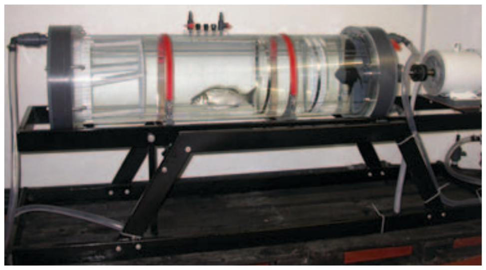
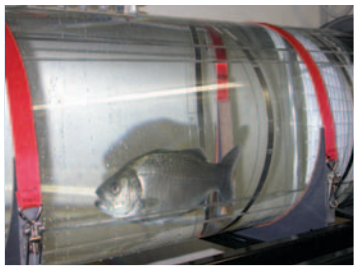
AQUATIC TELEMETRY

ADVANCES AND APPLICATIONS





Cover photographs:
EMG radio telemetry transmitter in front of a seabass *(Dicentrarchus labrax)* and seabass surgery (upper photos), courtesy of Pierluigi Carbonara, COISPA; seabass in a respirometer for a test of swimming performance (lower photos), courtesy of Giuseppe Lembo, COISPA.

AQUATIC TELEMETRY

ADVANCES AND APPLICATIONS

Proceedings of the
Fifth Conference on Fish Telemetry held in Europe
Ustica, Italy, 9–13 June 2003

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Preparation of this publication

This co-publication by FAO and COISPA is a compilation of 29 selected papers presented at the Fifth Conference on Fish Telemetry held in Europe which COISPA organized in Ustica, Italy, in 2003 to bring together researchers and fisheries biologists involved in telemetry and biotelemetry studies in marine and freshwater ecosystems. In line with its attempts to make the use of the aquatic resources more sustainable, the FAO Fisheries Department decided to publish these Proceedings to put emphasis on telemetry as a useful tool for gathering biological information to serve as a basis for management decisions.

The submitted papers examined and selected for publication by the Scientific Committee of the Conference and peer-reviewed by independent referees. Thus, this publication complies with the high international scientific standards. The document was compiled and technically edited by Maria Teresa Spedicato and Giuseppe Lembo, COISPA, in cooperation with Gerd Marmulla, FAO. The desktop processing was done by Linopuglia (Bari, Italy).

The views expressed in this publication are those of the authors and do not necessarily represent those of the Food and Agriculture Organization of the United Nations or COISPA.

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We express our gratitude to the Italian Association of Marine Biology (S.I.B.M.), the Italian Ministry of the Environment and the Italian Ministry of Agriculture and Forestry Policy that provided support for the organization of the Conference. We also like to thank all the attendees for participating in, and contributing to, the Conference as well as all those who assisted in the Conference arrangements. We wish likewise to thank the members of the Secretariat, the Scientific and Organizing Committees and the referees for helping to improve the manuscripts.

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Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9-13 June 2003.
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Abstract

This volume includes 29 peer-reviewed papers presented at the Fifth Conference on Fish Telemetry held in Europe (Ustica, Italy, 9-13 June 2003). The papers cover a wide range of topics on the application of aquatic telemetry in the field of human impact, fishery management and aquaculture. Evaluations of the barriers' effects on the migrations of both juvenile and adult fish are presented and discussed. New results on migratory patterns and habitat utilization are reported, elucidating behavioural ecology of several freshwater and marine species. Advances in methodology and new technology are also described and examined.

Foreword

Freshwater and marine resources, especially fish, have long provided a valuable source of food for mankind. However, heavy fishing pressure and the environmental impacts associated with the fast growing human population are increasing the stress on the aquatic resources and this calls for the strict application of management regulations. To protect biodiversity and assure the sustainability of the resources for the future, sound and responsible management is today more important than ever before. Ideally, current regulations are to be based on various criteria including the biology of the species concerned, as outlined in the FAO Code of Conduct for Responsible Fisheries and the related Technical Guidelines.

Telemetry, i.e. the remote measurement of biological variables, is a viable tool to obtain, in a limited time, information on the biology and the behaviour of the animals, one of the important preconditions for management decisions. The use of this technology in the aquatic environment has seen a rapid increase in the last two decades, as evidenced by the growing number of studies being undertaken.

The Fifth Conference on Fish Telemetry held in Europe, organized by COISPA Tecnologia & Ricerca in June 2003, brought together researchers and fisheries biologists involved in telemetry and biotelemetry studies on marine and freshwater ecosystems. The central theme of the conference was the interdisciplinary approach to provide the scientific basis for the conservation and rational management of natural resources. With the present book, FAO and COISPA are now publishing the Proceedings of a conference that was of particular relevance to all those involved in the field of fish ecology, aquaculture and fisheries management.

In an attempt to make the use of resources more sustainable, FAO is promoting the idea of using telemetry to study characteristics of fish, with a view to increase benefits for fisheries and aquaculture while maintaining a balance between exploitation and conservation. As part of its work under the Major Programme on Fisheries, the FAO Fisheries Department is active in raising the awareness of managers and scientists regarding the potential use of telemetry for supporting the management decision process[1]. In this context, the FAO Fish Telemetry Web site[2], which was launched on the occasion of the Fifth Fish Telemetry Conference, provides access to technology to help foster sustainability, addresses key management issues, and promotes information and technology exchange between managers and researchers in fisheries and aquaculture. FAO also co-financed a pilot workshop on the application of biotelemetry to fish studies for the management of inland fisheries in West Africa and is planning to provide inputs to training courses in future. Furthermore, a manual on telemetry is in preparation.

We trust that the compilation of excellent papers in these Proceedings, intended to serve as a showcase for the latest developments in aquatic telemetry and to give technical guidance to managers, will help provide concrete answers to questions in relation to fisheries management.

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[1] http://www.fao.org/english/newsroom/news/2003/19343-en.html

[2] http://www.agsci.ubc.ca/gbi/FAO%20Fish%20Telemetry/

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Introduction

The Fifth Conference on Fish Telemetry held in Europe was convened in Ustica, Italy, from 9 - 13 June 2003. The aim of the Conference was to promote the exchange of knowledge and experiences among researchers involved in telemetry and biotelemetry studies on marine and freshwater ecosystems. The central theme of the Conference was the inter-disciplinary approach to provide scientific basis for the conservation and sustainable management of natural aquatic resources.

The Fifth Conference, which attracted 105 delegates from 20 countries of five continents, continued the tradition that began with the first telemetry conference held in Liege, Belgium (1995), followed by conferences in La Rochelle, France (1997), Norwich, United Kingdom of Great Britain and Northern Ireland (1999) and Trondheim, Norway (2001).

The presence of "new" participants indicated an increasing interest in the field of aquatic telemetry and the growth of the scientific community, as evidenced also by the about 3 000 visitors of the Conference Website.

The presentations and posters covered the most recent applications and developments in the field of telemetry research and 29 manuscripts were selected, after peer-review by referees, for inclusion within these proceedings.

In the last eight years, there has been seen an enormous progress in aquatic telemetry research. In addition to salmonids, many other species have been studied, which indicates that telemetry is now widely being applied for investigating aquatic animal behaviour. Besides the traditional high-class research on the effects of dams and obstacles on the migrations of both juvenile and adult fish, and in addition to its use in elucidating movements and migrations in studies on the population dynamics of marine stocks, the application of telemetry systems has also continued to develop in aquaculture, e.g. for providing advice for improved welfare of cage-reared fish. A recent field of advanced application, discussed with great interest at the Ustica Conference, is the contribution of aquatic telemetry to the estimation of home range and site fidelity of key species in Marine Protected Areas, thus providing essential data for the evaluation of the reserve effect and the management of fishery resources.

Since the first conference on aquatic telemetry, there was always synergistic relationship between the biologists and engineers for the development of specific systems to address particular problems. This fruitful collaboration has led to the development, application and routinely use of technologies such as Data Storage Tag and miniature pingers. Further improvement of miniaturisation, integration of tracking data with the Geographical Information System and environmental variables, developing sensors to monitor the physiology and environment of free ranging fish are a challenge for the next future. The dissemination of information through the FAO fish telemetry web-site will contribute to expand the popularity and use of aquatic telemetry.

FAO's support in the production of this special issue of the Conference Proceedings is thankfully acknowledged.

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HUMAN IMPACT, FISHERY MANAGEMENT AND AQUACULTURE

Spedicato, M.T.; Lembo, G.; Marmulla, G. (eds.)
Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9-13 June 2003.
Rome, FAO/COISPA. 2005. 295p.

Using electromyogram telemetry to study the spawning migration of sea lamprey (*Petromyzon marinus* L.)

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Key words: EMG telemetry, swimming performance, activity effort, obstacle negotiation, River Mondego, Portugal.

Abstract

Laboratory and field experiments were conducted to assess activity patterns in adult sea lamprey (*Petromyzon marinus* L.) using electromyogram (EMG) telemetry. The good correlation between EMG values and sea lamprey activity levels observed during laboratory trials, allowed us to study *in situ* the behaviour of these animals during their spawning migration. Special attention was given to the sea lamprey activity patterns observed during the upstream migration when negotiating obstacles in specific reaches of the River Mondego, Portugal. High activity levels were usually associated with subsequent periods of low activity or rest periods. When swimming through stretches free from obstacles, the EMG values showed a constant pattern of activity. Intense activity peaks were frequently observed when lamprey negotiated difficult passage areas, less common during negotiation of smaller obstacles, and seldom recorded for stretches free from obstructions.

Introduction

During the course of evolution, anadromous fish populations' evolved genetically determined strategies that maximize fitness, and presumably become adjusted to the natural obstructions that they encounter in their upstream spawning migration (Gross, 1987; Clay, 1995). Usually these species stop feeding prior to migration, so the allocation of energy reserves must guarantee migration and spawning success. Such a delicate balance is often disrupted as a result of the modifications made in watersheds by human actions. Hinch *et al.* (1996) stated that river conditions that delay migration or require great energy expenditure to negotiate, are responsible for a post spawning mortality increase in sockeye salmon *Oncorhynchus nerka* (Walbaum).

Recent works using electromyogram (EMG) telemetry on free-swimming specimens have been successfully applied to different species, e.g., lake trout *Salvelinus namaycush* (Walbaum) (Weatherley *et al*., 1996), largemouth bass *Micropterus salmoides* (Lacépède) and smallmouth bass *M. dolomieui* Lacépède (Demers *et al*., 1996), sokeye salmon (Hinch *et al*., 1996) and Atlantic salmon *Salmo salar* L. (Booth *et al*., 1997; Økland *et al*., 2002). Telemetry techniques have been developed for the detection and transmission of electromyograms produced during muscle activity of free swimming fish (e. g. Ross *et al*., 1981; Rogers *et al*., 1984; Kaseloo *et al*., 1992; Demers *et al*., 1996; Hinch *et al*., 1996; Weatherley *et al*., 1996; Booth *et al*., 1997; Thorstad *et al*., 2000). Electromyograms are bioelectrical voltage changes that are strongly related with strength and duration of muscle contractions (Kaseloo *et al*., 1992)

In previous studies developed in the River Mondego, Almeida *et al*. (2000, 2002) described the migratory behaviour of sea lamprey *Petromyzon marinus* L., and identified the main obstacles and difficult passage reaches present in the migratory route of these animals. In the present study the exercise and activity patterns of sea lamprey during obstacle negotiation and movement through difficult passages areas was investigated using EMG telemetry. The results presented here are to the authors' knowledge the first that document the potential of using the electromyogram telemetry technology in lampreys.

Materials and methods

Five migrating adult sea lampreys (Table 1) were purchased from professional fishermen at the Mondego estuary (Portugal) and tagged with EMG radio transmitters manufactured by Lotek Engineering Inc. Newmarket, Ontario, Canada. Transmitters were cylindrical, weighed 18.3 g in the air, 8.0 g in water, and were 53.0 mm long by 16.2 mm diameter. The two Teflon-coated stainless steel electrodes were hooked and held in position in the swimming muscle using 18 carat gold tips (7 x 1 mm), as described by Hinch *et al.* (1996) and Thorstad *et al.* (2000). The transmitters detected signals over 1-2 μV in amplitude, and a radio pulse was transmitted whenever the 150 μV factory-determined threshold was exceeded (Kaseloo *et al.*, 1992). Consequently, the intervals between pulses correlated with the frequency of muscle contraction. A combined receiver and data logger model SRX-400 (Lotek Engineering Inc.) recorded the pulses as intervals (ms) between successive radio signals transmitted on a frequency (142.076 – 142.357 MHz), unique to each transmitter.

Prior to the implantation of the EMG transmitters, the surgical procedure and the animals' adaptation to the experimental conditions were tested in two lampreys, using dummy transmitters with dimensions similar to the EMG transmitters.

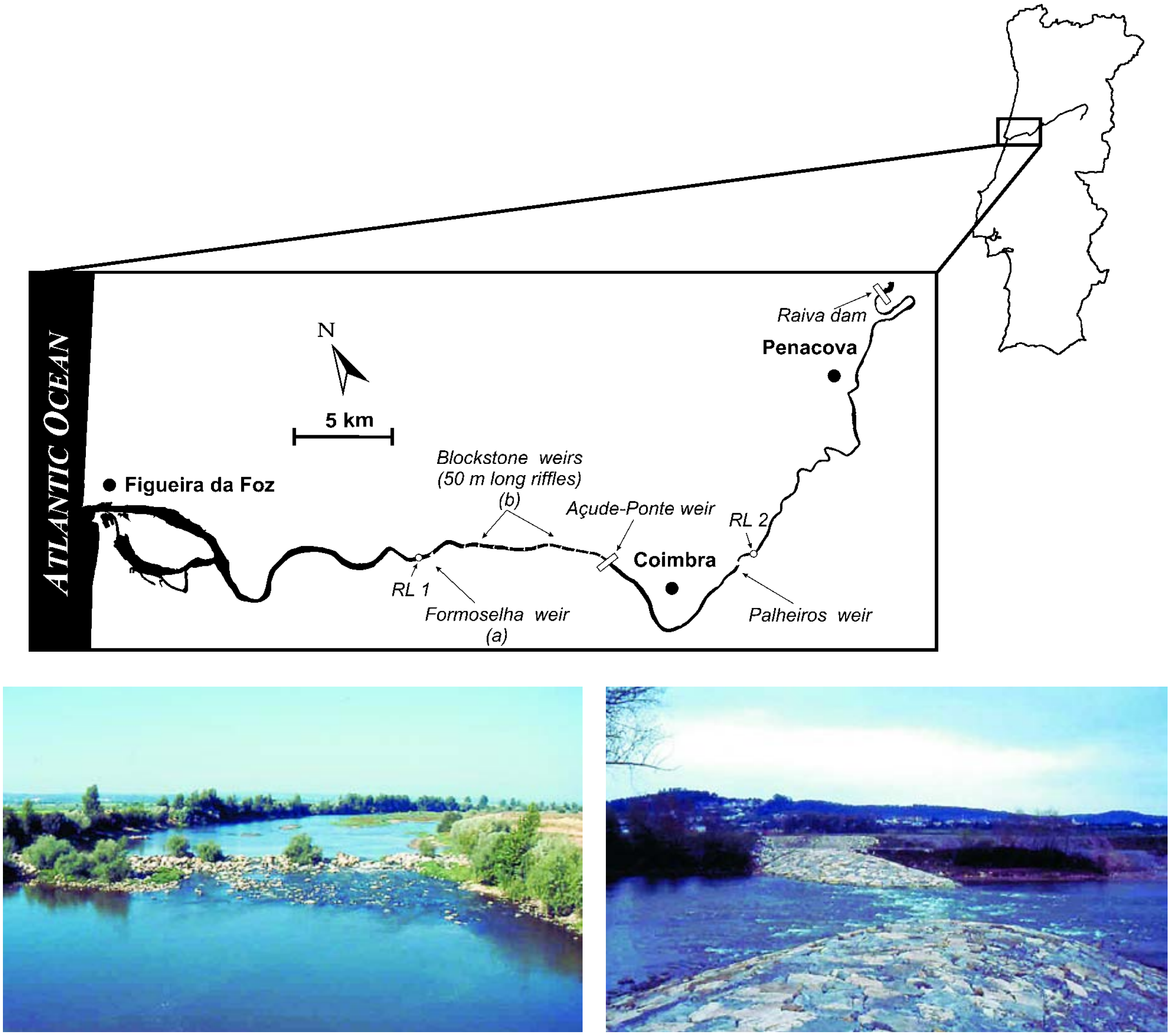
The lampreys were anaesthetised in a 0.5 ml 2-phenoxyethanol *per* liter water and a tag was surgically implanted in the body cavity of each fish. Surgery was initiated when the lamprey released its sucking disk from the container wall and stopped reacting to manipulation. The abdominal region was disinfected with an iodine solution (Betadine®) and a 3 cm incision was made in the midventral line, 8 cm from a point corresponding to the projection of the anterior insertion of the dorsal fin. The whip antenna was run through a hole in the abdominal wall, pierced with a blunt needle, leading the antenna to exit posterior.

The two gold-tipped electrodes (5-10 mm apart) were placed into the red lateral musculature, under the skin at the mid position, via an incision in the ventral region, using plunger devices (McKinley and Power, 1992). The incision was closed with 4-6 independent non-absorbable polyamide monofilament sutures (2/0 Dafilon DS24) and disinfected with Betadine. The complete procedure took 10-12 minutes. All lampreys were successfully revived in a 2-m^3 holding tank, and were left to recover for a period of 8 days under a light cycle of 10 h light: 14 h darkness. They were then carried to the River Mondego and released at two locations, one downstream from the Formoselha weir (RL1), and the other upstream from the Palheiros weir (RL2) (Fig. 1).

Table 1 – General information about the EMGs tracking sessions.

ID	TL (mm)	TW (g)	SD	RD	RL	TTT (h)	TDM U/D (m)	(ºC)
Lp 3	945	1445	03/03/02	18/03/02	*RL1*	78	7014/0	12.4
Lp 4	990	1800	25/03/02	01/04/02	*RL1*	161	5867/0	17.5
Lp 5	990	1900	09/04/02	15/04/02	*RL1*	163	3944/0	15.7
Lp 6	960	1700	23/04/02	06/05/02	*RL2*	158	7926/2892	16.1
Lp 7	930	1431	05/05/02	15/05/02	*RL2*	161	14267/10017	18.8

ID-animal identification, TL-tagged sea lampreys total length (mm), TW-tagged sea lampreys total weight (g), SD-surgery date, RD-release date, RL-release location, TTT-total time tracked, TDM U/D-total distance moved upstream/downstream (m), mean water temperature (ºC).



(a) (b)

Fig. 1 – Map of the River Mondego showing details of the study area. Photographs illustrate a view of the Formoselha weir (a) and of one riffle zone caused by a submerged blockstone weir (b). RL–releasing points.

During the recovery time, we tested the transmitter response to forced lamprey movements. For each animal, an EMG interval was associated with one of four different behaviour categories: i) *resting*, corresponding to periods when the lamprey used the sucking disk to remain motionless on the bottom or on the wall of the holding tank; ii) *low activity*, slow swimming movements typically made in the same direction, avoiding sudden changes of depth; iii) *medium activity*, fast swimming with regular changes of direction; iv) *high activity*, fast swimming with some burst accelerations, attempts to escape from the holding tank raising the head out of the water, swimming with one third of the body out of water and occasional jumps out of water.

Following release of the lampreys, a three-element hand-held (Yagi) antenna was used to track the location of lampreys and to monitor the EMGs. The tagged lampreys were tracked continuously, following the procedure described by Almeida *et al*. (2000; 2002). Data were downloaded to a laptop computer via an RS-232 serial communication port.

Results

The two animals that were tagged with the dummy transmitters survived the experimental procedure and indicated that the EMG transmitters could be successfully implanted into adult sea lamprey. After eight weeks the animals were euthanized and a *post mortem* observation revealed no internal damage and that gonad continued its maturation process.

Laboratory observations of the five EMG tagged lampreys indicated a clear difference between EMGs recorded when all lampreys were resting motionless and attached via the sucking disk, and periods of active swimming (Fig. 2). Resting periods corresponded to a steady high EMG pulse interval, and movement intensity lowered EMG pulse intervals. Pulse intervals during activity were highly dependent on the swimming speed, giving an accurate report of the animals' behaviour (Fig. 3). Laboratory records showed that lamprey were particularly active during the dark hours (Fig. 2).

The three animals that were released downstream from the Formoselha weir spent 21 hours, 27 hours and 93 hours passing this obstacle (Table 1). Two of them halted their upstream migration halfway between the Formoselha weir and the Açude-Ponte dam (Fig. 1). The lamprey that took longer to negotiate the Formoselha weir moved 3.4 km upstream in the next two nights, died and was recovered 1.3 km downstream. A closer look at the incision of the deceased specimen revealed that it was open, probably as a result of the intense exercise made by the animal while passing the Formoselha weir, although the electrodes maintained the position following surgery.

The two lampreys that were released upstream from the Palheiros weir (Fig. 1) presented two different types of behaviour. One moved 7.9 km upstream during the first night, and on the second night moved 2.9 km downstream and halted near the confluence of a small tributary for the rest of the tracking period (Table 1). The other animal made a short downstream movement just after being released, and passed over the Palheiros weir. During the first night the lamprey continued to move downstream for another 10 km, ending in the reservoir of the Açude-Ponte dam. On the next night the lamprey moved upstream and reached the Palheiros weir, where it stopped for the next two nights. Finally, on the fourth night the lamprey passed the weir and halted after moving 5 km upstream. No other movement was observed for the rest of the tracking period.

All five lampreys showed a preference for moving during the night. They spent 93% of the time resting during the day and only 44% of the time resting during the night. The cruising ground speed (*GS*) attained by the three lampreys released downstream from the Formoselha weir on the stretches free from obstacles was 11.1 BL (Body Length) min^{1}. For an animal with a total length of 85 cm, this value represents a GS of 0.6 km h^{-1}. The two sea lampreys released upstream the Açude-Ponte dam in the upper reaches of River Mondego attained a cruising GS of 23.9 BL min^{1}. A lamprey with 85 cm of total length would attain a GS of 1.2 km h^{-1}.

There were small variations in the EMG pulse intervals among individual lampreys with the resting EMG records, which corresponded to a steady high EMG baseline, with different values for each tagged animal. When comparing the percentage of time spent by the lampreys at each activity level throughout the different river habitats it was noticed that the lampreys showed similar behaviours when passing through river stretches morphologically identical. The lamprey *Lp 4* demonstrated a considerably more energetic swimming than the rest of the released animals, with a higher percentage of time corresponding to a more active behaviour (Table 2).

The EMGs records showed high activity when the lampreys were negotiating the Formoselha weir. This indicates that this obstacle is difficult to pass and demands intense exercise for a substantial period of time (Fig. 4). On average 28 percent of the total time was spent to passing the weir.

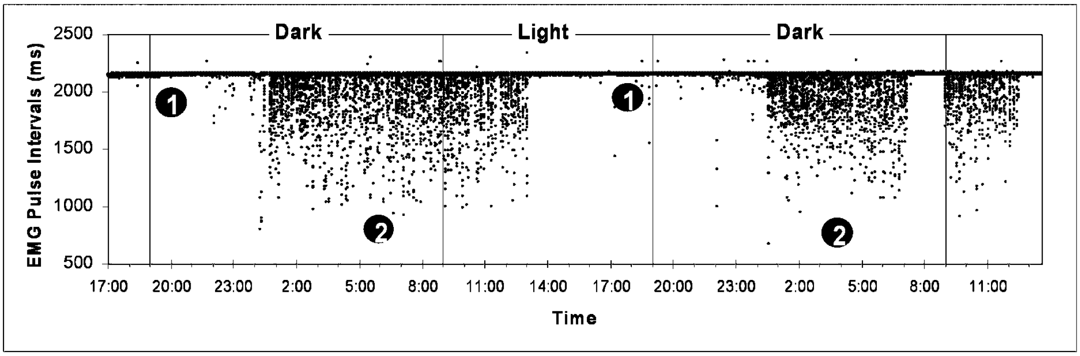


Fig. 2 – Records of radio transmitted EMG pulse intervals from axial swimming muscle of a representative sea lamprey (*Lp 7*) during laboratory trials. 1-Resting motionless; 2–Active swimming.

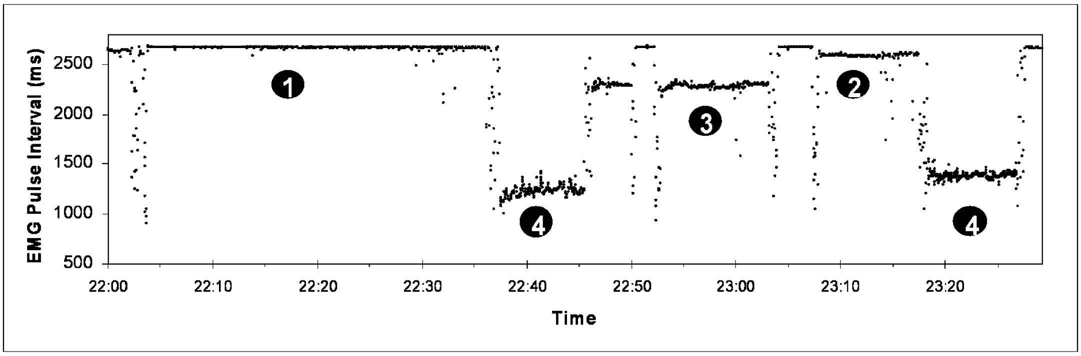


Fig. 3 – Records of radio transmitted EMG pulse intervals from axial swimming muscle of a representative sea lamprey (*Lp 6*) during laboratory trials. Activity levels: 1–Resting; 2–Low; 3–Medium; 4–High.

Table 2 – Percent of time spent by tagged lampreys at each activity level in the distinct river habitats.

River habitat		Activity level	*Lp 3*	*Lp 4*	*Lp 5*	*Lp 6*	*Lp 7*
Free stretches	% time spent each activity level	*Rest*	4.6	9.9	2.9	14.0	17.5
		L_act	5.8	28.0	42.7	5.5	8.3
		M_act	86.5	41.3	52.1	72.2	72.0
		H_act	3.1	20.9	2.3	8.2	2.1
Blockstone weir		*Rest*	7.7	0.8	1.0	—	—
		L_act	29.3	31.8	31.3	—	—
		M_act	49.2	40.3	60.3	—	—
		H_act	13.8	27.1	7.4	—	—
Formoselha weir		*Rest*	12.6	9.6	5.9	—	—
		L_act	18.4	9.5	26.5	—	—
		M_act	53.5	33.6	46.4	—	—
		H_act	15.5	47.2	21.2	—	—
Palheiros weir		*Rest*	—	—	—	29.3	—
		L_act	—	—	—	29.3	—
		M_act	—	—	—	33.3	—
		H_act	—	—	—	8.0	—

Rest – resting, L_act – low activity, M_act – medium activity, H_act – high activity.

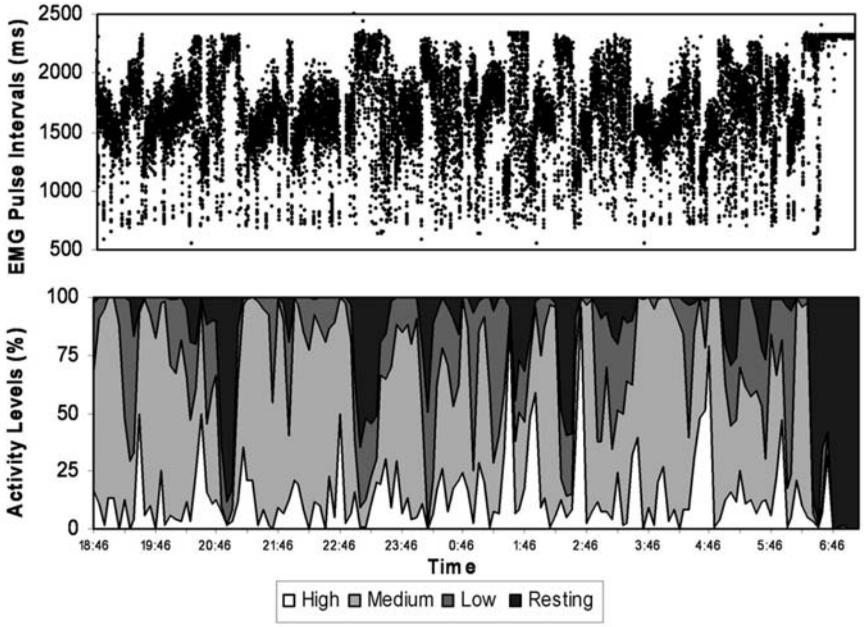


Fig. 4 – EMG records and proportion of time spent in each of the behaviour categories corresponding to sea lamprey *Lp3* during the Formoselha weir negotiation.

Submerged blockstone weirs created riffle zones where the lamprey changed their behaviour. The uniform pattern of EMGs observed in river stretches that separated the riffle zones changed to a sequence that shows peaks of high intensity movements, usually associated with low activity and resting moments (Fig. 5).

Movements through river stretches free from obstacles, like the river section upstream from the Palheiros weir (Fig. 1), exhibited a regular pattern of EMGs pulses, occasionally interrupted by high activity episodes and resting moments (Fig. 6). These probably resulted from changes in the morphology of the river bed.

Discussion

Lampreys tagged with EMG transmitters exhibited the same circadian activity patterns as lamprey bearing smaller radio or acoustic transmitters (Almeida *et al*., 2000; 2002). EMG transmitters registered efficiently all the animals' movements, even slight oscillations of the body when sea lampreys were attached to the wall, or to the bottom of the holding tank. During the laboratory trials it was observed that the EMG pulse rate varied depending on the position adopted by the lamprey. For instance, if lampreys were resting on the wall of the tank, the EMGs values were lower than when lampreys were resting in the bottom.

Constant swimming in the river stretches free from obstacles also gave indications of variations in EMGs. Because the electrodes were located in the left axial swimming muscle, it is possible that contractions of the right side muscle were not registered, which would produce a high EMG pulse interval. Økland *et al*. (2002) described a similar situation in an EMG telemetry study conducted with Atlantic salmon.

Lampreys take advantage of their sucking disk to rest motionless in areas of the riverbed where the current is high. This behaviour explains the resting moments that usually were associated with fast swimming periods and burst swimming episodes. This sequence of events was normally observed when the animals were migrating through difficult

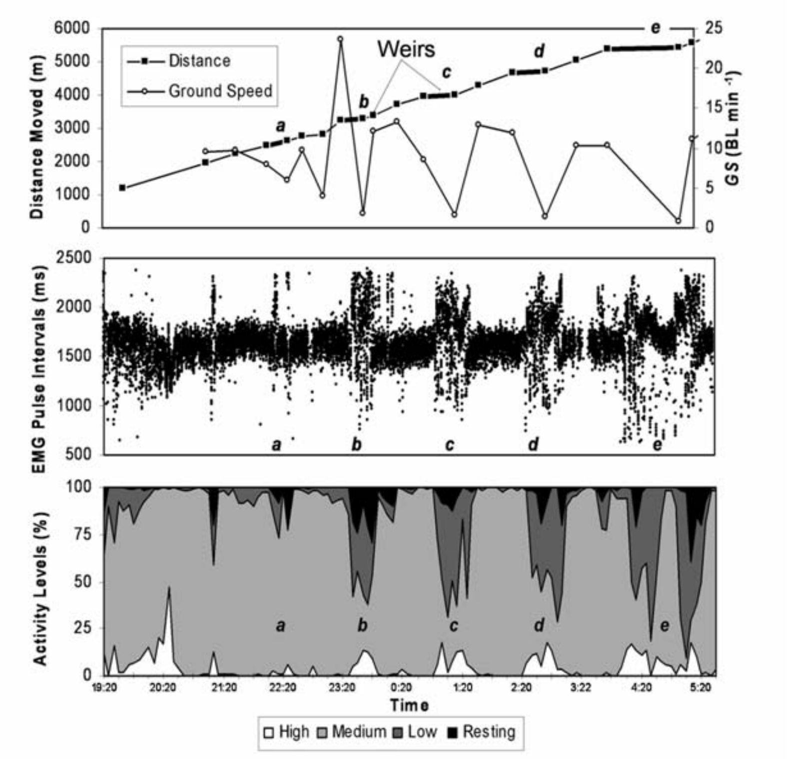


Fig. 5 – Distance moved from the Formoselha weir, ground speed, EMG records and proportion of time spent in each of the behaviour categories corresponding to sea lamprey *Lp3* tracked in the river stretch between the Formoselha weir and the Açude-Ponte dam. Also identified the location of the submerged blockstone weirs (a, b, c, d and e) throughout.

passage zones (*e. g.* riffles), or during negotiation of obstacles (*e. g.* Formoselha weir).

The results demonstrated that the ground speed estimates made in the past using conventional radio and acoustic telemetry gave a rough idea about the behaviour of the animals in difficult passage zones. In fact, Almeida *et al.* (2000; 2002) assumed that sea lampreys were moving continuously through the riffle areas, when the animals probably were alternating between resting moments and burst swimming, as a strategy to overcome these fast current stretches as observed in the present study.

Comparing the results obtained by Almeida *et al.* (2000; 2002) studies, which used externally attached radio or acoustic transmitters, with the cruising GS of sea lampreys tagged with surgically implanted EMG transmitters it was possible to notice that, apparently, lampreys with EMG transmitters migrate more slowly than with external tags. It is possible that internal implantation might affect the swimming performance of the sea lampreys not only because it is a more intrusive technique, which may provoke additional stress, but also due to the necessary recovering period in laboratory after the tagging procedures which may alter to some extent the normal behaviour of the migrating sea lamprey. Mesa *et al.*, (2003) work which evaluated the effect of surgically implanted telemetry transmitters on the swimming performance of adult Pacific lampreys (*Lampetra tridentata*, Richardson) showed significant but minor effects.

Lucas *et al.* (1991) and Demers *et al.* (1996) concluded that using conventional telemetry tracking-based swimming speeds as an index of fish activity could be misleading. This is particularly the case when one wants to estimate the metabolic cost

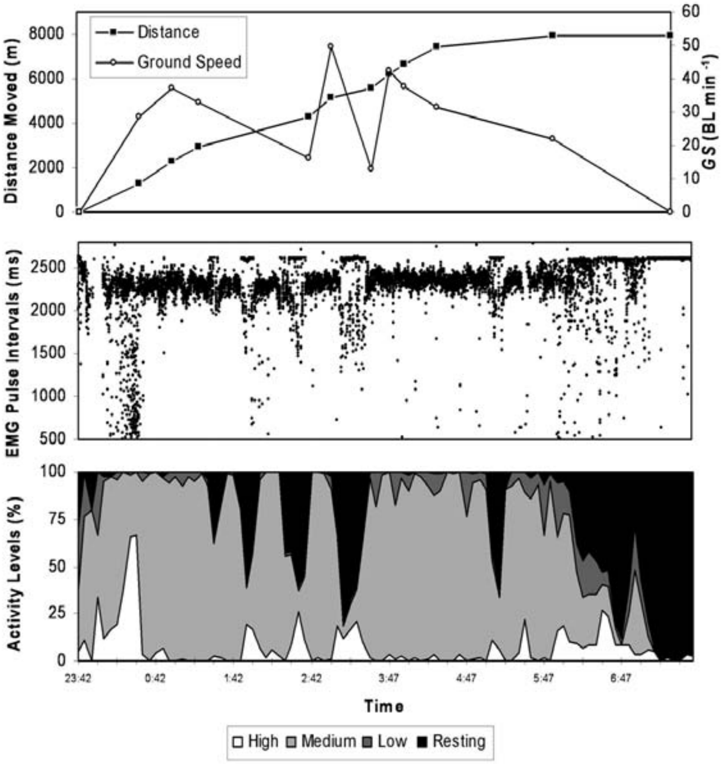


Fig. 6 – Distance moved from the Palheiros weir, ground speed, EMG records and proportion of time spent in each of the behaviour categories corresponding to sea lamprey *Lp6* tracked in the upstream stretch of River Mondego.

associated with an apparent swimming speed. The present study supports this conclusion, because movement through difficult passage areas (*e. g.* riffles zones) produced an increase in EMG pulse rate, although the ground speed decreased through these river stretches.

Sea lampreys recover rapidly from post-exercise metabolic and respiratory acidosis (Wilkie *et al.*, 1998), which means that they are able to continue their migration shortly after an exhaustive exercise episode. However, the energy spent negotiating obstacles and migrating through a sequence of difficult passage zones, like the riffle areas in the River Mondego, may increase the amount of energy allocated to migration and, consequently, limit spawning success. Further investigations are necessary to establish whether the excessive energy costs of migration through anthropogenic or natural obstacles affects the overall spawning success of sea lamprey.

Acknowledgements

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Radio-tracking: a useful tool for the Aulne Atlantic salmon rehabilitation program

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Key words: radio-tracking, Atlantic salmon, upstream migration, weirs.

Abstract

A two-year radio-tracking study of Atlantic salmon was conducted on the Aulne, a small French coastal river. The behaviour of 129 salmon was studied from early July 1999 to mid-December 2000. The objective was to investigate patterns of upstream migration of salmon, in particular through the lower 70 kilometres of the river which is canalised. This enabled us to compare the passability of weirs and how this varied according to the type of fish-pass facility. The technique of the cumulative effect of the obstacles indicates that less than 5 percent of the population is likely to get through the canalised part and reach areas that are suitable for spawning. The most serious obstacles were presented by the weirs located the furthest downstream and two others in the middle of the river. The study also enabled both an estimation of the impact of fishing activities and a comparison of the upstream migration capacities of wild and reared salmon. Radio-tracking thus provides managers with a tool for assessing the restoration plan in order to improve its efficiency.

Introduction

The Aulne is a small coastal river in Brittany in north-west France. A seventy-kilometre stretch of the downstream watercourse has been canalised and includes 28 weirs. The river supports salmon; annual rod catch data indicate relatively constant catches from the early 1950s to the 1970s, followed by a sharp decrease, before levelling off at a low level until the mid-1980s. At this time, a plan was initiated to improve runs of salmon into the river.

To compensate for the decrease, various actions were undertaken. The first one involved restocking with juveniles from spawners captured in their natural environment, mainly in its estuary tributary, the Douffine. This restocking was done from the end of the 1980s, with parr and smolts being released directly into the Aulne, or into its estuary tributary, the Douffine. Another action involved making a census of juveniles production zones. This revealed that most of these zones (74% of the total surface area) were in the natural part of the Aulne, upstream of the canalised section (FDPPMA 29, 1996). The remaining production areas were distributed along various tributaries of the canalised section, mainly in the biggest of them, the Ster Goanez, on which we found more than 12% of the production zones. In addition, an effort was made from 1994 to improve the passability of weirs by building new fish passes. Today, 18 of the 28 weirs on the canalised section of the Aulne have been fitted with modern facilities.

These actions have led to an increase in the number of adults returning to the downstream part of the Aulne, an increase in the number of salmon caught by anglers (Fig. 1) and an increase in breeding potential even after fishing. Nevertheless, the increase of capture figures levelled off in the middle of the 1990s and then decreased again until 2002. Moreover, an initial biological assessment (count of effective spawning and juvenile abundance indices) indicates that there is very limited natural reproduction, especially upstream the canalised part of the river (FDPPMA 29, 2002). Thus, in spite of significant restoration efforts, the results are disappointing.

The main hypothesis for explaining the scarcity of natural juvenile production is a migratory blockage preventing adults from reaching the spawning grounds in the natural part of the Aulne, upstream of the canalised part. Therefore, it was decided to radio-track adults during their upstream migration in 1999 and 2000. The objective was to investigate upstream migration of returning salmon in the Aulne under current environmental conditions and to assess the impact of the numerous obstacles to migration.

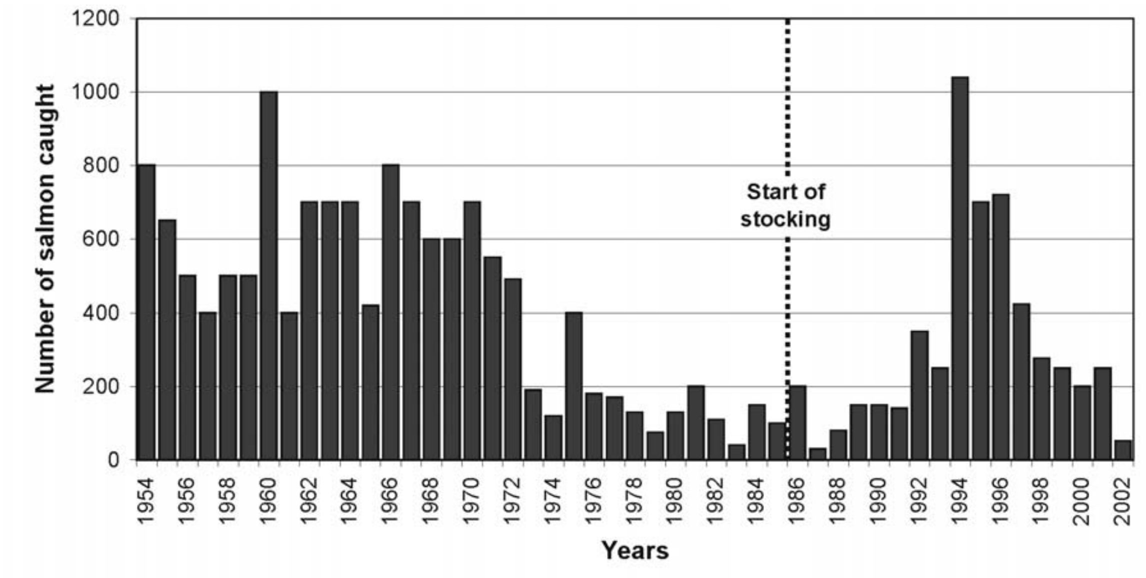

Fig. 1 – Rod catch of salmon on the River Aulne from 1954 to 2002 (source: CSP).

Materials and methods

Experimental site

The river Aulne is located in north-west France (Fig. 2). It is 145 km long in all and 70 km of its downstream part is canalised. Its catchment area covers 1,495 km^2. Salmonids predominate in the natural part of the river, and cyprinids in the canalised part.

About halfway along the canalised part of the Aulne (supplied by a catchment area of 1,224 km^2), there is a flow gauging station. The Aulne's mean annual discharge is 21.2 m^{3}s^{-1}. The river's regime is pluvial. The catchment area is affected by a particularly well-defined ocean climate, with heavy precipitation – about 200 days of rain per year, with mean annual rainfall ranging between 1,000 and 1,200 mm. The water level can rise dramatically (more than 400 m^{3}s^{-1}) or drop to drastic levels (less than 1 m^{3}s^{-1}). The lowest levels are recorded from July to September, with the heaviest flows in winter.

The physical/chemical quality of the Aulne's water is generally poor (Troadec and Le Goff, 1997). This appears to be due to the large quantities of run-off containing nitrates and phosphates from agricultural sources.

The 28 weirs in the 70-kilometre canalised part of the Aulne are designed to maintain water depths of one to two metres. They are nearly all chevron-shaped weirs – the point of the "V" being the furthest upstream – and include a lock for boats near the right bank and a discharge gate on the left bank to lower the amount of water upstream. The only rectilinear weirs, at right angles to the bank, are numbers 1, 2 and 6. The reaches between the weirs are between two and three kilometres long on average. The height of the weirs varies between 1.3 and 2.3 m, but usually lies around 2 m.

From 1994 to 1999, 18 weirs were fitted with new fish pass facilities (Fig. 2), generally chevron-type baffle fishways with a downstream pre-barrage. All the fish-passes at chevron-shaped weirs were positioned in the middle of the weir. The pre-barrage, at the foot of the canal, reduces the drop. Two other weirs (numbers 20 and 21), initially fitted with only a notch around 40 cm deep in the middle, have now been fitted with a baffle fishway near the right bank. Even though these facilities were installed before the start of the restoration plan, these two weirs are included in the category of weirs fitted with a new fish-pass.

Seven weirs still have older fish pass facilities, generally pool fishways with overflow weirs. On the Aulne, the pools are too small and cannot dissipate energy well, especially during fast flows. All the pool fishways are in the middle of the weir, with the exception of weir 3, where it is located near the right bank.

Weir 17 does not have a real fish-pass, only a gently sloping ramp without any baffles to dissipate energy and reduce water velocity.

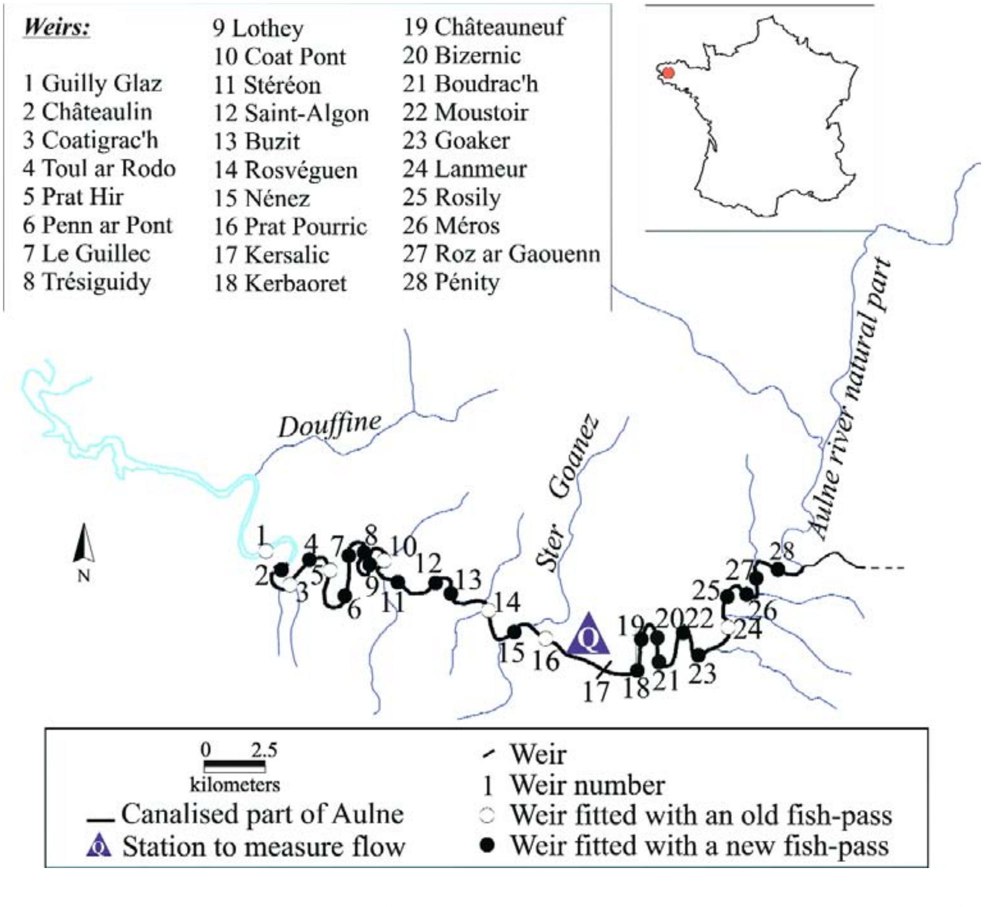

Fig. 2 – Map of the River Aulne, indicating the location of weirs and the different types of fish pass facilities at each.

Research period

The migration of salmon up the Aulne was studied over a two year period, 1999 and 2000. The 1999 study was initiated on July 5 and only covered grilse, salmon that have spent one winter at sea. The 2000 study began with the arrival of the first fish in late February and included both grilse and multi-sea-winter 'spring' salmon, fish which have spent two or more winters at sea. Individual fish were trapped in both years through to the end of October. The daily tracking of fish ended in mid-December, although several fish continued to be tracked at less frequent intervals up to the end of January.

Capture and radio-tagging of fish

The fish were caught in the pool fishway at Châteaulin (weir 2), representing the tidal limit. The fishway's upstream pool was transformed for the purposes of this study into a trap as described by Travade and Larinier (2002).

The fish-pass was shut at least twice a day – during the morning and early evening – and up to four times a day during the busiest migration period to check the trap for salmon. These times were chosen so as to limit the amount of time that fish spent in the trap, as over 85% of fish enter the pass during the daytime (Chanseau *et al*., 1999).

The trapped salmon were anaesthetised using a solution of diluted 2-phenoxyethanol (0.25 mll^{-1}). They were then measured. No injured, small (total length less than 55 cm) or descaled fish were radio-tagged.

In the two years of study, 132 salmon were radio-tagged by inserting a transmitter into their stomachs through a plastic tube. This method was chosen as the most suitable for adult salmon during upriver migration (Stasko and Pincock, 1997; Solomon and Stroreton-West, 1983).

All fish were tagged with ATS (Advanced Telemetry System) radio transmitters. These have an external antenna and are cylindrical (60 mm long x 20 mm in diameter). In air, they weigh 20 to 22 g, which is less than 1.5% of the weight of the tagged fish. This is well below the 2.5% threshold above which certain species buoyancy is affected (Baras and Lagardère, 1995). The transmitters operated within the 48 to 49.9 MHz frequency range at 20 kHz intervals. The transmitters have a guaranteed life of 220 days. Actually, almost all worked for over ten months, thus covering the study period. The mortality indication option was chosen from available options. This meant that if the transmitter remained immobile for six hours, the pulse rate changed to alert listeners.

Transportation and release

In all, 79 salmon were released immediately upstream of their place of capture (i.e. upstream of weir 2). However, due to the difficulties encountered by these salmon in clearing the lower obstacles and in order to study the impact of each weir in the canalised section, the other tagged adults were transported and released at different points along the migration route. Thus 4, 7, 10, 3, 1, 10, 7, 5 and 6 fish were released upstream of weirs 3, 5, 8, 9, 10, 11, 14, 16 and 19, respectively. Consequently at least ten fish reached each of the 26 weirs being studied, upstream of the place where they were captured.

The fish transported upstream were placed one at a time in a transport tank containing 180 litres of diluted anaesthetic (0.075 mll^{-1}). A pump permitted to deliver compressed air to ensure the fish had enough oxygen in the water.

Radio-tracking

Automatic listening stations (ALS) were set up at 13 of the 26 weirs studied to record the times of arrival and departure of the tagged fish and thus the length of time spent at each weir and the ensuing migration delays. Between the various weirs along the canalised part of the Aulne and at weirs without an ALS, salmon movement was tracked manually, either on foot, by car or, occasionally, from aircraft. As far as possible, we tried to locate each radio-tagged salmon at least once a day while they remained in the canalised part. For weirs without an ALS, the minimum and maximum lengths of time the fish were held up by obstacles were determined from manual tracking records.

Results

Although 132 salmon were radio-tagged, only 129 were tracked. This is because one transmitter stopped working as soon as the fish was put back into the water and two other fish quickly regurgitated their tag. We obtained information from only 126 of the 129; two salmon were injured during the release operation and a third died soon after tagging, probably as a result of the handling.

Passability of weirs

To assess the passability of the weir, we determined the mean passage percentage and migration delay at each weir. Some fish were captured by anglers just downstream of several weirs and they were not taken into account when evaluating the passability of weirs.

The overall impact of the canalisation was estimated by adding together the impacts of each weir. This assessment was only possible in 2000. Work on the weirs or locks in 1999 required discharge gates at several weirs to be opened, and this atypical operation affected migration of the fish. There were not enough fish at each weir during the 1999 study to be able to reliably estimate how easily the weirs were passed in their usual mode of operation (i.e. discharge gate shut).

In terms of the cumulative percentage of fish clearing the weirs, it appears that 39.6% of salmon are likely to reach the Ster Goanez, the main tributary of the canalised section upstream of weir 15, where 12% of the catchment's salmon spawning grounds are found. Only 4.3% of salmon reach the natural part of the Aulne river (Fig. 3), where most of the spawning grounds are situated. The most obvious obstacles were those furthest downstream on the migration route (weirs 3 to 5 with a passage percentage of 76% to 91%) and two others in the middle section (weirs 16 and 17 with respectively a passage percentage of 31% and 67%).

The passability of weirs appears to depend on fish-pass type. Leaving weir 17 out of the analysis, it being an obstacle without a real fish-pass, we observed that the mean fish passage percentage observed at weirs fitted with older fishways is lower than at weirs with the more recent passes (73.7%±7.7 compared with 95.9%±1.2). This difference is statistically significant (Mann Whitney: $U=7.0$; $p<0.001$).

The delays noted at weirs fitted with older fishways (9.9±1.7 days) are greater than at weirs with the new fish-passes (3.8±0.7 days). This difference is also statistically significant (Test t: $t=3.20$; $p<0.01$).

It appears that the passability of weirs also depends on their position along the migration route. In 2000, some of the poorest passability ratings were observed for weirs 3 to 5, which are the furthest downstream in the canalised part of the river. In 1999, the lowest fish passage percentage was observed at weir 3 (33.3%). This weir is a special case in that it is the only chevron-shaped weir on the Aulne to be fitted with an older pool fishway placed on the right bank, instead of in the middle of the weir. In 1999, the lowest passage percentage at weirs with recent fishways was at weir 4. The passage percentage at this obstacle was significantly lower than that observed at weirs with a similar design, fitted with the same new fish-pass, but located further upstream on the migration route (Fig. 4): 77.8% at weir 4 compared with a mean of 95.2% for the other weirs (Test-t for a single sample: $t=5.014$; $p<0.001$). The passage percentage at weir 5 was also lower than that at weirs with the same design fitted with the same type of fishway but further upstream along the migration route: 57.1% at Prat Hir compared with a mean of 72.2% at the other weirs. Nevertheless, this difference is not statistically significant (Test-t for single sample: $t = 0.624$; $p = 0.577$).

Downstream migration

In 1999, 14 salmon (35% of the study sample) left the canalised part of the Aulne before spawning and migrated up other nearby rivers (Fig. 5) – eight up the Douffine, an estuary tributary of the Aulne, and six up other coastal rivers with mouths near the Aulne (one up the Camfrout, two

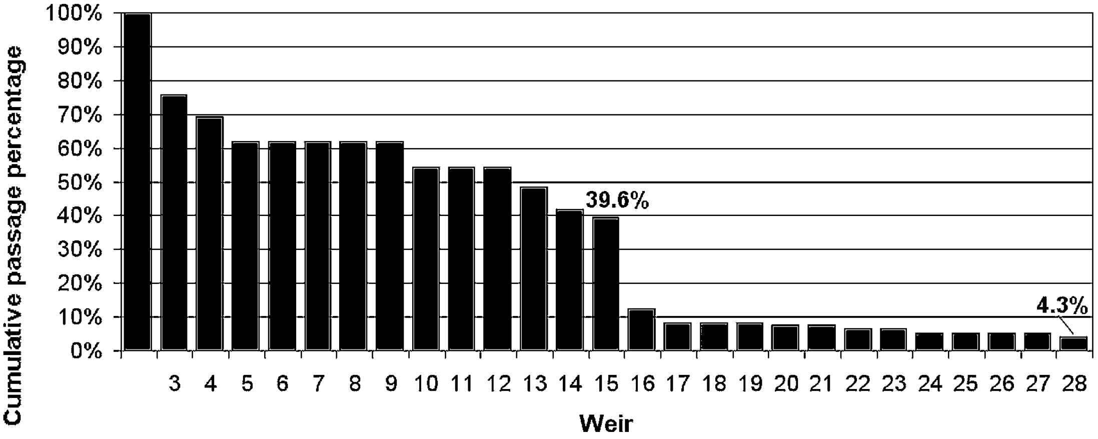

Fig. 3 – Cumulative percentage of salmon clearing the weirs along the canalised part of the River Aulne in 2000.

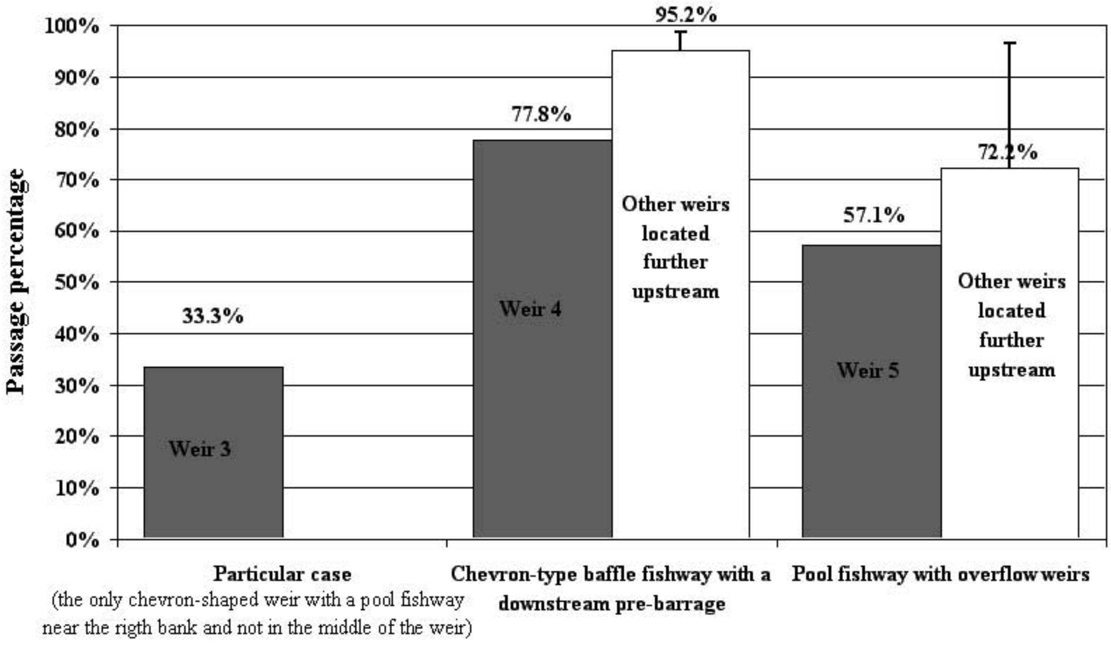

Fig. 4 – Passage percentage observed at the three weirs furthest downstream compared with all other weirs with similar fish pass designs.

up the Elorn and three up the Faou). The eight salmon swimming up the Douffine were held up at the foot of the first dam because its fish elevator was out of order. Most of these fish were subsequently detected in Brest harbour before the breeding period (one fish was found in the Camfrout, one in the Elorn and one in the Mignonne estuary).

Nineteen salmon (22% of the study sample) also left the Aulne in 2000 without having spawned there; only nine were subsequently found in other watercourses. Of these, eight were found in the Douffine and one in the Faou (Fig. 5). Radio-tracking was made very difficult at the time of downstream migration because of a combination of heavy flow, which limited access to the watercourses, and poor weather, which ruled out flying over the study area.

Impact of fishing

The study also enabled us to quantify the impact of angling.

The 40 salmon monitored in 1999 were grilse. Eight of them –20% of the study population– were caught by anglers, with seven being caught immediately below weirs. In 2000, only 4 of the 67 grilse radio-tracked (6%) were caught by fishermen. Three of these were also captured just downstream of a weir, the fourth being caught about 500 m downstream of weir 10. Over the two years, 12 of the 107 radio-tagged grilse (11%) were therefore captured by anglers.

The cumulative percentage of grilse passing the weirs in 2000, based on all individuals, whether or not they were captured by anglers, indicates that 32.8% passed the weir 15 and only 3.5% passed the last weir of the canalised section (Fig. 6). Excluding the grilse taken by anglers, the percentage of individuals passing over the weir 15 was 41.3% and the percentage of those passing over the most upstream weir of the canalised part was 4.4%. Therefore, angling activities reduced by 8.5% the number of potential spawners which passed weir 15 and were hence likely to migrate up the main tributary of the canalised Aulne, and

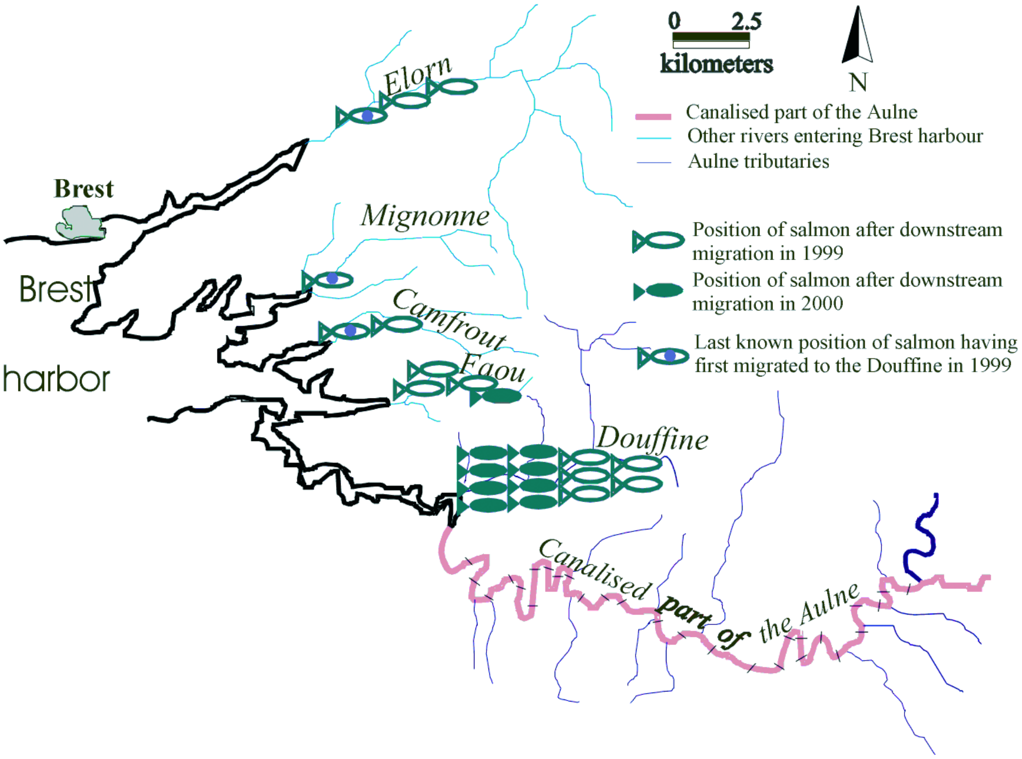

Fig. 5 – Position of radio-tagged fish having migrated down the Aulne before the breeding season.

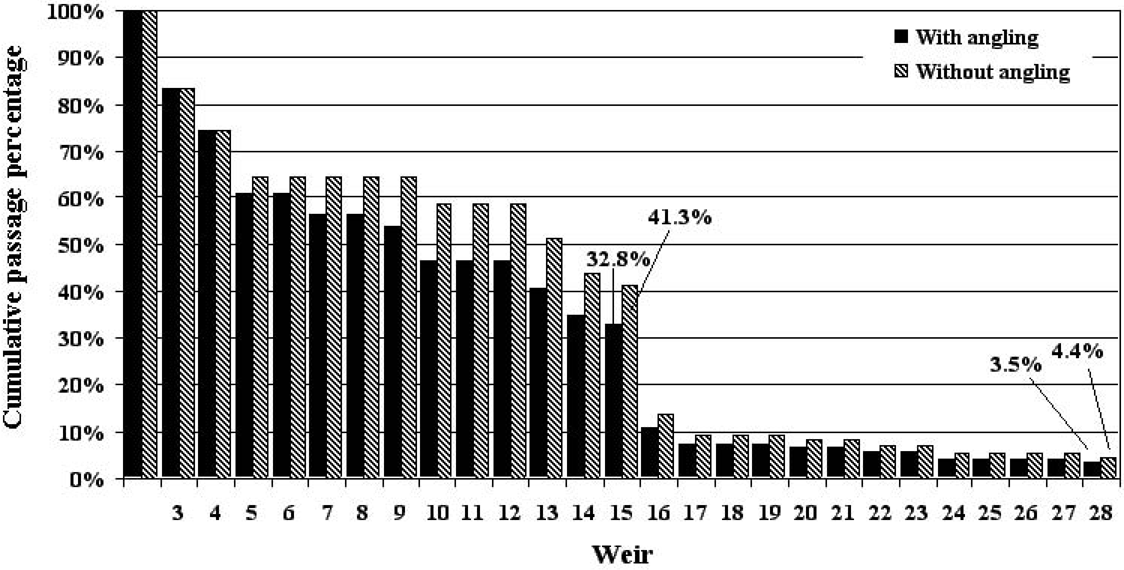

Fig. 6 – Estimated cumulative passage percentage of grilse in 2000 with and without angling.

by 0.9% the number of potential spawners likely to reach the spawning grounds in the upper Aulne.

For spring salmon, the impact of fishing was investigated only in 2000 and only on the downstream section of the Aulne (up to weir 10), since the number of individuals passing over the tenth weir was too small to enable evaluation of a passage percentage for more upstream obstacles. Nine of the 19 individuals radio-tracked –47% of the study population– were caught by anglers. Eight of them were captured just downstream of a weir, the ninth being fished about 400 m downstream from weir 3. The cumulative percentage of spring salmon passing over the tenth weir, based on all individuals, whether or not they were captured by anglers, was just 16.7% (Fig. 7). Excluding the spring salmon taken by anglers, the percentage of individuals passing over the tenth weir was 46.2%. The impact of angling activities is thus greater on spring salmon as fishing reduced by about 30% the number of potential spawners likely to reach the tenth weir of the canalised section.

Comparison between wild and reared salmon

Most of the hatchery-reared fish released to the river have been marked with an adipose fin clip. Only some of the 0^+ parr released in 1995 and 1997 and some of the 1^+ smolts released in 1997 have been introduced without such marking. We can be sure that salmon without an adipose fin were hatchery-reared fish but the opposite is not true, as salmon with an intact fin might be either reared or wild. Scale reading of all individuals tagged in 2000 enabled us to determine the number of years fish had spent in the river and the number of years they had spent at sea. With this additional information, we were able to determine the origin (wild or reared) of most (69/86) of the individuals studied in 2000. No scales were taken from individuals tagged in 1999. Thus comparison of wild and hatchery-origin fish is limited to just those 69 tagged during 2000.

The first comparison between wild and reared salmon concerns weir clearance. The number of obstacles with normal configurations (i.e. with discharge gate closed) cleared by fish was on average

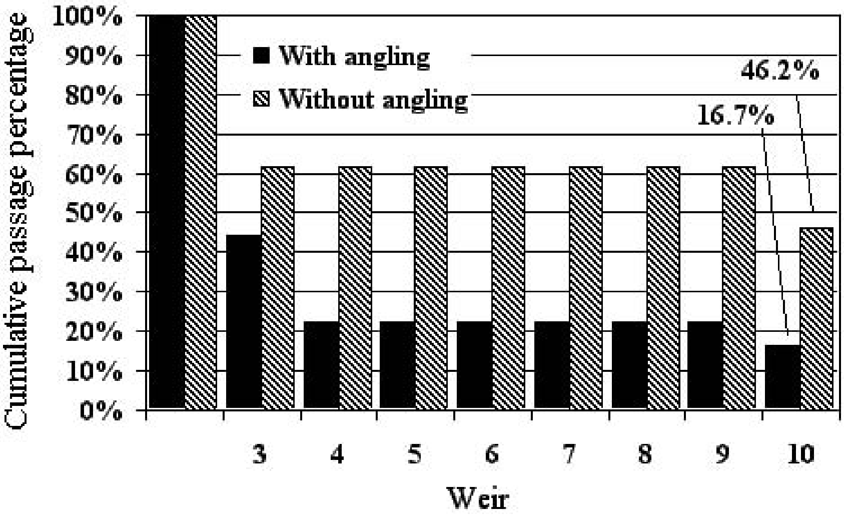

Fig. 7 – Estimated cumulative passage percentage, up to weir 10, of spring salmon in 2000 with and without angling.

5.7±1.7 for wild salmon as opposed to 8.0±1.9 for reared ones; this difference is not statistically significant (Mann Withney: U=71.0; p=0.574).

It is also possible to compare the percentage passage obtained for each weir, by limiting analysis to weirs with normal configurations, visited by at least five individuals from each category. This allows comparison for weirs 3 to 16, but there was no difference between wild and reared salmon (Wilcoxon: Z= -0.059; p=0.953) (Fig. 8).

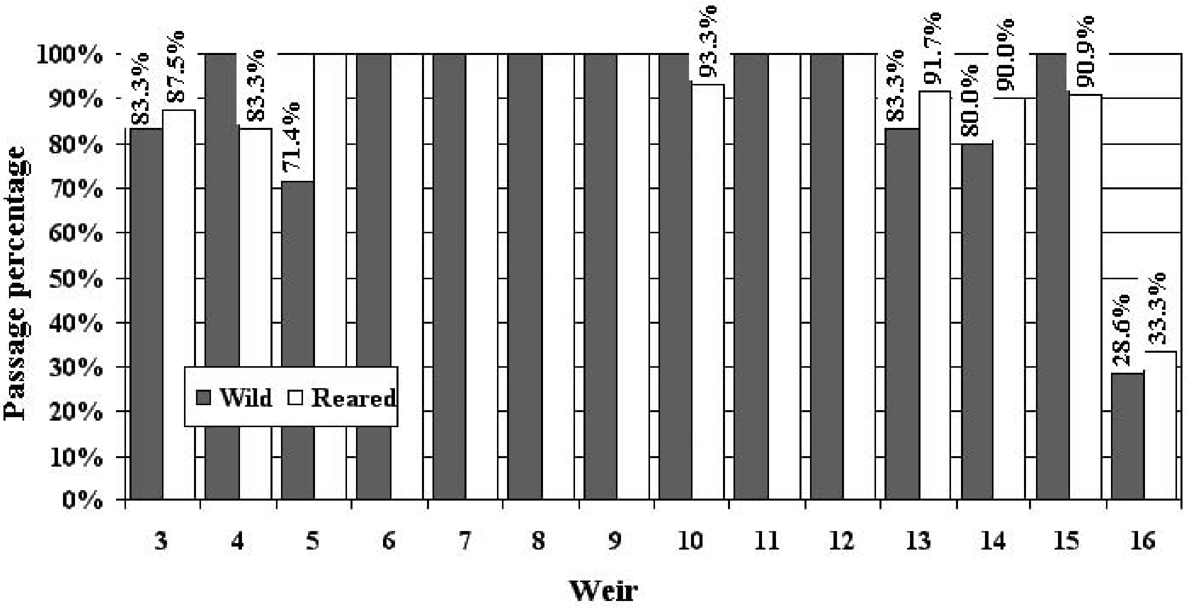

Fig. 8 – Comparison of passage percentage between wild and reared salmon up to weir 16.

Analysis of the fate of the fish (Table 1), divided into four categories (downstream migration before breeding, survival on the Aulne until breeding, caught by anglers and dead), indicated a statistical difference between wild and reared salmon (Chi-squared test: χ^2=25.9; p<0.001). More reared individuals undertook a downstream migration and more mortality was observed among wild fish. The greatest part of mortality appeared in summer (43%), with low flow and high temperature for salmon (until 23°C). Mortality was also noted after injuries during weirs passage attempts, particularly where rocks are abundant just downstream of weirs (28.5%). Lastly, several cases of mortality (28.5%) occurred just after flow increase.

Table 1 – Fate of wild and reared salmon radio-tracked during 2000.

Destiny	wild	reared
Survival on the Aulne until breeding	9 (42.9%)	17 (35.4%)
Downstream migration before breeding	2 (9.5%)	12 (25.0%)
Caught by anglers	1 (4.8%)	6 (12.5%)
Dead	9 (42.9%)	13 (27.1%)

However, if the comparison is limited to just two categories (survival on the Aulne until breeding and absence of survival on the Aulne until breeding), there was no statistical difference between wild and reared salmon (Chi-squared test: χ^2=0.511; p=0.475).

Discussion

The canalised part of the Aulne appears to represent a major obstacle to migrating adult salmon, since only 4.3% of the tagged fish were able to reach the natural part of the Aulne where most of the areas favourable for breeding and growth of juveniles are found. This result is even more alarming given that it was based on the radio-tracking investigation in 2000, a year with exceptionally heavy flows which helped the fish to progress. During most of the salmon migration period, monthly mean flows were around twice that of reference flows. This difficulty in clearing the canalised sector appears to be partly due to the poor performance of the old fish pass facilities which were badly installed and are too small. The worst clearance results, both in terms of percentage passage and migration delay, appear to be at the weirs which are still fitted with outdated fish passes, or at weir 17 which doesn't have a proper pass. The effort made to date for the restoration plan have not been useless as fish passage is somewhat better at weirs fitted with new fish pass facilities. Moreover, the problem of passability is particularly evident on the downstream part of the migration route at the first three weirs studied (3 to 5). Weir 3 (Coatigrac'h weir) is fitted with an older fishway which is not only too small but is also positioned near the bank, while the weir itself is chevron-shaped. At the Toul ar Rodo and Prat Hir weirs, even though the fishways are positioned in the middle of the weirs, they are less passable than similar weirs further upstream, fitted with identical fishways. The nature of the obstacle and the fishway design cannot fully explain the poor clearance results observed. Other environmental factors could limit the progression of salmon in this part of the river. Salmon are used to rough water and might hesitate to migrate upstream through this canalised section where flow is light and the water of a poor quality. This is partly perhaps why several salmon migrate downstream before the breeding period.

As previously shown in studies on other European rivers (Chanseau *et al.*, 1999; Gerlier and Roche, 1998), radio-tracking can be very useful for evaluating the impact of in-river obstructions on salmon migration.

Gentle insertion of radio transmitters into fishes' stomachs via the oesophagus did not prevent fish being caught by anglers. This has previously been reported for other studies, for example on the River Tummel (Gowans *et al.*, 1999), on the River Pau (Chanseau *et a*l., 1997, Chanseau *et al.*, 1998) or on the River Scorff (Prévost, 2002), as well as during the 2 investigations conducted on the Aulne (Croze *et al.,* 2000, 2002). Angling appears to have had a noticeable impact on the stock of radio-tagged grilse in 1999 and 2000, as up to 20% of the stock was caught. Likewise, fewer adults reach the main tributary of the canalised part and the natural part of the Aulne because of angling. However, fishing does not appear to be the one factor limiting the widespread presence of one-sea-winter adults in areas favourable to breeding: without this activity, the percentage of one year old sea salmon reaching the Aulne river remains very low. The impact of angling on the spring salmon population was found to be far greater, as half of the fish were caught before reaching weir 10. As angling limits the number of fish successfully clearing this weir, this will reduce the numbers of fish able to reach even the reproduction areas located on the main tributary of the canalised sector.

Suggestions that the origin of the salmon returning the Aulne, whether wild or hatchery-origin, might affect the migratory behaviour of the fish were not borne out by this investigation. In terms of the capacity to clear obstacles, the performances of wild fish and reared fish were quite similar. Indeed, there was no difference in the mean number of weirs cleared by the two groups of fish, or the clearance percentages observed at the various weirs. The use of reared salmon does not therefore appear to be responsible for the very low success rate in passing the canalised sector.

On the other hand, differences were observed between these 2 categories with respect to the fate of individuals. The percentage of salmon descending the Aulne in 2000 was greater for reared individuals (25%) than for wild ones (9.5%). This phenomenon might be at least partly explained by the choice of release sites for the young stocked fish. Even though most of them were freed on the Aulne, several thousand smolts were released up to 2001 on the estuary tributary of the Aulne, the Douffine. In 2000, it was observed that all of the salmon descending the Aulne then ascending this tributary were reared salmon. These eight fish might thus come from batches released on the Douffine which were returning to it after having mistakenly entered the Aulne. Mortality, apart from fishing, appears to be less significant for reared fish (27%) than for those assumed to be wild (43%). This result might be partly explained by a greater percentage of reared fish among those descending the Aulne, since individuals which had left the Aulne could obviously not die there. On the other hand, the proportions of individuals which survived up to the reproduction period did not appear to be different when wild populations and reared ones were compared. The reared individuals are thus just as likely to reproduce as wild ones.

In conclusion, this radio-tracking study explains why there is a lack of wild juvenile salmons on the spawning grounds in the natural part of the Aulne upstream of the canalised part. The lack of young fish is due to the difficulties that salmon face when trying to reach these breeding areas, particularly those on the natural part of the river. The percentage of adults likely to reach the natural part is too low to enable sufficient natural reproduction in this catchment area. This poor result is probably due to the environmental conditions caused by canalisation, with a multitude of weirs along the canalised part and sluggish flows which undoubtedly intensify problems due to poor water quality. This study also revealed the high impact of angling, especially on spring salmon, and showed that use of reared individuals cannot explain the lack of passability of the canalised part, nor the low amounts of natural fry produced on the Aulne.

The study has thus provided managers with a means of assessing the restoration plan. We recommend that several steps are taken to pursue this plan: (1) new fish-passes should be built at weirs 3 to 5, at weir 17 and at all weirs fitted with old fishways, (2) the migration environment should be improved by improving water quality and increasing the flow speed, for instance by opening weirs and (3) fishing activities should be prohibited during the spring salmon migration period.

Radio-tracking was used on this watercourse to aid decision-making. It was used not only to assess the salmon restoration plan for the Aulne river, but also to point out likely alternatives to authorities, to help maintain one of the salmon populations that, in the past, enabled the biggest catches in all of Brittany's waterways.

Acknowledgements

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3-dimensional positioning of salmon in commercial sea cages: assessment of a tool for monitoring behaviour

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Key words: acoustic telemetry, aquaculture, 3-dimensional positioning, chinook salmon, *Onchorhynchus tshawytscha*.

Abstract

In aquaculture, telemetry may provide a valuable tool for monitoring fish in sea cages non-invasively. A 3-dimensional positioning system was assessed by tracking the movement of commercially farmed chinook salmon (*Oncorhynchus tshawytscha*, Walbaum, 1792) in a sea cage. The accuracy and reliability of the data generated is presented in terms of noise and position precision. Algorithms were used to test the ability of the system to measure and furthermore identify known activity patterns. Differences in night and day activity patterns were picked out by the classifier which was further refined to enable the identification of distinct feeding times in each of three commercial cages.

Introduction

Acoustic telemetry is widely utilised in ecological studies. Archival tags have been used to document seal and whale diving (Le Boeuf *et al*., 2000; Johnson and Tyack 2003) and basic transmitters facilitate real-time tracking of salmonid migration (Thorpe *et al*., 1981; Smith *et al*., 1998). In addition, automated fixed tracking stations can be positioned in arrays to cover specific important areas e.g. salt ponds (Lagardère *et al*., 1990) or marine reserves (Lembo *et al*., 2002).

In aquaculture, telemetry may provide a valuable tool for remotely monitoring fish swimming behaviour in sea cages. Previously, farmers could conduct a basic assessment of health and welfare whilst hand feeding fish. However, the advent of automated feeding systems (e.g. Storvik AS, Norway; Akvasmart, Norway) has resulted in fish feeding lower in the water column (Fernö *et al*., 1995; Hevrøy *et al*., 1997). Hence, cameras are used to assist with feeding and health assessment, but they do not provide information on individuals nor is it known what proportion of the population is viewed at any given time.

To date, aquaculture-based studies have focused on a few individuals in small-scale experimental cages rather than large-scale commercial operations (Juell and Westerberg 1993; Bégout Anras *et al*., 2000). Recently, the accuracy of acoustic positioning systems has been measured and assessed in order to optimise position accuracy (Smith *et al*., 1998; Ehrenberg and Steig 2001; 2003). The described study tested similar technology with replicated groups of fish held under commercial conditions.

As the collection of data is highly automated in fixed array positioning systems, the amount generated can be very large, even over a short time period. This provides problems in processing and analysis. One solution to this is to utilise algorithms to detect interesting features in the data (e.g. McFarlane *et al*., 2004).

The aim of the described study was to assess the use of a 3-dimensional positioning system in tracking the movement of commercially farmed chinook salmon (*Oncorhynchus tshawytscha*) in sea cages. The accuracy and reliability of the data generated was assessed in terms of noise and positioning and algorithms were used to test the ability of the system to measure and furthermore identify known activity patterns.

Materials and methods

Site and Fish

The study was carried out at the Marine Harvest Young Pass sea site (50°36’40N, 125°34’66W) Vancouver Island (BC, Canada) between the 2nd and the 27th of December 2002. During the study the fish were held in three adjacent net cages, 30 m x 30 m, maximum depth 20 m, hanging from a steel frame (Fig. 1). As the cages were in a 2x4 arrangement, cages 2 and 3 were at the end of the system, furthest from the generator and the majority of boat activity, and cage 1 was adjacent to cage 2. The cages were surrounded by a steel walkway, 1 m wide on the outside and 2 m wide in the middle (between cages 2 and 3). The cage system was stabilised and anchored using large buoys situated approximately 1 m from the walkway on the two outside corners of cages 2 and 3.

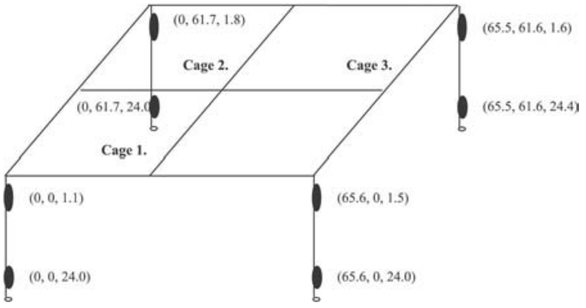

Fig. 1 – Schematic of system, lines are not to scale. Hydrophones are denoted by black ovals, and co-ordinates are displayed in metres.

Thirty-nine chinook salmon (mean ± s.e: 826.41 g ± 24.75) were obtained during routine transfer from one pen to another. All fish on the farm were female. The subjects were fitted internally with CAFT 11-3 acoustic tags (11x46 mm, 8.4 g in air, 4.2 g in water). Before undergoing surgery, individuals were anaesthetised in clove oil at 60 ppm until the operculum rate became slow and irregular. During surgery, the gills were irrigated with clove oil at 30 ppm to maintain anaesthesia. Each individual was weighed and measured and a 2 cm mid-ventral incision was made, anterior to the pelvic girdle, to allow insertion of the acoustic tag into the body cavity. The incision was then closed using 3 separate absorbable monofilament sutures (3-0 Ethicon). Surgery took no longer than 3 minutes and the entire procedure including anaesthetisation, a maximum of 7 minutes. Individuals were then held in a 1 m^2 tank until equilibrium and normal swimming behaviour were recovered and 13 fish placed in each of three cages. The fish were divided equally into 3 pens containing an average of 6000 fish in each resulting in a density of 3.7 kgm^{-3}. There was no significant difference in the weight of tagged fish placed in each cage (Kruskal-Wallis: $\chi^2=0.720$, d.f.=2, $p=0.698$, median: cage 1=815 g, cage 2=755 g, cage 3 =820 g)

During the study the fish were fed on commercial regimes; each cage was fed in turn for 30 minutes with 10 minutes in between. Feeding times were as follows (24 hour clock): Cage 1: 10:40-11:10, cage 2: 12:00-12:30, cage 3: 12:40-14:10. Due to the layout of the farm, there was a longer delay between feeding in cages 1 and 2 than there was between cages 2 and 3.

Positioning system

Positioning data were collected using 8 Lotek LHP_1 hydrophones (bandwidth 20-80 kHz), arranged in rectangular array suspended by four ropes, each with a 7 kg weight attached (Fig. 1). The hydrophones were suspended from the outer buoys of the farm in order to minimise transmission error (Ehrenberg and Steig, 2001). The acoustic tags emitted a coded pulse sequence (76.8 kHz, 86 dB) every 5 seconds. The information regarding the identity and the time that this signal was received by each hydrophone was transmitted via cable to the MAP_500 receiver. The signal was then digitally processed in order to remove noise, find acceptable codes and record the times that individual hydrophones received these codes. This information was transferred to a computer twice daily using 80 Mb flashcards.

Data were collected and stored continuously by the MAP system once tagged fish were placed in the cages. In order to reduce possibility of spurious behaviour due to recovery from surgery, data from the first 10 days following surgery has been omitted from the present study.

Setup and accuracy of system

Following deployment of the hydrophones, a reference tag was submerged at various important positions in the array to ensure that tag signals could be detected throughout the array and to set the receiver offset and gain values. Using this, the receiver gain and offset were adjusted to maximise the total number of received signals whilst minimising the number of spurious data points. The desired ratio of one spurious data point to 10 accurate points was achieved at a gain of 70 and an offset of 65.

In order to assess the position accuracy of the system, a stationary reference tag was anchored at the centre of the array (x=34.5 m, y=31.0 m, z=5.0 m) for the duration of the study. In addition, acoustic interference in the transmission of signals was determined by measuring the intervals between received tag signals for each tag. Data collected at the end of the study (December 26th) was used for these analyses as any technical errors in the tags would be present to the greatest extent at this point.

Data Processing

Files collected by the MAP 500 system were processed using the BioMAP program (Lotek Wireless, St Johns, Canada) to provide raw positioning data. These data were then filtered to remove extraneous and unreliable data points. Initially, fish positions recorded on fewer than 4 hydrophones were removed (the minimum for a three-dimensional position), as were positions outwith the physical boundaries of the cages. Subsequently, points of poorer accuracy were identified using a reliability index and geometric diffusion of precision (GDOP). Since the MAP system calculated positions from hyperbolae of possible points from each receiver, the degree that these hyperbolae overlap, and therefore the degree of noise/error was related to the geometry of the receivers (Smith *et al*., 1998 and Ehrenberg and Steig, 2003 for discussion). The GDOP calculated the area of error that occurred as a result of the geometry of the hydrophones and was set at 0.3; data with a value greater than this were rejected.

Identification of known activity patterns

Initially, behavioural characteristics such as column position and absolute velocity were calculated from the data and assessed by eye for differences in night and day activity. This determined the occurrence of trends in activity and identified key behavioural characteristics. Following this, a fuzzy K-Means classifier (Duda *et al*., 2001) was used to distinguish trends in fish activity levels with respect to night and day and feeding times.

Twenty-two behavioural characteristics that were likely to indicate broad changes in activity were derived from the position time series data. They consisted of means and standard deviations of 11 measurements (Table 1). One behavioural characteristic was created for each fish within a specified time window by averaging the data available for that interval to create a single datum. This moving window was used to provide a smoothing effect to facilitate the identification of clusters as the data were often erratic.

The classifier provided a degree of membership (from 0 to 1) for each feature in a predetermined number of classes, chosen as an input parameter to the algorithm. The sum of the degree of memberships was 1, similar to a probability distribution. Naturally occurring clusters were identified within these behavioural characteristics using an iterative process that calculated the metric distance from the centre of each of the classes to each of the behavioural characteristics. The degree of membership of each behavioural characteristic to each class was then used to adjust the class centre until it no longer moved; thus identifying a naturally occurring cluster.

Classifications were initially performed on all the behavioural characteristics using all fish and time data. Naturally occurring classes were identified, and the data was deconstructed into its original order, by time and fish number. Following the initial classification the classifier was refined in order to minimise variation in behaviour between cages and between night and day. The classifier was run individually for each cage using only daylight hours. In addition, the number of behavioural characteristics was reduced to 6; the mean and standard deviation of radial position (distance from cage centre), absolute velocity (speed, regardless of direction) and column position (distance to the water surface).

Table 1 – Description and formulae for calculation of the parameter vectors used for classification

Name	Description	Formula
Absolute Velocity	Speed, regardless of direction.	$AbsVel = \sqrt{\left(\frac{\Delta X}{\Delta t}\right)^2 + \left(\frac{\Delta Y}{\Delta t}\right)^2 + \left(\frac{\Delta Z}{\Delta t}\right)^2}$
Absolute Acceleration	Fish acceleration regardless of direction	$AbsAcc = \sqrt{\left(\frac{\Delta(\Delta X)}{\Delta t}\right)^2 + \left(\frac{\Delta(\Delta Y)}{\Delta t}\right)^2 + \left(\frac{\Delta(\Delta Z)}{\Delta t}\right)^2}$
Radial Position	Fish distance from cage centre	$AbsAcc = \sqrt{(X_{fish} - X_{centre})^2 + (Y_{fish} - Y_{centre})^2}$
Radial Velocity	Rate of change of the distance from cage centre	$AbsAcc = \sqrt{\left(\frac{\Delta(X_{fish} - X_{centre})}{\Delta t}\right)^2 + \left(\frac{\Delta(Y_{fish} - Y_{centre})}{\Delta t}\right)^2}$
Radial Acceleration	Rate of change of speed with respect to the cage centre	$AbsAcc = \sqrt{\left(\frac{\Delta(\Delta(X_{fish} - X_{centre}))}{\Delta t}\right)^2 + \left(\frac{\Delta(\Delta(Y_{fish} - Y_{centre}))}{\Delta t}\right)^2}$
Column Position	Distance to the water surface	$AbsAcc = Z_{fish}$
Column Velocity	Rate of change of the distance to the water surface	$AbsAcc = \sqrt{\left(\frac{\Delta Z_{fish}}{\Delta t}\right)^2 + \left(\frac{\Delta Z_{fish}}{\Delta t}\right)^2}$
Column Acceleration	Rate of change of speed with respect to the cage centre	$AbsAcc = \sqrt{\left(\frac{\Delta(\Delta Z_{fish})}{\Delta t}\right)^2 + \left(\frac{\Delta(\Delta Z_{fish})}{\Delta t}\right)^2}$
Arc Length	The angular distance with respect to the centre of the cage	$\sqrt{(X_{fish} - X_{centre})^2 + (Y_{fish} - Y_{centre})^2} \cdot \arctan2((X_{fish} - X_{centre}),(Y_{fish} - Y_{centre}))$
Angle Velocity	Rate of change of angular position to the cage centre	$\frac{\Delta\left(\sqrt{(X_{fish} - X_{centre})^2 + (Y_{fish} - Y_{centre})^2} \cdot \arctan 2((X_{fish} - X_{centre}),(Y_{fish} - Y_{centre}))\right)}{\Delta t}$
Angle Acceleration	Rate of change of angular velocity with respect to the cage centre	$\frac{\Delta\left(\Delta\left(\sqrt{(X_{fish} - X_{centre})^2 + (Y_{fish} - Y_{centre})^2} \cdot \arctan 2((X_{fish} - X_{centre}),(Y_{fish} - Y_{centre}))\right)\right)}{\Delta t}$

Results

System Accuracy

The median pre-programmed time for tag transmission was 5 seconds. However, the overall average time between received signals on December 26th was 17.3 seconds. This ranged from an average of 7.4 to 491.0 seconds for each tag.

The reference tag provided an index of positioning accuracy. From this, it was determined that the overall standard deviation of the noise in the position measurement was 74.6 cm. Thus, 99.7% of the position points are within 2.2 m of the actual position overall. The depth plane has the largest affect on position accuracy as the standard deviation of this plane is 2.6 m compared with 0.5 m and 0.7 m on the X and Y planes respectively.

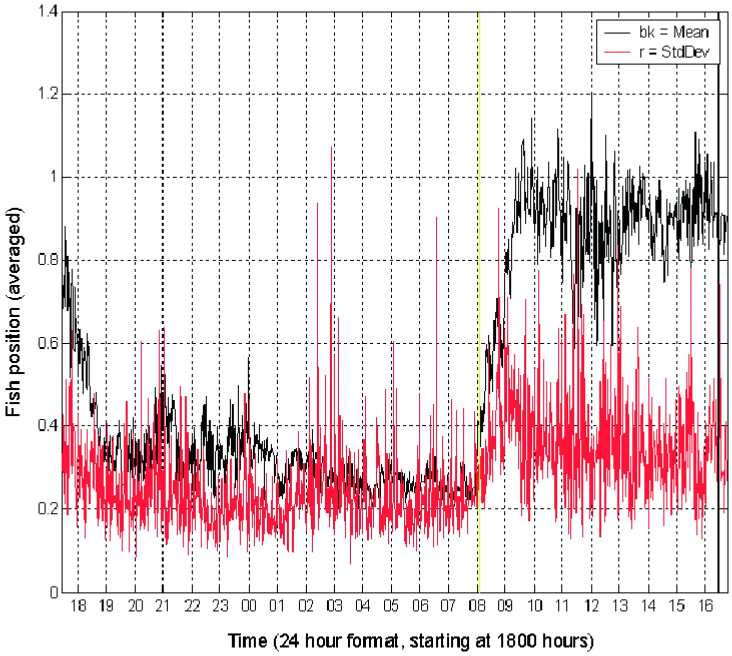

Fig. 2 – Fish position (averaged for all fish) over one day.

Detection of activity patterns

Initially, the mean and standard deviation of the behavioural characteristics were calculated, normalised and filtered (see methods). Differences between day and night were evident in mean and standard deviation of absolute velocity, absolute acceleration, angular velocity, mean radial velocity and radial acceleration, standard deviation of angular acceleration, column acceleration and column velocity. These differences were most pronounced in column position (Fig. 2); the fish were much lower in the water column during daylight (from 08:00 h to 18:00 h) than during darkness. Three-dimensional positions for each individual enabled tracks to be plotted showing the distribution of fish in the cage over time (Fig. 3).

Classification was then performed using one day of data and all behavioural characteristics. The behavioural characteristics were normalized and the Euclidian metric distance was calculated. Overall, a general trend was apparent, with the majority of fish classified into same class at any given time. However, the occurrence of differential class membership is indicative of small differences in individual behaviour.

In order to minimise the variation in behaviour between cages and between night and day, the classifier was refined. The resulting class membership is illustrated in Fig. 4 over a seven day period. Similar

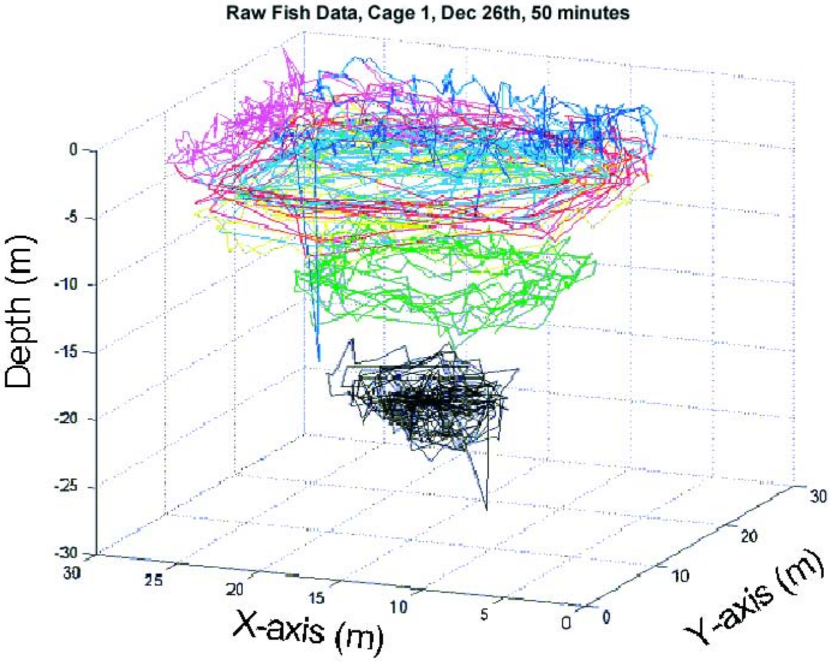

Fig. 3 – Raw data illustrating 50 minutes of fish position data for many individuals in one cage.

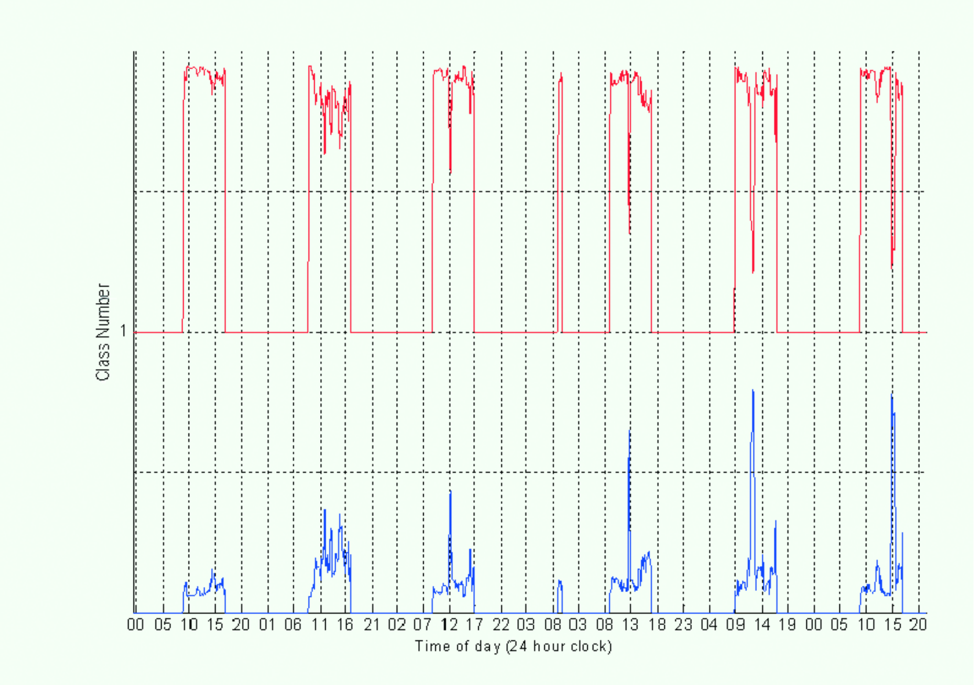

Fig. 4 – Graphical representation of class membership (0 or 1) of one cage of fish over seven days. The x-axis is labelled with the first two digits of the 24 hour clock in five-hourly intervals.

classification patterns were present each day although there was some variation between days. However, there was a spike in class 0 (the lower class) around the same time everyday which corresponds to the time that the fish were fed. This time was different in each tank, no tank had an overlap in the timing of the spike and they occurred in the same order as the cages were fed on the farm.

Discussion

The mean interval between received signals was much greater than the interval between signal transmission. This reflects the extent of noise in the environment; preventing the signal from reaching the hydrophones or slowing it down. Random noise can make an extensive contribution to the errors encountered in tracking positions of individuals (Smith *et al*., 1998). The present study was carried out upon a commercial farm where noise in the data can potentially result from boats, generators and automatic feeders in addition to noise inherent to the seawater environment.

Overall, the positioning accuracy of the system was lower than similar studies; Chapman *et al*. (1975) documented an error of ± 1 m when tracking Norway lobster and Juell and Westerberg (1993) estimated an error of 0.1 m in the centre of a sea cage. Ehrenberg and Steig (2003) quoted standard deviations of 0.16 m, 0.14 m and 0.26 m on the X, Y and Z planes, respectively using a similar sized hydrophone array. These are 4 times lower than those quoted in the present study for X and Y co-ordinates and 10 times lower for the Z co-ordinates. Smith *et al*., (1998) used an array approximately seven times larger than that described here, however the average position accuracy of 5 tags was also seven times greater (3.3 m). In the present study the reference tag was suspended in the water with no weight attached, potentially giving a lower accuracy of positioning than from the subjects themselves. Unfortunately, it was not possible to increase the accuracy of the data further using the GDOP or Reliability index. Other data filtering techniques such as Kalman filtering, which uses information available about noise to determine the actual position of a target, given consecutive position measurements, may improve the accuracy. However, this level of filtering is outwith the scope of the present paper.

In the described study, the hydrophone array was positioned to surround the cages, but this resulted in the depth plane being shorter than the rest so the formation was not a true cube shape with sides of equal length. This has been shown to result in a larger position error in the centre of the cage, especially in the depth plane (Ehrenberg and Steig, 2003). Therefore, in order to improve accuracy, hydrophone arrays should be positioned in a cube formation wherever possible.

The data analyses performed did not utilise absolute points, but rather scanned large sections of data for trends. This method is less likely to be affected by inaccuracies in positioning. The clear differences in diel behaviour that were documented have also been exemplified in farmed Atlantic salmon (e.g. Bégout Anras *et al*., 2000; Oppedal *et al*., 2001) and are likely to be influenced by feeding and surface light avoidance (Fernö *et al*., 1995).

In addition to diel patterns, differences in activity were identified in relation to feeding times. Although these trends were picked out by the classifier, there was a great deal of variation between individuals and between days. For example, the spikes that indicate abrupt changes in class membership at feeding times are not always present to the same degree if at all (Fig. 4). This could be a result of particular sets of circumstances replicating the feeding spikes or more likely, some external stimulus affecting the fish behaviour. The classifier was run in multiple iterations, meaning that different starting points give different end clusters whilst naturally occurring clusters are identified. In the present study, extraneous clusters may occur in the data as a result of sunrise or sunset, watercraft, predators, or environmental anomalies. However, the appearance of similar membership spikes over multiple days does indicate a re-occurring phenomenon.

In conclusion, the classifier was able to identify known changes in activity that occurred in commercial sea cages. Daytime swimming activity was differentiated from that at night and distinct membership patterns indicative of feeding were identified in each of three commercial cages. Therefore, this system could provide a valuable tool for farmers to monitor their stock. Automation of this system could potentially provide a tool that would monitor feeding activity daily and pick out differences as they occur, warning farm staff that there is a problem in terms of disease or predation.

The ability to quantify swimming behaviour of farmed fish in sea cages has widespread implications. There are many unanswered basic questions such as the issue of social interactions in the large, high-density groups found in aquaculture. Furthermore, recent documents and legislation on the welfare of farmed fish (e.g. FSBI, 2002) call for a greater understanding of the basic behaviour of caged fish in response to husbandry stressors and routine procedures such as feeding.

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Effect of hydropeaking on migrations and home range of adult Barbel (*Barbus barbus*) in the river Meuse

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Key words: rheophylic fish, home range, migration behaviour, flow regime, telemetry.

Abstract

The non-navigable part of the River Meuse, forming the border between Belgium and the Netherlands, is 60 to 100 metres wide and has an average slope of 0.45 mkm^{-1}. The river has been modified by gravel extraction, bank stabilization, summer dykes and flow modifications. To document fish use of this system, fourteen adult and female (Fork Length: 47.5–57 cm) barbel (*Barbus barbus*) were radio tagged (40 MHz): 5 in May 2001, 3 in October 2001 and 6 in April 2002. From May 2001 till September 2002 fishes were localized weekly throughout the year and daily in April and May to identify spawning grounds and investigate seasonal migrations and home range. In winter, when flows ranged from 250 to 2 800 m^{2}s^{-1}, barbel were found in the main river bed at all times. No downstream migrations to sheltered parts of the river were observed. In spring, both upstream (0.2 km) and downstream (up to 2.6 km) migrations to spawning grounds were observed. Individual barbel, in the mouth of a tributary, showed different migrations towards spawning areas and holding locations under low flow conditions. Migrations in summer and autumn were directed by changes in flow and habitat suitability. The home ranges of the barbel ranged from 1.05 to 27.3 km and differed significantly in size for different parts of the river. Resident habitat suitability is determined by discharge, water depth, water current and bottom structure. Total home ranges of barbel, occupying a highly structured part in the river with continuous availability of suitable habitat for spawning, resting and foraging were significantly smaller (1490 m) than those for barbel initially caught in areas with less habitat diversity (12.5 km).

Introduction

Spatial and temporal change in habitat use by aquatic species in response to changes in discharge and water level is typical in river systems. While these animals have adapted to the timing, amplitude and predictability of seasonal flows, man-made changes to water courses have resulted in strong variations in water quality, hydrology and marked habitat fragmentation. These modifications have largely affected populations of aquatic invertebrate species (Céréghino and Lavandier, 1998, Growns and Growns, 2001, Céréghino *et al*., 2002, Cortes *et al*., 2002). In particular, these changes have modified the drift of invertebrates (Lauters *et al*., 1996, de Crespin de Billy *et a*l., 2002), reduced the availability of key habitats for fish or their access to these habitats (Raat, 1996, Baras and Lucas, 2002, Brown and Ford, 2002, Pretty *et al*., 2003, Vehanen *et al*., 2003).

