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Studies on downstream migrating silver-phase European eels (*Anguilla anguilla*) in hydropower-regulated rivers.

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I certify that this thesis is my own work and I have not obtained a degree in this University, or elsewhere, based on this work.

Ethics statement

The handling of eels during this study was conducted under project authorisation AE19125/P035 issued by the Health Products Regulatory Authority (HPRA), Ireland's competent authority responsible the implementation of EU Directive 2010/63/EU.

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Abstract

Within the last 50 years, the European eel has gone from one of the largest freshwater fisheries resources throughout its range to being listed as critically endangered. A variety of factors have been implicated in this decline, but the exact causes remain poorly understood. However, during their downstream spawning migrations from rivers and lakes to the ocean, silver eels are exposed to considerable interference from in-channel structures and the biomass of eels successfully escaping from European rivers has greatly diminished. As a result of this decline, the European Union introduced Regulation EC No. 1100/2007. The key goal of this regulation is to enable, with a high probability, the escapement to the sea of at least 40% of the silver eel biomass that would exist under pristine conditions. All Member States with natural eel habitats were required to establish eel management plans (EMPs) that outlined measures to reduce anthropogenic mortality and to develop monitoring programmes to assess compliance with management targets.

In this study, two mitigation measures aimed at reducing hydropower mortality were assessed. In the hydropower regulated rivers Shannon and Erne, eels are captured upstream of dams and transported downstream to river sections with good seaward connectivity. The efficiencies of these 'trap and transport' (T&T) programmes were evaluated. It was found that 630 tonnes of eels have been captured and released to date (2009 – 2019) and the quantities released have proven important for reducing anthropogenic mortality rates in line with the EU regulation. However, clear differences exist between the efficiencies of the Erne and Shannon programmes and it was found that the effectiveness of T&T as a mitigation measure is directly linked to the number of hydropower stations bypassed. Trap and transport is only intended as an interim solution while non-intrusive alternative methods are developed. An underwater strobe light array was evaluated in the lower River Shannon to determine its potential to deflect silver eels during their downstream migrations. Eels displayed strong negative phototaxis, with strobe lights reducing the biomass of eels passing a river section by 80.3%. The results of this study suggest that light arrays could be used in future to prevent eels from entering turbines, guide eels to safe bypass routes or to increase the capture efficiency of trap and transport operations.

Monitoring programmes are required to assess the effectiveness of EMP measures and to assess compliance with the EU escapement target (40%). This requires that silver eel production (i.e. population size) and escapement are calculated annually. These values have traditionally been quantified using fisheries catch data. However, catch data is only considered robust where fishing is more or less constant throughout the migration period. Unfortunately, gaps frequently occur due to unfavourable environmental conditions or the implementation of fisheries regulations. This prompted the development of alternative monitoring protocols to quantify eel migrations. An acoustic camera (DIDSON) was used to observe eels swimming downstream of an eel fishing site on the R. Erne. A highly significant relationship was observed between nightly DIDSON eel counts and catch at the fishing site ($R^2 = 0.968$, $p < 0.001$) and will enable fisheries-independent estimation of spawner biomass in future. The acoustic camera was also used to investigate eel route selection at a water regulating structure in the lower R. Shannon. It was found that the proportion of eels migrating via alternative migration routes was strongly related to the proportion of total flow diverted to each route ($R^2 = 0.827$, $p < 0.001$). Improved knowledge of route selection will assist with the calculation of spawner escapement but also with the development of conservation strategies and the detection of mortality hotspots.

Generalised Additive Models were used to model daily catches of silver eels in the Shannon and Erne based on a variety of environmental variables. Final models were used to retrospectively complete discontinuous catch records and increased estimates of production by 9.3% on the Shannon and by 2.8 – 3% on the Erne, compared to estimates of production based on incomplete catch records alone. Finally, the ability of sequentially placed nets to generate quantitative estimates of silver eel production were assessed at a lake and riverine site. It was found that this method was an appropriate sampling protocol for the riverine site, but when applied to lake populations, estimates were highly biased relative to population estimates based on mark-recapture experiments. It is essential that data collection embraces both fisheries and non-fisheries data sources and the monitoring protocols developed in this thesis will facilitate the calculation of production and escapement in future.

Chapter 1: General Introduction

1.1. Anguillid eels

The 'true eels' belong to the order Anguilliformes. All 19 families within this order are strictly marine, with the exception of the Anguillidae. This family contains a single genus, *Anguilla*, consisting of 19 species and sub-species. Anguillid eels are teleosts, characterised by distinctive, elongate morphologies (Figure 1.1) and catadromous lifecycles, with feeding and growth occurring in freshwater and coastal areas and spawning occurring in the ocean. Anguillid eels are widely distributed throughout the world's oceans in both temperate and tropical waters, with the notable exception of the southern Atlantic Ocean, the west coasts of the Americas and the Polar regions (Aoyama, 2009). The North Atlantic is home to two species of eel, the European eel (*Anguilla anguilla*) and American eel (*A. rostrata*).

Figure 1.1. The European eel (Photo: Eamonn Lenihan)

1.2. The European eel (*Anguilla anguilla*)

Within its range (Figure 1.2), the European eel (*Anguilla anguilla*) can be found in all coastal and continental waters connected to the Atlantic Ocean, North Sea, Baltic Sea and Mediterranean Sea. In fact, within the ICES (International Council for the Exploration of Seas) area, no fish stock is more widely distributed. As a catadromous species, the European eel has a remarkably complex lifecycle that involves two metamorphoses and two oceanic migrations (Figure 1.3). The collection of newly

hatched larvae from ichthyoplankton surveys suggests that life begins in the Sargasso Sea (23º to 29.5º N, 48º to 74º W) in the western Atlantic (Schmidt, 1923; Miller et al., 2019). Larvae are thought to hatch from eggs deposited in the upper ~300 m of the ocean (Miller et al., 2019). Following hatching, eggs develop into transparent, leaf-like leptocephali larvae and drift eastward with the Gulf Stream and North Atlantic Drift (Tesch, 2003). Larval dispersion is considered to be random. Upon arriving at the European continental shelf, 10 months to two years later (Bonhommeau et al., 2009), leptocephali metamorphose into typically 'eel-shaped', transparent juveniles called glass eels (Tesch, 2003). Glass eels are considered to orientate themselves using lunar and magnetic cues in pelagic waters, chemical cues in coastal zones and odours, salinity gradients and currents in estuaries (Cresci, 2020). Eels enter rivers all year round, although migration peaks occur in September – October in southern Europe, and from March – May in more northern latitudes (Tesch, 2003). The immigration of glass eels is commercially harvested across much of Europe. These eels are largely used for stocking purposes and as seed for aquaculture enterprises (ICES, 2019).

