# Early marine migration of European silver eel (*Anguilla anguilla*) in Northern Norway

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## ABSTRACT

To study migratory behaviour in wild northern European silver eel (*Anguilla anguilla*) during sea entry and early marine migration, 32 individuals were tagged with acoustic transmitters and registered at four automatic listening station arrays from the mouth of the north Norwegian River Alta and throughout the Alta Fjord. The *A. anguilla* entered the fjord during all parts of the tidal cycle and did not seem to utilize the outgoing tidal currents. They migrated mainly during the night, both in the river mouth and fjord. On average, they spent 2.7 days travelling from the river mouth to the outermost array, 31 km from the river mouth, corresponding to anaverage migratory speed of 0.5 km $h^{-1}$. The *A. anguilla* generally migrated in the central part of the fjord and in the uppermost 10–25% of the water column, but with frequent dives to greater depths. Already 4 km after sea entry, *A. anguilla* were observed diving deeper than 130 m within 20–30 min periods. Hence, this study demonstrated that *A. anguilla* may perform an active diving behaviour already during the early marine migration. The study took place in a pristine area with a minimum of anthropogenic interventions and by individuals from a population still uninfected by the introduced parasite *Anguillicoloides crassus*. The results may therefore be used as a base-line for future studies of the *A. anguilla*early marine migration.

**KEY WORDS:**acoustic telemetry;*Anguillicoloides crassus*; diurnal migration; diving behaviour; migratory speed; sea entry.

## INTRODUCTION

The biology of the European eel *Anguilla anguilla* (L.) has been examined for more than 100 years (van Ginneken&Maes, 2005). However, many components of the intriguing life cycle and long distant migrations are still unknown. The species is found and exploited in fresh, brackish and coastal waters in almost all of Europe and along the Mediterranean coasts of Africa and Asia. The stock has shown a strong decline in the entire distribution range during recent decades, but the causes are unknown (Dekker, 2004; ICES, 2009).

As catadromous fishes, *A. anguilla* spend most of their life in freshwater until they return to the spawning grounds in the Sargasso Sea, although part of the population never enter freshwater but reside in brackish and marine areas near the coast (Tsukamoto *et al.*, 1998;Arai *et al.*, 2006; Daverat *et al.*, 2006). Before the return migration, *A. anguilla* undergo a transition as preparation for the oceanic life and are termed silver eel (Tesch, 2003). The silver eel migration is one of the life stages that isstill poorly understood. Potentially, migration timing and progression rates may impact survival, and such information may be crucial for the development of successful protective measures (Aarestrup *et al.*, 2010). Therefore, in order to identify critical life stages, and to be able to implement effective mitigation measures, it is necessary to obtain information on their seaward migratory behaviour and performance. Some studies have revealed important elements of the *A. anguilla* silver eel downriver (*e.g.* Vøllestad *et al.*, 1986; Breukelaar *et al.*, 2009) and open ocean migration (*e.g.* Tesch, 1995; Aarestrup *et al.*, 2009), however only limited information exists on the migratory behaviour through the near coastal areas (Aarestrup *et al.*, 2010).

In many watersheds and near coastal areas, *A. anguilla* need to pass migratory obstacles like dams, fish farms, harbours and industrial developments during their spawning migration, thus anthropogenic factors might influence their migratory routes and behaviour. To collect basic information about the generally preferred seaward migration pattern in *A.*

*anguilla*, the ideal situation is to study the migration in a natural environment with minimal anthropogenic factors possibly influencing the migratory behaviour and progression. Such information is required when evaluating the movements in declining populations from areas more heavily influenced by obstacles, altered water currents, or contamination. Northern areas, like the Alta Fjord where this study was performed, are pristine when compared to Norway and central Europe, with a sparse human population and little industrial development and other constructions. Information about fish migration in these areas may therefore be important in understanding basic migratory behavior in a pristine area. No published information appears to exist about *A. anguilla* migratory behaviour in northern areas. However, *A. anguilla*is reported to occur in freshwater habitats and near coastal areas along the entire coast of northern Norway (Bergersen&Klemetsen, 1988), and they are occasionally observed in the Russian River Tuloma on the Kola Peninsula (Sergey Prusov, pers. com.).

Another factor that may influence the behaviour of *A. anguilla* is the introduced parasitic swimbladder nematode *Anguillicoloides crassus*. This parasite may cause severe pathology and dysfunction of the swimbladder (Van Banning&Haenen, 1990; Würtz&Taraschewski, 2000; Abdelmonem *et al.*, 2010; Neto *et al.*, 2010). In laboratory experiments, *A. crassus* infected *A. anguilla* has shown severely impaired swimming performance (Palstra *et al.*, 2007) and Sjöberg*et al.*(2009) suggested that the parasite-induced damage to the swimbladder may inhibit vertical migrations and cause infected fish to migrate in shallower coastal waters, closer to the shore. *Anguillicoloidescrassus* has recently been introduced to Norway and so far, it has been found in rivers up to 59 °N (Mo, 2009). It is likely that the parasite will continue its spread northwards but so far surveys have not been performed in Northern Norway. Thus, examination for *Anguillacrassus* of *Anguillaanguilla* from the study area in the Alta Fjord at 70°N was included to determine the likelihood of individuals being infected with this parasite.

The aim of this study was to analyse the individual migration pattern of *A. anguilla* silver eels during the first days of their seaward migration in a pristine northern fjord. The main aspects examined were effects of tidal water on timing of sea entry, diel migratory behaviour patterns, migratory speeds, horizontal distribution and swimming depth.

