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Experimental study of the influence of photoperiod and temperature on the swimming behaviour of hatchery-reared Atlantic salmon (*Salmo salar* L.) smolts

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ABSTRACT

The impacts of photoperiod and temperature on the swimming behaviour of hatchery-reared Atlantic salmon smolts were investigated, with a view to optimising salmon restoration strategies in the Loire-Allier basin. A novel experimental design was developed to study individual tagged fish in 9 m diameter hatchery tanks. Movements and swimming speeds were recorded over a period of eight months (January to August), repeated over four consecutive years (2005–2008). Fish switched from positive rheotactic behavior in January-February, to negative rheotactic behaviour at mid-March or April depending on the year, a period corresponding to the start of the downstream migration of wild smolts from the upper river spawning areas. Daily variation in movement and swimming speed occurred with high swimming speeds with the flow during the day and much lower speeds during the night. Swimming speeds could exceed water current velocity, showing hatchery-reared salmon can actively swim with the flow during the day. Experimental changes of photoperiod (constant light or constant darkness) allowed confirmation of the role of photoperiod in the daily variation of swimming activity. Analysis of the relationship between water temperature and swimming speeds over the four year experiments suggested a major role for water temperature in the modulation of swimming activity. Maximal swimming speed was recorded at 10.5 °C and swimming speed was reduced by 80% for temperatures under 4 or above 17 °C. Fish stopped moving above 20 °C. The data highlight the importance of temperature for the modulation of downstream movement, as well as the potential deleterious impact of the anthropogenic increase in river temperature below the spawning and juvenile habitat in the Allier tributary on the success of downstream migration. Better understanding of temperature effects on actual population-specific in-river migration patterns is required to allow managers to identify mitigation measures needed to improve migration success.

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1. Introduction

During the Atlantic salmon (*Salmo salar* L.) parr-to-smolt transformation (smoltification), morphological, physiological and behavioural changes occur that prepare the fish for its future ocean life (Boeuf, 1993; Hoar, 1976; McCormick and Saunders, 1987; McCormick et al., 1998). Salmon parr are territorial but become less aggressive as smolts, adopting a characteristic shoaling behaviour (Jonsson and Jonsson, 1993; Thorpe, 1994). Smolts usually start their downstream migration at the beginning of March-April for individuals from southern latitudes (e.g., France and Spain: Boeuf, 1993; Utrilla and Lobon-Cervia, 1999), in early June–July for the individuals from the northernmost latitudes (Davidsen et al., 2005) and as late as early August in some northern Icelandic rivers (Antonsson and Gudjonsson, 2002).

The timing of a smolt's arrival at the sea is crucial for its successful acclimatization and survival. The period during which smolts are able to adapt to seawater ("physiological smolt window") is limited (Berglund et al., 1992; Boeuf et al., 1985; McCormick et al., 1998). Delays in downstream migration can be lethal due to the loss, firstly, of the "physiological smolt window" and, secondly, of the "ecological smolt window," with an increased probability of encountering unfavourable environmental conditions such as high temperature, low dissolved oxygen concentrations or pollution (Antonsson and Gudjonsson, 2002; Hvidsten et al., 1998; Jutila et al., 2003, 2005; McCormick et al., 1998). Timing can be expected to be of greater importance in very long river systems, where climatic and anthropogenic conditions (temperature, flow, pollution and obstructions) have the potential to considerably delay downstream migration (McCormick et al., 2003). With spawning areas located 920 km from the ocean, the Loire-Allier River is the longest migration distance for Atlantic salmon in the northeast Atlantic region.

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Downstream migration begins with a change in rheotactic behaviour, from predominantly positive (facing the flow) in parr to predominantly negative in smolts. Riley (2007) suggested that the initial downstream movement of Atlantic salmon smolts is solitary, presumably followed by schooling behaviour further downstream (Hansen and Jonsson, 1985; Hvidsten et al., 1995; Olsen et al., 2004).

The environmental mechanisms influencing downstream migratory behaviour are not fully known but multiple factors are probably involved and synergies between these factors are potentially important (Groot, 1981). River flow, temperature and photoperiod have all been reported to be external factors in migration initiation and control (McCormick et al., 1998). In freshwater it is believed by some authors to simply entail passive displacement with the current (Huntsman, 1939; McCleave, 1978; Mills, 1964; Thorpe et al., 1981; Tytler et al., 1978). However, smolts have been observed to swim actively (Davidsen et al., 2005; Fångstam, 1994; Hansen and Jonsson, 1985; Kallenberg, 1958; Solomon, 1978) and to seek areas of high velocity (Jonsson et al., 1991).

Restocking programmes aimed at restoring salmon in the basin of the Loire-Allier River have been underway for nearly 80 years. Initially they involved releasing fingerlings of different origin (Canada, Scotland, Norway, Iceland, Poland, and Denmark). In contrast, from 1985 onward only salmon caught in the Allier River have been used as broodstock. Since 2001, stocking at the smolt stage has significantly increased, with an annual release of approximately 250,000 smolts. However, artificial rearing can produce fish that are poorly adapted to the wild (Aprahamian et al., 2003). This led us to investigate the migratory behaviour of hatchery-reared smolts with regard to environmental conditions such as photoperiod and temperature. The study was carried out with a view to optimising release strategies for salmon restoration in the Loire River. On the Loire/ Allier axis, the distance to the sea is long, with dramatically fluctuating environmental conditions and numerous potential obstructions to fish migration (28 dams or barriers). Additionally, the middle catchment river temperature can reach 30 °C in July and August, and mean river has risen 2 °C over the past 24 years (Gosse et al., 2008; Lair and Reyes-Marchant, 2000). Temperature is an essential element in the development and loss of seawater tolerance (Handeland et al., 2004; McCormick et al., 1999) and in the initiation and termination of migration (Zydlowski et al., 2005). The impact on the initiation and progress of downstream migration of natural photoperiod, constant darkness and constant light along with the influence of natural water temperature variations was also investigated.