Figure 1.2. The range of the European eel (Modified from Jacoby et al., 2015)

In the past few decades, the long-held belief that anguillid eels demonstrate obligatory catadromy (i.e. marine spawning followed by exclusively freshwater residency) has been disproved for many species of eels in the genus *Anguilla*, including the European

eel. Instead, it has been shown, primarily by otolith microchemical analyses, that eels are facultatively catadromous with some glass eels never entering freshwater and completing their life-history in brackish or marine waters (Tsukamoto et al., 2001; Arai et al., 2019).

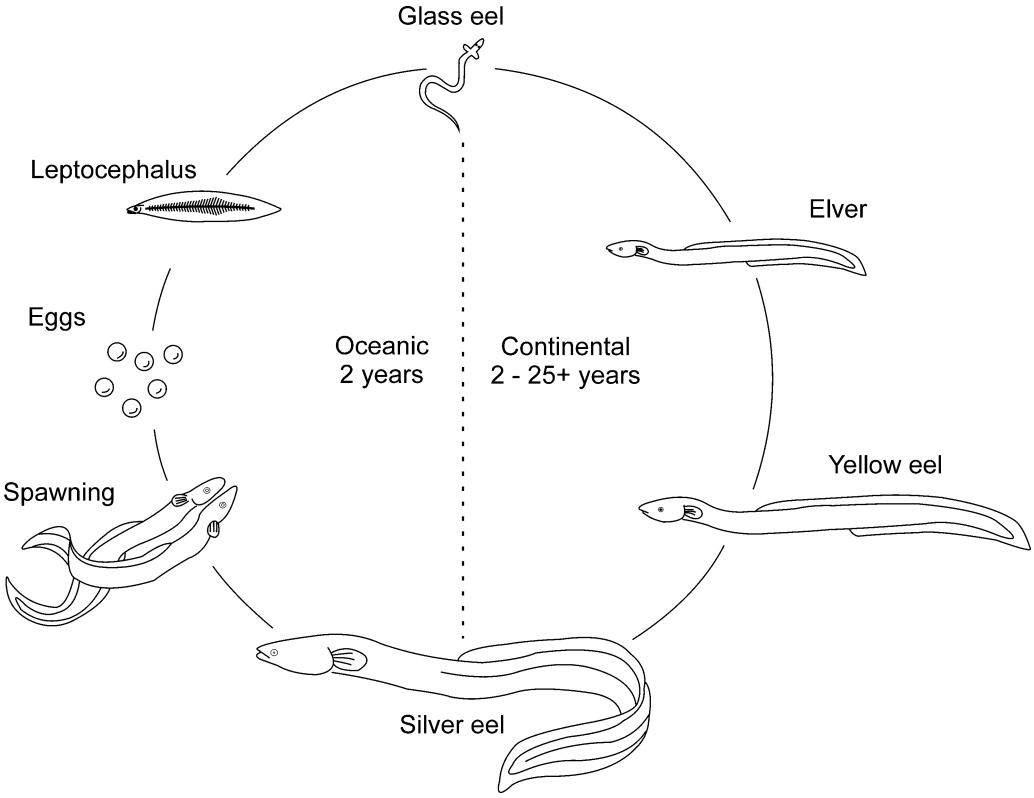

Figure 1.3. The lifecycle of the European eel (modified from Dekker, 2000).

As glass eels travel further into estuaries, pigmentation occurs. Pigmented eels become known as elvers and continue to migrate upstream, colonising all available habitat. Eels arriving in catchments are sexually undetermined. It appears that population density is the most important factor determining whether eels become male or female. The general pattern is that males dominate in the lower sections of catchments where density is highest (Laffaille et al., 2006) and a greater proportion of females are observed in the upper sections of catchments were density is lowest (MacNamara et al., 2017). Once individuals attain a certain size (usually 30 cm), they become known as yellow eels because of their colouration. Yellow eels are the feeding and growth life-stage (Moriarty, 2003). During this sedentary phase, eels accumulate sufficient somatic reserves to power the long-distance swimming associated with their marine migrations. However, females also require additional energetic stores in order to

produce eggs. Therefore, males tend to reach sufficient reserves for migration at shorter lengths (< 440 mm; Laffaille et al., 2006; McCarthy et al., 2014), while females migrate at greater lengths (approximately 440 to 1000+ mm; McCarthy et al., 2014). Female length is also linked to fecundity (MacNamara and McCarthy, 2012) and therefore it is thought that females optimise their size in order to increase reproductive output. This leads to different life-history strategies and marked sexual dimorphism in maturing male and female eels. The duration of the yellow eel stage is highly variable among individuals and sexes, but typically lasts from 3 – 25 years (ICES, 2019).

Once sufficient reserves are accumulated, eels transition to the migratory life-stage (i.e. silver eels). Metamorphosis occurs weeks to months in advance of migrations (Fontaine, 1994), and involves a series of morphological and physiological changes that prepare them for oceanic migrations. Morphological changes include an enlargement of the eyes and an increase in the number of rods "males tend to reach (an adaption of deep sea fishes), elongation of the pectoral fins, thickening of the skin and the development of counter-colouration, with the ventral surface whitening and the dorsal surface adopting a dark, silver appearance. Important physiological changes also occur. Eels acquire salinity tolerance prior to entering oceanic waters (Durif et al., 2009). Long-distance migrations are energetically taxing, and as a result, eels cease feeding to save energy. Instead, they rely on somatic reserves, with fat content increasing to ~ 28% at the point of migration (Bergersen and Klemetsen, 1988). Power output from muscles increases to economise long-distance migrations (Lokman et al., 2003). Finally, the gonadotropic axis is initiated, and gonad development begins (Dufour et al., 2003). Once silvering is complete, eel behaviour changes and they become more perceptive to environmental cues that encourage downstream migrations.

Mass migrations typically occur in autumn and winter (Tesch, 2003). There is no literature to suggest that there is a social component to silver eel migrations. Instead, migration events are thought to be triggered by a complex combination of environmental factors (Sandlund et al., 2017). These factors can be hydrological, climatic or related to light (e.g. lunar phase and day-length). Which environmental cues are important tends to be catchment specific. All life-stages of eel are photophobic (light-shy) and silver eel migrations typically occur at night and during the darker phase of the moon. Peaks in eel migration are also frequently associated

with increasing river flow, reducing water temperature, heavy precipitation and lower atmospheric pressure (Cullen and McCarthy, 2003). While environmental factors can act as releasing factors, encouraging eels to migrate, they can also act as inhibiting factors (Figure 1.4).