During the nineteenth and twentieth centuries the River Meuse was dredged in Belgium, banks were rectified and originally 23 weirs and dams were erected for navigation and flow control (Mischa and Borlee, 1989). Presently 6 dams remain of which only a fraction are equipped with operational fish passes (Baras *et al*., 1994, Prignon *et al*., 1998). Additionally, several dams are equipped with small hydropower plants that operate in a discontinuous discharge mode. These plants cause the water level and velocity to vary beyond the range of natural fluctuations. For example, water level fluctuations that typically took place between seasons can now occur on a single day or within a few hours. These marked changes have resulted in the extinction of local populations of diadromous species

(Philippart *et al*., 1988; 1994) and declines in abundance potamodromous species, such as the common barbel (*Barbus barbus* L).

Previous studies have highlighted the behaviour of barbel in rivers with restricted anthropogenic interference, i.e. no man-made obstacle to upstream or downstream movement, no or little change in the natural flow regime and no major loss of habitat (for the River Meuse basin, see Philippart 1977, Baras, 1992; 1994; 1995; Philippart and Baras, 1996). Information on how barbel react to man-made obstacles can be found in Baras *et a*l. (1994) and Lucas and Frear (1997). In contrast, little or no information is at hand on how barbel react to man-made variations in the flow regime, even though such information might be crucial for management of their populations in rivers that undergo flow management and hydropeaking. Flow modification can strongly affect the eggs (Baras and Philippart, 1999), the larvae or juveniles (Baras and Nindaba, 1999) or the adults themselves, although a greater plasticity and resilience of the more agile adults.

Here, we provide a first account of the behaviour of barbel in the Border Meuse, which still provides natural habitats but is strongly modified by hydropeaking. The study focused on the home range, migration, habitat use of adult female barbel, as revealed by radio tracking. Female barbel attain sexual maturity at an older age and larger size than males (Philippart, 1977) and they are the true limiting factor of the population. Additionally, the final selection of the spawning site is done by females (Hancock *et al*., 1976, Baras, 1994).

Material and methods

Study area

The so-called "Border Meuse" is a 40-km stretch where the river forms the border between Belgium (left bank) and the Netherlands (right bank), in between the dams of Borgharen (upstream) and Linne (downstream), which are both sited in the Netherlands (Fig. 1). The dam of Borgharen is impassable to fish during periods of low flow. In between these two dams, there is no man-made obstruction to flow or fish movement, thereby making the Border Meuse one of the sole free-flowing stretches of the lowland River Meuse.

The banks of the river were stabilized for flow control over almost the entire length of the Border Meuse. The riverbed was locally dredged and lowered 1 to 3 m but some parts are nearly unaffected. This part of river was not dredged substantially as other parts of the Meuse, because this stretch of the river is bypassed by two lateral canals for navigation. The alternation of pools and riffles is thus largely maintained in the Border Meuse. The width ranges from 60 to 100 m (within summer dykes) and the mean slope is 0.40‰. Depth in pools can be in excess of 3 m during summertime. The substratum is of cobbles rather than gravel, due to high erosive forces in the riverbed. Low base flows are less than 10 m^3s^{-1} during summer and relatively high peak flows can attain 2800 m^3s^{-1} during rainy winters (Heylen, 1997).

The flow regime in the Border Meuse is strongly dependent on the operation of upstream hydropower dams, in particular that of Lixhe, in between the cities of Liège and Maastricht, about 30 km upstream of the centre of the study area (near Maasmechelen, Fig. 1). At the dam of Lixhe, the maximum drop at the weir is 7.5 m and the turbines operate in a discontinuous mode. This results in an alternation of water retention and hydropeaking, especially during periods of low flow. This alternation causes daily changes in discharge and water level (85 m^3s^{-1} or 0.8-1.1 m in April-May 2001 and 2002), but no substantial variation in oxygen content between different habitats in the Border Meuse (Witteveen and Bos, 2000). Changes in discharge are frequently more than 170 m^3s^{-1} or 2.2 m in height within one our.

Tagging and tracking

Female barbel (47.5-57.0 cm Fork Length, 1,580-2,813 g in weight, *n*=14) were captured with electric fishing (DEKA 7000, DC 250-350 V, 4-8 A) during May 2001 (*n*=5), October 2001 (*n*=3) and April 2002 (*n*=6). The adult female barbel were caught in deep (>80 cm) and fast flowing (>1.5 ms^{-1}) riffles, externally identified as female prior to implantation and checked by internal gonad con-

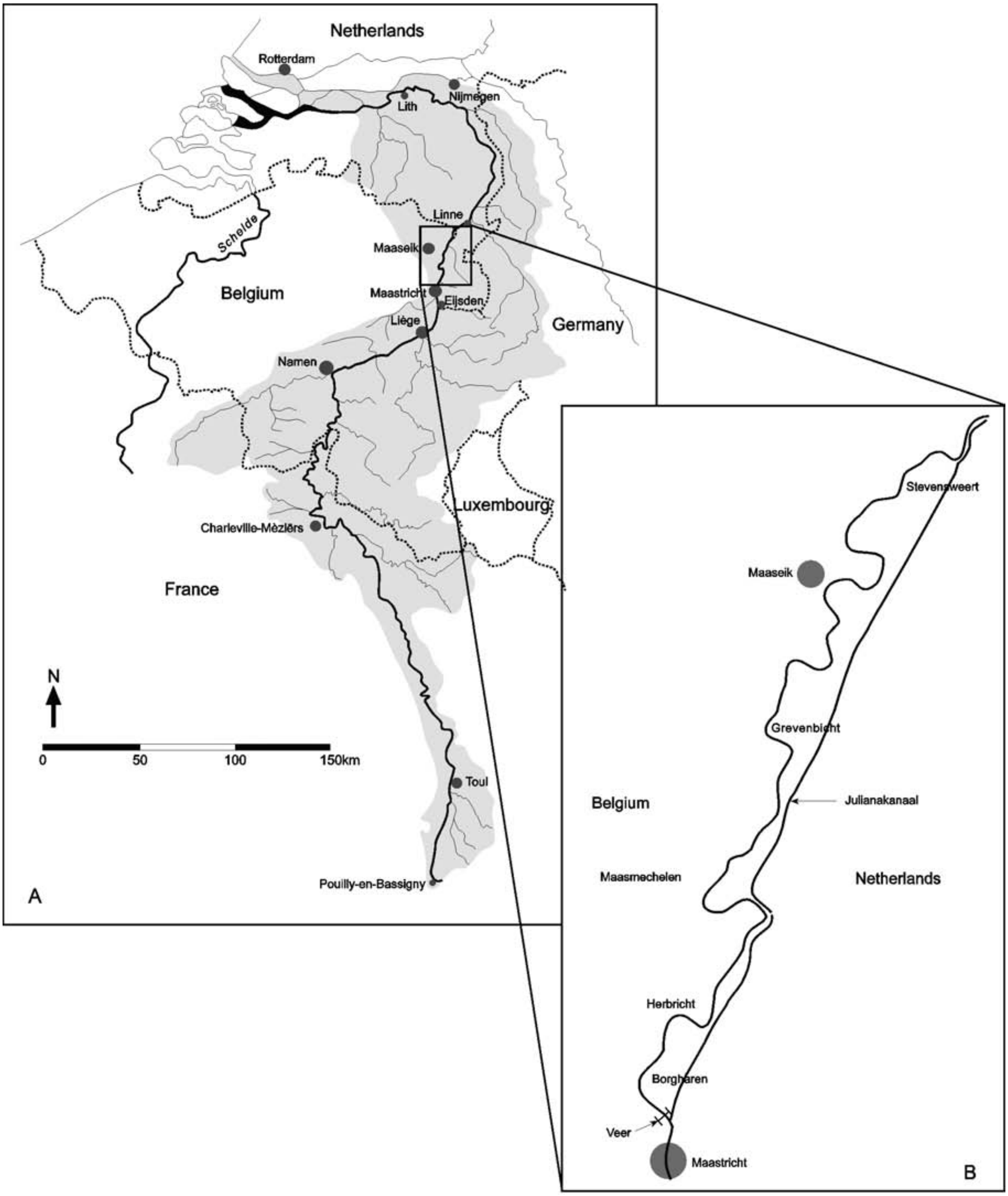

Fig. 1 – Location of the study area on the river Meuse. The Border Meuse is situated between Borgharen (downstream Maastricht) and Maaseik.

trol during implantation of the transmitter. Barbel were exclusively captured in Herbricht (*n*=6) and Maasmechelen (*n*=8) respectively 22 and 33 km downstream of Eijsden (Fig. 1). Maasmechelen is characterised by a steep slope (up to 1.7‰) and the presence of two permanent islands and large gravel bars. In Herbicht, the slope does not exceed 0.45‰, and no permanent island is present, only a few lateral gravel bars. However, this station is at the confluence with the tributary Geul, which is the sole tributary of the Border Meuse that is large enough for adult barbel.

Within the hour following capture, barbel were anaesthetised with 2-phenoxy-ethanol (0.4 mll^{-1}) and surgically tagged with radio transmitters, through an incision opened in between the pelvic girdle and the papilla. The incision was closed with separate stitches made of Vicryl, which absorbs within 6 months (for detailed information on surgery, see Baras, 1992). Radio transmitters (ATS Inc., 40 MHz) were equipped with coil antennae, to minimize the risks of drag, entanglement or pathological outbreak after the barbel had healed (for a synthesis, see Jepsen *et al*., 2002). Radio frequencies were spaced 10 kHz apart, to minimize risks of interference between transmitters, and to permit straightforward manual scanning with a simple receiver (Fieldmaster 16 channels, ATS Inc.). Each transmitter was equipped with an activity tilt, which shifted the tag's pulse rate from 40 to 80 pulses per minute, thereby allowing identification of active and inactive fish. Fish were released in calm places approximately 20 m downstream the capture site.

From May 2001 to September 2002, fish were tracked at weekly intervals, as this interval was shown to allow accurate estimation of home range in barbel (Baras, 1998). However, during the spawning period (April-May) fish were tracked every day, since females might spend no more than one or two consecutive days on the spawning grounds (Baras, 1994; 1995). Searches were made on foot or by car from the elevated riverbanks for 18 months. Upon detection of a signal, its position was determined by triangulation with a loop antenna, which gives a sharp null peak. Information of 11 fishes tracked for at least 12 months has been processed (Herbricht *n*=4, Maasmechelen *n*=7).

Home range was defined as the distance between the upstream-most and downstream-most locations. Home range and distances moved by barbel were measured by reference to landmarks, the position of which was determined by GPS (nearest 6 m). Data on the hourly discharge at Lanaken (between Borgharen and Herbricht, Fig. 1) were provided by the Flemish administration (AWZ). Data on water temperature were derived from RIZA at Eijsden. Because year round habitat use of the barbel often showed a distinct, binary nature, logit regression was used to detect and quantify major changes in habitat utilisation of individual fishes in relation to discharge (Statistica, StatSoft).

Results

The behaviour of barbel varied substantially depending on capture location. The fish from Herbricht showed long-range seasonal migrations, whereas those from Maasmechelen remained all year round in the vicinity of their capture site. Migrations during high peaks were not observed. Low peaks sometime force individual barbel to move to deeper resident habitats. The average annual home range was 1.5 km in Maasmechelen (1.05-4.0 km), and 12.5 km in Herbricht (5.9-27.3) (Fig. 2a). Therefore, we describe the annual movements of these fishes in separate paragraphs.

Two of the six barbel tagged in Herbricht, near the mouth of the Geul, could only be tracked four less than three days. The other four barbel moved in between this tributary and the River Meuse. Typically, habitats in the tributary were colonized during spring and early summer, until the water level dropped substantially in July-August. Two barbel that showed strong residency in the Geul then left the tributary, entered the Meuse and moved downstream several kilometres (5.9 and 27.3 km). A third barbel moved in and out the tributary during spring. It moved as far as 6.7 km upstream. The fourth barbel moved 10 km downstream to the station Maasmechelen. Hence, barbel

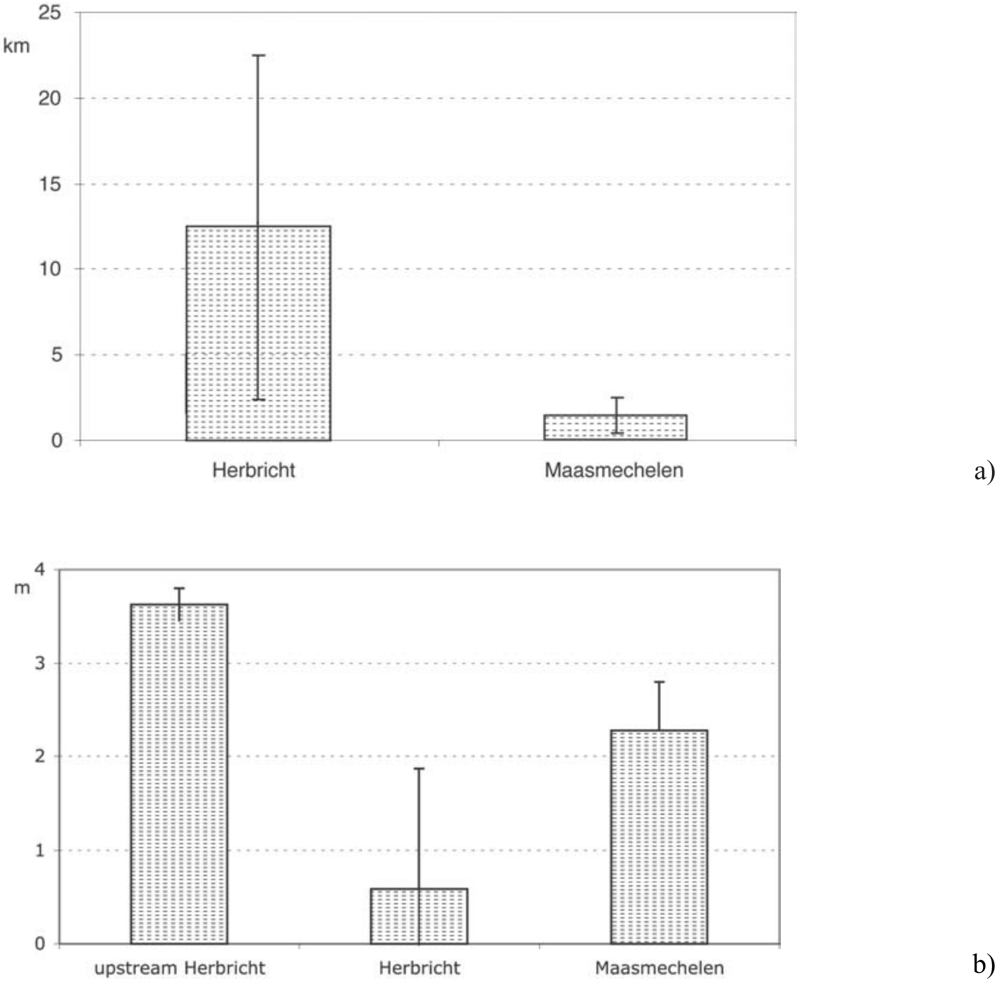

Fig. 2 – a) Average home range of barbel in the station Maasmechelen (n=7) and Herbricht (n=4). Error bars indicate standard deviations. b) Average maximum depth in cross sections in the river Meuse upstream Herbricht, from Herbricht to Maasmechelen and at Maasmechelen. Error bars indicate standard deviations.

that originated from the same area spread over about 35 km during summer or nearly the total length of the free-flowing part of the Border Meuse. The length of the migrations is strongly related to the presence of deeper riffles or pools in the river. Upstream Herbricht and in Maasmechelen deeper holding places are present. From Herbricht up to Maasmechelen maximum depth at low discharge (10 m^3s^{-1}) is in average only 0.6 m (Fig. 2b).

In contrast, the fish captured near Maasmechelen (*n*=7) showed restricted movements at all times of the year. During autumn and winter, under low temperatures and high flows, barbel (*n*=4) showed almost no movement. They consistently remained in deep runs with large boulders unless flows exceeded 800 m^3s^{-1}, when they moved to riparian shelters. The shelters were flooded willow trees or big boulders on flooded riverbanks. In spring, barbel (*n*=11) moved over distances ranging from 50 to 2600 m and gathered in the pools and runs along one of the permanent islands when water temperature in the morning reached 13.5°C. Five to seven days after migration towards the spawning site, all barbel moved back to previously used habitats up- or downstream the spawning site. During late spring and summer, when flows decreased, the barbel in Maasmechelen also made restricted movements. For some (*n*=6), there was an obvious relationship between discharge and movement. For example, one of the barbel consistently moved between locations when flow reached 250 m^3s^{-1}, which accounted for its movements in between successive locations (Fig. 3). Another example is of two barbel that were tagged in April 2002 in a newly formed connection between a lateral gravel pit and the main stream. When minimum flow dropped below 150 m^3s^{-1} both barbel moved to residence places 1.6-2.6 km downstream or 4 km upstream respectively. When the minimum discharge exceeded 150 m^3s^{-1} again, both fishes migrated back to the gravel bank and entered the gravel pit. Three days later, when the minimum water level dropped again below 150 m^3s^{-1} both barbel returned to the places they occupied during the former low-flow episode. In contrast, other fish behaviour did not exhibit such clear-cut relationships (Fig. 4).

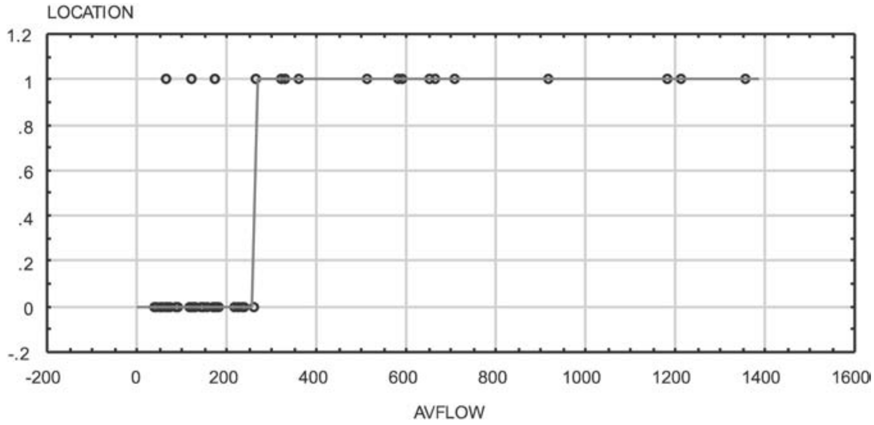

Fig. 3 – Two dimensional function plot with logit regression where average discharge (avflow in m^3s^{-1}) explains 75% (Barbel 2, N=60) of the variance in the occupation of the macrohabitats (locations coded 0 and 1).

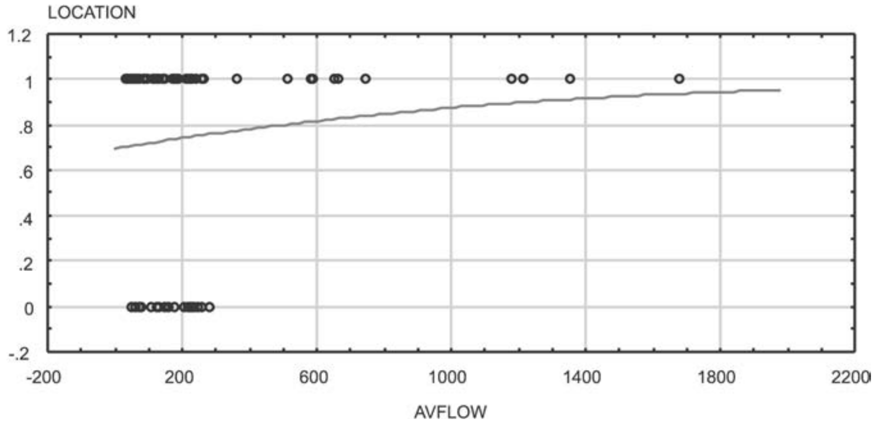

Fig. 4 – Two dimensional function plot with logit regression where average discharge (avflow in m^3s^{-1}) explains only 2% (Barbel 5, N=83) of the variance in the occupation of the macrohabitats (locations coded 0 and 1).

Discussion

The striking feature of this study is that the mean annual home range in Maasmechelen (1.5 km) was almost identical to the values that were determined for barbel in the undisturbed River Ourthe, either by conventional tagging or radio tracking (1.17 km in both cases) (Philippart, 1977; Baras, 1992; Philippart and Baras, 1996). Baras (1992) suggested that restricted home ranges in the River Ourthe were due to the availability of suitable habitats for resting during summer time and wintertime, thereby implying no need for long-range migrations in autumn or early spring. The same applies to station Maasmechelen, where both deep calm places and shallow fast-flowing places are available all year-round. This year-round availability of suitable places was only compromised under low summer discharge when water temperature exceeded 25°C and under very high winter flows, when some residence places became unsuitable and barbel moved towards the calmer places near the banks. Similar lateral and longitudinal movements were observed in the barbel tracked in the River Ourthe following spates during winter or spring (Baras, 1992). When flow decreases in summer, the individual differences in habitat selection suggest that the occurrence and the length of these movements is largely dependent on the habitat occupied under higher flows rather than on the value of discharge itself.

Other authors described movements over shorter or longer distances for *Barbus* spp.. In particular, the Mediterranean barbel *B. haasi* and *B. sclateri* are fairly resident in small Spanish rivers, with an average home range approximating 100 m (Aparicio and de Sostoa, 1999; Prenda and Granado-Lorencio, 1994). In contrast, Lucas and Frear (1997) reported seasonal movements of up to 20 km for *B. barbus* in the River Nidd (England). The compilation of a series of experiments in the River Ourthe (1988-1999) indicates that female barbel can also move short (a few hundred metres) or long distances (up to 20 km) (Baras, 1992; Philippart and Baras, 1996). Additionally, females that were tracked up to three years in a row showed consistent fidelity to the same spawning grounds and summer holding areas (Baras et al., unpubl. data), regardless of whether these were close or far from their residence areas. This may result because some habitats become unsuitable either because of high water velocities under high flow conditions in winter or reduced depth in summer. Hydropeaking, generating significant fluctuations in flow, results in major changes in physical conditions of the fish habitat. River stretches with high variation in stream morphology are less affected by the hydropeaking. The availability of refugia, during high and low flow conditions is particularly crucial for stream fish (Valentin *et al.*, 1996).

Barbel tends to select habitats that were as close as possible to their preferences (Baras, 1992; 1995), whatever the distance between these habitats. In the Border Meuse, both the Maasmechelen and Herbricht stations offer a wide variety of habitats which might accommodate the habitat preferences of barbel, either for residence areas or foraging areas at all times of the year. At least, this is the case under normal flows. Under very low flows, as those produced during the episodes of water retention in Lixhe, places with depth greater than 0.8 m (i.e. the preferred depth for the residence areas of adult barbel) can be found in sufficient number during summer in Maasmechelen, but are more rarely present in Herbricht. Additionally, the riffles in Herbricht are much shallower than those in Maasmechelen and their depth does not exceed a few centimetres during the episodes of water retention. Furthermore, the mouth of the Geul stream is largely impounded and shallow during summer, thereby discouraging or preventing the movements of large fish under very low flows. Finally, water temperature in the Border Meuse frequently exceeds 23-25°C during summer and during water retention, an additional warming by at least 1°C can occur. Such warm temperatures are in excess of the preferred thermal range of large adult barbel (Baras, 1995). In the River Ourthe, barbel were found to exhibit behavioural thermoregulation at temperatures in excess of 22-23°C, either through time-budgeting or through the utilisation of areas of cooler water. No such possibility exists in the Border Meuse, so thermoregulation can only be achieved by long-range movements to deeper or faster flowing stretches.

The Border Meuse offers a wide range of gravel bars that might serve as spawning grounds for barbel under a particular range of flows. The variations in water level and velocity that result from the hydropeaking at Lixhe have direct and indirect consequences on the adequacy of these habitats. As shown here, drops in water level are likely to cause barbel to stop spawning or to abandon the spawning grounds. The marked variations in water level are also likely to dry up places where eggs were laid, thereby resulting in the death of the all offspring in these habitats. Finally, the variations in water velocity that result from hydropeaking schemes are likely to result in the siltation of gravel bars. The barbel is a lithophilous pit-spawner: eggs are laid in 5-10 cm deep pits dug by the female in the cobble-gravel layers, so siltation might complicate the digging by spawners or reduce the intra-gravel flow, thereby jeopardising the eggs.

Maasmechelen is the sole station in the entire Border Meuse that provides a sufficient diversity of habitats for barbel all year round, including during the episodes of water retention at Lixhe. This station offers permanent islands and gravel bars with contrasting depths, which offer suitable spawning grounds and nursery habitats for barbel under the entire range of water level fluctuation. Two consecutive surveys (2001 and 2002) where the abundance of young-of-the-year barbel was examined in the Border Meuse, concluded that the Maasmechelen station hosted the highest density of 0-age barbel (De Vocht *et al.*, in prep). Hence, it is possible that this station is the sole sanctuary for this species in the Border Meuse. Other sites, such as Herbricht, offer some of the key habitats, but they cannot host self-a sustaining population of barbel.

To protect barbel it is thus imperative that habitat diversity in Maasmechelen is preserved and that future dredging schedules spare this area. The barbel is representative of the community of rheophilic fishes that use similar habitats. In particular, the spawning habitats are known to be shared by chub *Leuciscus cephalus*, river bleak *Alburnoides bipunctatus* and grayling *Thymallus thymallus*. In the long term, more attention should be dedicated to suppressing the hydropeaking, either by changing the type of turbine in Lixhe or by decommissioning this dam.

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Linking individual migratory behaviour of Atlantic salmon to their genetic origin

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Key words: telemetry, genetic background, mixed stocks, migration

Abstract

Many stocks of fish consist of mixtures of individuals originating from different populations. This is particularly true for many salmon and trout stocks, where fish of different genetic background are being found in the same rivers and/or lakes due to stocking activities or straying caused by increased aquaculture activities. The interpretation of results from studies of survival and behaviour of fish from such "mixed stocks" require information of the genetic background of individual fish. We used genetic analysis combined with radiotelemetry to study upstream migration of Atlantic salmon (*Salmo salar*) in a Danish lowland river. The river has a small population of native salmon, but salmon juveniles from Irish, Scottish and Swedish populations have been stocked and return as adults. A total of 39 salmon were caught by electrofishing and tagged by surgical implantation. A tissue sample (fin clip) from each tagged salmon was analysed using microsatellite DNA analysis of 6 loci. Assignment tests were used to infer the population of origin. The results showed that the salmon run was composed of approximately 1/3 "native fish", 1/3 foreign stocked fish and 1/3 escaped farmed salmon. The results indicate that stocked, foreign salmon had a slightly higher mortality and moved more up and down in the river than the native salmon did, but all salmon had problems passing the physical obstructions in the river. The DNA analyses enabled us to compare the behaviour of fish of different genetic origin, but the interpretation of the results was hampered by a high mortality of tagged fish. This study demonstrates that the combination of recent genetic methods and telemetry provides a potent tool for better management of mixed stock fisheries.

Introduction

In many rivers, with dwindling stocks of wild Atlantic salmon, attempts have been made to enhance populations through stocking programs. In several cases, broodstock from near or far rivers have been used. The results obtained from biotelemetric studies of the behaviour and migration of salmon are often inconclusive due to lack of knowledge of the genetic background and life-history of each tagged fish (e.g. Gerlier and Roche, 1998; Chanseau and Larinier, 2000; Thorstad *et al*., 2003). As many Atlantic salmon runs now consists of various proportions of individuals of different origin, such as: 1) wild natural born salmon, 2) hatchery reared offspring from wild (native or non-native) fish released at different life stages (½ year, yearlings or smolts), 3) escaped farmed salmon and 4) strays from hatchery reared fish from other rivers, it becomes very important for researchers to get background information of each fish's genetic and ecological background (wild/released). Recently, the development of new and more sensitive population genetic markers, such as DNA microsatellites have been used to provide detailed information on the genetic structure of trout and salmon (see for example Nielsen *et al*., 1999; 2001a; Hansen *et al*., 2000; 2001). Not only salmonids, but also several other fish species have been shown to exhibit heterogeneous population structure. Thus, even "classical" marine fishes (i.e. wide distributions, large population sizes, high fecundity, and pelagic eggs and larvae) like cod (*Gadus morhua*) form separate populations (see for example Ruzzante *et al.*, 1998; Nielsen *et al.*, 2001a) that may overlap spatially at certain times, such as mixed feeding aggregations, but nonetheless form isolated spawning populations. The objective of this paper is threefold: 1) to discuss the importance of linking observed behaviour with genetic background, 2) present a method to obtain information of the genetic origin of experimental fish and 3) to present a case study where this method was used.

Materials and methods

Capture and tagging

Salmon for tagging were obtained by electric fishing from boat in the river downstream of a hydropower dam and from a trap established in one of the uppermost chambers of the fish ladder at the hydropower station. Upon capture salmon selected for tagging were anaesthetised in a 5 mgl^{-1} solution of clove oil and a radio transmitter with a trailing external antenna (ATS model F1835, 3.4 g in water) was inserted in the body cavity by standard surgical procedures (Jepsen *et al.*, 2002). The incision was closed with two separate monofilament sutures and the tagged fish were released immediately after recovery. Salmon were released close to or at the position of capture, meaning that tagged salmon were released from the powerstation and approximately 10 km downstream. All salmon were measured to nearest cm and a small tissue sample (fin-clip) was taken for genetic analysis. The experimental procedures used in this study conform to the guidelines for the use of animals in research and local ethical conventions.

Study area

Varde River is a typical Danish lowland river with a catchment area of 1090 km^2, mainly farmed land (75%). Discharge range from 10,000 – 25,000 ls^{-1}. Through the late 1800 – early 1900, the river was heavily regulated to accommodate agricultural interests and in the 1920's a hydropower station was built. This station was further developed in 1940 and gave the river its present form (Fig. 1). The main spawning areas for salmon are situated upstream of the hydropower dam, where passage is only possible through an old (chamber-type) fish ladder with approximately 150 ls^{-1}. Upstream of the dam there is a shallow reservoir (35 ha) with dense vegetation during summer.

The regulation in combination with pollution (industrial and agricultural) caused a rapid decline in the run of Atlantic salmon and after World War II, the salmon stock was considered extinct. A few salmon were still caught, but were thought to be strays from the nearby Skjern River or other rivers. In 1993 a stocking program was initiated and every year a high number of salmon juveniles from different foreign populations (Burrishoole, Corrib, (Ireland), Lagan (Sweden), Conon (Scotland)) were released in Varde River. In 1999, samples from 101 adult and juvenile salmon caught by angling and electric fishing were analysed using DNA microsattellites (6 loci) and the results compared to those from the original (indigenous) salmon population. Old scale samples from the 1910's (N=37) were analysed to give information about the genetic composition of the original Varde salmon. The comparison of genetic profiles led to the conclusion that the salmon population in Varde River had persisted (see Nielsen *et al.*, 2001b for details), but at a very low level (small effective population size). This conclusion resulted in immediate management measures: cessation of stocking of salmon of foreign origin and a protection of the adult salmon in the river (only catch and release allowed). In order to facilitate additional protective/supportive measures, knowledge of the main spawning areas of the wild salmon was needed. Thus, a radiotelemetry project was planned to provide such information during the season of 2002.

Tracking

The tagged fish were tracked manually from boat or river banks approximately once a week from tagging through the spawning period. Fish posi-

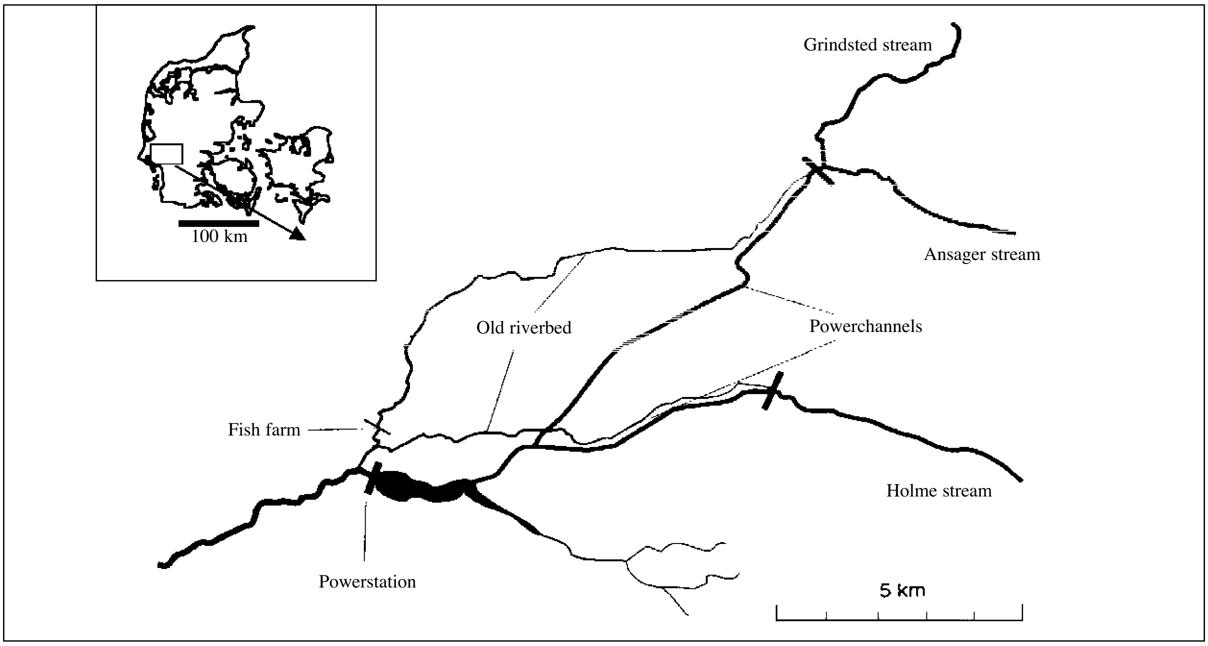


Fig 1 – Map of the study area. Vertical bars show major dams/obstacles in the system.

tions were marked by a Garmin GPS (e-trex) with fidelity of <10 m and analysed in Mapsource. Tracking was concluded in January 2003. In addition 7 automatic listening stations (ALS) were installed along the river and the tributaries.

DNA analysis

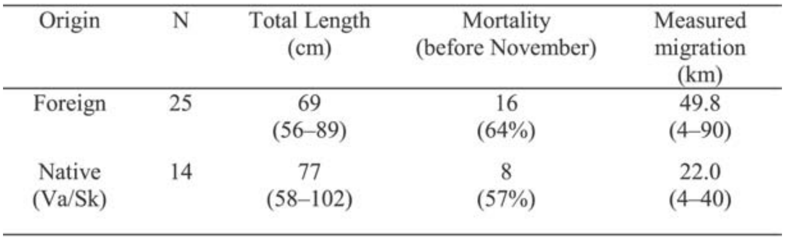
Six microsatellite loci were assayed: *SsoSL 85, SsoSL 311, SsoSL 417, SsoSL 438* (Slettan *et al.*, 1995), *Ssa 85* and *Ssa 202* (O'Reilly *et al.*, 1996). "Selfclassification tests", i.e., the assignment of individuals of known origin in baseline samples, to determine assignment power among populations and assignment of present population samples of unknown origin, were done using the program GeneClass (Cornuet *et al.*, 1999). We used the "Bayesian method" option (modified from Rannala and Mountain, 1997). The probability of correct assignment depends largely on the relatedness of the different populations. The percentage of correctly assigned foreign individuals was rather high (98.8–99%), whereas the probability of distinguishing between individuals from the closely related Varde and Skjern populations was rather low, so we chose to group these together in Fig. 2. For further details on the assignment of individuals to populations of origin in Varde River or exogenous populations, see Nielsen *et al.* (2001b).

Results

From June 18 to September 17, a total of 59 salmon (56–102 cm Total Length) were caught by electric fishing in the lower river and in the fish ladder trap. Of these, 39 (35 electro-fished, 4 trap-caught) were radio-tagged by surgical implantation (Table 1). The results of the DNA analysis (Fig. 2) showed that nearly one third of all salmon caught were most likely of Varde/Skjern origin and most likely wild fish.

Nineteen salmon were tagged from mid-June to mid-July, where the water temperature rose to above 15 ^{0}C and we decided to postpone further tagging until the temperature decreased. The tagged fish generally moved little in the lower river and none approached the dam in attempt to move upstream during the first weeks. Most fish moved downstream after release and one of the tagged salmon apparently left the river and was not recorded again. In late July, water temperatures rose to above 20 ^{0}C and stayed very high for an unusually long period of time (6-7 weeks). During the first week of August we concluded that 13 of the tagged salmon had died. We managed to recover seven dead fish and found 4 transmitters on the bank, whereas the remaining two transmitters were irretrievable from the bottom of the river. The dead salmon and the transmitters were found close to the place of last location from tracking. Some of the dead fish were still quite fresh and examination of these revealed no apparent cause of death. One of the dead salmon had been tagged 42 days before and the incision was fully healed and the sutures shed. Two tagged salmon disappeared and were not later recorded during the period with high mortality. In September when water temperatures decreased to about 15 ^{0}C, we resumed tagging and in the period from 17 to 24 September 20 salmon were tagged. Of these, three died within few days after tagging, while the remaining were tracked for a long period through the spawning season.

Table 1 – Comparison of mortality (number and percentage) and migration (average and range) of foreign and native salmon (mean Total Length and range are given) The group of foreign fish are composed of 9 Burrishoole, 9 Corrib, 5 Conon, 1 Lagan and 1 farmed salmon. Mortality includes fish that disappeared from the river before the spawning period. There was statistical significant difference in measured migration length between the groups (Mann-Whitney U-test; W=7.5; p=0.02)



Origin	N	Total Length (cm)	Mortality (before November)	Measured migration (km)
Foreign	25	69 (56–89)	16 (64%)	49.8 (4–90)
Native (Va/Sk)	14	77 (58–102)	8 (57%)	22.0 (4–40)

The results from the tracking of the remaining 20 tagged salmon (3 surviving fish from the early tagging + 17 from the later tagging) showed several major problems for upstream migration in the river. Only seven tagged salmon used the fish ladder to enter the reservoir and the upper river (Fig.3). Five tagged salmon entered the old river channel that has a very limited flow and only gives access to a few spawning areas. Of these five, three got into a fish farm, despite 30 mm fencing. Later we electro-fished a part of the outlet channel of the fish farm and estimated that 15-25% of the total spawning run of salmon was trapped there. Of the seven fish, that passed the power station, two (one Varde/Skjern 272, one foreign 083; Fig 4) moved relatively directly up to known spawning areas and stayed there during the spawning season (Nov.-Dec.). The remaining five (two Varde/Skjern, three foreign) moved in a more erratic manner and were recorded in two or three different tributaries. Two of these moved down through the fish ladder again and one later entered the fish farm, whereas the other jumped out of the fish ladder and died.

Some (3) of the tagged salmon that did not pass the hydropower station, left the lower river (to enter other rivers?), one was caught by an angler (released, but found dead six days later) and some (4) stayed in the lower river throughout the spawning period.

Generally the foreign stocked salmon moved longer distances than native salmon did (Table 1) and three of the tagged fish (Fig. 4, Fish 161) classified as Varde/Skjern, stayed in the lower river

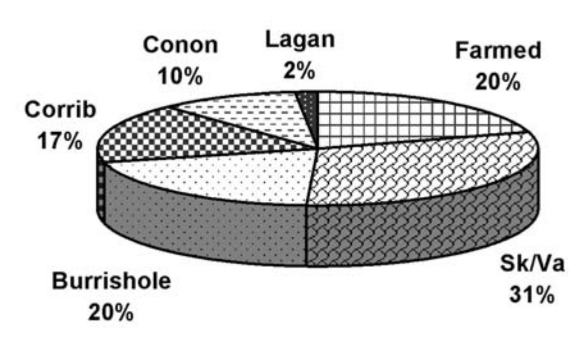


Fig. 2 – The genetic distribution resulting of the assignment test of samples from 59 adult salmon caught in Varde River in 2002.

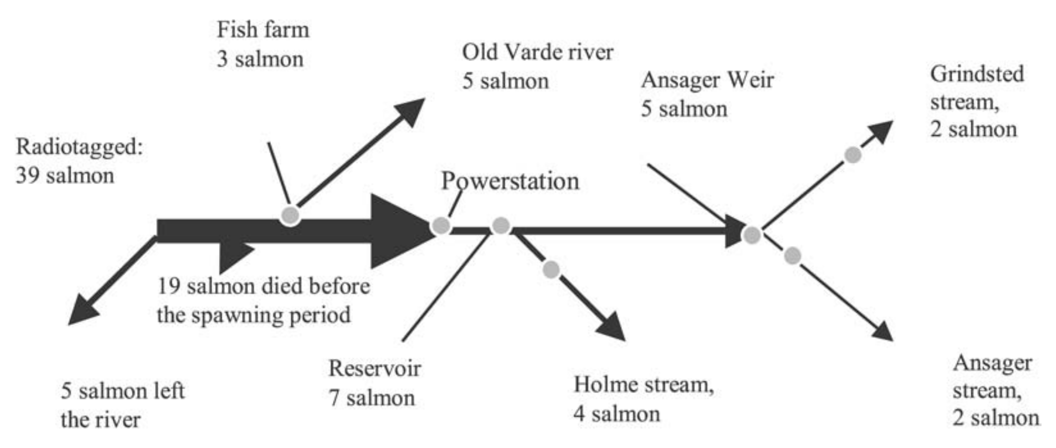


Fig. 3 – Schematic view of the spatial distribution of radio-tagged salmon in the Varde River system. The circles show position of Automatic listening stations (ALS). Note that numbers don't add up because some of the tagged fish were observed in several tributaries (see text).

and did not approach the dam at any time. During the spawning period these individuals showed clear preference for a certain area, where there was good current and coarse gravel on the bottom. During very low flow, it became clear that some fish had actually spawned there as reds were visible. Earlier this area was not judged as suitable spawning area because of depths of >1 m, but attempts will be made to find juveniles in the area using electric fishing.

Discussion

The expected difference in behaviour between native and introduced fish was not documented by the present results. This was partly due to the high mortality of the fish and to the many problems caused by man made obstacles in the river system. However, the fact that only one of the tagged native fish showed distinct homing behaviour to a tributary, whereas three presumably spawned in

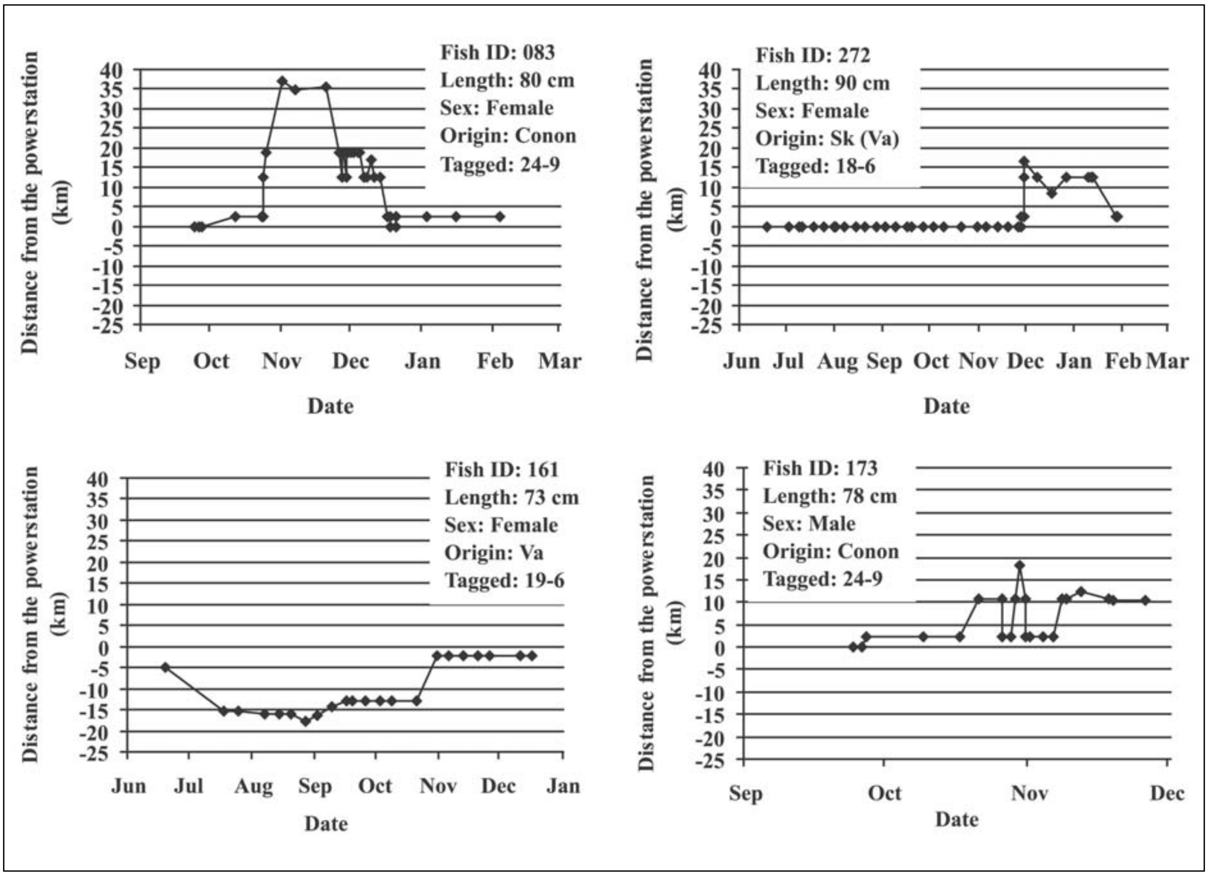


Fig. 4 – Examples of migration of radio-tagged salmon in Varde River.

the river downstream of the power station, indicate that this area may be very important for the persistence of Varde salmon as long as the obstacles exist.

The use of genetic analyses proved to be very valuable in the study of the salmon in Varde River, but even with sophisticated analyses like this one, the picture was not black and white. The genetic profiles can give information (with a certain probability) of what population each fish belongs to, but not about whether it is hatchery reared for supportive breeding or wild fish. During the last three years the salmon used for stocking in Varde River are all offspring from broodstock that was genetically tested and assigned to be Varde/Skjern salmon (supportive breeding), so we could never be 100% certain that a tagged fish was indeed a wild indigenous salmon. A comparison of the behaviour of native *vs*. foreign fish reveals that in both groups there are fish that move erratically up and down the river and also (fewer) fish that show a much more determined migration. However, the comparison of distance moved (Table 1) indicate that the foreign, stocked fish show more of this up and downstream movement than the native fish. This is in accordance with the results from a study of stocked salmon in River Gudenaa, Denmark where most salmon showed extensive erratic up- and downstream movements (Aarestrup *et al*., 2000).

The high mortality of the tagged fish came very suddenly and unexpectedly. It was probably caused by unusual weather conditions. The fact that the majority of the fish died within a short period of few days, despite the fact that they were tagged 5-42 days earlier, indicates that it was unlikely that handling and tagging was directly responsible for the deaths. In the same period we did find dead, untagged salmon and trout in the lower river. Electric fishing in the river after the deaths, provided very poor catches (of sea-trout and salmon) compared to earlier and knowing that no fish had passed upstream, we concluded that untagged salmon and trout either had died or left the river. However, we cannot rule out the possibility that the combined effect of capture, handling and tagging made the tagged fish more vulnerable to hostile environmental conditions.

Despite the fact that the high mortality left us with few fish to analyse, the results have highlighted several important problems to be solved in order to secure the existence of salmon in Varde River. The study also provided an indication of how the salmon population may have been able to persist by utilising the lower river for spawning. The current data cannot be used as documentation of successful spawning in unexpected areas, but future research may provide that. The results have directly effected management decisions regarding the monitoring of escaped farmed salmon in several rivers, monitoring the environmental conditions during summer in the lower Varde River and increased the political pressure to secure passage at the power station. In addition it has been decided to focus more research on how to prevent fish from entering into fish farms.

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The use of radio telemetry for optimizing fish pass design

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Key words: Atlantic salmon, upstream migration, hydroelectric plant, fish pass, radio telemetry.

Abstract

A radio telemetry study of adult Atlantic salmon (*Salmo salar L.*) was conducted in 2000 and 2001, for the purpose of optimizing the design of a new fish passage facility at the Baigts hydroelectric plant, located on the Gave de Pau river in the southwest of France. The efficiency of the old Denil fish pass, located on the bank opposite the tailrace, had previously been evaluated at 30-40% of its potential. The decision was taken to build a new fish lift at the only possible location on the site, i.e. at the existing fish pass entrance. Initially, only the lower part of the fish lift was built and its efficiency evaluated. The behaviour of 70 wild salmon was studied from early July 2000 to mid-December 2001. They were trapped, radio-tagged and released at the Puyoo dam, 8 km downstream from the plant. During the 2000 study, the spill discharge at the dam varied significantly, notably during a prolonged stoppage of the plant. The efficiency of the fish pass was increased to 80%, but part of this increase, which was difficult to assess, was for the period when the turbines were closed and all of the river flow spilled over the dam. Following the first year's results, attraction flows varying from 7.5 m^3s^{-1} to 11.5 m^3s^{-1} were tested in 2001. The auxiliary attraction discharge was nevertheless relatively dispersed, being divided between the fish lift entrance, an existing radial gate, a flap gate and the existing downstream bypass channel. The rates of average upstream passage increased to 87%, which may be partly attributed to (i) increased fish pass attractivity due to higher dam spillage via the nearest flood gate and (ii) longer times spent by fish inside the first pool of the fish facility due to an anti-return device installed at the fish pass entrance. In addition, migration delays were greatly reduced with the median blockage duration decreasing from 53 days in 2000 to 9 days in 2001. Nevertheless, considering the migration delays and the position of the obstacle on the river, a long way downstream from major spawning grounds, the efficiency of the fish pass still has to be improved. This will be done by concentrating all attraction discharge release very close to the fish lift entrance. A small turbine (with a maximum discharge of 10 m^3s^{-1}) will be installed in the near future.

Introduction

Since the beginning of the last century, thirty-eight obstacles (dams or low weirs) have been built on the *Gave de Pau* river with the result that Atlantic salmon (*Salmo salar* L.) have almost entirely disappeared from the river. A restoration plan was undertaken about twelve years ago and led to the building of facilities at obstacles that had previously not been equipped with fish passes. A first radio telemetry study was performed from 1995 to 1997 (Chanseau *et al.*, 1999) to assess the impact of the different obstacles. It concluded that the Baigts hydroelectric power plant, with its sixty-year old fish pass, remained one of the most severe obstacles to salmon migration. This lack of efficiency, evaluated at 30 to 40% of its potential, was due to the poor design of the fish pass, its limited discharge and the location of the entrance, on the left bank, on the opposite side of the river from the tailrace. However, most of fish visited the fish pass entrance (Chanseau and Larinier, 1999).

In the light of these results, it was decided that a new fish passage should be built. The best location for this new fish pass was unquestionably on the right-hand bank near the tailrace. However, given the limited available space on the bank and the particular layout of the intake screens, it would have been difficult and also very expensive to build a fish pass there.

The decision was thus taken to install a new fish lift at the only reasonably feasible location on the site, i.e. at the existing fish pass entrance. At first, only the lower part of the fish lift was built and its efficiency evaluated through a provisional fish trap. The second stage of work was only to be launched if the relevant authorities found that the fish lift, after radio telemetry assessment, was efficient enough.

This paper describes the main results of the two-year radio telemetry study conducted in 2000 (Chanseau and Larinier, 2001) and 2001 (Bau *et al*., 2002a), prior to the final design of the fish lift, describing only those results that directly influenced the design of the fish pass for Atlantic salmon (*Salmo salar* L.).

Materials and methods

Study site

The Baigts hydroelectric power plant is located in the southwest of France, on the *Gave de Pau* River, 20 km above its confluence with the *Gave d'Oloron* river and approximately 50 km from the estuary. The annual mean flow is around 80 m^3s^{-1}. The plant consists of a powerhouse located on the right bank and a dam 57 m long located on the left bank. The maximum turbine discharge (there are three Kaplan turbines) is 90 m^3s^{-1} and the rated head is around 13 m. The spillway has two radial gates and a smaller flap gate surmounting a bottom slide gate adjacent to the power intake. A downstream bypass is located at the downstream end of the intake screens while a steep open channel, 1 m wide, conveys downstream bypass flow to the tail water. The old Denil fish pass is located on the left bank, on the opposite side from the tailrace and is 80 m long (Fig. 1).

The future fish facility, once completed, will be located on the left bank, at the base of the dam, very close to the existing fish pass entrance. Its lower part comprises a large holding pool and a 1.2 m wide, gated entrance. A provisional trap has been installed in the upstream part of this pool. The facility is partly fed through the old fish pass (1 m^3s^{-1}) and partly directly from the headpond (maximum 2.5 m^3s^{-1}) after the energy has been dissipated by passing through several pools. One part of the flow is injected upstream from the trap and the other part laterally, downstream from the trap, through a vertical screen. An electrical winch is used to raise the trap and to free fish upstream (Fig. 2) from the pass.

In 2001, it was decided to increase the proportion of the fish pass flow passing through the trap and to install a V-trap at the downstream pool entrance.

Tagging and Fish movement

Over the two years 2000 (170 days from 19 June to 4 December) and 2001 (182 days from 18 June to 16 December), 70 (29 in 2000 and 41 in 2001) wild Atlantic Salmon (mainly grisle 60-89 cm total leugth) were captured in the fish pass located at the Puyoo dam, 8 km downstream from the study site and were anesthetised (with 2-phenoxyethanol, 0.25 mll^{-1}, then clove oil, 26 $mmoll^{-1}$) before being tagged with radio transmitters (Advanced Telemetry System; with a frequency range of 48 to 49.9 MHz ; 60x20 mm; 20-22 g in air; lifetime: 220 days; pulse rate: 56 to 58 per minute) that were introduced into the fishes' stomachs via the oesophagus. Each radio tag had a unique output frequency. The tagged fish were released just upstream of the Puyoo fish pass. The tagging and tracking procedures are similar to those used by Solomon & Storeton-West (1983) and have been described by Chanseau *et al*. (1999).

The fish movements were determined using five automatic listening stations (Advanced Telemetry System; receiver model R2100; DCC II model D5040) to define 6 principal detection zones: zone 1 (Z1) corresponding to the tailrace, zone 3 (Z3) to the dam, zone 2 (Z2) to a zone located between the two preceding zones at the downstream end of the dividing wall, zone 4 (Z4) at the fish pass entrance, zone 5 (Z5) at the downstream entrance pool to the fish lift and finally zone 6 (Z6) at the holding trap of the fish lift (Figs. 1 and 2). Daily manual tracking (either on foot or by car) was used to complete the automatic radio monitoring.

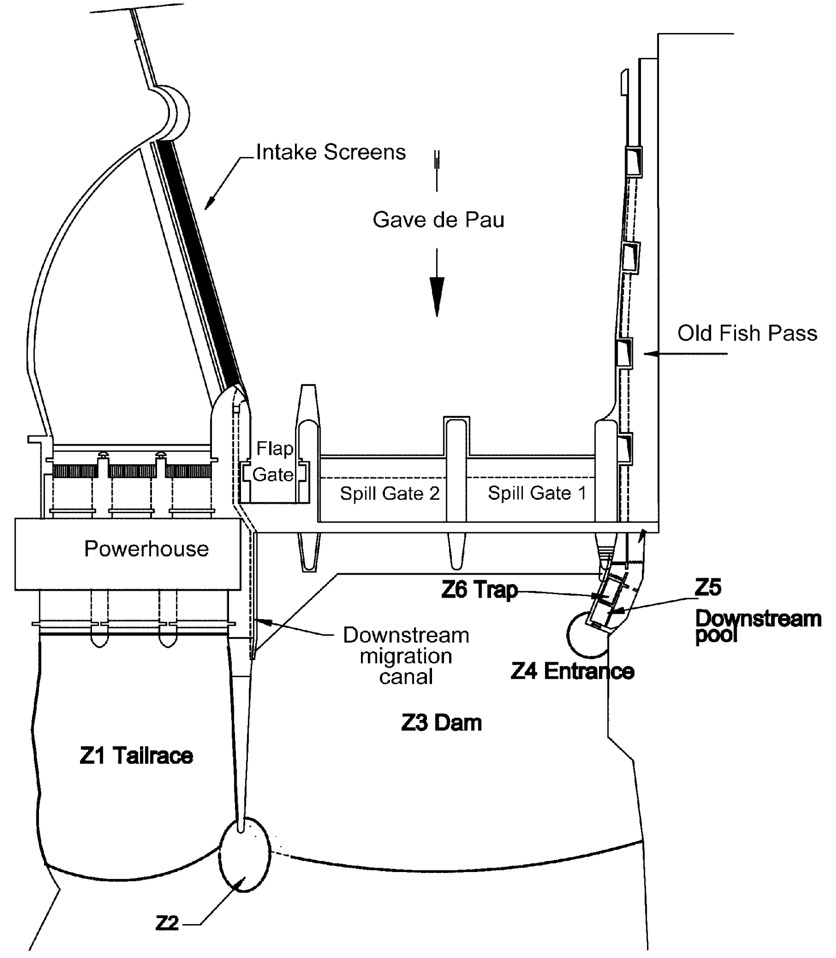


Fig. 1 – Plan of the Baigts power plant.

Water temperature, river flow and turbine operation

Water temperature (°C), and river flows downstream of the plant (m^3s^{-1}) were recorded automatically and saved at 1-hour intervals. Turbine operation was monitored every 3 minutes to estimate flow in the tailrace at any given time.

In 2000, four separate periods could be distinguished according to the rate of flow spilling over the dam:

i) 1st period: before 8 March 2000, when all discharge on the dam side passed through the fish pass (2.5 m^3s^{-1});

ii) 2nd period: from 8 March 2000 to 24 September 2000, when 2.5 m^3s^{-1} passed through the fish pass and 1 m^3s^{-1} more through the downstream migration channel;

iii) 3rd period: from 24 September 2000 to 25 October 2000, when the turbines were stopped and all river discharge passed under the dam gates;

iv) 4th period: from 25 October 2000 to 5 December 2000, when 4 m^3s^{-1} passed through the flap gate, 3.5 m^3s^{-1} through the fish pass, i.e. a minimum spill discharge on the dam side of 7.5 m^3s^{-1}. During this period, increase in river discharges resulted in more important spillage, which generally varied from 25 to 33 m^3s^{-1}.

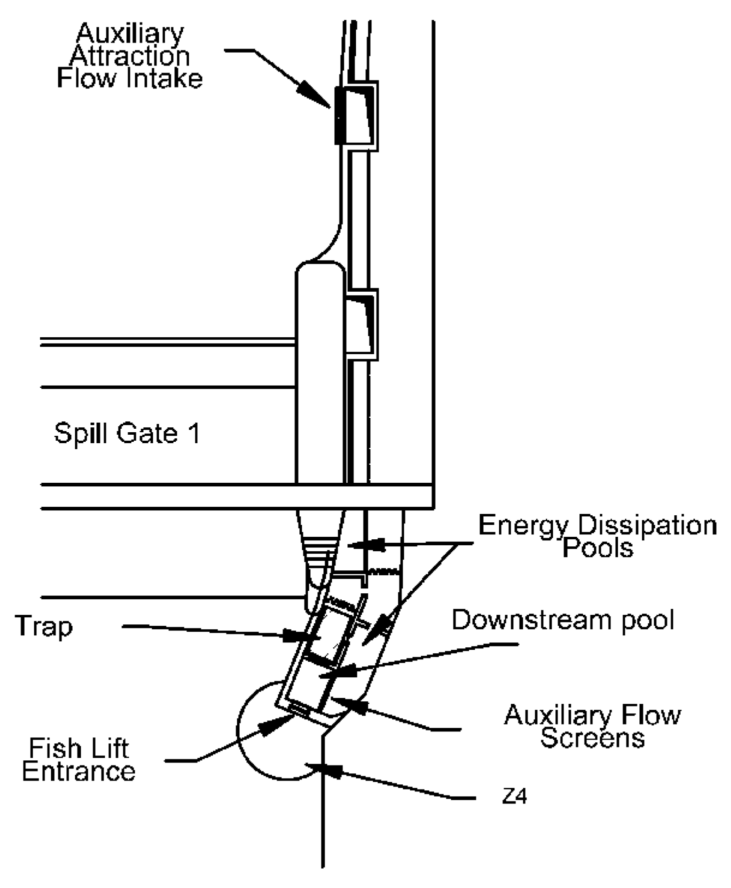


Fig. 2 – Plan of the left bank showing the old fish pass and the new fish lift entrance.

In 2001, in the light of the results for 2000, it was decided to let the attraction discharge at the dam vary from 7.5 m^3s^{-1} to 11.5 m^3s^{-1}, depending on the turbine discharge (Table 1). The attraction discharge release was nevertheless relatively dispersed, between the fish lift entrance (3.5 m^3s^{-1}), through the existing downstream bypass channel (2 m^3s^{-1}), the flap gate (2 m^3s^{-1}) and one of the two radial gates (2 to 4 m^3s^{-1} under the gate then through a siphon pipe above the gate).

Table 1 – Variation of attraction discharge at dam according to the turbine discharge (in 2001)

Turbine discharge (m^3s^{-1})	Fish pass discharge (m^3s^{-1})	Downstream migration canal discharge (m^3s^{-1})	Flap gate discharge (m^3s^{-1})	Radial gate or siphon pipe discharge (m^3s^{-1})	Total discharge (dam side) (m^3s^{-1})
0-40	3.5	2	0	2	7.5
40-60	3.5	2	0	4	9.5
60-90	3.5	2	2	4	11.5

Results

Fish passage

In 2000, of the 29 salmon tagged, 25 were recorded near the plant. Two never showed up at the plant and two others probably either regurgitated the transmitter or died. Three other fish which had been tagged during another study undertaken at the same time in the estuarine part of the Adour basin, reached the plant and were monitored. Three individuals died during the study. Twenty fish were trapped in the facility and passed over the Baigts plant, i.e. 80%. However, part of this increase, which was difficult to assess, can be attributed to the period when all of the river flow spilled over the dam. Only 12 fish (48%) were trapped while the plant was in operation. Eight individuals were trapped during a prolonged stoppage of the plant due to work on the intake screens (from 29 September 2000 to 25 October 2000). As it was difficult to judge whether these fish could have passed while the plant was operating, we can only assume that the efficiency of the facility is between 48% and 80% (as compared with 34% for 1995-1997). The first quartile and the median of the delay for the trapped fish were respectively 23 and 53 days.

In 2001, of the 41 salmon tagged, 31 were recorded near the plant. Two other fish, which had been tagged for another study undertaken at the same time in the estuarine part of the Adour basin, reached the plant and were also monitored. Only 30 individuals were taken into account since three of the 33 individuals had disappeared prematurely. Twenty six fish were trapped in the facility and passed over the Baigts plant. The overall efficiency can be estimated at 87%. The first quartile and the median of the delay for the trapped fish were respectively 0.7 and 9 days.

Influence on fish position of discharge spilling at dam

In 2000, the distribution of the duration of visits of the radio tagged fish to the different reception zones (Z1, Z2, Z3 and Z4) were compared (ANOVA) in relation to flow discharges spilling over the dam (periods 1 to 4). Fish spent proportionally more time in the tailrace during periods 1 and 2 than during periods 3 or 4. Fish stayed for a longer time at the fish pass entrance during the fourth period than during the third period when all the river discharge was spilling through the gates, which partly masked the entrance of the fish pass (Table 2).

Table 2 – Distribution of the percentage of presence in the different zones (Z1, Z2, Z3, Z4) during the four distinct periods and ANOVA results.

Zone	Period				F	p value	Homogeneity of groups
	1	2	3	4			
Z1	25.8	32	30.8	16.5	0.7	0.55	1=2=3=4
Z2	55.9	56.4	22.3	0	9.03	0.0001	(1=2) ≠ (3=4)
Z3	17	11.1	45.5	65.1	14.3	< 0.0001	(1=2) ≠ (3=4)
Z4	1.2	1.2	0.47	18.4	29.4	< 0.0001	(1=2=3) ≠ 4

General fish behaviour

During the two year study, fish spent most of their time in a pool about 500 m to 1,200 m downstream from the plant. The salmon moved many times between this pool and the dam, with 1,557 out of the 2,311 approaches recorded in 2000 and 1,590 out of 1,961 approaches recorded in 2001 lasting less than 3 hours.

In 2000, the number of approaches per day to the plant varied from 1 to 15, while 66% of the number of visits was between 1 and 3. In 2001, the number of visits varied from 1 to 17 with 70% of the number being included between 1 and 4.

In 2000, 15 of the 27 fish, when present below the plant, preferred to stay in the tailrace (Z1), 7 downstream from the dam (Z3) and 5 near the dividing wall (Z2). The duration of visits in these zones was relatively short with 50%, 81% and 68% of the visits to Z1, Z2, Z3 lasting less than 1 hour. In 2001, 17 of the 33 fish preferred to stay in the tailrace (Z1), 7 downstream from the dam (Z3) and 9 near the dividing wall (Z2). The duration of visits in these zones was also relatively short with 60%, 81% and 86% of the visits to Z1, Z2, Z3 lasting less than 1 hour.

Fish behaviour at fish pass entrance

In 2000, while visits to the fish pass entrance (Z4) were relatively frequent (1,250), most were short, with 60% lasting less than 1 minute and 86% less than 5 minutes. All fish visited the fish pass entrance at least once (the mean was 45 times and the median 20 times). Sixty-six percent of the fish were generally monitored near the entrance less than 24 hours after their initial approach (median delay 13 hours).

In 2001, the visits to the fish pass entrance (Z4) were relatively frequent (506), most were short, 76% lasting less than 1 minute and 95% less than 5 minutes. All fish visited the fish pass entrance at least once (with a mean of 15 times and a median of 5 times). Seventy-four percent of the fish were generally monitored near the entrance less than 24 hours after their initial approach (median delay 7.2 hours).

In 2000, the results showed that 1,250 out of 2,198 (57%) visits to the site were followed by a visit to the fish pass entrance (Z4); 264 out of the 1,250 (21%) visits to the fish pass entrance were followed by the fish actually entering the downstream entrance pool (Z5); 20 out of the 264 (7.5%) visits to the downstream pool were followed by the fish entering the trap (Z6), thus enabling them to pass over the dam. Each trapped fish visited the downstream pool an average of 13 times, the fish pass entrance an average of 63 times and the site itself an average of 110 times.

In 2001, 506 out of 1,961 (26%) visits to the site were followed by a visit to the fish pass entrance (Z4); 176 out of the 506 (35%) visits to the fish pass entrance were followed by the fish actually entering the downstream entrance pool (Z5); 26 out of the 176 (15%) visits to the downstream pool were followed by fish entering the trap (Z6). On average, each trapped fish visited the downstream pool 7 times, the fish pass entrance 20 times and the site 75 times.

Discussion

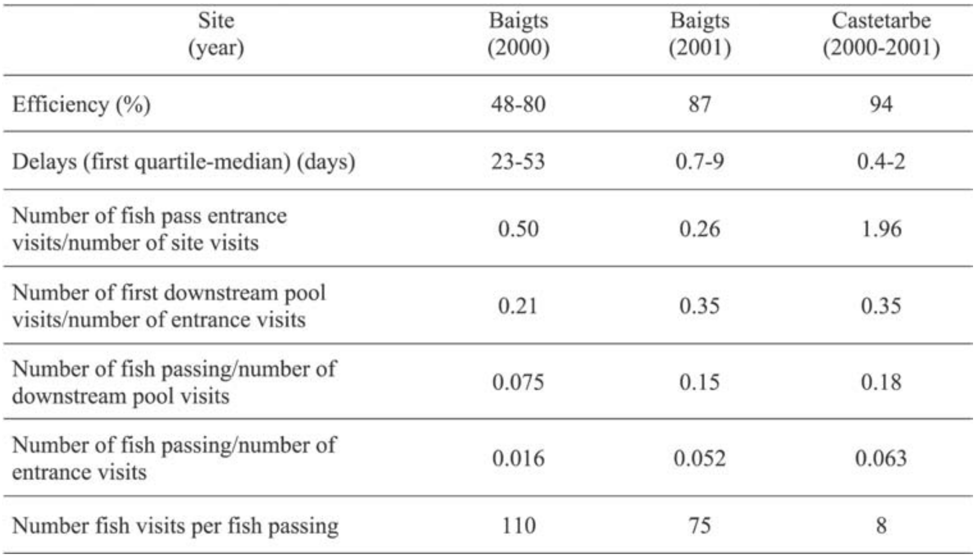
Even though it is difficult to compare the results of the two successive years, considering the difference in river flow conditions, it seems that the passability of the dam increased from between 48 and 80% in 2000 to 87% in 2001. The improvement is obvious concerning the delays, as the first quartile and median delays decreased from 23 and 53 days in 2000 to 0.7 and 9 days in 2002.

The general behaviour of fish is very similar in 2000 and 2001. The main differences concern fish behaviour at the fish pass entrance. The modifications in 2001 (installation of a V-trap at the downstream pool entrance and increase of the flow passing through the trap) have made it possible to reduce the number of visits to the facility entrance before entering the trap and passing upstream.

There is little information on fish behaviour and especially Atlantic salmon, with respect to obstacles to migration and to entrances of fish passes (Gowans *et al*., 1999; Northcote, 1998). In order to be able to evaluate the potential for further improvement, it seemed a good idea to compare fish behaviour at the Baigts plant to that observed at the Castetarbe plant, located 6 km upstream on the same river. The fish pass sited at the Castertarbe plant is recent and well located, on the tailrace side. The Castetarbe fishway was assessed by radio telemetry in 2001, with practically the same fish (Bau *et al*., 2002b). This pass is considered to be efficient and can be used as a reference for the Baigts fish pass (Table 3).

Overall efficiency was estimated at 94% at Castetarbe (versus 87% at Baigts). The first quartile and median of the delay for the trapped fish were 0.4 and 2 days (versus 0.7 and 9 days at Baigts). The percentages of visits to the fish pass entrance followed by fish entering the downstream pool were not very different (26-35%). The percentages of visits to the first downstream pool followed by fish passing upstream were close (18% at Castetarbe versus 15% at Baigts).

Table 3 – Comparison of Castetarbe fish pass and Baigts fish lift in terms of rate of efficiency, delays and frequency of visits.



Site (year)	Baigts (2000)	Baigts (2001)	Castetarbe (2000-2001)
Efficiency (%)	48-80	87	94
Delays (first quartile-median) (days)	23-53	0.7-9	0.4-2
Number of fish pass entrance visits/number of site visits	0.50	0.26	1.96
Number of first downstream pool visits/number of entrance visits	0.21	0.35	0.35
Number of fish passing/number of downstream pool visits	0.075	0.15	0.18
Number of fish passing/number of entrance visits	0.016	0.052	0.063
Number fish visits per fish passing	110	75	8

The main difference between the two sites is the frequency of fish visits to the pass entrance. Each visit to the site was followed by an average of 2 visits to the fish pass entrance at Castetarbe, versus 0.3 visit at Baigts.

On average, each fish which passed upstream of the Castetarbe plant had previously visited the site 8 times versus 75 at Baigts.

Fish behaviour at the fish pass entrance was similar at both Baigts and Castetarbe: the problem of fishes' reluctance to enter the trap entrance, observed at Baigts, seems to have been solved. The main factor explaining the difference in efficiency and delays remains the lower frequency of visits to the fish pass entrance at Baigts as compared to Castetarbe.

In conclusion, the increase of spill discharge on the dam side and the changes made to the trap and the downstream pool of the fish pass significantly increased the efficiency of the Baigts fish pass. While the efficiency rate (87%) seems to be fairly satisfactory, the migration delays remain too long considering the downstream location of the dam on the river. The efficiency still has to be improved. When the fish behaviour is compared to that observed at the Castetarbe plant, it appears that there is still a lot of potential for improving the Baigts fish pass, by increasing the frequency of fish visits to the pass entrance.

In 2001, an attempt was made to improve fish pass efficiency by attracting fish more frequently on the left bank by increasing the spilled discharge on the dam side. However, it will not be possible to release a significant, concentrated flow near the fish pass entrance, unless significant construction is undertaken and this was hardly conceivable for an experimental preliminary stage. All attraction discharge on the left bank should be concentrated close to the fish pass entrance. It was thus decided to install a special small turbine discharging 8 to 10 m^3s^{-1} at the fish pass entrance.

Fish guidance towards the pass entrance should also be improved with the reinforcing of an existing rip-rap groin guiding the flow, stretching from the left bank diagonally towards the end of the dividing wall and the tailrace.

These two modifications should increase the frequency of fish visits to the fish pass entrance and significantly reduce the delay before passage which was the limiting factor when compared to the Castetarbe fish pass reference.

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Factors affecting adult Pacific lamprey passage rates at hydropower dams: using "time to event" analysis of radiotelemetry data

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Abstract

Adult Pacific lamprey (*Lampetra tridentata* Gairdner) encounter up to nine mainstem hydropower dams during their pre-spawning migration in the Columbia River Basin, USA. Radiotelemetry studies indicate that lamprey passage efficiency (the proportion that pass at each dam) is low relative to that of adult salmonids. In addition, lamprey migration is often delayed for over 5 days as they negotiate fishways designed to facilitate salmonid passage. We applied 'time-to-event' analyses (here, time to passage) to 4 years of lamprey passage data by setting the 'hazard rate' of traditional epidemiological studies equal to passage rate. Lamprey passage rates varied as a function of time, along with time-varying predictor variables (such as water temperature, river flow and spill). We used the Akaike Information Criterion to compare several competing versions of the model (each using a different predictor variable). Thus, we were able to distinguish the relative contribution of various factors to migrational delay. By fitting the model with a log-likelihood function, we incorporated information from individual fish rather than aggregated groups of fish. Consequently, this method is able to derive more information from small data sets than more traditional approaches. Moreover, models of this kind allow examination of multiple functional relationships to better explain patterns of fish behaviour obtained from fish telemetry programs.

Introduction

Pacific lamprey (*Lampetra tridentata* Gairdner) are anadromous and may swim hundreds of kilometers to reach spawning locations in the Columbia and Snake Rivers of northwestern USA (Moser and Close, 2003). Although adult Pacific lamprey are parasitic during the marine phase of their life cycle, they detach from their host prior to undertaking this prespawning migration. Therefore lamprey spawning movements are fueled by endogenous reserves, as in many other anadromous species. A notable difference however, is that Pacific lamprey enter fresh water a year prior to spawning (Beamish, 1980). Consequently, the energetic constraints on lamprey movements may be substantially higher than those on other anadromous fish migrations.

Pacific lamprey exhibit low passage efficiency and are delayed at the hydropower dams they encounter on the lower Columbia River (Fig. 1). Whereas 90% or more of the salmonids (*Oncorhynchus* spp.) approaching these dams pass successfully, on average only about 50% of the lamprey pass each of the three mainstem dams that are farthest downstream on the Columbia River (Moser *et al.*, 2002). Moreover, lamprey require a median time of 4–6 days to pass the first dam they encounter (Bonneville Dam, Rkm 235), while adult salmonids typically negotiate the fishways at this dam in less than 1 day.

Migration delay at the lower Columbia River dams may reduce lamprey fitness. Negotiating complex fishways and residing in areas of high current velocity is energetically costly (Mesa *et al.*, 2003). Lamprey energy reserves are limited, so added time spent migrating and exposure to higher water temperatures during delays may result in reduced spawning success or even inability to reach spawning areas. Also, delay at the dams may expose lamprey to greater predation risk. For example, key predators such as sturgeon and sea lions aggregate below Bonneville Dam and may target lamprey holding at the base of dam (R. Stansell, personal communication, 2004).

In this study, we investigated the factors affecting migration delay of Pacific lamprey by applying "time-to-event" analysis to adult Pacific lamprey passage times. Radiotelemetry was used to obtain the time each individual lamprey required to pass over each dam. The variability in passage time was then related to such abiotic and biotic variables as water temperature, flow, spill, time of day, lamprey size, and the abundance of other species in the fishways. By computing Akaike's Information Criterion we were then able to compare competing models to identify those variables that contributed most significantly to lamprey delay at each dam.

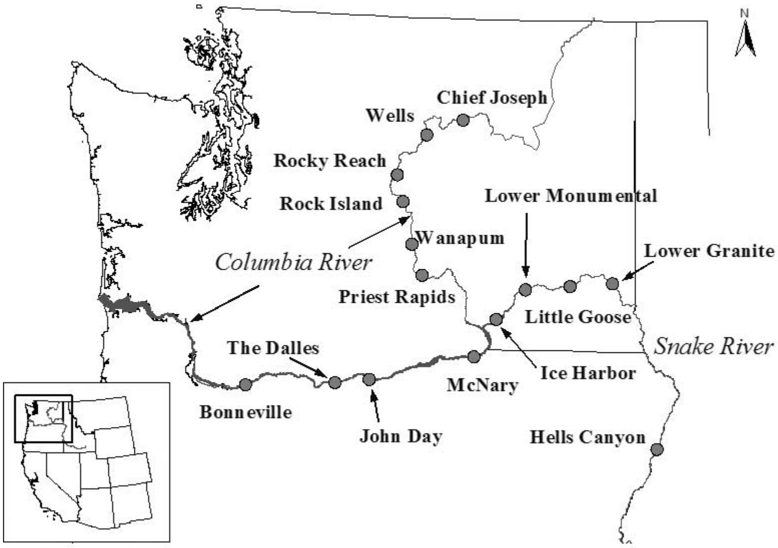

Fig. 1 – The Columbia and Snake River system. Dots indicate the location of mainstem hydropower dams.

Materials and methods

In 1997, 1998, 2000, and 2001, we captured migrating adult Pacific lamprey in a trap deployed nightly at Bonneville Dam (Fig. 1). Fish were anaesthetized (with either 70 ppm tricaine methane sulfonate or 60 ppm clove oil), weighed (to the nearest gram), and measured (to the nearest cm). Using surgical techniques described by Moser *et al*. (2002), a uniquely-coded radio transmitter that represented less than 2% of lamprey body weight was implanted in the body cavity of each fish. The fish were then released 3 km downstream from the dam.

As the lamprey swam back to the base of the dam, they were detected via an extensive array of fixed-site radio receivers (Moser *et al*., 2002). We divided the passage time into two segments. First, the time lamprey spent in the dam tailrace prior to fishway ascension ("tailrace" time) was defined as the time from the first detection at an entrance to a fishway to the time of last entrance into a fishway. Second, the amount of time lamprey required to negotiate the fishway, or "ladder" time, was defined as the time from the last entrance into the fishway to the last detection as the lamprey exited the top of the fishway and moved into the dam forebay. Fish that did not successfully pass over the dam were removed from analysis. Passage times were determined in the same way for lamprey that approached The Dalles Dam (Rkm 308, Fig. 1).

Hourly flow, water temperature, and spill (amount of water released over the dam spillway) were recorded by the US Army Corps of Engineers and these data were downloaded from a website maintained by the University of Washington (DART, 1995). We were also interested in whether crowding by other species in the fishways would affect lamprey passage times. The most abundant fish in the fishways during lamprey migration are American shad (*Alosa sapidissima* Wilson). Daily counts of American shad were taken at each dam and we downloaded these data from DART (1995).

We employed modeling techniques that were initially developed to analyze survivorship in epidemiological studies (Kalbfleisch and Prentice, 1980; Hosmer and Lemeshow, 1999). Researchers have recently generalized these types of analyses from time to death to any "time-to-event" process (Hosmer and Lemeshow, 1999), which in this case was time to passage. Thus, the "survivorship" curve was the proportion of individuals that had not passed as a function of time. The shape of the passage curve is defined by the instantaneous rate of passage, $\lambda(t)$, which can vary through time depending on ambient conditions. In the simplest case, where passage rate is constant with respect to time ($\lambda(t) = \alpha$), the probability that lamprey will remain downstream from a dam as a function of time is an exponential function:

$$\text{Prob(delaying } t \text{ or more days)} = \exp(-\alpha t) \qquad (1)$$

where α is the passage rate parameter. With this formulation, an underlying Poisson process describes time to passage, and the mean delay time is $1/\alpha$ (Ross, 1993). Thus as α increases, mean delay time decreases.

We can also express the passage rate as a time-varying function, which is important if individuals face variable conditions during the delay period. In this case, time to passage is described by a nonhomogeneous Poisson process (Ross, 1993), and the delay equation is slightly more complicated:

$$\text{Prob(delaying } t \text{ or more days)} = \exp(-\int_0^t \lambda(\tau)d\tau) \qquad (2)$$

This equation integrates over an individual's experience up until time t. Usually the term inside the integral is a simple function and easy to integrate. As an example, we developed a diel model, where passage rate varied according to time of day:

$$\lambda(\mathrm{t}) = \begin{cases} \alpha_N \textit{ during night hours} \\ \alpha_D \textit{ during day hours} \end{cases} \qquad (3)$$

Based on passage distributions, we defined day as 06:00 to 21:00 and night as the remaining hours.

Next we expanded this model to relate passage rate to predictor variables: lamprey size, flow, spill, water temperature, time of year and shad abundance (in thousands) in the fishways. Since the majority of passage occurs at night, we included only the predictor variables in the night passage rate:

$$\alpha_N(t) = \alpha_0 + \alpha_1 \cdot X_\tau \qquad (4)$$

where X_t is a predictor variable (which may be time-varying) and α_0 and α_1 are fitted parameters.

Model parameters were estimated by maximizing the log-likelihood function with respect to the model parameters using the downhill simplex method (Nelder *et al*., 1965; Press *et al*., 1988). The likelihood function is based on the probability density function for delay time t:

$$f(t) = \lambda(t)\exp(-\int_0^t \lambda(\tau)d\tau) \qquad (5)$$

The log-likelihood function is then defined as:

$$\log L = \sum_{i=1}^{N} \log \mathrm{f}(t_i \mid \alpha) \qquad (6)$$

where t_i is the delay time for the ith individual, N is the total number of individuals at a particular dam, and α is the vector of model parameters.

We bootstrapped the data (Efron and Tibshirani, 1986) to obtain approximate 95% confidence intervals (CIs) with the number of bootstrap iterations set at 200. The CIs served to determine the precision of the parameter estimates and to assess whether parameters were significantly different from zero. If the CI for a parameter contained zero, this parameter was not significantly different from zero.

We used Akaike's Information Criterion (AIC) (Akaike, 1973; Burnham and Anderson, 1998) to determine the relative influence of various factors on delay. We considered the diel model to be our null model and determined the importance of various predictor variables by adding spill, flow, water temperature, fish length, shad abundance and time of year to the diel model separately (Equation 4). We quantified the extent of improvement for each alternative model by computing the difference between AIC values for it and the diel model (Δ AIC).

Consequently, the magnitude of the Δ AIC corresponded to the level of improvement in model fit.

Results

The number of lamprey that passed over each dam and were subsequently used in this analysis varied among years and dams (Figs. 2 and 3). The total length of tagged lamprey ranged from 61 to 79 cm (mean=70 cm). The median yearly tailrace time below Bonneville Dam ranged from 0.93 to 3.10 d. At The Dalles Dam, median yearly tailrace time ranged from 0.03 to 1.24 d. After their final entry into the fishway, lamprey also exhibited longer median ladder times at Bonneville Dam (1.09-2.25 d) than at The Dalles Dam (1.01-1.84 d) in each year. In most years, approximately half of the lamprey delayed in the tailrace below the dam for less than an hour before making their final entrance into a fishway (Fig. 2). Fish that did not pass within the first hour sometimes remained below the dam for weeks, and passage patterns for these fish were quite variable across years. In contrast, the passage patterns of lamprey in the ladder were remarkably similar among years within sites, with no statistical difference in passage curves across years at Bonneville (P=0.109, log-rank test) or The Dalles Dams (P=0.306). However, the shape of these curves was significantly different between dams (P<0.001), indicating that lamprey passed through The Dalles Dam fishways faster than through those at Bonneville Dam (Figs. 2 and 3).

Because of the bimodal behavior in delay exhibited by lamprey in the tailrace prior to fishway ascension (Fig. 2), we used only fish that had tailrace times of greater than an hour to model tailrace passage. We used all fish for the analysis of ladder passage since there was no apparent bimodal behavior associated with ladder passage times.

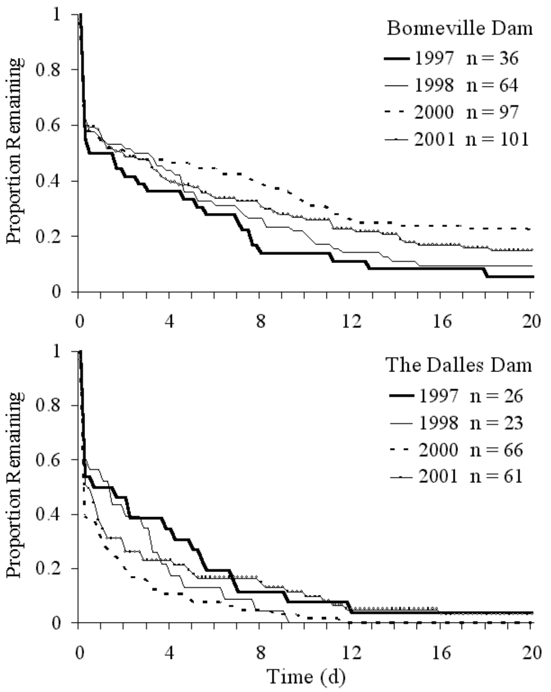

Fig. 2 – The proportion of radio-tagged lamprey that remained in the tailrace below Bonneville (top panel) and The Dalles (bottom panel) dams as a function of time in each year.

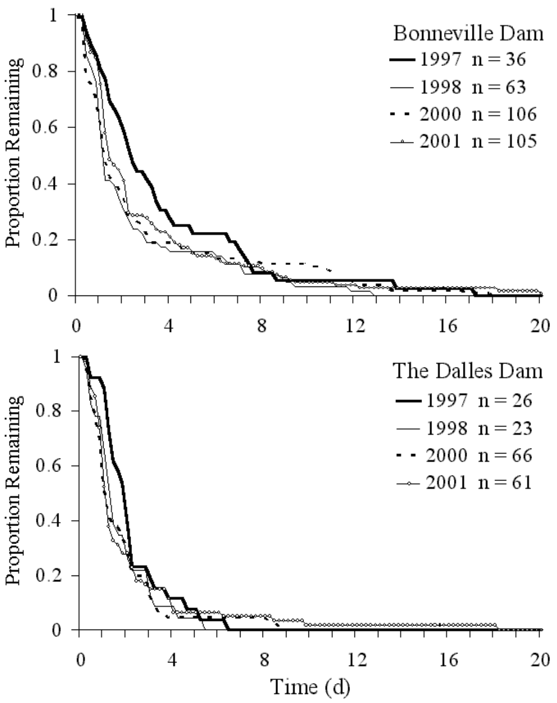

Fig. 3 – The proportion of radio-tagged lamprey that remained in the ladder at Bonneville (top panel) and The Dalles (bottom panel) dams as a function of time in each year.

The diel model (where passage rate varied according to time of day) for both measures of passage time (tailrace and ladder) represented a considerable improvement over the simple model (Tables 1.a-1.d). Passage rates at night (α_N) were significantly higher than daytime rates (α_D) based on the absence of overlap in the 95% confidence intervals for the parameter estimates in nearly every dam and year combination. Due to the obvious nocturnal pattern in lamprey passage rates, we used the diel model as our null model in assessing the effects of other variables.

We determined the improvement in AIC values for each variable and plotted the resulting Δ AIC (Figs. 4 and 5). For both time in the tailrace and the ladders, there were few consistent trends in the effects of a wide range of variables. We assessed the effects of flow and spill on lamprey delay in the tailrace, but not in the ladder because they would not be exposed to these effects in the ladder. Similarly, we only examined the effects of shad abundance in the ladder, as this is where we would expect to see an effect of crowding on lamprey passage rate.

The most consistent effect was that of date. Lamprey that migrated later in the year exhibited less delay in the tailrace than those migrating earlier in the year for 1998 and 2001 at Bonneville Dam and for 1998, 2000, and 2001 at The Dalles Dam (Fig. 4). For the time spent in the ladder, the date model showed substantial improvement in AIC at Bonneville Dam in 2000 and 2001 (Fig. 5). Moreover, at Bonneville Dam in 2000 and 2001, and at The Dalles Dam in 2000, water temperature (which is positively correlated with date) was also negatively correlated with lamprey delay (i.e., lamprey exhibited less delay as water temperature increased, Fig. 5).

There was no indication that lamprey length had any effect on either delay in the tailrace or in the ladders (Figs. 4 and 5). Similarly, spill apparently had no effect on lamprey delay (Fig. 4). Flow was only a significant factor at The Dalles Dam tailrace in 1998. Shad abundance significantly increased lamprey delay in the Bonneville Dam ladders in 2001, and there was no effect of shad on lamprey delay at The Dalles Dam ladders (Fig. 5).

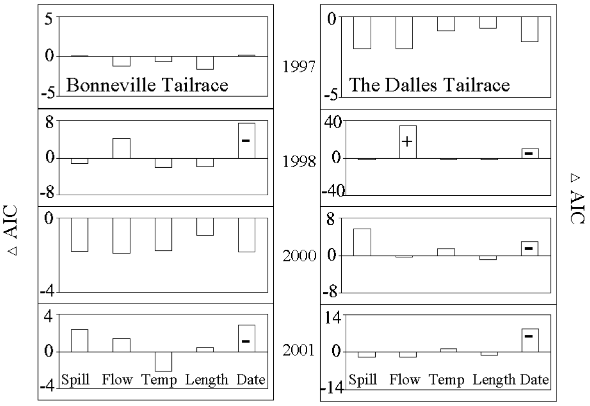

Fig. 4 – The change in AIC (Δ AIC) value with the addition of various factors (spill, flow, water temperature, lamprey length and date) to the null diel model of passage through the tailrace below Bonneville (left panel) and The Dalles (right panel) dams in each year. Symbols in the bars indicate significant effects and the direction of the correlation with delay (i.e., negative relationships indicate that increasing this factor reduces delay).

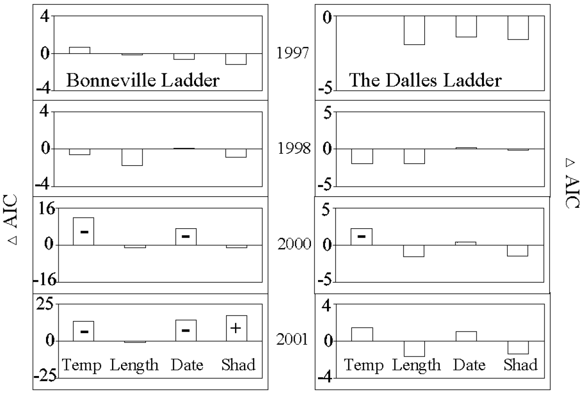

Fig. 5 – The change in AIC (Δ AIC) value with the addition of various factors (water temperature, lamprey length, date and shad abundance) to the null diel model of passage through the ladders at Bonneville (left panel) and The Dalles (right panel) dams in each year. Symbols in the bars indicate significant effects and the direction of the correlation with delay (i.e., negative relationships indicate that increasing this factor reduces delay).

Table 1.a – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (Bonneville-Ladder).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
		Simple	0.275	(0.206, 0.398)					82.53	
		Diel	0.136	(0.067, 0.224)	0.497	(0.372, 0.726)			75.41	12.24
	1997	Temperature	0.136	(0.066, 0.229)	-1.271	(-4.241, 1.094)	0.098	(-0.019, 0.306)	74.08	12.88
	n=36	Length	0.136	(0.069, 0.243)	-3.131	(-13.824, 2.551)	0.052	(-0.026, 0.257)	74.48	12.09
		Date	0.136	(0.075, 0.232)	-1.060	(-3.522, 3.269)	0.008	(-0.004, 0.024)	74.74	11.57
		Shad	0.136	(0.074, 0.225)	0.560	(0.308, 1.300)	-0.003	(-0.020, 0.007)	74.98	11.08
		Simple	0.422	(0.322, 0.570)					117.32	
		Diel	0.131	(0.078, 0.208)	0.887	(0.636, 1.343)			93.52	45.60
	1998	Temperature	0.131	(0.075, 0.213)	0.538	(0.109, 1.260)	0.021	(-0.012, 0.346)	92.83	44.99
	n=63	Length	0.131	(0.074, 0.221)	2.238	(-2.022, 10.160)	-0.019	(-0.098, 0.047)	93.40	43.85
		Date	0.131	(0.076, 0.218)	-0.907	(-5.896, 2.432)	0.010	(-0.007, 0.042)	92.46	45.73
Bonneville Ladder		Shad	0.131	(0.079, 0.203)	0.926	(0.673, 1.401)	-0.003	(-0.009, 0.005)	92.96	44.72
		Simple	0.365	(0.283, 0.491)					208.77	
		Diel	0.121	(0.075, 0.196)	0.749	(0.581, 0.995)			172.34	70.85
	2000	Temperature	0.121	(0.074, 0.183)	-2.081	(-3.892, -0.387)	0.148	(0.074, 0.292)	165.44	82.65
	n=104	Length	0.121	(0.075, 0.183)	-0.757	(-4.601, 4.384)	0.022	(-0.036, 0.092)	171.95	69.64
		Date	0.121	(0.073, 0.200)	2.457	(0.574, 3.877)	-0.008	(-0.013, 0.003)	167.80	77.94
		Shad	0.121	(0.078, 0.186)	0.755	(0.566, 1.056)	-0.005	(-0.031, 0.012)	171.91	69.73
		Simple	0.325	(0.255, 0.455)					140.18	
		Diel	0.089	(0.035, 0.171)	0.697	(0.545, 0.988)			112.53	53.30
	2001	Temperature	0.088	(0.040, 0.167)	-3.738	(-6.068, -1.731)	0.246	(0.140, 0.430)	104.90	66.55
	n=66	Length	0.089	(0.045, 0.168)	3.124	(-0.508, 7.907)	-0.033	(-0.090, 0.027)	111.87	52.61
		Date	0.089	(0.041, 0.169)	-3.523	(-5.509, -1.292)	0.024	(0.013, 0.040)	104.59	67.17
		Shad	0.089	(0.043, 0.175)	1.013	(0.751, 1.510)	-0.013	(-0.024, -0.007)	102.98	70.40

Table 1.b – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (Bonneville-Delay).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
		Simple	0.171	(0.111, 0.314)					77.49	
		Diel	0.174	(0.102, 0.329)	0.165	(0.090, 0.338)			77.48	-1.98
	1997	Spill	0.175	(0.076, 0.330)	0.225	(0.047, 0.304)	-0.000	(-0.004, 0.038)	77.42	-1.86
	n=28	Flow	0.175	(0.104, 0.357)	0.350	(0.059, 0.488)	-0.001	(-0.012, 0.020)	77.10	-3.22
		Temperature	0.174	(0.085, 0.354)	-0.583	(-3.049, 0.644)	0.042	(-0.014, 0.357)	76.78	-2.57
		Length	0.174	(0.096, 0.417)	-0.401	(-2.057, 4.384)	0.008	(-0.043, 0.056)	77.31	-3.65
		Date	0.175	(0.096, 0.388)	-2.048	(-15.801, 3.537)	0.012	(-0.009, 0.114)	76.38	-1.78
		Simple	0.144	(0.111, 0.214)					149.67	
		Diel	0.063	(0.036, 0.103)	0.278	(0.200, 0.442)			136.87	23.60
	1998	Spill	0.064	(0.038, 0.101)	0.385	(0.152, 0.409)	-0.001	(-0.005, 0.025)	136.47	22.38
	n=51	Flow	0.063	(0.040, 0.132)	0.560	(0.154, 0.595)	-0.001	(-0.008, 0.019)	133.81	27.72
		Temperature	0.064	(0.040, 0.105)	0.281	(0.144, 0.630)	-0.000	(-0.011, 0.012)	136.87	21.60
Bonneville		Length	0.064	(0.037, 0.104)	-0.057	(-3.170, 1.938)	0.005	(-0.019, 0.053)	136.81	21.70
Delay		Date	0.064	(0.036, 0.103)	-0.837	(-2.107, 0.081)	0.006	(0.002, 0.019)	132.19	30.96
		Simple	0.064	(0.051, 0.085)					243.80	
		Diel	0.035	(0.022, 0.054)	0.112	(0.085, 0.156)			232.97	19.68
	2000	Spill	0.035	(0.023, 0.055)	0.126	(0.079, 0.224)	-0.000	(-0.001, 0.001)	232.87	17.86
	n=65	Flow	0.035	(0.022, 0.059)	0.090	(-0.089, 0.358)	0.000	(-0.001, 0.001)	232.91	17.78
		Temperature	0.035	(0.022, 0.053)	0.028	(-0.329, 0.474)	0.004	(-0.013, 0.025)	232.84	17.93
		Length	0.035	(0.023, 0.059)	-0.227	(-0.898, 0.430)	0.005	(-0.003, 0.016)	232.43	18.75
		Date	0.035	(0.023, 0.053)	0.064	(-0.122, 0.402)	0.000	(-0.001, 0.001)	232.89	17.84
		Simple	0.099	(0.079, 0.133)					251.58	
		Diel	0.031	(0.018, 0.047)	0.211	(0.152, 0.293)			222.83	55.50
	2001	Spill	0.032	(0.017, 0.048)	0.182	(0.127, 0.273)	0.003	(0.000, 0.010)	220.63	57.89
	n=76	Flow	0.032	(0.019, 0.054)	-0.025	(-0.309, 0.277)	0.002	(-0.000, 0.006)	221.12	56.92
		Temperature	0.032	(0.020, 0.053)	0.231	(-0.445, 0.611)	-0.001	(-0.016, 0.039)	222.88	53.40
		Length	0.032	(0.019, 0.053)	1.211	(-0.023, 2.991)	-0.014	(-0.034, 0.005)	221.62	55.92
		Date	0.031	(0.017, 0.052)	-0.302	(-0.721, 0.347)	0.003	(-0.000, 0.006)	220.39	58.38

Table 1.c – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (The Dalles-Ladder).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
The Dalles Ladder	1997 n=22	Simple	0.891	(0.703, 1.223)					24.53	
		Diel	0.135	(0.052, 0.397)	2.038	(1.528, 2.644)			11.77	23.52
		Temperature	0.134	(0.055, 0.356)	-7.961	(-62.379, -2.659)	0.496	(0.268, 4.495)	10.77	23.52
		Length	0.135	(0.055, 0.410)	-2.202	(-23.530, 17.309)	0.058	(-0.200, 0.409)	11.72	21.61
		Date	0.134	(0.059, 0.444)	-2.870	(-9.395, 1.519)	0.024	(0.006, 0.071)	11.46	22.13
		Shad	0.135	(0.053, 0.471)	2.019	(1.472, 2.583)	-0.053	(-0.478, 0.290)	11.56	21.94
	1998 n=23	Simple	0.622	(0.466, 0.955)					33.92	
		Diel	0.357	(0.160, 0.713)	1.029	(0.720, 1.560)			30.80	4.24
		Temperature	0.368	(0.167, 0.737)	1.023	(-56.117, 1.533)	0.000	(0.000, 3.839)	30.80	2.25
		Length	0.357	(0.138, 0.754)	1.011	(-27.282, 33.700)	0.000	(-0.270, 0.929)	30.80	2.24
		Date	0.357	(0.163, 0.728)	-5.744	(-12.733, 3.158)	0.037	(-0.003, 0.081)	29.68	4.49
		Shad	0.357	(0.159, 0.619)	1.204	(0.713, 2.405)	-0.016	(-0.104, 0.022)	29.88	4.09
	2000 n=66	Simple	0.598	(0.486, 0.795)					99.97	
		Diel	0.203	(0.124, 0.349)	1.256	(0.941, 1.675)			76.48	44.96
		Temperature	0.203	(0.123, 0.316)	-2.499	(-8.261, 1.660)	0.187	(0.001, 0.495)	75.35	47.23
		Length	0.203	(0.123, 0.340)	-1.006	(-5.386, 4.861)	0.033	(-0.038, 0.111)	76.27	43.40
		Date	0.203	(0.112, 0.358)	3.879	(0.212, 9.103)	-0.012	(-0.028, 0.011)	75.28	45.38
		Shad	0.203	(0.117, 0.354	1.226	(0.913, 1.705)	-0.000	(-0.240, 0.375)	76.21	43.51
	2001 n=61	Simple	0.512	(0.395, 0.752)					101.80	
		Diel	0.258	(0.171, 0.460)	0.926	(0.693, 1.353)			90.02	21.57
		Temperature	0.258	(0.144, 0.395)	-1.383	(-4.908, 2.483)	0.116	(-0.058, 0.315)	89.29	23.03
		Length	0.258	(0.140, 0.495)	-0.785	(-6.875, 7.240)	0.024	(-0.063, 0.119)	89.85	19.90
		Date	0.258	(0.161, 0.449)	2.936	(-2.836, 5.271)	-0.009	(-0.018, 0.020)	88.48	22.65
		Shad	0.258	(0.143, 0.444)	0.902	(0.626, 1.395)	0.003	(-0.046, 0.019)	89.69	20.22

Table 1.d – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (The Dalles-Delay).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
The Dalles Delay	1997 n=18	Simple	0.183	(0.111, 0.413)					48.52	
		Diel	0.081	(0.026, 0.240)	0.355	(0.197, 0.752)			44.03	6.98
		Spill	0.082	(0.024, 0.238)	0.324	(0.114, 0.787)	0.000	(-0.001, 0.077)	44.03	4.98
		Flow	0.081	(0.025, 0.245)	0.372	(0.113, 0.878)	-0.000	(-0.020, 0.052)	44.03	4.98
		Temperature	0.081	(0.028, 0.244)	2.014	(-7.612, 9.581)	-0.086	(-0.390, 0.526)	43.46	6.12
		Length	0.082	(0.018, 0.202)	-1.404	(-11.362, 3.152)	0.026	(-0.028, 0.249)	43.39	6.27
		Date	0.081	(0.021, 0.202)	1.520	(-9.205, 6.360)	-0.006	(-0.023, 0.081)	43.80	5.44
	1998	Simple	0.325	(0.227, 0.553)					33.99	
		Diel	0.098	(0.028, 0.204)	0.704	(0.386, 1.306)			27.56	10.85
		Spill	0.098	(0.031, 0.213)	1.341	(0.181, 5.539)	-0.006	(-0.034, 0.016)	27.09	9.80
		Flow	0.097	(0.034, 0.150)	18.941	(3.128, 42.556)	-0.086	(-0.149, -0.006)	9.04	45.90
		Temperature	0.097	(0.033, 0.202)	0.844	(-11.636, 1.634)	-0.008	(-0.039, 0.871)	27.52	8.93
		Length	0.098	(0.030, 0.210)	2.611	(-7.763, 14.620)	-0.027	(-0.164, 0.144)	27.50	8.98
		Date	0.098	(0.032, 0.196)	-9.955	(-73.188, -5.578)	0.059	(0.035, 0.458)	21.45	21.08
	2000 n=31	Simple	0.367	(0.272, 0.611)					62.10	
		Diel	0.113	(0.040, 0.234)	0.797	(0.552, 1.479)			49.76	22.68
		Spill	0.113	(0.037, 0.220)	1.762	(0.404, 1.521)	-0.020	(-0.010, 0.107)	45.92	28.35
		Flow	0.113	(0.046, 0.221)	1.576	(0.455, 1.962)	-0.006	(-0.040, 0.055)	48.94	22.31
		Temperature	0.113	(0.037, 0.247)	6.119	(0.690, 14.463)	-0.256	(-0.596, 0.003)	48.03	24.15
		Length	0.113	(0.037, 0.244)	3.318	(-2.959, 14.737)	-0.036	(-0.147, 0.064)	49.21	21.77
		Date	0.113	(0.038, 0.233)	-2.319	(-7.498, 0.321)	0.014	(0.004, 0.055)	47.22	25.75
	2001 n=42	Simple	0.203	(0.138, 0.387)					108.99	
		Diel	0.061	(0.027, 0.162)	0.445	(0.252, 1.134)			91.88	32.22
		Spill	0.061	(0.027, 0.138)	0.472	(0.185, 1.927)	-0.002	(-0.007, 0.070)	91.79	30.39
		Flow	0.061	(0.022, 0.153)	0.527	(0.205, 1.481)	-0.001	(-0.031, 0.046)	91.84	30.31
		Temperature	0.061	(0.024, 0.165)	-1.169	(-8.827, 3.202)	0.080	(-0.098, 0.612)	90.32	33.35
		Length	0.061	(0.025, 0.181)	2.326	(-0.772, 8.992)	-0.026	(-0.087, 0.041)	91.34	31.29
		Date	0.061	(0.024, 0.169)	-1.779	(-5.902, -0.060)	0.011	(0.003, 0.047)	86.47	41.03

Discussion

The time-to-event analysis we used to examine lamprey delay offers some decided advantages over more traditional approaches. This method takes into account the temporal variability in environmental predictors that is not distinguished by methods that group passage times into bins. In cases where environmental data are available on fine temporal scales (in this case hourly), time-to-event analyses incorporate this information and increase the precision of correlations. In addition, these analyses require smaller sample sizes because each fish is treated independently and the outcomes are not affected by the non-normal distribution characteristic of passage rates in fish.

