Contents

1. Introduction

The European eel (*Anguilla anguilla* L.) is a catadromous species, which means it feeds in freshwater and migrates downstream to sea to spawn. The life-cycle (Fig. 1) is believed to begin in the Sargasso Sea (Schmidt, 1922), from where the larvae are transported along the Gulf Stream and North-Atlantic Drift to the European continental shelf (van Ginneken & Maes, 2005; Righton *et al*., 2012). At this stage, the larvae metamorphose into glass eels and proceed into freshwater or coastal habitats across Europe, North Africa or Mediterranean Asia, where they feed and grow for about 5–50 years as yellow eels (Tesch, 2003; Dekker, 2004). *Anguilla* spp. are semelparous, meaning that they reproduce only once per lifetime. Reproductive migration is preceded by an adaptive process known as "silvering", which prepares the partially mature adults for the oceanic conditions to which they will be subjected (Tesch, 2003; Righton *et al*., 2012). Feeding ceases once silvering is complete and therefore adequate lipid reserves are required to cover the extensive journey to the spawning ground, as well as to fuel gonad maturation (Tesch, 2003). It is therefore believed that reproductive migration only occurs in eels with sufficient lipid stores (Palstra & van den Thillart, 2010). In addition to internal biological factors, the silvering process is thought to be triggered by external factors, namely a sudden decrease in water temperature and low light levels (Vøllestad *et al*., 1986; Durif *et al*., 2002; Bruijs & Durif, 2009). Downstream movements have been related primarily to increased water flow during the dark of the moon, between sunset and midnight (Frost, 1950; Lowe, 1952; Haro, 2003).

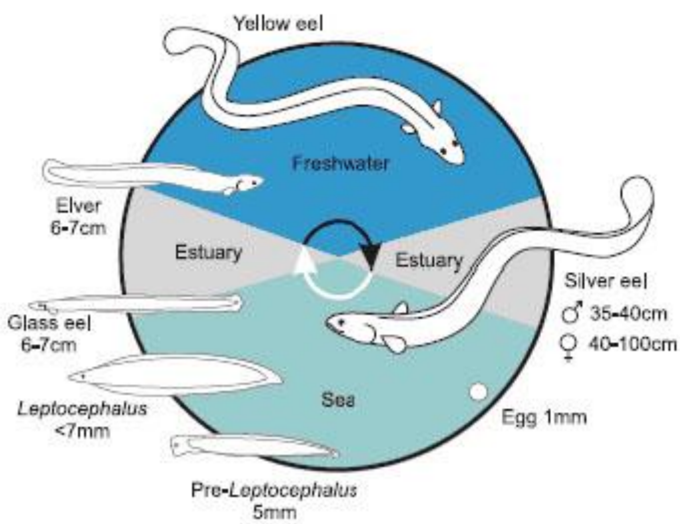

Figure 1. Life-cycle of the European eel. Image courtesy of www.cefas.defra.gov.uk.

The increasingly high socio-economic value of eels means that they are heavily exploited during various life-stages, including the silver phase (Dekker, 2000, 2004; Tesch, 2003; Cottrill *et al*., 2006). Recruitment of elvers has dwindled to about 1% of that in the late 1970s, with the entire European standing stock showing steep decline (Dekker, 2000, 2003, 2004). Fewer silver eels returning to sea to spawn, as a result of reduced spawner production (Anonymous, 2009; MacNamara & McCarthy, 2013) and human activities along the reproductive migratory route (e.g. Durif *et al*., 2002; Winter *et al*., 2006; Acou *et al*., 2008), is often imputed as a significant contributing factor to the decline. Accordingly, the International Council for the Exploration of the Sea (ICES) have raised the importance of reducing such activities until stock recovery is achieved (ICES, 2009, 2010, 2012). In line with ICES recommendations, the European Union (EU) produced an eel recovery plan, the key feature of which is to "reduce anthropogenic mortalities so as to permit with high probability the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock" (EU, 2007). Escapement rates of migrating silver eels must therefore be quantified in each EU member state's eel management units to aid recovery to such a state, with research focused on identifying factors that may be contributing to downstream mortality in migrating eels (Winter *et al*., 2007).

When *A. anguilla* enter their freshwater habitats as elvers it takes 6–10 years on average until they egress to sea to spawn as silver eels (Tesch, 2003). The time period between silver eels beginning their reproductive journey and their offspring reaching Europe is 14–16 months (van Ginneken & Maes, 2005). Therefore, the shortest step in recovery is between silver eel and elver, making the silver eel life-stage the critical component of European eel stock recovery (MacNamara & McCarthy, 2013). Consequently, considerable interest has grown regarding silver eel behaviour and their ability to reach the sea; the understanding of which is crucial for developing successful protective measures (Bruijs & Durif, 2009; Aarestrup *et al*., 2010; Davidsen *et al*., 2011).

The influence of external factors on silver eel reproductive migrations varies within and between localities (Vøllestad *et al*., 1994; Durif & Elie, 2008; Breukelaar *et al*., 2009), meaning that regional accumulation of data is necessary (Aarestrup *et al*., 2010). As such, studies have been carried out on silver eels in numerous river systems across Europe to determine the factors governing migratory behaviour (e.g. Vøllestad *et al*., 1986; Durif &

Elie, 2008; Davidsen *et al*., 2011) and impacting survivorship (e.g. Durif *et al*., 2002; Aarestrup *et al*., 2010; Simon *et al*., 2012). Yet, basic quantitative silver eel data are lacking for many European rivers (Breukelaar *et al*., 2009; MacNamara & McCarthy, 2013). Such information is essential to the development of Eel Management Plans (EMPs) which are drawn up for each EU member state and adjusted to regional and local conditions (EU, 2007). European silver eel research must therefore extend to less-studied areas in support of EMPs. Gathering empirical information from additional river systems is also important for enhancing existing knowledge, as regional variation means that results obtained from a particular system are not transferable into another (Simon *et al*., 2012).

European eels have been shown to migrate in large groups during narrow temporal windows, typically in autumn (Frost, 1950; Bruijs & Durif, 2009). The efficiency of managing human activities which affect silver eel survival depends partly on the ability to predict their behaviour during the downstream migration (Breukelaar *et al*., 2009). Yet, being able to precisely predict the timing of downstream runs has proven difficult due to site-specific responses to different cues (Durif & Elie, 2008). Lowe (1952) attributed the number of conspecific migrants available in the system, as well as the eel's responsiveness to external conditions, as being a determinant in the timing of downstream movement. Added to the variation in hydrology and man-made obstacles at different localities (Winter *et al*., 2007; Simon *et al*., 2012), the challenge associated with modelling migration patterns becomes apparent. Water flow is generally regarded as the most important parameter governing silver eel migration, followed by darkness/turbidity (Durif *et al*., 2002; Bruijs & Durif, 2009). However, there is still much uncertainty surrounding the nature of the relationship between silver eel movement and external factors (Durif *et al*., 2008), with most of the knowledge coming from the commercial fishing industry (Bruijs & Durif, 2009). This uncertainty is highlighted by studies in which eel migration was not related to some of the factors which are regarded as being influential (e.g. Sloane, 1984; Behrmann-Godel & Eckmann, 2003; Durif *et al*., 2008).

The nocturnal and rather poorly known nature of the silver eel run has often made the collection of escapement data challenging for researchers (Davidesen *et al*., 2011; Verbiest *et al*., 2012). Conventional mark/recapture methods using numbered identification tags have been valuable for estimating silver eel escapement, particularly in commercial fisheries (e.g. Rosell *et al*., 2005; Breteler *et al*., 2007; Prigge *et al*., 2013). However, these methods are based upon recaptures by fisheries only (Rosell *et al*., 2005), and hence the data collected may not tell the full story. More recently, the ability to estimate silver eel escapement from river systems has been improved by advances in biotelemetry (Arnold & Dewar, 2001). Unlike the traditional mark/recapture approach using identification tags, telemetry can assign eel losses (e.g. mortality, removal in illegal fisheries) to specific parts of the river through multiple detections ('recaptures') of individuals during downstream passage. Specifically, (passive) acoustic telemetry involves the eel being equipped (externally or internally) with a transmitter which relays signals to a fixed array of automated receivers as the eel moves through the river (Fig. 2). This allows for more refined estimates of escapement by holding up recaptured and lost individuals against the number of eels successfully passing a receiving station at or near the river outflow. This approach eliminates the potential for eels becoming stressed by physical recapture (Bridger & Booth, 2003). Behavioural data which would otherwise be unobtainable can be gathered using biotelemetry (Cottrill *et al*., 2006). Tracking emigrating eels provides better understanding about environmental cues regulating migration when movement is related to external conditions (e.g. Behrmann-Godel & Eckmann, 2003; Jansen *et al*., 2007; Davidsen *et al*., 2011), as well as the impact of human activities such as fishing (Winter *et al*., 2006; Simon *et al*., 2012) and hydroelectric power generation (e.g. Winter *et al*., 2006; Carr & Whoriskey, 2008; Travade *et al*., 2010). Knowledge gained from telemetry therefore allows researchers to not only refine estimates of silver eel escapement, but also note survival impacts along the eel's downstream transit and improve understanding about the factors regulating migration.

