Original Article

European eel *Anguilla anguilla* compromise speed for safety in the early marine spawning migration

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There are substantial benefits to potential fitness conferred to animals that undertake migrations. However, animals must make compromises to maximize survival and compensate for the risks associated with long-distance movement. European eel (*Anguilla anguilla*), a migratory catadromous fish, has undergone population declines owing to changes in marine and freshwater habitat and interactions with human infrastructure, instigating research to investigate the mechanisms controlling their migration. Yellow-phase European eels from the local River Opo and silver-phase European eels transplanted from River Imsa, Norway, were implanted with acoustic transmitters and released within a network of receiver stations in the Hardangerfjord, Norway. Silver-phase eels exhibited more movement within the array than yellow-phase eels, signifying the onset of migration. Silver-phase eels moved through the fjord nocturnally, arriving at gates predominantly at night. Eels had slower rates of migration than expected based on models predicting continuous movement, suggesting that movement ceased during daylight hours. Reduced net rates of travel supported the hypothesis that eels compromise speed for safety during the early marine migration by avoiding predators and not actively migrating during daylight. The silver eels were capable of directed movement towards the ocean and were not recorded by receivers in bays or dead ends. European eels must successfully transit this coastal zone, where their residence is prolonged because of the relatively slow speeds. These results suggest that the early marine phase of the European eel spawning migration be a focal period for European eel conservation efforts.

Keywords: asset protection principle, conservation behaviour, exploitation, fjord, telemetry.

Introduction

Migration is a behaviour that pervades among invertebrate and vertebrate taxa in the animal kingdom (Dingle and Drake, 2007). Animals evolved migratory behaviour to cope with seasonal changes in their environment and exploit highly productive areas to enhance reproductive potential by accelerating growth, avoiding predators (Zaret and Suffern, 1976; Gliwicz, 1986), or mitigating disease risk (Altizer *et al.*, 2011). The behaviour confers substantial resource advantages to individuals but also involves considerable risk (Hebblewhite and Merrill, 2007). Long-distance migration is energetically taxing and many animals forego feeding while migrating, meaning that migration must be powered by limited somatic energy stores (Stephens *et al.*, 2009).

Hormones associated with the glucocorticoid stress response (e.g. cortisol; Lobato *et al.*, 2010; Cornelius *et al.*, 2013) and oxidative stress products (Bombardier *et al.*, 2010) incurred along the migration have the potential to negatively affect the individual and require physiological and behavioural adaptations to manage stress and maintain fitness. The asset protection principle predicts that animal behaviour should be increasingly cautious with increasingly valuable reproductive assets (Clark, 1994). Older age, larger body size, or greater gonadal investment should therefore increase vigilance in animals (Lenormand *et al.*, 2004; Halttunen *et al.*, 2013).

The European eel is a highly migratory fish that colonizes rivers or coastal areas throughout the European continent (van

Ginneken and Maes, 2005). Eel larvae recruit to coastal areas and freshwater systems and may remain up to 50 years while feeding, growing, and preparing to return to the Sargasso Sea (Poole and Reynolds, 1998). After sufficient energetic reserves have been accumulated, yellow-phase European eels transition to the migratory life stage, which may be characterized by a change in colouration (Lokman et al., 2003; Durif et al., 2005; Bruijs and Durif, 2009). Migratory eels undergo a whitening of the ventral skin, darkening of the dorsal skin, expansion of the eye width, and lengthening of the pectoral fins for marine life (Durif et al., 2005; but see Pankhurst and Lythgoe, 1982). Physiological changes to the silver-phase eel include increased muscle power output to economize energy during the non-feeding migratory life stage (Ellerby et al., 2001; Lokman et al., 2003). The long-distance movements of European eel in the marine environment were unknown until recently (see Aarestrup et al., 2009; Righton et al., 2012, 2016) and based on field observations and fishery interceptions of migrating eels (Ernst, 1977; Bast and Klinkhardt, 1988) without empirical data on the actual marine life of adult eels. Advances in animal biotelemetry provide evidence that silver eels swim in excess of 5000 km through the marine environment to reach spawning grounds in the Sargasso Sea (Aarestrup et al., 2009; Righton et al., 2016). Eels encounter competing pressures of speed and safety after entering the marine environment as they must avoid predation and energetic exhaustion to reach spawning grounds in synchrony with conspecifics at the appropriate time.

