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Synchrony in the downstream migration of smolts and upstream migration of adult Atlantic salmon in the subarctic River Utsjoki

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Seasonal and diel migration timing of wild Atlantic salmon *Salmo salar* smolts and adults were investigated annually (2001–2004) in the subarctic River Utsjoki, a tributary of the large River Teno (70° N), using underwater video monitoring. Submerged video cameras provided information on the exact timing and intensity of both migrations in a natural river channel, without disturbing the fish. In contrast to the mainly nocturnal migration pattern described from temperate rivers, the River Utsjoki smolts and adults migrated throughout the day. Smolts migrated most intensively during hours of rising (0300–0900 hours) and high sun (0900–1500 hours), while adults favoured the period of low sun (2100–0300 hours). Smolt migrations started in June and lasted on average 42 days. Adults usually ascended the site 2–3 weeks before the first descending smolts were observed and the adult migrations extended to the end of August. Seasonal synchrony was observed between smolt and adult migrations in years of slowly warming water, whereas in a year of exceptionally warm early summer (2002), smolts migrated earlier than adults. Thus, water temperature seemed to be an important environmental factor triggering the smolt migration, while the migration of adults was probably more fixed to a certain season. Weak positive correlations between fish counts and water temperature were observed, indicating that increasing water temperature may have promoted both smolt and adult migrations. The influence of discharge was negligible, although increasing discharge late in the season may have activated the remaining individuals in both groups.

Key words: migration timing; *Salmo salar*; subarctic; synchrony; video monitoring.

INTRODUCTION

Anadromous Atlantic salmon *Salmo salar* L. perform extensive migrations between fresh and sea water during their life cycle, and show precise homing to the natal river they left as smolts (Hansen *et al.*, 1989; Youngson *et al.*,

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1994). Therefore, Atlantic salmon is an excellent species for migration studies by static, point observation methods enabling the monitoring of migration timing and intensity. Typically, smolt migration occurs during a relatively short period in spring or early summer (Österdahl, 1969; Hesthagen & Garnås, 1986; Davidsen *et al.*, 2005), whereas the upstream ascent of adults to rivers is known to last at least some months (Jensen *et al.*, 1986; Niemelä *et al.*, 2000) or it may extend throughout the year (Hawkins, 1989; Welton *et al.*, 1999). The diel or seasonal variations in the timing of migrations are affected by environmental factors (Jonsson, 1991).

The timing of Atlantic salmon smolt migration is considered to be crucial for later survival (Hansen, 1987; Hvidsten *et al.*, 1995) because optimal periods for seawater entry may be brief. If the smolt migration is either too early or delayed, smolts can meet unfavourable oceanic temperatures and feeding conditions and suffer increased mortality (Jonsson & Jonsson, 2004). Obviously, evolutionary mechanisms have evolved to ensure the smolts migrate at the right time of the year (Österdahl, 1969). Photoperiod is considered to be the mechanism preparing juveniles to undergo parr–smolt transformation and thus be prepared for migration (McCormick *et al.*, 1987). Water temperature and discharge have been identified as the most important factors affecting the overall timing of the migration, although the proximate factors triggering smolt migration may vary between streams (Österdahl, 1969; Hesthagen & Garnås, 1986; Jonsson, 1991; Erkinaro *et al.*, 1999; Byrne *et al.*, 2003).

For adult Atlantic salmon, the timing of river entry and subsequent upstream migration is a major factor affecting their survival, because of human fishing pressure and environmental conditions (Solomon *et al.*, 1999; Opdahl, 2005). For example, Atlantic salmon ascending at the time of peak fishing effort may suffer from elevated fishing mortality, whereas low water-flow conditions in small rivers may adversely affect the survival of ascending Atlantic salmon (Solomon *et al.*, 1999). Atlantic salmon from different parts of a river system may ascend at different times (Stewart *et al.*, 2002), indicating a genetic influence on run timing. Environmental factors like water temperature and discharge, however, affect the initiation and intensity of Atlantic salmon ascent in several rivers (Jensen *et al.*, 1989; Jonsson *et al.*, 1990; Gowans *et al.*, 1999).

Usually, Atlantic salmon migration studies have focused on either seaward migration of smolts or upstream migration of adults, and their possible links may have remained undetected. For example, it is possible that both smolts and adults react similarly to changing environmental conditions in the spring and early summer, which may be seen as synchronous migration timing. The point observation methods normally require man-made constructions extending across the whole river, forcing fish to swim through an observation zone or device. This may alter the migratory behaviour of Atlantic salmon, leading to biased results (Banks, 1969; Whalen *et al.*, 1999). Underwater video surveillance, enabling undisturbed observations, has been used to count ascending Atlantic salmon or descending smolts during the last 20 years (Irvine *et al.*, 1991; Hatch *et al.*, 1994; Lamberg *et al.*, 2001; Welton *et al.*, 2002), but it is only recently that the method has been used to monitor both migrations simultaneously (Orell, 2003). Although video recording systems have usually been placed in association with man-made structures, like fish ladders or counting fences (Lamberg *et al.*, 2001), they can also be utilized in natural channels (Davidsen *et al.*, 2005).

