

1 **Early marine migration of European silver eel**

2 ***(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 an average 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.

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INTRODUCTION

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

54 As catadromous fishes, *A. anguilla* spend most of their life in freshwater until they
55 return to the spawning grounds in the Sargasso Sea, although part of the population never
56 enter freshwater but reside in brackish and marine areas near the coast (Tsukamoto *et al.*,
57 1998;Arai *et al.*, 2006; Daverat *et al.*, 2006). Before the return migration, *A. anguilla* undergo
58 a transition as preparation for the oceanic life and are termed silver eel (Tesch, 2003). The
59 silver eel migration is one of the life stages that is still poorly understood. Potentially,
60 migration timing and progression rates may impact survival, and such information may be
61 crucial for the development of successful protective measures (Aarestrup *et al.*, 2010).
62 Therefore, in order to identify critical life stages, and to be able to implement effective
63 mitigation measures, it is necessary to obtain information on their seaward migratory
64 behaviour and performance. Some studies have revealed important elements of the *A. anguilla*
65 silver eel downriver (*e.g.* Vøllestad *et al.*, 1986; Breukelaar *et al.*, 2009) and open ocean
66 migration (*e.g.* Tesch, 1995; Aarestrup *et al.*, 2009), however only limited information exists
67 on the migratory behaviour through the near coastal areas (Aarestrup *et al.*, 2010).

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

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

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

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

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MATERIAL AND METHODS

104 STUDY AREA

105 The Alta Fjord, northern Norway (70°N 23°E), is a large subarctic open fjord, which is 15 km
106 at its widest and 488 m at its deepest (Fig. 1). The fjord opens through three channels into the
107 Barents Sea. The tidal range is 1.5–2.5 m. The 20 km long River Halselva (Fig. 1), with a
108 catchment area of 143 km², drains into the Alta Fjord. The mean annual water discharge is 5
109 m³ s⁻¹ and the water temperature reaches a maximum of about 12° C in early August. A fish
110 trap (wolf trap) is located about 200 m upstream from the river mouth and is operated during
111 the ice-free period from April to November. From 2000 to 2010, the mean number of seaward
112 migrating *A. anguilla* was 33 per year (range 4–88, S.D. = 59, Fig. 2). The River Alta (Fig. 1),
113 with a catchment area of 7 400 km², is the major river draining into the Alta Fjord and is
114 situated in the innermost part of the fjord. The mean annual water discharge is 75 m³ s⁻¹. The
115 shortest distance through the fjord from River Halselva to River Alta is 19 km. A small town
116 with 12 000 inhabitants is situated at the mouth of the River Alta, whereas 439 inhabitants
117 live along the River Halselva.

118

119 FISH CAPTURE AND TAGGING

120 During the downstream migration in 2007 (5 June – 12 October), 32 wild *A. anguilla* silver
121 eel (L_T : mean 629 mm, range 370–765 mm, S.D. = 75, mass: mean 427 g, range 204–694 g,

122 S.D. = 123) were captured in the wolf trap in River Halselva and kept up to four months in a
123 holding tank at the catch site until tagging. This is a gentle catch method as the fish swim
124 freely inside the trap, usually uninjured. Twenty-one fish were tagged with individually coded
125 acoustic depth sensing transmitters [Thelmabiotel AS, Norway
126 (www.thelmabiotel.com) model ADT-MP-9-long, 9 x 39 mm, mass in water/air of 4.3/6.8 g,
127 battery life 130 days] and eleven fish with transmitters without depth sensors (Thelmabiotel
128 AS, Norway, model MP-9-long, 9 x 28 mm, mass in water/air of 3.3/5.2 g, battery life 203
129 days). The depth sensing transmitters recorded depth with a pressure sensor (range 0–130 m,
130 depths deeper than 130 m were shown as 130 m) and transmitted this information together
131 with the fish identity code.