Migratory species are exposed to additional risks because of their movement through multiple habitats (Hebblewhite and Merrill, 2007). Long-distance movements by European eel up and down major river systems and through estuaries and fjords to the open ocean expose them to considerable interference from human infrastructure that has contributed to their imperilment (Dekker, 2003; ICES, 2009). An effective recovery plan for eels requires accurate knowledge of the behaviour and survival throughout the life history and better information of the early marine phase is needed to contribute to such a framework (Davidsen et al., 2011; Bultel et al., 2014). In Norway, silver eels exit rivers into fjords, which form relatively narrow channels to the open ocean. Compared to rivers that discharge into the open ocean, long networks of fjords provide an opportunity for accurate tracking of the early marine phase of eel migration (e.g. Davidsen et al., 2011) because they travel through a channel that can be adequately covered by arrays of acoustic receivers. Yellow- and silver-phase eels were implanted with transmitters in Norway's second longest fjord system with receiver gates positioned in the fjord en route to the North Sea to track the speed, periodicity, and success of eels exiting the fjord. The array was used to observe the early marine migration of acoustically tagged European eels and to test the hypothesis that European eels trade off safety and speed in their migration.

Methods

The 179 km Hardangerfjord is the world's fourth longest fjord and the second longest in Norway. The Hardangerfjord is a network of smaller fjords, creating a large, branching area that must be navigated by migratory species that use the fjord including sea trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), and European eel that enter local rivers. To study the movement of eels during their spawning migration, trap nets were set from 25 August to 15 September 2006 in the Hardangerfjord (60.072210°N, 6.549732°E) near the confluence of the River Opo

at the town Odda to capture European eel. Seventeen female yellow-phase eel were captured (56.6 ± 20.2 cm SD TL, range = 47.4–73.7-cm TL). Because of an absence of silver-phase eel, 56 female silver-phase eel were captured in a Wolf trap 100 m from the sea in the River Imsa (58.903324°N, 5.963514°E) during their downstream migration (59.7 ± 18.1-cm TL, range = 51.0–89.7-cm TL) and transported by car to the same site in the Hardangerfjord for release on 14 September 2006. Eels were individually anaesthetized (40 mg l^{-1} metomidate, Aquacalm, Syndel Laboratories Ltd, Canada; Iversen et al., 2013) and a 9- or 13-mm acoustic transmitter (Thelma Biotelemetry, Trondheim, Norway) was implanted into the intraperitoneal cavity using methods described by Økland and Thorstad (2013) and Thorstad et al. (2013). The incision in the body cavity was closed with sutures and the eels were allowed to recover prior to release. Thorstad et al. (2013) found tag expulsion rates after six months of 12% using similar methods. Following tagging, eels were recovered for 1–6 h such that all were released simultaneously on two tagging days, either 14 September 2006 at 20:25 or 15 September 2006 at 15:34.

Underwater acoustic telemetry receivers (VEMCO VR2, Halifax, NS, Canada) were deployed in a gate configuration (see Donaldson et al., 2014) at six points in the fjord and in some bays and dead ends. The gates, G1 (*n* = 2 receivers), G2 (*n* = 6), G3 (*n* = 6), G4 (*n* = 2), and G5 (*n* = 8), were placed 2.0, 9.6, 34.8, 73.6, and 94.7 km from the release location and remained active from September 2006 to March 2007. The first gate was placed 2.6 km from the confluence of the River Opo (Figure 1). This receiver network permitted the identification of migratory activity through the fjord and a determination of survival. Calculating survival was only possible up to Gate 4 because of gaps in coverage at subsequent gates. Migration speed was calculated between gates to determine the average rate of movement through the fjord.