In the present study, the temporal migration patterns of descending Atlantic salmon smolts and ascending adults were studied in the subarctic River Utsjoki in a 3 year period (4 year period in diel timing analysis). By use of an array of submerged video cameras covering the water column across the river, the exact timing of both migrations were monitored simultaneously without influencing the fish behaviour. The main goal of this study was to detect possible seasonal and diel relationships in timing between descending smolts and ascending adults. In addition, the possible role of environmental factors, like water temperature and water discharge, affecting the migration initiation and activity of the fish was studied.

MATERIALS AND METHODS

STUDY AREA

The River Teno (Tana in Norwegian) watercourse (catchment area 16 386 km^2) is located in Northern Europe between Finland and Norway (70° N; 28° E) and it drains *via* Tanafjord to the Barents Sea (Fig. 1). It is one of the largest and most productive Atlantic salmon rivers in Europe, with annual river catches between 100 and 250 t (Niemelä *et al.*, 2005) and >1200 km of the river stretches, including tributaries, accessible to ascending Atlantic salmon. The River Utsjoki (catchment area 1665 km^2) is one of the largest tributaries of the River Teno, flowing 66 km in a mountain valley before connecting to the River Teno mainstem some 106 km upstream from the sea. The mainstem of the River Utsjoki comprises large numbers of deep lakes with connecting river stretches. Two major tributaries, the Rivers Geavojohka and Carsejohka, drain to the middle part of the River Utsjoki (Fig. 1). The Atlantic salmon stock of the River Utsjoki consist of several distinct substocks (Elo *et al.*, 1994) with grilse [one sea-winter (SW) Atlantic salmon, 1 SW] populations in the two major tributaries, whereas 2–4 SW spawners form a considerable portion of the spawning stock in the mainstem. Smolt ages in the Utsjoki system vary between 2 and 7 years, but most smolts migrate at 3 to 5 years of age (Englund *et al.*, 1999).

The active upriver migration of Atlantic salmon in the River Utsjoki normally takes place between early–mid June and late July (Opdahl, 2005). The spawning period is usually between late September and early October (Karppinen *et al.*, 2004). Smolt migration usually occurs over a 4–5 week period in June and July (Davidsen *et al.*, 2005; Palerud & Reisz, 2005). A more detailed description of the study area and the fish fauna both in the mainstem (River Teno) and River Utsjoki is given by Niemelä (2004).

Because the River Teno catchment is situated in a subarctic area, the winter conditions are extreme; ice covers the rivers for *c.* 6–7 months from October to November until late May. Spring flooding usually takes place between mid-May and early June and it lasts *c.* 2–3 weeks. The mean annual discharge in the River Teno mainstem is *c.* 200 m^3 s^{-1} and that of the River Utsjoki in 2001–2004 was *c.* 13·4 m^3 s^{-1} (measured 20 km upstream from the outlet of the River Utsjoki). During the study period (May to August), the discharge varied between *c.* 4 and 40 m^3 s^{-1}. The many lakes in the River Utsjoki watercourse stabilize the variation in the water level (Fig. 2). Water temperatures vary considerably between months, from October to May water temperature is constantly <1° C and in summer (June to August) it may occasionally exceed 20° C. In 2002–2004, mean daily water temperatures in the River Utsjoki over the study period varied between 3·5 and 19·8° C (Fig. 2). Polar day conditions, 24 h sunlight, prevail over 2·5 months from mid-May until the end of July.