## MATERIAL AND METHODS

### STUDY AREA

The Alta Fjord, northern Norway (70°N 23°E), is a large subarctic open fjord, which is 15 km at its widest and 488 m at its deepest (Fig. 1). The fjord opens through three channels into the Barents Sea. The tidal range is 1.5–2.5 m.The 20 km long River Halselva (Fig. 1), with a catchment area of 143 $km^2$, drains into the Alta Fjord. The mean annual water discharge is 5 $m^3 s^{-1}$ and the water temperature reaches a maximum of about 12° C in early August. A fish trap (wolf trap) is located about 200 m upstream from the river mouth and is operated during the ice-free period from April to November. From 2000to 2010, the mean number of seaward migrating *A.anguilla* was 33 per year (range 4–88, S.D. = 59, Fig. 2). The River Alta (Fig. 1), with a catchment area of 7 400 $km^2$, is the major river draining into the Alta Fjord and is situated in the innermost part of the fjord. The mean annual water discharge is 75 $m^3 s^{-1}$. The shortest distance through the fjord from River Halselva to River Alta is 19 km. A small town with 12 000 inhabitants is situated at the mouth of the River Alta, whereas 439 inhabitants live along the River Halselva.

### FISH CAPTURE AND TAGGING

During the downstream migration in 2007 (5 June – 12 October), 32 wild *A. anguilla* silver eel ($L_T$: mean 629 mm, range 370–765 mm, S.D. = 75, mass: mean 427 g, range 204–694 g, S.D. = 123)were captured in the wolf trap in River Halselva and kept up to four months in a holding tank at the catch site until tagging. This is a gentle catch method as the fish swim freely inside the trap, usually uninjured. Twenty-one fish were tagged with individually coded acoustic depth sensing transmitters [Thelmabiotel AS, Norway (www.thelmabiotel.com)model ADT-MP-9-long, 9 x 39 mm, mass in water/air of 4.3/6.8 g, battery life 130 days] and eleven fish with transmitters without depth sensors (Thelmabiotel AS, Norway, model MP-9-long, 9 x 28 mm, mass in water/air of 3.3/5.2 g, battery life 203 days). The depth sensing transmitters recorded depth with a pressure sensor (range 0–130 m, depths deeper than 130 m were shown as 130 m) and transmitted this information together with the fish identity code.

Before tagging, the *A. anguilla* was anaesthetized in an immersion of 40 mg $l^{-1}$ Metomidate [Marinil ™, Wildlife Labs., Inc., Fort Collins, Colorado, U.S.A. (www.zoopharm.net)]. After anaesthetization, length (nearest 5 mm) and mass (nearest g) were recorded before the fish was placed ventral side up on a wet surgical cradle. A 14–19 mm incision was made on the ventral surface of the fish. The acoustic tag was inserted into the incision and pushed anteriorly away from the incision. The incision was closed with 3–4 independent sutures [2/0 Ethicon Inc. braded silk suture (www.ethicon.com)]. All individuals were characterised as silver eels, based on the silvery appearance (Tesch, 2003).

After 1-3 h of recovery, the fish were transported (travelling time 1 h) in a 750 l aerated water tank to the release site in the River Alta. Twenty-six *A. anguilla* were released 5 km upstream from the river mouth 1745 hours on the 3 October. Six*A. anguilla*were released 0.5 km upstream from the river mouth at 2130 hours on the 23 October. The release in the River Alta instead of the capture site was chosen for optimal use of the automatic listening stations arrays already deployed in the fjord for other purposes.

During the downstream migration in 2009, 14 wild *A. anguilla* silver eel were captured in the wolf trap in the River Halselva, killed by an overdose of anaesthetic and kept in a freezer until examination in 2010. The eels were thawed, the abdomen opened with a scalpel and the swimbladder removed with a pair of pincers. Each swimbladder was opened with a pair of scissors and examined for the presence of *A. crassus* under a stereo microscope at 10-20 x magnification.No *Anguillacrassus* were observed in the swimbladder of the 14 examined *Anguillaanguilla*.

RECORDING OF THE FISH BY AUTOMATIC LISTENING STATIONS AND MANUAL TRACKING

The fish behaviour was monitored using 48 automatic listening stations [ALS, Vemco Inc.(www.vemco.com) model VR2]from 3 October to 7 November 2007. Two ALSs were deployed 2 m below surface in the mouth of the River Alta (Fig. 1). Three ALS arrays were deployed across the fjord at 4 km (11 ALSs, 3.8 km wide), 17 km (14 ALSs, 4.5 km wide) and 31 km (21 ALSs, 8.3 km wide) from the river mouth (Fig. 1). The ALSs within each array were deployed 5 m below surface and separated horizontally by 400 m. The fjord was divided into zone 1 (river mouth – first ALS array), zone 2 (first – second ALS array) and zone 3 (second – third ALS array) (Fig. 1). The depth in the river mouth was 3 m, at the first ALS array 13–130 m, at the second array 40–400 m and at the third array 20–450 m. For analyses of horizontal distribution, each array was divided into eastern side (three ALSs from east), western side (three ALSs from west) and central part (remaining ALSs). Individuals were designated to the ALS with the largest number of recordings if simultaneously recorded by more than one ALS. The ALSs recorded the acoustic identity code of the tagged *A. anguilla*, depth (for 21 of the tags) and the exact time from when they were within a range of 100–600 m from the ALS (the detection range depended on environmental conditions). The last registration of individual fish in the river mouth was used as the time of sea entry. At the three arrays in the fjord, the first registration was used as the time of arrival at the array. Manual river tracking was performed on 18 October using an acoustic receiver with an omnidirectional hydrophone (Vemco Inc., model VR100) to detect if any individuals from the first release group remained in the river.

## ENVIRONMENTAL VARIABLES

The tidal range was recorded during 3 October – 7 November 2007. This was done by recording the depth every 10 min using a depth sensing data storage tag (Star-Oddi, Iceland (www.star-oddi.com) model DST-milli-L) placed at the fjord bottom 1 km from the mouth of the River Alta.