Data analysis

Time to enter the array was compared between silver- and yellow-phase eels with a Welch's two-sample t-test, implemented with the t-test function in R (R Core Team, 2017). Lunar phases were determined using the *lunar.phases* function in the R package lunar (Lazaridis, 2014). Diel migratory activity was tested by the Rayleigh test of uniformity, implemented with the *r.test* function in the R package CircStats by converting hour of the day to degrees (Lund and Agostinelli, 2012). To determine whether eels arrived at gates predominantly at nighttime, the onset and cessation of darkness were determined using the *getSunlightTimes* function in the R package suncalc returning the time of night and nightend (Agafonkin and Thieurmel, 2017). Migratory behaviour of yellow- and silver-phase eels was modeled using time to event analysis. Visual comparison of the migration of yellow- and silver-phase eels was plotted with Kaplan-Meier Survival curves using the *ggsurvplot* function in the survminer package (Kassambara and Kosinski, 2016). Cox proportional hazards regression was then applied using the *cph* function in the survival package (Therneau, 2015) to compare the migratory behaviour of yellow- and silver-phase eels in the Hardangerfjord. Proportionality of hazards assumption was tested by extracting Schoenfeld residuals from the model and testing for violation at α = 0.05. Time to event analysis relies on a continuous response variable associated with the time at which an event is recorded (or censorship is assigned); for our purposes, we used the spatial variable (Gate number) instead of time as the
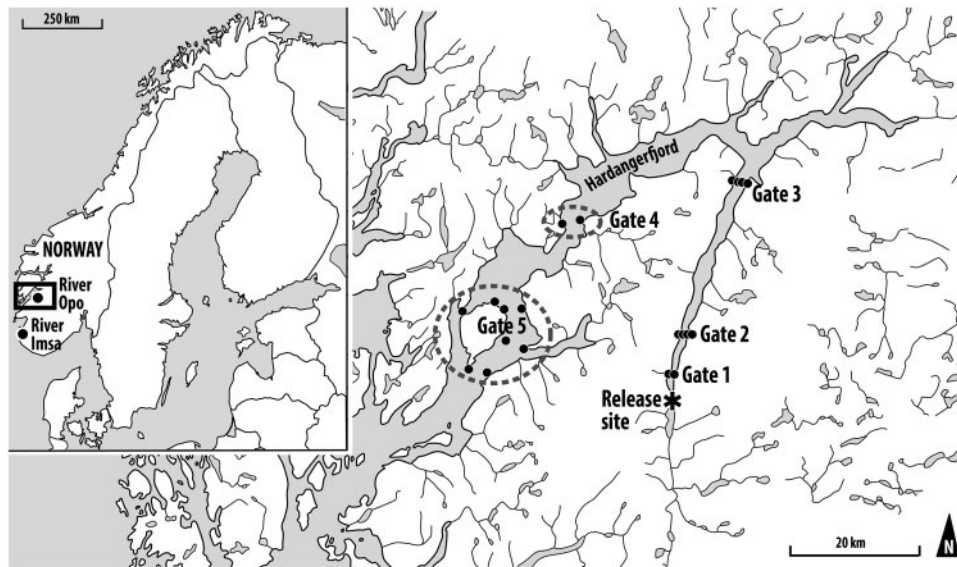
Figure 1. Site diagram of the migration arena used to investigate the estuarine progress of European eels (*Anguilla anguilla*). Yellow eels were captured from the River Opo and silver-phase eels were captured and transported from the River Imsa (inset). Gates are shown in the main figure consisting of Vemco VR2-W type acoustic receivers to detect movements of eels out of the fjord towards the Atlantic Ocean.

response variable. The model was therefore comparing the migratory activity of yellow- and silver-phase eels based on detections at the gates. For example, eels that were detected up to Gate 4 were coded as having an event occur at $t(4)$. Time to event analysis also allows individuals to be censored when they drop out of a study; eels not detected at Gate 5 could not be determined to have died but instead were censored at Gate 4. The dataset is therefore right censored because eels that were detected at all gates never experienced an event but instead were censored at $t(5)$. Censorship of eels with unknown fate allowed us to account for the uncertainty associated with incomplete receiver array coverage of Gates 4 and 5 while maximizing the amount of data available for modelling (i.e. because we did not have to entirely remove fish with unknown fate).

Average migration rates were calculated for eels as the time between last detection at a gate to the first detection at the subsequent gate in kilometers per day. Detection efficiencies were calculated by Plantalech Manel-La *et al.* (2011) between 100 and 500 m depending on the environmental conditions at the time of tag transmission, with 99% efficiency at G2 and 94% at G3. Rate of movement was compared among gates with a linear model (*lm* function in R) to determine whether distance between gates influenced the time taken to migrate within the array with multiple comparisons calculated by a Tukey HSD test with the *glht* function in the multcomp package (Hothorn *et al.*, 2008). Figures were plotted using ggplot2 (Wickham, 2008) and the extension ggridges (Wilke, 2017; Figures 2 and 3).