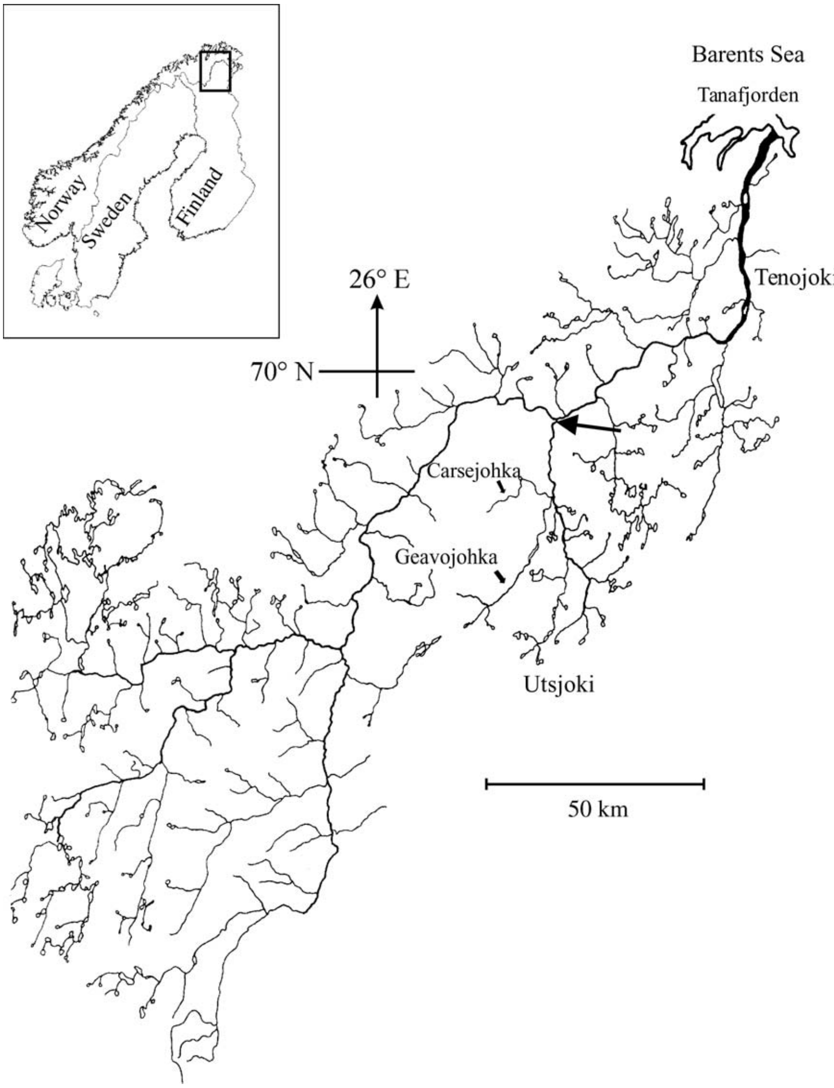

FIG. 1. The map of the River Teno watercourse showing the location of the River Utsjoki and its major tributaries. →, the location of video cameras.

SAMPLING METHODS

The descending smolts and ascending adult Atlantic salmon were monitored by underwater cameras *c.* 200 m upstream from the confluence of the Rivers Utsjoki and Teno. In the pilot phase of the study (2001), only one camera was used, but in other years (2002–2004) eight cameras were installed in the river. Videotaping was initiated after the ice break-up and spring flooding, as soon as it was possible to work in the river and conducted mainly between June and August (Table I). The installation and the use of the cameras, as well as the video recording system, is described in detail by Davidsen *et al.* (2005) (Fig. 3). The shallow-water area, between riverbanks and bridge pillars, was only monitored in 2004 and the observations showed that migrating adults did not use this area at all and only a negligible proportion of smolts (*c.* 2%)

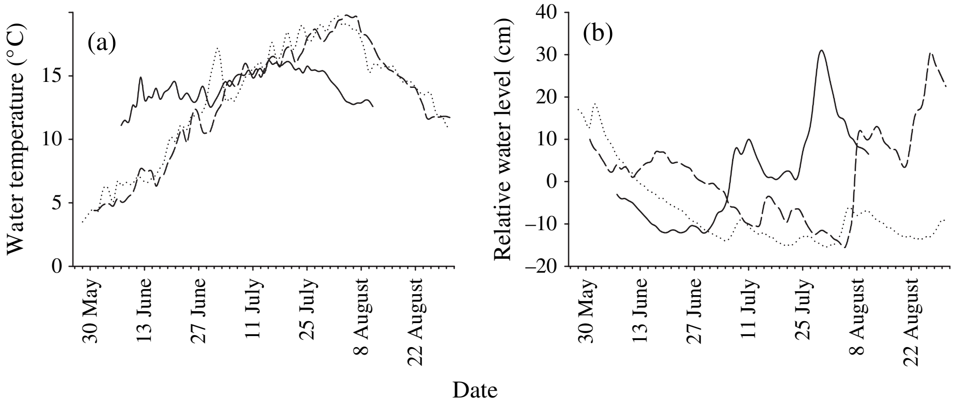

FIG. 2. Mean (a) daily water temperatures and (b) relative water levels in the River Utsjoki in 2002 (——), 2003 (-----) and 2004 (- - -).

migrated through this area (Fig. 3). Artificial infra-red light (wave length *c.* 730 nm) illumination was used at nights after *c.* 10 August in 2003–2004. This was not possible in 2002, and the monitoring was finished on 11 August, because of dark nights.

The videotapes were analysed with Panasonic video recorders (AG-TL 700 and AG-7355; Panasonic, Kadoma, Japan) and black and white monitors (JVC TM-A140PN; JVC, East Kilbride, Scotland, U.K., and Panasonic WV-CM 140) by experienced staff. Numbers of descending smolts and ascending adults and the date and time they passed the cameras were recorded. Every individual adult Atlantic salmon was counted, whereas estimation of the numbers of smolts (repeated counts, numbers round up to nearest 10) was occasionally necessary, when smolts migrated in a dense school. The video equipment, however, enabled frames to be frozen and slow motion pictures from several cameras were used to count the numbers of fish in a passing school, increasing the estimation accuracy.