## DATA ANALYSES

To test the diurnal migratory behaviour, day time was defined as 0700 – 1700 hours, which corresponded to sunrise and sunset onthe 15 October. Chi-square tests were used to test for differences between sea entry at day or night and during different phases of the tidal cycle (divided into 3 h phases: high, ebbing, low or flooding tide). The migratory speeds in the three fjord zones were calculated for fish registered at two subsequent ALS arrays. Since some *A. anguilla* were not registered by all arrays, the sample sizes for these analyses were smaller than the total number registered. Migratory speed was estimated as individual total lengths ($L_T$) per second, and as km $h^{-1}$ by using the shortest distance between the arrays and the river mouth, thus giving minimum estimates (Thorstad *et al.*, 2004). Migratory speed was log transformed in order to perform a one-way ANOVA test to test for difference in swimming speed between the fjord zones. A fish was located to several ALS in the analyses of horizontal distribution if it was detected on these on independent occasions (> 30 min without detections). When analysing the swimming depths and diving behaviour, individual mean values were used to calculate the populations mean in order to keep the data points independent. The depth sensor range stopped at 130 m, so individual dives may have been deeper. However, in these situations 130 m was used in the analyses, and individual average depths may therefore have been underestimated.

## RESULTS

### PERFORMANCE

In total, 26 (81%) of the 32 *A. anguilla* were registered in the river mouth and/or in the fjord following release (20 from the first group and all six from the second group). Twenty-two (69%) were registered at the first ALS array, 13 (41%) at the second array and 16 (50%) at the third array. The remaining six fish were never registered in the fjord or river after release. Total length (Welch's *t*-test, d.f. = 30, $P > 0.05$) or mass (Welch's *t*-test, d.f. = 30, $P > 0.05$) did not differ between those registered and those not registered after release. Further, there were no differences in total length (Welch's *t*-test, d.f. = 30, $P = 0.05$) or mass (Welch's *t*-test, d.f. = 30, $P > 0.05$) betweenthoserecorded and those not recorded at the third transect.

### TIMING OF SEA ENTRY AND DIEL MIGRATORY PATTERN

The first individual was detected in the river mouth on 3 October (same day as release) and the last on 6 November (14 days after release). The proportion of *A. anguilla* entering the sea did not differ among the four phases of the tidal cycle (high 8 (31%), ebbing 7 (27%), low 8 (31%) flooding 3 (12%); $\chi^2$ test, d.f. = 3). Fifteen *A. anguilla* (58%) entered the fjord at high or ebbing tide, while 11 *A. anguilla* (42%) entered at low or flooding tide. All individuals except one (96%) entered the fjord during night time ($\chi^2$ test, d.f. = 1, $P < 0.001$). This clear nocturnal migratory pattern continued as the *A. anguilla* migrated outward through the fjord (Table I).

MIGRATORY SPEED

Time spent from the river mouth to the last array 31 km from the river mouth varied between 24 and 262 h (average ± S.D. = 65 ± 73 h). This corresponds to anaverage migratory speed of 0.25 $L_T$ $s^{-1}$ (range 0.1–0.6), or 0.5 km $h^{-1}$ (range 0.1–1.3). The average migratory speed was lower in zone one (0.2 km $h^{-1}$/0.1 $L_T$ $s^{-1}$) than in zone two (0.6 km $h^{-1}$/0.4 $L_T$ $s^{-1}$) (ANOVA, d.f. = 7, $P < 0.001$). There was no difference in migratory speed between zone two and zone three (0.7 km $h^{-1}$/0.4 $L_T$ $s^{-1}$) (ANOVA, d.f. = 6, $P > 0.05$) (Fig. 3). The migratory speed (km $h^{-1}$) from the river mouth to the third ALS array did not depend on total body length (linear regression, d.f. = 8, $r^2 = 0.025$, $P > 0.05$).

HORIZONTAL DISTRIBUTION

The *A. anguilla* tended to migrate along the eastern side of the fjord at the time they passed the first ALS array (26 of 50 registrations, Fig. 4). When passing the second and third ALS array they migrated mainly in the central part of the fjord, but with a distribution skewed towards the western part of the fjord (Fig. 4).

SWIMMING DEPTH AND DIVING BEHAVIOUR

Fourteen of the *A. anguilla* tagged with depth sensing transmitters were registered by one or more ALS arrays. Mean swimming depth was 24 m when passing the first array, 64 m at the second array and 48 m at the third array (Table II and Fig. 5). This indicates that the *A. anguilla*did not migrate close to the bottom but stayed in the uppermost 10–25% of the water column. There was no difference in swimming depth between day and night (Welch's *t*-test, d.f. = 34, *P*> 0.05). The individual variation in mean swimming depth was large and varied from 0 to >130 m (Table II). Further, individuals often changed swimming depth within a short time period. Three individuals were observed to change from 110–130 m depth to < 10 m depth within 15 min. Dives to 130 m depth or more were observed at all three ALS arrays. Twelve individuals had dives deeper than 50 m and seven of these had dives deeper than 100 m.

## DISCUSSION

### PERFORMANCE

The registration of 50% of the *A. anguilla* 31 km outward the fjord is a minimum estimate of the survival. Four of the automatic listening stations in the third array were lost before the study ended and some fish may therefore have passed the array without being registered. Six (19%) of the fish were never registered after release, which may be due to predators bringing the *A. anguilla* out of the river, malfunctioning transmitters, or the fish moving to a place in the river where the detection efficiency was low (like rapids with high current speeds) (Davidsen *et al.*, 2009). Winter *et al.* (2005) studied tagging effects in *A. anguilla* silver eel, and recorded no transmitter expulsion or mortality related to tagging. Moreover, they found no effects of tagging on timing of activity.*A. anguilla* silver eels havealso been successfully tagged with similar transmitters in several other studies (*e.g.* Baras&Jeandrain, 1998; Behrmann-Godel&Eckmann, 2003). Hence, transmitter implantation was not expected to largely affect fish behaviour or survival.

### TIMING OF SEA ENTRY AND DIEL MIGRATORY PATTERN

The *A. anguilla* entered the sea during all parts of the tidal cycle and did not seem to utilize the outgoing tidal currents. Selective tidal stream transport is a behavioural mechanism that allows organisms to quickly pass through the transition zone between the freshwater and saline habitat by using the outgoing tidal current speeds. Such behaviour may be important for many diadromous fish species due to the often high predation pressure in estuaries (Dieperink *et al.*, 2002; Jepsen *et al.*, 2006). American silver eel *Anguilla rostrata* (Lesueur) have in some studies been found to use tidal currents as a transport mechanism (Parker&McCleave, 1997; Hedger *et al.*, 2010), while in a recent study, timing of sea entry had little or no relation to the tidal cycle (Carr&Whoriskey, 2008). In *A. anguilla* silver eel, selective tidal stream transport has been suggested during open ocean migration (Arnold&Cook, 1984), but there appear to be no studies that document such behaviour during sea entry.