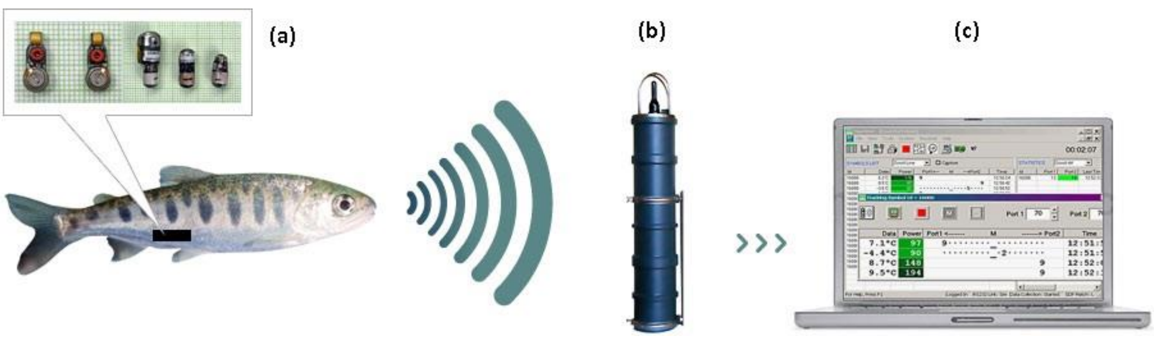

Figure 2. Acoustic telemetry system. As the tagged fish moves through the water the fish identity and sensor data (if available) are relayed by the transmitter (a) at a specific rate to a manual receiver or a set of receivers (b) either submerged or floating on the water (Dagorn et al., 2007). Stored data are collected from receivers and uploaded to a computer (c) for analysis. Image courtesy of www.biosonicstelemetry.com.

Biotelemetry has shown that silver eels conduct a range of behaviours during riverine transit (e.g. immediate passage, 'stationary behaviour', and 'recurrence behaviour') which partially dictate the time spent descending the river (Jansen *et al*., 2007). High individual variation in behaviour within migrating silver eel populations has been observed in previous studies (e.g. Winter *et al*., 2006; Davidsen *et al*., 2011; Verbiest *et al*., 2012). This variation presents challenges when attempting to precisely predict migration events in reference to managing human activities along the eel's freshwater migration route so that escapement targets are met. Thus, more research into downstream migration patterns is required.

This study was carried out in Europe's largest commercial wild eel fishery, Lough Neagh in Northern Ireland (ICES, 2012). The Lough Neagh and lower River Bann commercial eel fishery has been owned and managed by the Lough Neagh Fishermen's Co-operative Society (LNFCS) since 1971. Single ownership of all elements of eel fishing rights permits a unique co-ordinated management system committed to long-term sustainability (Rosell *et al*., 2005; Anonymous, 2009). The eel stock is regulated under the terms of the Neagh/Bann Eel Management Plan (Anonymous, 2009). The significant cultural and commercial importance of Lough Neagh eels has been highlighted by the recently awarded EU Protected Geographical Indication status under EU law (EU, 2011). Historically, annual recruitment of elvers to the lough averaged in excess of 11 million, until a dramatic pan-European decline in 1983 saw just 726,000 individuals being recruited (Anonymous, 2009); which fell further to approximately 48,000 in 2011 (ICES, 2012). Natural recruitment in Lough Neagh has been supplemented by the purchase of elvers from outside the River Basin District (RBD) since 1984, with silver eel fishing subsidising this stocking (Anonymous, 2009; ICES, 2012). However, silver eel catches in the RBD are declining, totalling just 73 tons in 2011, the lowest on record (ICES, 2012). Should management regime changes result in further catch reductions, cash revenue available for supplemental elvers would be jeopardised. This situation would ultimately lead to a collapse in annual spawner production and, eventually, the entire fishery (Anonymous, 2009). Therefore, biological production and commercial sustainability of Lough Neagh eels depend on adequate escapement being demonstrated in order to meet compliance, yet retain and support the current management regime.

Since 2003, an annual mark/recapture tagging programme using Floy™ (hereafter floy) tags has been employed to estimate silver eel escapement past the weir fisheries, which operate during a three month fishing season and are subject to a trap-free gap in the river and inefficient fishing during very high river flows (ICES, 2012). As of 2011, 4,920 Lough Neagh silver eels had been tagged with floy tags and recaptures recorded at both silver eel fishing sites to derive an escapement estimate (Anonymous, 2009; ICES, 2012). However, this approach does not provide information on eel mortality during river descent (Anonymous, 2009). Consequently, EU assessors have requested that acoustic telemetry be used to investigate the presumption that all eels escaping past the fishing weirs reach the sea (Anonymous, 2012). The cost differential between floy tagging (£0.10 per tag) and acoustic telemetry (present study: £24,000) studies makes the continuation of the floy tagging programme a key objective of the EMP. However, the efficacy of floy tagging for estimating escapement must be verified. Hence, this was a corroborative study into the recapture rate of floy tags vs. acoustic tags. The aims and objectives were to:

(i) Demonstrate that floy tagging is comparable to acoustic tagging for assessing recapture rates of silver eels, and therefore catch efficiency of the silver eel fishing weirs on the river, which is then extrapolated into an escapement estimate to measure compliance with the EU conservation target.

(ii) Demonstrate that those silver eels which are not recaptured but which do migrate downstream actually make it to sea (Anonymous, 2012).

(iii) Investigate spatial patterns of downstream migrant losses and identify possible bottlenecks (i.e. areas where mortality is high) along the downstream migration route.

(iv) Assess silver eel behaviour during downstream transit by tracking movement patterns. Migration timing and rates of travel may impact survival, making knowledge of these behaviours crucial for the development of successful protective measures (Aarestrup et al., 2010). As no prior knowledge of the behavioural time budgets exists for silver eels in the RBD, this study aimed to identify behavioural patterns and relate these patterns to escapement success, as well as provide a basis for future research into the drivers of such behaviours.

2. Methods

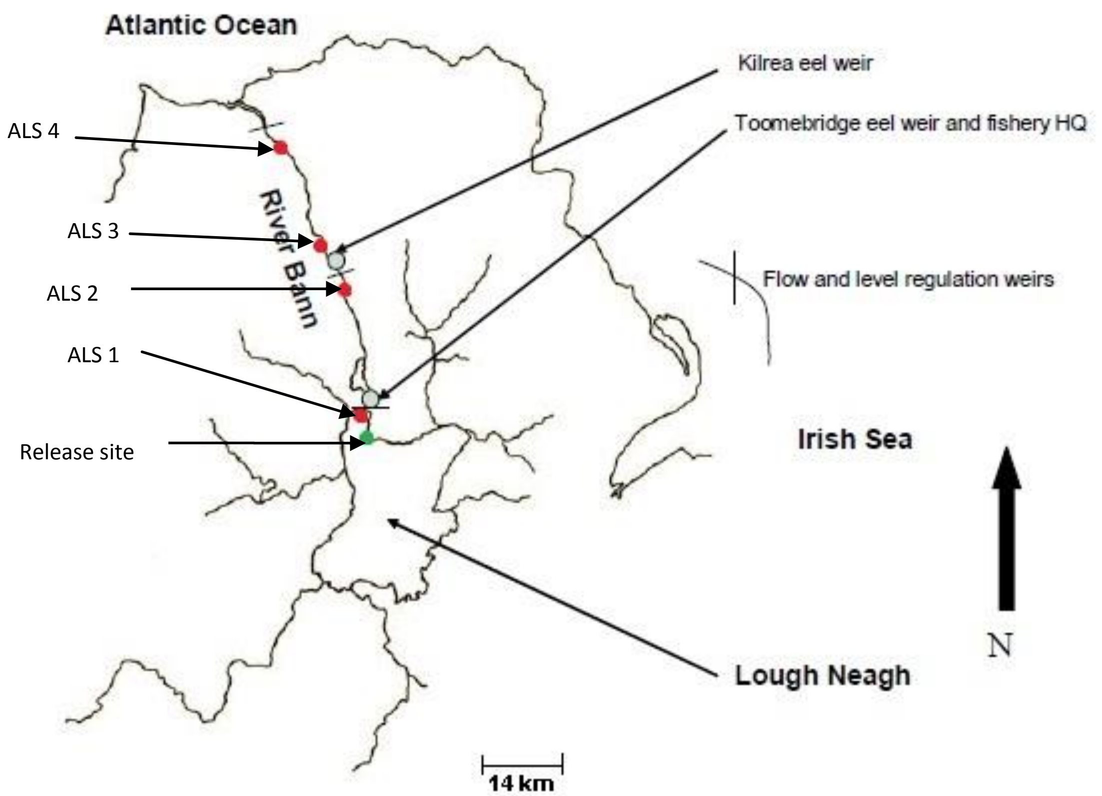

Figure 3. The study area showing the active fishing weirs and sluices, along with the release site (green) and the acoustic receivers (red). Image adopted from the Neagh/Bann Eel Management Plan (Anonymous, 2009).