ENVIRONMENTAL DATA

Daily river discharge data were obtained from the Finnish Environment Institute (SYKE). River water temperatures were collected by automatic data loggers (TinyTalk II) placed on the river bed at the monitoring site. The temperature logging interval was between 1 and 4 h, with mean daily temperatures calculated from these data for use in subsequent analyses. Relative water level was measured with a stationary water level stick placed near the video monitoring area.

TABLE I. The duration of study periods, number of smolts and adult Atlantic salmon registered and number of underwater cameras used in 2001–2004

Year	Study period	Smolt (*n*)	Adult (*n*)	Camera (*n*)
2001	23 June to 20 July	6081	4660	1
2002	7 June to 11 August	12 851	3574	8
2003	28 May to 31 August	14 969	3041	8
2004	31 May to 31 August	26 380	1429	8

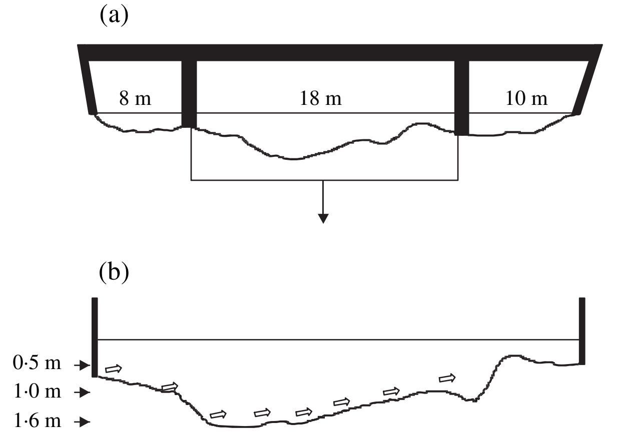

FIG. 3. Profile of the (a) bridge and river bed in the River Utsjoki and (b) centre channel river bed (⇨, the positions of the video cameras and the direction of observations in 2003–2004. In 2002, the cameras were slightly more apart from each other and the direction of observations were opposite).

STATISTICAL ANALYSES

The effect of diel solar cycle (light conditions) on smolt and adult migrations were analysed by dividing each day into 6 h periods according to the position of the sun: low (2100–0300 hours), rising (0300–0900 hours), high (0900–1500 hours) and sinking (1500–2100 hours). The frequency distributions of descending smolts and ascending adults in each period of the solar cycle were compared using the χ^2 test (Zar, 1996). In addition, the diel frequency distributions between smolts and adults were compared with the χ^2 test, the null hypothesis being: no differences in diel migration pattern between smolts and adults. Analyses were made separately for each year (2001–2004) and for pooled data (years combined).

The differences in the timing of migrations between smolts and adult Atlantic salmon in years 2002–2004 were analysed with the Mann–Whitney *U*-test (Zar, 1996). Daily numbers of both migrations were used in these analyses. Synchrony between the daily numbers of smolts and adult Atlantic salmon in each year was analysed by Spearman rank correlation (Zar, 1996). These correlations were calculated only for the yearly period when smolts were migrating (range 39–44 days). Spearman correlations were also used to analyse the synchrony in the daily numbers within smolt and adult migrations between years. The first day of migration, median date of migration (that is the day when 50% of smolts or adults had migrated through the video monitoring area), lower (Q_1) and upper quartile (Q_3) dates of migration (when 25 and 75% of smolts or adults had migrated, respectively) and the peak day of migration were calculated for each year for both smolt and adult migrations. The duration of migrations was defined for smolts, but not for adults, because a few Atlantic salmon enter the river very early or very late in the season, when the video monitoring is not conducted.

The possible effects of water temperature and discharge on the daily numbers of smolts and adults were analysed by cross correlation analysis (SYSTAT, 1996). As significant autocorrelation was observed in all the time series (temperature, discharge, number of smolts and number of adults), they were differenced once to remove the trend and render them stationary. Cross correlations (CCR) between Atlantic salmon count series and time series of water temperature or discharge were estimated with time lags of ± 5 days. A correlation for a positive time lag indicates a relationship between Atlantic salmon count series and environmental variables that number of days earlier.

The significance of the correlations (CCR) was accepted if the *c.* 95% CL for the correlation were exceeded, as presented by SYSTAT (1996).

The migration behaviour of smolts in 2002, *e.g.* swimming direction and position in the water column, has been analysed in an earlier paper (Davidsen *et al.*, 2005).