A majority (96%) of the *A. anguilla* entered the sea at night and continued this nocturnal behaviour pattern as they migrated outward through the fjord. This result is supported by other studies of the early marine phase of the *A. anguilla* spawning migration (Lowe, 1952; Aarestrup *et al.*, 2008; Aarestrup *et al.*, 2010) and of their downstream migration in freshwater habitats (Vøllestad *et al.*, 1986; Tesch, 2003). Absence of day activity in freshwater and near coastal habitats is probably a light avoidance behaviour, perhaps to avoid predators (Vøllestad *et al.*, 1986). However, when the *A. anguilla* reach the open sea, they seem to migrate both day and night (Tesch, 1995) and instead migrate deeper during the day (Aarestrup *et al.*, 2009).

MIGRATORY SPEED

The migratory speed out of the fjord (average 2.7 days during the first 31 km) was much faster than observed in a similar study in near coastal waters (Aarestrup *et al.*, 2010), but slower than in the open ocean (Tesch, 1974; Tesch *et al.*, 1991; Aarestrup *et al.*, 2009).

Asalso recorded for Japanese eels*A. japonica* (Temminck& Schlegel; Aoyama *et al*., 2002), the migratory speed increased as the *A. anguilla* moved outward through the fjord, however there was a large individual variation. This may indicate that the individuals encountered different current speeds and directions at sea entry or alternatively an indication of individual behaviour patterns (Davidsen *et al.*, 2009). The migratory speed was 43% lower than for Atlantic salmon (*Salmo salar* L.) post-smolts (Davidsen *et al.*, 2009) and 48% lower than for adults (Halttunen *et al.*, 2009) in the same fjord the same year. Studies in swim-tunnels indicate that *A. anguilla* can swim four to six times more efficiently than non-anguilliform fish, however high speed is not characteristic of the pure anguilliform mode (van Ginneken&Maes, 2005). The difference in early seaward migratory speed between *S. salar* and *A. anguilla* in the Alta Fjord, and the observation of no correlation with the tides during sea entry for *A. anguilla*, but for *S. salar* post-smolts (Davidsen *et al.*, 2009), may indicate that the predation pressure for *A. anguilla* during the first phase of the seaward migration is much lower than for *S. salar* post-smolts.

## HORIZONTAL DISTRIBUTION

The *A. anguilla* generally used the central part of the fjord. This tendency to not swim along the coastline may be the first step in their navigation towards the open ocean and hence the spawning areas in the Sargasso Sea. In experiments, *A. anguilla* silver eels have been found to prefer swimming routes with the highest water velocity (Hadderingh *et al.*, 1999). However, in the current study, there is no information available about the differences in the current speeds across the fjord. Another reason for the preference of the central part of the fjord may be that the *A. anguilla* seemed to utilize the greater depths found here.

## SWIMMING DEPTH AND DIVING BEHAVIOUR

The *A. anguilla* generally migrated in the uppermost 10–25% of the water column, but stayed deeper as they moved outward through the fjord. Already 4 km after sea entry, *A. anguilla* were observed diving to depths deeper than 130 m and the fish displayed a very active diving behaviour throughout the fjord migration, including dives with more than 130 vertical meters within 20–30 min. Such behaviour has until now only been described for the open ocean part of the spawning migration, where several studies have shown that *A. anguilla*migrates at depths down to 500–700 m (Tesch, 1978, 1989, 1995; Aarestrup *et al.*, 2009). However, studies of the New Zealand Longfin eel*A. dieffenbachia* (Gray) also showed that the migration took part in the open water column during the early seaward migration (Jellyman& Tsukamoto, 2002, 2005). The active diving behaviour observed a short time after leaving the river may indicate that the *A. anguilla* is well adapted to the saline habitat already at the time of sea entry. Less adapted fishes would be expected to stay in the brackish water layer at the surface. There was no difference in swimming depth between night and day, in contrast to the open ocean recordings by Aarestrup *et al*. (2009), however this may be due to a limited number of registrations during day time in the present study. Frequently diving to mid-water or to the bottom is common in many fishes and has often been suggested to serve several functions, from a searching strategy for prey and olfactory cues to determination of current direction (Greer Walker *et al.*, 1980; Holland, 1990; Arnold&Greer Walker, 1992; Metcalfe *et al.*, 1993). During the spawning migration, *A. anguilla* do not feed (Tesch, 2003), however the frequent dives may be a part of the navigation towards the open sea.

In this study, *A. anguilla* were often found to migrate deeper than 130 m, but since the acoustic tags were not able to record depths deeper than 130 m, no information exists about the maximum depths. Therefore, average swimming depths given in the present study are minimum estimates.

Since the swim bladder nematode *A. crassus* may severely injure the swim bladder and possibly affect the vertical migration of *A. anguilla*(Van Banning&Haenen, 1990; Würtz&Taraschewski, 2000; Abdelmonem *et al.*, 2010; Neto *et al.*, 2010), it may be argued that the observed behaviour with fast vertical movements up and down the water column may be a result of *A. anguilla* not being able to keep a steady depth possibly due to being infected by this parasite. It was therefore important to document that this study represents parasite-free individuals. The *A. anguilla* in the present migration study were sampled in 2007 while the *A. anguilla* examined for the presence of the swimbladder nematode *A. crassus* were sampled in 2009. As the prevalence and abundance of *A. crassus* in *A. anguilla* have increased to high numbers within a short period when introduced to other Norwegian rivers (Mo, 2009), it is unlikely that *A. crassus* was present in River Halselva in 2007 but not observed in 2009. However, it may be argued that the spread of *A. crassus* among *A. anguilla* in the northernmost Norwegian rivers would be slow due to the cold climate and that the sample of 14 *A. anguilla* was too small to detect the parasite. If the parasite was present in 2007, the prevalence and abundance of the nematode were likely so low that the effect on the seaward migratory behaviour of *A. anguilla* was neglectable.