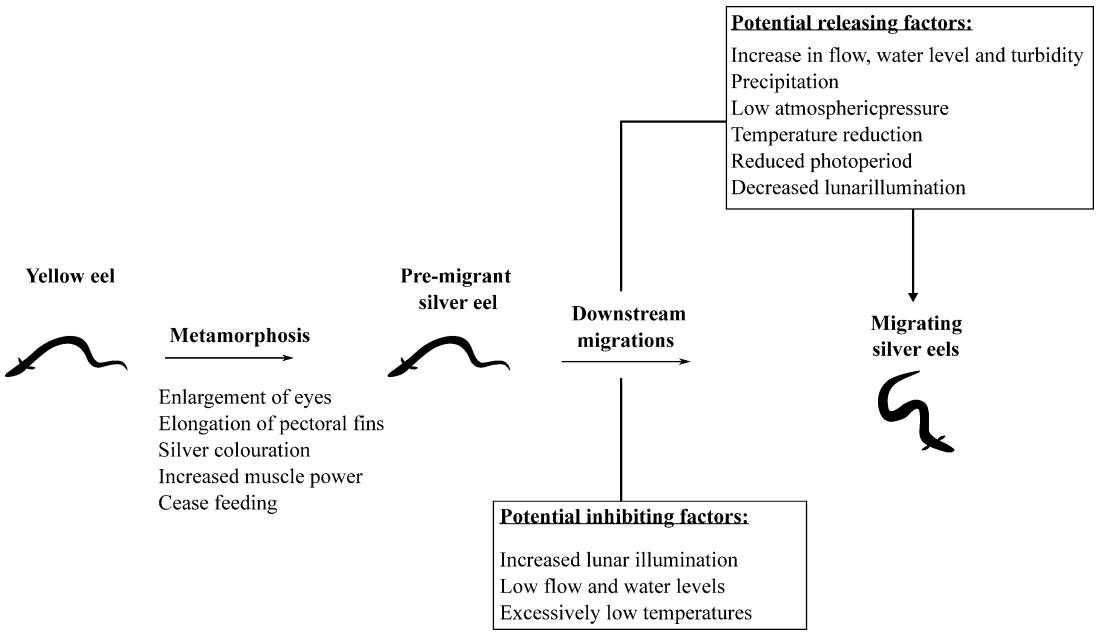

Figure 1.4. Following metamorphosis, silver eel migrations are controlled by environmental cues that can act as inhibiting or releasing factors (Modified from Haro, 2003).

Once eels leave rivers and enter the ocean, relatively little is known about their spawning migrations. The length of this migration varies in distance with geographical location within the species range. For example, eels leaving the Azores face a migration of *c*.2,500 km, while those leaving northern Scandinavia must migrate *c*.6,500 km. The timing of silver eel escapement from different catchments reflects this, with eels leaving the Baltic earlier than those leaving western Europe (Righton et al., 2016). Silver eels are likely to reach the Sargasso Sea by the following February to June (Fricke and Kaese, 1995). In recent years, the advancement and miniaturisation of telemetry technology has allowed for the tracking of portions of the oceanic migration (Righton et al., 2016).

The exact location of spawning grounds in the Sargasso Sea remains unknown and therefore it has not been possible to capture or observe spawning in the wild. Existing knowledge on the reproductive biology of eels comes from the artificial maturation of

eels in captivity. Eels are semelparous, meaning that upon reaching the spawning grounds, individuals are presumed to die after repeated spawning events (Tsukamoto et al., 2011). Although European eels have a wide geographical range, all eels spawn in the Sargasso Sea and form one panmictic population, meaning the stock consists of a single randomly mating population (Als et al., 2011).

1.3. European eel stock decline

Eels can be found in all available habitats, including coastal waters, estuaries, lagoons, lakes, rivers and wetlands (Harrod et al., 2005; Arai et al., 2019) and, historically, accounted for in excess of 50% of the fish density and biomass in many European waterways (Moriarty and Dekker, 1997). From the early 1900's, the eel population was increasingly impacted by human factors. For example, within Europe, it is estimated that of approximately 124,000 km^2 of potential eel habitat available, 33% (42,000 km^2) is now inaccessible due to the presence of anthropogenic structures (Moriarty and Dekker, 1997). Additionally, fishing pressure increased during this time as fisheries shifted from small scale subsistence fisheries to large scale commercial operations (Dekker, 2019).

The stock status is usually assessed based on time series of juvenile recruitment (either as glass eels or elvers) to rivers across Europe (ICES, 2019). These time series have revealed that recruitment across Europe has declined by more than 90% since the early 1980s (Bornarel et al., 2018; ICES 2019). However, this recruitment decline was preceded by reductions in fisheries yields of yellow and silver eels in the 1960's (Dekker, 2003) and 1970's (Aalto et al., 2016). This led to the conclusion that the recruitment collapse may have been the result of insufficient spawners. It is also likely that depensatory mechanisms and Allee-effects are impacting on stock-recruitment (Allee 1932; Dekker, 2004). In Ireland, the recruitment of glass eels and elvers to rivers is monitored in a series of hydropower regulated and free-flowing catchments. In the Rivers Shannon and Erne, which are regulated for hydropower in their lower reaches, elvers are recorded in traps downstream of barriers and transported and released upstream. Glass eel or elvers are trapped in six other free-flowing rivers by Inland fisheries Ireland and the Marine Institute (SSCE, 2012), with eels subsequently released to the same river. In Northern Ireland, elvers can recruit naturally to Lough Neagh, Europe's largest commercial eel fishery. However, the fishery is heavily

supplemented by re-stocking with eels imported from France, Spain and the United Kingdom. Between 2000 and 2008, recruitment to Irish catchments declined to between 4% (River Shannon) and 23% (R. Erne) of historic levels (1979 – 1984; Figure 1.5A). Commercial catches in Ireland did not decline as early as in continental Europe but instead coincided with declines in recruitment in the 1980's. Commercial catches of silver eels on the R. Shannon declined from a mean annual catch of 46.5 t in the 1980's (Quigley and O'Brien, 1996) to an annual mean catch of 26 t in the periods from 2000 - 2008 (Figure 1.5B). Although not as dramatic as the decline in recruitment, declining silver eel catches resulted in increased fishing effort. For example, in the 1980's only three sites were fished in the Shannon, yet in the 1990's this increased to a maximum of 29 fishing sites (McCarthy and Cullen, 2000) and similar effort continued into the 2000's, meaning the true extent of the decline was likely masked.

As a result of this decline, the European eel was classified as critically endangered by the International Union for the Conservation of Nature in 2008 (Jacoby and Gollock, 2014). Long-distance movements by eels up and down rivers, through estuaries and the open ocean mean they are exposed to considerable interference during their life cycle. A variety of factors have been implicated in the decline of the eel stock, with effects acting synergistically and varying between life stages (reviewed by Jacoby et al., 2015; Drouineau et al., 2018). Oceanic factors include overfishing of glass eels (Dekker, 2000), natural and human-driven changes in oceanic circulation patterns (Knights, 2003), and changes in sea surface temperature (Bonhommeau et al., 2008) have been considered. Eels are also affected by a range of factors during their continental lifecycle, including fisheries (for yellow and silver eels), introduced pathogens such as the Asian swimbladder nematode *Anguillacola crassus* (e.g. Sjöberg et al., 2009), viruses (e.g. McConville et al., 2018) and bioaccumulation of toxins/pollutants (Capoccioni et al., 2020). In-channel structures for hydropower generation, navigation, water-abstraction, flood control and water security are considered to have a particularly significant impact on eels.