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

140 After 1–3 h of recovery, the fish were transported (travelling time 1 h) in a 750 l
141 aerated water tank to the release site in the River Alta. Twenty-six *A. anguilla* were released 5
142 km upstream from the river mouth 1745 hours on the 3 October. Six *A. anguilla* were released
143 0.5 km upstream from the river mouth at 2130 hours on the 23 October. The release in the
144 River Alta instead of the capture site was chosen for optimal use of the automatic listening
145 stations arrays already deployed in the fjord for other purposes.

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

153

154 RECORDING OF THE FISH BY AUTOMATIC LISTENING STATIONS AND MANUAL 155 TRACKING

156 The fish behaviour was monitored using 48 automatic listening stations [ALS, Vemco
157 Inc.(www.vemco.com) model VR2]from 3 October to 7 November 2007. Two ALSs were
158 deployed 2 m below surface in the mouth of the River Alta (Fig. 1). Three ALS arrays were
159 deployed across the fjord at 4 km (11 ALSs, 3.8 km wide), 17 km (14 ALSs, 4.5 km wide)
160 and 31 km (21 ALSs, 8.3 km wide) from the river mouth (Fig. 1). The ALSs within each array
161 were deployed 5 m below surface and separated horizontally by 400 m. The fjord was divided
162 into zone 1 (river mouth – first ALS array), zone 2 (first – second ALS array) and zone 3
163 (second – third ALS array) (Fig. 1). The depth in the river mouth was 3 m, at the first ALS
164 array 13–130 m, at the second array 40–400 m and at the third array 20–450 m. For analyses
165 of horizontal distribution, each array was divided into eastern side (three ALSs from east),
166 western side (three ALSs from west) and central part (remaining ALSs). Individuals were
167 designated to the ALS with the largest number of recordings if simultaneously recorded by
168 more than one ALS. The ALSs recorded the acoustic identity code of the tagged *A. anguilla*,
169 depth (for 21 of the tags) and the exact time from when they were within a range of 100–600
170 m from the ALS (the detection range depended on environmental conditions). The last

171 registration of individual fish in the river mouth was used as the time of sea entry. At the three
172 arrays in the fjord, the first registration was used as the time of arrival at the array. Manual
173 river tracking was performed on 18 October using an acoustic receiver with an
174 omnidirectional hydrophone (Vemco Inc., model VR100) to detect if any individuals from the
175 first release group remained in the river.

176

177 ENVIRONMENTAL VARIABLES

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

182

183 DATA ANALYSES

184 To test the diurnal migratory behaviour, day time was defined as 0700 – 1700 hours, which
185 corresponded to sunrise and sunset on the 15 October. Chi-square tests were used to test for
186 differences between sea entry at day or night and during different phases of the tidal cycle
187 (divided into 3 h phases: high, ebbing, low or flooding tide). The migratory speeds in the three
188 fjord zones were calculated for fish registered at two subsequent ALS arrays. Since some *A.*
189 *anguilla* were not registered by all arrays, the sample sizes for these analyses were smaller
190 than the total number registered. Migratory speed was estimated as individual total lengths
191 (L_T) per second, and as km h^{-1} by using the shortest distance between the arrays and the river
192 mouth, thus giving minimum estimates (Thorstad *et al.*, 2004). Migratory speed was log
193 transformed in order to perform a one-way ANOVA test to test for difference in swimming
194 speed between the fjord zones. A fish was located to several ALS in the analyses of horizontal
195 distribution if it was detected on these on independent occasions (> 30 min without

196 detections). When analysing the swimming depths and diving behaviour, individual mean
197 values were used to calculate the populations mean in order to keep the data points
198 independent. The depth sensor range stopped at 130 m, so individual dives may have been
199 deeper. However, in these situations 130 m was used in the analyses, and individual average
200 depths may therefore have been underestimated.