2. Materials and methods

2.1. Fish

The study was carried out at hatchery of the Conservatoire National du Saumon Sauvage, Chanteuges (south central France: N 45°04'48, E 03°31'55). The hatchery produces juvenile salmon which are released into the river at different developmental stages as part of a restoration programme to enhance the salmon population of the Loire-Allier basin. Wild males and females adult salmon, caught in the Allier River at a location 820 km from the sea, were used to produce 1st generation hatchery-reared progeny. In October of each year (2005–2008, inclusive), at ~8 months old, 1500 fish exceeding 145 mm ("upper mode": Boeuf, 1993; Thorpe, 1977) were transferred to the experimental tank.

2.2. Experimental set-up

A circular tank (9 m diameter; depth range 0.5 m at the periphery to 0.7 m in the centre) was supplied with natural running water from the River Allier or one of its tributaries (the River Desges), without filtration or disinfection. Water temperature ranged from <1 °C in

January to >20 °C in July/August), measured using temperature probes (Johnson control, Colombes, France; TS 9101: accuracy ± 0.2 °C). An anti-clockwise flow was achieved by a tangentially orientated water inlet at the periphery of the tank and a central drain (Fig. 1A). The flow was maintained at 3 l s^{-1} until April then progressively increased to 7 l s^{-1} (when water temperature reached values above 13 °C) in order to ensure a concentration of dissolved oxygen higher than 7 mg l^{-1} . Water velocity was monitored at 32 points in the tank, at two depths and at three different overall water flows (3, 5 and 7 l s^{-1}) using an electromagnetic flow meter (Marsh-McBirney Flo-Mate 2000, accuracy $\pm 2\%$, HACH Company, Frederick, MD, U.S.A.), in order to compare the swimming speed of the fish with the water velocity (Fig. 1B). Natural photoperiod was maintained by an external light sensor that controlled a 125 W high pressure mercury vapour light situated above the tank producing a white light with an intensity of 50 lx on the tank surface. Except during the constant darkness experiment, fish were fed by hand 6 to 8 times a day *ad libitum* with commercially available food (Skretting, Fontaine Les Vervins, France), between 7:45 am to 4:00 pm Universal Time (UT) from January to March, and from 6:45 am to 1:30 pm (UT) from April to August. Fish mean length increased from 14.9 ± 20 (SD) mm in February to 272 ± 27 (SD) mm at end of August.

2.3. Movement monitoring

The experimental tank contained 1500 fish including tagged individuals. Fish movements were continuously monitored in the experimental tank from January to August under natural conditions of photoperiod and temperature. The experiment was repeated during four years (2005–2008).

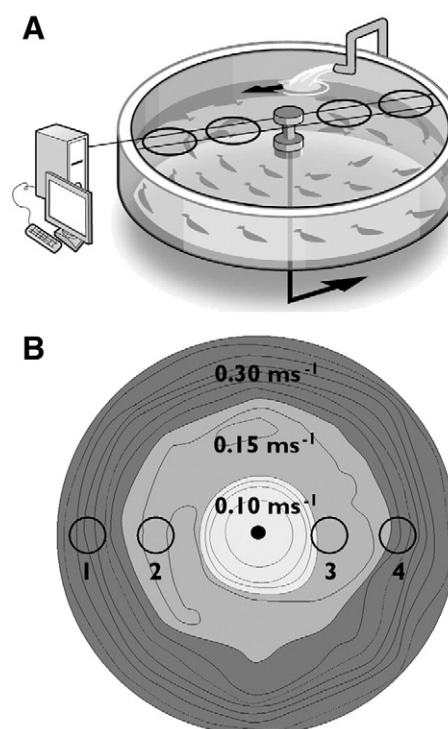


Fig. 1. Diagram of the experimental tank and swimming activity monitoring system. The 9 m diameter experimental tank with 1,500 juvenile salmon was supplied with running natural river water, under natural photoperiod. An anti-clockwise water flow was produced by tangent water supply and evacuation via a central drain (A). The various water flow speeds in the tank for 5 l s^{-1} water supply are represented by 0.025 m s^{-1} isochrones (B). The 4 detection antennas were held by two cables on the surface of the water. Swimming activity of 7 individually tagged fish was recorded continuously from January until August.

Visual observations of overall fish swimming behaviour were made every day at feeding time and classified as: fish facing the current (positive rheotactic behaviour) with no movement; fish facing the current (positive rheotactic behaviour) and swimming upstream against the current; fish swimming downstream with the current (negative rheotactic behaviour). Some observations were also made at night under quick lighting or under red light.

A new PIT tag detection system, using radio frequency, was developed to monitor detailed movements of some individuals. It was composed of a series of four antennas (each 85 cm in diameter) placed across the diameter of the tank, 8 cm above the water surface (Fig. 1A–B). The horizontal position of the antennas above the water surface allowed the antennas to detect transponders located directly below them with 100% efficacy up to the tank maximal depth of 0.7 m. The system was multiplexed to avoid interference between antennas. An antenna was activated for 50 ms then read for 200 ms before moving to the next antenna, thus performing a complete cycle in 1 s. Each time a PIT tagged fish was detected by an antenna, the software system recorded the tag number, the antenna number and the date and time of detection. After simulation of fish detection using Matlab (MathWorks, Natick, MS, USA) and preliminary tests, the number of PIT tagged fish in the experimental tank was limited to 7, in order to avoid the risk of detection interferences between different tagged fishes.