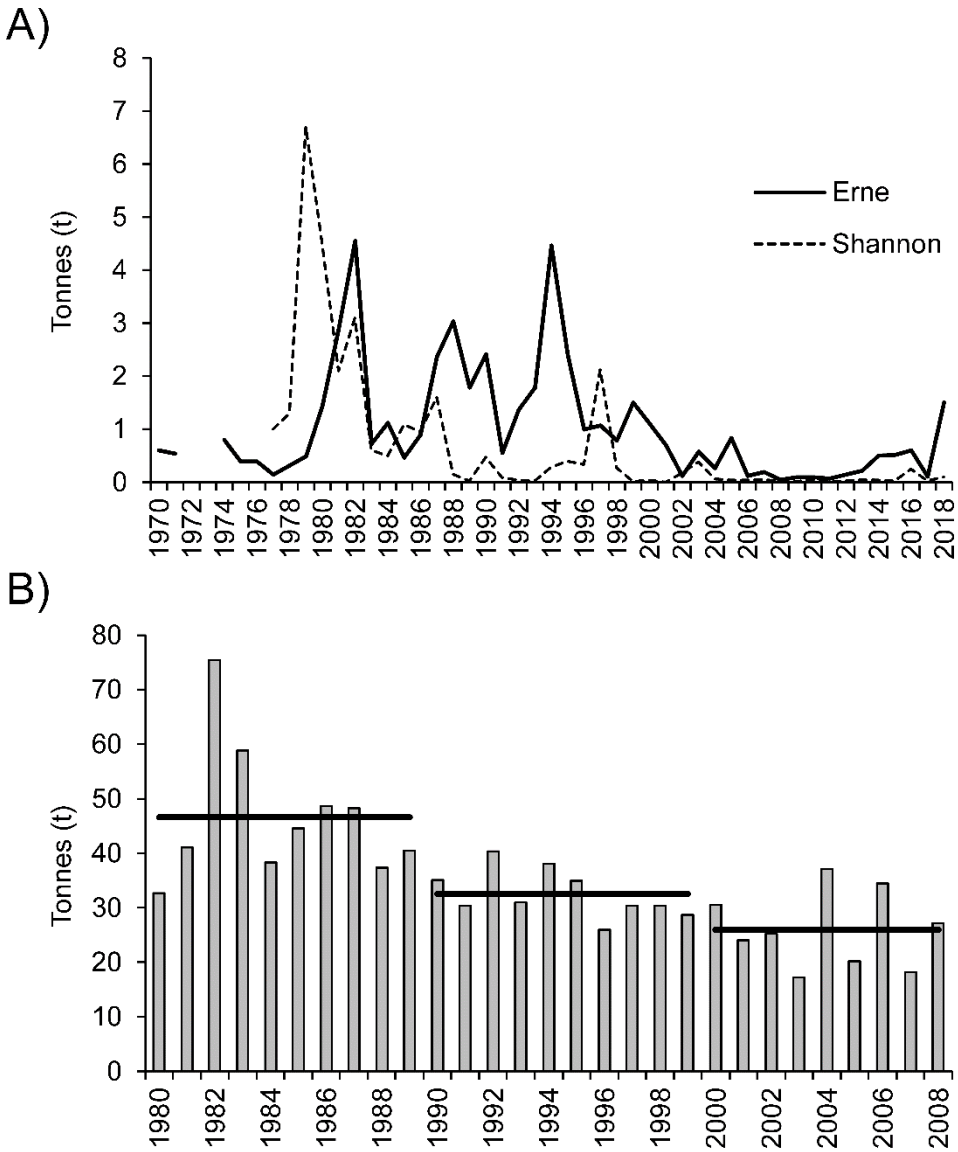

Figure 1.5. A) Catches recorded at elver trapping stations on the Erne (Cathaleen's Fall) and Shannon (Ardnacrusha). B) Commercial silver eel catches in the Shannon, black lines represent mean annual catch each decade (1980's = 46.5 t, 1990's = 32.5 t, 2000's = 26.0 t). Data supplied by Electricity Supply Board (ESB).

1.4. Protection and legislation

The latest advice from ICES is that the status of eel stock remains critical with glass eel recruitment to Europe in 2020 only 6.5% of historic levels (1960–1979; ICES 2020). As such, all anthropogenic mortality (e.g. recreational and commercial fishing, and hydropower) affecting silver eel escapement should be reduced to as close to zero

as possible. The decline of the European eel throughout its range prompted the European Union (EU) to introduce regulation EC No. 1100/2007. This regulation required all EU Member States that contain natural European eel habitat to adopt national eel management plans (NEMPs). Each country's NEMP was to outline actions that would be adopted in order to reduce anthropogenic mortality to permit escapement to the sea of at least 40% of the silver eel biomass that would have existed in the absence of anthropogenic impacts. Targets are set relative to the silver life stage because the enhancement of potential spawner escapement from continental habitat is seen as the most effective way of enhancing the spawning stock and subsequent recruitment (Robinet et al., 2007). Irelands NEMP was submitted to, and accepted by, the EU in 2009. It specified four main management actions:

1) The cessation of commercial fisheries for yellow and silver eels
2) Facilitation of the upstream migrations of juvenile eels at barriers
3) Improvements to water quality
4) The introduction of a trap and transport programme to mitigate against the impact of hydropower on downstream migrating silver eels

In Ireland, pristine escapement was estimated using historic silver eel catch records and fishing efficiency rates from five 'index' rivers (DCENR, 2008). Estimates were raised to account for unreported and illegal fishing. Estimates of productivity from these index rivers were extrapolated to data poor catchments based on habitat characteristics and a national estimate of pristine escapement was calculated to be 594 metric tonnes before the stock was impacted by anthropogenic factors. Current escapement is also calculated in these index rivers using silver eel catch data from experimental fisheries and estimates of efficiency. Again, information collected in these data rich rivers is extrapolated to data poor catchments. Current escapement is calculated annually and expressed as a percentage of the historic escapement to report on compliance with the EU escapement target (40%).

At present it is not possible to define a timeframe to achieve the EU biomass target. Instead, Ireland has set an alternative target outlining the timeframe to full recovery of recruitment. According to the stock assessment of Åstrom & Dekker (2007), reducing anthropogenic mortality by 85% of pre-NEMP levels should enable recruitment to recover within 90 years. This recovery in recruitment should

subsequently enable the achievement of the EU silver eel escapement target (40%) within a similar, or shorter, timeframe. With the proposed management actions as part of Ireland's NEMP, fishing mortality should be eliminated and turbine mortality markedly reduced. Therefore, it is anticipated that the lifetime mortality rate imposed on eels should enable recovery of recruitment within 100 year or less.