This is the first study to describe the early seaward migratory behaviour of *A. anguilla* in northern areas. Since the migration took place in a pristine area with a minimum of anthropogenic interventions and with individuals from a population which still is uninfected by the introduced parasitic swimbladder nematode *A. crassus*, the results from this study may be used as a base-line for future studies of the *A. anguilla* early migration.

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TABLE I: Comparisons of the number and per cent of *Anguilla anguilla* silver eel leaving the mouth of River Alta and passing three arrays of automatic listening stations (ALS) in the Alta Fjord during day and night. $\chi^2$ tests were used to test for differences between the percentages.

| | River mouth | 1st ALS Array | 2nd ALS Array | 3rd ALS Array |
|---|---|---|---|---|
| Total | 26 | 22 | 13 | 16 |
| Day | 1 (4%) | 1 (5%) | 2 (15%) | 3 (19%) |
| Night | 25 (96%) | 21 (96%) | 11 (85%) | 13 (81%) |
| *P* value | < 0.001 | < 0.001 | < 0.05 | < 0.05 |

TABLE II: The mean swimming depths of *Anguilla anguilla* silver eel as they passed three arrays of automatic listening stations (ALS) in the Alta Fjord during their seaward migration. *n* is the number of individuals registered at each array. Since the tags only recorded depths < 130 m, 130 m means that the *A. anguilla* was at 130 m depth or deeper.

| | 1st ALS array | | 2nd ALS array | | 3rd ALS array | |
|---|---|---|---|---|---|---|
| | Day | Night | Day | Night | Day | Night |
| *n* | 5 | 12 | 3 | 7 | 2 | 7 |
| Mean (m) ± S.D. | 23 ± 40 | 26 ± 26 | 88 ± 52 | 63 ± 25 | 112 ± 30 | 44 ± 45 |
| Min - max (m) | 0-130 | 0-112 | 3-130 | 0-130 | 50-130 | 0-130 |

Figure captions:

FIG 1: Map of the Alta Fjord, River Alta and River Halselva showing the position of the fish trap (■), release sites (★ the threeautomatic listening station (ALS) arrays in the fjord (.....) and the twoALSs in the river mouth (.). The map also shows the division of the three zones (Z1–Z3).

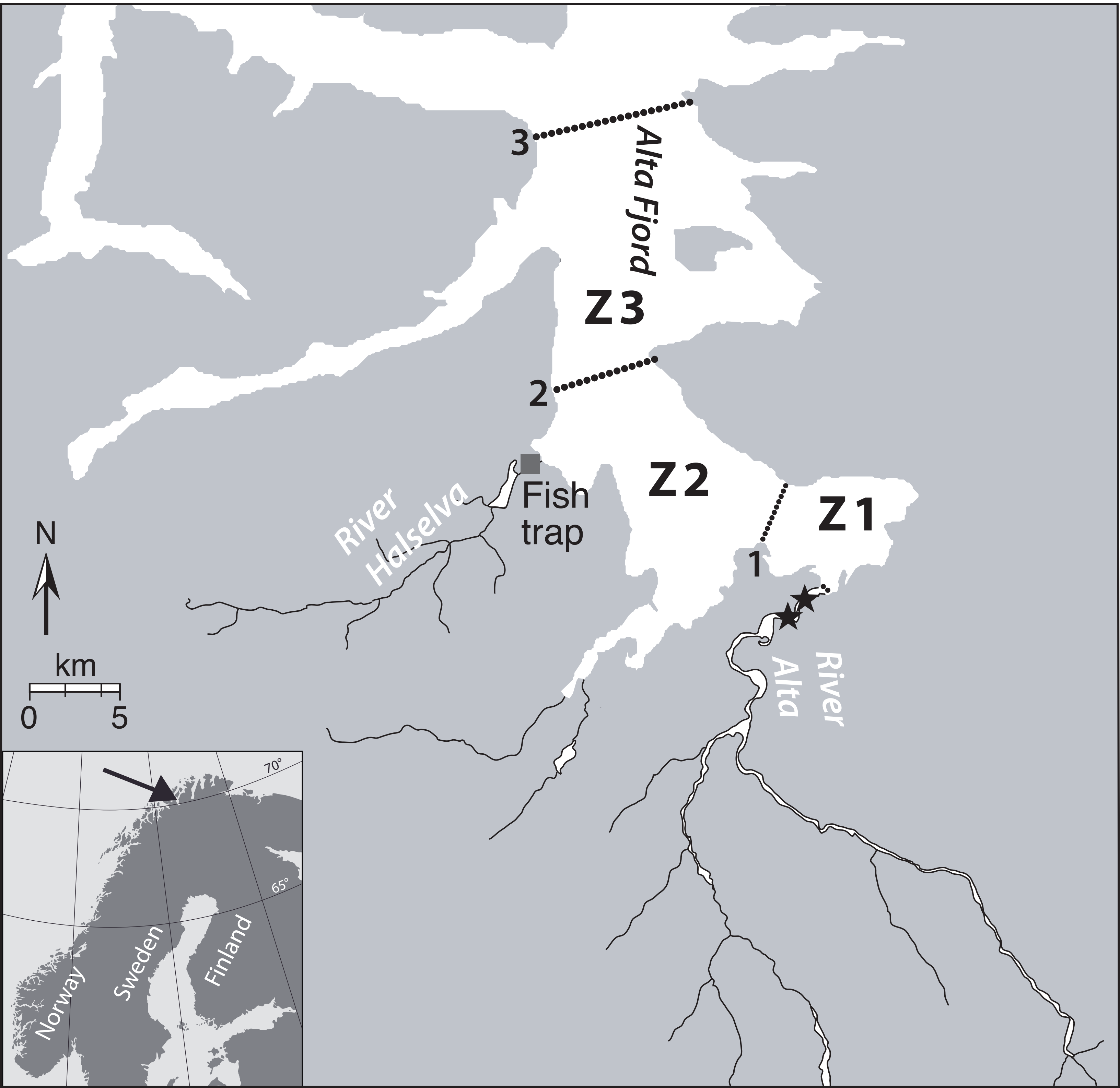
FIG 2: Seaward migration of *Anguilla anguilla* in River Halselvafrom year 2000–2010.