Predictive models of this type may be useful for management of hydropower dams to benefit fisheries resources. Our analysis indicated that there were significant differences in passage rates at the two dams we examined. Although we dissected the lamprey passage into two distinct phases (delay in the tailrace and in the ladder), our analysis indicated that there were significant and consistent improvements in both measures at The Dalles Dam relative to Bonneville Dam. Subsequent analysis did not indicate that environmental factors affected by dam operation, such as flow or spill, were important predictors of lamprey delay at either dam. We hypothesize that differences in fishway construction at the two dams affected passage rate, as they do passage efficiency (Moser *et al*., 2002). An alternative hypothesis is that lamprey at The Dalles Dam are more motivated or more able to negotiate the fishways due to the date of passage. In our analysis of a variety of predictor variables, the only consistent improvement to the diel model resulted when we added the effects of date. It is unlikely that this effect was due to the stage of reproductive maturity, as Pacific lamprey in this system do not spawn until the year after river entry. We found that lamprey exhibited decreased delay below the dams as the season progressed. Moreover, they exhibited some decreases in delay with increasing water temperature (which is correlated with date) in the ladders. Consequently, improved passage at The Dalles Dam may be partly attributed to the fact that lamprey passed this dam later in the year.

Recent laboratory measurements of lamprey swimming performance indicated a slight, yet significant decrease in swimming performance of radio-tagged lamprey when compared to controls (Mesa *et al*., 2003). If there was a significant effect of relative tag size on lamprey passage rate, it would have been reflected in an improvement in AIC values when we modeled the effects of lamprey length. Instead, we found that there was a consistent decrease in AIC when we added the length variable, indicating that there was no effect of lamprey size on delay either in the tailrace or in the fishways.

The clear improvement in the diel model over the simple exponential function describing the probability of delay indicated that our analysis is sensitive to patterns of lamprey behavior. While the fact that adult lamprey are primarily nocturnal is well-documented (Steir and Kynard, 1986; Almeida *et al*., 2002), the effects of other abiotic and biotic variables on passage rate have not been described. We found that the date of passage was an important factor affecting lamprey delay, but that other abiotic predictor variables did not have any significant or consistent effect on delay. Almeida *et al*. (2002) noted that adult sea lamprey (*Petromyzon marinus* Linnaeus) migration in the River Mondego, Portugal, was stimulated by increased flow. However, we found no evidence that Pacific lamprey delay was negatively correlated with flow. This may be due to the fact that increased flow at the base of dams is associated with increased turbulence, whereas increased flow in reservoirs, like the River Mondego results in higher velocity, uni-directional currents.

Interestingly, we found that abundance of shad in the fish ladders at Bonneville Dam was positively correlated with lamprey delay in 2001. Of the four study years, 2001 was the year with the highest total shad abundance and the lowest water levels. Consequently, negative effects of shad on lamprey passage rates would be most pronounced in 2001. It is possible that this result is spurious, as no significant effect of shad abundance was found at The Dalles Dam ladders or in any other year. However, this finding suggests that further investigation of biotic interactions in the fish ladders is warranted. We caution that the data used in our analysis represent only a fraction of the adult Pacific lamprey migrating through the lower Columbia River. The fish were initially collected in a fishway at Bonneville Dam, and therefore are not representative of the entire population downstream of the dam. We also eliminated from analysis those fish that did not successfully pass over a dam. Moreover, for the analysis of tailrace delay, we eliminated the lamprey that required less than 1 hour to make a final entrance into a fishway. Consequently, while the sub-sample we used illustrates the use of this technique, it does not necessarily provide a comprehensive analysis of all lamprey behaviours.

The approach we present is a simple comparison of single factor models. The time-to-event analysis allows construction of more complex multifactorial models that may be necessary to distinguish the effects of environmental variables that are correlated (such as time of year and water temperature). In addition, there are a host of other predictor variables that could be tested. For example, we found that delay below the dam was distinctly bi-modal, which may be due to reproductive readiness. A physiological marker of reproductive condition may therefore be a useful predictor of lamprey delay. Nevertheless, the simple methods employed here indicated that time-to-event analysis is useful in describing lamprey passage rates and can be used with relatively low sample sizes. Efforts to reduce lamprey delay at hydropower dams will benefit from an even more comprehensive assessment of factors to allow prediction of lamprey behaviour.

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No-take zones: does behaviour matter?

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Abstract

No-Take Zones (NTZs) or strict Marine Protected Areas are being widely promoted as a powerful tool against overexploitation of fish stocks. Increased catches and sustainability of adjacent fisheries are proposed to result through two mechanisms: spillover of maturing adults, and export of larvae from spawning within the NTZ. However, the effectiveness of NTZs will depend on various factors, including the behaviour of the fish species concerned. Species with smaller territories or home ranges, such as small serranids, will show less spillover of adults than those with larger territories or home ranges, such as carangids. On the other hand, species whose home ranges are large in comparison to an NTZ will receive little protection from it. Fish, such as rabbit fish (Siganidae) or Napoleon wrasse (*Cheilinus undulatus*), that show diel or other regular movements to forage or spawn in adjacent areas, will be vulnerable to exploitation outside NTZs, unless protected areas are extended to incorporate the range of particular populations. Similarly, species such as large serranids, lutjanids and lethrinids, that show seasonal migrations to regional spawning sites, are vulnerable to being targeted, unless spawning aggregation sites are also protected. The reproductive behaviour of species, for example whether they show sex reversal in response to growth or social status, may also influence the effectiveness of management interventions. The behaviour of fish larvae can also be important in determining the extent to which they recruit to their natal area. Increasing evidence suggests that larval behaviour may be adapted to promote local recruitment, as well as wide dispersal, to a greater extent than previously supposed. The effects of protection against fishing will also depend on the trophic level of species. Both fish and invertebrates that are either prey or competitors of the principal exploited species commonly show reduced abundance within NTZs, and enhanced abundance in areas where fishing is more intense. Thus knowledge of the ranging and migratory behaviour, not only of individual species but also of specific populations, is required to inform the design of networks of NTZ; data on foraging, social and reproductive behaviour are important for predicting the effects of protective measures. Tracking individuals by telemetry can provide information critical to the conservation and sustainable management of stocks.

Introduction

In the face of declining and even collapsing marine fish stocks globally (FAO, 2003), protected areas closed to fishing, known as No-Take Zones (NTZs), or Strict Marine Protected Areas (sMPAs), have in the last few years been widely promoted as a powerful tool against overexploitation of fish stocks (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994; Bohnsack, 1998; Roberts and Hawkins, 2000). This paper will consider the importance of the behaviour of species at different life stages with regard to the effectiveness of NTZs, primarily focusing on reef areas and coastal species. As will be illustrated, hydro-acoustic telemetry of tagged fishes provides a valuable tool for assessing the relevant behaviour of adult fish and increasingly of juveniles also.

Initially, NTZs were adopted in tropical coral reef areas as a measure to protect pristine coral reef communities for conservation purposes, or as an alternative to standard estimations of maximum sustainable yield and allocation of quotas. Determination of Total Allowable Catches (TACs) for the more than 100 species commonly present in tropical reef catches would be impracticable, and enforcement of quotas among uneducated, artisanal fishers in remote areas almost impossible. NTZs represent a simpler solution to such problems: any fisher observed within the NTZ is presumed to be in breach of regulations. In principle by assuming a degree of site fidelity among exploited species, fishing effort can be regulated by adjusting the proportional extent of NTZs in relation to fished area. With fish telemetry studies, the actual movement and location of fish can be related to areas, allowing a more practical definition of NTZs boundaries to be made.

A series of related fisheries and environmental benefits have been argued in relation to NTZs (Bohnsack, 1998). It has been anticipated that they can:

- prevent loss or extreme depletion of a stock, so safeguarding the potential for future recovery;
- protect spawning sites, or a portion of the stock, to ensure effective spawning, thus reducing the risks of recruitment-overfishing of stock;
- maintain or enhance fisheries yields in adjacent areas, by protecting fish within the NTZ until they have grown to larger size and emigrate to fished areas;
- buffer the stock against extremes, thus reducing uncertainty and variability in yield;
- protect genetic diversity if multiple NTZs can be located so as to protect portions of genetically separable populations or sub-populations;
- provide data on unexploited stock levels and on natural mortality, required to model maximum sustainable yields;
- provide reference sites for distinguishing effects of environmental change from ecosystem effects of fishing;
- protect other non-target species that may be important for ecosystem structure and function, e.g. keystone predators of echinoids.

Of the potential benefits, the most important is the anticipated gain to adjacent fisheries. The extent to which this may occur is still in dispute, and the mechanisms are the key subjects of considerable research.

The Reserve Effect

It is now widely accepted that, in regions subject to significant fishing pressure, there are positive effects of establishing a NTZ. These include an increase in fish abundance and biomass within the NTZ, and commonly an increase in mean fish length. These effects have become known as the reserve effect. Prior to the 1980s, fish population biologists tended to believe that fish recruitment was independent of spawning standing stock, and spawning standing stock would therefore not be affected by fish catch. The first evidence that a reserve effect would develop within a NTZ came from work in heavily fished tropical regions of South-east Asia (Alcala, 1988; Alcala and Russ, 1990). Among well-known examples was the observation by Russ (1985) of a fourfold increase in abundance of predatory fish in the Sumilon Island reserve, Philippines, over eight years following protection of the area. Subsequently, similar effects were described from NTZs or sMPAs in southern Africa (Buxton and Smale, 1989), Eastern Africa (McClanahan and Muthiga, 1988; Watson and Ormond, 1994), and the Caribbean (Polunin and Roberts, 1993).

To date, there have been 80 or more studies on the effect of establishing NTZs (see recent reviews by Halpern and Warner, 2002; Halpern, 2003). These studies compare fish stocks within an NTZ reserve either with those in the same area before protection, or with those in a similar adjacent area not given protection. The overwhelming majority of studies have recorded greater abundance, biomass, size and diversity of fish within the NTZ.

NTZs have also proved effective in increasing the stocks of commercially exploited invertebrates. For example, there has been an increase in the rock lobster, *Pagurus auratus,* by a factor of 5.8-8.7 inside the Leigh Marine Reserve, New Zealand (Babcock *et al*.,1999). A greater number of gray snapper above legal fishable size (>25.4 cm) have been recorded within a mangrove area set aside within the Everglades National Park to protect alligators (Faunce *et al*., 2002). This latter example is interesting as it demonstrates an effect of protection in the USA, where the authorities and sports fishermen have been very resistant to establishing any NTZ as a purely fisheries management measure.

Effects on Fish Catch

That protection usually results in an increase in fish abundance within protected areas is beyond doubt. More critical in relation to fisheries management is whether or not the establishment of NTZs can result in an increase in the same stock in adjacent areas, outside of any NTZ, and in particular whether it can result in an increase in catch from surrounding areas.

There are now some ten studies that have documented an increase in stock or catch. In perhaps the earliest well-known study, Russ and Alcala (1996) recorded a steady increase in the abundance of predatory fish immediately adjacent to the Apo Island Reserve in the Philippines. The ratio of their abundance inside versus outside the NTZ increased, as protection first influenced abundance within the reserve, and then decreased, as fish also increased their abundance outside the reserve (Fig. 1).

The most dramatic apparent benefit to fish catch from adjacent areas with which the authors are familiar occurred in the Shimoni area of the coast of Kenya (Watson and Ormond, 1994; Watson *et al.*, 1997). Here the large MPA incorporated a series of offshore reefs and islands, divided into two comparable portions. In one of these, the Mpunguti Marine Resource Area, fishing by local artisanal fishers was permitted. In the other, the

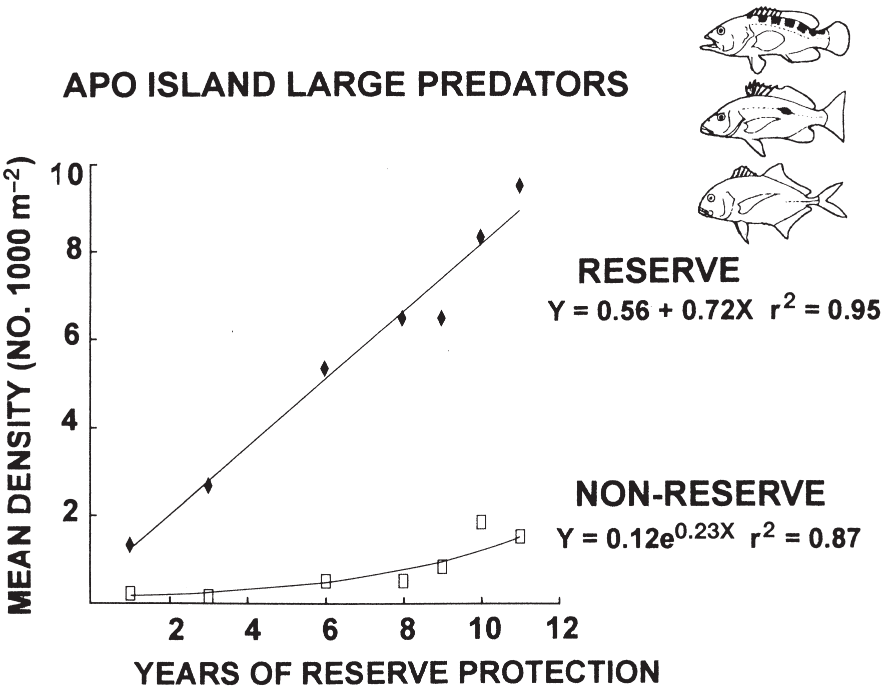

Fig. 1 – Increasing abundance of predatory reef fish both within and outside Apo Island reserve in the Philippines, with increasing time from the establishment of the protected area (from Russ and Alcala, 1996).

Kisite Marine National Park, fishing was in principle prohibited, although this prohibition was rarely enforced through the 1970s and 1980s. During the 1980s, there was a sharp decline in fish landings in the Shimoni region. Subsequently, in 1988, the Kenya Wildlife Service began enforcing the prohibition on fishing in the National Park. This was supported by a campaign of environmental education directed at local fishing communities, to persuade them of the potential benefits to the fishery of enforcing the National Park as a no-take area. By 1995, the fish stocks within the National Park area had increased to up to ten times that within the fished Mpunguti Marine Resource Area, and the fish catches from the remaining marine areas had recovered to the earlier higher level, despite a reduction in the area being fished (Fig. 2). Among more recent similar studies is a clear improvement in fish catches of between 46 and 90% within the fished areas between five small No Take Areas, established on the Caribbean island of St Lucia (Roberts *et al.*, 2001).

Mechanisms of Fisheries Enhancement

Any benefits to adjacent fisheries from the establishment of NTZs are presumed to arise through two distinct, but related, mechanisms. Firstly, if there is an increase in spawning stock within an NTZ, then an increase in the production and dispersion of larvae should result in increased 'larval export' to other areas. If stocks in neighbouring fished areas have through fishing become recruitment limited, then they may be enhanced through resulting increased

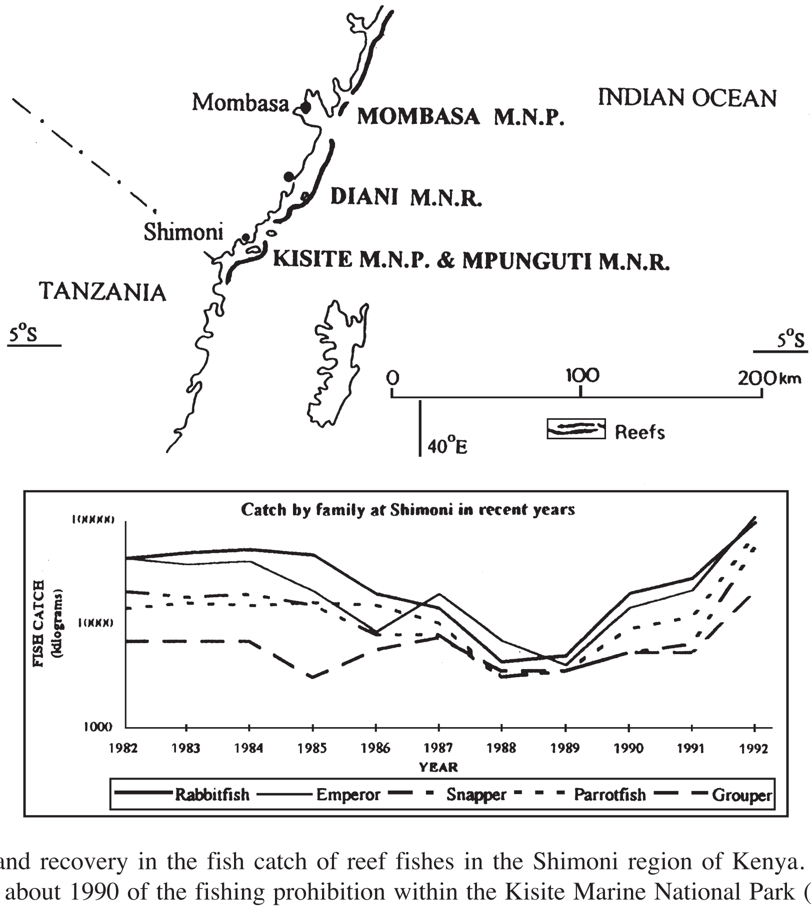

Fig. 2 – Decline and recovery in the fish catch of reef fishes in the Shimoni region of Kenya. Recovery followed enforcement from about 1990 of the fishing prohibition within the Kisite Marine National Park (from Watson *et al.*, 1997).

recruitment. Secondly, if there is an increase in abundance of adult or juvenile post-recruitment fish within the NTZ as a result of protection, then some of these fish may be expected to move out of the NTZ to surrounding areas where population densities have been depleted as a result of fishing. Even where there is no significant movement in response to a population gradient, individuals with home ranges towards the edge of an NTZ may have their home range extending over an NTZ boundary, and so may be liable to capture. The movement of post-recruitment and adult fish out of an NTZ has been termed 'spillover'.

The extent of larval export and spillover from NTZs to fished areas has become a subject of considerable topical interest. Spillover from an NTZ will clearly be influenced by the ranging and migratory behaviour of the fish. Local fishers implicitly acknowledge the occurrence of spillover by fishing close to the boundary of an NTZ, a practice often referred to as 'fishing the line'. Evidence for spillover may be relevant to local fisheries managers in seeking the support of local fishers for the establishment or maintenance of an NTZ. By contrast, it has been assumed that local fishers are less likely to experience a benefit from enhanced larval export, since fish larvae were presumed to be carried passively by ocean currents to areas a considerable distance away. This view, however, is being revised as a result of new knowledge about fish larval behaviour. We will consider the influence of fish behaviour first on spillover, and then on larval export.

Spillover and Species Mobility

The mobility of post-recruitment fish will determine the extent of spillover from an NTZ. As pointed out by Bohnsack (1996), however, the degree of protection afforded a population through the establishment of an NTZ will itself be inversely related both to species mobility, and to the size of the protected area. Thus species with large home range size, compared to the size of an NTZ, will receive relatively little protection from the enforcement of the NTZ (Holland *et al*., 1996). In the extreme case, migrant or free-ranging species will receive no benefit from the creation of NTZs, except where critical areas, such as spawning grounds or migration bottlenecks (e.g. for tuna passing through the Straights of Messina), can be protected.

These conclusions were supported by Kramer and Chapman (1999) who modeled species mobility and spillover influence on abundance differences between NTZs and surrounding fished areas. They found that:

a) increases in abundance will be higher in reserves that are larger or have higher area to edge ratios;
b) species with low mobility will show greatest increase within the NTZ, and hence greatest potential increase in larval export;
c) species with intermediate levels of mobility will provide the greatest spillover benefit to nearby fisheries.

This latter conclusion arises because i) although fish with very high mobility will not receive protection from the creation of an NTZ, ii) fish with very low mobility will develop increased abundance in the NTZ as compared with the fished area, but will show minimal spillover. A variety of other models have sought to predict the effect of NTZs on fish catch (e.g. Polacheck, 1990; DeMartini, 1993).

Fish species that are territorial will be least mobile. In behavioural studies, a territory is defined as an area that is both exclusive to one or more individuals, and is defended against other individuals (Wilson, 1975). A high proportion of coral reef fish are territorial, though once territories have been established, individuals may show agonistic behaviour only occasionally and even appear to tolerate the presence of neighbours. Territories may be occupied and defended not only by single fish, but by bonded pairs, as in many butterflyfishes (Chaetodontidae), or by larger social units, as in many wrasse (Labridae), parrotfish (Scaridae) and groupers (Serranidae) (Reese, 1975; Robertson, 1972; Kuwamara, 1984; Van Rooij *et al*., 1996). In many reef groupers, a dominant territorial male defends a large area within which females occupy a series of overlapping home ranges, or non-overlapping sub-territories within it (Shpigel and Fishelson, 1991). The size of territories varies considerably between species from only a metre or two, as in the some damselfishes, such as *Stegastes*, (Sadovy, 1986) to hundreds of metres in the case of the largest parrotfish (e.g. *Cetoscarus bicolor*) (unpubl. data RFGO) and grouper (e.g. *Plectropomus* spp.) (Zeller, 1997). As in other vertebrate groups, the size of territories varies inversely with food abundance, but broadly speaking the size of territory increases with the biomass of the species.

Home ranges differ from territories in being areas that are neither exclusive nor defended (Wilson, 1975). They too vary considerably in size, but usually they are larger than territories for the same or comparable species. Home range size depends on species and habitat, but is generally proportional to body size, both across species (Kramer and Chapman, 1999) and within a species, as described for coral trout, *Plectropomus leopardus* (Goeden, 1978).

Reef fish territories can be plotted by following (e.g. with SCUBA) and mapping the movements of individual fish for as little as a few hours. Where individuals can be recognised through tagging or individual variation in colour pattern, more precise plots can be obtained. By contrast, it can take much longer to plot the full extent of an individual's home range, since some parts of the range may be visited relatively infrequently. Hence acoustic tracking may be a more effective method, particularly for larger fish species with correspondingly greater home ranges. Zeller (1997) plotted the territories of coral trout, *Plectropomus leopardus,* at Lizard Island, Australia, by ultrasonic telemetry (Fig. 3). Fish were recorded for a maximum of 202 days, observed to use regular locations, moved a mean of 192 m with a maximum distance of 1122 m, and had average minimum polygon home ranges of 10458-3188 m^2, that were observed to be stable within and between tracking sessions.

An example of a study using telemetry to map the home ranges of a species within a small marine protected area (<1 km^2) was carried out on Coconut Island, Kaneohe Bay, Hawaii (Meyer *et al.* 2000). The home ranges of five Hawaiian white-saddle goatfish were determined using acoustic tags and fixed hydrophones. All of the fish remained within the reserve, but showed consistent diel behaviour patterns, refuging in holes within preferred areas by day, and foraging over extensive areas of sand and coral rubble by night. Another study at the same site illustrates how some species often assumed to be wide ranging may in fact have relatively well defined home areas. Holland and colleagues (1996) tagged blue trevally, *Caranx melampygus,* with both acoustic transmitters and plastic tags; 75.5% were recaptured or relocated within 0.5 km after 4-454 days, but the distance from site of first capture was not related to time at liberty.

Dispersion

While many reef fish species are territorial, or have fairly well defined home ranges, others may be essentially vagrant, wandering over broader regions in search of food and shelter. Some may adopt temporary home ranges on encountering suitable habitat or abundant food, before moving when conditions become less favourable. The degree of protection afforded such species by an NTZ will depend on two factors. These are the length of time that individuals typically remain in an area, and the rate at which individuals present within the area at any one time disperse over a wider region.

Information on the extent and rates of dispersion of such species has come as a by-product of mark-recapture studies using conventional tags. Of 2,932 red snapper tagged on artificial reefs in the Gulf of Mexico, approximately half were recaptured locally, while others moved a mean of 29.6 km, and a maximum of 352 km (Patterson *et al.*, 2001). Similarly, in a mark-recapture study of five temperate reef fish species, 7.4% of one species, *Petrus rupestris,* were found to have moved 200-1000 km towards distant aggregations of the same species. Among the other four species, 57-93% of individuals had not moved away, and the remain-

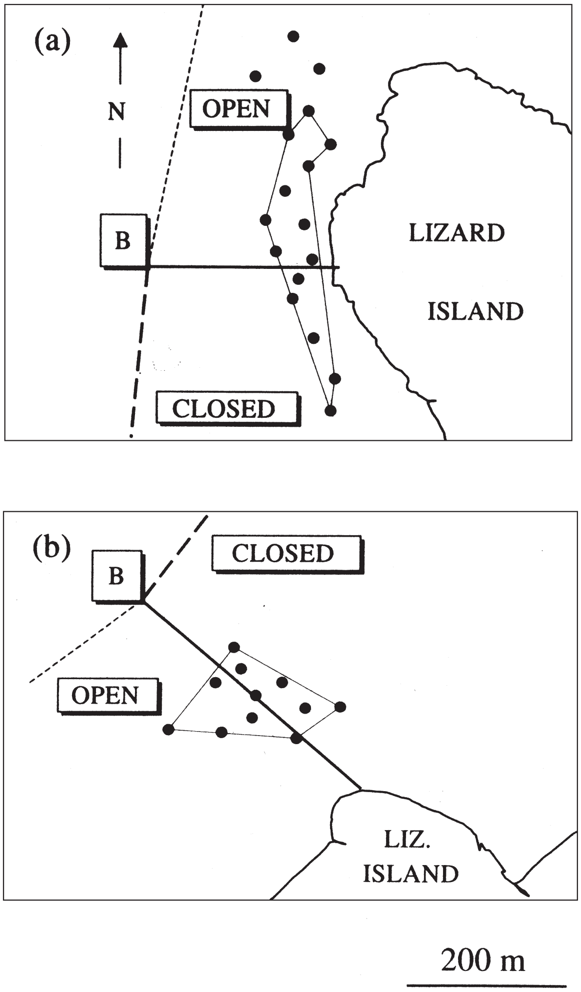

Fig. 3 – Two examples of the home ranges of coral trout, *Plectropomus leopardus,* at Lizard Island, Great Barrier Reef, as determined by ultrasonic telemetry. The polygons show the minimum area polygons for the individual fish, whose home ranges in these cases straddle the boundary between areas open and closed to fishing (from Zeller and Russ, 1998).

der had moved only short distances from the site of first capture (Griffiths and Wilke, 2002). However, it is not always easy to know how such results should be interpreted, because there are issues of fish mortality and tag loss, which can be high in reef fish (Whitelaw and Sainsbury, 1986). The behaviour of the fish recovered, or those that have been tagged, may not be representative of the population. For example, many of the fish not recovered may be those that moved out of the search area. Capture and tagging activities may provoke affected fish to move more when they might not otherwise have done.

Direct Observation of Spillover

A number of studies have been undertaken with a view to monitoring movement of fish out of a protected area. Attwood and Bennett (1994) tagged 11,022 fish over 5.5 years within the 50 km long Tsitsikama coastal reserve, South Africa. Of the 9.1% that were recaptured, 17.8% had moved outside the reserve. Other studies have used underwater observers as a means of re-recording tagged fish. Beinssen (1988) tagged 273 coral trout at Heron Island, on the Great Barrier Reef, Australia, of which 13.9% were resighted. Most of these had moved only short distances (500-1500 m), and were presumably still within their original territory; only one crossed the boundary to move out of the Heron Island reserve. Chapman and Kramer (2000) used both recapture and underwater observation to re-record fish tagged on capture in Antillean fish traps in the Barbados Marine Reserve and adjacent non-reserve. Standardised recapture distances ranged from 0 to 116 m, and weighted median re-sighting distances from 0 to 44 m, depending on the species. The greatest re-sighting distance was 538 m, and the greatest recapture distance 616 m; despite these figures no emigration from the reserve was recorded.

Hydro-acoustic telemetry is increasingly providing an alternative tool for such studies, since individuals can be relocated and tracked on a more reliable basis, and tracking can be undertaken in deeper water that is unsuitable for work using SCUBA. Eristhee and Oxenford (2001) tracked Bermuda chub by acoustic telemetry. They found consistent overlapping individual home ranges that were similar in size between reserve and non-reserve sites. Similarly, Zeller and Russ (1998) used ultrasonic telemetry and underwater observation of freeze-branded individuals to compare movement of coral trout, *Plectropomus leopardus,* in and out of NTZs at Lizard Island, Australia. The density of coral trout was 20% higher in the NTZs, but the difference was not significant: 93 of the 183 freeze-branded fish subsequently observed underwater had not crossed the NTZ boundary within the 2 month study period. Using data from ultrasonic transmitters, they found that fish with home ranges on the boundary of an NTZ crossed boundaries a mean of 15.3 times per month. Curiously, the mean distance moved by fish was greater within the NTZs than outside, when estimated by underwater observations. This difference was not evident in the telemetry data, and so was interpreted as an artefact associated with the direct observation protocol.

In principle, either direct observation (e.g. by SCUBA) or tagging (e.g. conventional tags or acoustic transmitters) could be employed to monitor movement across the boundaries of an NTZ, and so detect any net emigration or spillover. It may be difficult in practice, however, to detect any net emigration, as this would probably be hidden as a tiny fraction of the huge number of fish movements that take place every day, as a result of the normal activity of fish whose home ranges straddle the boundary. In the cases of conventional tagging or acoustic telemetry, the problem would be exacerbated by the low proportion of the fish population that is recovered or being monitored. In addition, it may be that most emigration is by sub-adult or fugitive fish that are less susceptible to capture and tagging, and less easy to observe. Thus determination of spillover from direct observation of fish movement across a boundary may prove impractical.

Density Gradients across Boundaries

As an alternative, researchers have also looked at patterns in fish abundance across NTZ boundaries to deduce evidence of spillover. If there was no net emigration of fish across the boundary of an NTZ, a sharp divide might be predicted between an area of higher fish abundance within the NTZ, and one of lower abundance in an adjacent fished area. Where instead there is net movement or spillover of fish from the NTZ, a gentler gradient in abundance would be expected from within the NTZ to within the adjacent fished zones. Such gradients in abundance have been observed across the boundaries of NTZs in several studies. Perhaps the best known case is the reduction in catch by fish traps with increasing distance from the centre of the Barbados Marine Reserve (Fig. 4), observed by Rakitin and Kramer (1996).

We too have observed similar density gradients in fish abundance across the boundaries of NTZs contained within the Marine Protected Area at Nabq, South Sinai, Egypt (Ashworth and Ormond, 2005). Within the fished portions of the MPA, fishing is permitted only to Bedouin who have traditional rights. In 1995, the Bedouin community agreed to the establishment of five NTZs, which by 2000 had resulted both in differences in fish family abundance between fished and unfished zones, and an increase in catch per unit effort (CPUE) from 0.79 to 1.31 kg unit gear^{-1}hr^{-1} within the open areas (Galal *et al*., 2002). Subsequently, we observed gradients in fish abundance on transects between one of the NTZs and the adjacent fished zones (Fig. 5). The gradients in abundance varied in slope, depending both on the species concerned and on the intensity of fishing, which was greatest on transects nearer the shore.

Other Regular Movements

The effectiveness of NTZs and the degree of spillover into a fishery will also be affected by other types of fish movement. Firstly, many species of rabbitfish (Siganidae), grunts (Haemulidae), snappers (Lutjanidae), and cardinal fish (Apogonidae) show diel or other regular foraging movements between distinct roosting and foraging areas. Normally both roosting and foraging areas would be considered as parts of the home range, but the two areas may be some distance apart. Brown surgeonfish (*Acanthurus nigrofuscus*) migrate up to 1.5 km between fore-reef and reef flats at sunrise and sunset (Mazeroll and Montgomery, 1995; 1998), with movement being triggered by ambient light levels (Myrberg *et al*.,1988).

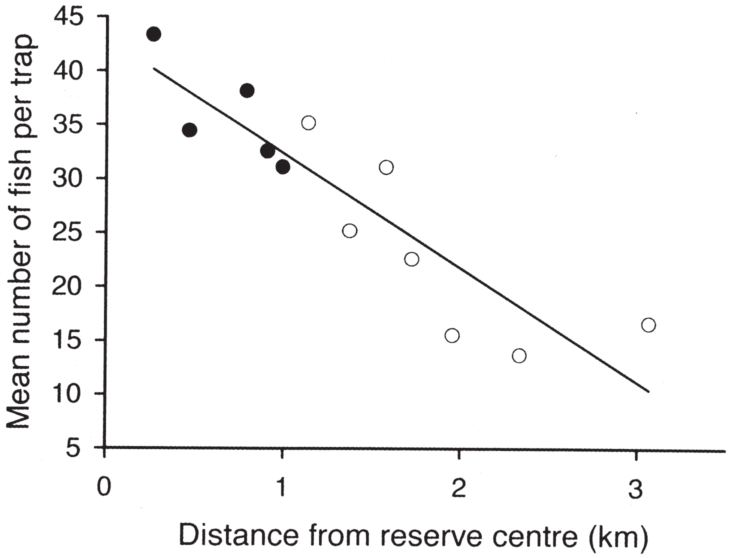

Fig. 4 – Catch per unit effort of fish traps with increasing distance from the centre of the Barbados Marine Reserve. The decline in catch with increasing distance from the centre, within (solid symbols) as well as without (open symbols) the reserve, are considered due to decreasing abundance of fish as they move out of the reserve and are caught (from Rakitin and Kramer, 1996).

Similar considerations apply to spawning movements. Many fish show movement on an occasional or daily basis to suitable spawning sites within their regular home ranges. These species have been termed resident spawners (Thresher, 1984; Domeier and Colin, 1997). They include some species of grouper such as coney, *Epinephelus fulvus,* as well as most species of wrasse (Labridae) and parrotfish (Scaridae) (Randall and Randall, 1963; Warner, 1987). Other species, termed transient spawners, migrate seasonally to locations outside their daily home range. Typically, fish are drawn from a large area and travel for days or weeks to reach local or regional spawning sites, where they remain for a period often extending over one or two lunar phases. Transient spawners include various species of grouper (Serranidae), snapper (Lutjanidae), and emperor (Lethrinidae). (Shapiro, 1987; Sadovy *et al*., 1994).

A prime example of a transient spawner is the Nassau grouper, *Epinephelus striatus,* that migrates to spawn at specific sites at full moon, in the southern Caribbean in December and January, and in the northern Caribbean in May and June. These movements have been studied using both conventional and acoustic tags. Bolden (2000) studied the movements of Nassau grouper in central Bahamas using Floy dart tags and acoustic transmitters that enabled fish to be tracked for 24 hrs a day. Fish were observed to travel up to 220 km to reach a spawning site, where their mean stay was 46 days. Other serranid genera in the Pacific tend to travel shorter distances to more local spawning sites. Zeller (1998) studied spawning of coral trout, *Plectropomus leopardus,* at Lizard Island, Great Barrier Reef, Australia. He used ultrasonic tags to track 35 fish that used four spawning sites between 220 and 5,210 m from their home range sites. Only 31% of fish participated in spawning, which peaked at new moon; females tended to make overnight visits, but males made multiday visits to spawning sites.

Such spawning sites are very vulnerable to overexploitation by fishers. Unregulated exploitation can completely eliminate a spawning aggregation; for example, 33% of Nassau grouper spawning aggregations have disappeared from Belize

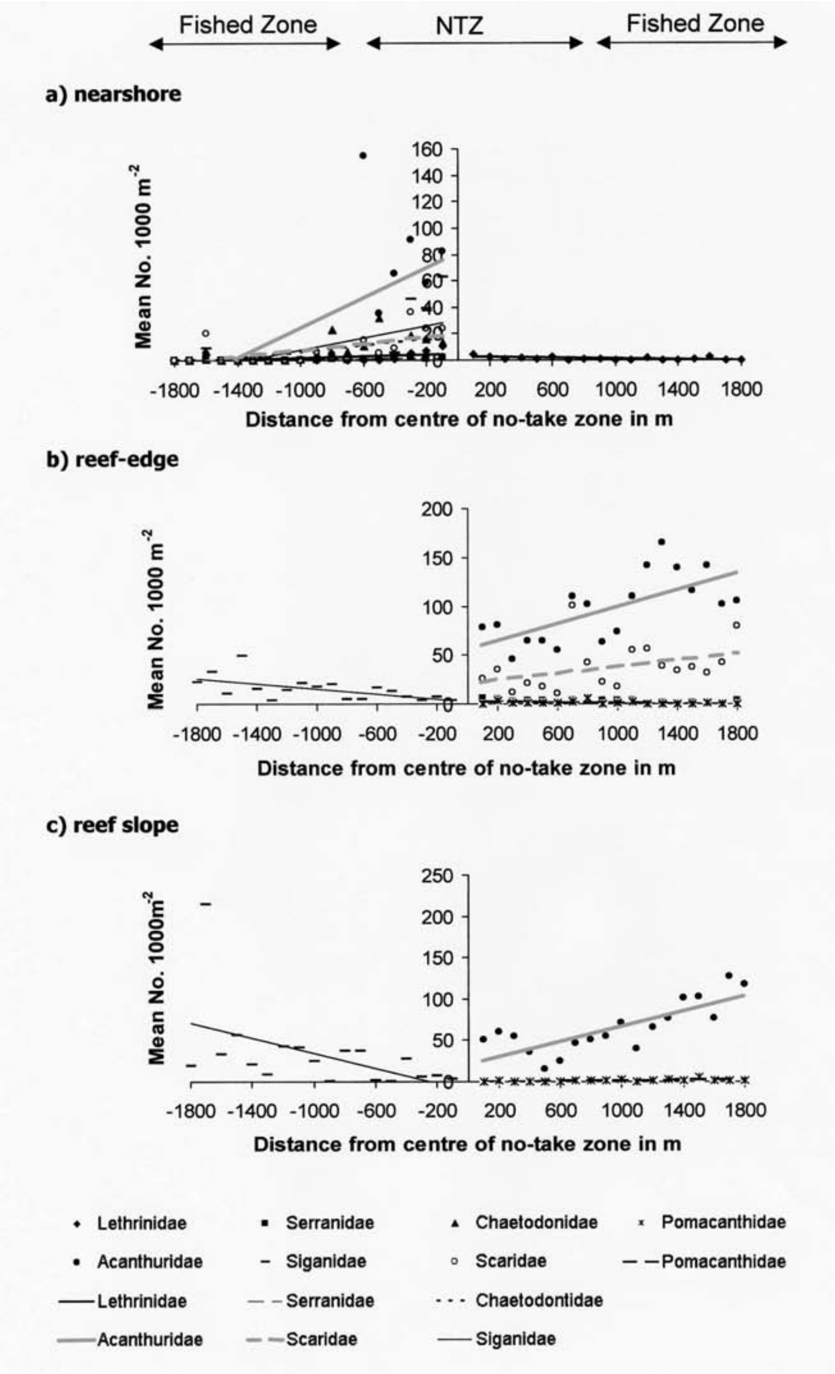

Fig. 5 – Abundance of fish as observed by underwater visual census along transects at three different depths moving from the centre of a No-Take Zone into both the adjacent fished areas within the Nabq Marine Protected Area at Nabq, South Sinai, Egypt. Only families showing a statistically significant trend are included. Nearer the shore most families show a significant decline in abundance moving out of the NTZ, but furthest from the shore some families are less abundant in the NTZ than in the fished zones (after Ashworth and Ormond, 2005).

and the Caribbean due to overfishing (Sala *et al*., 2001). One of the largest remaining sites has been reduced from 15,000 to less than 3,000 fish within 25 years. It is therefore desirable to include major spawning aggregations within MPAs whenever possible. The ease with which seasonal aggregation sites can be overlooked is demonstrated by a recent study by Eklund and colleagues (2000). They described how a new NTZ in the Florida Keys National Marine Sanctuary was established without it being appreciated that a spawning aggregation of 96 black grouper, *Mycteroperca bonaci*, was located less than 100 metres outside of the NTZ.

The effect of heavy exploitation can be compounded in sex reversing species, which includes most groupers (Serranidae). Fishing typically results in heavier mortality of larger individuals, and in the scarcity of the larger sex (Punt *et al*., 1993, Hunstman and Schaaf, 1994). This is especially so if sex reversal occurs at a fixed age, and less so where sex change is mediated socially (Vincent and Sadovy, 1998). Epinepheline groupers have female-biased sex ratios (Moe, 1969; Shapiro, 1987), although occasional male-biased populations have been reported. These have attributed to heavier exploitation of the smaller females, because they tend to occur nearer to shore (Johannes *et al*., 1996). An illustration of the effects of exploiting aggregations in protogynous species is provided by Coleman and colleagues (1996), who describe how fishing reduced the proportion of males from 17% to 1% in gag, *Mycteroperca microlepis,* and from 36% to 18% in scamp, *M. phenax,* but produced no change in sex ratio in the non-aggregating red grouper, *Epinephelus morio*.

Larval Export

While the production of larvae is critical, so to is their fate. In particular the import and export of larvae may determine both fish populations within an NTZ, and the extent that these populations contribute towards replenishment of stocks in surrounding areas. Fish can remain as larvae from 3-6 weeks, depending on food availability and ambient temperature (Moloney *et al*., 1994; Bingham, 1992). It has been presumed that larval recruitment from a spawning location occurs over a large area, encompassing hundreds to over a thousand kilometers (Boehlert, 1996; Roberts, 1997). Shanks and colleagues (2003) examined the dispersal distance of propagules of marine benthic organisms. They estimated dispersal distances for 32 taxa, and the time spent dispersing for 25 of these taxa. They found that the more time spent in water, the further the propagules were generally dispersed. The curve of frequency distribution and dispersal distance is bimodal with, however, a gap between 1 and 20 km. The model suggested that at less than 1 km distance dispersed, the larvae tend to spend less than 100 hours as plankton. If the larvae spend longer than this, then they probably remain in near-bottom waters. Larvae dispersing further than 20 km tended to spend more than 300 hours as plankton. Shanks and colleagues (2003) suggest that there may be evolutionary constraints against a mid-range dispersal strategy covering the gap between 100 and 300 hours in the plankton. From their results, they propose that marine reserves need to be large enough (at least 4-6 km diameter) to contain short-distance propagules, but far enough apart (10-20 km) that long-distance propagules can settle in an adjacent reserve.

Is Recruitment Supply Driven?

Irrespective of the distance to which larvae may be carried, two key issues have arisen in relation to the effects of larval dispersal on fish recruitment. First, is recruitment supply driven? Second, does significant retention of larvae occur on their reefs of origin? Considering the first of these issues, there are a number of factors that may drive the supply of larvae, including timing of spawning, pelagic larval duration, lunar and tidal cues, and stochastic factors including larval growth and mortality, and oceanographic processes (Valles *et al*., 2001). Thus recruitment of damselfishes (Pomacentridae) on the Great Barrier Reef, Australia, has been found to match seasonal patterns in larval abundance (Milicich *et al*., 1992). In turn, annual variation in the abundance of adults on the Great Barrier Reef has been found to vary with recruitment (Williams, 1979; Doherty and Fowler, 1994). Consistent differences in levels of recruitment were observed between sites, however, and presumed to be related to habitat characteristics (Milicich and Doherty, 1994). By contrast, Robertson (1988a, b) found no relationship between larval abundance and adult populations in several families of Caribbean reef fish.

The relative importance of pre- and post-recruitment processes may differ between species and locations. An interesting study in this context is that by Sponaugle and Cowen (1996) who compared larval supply and juvenile recruitment in two reef fish in Barbados. One, the bicolour damselfish, *Stegastes partitus*, is a small, solitary, relatively sedentary territorial herbivore with benthic eggs, while the other, the ocean surgeon, *Acanthus bahianus,* is a larger, mobile schooling herbivore, with pelagic eggs. They found that *Stegastes* larvae were more abundant in the south, and *Acanthurus* larvae more abundant in the north, suggesting that larval supply was not simply the result of passive transport. The abundance of juvenile *Stegastes* matched that of the larvae, although it was less variable spatially. By contrast, the pattern of abundance of juvenile *Acanthurus* was the inverse of the larval supply pattern, implying that post-settlement processes were influencing juvenile abundance. More generally, it has been argued that recruitment patterns are likely to be affected by a range of ecological processes, such as predation, competition, behaviour, habitat selection, facilitation, and resource availability (Hixon, 1991; Jones, 1991; Leis, 1991; Cowen and Sponaugle, 1997).

Spatial differences in fishing pressure can result in changes in resident fish community structure (Russ, 1991; Roberts, 1995; Bohnsack and Ault, 1996). This suggests that fisheries-related differences in ecology between an NTZ and a neighbouring fished area could result in differences in rates of recruitment, or in post-settlement survival. Even without such differences, larval supply may differ between adjacent areas. Valles and colleagues (2001) compared the supply of larvae of the bicolour damselfish, *Stegastes partitus*, to a marine reserve (Anse Chastenet) with that for an adjacent fished area (Grand Caille) within the Soufriere Marine Management Area (SMAA), St Lucia, over a single autumn period. They found a consistently higher abundance and diversity of larvae arriving at the fished area, despite the proximity of the two sites. This difference was attributed to local scale variation in hydrodynamics and biological features.

Is Larval Retention Significant?

The second issue, particularly relevant to the role of NTZs, is whether significant retention of larvae occurs on their reefs of origin. As described above, it has long been presumed that most marine larvae are carried long distances by prevailing currents. Hence it was anticipated both that larval recruitment to a location is independent of local reproduction (Sale, 1991; Caley *et al*., 1996), and that a high proportion of larvae are lost after transport away from their sites of origin (Dight *et al*., 1990). Subsequently, it was suggested that recirculatory features in the lee of reefs might entrap dispersing larvae, increasing the likelihood of successful recruitment locally (Kingsford *et al*., 1991; Dight and Black, 1991). Further, hydrographic models incorporating this feature have suggested that, because most larvae that are carried away fail to survive, local recruitment could be up to 10 times more likely to occur than recruitment downstream (Black, 1993).

Direct evidence that local retention may be more important than distant recruitment is not easily obtained. Swearer and colleagues (1999), however, noted that coastal waters typically have higher concentrations of nutrients and trace elements than the open ocean, and they used differences in tissue concentrations of these chemicals to distinguish larvae that experienced these two environments. They compared chemical signatures of otoliths in juvenile bluehead wrasse (*Thalassoma bifasciatum*) from windward and leeward reefs at St Croix, (US Virgin Islands). They found that larvae on the two types of reef appeared to have experienced different larval environments. The leeward reefs recruited largely retained larvae, while windward reefs mainly received larvae that had experienced oceanic conditions. Accordingly, Swearer and colleagues (1999) argued that in the Caribbean larval dispersal processes operate at different spatial scales: between islands (>100 km) and within islands (<10 km). They suggested that reefs over time receive both locally retained and ocean-dispersed larvae, but as more than 70% of settlement was on the leeward reefs, a majority of recruits originated from locally retained larvae.

Larval Behaviour

It was also long presumed that larvae are dispersed passively by ocean currents, and are unable to affect their destination. However, increasing evidence suggests that larval behaviour is adapted to promote local recruitment as well as dispersal. Some larval fish are capable of remarkable swimming speeds. Larval fish in swimming chambers have been shown to attain speeds up to 13.5 cms^{-1}, although with a 25-fold variation in abilities between species (Stobutzki and Bellwood, 1997). In studying the swimming speed of late pelagic larvae *in situ* around Lizard Island and Rangiroa Atoll, Leis and Carson-Ewart (1997) measured the speed of 50 species in 15 families of mainly perciform fish (Fig. 6). Speeds were very high for these small fish (0.7-5.5 cm), averaging 20.6 cms^{-1} or 13.7 body-lengths s^{-1}, depending on the taxa. Apogonids and nemipterids were slowest, pomacentrids and chaetodontids speeds varied with species, and acanthurids, lethrinids and serranids were fastest. Crucially, all but apogonids and nemipterids were found to have mean speeds greater than average ambient current speed. That is, late larval fish are capable of swimming fast enough to influence their dispersal destination.

The potential effect of active swimming by late stage larval reef fish has been modeled by Armsworth (2000), distinguishing between strong and weak swimming ability, and between responsiveness to current-dependent and current-independent cues for orientation. Armsworth (2000) concluded that purely hydrodynamic effects leading to incidental recruitment or passive entrainment in re-circulatory features around reefs were less important than larval swimming abilities. Rather, the model suggested that the ability of larvae to respond to sensory cues was critical. Acanthurids have specialised larvae that are strong swimmers during their late stage, capable of directed motion and selective of their benthic habitats. Thus local currents are not likely to be a constraint for acanthurids. Armsworth (2000) suggests that for these and similar species recruitment would be relatively predictable in space and time. Larval apogonids, by contrast, are weak swimmers. Armsworth (2000) notes that they might be expected to have a shorter pelagic larval duration and employ advection avoidance mechanisms, show vertical migration, and exploit the benthic boundary layer, making it more likely that they would be retained near to a reef. The idea that larval fish may home towards suitable reefs from considerable distances has been given strong support by recent evidence both that larvae are sensitive to ocean sounds, and that they will recruit preferentially to locations fitted with loudspeakers emitting characteristic reef sounds (Tolimieri *et al*., 2000; Leis *et al*., 2003). If larvae can respond to current-independent auditory stimuli, such as the sounds of wave action and currents on reefs, and swim against moderate currents to reach source reefs, then larval recruitment may be very far from the passive process hitherto imagined.

Trophic Effects

A final aspect of behaviour that may influence the response of fish stocks to the establishment of No-Take Zones is the feeding ecology and trophic role of the species concerned. The review by Halpern (Halpern and Warner, 2002; Halpern, 2003) of some 80 studies into the effects of NTZ establishment included consideration of the effects on the

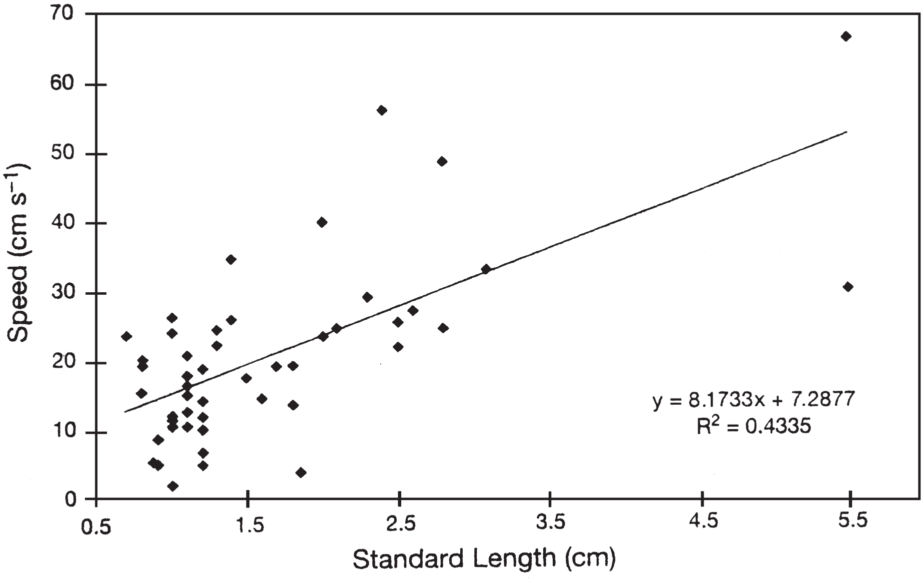

Fig. 6 – Relationship of mean swimming speed to mean size (standard length) in late stage larvae of 53 species of coral reef fish (from Leis and Carson-Ewart, 1997).

density, biomass, organism size of lower trophic groups. They concluded that the abundances of herbivorous fishes and invertebrates in NTZs is usually lower than, or similar to, that in adjacent fished areas. However, a number of studies have reported a decrease within NTZs in some fish that are either herbivores (Roberts and Polunin, 1991; 1992) or competitively inferior predators (Watson and Ormond, 1994; Sluka *et al.*, 1998; Chiappone *et al.*, 2000). Such effects seem likely to be the result of a decrease in the predation or competition due to preferentially exploited species such as larger grouper (Russ, 1985). It has also been suggested that mortality of juveniles may be higher in reserves than outside, as a result of competition or predation (Dufour *et al.*, 1995). Similar effects have also been reported for invertebrates, notably for echinoids (McClanahan and Shafir, 1990; Watson and Ormond, 1994; McClanahan *et al.*, 1999; Ruttenberg, 2001, Ashworth *et al.*, 2004), and smaller molluscs (McClanahan, 2002; Ashworth *et al.*, 2004). Again it seems most likely that these effects are due to an increase in abundance of fish predators. Thus some species may show a reduced abundance within NTZs. This will clearly have implications for conservation plans designed to sustain species abundance and maximise diversity.

A recent study in which we have participated (Ashworth and Ormond, 2005) suggests an explanation for the variable response of herbivore and invertebrate populations to NTZ establishment. As described above, five NTZs were established in 1995 at Nabq, Egypt, within which there have been significant increases in the abundance of some fish families (Galal *et al.*, 2002). A more detailed study of one of these areas has shown that the response of fish stocks varies with fishing effort. Nearer the shore where fishing effort is greatest, 9 out of 10 families were more abundant in the NTZ (Fig. 5). With increasing distance from the shore, fewer families showed this response. Furthest from the shore, fishing pressure was least and only two herbivore families (Acanthuridae and Siganidae) showed significant differences between the fished areas and the NTZ, with both being more abundant in the fished areas. The explanation for this effect must be that whereas more intense fishing using non-selective gear reduces the abundances of all families, relatively light fishing using more selective gear may reduce the numbers only of some families. If this light fishing only reduces the numbers of larger predatory fish, the numbers of some prey families may increase as a result of reduced predation pressure. If a large variety of predatory species is being exploited, but only a few prey species being released from predation, the change in abundance of these prey species may be greater than that of any predator species. Thus the response of fish populations to NTZ establishment will depend on both trophic status and fishing pressure.

Conclusions

The idea that overfishing can be regulated by protecting portions of the marine environment is easy to grasp. However, the extent to which species abundance increases within a No-Take Zone (NTZ), and the extent to which this increases fish catch in adjacent fished areas, depends on a number of factors. The ranging and migratory behaviour of species is critical in determining both the extent to which fish within an NTZ are protected from exploitation, and the extent to which spillover of denser populations within the NTZ will supplement stocks and enhance fisheries in adjacent fished areas. Species vagility may be influenced by, among other factors, the social and reproductive behaviour of species. Also key is the patterns of larval export from an NTZ. These will be greatly influenced by fish larval behaviour, specifically the extent to which larvae can be entrained with circulatory features nearshore, or detect and swim against the current towards suitable benthic habitat. Finally, the trophic and competitive status of a species may influence its response to cessation of fishing. Where fishing pressure is less intense, species that are prey, or inferior competitors of exploited predatory species, may actually increase in abundance as a result of the removal of their principal predators. Hydro-acoustic tagging of adults and chemical profiling of larvae are methods offering the possibility of monitoring spillover and export of adults and larvae respectively, so as to assess the effectiveness of NTZs.

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Telemetry studies of the passage route and entrainment of downstream migrating wild Atlantic salmon (*Salmo salar*) smolts at two hydroelectric installations on the Exploits River, Newfoundland, Canada

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Abstract

The Exploits River is the largest river in insular Newfoundland, Canada, supporting an anadromous wild Atlantic salmon *(Salmo salar* L.*)* population of up to 30,000 returning adults annually. Since 2001, telemetry studies have been conducted at hydroelectric plants at Bishops Falls and Grand Falls-Windsor, 10 and 22 km upstream from the mouth of the river respectively, to address downstream fish passage issues. In 2001, studies were focussed on smolt passage at Bishops Falls and 35 tagged smolt were released 100-200 m above the facility from June 6 to 23 in 7 separate releases. Nineteen (19) of these fish entered the forebay while the remaining 16 fish remained in the river mainstem and passed over the dam in spillage. Fish remained in the forebay on average 14.1±3.0 hours (mean ±s.e.). Fish spent most of their time (9.0±2.1 h) in a quiet water area in the proximity of a bypass and lesser time in other locations (0.05±0.05 h in front of the trashracks; 0.3±0.3 h in the middle of the forebay; 4.5±2.1 h below the entrance gates to the forebay). Thirteen (13) fish exited the forebay through the bypass facility (reverse fishway). Three (3) fish were determined to have passed through the turbines and survived turbine passage. In 2002, 23 smolt were released 5.0 km upstream of the Grand Falls facility from June 3 to 18 in 5 separate releases. Fish took an average of 78.8±12.8 hours to reach the dam and/or power canal of the plant. Twelve (12) fish subsequently went over the dam and 11 were entrained into the power canal. Of the 12 fish that went over the dam, one went through an opening specifically intended to facilitate smolt out migration while 6 transmitters were found at a gull colony below the dam indicating apparent predation. Once in the power canal, fish moved through the canal quickly, on average 11.0±2.0 minutes, before being bypassed (n=5), passing through the turbines (n=5), or swimming out of the canal entrance (n=1). These telemetry studies have been important in elucidating the various passage routes downstream migrating Atlantic salmon smolt are using at hydroelectric facilities and are part of a continuing effort by government and industry to maintain and enhance the salmon population on the Exploits River.

Introduction

Dams are barriers to movement of migratory species, such as anadromous salmonids, that must be traversed in order to maintain the population that is spawning and rearing upstream of the barrier. Loss of smolt during downstream migration represents a population reduction in a life stage that does not allow for normal biological compensatory mechanisms to mitigate the potential population loss. Mortality at the smolt stage will adversely affect adult recruitment and hence potential yield from the stock originating from spawning and rearing areas above a hydroelectric development (Ruggles *et al*., 1993). Smolt descent in rivers is a naturally hazardous period in the life history of Atlantic salmon and the passage of falls and dams, desmoltification, and predation from other fishes, birds, and mammals are major sources of mortality for migrating juveniles that has the potential to seriously affect the sustainability and viability of salmon populations (Hvidsten and Johnsen, 1997). Understanding the potential for turbine entrainment and design and operation of fish bypasses at hydroelectric installations requires knowledge of swimming ability and behaviour, environmental cues for migration, and orientation and direction of movement. Fish have several potential passage routes as they approach and move past a hydroelectric facility. They can enter the forebay or turbine intakes (e.g. penstocks), where they can be directed to a bypass or pass through the turbines, or they can pass over the dam and/or spillways, depending on the design and operation of the power plant. A fundamental behaviour pattern of salmon smolts approaching dams is that they are surface oriented and generally follow the maximum flow patterns, therefore, fish may be more readily passed in spillage during high flow periods and may have to actively avoid entrainment during lower flows, when more of the bulk flow is directed to the power plant (Coutant and Whitney, 2002). Passage of downstream migrating juveniles has been a particularly difficult aspect of hydroelectric development to manage and efforts to divert smolts from turbines by spills or bypasses have met with varying degrees of success (U.S. Congress, 1995). Smolt must reach salt water in a defined time period or they may cease their migration and desmoltify and significant delays associated with passage of hydroelectric facilities may be important in initial smolt survival when they first encounter the sea (Ruggles, 1980). Fish guidance systems are influenced by fish behaviour and behaviours that lead to successful guidance will vary by species, fish size, physiological condition, etc. Mechanical, structural, and operational features of hydropower installations are important primary features that will influence potential for successful guidance and downstream passage. Studies are needed to relate fish behaviour and movements to hydraulic (flow direction and velocity) and other environmental cues encountered by fish as they approach a dam and enter forebays, bypasses, or turbine intakes (Coutant, 1999).

The Exploits River is the largest river in insular Newfoundland, Canada, supporting an anadromous wild Atlantic salmon population of up to 30,000 returning adults annually. Upstream fish passage facilities have been installed at several major natural and man made barriers on the river to provide access to most of the watershed. Two hydroelectric plants were developed in the early 1900s in the lower reaches of the river at Bishops Falls and Grand Falls-Windsor, 10 and 22 km upstream from the mouth of the river, respectively. In the mid-1990’s a downstream fish protection system (floating louver and bypass) was installed at Grand Falls-Windsor and the effectiveness of that system has been assessed since 1997 (Scruton *et al*., 2002b). In 2001, telemetry studies were conducted at the Bishops Falls hydroelectric plant to address entrainment into the forebay, residency in the forebay, passage routes including turbine entrainment, and potential migratory delays. This work was conducted as a precursor to a major refit of this power plant in 2002/2003, including installation of a new surface bypass system, in order to consider existing downstream migration routes in the design and operation of this new bypass. In 2002, a similar telemetry study of smolt entrainment and passage was conducted at the Grand Falls-Windsor facility, in order to provide comparable information to further improve the operations of the plant and bypass system to optimize downstream passage success. This paper reviews the results of these telemetry studies in the context of the comprehensive resolution of downstream fish passage issues on the Exploits River.

Materials and methods

Exploits River

The Exploits River is the longest river (246 km in length) and largest drainage basin (11,272 km^2) on the island of Newfoundland and has a mean annual discharge of approximately 290 m^{3}s^{-1}. The river sustains one of the largest runs of wild adult Atlantic salmon in North America which was developed through a major enhancement program including adult transfers and stocking of unfed fry throughout the drainage (Taylor and Bauld, 1973). The river was originally obstructed to upstream migration at Bishop's Falls and Grand Falls, approximately 10 and 20 km from the estuary, respectively, and several major tributaries were also obstructed, and, prior to enhancement, only 10% of the watershed was accessible and the adult run was estimated at 1600 fish (1960) (O'Connell and Bourgeois, 1987). A fishway was constructed at Bishop's Falls (1958) providing access to major tributaries and the returning adult population grew to about 16,000 fish (1985). Fish passage was subsequently provided at Grand Falls (1991) and Red Indian Lake (1989) permitting access to much of the watershed. Adult production potential, based on habitat productive capacity, was estimated at 80-100,000 fish and returns at Bishop's Falls peaked at 33,000 fish in 1996, and have averaged 22,000 over the 1990s (O'Connell *et al*., 2003).

Hydroelectric facilities, at Bishop's Falls and Grand Falls-Windsor, were installed by Abitibi Consolidated Company of Canada (ACCC) in the early 1900's to supply power to a pulp and paper mill at Grand Falls-Windsor (Fig. 1). At Grand Falls, the water supply to the generating facility enters a forebay through a series of vertical gates and then through a power canal with submerged intake gates leading to Francis turbines operating under a 'run of river' regime. Flows under normal operating regimes are 183 m^{3}s^{-1} (ranging from 160 to 210 m^{3}s^{-1}) and during the smolt run, 28.3 m^{3}s^{-1} of water is spilled over the dam through 21.3 m opening and at the north end to facilitate smolt migration ('smolt water'). Passage routes for downstream migrating smolts are: (i) over the dam, (ii) through the 'smolt' opening in the dam, (iii) through spillway gates in the dam (only during the early part of the run), (iv) into the power canal and bypassed back into the river, and (v) into the power canal but past the louver guidance system and through the turbines (Fig.2).

At Bishops Falls, the water supply to the generating facility enters a forebay through a series of

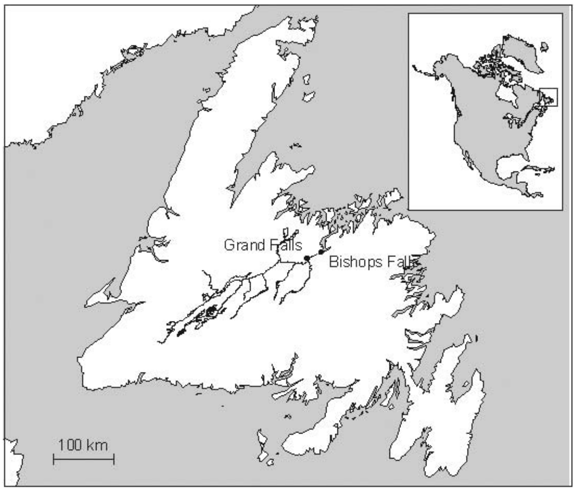

Fig. 1 – Map of the Exploits River watershed, insular Newfoundland, Canada showing the location of the Bishops Falls and Grand Falls generating stations.

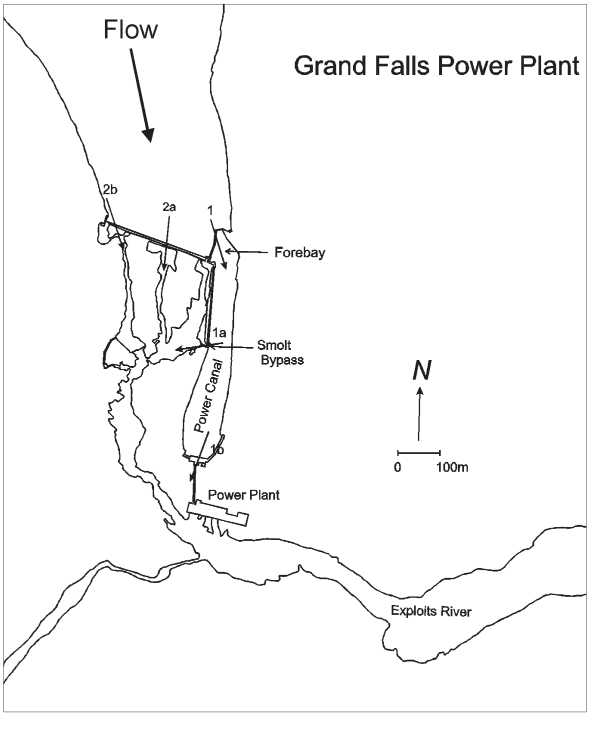

Fig. 2 – Configuration of the Grand Falls dam and power plant in the Exploits River showing the various passage alternatives for downstream migrating Atlantic salmon (*Salmo salar*) smolt. 1) entry into the forebay and power canal, 1a) turbine passage, 1b) passage through louver and bypass (reverse fishway), 2a) passage over the dam, 2b) passage over the dam through smolt water opening.

bottom opening vertical gates and then directly into the turbine intakes. During the smolt run, 28.3 $m^3s^{-1}$of spillage is provided through a 17.3 m opening on the north end of the dam to facilitate smolt migration ('smolt water'). A reverse fishway at the south end of the turbine intakes was installed as a downstream passage alternative for fish entering the forebay. Bottom opening control gates for spillage are located on the southeast end of the dam. Passage routes for downstream migrating smolts are: (i) over the dam, (ii) through the 'smolt' opening in the dam, (iii) through spillway gates in the dam (only during the early part of the run), (iv) into the forebay and bypassed back into the river through the reverse fishway, and (v) through the turbines (Fig 3).

Bishops Falls Smolt Tracking 2001

In 2001, studies were focused on downstream smolt passage at Bishops Falls and 35 radio tagged smolt were released 100-200 m above the facility from June 6 to 23, 2001. Seven separate releases, involving five fish per release, were staggered over the 17 day study period to allow maximize coverage by the fixed stations. Fish were initially captured at the fish protection system (floating louver, bypass) at the Grand Falls power canal where radio transmitters were surgically implanted. After recovery fish were transported in insulated containers to their release point.

Smolt were surgically implanted with radio transmitters (Advanced Telemetry Systems, model F1420, 7 mm in diameter, 18 mm long, 1.3 g in water) after procedures described in Scruton *et al.*

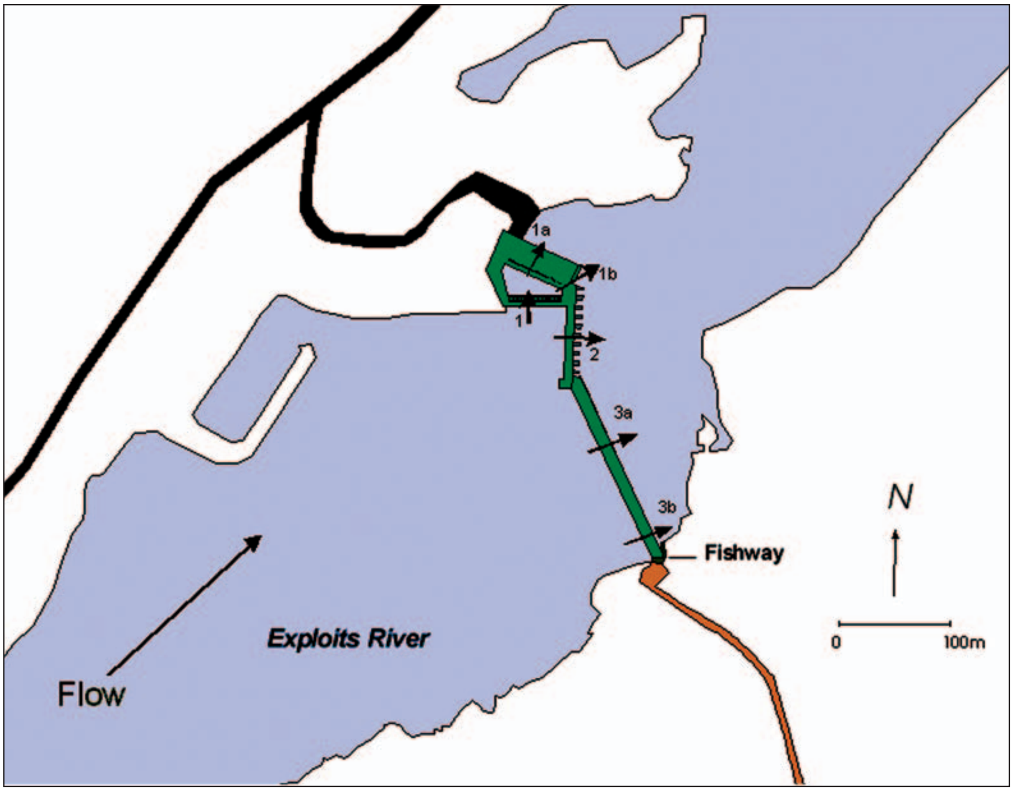

Fig. 3 – Configuration of the Bishops Falls dam and power plant in the Exploits River showing the various passage alternatives for downstream migrating Atlantic salmon (*Salmo salar*) smolt. 1) entry into the forebay, 1a) turbine passage, 1b) passage through bypass (reverse fishway), 2) passage through spillway gates, 3a) passage over the dam, 3b) passage over the dam through smolt water opening.

(2002a). Fish were anesthetized in 10 l of river water with 1-2 ml clove oil/ethanol solution as described in Anderson *et al*. (1997). After regular opercular movement had ceased and fish had lost equilibrium (approximately 2 min), fork length (FL, centimeters) and weight (WT, grams) were determined. Fish were then placed dorsal side down on foam padding which kept them moist and held them in position during surgery. A 1 cm incision was made posterior to the pelvic fin. Using an 18 G hypodermic needle, a small puncture wound was made just below and lateral to the incision, through the body cavity. The antenna of the transmitter was threaded through the body wall using the hypodermic needle. The transmitter was then inserted into the body cavity and the incision closed with 2 sutures of 4-0 Ethicon braided silk. Upon completion of surgery, fish were placed in insulated holding containers and were allowed to recover for a 12 hour recovery period.

A combination of both manual tracking and fixed stations were used to monitor fish movements. Three automatic data logging stations (Lotek Wireless Inc. SRX_400 receivers with a combination of coaxial [underwater] and Yagi antennas) were setup to monitor discrete areas in the forebay and other parts of the power plant and dam. Set up with calibration delineated 4 discrete areas in the forebay: (i) in front of the submerged entrance gates to the forebay, (ii) in the main area (middle) of the forebay, (iii) at the trash racks in front of the submerged turbine entrances, and (iv) in a quiet water area near the spillway gates and the downstream fishway (Fig. 4). Additional antennae monitored potential passage over the dam and spillways as well as turbine passage. Fixed station data were downloaded daily. Scanning rate varied by receiver and in relation to the transmitters deployed and the maximum scan time was 2 minutes at any one receiver. Manual tracking from both the river shoreline and boat, was conducted each evening after release, and opportunistically, during

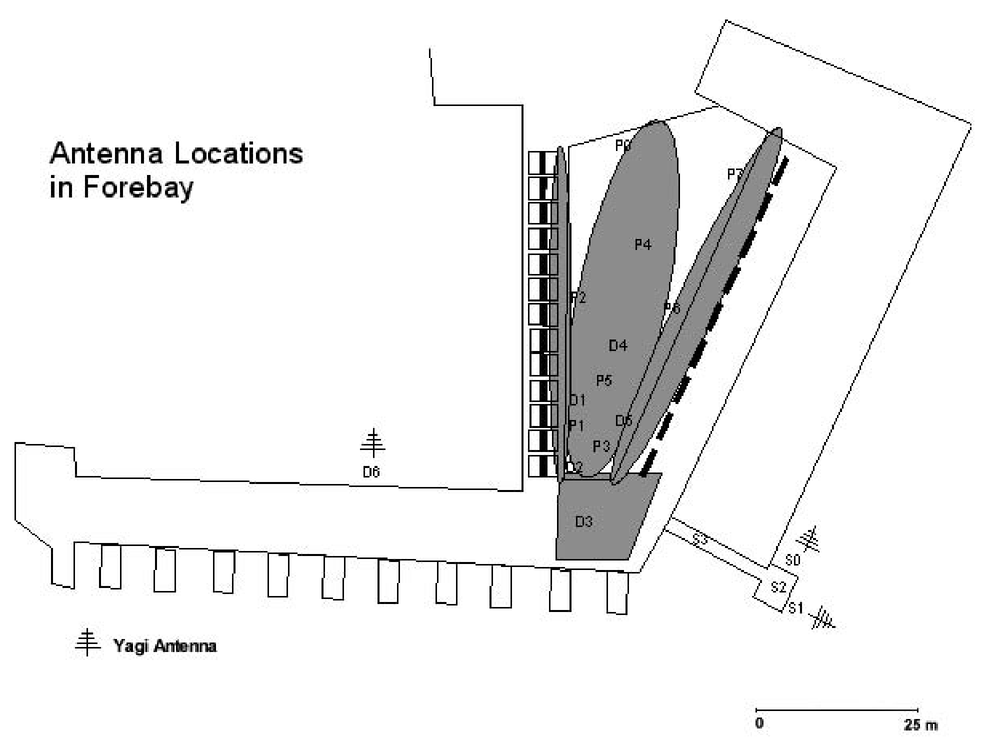

Fig. 4 – Bishops Falls forebay showing the location of coaxial and Yagi antennae and the discrete detection zones used in the fixed station telemetry monitoring of smolt movements.

daylight hours. Manual tracking was also used to locate fish and follow movement downstream after having passed through the facility to determine survival after turbine passage.

Grand Falls Smolt Tracking 2002

In 2002, studies focused on downstream smolt passage at Grand Falls and 23 radio tagged smolt were released from June 3 to 18, 2002. Five separate releases, involving three to twelve smolt per release, were staggered over the 15 day study period. Fish were captured from the fish protection system (floating louver, bypass) at the Grand Falls power canal and radio transmitters were surgically implanted as described above. After recovery fish were transported in insulated containers to their release point, approximately 5.0 km above the entrance to the Grand Falls forebay. Fish were released at 3 locations, from the right hand bank (looking upstream) (n=10), from the left hand bank (n=13), and from mid-river (n=9), to determine if release location (i.e. migration trajectory) had any influence on entrainment into the Grand Falls facility.

Again, a combination of both manual tracking and fixed stations were used to monitor fish movements. Three automatic data logging stations (Lotek Wireless Inc. SRX_400 receivers with a combination of coaxial [underwater] and Yagi antennas) were setup to monitor discrete areas along the dam, the entrance to the forebay, and the floating louver, fish handing and bypass system (Fig. 5). Fixed station data were downloaded daily. Scanning rate varied by receiver and in relation to the transmitters deployed and the maximum scan time was 30 s at any one receiver. Manual tracking, as above, was also used to track fish from their release point until detected by the fixed stations.

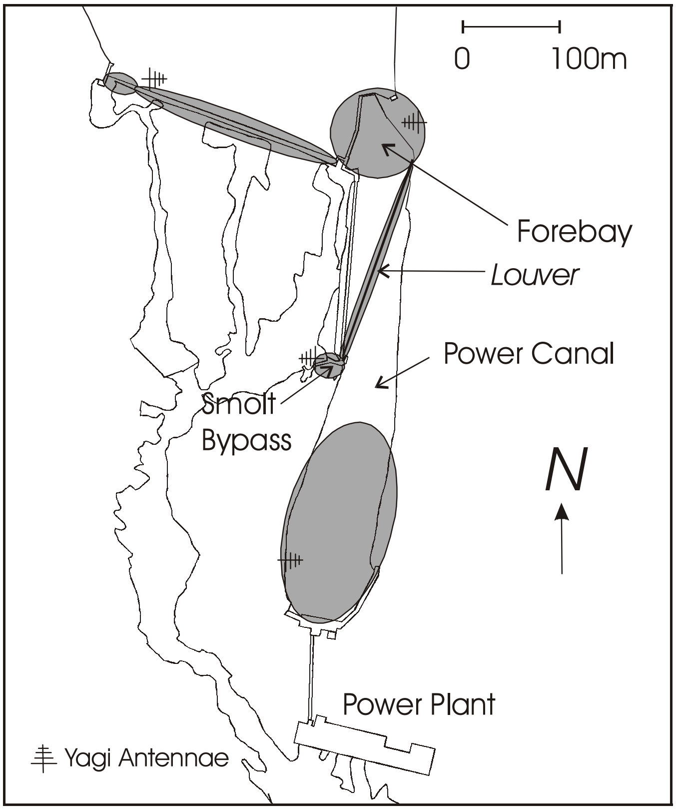

Fig. 5 – The approach to and the Grand Falls forebay and power canal showing the location of discrete detection zones used in the fixed station telemetry monitoring of smolt movements.

Results

Bishops Falls Smolt Tracking 2001

In 2001, studies on downstream smolt passage at Bishops Falls involved the release and tracking of 35 tagged smolt from June 6 to 23 in 7 separate releases. Smolt used in telemetry studies ranged in length from 144 to 233 mm (mean of 175.3, s.e.±2.99) and in weight from 30-103 g (mean of 50.4, s.e.±2.33). Nineteen (19) of these fish entered the forebay while the remaining 16 fish remained in the mainstem of the river and passed over the dam (Fig. 6). Fish remained in the forebay from 0.2 to 42.0 hours (average 14.1±3.0 hours). Fish spent most of their time, from 0.1 to 30.0 hours (average 9.0±2.1 hours) in a quiet water area in the proximity of the bypass. Fish spent a lesser time in the other locations; from 0.0 to 1.0 hours (average 0.05±0.05 hours) in front of the trashracks; from 0.0 to 5.0 hours (average 0.3±0.3 hours) in the middle of the forebay; and from 0.0 to 35.0 hours (average of 4.5±2.1 hours) below the entrance gates to the forebay. One fish was detected at the entrance gates to the forebay for a total of 102 hours, and may have been injured or dead, and the data on this fish was removed from more detailed analyses. Thirteen fish exited the forebay through the bypass facility (reverse fishway) and 3 fish were determined to have passed through the turbines. Manual tracking downstream of the power plant determined these 3 fish had survived turbine passage as fish were verified to be continuing their migration in the lower reaches. Monitoring frequency did not permit a rigorous assessment of survival of turbine passage.

Grand Falls Smolt Tracking 2002

In 2002, a total of 23 smolt were released 5.0 km upstream of the Grand Falls facility from June 3 to 18 in 5 separate releases. Smolt used in telemetry studies ranged in length from 161 to 209 mm (mean of 180.4, s.e.±1.83) and in weight from 40-77 g (mean of 50.7, s.e.±1.56). Fish took an average of 78.8±12.8 hours to reach the dam and/or power canal of the plant. Twelve (12) fish subsequently went over the dam and 11 were entrained into the power canal. Of the 12 fish that went over the dam, one went through an opening specifically intended to facilitate smolt out migration while 6 transmitters were found at a gull colony below the dam indicating predation (either active on live smolt, or passive on smolt that may have been killed during dam passage) (Fig.7). Once in the power canal, fish spent on

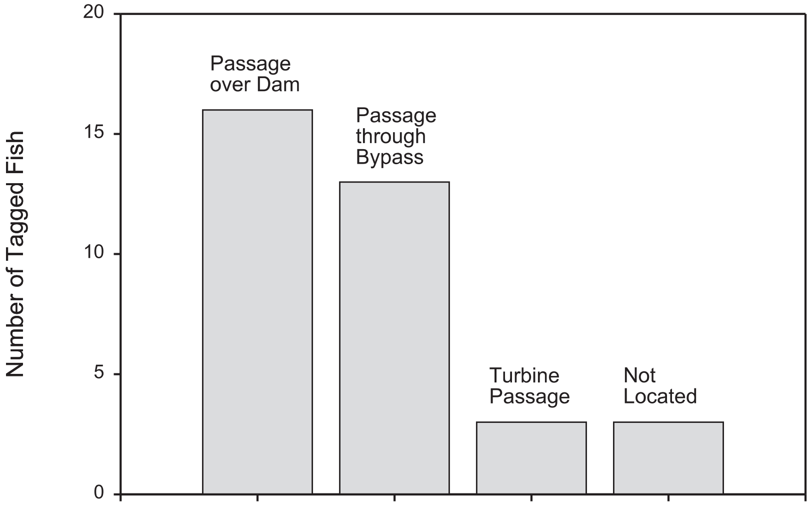

Fig. 6 – Proportion of downstream migrating Atlantic salmon (*Salmo salar*) smolt using various passage alternatives at the Bishops Falls dam and power plant in telemetry studies in 2001.

average 11.0±2.0 minutes in the canal before being bypassed (n=5), passing through the turbines (n=5), or swimming out of the canal entrance (i.e. returning to the forebay/main river; n=1).

Discussion

In the 2001 Bishops Falls study, 19 (54%) of 35 fish released entered the power plant forebay while the remaining 16 fish were deemed to have passed over the dam. Fish passing into the forebay would have to sound some 1.2 m below the water's surface to do so. Generally, many species of salmon smolt are reluctant to sound to submerged outlets at dams (Ruggles and Murray, 1983). Orientation of smolt in the upper portion of the water column will result in them having a greater likelihood of being deterred from bottom opening entrance gates or deep turbine intakes and finding alternative surface passage routes (Haro *et al*., 1998). Fish generally do not descend into the lower two-thirds of the water column in dam entrances or forebays, unless there is no alternative passage route, and several studies have demonstrated that migrating salmonids only sound to great

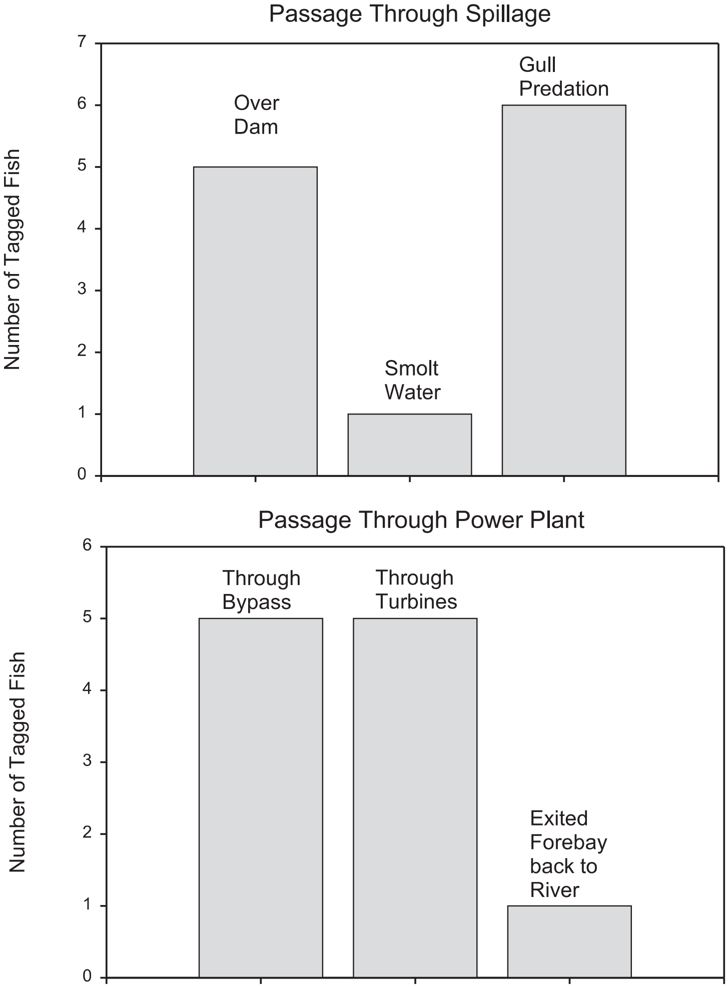

Fig. 7 – Proportion of downstream migrating Atlantic salmon (*Salmo salar*) smolt using various passage alternatives at the Grand Falls dam and power plant in telemetry studies in 2002.

depths as a last resort (Coutant and Whitney, 2002). Salmon smolts are able to sound to considerable depth to escape from reservoirs however their migration can be delayed for considerable periods (Ruggles and Murray, 1983).

Fish will use alternative pathways for downstream migration, other than turbine passage, if suitable conditions can be provided for fish to locate and use alternative routes. In both the 2001 Bishops Falls studies and the 2002 Grand Falls studies, 45% and 56% respectively, used alternative passage routes other than going through the power plant infrastructure. Atlantic salmon smolts that did enter the forebay at Bishops Falls resided in the forebay from 0.2 to 42.0 hours (average of 14 hours) and did not appear to demonstrate any significant delay in their migration. At Grand Falls in 2002, smolts spent, on average, 79 hours to traverse the 5.0 km from their release location to the power plant, however, once they were entrained into the forebay and power canal, took an average of 11.0 minutes to be bypassed. Salmon smolt migration is often interrupted once fish reached impounded waters associated with a hydroelectric dam and the general pattern is also for smolt to be delayed in the surface waters of forebays (e.g. Giorgi *et al*., 1988). The time taken by smolts to reach Grand Falls power plant, from release, suggest they may have been delayed owing to an impoundment associated with Goodyear's Dam, approximately 3.5 km above the power plant. Once fish passed Goodyear's dam they arrived at the Grand Falls power plant very quickly. Atlantic salmon smolt can also be delayed at bypass systems and have been observed to gather in large numbers before being bypassed *en mass* as a school (Nettles and Gloss, 1987). This appears to be the situation for fish that entered the Bishops Falls forebay in 2001. Once in the forebay, fish appeared to locate the quiet water area in front of the smolt bypass locations (reverse fishway) and large accumulations of smolt were observed in this area. Tagged smolt resided in this area for 9.0 hours on average before 13 of them were subsequently bypassed, mostly at night.

Forebay bathymetry often results in turbulent flow conditions and will determine smolt distribution, both vertically and horizontally, under these conditions. Conditions in the Bishops Falls forebay are extremely turbulent and, during the peak smolt run, fish were observed to be buffeted in the standing waves in the forebay and, on occasion, have been seen to be tossed into the air. Fish spent very little time in the highly turbulent areas in front of the entrance gates, in the middle of the forebay and in front of the trash racks and were able to locate and remain in the quiet water areas of the forebay. Despite the apparent disorientation of smolts related to water turbulence at the Bishops Falls forebay, the majority of the tagged fish were able to locate and utilize the downstream bypass system. Of the three fish that went through the turbines, they spent more time in the forebay (average of 18.3 hours), and considerable time (average of 10.6 hours) in the quiet water area, before turbine entrainment. It is unclear why these fish selected turbine passage and were unable to find and use the downstream bypass.

The location of fish as they approach hydro power installations, in relation to possible passage through spillage routes, is important in the context of overall passage of hydroelectric facilities, and the particular physical configuration of power plants and spillways will play a large role in the overall effectiveness of spillage in passage. A large proportion of the tagged smolts at Bishops Falls and Grand Falls were not entrained into the power plant's infrastructure (i.e. forebays and power canal) and utilized spillage over the dams as the preferred downstream migration route. At both facilities, water is released throughout the smolt run, in addition to openings in the dams on the opposite side of the river from the power plants, specifically for the purpose of encouraging smolt to use these passage routes.

At Grand Falls, half of the fish that went over the dam (6 of 12) were predated upon by herring gulls (*Larus argentatus*). A large gull colony has been established at Grand Falls presumably, at least in part, because of food supply from migrating smolts during the nesting period. Additionally, the configuration of Grand Falls, with most water spilling on top of rock outcrops, would result in a high natural rate of mortality. Stress associated with tagging, or possibly the obvious appearance of the antennae, could also have made tagged fish more susceptible to predation. If rates of mortality and/or predation are a true indication mortality associated with dam passage, the preferred passage route in terms of overall survival may be through entrainment into the power canal, and subsequent bypass back into the river from the louver protection scheme as previous studies have determined a bypass efficiency up to 75% (Scruton *et al.*, 2002b). This observation may result in modifying the current operation of the facility, which spills water during the smolt run to encourage fish to use alternative passage routes, to increasing entrainment into the power canal for subsequent bypass. The apparent high rate of mortality and/or predation is of importance and may warrant additional study.

Migration delays can potentially cause smolts to de-smoltify and reside in the river for an additional year, could delay there entrance into the ocean resulting in exposure to unfavourable environmental conditions, can result in depletion of energy reserves, and could expose fish to increased rates of predation (Ruggles, 1980). Reductions in the delay that smolt experience as they enter forebays and are bypassed by hydroelectric projects is considered a critical element of enhancing fish passage and survival (Haro *et al.*, 1998). The telemetry studies at Bishops Falls in 2001 and Grand Falls in 2002 suggest no major migration delays associated with passage of the two facilities. Further, school integrity during downstream migration and passage of hydroelectric facilities will reduce stress and predation risk (Haro *et al.*, 1998) and downstream passage can be inhibited by obstacles that prevent fish from maintaining schools (Bakshtansky *et al.*, 1993). Accumulation of smolt, through schooling behaviour, may be playing a role in the successful bypass of fish entering the Bishops Falls forebay.

The telemetry studies conducted at Bishops Falls and Grand Falls, in 2001 and 2002 respectively, have been important in elucidating the various passage routes downstream migrating Atlantic salmon smolt are using at hydroelectric facilities on the Exploits River. These studies, in addition to assessing the effectiveness of existing fish protection schemes at these facilities, will be important in determining the overall successful downstream passage of smolts from the watershed. Additionally, with a knowledge of the utilization of the various passage alternatives, the operation of the two facilities, including discretionary spillage during the smolt migration period, can be optimized to improve overall successful passage of hydroelectric facilities. These studies are part of a continuing effort by government (Canadian Department of Fisheries and Oceans) and industry (Abitibi Consolidated Company of Canada) to maintain and enhance the salmon population on the Exploits River and to minimize the impacts of hydroelectric development on migrating fish.

Acknowledgements

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Insight into the homing behaviour of the dusky grouper (*Epinephelus marginatus* Lowe, 1834) around the island of Ustica, Italy

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Key words: *Epinephelus marginatus*, juvenile/pre-adult migrations, homing behaviour, hydroacoustic telemetry, marine protected areas.

Abstract

Knowledge about the migratory behaviour of a threatened nearshore fish, *Epinephelus marginatus*, is critical for the effective conservation and management of the species, particularly in terms of designing and regulating Marine Protected Areas (MPAs). Homing and site fidelity of adult dusky groupers (2-17 kg) were already documented using a hydroacoustic telemetry study. In addition, site fidelity of juveniles (less than 1 kg) was also demonstrated using a wireless communication system combined with manual tracking events. However, the life stage at which homing behaviour becomes established remains unknown, as well as the duration of the home memory when the fish is kept far (e.g. in captivity) and then re-introduced in its environment. Indeed, these aspects are particularly relevant when re-stocking is envisaged as a possible management option. The objective of our study was to determine the homing and migratory behaviour of two age categories of the dusky grouper. Four juveniles (343-679 g) and three pre-adult individuals (1350-1450 g) were captured in a no-take zone of a marine protected area and outfitted with acoustic transmitters. Juveniles were released within two months after capture, while the pre-adults were kept in captivity for about 15 months. The releasing sites for both groups were about 5 km far from the capture site. One juvenile precisely homed within four days, other two were found moving towards the capture site and the fourth one disappeared. Among the pre-adult groupers, two fish were remained in the vicinity of the release site for two successive months, while the third individual disappeared few days after being released. These preliminary results suggest that homing behaviour is likely established in juvenile dusky groupers and prolonged captivity may affect homing ability.

Introduction

Over the past two decades Marine Protected Areas (MPAs) have been established worldwide for species, habitat and biodiversity conservation (e.g. Agardy, 1997). More recently, MPAs have also been proposed as a valuable tool for mitigating the effects of mismanagement of fishery resource (e.g. Lauck *et al*., 1998) and for providing additional benefits to those obtained from simple fishing effort control (Apostolaki *et al*., 2002). The benefits of MPAs are related to their ability to act as harvesting refugia and sources of recruits to fisheries (Nowlis and Roberts, 1999), although their effectiveness mainly relies upon size, location, designing (i.e. subdivision in zones with different degree of protection), (Côté *et al*., 2001), habitat quality (Rodwell *et al*., 2003) and movement pattern of the species. For example, species typically exhibiting small home ranges may be well protected by small harvest refugia (Holland *et al*., 1993). Thus, studies on movement dynamics of overexploited, long-living and top-predator species, such as rockfishes (e.g. Soh *et al*., 2000; Starr *et al*., 2002) and groupers (Zeller, 1998; Lembo *et al*., 1999a; Bolden, 2000; Sala *et al*., 2001; Whaylen *et al*., 2004), have increased in the last years, focusing on the implication of managing MPAs targeting these fish.

Hydroacoustic telemetry proved to be a powerful technique for generating complete information on individual fish movements over time, including in and out protected areas, thus providing data on home range and site fidelity that are crucial for species conservation and designing/management of MPAs (O'Dor *et al*., 2001).

Along the Mediterranean coasts, several MPAs have been established and the dusky grouper (*Epinephelus marginatus*, Lowe, 1834) has been considereded the key-species. (e.g. Ustica Island, Italy; Medes Islands, Spain; Straits of Bonifacio, France). Knowledge about the movement dynamics of this threatened nearshore fish is critical for the effective conservation and management of the species, particularly as it applies to the regulation of marine reserves.

Homing and site fidelity of adult dusky groupers (2-17 kg) were documented using a hydroacoustic telemetry study (Lembo *et al*., 1999a; 1999b). In addition, site fidelity of juveniles (less than 1 kg) was also demonstrated using a wireless communication system combined with manual tracking exercises (Lembo *et al*., 2002). However, the life stage at which homing behaviour becomes established remains unknown, as well as the duration of the homing behavioiur when the fish are kept in captivity and then re-introduced. These aspects are particularly relevant to the restoration of the species through re-stocking and re-location events within MPAs.

To address these issues, preliminary experiments were conducted within a MPA on the island of Ustica (Italy) using two age groups of the dusky grouper: four juveniles (343-679 g) and three pre-adult specimens (1350-1450 g), to determine their homing and migratory behaviour.

Materials and methods

Study area

The study was conducted in Ustica, a volcanic island (area 8.7 km^2 and circumference 9 km) situated in the Mediterranean Sea, 60 km north off the Sicilian coast of Italy (38° 42' N, 13° 10' E) (Fig. 1), where a MPA has been established since 1986. Coastline is rocky and uneven and the core area of the marine reserve (A zone), which is fully protected, is located on the northwest side of the island. It stretches ca. 1.5 km along the coastline and ca. 400 m out from the shore, covering an area of ca. 0.5 km^2. In the B zone commercial fishing is permitted only with special authorisation, while in the C Zone fishing is permitted with some limitations.

Tagging and tracking

Two age categories: four juveniles (mean total length = 31.1±3.5 cm; mean total weight = 470.5±147.7 g, Table 1) and three pre-adult specimens (mean total length = 43.7±1.5 cm; mean total weight = 1400±50 g, Table 1), the former for homing experiment and the latter for testing home memory were used.

The transmitters (CAFT 8_6, Lotek Wireless, Inc., Canada) used for the juveniles were cylindrical in shape and operated at 76.8 kHz with a pulse rate of 5 s. Power output, as specified by the manufacturer, was 148 dB and nominal longevity 35 days. Transmitter length was 38.0 mm, diameter 8.5 mm and the weight in air and salt water was 5.0 and 3.3 g, respectively.

Also the transmitters employed for pre-adult dusky groupers operated at 76.8 kHz (CAFT 16_4s, 12 hours on, 12 hours off), but pulse rate was 10 s, power output 161 dB and nominal longevity 270 days. Transmitter length, diameter, weight in air and salt water were 62 mm, 16 mm, 29 and 14 g, respectively. All the transmitters employed a digital coding scheme.

The dusky groupers were captured by hook and line in the no take area (A zone) of the MPA at Ustica (at 5-7 m depth the juveniles and at 5-12 m depth the pre-adults) and surgically implanted with acoustic transmitters, following the technique reported in Økland *et al*. (1999).

The fish of the juvenile group were kept in tanks almost 2 months between catch and surgery, and 1-4 days between surgery and release (Table 1) that took place about 5 km far from the capture site at 9 m depth. Pre-adult dusky groupers were kept in captivity at COISPA Experimental Station, based on the mainland, for about 15 months. The three dusky groupers were transported (about 20 hours trip duration) using a 400 l tank continuously supplied with

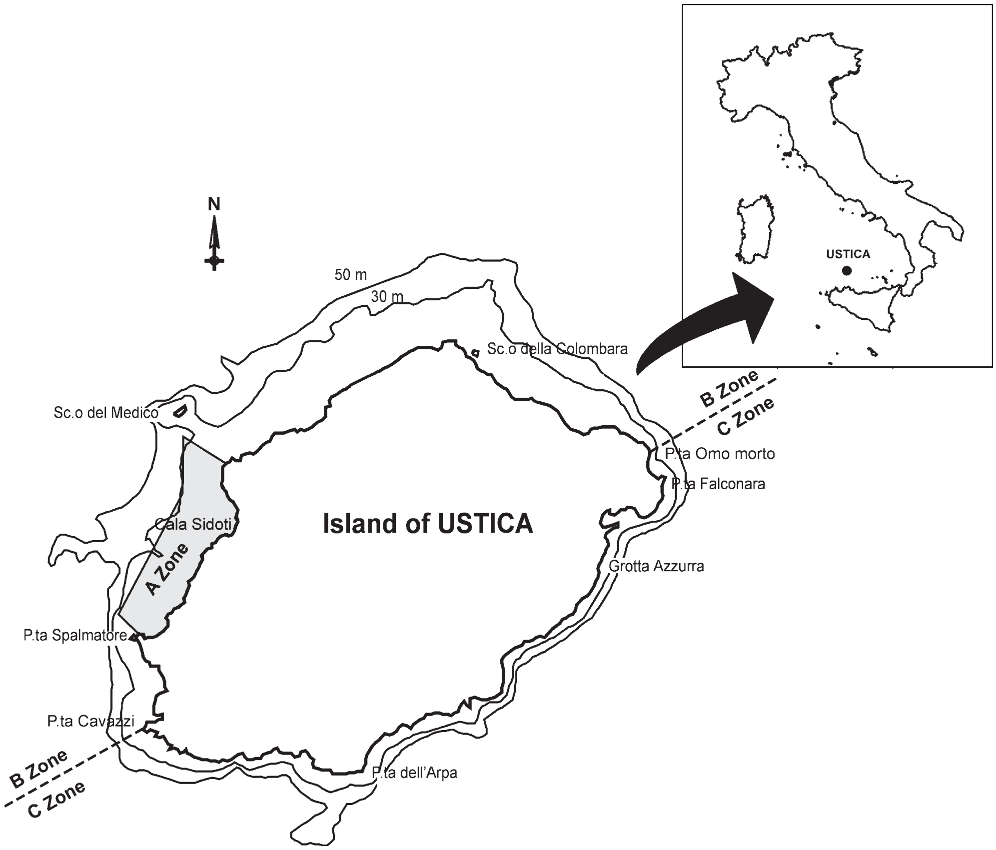

Fig. 1 – Ustica Island depicting areas with different degrees of protection (A zone=core area of the MPA-all activities forbidden; B zone=commercial fishing permitted only with special authorisation; C Zone=fishing permitted with some limitations).

Table 1 – Transmitter code, fish length and weight, transmitter/body weight ratio (weight of transmitter in air), capture, surgery and releasing dates of the two groups of dusky grouper used for the homing tests.

	Transmitter Code	Total length (cm)	Total weight (g)	Transmitter /body weight ratio	Capture date	Surgery Date	Releasing Date
Group 1 juveniles	5	36.0	679	0.74	06.06.01	29.07.01	30.07.01
	6	29.5	395	1.27	07.06.01	29.07.01	30.07.01
	11	28.0	343	1.46	11.06.01	29.07.01	03.08.01
	12	31.0	465	1.08	10.06.01	29.07.01	03.08.01
Group 2 pre-adults	154	42	1350	1.86*	23.10.00	31.01.02	01.02.02
	161	45	1400	1.07*	23.10.00	31.01.02	01.02.02
	167	44	1450	1.37*	30.10.00	31.01.02	01.02.02

*calculated on the final weight of 1570 (code 154), 2700 (code 161) and 2120 (code 167) g.

oxygen. When at the rearing facilities, the fish were maintained at density of 4-5 kg$(m^3)^{-1}$, water renewal of 5-6 volumes(day^{-1}), natural photoperiod and fed fresh food (mainly cephalopods) *ad libitum*. The fish growth was monitored and the weight before releasing was 1570, 2700, 2120 g for the fish code 154, 161 and 167 (Table 1). Thus their gain in weight was respectively 15, 92 and 46%. Once again at Ustica the fish were implanted with acoustic transmitter and released about 5 km far from the capture site at 16 m depth.