1.5. Barriers to eel migrations

The construction of anthropogenic obstacles means that large free-flowing rivers are now largely absent from Europe (Grill et al., 2019), resulting in river fragmentation and flow regulation. Diadromous fish have undergone a dramatic decline (Limburg and Waldman, 2009) and the construction of barriers, particularly dams, has been found to severely impact diadromous fish diversity (Halvorsen et al., 2020). Dams store water to convert kinetic energy to potential energy. When released over, under or through a structure, the water velocities created can far exceed the swimming ability of juvenile eels, effectively making structures impassable under certain conditions. In Irish hydropower regulated rivers recruiting juvenile eels are captured in traps downstream of dams and stocked upstream. However, river connectivity is a 'two-way street' (Calles et al., 2009) and it is therefore necessary to ensure that these stocked eels are protected during downstream migrations following their continental residency.

Downstream migrating eels tend to 'go with the flow' (Jansen et al., 2007) and increased flow velocities in front of turbine intakes are thought to act as an attractant for eels. Riverine obstructions frequently result in delays (Besson et al., 2016), injury (Bolland et al., 2019), and mortality (Winter et al., 2007; Calles et al., 2010). Because of their distinctive elongate morphology, eels are particularly vulnerable at hydropower intake screens and during turbine passage (Boubée and Williams, 2006; Calles et al., 2010). Trash screens are designed to prevent large debris from entering turbines. However, when flow velocities approaching these screens exceed the swimming speed of eels, these fish can become trapped, or 'impinged', against these screens. When bar spacing on trash screens exceeds 10 mm, eels will simply pass through screens and enter turbines (Adam et al., 2005). During turbine passage, eels suffer injury and mortality due to contact with the turbines. Eels also experience a

range of injuries and mortality related to rapid changes in pressure, including gas embolisms in tissues and organs, and ruptured swimbladders. Mortality rates from hydropower stations have been widely reported for eel species but generally range from 15 – 25% (Bruijs and Durif, 2009). Mortality rates up to 100% have been reported (Montén, 1985) and the rate is a function of turbine type and operation as well as fish length. The problems associated with dam mortality are exacerbated where there are multiple dams located on the migration axes of eels (Dönni et al., 2001).

Eels surviving turbine passage are frequently injured, suffering lacerations, fractures and damage to internal organs. Fish that survive passage potentially tend to be disorientated and have a higher risk of predation by predatory fish and piscivorous birds (Doherty and McCarthy, 1997). Therefore, the impact of anthropogenic obstacles on silver eel migrations is considered a key factor in the decline of eel population and has been the focus of much research (Winter et al., 2007; Verbiest et al., 2012).

1.6. Silver eel trap and transport

Although 'fish-friendly' turbines are being developed (Hogan et al., 2014) the general consensus remains that the entrance of fish to turbines should be minimised where possible (Fjeldstad et al., 2018). No globally accepted standard for fish passage solutions exist, however, to achieve safe downstream migration past hydropower, fish must be prevented from entering turbines and safe alternative routes provided. In many older hydropower facilities, it is frequently not considered practical, or cost effective, to retrofit structures with built fish passage solutions. 'Trap and transport' (T&T; also known as assisted migration) is considered a practical solution to enhancing silver eel escapement (Richkus and Dixon, 2003) and often represents the only viable mitigation measure. In the case of silver eels, T&T involves capturing downstream migrating eels and transporting them to a river section with good seaward connectivity in order to continue their migrations.

Approximately 50% of the freshwater habitat available to eels in Ireland is located above hydropower dams. Therefore, in order to enhance silver eel escapement as required by the EU regulation, T&T programmes were initiated on Ireland's three main hydropower impacted rivers, the Shannon, Erne and Lee. The R. Lee T&T

programme is a relatively small scale programme, aiming to release 500 kg of eels annually, and is not dealt with in this thesis. Prior to Ireland's NEMP, the Shannon and Erne both hosted commercial fisheries for yellow and silver eels. Following the adaption of the EMP in 2008, commercial fishing ceased and in their place, catchment-wide conservation fisheries were established.

Trap and transport was introduced as an interim solution while alternative non-intrusive measures are investigated. Ireland's NEMP determined that T&T would remain in place until a suitable 'engineered solution' with high efficiency was in place (DCERN, 2008). Engineered solutions may involve alterations to turbine design, alternative generating protocols, creation of alternative migration routes or the use of guidance devices. The most attractive solution to date appears to be the use of behavioural guidance barriers, such as artificial light arrays, to guide eels towards safe routes. However, evaluations of efficiency are lacking for most deflection systems.

1.7. Production and escapement

Pristine production is calculated for the Shannon based on catchment characteristics and productivity estimates extrapolated from other Irish rivers. On the Erne, pristine production is estimated using historic silver eel catch records and fishing efficiency rates (Matthews et al., 2001). Estimates were raised to account for unreported and illegal fishing (DCENR, 2008). In the Shannon and Erne catchments, pristine production was estimated to be 189,079 kg and 107,388 kg respectively. In order to assess compliance with the EU regulation, the estimation of present day production and escapement is required. Production is the biomass of silver eels in a catchment capable of escapement. Escapement can be defined as the biomass of silver eels that successfully circumnavigate all sources of human-related mortality (e.g. fisheries and hydropower generation) on their migrations from continental habitats to the ocean for spawning.

Directly assessing production and escapement requires intensive monitoring from the beginning to the end of the migration periods and is a difficult and often costly process. The primary means of estimating production rely on direct estimates based on intercepting eels during their downstream migrations (Robinet et al., 2007). This is most commonly achieved using catch records (from commercial or experimental

fisheries). Depending on their location and scale, fisheries can provide robust data for the estimation of silver eel production and escapement when combined with mark-recapture experiments to determine fishing efficiency. ICES (2019) noted that 75% of escapement and 25% of production values reported to the EU were calculated using commercial fisheries data (e.g. Rosell et al., 2005; Amilhat et al., 2008). Since Ireland's NEMP specified the closure of commercial fisheries in the Rivers Shannon and Erne, catch data collected as part of T&T programmes represents the only data source from which to estimate silver eel production and escapement in the Rivers Shannon and Erne. Eels are caught at several points throughout these catchments, with mark-recapture experiments conducted in the lower catchments to establish the remaining eels that are not caught. Escapement is calculated by subtracting estimates of anthropogenic mortality from production. However, the use of catch data, whether from commercial or experimental fisheries, requires that the entire migration period is covered (Robinet et al., 2007). Difficulties can arise when discontinuities occur in catch records due to fluctuations in river flow leading to periods of crew inactivity, or due to the imposition of management measures. In both scenarios valuable catch data is missed and can result in biases being introduced into calculations. As a result, new quantitative monitoring protocols are required to facilitate the quantification of eel migrations. Recent advances in modelling techniques and hydroacoustic devices might represent viable alternatives to catch-based methods of calculating production and escapement.