FIG 3:Migratory speeds of *Anguilla anguilla* silver eel during migration through different zones in the Alta Fjord. The box-and-whisker plots give the median values (black lines), the interquartile ranges (box, 50% of the data falling into this) and the $5^{th}$ and $95^{th}$ percentiles (whiskers).

FIG 4: Horizontal distribution of *Anguilla anguilla* silver eel during migration through the Alta Fjord. a) is the distribution of registered eel at the third automatic listening station (ALS) array (21 ALSs), b) distribution at the second array (14 ALSs) and c) distribution at the first array (11 ALSs). The black bars represent recordings at single ALSs in each of the three transects. West (three ALSs from the western side of the fjord), east (three ALSs from the eastern side) and central (remaining ALSs) refer to different zones of the transects used in result analyses.

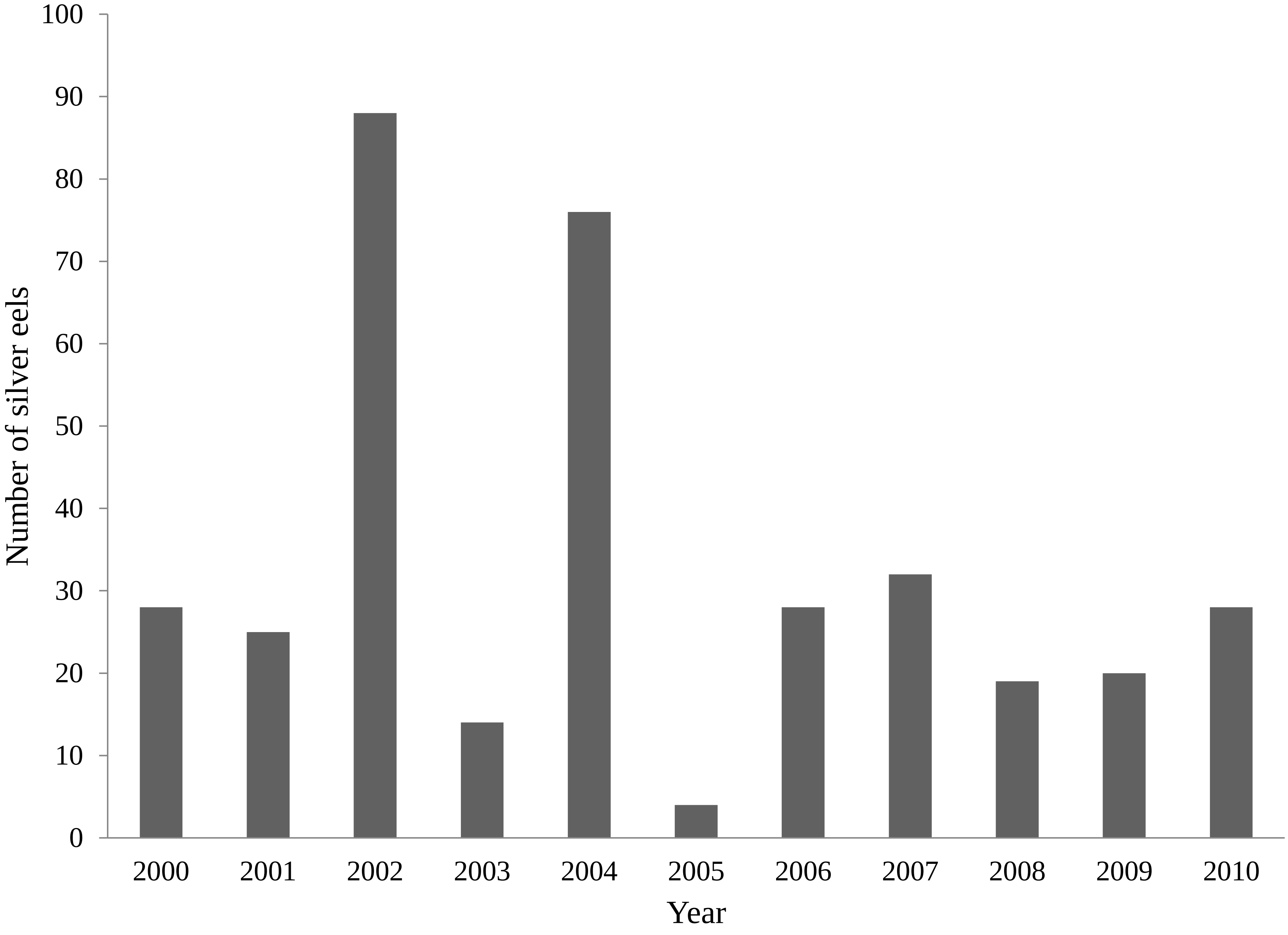
FIG 5: Depth distribution of *Anguilla anguilla* silver eel during migration through the Alta Fjord. a) shows results at the third automatic listening station (ALS) array (21 ALSs), b) at the second array (14 ALSs) and c) at the first array (11 ALSs). Depths data are given for each of the ALSs in each transect. The number above each box indicates number of fish. A fish may be shown at several ALS if it was detected on these on independent occasions. The solid line indicates the depth profile of the fjord. Maximum depths in the central areas of the second and third array are 400–450 m, but the y-axes only cover the 130 m range of the transmitters.