2.1. Study area

Lough Neagh (54.6183° N, -6.3953° W) drains 43% of the land area of Northern Ireland through six major and numerous minor affluent rivers, discharging into the Atlantic Ocean via the lower River Bann. The lower Bann is approximately 60 m wide for most of its length, flowing 58 km north from where it leaves Lough Neagh at Toome to where it enters the sea near Castlerock (Frost, 1950). Water level on the river is mediated by the Rivers Agency of Northern Ireland using a series of weirs and sluice gates (Fig. 3), whereby the discharge can fluctuate dramatically as the sluices are operated (Rosell *et al*., 2005; Anonymous, 2009). As such, water flows are variable and tend to alternate between periods of high flow in excess of 300 $m^3.s^{-1}$ and lower flows less than 50 $m^3.s^{-1}$ (Anonymous, 2009). Mean (± SD) water flow on the lower Bann is 90.1 $m^3.s^{-1}$ ± 83.2 (based on 1980–2009 records). During the study period, all sluice gates were open and the river was in full flow, with a rate of approximately 250 $m^3.s^{-1}$ (Derek Evans, AFBI, Personal Communication).

The lower Bann is the sole migration route for silver eels out of Lough Neagh and an active fishery allows annual mark/recapture studies of silver eel escapement. Eels used in mark/recapture studies are captured at Toome fishing weir and tagged, before being taken back upstream and released (Anonymous, 2009). The eels are released upstream so that they can approach the weir in their normal manner, as opposed to being released at the fishery and possibly heading downstream immediately, which would result in biased recaptures. Commercial silver eel fishing occurs in autumn and winter at two fixed stations on the river (Fig. 3), with highly concentrated eel runs being intercepted in coghill nets (Frost, 1950; Rosell *et al*., 2005). The main weir at Toome is most effective during high river flows, while two weirs at Kilrea (24 km downstream) are more effective at low river flows. As a result, fishing at Kilrea weirs is frequently prevented by floods, resulting in increased silver eel escapement from the RBD (Anonymous, 2009). An additional fishing weir is located downstream from Kilrea but has not been fished since 1995. As a conservation measure, active silver eel fisheries on the Bann must maintain a free gap of 10% of the river width, and are only fished at night. Fishing ceases when catches decline to below economically viable levels, usually around the beginning of December. In total, there are three fishing weirs and three sets of sluice gates on the river. There are no turbines, hydroelectric power stations or major water abstractions that might impede silver eel escapement to sea in the Bann River system. There is also no authorised recreational eel fishing in the Neagh/Bann system (Anonymous, 2009; ICES, 2012).

2.2. Capture and external tagging

This study was part of a wider PhD. project. Migrating silver eels were caught on the night of 12th November, 2012 at the beginning of the out-flowing River Bann at Toome using fixed coghill nets of 35 mm mesh size. Eels were examined macroscopically and determined to be silver based on external characteristics (large eyes and silvering body, Tesch, 2003). The eels were kept overnight in a perforated holding tank submerged in the river. On 13th November, 2012, 60 eels were externally tagged (Fig. 4) with Thelma Biotel acoustic transmitters (size: 7.3 × 18 mm; mass in air: 1.9 g; mass in water: 1.2 g; pulse interval: 15 sec; battery life: 60 days). Tests were performed prior to tagging using a VEMCO-VR100 ultrasonic manual receiver to ensure that each transmitter was working properly. Each transmitter was attached to the middle of a length (approximately 10 cm) of monofilament line by wrapping thread around both line and transmitter and securing with glue before leaving to dry overnight. Prior to attachment, the fish were anaesthetised using clove oil buffered with acetone (2% aqueous solution). The total length (L_T) of each eel was measured (to the nearest 0.1 cm). The mean L_T (± SD) was 62.5 cm ± 4.9 (range: 53–82 cm). Based on historical records of total lengths of emigrating male and female silver eels in the River Bann (Tesch, 1977), all fish were identified as being female. Eel mass was not estimated. The mean (± SD) mass of female silver eels emigrating from Lough Neagh from 2004–2011 was 375.3 g ± 9.9 (ICES, 2012). Using this mean value as a proxy, transmitters weighed an average of 0.5% of eel body mass in air. Transmitters were attached by piercing the dorsal side of the fish using a curved hypodermic needle to run the monofilament line underneath the skin and back out. Fishing beads and crimps were used to secure the transmitter in place. The hypodermic needle was sterilised using ethanol after each attachment procedure.

Concurrent to acoustic tagging, 60 silver eels were tagged with floy tags. These tags are analogous to those used to attach prices to clothing and were inserted with a gun which can be loaded with one or a clip of floy tags, making the tagging of eels quick and easy. All tagging (acoustic and floy) took place at Toome eel fishery. Following tag attachment, the eels were held in a tank of fresh river water (replaced every 5 minutes) until release.

Figure 4. Acoustic transmitter attached to the dorsal side of a silver eel.

2.3. Release and tracking

The eels were transported in tanks (travelling time 10 minutes) 4.9 km southeast of the capture site and released on the north coast of Lough Neagh (Fig. 3) on the afternoon of 13th November, 2012. The silver eel fishery at Toome remained active until 3rd December, 2012 and was visited on a nightly basis to gauge the strength of eel runs and ensure that there was no interference with tagged individuals. The fishery at Kilrea was only active from 16th November, 2012 to 19th November, 2012. Recaptures were used to assess fishery-induced mortality in the river. All floy tagged eels were removed from the catch, with the capture site and tag number being recorded. Recaptured acoustically tagged eels were identified by transmitter identification number and released back into the river system, but were excluded from further analyses of the downstream migration as they were considered as 'fishery mortalities'.

Eel downstream travel was tracked by four fixed VEMCO-VR2W-69kHz single channel receivers distributed along the length of the river. Receivers were placed downstream from the release site at distances of 4.6 km, 27.9 km, 30.5 km, and 48.6 km respectively (Fig. 3). The first automatic listening station (ALS) was located approximately 260 m upstream from Toome fishing weir. The second and third ALSs were located approximately 1 km either side of Kilrea fishing weirs. Each receiver recorded and stored transmitter code and time (to the nearest second) of each eel passing through its range. The detection range of each receiver was approximately 150 m either side. ALSs were in continuous operation until the middle of March, 2013. A fifth receiver had been stationed 62 km downstream from the release site, where the river enters the sea, but could not be retrieved due to boat engine failure (resulting in an unsuccessful retrieval attempt) and unforeseen weather conditions. However, based on a 2011 pilot study (Warren Campbell, QUB PhD student, Personal Communication), all individuals that passed the penultimate ALS (i.e. the fourth ALS in this study) also passed the final ALS near the river outflow. This set a precedent for using the penultimate ALS data as a proxy for escapement.

2.4. Tagging effects

A controlled tank experiment was carried out to assess the effects of tagging on eel survivorship. 30 eels were fitted with dummy transmitters (simulating the Thelma Biotel 7.3 mm transmitter) and a further 30 were tagged with floy tags. Tagged eels were placed with

30 untagged eels in a perforated holding tank (15 m x 8 m x 1.5 m) submerged in the river for thirty days. This ensured that the control eels experienced the same environmental conditions as the experimental eels. The health status and longevity of the control eels, as well as any tag losses, were monitored daily.

2.5. Assessing the efficacy of conventional mark/recapture approach

Floy tag recaptures were held up against acoustic tag recaptures to verify that eels equipped with either tag returned to the river at a similar rate, thus allowing the corroboration of results from mark/recapture studies with results from hydroacoustic studies. The theoretical maximum escapement estimate, defined as the proportion of the total number of floy tagged eels not recaptured by the fisheries, was compared with escapement of acoustically tagged eels in order to assess whether floy tagging is a suitable method for deriving silver eel escapement estimates. Any inference made here would also rely on the premise that all tagged individuals, which were displaced 4.9 km southeast of the capture site, returned to the river to migrate. The acoustic tagging tested the validity of this presumption.