Manual tracking of juveniles was carried out from a boat during daylight in the period 1-9 and 23-28 August 2001. Tracking of pre-adults was conducted on the following dates: 2, 7, 8, 9, 10 February; 1-2 March, 20-23 April, 20-22 May and from 29 June to 4 July 2002. A receiver (Lotek SRX_400A with W5 CODE_LOG software), an ultrasonic upconverter to radio signals (Lotek UUC-142) and an omni-directional hydrophone (Lotek HPA-D-2) were used. Tracking accuracy was estimated as the mean distance between the exact position of a reference transmitter (determined by GPS Model: Garmin 12 XL; precision ±5 m) and the position determined by a naive tracker during six trials. The accuracy of positioning, for the same person that conducted manual trackings, was 18 m (sd=4.6; C.V.=25.6%).

Results

One juvenile dusky grouper (code 5) precisely homed within four days after releasing (August 3, 2001), covering a distance of 5119 m, calculated as shortest route between the capture and releasing site (Fig. 2). During the subsequent 6 days (4÷9 August, 2001) this individual moved on average 63±14 m from the capture site in a depth range of 7-14 m. The second fish (code 6) was found 2080 m

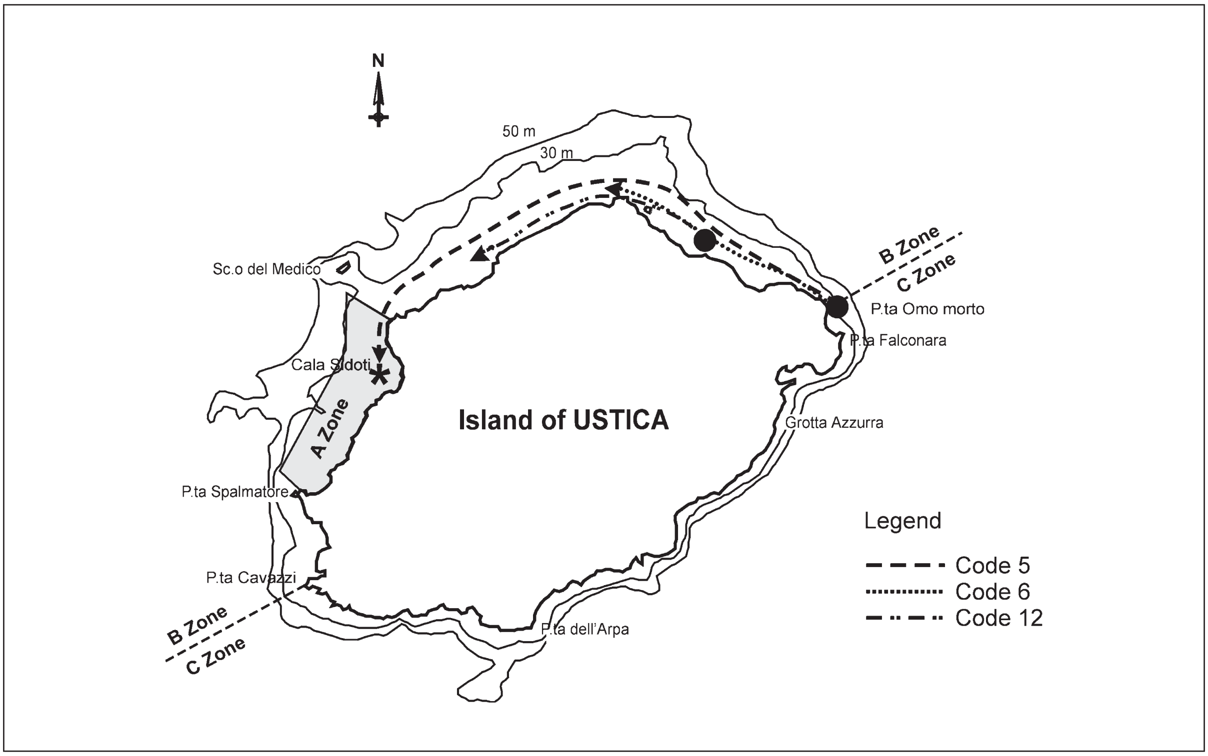

Fig. 2 – Movements of the fish code 5, 6 and 12 (*) Capture site and releasing sites (●) are indicated. The dotted lines represent the possible shortest routes followed by the fish.

far from the releasing site after 24 days at liberty (23 August, 2001) and it moved on average 59±17 m in the following 5 days (24÷28 August, 2001) in a depth range of 15-17 m. The third juvenile (code 12) showed a displacement of 767 m two days after releasing (5 August, 2001) and travelled 1000 m further on the 3rd day, while in the successive 3 days (7÷9 August, 2001) it moved on average 63±15 m in a depth range of 8-14 m. At the end of August we could no longer locate the individual. The fourth fish (code 11) never was found after release. All tracked fish moved north-westward direction from the releasing to the capture site (Fig. 2).

Among the dusky groupers of the second group, fish were located 50 m (code 154), 36 m (code 161) and 56 m (code 167) from the releasing site few hours after they were at liberty. In the following monthly tracking occasions, from 2 February to 22 May 2002, the fish code 167 was found on average 164±20 m from the releasing site in a depth range of 7-19 m, while the fish code 161 was localised in the range of 995±22 m (9-19 m depth) from the releasing site. This fish disappeared from the tracking on April 2002, while the former was no more localised from the end of June 2002, when the tracking was conducted at a fine scale around the Island perimeter. The fish code 154 disappeared in the week following the release.

Discussion

The results obtained in the present study, although preliminary due to the limited number of individuals and tracking occasions, suggest that homing is already established in juvenile dusky groupers and that prolonged captivity may affect home memory. The outcomes achieved so far evidenced that one juvenile dusky grouper (weight: 679 g, code 5) precisely homed within four days at liberty, after a short-term captivity of about 9 weeks. This behaviour is very similar to that of adult dusky groupers (2-17 kg; adulthood approximated by the lowest limit of the size at first maturity) returned within 3-6 days from the core area of the MPA (releasing place) to their sites of capture, after a short-term captivity (1-7 wks) (Lembo *et al*., 1999a; 1999b). Also the travelled distance (5119 m) is comparable to the longer route estimated for adults (5904 m; unpublished data). In the days after releasing the juvenile dusky grouper showed limited displacements (average: 63±14 m) and a preference for shallower waters (7-14 m), as expected on the basis of the site fidelity behaviour, characterized by small scale movements (9-93 m) at early life stages (113 g) (Lembo *et al*., 2002), and from the nearshore distribution of younger fish (e.g. Lo Bianco, 1909).

Very similar range of restricted daily movements in shallower water was also observed for the other two fish (weight 395 g, code 6; weight 465 g, code 12) located during manual tracking exercises. These juveniles, however, did not show the same precise homing behaviour of the fish code 5. They travelled toward the core area of marine reserve in the days after releasing, but never reached their site of capture, at least during our last monitoring period. Observations were limited by operational conditions due to a number of factors, i.e. the longevity of transmitters, the signal strength compared to the area to be explored during the fish searching, and the ambient noise (e.g. rocky bottom, breaking waves and air bubbles in the water; Stasko and Pincock, 1977). The fate of the fourth fish (weight 343 g, code 11) is unknown but maybe due to its subsequent death in a cave where it would not be possible to receive a signal from the transmitter. (Lembo *et al*., 1999a).

Two of the pre-adults fish that experienced prolonged captivity (codes 161 and 167) never came back to the capture site in the core zone of the MPA, but remained rather close (164±20 m) or bit far (995±22 m) from the releasing site, at least within 2-3 months at liberty. This behaviour is contrasting with the previous observations on the homing of adults occurring in few days (Lembo *et al*., 1999b), thus the captivity could have affected the home memory. Additional tests with a higher number of fish and longer monitoring time are though necessary to confirm this outcome. The fate of these two fish after 2-3 months is unknown like that of the fish code 154, soon disappeared probably as consequence of capture.

The behavioural pattern of dusky groupers, characterised by homing associated with site fidelity, makes this species particularly fragile and susceptible of localised stock depletion. In the Ustica MPA visual census estimates of dusky grouper population (Vacchi *et al*., 1999) reported higher abundance of 21-30 cm size class individuals in the core area of the reserve, while density of smaller fish among the zones was comparable. This result would imply that the shallow rocky shores of all the three zones of the MPA are suitable for the post-settlement phase of early juveniles, having similar potential of recruitment. Conversely diverse fish density among zones might be a consequence of fishery exploitation. Effects of protection on dusky grouper have been also observed in the Cabrera Arcipelago National Park, where fish density, mean and modal sizes resulted higher than in adjacent areas open to the fishery (Reñones *et al*., 1999).

At our current state of knowledge, the homing behaviour and site fidelity of dusky grouper suggest that only the proportion of the population (both juveniles and adults) resident in the core of the MPA at Ustica could be considered protected by the no-take zone. Thus, the effect of reserve on the adjacent areas may only related to the larval dispersal or, eventually, to the occurrence of spawning migrations (not yet proved) around the Island. Re-stocking using individuals in the range size of 0.3-17 kg cannot thus be viewed as an effective management option for stock restoration, unless home memory of re-located individuals is affected by prolonged captivity.

Further investigations are however necessary to confirm the findings of this study as well as to clarify the mechanisms of homing.

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Upstream migration of Atlantic salmon in three regulated rivers

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Key words: *Salmo salar*, hydropower development, power station, residual flow, artificial freshets, radio telemetry.

Abstract

Atlantic salmon (*Salmo salar* L.) were studied during their upstream migration in three Norwegian regulated rivers; the Rivers Mandalselva, Nidelva and Orkla (mean annual water discharge 88, 123 and 71 m^3xs^{-1}, respectively). A total of 169 salmon (body length 51-108 cm) were radio tagged during 1996-2002. The studies were focussed on migration past power station outlets, residual flow stretches (6, 2.6 and 22 km long, respectively), over dams and weirs and on the effects of artificial freshets. The salmon were delayed at power station outlets. The behaviour at the outlets seemed dependent on water discharge and design of the outlet. The salmon were further delayed by low water discharge (3-5 m^3s^{-1}) and a number of weirs and dams on the residual flow stretch in the Rivers Nidelva and Mandalselva. Some salmon even reversed direction and migrated downstream again after entering the residual flow stretches, probably due to confusion by the much lower water discharge than in the river below the power station outlet. In contrast, the higher residual flow in the River Orkla (10-20 m^3s^{-1}) did not seem to delay the upstream migration, although the dam at the power station intake did. The studies showed that even dams and weirs that seemed not physically difficult for salmon to pass acted like migration barriers. Positive effects on the upstream migration by artificial freshets were found in the River Mandalselva one of the years, but not in the River Orkla (artificial freshets were not studied in the River Nidelva). However, the migration speeds in the River Mandalselva were so low, and the movements generally so erratic, that the importance of the freshets in stimulating the salmon to pass the residual flow stretch was insignificant.

Introduction

The installation of hydroelectric power stations on rivers may hinder or harm migrating salmonids. Downstream migrating smolts are reported to suffer mortality when passing through dams or turbines (Raymond, 1988; Hvidsten and Johnsen, 1997). Upstream migration to the spawning grounds may be affected by altered water discharges, dams, weirs, fish passages and other migration barriers (Webb, 1990; Laine *et al.*, 2002; Karppinen *et al.*, 2002). Outflows from hydropower stations may also attract fish and delay the upstream migration (Andrew and Geen, 1960; Brayshaw, 1967; Arnekleiv and Kraabøl, 1996).

Water discharge is the factor most frequently reported to control the upstream migration of salmonids (Banks, 1969; Jonsson, 1991). Water discharge appears to be an important factor stimulating adult Atlantic salmon (*Salmo salar* L.) to enter rivers from the sea (e.g. Huntsman, 1948; Saunders, 1960; Potter, 1988; Smith *et al.*, 1994). Upstream migration in rivers also appears to be stimulated by elevated flow (e.g. Huntsman, 1948; Hayes, 1953; Dunkley and Shearer, 1982; Baglinière *et al.*, 1990). However, the relationship between physical factors and migration is complex, and many other factors may also affect the migration (Banks, 1969;

Jonsson, 1991). In regulated rivers with possibilities of controlling the water discharge, artificial freshets may be used to stimulate the upstream migration of Atlantic salmon (Huntsman, 1948; Hayes, 1953; Banks, 1969). However, little is known about the effects of different water discharges and duration of such freshets on migration.

The aim of this paper is to present and synthesise results from studies of upstream migration of radio tagged Atlantic salmon in three Norwegian regulated rivers; with focus on power station outlets, residual flow stretches, dams and weirs and on the effects of artificial freshets. The purpose is to determine factors important for the passage of salmon past hydropower installations and affected river stretches.

Materials and methods

Study area

Atlantic salmon were studied during their upstream migration past power stations in the Rivers Mandalselva, Nidelva and Orkla (Fig. 1). The power stations are similar in that they have water intake just above a dam in the main river and the outlet in the main river some km downstream (Fig. 2). The river stretch between the intake and the outlet (residual flow stretch) has a reduced water discharge. The rivers differ in mean annual water discharge, minimum discharge in residual flow stretch, discharge of artificial freshets, number of weirs/dams in the residual flow stretch and origin of the salmon (Table 1).

The fish populations in the Rivers Mandalselva and Nidelva are negatively affected by acid precipitation. The native Atlantic salmon populations are extinct, and the Atlantic salmon entering these rivers during the 90s were non-native, mainly originating from neighbouring rivers and salmon farm escapes. (The River Mandalselva is currently limed and a salmon population being re-established.) The River Orkla has a native salmon population. The rivers and power stations are described in further detail in Hvidsten (1993), Thorstad and Heggberget (1998) and Thorstad *et al*. (2003).

Capture and tagging of fish

A total of 169 Atlantic salmon were captured and radio tagged during 1996-2002 (Table 1). In the River Mandalselva, the salmon were captured in a fish passage and released in the lower part of the residual flow stretch, just above the tunnel outlet. In the River Nidelva, the fish were captured in bag nets and released 2 km downstream from the power station outlet, or collected in the fish passage at the dam and transported downstream to the same release site. No differences were found between salmon collected at the dam and salmon captured in bag nets in migratory speeds or behaviour (Thorstad *et al*., 2003). In the River Orkla, the fish were captured by hook and line and released in the pool downstream the power station outlet. Ideally, the fish should be captured in the sea outside the river mouth for studies of upstream migration, since capture in the river may disturb the migration pattern. However, resources for capture in the sea were not available for these studies, and fish were caught in bag nets in the river or collected from fish ways, which are also gentle catch methods. In the River Orkla, where there is no fish ways (and no bag nets available), the fish had to be captured by hook and line. In all three rivers, the fish were either tagged and released immediately after captured or kept for up to 12 days (most of the fish less than six days) in a net pen or wooden boxes until tagging and release. This was done to standardise release dates for groups of fish. Negative effects of keeping fish like this is not known.

Radio transmitters (Model 2040 or 2120, Advanced Telemetry Systems, ATS) were externally attached to the fish below the dorsal fin, as described in Økland *et al*. (2001). The transmitters had weight in air of 10-11 g and weight in water of 6-8 g. Swimming performance of similarly sized salmon was not affected by such transmitters in laboratory trials (Thorstad *et al*., 2000). To recognise individual fish, each radio tag had a unique combination of frequency and pulse rate.

Recording of the fish after release

During upstream migration, the fish were positioned by manual tracking (within ± 250 m or less, receiver model R2100, ATS) every third day in the

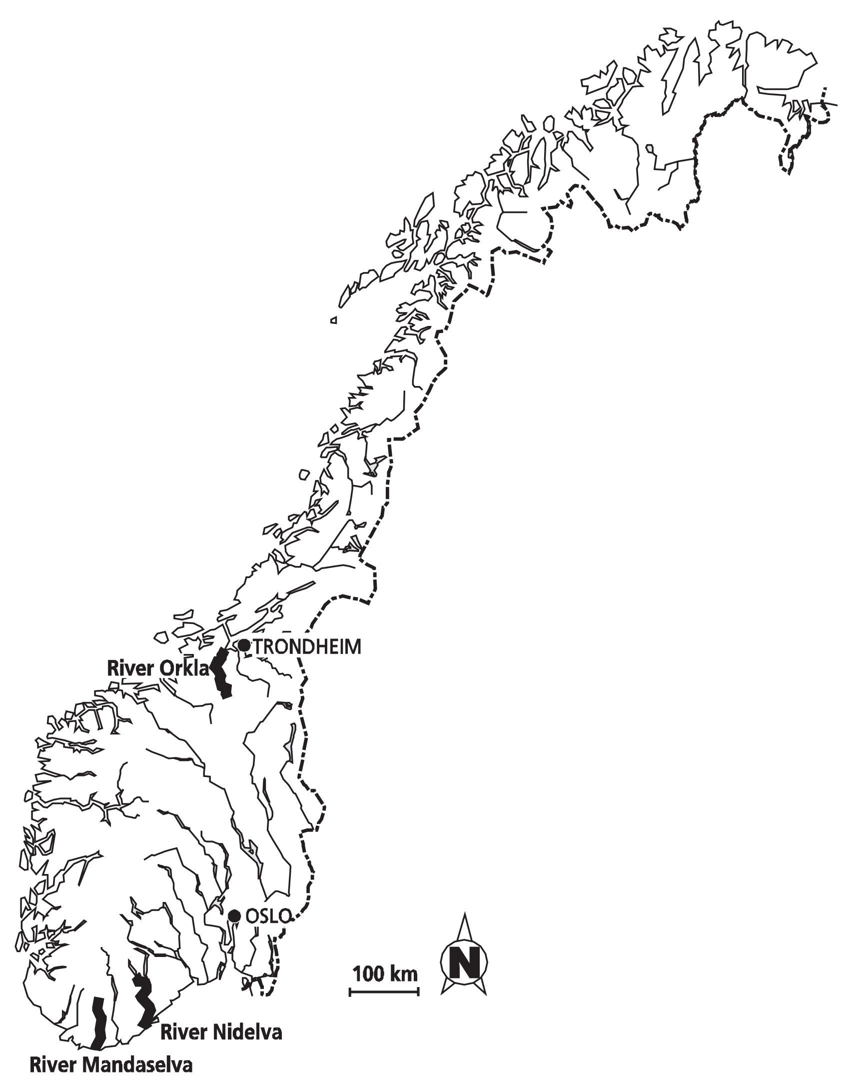

Fig. 1 – Map of Norway showing the Rivers Orkla, Nidelva and Mandalselva.

River Mandalselva and in the River Nidelva in 1999, every forth day in the River Nidelva in 1997 and every second day in the River Orkla. After the upstream migration period, the fish were tracked less often, but after standardised tracking schemes, until December or January. During artificial freshets in the Rivers Mandalselva and Orkla, the fish were located just prior to every freshet, twice a day during the freshets (morning and evening) and the morning after the freshets.

In the River Mandalselva in 1996, a data logger (DCC II, ATS) was installed at two of the weirs locally considered as migration barriers to continuously and automatically record tagged fish in these areas. In the River Nidelva, a data logger was installed at the tunnel outlet both years. A multiplex (ATS) connected to the DCC II provided the ability to automatically select and monitor four antennae separately. Antenna 1 covered the area downstream the tunnel outlet, antenna 2 the area outside the out-

Table 1 – Information on studies of radio tagged salmon past Laudal power station in the River Mandalselva, Rygene power station in the River Nidelva and Svorkmo power station in the River Orkla. Information on water discharges is given for the study periods, except mean annual water discharge.

	River Mandalselva	River Nidelva	River Orkla
Mean annual water discharge (m^3s^{-1})	88	123	71
Minimum water discharge in residual flow stretch (m^3s^{-1})	3	3-5	10-20
Water discharge through power station (m^3s^{-1})	0-110	36-176	0-60
Length of residual flow stretch (km)	6	2,6	22
Number of weirs/dams on residual flow stretch	12	4	1
Screen to prevent fish from entering the power station tunnel	yes	no	yes
Study period	1996 and 1997	1997 and 1999	2002
Number of salmon tagged	76	59	34
Origin of salmon	non-native	non-native	native
Body size of tagged salmon (cm)	51-96	52-108	58-108
Catch method	fish trap	bag net and fish way	angling
Period when tagged salmon were released	9 Aug-18 Sept	21 Aug-2 Oct	15 Jun-27 Jul
Studies carried out at power station outlet	no	yes	yes
Studies carried out in residual flow stretch	yes	yes	yes
Studies on artificial freshets	yes	no	yes
Water discharge of artificial freshets (m^3s^{-1})	8-13	-	23-30
Water discharge in residual flow stretch prior to artificial freshets (m^3s^{-1})	3	-	10-21
Duration of artificial freshets (h)	8-48	-	6-15

let, antenna 3 (underwater antenna) a small area just outside the outlet, and antenna 4 the area upstream the outlet. It was thus possible to record when fish stayed outside the outlet, or when they entered the tunnel and the residual flow stretch (see Thorstad *et al*. 2003). In the River Orkla, a data logger was installed at the power station outlet and at the dam at the power station intake.

Study design

In the River Mandalselva, migration in the residual flow stretch (3 m^3s^{-1}) and further upstream, and the effects of artificial freshets in the residual flow stretch, were studied for two years (Table 1). The design of the dam limited the maximum rate at which water could be released to 13 m^3s^{-1}. Six different freshets were released in 1996 (Thorstad and Heggberget, 1998), and two similar freshets in 1997 (each freshet consisted of increased water discharge to 13 m^3s^{-1} in two following days from 8:30 to 20:30 hours).

In the River Nidelva, migration past the power station outlet and in the residual flow stretch was studied for two years; one year with residual discharge of 3 m^3s^{-1}, and the following year of 5 m^3s^{-1}, to see if increased discharge stimulated the migration (Table 1).

In the River Orkla, migration past the power station outlet, in the residual flow stretch and further upstream was studied for one year (Table 1). The effects of artificial freshets in stimulating salmon to pass the power station outlet and residual flow stretch were studied during four freshets (lasting from 6 to 15 hours, with water discharge of 23-30 m^3s^{-1}, Table 1). Two of the freshets were released in connection with rain and a natural increase in water discharge. The residual discharge in the River Orkla was minimum 20 m^3s^{-1} until 1 September and 10 m^3s^{-1} thereafter (Fig. 3). Salmon that migrated downstream after catch and release and stayed in the downstream parts of the rivers, were not included in the analyses.

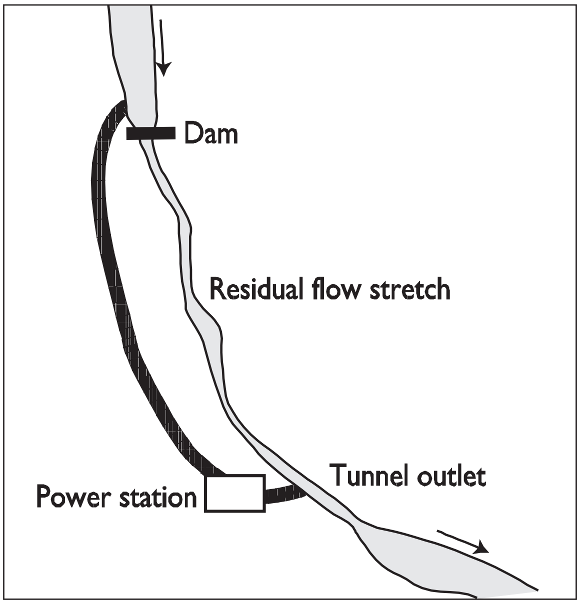

Fig. 2 – Schematic outline of the Laudal power station in the River Mandalselva, Rygene power station in the River Nidelva and Svorkmo power station in the River Orkla, which all have intake and outlet in the main river.

Previously published results

Two previous publications are produced from these studies. One publication analysed the effects of artificial freshets in the River Mandalselva in 1996, concluding there were no significant effects of the six freshets released (Thorstad and Heggberget, 1998). The other publication analysed the results from the River Nidelva in 1997, concluding that salmon were delayed by the power station outlet and in the residual flow stretch at a water discharge of 3 m^3s^{-1} in the residual flow stretch (Thorstad *et al.*, 2003). Previously published results are not repeated in this paper, but are referred to as a basis of comparison to the new results presented in this paper.

Data analyses

The data did not meet the assumptions of parametric tests, and non-parametric tests were therefore used. Mann-Whitney U tests were used to test whether two independent samples came from the same population. The Kruskal-Wallis test was used in the case of more than two independent samples, whereas the Wilcoxon signed ranks test was used when comparing two related samples. A Yates-corrected Chi-square calculation was used to compare observed and expected frequencies in two categories to test whether the categories contained the same proportion of values.

Results

Delays at power station outlets

In the **River Nidelva** in 1999, when water discharge in the residual flow stretch was 5 m^3s^{-1}, 74% (n=31) of the tagged salmon migrated upstream to the tunnel outlet after release, where they stopped for on average 4.1 days (range 0-39). This was a shorter stop than in 1997, when the residual discharge was 3 m^3s^{-1} (average 22.4 days, Mann-Whitney U test, U=91.0, P<0.001). However, the fish seemed to be attracted by the tunnel outlet also in 1999, and returned to the outlet one or more times after up- or downstream movements. In total, the fish was recorded at the outlet on average during 27% (range 0-92%) of the tracking surveys. Results from the data logger and manual tracking showed that in 1999, the fish rather stayed outside the power station tunnel, instead of entering the tunnel and mainly staying inside the tunnel as they did in 1997. In 1999, only seven salmon had a longer stay than 1 h inside the tunnel (up to 77 h). However, the proportion of salmon entering the residual flow stretch was not different between the two years (10 of 17 in 1997 *versus* 25 of 31 in 1999, Yates-corrected Chi-square calculation, χ^2=2.65, P=0.20).

In the **River Orkla**, salmon also stopped at the power station outlet, before migrating further upstream (on average 42 days, range 0-101, n=25). The salmon were not recorded immediately at the tunnel outlet, but stayed in the pool 150-200 m downstream from where the water from the tunnel and the residual flow stretch run together.

Migration on residual flow stretches

In the **River Mandalselva**, 17% (n=9) of the radio tagged salmon passed the residual flow stretch and

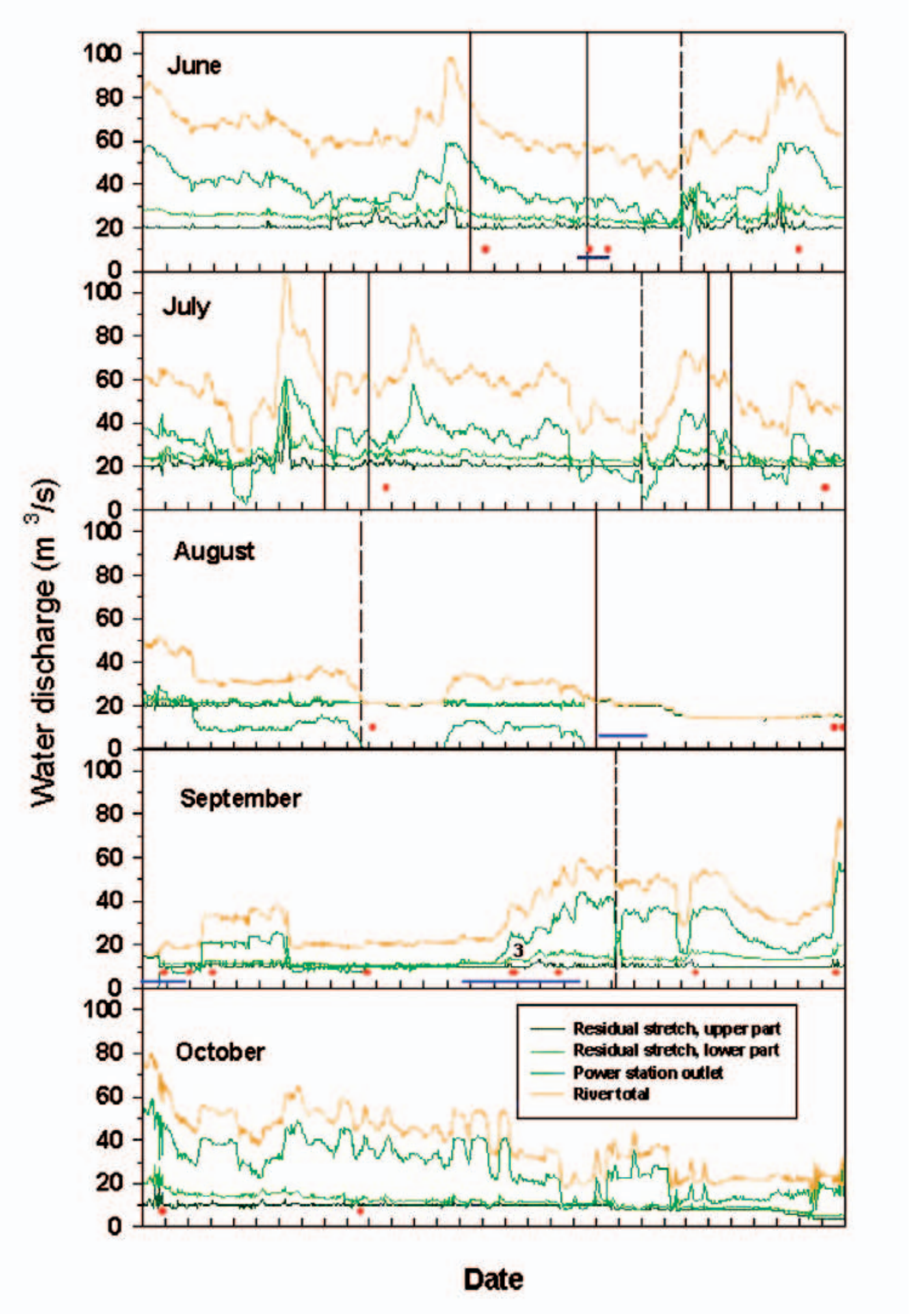

Fig. 3 – Timing of upstream migration of individual salmon (red dots [note that three salmon passed the same day in mid September] or blue lines when the exact timing was uncertain) from the tunnel outlet in the River Orkla in relation to artificial freshets (dotted vertical lines) and water discharge. Solid vertical lines indicate dates when salmon were radio tagged. Data on hourly water discharge during 1 June to 31 October was provided by the Power Stations in Orkla (KVO), and is shown from the first to the last date every month.

migrated further upstream the river. This was a larger proportion than in previous years with a lower residual discharge (0.25 m^3s^{-1} in 1993 and 1.5 m^3s^{-1} in 1994-1995), when 1.5% (1993) and 3.7% (1994-1995) of the salmon passed the residual flow stretch according to results from fish traps catching all salmon entering and leaving the stretch those years (Yates-corrected Chi-square calculation, χ^2=5.20, P=0.023). The radio tagged salmon spent on average 42 days (range 14-69) in passing the residual flow stretch, corresponding to a migration speed of 0.15 km(day^{-1}). After passing the residual flow stretch, average migration speed for the same individuals increased to 3.6 km(day^{-1}).

In the **River Nidelva**, none of the salmon managed to pass the dam at the power station intake. Both in the **River Mandalselva** and **River Nidelva**, salmon distributed themselves over the entire residual flow stretch, and generally showed an erratic movement pattern with up- and downstream movements. Based on where the salmon stopped, or turned and migrated downstream in the two rivers, none of the weirs could be identified as more serious migration barriers than the others, except the dam at the power station intake and one of the other weirs in the **River Mandalselva**. The two weirs locally considered as migration barriers in the River Mandalselva did not appear to delay salmon more than the others. Some of the salmon turned and migrated downstream again just after entering the residual flow stretch. This was especially notable in the **River Nidelva** in 1999, where 24% (n=6) of the salmon moved downstream again after being recorded just upstream the outlet, and they did not enter the residual flow stretch again later in the season.

In the **River Orkla**, salmon seemed not to be delayed in passing the residual flow stretch. The salmon spent on average 9.7 days in passing the stretch, which corresponded to an average migration speed of 3.1 km(day^{-1}). This was not different from the migration speed further upstream the river, which was on average 3.7 km(day^{-1}) for the same individuals (Wilcoxon signed ranks test, Z=-0.31, P=0.75). However, the salmon seemed to be delayed at the dam at the power station intake, where they spent on average 11 days (range 2-24) before passing.

Effects of artificial freshets

In contrast to no effects in 1996, positive effects of the artificial freshets on the upstream migration were found in the **River Mandalselva** in 1997. Number of weirs passed per hour was higher during both of the freshets (including a 10-13 hour period after the freshet) than during the remaining upstream migration period (Wilcoxon signed ranks tests, Z=-2,28, P=0.023; Z=-2,11, P=0.035), and distance moved was higher during one of the freshets (Wilcoxon signed ranks test, Z=-2,58, P=0.010). However, the migration speeds in question were so low (0.2-0.5 km(day^{-1}) during freshets and 0.08 km(day^{-1}) during the remaining upstream migration period), and the movements generally so erratic, that the importance of the freshets in stimulating the salmon to pass the residual flow stretch was insignificant. Freshets were not obligatory for the passage of any of the weirs, as all the weirs at some occasion were passed during residual water discharge.

The upstream migration from the power station outlet in the **River Orkla** were not highly stimulated by freshets, as only one salmon (4%) migrated upstream during a freshet (Fig. 3). Of the salmon migrating upstream later in the season, 17 (68%) stayed outside the outlet during at least one of the freshets without passing (two of the salmon stayed during four freshets, two salmon stayed during three freshets and four salmon stayed during two freshets). The upstream migration happened during a wide range of water discharges, both in the residual flow stretch (between 11 and 28 m^3s^{-1}) and from the tunnel outlet (0-55 m^3s^{-1}), during increasing, decreasing and stable water discharges (Fig. 3). Water discharge from the power station varied from 0 to 2.8 times higher than from the residual flow stretch when salmon passed the tunnel outlet and migrated further upstream (this relationship varied between 0 and 3.6 during the season, and was on average 1.3 times). Migration in the residual flow stretch also did not seem to be stimulated by the freshets, but the sample size was low, except during the last freshet, when there was no difference in distance moved between the days before, during and after the freshet (Kruskal-Wallis test, n=14, χ^2=1.5, P=0.46).

Discussion

Delays at power station outlets

Results in the present study showed that both native and non-native salmon were delayed at power station outlets during their upstream migration, even though the localities in the River Nidelva and River Orkla did not seem to imply any physical migration barriers (passage of power station outlet was not studied in the River Mandalselva). Salmon may naturally stop in some pools during their upstream migration, but the stops at the tunnel outlets both in the River Nidelva and Orkla were much longer than what was observed in comparable pools in the River Tana (average 5-9 days in the most popular pools, Økland *et al*., 2001). The shorter delay observed in the River Nidelva than in the River Orkla may be because the salmon were tagged later in the season, closer to spawning. The results in the present study are in accordance with other studies describing delays at power station outlets (Andrew and Geen, 1960; Brayshaw, 1967; Webb, 1990; Chanseau and Larinier, 1999).

Behaviour at the outlets seemed to be affected by both water discharge and the design of the outlet. Effects of water discharge were demonstrated in the River Nidelva, where the salmon mainly stayed inside the power station tunnel the first year of the study (Thorstad *et al*., 2003), whereas they mainly stayed in the river outside the outlet the second year, when the residual discharge was higher. No other factors were known to differ between the two years. However, the increase in water discharge was not sufficient to increase the proportion of salmon entering the residual flow stretch. The design of the outlet seemed to affect where the fish stayed at the outlets. In the River Nidelva, where the tunnel empties straight into the river, the most "natural" migration route is into the tunnel, and salmon must keep slightly to the right to enter the residual flow stretch. In the River Orkla, the tunnel empties into a side stream, which run together with the residual flow stretch 100 m downstream from the tunnel outlet. Upstream migrating salmon must either turn left to enter the side stream from the tunnel outlet, or slightly to the right to enter the residual flow stretch. These differences between the rivers may be the reason why the fish stayed inside or just outside the tunnel outlet in the River Nidelva, whereas they stayed in the pool downstream from where the water from the side stream and the residual flow stretch run together in the River Orkla.

One may think that factors such as water discharge in the residual flow stretch, water discharge from the power station, or the relationship between these two, would affect the upstream migration past tunnel outlets. However, the artificial freshets did not seem to affect the upstream migration from the outlet in the River Orkla, and the passage by individuals happened during a wide range of water discharges in the residual flow stretch and through the power station in both rivers (for results from the River Nidelva, see Thorstad *et al*., 2003). In the River Orkla, the water discharge was usually 1-2 times higher from the tunnel outlet compared with the residual flow stretch when upstream migration from the outlet occurred. The power station was closed for a period in August, without stimulating the migration, which may be due to unusually warm weather conditions and low water discharges during the period. Closing the power station in a period with rain and higher water discharge would maybe stimulate the upstream migration.

It can be concluded from these studies that relatively short and small artificial freshets in large regulated rivers may be a waste of water and money in stimulating Atlantic salmon to pass power station outlets. However, Arnekleiv and Kraabøl (1996) found positive effects by artificial freshets on trout (*Salmo trutta*) migration past a tunnel outlet, and effects by water discharge also on Atlantic salmon cannot completely be ruled out. Complex relationships may exist, and for example changes in water discharge or quality on a micro scale may be important. Furthermore, water discharge may not be important until the salmon is motivated for migration.

Migration on residual flow stretches

A water discharge of 20 m^3s^{-1} in the residual flow stretch in the River Orkla did not seem to reduce the migration speed. The migration speed was both comparable to migration speeds on river stretches upstream the residual flow stretch and in other rivers (e.g. Johnsen *et al*., 1998; Hayes *et al*., 1953; Smirnov, 1971), although other studies have reported higher migration speeds, such as Hawkins and Smith, 1986; Aarestrup *et al*., 2000). In contrast, the much lower residual flow in the Rivers Mandalselva and Nidelva seemed to delay the migration, probably together with a number of weirs constituting migration barriers (see below). The importance of increased water discharge on residual flow stretches was also demonstrated by the fact that an increase in residual discharge in the River Mandalselva from 0.25 to 3 m^3s^{-1} increased the proportion of salmon passing the residual flow stretch.

Large-grown salmon and sea trout may enter small rivers (3-5 m^3s^{-1}) seemingly without any problems. The delays seen in the residual stretches in the River Mandalselva and Nidelva is, therefore, probably related to salmon entering a big river and then suddenly finding themselves on a river stretch with a much lower water discharge. This may also have been the reason why some salmon turned and migrated downstream again after entering the residual flow stretch. Such behaviour was also observed for sea trout entering fish passages, and it was speculated that the fish tried to find an alternative route or wait for better conditions (Aarestrup *et al*., 2003). As for passage of power station outlets, relatively small and short artificial freshets did not seem to stimulate migration in residual flow stretches to a large extent, although small effects were found one of the years in the River Mandalselva. A large number of studies have reported that increases in water discharge have stimulated the upstream migration of salmon (see e.g. references in the introduction). Strikingly few studies have reported that they found no relationship between upstream migration and water discharge (but see Hawkins and Smith, 1986; McKinnell *et al*., 1994). One may speculate that studies finding no effects are under-reported and, thus, the effect of water discharge on the upstream migration exaggerated, especially in large rivers with a generally high water discharge.

Migration barriers

Dams and weirs delayed upstream migration in all the three rivers, although none of them seemed to be physically difficult migration barriers. In the Rivers Mandalselva and Nidelva, there were no weirs where all salmon stopped or where they only passed at increased discharge, and it seemed like the motivation to migrate was reduced due to a combination of low water discharge and a high number of obstacles. Salmon in the Rivers Mandalselva and Nidelva probably had no previous experience of the rivers, which may have decreased their motivation to migrate upstream compared with native salmon. However, escaped farmed salmon in two other Norwegian rivers appeared motivated to migrate upstream and distributed themselves further upstream than the wild salmon during spawning (Økland *et al*., 1995; Heggberget *et al*., 1996; Thorstad *et al*., 1998). The lack of motivation to migrate upstream in the Rivers Mandalselva and Nidelva may, therefore, not be explained by origin or lack of river imprinting. This was confirmed by the results from the River Orkla, where native salmon also seemed to be delayed by the dam, although it seems not to be a physically difficult obstacle to pass. It can be concluded from the results in this study that seemingly easy obstacles to pass may considerably delay salmon in their upstream migration. Ovidio and Philippart (2002) concluded from a five-year study in the same way that some small obstacles are not as insignificant as initially thought and can significantly disrupt and/or obstruct fish upstream movements.

Delays in the upstream migration may obviously create conflicts in the organisation of a sport fishery when salmon arrive in the upper parts of the watershed later after hydropower development. However, the biological importance of such delays is not known, as long as the salmon arrive on the spawning grounds in time for the spawning season. Atlantic salmon often enter the rivers several months before spawning (Nordqvist, 1924; Hawkins and Smith, 1986), and may hold position at the spawning grounds for one to two months before spawning (Økland *et al*., 2001). As pointed out by Fleming (1996), there is no satisfactory adaptive explanation for the early river entry time of adult Atlantic salmon. If the early river entry is associated with some kind of advantages, delays during the upstream migration will involve corresponding disadvantages.

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MIGRATORY PATTERNS, HABITAT UTILIZATION AND BEHAVIOURAL ECOLOGY

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Mekong giant catfish tracking project (MCTP): preliminary results in 2002

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Key words: Mekong giant catfish, pla buk, *Pangasianodon gigas*, biotelemetry, coded ultrasonic transmitter.

Abstract

The Mekong giant catfish (*Pangasianodon gigas* Chevey, 1931), or the pla buk in Thai, is one of the largest freshwater catfish in the world. It is endemic to the Mekong River basin. The biggest fish recorded was about 300 kg with a total length of about 3 m. Although it is listed as a highly endangered species in the IUCN Red List, little is known of its ecology or feeding habits. The Mekong giant catfish tracking project (MCTP) was initiated to investigate the migration behaviour of the catfish using ultrasonic biotelemetry, at the request of the Department of Fisheries, Ministry of Agriculture and Cooperatives of the Government of Thailand in 2001. This request included the following issues: to develop a methodology for tracking the Mekong giant catfish; to clarify the migration behaviour of the mature catfish after spawning and their habitat; to evaluate the resource enhancement achieved by releasing fingerlings into the Mekong River; and to conserve this resource in Thailand. We began by developing the methodology in the Mekong River. In 2002, ten Mekong giant catfish were released into the Mekong River with coded ultrasonic transmitters implanted inside their body cavities. They were monitored by five ultrasonic receivers covering a range of about 110 km. Five of ten catfish were tracked successfully for 10 days after release, four of which went upstream for about 60 km and the other went downstream for about 50 km.

Introduction

The Mekong River is the largest river in Southeast Asia. It flows through six countries including China, Myanmar, Thailand, the Lao People's Democratic Republic (Lao PDR), Cambodia, and Viet Nam from its source in the Tibetan Himalayas, and covers a distance of more than 4,400 km before reaching the South China Sea. The river basin covers an area of nearly 800,000 km. An estimated 1,700 species of fish are believed to inhabit the Mekong River and its basin, including the Mekong giant catfish (Bao *et al*., 2001).

The Mekong giant catfish (*Pangasianodon gigas*), or pla buk in Thai, is endemic to the Mekong River. As its vernacular and English names indicate ("buk" means colossal or strong), pla buk is known for its huge size, attaining a length of 3 m and a weight of more than 300 kg in adults (Akagi *et al*., 1996). It is classified as an endangered species on the 2000 International Union for the Conservation of Nature (IUCN) Red List and also listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Therefore, the fishing of catfish is strictly regulated in Thailand. The only fishery cooperative permitted to catch the Mekong giant catfish in Thailand is located in the Chiang Khong District in the northern part of Thailand. The fishermen in the cooperative use gill nets with a height of 3 m and a mesh width of 40 cm. The fishing season starts in April and finishes by the end of the dry season at the end of May. Recently, the number of fish in these catches has decreased dramatically.

An artificial insemination project, using captive pla buk males and females, was begun in 1981 as a conservation strategy by the Department of Fisheries, Ministry of Agriculture and Cooperatives of the Government of Thailand. Its first success was achieved in 1983. A demonstration of the release of captured pla buk was conducted in 1996 (Akagi *et al*., 1996). However, little is known of the ecology or feeding habits of wild or artificially released pla buk. In particular, the migration behaviour of the Mekong giant catfish is cloaked in mystery because very few mature fish have been caught in the limited area described above.

The Mekong giant catfish tracking project (MCTP) was initiated in 2001 to investigate the migration behaviour of the catfish, using ultrasonic biotelemetry, at the request of the Department of Fisheries, Ministry of Agriculture and Cooperatives of the Government of Thailand. The request included the following issues: to develop a methodology for tracking the Mekong giant catfish in the Mekong River; to clarify the migration behaviour of the mature catfish after spawning and their habitat; to evaluate the effectiveness of the resource enhancement achieved by releasing fingerlings; and to conserve this resource not only in the Mekong River but also in reservoirs in Thailand. At the outset of the cooperative project, we began to develop a methodology to track the Mekong giant catfish in the Mekong River. Our preliminary results are introduced in this paper.

Materials and methods

Study site and experimental fish

The study was conducted in 2002 in the middle reaches of the Mekong River, covering around 110 km within the Nakhon Phanom Province (Fig. 1).

We studied ten Mekong giant catfish in 2002. These experimental catfish were artificially inseminated in the Chiang Rai Inland Fisheries Research and Development Center and reared at the Nakhon Phanom Inland Fisheries Station (Table 1).

Fig. 1 – Location of the study area of the Mekong giant catfish tracking project (MCTP) in 2002.

Table 1 – Characteristics of the Mekong giant catfish used in this study. The fish were tagged with coded ultrasonic transmitters placed inside their body cavities on June 25, 2002 at the Nakhon Phanom Inland Fisheries Station. The fish were released at the mouth of the Song Khram River on June 27, 2002, at the noted release times.

ID	Fork length (cm)	Body weight (kg)	Release time (June 27, 2002)
1	103.5	15.0	17.00
2	86.5	9.0	12.07
3	105.0	17.2	16.58
4	91.0	12.0	17.02
5	103.5	15.0	12.11
6	67.5	4.2	17.01
7	67.0	4.7	17.03
8	72.0	5.2	9.06
9	69.0	5.4	8.58
10	70.5	5.4	16.59
Average	83.6	9.3	-
s.d.	15.4	4.8	-

Transmitters

We used coded ultrasonic V16-4H transmitters (Vemco Co., Ltd., Canada). They are 16 mm in diameter, 65 mm long, and weigh ca. 10 g in water. The frequency of the transmitters was 69 kHz. The power of the acoustic signals was 153 dB and the interval of transmission was about 45 seconds, on average. The battery lasted over two years. The transmitters transmit complex codes consisting of six pulses per transmission. If the receiver picks up all the six pulses of a transmitter perfectly, it can identify and record the ID number of that transmitter. If the receiver cannot identify the ID number, it records only the number of pulses. Two hundred and fifty-six different fish have been identified on the same frequency using this transmitter (Voegeli *et al.*, 1998 & http://www.vemco.com/).

Experimental deployment

Before the main experiment, we carried out preliminary tests to determine the effects of external and surgical transmitter attachments on the fish in the Kalasin Inland Fisheries Research and Development Center using dummy transmitters, from May 3 to June 19, 2002. No external attachment transmitters remained after the experiment. Therefore, all the transmitters were implanted surgically into the abdominal cavities of the catfish under anaesthesia, using our previously described method (Mitamura *et al.*, 2002). We implanted the transmitters at the Nakhon Phanom Inland Fisheries Station on June 25, 2002. After surgery, the fish were kept in indoor tanks for at least 24 hours, so that their physical condition could be observed before the release experiments.

The sample catfish were released on June 27, 2002, at the mouth of the Song Khram River, which is one of the branches of the Mekong River (Table 1, Fig. 1).

Tracking system

We used VR1 receivers (Vemco Co., Ltd., Canada) to track the catfish carrying the coded ultrasonic transmitters. The VR1 receivers were installed in water of medium depth to record the presence of the catfish carrying the transmitters. The dimensions of the VR1 receiver are 60 mm in diameter and 205 mm in length, and it is powered by a lithium battery that lasts for 180 days. It has flush-memories inside to record the data. Information, including the ID number and the time, were recorded when the tagged fish passed within the detection range of the receiver. According to a test of the detection range, the receiver was able to detect signals from transmitters within about 300 m in the main stream of the Mekong River. Therefore, the receivers were unable to completely cover the area up to the opposite side of the river (i.e. the Lao PDR side) in the flood season because the width of the river expands to about 500–600 m.

Tracking periods and placement of fixed stations

We installed five VR1 receivers, No. 1–5, in the Mekong River. Two (No. 3 and 4) of the five receivers were set up near the release point. One (No. 5) receiver was set up in the Song Khram River, which is a branch of the Mekong River. Another (No. 1) receiver was set up at a place about 60 km upstream from the release point, in the Bannakhae district of the Nakhon Phanom Province. The fifth receiver (No. 2) was set up about 50 km downstream from the release point in front of the River View Hotel in the downtown sector of Nakhon Phanom. The data from the five VR1 systems were downloaded on August 18, 2002. After downloading, the locations of two VR1 receivers were changed to cover further areas 100 km upstream (Fig. 2). The second downloading was conducted on November 23, 2002.

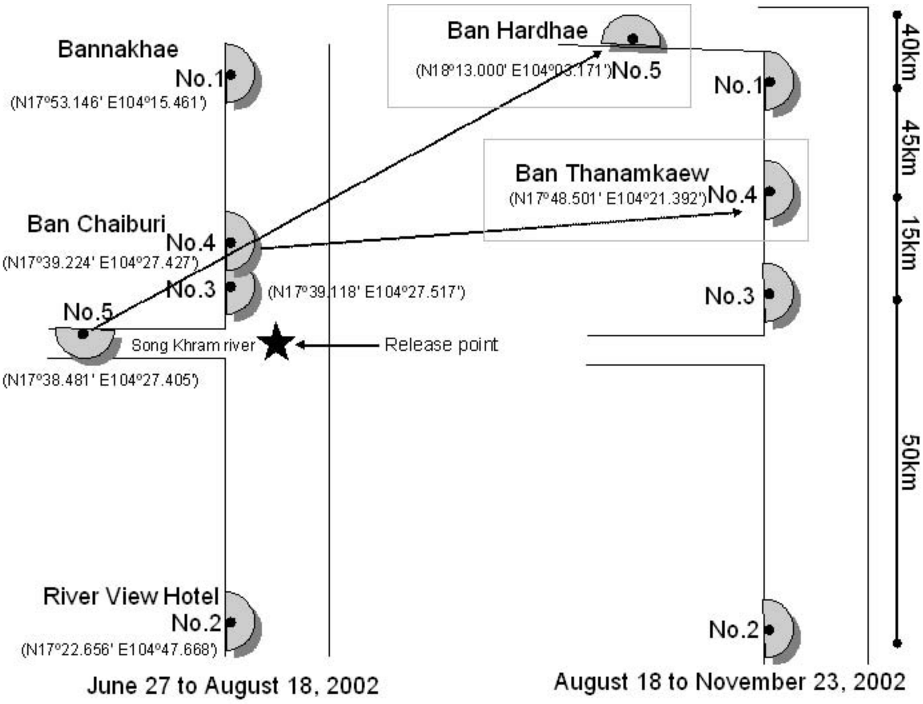


Fig. 2 – Distribution of the VR1 receivers between June 27 and August 18 and between August 18 and November 23, 2002.

Results

All the VR1 receivers worked well and detected signals from the coded ultrasonic transmitters in the sample catfish. Figure 3 shows a summary of the results of the tracking study. The No. 3 receiver, nearest to the release point, recorded data for all the sample fish on July 27, 2002, when the fish had been released. This indicates that all the transmitters were working well inside the catfish.

We describe in detail the attendance of each fish at the receivers as follows: ID 1 went out of range of receiver No. 3 just after its release at 17:00 hours on June 27, 2002. Then it returned to the release point and stayed between receivers No. 3 and 4 from June 27 to July 1, 2002. At 20:58 hours on July 1, it went out of range of receivers No. 3 and 4. It appeared again 60 km upstream from receiver No. 1 at 11:00 hours on July 4 and stayed around receiver No. 1 for 01.02 hours.

ID 2 was released at 12:07 hours and stayed for 10.34 hours around the release point, then disappeared.

ID 3 was released at 16:58 hours and stayed there for two hours. It was also detected in the branch stream, at receiver No. 5, soon after. It disappeared between June 28 and July 3, and then returned to receiver No. 4. It went upstream again at 06:55 hours on July 4 and arrived at receiver No. 1 at 11:00 hours on June 6.

ID 4 moved out from the release point just after release and never returned.

ID 5 was released at 12:11 hours and stayed around the release point for five days. On June 29 and 30, 1,367 and 1,555 signals from its transmitter were detected by receiver No. 3, respectively.

ID 6 was released at 17:01 hours and moved into the branch stream, around receiver No. 5, on June 28 and stayed there for three days. On June 28, 29, and 30, 1670, 2110, and 1753 signals from the transmitter were detected by receiver No. 5, respectively. The fish then moved into the main stream at 09:33 hours on July 1, 2002 and swam 60 km upstream and passing the No. 1 receiver at 0:42 hours on July 3.

ID 7 was released at 17:03 hours and stayed at the site for two hours. It then moved away from the release point and appeared around the mouth of the branch stream on July 3, 2002. ID 8 was released at 09:06 hours, stayed for 5.16 hours, and then disappeared. After six days, it appeared about 500 m upstream from the release point. It then moved upstream at 14:50 hours on July 4 and arrived at receiver No. 1 at 11:28 hours on July 6.

ID 9 was released at 08:58 hours and moved out from the release point. It appeared again 50 km downstream on July 4 and passed receiver No. 2. The signals were recorded between 09:58 and 10:53 hours by receiver No. 2.

ID 10 was released at 16:59 hours, disappeared immediately, and never returned to the vicinity of any receiver.

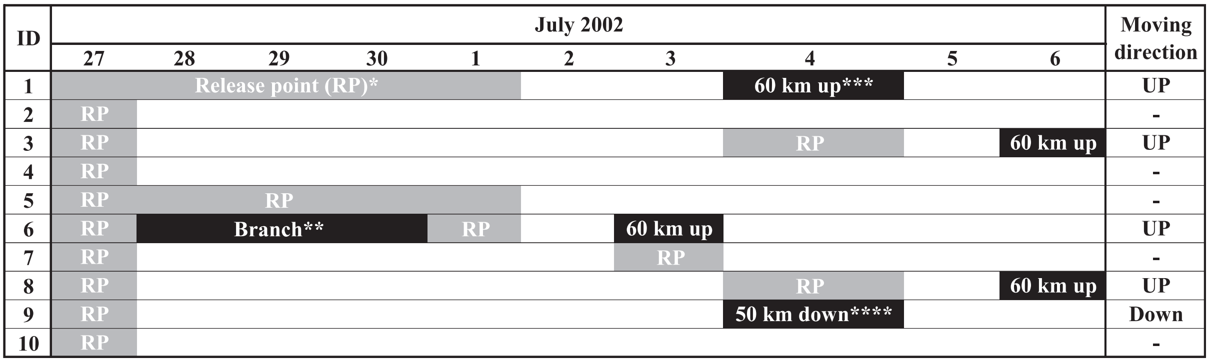
We downloaded the data from all the receivers on November 23, 2002. We found that no IDs were recorded on all the receivers, although there were many pulses recorded, as shown in Table 2.

Discussion

All the VR1 receivers successfully recorded the ID numbers of the sample Mekong giant catfish in a wide area ranging along about 110 km of the river. However, the detection range of the VR1 receivers was limited to within a radius of about 300 m, so that it was impossible to detect signals when the catfish moved to the opposite side of the river, i.e., the Lao PDR side. Disappearance of IDs 2, 4, and 10 just after release indicates that they moved out of the detection range. In future, receivers should also be installed on the Lao PDR side of the river to track the catfish completely.

The V16 coded transmitters sent ultrasonic signals every 45 seconds on average. The signal interval varied randomly ranging from 20 to 90 seconds, in order to avoid crosstalk. Therefore, the number of detection events should be less than around 1920 per day on average. ID 5 was detected on June 29 (1367 times) and on June 30 (1555 times) at the No. 3 receiver, and ID 6 was detected on June 28, 29, and 30 (1670, 2110, and 1753 times, respectively) at receiver No. 5, indicating that these fish were continuously within a 300 m radius of the respective VR1 receiver. Moreover, it is clear that ID 6 entered the Song Khram River on June 28 and stayed there until June 30 (Fig. 3).

The data from the VR1 receivers show us the times at which fish were present in an area with a 300 m radius. This constitutes an attendance book for the fish. We can infer the fish's movements using two attendance books. ID 1 moved away from receiver No. 4 at 20:58 hours on July 1 and was detected at receiver No. 1 at 11:00 hours on July 4. It took 38 hours and two minutes to move from receiver No. 4



ID	July 2002										Moving direction
	27	28	29	30	1	2	3	4	5	6	
1	Release point (RP)*							60 km up***			UP
2	RP										-
3	RP							RP		60 km up	UP
4	RP										-
5	RP	RP									-
6	RP	Branch**			RP		60 km up				UP
7	RP						RP				-
8	RP							RP		60 km up	UP
9	RP							50 km down****			Down
10	RP										-

* Release point included data of Nos. 3 and 4 VR1 receivers

** Branch was No. 5 VR1 receiver data

*** 60 km-up was No.1 VR1 receiver data

**** 50 km-down was No. 2 VR1 receiver data

Fig. 3 – Summary of the results of the Mekong giant catfish tracking project using coded ultrasonic transmitters and VR1 receivers in the Mekong River in 2002.

Table 2 – Number of pulses recorded by the VR1 receivers between August 18 and November 23, 2002.

VR1 location	Number of pulses
No. 1	344
No. 2	67
No. 3	1688
No. 4	7089
No. 5	364

to receiver No. 1. In the same way, IDs 3, 6, and 8 took 52 hours and 8 minutes, 55 hours and 49 minutes, and 44 hours and 38 minutes, respectively, to move between these points. They swam about 60 km from receiver No. 4 to receiver No. 1 in 49 hours and 39 minutes, on average. If the catfish swam 12 hours a day, the average swimming speed was 178 cms^{-1}, taking into consideration the velocity of the river current, which was about 2 kmh^{-1} (measured by a global positioning system [GPS] on the boat). The average body length (BL) of the fish (l) was 87 ± 20 cm, so that 178 cms^{-1} can be converted to two body lengths per second (2 BLs^{-1}). This is a reasonable value according to previous studies (Bainbridge, 1958; Wardle, 1975).

Only ID 9 appeared at receiver No. 2, 50 km downstream from the release point, on July 4, 2002. We should interpret downstream movement with caution because dead fish will also drift downstream with the current. If the fish were dead, it would move across the 600 m diameter of the detection range of receiver No. 2 in 18 minutes, if the velocity of the river were 2 kmh^{-1}. Therefore, because the signals for catfish ID 9 were recorded for 55 minutes, from 09:58 to 10:53 hours, on July 4 by receiver No. 2, it appears to have been alive, although there is no other evidence to support this inference. The second downloading on November 23, 2002, gave us no ID number at all. However, fractions of ultrasonically coded signals were recorded by all the VR1 receivers, as shown in Table 2. The No. 4 receiver, located 15 km from the release point, stored 7089 pulses for 97 days, from August 18, 2002 to November 23, 2002. This indicates that some experimental catfish occupied an area near receiver No. 4, but slightly outside the detection range of the neighbouring VR1s or inhabited areas on the opposite side of the river, i.e. on the Lao PDR side of the Mekong River.

In this study, we used artificially reared Mekong giant catfish instead of wild fish to circumvent the difficulties in preparing wild catfish that result from the serious decrease in recent catfish catches. Therefore, we should interpret the results of this analysis of catfish behaviour with caution. However, the results will provide useful information for understanding the resource enhancement achieved by releasing catfish fingerlings in the future, as has been requested by the Government of Thailand. We are also preparing tracking experiments using wild catfish in accordance with the recommendations of the Government of Thailand but it may be too late to proceed with this because there has been no catch for some years. Against this background, we have started another tracking experiment in an artificial reservoir, the Mae-puem Reservoir in Phayao Province. The Mae-puem Reservoir has an area of about 816 km^2, and was completed in 1982 for irrigation water. The Government of Thailand has undertaken to create new catfish resources in reservoirs. Therefore, we are attempting to clarify the behaviour of reared Mekong giant catfish in order to conserve them in the reservoirs of Thailand.

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Movements of juvenile and adult spider crab (*Maja squinado*) in the Ría da Coruña (N-W Spain)

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Key words: *Maja squinado*, movements, maturity, ultrasonic telemetry, Ría da Coruña, North-West Spain.

Abstract

In July 2002, 12 juvenile and 12 adult (recently terminal moulted) spider crabs were tagged using ultrasonic pingers (Sonotronics, USA) in the Ría da Coruña (N-W Spain). Both adults and juveniles were released in the same sandy shallow bottoms (5-10 m) in which they were caught. This area, as known from previous studies, is a typical juvenile area where spider crabs carry out their terminal moult before the autumn migration to deep bottoms. The tracking was carried out daily for a period of two weeks, although not all the crabs were located every day. Juvenile crabs were found to move small distances, performing non-directional movements near the coast, in protected areas up to 10 m deep. Two of the adult crabs performed small-scale movements in the outer (more exposed) part of the estuary, at depths up to 20 m. The rest of the adult crabs remained in the juvenile area, performing the same non-directional movements as the juveniles. Four male adult crabs were recaptured by commercial fisheries in the following months, three of them at more than 40 m deep, in the central channel of the estuary, probably while performing their seasonal descent migration. A female carrying eggs was recaptured in December near the coast.

Introduction

The spider crab, *Maja squinado* (Decapoda, Majidae) (recently splitted into *Maja squinado* (Herbst, 1788), inhabiting Mediterranean coasts, and *Maja brachydactyla* Balss, 1922, in the Atlantic coasts of Europe (Neumann, 1996)), is a species that lives at depths ranging from subtidal level to more than 150 m (González-Gurriarán *et.al*., unpublished data). There is strong evidence that spatial segregation exists between juveniles and adults; these habitat differences are variable according to the season (Corgos *et al*., 2002). In the Ría da Coruña (N-W Spain), juveniles (carapace lenght < 120-140 mm) inhabit predominantly shallow waters characterized by mixed hard-and-soft bottoms. One or two months after the terminal moult that takes place in their second year, through which they attain maturity, females start their gonad maturation (González-Gurriarán *et al*., 1998). Some behavioural changes are also defined in this period, leading to migratory movements to deeper waters (Latrouite and Le Foll, 1989; González-Gurrirán and Freire, 1994; Hines *et al*., 1995). The adults inhabit deep areas where they are the target of a tanglenet fishery (González-Gurriarán *et al*., 1993; González-Gurriarán and Freire, 1994). Movements and habitat use of this species is highly important for the fishery, given that catches are directly related to the activity rhythms and migrations. Although many studies have been carried out analyzing migration movements using mark-recapture methods (Camus, 1983; Kergariou, 1976; Le Foll, 1993; González-Gurriarán *et al*., 2002), little information is available on the animal's activity in the coastal shallow areas in the months prior to migration (González-Gurriarán and Freire, 1994).

The objective of this study was to describe patterns of movement and habitat use in the summer period when shallow areas, determined by previous studies, are shared by juveniles and young adults (recently moulted to maturity). Local movements between habitats or areas within a habitat as well as aggregation patterns are aspects of interest as yet to be established.

The study used ultrasonic telemetry, previously shown to be an efficient tool to obtain accurate data on crab small-scale movements and migrations (Maynard and Webber, 1987; Wolcott and Wolcott, 2002). It has also been successfully used in the spider crab (Freire and González-Gurriarán, 1998; González-Gurriarán and Freire, 1994; González-Gurriarán *et al*., 2002; Hines *et al*., 1995).

Materials and methods

In July 2002, 24 spider crabs were tagged using ultrasonic pingers in the Ría da Coruña (NW Spain) (Fig. 1). The tagging took place in Bastiagueiro, a shallow sandy bottom area in the inner part of the Ría da Coruña (43° 21' N, 8° 22' W), between the 8th and the 10th July 2002. Twelve juvenile (with carapace length between 84 and 135.5 mm) and twelve adult (recently moulted to maturity; carapace length between 112 and 173 mm) spider crabs were tagged using Sonotronics IBT-96-2 and CHP-87-S pingers, respectively. The first has a weight of 2.5 g in water and dimensions of 28 by 9.5 mm. The battery lasts for 60 days, and the operating frequency is 69 or 76.8 kHz. Under ideal oceanographic conditions the pingers can be detected from distances up to 500 m (Sonotronics' technical specifications). The pingers used for the tagging of adult crabs weighted 8 g in water, and their dimensions were 67 by 18 mm. The battery lasts for 7 months and the transmission frequency is 75 kHz. They can be detected from distances up to 3000 m in ideal conditions.

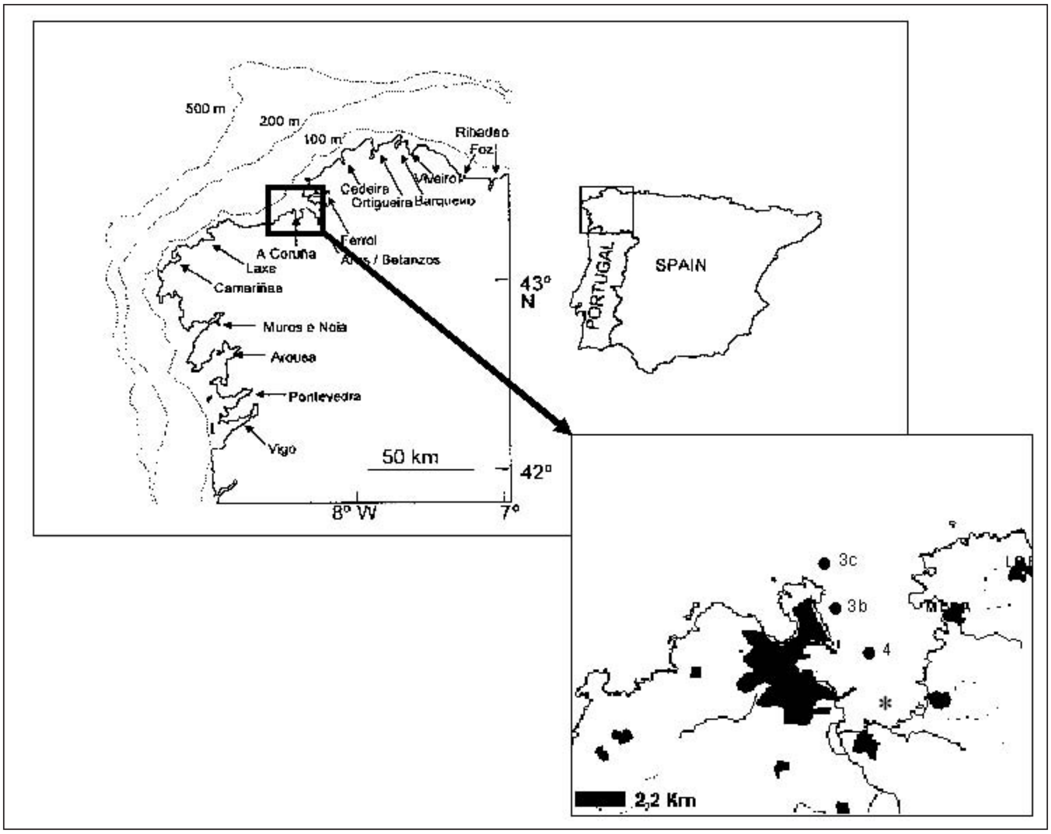

Fig. 1 – Ría da Coruña (NW Spain), showing tagging area (*) and oceanographic data collection stations (4, 3b and 3c).

The spider crabs were captured using pots. Algae and other epiphytes were cleaned off the dorsal part of the carapace by scrubbing them with a brush. Then the area was dried using alcohol and acetone in a cloth. Tags were then attached to the clean, dry carapace on the dorsal side, using quick epoxy. Adult crabs' tags, which are bigger, could be labelled by writing UDC´s (Universidade da Coruña) telephone number and the word "reward" on its surface. Smaller tags used for juveniles allowed no writing on their surface. Thus, the labelled part of a T-bar anchor tag was also attached to the carapace, using the same quick epoxy. The tagging process was as quick as possible (<20 minutes), in order to avoid long air exposure.

A Sonotronics USR-5W receiver with a Sonotronics DH-2 directional hydrophone was used to locate the tagged crabs on a daily basis (although some of the crabs were not located every day due to unfavourable weather and oceanographic conditions, crab loss, lack of time, etc…), using a small boat equipped with echosounder and GPS. The telemetry experiment started the 8th July 2002 and ended the 24th July 2002.

Distance between consecutive locations and movement direction in relation to the north was estimated from GPS positions of located crabs. The distance between locations was assumed to be the minimum distance travelled by the animal between observations. Speed (mday^{-1}) was calculated as distance between locations in consecutive days. Distance between locations, speed and mean depth was calculated omitting the release observation. The statistic r was computed, which is equal to the mean vector length and represents a measurement of concentration of the different movement angles. The length will range from 0 to 1; larger number indicates that the observations are clustered more closely around the mean than lower numbers. The Rayleigh test was performed to determine if the movement of each animal presented a significant directional orientation. The test calculates the probability of the null hypothesis that the data are distributed in a uniform manner (Batschelet, 1981).

Some recaptures were obtained from commercial fisheries in the following months. Data such as fishing date, position and depth were taken. In the only case of a recaptured female, dissection was performed to determine gonad and egg maturation stage and number of sperm masses (González-Gurriarán *et al.*, 1998).

Oceanographic data, recorded monthly, were provided by the Instituto Español de Oceanografía (Centro Costero de A Coruña). These included temperature and salinity in three sampling stations in the tagging area and outer part of the estuary, from 20 to 40 m depth. Two data loggers, that recorded temperature data every two hours, were placed in the tagging area, at fixed depths of 5 and 10 m.

Results

From a total of 24 tagged crabs, four were never located (lost after release) and one crab was located only once. These five crabs were all adults. Mean number of position fixes per crab was 10 (range: 4-12). During the tracking period, both juvenile and adult spider crabs performed small-scale movements within the inner part of the estuary (Fig. 2). The mean distance between locations was 187 m for juveniles and 179 m for adults (range: 94-517 and 114-250, respectively) and the mean speed 154 mday^{-1} for juveniles and 159 mday^{-1} for adults (range: 58-272 and 100-250, respectively). These movements were carried out in shallow sandy bottoms. Mean depth was 6.5 m for juveniles and 9.5 m for adults.

Figure 3 shows the distance between crabs during the experiment. Crabs moved up to 187 mday^{-1}, and average distance between crabs was 80 m (range: 17-106 m).

One juvenile crab showed significant directionality (SW) in its movements (r=0.57, p=0.03). Two crabs that were lost for more than one week during the tracking were excluded from the directionality analysis. The rest of the crabs did not show significant directionality in their movements (tests of Rayleigh, p>0.05; Figs. 2 and 4); r statistic ranged between 0.08 and 0.4.

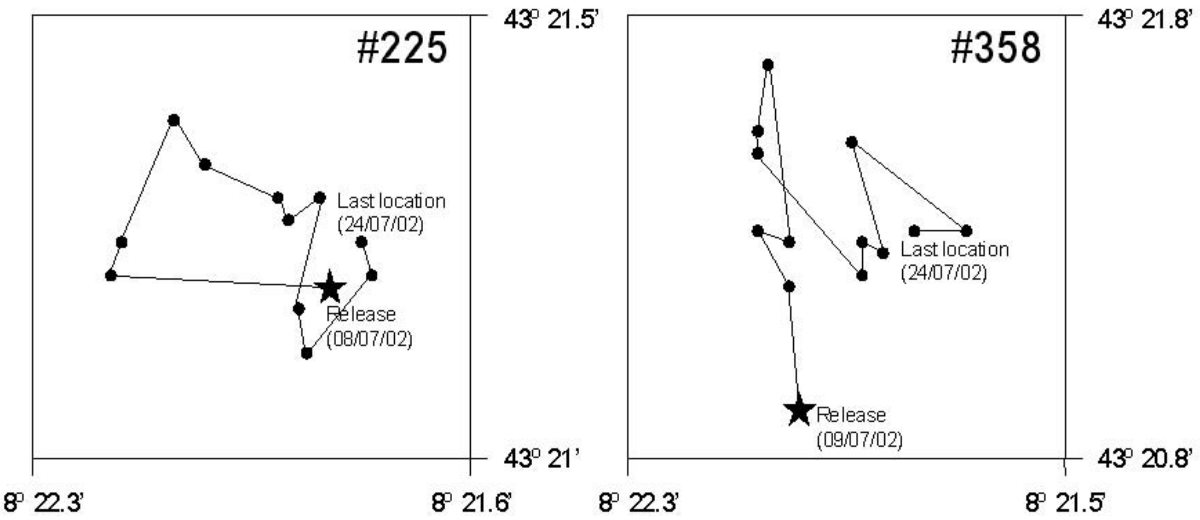

Fig. 2 – Examples of movements of two juvenile crabs (#225 and #358).

In late August, one month after the end of the tracking, three adult males were recaptured by commercial fisheries. One of them was recaptured in the inner part of the estuary, at a depth of 17 m. The other two were recaptured in the central channel, outside the estuary, at a depth of 50 m. Another male was recaptured outside the estuary in May 2003, at a depth of 45 m. A female carrying eggs was recaptured in late December 2002 in coastal shallow waters.

Oceanographic data (Fig. 5, a and b) show a stable pattern of both temperature and salinity during the late spring-summer period (May to September). Mean temperatures show an oscillation of 2 ºC and salinity initiates a slow decrease in September, related to the first autumn rains.

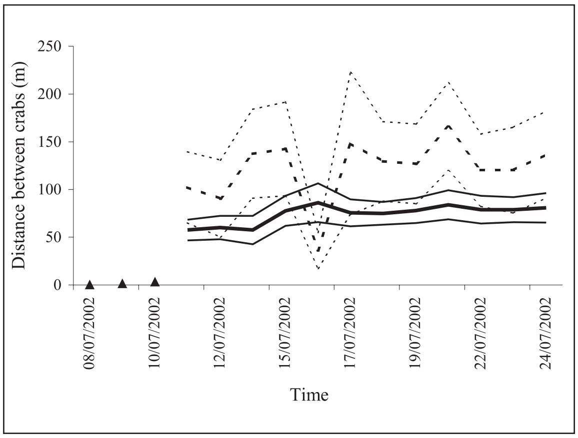

Fig. 3 – Average distance (m) between crabs (both juvenile (solid line) and adult (dotted line) from release to the end of the experiment. Thinner lines show the confidence interval. Triangles represent release dates.

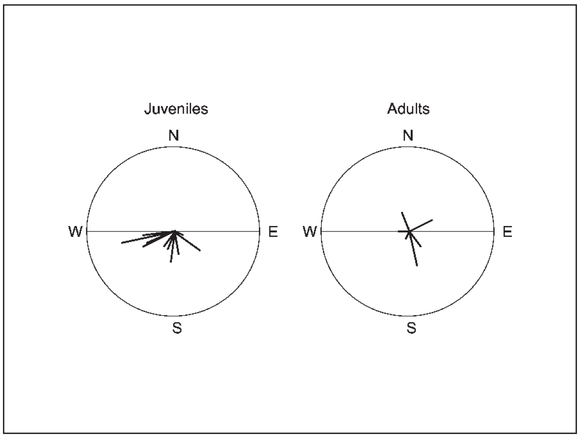

Fig. 4 – Average angles of movements in juveniles and adults. Vector length is proportional to directionality of movement (statistic *r*; radius of the circumference=1).

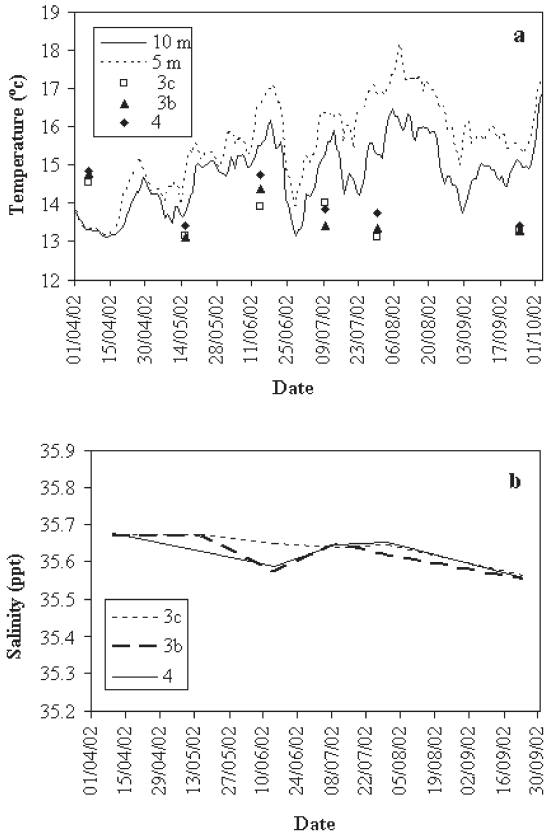

Fig. 5 – **a**, Bottom temperature at stations 4, 3b and 3c (20, 35 and 40 m depth, respectively), and temperature at 5 and 10 m in the tagging area. **b**, Bottom salinity at stations 4, 3b and 3c.

Discussion

In the Ría da Coruña, juvenile spider crabs show a clear aggregative pattern in shallow areas, probably to avoid predation risk (Corgos *et al*., 2002). During late summer, both juveniles and recently moulted to maturity adults carry out small-scale, non-directional movements. This kind of short, random movement in shallow areas has also been observed in other crabs, such as *Cancer pagurus* (Skajaa *et al*., 1998), and in *Homarus americanus* (Watson *et al*., 1999).

González-Gurriarán and Freire (1994), describe a two-phase movement pattern for these young adults, while gradually increasing their gonad, muscle and hepato-pancreas condition. The first stage is characterized by movements that follow the same pattern as those of juveniles. We found, for both juveniles and adults, that the average distance between animals was smaller than the average distance between consecutive locations. Taking into account the potential movement of the crabs (up to 187 mday^{-1}), the average distance between crabs during tracking (80 m) would point to an aggregative pattern as suggested in previous studies (Corgos *et al*., 2002).

An increase in movement scale and directionality was found in the second phase, prior to migration (González-Gurriarán and Freire, 1994). Right before the descent autumn migration, adults move progressively to the outer part of the shallow area, leaving it coordinately in September (males) and October (females) (Corgos *et al*., 2002). Our results show recaptures in the central channel outside the estuary, at a depth of 50 m, suggesting the beginning of movements to deeper areas. Seasonal migrations have been described in decapods such as blue crab (Skajaa *et al*., 1998; Wolcott and Wolcott, 2002), snow crab (Maynard and Webber, 1987), king crab (Fotheringham, 1975) and swimming crabs (Venema and Creutzberg, 1973).

The beginning of the descent migration, which tends to occur in late summer or autumn, has been found to be strongly related to oceanographic parameters together with ontogenetic aspects (Venema and Creutzberg, 1973; Latrouite and Le Foll, 1989; González-Gurriarán and Freire, 1994; Tankersley *et al*., 1998; Watson *et al*., 1999; González-Gurriarán *et al*., 2002; Wolcott and Wolcott, 2002). The period in which our tracking was performed corresponds to the first stationary phase described by González-Gurriarán and Freire (1994). Mating might take place in deep areas (González-Gurriarán *et al*., 1998) where a lek mating system has been suggested by Corgos *et al*. (2002).

The possibility of fertilizing eggs with sperm from previous matings would give the females the opportunity to spawn two o three times without remating (González-Gurriarán *et al*., 1998). The hypothesis of a late winter-early spring ascent migration towards shallow coastal areas, where higher temperatures would favour egg development, was suggested by González-Gurriarán *et al*. (2002). Spawning migrations have also been described for *Callinectes sapidus* (Carr *et al*., 2002; Tankersley *et al*., 1998; Wolcott and Wolcott, 2002). Male spider crab recaptures still occur in spring in deep areas, thus supporting the hypothesis of a just-female ascent migration. Breeding female recaptures in shallow waters occur from December on, as it is the case in our study, supposedly after performing both migrations.

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Landlocked Atlantic salmon: movements to sea by a putative freshwater life history form

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Key words: landlocked, Atlantic salmon, acoustic telemetry, strontium.

Abstract

Certain populations of Atlantic salmon (*Salmo salar*) have become landlocked, and live their entire life history out in freshwater. On the Magaguadavic River, New Brunswick, Canada, hatchery and wild origin landlocked salmon were detected moving downstream towards the ocean, and subsequently back upstream in the river. High levels of strontium, indicative of ocean residence, were found in the scales of these fish. In 2002 and 2003, 23 and 13 landlocked salmon, respectively, from this river were fitted with acoustic tags, and their movements in the lower river and adjacent coastal area were monitored. Some fish covered long distances, eventually moving beyond our tracking array. Others remained in coastal waters in close proximity to the river and its estuary. Two fish that returned early to the river were infested with sea lice, and were detected in areas close to commercial salmon farms.

Introduction

Atlantic salmon exist in both anadromous and non-anadromous forms (Power, 1958; Berg, 1985). Anadromous salmon typically migrate to sea as juveniles (smolt) and return as adults to their natal stream to spawn. Non-anadromous or resident (landlocked) salmon spend their entire life cycle in freshwater, typically using lakes in the watershed as feeding areas for larger fish. Landlocked parr, similar to the anadromous form, inhabit riffle areas. The occurrence of anadromous and landlocked Atlantic salmon is widespread in eastern North America (Scott and Crossman, 1964). Often the two forms are sympatric within a river system. New Brunswick's Magaguadavic River has both anadromous and landlocked forms of Atlantic salmon. In this river, the history of the landlocked salmon population was uncertain prior to the establishment of a hatchery stocking program. Stocking of landlocked salmon into lakes in the Magaguadavic watershed by federal and provincial government agencies began in 1980, and continues now. Some of these fish now reproduce naturally in the river. The history of the anadromous Atlantic salmon has been well documented for the river (Martin, 1984; Carr, 1995; Carr *et al.*, 1997). However, little information is available on the non-anadromous form other than stocking records.

An anadromous salmon monitoring program detected landlocked salmon moving downstream towards the ocean, and subsequently back upstream in the river. It was not known if the fish took up residency in seawater, and if so, how far out to sea they ventured. We also did not know if these were passive movements, driven by spring freshets, or if the fish were showing active migratory tendencies.

Strontium (Sr) has been measured in scales and otoliths by various researchers to document fish movements between freshwater and marine environments (Bagenal *et al.*, 1973; Kalish, 1990; Coutant and Chen, 1993; Halden *et al.*, 1995; Babaluk *et al.*, 1997; Eek and Bohlin, 1997). As fish grow, their scales develop concentrations of trace elements (i.e. Sr) in the calcified matrix that are proportional to those in the environment in which they live. Since Sr concentration is enriched in seawater, a high Sr level (as measured by the standardized Sr/Ca ratio) in some portions of the scales would indicate periods of life spent in seawater. The objectives of this study were: (1) to determine whether the landlocked salmon did move into the marine environment by assessing Sr concentrations in their scales, (2) to determine whether the downstream movement patterns of landlocked salmon are similar to those of anadromous salmon smolts, and (3) to assess marine survival and movement patterns of downstream moving landlocked salmon by acoustically tagging and tracking them through the lower river and out into the surrounding marine environment.

Materials and methods

Study area

The Magaguadavic River is the sixth largest river in New Brunswick. It originates in Magaguadavic Lake in the southwestern part of the province and flows southeasterly 97 km to Passamaquoddy Bay (Fig. 1). There are 103 named tributaries and more than 55 lakes within a drainage area of 1812 km^2. A 13.4 m high dam (built in 1903) located at the head of the tide is equipped with Francis runner-type turbines that generate about 3.7 megawatts of power. A pool and weir fishway bypasses the dam for upstream fish passage. All fish ascending the river from seawater must pass through a collection trap in the fishway. A sluiceway intended for downstream fish passage is situated adjacent to the penstock. The Magaguadavic River drainage supports a sport fishery for landlocked Atlantic salmon, brook trout (*Salvelinus fontinalis*), and introduced smallmouth bass (*Micropterus dolomieui*). The sport fishery for the anadromous salmon run has been closed since 1992 as a result of precipitous declines in the run.

Landlocked salmon were first stocked into Magaguadavic Lake in 1980. From 1985 to 1997, progeny from wild origin broodstock from four New Brunswick lakes (Skiff, Oromocto, Grand, Chamcook) and from Grand Lake, Maine were released into the river. Since 1998, all source broodstock for the stocking program have originated from lakes within the Magaguadavic drainage. Landlocked salmon stocked into the river are all fin clipped to permit identification. Most hatchery fish are released as one year olds, and stocking densities generally range from 1000 to 8000 fish annually.

Identification of landlocked salmon

Salmon were classified as anadromous or landlocked on the basis of fin clips, size, and scale analysis. Stocked hatchery landlocked salmon often have fin clips corresponding to release years and locations. Fork length was recorded to the nearest mm, and a sample of scales was taken to identify the fish. Freshwater ages were determined from circuli patterns on the scales. All Magaguadavic origin wild anadromous salmon smolt move to sea at 2 to 3 years of age, and their fork lengths range from 13 to 25 cm. Wild landlocked salmon leaving the river have been 3 to 7 years of age, with sizes ranging from 31 to 58 cm. Hatchery origin landlocked salmon were stocked as one-year-old at sizes generally greater than 25 cm. Two-year-old hatchery fish have been documented leaving the river at sizes greater than 30 cm.

Strontium Analysis

The analysis of Sr was done using a wavelength dispersive X-ray electron microprobe (WD-EM at the University of New Brunswick, Canada). We analysed scales collected from 34 landlocked salmon returning to freshwater from the sea that were captured at the head of tide fishway trap (13 from 1996, 2 from 1997, 12 from 1998, and 7 from 1999). The scales were embedded in an epoxy matrix (Epofix©) and a transverse cut was made along the long axis of the scale, through the focus, using a steel blade microtome. The smooth surface necessary for the use of WD-EM was attained with a finishing cut using a glass-knife ultramicrotome and the finished blocks were carbon-coated.

We analysed the first five contiguous circuli and 15 additional points were sampled at every other circulus, when possible, covering a region corresponding to approximately the 35 last-laid circuli. Since between 8 and 12 circuli are formed each year in the case of the Atlantic salmon (Summerfelt and Hall, 1987), we investigated the past three or four years of these fish, at a one or two month time resolution. Further details on the methods are given in Courtemanche (2003).

measured, and a sample of scales and fin tissue was taken. Salmon were kept for tagging if they exhibited no external deformities or injuries. All other fish were released downstream of the collection device.

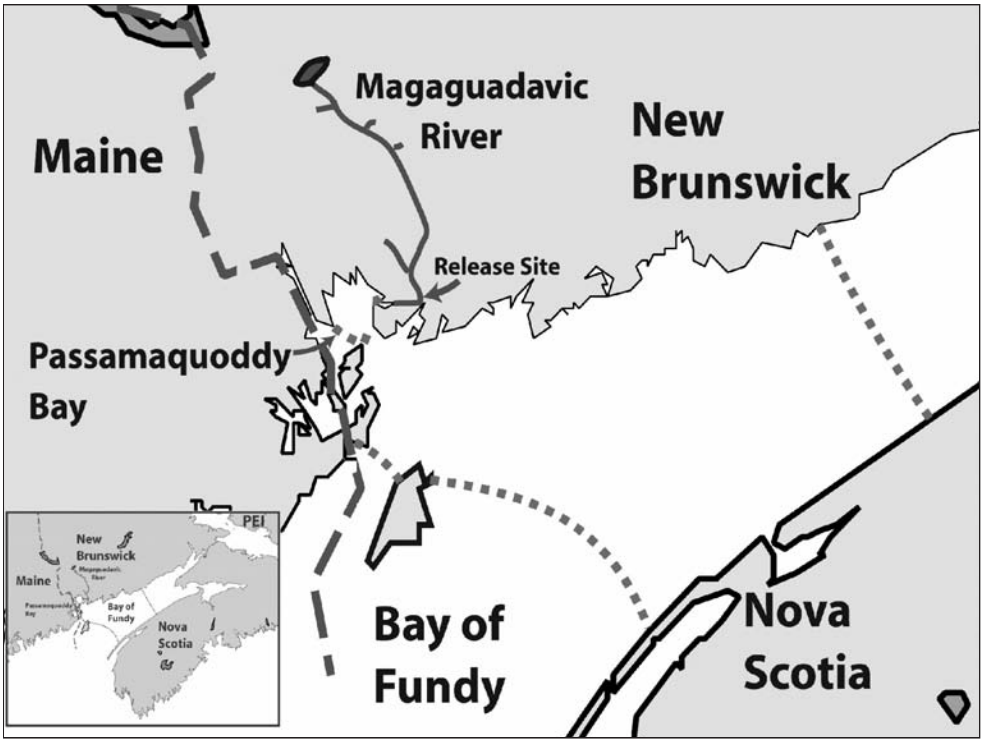

Fig. 1 – Map of study area showing the release site for tagged salmon and the three tracking zones: Magaguadavic River release site to it's confluence with the Passamaquoddy Bay (Zone 1), Passamaquoddy Bay (Zone 2), and the Bay of Fundy (Zone 3). The tracking array in the bays are shown by small squares. The international border is shown by a dashed line.

Tagging Program

Downstream moving landlocked salmon were captured in a smolt counting fence trap (operational from 18 April to 14 June 2002, and from 30 April to 17 June 2003) situated in a bypass stream below the downstream fish passage facility. The trap was monitored daily and fish were classified as landlocked salmon based on size, fin clips, and scale analysis. All fish captured were

Tagging Procedures

V16-4H-R04K coded ultrasonic pingers (65 mm length x 15 mm diameter; weight 26 g, produced by Vemco Limited, Shad Bay, Nova Scotia) were used to tag landlocked salmon. Pingers had a frequency of 69 kHz, minimum and maximum off delays of 10-35 seconds, and an expected life of 366 days.

Pingers were surgically implanted in the peritoneal cavity of the fish. The anaesthetized (using clove oil [40 mgl^{-1}]) salmon were placed ventral side up in a V-shaped trough with moist paper toweling for support. Germex was used to sterilize all surgical tools, sutures, and pingers. Furacin was used to clean the ventral surface of the fish prior to making a 2 cm mid-ventral incision beginning 1 cm anterior to the pelvic fins. The pinger was inserted into the peritoneal cavity under the incision. Three to four sutures (4-0 Ethilon black monofilament nylon with FS-2 circular cutting needle) were applied to close the incision and a tissue cement (Vetbond) was used to seal the incision and stitches. Furacin was sprayed on the closed incision. Fish recovered in less than 10 minutes from the anesthesia and were able to quickly equilibrate after pinger insertion. The salmon were monitored in an oxygenated tank for 24 hours before being released. No post tagging mortalities occurred prior to release.

Releases

In 2002, a total of 23 landlocked salmon were tagged and released from 9 May to 14 June 2002. In 2003, thirteen landlocked salmon were tagged and released from 29 May to 17 June. All fish were released in the Magaguadavic River estuary, situated 500 m below head of tide. Tagged salmon were released between 06:00 and 20:00 hours. No significant differences were observed among fork length or tag to body weight ratios of tagged fish among the release dates and times in each of the years ($P>0.05$).

Tracking

Movements of tagged fish were monitored by positioning submersible receivers (VEMCO VR2-Monitor), each having a built-in omni directional hydrophone with data logging components programmed to decode and identify individual tagged fish at various points (Fig. 1). Weekly active searches for tagged fish were performed (9 May to 11 September in 2002, and on 14 August and 12 September 2003) using a boat equipped with a land-based receiver (VEMCO VR60) having either directional (VEMCO V10) or omni directional (VEMCO VH65) hydrophones. The marine arrays placed in the Bay of Fundy were part of a joint tracking program between the Department of Fisheries and Oceans and the Atlantic Salmon Federation. There were no tracking arrays in the Bay of Fundy in 2003.

Due to the small sample sizes, statistical comparisons were made by non-parametric tests (χ^2, Mann-Whitney, Kruskal-Wallis). The SAS generalized linear model (GLM) was used for comparison of samples of unequal size. The Pearson correlation coefficient was used to test the strength of association of environmental parameters between fish captures.

Results

High levels of strontium were detected in 91% (31) of the landlocked salmon scales analysed (Fig. 2). Only 9% (3) fish had no strontium in their scales (Fig. 2). The mean fork length of the 34 fish sampled was 44.2±4.9 cm. The mean fork lengths of the fish with scales with and without strontium were 46.3±4.3 cm and 44.0±5.0 cm, respectively. Ages of the fish ranged from two to five years. There was no significant difference in fork length or ages between the salmon with scales showing the presence or absence of strontium ($P>0.05$).

A total of 62 landlocked salmon were captured moving seaward during the anadromous smolt run in 2002, and their mean fork length was 35.7±5.2 cm. Most of the 2002 landlocks (75%) and anadromous smolt (89%) were captured over a 29-day period when water temperatures and water discharges averaged 13.9±2.2 °C and 19.7±10.3 m^{3}s^{-1}, respectively (Fig. 3a). A total of 21 landlocked salmon were captured moving seaward during the anadromous smolt run in 2003, and their mean fork length was 42.2±5.67 cm. Most of the 2003 landlocks (76%) and anadromous smolt (68%) were captured over a 7-day period when water temperatures and water discharges averaged 13.7±0.69 °C and 30.9±6.50 m^{3}s^{-1}, respectively (Fig. 3). There was no significant correlation between numbers of salmon captured and any of the environmental parameters (water temperature and discharge) measured in each of the years (P>0.05).

The mean fork length and tag to body weight ratio of tagged salmon in 2002 was 40.7±4.5 cm and 4.7±1.0 %, respectively (Table 1). Their ages ranged from 2 to 5 years (Table 1). The mean fork length and tag to body weight ratio of tagged salmon in 2003 was 43.8±5.4 cm and 4.1±1.3%, respectively (Table 1). Their ages ranged from 3 to 7 years (Table 1). No significant differences were observed in fork lengths, tag to body weight ratios, or ages between wild and hatchery landlocked salmon in each of the years (P>0.05, see Table 1). However, fork lengths of the tagged salmon in 2003 were slightly larger than the tagged fish in 2002 (P<0.05). No differences were found in tag to body weight ratios between the two years (P>0.05).

Three (13%) and one (8%) of the tagged salmon did not leave the seawater section of the Magaguadavic River in 2002 and 2003, respectively (zone 1, see Fig. 1). Those fish moved 8 km from the release site to the mouth of the river where they resided (within a 1 km section inside river mouth) throughout the study. A total of 14 (61%) and 9 (69%) of the tagged fish moved into Passamaquoddy Bay in 2002 and 2003, respectively (zone 2, Fig. 1). Five salmon tracked in 2002 were detected on receivers in the Bay of Fundy (zone 3, Fig. 1). No receivers were positioned in the Bay of Fundy in 2003.

It took the tagged salmon from 1 to 22 days to reach the mouth of the river (8 km) in 2002, significantly longer than the 1 to 4 days it took for the tagged fish in 2003 to cover the same distance (P<0.05, see Table 2). The sizes of the tagged salmon tracked to the mouth of the river in 2003 were significantly larger than the fish tracked in 2002 (P<0.05, see Table 2). The tag to body weight ratio for the same group of fish in 2003 was lower than those in 2002 (P<0.05, see Table 2). The ultimate destination of individual fish did not significantly influence the time taken to reach the river's mouth within each year (P>0.05, see Table 2). There was no difference between years in the fraction of tagged fish moving out of the river and into the bay (P>0.05).

The final positions for the 14 tagged fish that left the river in 2002 was as follows: six signals were last recorded in Passamaquoddy Bay, four signals were last detected in the anadromous salmon smolt migration route between Grand Manan NB, and Nova Scotia, and four fish had returned to the river. The latter group spent from 1 to 31 days at sea before returning to the river. Of the fish returning to the river, two were recaptured in the fishway trap at head of tide 45 and 55 days after initial release. One of the recaptured fish had travelled to the inner Bay of Fundy, more than 150 km from the initial point of release (see inner bay arrays, Fig. 1). Both recaptures had heavy sea lice (*Lepeophtheirus salmonis*) infestations and extensive external damage along the head, typical of sea lice attachment. The fish had increased in length by 1.4 and 1.7 cm respectively, during their residence at sea.

The final positions for the tagged salmon in 2003 was as follows: four signals were last detected on receivers in Passamaquoddy Bay, five signals were never detected after the fish left the Magaguadavic River, and the signal from one fish remained near the mouth of the Magaguadavic River. It is unknown whether any tagged fish left Passamaquoddy Bay since no receivers were positioned in the Bay of Fundy in 2003. Although no tagged fish returned to the river in 2003, there was no significant difference in fractions of active tracked fish returning to freshwater (9% in 2002, 0% in 2003) between the two years (P>0.05).

Six (26%) and three (23%) of the tagged fish were suspected to have died within 3 km downstream of the release site in 2002 and 2003, respectively since their signals were either lost or tag positions remained stationary within two days after release. The tag to weight ratios for the six (2002) and three (2003) lost signals was 4.0±1.3 and 4.4±0.6%, respectively (Table 2). There was no significant difference in the fractions of signals lost between years (P>0.05). The pooled data (2002 and 2003) showed no significant difference in both tag to weight ratios and fish sizes for lost signals and fish tracked in zones 1 to 3 (P>0.05, see Table 2).

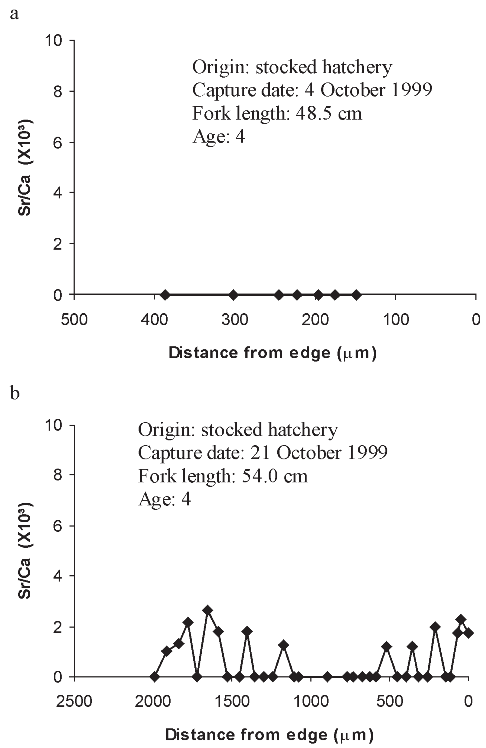

Fig. 2 – Representative Sr/Ca analysis from two different fish that had returned to freshwater from the sea, and showing (a) no strontium and (b) high frequencies of strontium. Scales were analyzed from landlocked salmon captured at a head of tide fishway in the Magaguadavic River.

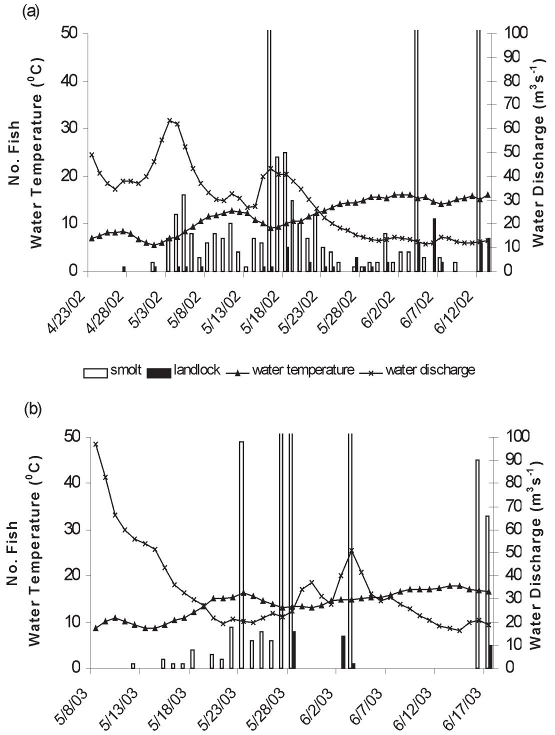

Fig. 3 – The daily numbers of landlocked salmon and anadromous smolt captured in a counting fence trap below the outlet of a downstream fish passage facility in the Magaguadavic River in (a) 2002 and (b) 2003. The water temperatures and discharges are also presented.

Table 1 – Total numbers, origins, fork lengths, tag to body weight ratios, and ages of acoustically tagged landlocked salmon in the Magaguadavic River in 2002 and 2003.

Year	Origin	No. Fish	Fork length (cm)		Tag to body weight ratio		River age
			Mean±s.d.	Range	Mean±s.d.	Range	Mean (range)
2002	Wild	3	44.2±11.7	36.7-57.7	4.6±2.8	1.4-6.5	4.0 (3-5)
	Hatchery	20	40.1±2.6	37.3-41.8	4.8±0.7	3.9-6.7	3.2 (2-4)
	Total	23	40.7±4.5	36.7-57.7	4.7±1.0	1.4-6.7	3.3 (2-5)
2003	Wild	4	42.0±3.0	39.3-45.5	4.0±0.7	3.1-4.8	3.8 (3-5)
	Hatchery	9	44.7±6.1	39.5-59.6	4.2±1.5	1.1-5.9	4.1 (3-7)
	Total	13	43.8±5.4	39.3-59.6	4.1±1.3	1.1-5.9	4.0 (3-7)

Table 2 – Total numbers, fork lengths, tag to body weight ratios, and number of days to reach river's mouth of tagged fish in the three tracking zones. The biological data is also presented for tagged fish that were lost (signified as 'dead') shortly after initial release. The tracking zones are as follows: Zone 1: seawater section of the Magaguadavic River; Zone 2: Passamaquoddy Bay; Zone 3: Bay of Fundy. No tracking arrays were in Zone 3 during 2003.

Year	**Zone**	**No. Fish**	**Fork length (cm)**	**Tag to body weight ratio (%)**		**No. days to river mouth**	
			Mean±s.d.	Mean±s.d.	Range	Mean±s.d.	Range
2002	1	3	39.7±1.2	4.7±0.3	4.5-5.1	4.7±0.3	1-5
	2	9	38.3±0.9	5.1±0.7	4.5-6.5	5.1±0.7	2-22
	3	5	40.9±2.9	4.9±1.2	3.9-6.7	4.9±1.2	2-21
	Dead	6	44.4±7.4	4.0±1.3	1.4-5.1		
2003	1	1	41.5	5.9	5.9	5.9	1
	2	9	44.9±6.2	3.8±1.3	1.1-5.6	3.8±1.3	1-4
	Dead	3	41.6±3.4	4.4±0.6	3.7–4.8		
Combined	1	4	40.2±1.3	5.0±0.6	4.5-5.9		
	2	18	41.6±5.4	4.5±1.2	1.1–6.5		
	3	5	40.9±2.9	4.9±1.2	3.9–6.7		
	Dead	9	43.5±6.2	4.1±1.1	1.4-5.1		

Discussion

The detection of strontium in landlocked salmon scales showed that these fish were indeed moving into the ocean. We had hoped that by analyzing Sr/Ca ratios for individual circuli, we might be able to arrive at a rough estimate from growth rates of the duration the fish spent at sea. Unfortunately, the elemental composition of scales appears to be somewhat unstable, at least for strontium (Courtemanche, 2003), which makes this analysis unworkable.