Figure

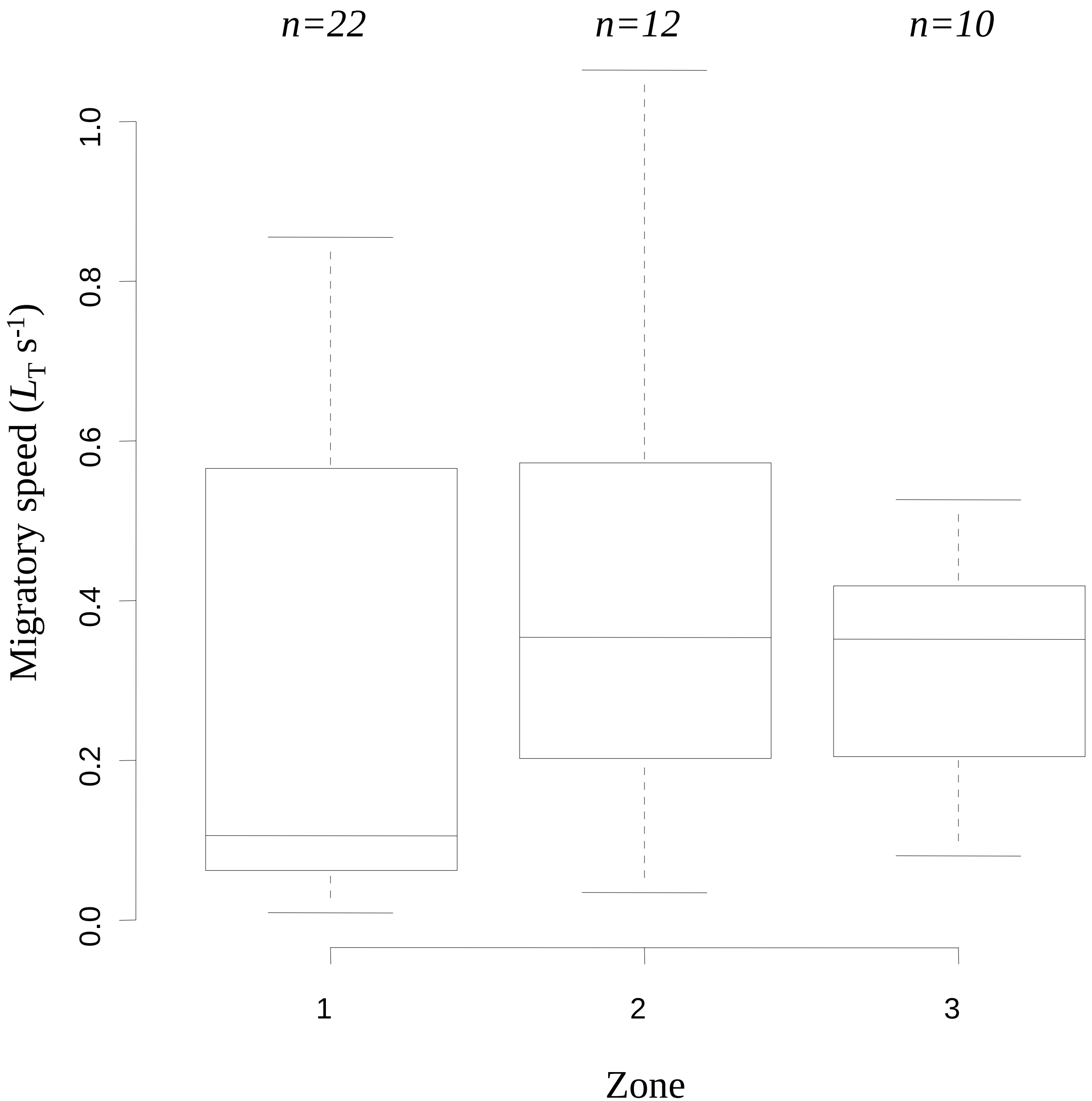


3
Alta Fjord
Z3
2
Z2
Z1
1
Fish trap
River Halselva
River Alta
N
km
0
5
70°
65°
Norway
Sweden
Finland

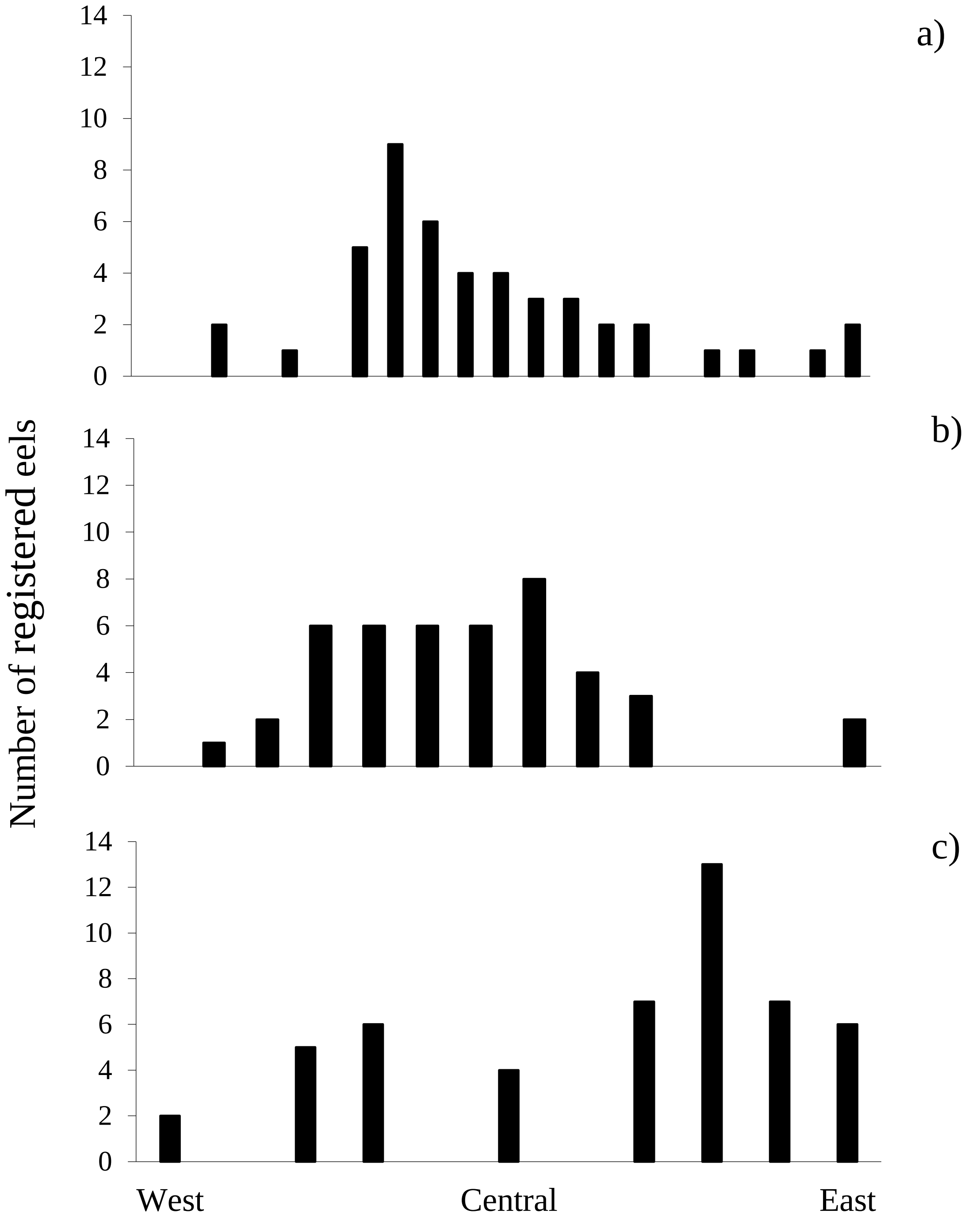
Figure


100
90
80
70
60
50
40
30
20
10
0
Number of silver eels
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
Year

Figure