1.8. Study areas

1.8.1 The River Shannon

1.8.1.1. The Shannon catchment

The River Shannon (Figure 1.6) is Ireland's largest river, draining approximately one-fifth of the island. The vast majority of the river lies in the Republic of Ireland, with 6 km^2 extending into Northern Ireland. The river is 360 km long, including a 97 km estuary, and enters the Atlantic on the western coast. The main river stem flows through a number of lakes, the largest of which are Lough Allen (35 km^2), L. Ree (105 km^2) and L. Derg (117 km^2). The Shannon lakes are generally characterized as mesotrophic to eutrophic and shallow, although the three mains lakes contain considerable areas of deep water. The principle tributaries of the river are the Rivers Inny, Suck and Brosna. The river is characterized as slow flowing, dropping only 17 m from L. Allen to Killaloe (a distance of 200 km). In the remaining 25 km, between Killaloe and Limerick City, of the freshwater section, the river drops by a further 30 m. As a result of this drop, it was decided in the 1920's that the lower catchment was the ideal location for the construction of a hydropower scheme. The cascade catchment, the area above the dam, is 10,400 km^2. The total wetted area of the cascade catchment includes 38,771 hectares (ha) of lake habitat and 3,695 ha of fluvial habitat (42,466 ha total).

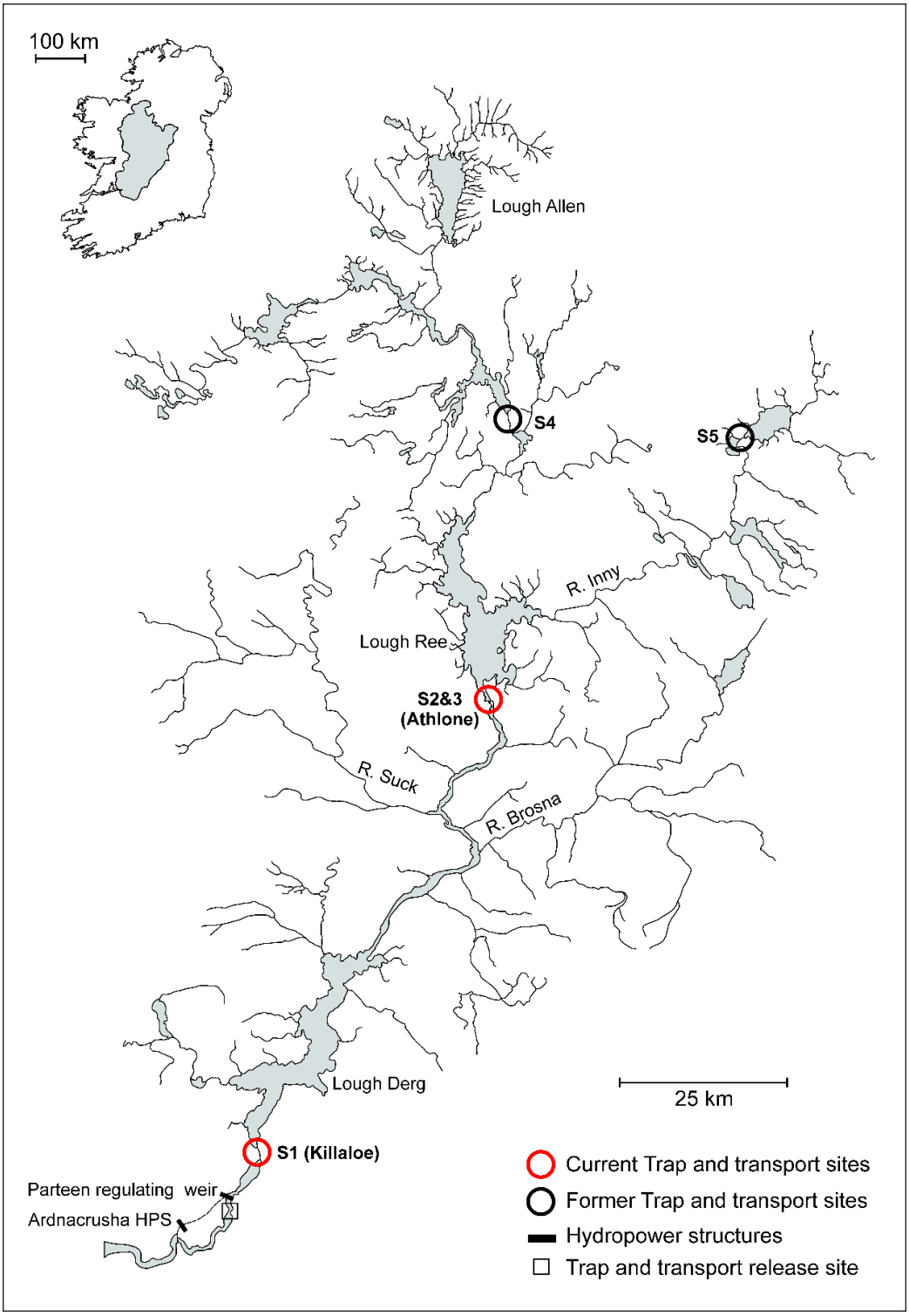

Figure 1.6. Map of the Shannon catchment, showing the locations of hydropower structures in the lower catchments and trap and transport fishing and release sites. Fishing, as part of trap and transport, stopped at sites S4 and S5 in 2016.

1.8.1.2. Hydropower

Ardnacrusha hydropower station (HPS) (86 MW) has a hydraulic head of 28.5 m and contains one Kaplan (167 rpm) and three Francis turbines (150 rpm). A 12.8 km artificial headrace canal supplies Ardnacrusha with up to 380 $m^3 s^{-1}$ of water, which is required for maximum generation. A 2.4 km tailrace returns station discharge to the River Shannon. Parteen weir is located at the start of the headrace canal and serves to divert the main flow away from the River Shannon to the headrace canal (Figure 1.7A). At the HPS, a number of migration routes are available in principle, including passage through turbines, a Borland lock type fish pass, a spillway and a navigation canal lock (Figure 1.7B). However, eels rarely utilise the Borland lift or navigation canal, and spillage, which only occurs rarely, is minor compared to overall flow. The turbine intake trash screen has vertical bars with a spacing of 60 mm, which is insufficient to exclude eels from entering turbines. Therefore, essentially all eels are considered to pass via the turbines and surviving individuals may proceed to the estuary via the tailrace. Turbine passage mortality for silver eels entering Ardnacrusha HPS was previously determined by means of acoustic telemetry, using protocols described in several reports (e.g. SSCE, 2012). An average mortality of 21.15% (range 16.6 – 25%, n = 103 eels) was established.