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RESULTS

204 PERFORMANCE

205 In total, 26 (81%) of the 32 *A. anguilla* were registered in the river mouth and/or in the fjord
206 following release (20 from the first group and all six from the second group). Twenty-two
207 (69%) were registered at the first ALS array, 13 (41%) at the second array and 16 (50%) at the
208 third array. The remaining six fish were never registered in the fjord or river after release.
209 Total length (Welch's *t*-test, d.f. = 30, $P > 0.05$) or mass (Welch's *t*-test, d.f. = 30, $P > 0.05$)
210 did not differ between those registered and those not registered after release. Further, there
211 were no differences in total length (Welch's *t*-test, d.f. = 30, $P = 0.05$) or mass (Welch's *t*-test,
212 d.f. = 30, $P > 0.05$) between those recorded and those not recorded at the third transect.

213

214 TIMING OF SEA ENTRY AND DIEL MIGRATORY PATTERN

215 The first individual was detected in the river mouth on 3 October (same day as release) and
216 the last on 6 November (14 days after release). The proportion of *A. anguilla* entering the sea
217 did not differ among the four phases of the tidal cycle (high 8 (31%), ebbing 7 (27%), low 8
218 (31%) flooding 3 (12%); χ^2 test, d.f. = 3). Fifteen *A. anguilla* (58%) entered the fjord at high
219 or ebbing tide, while 11 *A. anguilla* (42%) entered at low or flooding tide. All individuals
220 except one (96%) entered the fjord during night time (χ^2 test, d.f. = 1, $P < 0.001$). This clear

221 nocturnal migratory pattern continued as the *A. anguilla* migrated outward through the fjord
222 (Table I).

223

224 MIGRATORY SPEED

225 Time spent from the river mouth to the last array 31 km from the river mouth varied between
226 24 and 262 h (average \pm S.D. = 65 ± 73 h). This corresponds to an average migratory speed of
227 $0.25 L_T s^{-1}$ (range 0.1–0.6), or 0.5 km h^{-1} (range 0.1–1.3). The average migratory speed was
228 lower in zone one ($0.2 \text{ km h}^{-1}/0.1 L_T s^{-1}$) than in zone two ($0.6 \text{ km h}^{-1}/0.4 L_T s^{-1}$) (ANOVA,
229 d.f. = 7, $P < 0.001$). There was no difference in migratory speed between zone two and zone
230 three ($0.7 \text{ km h}^{-1}/0.4 L_T s^{-1}$) (ANOVA, d.f. = 6, $P > 0.05$) (Fig. 3). The migratory speed (km h^{-1})
231 from the river mouth to the third ALS array did not depend on total body length (linear
232 regression, d.f. = 8, $r^2 = 0.025$, $P > 0.05$).

233

234 HORIZONTAL DISTRIBUTION

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

239

240 SWIMMING DEPTH AND DIVING BEHAVIOUR

241 Fourteen of the *A. anguilla* tagged with depth sensing transmitters were registered by one or
242 more ALS arrays. Mean swimming depth was 24 m when passing the first array, 64 m at the
243 second array and 48 m at the third array (Table II and Fig. 5). This indicates that the *A.*
244 *anguilla* did not migrate close to the bottom but stayed in the uppermost 10–25% of the water
245 column. There was no difference in swimming depth between day and night (Welch's *t*-test,

246 d.f. = 34, $P > 0.05$). The individual variation in mean swimming depth was large and varied
247 from 0 to >130 m (Table II). Further, individuals often changed swimming depth within a
248 short time period. Three individuals were observed to change from 110–130 m depth to < 10
249 m depth within 15 min. Dives to 130 m depth or more were observed at all three ALS arrays.
250 Twelve individuals had dives deeper than 50 m and seven of these had dives deeper than 100
251 m.