2.6. Assessing the fate of tagged eels

Escapement from the system was defined as the number of acoustically tagged eels passing the final ALS as a proportion of the original number of acoustically tagged eels that entered the river. In addition to demonstrating the proportion of silver eels that make it out to sea, this revealed whether success in making it past the fishing weirs could serve as a predictor of successful escapement to sea.

Spatial patterns of downstream migrant losses were investigated by identifying areas where tagged eels that did not pass the final receiver were last detected. This allowed for the mapping of bottlenecks along the freshwater phase of the migratory route (i.e. areas where mortality is high). The study area was divided into four sections. The release site in the lough to ALS 1 in the river was termed section 0 and the river was divided into section 1 (ALS 1–ALS 2), section 2 (ALS 2–ALS 3), and section 3 (ALS 3–ALS 4).

2.7. Downstream migration patterns

Eel behaviour during downstream transit was based on number of detections and the duration between consecutive detections. The amount of time spent in each study section by each eel was determined by calculating the amount of time between the final detection at one ALS and the first detection at the next (or in the case of section 0, time of release to first detection at ALS 1). The length of each section was divided by the time spent in the relevant section to determine rate of travel. Time within each detection range was determined by calculating the time interval between the first and last detections at each ALS. Diurnal and daily patterns of movement (with reference to lunar phase) were also investigated.

2.8. Data analyses

Results from the tank-based controlled experiment to assess the effects of tagging were analysed using a G-test to compare acoustically tagged, floy tagged and non-tagged eel mortalities. Downstream transit data were stored at each ALS and retrieved in March 2013. Eels were considered to have resumed migration when detected at ALS 1. Two paired-samples t-tests were conducted to test the effect of eel body length on the decision to resume migration and survivorship during the downstream migration. The data for the first of these tests were $\log_{10}$ transformed to meet the requirements of parametric analysis. Rates of travel in the four study sections were compared using a Kruskal-Wallis test, followed by a pair-wise comparisons post-hoc test. Daily movement patterns were plotted to examine the relationship between silver eel migration and lunar phase. Lunar records were obtained online from www.timeanddate.com.

3. Results

3.1. Tagging effects

During the tank-based controlled experiment external tagging did not appear to affect eel survivorship as there was no significant difference in mortality between the acoustically tagged, floy tagged and untagged eels ($G_{2, 89} = -5.742$, $p > 0.05$). Therefore, it was expected that return rates between acoustically tagged and floy tagged eels would not differ. There was 100% retention for both acoustic transmitters and floy tags during the thirty day trial.

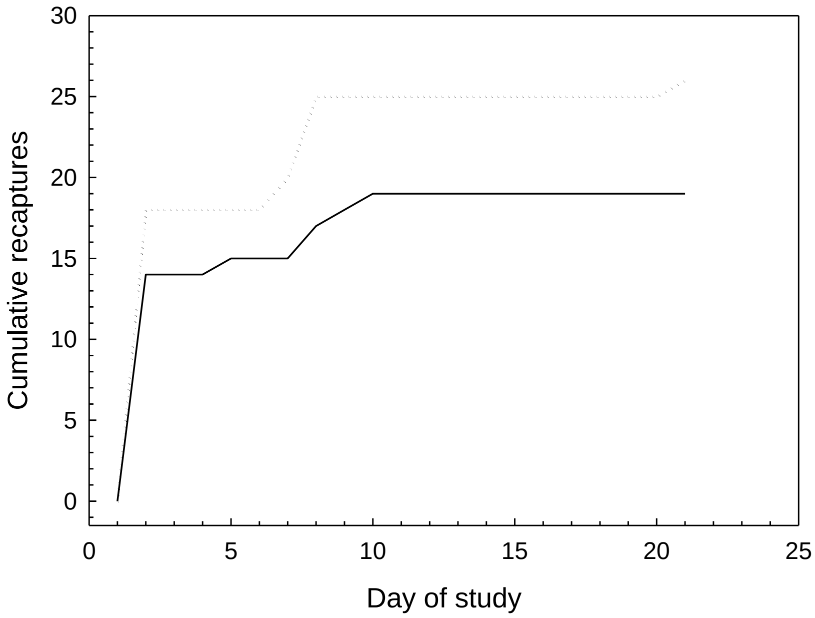

Figure 5. Cumulative recaptures of acoustic tags (solid line, n = 19) and floy tags (broken line, n = 26) during the period from when eels were released (13th November) until fishing stopped (3rd December).

3.2. Floy tag recaptures

Of the 60 floy tagged eels released, 43% (n = 26) were recaptured by the fisheries (Fig. 5). This figure is higher than the year on year average recapture rate of 29.6% demonstrated by the floy tagging programme from 2003–2011, and is the highest floy tag recapture rate observed to date (with the next highest being 39% in 2008, ICES, 2012). Eighteen floy tagged eels were recaptured within the first 24 h of release. All recaptures were taken at the fishing weir at Toome.

3.3. Fate of acoustically tagged eels released upstream

During the four month study period, 40% (n = 24) of the 60 acoustically tagged eels were not detected, and were therefore excluded from analyses of downstream moving eels. The remaining 60% (n = 36) were first detected at ALS 1 between 13th November, 2012 and 2nd January, 2013, and were presumed thus to have recommenced migration towards the Atlantic Ocean. The resumption of migration did not appear to be related to eel size, as body length did not differ between migrating and non-migrating eels ($p > 0.05$). Of the 36 acoustically tagged migrating eels, 53% (n = 19) were recaptured by the fishery at Toome (Fig. 5), with one being recaptured twice over four days. No acoustically tagged eels were recaptured at the second fishery further downstream. Of the 17 potential escapees leaving Toome, 10 were detected at ALS 2. Nine of these were detected at ALS 3. However, one eel which had not been detected at ALS 2 was detected at ALS 3 and ALS 4. Of the 10 eels which passed ALS 3, 8 made it to ALS 4. The major loss of eels (72%, Table 1) therefore occurred in section 1 of the river where they had to pass the main fishing weir. Excluding those with a known fate (i.e. fishery recaptures), 17% (n = 6) of eels entering the river were lost in section 1, 3% (n = 1) in section 2, and 6% (n = 2) were lost in section 3. The overall success of acoustically tagged eels reaching the sea was 22% (n = 8, Table 1). Thus, of the eels that made it past the fishing weirs, 47% (n = 8) reached the sea. There was no difference in body length between eels lost in the river with an unknown fate (n = 9) and those surviving riverine passage (n = 8) ($p > 0.05$), indicating that survivorship was not related to eel length. No tagged eels were detected during the period from January 11th to when the receivers were removed from the river in March.

Table 1. Number of migrating acoustically tagged silver eels detected at each automatic listening station (ALS), time spent (median; IQR) in each section (i.e. between ALSs), and overground rate of travel (median; IQR) in each section. Length of time (median; IQR) spent within the range of each ALS is also given. Detections at each section are those of the latter ALS (i.e. detections from section 2, or 'ALS 2 – 3', are from ALS 3). Nineteen eels were recaptured by the fishery between ALS 1 and ALS 2. *One eel was detected by ALS 3, but not ALS 2. Hence, 11 eels survived as far as section 2 of the river and 10 eels survived as far as section 3.

Transit from	*Release site – ALS 1 (section 0)*	*ALS 1 – 2 (section 1)*	*ALS 2 – 3 (section 2)*	*ALS 3 – 4 (section 3)*
No. of eels detected	36 (100%)	10* (28%)	10 (28%)	8 (22%)
Time (h) spent in study section	7:23 (5:29–60:08)	21:16 (10:31–46:12)	0:34 (0:32–0:38)	14:17 (6:54–22:35)
Rate of travel ($km.h^{-1}$)	0.63 (0.12–0.84)	1.1 (0.56–2.22)	4.47 (4.06–4.82)	1.9 (1.02–3.23)
Distance (km) from release site	4.6	27.9	30.5	48.6
Time (min) in detection range	10 (5–409)	6 (3–8)	2 (1–3)	2.5 (2–9)

3.4. Downstream migration patterns

Downstream migration occurred predominantly during the first two weeks of the study (Fig. 8). Twenty-six eels arrived at ALS 1 within 24 h of release (i.e. the night of 13th November/early morning of 14th November). Nine arrived during the following fourteen days, with the remaining one arriving at the beginning of January, 2013. Initial movement was nocturnal, with all individuals passing ALS 1 between the hours of sunset and 03:00 (Fig. 7). Diurnal patterns in eel movement were weaker during downstream passage, with 7 individuals being detected during daytime at the other three ALSs (2–4). The eels were released on the November new moon and therefore moved during this lunar phase. There was also movement during the light phases of the moon, but none during the study's other dark phase (Fig. 8).