Results

In total, 17 yellow-phase eels (62.2- ± 7.5-cm TL) were captured from the River Opo and 56 (64.7- ± 7.1-cm TL) silver-phase eels were imported from the River Imsa; both groups were released between 14 and 15 September 2006. No detections were recorded on receivers in dead ends or bays. Among 73 eels tagged, 26 were not detected on the first gate, most ($n = 16$) of which were yellow-phase eels from Opo. However, six silver- and one yellow-phase eel were later detected at Gate 4 (having never been

detected at any prior gates). Five silver-phase eels were never detected in the array (9%) and 22 (39%) were detected at the final gate; however, this gate did not have complete coverage and therefore the fate of eels that did not make it beyond Gate 3 is unknown. There was a significant difference in movement of the silver-phase eels of River Imsa origin compared with the movement of local yellow-phase eels according to Cox proportional hazards ($z = 6.22$, $p < 0.01$). Odds of movement within the array were 9.48 higher for silver-phase eels than yellow-phase eels.

Average silver-phase eel speed from release to Gate 1 was 4.2 ± 13.7 km d^{-1}, 44.5 ± 25.4 km d^{-1} Gate 1–2, 19.5 ± 18.8 km d^{-1} Gate 2–3, 9.8 ± 8.2 km d^{-1} Gate 3–4, and 13.9 ± 9.6 km d^{-1} (Gate 4–5; Figure 4). Modelled travel times between gates were significantly different from Gates 1–2 and all other gates (all Tukey $|t| > 5.78$, $p < 0.01$) and between release and Gate 1 and Gate 1–3 (Tukey $t = 3.89$, $p < 0.01$) such that shorter distances were transited faster.

Eels moved nocturnally and were first detected at each gate predominantly during nighttime hours (r-bar $= 0.99$, $p < 0.01$; Figure 1). Based on nighttime hours calculated from the suncalc package, eels arrived at gates predominantly during the night at Gates 1 (71% of those arriving), 2 (91%) and 3 (88%) Gate 4 (79%), and Gate 5 (95%). Arrivals at each gate were recorded predominantly on waxing (51%) and full (23%) moon phases, with a minority when the moon was waning (15%) or new (12%).

Discussion

The marine migration of Anguillid eels has presented one of the great mysteries of fish biology but the secrets are slowly being revealed by electronic tagging technologies (Righton *et al.*, 2012). Considerable effort has been expended to characterize the routes used by silver-phase eels migrating in the open ocean as they progress towards spawning grounds (Aarestrup *et al.*, 2008, 2010; Davidsen *et al.*, 2011; Righton *et al.*, 2016). However, movement through nearshore coastal areas such as fjords may be a significant bottleneck with disproportionately high mortality (as in
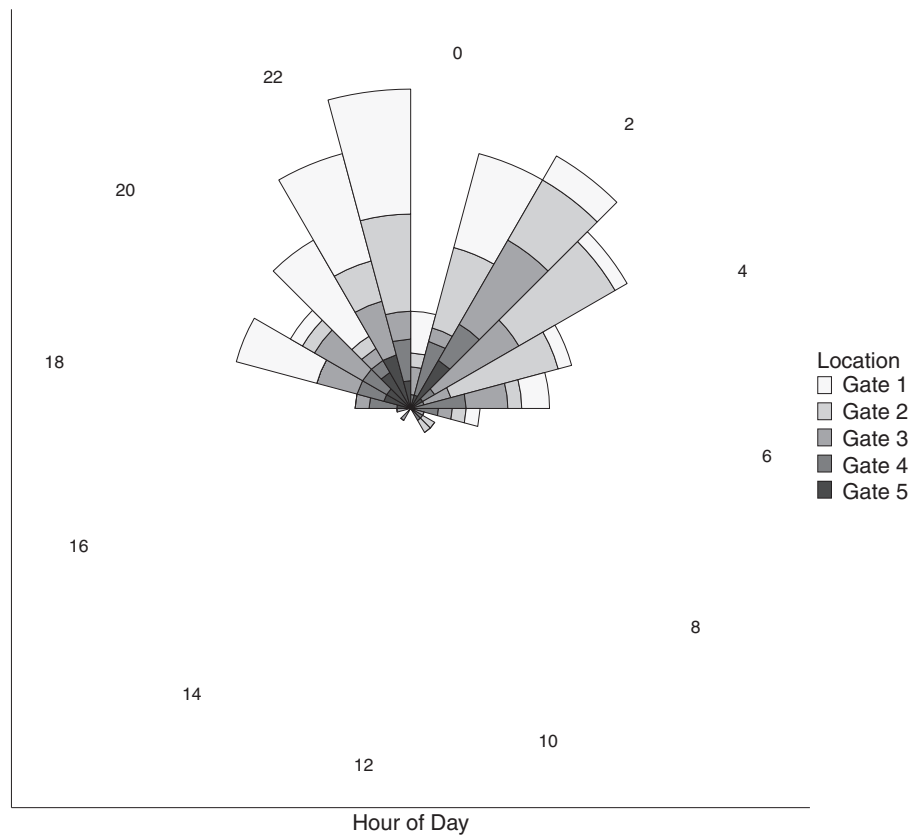
Figure 2. Polar histogram of entrance times recorded (i.e. first detection) for European eels (*A. anguilla*) at Gates 1–5 in an array of acoustic receivers in the Hardangerfjord, Norway. For the Rayleigh test of uniformity, hours were converted to degrees by dividing hour by 24 and multiplying by 360°.
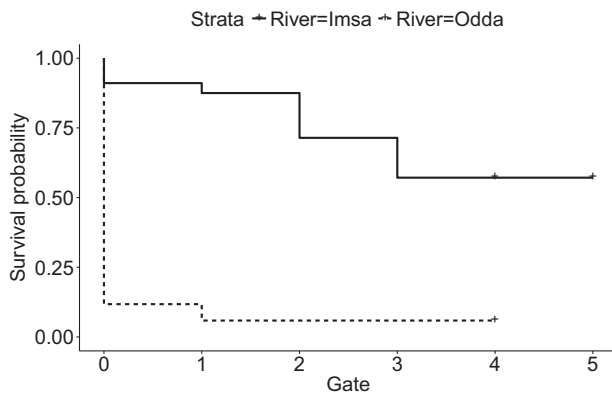