RESULTS

DIEL MIGRATION PATTERN

Although migration of smolts and adult Atlantic salmon occurred around the clock, the diel migration pattern of smolts and adults differed significantly from a uniform distribution in all years (2001–2004) (χ^2 test, d.f. = 3, $P < 0{\cdot}001$), and when years were pooled (χ^2 test, d.f. = 3, $P < 0{\cdot}001$) (Fig. 4). The diel migration patterns between smolts and adults were significantly different (χ^2 test, all years and pooled data, d.f. = 3, $P < 0{\cdot}001$). Highest proportions of smolts were usually (3 out of 4 years) observed to migrate during hours of rising sun (0300–0900 hours) and the lowest proportion either during hours of sinking (1500–2100 hours) or low sun (2100–0300 hours). On the other hand, ascending Atlantic salmon migrated most actively during hours of low sun, while the migration activity was at its minimum during hours of high sun (0900–1500 hours; Fig. 4).

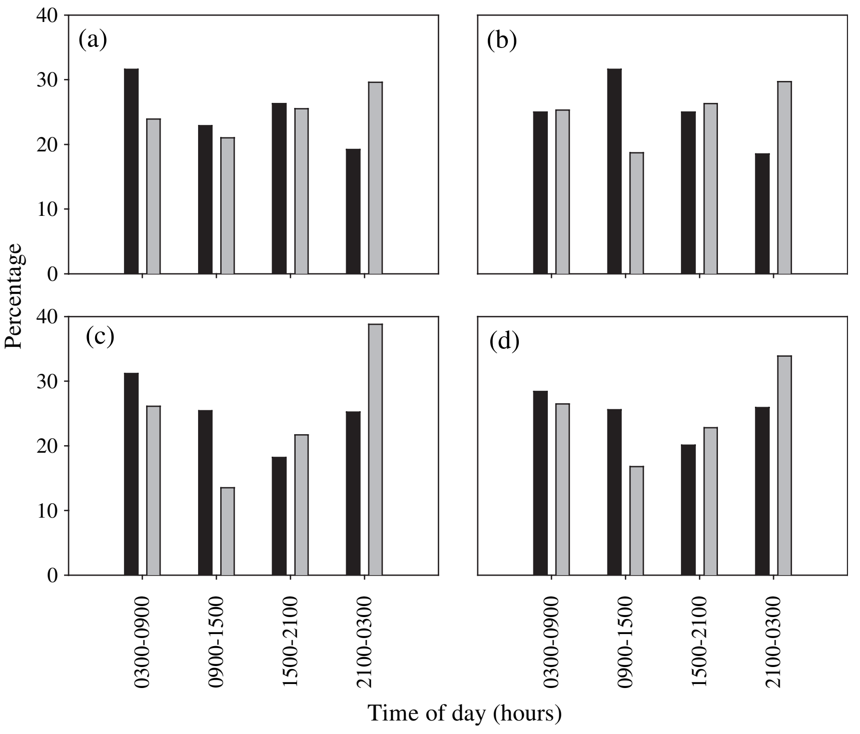

FIG. 4. Counts of smolts (■) and adult Atlantic salmon (□) in relation to diel solar cycle in (a) 2001, (b) 2002, (c) 2003 and (d) 2004 (smolts, n = 57 897 and adults, n = 12 487).

SEASONAL MIGRATION PATTERN

Smolt migrations started in June and they lasted on average 41·7 days (range 39–44 days) extending to the end of July (Fig. 5). Ascending adult Atlantic salmon were observed in the cameras at the end of May or beginning of June, *i.e.* at least some 2–3 weeks earlier than first smolts. In 2003 and 2004 when the river was monitored throughout June to August, 96 and 91% of adult fish migrated in June and July, respectively. Only small proportions were observed to ascend in August (Fig. 5). The migration timing between smolts and adults differed significantly in 2002 (Mann–Whitney *U*-test, $P < 0{\cdot}001$), whereas in 2003 and 2004 smolt and adult migrations occurred rather concurrently (Mann–Whitney *U*-test, all $P > 0{\cdot}05$) (Fig. 6). In addition, the daily numbers of migrating smolts and adults were highly correlated in 2003 (Spearman rank, $r = 0{\cdot}786$, $n = 39$, $P < 0{\cdot}001$) and 2004 ($r = 0{\cdot}838$, $n = 42$, $P < 0{\cdot}001$), while in 2002 the correlation was weaker, but significant ($r = 0{\cdot}332$, $n = 44$, $P < 0{\cdot}05$). In 2003 and 2004, the median day of migration was the same day for smolts and adults, whereas in 2002, smolts migrated 11 days earlier than adults (Table II). Thus, the migration timing between smolts and adults was more synchronous in 2003–2004 than in 2002 (Table II).