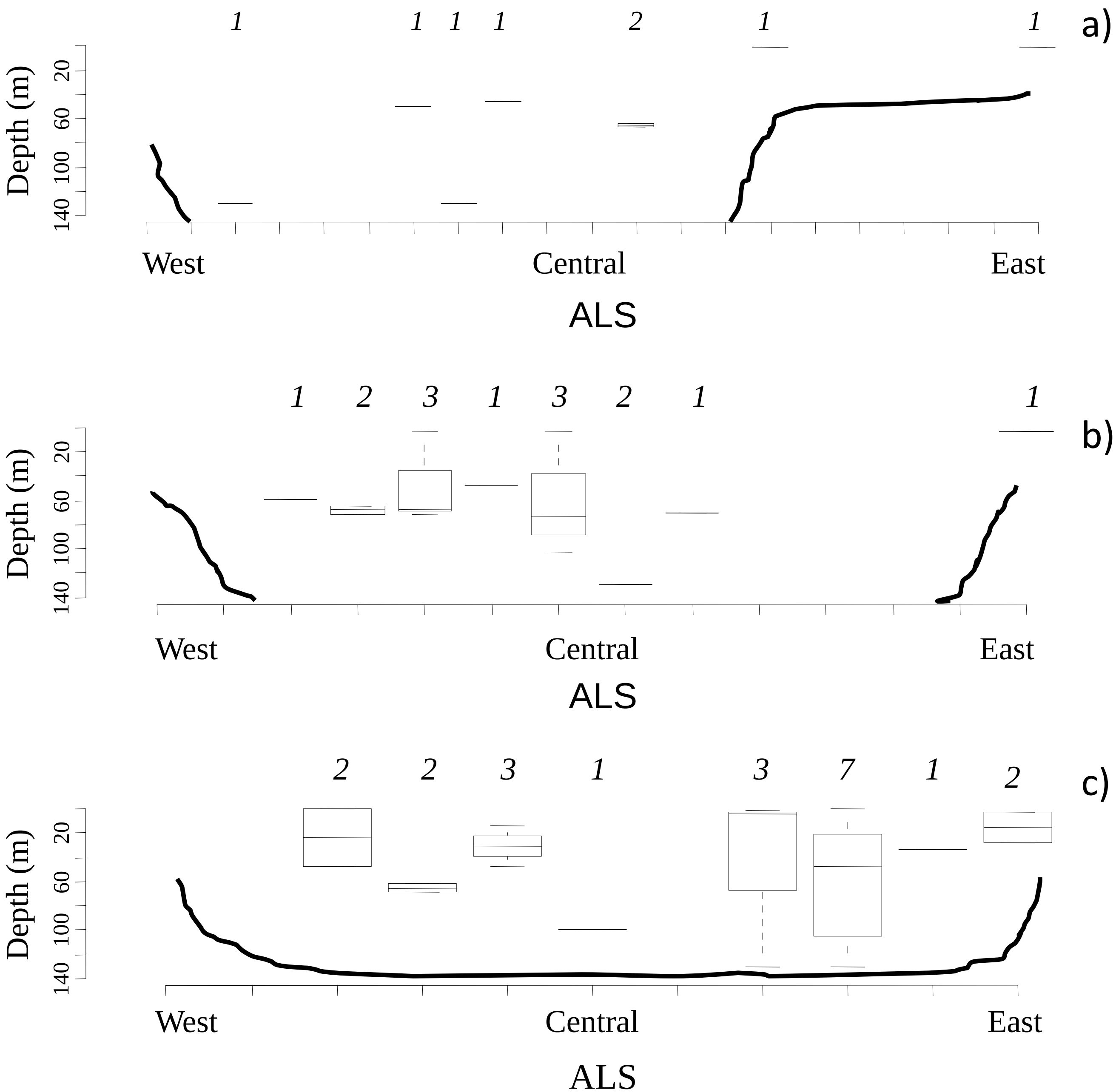


Figure



a)
b)
c)
Number of registered eels
0
2
4
6
8
10
12
14
West
Central
East

Figure



a)
1
1
1
1
2
1
1
Depth (m)
20
60
100
140
West
Central
East
ALS
b)
1
2
3
1
3
2
1
1
Depth (m)
20
60
100
140
West
Central
East
ALS
c)
2
2
3
1
3
7
1
2
Depth (m)
20
60
100
140
West
Central
East
ALS