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253

254

DISCUSSION

PERFORMANCE

255 The registration of 50% of the *A. anguilla* 31 km outward the fjord is a minimum estimate of
256 the survival. Four of the automatic listening stations in the third array were lost before the
257 study ended and some fish may therefore have passed the array without being registered. Six
258 (19%) of the fish were never registered after release, which may be due to predators bringing
259 the *A. anguilla* out of the river, malfunctioning transmitters, or the fish moving to a place in
260 the river where the detection efficiency was low (like rapids with high current speeds)
261 (Davidsen *et al.*, 2009). Winter *et al.* (2005) studied tagging effects in *A. anguilla* silver eel,
262 and recorded no transmitter expulsion or mortality related to tagging. Moreover, they found
263 no effects of tagging on timing of activity. *A. anguilla* silver eels have also been successfully
264 tagged with similar transmitters in several other studies (*e.g.* Baras & Jeandrain, 1998;
265 Behrmann-Godel & Eckmann, 2003). Hence, transmitter implantation was not expected to
266 largely affect fish behaviour or survival.

268

TIMING OF SEA ENTRY AND DIEL MIGRATORY PATTERN

270 The *A. anguilla* entered the sea during all parts of the tidal cycle and did not seem to utilize
271 the outgoing tidal currents. Selective tidal stream transport is a behavioural mechanism that
272 allows organisms to quickly pass through the transition zone between the freshwater and
273 saline habitat by using the outgoing tidal current speeds. Such behaviour may be important for
274 many diadromous fish species due to the often high predation pressure in estuaries (Dieperink
275 *et al.*, 2002; Jepsen *et al.*, 2006). American silver eel *Anguilla rostrata* (Lesueur) have in
276 some studies been found to use tidal currents as a transport mechanism (Parker&McCleave,
277 1997; Hedger *et al.*, 2010), while in a recent study, timing of sea entry had little or no relation
278 to the tidal cycle (Carr&Whoriskey, 2008). In *A. anguilla* silver eel, selective tidal stream
279 transport has been suggested during open ocean migration (Arnold&Cook, 1984), but there
280 appear to be no studies that document such behaviour during sea entry.

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

290

291 MIGRATORY SPEED

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

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

309

310 HORIZONTAL DISTRIBUTION

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

318

319 SWIMMING DEPTH AND DIVING BEHAVIOUR

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

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

344 Since the swim bladder nematode *A. crassus* may severely injure the swim bladder
345 and possibly affect the vertical migration of *A. anguilla* (Van Banning & Haenen, 1990;
346 Würtz & Taraschewski, 2000; Abdelmonem *et al.*, 2010; Neto *et al.*, 2010), it may be argued
347 that the observed behaviour with fast vertical movements up and down the water column may
348 be a result of *A. anguilla* not being able to keep a steady depth possibly due to being infected
349 by this parasite. It was therefore important to document that this study represents parasite-free
350 individuals. The *A. anguilla* in the present migration study were sampled in 2007 while the *A.*
351 *anguilla* examined for the presence of the swim bladder nematode *A. crassus* were sampled in
352 2009. As the prevalence and abundance of *A. crassus* in *A. anguilla* have increased to high
353 numbers within a short period when introduced to other Norwegian rivers (Mo, 2009), it is
354 unlikely that *A. crassus* was present in River Halselva in 2007 but not observed in 2009.
355 However, it may be argued that the spread of *A. crassus* among *A. anguilla* in the
356 northernmost Norwegian rivers would be slow due to the cold climate and that the sample of
357 14 *A. anguilla* was too small to detect the parasite. If the parasite was present in 2007, the
358 prevalence and abundance of the nematode were likely so low that the effect on the seaward
359 migratory behaviour of *A. anguilla* was neglectable.

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

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366

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

	River mouth	1 st ALS Array	2 nd ALS Array	3 rd 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%)
<i>P</i> value	< 0.001	< 0.001	< 0.05	< 0.05

4

1 TABLE II: The mean swimming depths of *Anguilla anguilla* silver eel as they passed three
 2 arrays of automatic listening stations (ALS) in the Alta Fjord during their seaward migration.
 3 n is the number of individuals registered at each array. Since the tags only recorded depths <
 4 130 m, 130 m means that the *A. anguilla* was at 130 m depth or deeper.