2.4. Fish tagging

For tagging, fish were anaesthetised in 0.04 ml l^{-1} eugenol. In 2005, external PIT tags (length: 31.2 mm, diameter: 3.85 mm, RI-TRP-RR2B read-only, Texas Instruments, Dallas, TX, USA) were attached on anchor tags implanted on the left side of the fish at the base of the dorsal fin, using a Floy Mark II tagging gun. The procedure was repeated in 2006, 2007 and 2008 using the same tags but with internal tags. A small incision was made with a scalpel along the ventral midline anterior to the pelvic fins in order to insert the tag directly in the abdominal cavity. The incision was sealed using Vet-bond Tissue Adhesive (3 M, St Paul, MN, USA), fish were placed in a temporary recovery tank, perfused with oxygen, for 30 minutes and returned to the experimental tank. Procedures were carried out under the supervision of authorized investigators (G.B and S.D.) in

accordance with the License for Animal Experimentation for Basic Scientific Research delivered by the French National Authorities.

2.5. Swimming speed evaluation

In the experimental tank, a PIT tagged salmon could be detected successively by the same antenna, the adjacent antenna or one of the two diametrically opposite antennas. Only detections between diametrically opposite antennas (e.g. 1–3, 1–4, 2–3, 2–4; Fig. 1A–B) were used to calculate distance travelled and swimming speed (Fig. 2A–B). Distance travelled was defined as mean circular distance between two opposite antennas. Computer data provided, for each tagged fish, cumulated distance travelled every hour. Results were then expressed as swimming speed (m s^{-1}) for each PIT tagged fish. The water velocity measured at 3 m from the centre of the experimental tank (the average distance of the antennas from the centre of the tank) was used to compare the swimming speed of the fish with the water velocity.

2.6. Experimental changes in photoperiod

The influence of natural photoperiod on fish swimming behaviour was assessed during the period of January to August during the four experiments (2005–2008). Additionally, fish movement was monitored under different experimental photoperiod regimes: constant dark and constant light during the period of highest swimming activity (from late April to early May, in 2005). For the constant light experiment illumination was kept constantly on for 103 hours with feeding maintained occurring as prior to light change. For constant darkness experiments, the tank was covered with an opaque black cover 6 hours before night-fall for a period of 76 h with no feeding.

2.7. Statistical analysis

Data are presented as mean swimming speeds (m s^{-1}) per hour (Figs. 2, 3, 5, and 6) or per month (Fig. 4) \pm SEM. The significance of the differences between means was assessed by Student's *t* test or ANOVA analysis. Nonlinear regression test was performed using GraphPad Prism version 5.00 for Windows (GraphPad Software, San Diego California USA).

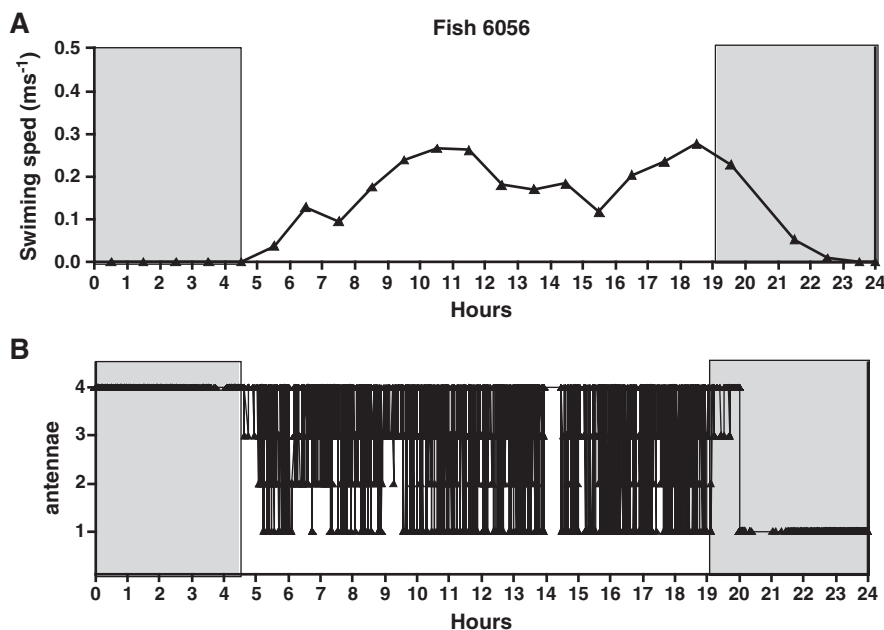


Fig. 2. Example of a daily recording of swimming activity via antenna detection for one individual fish. Fish swimming speed is expressed in m s^{-1} (A). Each detection by antennas 1 to 4 is plotted (B). The white and grey zones represent the duration of day and night, respectively (natural photoperiod).