The average time spent by the eels in section 0 (i.e. from their release in the lough to first detection at ALS 1) was 7 h 23 min; although individual variability was high (Table 1). One individual detected at ALS 1 within 24 h of release did not move further downstream until 55 days later on 7th January. This eel was detected a total of 509 times by ALS 1, which would suggest that it periodically resided at this site. However, no detections from 15th November to 4th January mean that the eel either moved back upstream before returning downstream, or moved downstream (but not as far as ALS 2) before returning upstream. This individual subsequently moved rapidly after reaching ALS 2 (4.16 km.hr^{-1}) and successfully made it past the final receiver. After entering the river the eels took an average of 21 h 26 min in reaching the second ALS, 23.3 km downstream of ALS 1. Again, this varied highly among individuals (Table 1), with the first and last individual entering the second river section 7 h and 51 days respectively after passing ALS 1. The latter of these eels was detected only once by both ALS 1 and ALS 2 (with no further downstream detections), suggesting prolonged stalling of migration between rapid downstream transits. The eels spent an average of 34 minutes in section 2 (smallest) and an average of 14 h 37 min in the final section. The amount of time spent in range of the ALSs (Table 1) shows that, when they were moving, the eels swam faster as they progressed downriver.

Rates of travel (distance over land) differed among the four study sections ($\chi^2_{3,\ 62}$ = 27.4, $p < 0.05$). A post-hoc test revealed differences in rates of travel between all sections ($p < 0.05$), except for between sections 1 and 3 ($p > 0.05$). One individual was not detected by ALS 2 and therefore was not included in the progression rate analyses for river sections 1

(ALS 1–ALS 2) and 2 (ALS 2–ALS 3). The average overall rate of travel from the release site to the final ALS was 2.02 km.hr^{-1} (IQR = 1.4–2.8). Rate of travel was lowest in section 0 (0.63 km.hr^{-1}, IQR = 0.12–0.84, Table 1, Fig. 6), owing to delayed onset of migration by 28% (n = 10) of eels. The eels showed increased progression rate in section 1 (1.1 km.hr^{-1}, IQR = 0.56–2.22, Table 1, Fig. 6), but with reasonably high individual variation. Transit through section 2 was rapid (4.47 km.hr^{-1}, IQR = 4.06–4.82, Table 1, Fig. 6), before declining in section 3 (1.9 km.hr^{-1}, IQR = 1.02–3.23, Table 1, Fig. 6) due to the fact that half of the eels travelled between 0.4 km.hr^{-1} and 1.3 km.hr^{-1}. Hence, section 3 had the largest interquartile range.

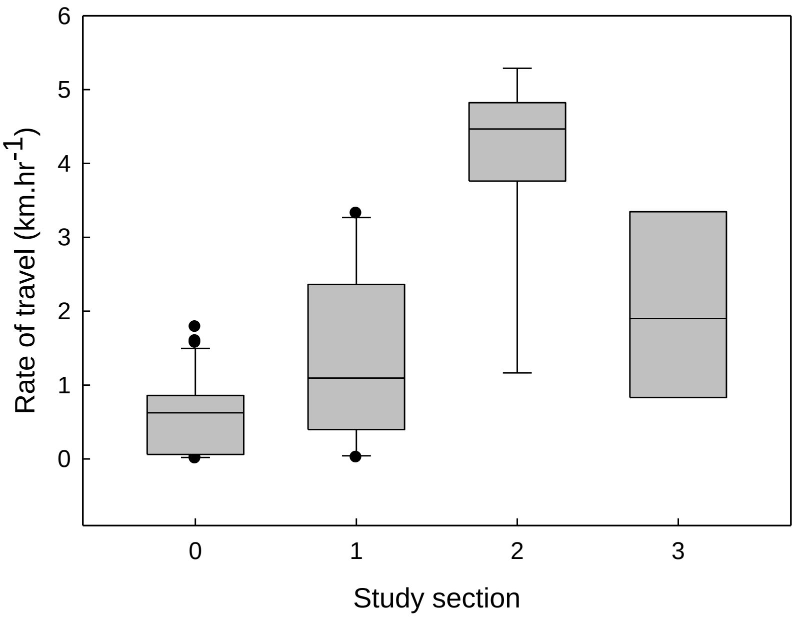

Figure 6. Rates of travel (distance over ground) in the four study sections for silver eels that resumed migration. The median is represented by the horizontal line within the boxes, and the lower and upper quartiles are represented by the bottom and top of the boxes. All observations within the 90th percentile lie within the whiskers. Any outlying plots represent observations beyond these limits.

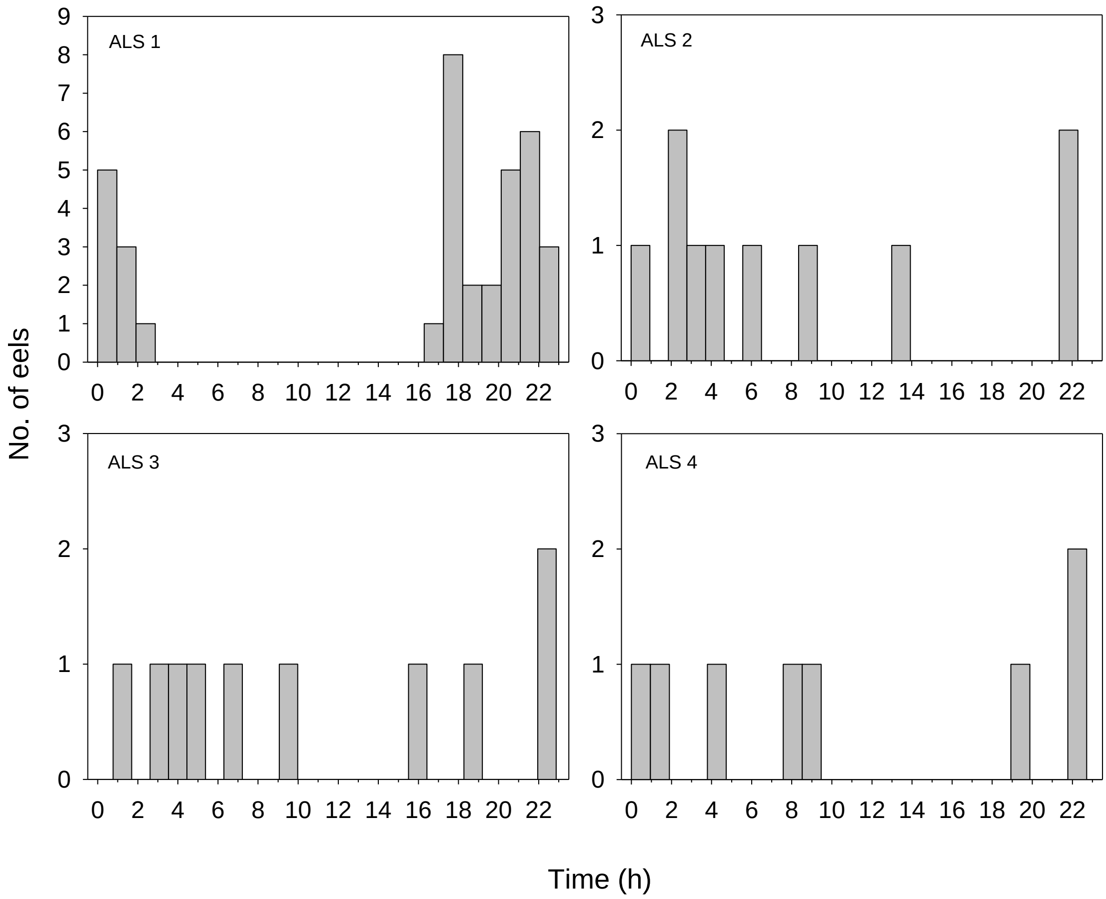

Figure 7. Time of day (0:00–23:59, denoted by hour of day) for passage by individual eels past each automatic listening stations (ALS). Passage is defined by the first detection at each ALS.