5

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

6

1 Figure captions:

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

6

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

8

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

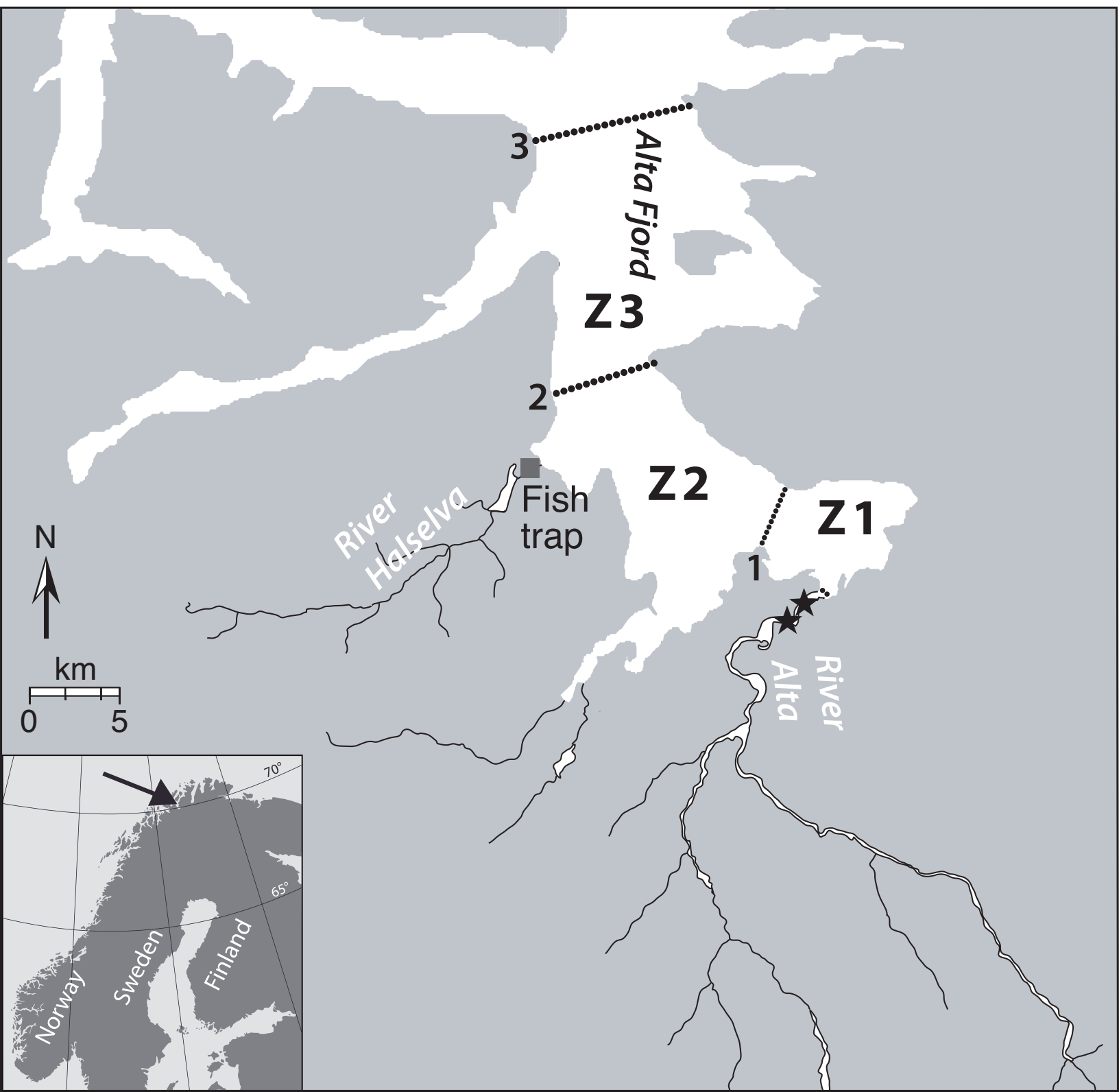
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14 FIG 4: Horizontal distribution of *Anguilla anguilla* silver eel during migration through the
15 Alta Fjord. a) is the distribution of registered eel at the third automatic listening station (ALS)
16 array (21 ALSs), b) distribution at the second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