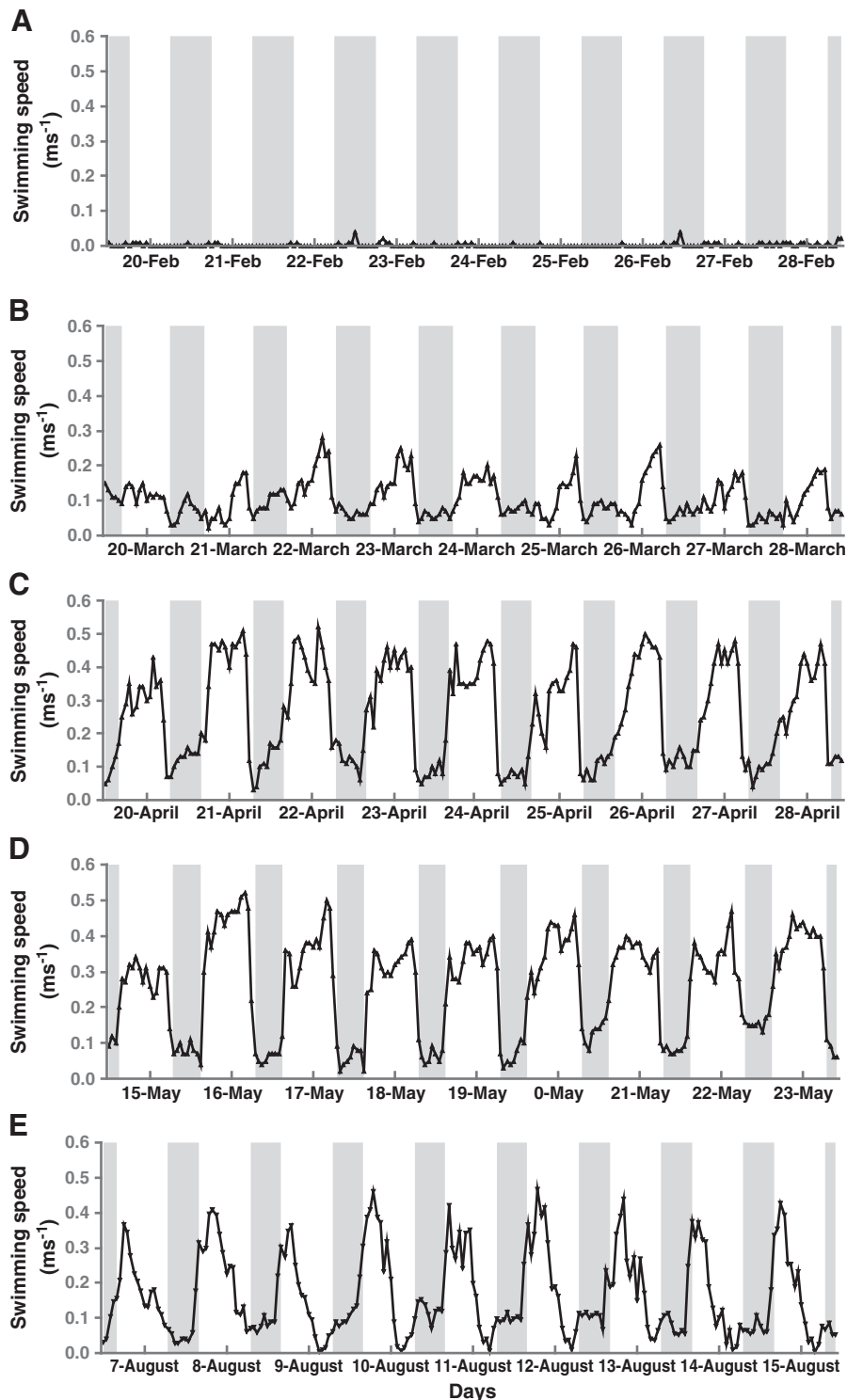


Fig. 3. Individual daily recordings of swimming activity from February to August 2005. Fish swimming speed is expressed in m s^{-1} . The white and grey zones represent the duration of day and night, respectively (natural photoperiod).

3. Results

3.1. Behavioural change

During the winter, all fish faced the current (positive rheotactic behaviour) and did not exhibit any net movement. However, some increased mobility was observed in relation to water turbidity from flooding events in the river (data not shown). During these periods, some fish swam against the flow while others slipped with the flow

until the water cleared, movement stopped and the fish resumed positive rheotactic behaviour.

In early spring, some of the fish started to exhibit down-flow movement independent of flooding events. This behaviour was intermittent, with phases of down-flow movement interrupted by sustained periods of positive rheotactic behaviour without significant movement. Then eventually all fish presented negative rheotactic behaviour and undertook a rotational shoaling movement until summer. The time when all fish in the tank started to exhibit the same negative

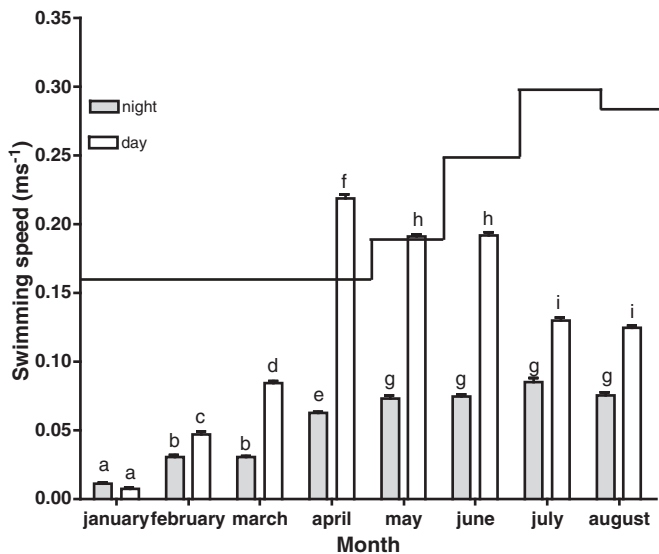


Fig. 4. Monthly variations in salmon nycthemeral swimming activity. Fish swimming speed is expressed in m s^{-1} . Data are presented as means \pm SEM of swimming speed for the 7 tagged fish during the day (white bars) and during the night (dark bars) for each month. For comparison with swimming speed, the water flow speed of the tank in m s^{-1} is represented by a black line.

rheotactic behaviour ranged from mid March to early April, depending on the year. Movement was maximal from April to May and then gradually declined.