Figure 3. Kaplan-Meier survival curves comparing the marine migration of European eel from River Opo (yellow-phase eel) and from River Imsa (silver-phase eel). Gates are used in lieu of time in the analysis; therefore, survival curves suggest the probability for an eel from each river (or of each colour) to be detected at each Gate (note- 0 is the point of release). Hashed marks indicate times at which censorship (i.e. removal because the fate beyond this time was unknown) was taken into account by the model given that Gates 4 and 5 had incomplete coverage of area in the fjord.

Atlantic salmon smolts; Thorstad *et al.*, 2012). Here, we used the branching geology of a long fjord complex to establish a receiver array in which acoustically implanted European eel can migrate and reveal the early marine migration through coastal waters

towards the open ocean. Our findings suggest a nocturnal migration that slows the average rate of progress out of the fjord, may prolong the overall migration, and could even delay the arrival at breeding grounds if there is no compensation later in the migration. We interpret this adaptation as supporting the asset protection principle (Clark, 1994) wherein the eels compromise speed for safety from predation during this phase of migration. Typical eel predators include marine mammals, sharks, and probably large bony fishes (Béguer-Pon *et al.* 2012; Wahlberg *et al.*, 2014), which may be more effective predators during diurnal periods.

Silver-phase eels in the Hardangerfjord were slower migrating between longer distances. It is unlikely that they were moving more slowly owing to physiological limits on swimming capacity. Experimental studies of eel swimming suggest that eels are capable of efficient swimming at higher speeds, with an optimum proposed by Palstra and van den Thillart (2010) of 0.80 bl s^{-1}. Correspondingly, we calculated average displacement of 0.81 bl s^{-1} across a short distance between Gates 1 and 2 (7.60 km). Between Gates that were farther apart, rates of transit were slower, not likely because they were swimming more slowly but most likely because they were only moving at night. Similar rates were observed by Davidsen *et al.* (2011), who calculated a speed of 0.25 bl s^{-1} across a 31-km fjord reach. Righton *et al.* (2016) also calculated speeds of 0.25 ± 0.12 bl s^{-1} for eels travelling in the open ocean. These speeds are slower than predicted by van den Thillart *et al.* (2004), who observed eels capable of steady swimming at 0.50 bl s^{-1} for long intervals, albeit at a temperature
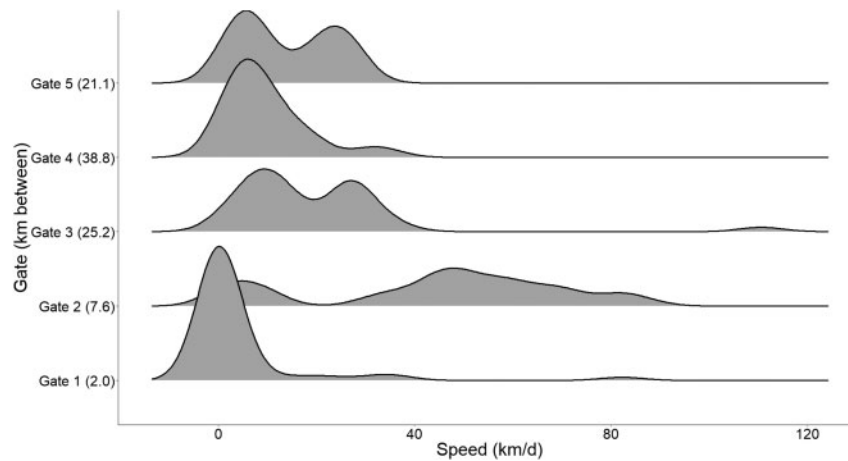
Figure 4. Ridge plot of densities representing the inferred speed between receiver gates moved by silver-phase eels (*A. anguilla*) in the Hardangerfjord. Speeds were calculated based on the first and last detection at each gate, if detections were missing for a gate it is excluded (i.e. if an eel was recorded at Gates 1 and 3 there is no speed reported for Gate 1–2 or 2–3). Note that Gate 1 represents the speed between the release site and Gate 1 and subsequent values are between gates (i.e. not cumulative).