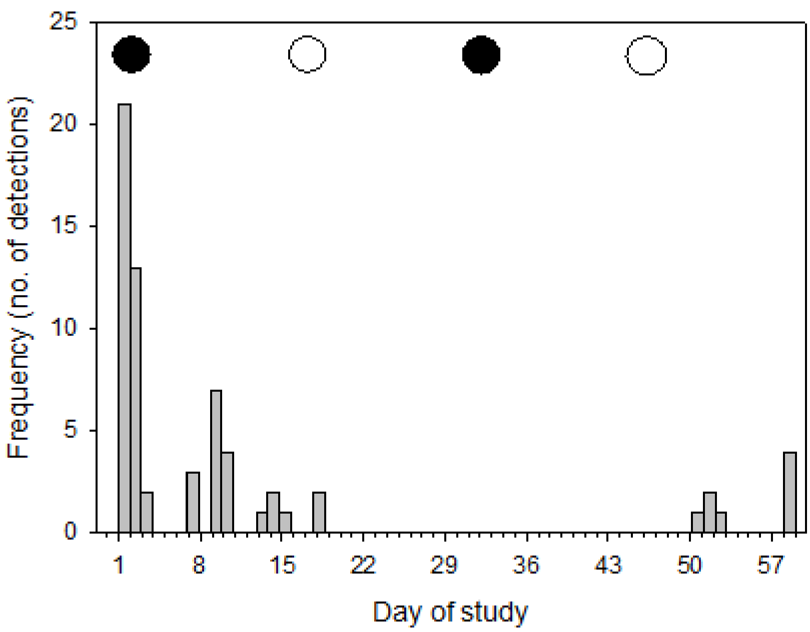

Figure 8. Daily movement of migrating eels in relation to lunar phase (• represents dark phase, i.e. new moon; o represents bright phase, i.e. full moon). Daily movement is measured by the first detection at any of the four ALSs on a given day.

4. Discussion

4.1. Efficacy of conventional mark/recapture approach

For the past decade, estimating silver eel escapement from Lough Neagh has been based on recapture efficiencies at the fishing weirs using floy tags, with the non-recaptured proportion of eels representing the escapement target estimate. From 2003–2011, average recapture rates were 29.6%; demonstrating approximately 70% escapement past the fisheries (ICES, 2012). However, because this estimate does not include mortalities in the wild, it may be an overestimation of the number of eels that reach the sea. The acoustic data suggest that this is indeed the case, as only 47% of acoustically tagged eels that made it past the fisheries reached the sea. However, it cannot be confirmed that eels lost in the river suffered mortality (discussed below) and therefore more research is needed to answer the question of whether escapement estimates from floy tag studies are overestimations.

When used to demonstrate the effectiveness of the fishing weirs (and thus escapement), floy tagging requires a 100% return rate of tagged individuals to the river, so as to specify recaptures as a proportion of the original tagged total, and not a fraction of that total. The telemetry data showed that escapement estimates using floy tags may indeed have been derived from a fraction of the total number of tagged individuals, as just 60% of acoustically tagged eels were detected. However, it is possible that some, if not all non-detected acoustically tagged eels did in fact migrate outside the study period (discussed below). Hence, it cannot be concluded that all tagged eels in floy tagging studies did not return to the river after release.

The use of acoustic telemetry in corroborating the traditional mark/recapture approach was verified by comparing the recapture rate of floy tags and acoustic tags. The data showed that a large proportion of acoustically tagged and floy tagged eels entered the river simultaneously (Fig. 5), supporting the notion of group migration (Frost, 1950; Bruijs & Durif, 2009). More importantly, however, these data validate the use of acoustic telemetry to corroborate floy tagging. Hence, the proportion of non-migrating acoustically tagged eels (40%) can be used as a proxy for the number of non-migrating floy tagged eels and applied to results from floy tagging studies (past and present). As a result of this corroboration, the 2003–2011 average recapture rate of 29.6% becomes 49.3% (or, 70.4% escapement past the fishing weirs becomes 50.7%). By the same token, floy tagged eels recaptured during this study would represent 72% (n = 26) of the total number of eels estimated to have resumed migration. This is a massive increase, even when compared with the hypothetically corrected recapture rate. The likely reason for this comparably high recapture rate is that the night of 13th November, 2012, when 71% of all tag recaptures (both floy and acoustic) were taken (Fig. 5), was the largest silver eel run of the year, with 8 tons caught. Had the study period covered the entire fishing season (early September – early December), the recapture rate may have been more typical of the 2003–2011 corrected average. The 2012 floy tag recapture rate (not including eels from this study) of just 19% (Derek Evans, AFBI, Personal Communication) substantiates this claim. The corroborative method applied in this study can also be verified by calculating acoustic tag recapture rate as a proportion of the total number of acoustically tagged eels, as opposed to the number that actually entered the river. In this case, the recapture rate would be 32% (as opposed to the true recapture rate of 53%); very similar to the average annual recapture rate demonstrated by floy tagging. The controlled tank experiment showed no significant difference in mortality between acoustically tagged and floy tagged eels, further validating this corroborative approach.

There have been many instances where small numbers of silver eels have been shown to begin downstream transit outside of the typical migration season (e.g. Winter *et al*., 2006; Simon *et al*., 2012; Verbiest *et al*., 2012). Reports of silver eels being caught amongst yellow eels in summer draft net catches indicate that this unpredictable migration pattern is true of Lough Neagh eels, contributing further to escapement (Anonymous, 2009). In the present study, the last eel to be detected by ALS 1 departed more than one month after fishing ceased. Therefore, because the floy tagging programme only covers the fishing season, inevitably there is additional escapement which is not being taken into account.

4.2. Non-detection of acoustically tagged eels

The maximum estimate of escapement demonstrated by floy tagging is based on the presumption that all tagged individuals released at the north of Lough Neagh return to the out-flowing River Bann to migrate. The results of the present study suggest that this presumption may be fallible, as only a fraction of eels (60%) that were captured and displaced actually travelled back towards the river. This finding is supported by studies in other European river systems in which not all eels were detected after tagging. For example, Davidsen *et al*. (2011) released 32 acoustically tagged silver eels approximately 16 km southeast of the site of capture. Twenty-two (69%) of these eels were detected at the first ALS, with just thirteen (41%) detected at the second ALS (i.e. the first point at which transit past capture site could be confirmed). Higher return rates were observed by Aarestrup *et al*. (2010), with 90% (n = 45) of acoustically tagged individuals being detected at the first ALS after they were released 2 km southeast (upstream, in a different tributary) of the capture site. Nevertheless, it is clear that despite having already begun migrating, not all silver eels immediately (or at least shortly there afterward) resume their seaward journey following capture/tagging/release. This may be attributed to the following reasons:

(i) The experimental procedure (i.e. capture, holding, handling, anaesthesia and tagging) may have negatively affected migrating eels. The success of any telemetry study relies upon the tagging procedure bearing minimal effects on the behaviour or physiology of the experimental animals (Bridger & Booth, 2003; Cottrill *et al*., 2006; Thiem *et al*., 2011). As such, a controlled experiment lasting thirty days was carried out to test tagging effects, showing no difference in mortality between tagged and non-tagged eels. Hence, external transmitter attachment was not expected to induce mortality in the test silver eels. However, unnatural behaviour (e.g. changes in swim performance) was not monitored in the controlled experiment. Swim performance is known to be a reliable indicator of any problems with tagging (Cottrill *et al*., 2006). In a study evaluating the effects of various tag attachment procedures on American silver eels (*Anguilla rostrata* L.), Cottrill *et al*. (2006) did not find a significant effect of external tagging on swim performance. Conversely, both Burgerhour *et al*. (2011) and Methling *et al*. (2011) found that energy expenditure, swim performance and efficiency were all significantly altered in migrating European eels with external tags, with both studies attributing drag as the crucial factor impairing swim performance. However, the tags used in their experiments (PSATs) were significantly larger than the acoustic transmitters used here. Nevertheless, it cannot be ruled out that transmitter attachment impaired eel performance.

(ii) Transmitters may have detached from the eel and become lost. Cottrill *et al*. (2006) observed a very low retention rate of external tags in American silver eels, with 11 of 12 transmitters becoming lost within 3–4 weeks post-tagging. However, in the present study, the controlled experiment to assess tagging effects showed a 100% tag retention rate. Thus, it is unlikely that tag loss contributed to the occurrence of non-detected eels.

(iii) Displacing migrating eels back upstream may have disrupted their orientation faculties. Although the mechanisms by which *Anguilla* spp. navigate during migration are not well understood (Righton *et al*., 2012), it is believed that they use water flow direction as an orienting stimulus (Jansen *et al*., 2007). This behavioural response is known as rheotaxis and is thought to be one of a number of orientation strategies (Hain, 1975). It would be expected that such additional cues are employed in the absence of directed water flow or alternative guideposts, such as in lakes or the open ocean (Durif *et al*., 2013). There is recent evidence to support the hypothesis that magnetic particles discovered in the lateral line system of European eels function in geomagnetic orientation (Moore & Riley, 2009; Durif *et al*., 2013). Durif *et al*. (2013) found that migrating eels have a magnetic compass with which they orient in a pre-registered direction. This means that, should migration be interrupted, eels would be able to resume movement along their old bearing. When compared with water inflow, orientation relative to the magnetic field was found to predominate in eels that have been displaced (Durif *et al*., 2013). These findings are highly relevant to the present study and provide a viable explanation as to why a significant proportion of tagged eels were never detected. When they initially began migrating before being caught, the eels would probably have come from all different directions of the lough to reach the out-flowing river. Because Lough Neagh is essentially a standing body of water, the eels would have had to have used compass cues in the absence of rheotactic cues to navigate towards the river. Removing the eels from the river and releasing them all at the same location in the lough could have prevented a significant proportion from finding their way back to the river due to their compulsion to follow their original bearing.