3.2. Pattern of activity

A distinct behavioural difference between diurnal and nocturnal activity was observed. All individual recordings based on PIT tags showed that activity was very low at night. During the night, tagged fish were either 1) not detected at all, 2) detected continually by the same antenna, or 3) detected at a low frequency between two opposite antennas. Visual observations confirmed that the fish were mostly immobile, facing the current. In contrast down-flow movements were recorded for all fish during the day, starting from mid March to early April, depending on the year.

A sample record of mean hourly swimming speed for different months of the year 2005 for individual fish is shown in Fig. 3. Fish showed no activity during the day or the night in February (Fig. 3A), but a high diurnal swimming activity was often recorded from March (Fig. 3B) until August (Fig. 3E). During this period the swimming activity was much lower during the night than during the day (Fig. 3B–E). This nycthemeral pattern of activity was observed in all years of study.

Mean monthly swimming speeds of all tagged fish (2005 to 2008), presented in Fig. 4, showed highly significant variations between day and night and between months (ANOVA $P < 0.001$). A significant difference between day and night speeds became apparent in February and was maintained until August ($P < 0.001$). Daytime speed increased sharply between March and April ($P < 0.001$), was flat until June, and then significantly decreased in July ($P < 0.01$). Daytime swimming speeds for April were above the average water velocity indicating active swimming.

3.3. Effects of experimental changes in photoperiod

Subjecting fish to constant darkness during the period of highest activity (from late April to early May) caused a change in swimming activity (Fig. 5A). As soon as the black cover was placed over the tank, a sharp decline in swimming speed was observed during the day, similar to that observed every night when the lights were

switched off. Recorded swimming speeds no longer reached the high values observed during the day but remained in the range measured during the night and the marked nycthemeral activity pattern observed under normal photoperiod conditions was strongly reduced. However, a weak “residual” cyclic activity was still detected and was concomitant with the recorded variations in water temperature (Fig. 5A). Swimming speed returned to high diurnal values immediately after the removal of the black cover and restoration of normal light conditions. The mean daily maximum swimming speed recorded during the 76 hours of constant darkness ($0.15 \text{ m s}^{-1} \pm 0.018$) was significantly lower ($P < 0.001$) than that recorded before ($0.32 \text{ m s}^{-1} \pm 0.02$) or after ($0.46 \text{ m s}^{-1} \pm 0.02$) constant darkness was imposed. The mean daily minimum swimming speed did not vary significantly throughout the experiment.

Applying constant light also induced a change in the daily pattern of activity (Fig. 5B). Swimming speed no longer decreased to the low value normally observed during the night. However, residual cyclic activity could still be observed as in the constant darkness experiment and was also concomitant with the daily variation in water temperature. When the natural photoperiod cycle was reinstated, nocturnal activity decreased drastically to values similar to those previously observed during the night. The mean daily minimal swimming speed recorded during the 103 hours of constant light ($0.21 \text{ m s}^{-1} \pm 0.01$) was significantly higher ($P < 0.001$) than that recorded before ($0.08 \text{ m s}^{-1} \pm 0.01$) or after ($0.01 \text{ m s}^{-1} \pm 0.01$) the experiment. The mean daily maximum swimming speed did not vary significantly throughout the experiment.

3.4. Role of temperature in the modulation of movement

An analysis of all mean hourly values of swimming speeds ($n = 13,600$) of all tagged fish (year 2005 to 2008) is shown in Fig. 6A. Swimming activity during the day increased with temperature, peaking at around 10°C and then slowly decreasing up to 13°C . For temperatures from 8 to 13°C , the swimming speed was higher than the water speed (0.16 m s^{-1}), indicating an active swimming behaviour. For temperature above 13°C , the water flow was increased to maintain oxygen level (see Material and Methods) where swimming speed remained constant from 13 to 19°C at which point it dropped significantly. For temperatures above 20°C the fish switched back to positive rheotactic behaviour but with no net movement (data not shown). Swimming speed was much lower during the night than during the day for temperatures above 3°C . A steady increase in night swimming speed was recorded for temperatures up to 10°C while a drop in night swimming speed was observed for temperatures above 17°C .

To infer the effect of temperature on activity under constant water flow, the reference water speed was set at the mean baseline of 0.16 m s^{-1} and the swimming speed differential was calculated for temperatures above 13°C (Fig. 6B). The correlations between water temperature and swimming speed corresponded to Gaussian distribution curves for day ($r^2 = 0.91$) and night ($r^2 = 0.48$). The calculated optimum temperature was 10.5°C (day) / 11°C (night), and swimming speed was reduced by more than 80% for temperatures lower than 4°C or higher than 17°C .