This study has shown that landlocked salmon can move to and survive in a marine environment for extended periods of time. Migration patterns were highly variable among the tagged fish. Some fish remained in the Magaguadavic estuary, others moved into Passamaquoddy Bay and Bay of Fundy, and some returned to freshwater after up to 55 days at sea. We do not know if these fish underwent a smoltification process similar to that observed for anadromous salmon juveniles moving to sea (Ruggles, 1980).

The out-migrant landlocked salmon seem to be exhibiting a movement pattern typical of many salmonids, however, their migration was not significantly influenced by temperature or water discharge. Anadromous salmon smolt runs typically peak at a water temperature of 10 °C or higher, and the migration period generally lasts for about 30 days (Elson, 1962; Jessop, 1975; Solomon, 1978; Ruggles, 1980; Moore *et al.*, 1998). Montgomery *et al.* (1983) reported that the onset of the downstream runs for anadromous brook trout and

Atlantic salmon smolt coincided with declining water levels and discharge.

Landlocked salmon individuals exhibited very different movement patterns, all typical of salmonids but some atypical of the species. The course tracks suggested a tendency for some tagged landlocked salmon to behave similar to sea run charr and trout. Brook trout, Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), and cutthroat trout (*Oncorhynchus clarki*) can move from freshwater in the spring of the year to marine environments (near their home river), and return to freshwater in the autumn or winter to spawn or overwinter (Dutil and Power, 1980; McCart, 1980; Castonguay *et al*., 1982; Jonsson, 1985; Trotter, 1989; Finstad and Heggberget, 1993; Gulseth, 2000; Curry *et al*., 2002).

Arctic charr have been documented to spend as few as 10 days at sea, whereas cutthroat trout have spent more than a year in the ocean (Trotter, 1989; Begout Anras and Gyselman, 1999).

Four tagged landlocked salmon moved into the open ocean and were last detected near Grand Manan Island. Anadromous Atlantic salmon postsmolts have been detected in the vicinity of Grand Manan Island on their way to ocean feeding grounds which can be as far away as Greenland (Lacroix, 1996). It is conceivable that this group of landlocks were heading to the species feeding grounds in the North Atlantic.

It is possible that the signals lost (or detected in the same position) in each of the years may have resulted from predation. Of the lost signals, 83% and 67% were from hatchery-reared fish in 2002 and 2003, respectively. Those fish were released during peaks in the anadromous smolt run, a run composed mostly of hatchery escapes from commercial salmon industries along the river. Avian and seal predators were frequently observed during that period just below head of tide.

The higher water discharge experienced in 2003 may explain the increased rate of tagged fish movements to the river's mouth. Aarestrup *et al.* (2002) reported that increased discharges might reduce predation on trout smolts. They suggested that a higher discharge results in higher turbidity, reducing visibility for predators. When smolts move faster, they also reduce their exposure time to riverine predation.

The results from this study suggest that the size of tags did not negatively influence fish survival, movements, and growth. Some studies have recommended that the tag to body weight ratios should not exceed 2% (Fried *et al.,* 1976; Paukert *et al*., 2001). However, Brown *et al*. (1999) reported that Atlantic salmon smolt swimming performance was not affected by tag to body weight ratios ranging from 6 to 12%. In our study, the tag to body weight ratios ranged from 1.1 to 6.7%. The tag to body weight ratios were lower for lost signals (dead fish) than for those fish that remained active for extended periods. We also found that the tagging incision on the two recaptured fish in 2002 had healed and mesentery tissue had begun to surround the tag in the body captivity, less than two months after initial tag implants. Each of the recaptures also had increased in length by about 4% (i.e. had actively fed) since their initial surgery.

The sea lice damage reported on the two recaptured landlocked salmon suggests that levels of infestations could pose a mortality risk to outmigrant salmon smolts, which could contribute to wild salmon declines in the region. Ten of 23-tagged landlocked salmon tracked into Passamaquoddy Bay during this study were detected near sea cages. Carr and Whoriskey (2004) reported sea lice infestations on 21 and 23% of wild anadromous adults and landlocked salmon, respectively, captured over an 11-year period ascending the head of tide fishway trap on the Magaguadavic River. Sea lice infestations have been a major cause of fish mortality and economic loss in the Bay of Fundy salmon aquaculture industry (MacKinnon, 1997).

These results may have major management implications. Some landlocked Atlantic salmon utilize the marine environment. The poor return rates (2 of 38 fish) suggest that there may be a high at sea mortality rate. Given that landlocked fish do maintain the capacity to adapt to seawater, and to undertake ocean movements, it may be possible for rivers that have endangered wild anadromous runs, to utilize landlocked salmon in the system as part of the broodstock in live gene banks for restoring sea-run populations. However, more research is needed to address whether any genetic similarities may exist between anadromous and landlocked populations, especially on a river-by-river basis.

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Spatial segregation of three anadromous salmonids in a northern Labrador (Canada) river during the spawning and over wintering periods

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Abstract

The range of anadromous Atlantic salmon (*Salmo salar*), Arctic charr (*Salvelinus alpinus*) and brook charr (*Salvelinus fontinalis*) overlap in coastal rivers of Labrador, Canada. These species have similarities in both life history characteristics and habitat requirements and it was thus hypothesised that their co-existence would lead to habitat segregation within a given river system. This hypothesis was tested in the English River where returning adults were surgically implanted with radio transmitters during July-August, 2001. The geographic location of these fish was investigated both in early and late October 2001 and again in January 2002 to elucidate spawning and over-wintering habitat utilisation. Additionally, a series of fixed stations, located at significant junctions within the river system, monitored the movement of the tagged fish from August 2001 to July 2002. While habitat utilisation varied within each species, a majority of the tagged individuals within a species exhibited similar behaviours. Although some overlap existed geographically, the three species occupied separate areas during spawning and the subsequent over-wintering periods. A detailed description of the habitat used and the differing behaviours exhibited by the three species are presented and discussed.

Introduction

Good scientifically defensible management of habitat is an important component of viable fisheries management strategies (Auster, 2001; Minns, 2001). Habitat managers however, are often faced with making decisions in absence of the scientific information they require and this increases the uncertainty within the decision making process (Minns and Moore, 2003). Habitat utilisation patterns are an important 'first step' in the habitat management process when trying to determine the potential a development has for harm to fishery resources (e.g. Bradbury *et al.*, 2001). Despite our advanced knowledge in many areas of fishery science, fish habitat associations for many species and geographic locations are still rudimentary (Minns, 2001; Minns and Moore, 2003). This is especially true in remote locations where little research has been conducted and physical and biological conditions can be quite different from areas where the scientific literature has been developed for any particular species.

Industrial development within Labrador has grown exponentially over the past three decades with many of the new projects expected to have significant interactions with freshwater habitats (i.e. mining; hydroelectric development; road building etc.). Despite this activity, very little habitat information for aquatic species has been collected in Labrador freshwater systems, due in large part to the remoteness of the area. The little habitat utilisation information we do have has generally been collected in conjunction with the larger development projects that have undergone environmental assessment (e.g. Ryan, 1980; Beddow *et al*., 1998). Experience gained from these environmental assessments has generally indicated a unique habitat utilisation pattern for most species sampled within the Labrador landscape. The reasons for these differences may be varied but most likely include differences due to colder environmental conditions, from the influence of the Labrador Current, and overall lower fish species diversity. Coastal Labrador systems are generally dominated by salmonids, which have similar life history patterns and overlapping ranges throughout Labrador, and lack predators and competitors from the Esocidae, Cyprinidae and Percidae as compared to other North American locales.

For the reasons cited above there was a need to improve our knowledge on the habitat utilisation patterns within Labrador Rivers. The use of telemetry vastly improves our ability to investigate usage patterns in large watersheds and the English River system supplied a unique opportunity as it contains three of the most valued anadromous salmonids in coexistence (Reddin *et al*., 2001). The three species, Atlantic salmon, brook charr and Arctic charr all are highly valued in commercial, recreational and aboriginal fisheries. Although the coexistence of anadromous populations of these three species may be considered rare throughout the world their ranges overlap throughout Labrador and it is quite common to find them in the same river system. The interaction of these species is poorly understood and a recent review of their freshwater habitat requirements failed to produce any information on the habitat requirements of Arctic charr or from rivers where they co-exist (Scruton *et al*., 2000).

It was thus hypothesised that the coexistence of these three anadromous salmonid species with similar life history patterns would result in distinct habitat use patterns due to competition for available habitat. These habitat use patterns were expected to differ from published reports or from observations made on the island portion of Newfoundland and Labrador where the low fish diversity has been associated with a niche expansion for many species (Gibson *et al*., 1993). Habitat utilisation was investigated for the three species within distinct life history stages (i.e. spawning and over-wintering) which is consistent with ongoing efforts to manage habitat within Newfoundland and Labrador (Bradbury *et al*., 2001).

Materials and methods

Study area

English River is located in northern Labrador with a catchment area of 545 km^2. It flows in an easterly direction into Kaipokok Bay at 54° 58’ N 59° 45’ W, approximately 8 km northeast of the town of Postville (Anderson, 1985; Fig. 1). The lower mainstem section of the river is characterised by braided channels, created by islands, with a predominance of cobble/gravel substrate. The upper part of the mainstem has a higher gradient with three small falls and larger substrate sizes. The entire mainstem section is only 700 m in length. The lower portion of the catchment is dominated by English River Pond with a surface area of 15.62 km^2. Four tributaries flow into English River Pond (Fig. 1) with the two major tributaries, Goudies Brook and Tilt Cove Brook comprising the majority of the fluvial habitat within the entire catchment.

Goudies Brook is comprised of a series of ponds that are connected by areas of ‘classical’ salmonid habitat with a good mix of cobble/gravel substrates. There is an impassable falls on Goudies Brook approximately 11 km from the confluence with English River Pond (Fig. 1). Tilt Cove Brook has two sub-tributaries which empty into Deer Pond (Fig 1). The first of these (Tilt 1) is comprised of good salmonid habitat with a mixture of cobble/gravel substrates and moderate gradients. The entrance to the second sub-tributary from Deer Pond has a high gradient with limited areas that would serve as resting areas for migrating salmonids and was thus deemed inaccessible.

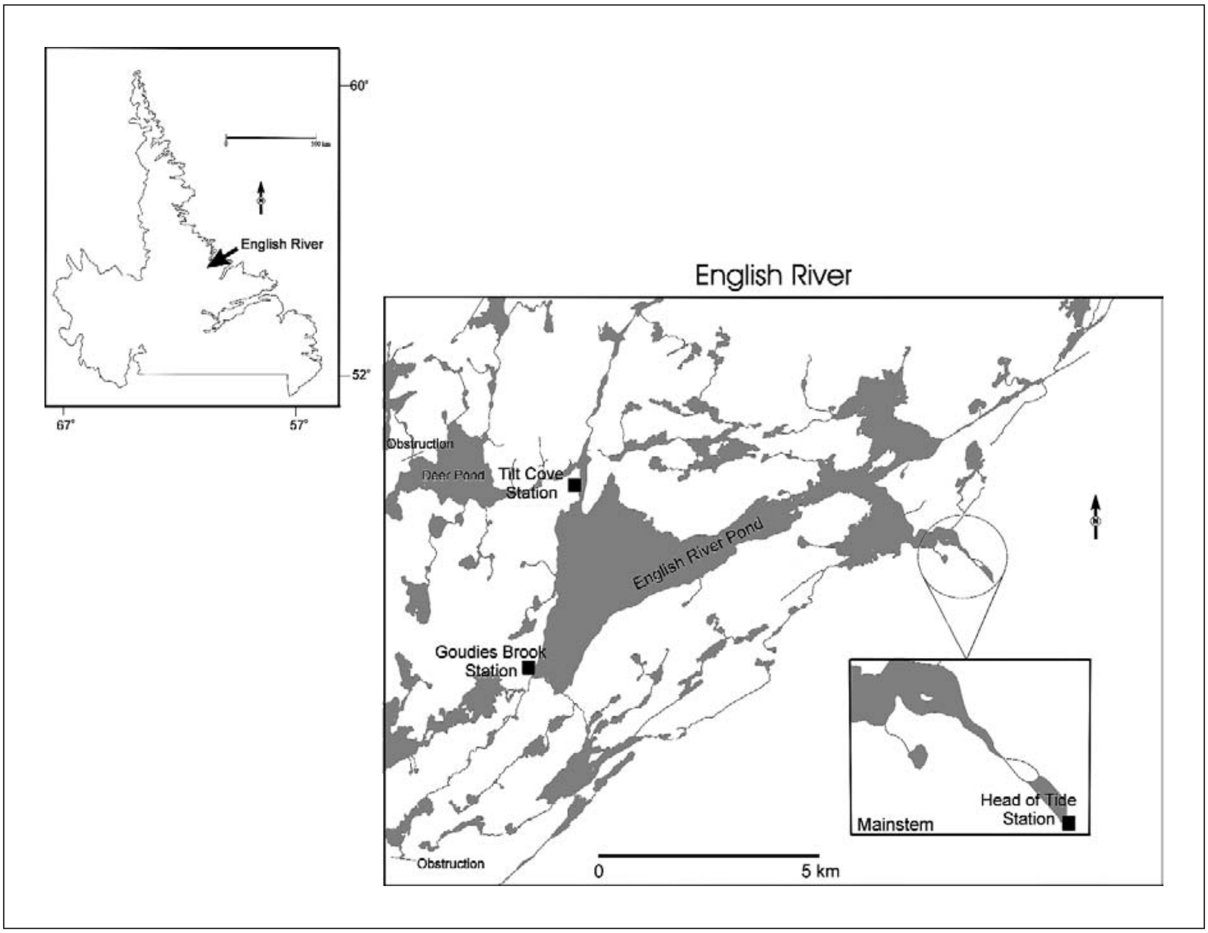

Fig. 1 – Location of the English River system with fixed station monitoring sites highlighted. Inset shows accessible portions of the watershed only.

Tagging and monitoring

Surgery and manual tracking procedures followed those as outlined by Clarke *et al*. (2001). Coded radio transmitters (Lotek model MCFT-3BM; 11x43 mm, 3.7 g in water), with an expected battery life of 278 days, were surgically implanted in twenty three Atlantic salmon, twenty eight Arctic charr and twenty brook charr during two surgery episodes in late summer 2001 (Table 1). Fish were collected from a complete counting fence operated just above head of tide. Fish were immersed in an anaesthetic bath until equilibrium was lost (3-5 minutes), anaesthetic consisted of clove oil (40 ppm) dissolved in ethanol. Fish were then placed on a V-notched table for surgery. During surgery fish were kept moist at all times and fresh water was continually passed over the gills via a small portable pump. Additional anaesthetic was periodically passed over the gills during surgery, ensuring that the fish stayed under the influence of the anaesthetic during handling. After surgery was complete (3-5 minutes), fish were held until the effects of the anaesthetic wore off and equilibrium was restored, at which time the fish were released into a pool just above the counting fence where they could be observed until they resumed their upstream migration.

Table 1 – Characteristics of tagged fish.

Species	July 25-27 N (tagged)	August 28-30 N (tagged)	N (tracked)	Average FL (range); (mm)
Salmo salar	23	0	19	550 (440 – 730)
Salvelinus fontinalis	1	19	18	350 (290 – 475)
Salvelinus alpinus	27	1	22	444 (360 – 560)

FL = Fork length.
N (tracked) = Number of tagged fish detected at least once through monitoring.

Monitoring consisted of both fixed-station sites at significant junctions within the catchment and three separate helicopter trackings. Fixed-station sites consisted of a Lotek SRX 400 receiver capable of detecting the coded tags with a date and time stamp. These stations utilised a 3-element Yagi antennae with an approximate range of 150 meters and were powered by a deep cycle 12 volt battery which was trickle charged by a solar panel. Two stations were set up on July 27, 2001, one at the junction of Tilt Cove Brook and English River Pond and the second at the confluence with Goudies Brook and English River Pond (Fig. 1). The Tilt Cove Brook station was in operation until October 2, 2001 and was subsequently moved to a site just above head of tide to monitor fish migrating out to sea. The Goudies Brook station was removed January 8, 2002. The lower station was installed on October 28, 2001 but did not operate properly for the entire winter, due to extremely cold temperatures. This station did operate properly from October 28 to November 14, 2001; December 12 to December 25, 2001; January 7 to January 23, 2002 and February 4 to July 18, 2002. Additional information about salmon migrating out to sea was derived from two recaptures that occurred within Kaipokok Bay during the aboriginal fishery of 2002. Three manual tracking episodes were conducted to locate fish positions. Two were conducted in the fall of 2001, October 2/3 and October 29, to elucidate spawning locations and one was conducted in mid winter, January 15, 2002 to elucidate over wintering locations. Tracking was conducted from a helicopter, affixed with an H-antenna and a Lotek SRX 400 receiver, moving at a speed of approximately 60-70 kmh^{-1} at an altitude of less than 100 meters above the river, which was well within the range of the transmitters. Once a tag was located its geographic position was recorded using a hand held Global Positioning System (GPS) (model: Garmin III Plus). The receiver was also set to log data during the helicopter flights, which augmented the manual recording of fish positions. Due to the large number of fish located within the mainstem, manual tracking from the ground was also conducted for this area during October 2, 2001. Fish locations were subsequently entered into a Geographic Information Systems (GIS) program (Map Info) and overlaid onto a 1:50,000 map (1:50,000) of the catchment to delineate likely spawning and over wintering areas for the three species within the system.

Results

Two of the tagged brook charr did not have any information collected during the monitoring exercise. One of these was found dead on the mainstem in September, 2001 (Table 1). Of the remaining 18 brook charr the majority (15) stayed within the mainstem area for the entire monitoring period (Fig. 2). The brook charr were located in two main aggregations within the mainstem. Six (6) fish stayed just above head of tide for the entire monitoring period returning to saltwater in June while seven (7) were located in the upper section of the mainstem, these fish also returned to saltwater in June. Two of the brook charr known to have returned to saltwater during the spring of 2001 were observed to re-enter freshwater in late summer 2002 after approximately 3 months in saltwater.

Only three (3) brook charr ventured past the mainstem into English River Pond and beyond (Fig. 2). One of these fish (code 58.1; see table 1) was located in Tilt Cove brook during the spawning season (October 2) and was located at the far end of English River Pond, near the entrance to Goudies Brook, during the winter (December 14, 2001). This fish had returned to the area just above head of tide on the mainstem by June 20, 2002 and remained in this area for one month before re-entering saltwater. One other brook charr entered Tilt Cove Brook on September 17, 2001 and was located in Deer Pond during both the October and January manual trackings. The final brook charr which was tracked successfully was located in a small pond off English River Pond (Fig. 2) during October, 2001 but was not located in subsequent tracking.

Sixty percent (13 of 23) of the tagged salmon passed the Goudies Brook station within a month of their release from the fence site. During the spawning season these fish were located throughout Goudies Brook (Fig. 3), which has a number of suitable spawning areas with good gravel and suitable velocities. The salmon remained in Goudies Brook throughout the winter either near their spawning sites or in one of the small ponds on the system (Fig. 3). Three of the salmon located in Goudies Brook were recorded returning to sea in late June 2002 which was almost two months later than salmon that used the lower part of English River (see below).

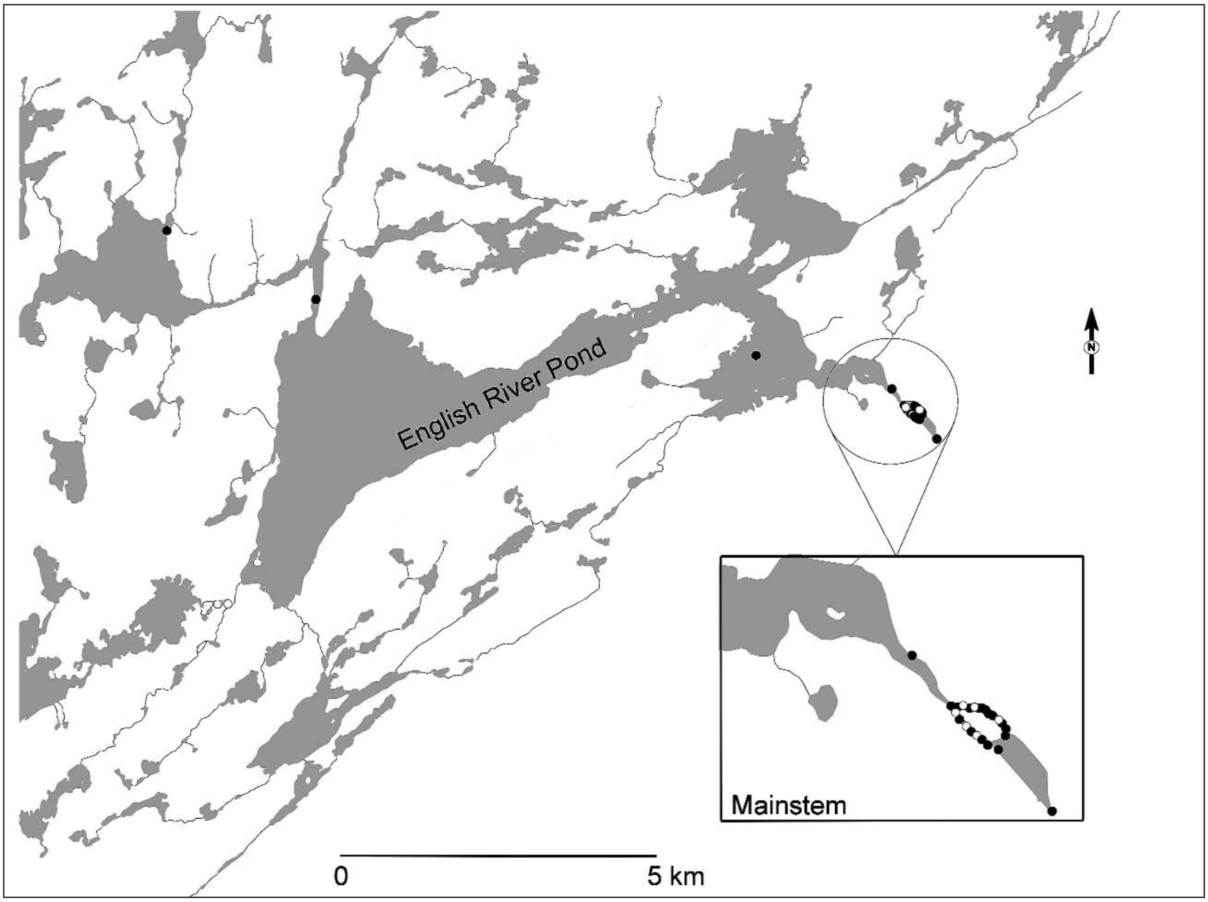

Fig. 2 – Location of brook charr (*S. fontinalis*) during fall (❍) and winter (●) monitoring periods.

A second aggregation of tagged salmon (N=5) used the upper portion of the mainstem just downstream of the English River Pond outlet (Fig. 3). These fish were observed spawning on isolated pockets of suitable substrate that are located in this area. These fish either over wintered in a similar area to their spawning locations or moved up into lower part English River Pond (Fig. 3). Two of the salmon using this area passed the downstream station on their way to sea in late April. Four of the tagged salmon were never located during the monitoring program (Table 1).

The largest aggregation (50%) of Arctic charr was located within English River Pond during both the fall and winter tracking period (Fig. 4). These fish were located at depth as indicated from the transmission power of the tags. Four charr were located over suitable spawning substrate within the mainstem. Five charr entered Tilt Cove Brook, two of which entered the eastern tributary and were located in suitable spawning habitat; the other three fish remained in Deer Pond. One charr entered Goudies Brook on September 23 but returned to English River Pond during the winter (January 15) and one charr was located over suitable spawning substrate in a small tributary off the Northeast coast of English River Pond (Fig. 4).

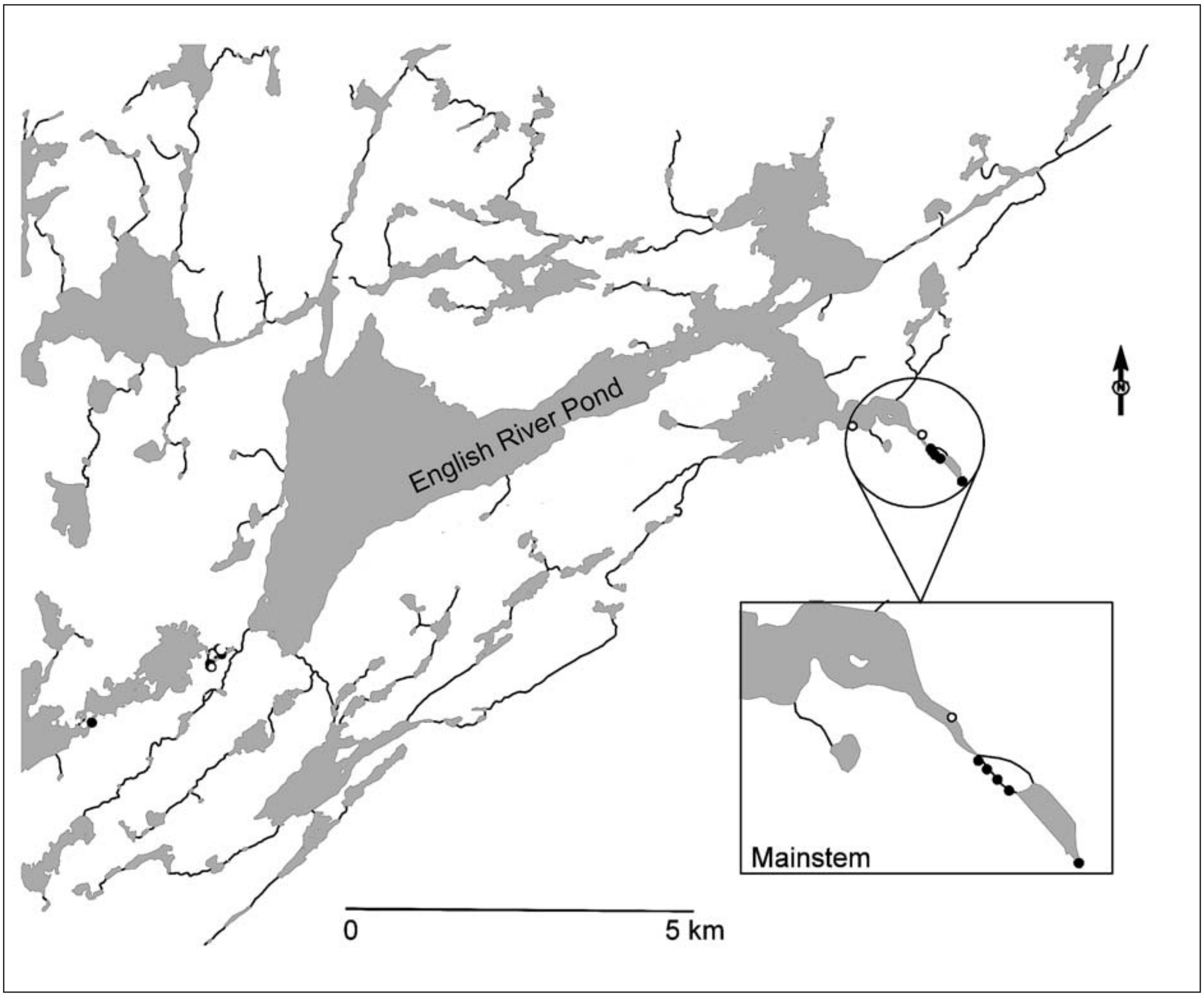

Fig. 3 – Location of Atlantic salmon (*S. salar*) during fall (❍) and winter (●) monitoring periods.

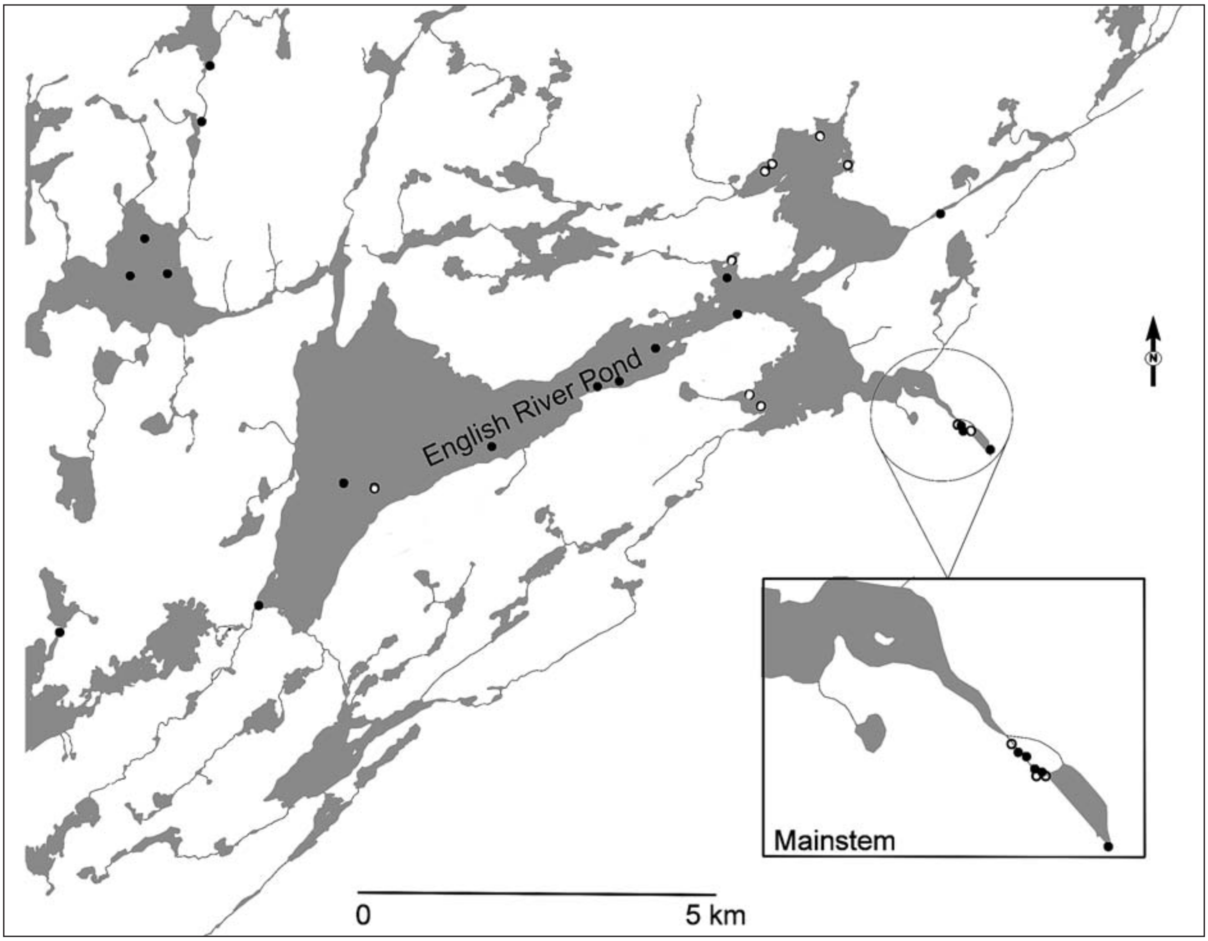

Fig. 4 – Location of Arctic charr (*S. alpinus*) during fall (❍) and winter (●) monitoring periods.

Discussion

The species that had the widest utilisation of the English River system and exhibited the most diverse behaviours was the Arctic charr. Over sixty percent (> 60%) of the charr monitored were located in lacustrine habitats during both tracking episodes in October 2001. These fish were located at depth and were not associated with shoals that may serve as spawning areas for this species (Dempson and Green, 1985). While it is quite possible that these fish moved from English River Pond to a small, unmonitored tributary to spawn either between or after our tracking episodes, previous work has indicated that this species does not spawn every year (Dempson and Green, 1985; see also review in Klemetsen *et al*., 2003) and many migrants move into freshwater to over-winter. Charr associated with spawning habitats were equally divided between those that remained in the mainstem and others that moved into two small tributaries in the upper areas of the watershed.

Both brook charr and Atlantic salmon exhibited fairly limited distributions within English River. Salmon either stayed within the mainstem on isolated pockets of suitable spawning gravel or they moved through English River Pond and entered Goudies Brook to spawn. Salmon that remained in the mainstem tended to use the upper section just downstream of the outlet of English River Pond.

Some of these fish subsequently moved up into the pond to over winter. From a management perspective it appears that Goudies Brook may be the most important producer of Atlantic salmon for the entire watershed and again lacustrine areas may serve as important over wintering areas for post spawned adults.

The brook charr were the most aggregated of the three species and for the most part showed very little migration into the English River system. Anadromy is not a well studied life history strategy for brook charr, but many authors have hypothesised that charr following this strategy make limited migrations between estuarine and freshwater habitats throughout the year (Power, 1980). The fish were located just above the head of tide, which has both areas of suitable spawning substrate and a large pool where fish may over winter. The head of tide area was found to be an important over wintering site for post spawned Atlantic salmon in the Miramchi, New Brunswick (Komadina-Douthwright *et al*., 1997). The authors hypothesised that this area would supply a relatively stable area with respect to environmental variables due to the influence of the salt water. Recent work on anadromous brook charr movements in eastern Canadian systems has also found that this was an important habitat for the populations studied (R. A. Curry, University of New Brunswick, personal communication). Since the head of tide area of English River, could supply both spawning and over wintering opportunities, and there was limited separation of the tagged individuals, it is difficult to say how many of the fish were using this area for either purpose. It is evident however, that this section of river is an important habitat for the anadromous brook charr of the English River system.

There was little movement by the majority of the fish between their selected spawning areas in October and over wintering sites in January but the manual tracking data was limited in temporal resolution. Salmon tended to move into lacustrine areas adjacent to their spawning sites and the charr species either remained in the lake for Arctic charr or at the head of tide for brook charr. There was some movement within the lake by Arctic charr with an aggregation of fish in the large bay to the Northeast side of English River Pond (Fig. 4). Also, the brook charr, which did migrate into the main catchment, over wintered in an outlet area on the southwest side of the pond (Fig. 3). It is possible that these areas have a preferred thermal habitat, possibly created by groundwater, which has been associated with over wintering sites for other salmonids (Power *et al*., 1999). The behaviour exhibited by the three species tended to separate them in space throughout the English River system with the most overlap occurring throughout the mainstem. Even within the mainstem salmon and charr used opposite ends of the river stretch but there was little separation between individuals of the two charr species using the lower sections of the river. Individuals that utilized the mainstem tended to return to sea earlier than those that migrated to the upper portions of the system. This behaviour would be expected to increase survival and production for these earlier returning individuals which, is an interesting hypothesis for future research.

It was apparent that a large proportion of the migrating adult charr were not on a spawning run but moving into freshwater to over winter. While not a unique observation for northern populations (Klemetsen *et al*., 2003; Power, 1980) this has important ramifications for fishery management decisions with respect to stock recruitment relationships and would make environmental assessment descriptions more difficult and time consuming to conduct for these species. Also, this behaviour as well as the post spawning movements of the salmon suggests that over wintering habitats play an important role in the production of these populations.

Although this work was limited in its sample size and temporal coverage of the upstream migration, with only two tagging episodes, it has revealed that the fish species studied exhibit a variety of behaviours. This work is thus, a good first step in the investigation of the habitat associations these species have during coexistence in coastal Labrador systems. Such information is needed by managers, who are faced with decisions regarding habitat alterations and their potential for harm as well as ways to mitigate and compensate for harmful encroachments. The diversity of fish behaviours observed is an important consideration from a management viewpoint. Many of the behaviours were unique to an individual species and may be viewed as differing from the norm for salmonids throughout more temperate climates.

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Movements and migrations of North Atlantic Bluefin tuna tagged with pop-up satellite tags

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Abstract

A total of 84 bluefin tuna were tagged with two types of electronic pop-up satellite tags and released in the Mediterranean and the Strait of Gibraltar between June 1998 and August 2000. Twenty-three tags (30%) were located by the Argos satellite system and the location rates were 21% and 52%, respectively for pop-up single-point tags (PTT-100 tag made by Microwave Telemetry Inc., Columbia, Maryland, USA) and pop-up archival tags (PAT tag made by Wildlife Computers Inc., Redmond, Washington, USA). Most tags surfaced in the western Mediterranean and eastern Atlantic, but one archival tag transmitted from a position south of Iceland and one single-point tag transmitted from the Greenland Sea. No transatlantic migrations were observed. Most tags released in the western Mediterranean surfaced near the tagging location, suggesting local residency. Residency and spawning site fidelity (which was also indicated by our data) offer the potential for overexploitation, if the industry progressively catches more large bluefin tuna for fattening. Tag experiments using pop-up archival satellite tags were conducted in collaboration with the Tuna Research and Conservation Centre, USA.

Introduction

Stock assessments of North Atlantic bluefin tuna (*Thunnus thynnus* L.) are currently carried out on the assumption that there are two stocks, the eastern Atlantic & Mediterranean and the western Atlantic, separated by a conventional boundary at 45° W. This two-stock hypothesis is supported by the presence of small to large bluefin tuna on both sides of the Atlantic, the occurrence of spawning in the Gulf of Mexico and in the Mediterranean at different times of the year, and the morphometric differences of bluefin tuna from the two grounds.

Analyses of conventional tagging data, which show a low mixing rate between west and east, with most tags recaptured in the area of release, also support the existence of two separate groups of bluefin tuna in the North Atlantic.

Recently, however, several electronic tagging programmes have been initiated to improve our knowledge of the migrations of North Atlantic bluefin tuna and investigate the occurrence of transatlantic movement (Block *et al*., 1998; 2001; Lutcavage *et al*., 1999).

In Europe, experiments with pop-up satellite-detected tags were carried out in the eastern Atlantic and Mediterranean between June 1998 and August 2000 as part of an EU FAIR Project. The aims of the project were: a) to identify and describe migrations and movements of bluefin tuna, both within the Mediterranean and between the Mediterranean and the Atlantic Ocean, in relation to spawning and nursery areas; b) to evaluate the practicalities of using pop-up satellite-detected tags; and to gain experience for future projects with large pelagic fish (De Metrio *et al*., 1999; 2001; 2002).

The present paper provides an overview of the results obtained during the EU FAIR Project. The findings, which have been partially reported to the international fisheries research community in several short ICCAT papers, are presented here for the benefit of the wider scientific community.

Material and methods

A total of 84 bluefin tuna were tagged with pop-up satellite-detected electronic tags in the Mediterranean and Eastern Atlantic, between June 1998 and September 2000. Types and number of tag used were: 61 PTT-100 pop-up single-point tags (Microwave Telemetry Inc., Columbia, Maryland, USA), which recorded a limited number of temperature measurements, and 23 PAT pop-up archival tags (Wildlife Computers, Redmond, Washington, USA), which recorded temperature, depth and daily longitude. Experiments with PAT tags were conducted in collaboration with the Tuna Research and Conservation Centre, Monterey, California, as part of the United States co-ordinated TAG programme.

Three bluefin tuna were tagged with PTT-100 tags, using an underwater gun, at the Stintino trap (Sardinia, Italy) in June 1998. Thirty-two bluefin tuna were tagged with PTT-100 tags by underwater gun or hand-held harpoon in the large bluefin tuna trap at Barbate (Spain), to the west of the Strait of Gibraltar, in July 1998 (9 fish) and in July 1999 (23 fish). Twenty-two bluefin tuna captured in the local sport fishery were tagged, either alongside the boat using a hand-held tagging stick (12 fish) or on deck (10 fish), in the Bocche di Bonifacio between Corsica and Sardinia during September 1999 and September 2000. Fifteen bluefin tuna were tagged (13 fish with PAT tags and 2 fish with PTT-100 tags) by hand-held harpoon and underwater gun in the aquaculture pens at Puerto Mazarròn (Cartagena, Spain) on 1st August 2000. Twelve bluefin tuna were tagged with PTT-100 tags in the Aegean Sea (Greece) in April and December 1999 and January and March 2000, using a short hand-held stick.

All tags were attached by a monofilament nylon leader to a nylon dart (PTT-100 tags) or a titanium anchor (PAT tags) embedded in the dorsal muscles of the bluefin tuna. For bluefin tuna tagged in the water, the nylon dart was embedded directly in the muscles. For bluefin tuna tagged on deck the titanium anchors were passed through the base of the second dorsal fin ray.

A series of charts of chlorophyll-a concentration were plotted for the Tyrrhenian Sea close to Corsica and Sardinia (central Mediterranean) and the eastern Atlantic to the south of the Strait of Gibraltar, the two areas in which most of the tags surfaced. Data were extracted from the SeaWiFS database (Parrish, 1996; IOCCG, 1999). Data for the first area were analysed for the period September 2000 to February 2001, obtaining a fairly homogeneous temporal coverage (about three good satellite acquisitions per month) apart from January.

A series of trials were made with five unused PTT-100 tags to test the ability of the Argos satellite system to detect these tags in the western Mediterranean (where there is now known to be substantial background noise and transmitter competition on the Argos radio frequency) and the eastern North Atlantic. A complementary analysis was carried out with the data received from the 12 PTT-100 tags that were both detected and located by Argos.

Results

Six tags were recovered from recaptured bluefin tuna, leaving 78 available to surface and transmit radio signals (Table 1). Twenty-three tags were located by satellite, giving an overall location rate of about 30% (23/78): all 23 transmitted valid data. Sporadic radio signals were received from a further six tags (four PTT-100 & two PAT tags) raising the overall detection rate to about 37% (Table 1). These six tags were, however, not located by Argos. Good temperature data were received from the four PTT-100 tags but no data were received from the two PAT tags.

Table 1 – Detection and location rates of tags attached to bluefin tuna in the Mediterranean Sea and eastern Atlantic Ocean between 1998 and 2000.

Tag type	Tagging location	No. of tags deployed n	No. of tags recovered from captured fish n	No. of tags available to surface on programmed date n	No. of tags detected n	No. of tags located n	Detection rate %	Location rate %
PTT-100	Barbate trap '98	9		9	4	4	44.4	44.4
	Stintino trap '98	3		3	2	2	66.7	66.7
	Total '98	*12*		*12*	*6*	*6*	*50.0*	*50.0*
	Barbate trap '99	23	1	22	4	3	18.2	13.6
	Bocche di Bonifacio '99	12	2	10	5	2	50.0	20.0
	Aegean Sea '99	5		5	1	1	20.0	20.0
	Total '99	*40*	*3*	*37*	*10*	*6*	*27.0*	*16.2*
	Puerto Mazarron cage '00	2	1	1				
	Aegean Sea '00	7		7				
	Total '00	*9*	*1*	*8*				
	Total PTT-100 tags	61	4	57	16	12	28.1	21.1
PAT	Puerto Mazarron cage '00	13	1	12	4	4	33.3	33.3
	Bocche di Bonifacio '00	10	1	9	9	7	100.0	77.8
	Total PAT tags	23	2	21	13	11	61.9	52.4
TOTAL (PTT-100 + PAT tags)		84	6	78	29	23	37.2	29.5

Location rates were about 21% (12/57) for the PTT-100 tags and 52% (11/21) for the PAT tags, which appeared to be less influenced by the high level of background noise and high density of Argos transmitters in the Mediterranean area than the PTT-100 tags. Detection and location rates of PTT-100 tags varied markedly between release sites and years (Table 1). In 1998, 4 (44%) of the 9 tags released at Barbate were detected and located, compared with 2 (67%) of the 3 tags released at Stintino. In 1999, however, the rate of detection for tags released at Barbate fell to 18% and the rate of location was only 14%. A slightly higher rate of location (20%) was experienced with tags released in the Bocche di Bonifacio and Aegean Sea in 1999, although at 50% the detection rate for tags released in the Bocche di Bonifacio was considerably greater. In 2000, none of the nine tags released at Puerto Mazarròn and in the Aegean Sea was detected.

Detection and location rates of the PAT tags also differed markedly between release sites. Only 4 (about 33%) of the 13 tags deployed on bluefin tuna in a holding pen at Puerto Mazarròn in the year 2000 were detected (and located) by satellite, although a further tag was recovered from a recaptured bluefin tuna before it was due to detach from the fish. In contrast, in Corsica in the same year the detection rate was 100%, with radio signals received from all 9 of the tags still available to surface on the programmed day. As mentioned above, however, two of these tags could not be located, possibly because they drifted ashore shortly after surfacing. A tenth tag was recovered from a recaptured bluefin tuna, again before it was due to detach from the fish, and the overall location rate from the releases in the Bocche di Bonifacio in 2000 was thus about 78%.

Most tags were located in the western Mediterranean or in the eastern North Atlantic off the coast of North Africa; one PAT tag surfaced south of Iceland and one PTT-100 tag transmitted from the Greenland Sea (Fig. 1). No tags were located in the western Atlantic suggesting no transatlantic migrations among the tagged fish.

Details of the tags that surfaced in the Mediterranean Sea and eastern Atlantic Ocean are given in Table 2, which summarises the dates and locations of deployment and pop-up, as well as the size of the tagged bluefin tuna.

Several tags showed interesting results. One PTT-100 tag deployed near the Strait of Gibraltar was detected in the Greenland Sea; another from the same release transmitted from the eastern Atlantic close to the southern limit of the eastern bluefin stock (Medina *et al*., 2002). A PAT tag deployed in the Mediterranean, close to Cartagena, was detected in the North Atlantic south of Iceland after 62 days at liberty. In contrast, most of the PAT tags deployed in the area of the Bocche di Bonifacio (Corsica) surfaced in the release area. Daily longitudes recorded by the tags indicated that all but one of these bluefin tuna remained close to the release area between longitudes 8° and 14°E. Maximum depths indicated that, while some bluefin tuna moved off into deep water (e.g. the Tyrrhenian Sea), the others most probably remained in the shallow water on the continental shelf around the islands of Corsica and Sardinia. The single tag that did not surface in the release area was located in the Golfe du Lion, to which the fish moved rapidly during its last few days at liberty.

Comparison of pop-up positions with the temporal set of chlorophyll-a maps shows a correspondence with higher pigment concentration areas. In particular, the central Mediterranean and the northern Tyrrhenian Sea show higher concentrations of chlorophyll-a than the other parts of the western Mediterranean and eastern Atlantic. Given the occurrence of persistent areas of high production in the areas where most of the tags were detected, especially to the east of Corsica, these may be feeding areas for both pre- and post-spawning bluefin tuna.

The rate of tag detection was much lower than expected from previous studies with the same type of tag in the western and central North Atlantic, where rates of 56 to 93% have been reported (Block *et al.*, 1998; Lutcavage *et al*., 1999; Lutcavage, pers. comm.). Because of this, and also because of the large difference in location rates (44% and 14%, respectively) between the tag deployments in Barbate in 1998 and 1999, a series of tests was conducted to compare the performance of five unused PTT-100 tags at a number of locations in Europe, Madeira and the United States. The results revealed a detection problem in the western Mediterranean Sea, where some of our tags were expected to surface. This problem could well have resulted in non-detection of tags that surfaced successfully in this area at the programmed time. The analysis of the data transmitted by the 12 PTT-100 tags located by Argos indicated the same problem. Tags that surfaced in the western Mediterranean had much lower detection and location rates (0.5-4.4 locations per day) than tags that surfaced in the North Atlantic (10-20 locations per day).

Discussion

Reasons for the low detection rate of the PTT-100 tags may include post-tagging mortality, bluefin tuna capture, premature tag release, failure of the tag as a result of exposure to high pressure and low signal-to-noise ratio during transmission. Whilst it is difficult to quantify some of these factors, our test results clearly indicate that the strength of the transmitted signal was sufficiently low to have compromised our ability to detect tags over a significant area of the western Mediterranean and north-western Europe. The ability to detect tags that surfaced in the Atlantic should, however, have been the same as that for tags of the same type attached to bluefin tuna in United States waters. In this context it is interesting to note that none of the pop-up positions of our tags were located in the central or western North Atlantic, but were confined to the eastern management area with no evidence of transatlantic migrations.

Fig. 1 – Pop-up locations of tags attached to bluefin tuna in the Mediterranean and eastern Atlantic from 1998 to 2000. Red circles, PTT-100 pop-up single-point tags; white circles, PAT pop-up archival tags.

Table 2 – Summary data for the tags located in the Mediterranean Sea and eastern Atlantic Ocean between 1998 and 2000. Dates and locations of deployment and pop-up are given, together with the size of the tagged bluefin tuna.

Type and IDs of tags			Fish biometry		Deployment dates and sites		Pop-up dates and sites		Days at liberty	Area
			W (kg)	FL (cm)						
1	PTT-100	09118	100	169	07/06/98	Tuna-trap of Stintino (Sardinia)	17/06/98	Central Tyrrhenian Sea	10	Mediterranean Sea
2	PTT-100	09119	100	170	07/06/98	Tuna-trap of Stintino (Sardinia)	29/06/98	Coast of North Africa	22	
3	PTT-100	09117	150	194	27/07/98	Tuna-trap of Barbate (Spain)	01/08/98	Alboran Sea	5	
4	PTT-100	23343	80	157	03/04/99	Aegean Sea	02/05/99	Aegean Sea	29	
5	PTT-100	06086	70	151	27/09/99	Bocche di Bonifacio (Corsica, France)	26/03/00	Bocche di Bonifacio	181	
6	PTT-100	07779	80	157	27/11/99	Bocche di Bonifacio (Corsica, France)	28/07/00	Bocche di Bonifacio	239	
7	PAT	99-759	100	172	01/08/00	Tuna-cages of Puerto Mazarròn (Spain)	01/01/01	Sardinia Channel	154	
8	PAT	99-531	160	198	01/08/00	Tuna-cages of Puerto Mazarròn (Spain)	01/10/00	Strait of Gibraltar	62	
9	PAT	99-526	170	202	01/08/00	Tuna-cages of Puerto Mazarròn (Spain)	01/09/00	Golfe du Lion	32	
10	PAT	99-679	78	156	09/09/00	Bocche di Bonifacio (Corsica, France)	04/10/00	Bocche di Bonifacio	30	
11	PAT	99-721	46	135	10/09/00	Bocche di Bonifacio (Corsica, France)	03/12/00	Bocche di Bonifacio	90	
12	PAT	99-736	75	154	12/09/00	Bocche di Bonifacio (Corsica, France)	02/01/01	Bocche di Bonifacio	120	
13	PAT	99-754	84	160	12/09/00	Bocche di Bonifacio (Corsica, France)	04/02/01	Central Tyrrhenian Sea	150	
14	PAT	99-735	42	131	14/09/00	Bocche di Bonifacio (Corsica, France)	06/12/00	Golfe du Lion	90	
15	PAT	99-716	48	137	14/09/00	Bocche di Bonifacio (Corsica, France)	06/12/00	Bocche di Bonifacio	90	
16	PAT	99-720	54	142	14/09/00	Bocche di Bonifacio (Corsica, France)	06/11/00	Bocche di Bonifacio	60	
17	PTT-100	23011	150	190	27/07/98	Tuna-trap of Barbate (Spain)	24/09/98	Madeira Island	59	Eastern Atlantic
18	PTT-100	23014	150	193	27/07/98	Tuna-trap of Barbate (Spain)	20/01/99	Cape Verde Islands	177	
19	PTT-100	23328	150	194	27/07/98	Tuna-trap of Barbate (Spain)	23/03/99	Greenland Sea	239	
20	PTT-100	23344	150	194	23/07/99	Tuna-trap of Barbate (Spain)	21/09/99	Eastern Atlantic Ocean	60	
21	PTT-100	23345	150	195	23/07/99	Tuna-trap of Barbate (Spain)	19/10/99	Canary Islands	88	
22	PTT-100	23327	150	195	23/07/99	Tuna-trap of Barbate (Spain)	16/01/00	Canary Islands	177	
23	PAT	99-606	230	223	01/08/00	Tuna-cages of Puerto Mazarròn (Spain)	01/10/00	Iceland Sea	62	

It was also noticeable that most of the tags deployed in the Mediterranean surfaced close to the original tagging location. This was especially true of the bluefin tuna released between Corsica and Sardinia, suggesting the existence of residency associated with the high productivity, together with other environmental characteristics of this area.

The recapture of a big bluefin tuna (290 kg) tagged with a PTT-100 tag at Barbate on July 1999 is of particular interest. This bluefin tuna - to which the (pressure-damaged) tag was still attached - was caught near the Balearic Islands in June 2001, suggesting fidelity to the western Mediterranean spawning area.

Spawning site fidelity and Mediterranean residency clearly offer the scope for overexploitation if the industry continues to catch more and more large bluefin tuna for fattening in cages, instead of starting to rear new fish from eggs.

Domestication of bluefin, which is the aim of the new EU funded Project "REPRO-DOTT", would need to extend to the control of all stages of the life history, including reproduction in captivity, rearing and weaning of larvae, and growth to market size, to be sure of avoiding this risk. In this new context, further researches on the bluefin tuna migrations need to be carried out in order to better understand the relations between environmental parameters and the behaviour and physiology of this species. Electronic tags offer an ideal tool for this purpose.

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Juvenile sturgeon (*Acipenser sturio*) habitat utilization in the Gironde estuary as determined by acoustic telemetry

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Key words: juvenile sturgeon, habitat, swimming behaviour, estuary, acoustic telemetry.

Abstract

A congregation area for young European sturgeon *Acipenser sturio*, an endangered species, was found in the Gironde estuary using acoustic telemetry. Between May and August 1999, sixteen young sturgeons, aged 4 to 5 years (total length: 82-122 cm, weight: 2.35-8.10 kg) were captured by trawling and tagged with a coded ultrasonic transmitter. Manual tracking was conducted 2 to 3 days a week until November 1999. Sturgeon movements were observed over periods of six hours, both during day or night. No significant behavioral differences in terms of swimming speed were observed between daytime and night-time. Most of the movements observed, occurred in the same direction than the tidal current, and their velocity was often slower than the flow. Only a few lateral movements were observed, and young sturgeons tended to congregate in an area located in the middle of the estuary, where the average depth is 7 m. The congregation area, obtained using the minimum convex polygon, represented a total surface of 32.6 km^2, but the Dirichlet tesselation with 95% of all positions showing a site fidelity, gave an area with a surface of 19.4 km^2. The use of a restricted portion of the estuary might be due to the very low number of individuals in the sturgeon population, but could also be due to the spatial distribution of polychetes worms, their favorite prey.

Introduction

The European sturgeon *Acipenser sturio* is one of the nine diadromous sturgeon species in the world (Rochard *et al*., 2001; Birstein, 1993). The species has already been extirpated from a large part of its former distribution area. The last zone where a population is still present, though scattered, and where individuals complete their life cycle is located in France (Lepage and Rochard, 1995; Williot *et al*., 1997). European sturgeons migrate along the Atlantic coast of Europe from the Bay of Biscay to the Bristol Channel and the North Sea (Rochard *et al*., 1997). It has been listed as an endangered species in France since 1982, and is now protected by national and international conventions (Lepage and Rochard, 1995; Pustelnik and Guerri, 2000), over all its current distribution area. In order to protect the species efficiently, knowledge on essential spawning and feeding habitats needs to be increased. The last known reproduction areas for the European sturgeon are in France: in the Garonne and Dordogne rivers (Castelnaud *et al*., 1991; Williot *et al*., 1997). A recent survey established that near 27 suitable spawning grounds were still available (Jego *et al*., 2002), but the feeding habitat remains poorly investigated (Brosse *et al*., 2000a). Before reaching the Atlantic Ocean, the young spend several months in the Gironde estuary (Magnin, 1959; Castelnaud *et al*., 1991). After a period of early acclimatization of 15 months, juvenile European sturgeons appear to be highly tolerant to salinity variations (Rochard *et al*., 2001). From 1995 to 1997, trawling surveys were conducted in the Gironde estuary to identify the estuarine habitat of the juveniles. Two areas of concentration were identified, and movements between these two areas occurred frequently.

This study aimed to identify the movements of the juveniles in the Gironde estuary and in particular the influence of tidal and nycthemeral cycles on their behaviour. The congregation area is described in terms of trophic habitat. A second objective was to control the presence of juvenile sturgeon in sectors which could not be sampled by trawling.

Materials and methods

Study area

The study area is the Gironde estuary in the south-west of France (Fig. 1). This estuary is the widest in Europe (635 km^2 of surface at high tide in the marine estuary). It drains 81,000 km^2, with a mean flow of about 1,000 m^3s^{-1} (Allen, 1972). Maximum width is 11 km. Mean depth is about 8 m at mid-tide. There are two navigation channels, a natural one on the right side, with depths ranging from 4 to 20 meters and an artificial one on the left side, with a depth ranging from 7 to 30 meters. Several islands lay between these channels, in the upper part and on sandy-muddy banks in the lower part. The bottom of the estuary is mainly a mixture of sand and mud with the sandiest part in the lower estuary and the muddiest part in the upper estuary. There are two ebb and two flood tides each day, lasting about 6.2 hours. The tidal range is approximately 5 meters. The salinity follows a gradient according to the strength of the tide and the river flow, it varies from 0 to 30 ppt from where the Garonne and Dordogne rivers meet to the mouth of the estuary. In the muddiest part of the estuary, the turbidity can be as high as 1 gl^{-1} near the surface and up to 50 gl^{-1} over the bottom in the maximum turbidity area (Latouche et and Jouanneau, 1994). This area, changing with the tide, can spread on 20 to 60 km, depending on the river outflow and the neap or spring tide (Sottolichio, 1999). The water temperature in the estuary ranges between 6 °C in January to 26 °C in July (Maurice, 1994).

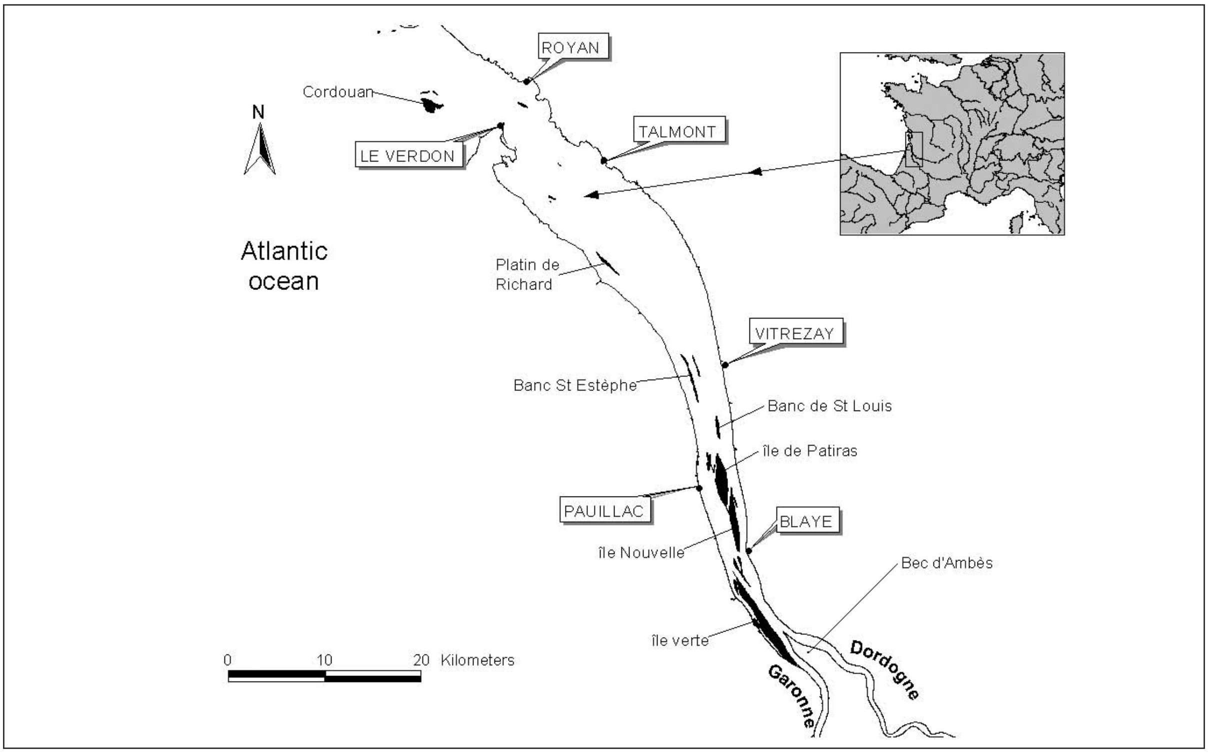

Fig. 1 – Gironde estuary

Capture and tagging

The juvenile sturgeons were captured during trawling surveys between May and August 1999 with a 12 m trawling boat. The duration of the tows was limited to approximately 30 minutes in order to catch live fish in good condition. When a juvenile sturgeon was captured, total length (TL) to the nearest centimeter below and the total weight (TW) to the nearest 50 g below were measured.

Sixteen juveniles were equipped with ultrasonic coded transmitter (model, CAFT 16-1 from Lotek) working on a frequency of 65.5 kHz. The fish weight ranged from 2.35 to 8.10 kg (mean ± s.d. 4.67 ± 1.46) and the fish length ranged from 82 to 122 cm TL (mean ± s.d. 99 ± 10.29). The weight of the tag never exceeded 1.06% of the fish weight. The lifetime of the tag was 225 days. Tracking was carried out over a period that did not exceed 167 days (Table 1).

The tags were attached externally at the base of the dorsal fin with a U shape stainless steel wire, generally used to make a spring, so that it kept the form we gave to it. A plastic cylinder was added on the free side of the wire before it was inserted into the muscle, through the base of the dorsal fin. We used a plastic cylinder instead of the plastic plate supplied by Lotek, since the round shape of the plastic cylinder prevented the wound caused by the cutting edge of the plastic plate. The fish were handled mostly in a tank with an air diffuser during tagging operations. Tagging did not last more than 3 minutes and most of the time less than 2 minutes with an experimented operator.

Table 1 – Capture and tagging histories for *Acipenser sturio* tracked between June and November 1999 in the Gironde estuary.

Fish number	Total length (cm)	Total Weight (kg)	Date of capture	Number of days at risk	Number of times located	Total time of tracking (h : mm)
71	96	3.30	27.5.1999	140	6	28:07
134	101	5.00	8.6.1999	127	6	25:04
121	122	8.10	8.6.1999	48	1	00:05
143	91	4.00	8.6.1999	-	0	00:00
115	95	4.30	8.6.1999	167	5	04:05
163	95	4.40	21.6.1999	155	8	29:25
142	100	4.70	21.6.1999	64	8	30:07
138	95	4.10	21.6.1999	64	5	16:08
109	106	5.10	22.6.1999	114	10	26:42
139	85	2.90	22.6.1999	153	12	21:16
74	100	5.30	21.7.1999	124	5	05:22
150	111	6.00	21.7.1999	124	7	11:25
165	114	7.00	21.7.1999	118	0	00:00
151	82	2.35	21.7.1999	-	0	00:00
168	97	4.30	21.7.1999	115	4	22:02
153	94	3.85	17.8.1999	-	0	00:00

Monitoring

The receiver used was the model SRX-400 (Lotek Marine Technologies Inc.) linked to an ultrasonic converter, that transforms the high frequency (HF) signal (65.5 kHz) to ultra high frequency (UHF)

(150.065 MHz). Then an omni directional hydrophone was fitted with a baffle in order to make it directional on 180 °. A 5 m boat powered with a 70 HP outboard engine was used for tracking, and the surveys were only carried out when weather conditions were good and safe for the people and equipment.

As the Gironde estuary is very large (11 km at the widest part) and the distance for signal detection was more or less 500 m with the engine stopped, we had to use a research grid traced on a marine map of the estuary in order to explore the whole estuary with its lateral sub tidal mud flat, navigation channels and sand banks. At each localization, the engine was stopped in order to minimize extraneous noises. The position of the fish was recorded using differential global positioning system (DGPS) with an accuracy of 2 m. The maximum distance determined for signal detection was 800 m, and for decoding 250 m; however these distances were reduced when turbidity was high. We avoided tracking fish on spring tide because of the high turbidity and because the high speed of the current resulted in a more difficult positioning. The implemented strategy was to monitor individual fish over a complete tidal cycle (flood-ebb). Part of the monitoring was performed so as to observe whether behaviours differed between daytime and night-time in terms of swimming speed. In order to obtain a good image of young sturgeon behaviour, we attempted to monitor a new fish for each survey. When tracking a fish during a complete tidal cycle, as many fish as possible were spot positioned without leaving the main tracked fish . Several tests were carried out to establish a relationship between the real distance and the signal strength obtained by the receiver. The variability of turbidity in the Gironde estuary prevented us from establishing any operational relationship between distance and signal strength. The position of the fish was recorded every 10 min during the continuous tracking. Every 30 min, we took a water sample from the bottom of the estuary in order to measure temperature, salinity, conductivity and suspended matter.

Over the 6-month monitoring period, 46% of the sturgeons were located from 7 to 10 times, 38% from 4 to 6 times, 15% only once, and 4 fish were never located. Twelve fish were tracked from 5 min to 30 hours in cumulative time. A total of 456 fixes were done in 26 effective days (Table 1).

For the first fish tracked in June 1999, we proceeded to a 24 hour tracking in order to have information on the stress period following handling of the fish and to compare the behaviour (route and swimming speed) with further trackings.

Data analysis

All the positions were reported on GIS (ESRI, ArcView, v. 3.2 and ArcView spatial analyst v.2.0a). Speed and distance between two positions were calculated with the same software. Only the points obtained from the continuous tracking were used for speed calculation. We used the minimum convex polygon to estimate the total surface used by the tagged fish during the six month tracking.

We performed a site fidelity test on each track using a user script “Animal movement v.2.04” (Hooge and Eichenlaub, 1997) under ArcView 3.2 in order to define if the trajectory showed a significant attachment to the site or not. We statistically compared each real track to a hundred randomly produced tracks composed of the same number of fixes. We made a Dirichlet tesselation on all the fixes in order to determine the main occupation area that can be considered as the preferred habitat (including 95 % of the fixes and excluding outliers). This method was chosen because of its poor sensitivity to autocorrelation (Wray *et al*., 1992).

The swimming speed was calculated using the distance and the time between two locations of a track. It was then considered as a ground speed. A mixed model with random effect “fish” on the intercept was used to compare swimming speeds by diel and by tidal phase.

The data concerning the habitat and the sturgeon diet, were provided by a study conducted over all the Gironde estuary (Brosse, 2003).

Results

Of the 16 tagged fish, 4 were never found by tracking: one of them was recaptured by trawl with a non functioning transmitter. No mortality was observed either during the tagging itself or after fish release in the estuary. We never found any sturgeon in the navigation channel during this monitoring period, neither on the left side of the estuary, nor around the wrecks or other sectors where we were not able to sample by trawling.

The fish that was tracked during 24 hours after being tagged had a swimming speed much higher during that period. It reached a maximum speed of 1033 cms^{-1} and had a mean swimming speed of 154 cms^{-1} whereas the mean speed of the same fish during its following tracking was between 26 cms^{-1} and 36 cms^{-1} depending on the day of tracking.

During the study, the water temperature close to the bottom ranged from 10.4 to 23.1 °C and the salinity ranged from 15.5 to 31.1 ppt. The fish were able to support a daily variation of salinity of 10.5 ppt.

Young sturgeons tended to stay in a congregation area (a maximum of 6 fish were identified at a given moment) located near the middle of the estuary (Figs. 2 and 3). When we consider all locations, the minimum convex polygon gave a surface of 32.6 km^2, but the Dirichlet tessellation with 95% of all positions showing a site fidelity, gave an area of 19.4 km^2 (Fig. 4) whereas the core of sturgeon activity occurred inside a narrow area of 2.6 km^2 (50% of all locations). We overlaid the result obtained by the Dirichlet tessellation and the map of the benthic fauna of the estuary (Fig. 4), and we noticed that tube dwelling polychetes were principally located in the congregation area.

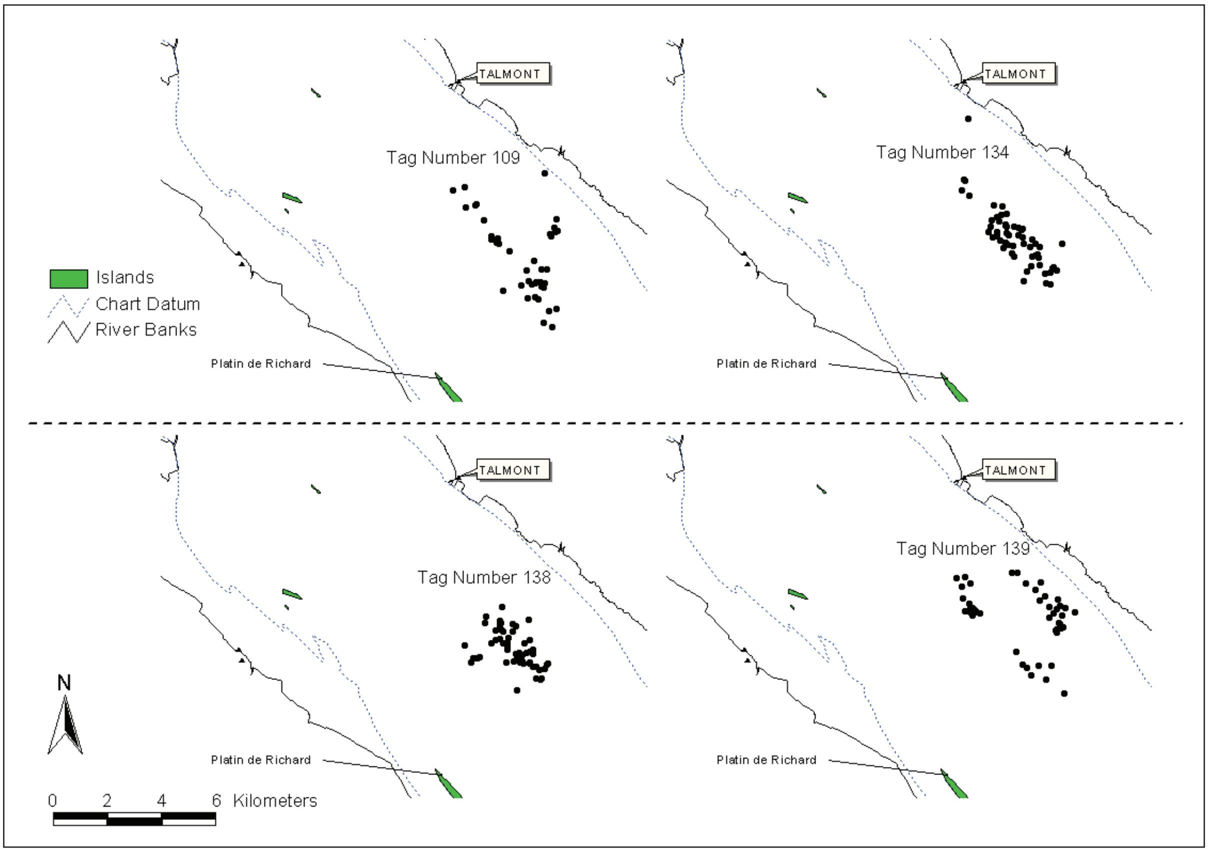

Fig. 2 – Maps of all the fixes recorded the six months tracking for the fish tag 109, 134, 138 and 139.

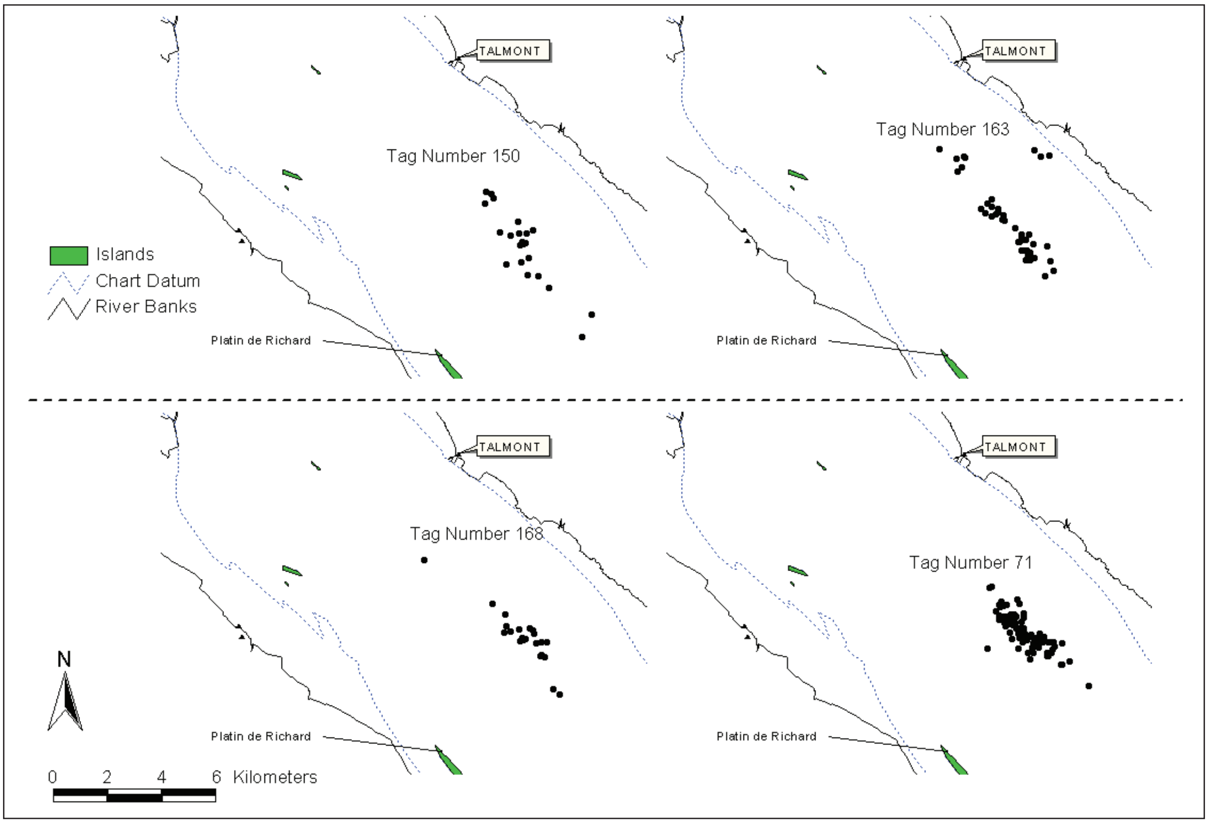

Fig. 3 – Maps of all the fixes recorded in the six months tracking for the fish tag 150, 163, 168 and 71.

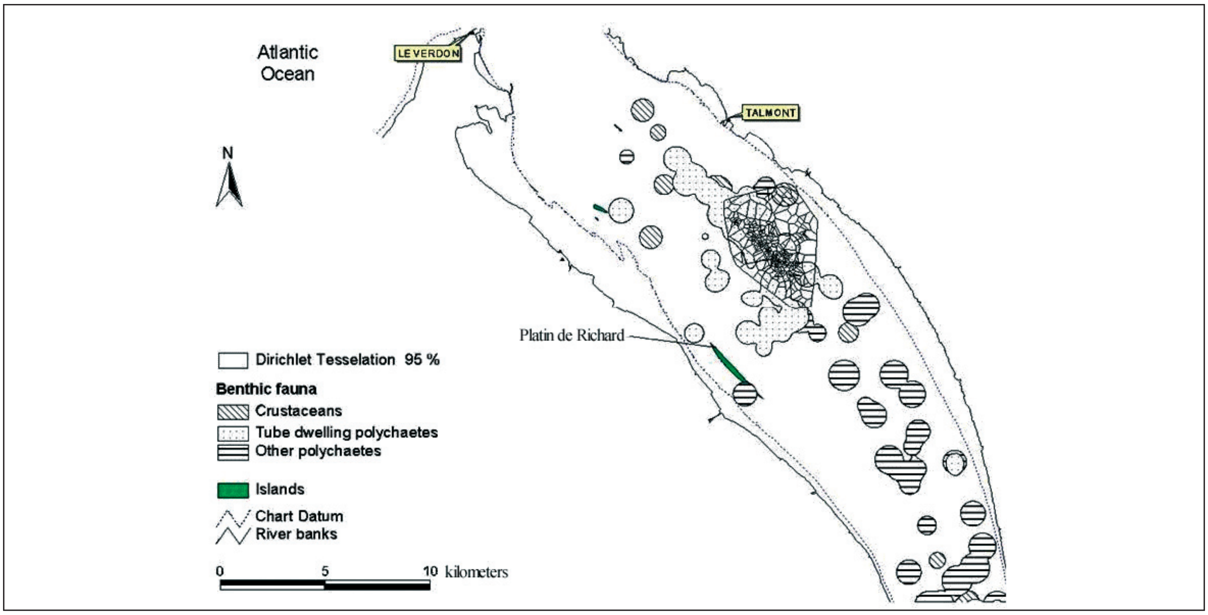

Fig. 4 – Congregation area estimated by Dirichtlet tessellation and details of the benthic fauna of the Gironde estuary.

Fish strayed away from their catching point by 400 m to 19 km (mean 4.2 km, s.d. 2.9 km) during the entire study period. Sturgeons exhibited movements mostly oriented following the direction of the tidal current: downstream movements during ebb and upstream movements during flood.

No significant diel interaction effects were observed on the swimming speed (mixed model, p =0.555) between daytime and night-time and no significant difference were observed in the swimming speed between flood and ebb tide (mixed model, p =0.278).

Discussion

We verified the stress caused by the capture and tagging, comparing the swimming speed and the total distance travelled immediately after being tagged and the observations done after 2 to 10 days. It appeared that the stress caused by the capture and handling of the fish affected the swimming speed of the fish for one full day. With Pacific salmon (*Oncorhynchus spp*.), handling of the fish shows to be disturbing and to affect their travel speed and direction during several hours after release (Ogura and Ishida, 1995).

After tagging, some sturgeons were released outside the congregation area, but all these fish homed back to this area (32.6 km^2). This zone represents less than 10% of the estuary's surface. Moser and Ross (1995) found that young Atlantic sturgeon *Acipenser oxyrhinchus* moved little and remained a long time in the same area. Use of discrete areas for extended periods of time seems to be common for sturgeon, and has been described for other species (Buckley and Kynard, 1985; Hall *et al*., 1991; Kieffer and Kynards, 1993; Bain, 1997; Foster and Clugston, 1997; Collins *et al*., 2000). A precise selection of the location where they live may indicate that they require a particular habitat. A high abundance of their favourite preys (polychetes worms) in the area could explain the congregation of sturgeon on this area (Brosse *et al*., 2000a). However, other factors could be important like bathymetry, sediment, fall of bed and current shed in the choice of this habitat. Nevertheless, very few individuals compose the sturgeon population at present and we must be careful in interpreting strictly these results to define what should be the feeding habitat for sturgeon in the estuary. Stomach content analyses show a diversity of 12 taxa of preys, and there were very few empty stomachs in young *A. sturio*, at least throughout the diurnal period (Brosse *et al*., 2000b). Monitoring using acoustic telemetry showed that the activity rhythm is similar between night and day. Therefore, it seems that these fish can eat throughout the day. A similar feeding activity was observed with shortnose sturgeon *Acipenser brevirostrum* (McCleave *et al.,* 1977). On a captive stock of *A. sturio* aged 1$^+$, activity rhythms were predominant during the night (Staaks *et al*., 1999). Over the study period, most of the observed movements consisted in short up or downstream movements (< 10 km) greatly influenced by the tidal cycle. Moser and Ross (1994) showed that swimming of *Acipenser oxyrhynchus* and *A. brevirostrum* in estuaries were well oriented to tidal current directions and mainly against the current. Swimming against the current could ensure that sturgeons do not drift too far from their feeding habitat. Salinity does not seem to be an important parameter for *A. sturio* as the fish were able to support a daily variation of salinity of 10.5 ppt.

This tracking experiment highlighted the behaviour of the juvenile sturgeon in the Gironde estuary. It confirms the use of the area which was determined by the trawling data (Rochard *et al*., 2001) and shows that juveniles do not forage in the shallow areas near the shore nor in the navigation channel where trawl sampling was impossible.

Acknowledgements

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Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK

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Key words: Pike, *Esox lucius*, spatial behaviour, static, mobile.

Abstract

Fifteen pike *Esox lucius* L. were radio tracked in the River Frome, UK, for between 8 and 25 months. Examination of the locations of seasonally determined cluster polygon home ranges, together with positional fixes recorded throughout the year, revealed that spatial behaviours could not be grouped into the simple 'static' and 'mobile' categories that had previously been proposed for the species. Rather, a continuum of spatial behaviours existed, from individuals that always remained within the same few hundred metres of river, to individuals that made repeated journeys over several kilometres on a broadly seasonal basis. Relocations were also observed, whereby pike moved to a distinctly different location to that which they had formerly occupied.

Introduction

The pike *Esox lucius* L. is a piscivorous fish, occurring in lakes and rivers in temperate and arctic regions of the northern hemisphere (Raat, 1988).

The spatial behaviour of pike in lakes has been well studied, and is known to be highly variable, both within and between populations with some individuals staying within a restricted area, whilst others move between two or three favoured areas, or wander more freely throughout the lake (e.g. Diana *et al*., 1977; Diana, 1980; Mackay and Craig, 1983; Chapman and Mackay, 1984; Cook and Bergersen, 1988; Lucas *et al*., 1991; Jepsen *et a*l., 2001).

Pike in rivers have received comparatively little attention. Riverine pike have been shown to be capable of extensive movements, with mean upstream spawning migrations of 7.7 km reported for pike in the Ourthe and Amblève rivers (Ovidio and Philippart, 2002). Movements >100 km, between summer and winter locations, occurred in an Alaskan wetland area (Burkholder and Bernard, 1994). These reports contrast with the results of a mark-recapture study, based in the River Frome, UK, during which most jaw tagged pike appeared to remain within the 3 km of study area after release, although some pike dispersed more widely, leading to the proposal that the pike population consisted of both static and mobile components, with the former comprising ca. 74% of the population (Mann, 1980). Gerlier and Luquet (1999) reported radio tagged pike occupying between 400 m and 12260 m of the River Ill, France, although interpretation of the results, in terms of static and mobile fish, is complicated by differences in release strategy and track duration.

Classic studies, which described limited movement (e.g. Mann, 1980), together with the adaptations of pike for fast-start swimming (Helfman *et al*., 1997) and the species preference for areas of slack water in rivers (Lamouroux *et al*., 1999), have led to reports of extensive movements being viewed as paradoxical (Ovidio and Philippart, 2002).

The present study aimed to describe the long-term spatial behaviour of riverine pike by referring to the locations of seasonally determined home ranges for radio tagged individuals and by interval tracking of these same fish throughout the year, including during the spawning period, which occurs in spring (Raat, 1988). Specifically, the hypothesis that pike populations comprise both static and mobile individuals (Mann, 1980) was to be examined.

Materials and methods

Study area
This study was based in the River Frome, Dorset, UK, a largely unmodified groundwater fed chalk stream in southern England. The river had a meandering main channel and was free to burst its banks under high flows, when water inundated the surrounding meadows. The main study area (SY 8686 and SY 8768), consisted of > 2000 m of river channel (mean width=14 m), flowing west to east, with adjoining drainage ditches and a millstream, this being the same area of river in which pike were marked and recaptured by Mann (1980) (Fig. 1). Whilst the East Stoke gauging weir, at the head of the weirpool (Fig. 1) formed a potential barrier to movement, there were no barriers downstream of the main study area. Submerged vegetation in the river consisted mainly of *Ranunculus* spp. and *Potamogeton* spp. Emergent vegetation (*Phragmites australis* (Cav.) and *Glyceria maxima* (Hartm.)) was rare and mainly confined to the banks. The majority of the river lay within areas of grazed pasture and there was little outstream shade. Discharge data (courtesy of the Environment Agency) and water temperature were recorded every fifteen minutes at the East Stoke gauging weir.

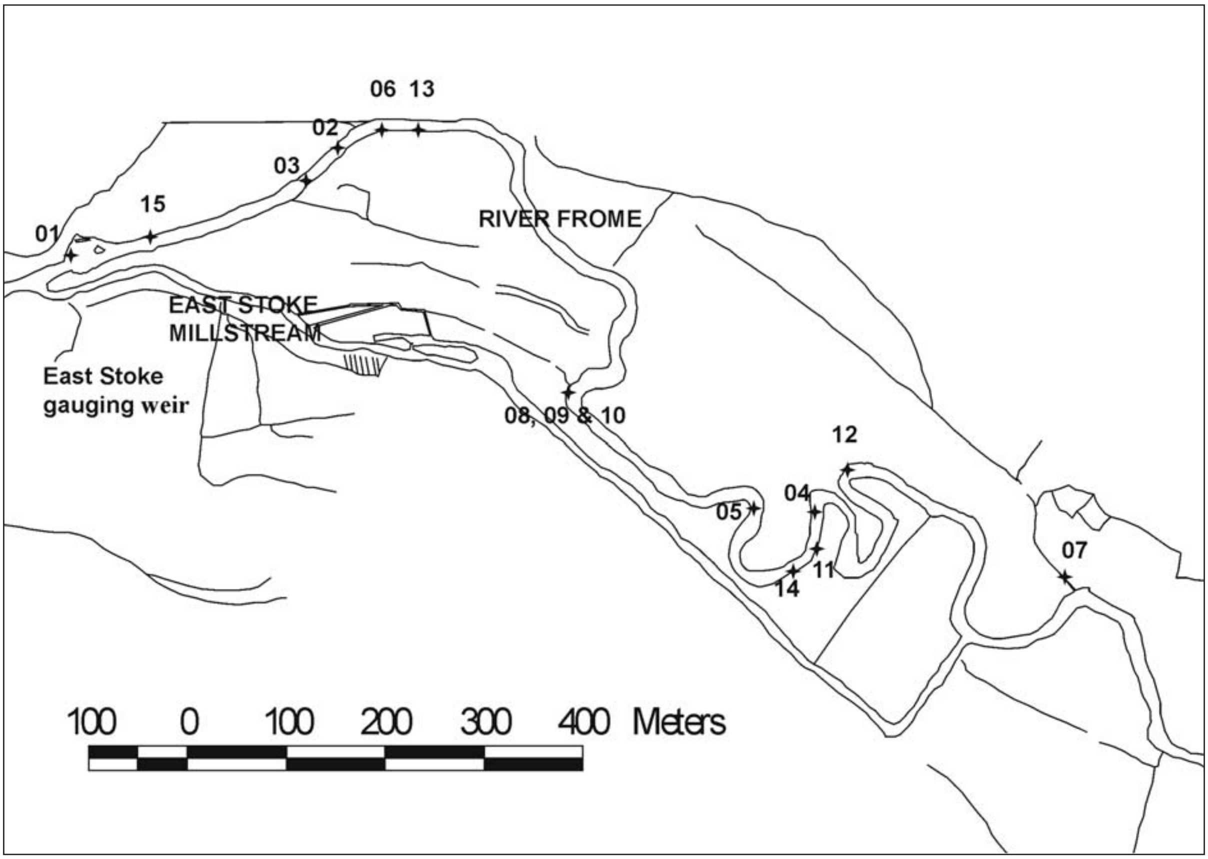

Fig. 1 – Capture locations for each pike (01, 02, 03 etc.) within the main study area.

Radio tagging

Fifteen pike, captured by angling or electric fishing within the main study area, were anaesthetised in a 1 mll^{-1} dilution of 2-phenoxyethanol in river water and implanted with TW-5 radio tags (Biotrack Ltd, Wareham, UK) under aseptic conditions, using sterilised instruments and tags, as described in full by Beaumont *et al*. (2002) (Table 1). Tagging was carried out in accordance with the UK Animals (Scientific Procedures) Act 1986. Tag dimensions were: length=8.0 cm, diameter=1.6 cm, weight=22 g in air, 7 g in water, and the antenna type was an internal coil. The ratio of fish weight to tag weight in water was <0.5% in all cases. Pike were sexed through external examination of the urogenital region (Casselman, 1974). Each pike was released at its capture location after recovery from anaesthesia (Fig. 1), this being considered less stressful than a prolonged period of post-operative captivity (Crossman, 1977). To avoid potential distortion of results following tag implantation, data were not recorded until at least ten days after tagging (Jepsen *et al*., 2001; Beaumont *et al*., 2002). Growth rates and condition factors have been shown to be unaffected amongst pike tagged using a similar procedure (Jepsen and Aarestrup, 1999). Pike 04 and Pike 08 died during the study, ca. 10 months and ca. 15 months after tagging. The deaths were assumed to be due to natural causes, although the remains of Pike 08 were too decomposed to allow for post-mortem investigation, and the body of Pike 04 could not be recovered (Masters, 2003).

Table 1 – Data collected for each pike, arranged in order of ascending TMLD. ‘No. fixes’ gives the number of fixes recorded for each pike whilst ‘No. days’ gives the number of days between the date of tagging and the date that the last fix was recorded. L_F and W are the fork length and weight at time of capture. The dates for home range tracks were: 1) July 2000, 2) September 2000, 3) December 2000, 4) March 2000, 5) July 2000, 6) September 2000, 7) December 2001 and 8) March 2002. TMLD and MCD are also given. Pike 08 was only present in the study area during home range track 4), therefore MCD could not be calculated. For Pike 01 and Pike 06, MCDs are based upon data from home range tracks 1) to 4) and 3), 4) and 8), respectively, during which the fish were within the main study area.

Pike	Date of tagging	Sex	L_F cm	W kg	No. fixes	No. days	Present in home range tracks	TMLD m	MCD m
15	8 Nov 2001	♂	64	2.3	130	240	7 and 8	162	20
13	31 Jul 2001	♀	52	1.7	232	346	6 to 8	231	167
10	17 Jan 2001	♂	64	2.8	310	542	4 to 8	546	264
12	22 May 2001	♂	69	3.2	218	416	5 to 8	653	447
05	23 Aug 2000	♀	60	1.7	401	689	2 to 8	762	541
03	08 Jun 2000	♀	66	3.0	500	748	1 to 8	781	325
11	22 May 2001	♂	58	1.7	225	416	5 to 8	1142	371
02	24 May 2000	♂	71	3.6	471	773	1 to 8	1385	333
14	4 Sep 2001	♀	54	1.4	166	316	6 to 8	1498	1377
07	30 Nov 2000	♀	93	8.2	296	581	4 to 8	1524	638
09	17 Jan 2001	♀	81	4.0	324	544	4 to 8	1899	1230
04	31 July 2000	♀	66	3.0	172	243	2 to 4	2694	1415
08	17 Jan 2001	♀	95	8.2	111	417	4	2857	n/a
06	16 Oct 2000	♂	87	>5.0	239	633	3, 4 and 8	5643	27
01	24 May 2000	♀	86	5.2	295	1276	1 to 4	5916	336

Tracking

The positions of radio tagged pike were determined from the riverbank, or from an inflatable boat, using hand-held radio receivers and three-element Yagi antennae. Tracks to establish short-term home ranges of pike were conducted on a seasonal basis. During these home range tracks pike were located three times a day (morning, midday and evening), for a period of 13 days, giving a maximum of 39 location records (fixes) per fish. Eight home range tracks took place during 2000-2002, occurring in 1) July 2000, 2) September 2000, 3) December 2000, 4) March 2001, 5) July 2001, 6) September 2001, 7) December 2001 and 8) March 2002. Time was usually insufficient to allow pike that had moved out of the main study area to be included in home range tracks.

Additional fixes were collected throughout the study, to provide longer term movement data. Due to the pike being tagged and released on different dates, the number of fixes recorded and the number of days upon which pike were tracked varies between individuals (Table 1). Time constraints did not allow pike that left the main study area to be located as often as those remained, resulting in relatively fewer fixes for these fish. Tracking concluded in July 2002.

Analysis

To compare long-term spatial behaviours between individuals, for each pike, the distance between the capture point and every fix was determined; distances being measured along the midline of the river using a modified version of RANGES V (Kenward and Hodder, 1996). Distance from the capture point was plotted against time, separately for each pike.

Spatial behaviour was further described using two indices, the Total Maximum Linear Displacement (TMLD) and the Maximum Core Displacement (MCD).

Total Maximum Linear Displacement (TMLD)

TMLD was the total longitudinal distance used by each pike during the entire period it was tracked, measured along the midline of the river i.e. the distance between the furthermost upstream downstream locations. Spearman's rank correlations were used to look for relationships between TMLD and a) pike length b) the number of fixes obtained for each pike and c) the number of days between the first and last fixes for each pike. Differences between the sexes were examined using a two-sample t-test (assuming unequal variation).

Maximum Core Displacement (MCD)

Convex cluster polygon home ranges were calculated for every individual in each home range track (using RANGES V) after removal of outlying fixes (Hodder *et al*., 1998; Kenward, 2001; Kenward *et al*., 2001). The cluster analysis technique used was the C_{tx} type, as defined by Kenward *et al*. (2001), clusters henceforth being referred to as 'core ranges.' The mean distance from the capture location of all the fixes within each separate core range was then calculated, this mean distance being termed the core "centre". Core ranges were 36±4 m long (mean ± s.e.), as measured along the midline of the river, making the core centre a suitable measure of location to describe long term spatial behaviour, over the scale of the river. MCD then, for each individual, was the distance between the furthermost upstream and downstream cluster centres, from all home range tracks combined. Whilst TMLD is a measure of the total length of river used by pike, MCD provides a measure of the longitudinal distance along which core areas of activity were distributed.

Use of side channels

This study focussed upon the spatial behaviour of pike within the main river channel, the behaviour of pike within side channels connected to the River Frome having been previously examined by Masters *et al*. (2002). In order to describe the linear movement of pike along the river channel, fixes occurring in side channels were recorded as the distance between the capture location and the point where the side channel connected to the river. By this method, a fix, for example, 10 m downstream of the capture location and 10 m along a drainage ditch, could not be confused with a separate fix, 20 m downstream of the capture location. To give an indication of the extent of side channel use in every home range track, the proportion of fixes occurring within the side channels was determined for each fish and a median value then calculated from all pike during that track.

Results

The results showed that considerable variation in spatial behaviour occurred between individuals, with TMLDs ranging from 162 m to 5916 m (Fig. 2, Table 1). There were no correlations between TMLD and either the length of time for which a pike was tracked (R_s=0.37, n=15, *P*=0.18), or the number of fixes recorded for each fish (R_s=-0.05, n=15, *P*=0.85), therefore the observed variation in TMLD was not simply a reflection of the different datasets. There was no significant difference in TMLD between the sexes (Two-sample t-test: DF=9, t=0.43, *P*=0.68). There was a significant positive correlation between TMLD and the fork length of pike (R_s=0.69, n=15, *P*<0.01), although TMLD could vary widely between similarly sized fish (e.g. Pike 03 and 04, Table 1, Figs. 2.a and 2.c).

Many of the pike, displayed a high degree of site fidelity, being found in the same few hundred metres of river throughout the time they were tracked (Pike 15, 13, 10, 12, 05, 03, 02; Figs. 2.a and 2.b), with MCDs being correspondingly low (20 m to 541 m, Table 1). In contrast, Pike 06 and 08 used widely separated areas of river at different times of the year (Fig. 2.c). Rather than a split into simple "static" and "mobile" groups then, a continuum of spatial behaviours existed, with pike displaying behaviours intermediate to the two "extremes" described above, for example, the behaviour of Pike 11 was similar to that of Pike 06 and 08 but on a smaller longitudinal scale, whilst Pike 07 showed periodic returns to its capture location whilst more commonly residing some 500 m upstream (Figs. 2.b and 2.c).

Short-term excursions were performed by several pike (Pike 05, 03, 02, 14 and 09) increasing the length of their TMLDs (Figs. 2.a and 2.b, Table 1), whilst MCD could also be increased if an excursion coincided with a home range track (Pike 05, 14 and 09, Figs. 2.a and 2.b, Table 1). Following excursions, Pike 05, 03, 02 and 14 all returned to their usual areas of residency. A permanent relocation was performed by Pike 01, which stayed within ca. 300 m of its capture site for ca. 11 months before ranging over several kilometres and settling 2000 m to 3000 m upstream (Fig. 2.c, Table 1).

Wide ranging movements similar to those of Pike 01 prior to relocation were also performed by Pike 04, which had shifted its area of residency downstream by some 500 m during November 2001, resulting in a high MCD for this fish (Fig. 2.c, Table 1).

The effect of season and/or discharge upon spatial behaviour

The timing of the movements of the two pike that used widely separated areas of river at different times of year (Pike 06 and 08) were broadly seasonal in nature, but discharge also appeared to be a factor; both pike moving upstream during a flood in December 2002 when more minor flood events earlier in the year had not resulted in upstream movements (Fig. 2.c). For several pike, excursive behaviour, or a more prolonged relocation, coincided with periods of flooding (Pike 05, 03, 14 and 04; Figs. 2.a and 2.c).

Increased movements during the spring were seen amongst some, but not all, of the pike (e.g. Pike 02, 14, 09, 04 and 01) and such movements were not necessarily repeated the following year (Pike 09 and 01, Fig. 2.b).

Utilisation of side channel habitats

Only two of the fifteen pike tracked were never found in side channels either during or between home range tracks (Pike 14 and 15). No pike were found in side channels during home range tracks 1) and 2) but pike were often found in side channels during home range tracks 3) and 4) (Fig. 3). Generally, lower percentage utilisation occurred in subsequent tracks, although one individual (Pike 12) made extensive use of a side channel during home range track 7) (Fig. 3).

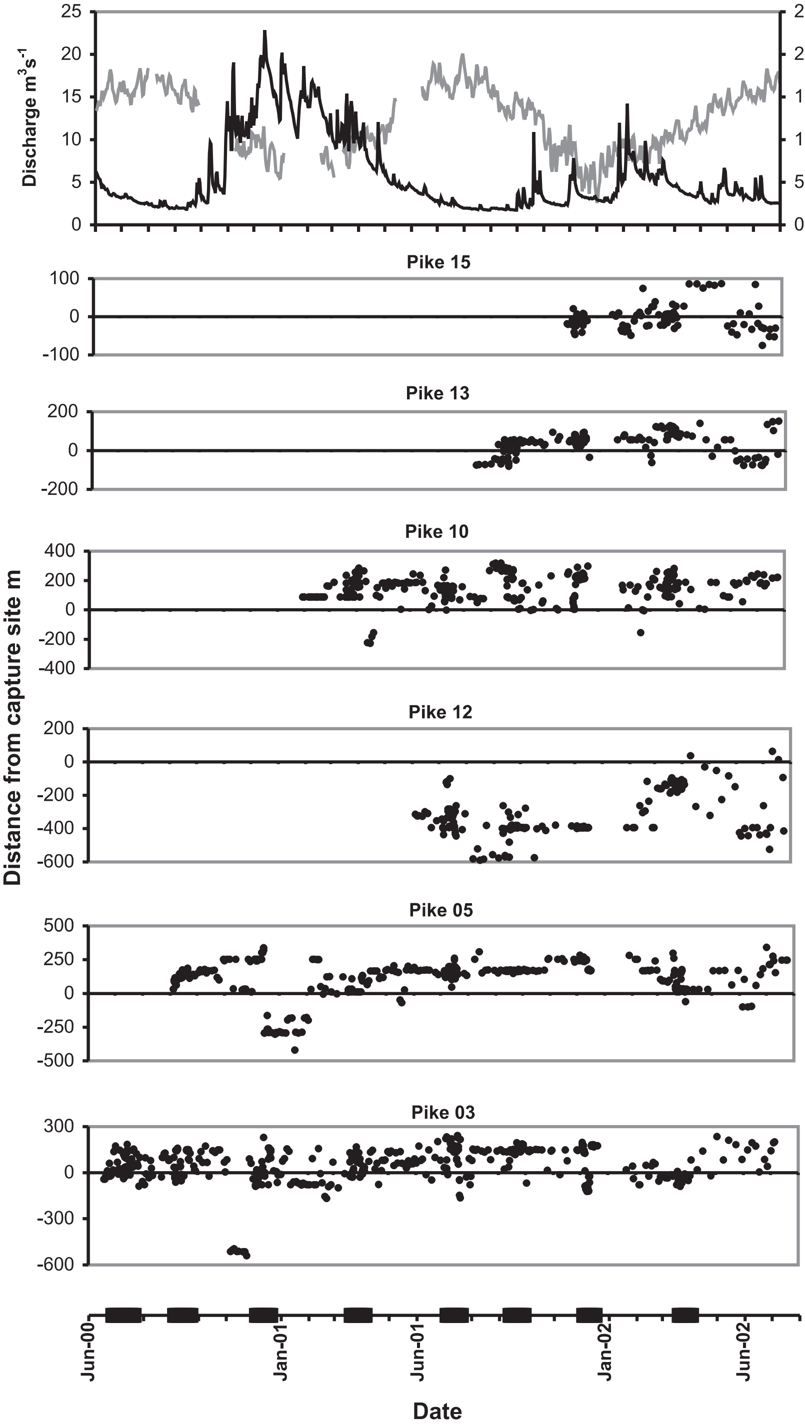

Fig. 2a – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 15, 13, 10, 12, 05, 03). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

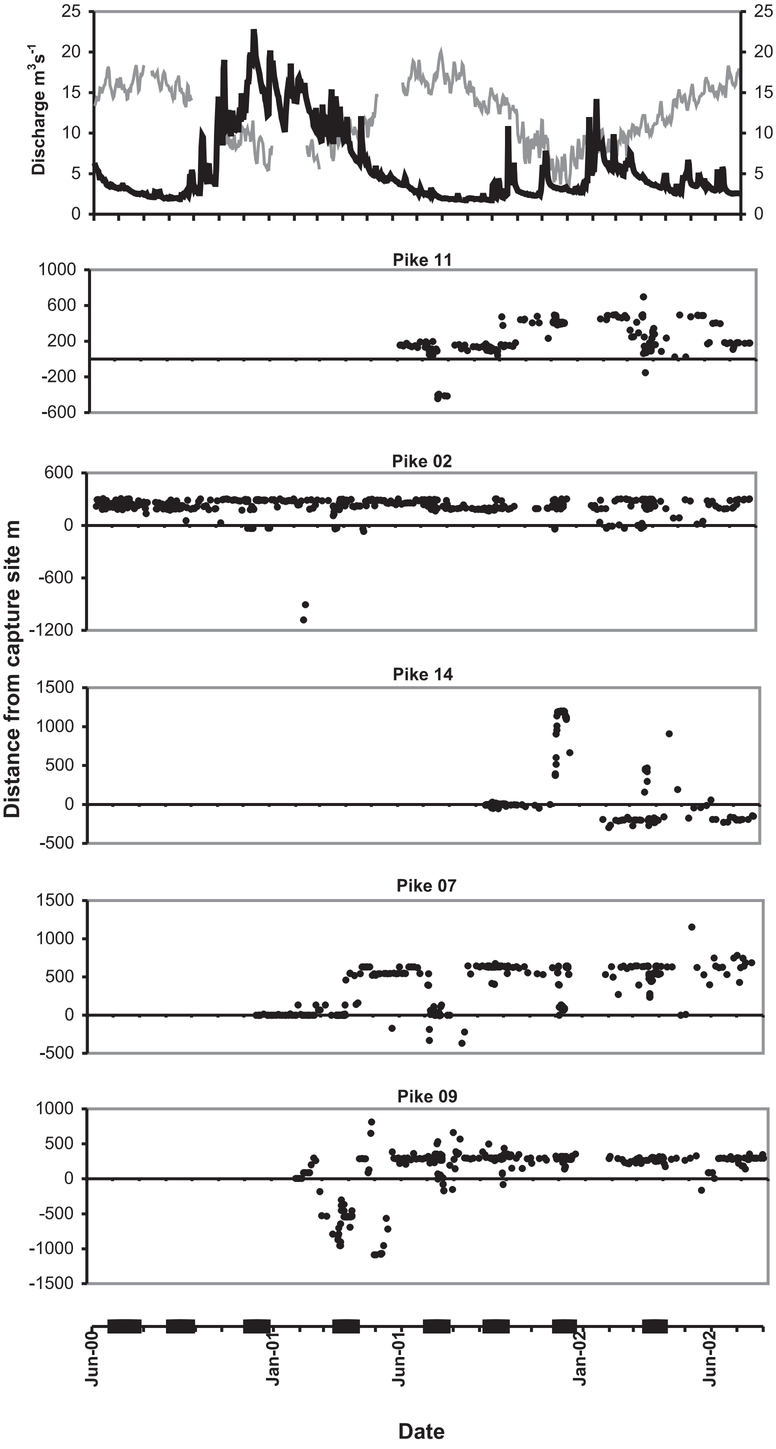

Fig. 2b – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 11, 02, 14, 07, 09). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

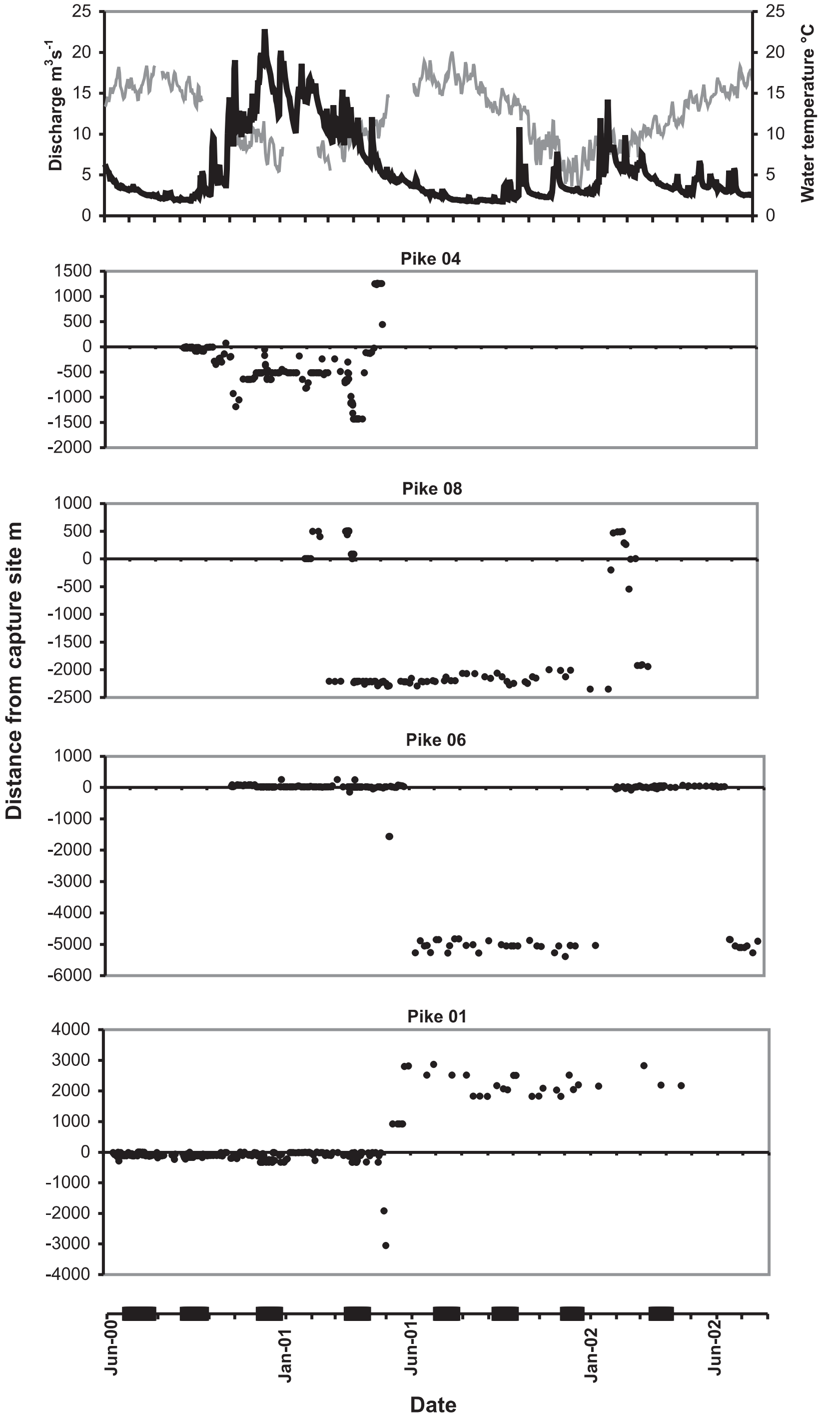

Fig. 2c – The distance from the capture location for every fix recorded from each pike over the entire time they were tracked, arranged in order of ascending Total Maximum Linear Displacement (Pike 04, 08, 06, 01). Mean daily discharge and water temperature data are also shown. Periods when home range tracking took place are indicated (■).