(19°C) higher than would be expected in the Hardangerfjord. At speeds ≤ 0.50 bl s^{-1}, eels power movement with posterior red muscle fibres without anaerobic white muscle (Gillis, 1998), which would avoid oxygen debt (Lee *et al.*, 2003). An alternate explanation for these observations would be inefficient migration by eels between gates if eels failed to find the correct route. If this were the case, movement would be slow but detections would be expected to be equally distributed throughout the day. Given that movements on receivers were recorded at night, the most likely explanation for our observations is that eels migrate predominantly during nighttime and have periods of diurnal inactivity that slow the average rate of movement as measured between gates.

Nocturnal movement of eels during the early marine migration results in slower average swimming speed and a prolonged migration through the fjord relative to their physiological capabilities. Other research has identified risk averse behaviours by eels that have been interpreted as adaptations to mitigate predation. Downstream migrating silver-phase eels exit rivers on longer, dimmer nights when their visibility to predators would be lower; eels also tend to move preferentially with conspecifics as a strategy for predator saturation (Bruijs and Durif, 2009; Sandlund *et al.*, 2017). Studies that have observed European eel migration in three dimensions have noted diel vertical migration, finding eels in warm, shallow water at night and cool, deep water during the day (Aarestrup *et al.*, 2009; Righton *et al.*, 2016). Aarestrup *et al.* (2009) suggested that this vertical migration serves to behaviourally thermoregulate rather than to avoid predators. However, Amilhat *et al.* (2016) found that eels exhibited diel vertical migration in the Mediterranean Sea in the absence of temperature stratification, suggesting that thermoregulation is not the primary motivation for daily dives. Temperature stratification in the Hardangerfjord is expected to be minimal and vertical movements would more likely allow eels to access different salinities or photic conditions rather than temperatures. Sjøtun *et al.* (2015) measured the halocline in the fjord and identified temperature stratification that might influence eel physiology and movement. However, we did not specifically measure depth or microhabitat of eels and this is an area for future research. In support of the

predator avoidance hypothesis, several studies have described predation on tagged eels, suggesting that the predator burden during the spawning migration is considerable (Wahlberg *et al.*, 2014; Amilhat *et al.*, 2016), which would drive evolution of behaviour. There may be benefits to eels using colder bottom water to delay maturation as they make slow progress towards the Sargasso Sea (Aarestrup *et al.*, 2009), but it seems likely that predator avoidance is an important driver of the behaviour of eels during their migration, including, as we have observed, diurnal inactivity.