4. Discussion

4.1. Experimental system for monitoring swimming activity

The experimental set-up using large hatchery tanks allowed us to follow the free movements and measure swimming speeds of individual tagged juvenile salmon in a large cohort (1,500 individuals) continuously over a period of eight months. The experimental period (January to August) spanned the period of natural downstream seaward migration. The experiment was repeated on independent

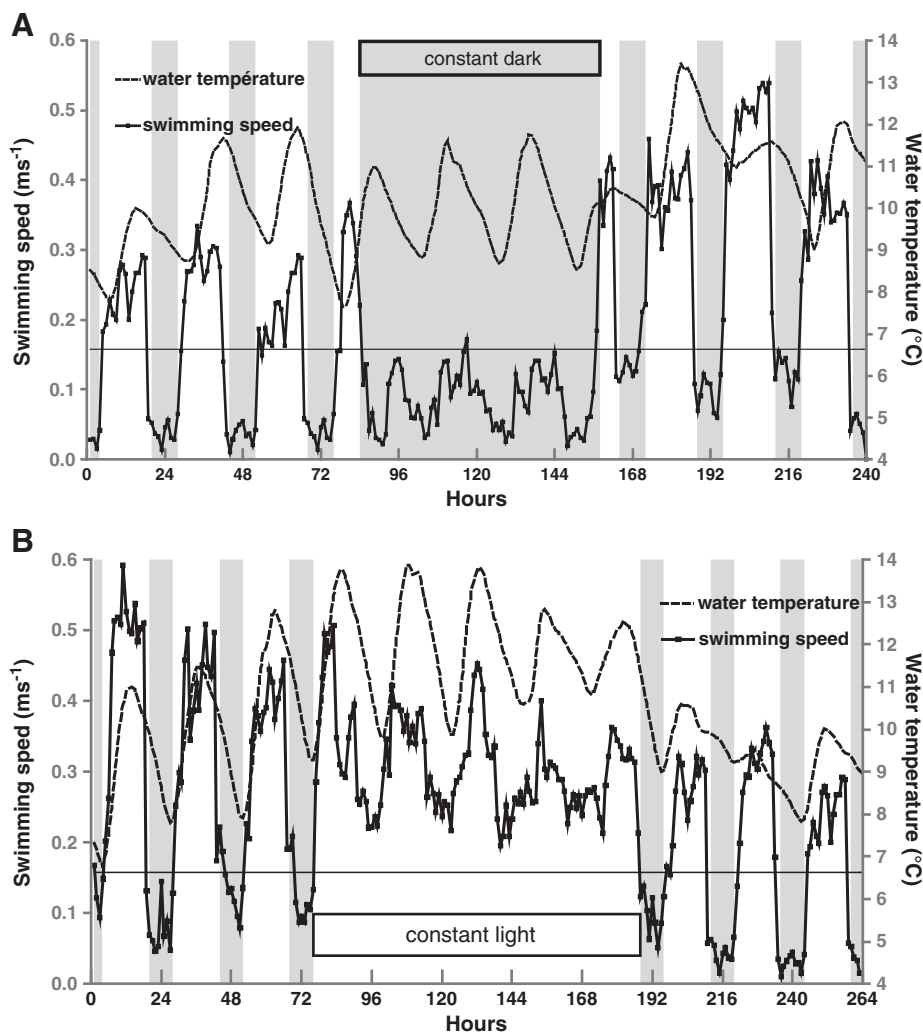


Fig. 5. Swimming activity during constant dark or constant light. Fish swimming speed is expressed in m s^{-1} . Each point represents the mean activity of the 7 tagged fish. The white and grey zones represent the duration of day and night, respectively (natural photoperiod). For testing the effect of constant darkness (A) the tank was covered with an opaque black cover. For testing the effect of constant light (B) the light was kept on. The dotted line indicates water temperature.

batches of fish during four consecutive years (2005–2008). Previous studies on Atlantic salmon and Brown trout (*Salmo trutta* L.) smolt behaviour in enclosed environments were carried out either in an elliptic channel or flume (Thorpe et al., 1988), or in smaller circular tanks (Pirhonen et al., 1998; Zydlewski et al., 2005) in which fish were forced to move within a restricted zone, guaranteeing detection using actograph technology (Moore et al., 1995, 1998a). Our system, with water input in the periphery and outlet in the centre of the tank, produced variable flows with gradients ranging from less than 0.1 to 0.5 m s^{-1} . This enabled smolts to use different zones characterised by different water speeds.

Juvenile salmon completed smoltification in the experimental hatchery tank during the study period, as indicated by various characteristic parameters such as silvering of body skin, increase in gill NaK-ATPase gene expression (maximum in April, Martin and Zydlewski, unpublished data), increase in pituitary thyrotropin and growth hormone gene expression (peak in April, Rousseau et al., 2011), in addition to the reported switch from positive to negative rheotactic behaviour.

Fish in January and February, exhibited positive rheotactic behaviour, facing the water current with no net movement but rapidly switched and showed typical negative rheotactic behaviour in mid March or April, depending on the year. This continued for the remaining months of the experiment. Comparison with captures of smolts in the river Allier at

the level of the hatchery indicated that the initiation of downstream migration occurred during the same period in the natural environment (data not shown).

4.2. Differential nocturnal and diurnal swimming activity

Many studies have reported the downstream migration of salmonid smolts to be predominantly nocturnal (Aarestrup et al., 2002; Antonsson and Gudjonsson, 2002; Greenstreet, 1992; Hansen and Jonsson, 1985; Hoar, 1976; Hvidsten et al., 1995; Mason, 1975; Moore et al., 1995, 1998a,b; Northcote, 1962; Thorpe et al., 1981). In contrast, others have reported diurnal downstream movement (Baglinière, 1976; Davidsen et al., 2005; Lacroix and McCurdy, 1996; Pirhonen et al., 1998; Solomon, 1978; Thorpe et al., 1988). Still others have demonstrated that smolts change from an overall pattern of initial nocturnal to later diurnal migration (Bangsgaard et al., 2006; Fångstam et al., 1993; Ibbotson et al., 2006; Lundqvist and Eriksson, 1985; McCormick et al., 1998; Moore et al., 1995; Österdahl, 1969; Thorpe and Morgan, 1978).