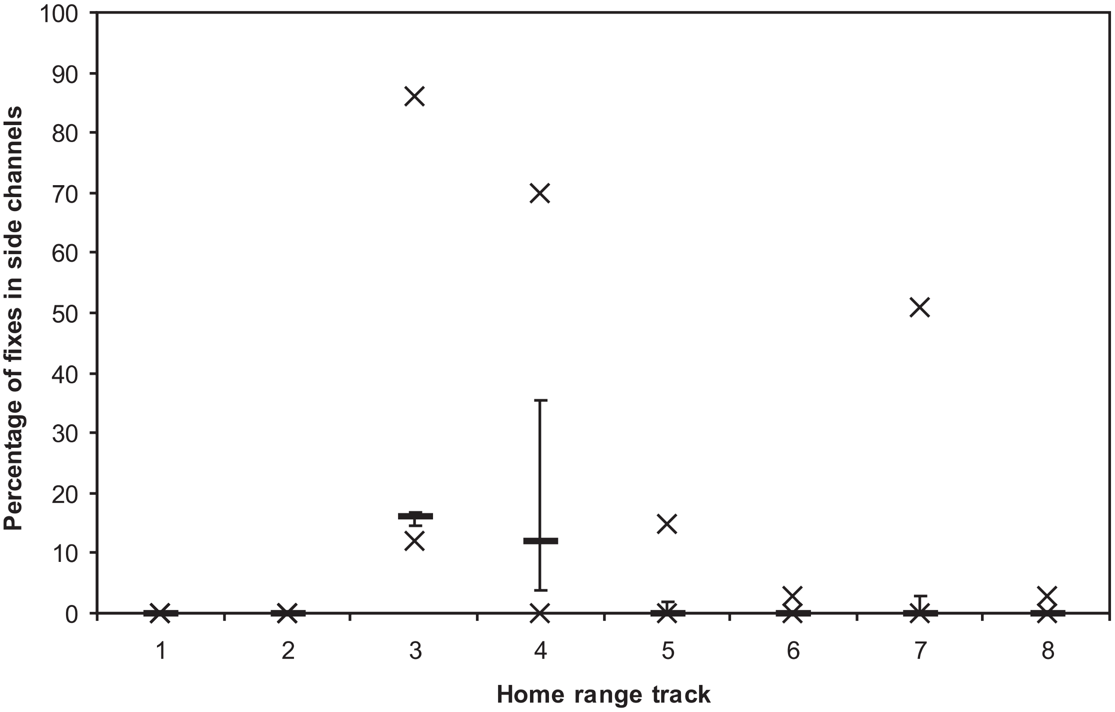

Fig. 3 – The median (▬), maximum (✕) and minimum (✕) percentage of fixes occurring in side channels in each home range track, together interquartile range, recorded from individual pike.

Discussion

Pike in the River Frome showed a highly variable repertoire of spatial behaviour that did not fit the previous model of static and mobile individuals (Mann, 1980). This result supports the view of pike as versatile predators (Chapman and Mackay, 1984) and reflects the variety of spatial behaviours reported for lacustrine pike. There was a continuum of spatial behaviours, from individuals that always remained within a few hundred metres of river (e.g. Pike 13, 15) to individuals that made repeated journeys of several kilometres (e.g. Pike 06, 08). Relocations could also occur, with Pike 01 moving to a distant stretch of river and not returning for the remainder of the study period.

The two indices used to describe spatial behaviour (TMLD and MCD) allowed for distinctions to be made between the total length of river used and the length of river in which activity was concentrated. However, MCD does require careful interpretation; larger values being obtained when home range tracks coincided with excursive behaviour by pike. Long-term radio tracking, between home range tracks, allowed such excursive behaviour to be placed in context with activity throughout the year.

Whilst pike that were always found within a few hundred metres of their capture site could be viewed as being “static”, we feel the term is inappropriate, as it would ignore both the movements within the length of river occupied, and also the occurrence of excursive movements. Pike 06 and 08 could easily have been described as ‘static’ fish, had they been involved in a mark-recapture or shorter-term radio tracking study. Despite both displaying repeated long distance movements between widely separated areas of river, within the upstream and downstream home ranges the patterns of fixes are similar to those of pike with the shortest TMLDs.

Explanations for the different spatial behaviours exhibited by the pike must of necessity be speculative at this stage. The positive correlation between pike length and TMLD suggests that larger pike may move more freely within the river than smaller pike; consistent with the hypothesis of Grimm and Klinge (1996) that smaller pike, being at greater risk of predation, show more restricted distributions.

The large upstream movements of Pike 06 and 08 were indicative of spawning migrations, although until such time as this behaviour can be shown to be of adaptive significance to the population (Lucas and Baras, 2001) the term 'migration' must be treated with appropriate caution. Both fish frequented known spawning grounds whilst residing in the main study area and Pike 08 was seen spawning in March 2001.

Upstream movement by Pike 06 and 08 appeared to be related to increased discharge in 2001. In November 2002, after the conclusion of the present study, Pike 06 again returned to the same upstream location, at the onset of a period of flooding (CEH, unpublished data), implying that a similar movement may have occurred prior to the fish being tagged in October 2000, when the period of major flooding had just begun. Downstream movements appeared to coincide with the end of the spawning period in both 2001 and 2002 and on the day after Pike 08 was seen spawning, the fish was detected in the main study area, and then subsequently >2000 m downstream, just 1.5 hours later.

Differences occurred between Pike 06 (♀) and 08 (♀), both in spatial behaviour within the main study area and in the timing of downstream movements. Whilst upstream, Pike 08 ranged more widely than Pike 06, and visited several different side channels, whereas Pike 06 was almost always found near the same channel where it had originally been caught and released. Pike 06 remained in the main study area longer than Pike 08 in both years. Without a larger sample size it was not possible to state whether these particular differences represented individual variation, or more widespread differences in behaviour between the sexes (Frost and Kipling, 1967; Lucas, 1992).

The spawning period is a time of increased activity for lacustrine pike (Lucas, 1992) and this appeared also to be the case for some riverine individuals, although others remained in one area throughout the spring. Miller *et al.* (2001) demonstrated the existence of natal homing amongst pike and it can be hypothesised that those individuals that showed the most restricted longitudinal distribution along the river remained within the vicinity of their natal spawning site for their entire life whereas wider ranging individuals may have dispersed away from the natal spawning site, possibly returning on a seasonal basis. However, during the spring pike were not necessarily restricted to one particular area (e.g. Pike 08 and 11) and different areas could be occupied in successive years (e.g. Pike 01 and 09). Natal homing alone cannot account for the variety of movement patterns displayed.

Langford (1979) noted that flood flows could lead to the displacement of pike, and this could account for some of the excursions recorded during the present study (e.g. Pike 03 and 05). Excursive movements perhaps lead to relocation, if a better quality habitat is found (in terms of increased prey availability or reduced competition) and this may have occurred for Pike 01.

Side channels are clearly of great importance to pike under certain conditions. These areas were known to be used for spawning (Mann, 1980), but were also found to be utilised extensively well in advance of the spawning period, particularly during elevated discharges in autumn/winter 2000/2001 (Masters *et al.*, 2002). Similar exploitation of side channels was noted by Gerlier and Luquet (1999). During summer months side channels were rarely occupied. Although some of the side channels in the study area became inaccessible to pike during the summer, due to shallow water at the mouth, others remained accessible, but were still rarely occupied. When pike left the main river channel, the side channels entered were usually those closest to the areas where they normally resided but it is notable that during the upstream movements of Pike 06 and 08, numerous side channels were passed during their return to the main study area.

In order to further study the variation in the spatial behaviours observed, ideally pike need to be followed throughout their lives and the importance of intraspecific and interspecific interactions also need to be considered. Studying pike throughout their lives is an aim for future studies, and can be achieved by techniques such as individually marking young-of-the-year pike prior to their dispersal from the spawning grounds, using Passive Integrated Transponders (Lucas, 1999), together with radio telemetry techniques adapted for use with small (Beaumont and Masters, 2003) and large pike.

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Long range seasonal movements of northern pike (*Esox lucius* L.) in the barbel zone of the River Ourthe (River Meuse basin, Belgium)

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Key words: telemetry, pike, annual movements, spawning activity, river.

Abstract

In order to study the annual activity cycle and reproductive ecology of northern pike (*Esox lucius* L.) in the River Ourthe (Belgian Ardenne), 6 fish (579-742 mm FL, 1605-4090 g, 2 females and 4 males) were captured by electric fishing in November 2000 and January 2001. They were surgically implanted with radio-transmitters and tracked for 149 to 349 days in a 30-km river stretch. During the pre-spawning period in winter, most movements were between distinct holding areas spaced from 40 to 550 m. All the pike began the upstream spawning migration between 8 February and 30 March 2001, when the mean water temperature varied from 6.7°C to 8.7 °C and the water flow from 52 to 199 m^3s^{-1}. The six pike travelled upstream, over distances ranging from 0.75 km to 15.7 km to reach their potential spawning sites. Pike arrived on their potential spawning sites between the 13 February and the 02 April 2001 and remained there from 5 to 25 days when the daily mean water temperature ranged from 2.9 to 10.0 °C. The six pike moved downstream after spawning and showed similar behaviour to those observed prior to spawning, but the distances between holding areas were more extended than during the winter pre-spawning period. When considering the entire tracking period, the longitudinal extension of the activity range varied from 1,421 to 24,798 m (mean 12,050 m).This exploratory study provided original observations on northern pike movements in a barbel zone of the River Meuse basin. Results contrast with the widely established view of pike being a sedentary predator and provide data on its behaviour throughout the annual cycle.

Introduction

As a top predator, northern pike (*Esox lucius* L.) play an important role in the regulation of fish community in rivers and lakes ecosystems (Prejs *et al*., 1994; Craig, 1996; Berg *et al*., 1997; Jepsen *et al*., 2001). They can tolerate a wide range of environmental conditions, but are primarily mesothermal or cool-water fish best adapted to shallow, productive, mesotrophic-eutrophic environments (Craig, 1996). Over the past half-century, eutrophication and habitat loss have significantly affected northern pike in Europe and North America (Casselman and Lewis, 1996) and there is an increasing need to conserve and enhance their populations. However, effective management programmes cannot be planned without an understanding of the biological requirements of the species throughout its life cycle.

Biotelemetry studies on the movements of pike have been almost exclusively performed in lakes and reservoirs (Diana *et al*., 1977; Diana, 1980; Cook and Bergesen, 1988, Rogers and Bergesen; 1995, Jepsen *et al*., 2001). Strangely, investigations in rivers ecosystems have been limited. Masters *et al*. (2002) studied the habitat utilisation during winter floods in an English river and a study on the movements of a single pike in an Irish canal was performed by Donnely *et al*. (1998). Currently, the established view of pike is of a largely solitary predator (Raat, 1988; Maitland and Campbell, 1993 in Rosell and MacOscar, 2002), migrating only in spawning season, and being relatively sedentary at other times. According to Lucas and Baras (2001) Esocids tend to display limited migration, altough local movement may be of key significance for population maintenance.

In order to study the seasonal activity cycle of *E. lucius* in the barbel zone of the River Ourthe (River Meuse basin), six individuals were radio-tracked during an annual cycle.

Materials and methods

Study site

The River Ourthe is the main sub-basin of the River Meuse in Southern Belgium. It runs through the Belgian Ardenne where it meets tributaries such as the Amblève and Aisne streams (Fig. 1). This section contains small weirs, of less than 3 m in height, which may sometimes interfere with the free movement of some species of fish (synthesis in Ovidio and Philippart, 2002). In the study area, the River Ourthe has a mean slope of 0.12%, a mean width and flow in summer of 25 m and 32 m^3s^{-1}, respectively. River Ourthe is typical of the barbel and grayling rivers and hosts a mixed cyprinid-salmonid fish assemblage (31 indigenous species) of which the main constituents are: the barbel, *Barbus barbus* (L.), chub *Leuciscus cephalus* (L.), nase *Chondrostoma nasus* (L.), grayling *Thymallus thymallus* (L.) and brown trout *Salmo trutta* (L.). The water temperature in the River Ourthe varies over the annual cycle, from 0 °C to 26 °C (mean: 10.5 °C, data from 1990 to 2000).

Fish tagging and environmental records

Six pike were captured by electric fishing (DEKA, 2.5 kVA) in an area situated in the vil-

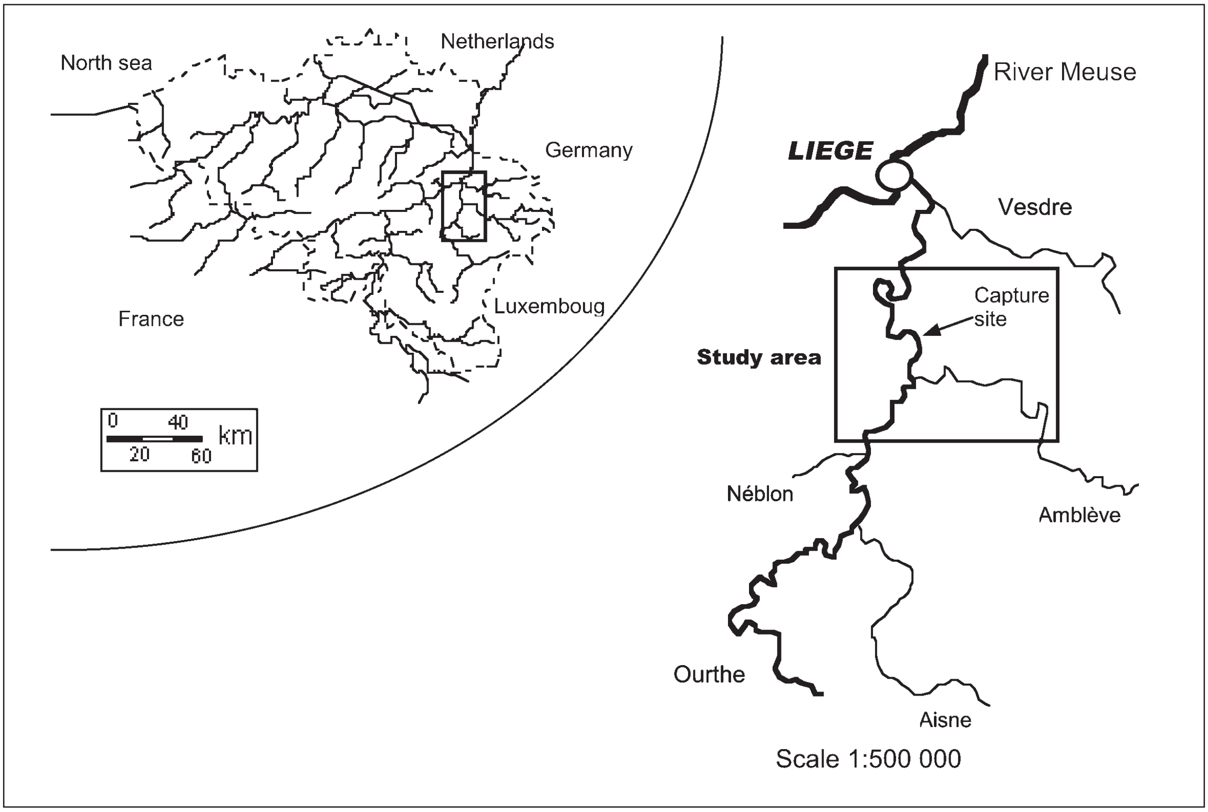

Fig. 1 – Location of the study area in Belgium and in the River Ourthe sub-basin (River Meuse basin)

lage of Poulseur (Fig.1). This area is characterised by the presence of two secondary river branches that contain immersed vegetation and that are commonly used by pike for reproduction since several years (Philippart *et. al.*, unpublished results). Three pike were captured in a river branch and the three others in the main course of the River Ourthe in November 2000 and in January 2001 (Table 1). Pike were anaesthetised in a 0.2mll^{-1} solution of 2-phenoxy ethanol then placed ventral side up into a v-shaped support adjusted to their morphology. A mid-ventral incision was made between the pelvic girdle and the anus and an alcohol-sterilised transmitter (ATS Inc., 40 MHz, internal coiled antenna, 20 g) was inserted into the body cavity. The incision was closed by three separate stitches, using sterile plain vicryl sutures. Fish were released at their capture site as soon as they had recovered posture and spontaneous swimming (about 10 min after surgery). This methodology minimises the possible biases originating from long term post-operative care. The sex of the pike was determined by visual inspection of the gonads through the incision, except for Pike 1 that was sexed after its recapture during the study. All the females were potentially mature and presented eggs under development in the ovaries.

Temperature in the River Ourthe and in the secondary branches was logged every 30 min using data loggers (TidBit Onset Corp.) installed in Poulseur with an accuracy of 0.16 °C. Water levels were measured daily in the River Ourthe and in the secondary branch with an accuracy of 1 cm, on limnimetric scales installed near the temperature loggers. Water flow was recorded continuously about 10 km downstream from the capture site (data from SETHY-MET).

Table 1 – Characteristics of the six tracked pike

Fish N°	Fork length (FL, mm)	Body weight (g)	Tag Ratio (%)	Sex	Date of capture	Date of last location	Tracking duration (days)
1	598	1 605	1.25	M	21 Nov. 2000	04 June 2001	196
2	607	2 170	0.92	F	21 Nov. 2000	01 June 2001	194
3	742	4 090	0.49	F	24 Jan. 2001	07 Jan. 2002	349
4	660	2 482	0.81	M	24 Jan. 2001	21 June 2001	149
5	662	2 310	0.87	M	24 Jan. 2001	13 Dec. 2001	324
6	579	1 630	1.23	M	24 Jan. 2001	07 Jan. 2002	349

Tracking

Fish were located once a week from 21 November 2000 to 29 January 2001. From the 30 January to the 1 April 2001, fish were located 6 times/week. From 2 April to 6 June 2001 they were located 3 times/week and then once every 10 days after 6 June 2001. Locations were made by triangulation from markers on the rivers' banks, using a mobile FieldMaster radio receiver and a loop antenna (ATS Inc.). Most locations were made during daytime, with accuracy between 5 to 20 m^2, depending on the distance between the fish and the observer and the width of the river. During the migration, distances between two locations were determined to the nearest 20 m using a decametre on the field or topographical map (1:5 000). The longitudinal extension of the activity range during distinct periods (pre- and post-spawning) was defined by the distance separating the most upstream and the most downstream location of each pike.

Results

Pre-spawning movements

During the winter pre-spawning period, pike demonstrated quite similar patterns of movements

(Figs. 2 and 3). Most movements were between resting-places 40 to 550 m apart. They usually moved upstream and downstream but the distances travelled between two locations rarely exceeded 300 m. Pike 1 travelled frequently between two resting-places situated in a secondary river branch and in the main course of the River Ourthe (Fig. 3). The resting-places of the other pike were essentially located either in the main course or in the secondary river branches.

Spawning migration

Pike began their spawning migration between 8 February and 30 March 2001 (Fig. 2). Individuals 1 and 3 started their migration on the same day (15 March). Migrations started when the mean water temperature was between 6.7 °C to 8.7 °C and the water flow between 51.6 and 199 m^3s^{-1} (mean flow the first day of migration: 124 m^3s^{-1}; mean annual flow in 2001: 54.3 m^3s^{-1}, Fig.3). Fish travelled upstream, over distances ranging from 0.75 km to 15.7 km to reach their potential spawning sites (Figs. 2 and 3). Some individuals migrated directly to the spawning sites whilst other moved discontinuously. Pike 5 moved 11.3 km upstream in 4 days, but, in contrast, pike 3 achieved a 4.5-km migration in 13 days (Fig. 2). Pike 2, 5 and 6 sometimes travelled more than 3.0 km upstream from one day to another in high water flow conditions (±100 m^3s^{-1}). On 8 March 2001 between 16:25 hours and 17:25 hours (7.7 °C and 79 m^3s^{-1}), pike 5 travelled 1.05 km upstream. This corresponds to a movement of 0.44 body $lengths^{-1}$. During it's 15.7 km upstream migration, pike 6 moved past three obstacles (Fig. 2).

Each pike used a different spawning site (Fig. 4). Pike 2 and 6 entered into the Amblève, a tributary of the River Ourthe. The four other individuals stayed in the main course of the River Ourthe or in a secondary branch for reproduction. The potential spawning areas were characterised by shallow (10-60 cm depth) and calm water and the presence of aquatic vegetation (*Ranunculus* sp., *Potamogeton* sp., *Carex* sp., *Scirpus* sp.) or immersed terrestrial vegetation (Gramineae). Pike 2 and 5 probably spawned in a secondary river branch. The other pike spawned in areas located along the banks of the Ourthe or Amblève.

Pike arrived on their potential spawning sites between the 13 February and the 02 April 2001 and stayed there 5 to 25 days (mean 11.2±7.8 days). During this period, the daily mean water temperature ranged from 2.9 to 10.0 °C (mean: 6.97 ± 1.75 °C) and the water flow from 41.4 to 259.0 m^3s^{-1} (mean: 99.8 ± 55.7 m^3s^{-1}) (Fig. 3). They left the spawning sites between 10 March and 13 April 2001.

In order to test if the pike effectively moved upstream to the spawning site, electric fishing was performed in June 2001 on habitats where pike 2 and 5 had migrated (Figs. 2 and 4). Juveniles were captured in the two sites, indicating their suitability for the pike's reproduction. Electric fishing was also achieved on the original capture sites of the six pike (Fig. 4) and juveniles were also observed at these places.

Downstream migration

The six pike moved downstream after reproduction (Figs. 2 and 4). Pike 1 returned to a previous resting-place used before the spawning migration. Pike 2 and 4 rapidly returned in a few days in an earlier resting-place, but several days later, they respectively moved 20 and 8 km downstream on 20 March and 10 May 2001. After it's downstream migration, pike 3 was located 800 m upstream of it's capture place, but never reintegrated the original resting-place. Pike 5 and 6 were located 10 and 3 km upstream of their capture and tagging site after the downstream migration.

During it's downstream migration fish 6 was confronted for the second time with the weirs of the Amblève, but in the direction of the water flow. The pike stopped its migration three days just upstream of each weir, indicating that the obstruction may interfere with the movement of pike in both directions (Fig. 2).

Post reproduction behaviour

After the downstream migration and until the end of the intensive tracking period (late June), pike

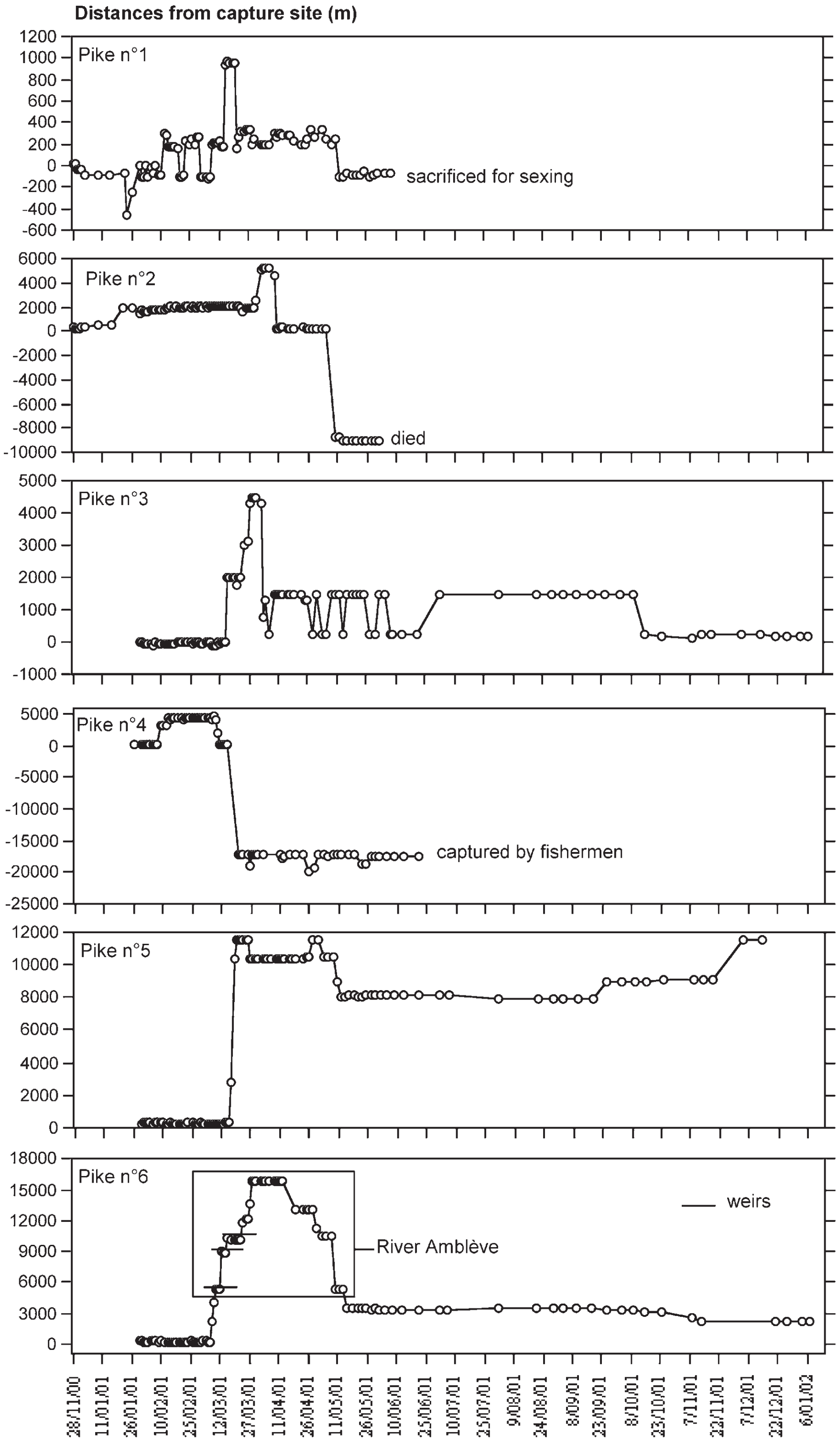

Fig. 2 – Movements in meters of the six pike radio-tracked in the river Ourthe sub-basin with reference to capture site.

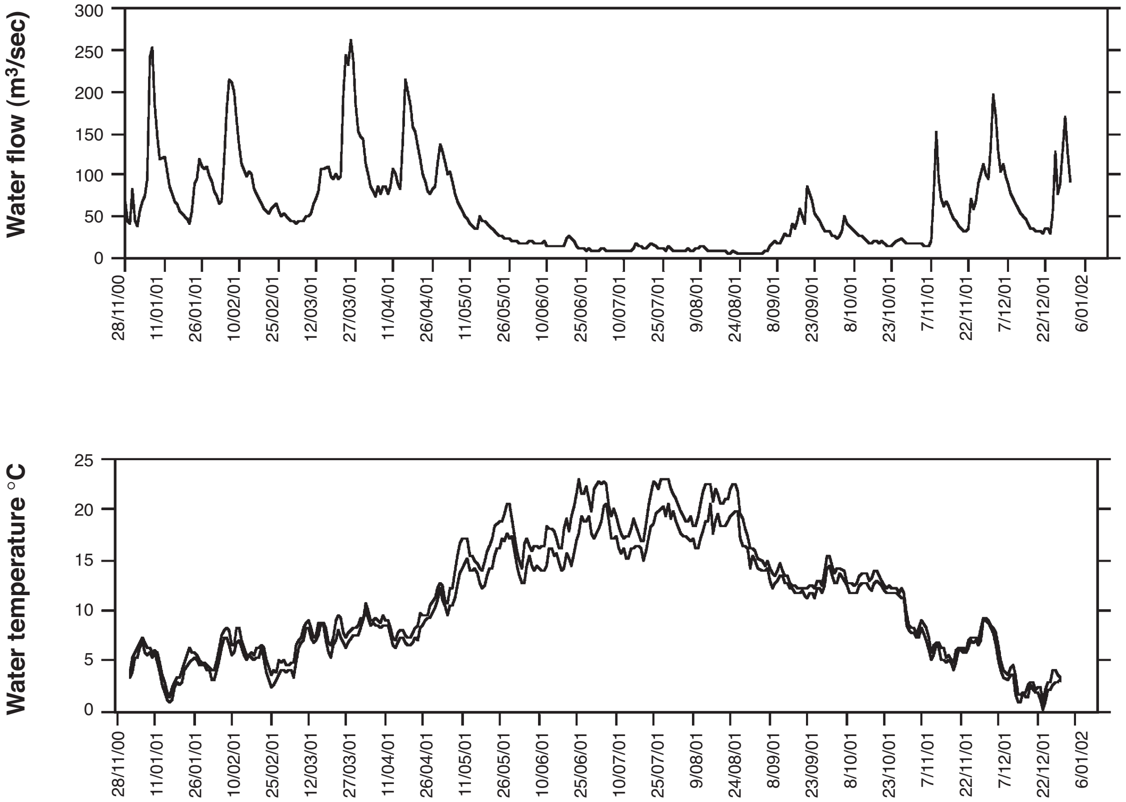

Fig. 3 – Variation of water level and water temperature (daily min. and max.) in the River Ourthe during the study.

showed similar behaviour to those observed prior to spawning, but the distances travelled between two resting-places sometimes exceeded 1.2 km (pike 3 and 4).

In June, three fish were no longer followed. Pike 1 was captured by electric fishing on 7 June 2001. It was covered by biting and fighting injuries (suggesting its participation to spawning activity) and was sacrificed for sexing. Pike 2 probably died as no movements were detected during the last days of tracking. Its transmitter was finally found in the water. A fisherman captured pike 4 and affirmed that the fish was in very good health and exempt of injuries.

Pike 3, 5 and 6 were followed less intensively after June 2001. Interestingly, pike 5 returned to the spawning site previously utilised in March 2001 in early December 2001 (Figs. 2 and 4), but the transmitter failed two days later. Pikes 3 and 6 stayed in the same sites until the end of the battery life of their transmitters.

Longitudinal extension of the activity range

Table 2 shows the longitudinal extension of the activity range of the pike before, and after the spawning migration as well as during the entire tracking period. Kruskal-Wallis test indicated significant differences between the 3 groups ($p<0.005$; $H=11.275$) suggesting an heterogeneity in the extension of movements from winter to summer. The longitudinal extension of the activity range is significantly longer after the spawning migration than before (Mann-Whitney; $P<0.05$; $Z=-2.082$). The longitudinal extension of the activity range was not correlated with the characteristics of the individuals (length, weight).

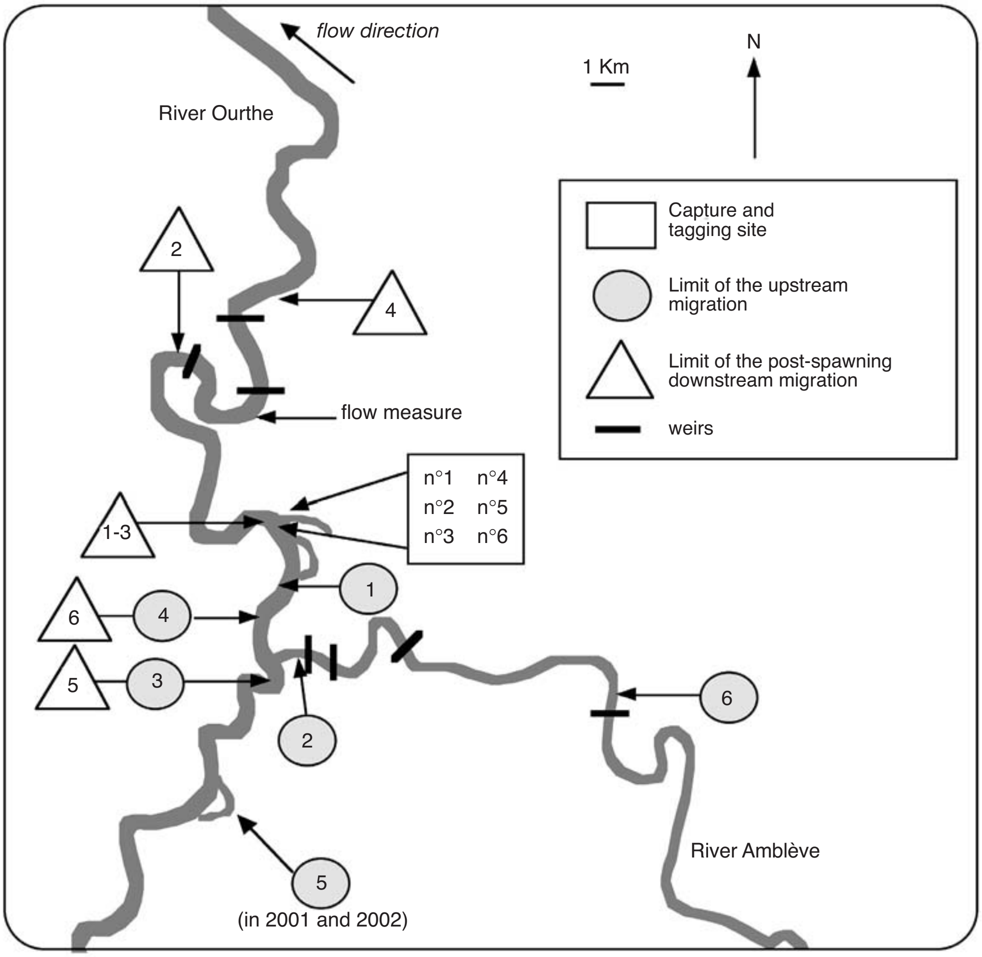

Fig. 4 – Geographical representation of the dispersion of the six radio-tagged pike before, during and after spawning.

Table 2 – Longitudinal extension of the activity range (m) of the six radio-tagged pike during three different periods.

Pike n°	Before spawning migration (m)	After spawning migration (m)	Total (m)
1	754	295	1 421
2	1 895	9 342	14 295
3	119	1 267	4 609
4	171	2 788	24 798
5	176	1 280	11 446
6	167	1 410	15 732

Discussion

This exploratory study provided original observations on northern pike movements in a barbel river. Results contrast with the widely established view of pike being a sedentary predator and bring data on its biological cycle and behavioural tactics throughout the annual cycle. Because the number of tracked fish was limited, results remain preliminary. But, by both the duration and the accuracy of the locations our study provides a better understanding of the behavioural ecology of northern pike in river ecosystems and constitutes a precious tool to improve the management of their populations.

Pike were tagged using surgical implantation. This method has several advantages over external attachment, including avoidance of vegetation entanglement, as well as less interference with swimming behaviour and speed (Winter, 1983; Mellas and Haynes, 1985; Herke and Moring, 1999). However, this tagging technique can be disadvantageous when tagging females just before spawning (Herke and Moring, 1999), but has been found to have no or very little adverse long-term effect on the growth and survival of pike (Jepsen and Aarestrup, 1999). In order to minimise this problem, fish were captured and tagged from three to two months before spawning, using transmitters representing a very low ratio of the fish body weight (<1.25% for the males and <0.92% for the females).

Annual movements

In the River Ourthe, pike were relatively mobile. The movements were more important during the spring upstream and downstream migration, but the pike still moved frequently outside the spawning periods. During the winter and summer seasons, the pike moved between distinct holding areas >1500 m apart. In an Irish canal a single radio-tracked pike moved in between different resting-places spaced out from up to 8 km. In the Lake Ste. Anne, Diana *et al*. (1977) found no differences in the level of movements between summer and winter, although during the winter, the tagged pike moved longer distances (>1000 m) more frequently than in the summer. In a Colorado reservoir, Cook and Bergesen (1988) found a small increase in number of pike movements, but a decrease in distance moved during winter. Rogers and Bergesen (1995) found no change in the level of pike movement from August to December despite drastic changes in temperature over the period.

Migration

Indirect proofs given by season, temperature, maturity of females during tagging, juvenile occurrence at the end of the spring and the characteristics of the potential spawning sites suggested that migration of pike were related to reproductive events.

Migrations started from 8 February to 30 March and ranged from 0.75 to 15.7 km. In the river "aux Pins" (Québec), Massé *et al*. (1991) performed factorial analysis after a capture-tagging-recapture study, and suggested that the spawning movements were facilitated by the river cues. In the River Ourthe, pike began their migrations during important flow conditions and during increasing water temperatures, ranging from 6.7 to 8.7 °C (mean daily temperature). From an ecological point of view, these cues may stimulate pike to migrate during thermal conditions that allow a sufficient swimming capacity and under high flows conditions associated with immersion of the terrestrial vegetation.

Two individuals entered in a tributary of the River Ourthe, and the others stayed in the main watercourse or in branches. Similar biotelemetry studies in rivers do not exist. Craig (1996) affirmed that northern pike living in rivers are rather sedentary but they have to migrate to reach the spawning grounds. A migration of 15 km (exceptionally 78 km) was reported by Carbine and Applegate (1948, in Craig, 1996) using capture-tagging-recapture methods. In our study, pike arrived on their spawning sites between 13 February and 02 April 2001 and stayed there 5 to 25 days (mean 11.2±7.8 days). During the spawning period, the mean water temperature ranged from 2.9 to 10.0 °C (mean: 6.97 ± 1.75 °C). Others studies reported that the spawners are present on the spawning grounds when water temperature is in the range 1-4 °C (Franklin and Smith, 1963; Dumont *et al*., 1980) and even 0 °C (Clark, 1950). In lake Windermere, spawning takes place at temperature range 6-14 °C (Forst and Kipling, 1967). Sukhanova (1979) observed pike spawning at temperature of 3.8-4.5 °C, but they were more active in the afternoon after 17:00 at 5-8 °C. In our study, potential spawning areas were located in shallow waters and were characterised by the presence of aquatic or immersed terrestrial vegetation, as it was already observed by several authors (synthesis in Craig, 1996).

Despite the fact that the tracked fish were captured and released near verified pike spawning areas, they all migrated upstream to spawn in distinct sites of the river basin. The first hypothesis is the existence of spawning site fidelity, expressed by the return of adults to previous years spawning areas. In our study, after its post-spawning downstream migration in April 2001 and a period of stability from April to November, pike 5 returned to the same spawning site in early December. This movement may correspond to the expression of spawning site fidelity. Spawning site fidelity has been shown in a number of esocids populations, including northern pike *Esox lucius* (Carbine and Applegate, 1948; Frost and Kipling, 1967; Bregazzi and Kennedy 1980; Karas and Lethonen, 1993) and muskellunge *Esox masquinongy* (Crossman, 1990). Rosell and MacOscar (2002) showed a high degree of specificity of return of individual fish to particular spawning areas, with 18 of 36 spawning season recaptures being found within 500 m of their previous years spawning site. Five were recorded at exactly the same spawning site. Individual returns, sometimes on many occasions, to spawning areas have been described before (Kipling and Lecren, 1984; Karas and Lehtonen, 1993). But the spawning site fidelity can also be the expression of natal-site fidelity. In order to verify this hypothesis in the future, we pit-tagged 150 young of the year pike in distinct spawning site in order to study their dispersal and possible return as adults to their natal site (homing behaviour). Another way to provide evidence of natal-site fidelity is to show genetic differences among spawning populations, which would result from reproductive isolation in cases of both natal-site and spawning site fidelity (Miller *et al*., 2001). Miller *et al*. (2001) showed significant differences between two spawning populations of northern pike in a single large reservoir by comparison of allele frequencies at five polymorphic microsatellites markers. The reproductive isolation suggested by these genetic differences could not occur if fish chose their initial spawning site randomly, even if they subsequently returned to those sites.

Dispersion of genitors during reproduction could also correspond to an adaptation strategy of the species that warrants a multiplication of the reproduction sites and allows a sufficient recruitment in case of problem (pollution, important diminution of the water level in the spawning site, predation) or to avoid genetic isolation.

During the spawning migration, one pike was confronted with several physical obstacles. This underlines the importance of considering the situation of northern pike in the different restoration programs in allowing the free movements of fish in rivers (Ovidio and Philippart, 2002).

Post spawning movements

After spawning, the tracked pike moved downstream. Some individuals returned to their initial capture site, even though some stayed between the capture site and the spawning area and others moved downstream of their capture site.

Similar upstream and downstream movements were observed by Koed *et al*. (2000) in adult pikeperch (*Stizostedion lucioperca*) in a Danish lowland river. Authors suggested that the pikeperch make a feeding migration during autumn and winter from upper reach to the lower reach and the estuary of the river Gudenaa, and an upstream spawning migration during the spring. The total distance annually travelled by pikeperch ranged from 47 to 226 km. In our study, distances travelled by fish were less important and the environmental conditions in the upper and lower limits of the pike's locations were not different. This suggests that in the River Ourthe sub-basin, the meaning of the post-spawning downstream migration could be partially or totally different. For a spawner, this downstream post-reproductive migration can be a way to avoid cannibalism on its own progeny or to return to a well-known river section that can be optimally exploited.

Longitudinal extension of activity range

The longitudinal extension of the activity range of the tracked pike was variable among individuals and period of the year. When considering the entire tracking period, including the spawning migration, the stretch of the river occupied by pike varied from about 1.5 km and 25 km. In an Irish canal, Donnely *et al.* (1998) tracked a single northern pike (81 cm FL, 3400 g) from January to June that occupied a longitudinal home range of about 9 km.

In artificial or natural lakes, contrasting results were collected on the extension of northern pike home-range. In Lake Ste. Anne (Alberta), Diana *et al.* (1977) affirmed that ultrasonic tagged northern pike did not have a well-defined home range, but rather appeared to move at random throughout a relatively narrow zone around the edge of the Lake. Several authors suggested that home range among pike is not very restricted (Bregazzi and Kennedy, 1980; Chapman and Mackay, 1984; Cook and Bergesen, 1988). Malinin (1969; 1970; 1971) found that pike are relatively sedentary with a home range of 50 to 150 m in diameter where the bottom is flat. Other studies revealed restricted movements among pike (Alessio, 1986; Karas and Lethonen 1993; Grimm and Klinge, 1996; Eklöv, 1997). Jepsen *et al.* (2001) observed different kinds of space utilisation between a lake and a reservoir in Denmark. In the lake, pike did not occupy restricted home ranges over long periods, but utilised most of the lake during the year. In the reservoir, pike showed three types of behaviour: i) staying in a restricted area, ii) moving between two or three “favourite areas” and iii) utilising larger habitats with frequent habitat shifts. Mann (1980) suggested that pike population is constituted of two groups of individuals. One group, mainly females, occupies restricted home range, and, the second group moves extensively.

In our study, six of the pike showed types of behaviour which, in our opinion, may not be placed in separate categories. We consider that dividing pike populations into “migrant” and “sedentary” fractions is too reductionist. It is probably a direct consequence of data-collecting methodologies likely to highlight extreme situations but not always suitable in accounting for tactics of intermediate resource utilisation. As in the case of the common trout *Salmo trutta* (Ovidio, 1999), pike seems capable of developing a multitude of behavioural tactics.

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Preliminary results from an exploratory translocation study at the Natural Marine Reserve of Miramare (Trieste, Italy)

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Key words: protected areas, marine conservation, telemetry.

Abstract

One of the conservation precautionary measures applicable to overexploited species is to implement protected population through translocation of exogenous individuals. The European lobster (*Homarus gammmarus* L. 1758) and the brown meagre (*Sciaena umbra* L. 1758) are species under strong fishing pressure. In summers 2001 and 2002 we released four translocated lobsters and two translocated brown meagres inside the Natural Marine Reserve of Miramare, where the species are naturally present. The spatial behaviour of the released animals was monitored using two different acoustic tracking systems (Track28 and VR1 receivers; Vemco Ldt). On the base both of bibliography and of our preliminary experimental outcomes, the lobsters were tagged by gluing the pinger to the dorsal surface of the cephalothorax and the brown meagres were tagged by implanting the pinger in the peritoneal cavity. All the animals, both lobsters and brown meagres, disappeared from the detection range of the hydrophones after a variable number of days (2-16 days of continuous monitoring). We suppose that they did not colonize the site, leaving the protected area. From the methodological point of view, VR1 mode proved to be a suitable tool to evaluate the colonisation of an area by transferred animals.

Introduction

One of the objectives of the Natural Marine Reserve of Miramare (Trieste, Italy) is to protect the local breeding populations from exploitation, maximising its density up to the extent permitted by local keystone resources. This is particularly relevant and precautionary for overexploited species and represents a buffer against mismanagement. In addition to protective measures, a management option for achieving this goal is to restock the local natural population with additional wild individuals, caught elsewhere, to increase the population's size and gene pool ('augmentation program'; Primack, 1993). This action assumes, however, that the released individuals will settle in the new area and avoid conflicts that are a potential hazard. A successful programme needs to consider the spatial behaviour of the released animals and therefore close monitoring is required.

In order to assess whether the reserve aided in restocking overfished species, the purpose of this preliminary project was (1) to monitor the behaviour of animals translocated into the protected area and (2) to evaluate the effectiveness of acoustic tracking methods as a tool for achieving the first goal. The target species were a crustacean, i.e. the European lobster (*Homarus gammarus* L.) and a teleost fish, i.e. the brown meagre (*Sciaena umbra* L.), which are naturally present in the reserve and are under strong fishing pressure outside the protected area. The small size of the marketed *H. gammarus* individuals throughout the Mediterranean Sea suggests that it is over-exploited (Relini *et al*., 1999). On the other side, the brown meagre, a soniferous fish, is included in the UNEP annex 3 of RAC-SPA protocol, i.e. the list of species whose exploitation has to be regulated (RAC-SPA Barcelona Convention, 1995, ratified in Italy in 1999; AA. VV., 1995).

Materials and methods

We monitored the spatial behaviour of four translocated lobsters and two translocated brown meagres in the Natural Marine Reserve of Miramare. The reserve is located about 8 km from Trieste at 45°42’08’’ latitude and 13°42’42’’ longitude (Fig. 1) and it extends for 1700 m coastline and for 121 hectares at sea. The area is divided in a core and in a buffer zone and the maximum depth reaches 18 m.

The animals were caught close to Pirano (Slovenia), at a coastal site facing the Trieste Gulf, tagged with acoustic transmitters and then released in the Reserve about 15 days later.

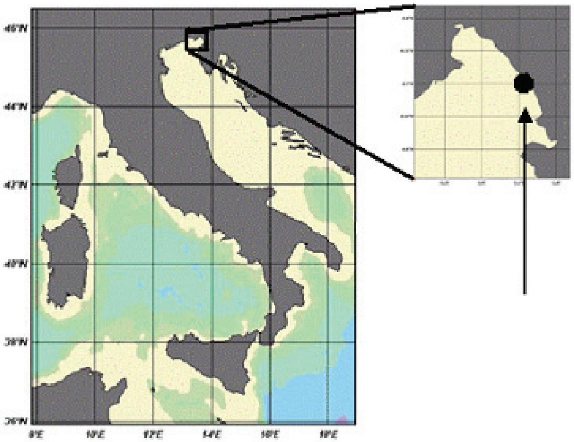


Fig. 1 – The Natural Marine Reserve of Miramare.

The tagging procedure was relatively easy for lobsters: the tag was glued to the dorsal surface of the cephalothorax with quick-setting epoxy resin after drying the carapace with alcohol (Van der Meeren, 1997). Four lobsters of different size (from 17 to 27 cm total length) were tagged with dummy transmitters and released in aquaria (3 m long, 3 m wide, 1 m deep) with ten blocks as shelters (50 cm long, 30 cm wide, 9-13 cm high). They were monitored over a period of 3 months and none of them lost its pinger throughout that time.

Tagging procedures for the fish were more difficult (for a review see Bridger and Booth, 2003). In aquaria, we tagged six brown meagres externally (423±28 gr body weight) i.e. securing a dummy transmitter onto one side of the fish by nylon wires inserted through the dorsal musculature (Baras and Lagardère, 1995). Other four brown meagres were tagged internally, two (441 gr and 443 gr) by forced ingestion of the dummy transmitter into the stomach (Hawkins and Urquhart, 1983) and two (424 gr and 380 gr) by surgical intra-peritoneal implantation (Thoreau and Baras, 1997). The transmitters never exceeded 2% of the body weight in water of the tagged fish. Four of the externally tagged fish shed their pingers within 24 hours and the other two kept pingers for about five days; all brown meagres showed wounds and infections on the skin around the pinger. Both fish regurgitated the transmitters located in the stomach within 48 hours, whereas the transmitters implanted in the peritoneal cavity were retained longer than 20 days. The latter brown meagres recovered within 24 hours from the operation, showing normal feeding and swimming behaviour. Buoyancy was also not noticeably affected by tagging. After 20 days of observations, the animals, in perfect health condition and still carrying the transmitter, were moved to a different, non-experimental tank, due to lack of space. Considering these preliminary outcomes, we concluded that intraperitoneal implantation was the best tagging procedure for our study.

In the field, the animals were tracked using two different acoustic systems: a four channel ultrasonic receiver, connected to a four element hydrophone array located under the research vessel (Track28, Vemco Ldt.) and four submerged automated acoustic receivers (VR1, Vemco Ldt.). The receivers VR1 were moored 1.5 m above the seafloor in proximity of two artificial rocky reefs of the reserve, where the target species are abundant. Mooring units consisted of a concrete filled box used as an anchor, a stainless steel bar and a sub-surface float providing positive buoyancy. The detection radius of each receiver ranged from 70 to 300 m, depending on bottom topography, but dropped to 15-20 meters from the source, when the pinger was located under the rocks.

The pinger used for the lobsters (8x38 mm, 5 gr in water) were the V8-1L continuous transmitters (©Vemco Ldt.), emitting one signal per second at

76.8 kHz (battery life 35 days) and the V8-2L-R256 coded transmitters (©Vemco Ldt.), emitting a train of six pings every 40-60 seconds at 69 kHz frequency (battery life 320 days).

The pingers used for brown meagres (5.5x30 mm, 3.3 gr in water) were the V8SC-6L continuous transmitters (©Vemco Ldt.), emitting one signal per second at 76.8 kHz (battery life 20 days) and the V8SC-6L coded transmitters (©Vemco Ldt.), emitting every 15-45 seconds at 69 kHz frequency (battery life 96 days).

Results

Tracking at sea: lobsters movements

On 16 May 2001 and 13 July 2001 two tagged lobsters (lobsters A and B; 17 and 32 cm TL, respectively) were released in different locations of the Reserve (Fig 2). The releases occurred at about mid-day at a depth of about 8 meters and the lobsters were then tracked continuously by means of the VR28 Tracking System. In both cases, even if shelters were present at the site, the animals moved away from the release point. They roamed around for the subsequent ten (A) and five (B) hours before settling inside (A) and outside (B) the core zone of the Reserve, respectively at 150 m and at 1100 m away from the release point. These sites had beach rocks present. Visual inspection by divers confirmed their positions. They remained at the same location for the following 26 hours (A) and 72 hours (B) respectively, alternating between sporadic short strolls and long residence in their shelter. After which time, the signal emitted by the transmitters was no longer detectable by the tracking system, even if visual inspections (17, 19 and 22 May 2001) revealed the presence of the lobster A at the same position previously defined acoustically. Lobster A found its shelter under a big rock of 1.5x3x0.5 m in size. Unfortunately after 22 May, the animal was no longer detected at its shelter nor at other locations inside the Reserve. A total of 130 and 150 hours of active search was carried out after the last received signal before ending the acoustic tracking session.

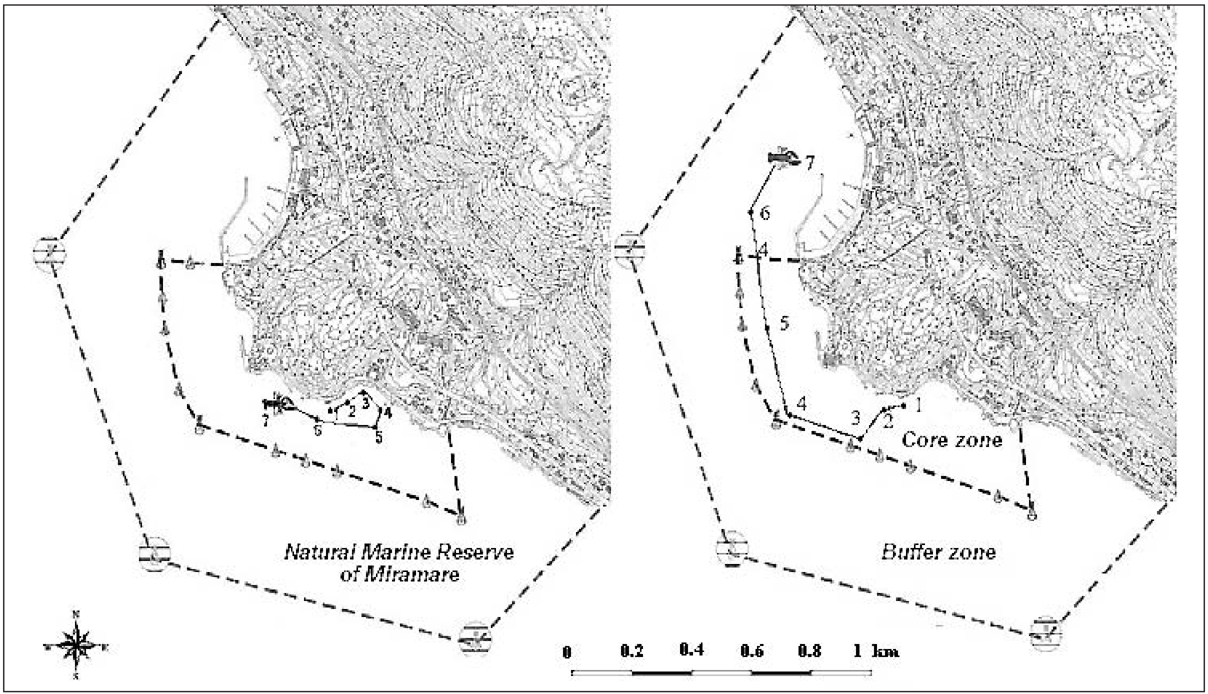


Fig. 2 – Movements of lobsters A (left) and lobsters B (right) at the Natural Marine Reserve of Miramare (number 1 represents the releasing point).

Two lobsters (lobsters C and D; 28 and 20 cm TL, respectively) were released on 13 May and 23 May 2002, respectively, at the rocky reef of Miramare (at 4 meters depth). Their presence was automatically detected by means of the VR1 Tracking System. Lobster C was also fitted with a V8-2L-R256 transmitter and it was therefore simultaneously monitored by both the VR28 and VR1 tracking systems. VR1 receivers demonstrated to be more effective in detecting the acoustic signals than the VR28, recording the presence of the animal also when the VR28 System did not reveal this. Visual observations showed that the individuals were detectable only when the lobsters projected themselves, or most of their body, out of the rocks, or when they moved to the muddy grounds facing the rocky reef. The animal was thus detectable only when the transmitter was clear from obstructions.

Lobsters remained inside the Reserve for the periods from 13 to 29 May (lobster C) and from 23 to 28 May 2002 (lobster D). Contrary to observations from 2001, lobsters C and D remained at the release point for one day after translocation. Subsequently, lobster C settled itself along the reef, building its burrow 150 m away from the release point (visual inspection confirmed the location of this shelter). Lobster D moved along the entire rocky reef for five days, stopping at different positions but never settling anywhere. A total of 7038 signals were detected by the four VR1 receivers (Fig 3): 1645 signals originated from lobster C and 5393 originated from lobster D.

In two cases, i.e. on 26 May from 01:00 to 04:00 and from 20:00 to 23:00 and on 27 May from 02:00 to 03:00, a large number of signals originating alternatively from lobsters C and D were detected by the same VR1 receiver, with an inter-pulses delay of 2–3 seconds. It is possible that the lobsters interacted with one another during these two periods, after which the animals disappeared permanently from the detection range of the hydrophones, one 20 hours after the other one.

Tracking at sea: brown meagre movements

On 31 July 2002, a brown meagre (individual a, 512 gr of weight) was released around midday at the rocky reef of Miramare at a depth of about 8 m. The animal was monitored by means of the VR28

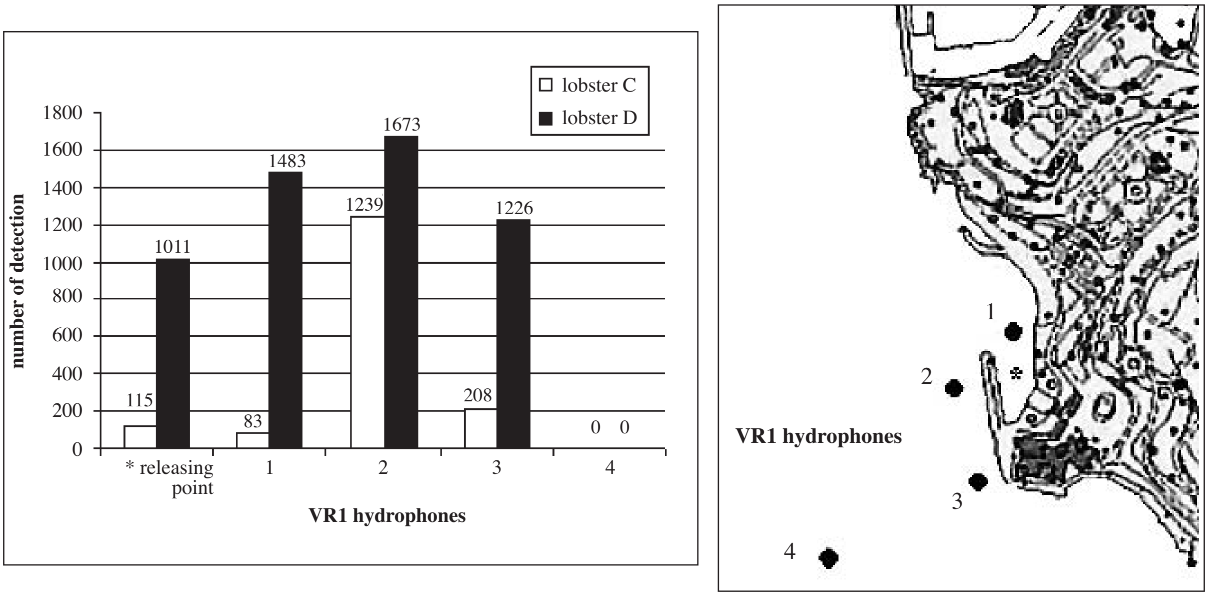
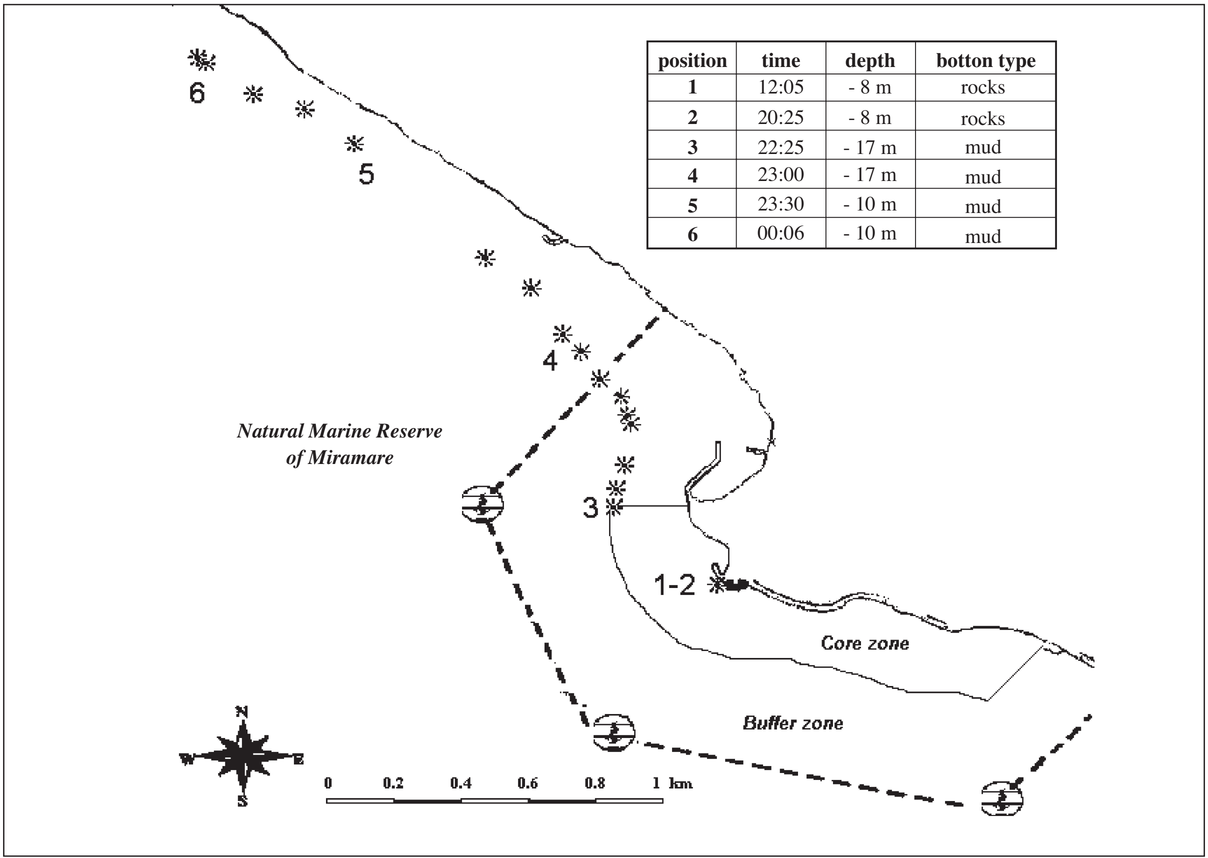


Fig. 3 – Number of detections of each VR1 hydrophones (on the left) – Position of the four VR1 hydrophones in the core area of the Natural Marine Reserve of Miramare (on the right).

Tracking System and, whenever possible, by visual inspection. Just after release, the animal hid in the rocky shelters present at the site, where it remained for the subsequent ten hours (till 22:20). That night, the fish moved away from the reef, leaving the protected area at about 23:00. At the same time, i.e. from about 19:00 till 00:20, acoustic emissions of *S. umbra* were recorded in the area facing the reef**,** indicating reproductive and agonistic activity within the local population (Bonacito, 2000; Bonacito *et al*., 2001). The released brown meagre swam along the coast with a north bearing (Fig 4) at a maximum recorded speed of 1.5 kmh^{-1}. The animal was detected until 00:06, when the monitoring was stopped due to bad weather conditions. The fish was no longer detectable in the area (2500 meters from releasing point) at 05:00 the following day. A total of 30 hours of active search was carried out in the following 15 days after the last received signal.



position	time	depth	botton type
1	12:05	- 8 m	rocks
2	20:25	- 8 m	rocks
3	22:25	- 17 m	mud
4	23:00	- 17 m	mud
5	23:30	- 10 m	mud
6	00:06	- 10 m	mud

Fig. 4 – Movements of the released brown meagre (individual a) in the gulf of Trieste.

Another brown meagre (individual b, 424 gr of weight) was released at the rocky reef of Miramare and its presence was detected by means of the VR1 Tracking System from 31 July to 7 November 2002. Out of the total of 2997 signals detected by the hydrophones, 638 signals were received almost simultaneously by different receivers (inter-pulses delay <1 sec) and allowed a better localization of the fish. Table 1 reports the first and the last signal recorded per day by the VR1 hydrophones (no signals were detected in between the reported recordings).

Table 1 – The first and the last signal from the brown meagre (individual b) detected per day by the VR1 hydrophones located in the Natural Marine Reserve of Miramare (the number of the VR1 refers to their position – see Figure 3).

	First detection of the day		Last detection of the day	
DATE	TIME	VR1 hydrophone	TIME	VR1 hydrophone
31 July	11:50	release point		
31 July			11:53	3
1 August	00:44	1		
1 August			21:17	4
2 August	04:32	4		
2 August			04:51	1
5 August	01:26	1		
5 August			21:18	4
30 August	20:34	4		
30 August			20:46	1
9 September	14:02	4		
9 September			14:22	4
7 November	07:10	4		
7 November			16:51	4

Discussion

The acoustic tracking systems proved to be an effective way to monitor movement and activity of individual animals without the need of direct observations. In our case, the active tracking system (VR28) was not ideal for tracking lobsters because the varied bottom structure and the shelter-seeking behaviour of this species did not allow the hydrophones to detect the signals originated by the pingers. Active tracking of brown meagres, however, was limited by time and overall weather constraints. We conclude that VR28 System is suitable only for very short-term studies, that require precise positioning (i.e. monitoring movement of translocated animals until their settlement). The automatic static monitoring system (VR1) provided continuous monitoring of many individuals simultaneously in the study-area, although the use of four hydrophones did not provide a complete coverage of the protected area of Miramare. It allowed for monitoring the two local rocky reefs (where most of the animals are usually located) with a degree of overlap between the ranges of the four hydrophones that permitted a rough triangulation. The spatial resolution obtained by the VR1 system was not amenable to analysis of fine-scale movements but daily activity and site fidelity patterns could be calculated by the VR1-data, provided the animal remains within the range of the receivers. We believe that VR1 mode is ideal for long-term monitoring of animal movements in a MPA and we consider it a suitable tool to evaluate the colonisation of an area by transferred animals.

The disappearance of the released animals, both lobsters and brown meagres, from the detection range of the hydrophones seems to indicate that they did not colonize the site, leaving the protected area after a variable number of days. This is particularly probable in the case of *S. umbra*: the data from the VR28 system showed clearly the departure of the tagged animal "a" from the reserve ten hours after the release; likewise, the erratic detections from the VR1 hydrophones suggest that brown meagre "b" did not establish at the reserve. On the other side, the fish seems to have been settled not very far from it, since its presence was recorded sporadically for about one month after the release and, interestingly, also three months later on. The translocated animal may have found a suitable habitat outside the MPA, where the brown meagre is distributed (Bonacito *et al.*, 2002).

The disappearance of *H. gammarus* is more difficult to interpret. We cannot exclude they lost their pinger, whereas it is rather difficult they have been preyed upon, because predators are not present in the area (except poachers). Out of four, only in one case (lobster "C"), the tagged animal seemed to start establishing itself at the reserve: data from VR1 indicated that for 13 days the animal movements were spatially restricted around an area, where a new burrow has been visually detected. Nevertheless, the animal disappeared later on.

Concluding, this study should be considered a very preliminary one; increasing sample size and additional research on the behaviour of both translocated and resident animals are necessary to better clarify these aspects.

Acknowledgements

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Habitat use by roach (*Rutilus rutilus* L.) and perch (*Perca fluviatilis* L.) in response to the presence of cormorants (*Phalacrocorax carbo* L.) and artificial refuges

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Key words: Cormorant, habitat use, artificial refuge, roach, perch, acoustic tags.

Abstract

The rise in cormorant numbers in England and Wales over the last 25 years and the greater use of inland feeding sites has increasingly brought these birds into conflict with freshwater fisheries. This has highlighted the need for effective management measures that will reduce the interaction between cormorants and their prey, and hence the level of impact on fish stocks and fisheries. One technique that is considered to have some potential in recreational coarse fisheries is the use of artificial refuges. In this study, the habitat of roach and perch was investigated in a small stillwater fishery in eastern England based on the movements of a small number of acoustically tagged fish and an acoustic positioning system. The main aims were to determine the extent to which the fish utilised natural and artificial refuges, and to assess whether cormorant foraging behaviour was influenced by the presence of artificial refuges. The results indicated that the tagged roach and perch both exhibited diurnal patterns of habitat use, utilising open water more by night. Roach tended to refuge in the marginal vegetation during the day and made no use of the artificial refuges. However, in the absence of cormorants the roach spent significantly more time in open water. The perch, in contrast, spent significantly less time in the marginal vegetation and more in one of the artificial refuges over the duration of the study; there was no significant increase in the use of open water. There was no evidence that cormorant foraging behaviour was influenced by deployment of the artificial fish refuges.

Introduction

The increase in cormorant, *Phalacrocorax carbo* (L.), numbers across Europe over recent years has raised growing concerns about their impact on fish stocks (e.g. Carss, 2002). The population of cormorants wintering in Britain has increased four-fold over the last 25 years (Wernham *et al.*, 1999) and, in England and Wales, cormorants have extended their range from coastal areas and now over-winter and feed in many inland areas (Russell *et al.*, 1996). This range extension and increase in numbers of birds has increasingly brought cormorants into conflict with inland fisheries.

There is clear evidence that the impact of cormorants can be significant at some sites (Feltham *et al.*, 1999), and this can have potentially serious economic implications for fisheries. In England and Wales, cormorants are protected under the Wildlife and Countryside Act (WCA) 1981, which implements the 1979 European Community Directive on the Conservation of Wild Birds (EEC/79/409). The WCA makes provision for killing or taking birds under licence for the purpose of preventing serious damage to fisheries, but licences only allow limited numbers of birds to be killed to reinforce the effects of other scaring methods, and where there are no other effective and practical alternatives. There is therefore a need for effective management measures that will reduce the interaction between cormorants and their prey, and hence the level of impact at affected sites.

As part of a review of potential cormorant management measures, M^{c}Kay *et al*. (1999) noted that underwater fish refuges might offer a relatively low cost option for reducing cormorant impact at certain sites, particularly smaller recreational (rod-and-line) coarse fisheries. Preliminary investigations indicated that underwater refuges could influence cormorant foraging behaviour and reduce levels of damage to fish (M^{c}Kay *et al*., 2003).

In England and Wales, cormorant numbers are highest on inland waters over winter, when natural cover for fish (e.g. weed beds) is at its lowest level and when fish swimming speeds are least (due to the low water temperatures). It is therefore envisaged that fish refuges might provide fish with additional cover and reduce their accessibility to cormorants at a period of the year when they might otherwise be particularly vulnerable to predation. In view of the fact that cormorants should be able to swim faster than most prey species over the winter months (Russell *et al*., 2003), to be effective, refuges would need to attract and 'hold' fish while providing protection from predators.

A preliminary appraisal (Russell *et al*., 2003) suggested that the features of artificial habitats most likely to attract freshwater fish are the presence of 'structure', to mimic natural habitat features, and overhead cover to provide shading and an enhanced ability to detect oncoming predators. To be effective as refuges from cormorants, structures designed to attract fish also need to provide additional protection from diving birds. For example, by surrounding potential fish holding sites with appropriate sized netting to make them unavailable to cormorants. An initial evaluation, which considered species' biology/ecology (Russell *et al*., 2003) suggested that freshwater refuges might be most suitable for fish such as roach, *Rutilus rutilus* (L.), and perch, *Perca fluviatilis* L., which are the species most commonly consumed by cormorants at inland fishery sites in England and Wales (Russell, unpublished data).

The use of weed cover and other submerged structures by many freshwater fish species is widely regarded as an adaptation to reduce the constant risk of predation by piscivorous fish (e.g. Savino and Stein, 1989). However, such refuging behaviour tends to restrict the spatial use a species makes of the available food and other resources, and represents a trade-off between the benefits of predator avoidance and the cost of lost feeding opportunities (e.g. Krause *et al*., 1999). It has been noted that predatory success (by piscivorous fish) in aquatic systems decreases as vegetation density increases (e.g. Jacobsen and Perrow, 1998). The consequences include both improved survival of the prey and reduced growth rates in the predator (e.g. Persson and Eklöv, 1995). However, the extent to which freshwater fish species might utilise potential refuge areas as an evasive strategy in response to attack by pursuit divers, such as cormorants, is less clear.

This study sought to describe the behaviour of roach and perch at a small stillwater fishery in Norfolk, eastern England, using acoustic tags and a high resolution positioning system. The aim was to investigate habitat use by the fish, determine the extent to which natural and artificial refuges were utilised, and assess whether fish behaviour was affected by the presence or absence of cormorants. Cormorant presence and activity was monitored simultaneously and related to refuge location and fish behaviour; cormorant foraging efficiency was also evaluated with and without refuges.

Materials and methods

Study site

The trial was conducted at Bawburgh Lakes Fishery, which is a complex of six lakes situated on the south-eastern outskirts of Norwich in eastern England (Fig. 1). The lake complex was created as a result of gravel extraction and is now managed as a recreational coarse fishery, supporting a range of species. The lake selected for the refuge trial, Works Lake, was one of the smallest lakes on the site (11,000 m^2) and was approximately rectangular in shape with a maximum depth of 5 m. The lake was known to hold reasonable numbers of roach and perch as well as a number of other cyprinid species and small numbers of pike (*Esox lucius* L.). Around

20 cormorants were recorded utilising the lake complex at the time of the study, using the site both for foraging and roosting (day and night). No active cormorant management was conducted at the site either before or during the study period.

Works Lake supports a relatively dense stand of submerged aquatic vegetation in the spring, summer and autumn, but at the time of the trial this had died back and the body of the lake was largely devoid of cover. However, the lake still had a strip of emergent vegetation around the margin, although this did not extend beyond 1-2 m in width (to a depth of about 1 m) at any point. The emergent vegetation was denser in some areas than others (Fig. 1).

Experimental Design

The refuge trial was conducted between 21st January and 19th February 2002 and comprised three sequential 10-day phases (Table 1), with each phase intended to provide data on a separate component of the fish/refuge/cormorant interaction. In phase 1, fish and cormorant activity was monitored in the absence of refuges, to provide baseline data. In phase 2, refuges were installed and monitoring was continued. In phase 3, active scaring, as necessary, prevented cormorants from alighting on this small lake and foraging, and fish behaviour was recorded in the absence of avian predators.

Two identical groups of refuges were deployed at the start of phase 2. The first (refuge 1) was located adjacent to the margin (~6 m from the bank), and the second (refuge 2) towards the centre of the lake in open water (Fig. 1). Each refuge group covered an area of approximately 7 m in diameter and had a volume of about 90 m^3; together the refuges comprised less than 1% of the lake volume. Each refuge comprised:

- four circular, 2 m diameter by 2 m high, free-standing cages constructed of 15 cm wire mesh and each incorporating overhead shade netting and internal ‘structure’ in the form of artificial weed;

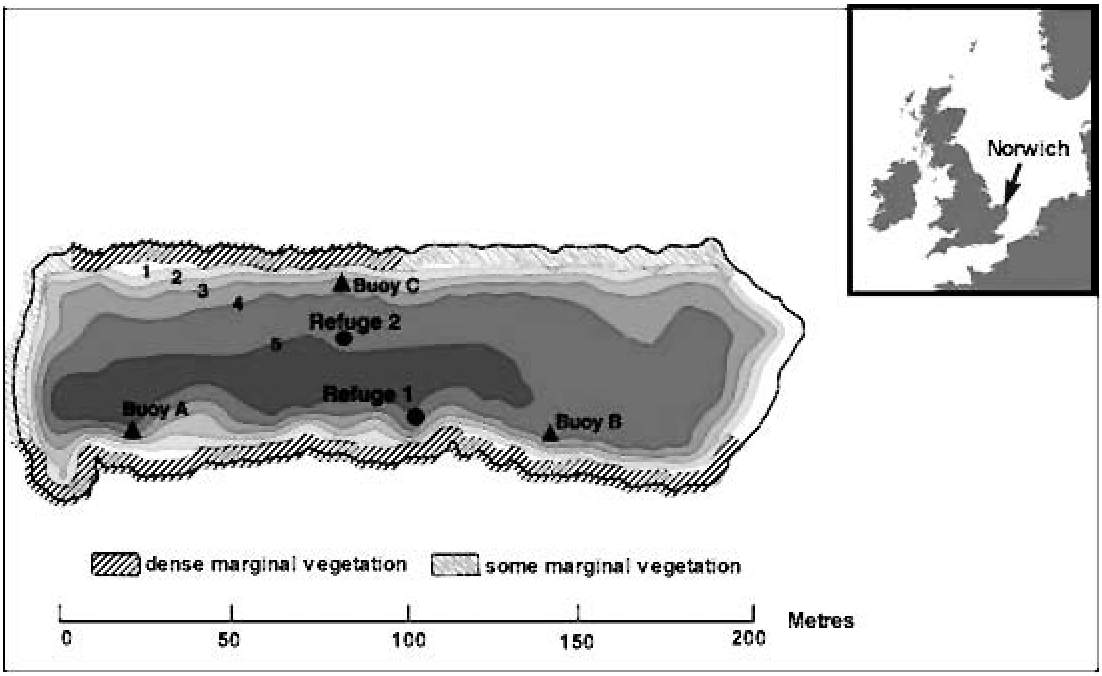

Fig. 1 – Schematic diagram of Works Lake indicating the dimensions, depth contours, refuge locations and the positions of the three fish positioning acoustic buoys, together with a map of the British Isles indicating the location of the study site in eastern England.

Table 1 – Timing and components of the three phases of the refuge trial.

Phase	1	2	3
Date	21 - 30 Jan.	31 Jan. - 9 Feb.	10 Feb. - 19 Feb.
Components	no refuges tagged fish cormorants	refuges tagged fish cormorants	refuges tagged fish no cormorants

- two rectangular floating cages (2 m x 2 m x 1 m), also made of 15 cm wire mesh, one fitted with overhead shade netting, and the other with a cover of rooted emergent vegetation planted in coir matting;
- one unit comprising ten land drainage pipes (2 m long by 33 cm diameter) strapped together in a pyramid formation;
- two square (2.5 m x 2.5 m) floating covers constructed of black plastic tubing (10 cm diameter) fitted with overhead shade netting.

The fish tracking system

A Vemco 'VRAP' high resolution tracking system (Vemco Ltd., Canada) was used to monitor fish behaviour during the study. Three acoustic tracking buoys were deployed in a triangular formation in the lake and the associated tracking system base station and attached PC were positioned on the nearby bank, in a secure weatherproof container. Data were downloaded on a daily basis throughout the 30-day trial.

Roach were captured from the lake margins by electrofishing, but it was not possible to capture perch in this way and fish for tagging were therefore obtained from another site. Both species were retained in a large holding cage in the lake for a few days prior to tagging to ensure there were no adverse effects following capture. Perch varied in size from 17.9-19.7 cm fork length (FL), while roach ranged from 15.6-17.8 cm. Fish were subsequently removed from the holding cage and tagged with miniature acoustic transmitters (Vemco V8Sc). Tags measured 20 mm in length by 9 mm diameter and weighed 2.3 g in air. Fish were anaesthetised using 2-phenoxy ethanol (0.4 mll^{-1}) and the transmitters surgically implanted into the peritoneal cavity (Home Office Project Licence No. PPL 80/612). Following full recovery (~15 minutes from tagging) fish were released to the lake. This technique of transmitter attachment has been shown to have negligible physiological and behavioural effects on salmon, *Salmo salar* L., smolts (Moore *et al*., 1990), and has been widely used in fish telemetry studies (e.g. Moore *et al*., 1996; Bridger and Booth, 2003), including investigations of roach behaviour (Jepsen and Berg, 2002).

At the start of the trial on 21st January, eight acoustically tagged fish were released, the maximum number possible with the positioning system, comprising four roach and four perch (Table 2). In the event, only three of these fish, 2 perch and 1 roach, were recorded throughout the 30-day experiment and some of the tagged fish 'disappeared' relatively soon after tagging (Fig. 2). Therefore, two further roach were tagged and released on 5th February, during phase 2.

Analysis of fish tracking data

The tracking system was able to record about 20 'fixes' per hour for each tag. After initial filtering, these data were assigned, initially, to one of four categories: open water, lake margins (including '*no solution*' and '*out of range*'), refuge 1 and refuge 2. The co-ordinates delimiting refuges 1 and 2 were characterised prior to the study by using a dummy tag deployed around the edges (within 1 m) of each refuge position. Fish were assigned to 'refuge 1' and 'refuge 2' even for phase 1 (when no refuges were actually present), in order to provide a control. Given the small size of the lake and its relatively uniform shape, it was noted that tags were never recorded as '*out of range*' when tested within open water areas. However, tags deployed within the marginal vegetation did constitute effec-

Table 2 – Fish tagging details (species, length, weight) and track duration.

Tag No.	Tag Freq kHz	Species	Fork Length cm	Weight g	Released		Last detection in open water		Track duration days
					Date	Time	Date	Time	
2131B	66	Perch	19.7	137	21-Jan	11:50	5-Feb	07:39	16
2138B	75	Perch	18.6	113	21-Jan	11:50	20-Feb	12:33	30
2133B	69	Perch	17.9	99	21-Jan	11:50	29-Jan	08:02	9
4834B	81	Perch	18.5	111	21-Jan	12:45	20-Feb	12:34	30
2136B	72	Roach	16.5	77	21-Jan	12:45	26-Jan	12:32	6
2129B	63	Roach	17.8	100	21-Jan	12:45	12-Feb	15:47	23
2139B	78	Roach	15.6	64	21-Jan	12:45	20-Feb	12:08	30
4837B	84	Roach	16.0	70	21-Jan	12:45	30-Jan	08:13	10
4836B	84	Roach	17.1	87	5-Feb	13:30	20-Feb	12:34	16
4831B	72	Roach	15.8	67	5-Feb	13:30	6-Feb	11:44	2

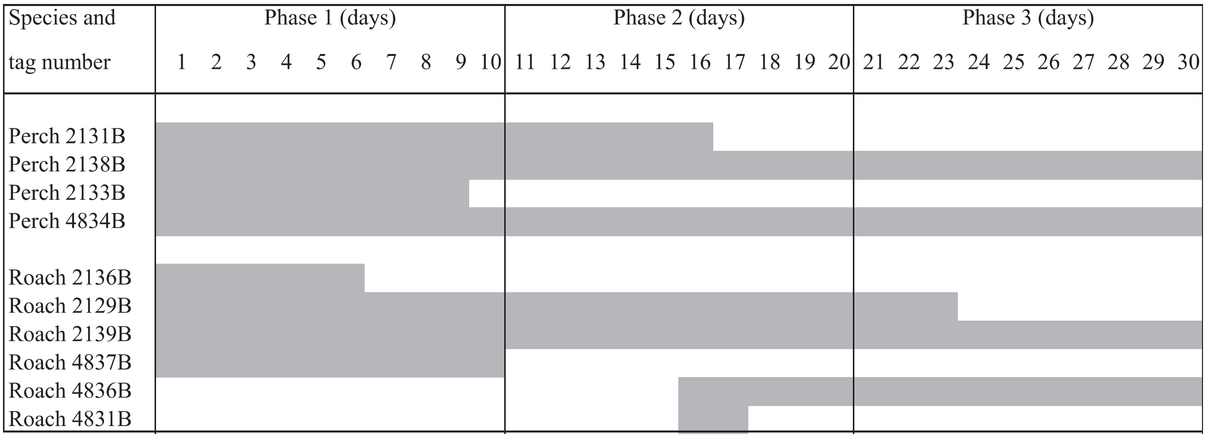

Fig. 2 – Schematic representation of the duration of each of the individual fish tracks (shaded blocks) relative to the three trial phases.

tive 'blind spots' for the tracking gear. Hence, for analysis purposes, fixes indicating '*no solution*' or '*out of range*' were also designated as being located in the lake margins.

The behaviour patterns exhibited by the roach and perch over the three phases of the investigation were assessed in two ways. For those individuals detected in all three periods (4 fish only), the data were expressed as histograms to illustrate the pattern of habitat use in each period. In addition, statistical analyses were applied to investigate the significance of particular behavioural changes. In view of the variable time periods over which tracking data were recorded, positional data for individual fish were aggregated by species to enable comparison of habitat use during the different phases. In view of concerns about auto-correlation, Monte Carlo randomisation procedures were carried out using the statistical package S-Plus (e.g. Venables and Ripley, 1994). Treatments were compared by randomly permuting the treatment labels before calculating the test statistic (e.g. the difference in means between the two treatments). This was repeated 1,000 times to obtain a simulated null distribution under the hypothesis that there was no difference between the treatments. A p-value was then calculated by comparing the observed value of the statistic against the null distribution.

Cormorant Foraging Parameters

Data on cormorant foraging behaviour were recorded using focal bird sampling techniques.

Individual cormorants using the study lake were observed continuously from time of arrival until time of departure. All observations were conducted from a hide located on the south bank of the lake between sunrise and around 14:30; initial observations indicated that cormorant activity was minimal outside this period. All cormorant activity was recorded with respect to GMT.

For each focal bird, the following data were recorded: (i) length of time present on the lake (foraging bout length), (ii) number of dives, (iii) duration of dives, (iii) total prey consumed, (iv) foraging efficiency (dives per prey item), (v) inter-dive duration, and (vi) total loafing time. Two measures of total prey consumption were calculated: total observed prey and total estimated prey. Total observed prey comprised all fish brought to and consumed at the surface, whilst total estimated prey comprised all observed prey plus prey considered to have been swallowed underwater, evidenced by the bird showing vigorous head and neck movements upon surfacing, as though swallowing an item of prey (Hughes *et al*., 1999). A successful foraging dive was counted when a fish was brought to the surface or if the bird was thought to have consumed prey underwater. Foraging efficiency of individual birds was expressed as the number of dives per prey item consumed. Total loafing time comprised the aggregated periods between arrival and first dive, the period between final dive and departure and any intervals >60 seconds between successive dives during the foraging bout. The number of other cormorants present on the pond was also recorded throughout the stay of the focal bird.

For each focal bird, mean or total values were calculated for each foraging parameter (*mean*: foraging bout length, dive duration, dives per prey item, inter-dive duration; *total*: dives, prey consumed, loafing time). The non-parametric Mann-Whitney U-Test was used to test for differences in cormorant foraging parameters between phases 1 and 2.

The study lake was partitioned into a number of sectors, each measuring approximately 44x14 m and these were further partitioned into edge, marginal and open water zones. The edge zone was defined as the water immediately adjacent to the bank out to a width of ~1.5 m, which included all emergent aquatic vegetation. The marginal zone extended for a further ~3.5 m out from the edge zone. The remaining area of the lake comprised the open water zone. During focal bird monitoring, records were made of the sector and zone in which each dive was initiated, that in which the bird resurfaced and that in which prey capture occurred. This also enabled foraging site preferences within the lake to be compared between the phases.

Variation in cormorant attendance between phases was investigated by comparing daily total counts of cormorant-visits to the trial lake, as it was not possible to identify repeat visits by the same birds in the unmarked population.

Results

Fish behaviour patterns relative to available habitat

The behaviour patterns exhibited by the two roach tracked throughout the study (Fig. 2) were broadly similar within each of the phases (Fig. 3). Both fish exhibited a diurnal pattern of behaviour, making extensive use of the marginal vegetation during the daylight hours and the open water at night. This diurnal pattern was retained throughout the study; randomisation tests confirmed that throughout all three phases roach made significantly more use of open water habitat during the hours of darkness than in daylight ($p<0.001$). However, the degree of marginal use was observed to fall markedly in phase 3. The mean number of ‘fixes’ per hour in the margins decreased from an average of 9.6 in phases 1 and 2 to 4.9 in phase 3. The Monte Carlo randomisation test indicated a highly significant increase ($p<0.001$) in the use of the open water in phase 3 compared with the earlier phases. Neither of the roach made positive use of the artificial refuge structures and there was no change in the degree of refuge use over the three phases.

The two perch tracked throughout the study also displayed reasonably similar behaviour patterns within each of the phases (Fig. 4). As with the roach, the perch displayed a diurnal pattern of behaviour, tending to favour open water during the night. The Monte Carlo randomisation test confirmed that, in all three phases, perch also made significantly more use of open water habitat during the hours of darkness than in daylight ($p<0.05$). However, in contrast to the roach, there was no significant increase in the use of the open water by perch in phase 3 compared with the earlier phases. The mean number of ‘fixes’ per hour in the margins for the perch decreased from an average of 8.1 in phases 1 and 2 to 3.7 in phase 3; a very similar reduction to the roach. The randomisation test of the pooled data confirmed that the perch used the margins significantly less ($p<0.001$) and refuge area 1 (located adjacent to the lake margins) significantly more ($p<0.001$) in phase 3 than phases 1 and 2. None of the tagged perch made more than passing use of refuge 2 during the investigation.

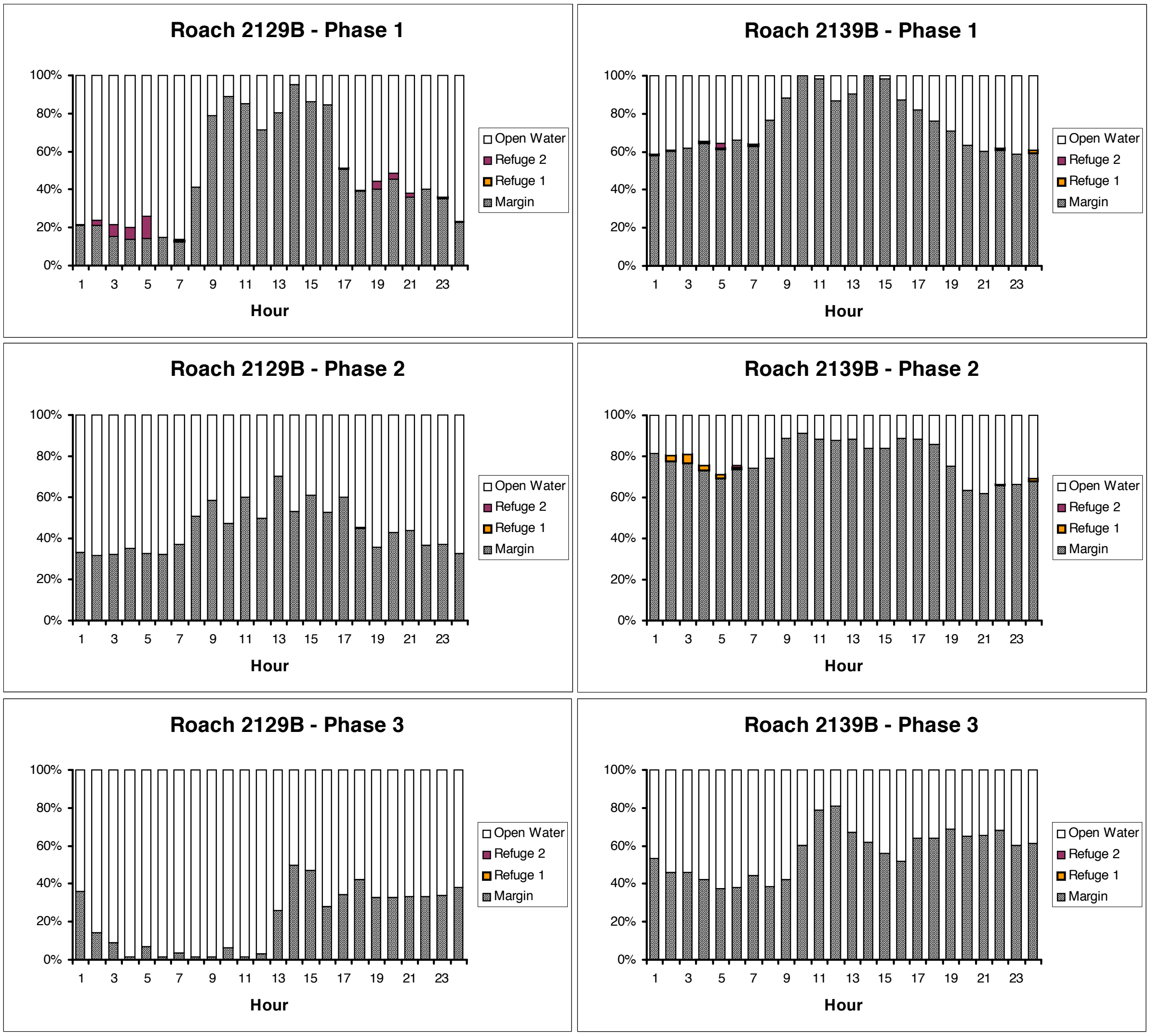
Roach 2129B - Phase 1
Roach 2139B - Phase 1
Roach 2129B - Phase 2
Roach 2139B - Phase 2
Roach 2129B - Phase 3
Roach 2139B - Phase 3

Fig. 3 – Relative habitat use for open water, refuge 1 (adjacent to the margin), refuge 2 (in open water in the centre of the lake), and the margins by two tagged roach tracked throughout the study period.

Cormorant foraging behaviour

Observations were conducted on seven days (totalling 48 hr 10 min.) in phase 1 and eight days (54 hr 40 min.) in phase 2. A total of 33 cormorants were recorded visiting the lake during phase 1 and 65 in phase 2. Focal observations were collected from 23 cormorants in phase 1 and 38 cormorants in phase 2. In phase 2, however, 7 of the 38 cormorants fed on mackerel that had been discarded by an angler; these birds, therefore, were omitted from the analysis. Birds were observed to have a diurnal attendance pattern, with peak numbers being recorded between 08:00 and 09:30 and again between 13:00 and 14:00. Although the total number of cormorant-visits virtually doubled in phase 2 compared to phase 1, the median daily number of cormorant-visits did not vary significantly between phases (Mann-Whitney U-Test: $U_{7,8}=18.5$, $p>0.05$).

Cormorant foraging parameters were compared between phase 1 and phase 2 to investigate

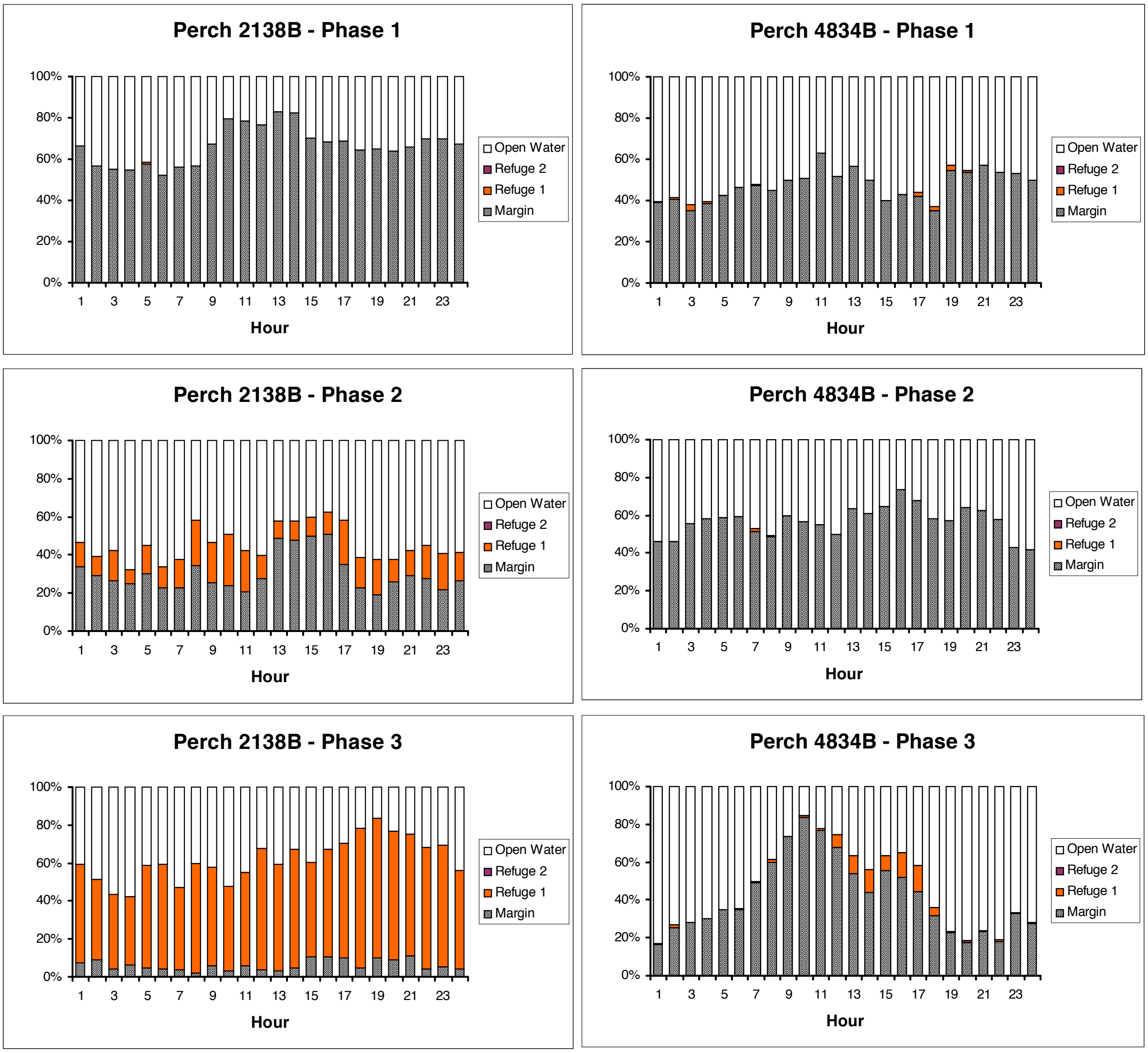

Fig. 4 – Relative habitat use for open water, refuge 1 (adjacent to the margin), refuge 2 (in open water in the centre of the lake), and the margins by two tagged perch tracked throughout the study period.

Table 3 – Comparison of cormorant foraging parameters between phases.

Foraging parameter	Phase 1 (no refuges)		Phase 2 (refuges)		n	U[#]	p
	median	range	median	range			
foraging bout (min)	7.6	1.4 - 40.2	13.6	1.2 - 42.5	20, 28	173	0.025
no. dives	13	1 - 56	15	3 - 53	21, 31	265.5	ns
dive duration (sec)	21	16 - 28	21	12 - 29	23, 31	316.5	ns
estimated prey consumed	2	0 - 9	2	0 - 8	21, 31	290	ns
observed prey consumed	2	0 - 9	1	0 - 6	21, 31	263.5	ns
dives/prey item	6.5	1.5 - 16	5.8	1.5 - 33	21, 27	242.5	ns
inter dive duration (sec)	10	4 - 18	10	5 - 24	22, 31	318	ns
total loafing time (min)	0.73	0.15 – 6.22	0.57	0.17 – 12.7	18, 25	208.5	ns

[#] Mann Whitney U-Test

whether foraging behaviour and/or efficiency differed in the presence of refuges. Foraging bouts were significantly longer during phase 2 compared to phase 1 (Mann Whitney U-Test, $p<0.05$). However, there was no significant difference in any other foraging parameter (Table 3). That is, although cormorants spent longer periods on the water during phase 2 there was no significant change in foraging intensity or efficiency.