In times of high flow, when Ardnacrusha has reached its maximum load (380 $m^3 s^{-1}$) and the water level above Parteen weir continues to increase, excess water is allowed down the natural "old river channel" (ORC) of the River Shannon through any or all of the set of three undershot sluice gates located at Parteen weir. This process is referred to as "spillage". The ORC has no barriers to migration and provides a safe migration route to the Shannon estuary, 21 km downstream. Therefore, seaward migrating silver eels have two routes available to them depending on flow conditions. A small flow (<10 $m^3 s^{-1}$) is released to the ORC at all times via a fish pass built to facilitate salmon (*Salmo salar*, L.) migrations. Previous analyses have revealed that eels do not use this route (McCarthy et al., unpublished) and therefore this migration route and its associated flow were excluded from this analysis. The mean annual flow through Parteen weir is 186 $m^3 s^{-1}$. The mean winter discharge is 274 $m^3 s^{-1}$, though flow may reach over 800 $m^3 s^{-1}$ in major winter floods.

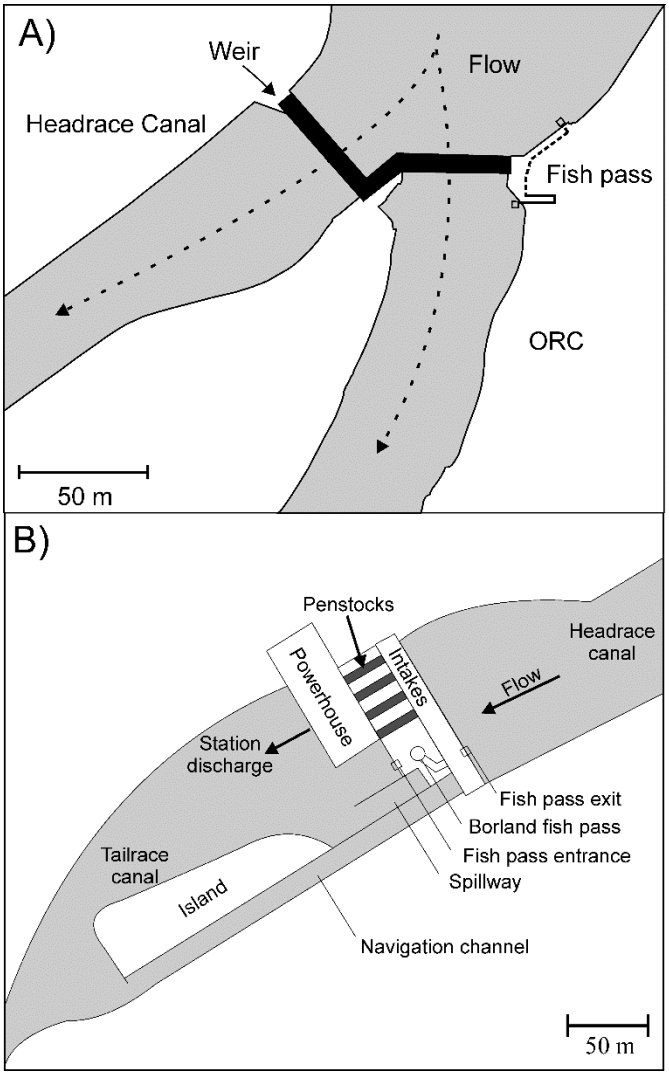

Figure 1.7. Schematic drawing of A) Parteen weir, which serves to divert the main river flow to the HPS via the headrace canal and B) Ardnacrusha HPS with various potential fish migration routes highlighted.

1.8.1.3. Shannon silver eel fishery

Following the construction of Ardnacrusha HPS, the Electricity Supply board (ESB) assumed the fishing rights to the Shannon. ESB-authorised fishing initiated in 1937 and extended until Ireland's NEMP specified the closure of fisheries in 2008. Extensive fisheries for both yellow and silver eels occurred throughout the catchment. Initially management of the fishery focused on the economic gains possible from development. This resulted in the Shannon Eel Management Programme which was established in 1992 by the ESB and called for a survey of eel stocks to determine the potential for job creation in eel fishing. This work was independently investigated by

the National University of Ireland Galway (NUIG). A report was compiled by NUIG based on work undertaken between 1992 and 1998 and determined that a more conservation-based management approach was required as a result of declining recruitment and silver eel catches (McCarthy and Cullen, 2000). This led ESB to establish a pilot-scale T&T programme in which various quantities of commercial catches in the lower catchment were released downstream of hydropower structures. Following the adoption of Ireland's NEMP, T&T was expanded to cover the entire catchment from 2009 onwards.

Initially (2009 – 2015), five sites were fished throughout the catchment as part of T&T (Figure 1.6). This declined to three sites from 2016. All eels captured are released to the natural river channel of the Shannon, downstream of Parteen weir. Killaloe eel weir (Site S1) is the lowermost fishing site in the catchment and accounts for approximately half of the eels captured annually. The fishing weir (Figure 1.8) consists of a metal walkway attached to the downstream side of a road bridge and extends across 90% of the river width. Up to 34 nets can be fished although in recent years only 19 have been fished. Over 99% of the cascade catchment is located upstream of Killaloe, making it the ideal location to carry out mark-recapture experiments for assessing fishing efficiency. Therefore, Killaloe is vital for the calculation of production and escapement in the Shannon catchment.

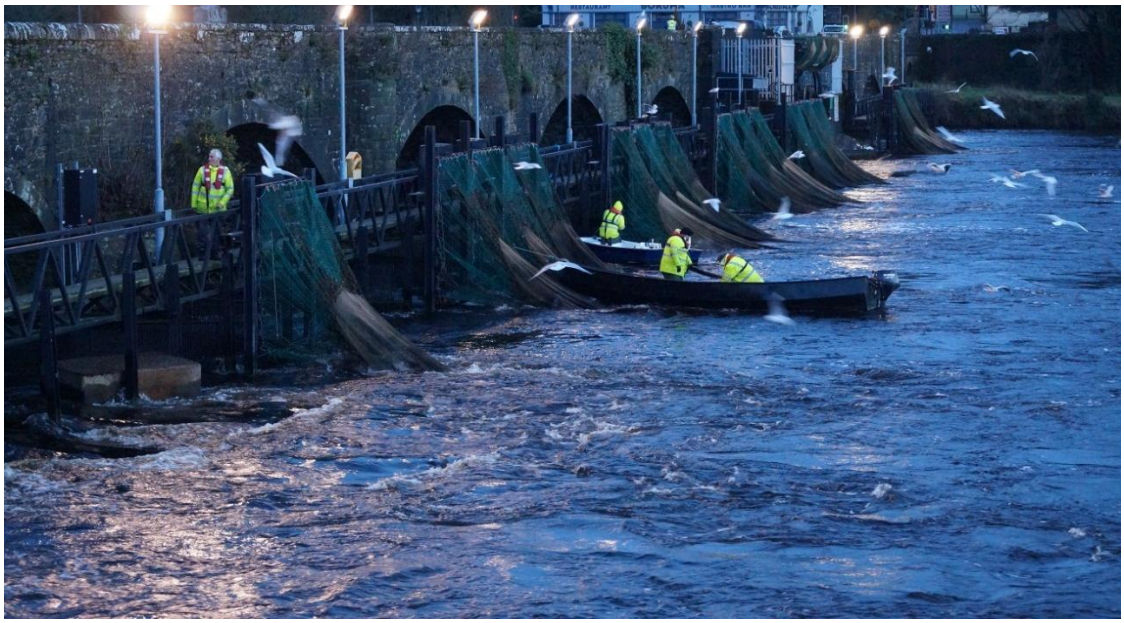

Figure 1.8. Silver eel fishing at Killaloe eel weir (Photo: Eamonn Lenihan).