Our observations clearly showed daily variations in swimming activity. During the day, high swimming speeds could be recorded in the experimental tank, with values sometimes greater than the velocity of the water. In contrast during the night, only very slight movements were observed, with fish mainly stationary. No change

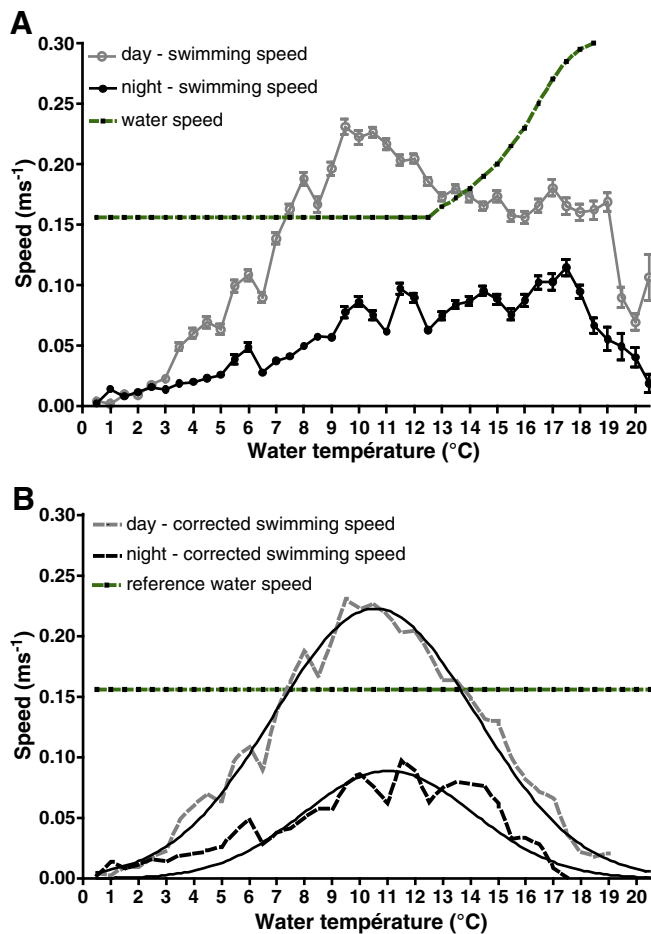


Fig. 6. Correlations between water temperature and diurnal or nocturnal swimming activity during the entire experiment. **A:** Fish swimming speed. Each point represents the mean \pm SEM of day (white) or night (black) swimming speeds of the tagged fish, for a given temperature, over the entire experiments (from January to August, and for the years 2005 to 2008). Water flow speed is represented by a dot line. Water flow had been progressively increased for temperatures above 13 °C to maintain constant oxygen level. **B:** Fish swimming speed after correction by considering a reference constant water flow in the tank. A non-linear regression using a Gaussian curve is presented for the day (mean 10.55, SD = 3.658, $r^2 = 0.91$) and for the night (mean 11.04, SD = 3.084, $r^2 = 0.48$).

in this cycle of activity was observed between different periods of study, across months and between years. This demonstrates that there is a major role of photoperiod in the daily rhythm of swimming activity.

The differential nocturnal and diurnal swimming activity was observed under natural photoperiod. Under the experimental changes of light regime, constant light prevented the large decrease in swimming speed normally observed during the night, while constant darkness prevented the large increase normally observed during the day. Initial daily changes in swimming speeds were recovered as soon as the normal photoperiod was re-established. This is consistent with Godin (1981) who demonstrated a circadian rhythm in the swimming activity of juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum), where an experimental change in the light cycle desynchronised their activity, with rapid resynchronisation when the previous light cycle was restored. However a residual daily variation in swimming speed could still be observed in our experiments under constant light or constant darkness. As these residual changes were concomitant with variations in water temperature, this suggests that daily temperature variations may also contribute to the differential nocturnal and diurnal swimming

activity. The observations that our hatchery-reared fish showed reduced swimming activity during the night (only 20% of the total distance travelled during the day) could well impact the duration of downstream migration especially in long river systems.

Salmon stock enhancement programmes that involve the hatchery-rearing of smolts for release to the wild should endeavour to ensure that the fish are behaviourally and physiologically in phase with local wild populations. Solomon (1982) and Moore et al. (1998b) argue that the presence of predators in the natural environment could be a factor driving the nocturnal migration of smolts. Furthermore, in the present study, unlike under natural conditions, regular and repeated actions associated with hatchery-rearing (including feeding) tend only to occur during the day. These actions could induce a biorhythm for the fish which can affect their behaviour and swimming activity. Further studies are required to compare daily swimming activity of hatchery-raised and wild salmon smolts, in the experimental setup in the hatchery, as well as in natural conditions using radio tracking.