No significant correlations were found in daily numbers of smolts between 2002 and 2003 and 2002 and 2004 migrations, but a strong correlation was evident between 2003 and 2004 ($r = 0{\cdot}924$, $n = 42$, $P < 0{\cdot}001$). All comparisons between adult migrations yielded significant positive correlations. The highest correlation was found between 2002 and 2003 ($r = 0{\cdot}774$, $n = 66$, $P < 0{\cdot}001$) migrations, followed by the 2003 and 2004 ($r = 0{\cdot}771$, $n = 94$, $P < 0{\cdot}001$) and 2002 and 2004 ($r = 0{\cdot}727$, $n = 66$, $P < 0{\cdot}001$) migrations.

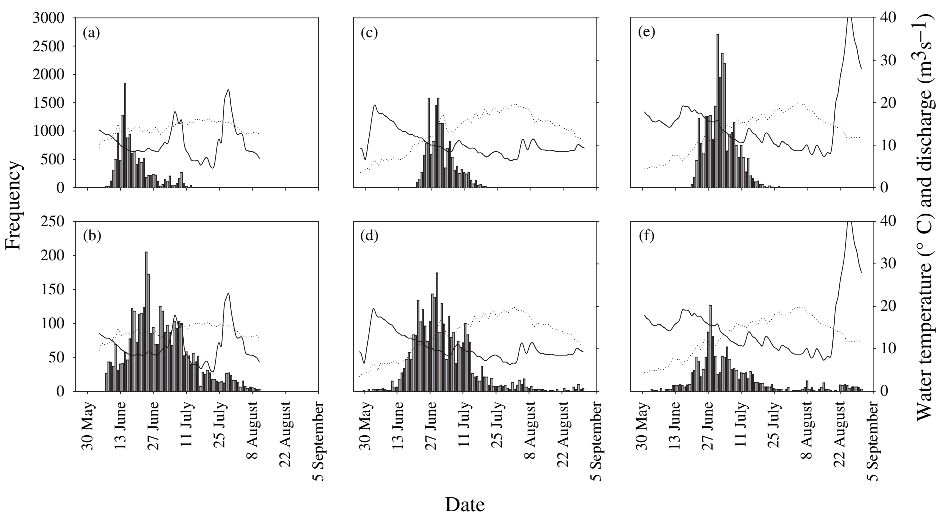

FIG. 5. Daily numbers of (a), (c), (e) smolts and (b), (d), (f) adult Atlantic salmon in relation to water temperature (-----) and discharge (——) in (a), (b) 2002, (c), (d) 2003 and (e), (f) 2004.

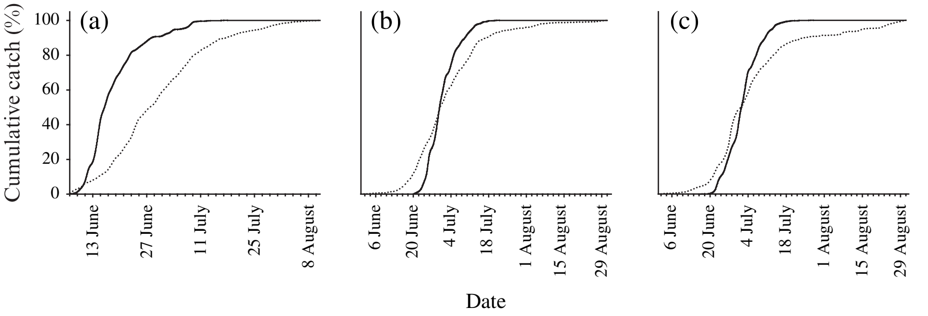

FIG. 6. Annual cumulative percentage number of smolts (——) and adult (-----) Atlantic salmon in (a) 2002, (b) 2003 and (c) 2004 through the seasons. Note the different time scales.

INFLUENCE OF ENVIRONMENTAL FACTORS ON SMOLT AND ADULT MIGRATIONS

The smolt migrations started at mean daily water temperatures between 8 and 11° C (Fig. 5). In the year of the earliest smolt migration (2002) water temperature was exceptionally high (9–11° C) at the beginning of June (Fig. 5). Some solitary adult Atlantic salmon migrated upstream at the very beginning of the monitoring period in 2003 and 2004, when the mean daily water temperatures were between 4 and 5° C. The adult migrations, however, were activated at temperatures ≥7–8° C (Fig. 5). Variation in the rate of the adult Atlantic salmon upstream migration was weakly correlated with changes in water temperature in 2002 (lag 3, $r = 0{\cdot}30$, $P < 0{\cdot}05$) and 2004 (lag 1, $r = 0{\cdot}28$, $P < 0{\cdot}05$), and similar weak relationship was detected for smolt migration in 2002 (lag 3, $r = 0{\cdot}34$, $P < 0{\cdot}05$).