(iv) Some eels may have delayed migration. Telemetric studies have shown that the beginning of silver eel downstream migration can vary over large timescales and that a protracted migration pattern is in fact normal (Bruijs *et al*., 2003; Winter *et* *al*., 2006; Simon *et al*., 2012). This variation in migration timing has been shown to occur in Lough Neagh by the annual mark/recapture programme, which, for seven of the past ten years, has been met with carry-over of some tagged silver eels from the year of marking to the next one or two (ICES, 2012). In the present study, initiation of downstream movement occurred over a fifty-one day period. Although the first ALS was in operation for a further two months, but detected no additional eels, it is possible that those tagged individuals that did not appear to resume migration did in fact migrate outside of the study period. It is also possible that non-detected eels may have migrated during the latter half of the study period without being detected due to transmitter battery failure. The battery life of the acoustic transmitters used in this study was 60 days. This means that any eels migrating after 12th January, 2013 would likely have gone undetected. The fact that the last detected eel began migrating on 2nd January suggests that additional individuals may have migrated during January – March when receivers were still in operation but transmitters were not.

Eels have been observed to resume migration quickly after being tagged and released (Durif *et al*., 2002; Simon *et al*., 2012). The present study supports these observations, with most (72%) of the acoustically tagged eels having arrived at ALS 1 within 24 h of being released. Eels that did not depart quickly may have lay in wait of favourable environmental conditions (Vøllestad *et al*. 1994; Acou *et al*., 2008), or were recovering from stress response after the tagging procedure. It may seem odd to suggest that individuals within a migrating population differ in their responses to external stimuli; however, while silver eel migration behaviour is relatively poorly understood, marked individual variation in behaviour is well documented (e.g. Winter *et al*., 2006; Davidesen *et al*., 2011; Verbiest *et al*., 2012). It is also well known that some silver eels halt their autumn migration and resume it the following spring or autumn (Tesch, 2003; Winter *et al*., 2006; Aarestrup *et al*., 2008). Hence, non-detected eels may have resided in and around the release site during the period covered by this study, before migrating at a later time. Because eels cease feeding at the silver-phase (Tesch, 2003), this behaviour could be energetically disadvantageous, as energy stores essential for migration and spawning would be used to sustain the fish during migration delay

(Acou *et al*., 2008). It is therefore possible that some silver eels resumed feeding by recovering yellow eel characteristics, as is known to occur (Svedäng & Wickström, 1997; Durif *et al*., 2005). Differences in growth phase (i.e. maturation stage) have been related to morphological size (Durif *et al*., 2005) and therefore it might be expected that life-stage reversion relates to body size. As there was no significant difference in body length between migrants and non-detected eels in the present study, it is unlikely that migration delay was related to regression of the maturation process.

(v) Non-detected eels may have migrated without being detected due to defective receiving equipment. One individual which was not detected by ALS 2 was detected further downstream by both ALS 3 and ALS 4. This suggests that missed detections are possible and calls into question the accuracy of the receiving equipment. Although only one case of missed detection was observed, it cannot be ruled out that eels not detected did in fact make it to sea without being picked up by the receivers. It is unlikely that missed detections were due to transmitter malfunction, as these were all tested before release. The potential for technological glitches in studies such as this should be minimised by frequent testing of receiving equipment during the study period.

(vi) Some eels may have died naturally because of predation or disease. There are a number of piscivorous birds and mammals present in the Lough Neagh system (Anonymous, 2009). In particular, the cormorant *Phalacrocorax carbo*, known to often consume high numbers of eels (Keller, 1995), feeds in large numbers throughout the year (Warke *et al*., 1994). However, mammalian and avian predator populations in the lough are not considered numerous enough to induce significant mortality in eels and therefore predation is not a likely cause of the high number of non-detections.

Some eels may have been affected by pathogenic disease such as “red pest”. The bacterium *Aeromonas hydrophila* was identified as the causative agent of an outbreak of this disease during a 2007 health screening of Lough Neagh silver eels (ICES, 2008). 10–15% of emigrating silver eels were affected with substantial mortalities recorded. The outbreak was related to the restriction of eel migration due to low autumnal rainfall and sluice gate closure (Anonymous, 2009).

Unusually low water levels during autumn 2012 (Derek Evans, AFBI, Personal Communication) might have brought about disease outbreak which contributed possibly to spawner mortalities during the study, although no such cases were reported and no empirical data to support this claim are presented here.

(vii) Eels may have been caught illegally. Silver eel fishing within the RBD occurs at two sites only, both of which are in the lower Bann (Anonymous, 2009). However, it cannot be excluded that illegal netting in the lough may have been responsible for the removal of some tagged eels before they were able to resume downstream migration.

4.3. Fate of downstream moving eels

Exploitation of silver eels by fisheries can vary widely between river systems (Simon *et al*., 2012). In the present study, 53% (n = 19) of acoustically tagged eels that entered the river were subjected to fisheries-induced mortality. Of those eels that entered the river, 22% (n = 8) reached the final receiver. As this ALS has been shown to be a viable proxy for escapement to sea (Warren Campbell, QUB PhD student, Personal Communication), it is inferred that 22% of migrating silver eels successfully reached the sea. Thus, 47% (n = 8) of acoustically tagged eels that escaped past the fishing weirs in the lower Bann were shown to have successfully reached the sea. Silver eel runs are known to vary year on year in Lough Neagh (Anonymous, 2009). Therefore, escapement estimates should be consolidated with data from successive studies in order to derive escapement from a multiennial average, analogous to the approach taken in the Atlantic salmon (*Salmo salar*) management strategy (NASCO, 2007). This approach would reduce potential bias associated with variation in eel runs and provide an improved estimate of escapement.

Of the 36 acoustically tagged eels that resumed migration, 25% (n = 9) were lost in the river with an unknown fate. Some of the possible explanations outlined for non-detected eels are applicable when considering migrant losses in the river; namely tagging effects, transmitter loss, defective receiving equipment, predation, and poaching. Keller (1995) found that the mean length of eel prey of *Phalacrocorax carbo* was 45.6 cm (range: 23.2–70.4 cm); smaller than the tagged eels in this study (mean length: 62.5 cm; range: 53–82 cm). Therefore, any tagged fish caught by cormorants would most likely have been the smaller individuals. However, body length did not differ between lost eels and those that survived downstream passage, indicating that lost fish were not the smallest in size, as would be expected had they been predated by cormorants.

It is more likely that eels lost in the river ceased migration and periodically resided in the river between the receiving stations in the same manner as that posited for non-migrating tagged eels (as discussed above). Eels are known to frequently halt downstream migration when environmental conditions become unfavourable (Tesch, 2003; Winter *et al*., 2006; Durif *et al*., 2013). This claim is substantiated by the marked variation in time spent in range of the first receiver and in the first two study sections (Table 1). For example, one eel took 55 days to pass ALS 1 after arriving. While this initially indicates that movement stopped, a 51 day gap without any detection suggests 'recurrence behaviour', where the fish approached an obstruction (in this case the fishing weir, 260 m downstream of ALS 1) and returned upstream, before subsequently descending back downriver to pass by the obstruction (Jansen *et al*., 2007). Although it is unlikely, it is also possible that the eel passed ALS 1 and remained in section 1, before swimming back upstream and again moving downstream. It must also be noted that this eel successfully escaped to sea after moving rapidly through sections 2 and 3 of the river. Although the reason(s) for this behaviour are unknown, it is a discernible example of migration delay during downstream transit. Another example of this was observed for a different eel which spent 51 days between ALS 1 and ALS 2 (section one, 23.3 km long), but was detected only once by each receiver. This indicated a protracted residency period between rapid downstream movements, as opposed to the eel continuously swimming at a slow rate.

The majority (67%) of acoustically tagged eels that were lost in the river were last observed reaching section 1, where the largest variation in time spent occurred (Table 1). Delays in migration have been known to occur during passage through lakes (Vøllestad *et al*., 1986). The presence of a lake in section 1 of the river therefore adds to the likelihood that lost migrants remained in this part of the river beyond the study period, possibly recommencing downstream movement at a later point. It cannot be known for certain whether these and the remaining three eels lost (one in section 2, two in section 3) ceased migration for an extended period or died. Were it the case that all eels lost in the river suffered mortality, it would mean that section 1 represents a significant bottleneck in the migration of Lough Neagh silver eels that have escaped past the main fishery. The uncertainty surrounding the fate of eels lost highlights the need for information gathered over a longer study period, as this could confirm the presence of any delayed migrants. Eels remaining lost over a long period would be attributed to them having died. Thus, inferring mortality is predicated on the availability of long-term data. Identifying mortality as the primary reason for eel losses in the river would require investigation into what is causing the eels to die, so that management strategies could be adjusted accordingly to meet the EU escapement target.