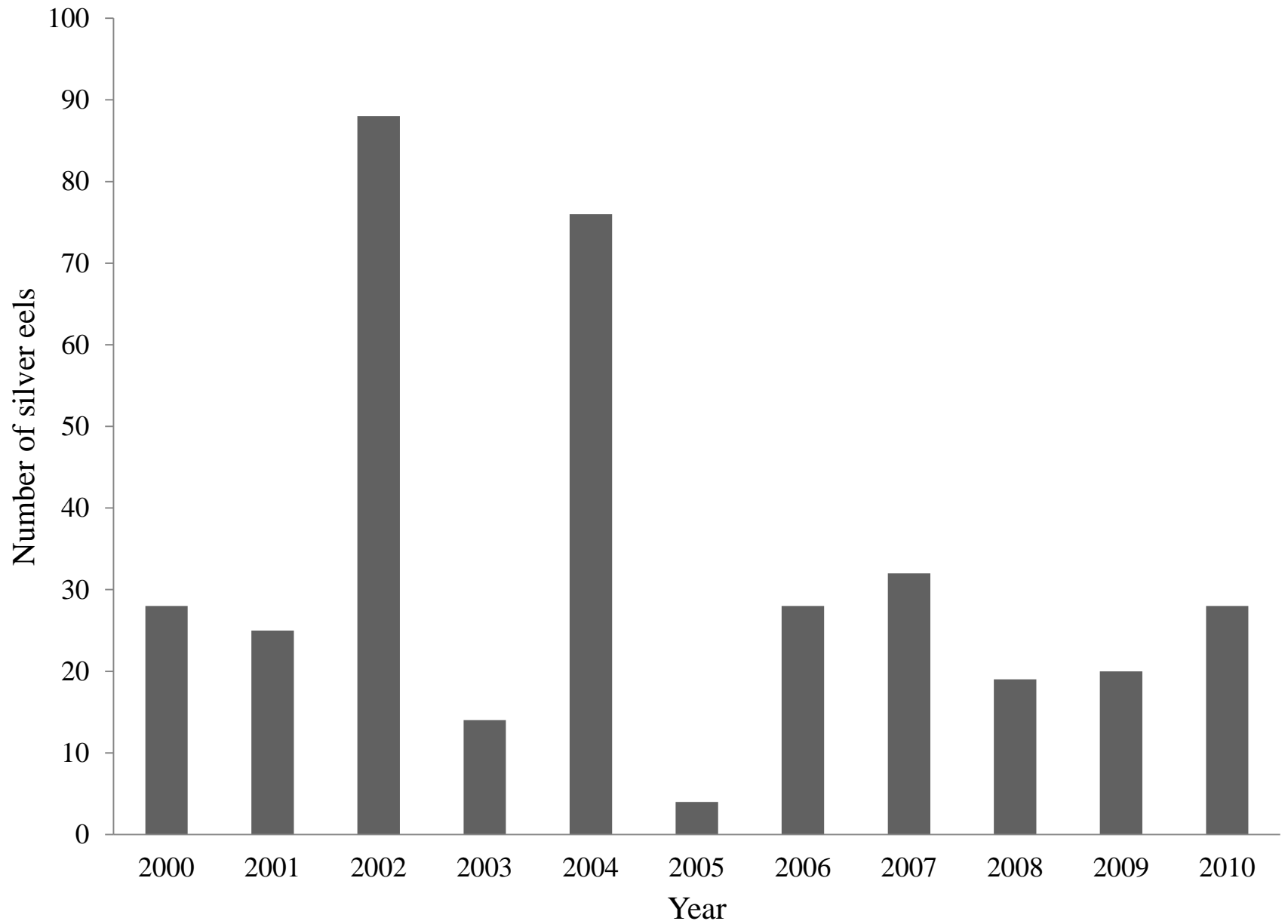
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22 FIG 5: Depth distribution of *Anguilla anguilla* silver eel during migration through the Alta
23 Fjord. a) shows results at the third automatic listening station (ALS) array (21 ALSs), b) at
24 the second array (14 ALSs) and c) at the first array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