Both smolts and adults migrated mainly during decreasing discharge in the river (Fig. 5). Daily variation in the rate of smolt or adult Atlantic salmon migration did not correlate with changes in discharge, although the migration

TABLE II. Timing (dates, time ranges) of smolt and adult Atlantic salmon migrations in the River Utsjoki in 2002–2004. Q1 and Q3 indicate the date when 25 and 75% of salmon have migrated through video monitoring area. Median date of migration is the date when 50% of fish have migrated

	Smolts			Adults		
	2002	2003	2004	2002	2003	2004
First migration day	7 June	19 June	17 June	—	30 May	3 June
Q1 date of migration	14 June	27 June	28 June	21 June	24 June	27 June
Median date of migration	17 June	30 June	2 July	28 June	30 June	2 July
Q3 date of migration	22 June	5 July	6 July	8 July	10 July	11 July
Peak day of migration	15 June	30 June	1 July	24 June	30 June	28 June
Range (days)	44	39	42	—	—	—

—, incomplete data.

activity of smolts (2002) and adults (2004) appeared to be related to increasing discharge late in the season (Fig. 5). No clear pattern between discharge and the initiation of smolt migration was evident.

DISCUSSION

In the River Utsjoki, Atlantic salmon adults and smolts migrated actively throughout the day, although the activity was somewhat higher in certain periods of the day. Differences were found between smolts and adults, smolts tending to migrate most actively in hours of rising and high sun (0300–0900 hours and 0900–1500 hours) whereas there was a slight tendency towards night-time (2100–0300 hours) migration in adults. These results are in contrast to those obtained from more southerly areas, where both smolt (Thorpe & Morgan, 1978; Youngson *et al.*, 1983; Hesthagen & Garnås, 1986; Jonsson, 1991; Riley *et al.*, 2002) and adult (Hawkins, 1989; Smith & Smith, 1997) migrations are predominantly nocturnal. Earlier studies conducted at higher latitudes, where midnight sun dominates the migration period, however, have revealed migration activity throughout the 24 h day (Erkinaro *et al.*, 1999; Lilja & Romakkaniemi, 2003; Carlsen *et al.*, 2004; Davidsen *et al.*, 2005) or have even indicated predominance of diurnal migration (Veselov *et al.*, 1998; Lilja & Romakkaniemi, 2003).

For smolts, migration during hours of darkness could be an adaptation to avoid potential sight-feeding predators, such as pike *Esox lucius* L. and goosander *Mergus merganser* (Solomon, 1982). In the subarctic area, like the River Utsjoki, midnight sun reduces any benefit associated with the cover of darkness, because light intensity remains on a high level throughout the 24 h. In these conditions, diurnal migration may even be an antipredator strategy (Davidsen *et al.*, 2005). In low water temperatures, the swimming capability of fish is reduced and they are relatively more vulnerable to endothermic predators (Veselov & Shustov, 1991). Increasing water temperatures during the daytime might, therefore, increase the ability of smolts to avoid certain predators (Davidsen *et al.*, 2005). Strong sunlight during daytime may favour the survival of smolts, because the capability of predators to detect smolts diminishes (Bakshtanskiy *et al.*, 1980). This is probably due to the combination of ripples on the water surface and bright sunlight, which produces underwater reflections, reducing the predation success of birds and fishes (Bakshtanskiy *et al.*, 1980). Similar interpretation was also suggested by Davidsen *et al.* (2005), who showed that hours of sunshine explained a significant proportion of the day-to-day variation in numbers of migrating smolts in the River Utsjoki in 2002.

The observed migration pattern of adult Atlantic salmon with peak migration at nights (2100–0300 hours) and weakest migration at midday (0900–1500 hours) is not easily explained in terms of predator avoidance, as adult Atlantic salmon have few natural enemies in the River Teno system. This tendency has been observed earlier in this system (Karppinen *et al.*, 2004). In the subarctic area, underwater light conditions are most stable during nights when reflections of sunlight are at a minimum. Night-time migration may offer the best underwater conditions, without suddenly changing light intensity between shady and sunny parts of river, which seems to disturb ascending Atlantic salmon (Orell, 2003). The weak or even missing diel rhythm in northern latitudes, however, might imply that for Atlantic salmon there is little or no advantage in migrating upstream at a certain time of day (Lilja & Romakkaniemi, 2003).

Seasonal synchrony was detected between smolt and adult migrations in 2003 and 2004, whereas in 2002 the smolt migration was earlier compared to adult migration, as described by the median date of migration. Nordeng (1977) has suggested that homeward navigation of adult Atlantic salmon is an inherited response to population-specific pheromone trails released from descending smolts. To follow this hypothesis, smolts should start their migration before adults, creating pheromone trails to river and inshore waters leading adults to the river of origin. The opposite is true, however, in the River Utsjoki as some adult individuals migrated earlier than the first smolts in all years and thus other factors may synchronize the migration patterns.