4.4. Downstream migration patterns

In common with previous studies (e.g. Lowe, 1952; Aarestrup *et al*., 2008; Davidsen *et al*., 2011), the onset of migration occurred after sunset during hours of darkness (Fig. 7). However, downstream passage was not strictly nocturnal as there were some instances of daytime movement in sections 1, 2 and 3. These results suggest that low light levels regulated the onset of migration, but that downstream movement may have been driven by additional overriding factors. Breukelaar *et al*. (2009) also observed downstream movement when using telemetry to track European silver eels in the lower Rhine. Migrating silver eels are not usually considered to be active during daylight, although they are known to move during heavily overcast conditions or when the water is turbid (Durif *et al*., 2002; Haro, 2003). Although no water composition data were collected during this study, the River Bann tends to be highly turbid during winter (Derek Evans, AFBI, Personal Communication), which might explain these findings. The collection of environmental data should be included in future telemetric studies of migrating Lough Neagh eels so that the occurrence of daytime passage can be explained better.

Reports on the effect of the moon on downstream migration are conflicting, with some studies citing a strong influence (Frost, 1950; Lowe, 1952; Deelder, 1954) and others finding an insubstantial association (Durif *et al*., 2002; Acou *et al*., 2008). Durif *et al*. (2002) concluded that the effect of the moon on silver eel migratory activity probably depends on luminosity, rather than an endogenous rhythm. As the eels in the present study were released on the November new moon, there was expected movement during this lunar phase. However, the observed movement during the light phases of the moon, but none during the study's other dark phase (Fig. 8), would suggest that lunar phase was not an important factor influencing silver eel movement in the River Bann. The findings of this study therefore support the claim by Durif *et al*. (2002) by showing no apparent relationship between movement and moon phase.

Rates of travel varied significantly between all sections of the river except for sections 1 and 3. There appeared to be a negative relationship between rate of travel and the number of non-recaptured migrants lost in the river. Of the three river sections, section 1 had the slowest rate of travel (1.1 $km.hr^{-1}$) and had the highest number of eels lost (n = 6). In section 2, where fewest eels were lost (n = 1), rate of travel was highest (4.47 $km.hr^{-1}$). Rate of travel in section 3 (1.9 $km.hr^{-1}$) was intermediate to the other two sections, as was the number of eels lost (n = 2). These data further support the notion of migration cessation by showing a relationship between slow riverine transit and missing eels. If the eels were predated or poached their rate of travel would not have slowed as a result, as removal from the water would have been sudden. It is therefore likely that reduced rate of travel was due to the cessation of migration by some individual(s) in the relevant river section.

Generally, over the course of the downstream migration, the acoustically tagged eels travelled slower than has been documented for *A. anguilla* in large rivers (2.7–3.9 $km.hr^{-1}$, Tesch, 1994). Rate of travel was slowest in section 0, which can be attributed to delay in the onset of downstream movement by 28% of individuals. This delay caused an underestimation of the actual rate of travel in this section. This was also the case in section 1 where there was considerable variation in rate of travel, possibly due to the presence of a lake (as discussed above; Vøllestad *et al*., 1986). Migration speeds were largely uniform and highest through section 2; four times that in section 1. This was the shortest study section and included one set of sluice gates and two weirs. The pace at which the eels moved past the fishing weirs in section 2 suggests that slow progression by some eels in section 1 was not attributed to the presence of the main fishing weir near its beginning. As the sluice gates were open during the study period, it cannot be determined whether the current water management in the lower River Bann precludes silver eels from reaching the sea. Transit through section 2 occurred over a relatively small spatial scale and therefore does not offer broad perspective of downriver migration speed. However, when compared with the slower, variable travel rate in section 3, the rapid, uniform movement through section 2 provides evidence that behaviour among migrants is not homogenous, downstream rate of travel is not constant, and cessation of downstream movement is common.

5. Conclusions

This study has shown that acoustic telemetry is a valuable technique for not only studying eel migration patterns and escapement to the sea, but for verifying the results from mark/recapture studies. In doing so, the acoustic results have suggested that it may be erroneous to assume that all tagged eels resume migration after being released. This calls the floy tagging programme into question due to the fact that recapture rates used to assess the efficiency of the fishing weirs, and therefore derive an escapement estimate, may be based on a fraction of the tagged sample. However, carry-over of floy tags from previous years, possible missed detections, and the likelihood of migration delay mean that it cannot be concluded from this short-term study that not all tagged eels eventually return to the river post-release. The fact that less than half of the acoustically tagged eels that passed the fishery reached the sea suggests that escapement estimates from floy tagging studies may be overestimations. However, it cannot be confirmed presently that eels lost in the river were subjected to mortality. Longer-term telemetric studies are needed to clear up these uncertainties, as well as to estimate the number of eels being overlooked by floy tagging studies (i.e. those migrating outside of the fishing season). As the use of acoustic telemetry to corroborate floy tagging has been validated, results from an extended acoustic study would serve to refine escapement estimates from floy tagging studies and allow the continuation of this method for estimating escapement. This is a key objective of the EMP due to the cost-effectiveness of floy tags.

For fisheries management it is essential to identify the number of non-migrants during studies of migrating silver eels, especially when attempting to demonstrate compliance with specific EU escapement targets. Clearly, not all tagged eels resume migration immediately after their release. The reasons for this are unclear, but it is plausible that orientation issues arise when migrating eels are displaced. Individual movement patterns and rates of travel data presented in this study suggest that non-detected eels, along with those lost in the river with an unknown fate, may have migrated after the study had ended (or, after transmitter batteries died). It is also possible that the downstream transit of some eels went undetected due to defective receiving equipment. In any case, this study raises new questions regarding escapement monitoring which must be addressed. Placing additional detection stations near and upstream from the release site, or manually tracking tagged fish (e.g. Verbiest *et al*., 2012) at the beginning of the river and into the lough, would help reveal information about the behaviour of individuals not participating in downstream migration. Fyke netting at the mouth of the river would complement regular testing of receiving equipment by identifying the occurrence of missed detections by intercepting any escapees which were not detected by the receiving equipment, and should also be considered.

The escapement estimate demonstrated in this study was below the conservation target. However, it remains to be determined to what extent the apparent failure to reach this target is due to mortalities rather than migration delay. If, after the aforementioned measures are taken, the number of eels reaching the sea lies below the 40% benchmark, action will be needed to reduce the mortality of migrating silver eels in the Neagh/Bann system.

6. Future Work

6.1. Longer-term study

The findings presented in this study are based on data collected over a limited time period. As a consequence, many questions remain unanswered and new questions have been raised. What is clear is that long-term investigation is needed in order to address these questions. Successive telemetric research on migrating silver eels in the Neagh/Bann RBD should increase the time interval at which transmitters relay their signals, thus extending battery life. This would enable longer-term monitoring of tagged eels and provide much needed insights into so called non-migrants and lost migrants. It would also help reveal the number of eels migrating outside of the fishing season, which should be taking into account when extrapolating escapement estimates from floy tag recapture rates.

6.2. Further testing of tagging effects

It is essential that the effects of tagging on eel swim performance are minimal, especially considering how quickly the majority of eels resume migration after their release. Future tagging work on migrating silver eels therefore should conduct swim trial validations (as described by Methling *et al*., 2011) for better assessment of the effects of their specific tag on eel behaviour and physiology. Steps could then be taken, if required, to ensure minimum impediment on eel swim performance.

6.3. Gathering environmental data

In addition to ensuring compliance with escapement targets, successful management requires the acquisition of empirical information relating to the eels' migratory movements and contextualising this information with environmental variables which are likely affecting migration. Research combining movement data with empirical information denoting the environmental conditions experienced by each tagged eel therefore should be carried out in the RBD. If refined estimates of escapement lie below the 40% conservation target, knowledge about the factors regulating migration could prove crucial for the implementation and timing of management strategies in the system. Although eel migration has been related to external factors in many European river systems (e.g. Behrmann-Godel

& Eckmann, 2003; Jansen *et al*., 2007; Davidsen *et al*., 2011), the influence of such parameters varies within and between localities (Vøllestad *et al*., 1994; Durif & Elie, 2008; Breukelaar *et al*., 2009). Thus, results from previous studies are not transferable into Lough Neagh (Simon *et al*., 2012) and must be accumulated locally.

7. References

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