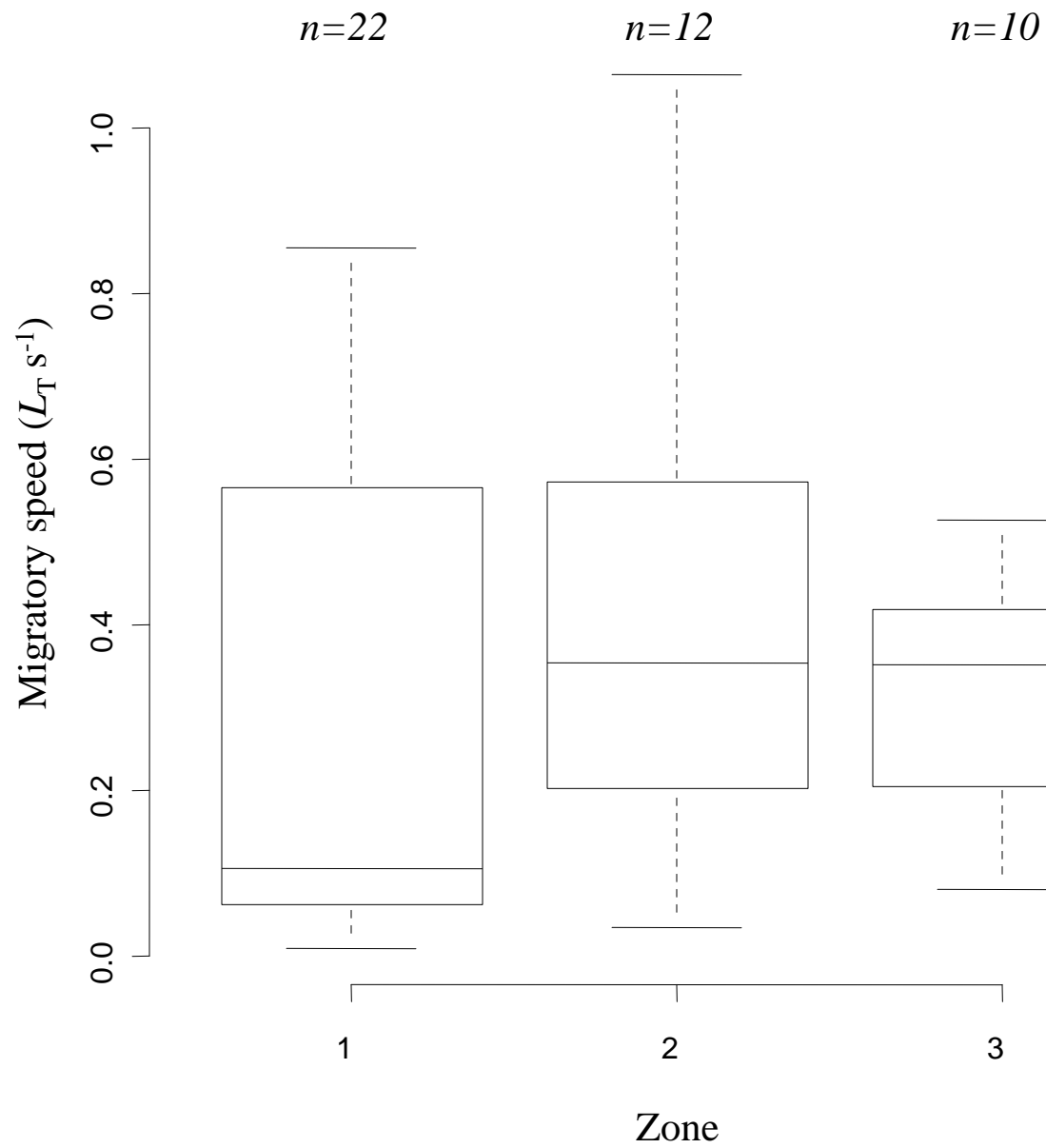
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