4.3. Passive or active swimming behaviour

Some authors have reported passive movement during the downstream migration of Atlantic salmon smolts under natural conditions (McCleave, 1978; Thorpe et al., 1981; Tytler et al., 1978). In an experimental study, Pirhonen et al. (1998) also reported that downstream migration of trout smolts was largely passive. However, other authors report active movement (Davidsen et al., 2005; Hansen and Jonsson, 1985; Kallenberg, 1958; Kennedy et al., 1984; Lacroix and McCurdy, 1996; Solomon, 1978). Fångstam (1994) indicated that smolts use river current for their downstream migration but also swim actively during about 10% of the time. Active swimming may enable smolts to avoid obstacles and seek areas of high velocity (Jonsson et al., 1991). Our experimental system allowed us to show that during day time the swimming speed in a down flow direction could be much higher than the average current speed, demonstrating active movements. For a water velocity of $0.16 \pm 0.12 \text{ m s}^{-1}$, swimming speed could reach a maximum of 0.55 m s^{-1} .

Pedersen et al. (2008) found that wild smolts had a greater swimming capacity than hatchery-reared smolts. Factors, such as condition factor, fin condition or selection, in which experimental fish used may differ, may explain this discrepancy. Our studies demonstrate that hatchery-reared smolts are able to perform active swimming but further studies are needed to compare the swimming speeds of hatchery-reared and wild smolts from the Allier River in order to evaluate their respective swimming capacities. These may differ.

4.4. Role of temperature in swimming activity

The present study did not directly address the effect of temperature on migratory behaviour. However, the comparison between the swimming speed and the natural variations in water temperature highlights the possible role of temperature in the initiation and progress of downstream migration. In our experiment, initiation of negative rheotactic behaviour occurred from mid-March up to beginning of April, depending on the year. This corresponds to a water temperature between 4 and 8 °C. This is potentially important as there is great variation between river systems and salmon populations regarding the temperatures reported to initiate downstream migration: they range from between 1.7 °C and 4.4 °C on the Orkla River in Norway (Hvidsten et al., 1995) to between 8.5 °C and 13 °C on the Varzuga River in Russia (Veselov et al., 1998). Thus the temperature needed to initiate downstream migration is probably an adaptive response of each population to its river environmental conditions.

Many studies have reported that an increase in temperature initiated downstream smolt migration (Baglinière, 1976; Fried et al., 1978; Jonsson and Ruud-Hansen, 1985; Jonsson et al., 1991; Mills, 1964; Österdahl, 1969; Raymond, 1979; Solomon, 1978; White, 1939). Some authors suggest the existence of a temperature threshold that must be reached before fish begin to migrate (Mills, 1964; Österdahl, 1969; Solomon, 1978; White, 1939). However, Zydlewski et al. (2005) report evidence that cumulative water temperature (degree-days) was more relevant to the initiation of downstream movement than temperature threshold. In contrast, our data suggest that an increase in temperature was necessary but not sufficient to initiate migration. Indeed, in 2008 the temperature rose by 3.5 °C to 7.5 °C over 6 days in March without the occurrence of downstream movement (data not shown).

In the present study, recorded fish activity suggests that temperature could modulate not only the initiation but also the progress of downstream migration. The ideal temperature for downstream movement was indicated to be between 7.5 °C and 13.5 °C with a maximal swimming speed for 10.5 °C. Swimming speed appeared to be reduced by more than 80% for temperature lower than 4 °C or higher than 17 °C and downstream movement was stopped for temperature above 20 °C.

These observations point to the possibility that elevated water temperature in the Loire river (2 °C increase over the past 24 years, Gosse et al., 2008; Lair and Reyes-Marchant, 2000), due to anthropogenic influence from cities, industries and nuclear plants, could negatively affect the progress of downstream smolt migration. At the same time there has been a reduction in water flow due to extraction for agriculture and industry and the presence of in-river obstructions such as dams. Collectively these factors could significantly delay, or even stop smolt migration in long rivers, with potentially severe implications for smolt survival and the viability of the Allier stock.

4.5. Local adaptation of populations and environmental changes

The results of the current study, taken in conjunction with other studies, suggest that each river stock or even individual tributary population may have a unique light/temperature response profile. This profile is likely to be shaped by natural selection to optimize migration behaviour for the particular environmental circumstance confronting each stock or population. It will match the ecological environmental window when migration is possible and optimal for completion of the life-cycle. In some rivers such as the Loire, the window for smolt migration, when temperatures (Moatar and Gailhard, 2006) along the whole length of the river are low enough for survival, can be very restricted. The same situation may prevail in some northern rivers in respect of estuary temperatures except that these may be lethally low (Jutila et al., 2005). These considerations suggest that most if not all salmon populations will be ecologically and environmentally constrained in respect of their downstream migration and that it is likely that each will be heritably different and locally adapted; heritable differences in smolt migration behaviour are known (Stewart et al., 2006). Understanding this aspect of local adaptation and how it might be potentially impacted by environmental changes is highly relevant to defining the restoration needs of threatened stock such as those of the Loire-Allier. Mismatch between the heritably defined profile and the environment brought about by anthropogenic environmental change will reduce fitness and, where change is to rapid, may be a factor underlying reduced stock abundance. Understanding the extent of heritable variant within and among populations may also manager to design habitat management supportive breeding programmes that minimize this mis-match.

5. Conclusion

Our study has provided new data on the swimming activity and behaviour of hatchery-reared smolts. Monitoring of swimming

speed revealed specific nycthemeral behaviour, with active down flow movement during daytime and very little movement during the night. Our data also highlight the importance of water temperature for the modulation of downstream movement. The development of temperature-dependent migratory profiles should allow restocking programme managers to select populations best-suited to local environmental conditions. Predictive models of changing habitat with climate change have been planned for diadromous species (Lassalle et al., 2008) including Chinook salmon (*Oncorhynchus tshawytscha*) (Battin et al., 2007). We advocate taking into consideration the thermal stress associated with downstream migration in the development of these models.

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