Within both phases 1 and 2, cormorants conducted a greater percentage of dives in open water than close to the margins. However, in general, while birds tended to dive in the open water/marginal zones they were observed to capture prey and resurface more in the edge/marginal zones. The percentage of total dives and resurfaces in the edge zone were 4% and 19% respectively in phase 1 (n=345), and 12% and 48% in phase 2 (n=534). With respect to the location of the two refuges, changes in the relative magnitude of cormorant dives (+4.3%, +1.2%), prey capture (+2.5%, 0%) and overall foraging efficiency (only 2 prey items caught near refuges) in areas adjacent to the refuges did not change disproportionately compared to non-refuge sectors following refuge deployment. Thus, cormorants appeared to be neither attracted to the refuges nor deterred by them.

Discussion

It is recognised that the fish behaviour data are based on only a very small sample. Only four of the eight fish initially tagged were recorded in each phase of the study, and a number of the other fish were only detected for relatively short periods (Fig. 2). While tag failure cannot be discounted, it is thought that these fish were more probably removed by predators. In two cases, cormorants were observed to be foraging on the lake at the time that the fish were last recorded. This is perhaps not surprising given the level of cormorant occupancy and small size of the lake. It is impossible to assess whether the tagged fish were any more vulnerable to predation. In any event, the results are based only on a small sample of fish and need to be interpreted with caution.

The behaviour of all the tagged perch and roach was consistent in indicating extensive use of the available cover within the lake and highlights the importance of habitat features for both these species. The tagged roach utilised the emergent marginal vegetation throughout the study, despite the relatively limited extent of this cover and the very close proximity of the adjacent reed stems. [N.B. Electrofishing of the margins, outside the study period, confirmed the presence of large numbers of roach, in particular, among this marginal vegetation].

Both the roach and perch displayed clear diurnal behaviour patterns, making significantly more use of the open water during the hours of darkness. This diel movement pattern has long been recognised in common prey species, such as roach and perch (e.g. Allen, 1935; Goldspink, 1990), often with peaks of activity at dawn and dusk (Cowx, 2001). The movements are thought to be influenced by the need to optimise feeding opportunities, mediated by the risk of predation. Movement by prey species is believed to carry a high risk of attracting predators (e.g. Ware, 1973) and fish migrations can affect levels of predation by cormorants (Adams *et al*., 1994; Neuman *et al*., 1997).

Cormorants are normally diurnal feeders and forage especially in the early morning (e.g. van Dobben, 1952), although a second feeding bout can also occur in the afternoon (Hughes *et al*.,1999). The early feeding bout thus coincides with peaks in activity and diel movements in certain key prey species and probably indicates a causative relationship. It has been noted that the precise timing and extent of diel movements by prey species is likely to influence the level of interaction with cormorants (Gliwicz and Jachner, 1992). In this study, the tagged roach were significantly more likely to be found in open water when cormorants were foraging, and the perch also displayed a similar tendency. Hence there was no evidence, in the short-term at least, that the fish were responding to the presence of the birds by moving into refuge areas, either the artificial refuges or the marginal vegetation.

Chub, *Leuciscus cephalus* (L.), have been shown to alter their behaviour patterns in response to the threat of avian predation (Allouche and Gaudin, 2001). Further, it has been noted that some populations of perch adopt ‘reverse’ diurnal behaviour patterns, feeding in open water by day and moving to the margins at night, suggesting some degree of flexibility and the ability to adapt to local situations (Cowx, 2001). In this study, it was evident that while an element of diurnal habitat use was retained, the roach made significantly more use of open water in phase 3 when there were no cormorants on the water. This suggests increased levels of foraging and may well represent a trade-off between predator avoidance and maximising feeding opportunities. It is difficult to assess the relative extent to which cormorant presence might impact upon fish stocks through lost foraging opportunities, slower growth or increased mortality, although Allouche and Gaudin (2001) suggested that in some circumstances fish-eating birds may affect local prey populations more through sub-lethal effects on growth rates than directly through death rates

There were no significant differences in the cormorant foraging parameters between phase 1 and phase 2, however, the duration of foraging bouts was significantly longer during phase 2. Thus, although cormorants spent longer on the water when refuges were present, there was no evidence that cormorant foraging intensity or foraging efficiency was affected by their deployment. In a previous study (M^{c}Kay *et al*., 2003), artificial refuges resulted in a significant increase in cormorant dive duration and also appeared to reduce the availability of fish to cormorants. Other, more recent studies have confirmed that fish refuges can reduce fish losses and cormorant foraging efficiency (Russell *et al*., unpublished data). The absence of such an effect in this investigation may reflect site-specific factors, for example, the extent of alternative cover or variability in the fish population.

While no significant effect of the refuges on cormorant foraging efficiency was detected, it might be noted that the trial was not designed specifically to investigate this. The principal aim of the trial was to investigate the extent to which fish utilised the refuges and whether usage was influenced by cormorant presence. The most important aspect of cormorant behaviour addressed by this trial was whether cormorants were attracted to possible fish activity in and around the refuges and consequently would focus their foraging activities there. Such behaviour may have important implications for the design and use of refuges. Despite some evidence for refuge use by the perch, there was no such indication of an influence on cormorant foraging location from this study. However, it was not possible to assess the overall extent of fish presence in the refuge areas.

Overall, there was no evidence that cormorant foraging behaviour was influenced by deployment of the fish refuges. That is, refuge deployment was not associated with either a decrease in cormorant foraging efficiency or a change in preferred foraging location, as predicted if refuges decreased the availability of fish. Likewise, there was no increase in either foraging efficiency or activity within the vicinity of refuges, as might be expected if refuges aggregated fish in vulnerable areas. Rather, cormorant foraging activity appeared to be, in the main, directed toward the natural marginal aquatic vegetation. This foraging strategy would be consistent with the evident extensive use of this habitat feature by the fish. By approaching the vegetation from open water cormorants may reduce the escape options available to fish and hence maximise their probability of prey capture.

On the basis of this investigation, it is not possible to make any clear assessment of the potential utility of fish refuges for reducing cormorant impact at freshwater fisheries. The work has provided some evidence that perch, at least, can be attracted to artificial refuge structures. Further, the work suggests that foraging opportunities for such prey species can be influenced by cormorant presence. Further work is required to assess whether refuge structures might be effective at reducing the overall impact of the birds at fisheries. It is probable that any potential benefits will vary from site to site and with the fish species present. The features of a fishery, particularly its size and the extent of existing natural cover, are likely to be important in deciding whether refuges might be effective and where they might be deployed.

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METHODOLOGY
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Influence of the light-dark cycle in the diel activity rhythms of sea lamprey's ammocoetes

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Key words: ammocoete, movement, PIT, diel activity rhythms.

Abstract

Ten sea lamprey ammocoetes, tagged with passive integrated transponders (PIT), were released in a tank (2 m^3 capacity) and their position monitored twice a day, for a period of one month. Ammocoetes' locomotor activity appeared to be conditioned by circadian rhythms. Differences in the proportion of detected activity *versus* apparent inactivity resulted mainly from the observations registered during the night. Ammocoetes were more active throughout the night period, particularly in the first and second weeks of trials. After an initial period of enhanced activity, differences between daily activity patterns tended to disappear. During the entire experimental period, ammocoetes spent most of the time stationary. There were no significant differences found when comparing the distance moved by the ammocoetes during the dark and light periods, through which they display a similar diel locomotor behaviour. On the other hand, since movements were more frequent at night, the total distance moved by the lampreys is clearly higher during the dark period. This method was found to be a valuable and effective technique to locate and identify individual ammocoetes burrowed up to 10 cm deep in the substrate, with acceptable accuracy and minimum disturbance.

Introduction

Many behavioural, biochemical and physiological processes of organisms exhibit daily fluctuations, which sometimes persist under constant conditions showing that they are driven by an intrinsic daily or circadian clock. External stimuli from the environment are responsible for the entrainment or synchronization of such rhythms (Meissl and Brandstätter, 1992). Pineal organ, eyes and photoreceptors of the tail region are thought to be associated with the circadian organization within lampreys, mediating distinct photobehavioural responses (Hardisty, 1979).

In spite of the striking contrasts in the habits of the ammocoetes and adult sea lampreys, it is interesting to notice that both should show rather parallel innate rhythms of activity. Throughout the spawning migration sea lampreys exhibit a strong diel pattern, being active in the hours of darkness and avoiding light during the daytime (Hardisty and Potter, 1971a; Hardisty, 1979, Almeida *et al.*, 2000; Almeida *et al.*, 2002). Although ammocoetes are relatively sedentary burrowing animals, they may leave their burrows predominantly during the night period suggesting a similar circadian pattern of activity (Hardisty and Potter, 1971b; Hardisty, 1979; Potter, 1980).

Portable passive integrated transponders (PIT) tag reading units have proved to be efficient to characterize movements of small fishes (Roussel *et al.*, 2000; Morhardt *et al.*, 2000). To determine ammocoetes' activity rhythms during the light-dark cycle, a portable PIT tag reader prototype, similar to the one described by Bubb *et al.* (2002) to track crayfish in shallow rivers and streams, was used. This technique is an useful alternative to standard radiotelemetry in small-scale environments because PIT tags can be implanted in smaller-bodied fishes, therefore making possible the assessment of individuals' fine-scale movements (Roussel *et al.*, 2000).

The objective of this study was to determine both the applicability and efficiency of PIT telemetry to characterize sea lamprey ammocoetes' movements and the influence of the light-dark cycle in ammocoets' diel activity rhythms.

Materials and methods

Telemetry equipment

Ammocoetes were marked with cylindrical PIT tags (122GL; Ukid Systems, Preston, U.K.). These transponders are housed in a biostable glass capsule, weigh 0.1 g in air and the external dimensions are 12 mm long by 2.1 mm diameter. The tags measured less than 3% of the experimental animals' body weight.

The portable PIT tags reader unit (UKID Systems, Preston, UK) is a full-duplex system operating at 125 kHz, powered by an integral 1500 mA/h NiMH battery pack, providing approximately seven hours of continuous use. It consists of a coil antenna (diameter: 180 mm), mounted on a pole (length: 1.5 m), connected to a decoding electronic module which displays the transponder's ID code when detected. The entire system weighs 2700 g, corresponding 800 g to the reader unit and 1900 g to the search antenna and pole.

Tagging procedures

The lampreys were anaesthetised in 1 ml 2-phenoxyethanol l^{-1} water, and surgery was initiated when lamprey stop reacting to stimulus. The abdominal region was disinfected with an iodine solution (Betadine®) and a 3 mm incision was made in the midventral line, 15 mm from a point corresponding to the projection of the anterior insertion of the dorsal fin. The PIT tag was then implanted into the peritoneal cavity and the incision was closed with one independent monofilament synthetic absorbable suture (Byosin® Glycomer 631, USP 6/0) and finally disinfected with Betadine®. Since ammocoetes are burrow dweller animals, a parafilm bandage was applied and fixed with cyanocrilate glue to ensure the protection of the incision's wound. The surgery procedure was conducted with the help of a dissecting microscope (Leica MZ6) and took 3 to 5 minutes.

Ammocoetes were revived in 500 litres holding aquariums with a bottom sediment composed of medium sand (0.25 mm ≤ MS < 0.5 mm), and were left to recover for a period of one month to ensure complete cicatrisation of the wound. There was no registered mortality during the recovering period.

Experiment trials

Experiment trials were conducted with ten sea lamprey's ammocoetes with an average total length (TL) of 154 mm (range: 135 – 168 mm), and an average total weight of 4.9 g (range: 2.9 – 6.5 g). Animals' adaptation to the experimental conditions was tested in a 2 m^3 indoor fiberglass holding tank, kept under a constant light-dark cycle (LD 10:14) for a period of one month. The bottom sediment of this tank was composed of a 10 cm layer of sand (59%, 0.5 mm ≤ coarse sand < 2 mm; 38%, 0.25 mm ≤ medium sand < 0.5 mm; 3%, 0.063 mm ≤ fine sand < 0.25 mm) to ensure the location of all tagged individuals. The water temperature was approximately 15 ºC during the entire laboratory experiment. Captive ammocoetes were fed weekly with powdered yeast *Saccharomyces cerevisae*.

Ammocoetes' positions were determined twice a day, at the end of the light and dark periods, using a simple structure located on the top of the tank. This location system consisted of a pole, placed on the top of a two axis structure, rotating as a clock hand, on which a plumb line was attached (Fig. 1). Ammocoetes' co-ordinates were determined according to the Pythagoras Theorem. When a tagged individual was detected, its position was identified with the plumb line and then both the distance to the centre of the axis (i.e. hypotenuse) and the projection of the ammocoetes' position to one of the axis (i.e. cathetus) were measured (Fig. 1).

During the tracking surveys, it was considered a valid move or activity whenever, on two consecutive detections, a minimum apparent distance moved (ADM) of 20 cm was covered by the tracked lamprey. Conversely, every time that the ADM was inferior to 20 cm it was considered inactivity or halt. The determination of the ammocoetes' position

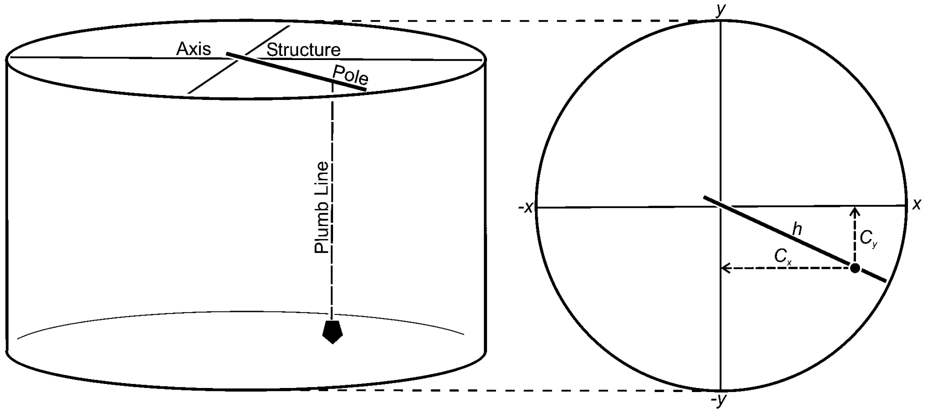

Fig. 1 – Diagram of the experimental tank with detail on the location system. Schematic representation of the method used for ammocoetes co-ordinates location. *h* (hypotenuse) – distance between the ammocoete position and the centre of the axis; c_x (cathetus x) – distance between the ammocoete position and the abscissa axis; c_y (cathetus y) – distance between the ammocoete position and the ordinate axis.

with the portable PIT tag reader unit had an associated average (± SD) detection error of 3.4 ± 1.9 cm. This detection error was calculated using a 2x2 m long opaque board on which 30 PIT tags were randomly attached and detected one by one. The positions of the tags were blind-searched by an operator unfamiliar with their locations. This equipment was also tested with success by Bubb *et al.* (2002) to identify and track crayfish in their natural environment. According to this author the operator could locate tagged individuals burrowed up to 15 cm deep on the stream bed with high efficiency (> 80% detection).

Non parametric statistics (G-test of independence, Mann-Whitney and Kruskal-Wallis tests) were applied according to Sokal and Rolf (1981).

Results

There were no deceased specimens during the experiment and all transponders remained operational. The experiment indicated that PIT tags can be surgically implanted in sea lamprey ammocoetes with success. The telemetry equipment was successful in locating and identifying individual ammocoetes burrowed up to 10 cm deep in the substrate.

Ammocoetes' locomotion activity appeared to be conditioned by circadian rhythms, being more active during the night period, particularly in the first ($G = 16.6$, $df = 1$, $p < 0.001$) and second ($G = 5.0$, $df=1$, $p<0.05$) weeks of trials. Nevertheless, after an initial period of enhanced activity, differences between daily activity patterns tended to disappear. Thus, throughout the third ($G = 0.1$, $df = 1$, $p = 0.74$) and fourth ($G = 1.8$, $df = 1$, $p = 0.18$) weeks no significant differences in the activity patterns during dark and light periods were identified (Fig. 2).

The ammocoetes' detected movements were caused either by swimming or burrowing activity. No significant differences were found in the apparent distance moved (ADM) by the ammocoetes between dark and light periods in each of the four weeks of study ($U_{1^{o}week} = 193.0$, $df = 33{,}13$, $p = 0.60$; $U_{2^{o}week} = 72.0$, $df = 19{,}9$, $p = 0.50$; $U_{3^{o}week} = 78.0$, $df = 14{,}12$, $p = 0.76$; $U_{4^{o}week} = 50.0$, $df = 15{,}9$, $p = 0.29$) (Fig. 3). Similar results were obtained for both the total ADM in the dark and light periods ($U=2274.0$, $df = 95{,}48$, $p = 0.98$), and the total ADM during the four weeks of study in the dark ($KW = 3.0$, $df = 3$, $p = 0.39$) and light periods ($KW = 1.9$, $df = 3$, $p = 0.58$), suggesting that even though the frequency of movements may differ within the light-dark cycle, the movements' covered distance remains identical.

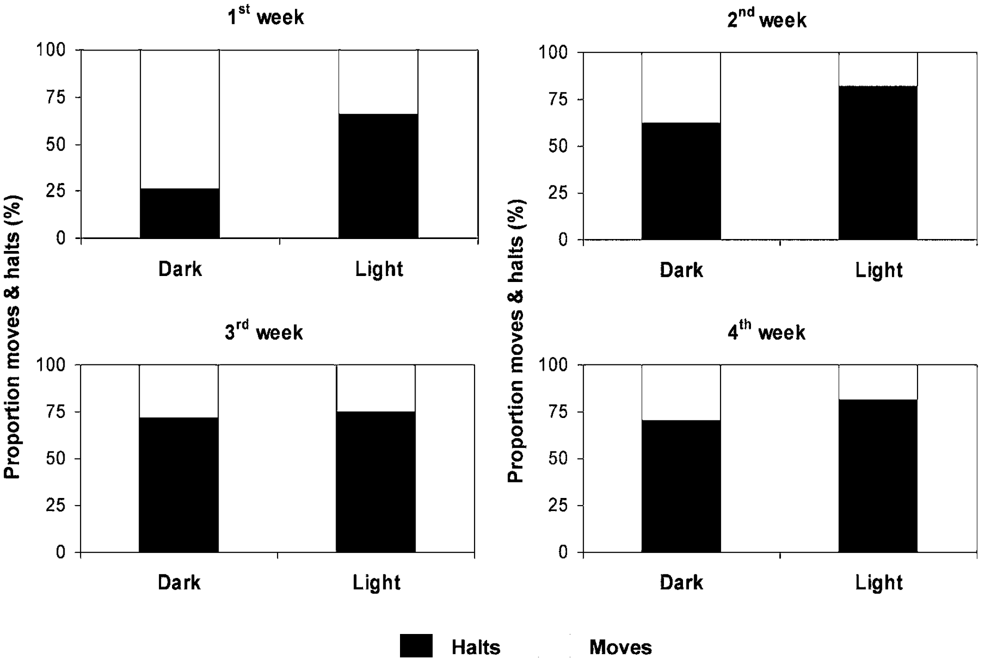

Fig. 2 – Proportion of moves and halts during the dark-light cycle throughout the four weeks of experiment.

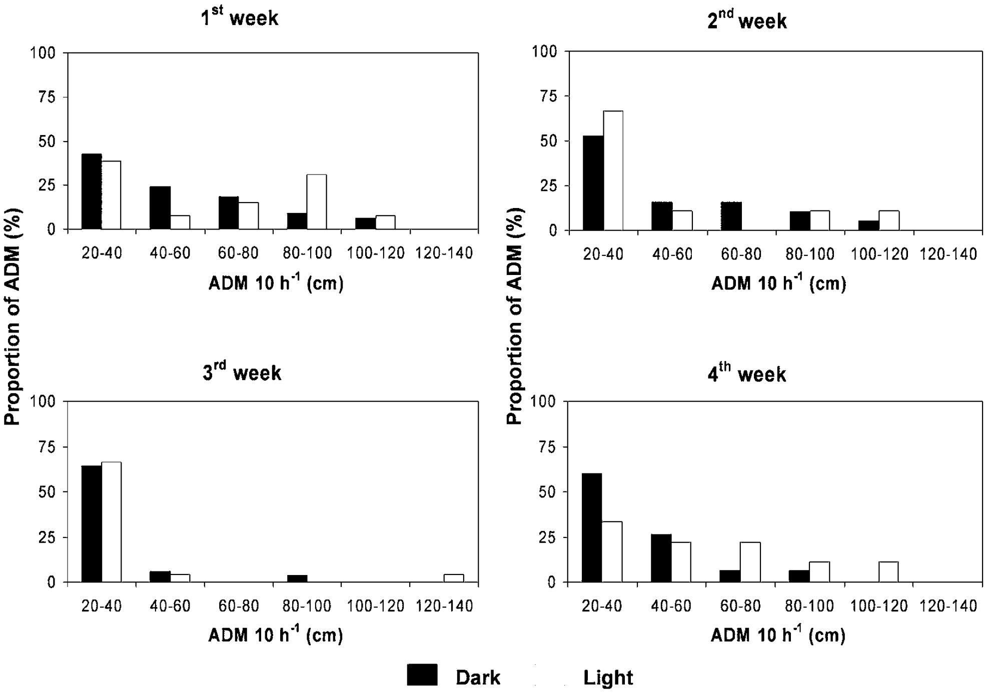

Fig. 3 – Proportion of apparent distance moved (ADM) during the dark and light period throughout the four weeks of experiment.

Discussion

The cryptic behaviour widely recognized for adult sea lampreys (Almeida *et al*., 2000; Almeida *et al*., 2002) also occurs among ammocoetes according to our results, supporting Hardisty and Potter (1971a) findings. This might indicates that after an adaptation period (i. e. first two weeks of experiment) during which the ammocoetes were more active, they tend to maintain their location, supporting earlier findings stating that lamprey larvae, living in stable and favourable environments, may remain in the same area for an undetermined period of time (Hardisty and Potter, 1971b).

There were multiple advantages and few disadvantages when using this new portable PIT tag detection method. As described by Morhardt *et al*. (2000), the prime advantage when using this technique on small fishes is that it avoids handling, which could influence their behaviour and health, every time individual fish positions need to be access. Unlike radio transmitters, PIT tags do not require batteries to work and continue to be functional throughout the life of the fish, can be implanted in smaller-bodied fishes, and are inexpensive making it possible to mark a large number of individuals (Morhardt *et al*., 2000; Roussel *et al*., 2000). Disadvantages of this system when applied to sea lamprey larvae include the need to use, due to tag size, ammocoetes larger than c. 120 mm; shallow water streams (<1 m deep) (Roussel *et al*., 2000); and the prolonged time needed to effectively probe a small area.

This method was found to be a valuable addition to the techniques available on the study of small fishes' movements. With this system it is possible to effectively locate and identify tagged ammocoetes in the sediment with acceptable accuracy and minimum disturbance. This experiment's results suggest that it might be viable to use this technique to monitor ammocoetes fine-scale spatial movements and assess microhabitat preferences in the natural environment.

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Activity patterns in pike (*Esox lucius*), as determined by motion-sensing telemetry.

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Key words: pike, telemetry, activity patterns.

Abstract

Activity patterns of pike fitted with motion-sensing radio tags were recorded using novel automated monitoring equipment. Activity was categorised into short duration (<5 s) and long duration (≥5 s) events. Pike displayed short duration activity events throughout the day and night. Long duration activity events were very sporadic and were often followed by long periods (>24 h) of quiescence. Experimental and observational records (based on over 8500 tracking observations) indicated that these long duration events followed by quiescent periods could be associated with the fish feeding. In total, active pulse patterns (both long and short duration) were only recorded for ~5% of the time that the fish were monitored. Analysis of the temporal patterns in the long duration activity events showed distinct diel patterns, and some seasonal variation associated with sunrise and sunset times. Results from the automated system are compared with results obtained from manual tracking. Data show that activity monitoring could be a useful method for determining the feeding periodicity of these fish and would enable a greater understanding of predator – prey interaction.

Introduction

The fish populations of the lower River Frome in southern England have been extensively studied, and much is known about the diet, numbers and age structure of the commonest species. In particular, research has concentrated on the pike (*Esox lucius* L.) (Mann, 1976; Mann, 1980; Mann, 1982; Mann and Beaumont, 1991) However, until recently little was known about the movements or activity and feeding patterns of these fish. As one of the top fish predators in northern European waters, knowledge of these factors would be of considerable ecological importance (and economic importance where predation on game fish is a factor).

The development of telemetry techniques has allowed some information on the movements of pike to be documented (Diana, 1980; Mackay and Craig, 1983). In addition, information regarding activity and feeding behaviour of pike has been collected by attaching heart-rate telemetry tags to fish (Armstrong *et al*., 1989; Lucas *et al*., 1991). Whilst these tags give excellent high precision data, tag longevity is low, and a maximum data run of only 90 hours was achieved by Lucas *et al*., (1991). All the above studies however are in still waters and the movement and activity patterns of pike in rivers are much less understood. Where data on movement in rivers does exist (Masters *et al*. 2002; Ovido and Phillipart, 2002) they have been shown to be capable of making extensive movements.

The interaction between pike and their prey in rivers is also poorly understood. Whilst Clough and Ladle (1997) proposed that the diel movement shown by dace in the river was a strategy to avoid predation by pike, Pitcher and Turner (1986) found that predators have an advantage at dawn when stalking shoaling prey. However it is not known whether pike activity patterns reflect this diel pattern and potential advantage at low light conditions. In addition, the hunting strategy of the pike in the river was not known. Pike are usually described as ambush predators (Savino and Stein, 1989); however, whether they attack their prey from a single, regular ambush site, or whether they move between several potential ambush sites has not been well established. Within lakes there is some evidence that pike are mobile between ambush sites (Diana, 1980); however, in a river environment, energetic cost associated with swimming against flow needs consideration. Pike are adapted for rapid acceleration rather than prolonged swimming (Jones *et al*., 1974; Webb, 1984) thus it was thought that in rivers they might exhibit a less active hunting technique. The study described here was designed to elucidate pike feeding strategy and timing in order to further investigate this hypothesis.

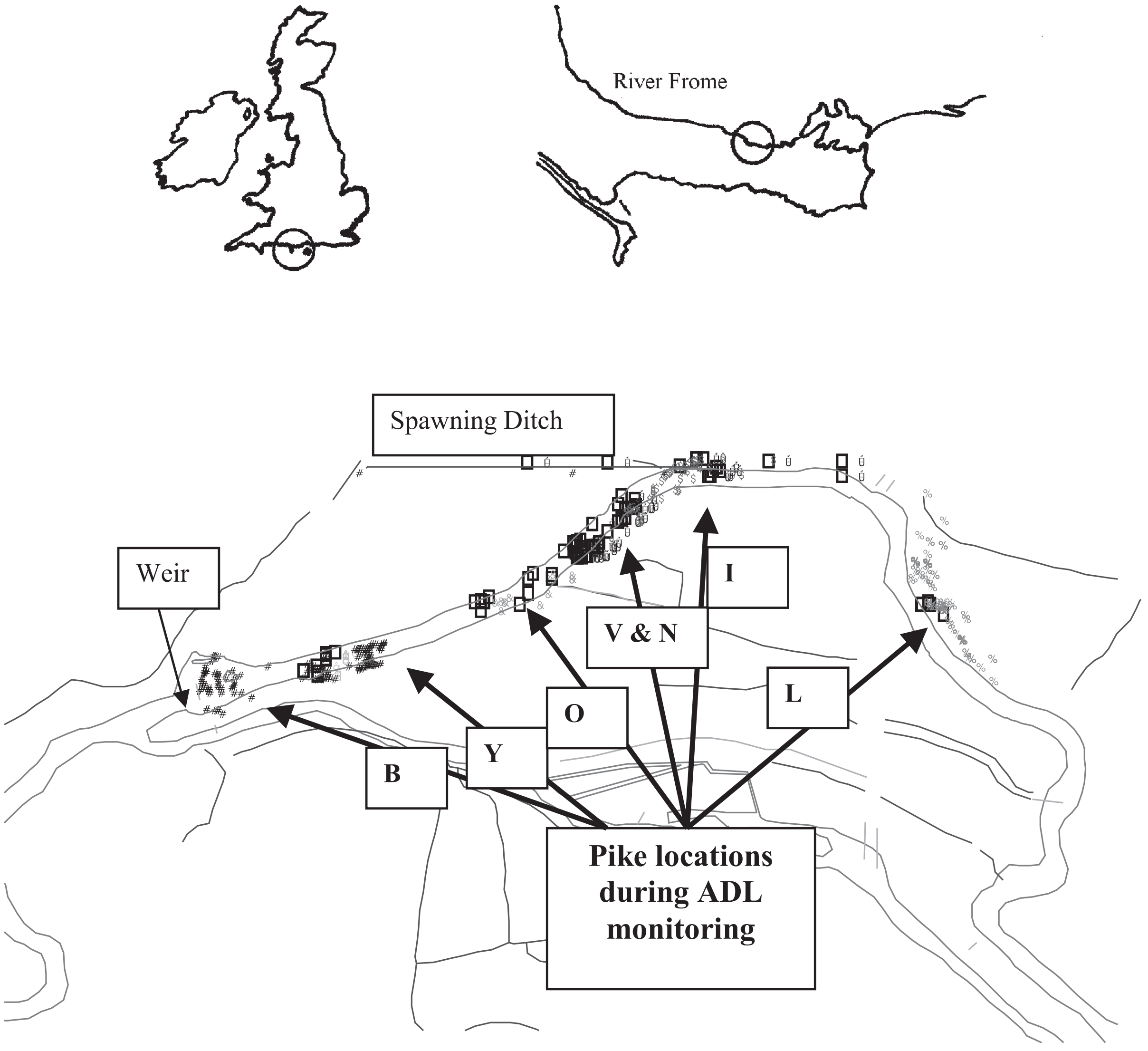

Fig. 1 – River reach studied and locations of fish during study period.

Materials and methods

Study Area

The part of river chosen for the activity study (Fig. 1) was about 500 m long and was an area known to contain several pike. At the upstream end of the area was a weir pool and near the mid-point was an area of gravel shallows. Also present was a small drainage ditch known to be used by pike for spawning. The study site was typical (apart from the weir pool) of much of the lower Frome. Sections encompassing the core home range areas (Kenward and Hodder, 1996) of the pike being automatically monitored were generally straight (Welton *et al.*, 2002). This made tag reception by the monitoring equipment simpler than if a very meandering section had been used.

Tagging

Pike were tagged with TW-5 activity sensing radio tags (Beaumont *et al.*, 2002), manufactured by Biotrack Ltd., Wareham, Dorset, BH20 5AX, UK. These tags react to high levels of omni-directional movement by reducing the interval between the pulses transmitted from the tag. Whilst normal swimming activity will not trigger the fast pulse rate, burst swimming will (e. g. during pursuit of prey or if the fish is startled). Tag life is dependent upon the degree of activity by the fish (due to the higher energy consumption of the tag whilst transmitting at high pulse rates) but in general a life of >2 years should be expected. In this study a maximum tag life of 2.5 years has been achieved.

The relatively large size of the tags (80 mm long, 16 mm diameter, weight 22 g in air 7 g in water) required that only pike longer than 500 mm (fork length) were tagged. The tags were implanted into the body cavity of the fish under general anaesthesia. Full details of the tagging procedure and logging system used to record the pulse intervals of the tags are described in Beaumont *et al.* (2002).

To date, during the three years of the study a total of 35 pike (comprising 15 males and 20 females) have been tagged in the river and over 8800 fixes recorded for them. Of the pike tagged, eight have been monitored by the Automatic Data Logger (ADL) system (Table 1).

Activity Data Logger (ADL)

Activity status of the tag was assessed by recording the number of activity events on a purpose designed Biotrack ADL. Unlike the majority of listening stations, where the logger records the presence or absence of a tag at pre-selected time intervals, the ADL system can be set to continuously record the time interval between tag radio pulses for a single tag. Based upon feeding experiments (Beaumont *et al.*, 2002), bursts of continuous high activity over a defined time period were considered to be potential feeding activity by the fish. In Beaumont *et al.* (2002) a ≥3-second time discriminator was used to categorise potential feeding events, however, experimental feeding data subsequent to that study (CEH, unpublished data) have led us to move to the use of a ≥5-second time discriminator. Activity data from the ADL was thus stratified into two categories, continuous periods of activity <5-seconds (minor activity events) and continuous periods of activity ≥5-seconds (major activity events). The time length of these major activity events could be >60 seconds duration.

The ADL was connected to a 3-element Yagi antenna mounted on a 4-metre mast. Both H-Adcock and dipole antennae were tested on the ADL, but reduced range (from the dipole) and null points (from the H-Adcock) in reception resulted in our favouring the Yagi. Due to the Yagi antennas directionality (5° peak reception), and its front loading characteristics, it was necessary to position the ADL at one end (upstream or downstream) of the pike core range with the antenna pointing towards the core range area. In this way maximum signal range with minimum null errors could be achieved. Receiving range of the ADL with the mast-mounted antenna was about 80 m. This was lower than the range for a standard receiver due to the signal strength required for the ADL to adequately discriminate true tag pulses from radio noise. Moderately high water conductivity (specific conductivity ~500 μScm^{-1}) may also have reduced received signal strength.

Table 1 – Details of pike monitored by ADL and duration of monitoring periods

Pike	Length (cm)	Weight (kg)	Sex	No. ADL monitoring runs	Time of year	Max time data run (Hrs)	Min time data run (Hrs)	Total time (Hrs)	% time gaps
B	71	3.6	M	18	Sept 01-Mar 02	469	0.2	1592	12
C	69	3.9	F	6	Sept 01–Nov 01	250	4	582	2
I	87	5.8	M	3	Feb 02–Mar 02	339	7	569	5
L	79	4.2	F	1	Jun 02	133	133	133	Not analysed
N	65	1.9	F	6	Jun 01			480	Not analysed
O	60	1.8	F	4	Oct 01–Nov 01	107	48	311	Not analysed
V	52	1.7	F	5	Mar 02–Apr 02	259	5	499	2
Y	64	2.2	M	6	Dec 01–Feb 02	576	18	1314	Not analysed
TOTAL				43				5480	5.3% (average)

Setting-up the ADL was a relatively complex procedure with several parameters requiring precise tuning to ensure a strong, clean signal for the ADL to record. In particular it was critical to set the threshold levels for the signal recognition in order to separate out extraneous noise from true signals. Unfortunately the precision required also meant that when the signal varied in intensity, and/or background noise levels varied after initial calibration, false data could be recorded.

Due to the very mobile behaviour of the pike, within the ADL data there were periods when no signal was received by the ADL. These periods varied from <1 second to several hours. Whilst the long duration gaps were a result of the fish moving out of range of the antenna, shorter periods could have been due to signal attenuation by aquatic vegetation or conductive material in the riverbed. The small null point at either end of the tag could also have caused gaps if the tag directly lined up with the antenna; these are likely to be of very short duration however due to the small angle of the null. Whilst gaps in the data only accounted for <4% of the time recorded by the ADL, the presence of the data gaps resulted in periods where we could not be certain that the fish had not had a ≥5 second activity (and thus potential feeding) event.

In addition to the gaps in the data, extraneous "noise" was also recorded by the ADL. These noise events were characterised by pulse widths less than the shortest duration pulses of the tag (c. 260 ms). The cause of this interference is not known but the area where the ADL was deployed is near an electric rail line, a military gunnery and tank training range and a fish counting facility running a computer (renowned for creating radio noise). Although generally infrequent and of very short duration these noise events did, on occasions, create false active signals (≥5 seconds duration) in the data.

The presence of the gaps and noise in the data presented considerable challenges for analysis of the data. The ADL produced considerable amounts of data: one record every 1300 ms while the fish was at rest and every 300 ms during active events. This resulted in between 66,000 and 288,000 data points per day. The computer programs written to analyse the data partially enabled some automation in detecting the gaps and noise in the data, however final manual editing of the data was still required.

ADL data was edited for gaps by collating activity data into minute intervals, and then recording whether any >5 second gaps occurred within that minute. Minutes where gaps of this duration did occur were coded.

Noise editing was carried out by filtering <260 ms pulse intervals from the data and assessing whether sufficient numbers of these "false" signals occurred during >5 second activity events to render the event invalid.

Manual Data Collection

In addition to the data being collected by the ADL, activity of the fish was also evaluated using manual tracking methods. During the manual tracking (3-tracks a day for 13-days at four different seasons) output from the tag was listened to for 5-minutes. The number of fast pulse "bursts" in that time was then recorded. No stratification into major and minor events was made with the data obtained from the manual tracking records. The number and identity of pike present during each track varied, due to immigration/emigration from the study section, natural mortality, and new pike being tagged after the beginning of the study (Table 2). All tagged pike within the study section were followed on each date shown in table 2 in order to provide as large a sample as possible from which to make inferences about the patterns of activity of the pike population. The inclusion of pike that did not reside within the section over the entire study period reduced the potential for bias that might have occurred had only 'resident' fish had been followed.

The proportion of five minute periods during which activity was detected was determined separately for each individual pike. The proportion of five-minute periods during which activity occurred (from all pike combined) were then compared between time periods morning (1-hour before sunrise to 2-hours after sunrise), mid-day (10:00 to 14:00) and evening (1-hour before sunset to 2-hours after sunset) using Kruskal-Wallis tests (Table 2).

In addition, the mean number of activity events heard in each time period was calculated for each pike individually. Mean numbers of activity events were then compared between time periods (for all pike combined), within each 13-day track, using Kruskal-Wallis tests (Table 2).

Activity data for individual pike collected at hourly intervals by manual tracking were also compared with concurrent data collected from the ADL to assess the comparability of the data collection methods.

Results

In excess of 5400 hours (228 days) of data has been collected from a total of 8 fish monitored by the ADL (Table 1). The longest run of data, without any gaps >5-seconds was approximately 4-days, and up to 12-days of almost continuous data have been obtained with some gaps of between 5 and 10-seconds duration. A 21-day run of data was obtained for one fish (including an 8-hour gap due to ADL battery failure).

Table 2 – The dates of manual tracks, together with the number of pike included in each track and results of Kruskal-Wallis tests for differences between time periods during each track.

Date	No. Pike tracked	K-W test significance–No. events			K-W test significance–Proportion		
		DF	H	P	DF	H	P
September 2000	5	2	2.13	0.34	2	2.77	0.25
December 2000	7	2	4.09	0.13	2	2.22	0.33
July 2001	8	2	5.02	0.08	2	2.63	0.27
September 2001	10	2	2.95	0.23	2	3.86	0.15
December 2001	11	2	1.48	0.48	2	0.74	0.69
March 2002	12	2	0.22	0.89	2	0.13	0.94

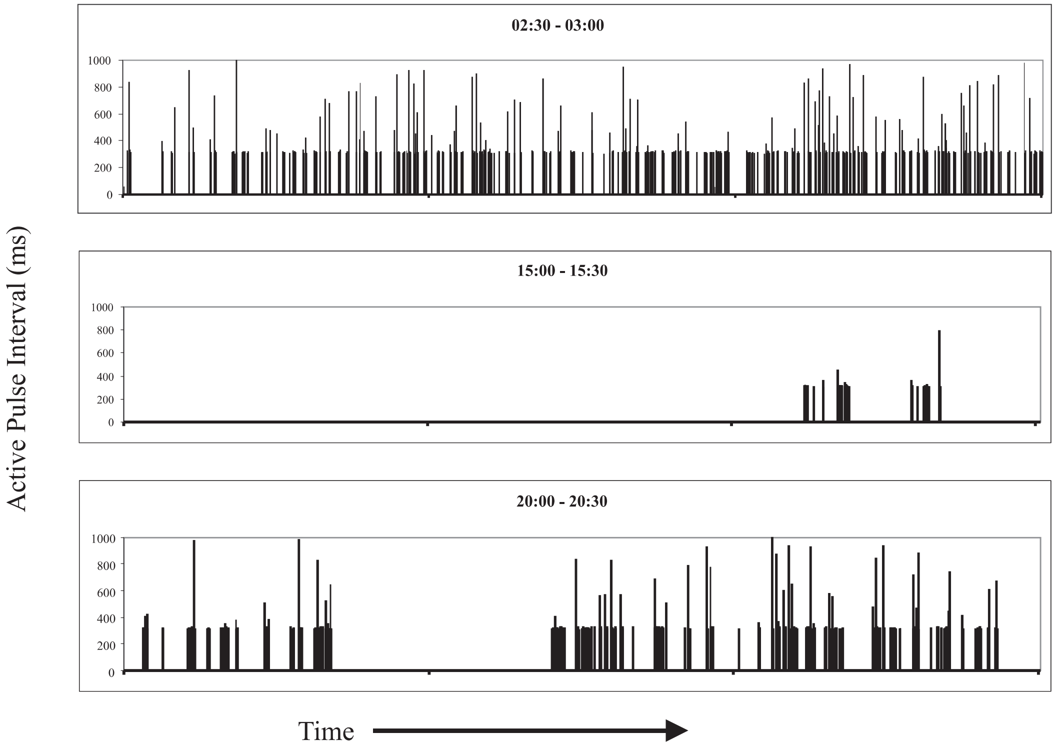

Fig. 2 – Total activity pulses recorded by ADL over three, 30-minute periods from pike N, June 2001.

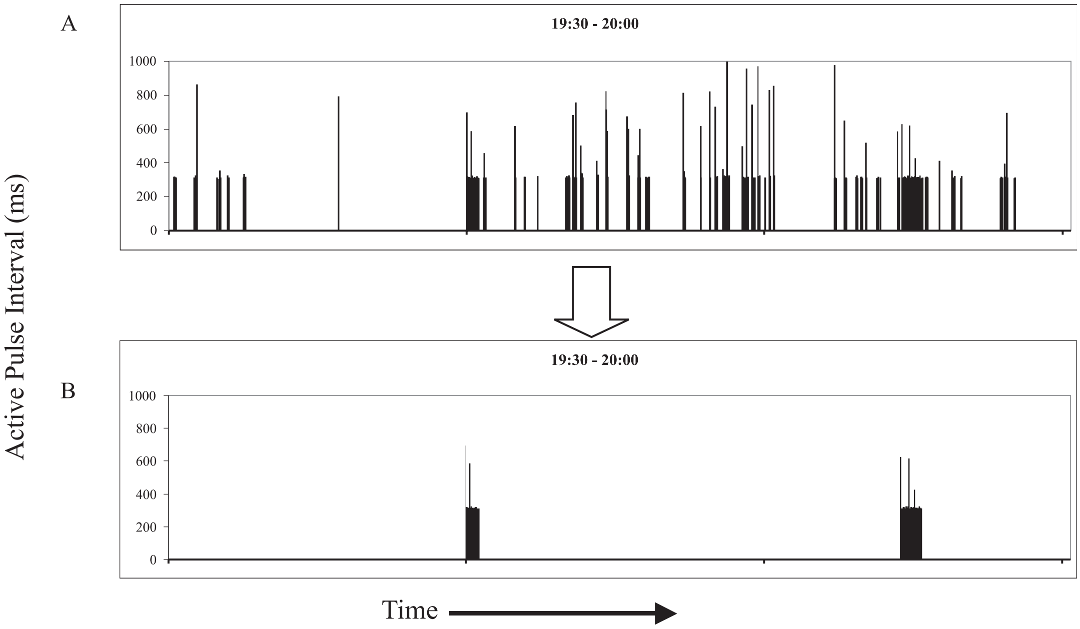

Fig. 3 – Total activity data between 19:30 to 20:00 for pike N June 2001 (A) and filtered ≥5-s activity data (B) for the same period.

In general, pike appeared to exhibit many minor activity events throughout the day and night with very few totally quiescent periods. Figure 2 shows an example of activity pulses recorded by the ADL for Pike N in June 2001 for three, 30-minute time periods throughout the day. When the minor activity events are filtered from the data however, a much-reduced pattern of major activity events is apparent (Fig. 3 A and B). Collation of these 'major events' into 1-hour time periods indicates activity peaks roughly corresponding with dawn and/or dusk: individual fish showing some variation between being predominantly active at dawn, dusk or both times (Fig. 4).

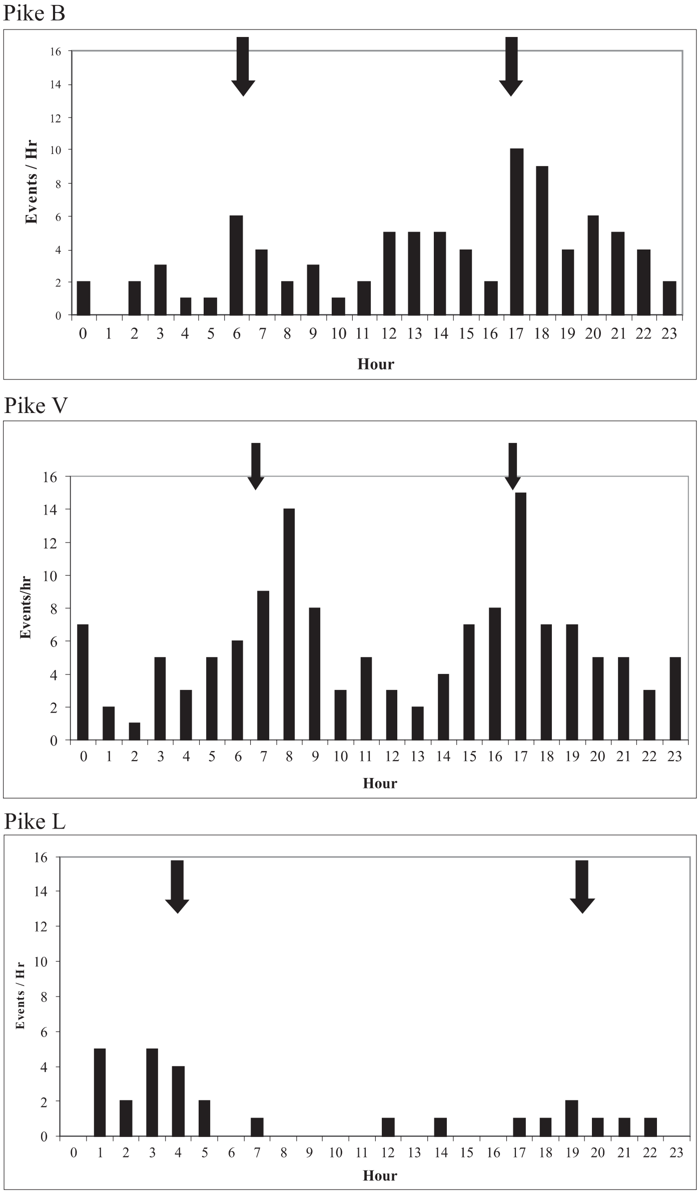

Fig. 4 – Major activity events per hour recorded by ADL for three pike: Pike B (collated over 12-day period in March 2002), Pike V (collated over 19-day period in March 2002), Pike L (collated over 5-day period in June 2002). Arrows indicate sunrise and sunset.

Hourly activity data for the male pike I, recorded in March 2002 (Fig. 5), did not conform to the pattern of movement observed in other fish: there was a much higher general level of activity (some days in excess of 1000 major activity events) and a higher proportion of major activity events occurring during the middle of the day. Fig. 6 shows data for one day (collated into activity per minute) of the high level of continuous activity (sometimes in excess of 60-seconds) exhibited by pike I during this period, and also shows an example of the high level of activity that occurred during the night on some occasions.

Data collected during the manual tracking were assessed for activity patterns. Whilst for individual tracking periods there appeared to be a trend towards lower proportions of activity events occurring during the day, as compared to during dawn or dusk, no significant differences occurred between the proportion of five-minute periods containing activity events in different time periods (Fig. 7, Table 2). Pooled data for all tracking periods also did not show any significant pattern (Kruskal-Wallis test: all d.f. = 2, H = 4.12, p = 0.13). Similarly, whilst there also appeared to be a trend towards lower median numbers of activity events for individual tracking periods being recorded during the day, no significant differences occurred between the number of activity events recorded in each time period for any of the tracks (Fig. 8, Table 2) or for the pooled data (Kruskal-Wallis test: all d. f. = 2, H = 2.49, p = 0.29).

Agreement between the ADL data and the hourly-recorded manual diurnal data was variable, but often showed good agreement for periods of high activity (Fig. 9). When the hourly data for fish being tracked manually (not all of which had been monitored by the ADL) were collated, and grouped into hourly activity events however, a clear pattern of crepuscular activity peaks similar to that registered by individual fish monitored by the ADL was found (Fig. 10).

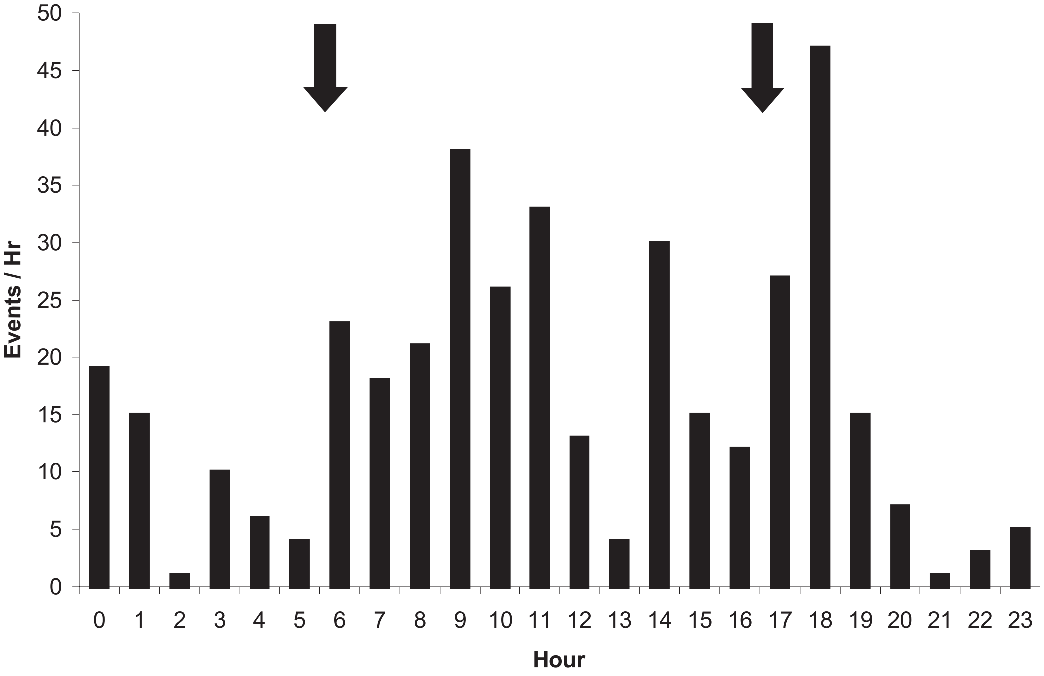

Fig. 5 – Activity events per hour recorded by ADL collated over 26-day period for pike I March 2002. Arrows indicate sunrise and sunset.

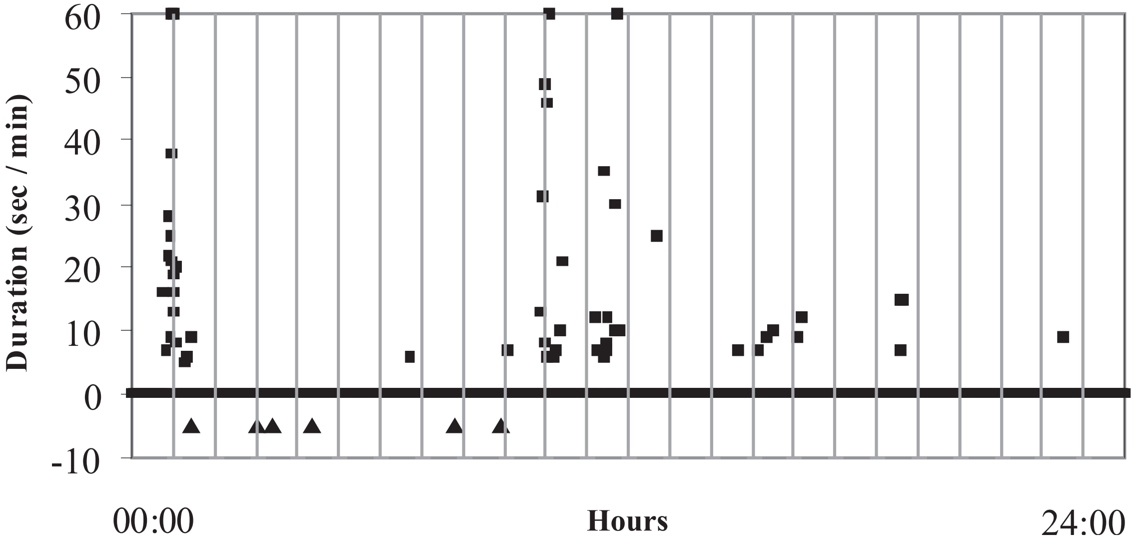

Fig. 6 – Major (≥5-second) activity events (seconds per minute) for pike I over one day (11-03-2002). Vertical lines indicate hours, triangles below baseline indicate the six, 1-minute periods where >5-seconds gaps in data exist.

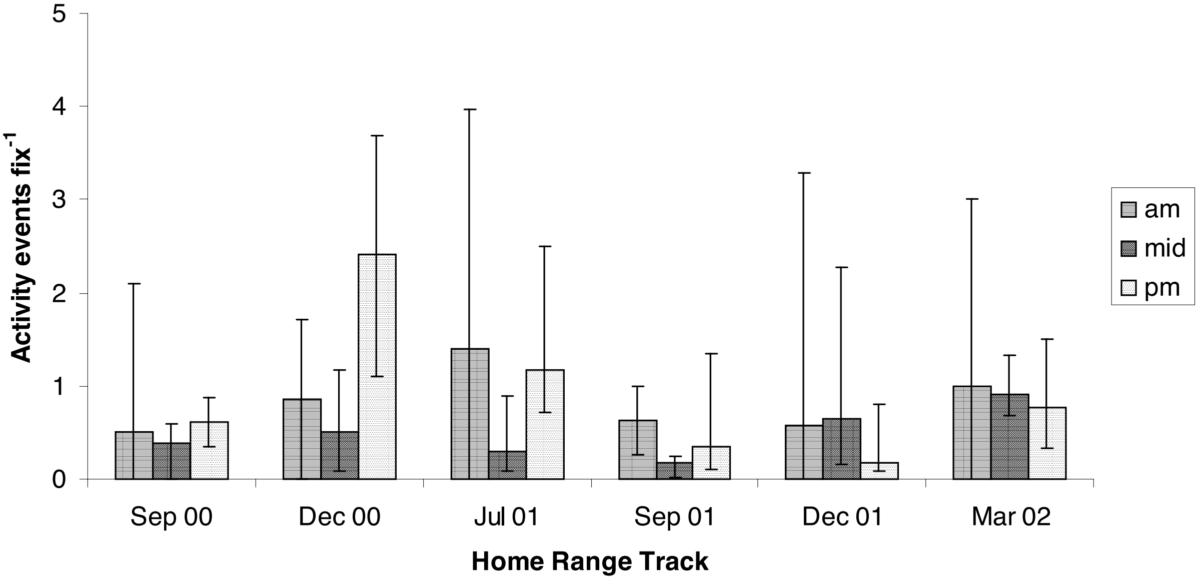

Fig. 7 – Proportion (median and interquartile range) of occasions where activity events were recorded during morning, mid-day and evening manual tracking.

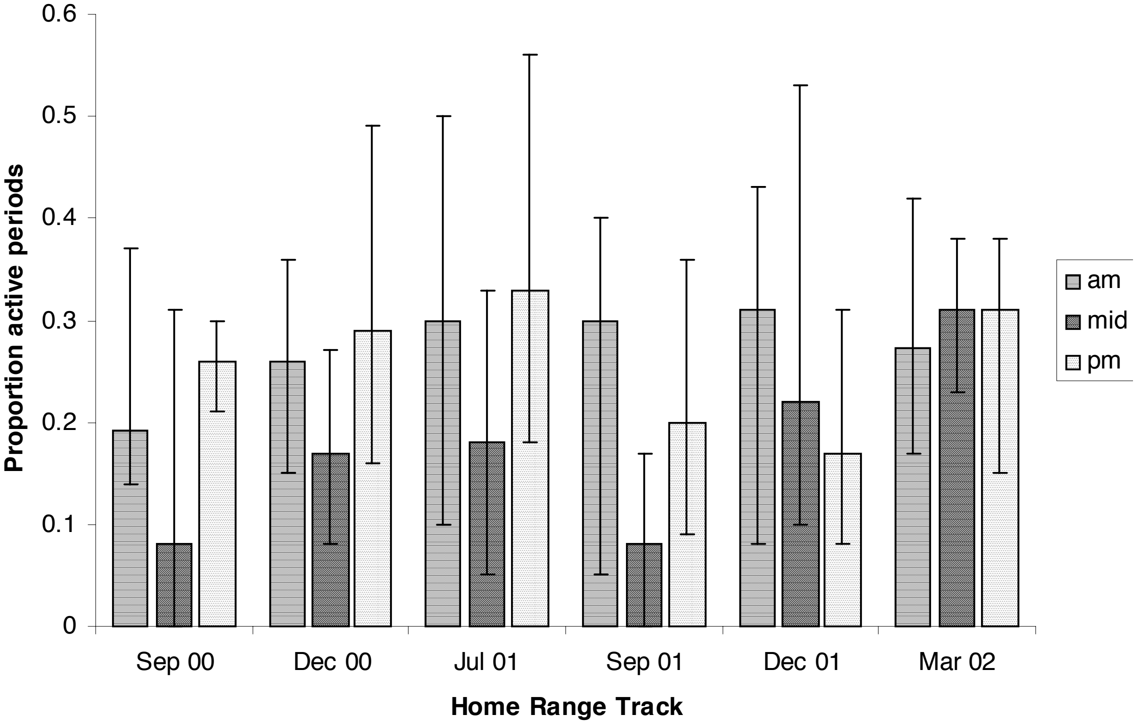

Fig. 8 – Mean number of activity events, from all pike, recorded during morning, mid-day and evening manual tracking (Median and interquartile range).

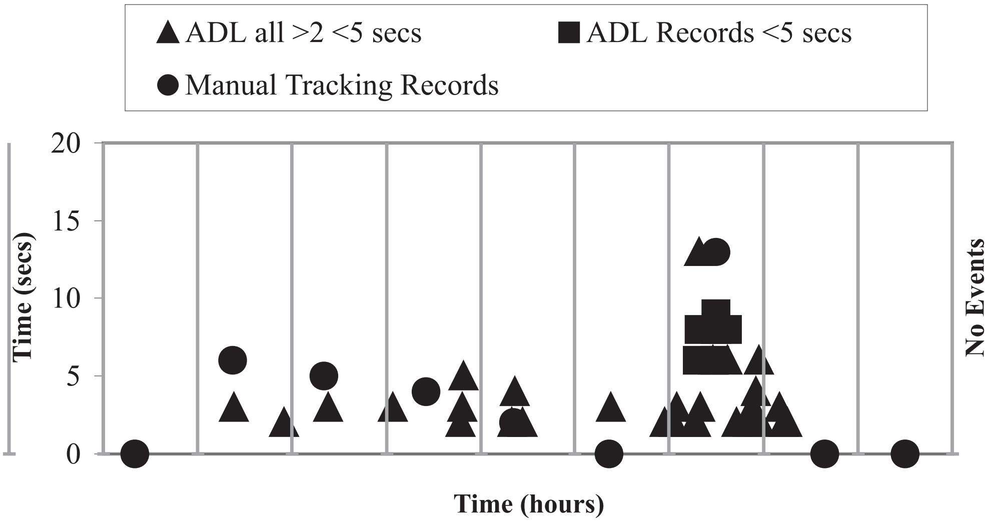

Fig. 9 – Comparison of activity status results obtained from ADL (duration of active events >2<5-seconds (triangles) and ≥5-seconds (squares) and manual tracking – the number of activity events in 5-minute periods per hour (circles). Pike I, 1-3-2002.

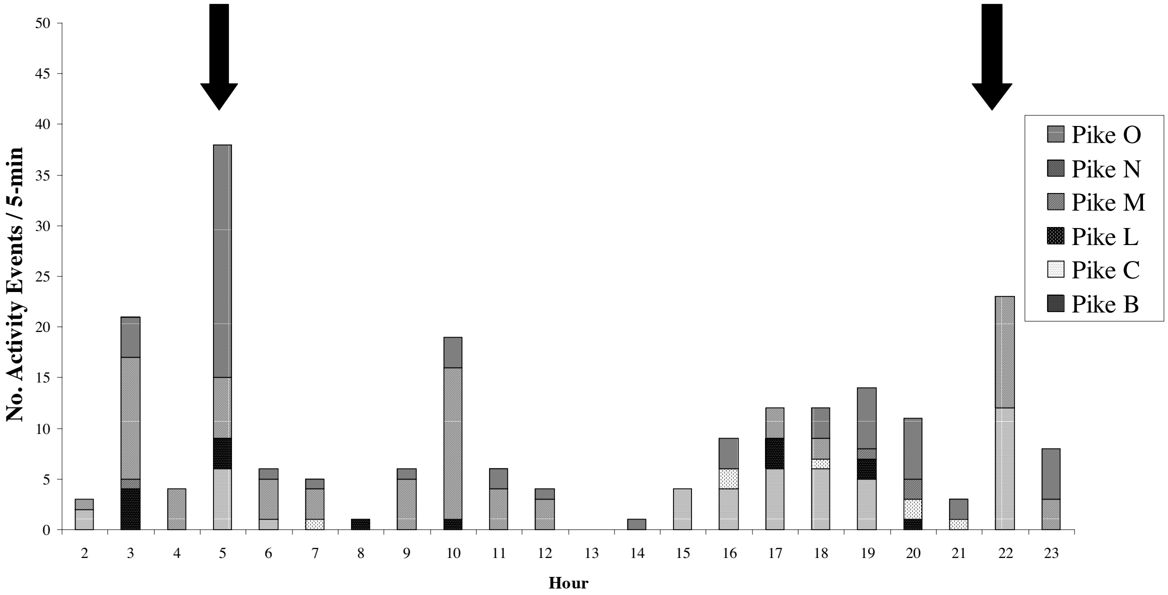

Fig. 10 – Number of activity events recorded by hourly manual tracking for all fish tracked over 24-hour period. Arrows indicate sunrise and sunset.

Discussion

The duration of the continual data from the ADL are far in excess of other previously published data on fish activity patterns and are also the only true "continuous" (notwithstanding the gaps in the data) data set known to exist. Other publications use the term continuous to describe frequent, but not continuous, records e.g. three records every 10 minutes (David and Closs, 2001).

Overall pike exhibited low levels of prolonged (≥5-seconds continuous duration) high-activity and confirms that the pike is a generally sedentary animal. Major activity events (≥5-seconds continuous duration) conformed to a pattern of night-time and mid-day minima and dawn and dusk maxima. These data correspond well to other published work on lake systems, where pike activity has been assessed on the basis of linear distance moved (Cook and Bergerson, 1988). They also support the hypothesis that pike feed at low light levels when they may have a competitive advantage over shoaling prey (the "twilight hypothesis"; Pitcher and Turner, 1986). The activity tag data indicated however that minor activity events could occur at any time over a 24-hour period. These findings are in contrast to other research (where pike are regarded as either being inactive or having low activity at night) where activity patterns based on linear movement of pike have been assessed (Diana, 1980; Lucas, 1992). Jepsen *et al.* (2001) found that pike in Lake Ring were predominantly nocturnal during June and July. However it is not clear from Jepsen's data whether fish movement occurred during true darkness or in the dawn, as data were only collected at 6-hour intervals. Whilst Diana (1980) considered that the slight movements he detected during the night-time were probably unimportant in overall time-energy budgets, the volume of activity pulses detected by the ADL during the night could indicate that cumulatively they may comprise an important component of the pike's overall activity energy budget.

The lack of a crepuscular activity pattern (as found for other pike) in the male Pike I corresponds well to other descriptions of increased pike activity patterns during spawning (Cook and Bergerson, 1988; Lucas, 1992). Lucas (1992) noting that male pike were significantly more active than females during the spawning period and that this activity was greatest during daylight hours. Whilst overall the highest peaks in activity for Pike I during this period were recorded during the day/dusk period, activity events were also recorded during the night. As Pike I moved away (5 km downstream) from the study area outside the spawning period, few data have been collected on its activity patterns at other times of the year (Masters *et al.*, this volume). Daytime activity levels however were in excess of those found for other pike monitored by the ADL at non-spawning periods. Based on the evidence from over 8500 manual tracking observations (Masters, 2003) it appears that in the river the pike adopts a very mobile hunting strategy and often ranges about the river before carrying out short duration active pursuits of prey. Attempts were made to monitor the interval between major activity/feeding events for pike being recorded by the ADL. The presence of gaps >5-seconds in the data set however, meant that even though the overall duration of these gaps only accounted for <4% of the time monitored, we could not be certain that the pike had not had major activity events in those gaps, and thus the periodicity of these events could not be assessed with any certainty. Analysis that has been possible to date has shown some differences in time intervals between major activity events in different seasons but these have not been significant (CEH, unpublished data).

Whilst activity patterns determined from the manual tracking generally showed higher activity events during the morning and evening, compared to the day, the differences were not significant.

Correlation between data collected simultaneously from hourly manual tracking of the fish, and the continuous ADL data, was variable. This would be expected when only listening for 5-minutes in every hour during manual tracking. When the manually collected data from several fish were pooled, however, similar crepuscular activity peaks to those found from the ADL data were apparent.

The fact that the information obtained from 5-minute manual data collection from the activity tag so well reflects (after pooling) the result obtained from the ADL is an important finding for other studies where manual assessment of activity tag output is carried out. The greater number of fish that can be assessed manually is also likely to give a better "population" perspective on activity patterns.

Given the energetic costs of moving against the flow in a river, the adoption of a very mobile hunting strategy by the pike was surprising but confirms data obtained from lake dwelling pike (Cook and Bergerson, 1988; Diana, 1980; Lucas *et al.*, 1991). The multi-nuclear nature of the home range area of the fish may also reflect this mobile hunting strategy within the river (Welton *et al.*, 2002).

Limitations of the prototype ADL system and the high mobility of the study species resulted in gaps in the data that limited the analysis possible. A multiple antenna system would solve some of the problems of fish moving out of range and modern electronics would probably also assist in reducing the proportion of false data collected. One drawback of the system is that time-energy budgets cannot be calculated; as is the case when using heart rate telemetry. However the system does provide a relatively simple system that enables an insight into fine time scale pike activity and, potentially, feeding patterns.

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Estimation of positioning error from an array of automated omni-directional receivers in an artificial reef area

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Key words: ultrasonic telemetry, receivers array, positioning errors, artificial reefs

Abstract

Artificial reefs (AR) have been shown to harbour increased numbers of fish compared to adjacent areas. To assess whether this is due to attraction through artificial structures or providing permanent habitat for the occupants, the behaviour of fish within ARs needs to be examined in more detail. Automated omnidirectional receivers and miniaturized pingers were applied to determine the hydrophones' detection range and study the variability of detections recorded at different distances, and to estimate pinger positioning error throughout the AR study area. Throughout the study site, positioning design and respective detection ranges of five receivers created 17 regions of overlap between two to five receivers. The detection range of the hydrophones was found to be 500 m. Weighted means of modified detection numbers were used to calculate the pinger's position in the study area. Pinger positioning error (Pe) was defined as the distance between the calculated geographical coordinates and the real ones. The artificial reef characterization results showed that the position error is related to the number of receivers overlapping. Minimal positional error was found in regions with four and five overlapping receivers (Pe is 54±24 m). The "barrier effect" of an artificial structure on signals detection depends on the distance between obstacle and transmitter. The omnidirectional hydrophones were unable to record any signal when the pinger was set inside the artificial structures. But, when the pinger was at least 1 m outside the pyramid, the positioning accuracy was found to be 132±54 m.

Introduction

Artificial reefs (AR) are submerged structures placed on the seabed deliberately, to mimic some characteristics of a natural reef (Jensen, 1998). They are being used worldwide for multiple purposes, but aim mainly at increasing fish production and protecting sensitive habitats (Bombace, 1997; Santos *et al.*, 1997). For three decades, scientific literature has been reporting successes and limits of AR but the question whether they contribute to attract or produce new fish biomass is still unresolved (Bohnsack, 1989; Lindberg, 1997). The attraction–production debate has provided the impetus to start studies dealing with the ecological processes (Miller, 2002) and fish behaviour (Santos *et al.*, 2002; Relini *et al.*, 2002; Workman *et al.*, 2002) in the artificial reef areas with the employment of more efficient monitoring techniques.

Since 1950s, telemetry has been considered a powerful tool consisting in the attaching of transmitters to animal bodies and "tracking" them in their natural environment by means of hydrophones (Ireland and Kanwisher, 1978). Generally, telemetric techniques have been employed for studying behavioural ecology (migration, home-range, habitat utilization, activity and movement, etc…) of marine and freshwater animals in different habitats (Bégout and Lagardère, 1995; Bridger *et al.*, 2001; Taverny *et al.*, 2002). The usefulness of tracking and habitat-use-data in telemetric studies depends on the accuracy and precision of tagged fish location estimates. Biased location estimates are often the result of the presence of physical obstacles (e.g. submerged vegetation, bottom topography) and of the oceanographic conditions (e.g. water flow, thermocline, turbidity) (Pincock and Voegeli, 1990). Hence, telemetry studies should be preceded by accuracy and precision assessments (Braun *et al*., 1997).

Low cost automated receivers are commonly deployed to study habitat utilization, by using simple presence/absence data within the range of each receiver (Klimley *et al*., 1988; Heupel and Hueter, 2001; Bridger *et al*., 2001; Lacroix and Voegeli, 2000; Voegeli and Starr, 2000; Voegeli *et al*., 2001). Recent application, based on overlapping automated receivers detection ranges, has increased the accuracy in locating fish throughout small areas (Arendt *et al*., 2001). Simpfendorfer *et al*. (2002) estimated tagged fish location by means of an algorithm which uses the number of detections recorded by the overlapping receivers. The authors also highlighted the importance of a correct arrangement of receivers throughout the study area to increase the positional accuracy. However, an unsolved question remains on the limit of accuracy of location estimates of this telemetric system, due mainly to the interference effects of natural (Simpfendorfer *et al*., 2002) and artificial obstacles on signal detection.

The Gulf of Castellammare (NW Sicily) is one of the largest Italian artificial reef area. Studies on the AR of the Gulf, have provided data on benthic and fish assemblages, the trophic relationships and the fishing yield, but no study has been aimed at the movements and activities of the AR fishes (Badalamenti *et al*., 2000). Few papers deal with the application of ultrasonic telemetry in the artificial habitats mainly due to the interference of the artificial structures on signal propagation (Collins *et al*., 2000; Smith *et al*., 2000).

In 2000, a research program started with the final goal of studying long-term fish movement by means of an array of automated omnidirectional receivers (D'Anna and Badalamenti, 2003).

In this paper we present the results of the application of automated omnidirectional receivers, aimed to:

1. determine the hydrophone detection range and study the variability of the number of detections recorded at different distances (Free-Water characterization);
2. estimate the positional error of calculated pinger positions throughout the study area, quantifying the interference effect of the single artificial structures (Artificial Reef characterization).

Materials and methods

Study site

The Gulf of Castellammare (Fig. 1) is a broad, crescent-shaped bay on the NW coast of Sicily (38° 03' N, 12° 52' E). The sandy seabed of the central gulf part is interrupted by the presence of *Cymodocea nodosa* patches (12-14 m depth) and two artificial reef areas. The largest artificial reef, chosen as the study site, is located off Alcamo Marina, 1 km offshore. In this area, 27 artificial structures are distributed over an area of 0.2 km^2 at depths between 14.5 and 21 m (Fig. 3). Each structure is built as a three-layer pyramid of 14 concrete blocks (total volume 150 m^3) (Badalamenti *et al*., 2002).

Five automated omnidirectional VR2 receivers (Vemco Ltd, Halifax, Canada) were deployed in the study area. Coded V8SC-1L, ultrasonic transmitters were deployed at known locations to assess the detection range of the hydrophones and accuracy of calculated positions upon number of detections.

Free-Water Characterization

To analyse the variability of the number of detection (*Nd*) versus the distance and to determine the hydrophones' detection range, an unobstructed line-of-sight (termed "Free-Water") between receivers and pingers was used.

Detection range & *Nd* variability – A total of 10 replicates were carried out, during which the environmental conditions were measured. Samples carried out during thermocline conditions and high water turbidity were not considered for the analysis. Size of Δt was fixed to 25 minutes, as a result of pre-survey tests upon pinger variability in the signal emission time (D'Anna and Badalamenti, 2003). Five hydrophones acoustic receivers were independently suspended 15 m from each other,

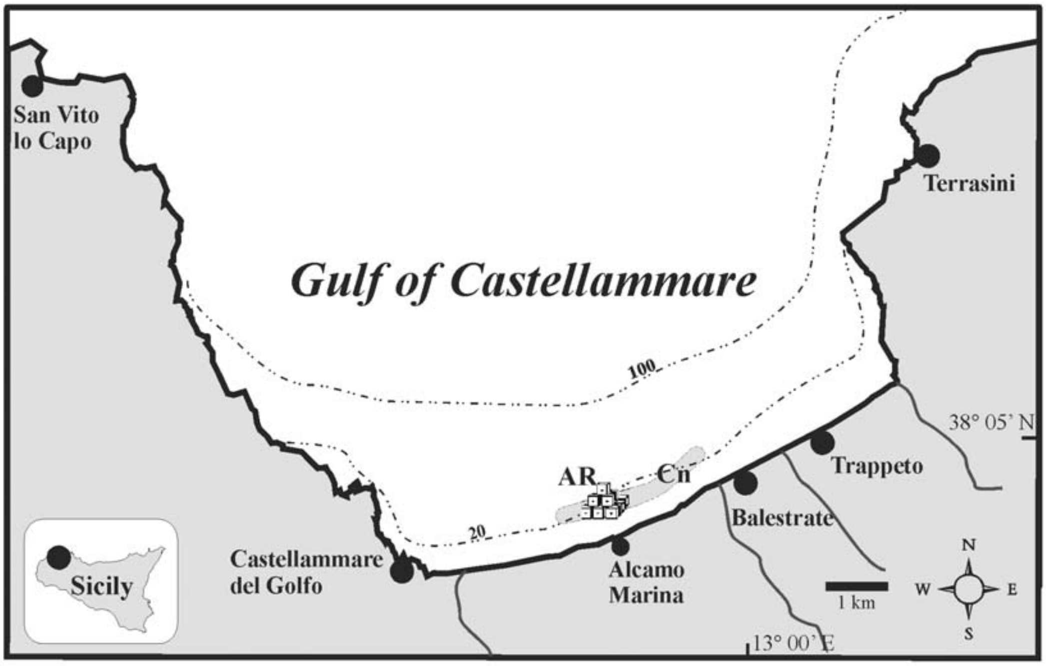

Fig. 1 – Map of study site in the Gulf of Castellammare showing the Artificial Reef (AR) area and the *Cymodocea nodosa* (Cn) patches

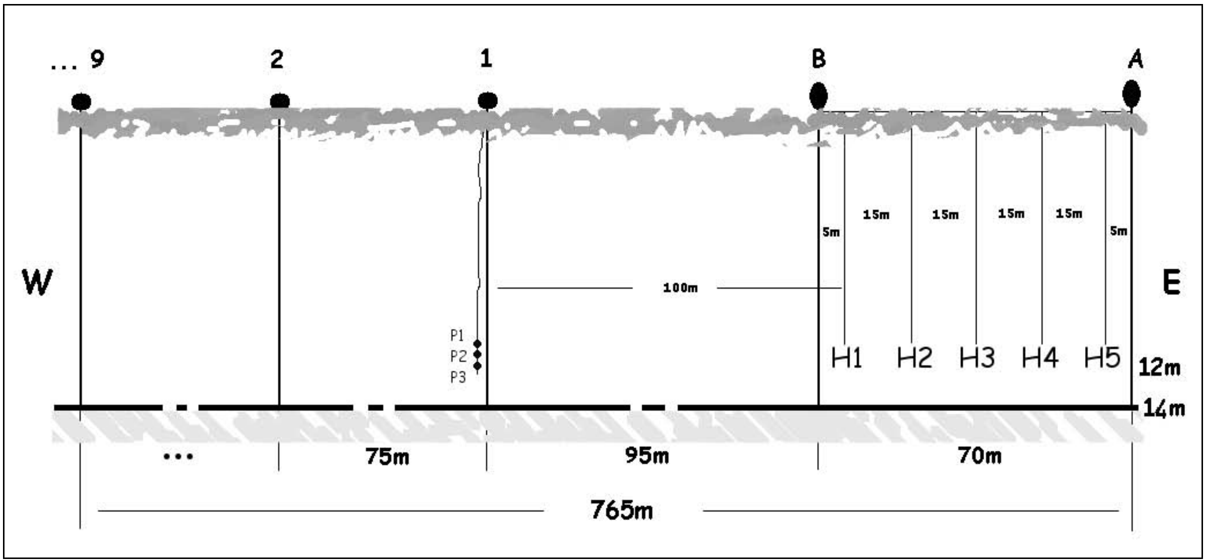

Fig. 2 – Sampling design for Free Water experiments. W = West, E = East; A, B, 1, 2,...9 = surface buoy; H1,…H5 = Hydrophones; • = Pinger (P1, P2, P3)

from east to west at a depth of 12 m (2 m above the seabed). Starting at 100 m from the westernmost receiver, 3 transmitters were suspended at the same depth for 25 minutes and moved to the west at consecutive distance intervals of 75 m (Fig. 2). During each trial 45 *Nd*-distance couples were recorded. The average *Nd* values from each pinger at different distances were tested with a two-way ANOVA using pinger (three levels) as random factor and distance (30 levels) as a fixed one.

ANOVA was carried out using "Gmav5" software after checking the homogeneity of variance with Cochran test. When differences were found, a-posteriori comparisons were made using the Student-Newman-Keuls (SNK) test (Underwood, 1997). A 10 percent detection threshold was chosen to assess the hydrophone detection range.

Artificial Reef Characterization

Three experiments were performed in order to estimate system error in calculated pinger position when placed (i) in the centre of each region of overlap (Study area tests), (ii) randomly inside the artificial reef area (Artificial reef area tests) or (iii) close to (out/inside) a single artificial reef structure (Pyramid "barrier effect" tests).

Based on the free-water experiments results, five receivers were deployed around and inside the artificial reef area (0.2 km^2) (Fig. 3). Each receiver was moored 2 m above the seabed, fixed to a thin rope anchored with a 4 kg lead barrel. A submersible plastic float was attached 3 m above the receiver to help it maintain a vertical orientation in the current, while a buoy was attached to the rope at the surface. The first receiver, called "C", was moored in the centre of the artificial reef area. The other receivers, labelled "N", "S", "E" and "W", were located 400 m, North, South, East and West of "C". This configuration resulted in the creation of 17 regions of overlap between two to five receivers and four zones, each unique to a particular receiver (N, S, E and W), covering a total area of 1.5 km^2.

Each recorded number of detections during *Δt* was replaced with the mean value of the respective *Nd* class according to free-water experiment results.

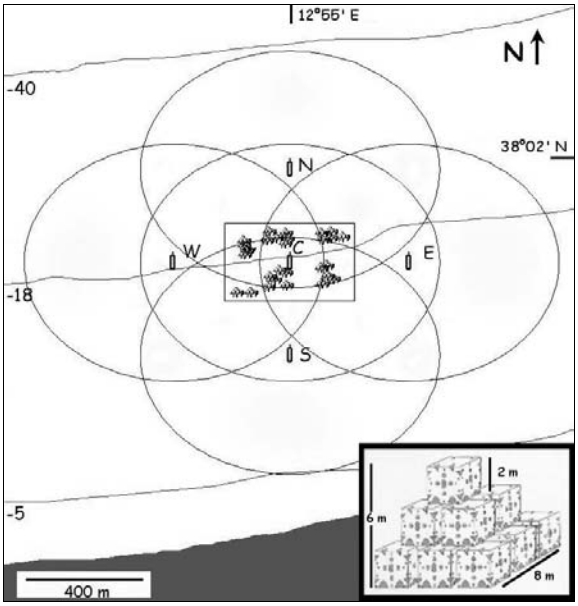

Fig. 3 – Receiver positioning design: circles represent the receivers (C, N, E, S, W) detection range, the square indicates the artificial reef area. In the corner a schematic picture of a single artificial pyramid.

The following weighted arithmetic mean was used to calculate the X- and Y- geographical coordinates of the pinger positions:

$$\overline{X}_{\Delta t} = \frac{\sum_{i=1}^{n} Nd_i X_i}{\sum_{i=1}^{n} Nd_i} \qquad \overline{Y}_{\Delta t} = \frac{\sum_{i=1}^{n} Nd_i Y_i}{\sum_{i=1}^{n} Nd_i}$$

where n is the number of receivers, *Nd* is the replaced number of detections for the *i*th receiver during *Δt*, X_i and Y_i are the X and Y coordinates of the *i*th receiver (based on Simpfendorfer *et al*. 2002). The pinger positioning error (Pe) was defined as the distance (in meters) between the calculated geographic coordinates and the recorded ones.

In all the experiments, a maximum of four pingers were used at the same time in order to avoid any code collision events (Lacroix and Voegeli, 2000). Pingers were independently attached to a thin rope, 2 m above the seabed. A 2 kg lead weight barrel was useful to prevent drifting. A sub-surface styrene float and a little white buoy were attached to the rope, 2 m above the pinger and on the sea-surface end respectively. A 25-minute time interval was chosen for each position in all tests.

A multi-probe and currentmeter were used to verify that the experiments were carried out under similar environmental conditions of those carried out in the Free-Water characterization. A non-differential handheld Global Positioning System (Garmin GPSII-plus) was used to locate pingers throughout the study area.

Analyses of variance of Pe estimates were carried out using "Gmav5" software after checking the homogeneity of variance with Cochran test. When differences were found, a-posteriori comparisons were made using the Student-Newman-Keuls (SNK) test (Underwood, 1997).

Study area tests – To estimate calculated position accuracy in overlapping areas the pingers were deployed in the centre of the 17 regions of overlap and Pe was calculated for each position. In order to detect differences in Pe between the overlap regions, an equal number of Pe values per region were randomly sorted (12) from the database then, a one-way ANOVA was applied with the factor location, fixed and orthogonal, and four levels (2, 3, 4 and 5) overlapping receivers.

Artificial reef area tests – We estimated the artificial structures' influence on position accuracy with pingers placed close (3 m) and far (at least 10 m) from the pyramids. Pe estimates from pingers located close to and far from the pyramid, were compared with one-way ANOVA with the factor location, fixed and orthogonal, and two levels (close and far).

Pyramid "barrier effect" tests – The most central pyramid with regards to each of the peripheral receivers was chosen to test whether the system was able to detect transmitters inside the pyramid. First, a scuba diver placed a pinger 1 m from each side of the pyramid. Then, the pingers were moved inside the pyramid among the concrete blocks. We then compared the estimated positioning error when the pinger was outside and inside the pyramid. This procedure was repeated 3 times.

Results

Detection range and Nd variability

The hydrophones' detection range was found to be 500 m (*Nd*=10 percent). Distance intervals over 535 m were not consider for ANOVA test because *Nd* values recorded were always under the 10 percent threshold. Significant differences ($p<0.001$) were found between distance intervals, while non-significant difference was found among pingers ($p=0.96$) and for the interaction between pingers and the distances ($p=0.77$). Post-hoc pairwise comparison highlighted five groups of distance intervals within which *Nd* does not vary significantly. The first group includes distances in the range between 0-265 m, the second group 266-310 m, the third 311-415 m, the fourth 416-490 m and the fifth group 491-535 m (Fig. 4). For each group, an averaged *Nd* value was calculated as shown in Table 1.

Table 1 – For each distance group, distance ranges and number of detection (*Nd*) class were found. Mean *Nd* values were calculated for positional estimation algorithm.

Distance group	1	2	3	4	5
Distance range (m)	0-265	266-310	311-415	416-490	491-535
Nd class	23-18	17-15	14.8	7.4	3.1
Mean *Nd*	21	16	11	6	2

Study area tests

The highest values of Pe were estimated in regions with two overlapping receivers (269±158 m), the lowest in the region with five overlapping receivers (36±32 m) as showed in Table 2. Pe among different overlap regions differs significantly (ANOVA, $p<0.001$). The Student-Newman-Keuls test showed that Pe values were equal in regions with 2 and 3 and with 4 and 5 overlapping receivers, with 2=3 > 4=5.

Table 2 – Mean values of Positioning error (Pe) and standard deviations (s. d.) calculated for each overlap region.

overlap with	Pe (m)	s. d.
2 hydr/5	269	158
3 hydr/5	197	139
4 hydr/5	71	57
5 hydr/5	36	32

Artificial reef area tests

Positioning error of pingers located close and far from the pyramid was 130±59 m and 54±24 m respectively. ANOVA found significant differences ($p<0.001$) in Pe between the two locations.

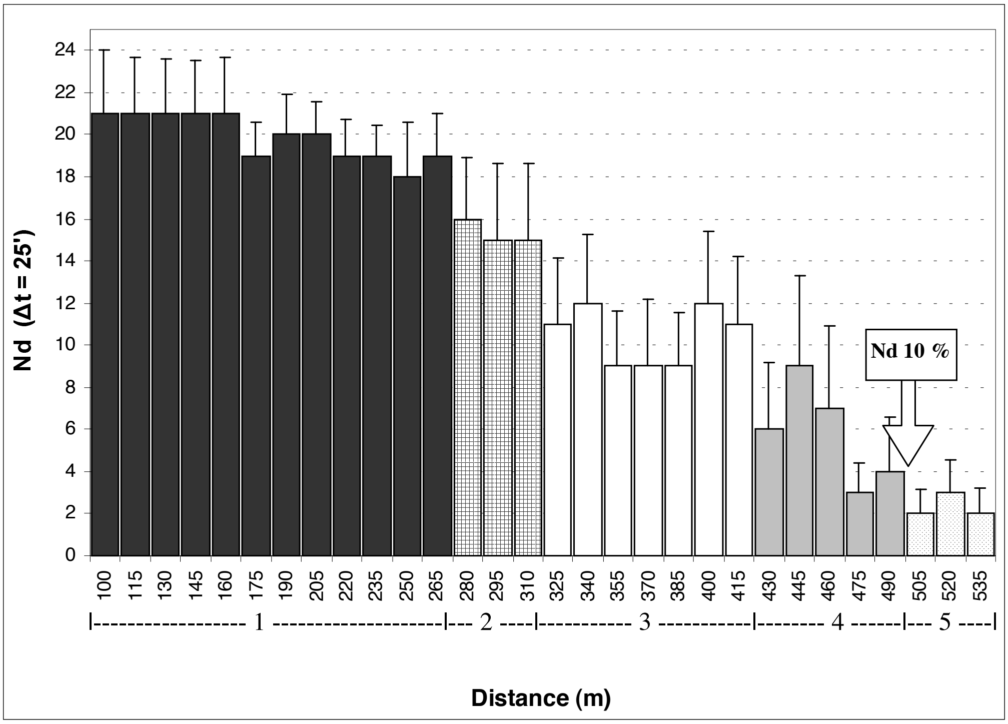

Fig. 4 – *Nd* means and standard deviation (s.d.) recorded at 15 m distance intervals. 1, 2, 3, 4, 5 = distance groups from Student-Newman-Keuls analysis.

Pyramid "barrier effect" tests

All receivers recorded *Nd*=0 when the pinger was inside the artificial structure and no estimated position and Pe were calculated.

When the pinger was placed outside the pyramid at a distance of 1 m from the blocks, Pe=132±54 m and the receiver on the opposite side of the pyramid with respect to the pinger, always recorded *Nd*=0.

Discussion

The results presented in this paper demonstrate that, using an appropriate arrangement of the receivers, it is possible to estimate the low-cost automated receivers' error in locating transmitters in an artificial reef area. Simpfendorfer *et al.* (2002) used an automated receiver system to estimate the location of tagged animals.

They applied an arithmetic mean of each receiver's geographic coordinates, weighted by the *Nd* recorded at a fixed time interval. However, that calculation algorithm is based on the assumption that a linear relation exists between *Nd* and distance from receivers even if the inverse-square law precisely relates sound intensity to distance from the transmitter (Ireland and Kanwisher, 1978). Moreover, a previous study conducted in the Gulf of Castellammare, confirmed a non-linear relation between the number of detections (*Nd*) recorded in a fixed time interval (Δt) and the distance between pingers and receivers (D'Anna and Badalamenti, 2003).

In fact, many environmental factors can strongly affect the *Nd*-distance relation, modifying the ultrasonic pulses strength and spreading (Pincock and Voegeli, 1990). Within a receivers array, the acoustic wave from transmitter creates different lines-of-sight for each receiver. Each line-of-sight could be differently affected by the intensity of single factors (i.e. water flow, submerged vegetation, presence of a fish shoal or artificial structures). As a consequence, two hydrophones would record different *Nd* values even if the pinger was located at the same distance from them. In this case, assuming a linear relation between *Nd* and distance, those values will correspond to different distances and their weight in the calculation algorithm will reduce the positional estimates accuracy. For this reason, we adopted the arithmetic mean *sensu* Simpfendorfer (2002) to calculate the pinger's geographic location but we applied a modification to the number of detections based on our *Nd* variability study. The main advantage is that different *Nd* values that are included in the same distance group are replaced by the *Nd* mean value of that group so that they have the same weight in the calculation algorithm. This finding represents a new approach in calculating the geographical coordinates of pinger positions taking into account the variability in the number of detection due to environmental factors effect.

The recognition of the importance of a correct receiver arrangement throughout the study area and of the resulting effects on the power of any telemetric system, has been highlighted by many authors (Stasko and Pincock, 1977; Lagardère *et al*., 1996; Braun *et al*., 1997; Simpfendorfer *et al*., 2002). The first application of a specific receiver placement design was based on the overlap between two receivers (Arendt *et al*., 2001). The authors created two reception zones, one for each receiver and a third common reception zone resulting from the overlap of the two receivers. Tagged animals were located by the receiver(s) that could detect any single pinger signal. This receiver arrangement contributed in reducing the area where the animal could be located.

The optimal receiver arrangement will vary depending on environmental characteristics of the study area and on the objective of research. In our case, with the presence due to artificial structures, increasing habitat complexity was likely to affect signal detection (McLeave, 1978; Matthews *et al*., 1990; Pincock and Voegeli, 1990; Smith *et al*., 1998). Our receiver placement design created seventeen overlap regions. This allowed us to locate pingers throughout the whole study area and, above all, to evaluate how Pe can be reduced through the increase of the number of overlapping receivers. In fact, in a region with five overlapping receivers, Pe was less than 85 percent when compared to Pe calculated in regions with only two overlapping receivers. The high values of Pe estimated in regions with two overlapping receivers (Pe=269 m) is due to a limit of the algorithm. In fact, the mean-position estimates always fall within the minimum convex polygon (MCP) described by the receivers location (Simpfendorfer *et al*., 2002). Thus, if we deploy a pinger outside the MCP, as in the case of our experiment (Fig. 3), the algorithm will locate it as if it was inside the MCP. This increases both the mean and the standard deviation values of Pe.

Another advantage of our receiver arrangement is that the AR area coincides with the region of highest overlap (four and five receivers, see Fig. 3). Our tests, conducted in the AR area, demonstrated that it is unlikely to detect pingers placed inside a pyramid. The limitations of such a system to detect signals, when the pinger is placed directly inside a physical structure, has been documented by other authors in previous studies (Matthews *et al*., 1990; Collins *et al*., 2000; Smith *et al*., 2000; Connolly *et al*., 2002). Nevertheless, when the pinger was placed 1 m outside the pyramid, its geographic location was calculated with Pe=132±54 m. This value decreased significantly to 54±24 m when the pinger was placed at least 10 m away from any artificial structure. The difference between these Pe values (78 m) can be named as the "barrier effect" of artificial structures.

The results of this demonstrative study can represent the base for future long-term research on fish activity patterns, home-range, and their use of artificial structures. The correct arrangement of high-overlap-based receivers, the temporal sequence of locations and the knowledge of positioning error estimates, could be helpful in discriminating different positions of tagged animals: (i) inside/outside the AR area, (ii) inside/near/outside a single structure. All this information could also contribute to better understand the role and the efficacy of artificial habitats.

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A brief discussion on the 2% tag/bodymass rule of thumb

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Key words: telemetry, tag weight, buoyancy, adverse effects.

Abstract

In the past two decades the number of researchers using biotelemetry to examine fish behaviour and survival has increased considerably. Associated with this has been a significant amount of literature on the effects of the transmitters on the measures under consideration. Despite this, some researchers still rely on a general rule of thumb, "the 2% rule", to indicate that the tagging protocol did not affect the results of a study. While it is clearly important to minimise the size of a transmitter and disturbance to a fish, such a general rule does little to advance our understanding of tag effects and may even hamper our ability to effectively study fish behaviour. This note will focus on the size specific effects of tags on fish and presents some recent results along with suggestions for future evaluations. We conclude that there is no generally applicable 'rule' for tag/fish size relationship and that the appropriate maximum relationship is driven by the specific study objectives, the tagging method and the species/life stage involved.

Introduction

In the book "Fisheries Techniques" published by American Fisheries Society (AFS) in 1983, and again in the 2nd edition (1996), J.D.Winter recommended that "Fish generally should not be equipped with transmitters that weigh more than 1.25% in water or 2% in air of the fish's weight out of water". Despite the fact that it was meant as a "rule-of-thumb", the recommendation has been widely accepted and used to validate many studies where it is often referred to as the "2% rule". Despite recent recommendations to abandon such a general rule (Brown *et al.*, 1999; Jepsen *et al.*, 2002), papers are still published in which the authors have not evaluated the effects of electronic tags on the fish, but merely state that they complied with the "2% rule".

We emphasise the need to avoid such a general statement and encourage researchers to be more proactive in establishing appropriate tag to body mass relationships. In the absence of information indicating the appropriateness of tag to body mass relationships it is incumbent on the authors to indicate that the potential effects of transmitters on fish performance are unknown. In this paper we present arguments and evidence against applying one general rule to fish of different species. When considering a tagging protocol, there are several factors that directly affect the performance of a fish, including tag weight in water (excess mass), tag volume, tag position and tag dimensions. Often overlooked, but just as important to consider, is the length and mass of an antenna and the antenna material (Cooke and Bunt, 2001). Equally important is the nature of the question being asked. The consequence of a large tag to a fish may be very different for studies that examine long term migrations (weeks), versus those that are only concerned with movement patterns over a 1-2 day period versus studies on survival or foraging behaviour. As an analogy, we might consider that a 20 kg backpack would considerably affect the performance of an Olympic sprinter, whereas the effect would be almost negligible to a person hiking 12 km on a mountain trail. It is also of importance where the tag is placed in or on the fish. Usually external tags are positioned further from the centre of balance of the fish than internal tags. Thus, external attachment can have additional effects on the balance and hydraulic properties of the fish. We argue that the appropriate tag mass to body mass ratios are relative to the specific objectives of each study and often tag volume, placement, dimensions or the presence of an antenna is more of a limiting factor than tag mass. This paper is not meant to be presenting a review of studies dealing with effects of tagging, but merely as a current comment to the discussion about tag/bodymass ratios. For a comprehensive and recent review of tagging procedures and effects, Thorsteinsson (2002) is recommended.

Tag/bodymass

While studies have shown adverse effects on fish tagged with transmitters heavier than 2% of their bodymass (McCleave and Stred, 1975; Ross and McCormick, 1981; Marty and Summerfelt, 1986; Eiler, 1990; Adams *et al*., 1998; Lefrancois *et al*., 2001), it is clear that there are many exceptions. For example, the swimming performance of rainbow trout (*Oncorhynchus mykiss*) smolts with tags of 6–12% tag/bm ratio (mass of the tag as a percentage of the fish's body mass) was not significantly impaired (Brown *et al*., 1999). In a study of Chinook salmon (*Oncorhynchus tshawytscha*) smolts tagged with 2.6-g dummy transmitters, most fish were well below the 2%ratio, but for some small (<50 g) individuals, the tag/bm ratio exceeded 5% (Jepsen *et al*., 2001). When physiological indices of stress were regressed against tag/bm ratios, no relationship was apparent 1, 7 or 21 days after tagging. The results of field studies suggest that in many cases tag size does not alter the behaviours under consideration. A comparison of recent data from the Columbia River (Schreck *et al*., 2001; 2002) with that of Ledgerwood *et al.* (2000; 2001), indicates that radio-tagged (2-10% tag/bm ratio) and PIT tagged (<1% tag/bm ratio) steelhead (*O. mykiss*) and fall Chinook salmon migrate at the same rate in the Columbia River between Bonneville Dam and the estuary (~180 km). This suggests that there is no compromise in the long term swimming performance of radio tagged fish. Similarly, the estimates of avian predation on the radio tagged smolts (Schreck *et al*., 2001; 2002) and PIT tagged smolts (Ryan *et al*., 2003) in the Columbia River are surprisingly similar, suggesting that the extra size and weight of the radio tag has little effect on predator avoidance.

In another study (Clements and Schreck, 2002), analysis of the effect of the tag size on the survival of hatchery-reared coho salmon (*O. kisutch*) suggests that there was no relationship between tag size and mortality. For fish that were implanted with radio transmitters the mean tag/bm ratio was 2.4±0.1% (mean ± s.e.) both for fish that were assumed to have survived and fish (transmitters) that were detected following predation by cormorants. Similarly, coho salmon were implanted with acoustic transmitters and the fish that were assumed to have survived had a mean tag/bm ratio of 9.2±0.4%, not significantly different for coho salmon that were assumed to have died due to predation (8.2±1.1%). In addition, the estimated estuarine mortality for fish tagged with the larger acoustic tag (70%) was almost identical to that for fish tagged with a radio tag (64%), suggesting that the size of the transmitter had a minimal and not statistically significant effect on predation (Clements and Schreck, 2002).

Few studies have systematically investigated the effects of different tag/bm ratios, and recommendations on maximum ratios often seem to be unfounded statements. Besides stress and growth, tag mass may influence buoyancy, equilibrium, swimming performance, feeding, wound healing, social rank and the propensity of fish to expel tags. Thus, to be able to put forward credible recommendations of tag mass to fish body mass ratios, effects of different ratios on all such characteristics of the fish may be necessary, depending on the objectives and duration of the study. Furthermore, it must be considered that the effects of different tag/bm ratios may depend on species, life stage, fish size, sex, general health of the fish, water temperature, water quality, habitat and tag attachment method.

Many researchers have found that the morphology of a fish species can be the limiting factor for tag size. In regards to internal tagging, this is the case for fish species with an elongated body form, such as eels, or vertically or laterally compressed fishes such as flatfishes or angelfish, where there is very little room in the body cavity. In predatory fish, the body cavity is usually larger and the body wall is more flexible than in omnivorous or planktivorous species (Jepsen *et al.*, 2002). For external tagging, it is important that the tag is not causing permanent postural disequilibrium and consequently irregular swimming (Thorsteinsson, 2002). For fast swimming species, the drag resistance of external tags can lead to reduced swimming ability, depending on the size, position and shape of the tag. Thus, fish morphology is important in determining the possible effects of tagging. For a number of species, tag volume and shape more than the tag/bm ratio limits the tag size. In these cases compliance with a tag/bm ratio of 2 % would be of little value in ensuring a minimal impact of the transmitter to the fish.

In cases when the transmitter can be placed internally or externally in a reasonable manner related to the morphology of the fish, the effect of the transmitter on buoyancy must still be considered. The transmitter will affect the buoyancy of the fish, and the ability of the fish to compensate for the additional mass is important for the discussion of maximum tag/bm ratios. Some fish, typically those associated with the substrate, are negatively buoyant while others have buoyancy aids such as oils, watery tissues and poorly ossified skeletons or swim bladders that match their densities to the water (McNeill, 1993). Many pelagic fish maintain a minimum forward cruising speed to generate enough lift to prevent sinking, for example elasmobranchs, scombrids and thunnids (e.g. Jobling, 1995). Most teleosts possess gas-filled swim bladders. In general, the swim bladder is approximately 5% of the volume of marine fishes, and approximately 7% in freshwater fishes, providing enough lift for neutral buoyancy. A fish with a gas-filled swim bladder can remain neutrally buoyant at different depths by secretion or absorption of gas to keep the swim bladder at constant volume as the ambient pressure changes (McNeill, 1993). In more primitive fish (such as salmonids and anguillids), the connection between the swim bladder and gut is retained as an open tube, and the fish are able to take in air at the surface and to vent it as they ascend upwards in the water column (physostomatous fish) (e.g. Bone and Marshall, 1982). The great majority of teleosts lose this open connection at early life stages, and the adult swim bladder is entirely closed (physoclistous fish). The swim bladder is filled either before the connection is lost, or by secretion of gas from special cells in its wall, a process that requires some time. While physostomatous fish may be neutrally buoyant most of the time, recent research suggests that most physoclistous fish are negatively buoyant much of the time (Arnold and Greer Walker, 1992), thus allowing for vertical migrations that would be impossible if the fish had to remain neutrally buoyant at all depths.

A neutrally buoyant tag can be made by increasing tag size or decreasing the density of components. Some neutrally buoyant archival tags are produced (Star-Oddi) and it would be very interesting to test the performance of fish tagged with such tags. Usually, tag size rather than mass is minimised and, thus, the tag represents additional weight in water which will affect the buoyancy of the fish. Perry *et al.* (2001) studied the buoyancy compensation of Chinook salmon smolts tagged with surgically implanted dummy tags. The results showed that even fish with a tag representing 10% of the body mass were able to compensate for the transmitter by filling their swim bladders, but the following increase in air bladder volume affected the ability of the fish to adjust buoyancy to changes in pressure. If a surgically implanted tag fills up a substantial part of the body cavity of a physostomatous fish, the fish may not be able to compensate, because there is simply not room enough for expansion of the swim bladder.

In a study of sea bass (*Dicentrarchus labrax*), Lefrancois *et al.* (2001) concluded that there is a certain threshold tag/bm ratio where the energy demand of a tagged fish increases rapidly. In this case fish with “tag weight in water/fish body-weight ratio” of 0 and 1% did not significantly increase metabolic oxygen demand, but when this ratio was increased to 4%, the fish had to use 28% of their total usable power to maintain buoyancy.

In fish that are naturally negatively buoyant, such as mackerels and tunas, part of the energy expended in swimming is used to provide hydrodynamic lift in order to keep the body from sinking (Jobling, 1995). This lift increases by increased swimming speed, and additional mass by a tag may thus necessitate an increase in the swimming speed. Arnold and Holford (1978) suggested that for plaice (*Pleuronectes platessa*), that have no swimbladder and are negatively buoyant, the additional mass of a tag will lower the energy expenditure by holding station on the bottom in a current of a given speed and also result in a reduction of work against the lift force exerted by the current. The addition of the tag could thus benefit a plaice opposing a current on the sea bed.