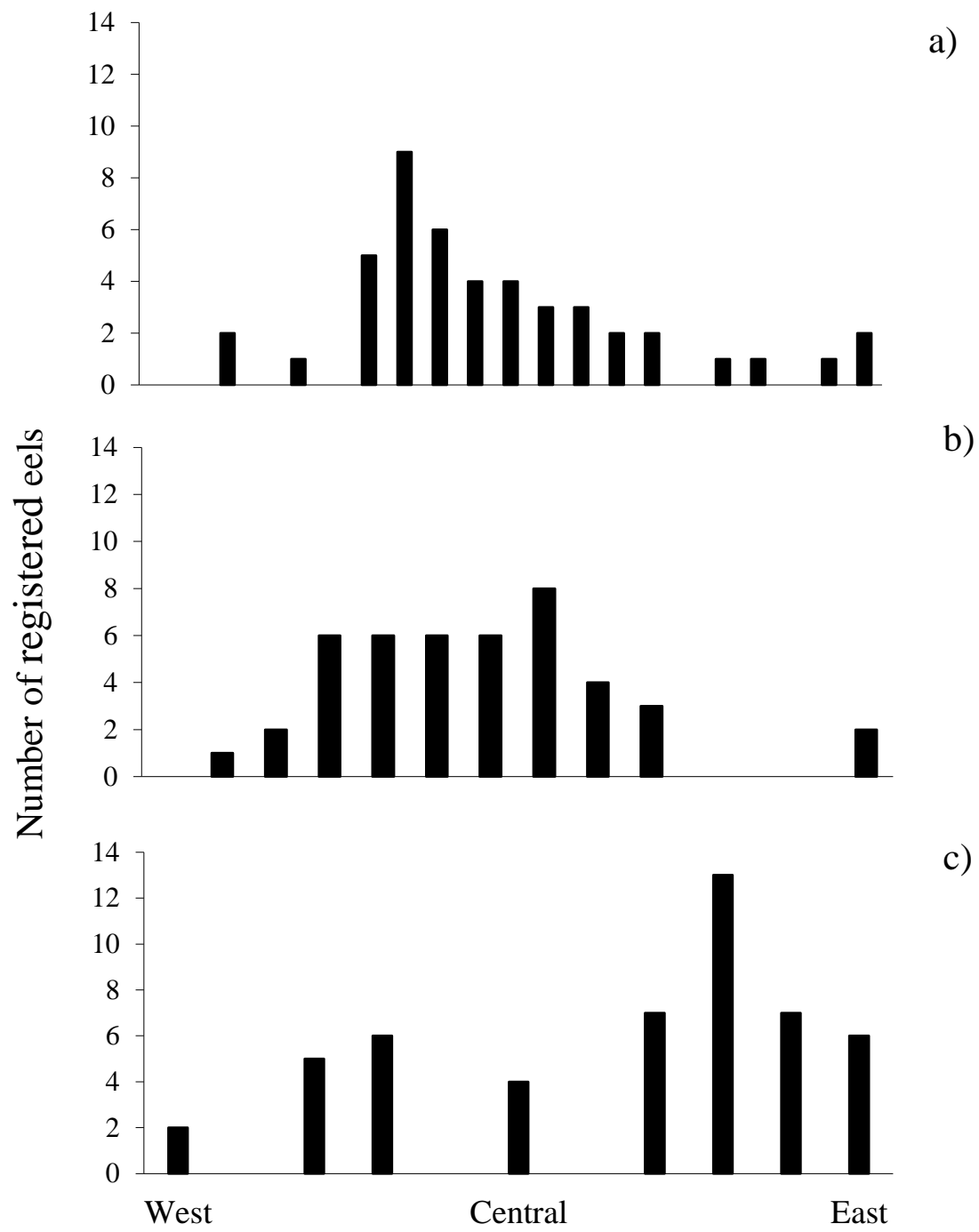
Figure



Figure



Figure



Figure