It is possible that both smolts and adults use similar environmental cues in their riverine migration securing an optimal timing to minimize the costs of the migration. Water temperature has been often suggested to be the major environmental factor triggering Atlantic salmon migration (McCleave, 1978; Jonsson & Ruud-Hansen, 1985; Jonsson, 1991; Veselov *et al.*, 1998; Whalen *et al.*, 1999; Antonsson & Gudjonsson, 2002; Jutila *et al.*, 2005). In the River Utsjoki, smolts and adults migrated synchronously in years (2003–2004), when water temperature were rising slowly in the beginning of summer, whereas in 2002, with an exceptionally warm early summer, smolt migration occurred earlier than the adults. This observation is in accordance with the suggestion of Jonsson & Ruud-Hansen (1985) and Zydlewski *et al.* (2005), who concluded that there is no temperature threshold triggering the smolt migration, but instead, it is controlled by a combination of temperature increase and temperature condition in the river during spring. Because smolts (or presmolts) are living in rivers, which warm up faster in spring than large sea areas, they have the possibility to react faster to unusually warm conditions, reducing the synchrony between the migrations. On the other hand, water temperature may be a less important cue for adults than smolts, as the first adult Atlantic salmon enter the river at low temperatures. This could mean that the initiation of smolt migration is strongly associated to water temperatures (Antonsson & Gudjonsson, 2002; Zydlewski *et al.*, 2005), whereas adult migration might be more fixed to a certain season. Adult Atlantic salmon at sea are unlikely to be able to detect environmental conditions in the river until they enter near-shore waters or river estuaries, where they can react to stimulating cues of the river environment. The timing of estuary entry, however, may be seasonally stable between years, giving adults a relatively narrow window to respond to the environmental stimuli from the river. This theory is supported by the present data, which indicate more stable seasonal migration timing of adults than that of smolts.

Changes in water temperature and daily smolt or adult numbers were poorly correlated, although some weak positive correlations were found with 1 and 3 daytime lags. This observation indicates that, in addition to the initiation of the migration, water temperature may have a slight influence on migration intensity within the season (Jonsson, 1991; Veselov *et al.*, 1998; Gowans *et al.*, 1999; Zydlewski *et al.*, 2005), as also observed earlier in small tributaries of the River Teno (Erkinaro *et al.*, 1998). As fishes are poikilothermic animals, their activity depends on the temperature in water (Jonsson, 1991). Furthermore, higher water temperatures have been shown to facilitate obstacle passage of adult Atlantic salmon (Banks, 1969; Jensen *et al.*, 1989; Gowans *et al.*, 1999). Increasing water temperature may therefore activate the river ascent to a certain level, after which higher temperatures depress the upstream migration (Hawkins, 1989).

Increasing discharge is suggested to initiate and stimulate both the smolt (Hesthagen & Garnås, 1986; Jonsson, 1991; Byrne *et al.*, 2003) and adult migrations of Atlantic salmon (Banks, 1969; Alabaster, 1970; Jonsson *et al.*, 1990). Opposite information, however, is available from other rivers, where low discharge is associated with the most active smolt (Veselov *et al.*, 1998) or adult migration period (Hellawell *et al.*, 1974) and where freshets have no effect or a negative effect on migration (Jonsson & Ruud-Hansen, 1985; Jensen *et al.*, 1989). This implies that different mechanisms may function in different rivers depending on adaptations to local environmental factors (Jonsson, 1991). In the River Utsjoki, the main smolt and adult migrations occurred only after the spring flood coinciding with decreasing discharge. No statistically significant correlations were found between changes in discharge and changes in smolt or adult numbers. Discharge peaks late in the migration period of both groups, however, may activate the migration of remaining fish, as observed in 2002 (smolt) and 2004 (adults). Thus, at times of low seasonal flow, migration of both groups may be associated with freshets, but during higher flows, migration is independent of increases in flow (Smith *et al.*, 1994; Davidsen *et al.*, 2005). Similarly, the response of adults to either increasing or decreasing flow appears to depend on the stage of migration; increased flow can increase movement into a river from an estuary, whereas Atlantic salmon migrating within the river may prefer decreasing flow (Trépanier *et al.*, 1996; Erkinaro *et al.*, 1999).

From the management point of view, the observed seasonal and diel stability in adult migration provides good possibilities to manage Atlantic salmon fisheries through temporal and technical regulation. Possible differences in migration timing between different tributary stocks, however, could complicate the overall management in a large river system, like the River Teno.

The present work is the first one where both smolt and adult Atlantic salmon migrations were simultaneously investigated by underwater cameras in totally natural conditions, and one of few studies in subarctic rivers, where environmental conditions markedly differ from those in rivers in temperate areas. These differences are especially pronounced in the diel migration pattern of both smolts and adults, as they migrate throughout the 24 h day in the north, instead of predominantly at night as seems to be the case in the southern rivers. Because of the harsh environmental conditions in northern Atlantic salmon rivers, the migratory window is short and both smolt and adult migrations take place during a brief period, which, under certain conditions, is common for both migratory groups. Underwater video monitoring proved to be an effective method and offered precise information on migration timing of both smolts and adult Atlantic salmon in a natural river channel.

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