The prevailing hypothesis is now that eels exit rivers predominantly before September–December and most spawning is completed in the early winter and springtime, with half the spawning complete by February (Righton *et al.*, 2016). Constant swimming at speeds of 0.5 bl s^{-1} (van den Thillart *et al.*, 2004) would be sufficient to place eels in the Sargasso Sea after 6 months (Ellerby *et al.*, 2001; van Ginneken, 2006) during the winter and spring when spawning is believed to occur (Righton *et al.*, 2016). However, this is likely after the peak spawning time (Righton *et al.*, 2016). Moreover, eels do not necessarily travel directly towards the Sargasso Sea, meaning that models predicting the travel time and distance are underestimates by using straight-line distances (Righton *et al.*, 2016). Our observation that eels migrate slower in the fjord suggests that silver-phase eels moving through fjords compromise speed for safety during their fjord migration; rather than making it to the Sargasso Sea as quickly as possible, migrating eels seem to take extra time, which we interpret as a means to improve safety. Given the speeds recorded in the open ocean (Righton *et al.*, 2016) and fjords (Davidsen *et al.*, 2011; this study), most eels must begin migrating to spawning grounds over a year in advance of their spawning time.

Individual variation in these data shows that some European eels may have a plastic migration, with some migrating more quickly than counterparts or migrating more than others during the day. This is consistent with the asset protection principle insofar as lower quality individuals (e.g. lower energetic reserves, less gonadal investment) are likely to accept more risky behaviour (Clark, 1994; Halttunen *et al.*, 2013). Migration is a highly plastic behaviour and many other species of fish exhibit intraspecific

adaptations in timing and speed (e.g. Jonsson *et al.*, 1990; Olsson and Greenberg, 2004). Although we were not able to test for mechanisms driving differences among individuals within our sample, our observations of variation suggest that future studies should compare somatic and gonadal energies for migrating eels to investigate what drives intraspecific differences in movement.

Silver-phase eels migrated farther in the acoustic array than yellow-phase eels, which aligns with predictions based on previous literature differentiating between life stages. Although the use of eel colouration as a predictor of migratory activity has been criticized (Pankhurst and Lythgoe, 1982), we found there was a significant difference between silver- and yellow-phase coloured eels. However, not all silver-phase eels migrated to the end of the array. Although the eels that did not continue in the array may have died, there is considerable plasticity in eel migration such that silver-phase eels should not necessarily be expected to migrate rapidly out of the fjord (Simon *et al.*, 2012). If the eels did perish, then the survival rate was still comparable to a 28.7 km stretch of a Danish fjord measured by Aarestrup *et al.* (2008, 2010), who tracked 17 and 43 eels entering the Randersfjord and 3 (18%) and 17 (40%) exiting the fjord in 2008 and 2010, respectively. In Randersfjord, these mortalities were attributed to fishery removals given that manual tracking failed to identify any tags remaining the fjord and that transmitters from predated eels would be detected from within the predator on the array. In the Hardangerfjord, no manual tracking was performed so eels could have been in areas between the arrays. If mortality did occur, natural mortality including predation would be the most likely cause; fisheries are not active in the Hardangerfjord and no significant tag effects are anticipated because Winter *et al.* (2005) studied transmitter implantation on silver-phase eels and identified 10% mortality but limited impacts on behaviour. The 10% tagging mortality could not account for the five silver-phase eels that never entered the array after release and is unlikely to explain the number of eels with unknown fate.

Conclusion

Mortality during the early marine migration has the potential to be a significant contributor to declines in European eel. Further research is needed to determine the actual fate of eels that disappeared within our array, whether they were predated, died of other causes, or were more simply no longer actively migrating. Indeed, the plasticity in the migration of European eel requires more attention to compare the exceptional individuals that travel slow or fast through the marine environment. A relatively high rate of disappearance by tagged silver-phase eels during this phase of the migration would be supported by other studies that have identified migration through fjords to be a risky phase in what is ultimately a small percentage of the total distance to spawning grounds. Even if mortality is not high, we found that the early marine migration through fjords is similar to rates observed in the marine environment. Transitional habitats such as estuaries and fjords are often overlooked phases of anadromous migration (Levings, 2016); however, the fjord migration is an important phase of eel migration and should be a focal point for eel conservation to improve overall spawning escapement.

Acknowledgements

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