In conclusion, the buoyancy regulating mechanisms of the fish determines the ability of the fish to adjust for the additional mass of a transmitter, and thus also the maximum size of transmitter that can be used for that fish. Physostomatous fish can regain buoyancy relatively fast by gulping air at the surface. The time until buoyancy is regained depends on the fish size, transmitter mass, physiology of the fish, water temperature and the depth the fish is held at. In order to judge the possible effects of the tags on buoyancy of the fish, and consequently on factors like behaviour, energy expenditure and growth, the weight of the tag in both air and water should be given.

Conclusion

There is no generally applicable "rule" for tag/fish size relationship and the appropriate maximum relationship is governed by the specific study objectives and the species/life stage involved. Thus, we recommend that all studies involving telemetric tags should include some kind of evaluation of tagging effects, preferably systematic investigations like the studies of Moore *et al.* (1990) and Peake *et al.* (1997). When laboratory studies that show little or no effect on the fish by the tag, caution must still be taken when evaluating the results of field studies as differences in environmental conditions and/or fish condition at tagging may lead to significant changes in behaviour and/or survival. It is important that the effects studied are relevant for the objectives/conclusions of a study – a study of swimming capacity or feeding cannot be used to draw conclusions about effects on growth or survival. An alternative method of validation is to compare the results from multiple simultaneous studies using different methods to monitor fish behaviour or comparing the results within one study: is the behaviour significantly different the first hours or days after tagging than later in the study? This may also give information on the duration of the tagging effects and on which results should be excluded from the data analyses. As it may be impossible to distinguish between the combined effects of capture, handling and tagging and the effect of tagging alone, details of capture methods must be provided. It is insufficient to assume that a tag/bm ratio of 2% is appropriate. Although numerous studies have examined tag effects (mainly on salmonids), there remain many avenues for research into the behavioural effects associated with tagging, as well as the role of the environment and fish condition at the time of tagging. Such studies are essential before it is possible to systematise information and state more general recommendations about maximum tag size for different fish species under various conditions.

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A new pass-through PIT tag detection system for marine use

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Key words: PIT tag, detector antenna, tag-recapture, trawl, cod

Abstract

In order to study the frequency of passages of juvenile fish through a trawl in areas of high fishing intensity, an underwater detector system for marine use of PIT tags was built. The system consisted of a cylindrical antenna coil with an inner diameter of 40 cm, connected to an underwater bottle (housing) that contained a battery, a detector board and a pocket PC for data logging. The system was built to operate at depths down to 500 metres. The system was been extensively tested in the laboratory and in a small-scale field experiment. One hundred per cent detection success was achieved with two groups, each of 10 juvenile cod (*Gadus morhua* L., 1758), where the tags had been injected into the dorsal musculature and abdominal cavity respectively. The detector was later used in a pilot study in which 329 cod were caught, tagged with PIT tags and Floy tags and subsequently released at the same location where they had been captured. The detector was mounted onto the open codend of a trawl and the area intensively fished. The 16 hauls taken swept 30% of the study area. Three tagged fish were detected as they passed through the trawl codend. Underwater video observations of fish behaviour directly in front of the antenna were made during four hauls. No fish with external Floy tags were observed on the video recordings, supporting the lack of PIT tag detections during the four tows when the video camera was used. The observed fish swam along the trawl, positioning themselves at a favourable angle for tag detection by the antenna. The recordings did not indicate that fish attempted to avoid passing through the antenna.

Introduction

The management of most commercially exploited fish stocks is based on a harvesting strategy that is designed to minimise the exploitation of juvenile, immature specimens (Gulland, 1977; Halliday and Pinhorn, 2002). This is generally achieved by the use of size-selective gears. The selectivity of trawls has traditionally been regulated by the specification of a minimum legal codend mesh size and during the last decades also by the use of grids, escape windows etc. A prerequisite for the efficacy of such technical devices is that the fish that escape through the meshes or other selective devices should survive. Published studies on the survival of cod indicate generally high survival rates for escaping fish of this species (DeAlteris and Reifsteck, 1993; Soldal *et al*., 1993). However, on intensively fished grounds, fishermen claim that multiple passages of fish through the meshes of the codend or through other size selective devices result in higher mortality rates than have been observed in the survival experiments. Visual observations of the capture process have shown that fish accumulate just ahead of the trawl opening. Some make escape attempts above or below the trawl, while the remainder swim with the trawl just ahead of the ground rope, where they maintain station until they tire and drop back into the body of the trawl (Main and Sangster, 1981). It is thus likely that fish that reach the extension/codend of a trawl are completely exhausted. If such fish manage to escape, it is likely that they will need a long period of time to recover physiologically. Should they be exposed to another trawl shortly after escaping, the added stress of a new escape response may severely affect their survival after being excluded, for example by a sorting grid. Moreover, fish that have been caught by the trawl but manage to escape through the meshes of the codend or through the bars of a sorting grid always run the risk of being injured, e.g. by scale loss (Chopin and Arimoto, 1995). This risk increases with each capture/escape episode.

A project to study the effect of multiple capture/escape episodes on the subsequent survival of fish escapees from towed gears began in 2000. The study required a methodology that enabled the number of passages of individual fish through the trawl to be monitored. The solution put forward was to apply the passive integrated transponder (PIT) technology that has been successfully used for individual tagging of juvenile salmonids (Prentice *et al*., 1990). PIT tag monitoring systems have been installed in hydroelectric dams and fish hatcheries (Prentice *et al*., 1990) and for deployment in streams (Roussell *et al*., 2000). A wide range of commercially produced antennae was also available. Of special relevance to our study is a detection system built for operation on a specially designed pair trawl in the Columbia River estuary (Ledgerwood *et al*., 2000). The system consisted of a 3-pipe bundle of 27 cm-diameter detection tunnels attached at the codend position of the trawl, and with electronics and power supply housed on a buoyant platform bridled to the surface-floating headline of the trawl.

The mentioned systems were all built for operation in fresh water and at shallow depths. The use of PIT tags for in situ detection of animals in the marine environment has been hampered because the equipment built to work in fresh water does not function in seawater, since the conductivity of seawater is higher than that of fresh water. The magnetic flux through seawater induces eddy currents that oppose the field responsible for their creation (Lenz's law) (Finkenzeller, 2000). This paper gives the design properties of a detector system built for marine applications and the results of tests of detection success. It also presents the results of a small-scale experiment that was intended to determine how often multiple encounters occurred.

Materials and methods

Technical description of detector system

The detector antenna is a multi-turn coil wound onto a 60 cm diameter cylinder made of epoxy and fiberglass. In order to insulate the coil from the seawater an epoxy layer 10 cm thick on the outside and 5 cm on the inside encapsulated the windings, producing a "pass through" cylinder of 50 cm inner diameter (Fig. 1). The length of the cylinder was 30 cm. The weight of the antenna was 95 kg in air, while in seawater it had a positive buoyancy of 13 kg. At each end of the cylinder a flange with a series of 10 mm holes was made for attaching the antenna to the trawl net. The inductance of the coil was 280 μH and a tuning capacitor of 7000 pF was connected in series with the windings. In order to situate the tuning capacitance as close as possible to the windings, a watertight housing was located on the outer surface of the antenna cylinder. A connector for the cable connection between the antenna and the detector board was attached to the lid of the housing. The maximum current in the antenna coil was obtained when the system is tuned to its resonance frequency. When the antenna was totally submerged in seawater the current was reduced by approximately 70% compared to the readings in air. Initial testing showed that the magnetic field still had enough energy to detect most kinds of PIT tags used in fish tagging experiments.

The detector was based on the PE105 transceiver board (Patten Engineering) and a data logging system on a pocket PC (Compaq iPAQ). The pocket PC was connected to the detector via an RS-232 serial cable. The PC and detector board were placed in an anodised aluminium bottle together with two rechargeable batteries. A 15 m long cable with low capacity (59 pFm^{-1}) connects the antenna to the detector board via two Subconn underwater connectors (Fig. 4). Whenever a PIT tag was within detection range of the antenna, the detector board transfered its *id*-code to the logger where the code was displayed and stored together with other information.

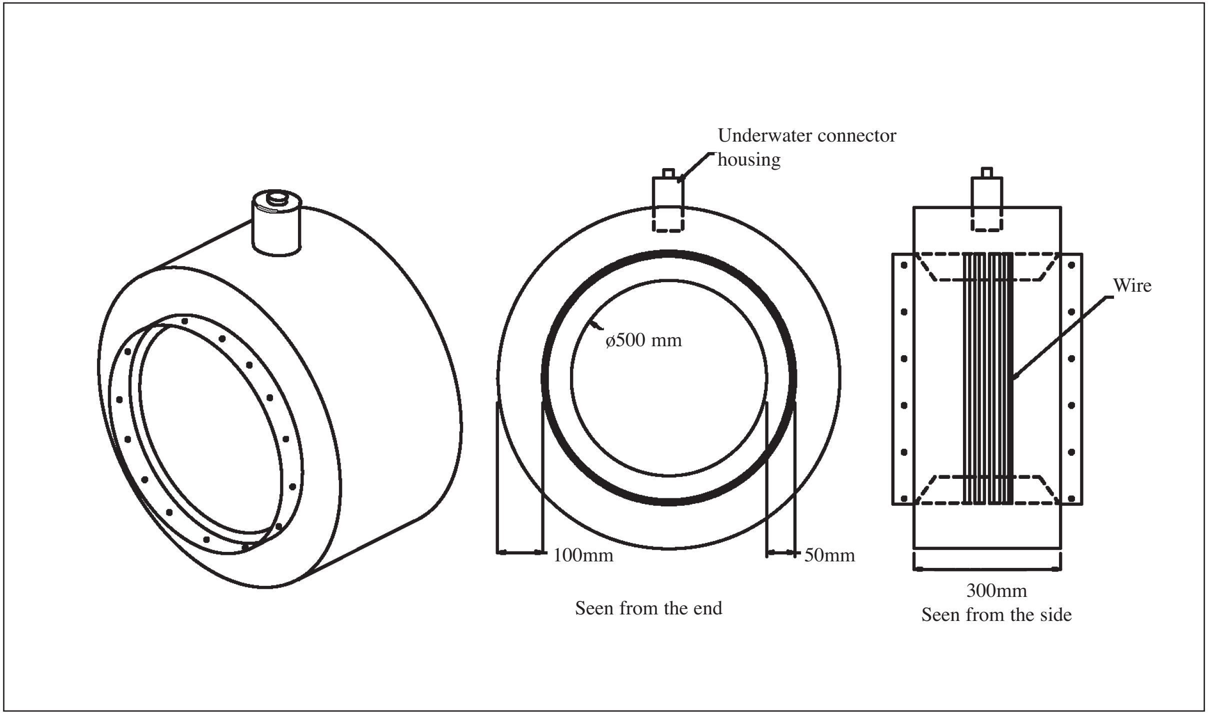

Fig. 1 – Construction drawing of the detector antenna. Note the insulating layers of epoxy on the inside and outside of the windings.

Laboratory tests of tagging procedure and detection success

To estimate tag loss and tagging injury and mortality, a total of 20 cod in the size range 35-40 cm were tagged with Destron TX1415BE tags (23.5x 4mm). The fish were anaesthetised prior to tagging. Ten fish had the tag injected into the dorsal muscle at the base of the first dorsal fin and ten had the tag injected into the abdominal cavity. The tags were injected using the Biomark MK10 injector with a gauge 6 needle. The fish were then transferred to a net cage and kept for 14 days after which they were inspected for tag presence, tag orientation and possible tagging-related injuries.

Tests of detection success were carried out with 35-40 cm cod tagged with TX1400BE (12.5x2 mm), TX1405BE (13.5x2 mm), TX1410BE (20x3 mm) and TX1415BE (23x3.4 mm) tags, all ISO tags operating at 134.2 kHz. The antenna was attached to a cylindrical net section connecting two net cages and the fish were forced to swim from one cage to the other. Trials to monitor detection range and sensitivity to tag orientation were also performed with hand-held tags and tags mounted to sticks or lines.

Field experiment

The field experiment was carried out in the Lyngen Fjord in northern Norway (Fig. 2). In order to facilitate trawling, a flat soft-bottom (clay) area of the fjord was chosen as the experimental site. The site topography and the presence of underwater cables crossing the fjord restricted the experimental site to a 2x1 nautical miles (6.86 km^2) area. The depth was 120 m.

Cod were caught by bottom trawl at the experimental site. On capture, the healthy fish (excluding fish with everted stomachs or otherwise injured by the capture process) were transferred to a net cage where they were kept for approximately one week in order to ensure that only fish that had fully recovered from the capture process were used in

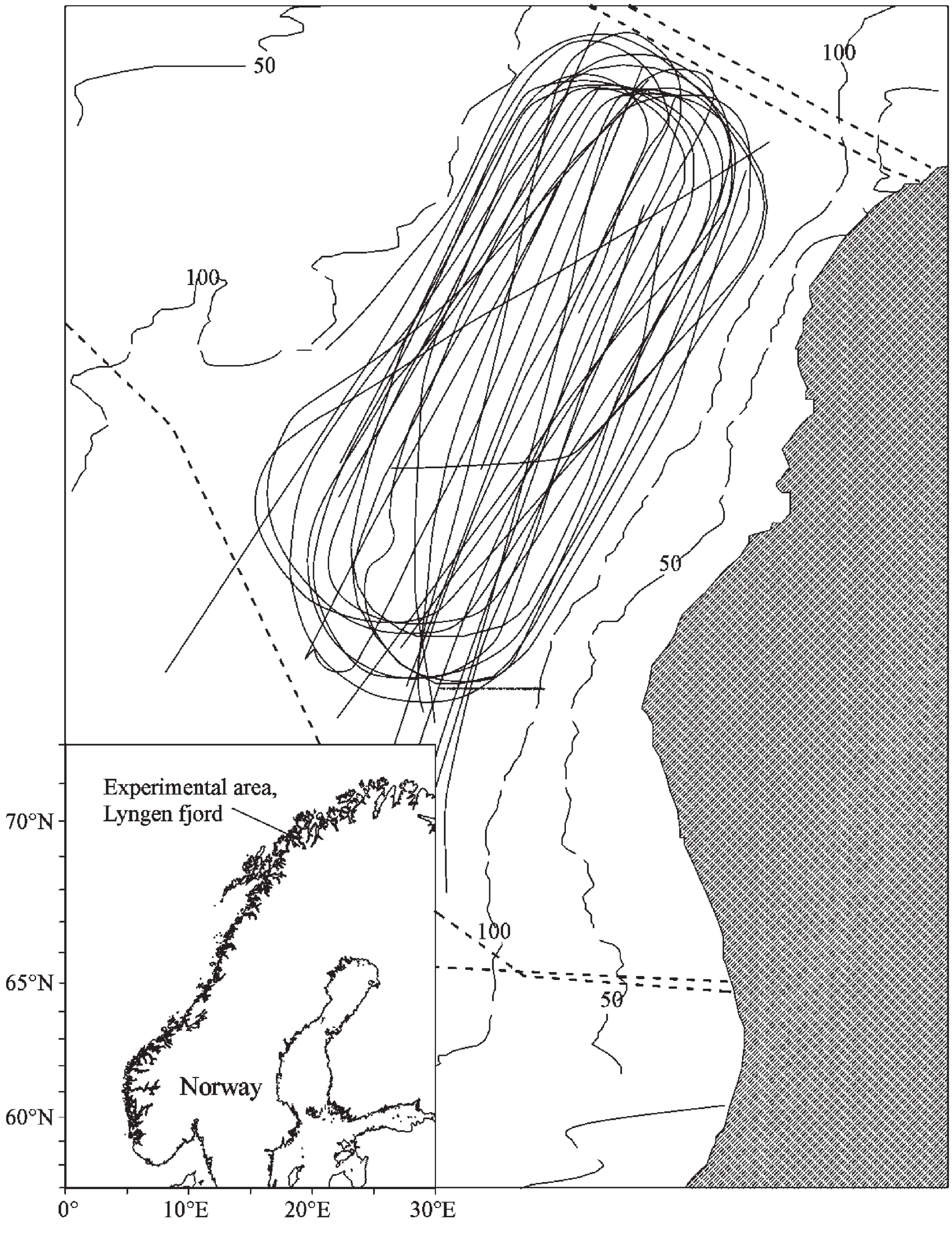

Fig. 2 – The experimental site of the tagging-recapture experiment. The tracks of the 16 recapture hauls are shown. The hatched lines indicate the position of underwater power cables crossing the fjord.

the tag-recapture experiment. A total of 329 cod were tagged, 127 with the Destron TX1410BE tag and the remaining 202 with the Destron TX1415BE. The tags were injected into the dorsal muscle as described above for the laboratory tests. Fish were also tagged with external Floy tags. All tagged fish exhibited normal swimming behaviour and had no external injuries. The tagged fish ranged in size from 29 to 98 cm (Fig. 3). After tagging the tag codes were read using the Destron FS2001-ISO reader kit and the fish were released in the centre of the experimental area.

The bottom trawl used in the experiment had a vertical opening of 7 to 8 m and a door-spread of 55 m, both measured in real time with Scanmar sensors. Towing speed was approximately 2.5 knots (1.29 ms^{-1}). During the recapture experiments, the antenna was mounted at the end of the open codend (Fig. 4). The aluminium cylinder with the detector board, logging unit and battery was attached to the extension, 12 m in front of the antenna. A total of 16 hauls were made with the detector. On four of these hauls (hauls no. 3, 4, 5 and 16), a SIT underwater video camera was used to study the behaviour of fish in front of the antenna and to verify the passage of fish past the antenna. The camera was attached to the inside of the roof of the extension piece, 1.5 m in front of the antenna and was looking towards the antenna. A light tube (11 W) was mounted on starboard side of the camera. The camera and light tube were connected to an aluminium bottle containing a video recorder and power supply (Fig. 4).

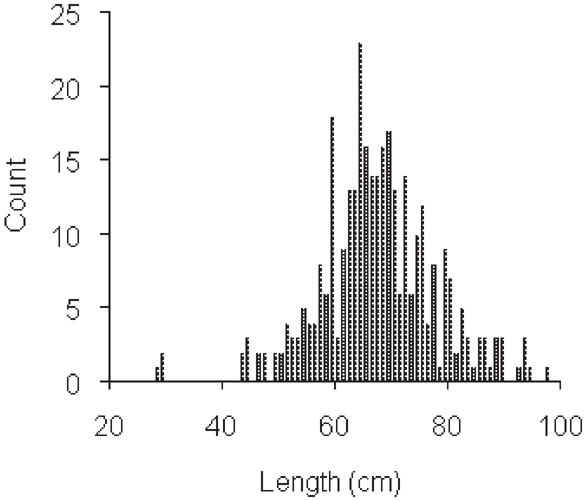

Fig. 3 – Size frequency distribution of the tagged cod.

Results

Laboratory tests of tagging procedure and detection success

No tag loss or mortality was observed for the 20 cod tagged in the laboratory study. The wounds left by the needle used to implant the tags had completely healed by the end of the two-week period in all but one fish. Dissection of the fish after the experiment had finished showed various orientations of the tags injected into the abdominal cavity, although the tags were all injected with the tags parallel to the long axis of the fish. There was no evidence of tag ejection for any of the tagged fish, nor that tags injected into the dorsal musculature had migrated further into the tissue. Three of the tags injected into the body cavity were showing indications of tissue encapsulation.

All tagged fish were successfully detected as they passed through the antenna during the laboratory tests. However, the manual test of the various tag sizes showed that the smaller tags (TX1400BE, TX1405BE) with shorter detection ranges were more likely to escape detection when they passed near the centre line of the antenna and at a large angle (>45 degrees) to the long axis of the detector cylinder.

Field experiment

The tracks of the trawl hauls in the study area are shown in Figure 2. The area swept by the 16 tows corresponds to roughly 30% of the designated study area. A total of three tagged fish were detected during the recapture tows, one fish during each of hauls 1, 8 and 10, respectively. Two of the fish (measuring 52 and 64 cm) were tagged with TX1415BE tags and one (64 cm) with the TX1410BE. The video

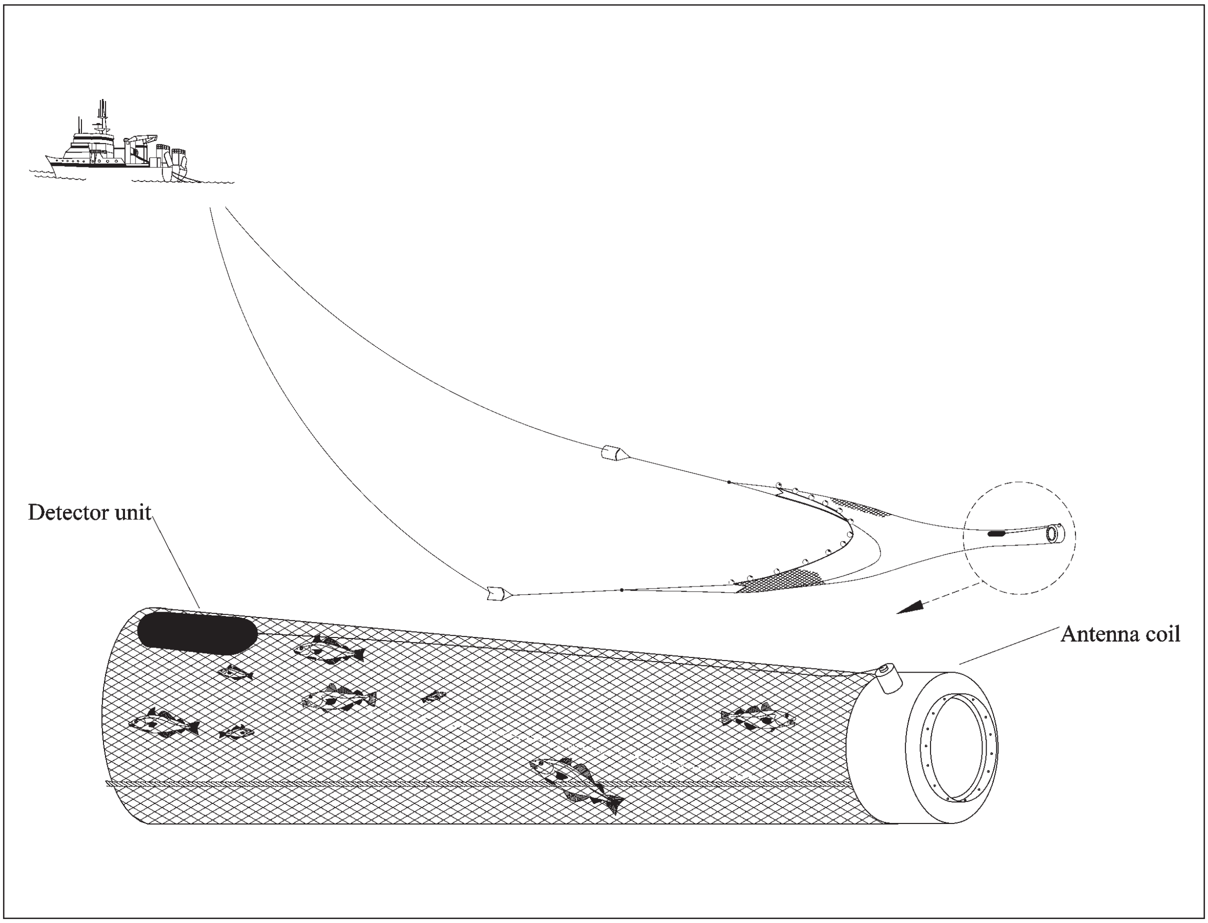

Fig. 4 – Sketch illustrating the mounting of the antenna at the end of an open codend.

recordings during hauls 3, 4, 5 and 16 did not indicate that any fish attempted to avoid passing through the antenna. The fish swam along the trawl, positioning themselves at a favourable angle for detection (i.e. parallel with the long axis of the cylinder). No fish with external Floy tags were observed on the video recordings, supporting the lack of PIT tag detections during the four tows when the video camera was used.

Discussion

The detector system for PIT tag detection in seawater has been successfully tested in both laboratory and field experiments. The antenna was specifically designed for mounting in the extension section of a trawl or at the end of an open codend to study repeated encounters of fish with a trawl on intensively fished grounds. The equipment is also suitable for other tagging-recapture situations, e.g. the monitoring of river/hatchery-tagged salmonids during their marine life stage. The advantage of this method for collecting "recapture" information is that the animal does not need to be brought onboard or even to the surface, thereby reducing recapture mortality to practically nil.

The antenna was built of epoxy, which has four main advantages. It has high electrical resistance, which reduces the occurrence of eddy currents. It also kept the antenna waterproof and extended the operating depth down to 500 m. Near neutral buoyancy in seawater and high mechanical strength improved the handling properties of the antenna and enabled it to be used on board commercial fishing vessels.

The field experiments were performed using the two largest of the four Destron tags tested, the TX1410BE and TX1415BE. The larger tags had a larger ferrite coil, and required less magnetic field strength to operate than the smaller coils. They could therefore be detected at a greater distance from the antenna and were less sensitive to the orientation of the tag than the smaller tags. To improve the detection success of the system, attempts will be made to increase the current throughput of the antenna by modifying the coil specifications. An auto tune option will also be implemented. Further planned improvements include an acoustic link between detector and vessel for real-time registration of detected tags.

No detection will take place if several tags are within detection range of the antenna simultaneously. Interference of the signals from the tags will in such cases result in a signal the detector cannot decode. Theoretically, some tagged fish could therefore avoid detection. However, the proportion of tagged individuals in sampled populations is normally very low, and the probability of simultaneous passages therefore negligible. This technical limitation of the system therefore has no practical consequences in a tag-recapture situation.

The recapture rate (three fish out of 329) in the field experiment was low. Assuming that the fish were uniformly distributed across the study area and accessible for capture by the bottom trawl, the expected number of recaptures would be 104. We speculate that some of the tagged fish may gradually have moved out of the study area due to the disturbance caused by the intensive trawling or moved up into the water column above the influence of the headline. However, this could not be verified as the ship was not equipped with a pelagic trawl and sampling outside the study area was prohibited because of electrical powercables crossing the fjord and by non-trawlable bottom (Fig. 2).

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Comparison of acoustic and PIT tagged juvenile Chinook, Steelhead and Sockeye Salmon (*Oncorhynchus*, spp.) passing dams on the Columbia River, USA

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Key words: acoustic tags, PIT tags, fish behaviour, fish movement, salmon smolt survival.

Abstract

The purpose of the study was to compare migration behaviour and survival of acoustic and passive integrated transponder (PIT) tagged juvenile salmonids passing dams on the Columbia River, Washington State, USA. Downstream migrating yearling chinook (*Oncorhynchus tshawytscha* Walbaum 1792), steelhead (*Oncorhynchus mykiss* Walbaum 1792), sockeye (*Oncorhynchus nerka* Walbaum 1792), and sub-yearling chinook smolts were individually implanted with either acoustic or PIT tags and monitored at Rocky Reach and Rock Island dams during spring and summer 2002. Travel times and detection rates were compared for acoustic ("A" tag weight 1.0 g and "E" tag weight 1.5 g) and PIT (tag weight 0.06 g) tagged fish released upstream of Rocky Reach Dam and detected at a Surface Collector Bypass Channel and further downstream at the Rock Island Dam project. Surface Collector Bypass Channel efficiencies were very similar for acoustic and PIT tagged fish. Surface Collector Bypass Channel efficiency and harmonic mean travel times for acoustic and PIT tagged smolts, for three different species and two year classes of chinook smolts, were not significantly different ($p>0.05$) for 13 of 16 comparisons. There were no significant differences between the four comparisons of 1.0 g and 1.5 g acoustic tagged steelhead smolts. Rock Island Dam project survival for PIT tagged ($\hat{S}_{RI} = 0.9555$, $\hat{S}E = 0.0249$) and acoustic tagged ($\hat{S}_{RI} = 0.9520$, $\hat{S}E = 0.0263$) yearling chinook smolts was not significantly different ($p>0.05$). The acoustic tag survival study required far fewer fish (798) than the PIT tagged survival study (90,000).

Introduction

Migrating juvenile salmon and steelhead (*Oncorhynchus* spp.) runs on the Columbia River (Washington State, USA) and its tributaries have been evaluated using passive integrated transponder (PIT) telemetry techniques over the past 20 years (Prentice *et al.*, 1990). PIT tags have been used to study survival, passage route determination, travel time, and smolt behaviour (Muir *et al.*, 2001). The results from these PIT telemetry studies are widely accepted and utilized by fisheries agencies and project managers for making smolt passage decisions. One limitation of PIT tag technology is that detection range of PIT tagged fish is approximately 0.30-0.61 m, and for this reason, PIT tag detectors are primarily installed in relatively small bypass pipes and fish ladders.

Acoustic tags have been used recently to study the behaviour and passage routes of migrating juvenile salmon and steelhead (Steig, 2000; Steig and Timko, 2000). Acoustic tags have the advantage that they can be detected over long ranges (up to 900 m) and detection rates are much higher than for PIT tagged fish, thereby reducing the total number of fish required for tagging. In addition, the three-dimension position of acoustically tagged fish can be determined (Ehrenberg and Steig, 2002; 2003). One major difference is that acoustic smolt tags are heavier than PIT tags (0.75-1.5 g in air versus 0.06 g for PIT tags).

Acoustic tags have been used to monitor fish movement for over 50 years (Steig, 2000; Ehrenberg and Steig, 2002). PIT tags have been used extensively since 1996 to determine information about salmon smolts passing Rocky Reach Dam in the mid-Columbia River in central Washington, USA and have been used to estimate proportion of fish bypassed with in-turbine diversion screens and passed through the Surface Collector Bypass Channel. PIT tags have also been used since 1998 to estimate the survival of fish passing through the mid-Columbia River dams, including Rocky Reach and Rock Island dams.

In 2002, studies were conducted to compare behaviour and survival of smolts implanted with acoustic and PIT tags during their outmigration past Rock Reach and Rock Island dams (Fig. 1). Species studied were yearling chinook, steelhead, sockeye, and sub-yearling chinook smolts. Comparisons were made of the travel times and detection rates of acoustic and PIT tagged fish released 40 km upstream of Rocky Reach Dam and detected at the Surface Collector Bypass Channel at the dam (Skalski and Ngouenet, 2002; Steig *et al*., 2003). In addition, comparisons of smolt survival from the tailrace of Rocky Reach Dam to the tailrace of Rock Island Dam (referred to as "Rock Island Dam project survival") were made for PIT tagged and acoustic tagged yearling chinook salmon smolts using a paired release-recapture study (Skalski *et al*., 2003) (Fig. 1).

Reports concerning use of acoustic tags with juvenile Pacific salmon are rare, several studies have investigated use of acoustic tags with juvenile

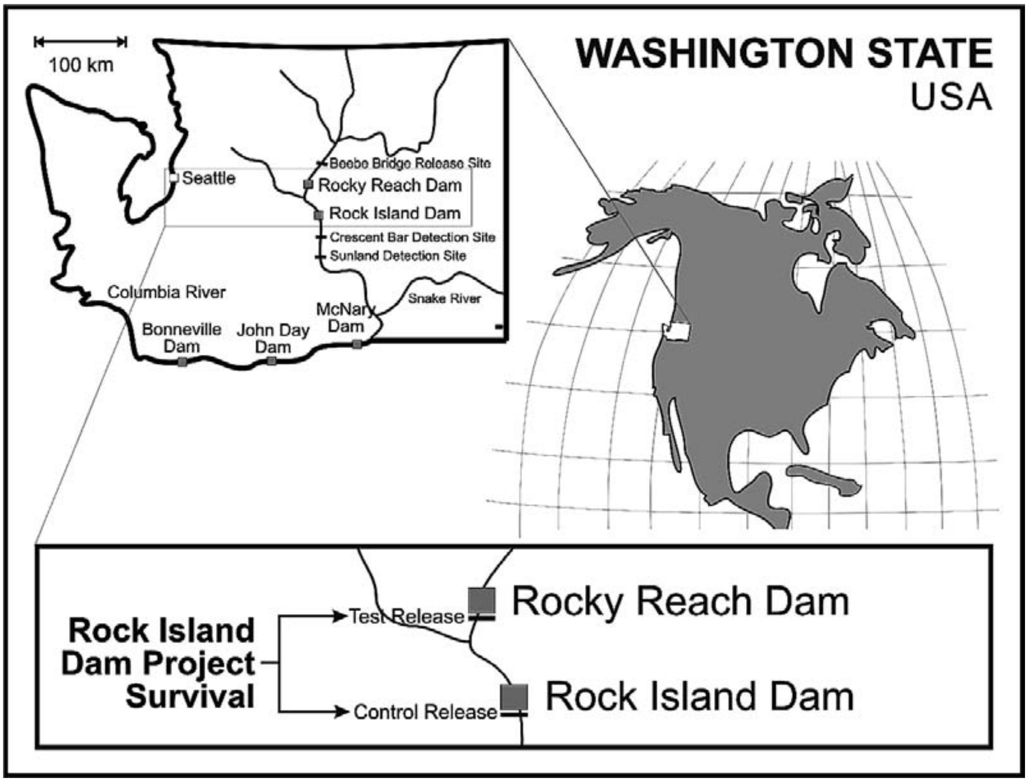


Fig. 1 – Location of release and detection sites on the Columbia River in Washington State, USA. Insert map of the mid-Columbia River basin shows the section of the river evaluated for yearling chinook smolt Rock Island Dam project survival study in 2002.

Atlantic salmon smolts (*S. salar*). Saddle tags significantly affected growth of fish <180 mm in length (Greenstreet and Morgan, 1989). McLeave and Stred (1975) found that both external tags and stomach-borne transmitters significantly reduced swimming speeds of Atlantic salmon smolts, but reduction was far less with internal tags. Surgically implanted tags showed no affect on smolts >120 mm and <190 mm in length (Moore *et al*., 1990). A recent assessment indicated it was feasible to use acoustic tags for three-dimensional positioning of Pacific salmon smolts at Lower Granite Dam (Steig and Timko, 2001). Anglea *et al*. (2004) conducted an investigation to compare the behavioural effects between fish implanted with 1.5 g "E" acoustic tags (up to 6.7% of the fish's body weight) and control fish. Implantation of acoustic tags in juvenile chinook salmon did not significantly affect swimming performance and did not result in greater predation susceptibility than to untagged fish.

Materials and methods

Study site

Rocky Reach Dam is located on the Columbia River, 11 km north of Wenatchee, Washington at river km 764 (Fig. 1). The dam's spillway is perpendicular and its powerhouse parallel to river flow (Fig. 2). During the 2002 Rocky Reach Dam behaviour study, PIT and acoustic tagged fish were released 40 river km upstream at Beebe Bridge (river km 803), in the center of the river. The Surface Collector Bypass Channel at Rocky Reach Dam was instrumented with four, 61 cm diameter circular coil PIT tag detectors spaced approximately 1.2 m apart. Similarly, the Surface Collector Bypass Channel was also instrumented with six acoustic tag hydrophones.

Rock Island Dam is located on the Columbia River at river km 729, 24 km southeast of Wenatchee, Washington and 35 km downstream of Rocky Reach Dam (Fig. 1). During the 2002 Rock Island Dam project survival study, PIT and acoustic tagged fish were released in the tailraces of Rocky Reach and Rock Island dams, in the center of the river. The PIT tagged fish were detected at juvenile collection facilities at McNary, John Day, and Bonneville dams, 262, 384, and 495 km downstream of Rock Island Dam, respectively that were instrumented with PIT tag detectors (Fig. 1). There were two downstream open river acoustic tag sampling sites located at Crescent Bar and Sunland Estates (Fig. 1). An array of evenly spaced hydrophones was placed in a straight line across the river at Crescent Bar and Sunland Estates used five and six hydrophones, respectively. A small trailer on the shore of the river at both detection sites housed the acoustic receivers.

Tagging

HTI *Model 795 Acoustic Tags* used during this study were 307 kHz encapsulated omni-directional pingers. The "E" tags were 20 mm long, 6.6 mm in diameter, and the weight in air was 1.5 g and 0.95 g in water. The in-water weight is important because that is the extra weight expressed by the tagged fish. The "A" tags were 17 mm long, 6.6 mm in diameter and the weight in air was 1.0 g and 0.55 gm in water. The only difference is that "A" tags are smaller and lighter than the "E" tags. Transmit power level for both the "A" and "E" tags were approximately 155 dB μPa @ 1 m. The acoustic tag pulse rates and pulse widths were programmable. The tags used in the 2002 study utilized standard CW pulses. Nominal pulse rate was 3.5-6.0 sec/pulse with a transmit pulse width of 0.5 msec. The useful life of the tag, once activated, averaged 28 days for the "E" tags and 14 days for the "A" tags.

PIT tags utilized in this study operated at a frequency of 134.2 kHz and were suitable for use with circular 30.5 cm and 61.0 cm diameter PIT tag detectors. PIT tags were 11.5 mm long, 2.1 mm in diameter and weighed approximately 0.06 g. The PIT tags had an operating temperature range of -40 to 70° C.

Fish handling procedures for the 2002 study were consistent with protocols used during the 1999, 2000, and 2001 juvenile survival evaluations. Fish selected for tagging were yearling and sub-yearling chinook (*Oncorhynchus tshawytscha*), steelhead (*Oncorhynchus mykiss*), and sockeye smolts

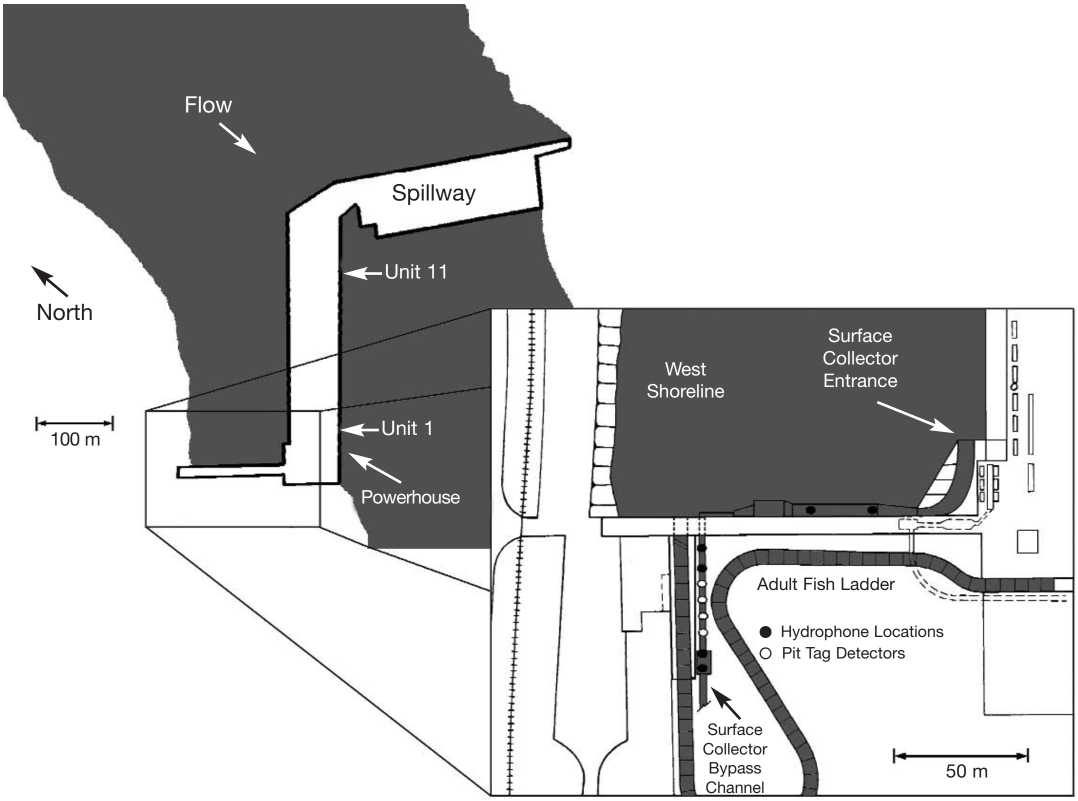


Fig. 2 – Plan view showing the orientation of Rocky Reach Dam on the Columbia River. The expanded plan view shows the hydrophone mounting locations and PIT tag detectors at the Surface Collector Bypass Channel at Rocky Reach Dam in 2002.

(*Oncorhynchus nerka*). Fish were collected from the Rocky Reach Dam Surface Collector Bypass Channel for the behavioural study and from the Turtle Rock Hatchery Facility for the survival study. Fish collected at the Surface Collector Bypass Channel were a combination of hatchery fish stocks (yearling chinook and steelhead) and natural fish stocks (yearling and sub-yearling chinook, steelhead, and sockeye). The fish were collected and transported to the tagging sites at both dams. Throughout the transport, dissolved oxygen levels were monitored and maintained between 7 and 12 ppm. Fish were held overnight after collection for recovery from handling stress prior to tagging. Fish were transferred from the holding tank to a tank containing a 100 mgl^{-1} solution of MS222. Fish were then placed into a V-shaped cradle and swabbed with iodine at the incision site. Acoustic tags were implanted through a 1 cm incision between the pectoral and pelvic fins, slightly off the mid-ventral line. The incision was closed with 2-3 internally knotted sutures followed by another application of iodine at the incision. Fish were placed into a recovery bucket prior to being returned to the holding tanks. PIT tags were implanted into the fish using standard methods as described by Prentice *et al*. (1990). All acoustic and PIT tagged fish were held together in 275-gallon tanks and supplied with fresh, de-nitrified river water throughout the holding period. All tagged fish were held up to 48 h prior to release to ensure fish survival, tag operation, and tag retention.

The acoustic receiver used for this study was the HTI *Model 290 Acoustic Tag Receiver;* designed to receive signals from up to 16 separate hydrophones. Signals received were synchronized in order to determine time of arrival for each detected pulse. Arrival time of the pulse at each hydrophone was used to determine the relative position of the tagged fish between hydrophones.

Rocky Reach Dam Behavioural Study

The Rocky Reach Dam behavioural study allowed for direct comparison between PIT-tagged fish and the two acoustic type tagged fish, since the Surface Collector Bypass Channel was equipped with both PIT tag detectors and acoustic tag hydrophones. Each tag type was tested for equal harmonic mean travel times. The mean travel time was computed using the harmonic mean ($\bar{t}_H$) calculated as follows:

$$\bar{t}_H = \frac{1}{\frac{1}{n}\sum_{i=1}^{n}\frac{1}{t_i}} = \frac{n}{\sum_{i=1}^{n}\frac{1}{t_i}} \qquad (1)$$

where

t_i=travel time from release to Rocky Reach Dam for the *i*th smolt recovered (i=1,...,n).

The variance for the harmonic mean travel time can be estimated by

$$\hat{Var}(\bar{t}_H) = \frac{\left(\frac{s^2_{1/t}}{n}\right)}{\left(\frac{1}{n}\sum_{i=1}^{n}\frac{1}{t_i}\right)^4} \qquad (2)$$

where

$$s^2_{1/t} = \frac{\sum_{i=1}^{n}\left(\frac{1}{t_i}-\hat{u}_{1/t}\right)}{(n-1)}, \qquad (3)$$

$$\hat{u}_{1/t} = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{t_i} \qquad (4)$$

Asymptotic (1-α) 100% confidence interval for harmonic mean travel time was computed as:

$$\bar{t}_H \pm Z_{1-\frac{\alpha}{2}}\sqrt{\hat{Var}(\bar{t}_H)} \qquad (5)$$

for both PIT and acoustic tagged smolts.

The statistical test of equal mean travel times for both tag types was performed using the Z-test of the form:

$$Z = \frac{\bar{t}_{H-PIT} - \bar{t}_{H-AT}}{\sqrt{\hat{Var}(\bar{t}_{H-PIT}) + \hat{Var}(\bar{t}_{H-AT})}}. \qquad (6)$$

Comparisons were also tested for independence of relative Surface Collector Bypass Channel efficiencies and arrival distributions using RxC contingency table tests (Skalski and Ngouenet, 2002; Zar, 1984).

Tagged fish releases occurred approximately 40 river km upstream of Rocky Reach Dam at Beebe Bridge (Fig. 1), in the center of the river. There were a total of 20 release groups, with 6 groups of yearling chinook, 10 groups of steelhead (5 each for the “A” and “E” tags), and 2 groups each of sockeye and sub-yearling chinook (Table 1).

A total of 472 acoustic tags were used during this study with 99 yearling chinook using “E” tags, 98 steelhead using “E” tags, 95 steelhead using “A” tags, 86 sockeye using “A” tags, and 94 sub-yearling chinook using “A” tags (Tables 1 and 2).

A total of 2,945 PIT tags were used during this study with 897 yearling chinook, 869 steelhead, 582 sockeye, and 597 sub-yearling chinook.

For statistical analyses, the yearling chinook and steelhead data were combined for time periods corresponding to the first half of the study (24 April through 5 May) and the last half of the study (17 through 26 May).

Acoustic “E” tagged fish lengths ranged between 145-200 mm (mean=165 mm) for yearling chinook and 150-220 mm (mean=193 mm) for steelhead smolts. Acoustic “A” tagged fish lengths ranged between 155-225 mm (mean=193 mm) for steelhead smolts, 116-150 mm (mean=136 mm) for sockeye smolts, and 120-152 mm (mean=127 mm) for sub-yearling chinook. PIT tagged fish lengths ranged between 105-210 mm (mean 141 mm) for yearling chinook, 125-235 mm (mean=193 mm) for steelhead smolts, 106-154 mm (mean=114 mm) for sockeye smolts, and 100-156 mm (mean=115 mm) for sub-yearling chinook.

The acoustic tag and PIT tag study designs compared six unique combinations of tag type (PIT tag, acoustic “E” tag, and acoustic “A” tag) and fish species (yearling chinook, steelhead, sockeye, and sub-yearling chinook), and study period, listed below and shown graphically in Table 2:

a) comparison of PIT tagged versus acoustic “E” tagged yearling chinook (a_1, and a_2, Table 2);
b) comparison of PIT tagged versus acoustic “E” tagged steelhead (b_1, and b_2, Table 2);
c) comparison of PIT tagged versus acoustic “A” tagged steelhead (c_1, and c_2, Table 2);
d) comparison of acoustic “A” tagged versus acoustic “E” tagged steelhead (d_1, and d_2, Table 2);
e) comparison of PIT tagged versus acoustic “A” tagged sockeye (e_1, Table 2);
f) comparison of PIT tagged versus acoustic “A” tagged sub-yearling chinook (f_1, Table 2).

Table 1– Releases of tagged fish upstream of Rocky Reach Dam at Beebe Bridge in 2002 (release dates, locations, fish species, tag-types, and sample sizes).

	Yearling Chinook		Steelhead			Sockeye		Sub-Yearling Chinook	
Release Date	Acoustic "E"	PIT	Acoustic "A"	Acoustic "E"	PIT	Acoustic "A"	PIT	Acoustic "A"	PIT
24/04/02	17	150	16	16	82				
28/04/02	17	149	14	16	112				
03/05/02	17	149							
08/05/02						42	284		
12/05/02						44	298		
17/05/02	18	150	20	21	225				
22/05/02	15	149	25	22	225				
26/05/02	15	150	20	23	225				
12/07/02								45	300
19/07/02								49	297
Totals	99	897	95	98	869	86	582	94	597

Rock Island Dam Project Survival

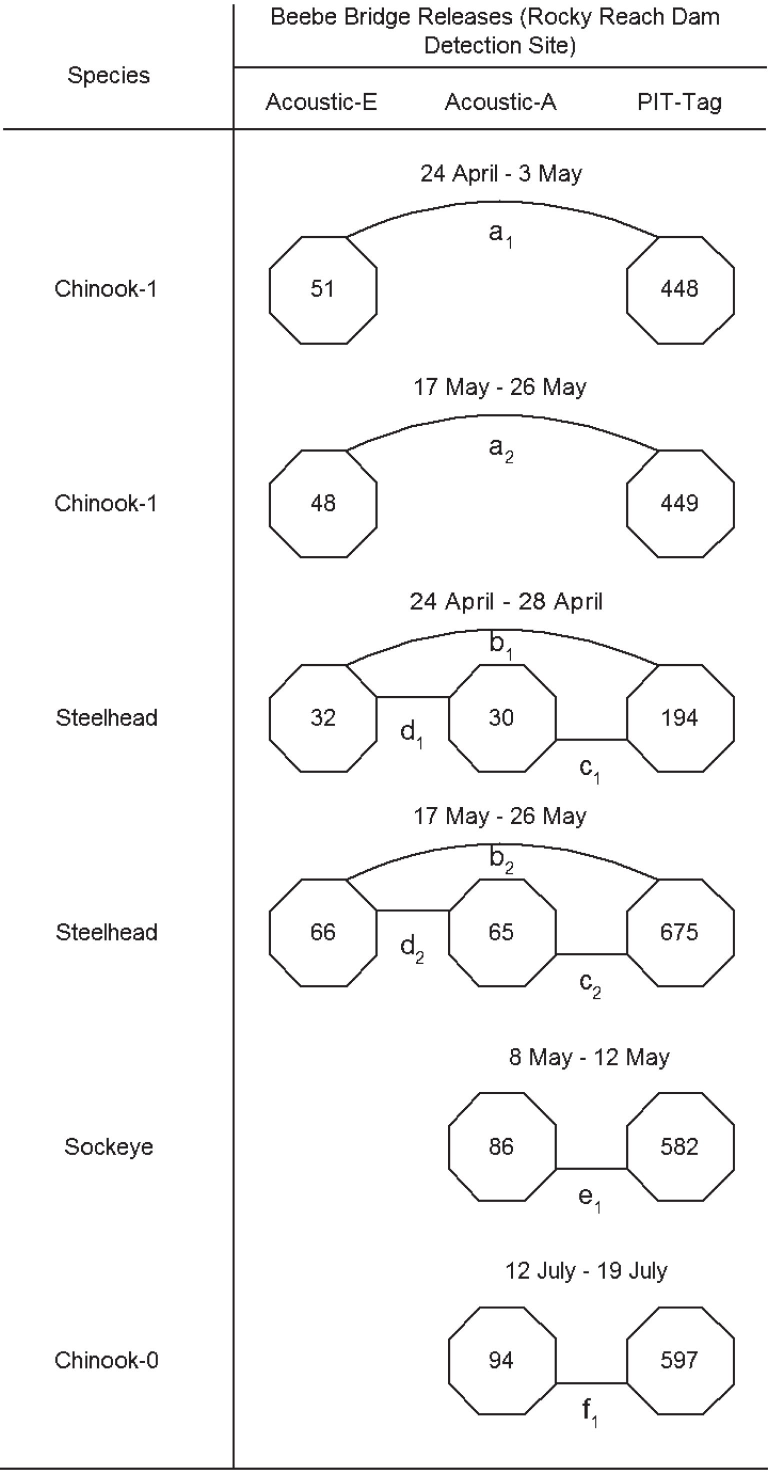
Project survival for the Rock Island Dam study was estimated by a paired release-recapture design. Rocky Reach tailrace releases were paired with Rock Island tailrace releases (Fig. 1). Releases occurred over 45 days, with 18 releases at each site, and included mixed groups of acoustic and PIT tagged smolts with approximately 22 acoustic tagged smolts (18x22; ≈400 per site) and approximately 2,500 PIT tagged smolts (18x2,500; ≈45,000 per site) in each release.

All releases occurred at approximately 08:00 each morning. Release-specific survival probabilities were computed for each paired-release. Study performance was measured by the average survival probability estimated across the 18 replicate releases. The project survival was estimated using the paired release-recapture models of Burnham *et al*. (1987).

The Rock Island Dam project results consisted of PIT tag and acoustic tag survival estimates. The analysis consisted of three elements: (a) tests of assumptions, (b) model fitting, and (c) estimation of project survival based on the paired-release design. Detailed methods and analysis are presented in Skalski *et al*. (2003).

The Rocky Reach Dam tailrace releases totaled 45,001 PIT and 399 acoustically tagged yearling chinook. The Rock Island Dam tailrace releases totaled 44,999 PIT and 399 acoustically tagged yearling chinook.

Table 2 – Statistically compared tag types and release groups of tagged fish upstream of Rocky Reach Dam in 2002.



Species	Beebe Bridge Releases (Rocky Reach Dam Detection Site)		
	Acoustic-E	Acoustic-A	PIT-Tag
		24 April - 3 May	
Chinook-1	51		448
		17 May - 26 May	
Chinook-1	48		449
		24 April - 28 April	
Steelhead	32	30	194
		17 May - 26 May	
Steelhead	66	65	675
		8 May - 12 May	
Sockeye		86	582
		12 July - 19 July	
Chinook-0		94	597

Table 3 – Acoustic and PIT tagged detection results for the 2002 Rocky Reach Dam study. Note that the detection rates are based on Surface Collector Bypass Channel tag detectors.

Tagged Fish Species	Tag Type	Total Fish Last Detected at Surface Collector	Total Fish Released	Percent Fish Last Detected at Surface Collector (%)
Yearling Chinook	PIT	157	897	17.50
Yearling Chinook	Acoustic “E”	23	99	23.23
Steelhead	PIT	251	869	28.88
Steelhead	Acoustic “E”	29	98	29.59
Steelhead	Acoustic “A”	26	95	27.37
Sockeye	PIT	23	582	3.95
Sockeye	Acoustic “A”	3	86	3.49
Sub-Yearling Chinook	PIT	14	597	2.35
Sub-Yearling Chinook	Acoustic “A”	5	94	5.32

Results

Rocky Reach Dam Behavioural Study

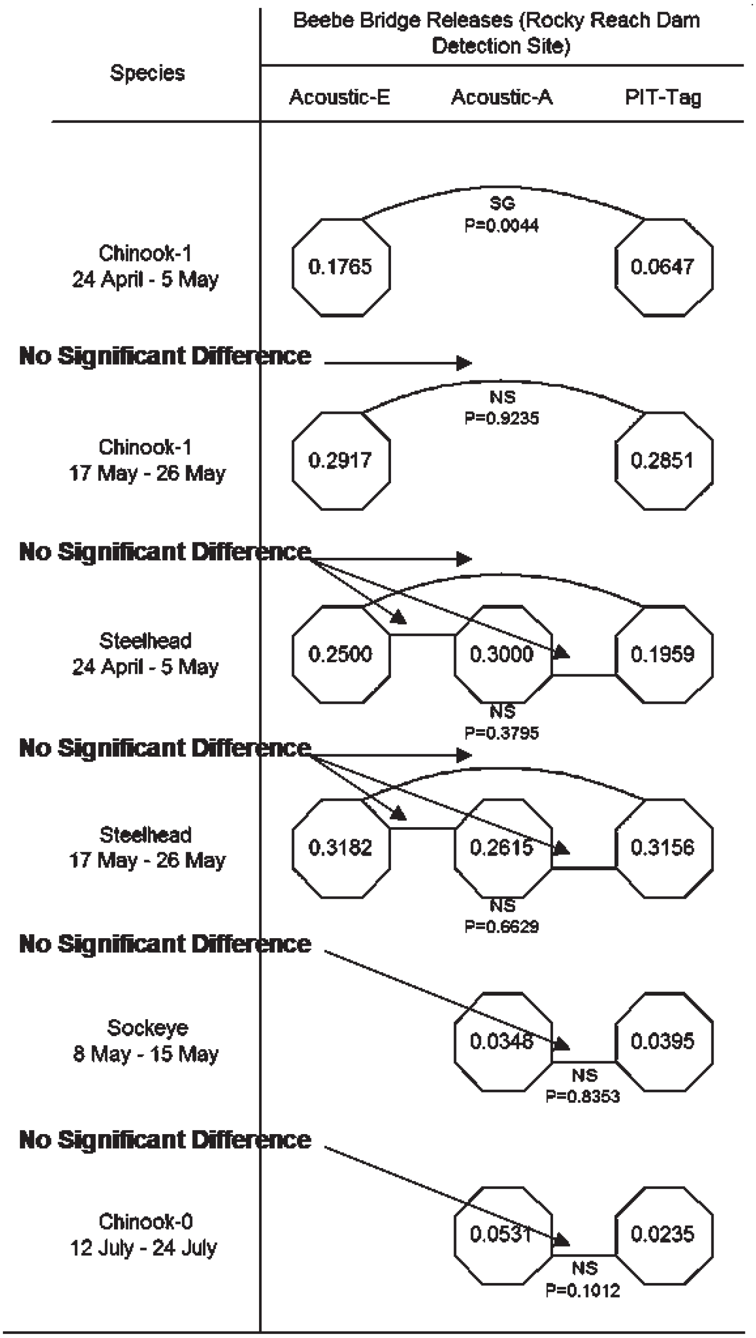
Percent of acoustic and PIT tagged fish detected at the Rocky Reach Dam Surface Collector Bypass Channel for each release is summarized in Table 3. Overall, Surface Collector Bypass Channel efficiencies were similar between acoustic and PIT tagged fish. Steelhead smolt collection efficiencies were 27%, 30%, and 29% for the acoustic “A”, acoustic “E”, and PIT tagged fish, respectively. Sockeye smolt collection efficiencies were similar for acoustic “A” tagged fish (3%) and PIT tagged fish (4%). Sub-yearling chinook smolt collection efficiencies were 5% and 2% for acoustic “A” and PIT tagged fish, respectively. Yearling chinook smolt collection efficiencies were slightly greater for the acoustic “E” tagged fish (23%) compared to the PIT tagged fish (17%).

Relative Surface Collector Bypass Channel collection efficiency for acoustic and PIT tagged fish indicated 9 of 10 tag type comparisons were not significantly different (P>0.05) (Table 4). Yearling chinook smolts released between 17 May and 26 May, steelhead, sockeye, and sub-yearling chinook collection efficiencies were not significantly different (P>0.05) between acoustic and PIT tagged fish. In addition, steelhead collection efficiencies were not different (P>0.05) between acoustic “A” and “E” acoustically tagged fish. Yearling chinook released between 24 April and 3 May were the only group found to have significantly different (P=0.0044) collection efficiencies (18% for acoustic tags, 6% for PIT tagged fish).

Mean harmonic travel times from release at Beebe Bridge to detection at Rocky Reach Dam indicated 8 of 10 tag type comparisons were not significantly different (P>0.05) (Table 5). Yearling chinook, sockeye, and sub-yearling chinook travel times were not significantly different (P>0.05) between acoustic and PIT tagged fish. Steelhead travel times were not significantly different (P>0.05) between acoustic “A” and “E” tagged fish. Steelhead released 24 April-28 April showed significantly different (P=0.0041) travel times between acoustic “A” and PIT tagged fish, but not between acoustic “E” and PIT tagged fish while steelhead released 17 May-26 May showed significantly different (P=0.0328) travel times between acoustic “E” and PIT tagged fish, but not between acoustic “A” and PIT tagged fish.

In summary, the statistical results showed that tagged fish were guided in similar proportions and with similar harmonic mean travel times, independent of tag type (PIT and acoustic) or tag size (acoustic “A” and “E”).

Table 4 – Summary of relative Surface Collector Bypass Channel efficiency comparing tag types (acoustic “E”, “A”, and PIT tagged fish). Dates, locations, fish species, and tag-types are presented for the various release groups. Comparisons denoted by lines are labeled with their level of statistical significance.



Species	Beebe Bridge Releases (Rocky Reach Dam Detection Site)		
	Acoustic-E	Acoustic-A	PIT-Tag
Chinook-1 24 April - 5 May	0.1765		0.0647
Chinook-1 17 May - 26 May	0.2917		0.2851
Steelhead 24 April - 5 May	0.2500	0.3000	0.1959
Steelhead 17 May - 26 May	0.3182	0.2615	0.3156
Sockeye 8 May - 15 May		0.0348	0.0395
Chinook-0 12 July - 24 July		0.0531	0.0235

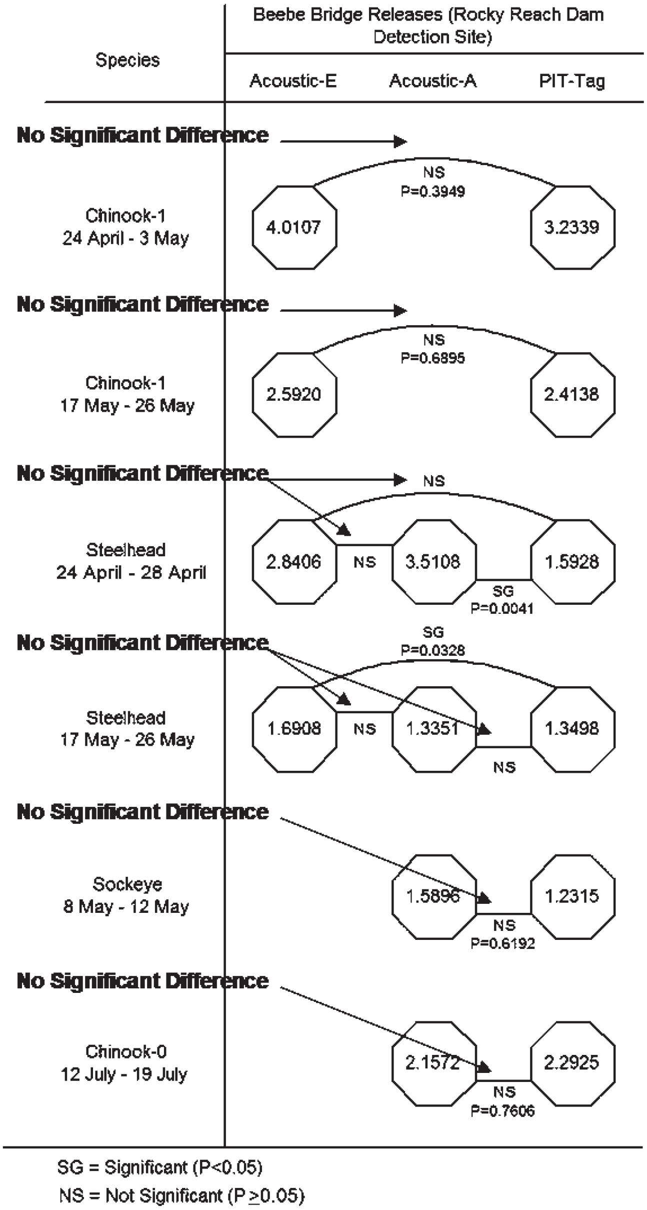
SG = Significant ($P<0.05$)

NS = Not Significant ($P \geq 0.05$)

Rock Island Dam Project Survival

Survival estimates, obtained utilizing 90,000 PIT tagged yearling chinook smolts and 798 acoustic tagged yearling chinook smolts, indicated that Rock Island Dam project survival for PIT tagged and acoustic tagged fish were in close agreement (Table 6). An arithmetic average across the two methods provided an estimate of project survival of ($\hat{S}_{RI} = 0.9538$, $\hat{SE} = 0.0146$).

Table 5 – Summary of the harmonic mean travel times from release to detection (in days) comparing acoustic “E”, “A”, and PIT tagged fish. Dates, locations, fish species, and tag-types are presented for the various release groups. Comparisons denoted by lines are labeled with their level of statistical significance from tests of homogeneity.



SG = Significant (P<0.05)
NS = Not Significant (P ≥0.05)

Table 6 – Results of yearling chinook smolts at Rock Island Dam in 2002 comparing PIT and acoustic tag results for project survival, standard error, and number of fish tagged.

PIT Tagged Fish Project Survival (Weighted Average)	PIT Tagged Fish Project Survival (Standard Error)	Number of PIT Tagged Fish
0.9555	0.0249	90,000
Acoustic Tagged Fish Project Survival (Weighted Average)	**Acoustic Tagged Fish Project Survival (Standard Error)**	**Number of Acoustic Tagged Fish**
0.9520	0.0263	798

Conclusion

Comparable study results were obtained between 1.0 g (“A”) acoustic, 1.5 g (“E”) acoustic, and PIT tagged fish. Acoustic tagged and PIT tagged yearling chinook salmon, steelhead, sockeye, and sub-yearling chinook smolts demonstrated similar migration dynamics as measured by survival, travel time and collection efficiencies at hydroelectric projects. In many applications, acoustic tags may utilize far fewer tags and fish to provide similar precision compared to PIT tags. Specific findings conclude the following.

1. The relative Surface Collector Bypass Channel efficiency and the harmonic mean travel times at Rocky Reach Dam comparing acoustic and PIT tagged fish for the 3 different species of salmon smolts and 2 year classes for chinook smolts were not significantly different ($P>0.05$) for 13 out of the 16 comparisons. In addition, there were no significant differences between the 1.0 g (“A”) and the 1.5 g (“E”) acoustic tags.
2. There was no significant difference between the survival estimates for acoustic or PIT tagged juvenile chinook smolts through the Rock Island Dam Project.
3. The acoustic tag survival study used 89,202 fewer chinook smolts to produce almost identical precision as the PIT tag survival study (798 versus 90,000, or <1%).

We conclude that acoustic tagged fish provide an effective alternative with comparable estimates to PIT tag survival studies. In addition, acoustic tags provide route specific fish passage results and three-dimensional fish paths. Acoustic tags also provide an effective alternative to PIT tag studies that may be advantageous when sample sizes are restricted as in the case of endangered or threatened species.

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Effects of surgically-implanted transmitters on survival and feeding behavior of adult English sole

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Key words: English sole, flatfish, tagging, telemetry, *Pleuronectes vetulus*, feeding.

Abstract

Acoustic telemetry studies of flatfish have typically relied on an external transmitter attachment. We propose to initiate long-term monitoring of adult English sole (*Pleuronectes vetulus* Girard) movements in Puget Sound, Washington, USA. The transmitters we use have a 2-year battery life, and we are concerned that external attachment might result in increased tag loss or predation risk over the course of this study. Consequently, we conducted a laboratory study to assess the feasibility of surgically implanting the transmitters. Dummy transmitters were constructed with the exact dimensions and weight of the study transmitters (5 g in air, 9x30 mm) and coated with an epoxy resin. We collected adult English sole (≥27 cm and 200 g) from Eagle Harbor, Washington, and tested insertion of a dummy transmitter into the peritoneal cavity from either the blind or eyed sides of the fish. A total of ten fish were assigned to each treatment group: blind-side insertion, eyed-side insertion and control. Two fish from each treatment were housed in each of five 1.2-m diameter tanks for 1 month. Fish were fed three times per week, and we noted their behavior for 10 minutes during each feeding. During the experiment, only one fish died (a control) and no transmitters were expelled. In addition, we found that fish from both treatments were active and exhibited normal feeding behavior relative to controls. At the conclusion of the experiment, all fish were weighed and sacrificed. Analysis of variance indicated no significant tank or treatment effects on weight gain. Necropsy revealed greater inflammation and fibrosis of the peritoneal side of the incisions made on the blind side relative to those on the eyed side. Therefore, we concluded that surgical implantation of transmitters into the peritoneal cavity is a viable option for long-term studies of flatfish movements, and we recommend insertion from the eyed-side of the fish.

Introduction

Acoustic telemetry studies of flatfish have typically relied on external transmitter attachment. Most of these studies either used large fish or were conducted over a relatively short time period (Greer Walker *et al*., 1978; 1980; Sureau and Lagardere, 1991; Metcalfe *et al*., 1993; Szedlmayer and Able, 1993). For studies using small fish, surgical implantation of the transmitter was not an option due to inadequate body cavity size. In studies using larger fish, the external attachment has apparently not affected fish movements or mortality over periods of greater than one year (G. P. Arnold, CEFAS Lowestoft Laboratory, Suffolk, UK, personal communication). We propose to use acoustic telemetry to conduct long-term monitoring of adult English sole (*Pleuronectes vetulus* Girard) movements in Puget Sound, Washington, USA. The transmitters we use have a 2-year battery life. We are concerned that external attachment of these transmitters on such a small flatfish for long periods of time might result in increased tag loss. Moreover, external attachment might affect fish behavior or make the tagged fish more vulnerable to predation during the course of the study. With the miniaturization of acoustic transmitters, it is now possible to surgically implant the transmitters into the body cavity of small flatfish. We therefore investigated the feasibility of surgically implanting acoustic transmitters into the peritoneal cavity of adult English sole of at least 27 cm total length.

A number of metrics have been used to assess the effects of surgically implanting transmitters in fish, including survival, growth, swimming performance, buoyancy compensation, physiological stress, dominance, predator avoidance and feeding (e.g., Mellas and Haynes, 1985; Moore *et al*., 1990; Adams *et al*., 1998a; 1998b; Martinelli *et al*., 1998, Thorstad *et al*., 2000; Jepsen *et al*., 2001; Perry *et al*., 2001). We felt that for English sole the most sensitive indicator of transmitter implant effects would be feeding behaviour, as the body cavity is small and the presence of the transmitter could physically affect the ability to feed to satiation. Therefore our objectives were to 1) determine whether sole would expel the transmitters as documented in other fish species (e.g., Chisholm and Hubert, 1985; Marty and Summerfelt, 1986; Lucas, 1989; Moser *et al*., 2000) and 2) determine whether feeding activity of English sole is affected by the presence of a transmitter in the peritoneal cavity. In addition, we compared the effects of transmitter insertion from both the blind and eyed sides of the fish to establish the best protocol for surgically implanting transmitters in this, and possibly other, flatfish species.

Materials and methods

Dummy transmitters were constructed with the exact dimensions and weight of an actual transmitter (5 g in air, 9x30 mm) and coated with epoxy resin. We collected adult English sole with an otter trawl from our study location in Eagle Harbor, Washington, USA. The fish were placed in a live tank onboard the vessel and those greater than 27 cm total length and 200 g in weight were transferred to the laboratory. The sole were acclimated to laboratory conditions in 1.2-m diameter, flow-through tanks for 1 week prior to implanting the transmitters.

Each fish was anaesthetized using a sedative dose of tricaine methanesulfonate (MS-222, 25 ppm) for 15 min and then transferred to a surgery bath with a higher concentration (80 ppm) for 5 min. We weighed (nearest g) and measured (nearest mm) each fish prior to surgery. A 2-cm horizontal, antero-posterior incision was made in the body wall on either the blind side or the eyed side (Fig. 1), and a dummy transmitter was inserted into the posterior region of the peritoneal cavity so that it rested in a dorso-ventral plane just anterior to the gonad. The incision was closed using two or three simple, interrupted, non-absorbable sutures closed with a surgeon's knot. We then irrigated the incision with oxytetracycline and swabbed it with a triple antibiotic ointment. Controls were handled but not anaesthetized.

There were a total of ten fish for each of the three treatments: blind-side incision, eyed-side incision and control. Two fish from each of the three treatments were then housed in each of five 1.2-m diameter tanks with running seawater at 17 °C for 1 month. After 1 week we initiated feeding experiments. The fish were fed chopped clams three times per week at a ration of 2.5% of their starting body weight as computed for each tank. During each feeding we noted their behaviour for the first 10 min after food was introduced into the tank and we recorded each time a fish ingested some food (referred to as a "bite"). At the conclusion of the experiment, all fish were weighed and sacrificed. We examined the tag and incision for signs of inflammation, incision closure and host reaction.

Results

Only one fish died (a control) and no transmitters were expelled. During the first two weeks of the experiment, most fish did not feed much and only certain individuals fed readily, regardless of treatment (Fig. 2). As the experiment progressed, more fish fed, and we found that fish from both tagged treatments were active and exhibited normal feeding behaviour relative to controls. We tested for treatment and tank effects on percent weight change (arcsin square root transformed; Zar, 1984) using analysis of variance. Because most fish lost weight during the course of the experiment (Fig. 3), we added 0.2 to the proportional change in weight recorded for each fish. We found no significant effects of tank, treatment, or tank by treatment interaction (p>0.05). Therefore, we pooled the data across tanks, but still found no significant treatment effect (df=2, F=0.29, P=0.75).

When we necropsied the fish, we found that all but three were females. In all fish the incision had closed completely and in many cases the scar was barely visible. However, we found that 30% of the fish tagged from the blind side had intraperitoneal

Fig. 1 – Typical locations of the incision made on the eyed- (top photo) and blind-(bottom photo) side of English sole (photos taken 2 weeks after surgery).

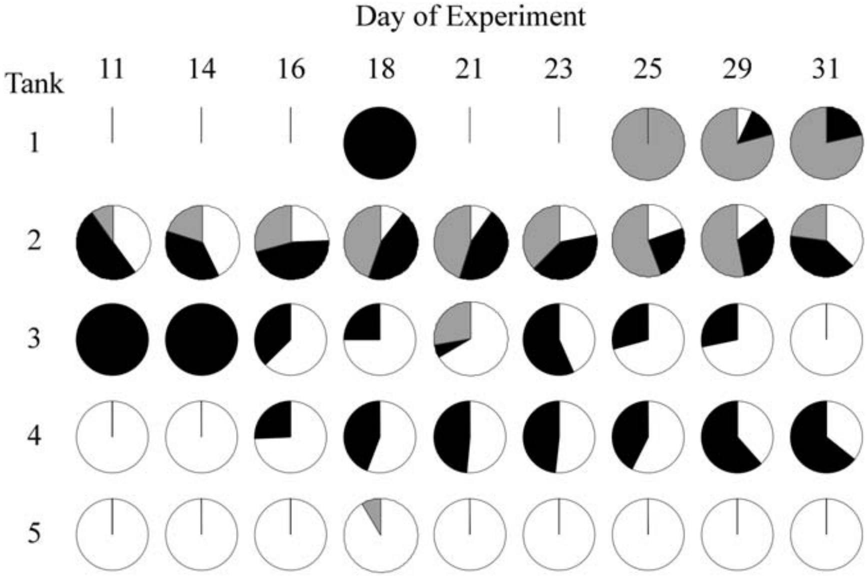

Fig. 2 – Percentage of bites made by fish of each treatment (controls in white, blind-side incision in black, and eyed-side incision hatched) in each tank during the course of the experiment. For example, on day 11 in tank 3 all bites were made by fish tagged from the blind side.

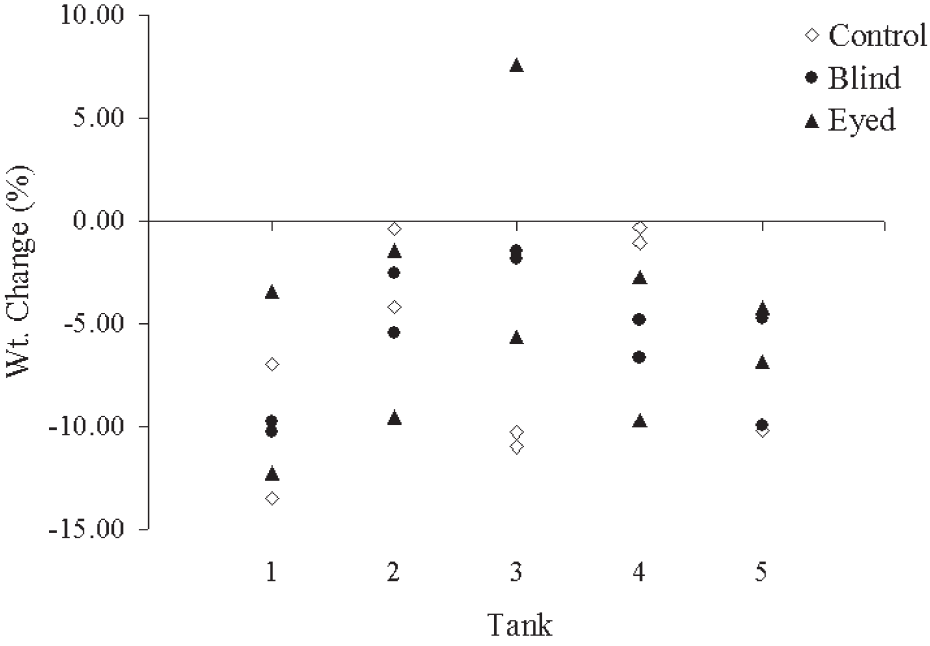

Fig. 3 – Change in weight during the course of the experiment for each treatment group: controls (open diamonds), blind-side incision (solid circles), and eyed-side incision (solid triangles).

fibrous adhesions to the incision and/or that the incision on the peritoneal side showed signs of inflammation (as opposed to 10% of the fish tagged from the eyed side). For both treatments, the tags were oriented in the same direction in the body cavity (perpendicular to the body axis and angled slightly with the ventral end of the tag more anterior than the dorsal end of the tag) and they did not appear to have shifted from their initial position at insertion. We found that opaque, fibrous tissue had started to encapsulate the tags in 30% of the fish tagged from the blind side and 40% of the fish tagged from the eyed side. However, there was no indication that the fibrous capsule was attached to the digestive tract nor evidence of muscle necrosis in the peritoneal wall adjacent to the tags in any of the fish.

Discussion

We concluded that surgical implantation of transmitters into the peritoneal cavity is a viable option for long-term studies of flatfish movements. As reported by Lucas (1989), we found some encapsulation of the tag, but there was no indication that this would result in future tag expulsion. The tags were probably too large for trans-intestinal expulsion (as in Marty and Summerfelt, 1986), and we found no evidence of muscle necrosis adjacent to the tag (a precursor of expulsion across the body wall, Lucas, 1989). Moreover, all incisions were completely closed, and in many cases the scars were barely visible after one month. There is some possibility that tag expulsion may occur as the gonads in English sole develop. However, due to the position of the tag in the body cavity, we believe that the risk of transmitter expulsion will be minimal.

While nearly all fish lost weight during the course of our study, there was no evidence that feeding was impaired by the presence of the transmitter in the body cavity. Similar studies of relatively large transmitter implants (2.3-5.5% of body weight) in juvenile chinook salmon (*Oncorhynchus tshawytscha*) also indicated that feeding was not affected by surgical implantation of the tags, while gastric implants did affect feeding (Adams *et al*., 1998a). We found leftover food in the tanks as much as 2 days after feeding, indicating that the ration was not limiting. Yet, individual variation in food intake by the English sole was high. Many fish (both tagged and controls) did not feed at all, while others consumed food regularly. This may have resulted from the relatively short time fish were allowed to acclimate to captivity prior to tag implantation. McCain *et al*. (1978) noted that adult English sole held in captivity required over 3 months to start gaining weight. Nevertheless, in our experiment some of the fish that ate most readily and took the most bites were those bearing tags, indicating that the tag did not prevent sole from feeding to satiation.

Our results suggested that inserting tags from the eyed side is preferable to blind-side insertion. This is primarily due to the fact that the incisions on the blind side were more subject to friction and abrasion during fish movements, and this could be more of a problem when the blind side of fish is exposed to sediment. Exposure of the blind-side incision to sediment not only increases the chance of abrasion, incomplete incision closure, and resultant peritoneal inflammation, but also increases the chances of opportunistic bacterial and viral infection and associated negative sequelae. In the only other pilot study that has used surgical implants of acoustic transmitters in flatfish, insertion was done on the eyed side of sole (*Solea solea*) for the same reasons (M. Begout-Anras, CREMA, L'Hommeau, France, personal communication).

Acknowledgements

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Behavioural effects of surgically implanting transponders in European eel, *Anguilla anguilla*

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Key words: behaviour, telemetry, surgical implantation, methodological effects, eel.

Abstract

The applicability of using transponders (Nedap Trail™) to tag European eel *Anguilla anguilla* (L. 1758) during their silver eel stage, was tested in a controlled tank experiment. Most studies on effects of implanted radio tags focus on the impact on mortality, disease, wound healing and growth. In this experiment we also measured individual activity continuously, which allowed to detect more subtle effects on behaviour as well. In total 40 silver eels (680-1685 g) were anaesthetized and injected with a micro PIT-tag. In 20 of these, dummy transponders similar in shape (cylindrical, 14x63 mm), weight (26.5 g in air, 16.0 g in water), volume (9.5 cm^3) and surface (glass) to Nedap-transponders were surgically implanted in the body cavity. All eels were placed in a Migromat®-tank with five compartments connected with openings that allowed free movement between compartments. Each opening was covered by an antenna recording individual passages. Because the tank was placed in the open, had transparent lids and was flowed with river water, eels could respond to 'natural' environmental stimuli, e.g. water temperature, turbidity, light and moon phase. The experiment was ended after 11 weeks (October-December). There was no significant difference in mortality rate between the control (15%) and experimental group (10%). All eel in the experimental group had closed wounds and none of the transponders was shed, nor any sign of expulsion was observed. In both groups one PIT-tag was lost. Individual activity level of the remaining eels was 38% lower in the experimental (n=17) than in the control group (n=16), indicating at least some effect of implanting transponders on the behaviour of eel. There was, however, no difference between groups in the timing of activity, neither during the entire period nor diurnal. Consequences for the interpretation of field telemetry experiments are discussed.

Introduction

Biotelemetry is a fast developing technology that is increasingly used to study fish behaviour (Lucas and Baras, 2001). In field experiments measurements are taken from tagged fish only, without the possibility of a control group. Therefore, it is important to determine potential bias in behaviour induced by the tagging procedure and materials on forehand in controlled experiments, especially since large differences in response to applied methodology are indicated for different species, life stages, and environmental circumstances (Jepsen *et al*., 2002). Most controlled experiments on the effect of applying telemetric tags, however, focus on effects such as mortality, disease, wound healing, and growth (e.g. Lucas, 1989; Martin *et al*., 1995; Martinelli *et al*., 1998; Walsh *et al*., 2000), whereas experiments with behavioural measurements are relatively few (Moore *et al*., 1990; Adams *et al*., 1998; Perry *et al*., 2001; Koed and Thorstad, 2001).

In the present study we focus on the possible effects of surgically implanted transponders on the behaviour of the European eel *Anguilla anguilla* (L. 1758) by means of a controlled tank experiment. In addition to more traditional parameters we also continuously recorded individual movements to detect possible differences in the timing and level of activity.

This study was performed within the context of a project to determine activity time patterns and serial mortality rates due to hydropower and fisheries in the River Meuse, the Netherlands (Bruijs *et al.*, 2003).

Materials and methods

Test fish and handling procedures

Eels were caught with fykenets by a professional fisherman at 8-9 October 2001 in the river Meuse at Ohé en Laak, The Netherlands. They were kept in oxygenated basins between catch and treatment on 10 October 2001. Only eels with a completely silver white ventral side were used, rejecting individuals with yellow or partly yellow ventral sides. We used 40 eels between 52.5 and 91.0 cm total length and 680 and 1685 g. Males do not grow that large before migrating (Dekker, 2000), thus all used fish were females.

Surgical implantation technique

All individuals were anaesthetized with 2-phenoxy-ethanol (0.9 mll^{-1}), weighed (g), measured (mm total length) and subcutaneously injected with an individual coded PIT-tag (Passive Integrated Transponder, TROVAN®) in the dorsal muscle near the head. In 20 eels, dummy transponders similar in shape (cylindrical, 14x63 mm), weight (26.5 g in air, 16.0 g in water), volume (9.5 cm^3) and surface (glass) to Nedap Trail™ transponders (Breukelaar *et al.*, 1998) were surgically implanted in the body cavity by making a mid ventral 2-3 cm incision in the posterior quarter of the body cavity. The used surgical procedure was the best among five different procedures tested for European eel by Baras and Jeandrain (1998). The incision was closed by commercial-grade cyanoacrilate adhesive (Loctite™) and a freshly cut 3-5 mm wide fragment of the eel's dorsal fin was applied over the drying adhesive to act as a biological bandage over the incision. Surgery lasted 3-5 minutes at a water temperature of 15 ºC. Eels were observed in a recovery tank until swimming behaviour reappeared and then released in the test tank.

Tank experiment

The experimental group with implanted transponders (n=20, length range 67-91 cm, mean±s.d.: 77.6±5.9 cm) and the control group (n=20, length range 53-90 cm, mean±s.d.: 66.3±8.8 cm) were placed together in one tank in order to avoid a possible tank effect. This Migromat® tank contained 5 m^3 water and consisted of five compartments connected by four square openings of 30 cm. Each of these openings was covered by an antenna loop that continuously registrated each individual passage (Adams and Schwevers, 1999; Fig. 1). Eels were free to move between the five different compartments and were found to do so, e.g. most eels visited several compartments more or less evenly distributed over the entire tank. The experiment was carried out from 10 October to 16 December, during the period of downstream migration, in the open field, with transparent lids and flowed with river water from the River Meuse, which enabled a response to 'natural' environmental stimuli, e.g. water temperature, turbidity, light and moon phase. A sediment layer of ca. 20 cm built up in the course of the experiment. During inspections dead or dying eels were removed from the tank. After 11 weeks at the end of the experiment, all remaining eels were checked and the presence of PIT-tags was determined. Eels of the treatment group were inspected for external and internal wound healing and the presence and location of the transponder. By external inspection it was determined whether the abdominal tissue or skin had closed, i.e. only scar tissue was visible. By internal inspection, after dissection, it was examined whether the transponder was still present, whether signs of expulsion were present, i.e. transponder enclosed in tissue, and what organ tissues were eventually grown to the abdominal tissue of the healing wound. Of all eels with implanted transponders pictures of the external and internal wound healing state were taken, allowing for later analysis of additional parameters.

Data analysis

Differences in mortality percentage between the experimental and control group were analysed using a *G*-test of independence (Sokal and Rohlf, 1995).

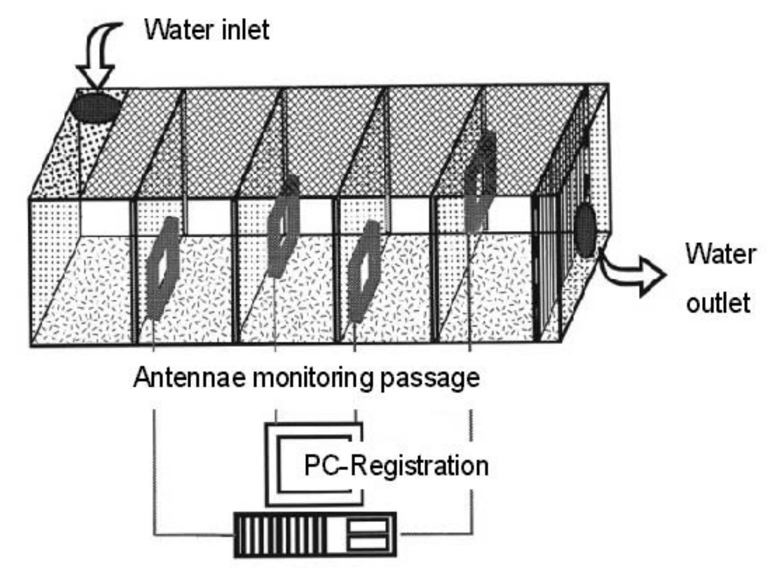

Fig. 1 – Schematic overview of the Migromat tank (1 m^3 water per compartment, 5 m^3 in total). The compartments are connected with openings covered by antenna loops that continuously monitor each passage of eels that move from one compartment to another.

For each individual, the number of passages through antenna loops was used as a measure for activity.

Because, unintentionally, the length distribution of the control group differed from the experimental group, we had to account for a possible length effect on activity when examining the effect of surgically implanting transponders. For this, we used a generalized linear model (GLM) that explained variance in activity for group, length and interaction between these two variables in the experimental tank:

$$A_{ij} = \mu + G_i + L + G_i{*}L + \varepsilon_{ij} \qquad (1)$$

where: A_{ij}=activity level of an individual eel (j), μ=mean activity, G_i=group (i=control, experimental), L=total length (cm), and ε_{ij}=error term.

However, due to the high colinearity between group and length, which are therefore not independent, in addition we used alternative tests for different groups of eels to examine a possible length effect on activity level. First, we examined the effect of length on activity by using data from an adjacent identical Migromat® tank, which will be further referred to as tank B where the experimental tank above will be referred to as tank A. Tank B was used for another experiment during exactly the same period (10 October-16 December 2001) to compare timing of activity in tanks with field data beyond the scope of this paper. However, the eels (n=30, length range 41-84 cm, mean±s.d. 66.4±11.5 cm) stocked in tank B were caught, handled, treated and implanted with a PIT-tag identically as described above for the control group in tank A. The following GLM model was used to examine the effect of length on activity in tank B:

$$A_j = \mu + L + \varepsilon_j \qquad (2)$$

where: A_j=activity level of an individual eel (j), μ=mean activity, L=total length (cm), and ε_j=error term.

Second, model (2) was applied to examine a possible length effect within the control group and experimental group of tank A, separately. Third, to compare a possible length effect between tanks, we examined a tank effect in combination with a length effect on the activity of eels that were given the same treatment, i.e. the control group of tank A and all eels in tank B, by using a GLM that explained variance in activity for tank, length and interaction:

$$A_{kj} = \mu + T_k + L + T_k{*}L + \varepsilon_{kj} \qquad (3)$$

where: A_{kj}=activity level of an individual eel with PIT-tags and without surgical implanted transponders (j), μ=mean activity, T_k=tank (k=tank A, tank B), L=total length (cm), and ε_{kj}=error term.

For the eels with implanted transponders in tank A we examined possible effects of external and internal wound healing state on activity by classifying them on the occurrence or absence of inflammation E_l (as a measure for external wound healing state) and the occurrence or absence of organ tissue grown to the healing wound I_m (as a measure for internal wound healing state). For this, variance in activity was tested with a GLM similar to model 2, where the parameter L was subsequently replaced by E_l=external healing (l=presence, absence of inflammation) and I_m=internal healing (m=presence, absence of tissue grown to wound tissue). For all GLM models, residuals were checked by a Shapiro-Wilk and Kolmogorov-Smirnov test on normality and interaction terms were removed from the models when these were not significant.

The timing of activity between the control and experimental group in tank A was examined on two different time scales. To compare timing between groups throughout the experiment, for each day the total number of antenna passages per group was determined. To compare timing between groups on a diurnal basis, for each of the 24 hours during the day the average number of antenna passages per group was determined. The correlation between groups was then determined for each of these two time scales (Sokal and Rohlf, 1995).

All statistical analyses were performed with SAS (version 8) software using α of 0.05.

Results

Mortality, disease, wound healing and tag retention

During the experiment from each group in tank A one eel died. In addition, one eel from the experimental group and two eels from the control group were removed, because they were near dead as a result of *Saprolegnia* sp. infection. Thus, total mortality rates were 10% and 15% for respectively the experimental and the control group, though not significantly different. In both groups at the end of the experiment, one healthy eel was found to have lost its PIT-tag, presumably during one of the first days after release in the tank since detections ceased shortly thereafter.

Within the treatment group at the end of the experiment, for all remaining 17 eels the wounds had closed, varying from completely healed with only scar-tissue visible to a closed abdomen but unhealed skin (Fig. 2). In 9 eels some organ tissue, mainly fat or intestine tissue was grown to the healed abdominal tissue. Inflammations were observed in 7 individuals. None of the eels had lost their transponder, which were all free laying in the body cavity and no signs of expulsion were observed.

Effects on activity level

Activity per eel in tank A was higher in the control group than in the experimental group (Fig. 3). When accounting for a group and length effect on activity level no significant effect was found for each of these parameters (model 1: group p=0.09, length p=0.91). Because group and length were not independent, we further examined a possible length effect on activity level. In tank B, where the length range was larger than in tank A, no significant effect of length on activity level was found (model 2: p=0.95). Also when testing the effect of length within the experimental group and the control group separately, no significant length effect was found (control: p=0.90, experimental: p=0.94). In addition, when combining all eels with only PIT-tags

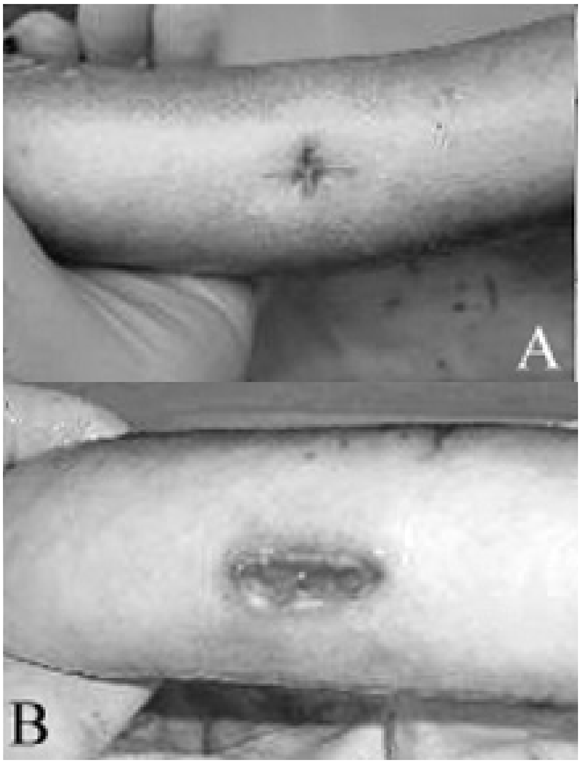

Fig. 2 – The range of wound healing state after 11 weeks. A: best healing, only scar tissue visible, B: worst healing, closed abdomen tissue but inflamed wound.

of tank A and B (model 3), again no significant effect of length was found (p=0.89). However, there was a significant effect between tank A and B (d.f.=2, F=4.25, p=0.05), where the average activity level of tank B was 36% lower than the control group in tank A, perhaps related to the number of eels in each tank (n=40 in tank A, n=30 in tank B). Because neither in tank B, nor in each of the groups in tank A, nor when combining the PIT-tagged eels of both tanks any indications for a length effect on activity were found, it appears justified to remove the length term from model 1. Then a significant effect of implanting transponders on the activity level was found (d.f.=1, F=5.44, p=0.03) where the model explained 15% of the variance. The average level of activity of the experimental group was 38% lower than of the control group.

When comparing average individual activity per group throughout the duration of the experiment (Fig. 3), several periods with different activity levels can be distinguished. The first 24 hours of the experiment, activity was nearly the same for each group. During 11 October-11 November, activity was relatively high in both groups with a peak on 12 October, and 38% less in the experi-

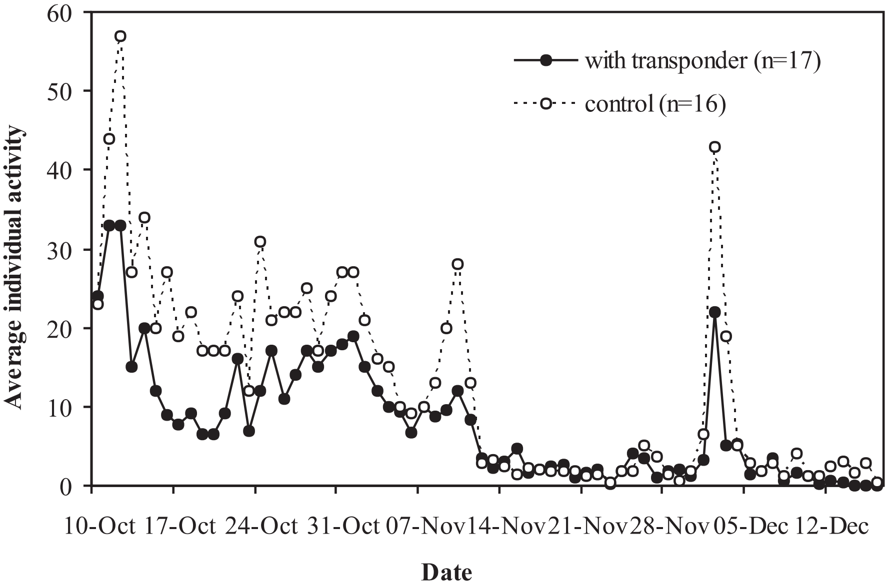

Fig. 3 – Average individual activity level per day for the experimental group with surgically implanted transponders and the control group during the entire period of the experiment in tank A from 10 October – 16 December 2001.

mental group. During 12-30 November, activity was very low for both groups and 10% higher in the experimental group. During 1-4 December, activity was high with a peak on 2 December, and 52% less in the experimental group. From 6-16 December activity was very low, and 55% less in the experimental group.

Within the experimental group, we did not find significant differences in activity patterns between eel with and without organ tissue growing onto the abdominal tissue (internal wound healing state, p=0.57) nor between eel with or without inflammations (external wound healing state, p=0.78).

Effects on timing of activity

When comparing average activity level of both groups during the day, a clear diurnal pattern was observed (Fig. 4). At night, especially between 18:00 and 22:00 hours, an increase in activity was observed, peaking at 20:00 hours. In the first five hours after sunset almost 40% of all activity took place. Very similar patterns were observed in all periods, also in the period when eel were relatively inactive (Fig. 3). Correlation between the activity level of the control and experimental group was highly significant both per day throughout the entire period (R^2=0.93, p<0.001) and diurnally per hour (R^2=0.95, p<0.001, Fig. 5).

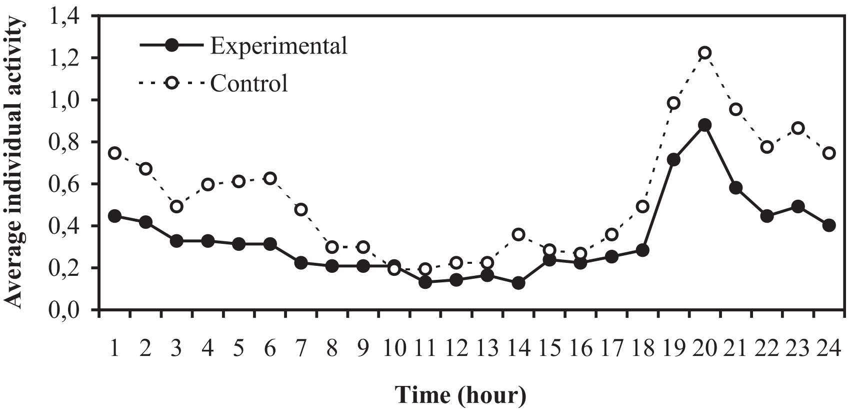

Fig. 4 – Diurnal patterns expressed as average individual activity level per hour during the entire period for the control group (broken line) and the experimental group (solid line) in tank A.

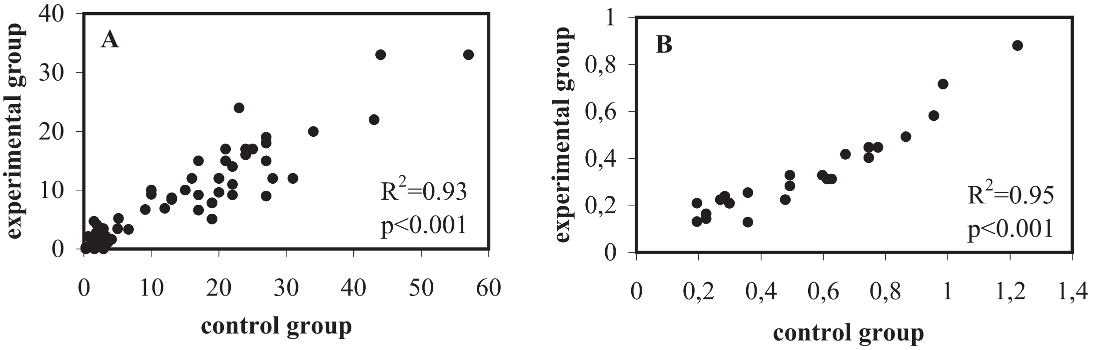

Fig. 5 – Correlation diagrams of mean activity level of the experimental group versus the control group in tank A for: A) each day during the entire period, B) each hour during the day (diurnal pattern).

Discussion

Because mortality rate was similar, even slightly less, in the experimental group than in the control group, and for the experimental group all wounds had closed abdominal tissues and no transponder loss or expulsion was observed during the 11 week period, it might be concluded by these commonly used criteria that surgically implanted Nedap-transponders are suitable to study silver eel migration.

When looking at the behaviour of eels in more detail, the timing of eel activity was very similar between both groups during the entire period as well as diurnal. Activity level, however, was 38% lower for the experimental than for the control group. Because no indications for a length effect on activity were found in tank B, within each group in tank A, or for all eels where no transponders were surgically implanted of tank A and B combined, it is unlikely that the uneven length distribution caused the differences between the experimental and control group in tank A and that the found effect was related to the surgical implantation of transponders. These eels were apparently less active. For this, we discuss two possible explanations.

First, the surgery and subsequent healing of the wound might have resulted in a lower activity level. If recovering from the treatment would be the main cause for the difference in activity levels between the two groups, it was expected that the impact decreased in time. The difference between both groups, however, showed no such trend, and the relative difference was even higher in the last part of the experiment (Fig. 3). Furthermore, no effect of wound healing state on activity level was found within the experimental group. It is therefore unlikely that this is the major cause for the observed difference.

Second, carrying the transponder may have inflicted lower activity. If this is true, it would be expected that the effect was relatively constant in time, which is close to what was observed. The transponder/body weight ratio was relatively high, ranging from 1.4 to 3.7%. In most eels it was higher than the often recommended ‘Winter’s 2% rule’ (Winter, 1996). Thus, in the individuals with a high ratio, i.e. the smaller individuals, it would be expected that the activity was lower. However, within the experimental group no effect of length was found. It might be that the effect in eels already occurs at ratio’s far lower than 2%. More studies have questioned this general rule of thumb (Jepsen *et al*., 2002), where sometimes effects well below 2% were found, and in other studies no effect could be demonstrated on behaviour in salmon smolts with ratios up to 10.7% (Brown *et al*., 1999). It is likely that eel, given its elongated body form and relatively narrow body cavity, flexible locomotion mode, efficiently fine tuned swimming endurance during the silver eel stage is relatively susceptible to carrying a transponder. We share the opinion of Gallepp and Magnuson (1972) and Jepsen *et al*. (2002) that it is unlikely that recommendations for a single weight ratio would be suitable in all species, or even within species. Some species and sizes of fish may be able to compensate for additional weight far better than others. But not only weight of the transponder might influence behaviour, volume might, especially for eel, be even more important. The relatively large transponder used in this experiment may fill much of the body cavity putting pressure on the internal organs, even though silver eel is supposed to cease feeding. Moreover, because of their anguilliform swimming mode, the relatively high transponder/body length (6.7-9.2%) might hamper their movements. Also, transponders proved to have detrimental effect on vertical stationing (Greensted and Morgan, 1989). Buoyancy is an important parameter, where the degree to which this can be compensated by means of filling the swim bladder varies between species (Lefrancois *et al*., 2001).

Within the current experiment, it can only be indicated whether the surgery treatment or carrying the transponder are more plausible explanations underlying the found effect on activity level as described above. However, to disentangle the effects of the surgical treatment and carrying the transponder, additional experiments are required that also include a ‘sham’-tagged group, undergoing the same surgical procedure but without actually implanting a transponder (Brown *et al*., 1999). In contrast to effects on the level of activity, no effects on the timing of activity were found. Both groups showed very similar patterns throughout the experiment and throughout the day. The very high activity during the first days of the experiment might be attributed to adjusting to the tank. The prolonged occurrence of higher activity thereafter, until 12 November, is probably at least partly due to a reaction on external stimuli, because commercial catches of silver eel in the River Meuse were also high during these weeks (Bruijs *et al*. 2003). The observed peak in early December is probably also initiated by external stimuli, although no commercial catch data of this week was available. Eels proved to be essentially nocturnal (Muller, 1972) and activity is normally peaking in the first two hours following sunset (Hain, 1975). This diurnal pattern is clearly reflected by the results of this tank experiment. Both groups tend to show rather 'natural' behavioural patterns in relation to external stimuli.

Implications for field telemetric studies

Studying timing and onset of downstream migrating silver eel in relation to trigger factors or environmental cues with Nedap-transponders seems to be justified, because no effects on timing of activity or mortality were observed. Given the lower activity of eels implanted with transponders one should be aware that at least some bias in observed behaviour might occur. For instance measured migration speeds might be underestimated or the length of travelled distances might be less. It is recommended to collect independent data from more conventional methods like monitoring downstream migrating eels or tag recapture experiments besides a field telemetry experiment to examine eventual aberrant behaviours related to the used methods.

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