1.8.2. The River Erne

1.8.2.1. The Erne catchment

The Erne is a trans-boundary catchment (Figure 1.9), with portions in the Republic of Ireland and Northern Ireland. It is the fourth largest catchment in Ireland and drains an area approximately 4,375 km^2. The river is approximately 130 km long and enters the Atlantic Ocean via a short estuary located in Ballyshannon, County Donegal. The catchment contains extensive lake habitat and drains in a north-westerly direction through L. Gowna, L. Oughter, and Upper and Lower L. Erne, the latter being the sixth largest lake in Ireland (110 km^2).

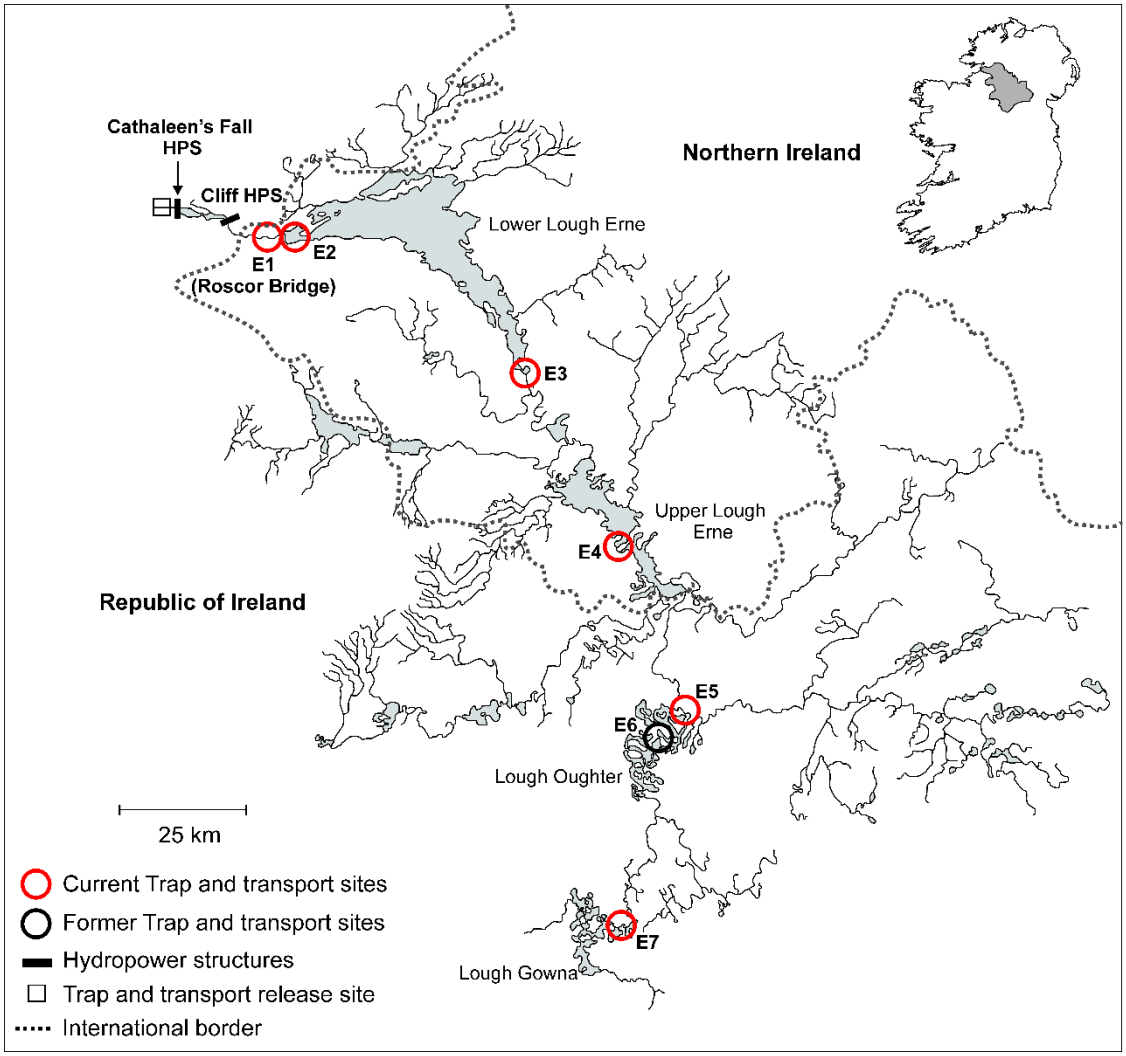

Figure 1.9. Map of the Erne catchment, showing the locations of hydropower stations (HPS) in the lower catchment and trap and transport fishing and release sites. Fishing stopped at site E6 in 2016.

1.8.2.2. Hydropower

The River Erne has two hydroelectric power stations on its lower reaches (Figure 1.9), which were commissioned in the early 1950s. Cathaleen's Fall HPS (45 MW) is located at the tidal limit on the river in Ballyshannon, and has a head height of 27 m. A second, smaller (18 m head, 20 MW) HPS is situated at Cliff. The two HPSs are 5.2 km apart and are separated by an artificial reservoir known as Assaroe Lake (235 ha). Flow patterns, which affect silver eel migrations, are controlled at the HPSs. Each HPS houses two Kaplan turbines with a maximum generating load of 180 m^3s^{-1}. When maximum generation is achieved and water level upstream continues to rise, excess water can be released via spillgates (three gates at each HPS). Spillage is achieved by raising gates by a determined amount to give a particular discharge rate. The average annual discharge through the Erne system is 92 m^3s^{-1}, ranging from < 10 m^3s^{-1} to a maximum recorded rate of 382 m^3s^{-1}.

Eels not captured as part of T&T continue downstream to hydropower structures. Previous telemetry analyses established mortality rates at Cliff and Cathaleen's Fall HPSs (SSCE, 2012). At both HPSs turbine intakes have trash screens with a bar spacing of 38 mm, which is insufficient to exclude eels. Therefore, during generation all eels enter turbines. Alternatively, the release of water via spillways presents eels with another migration route. Daily mortality rates are applied based on dusk to dawn hydrometric data and the results of telemetry studies that found mortality was dependant on flow to alternative routes (summarised in Table 1.1). Fish passes for ascending Atlantic salmon are present at both dams, although previous studies suggest that eels generally do not use these (McCarthy et al., unpublished)

Table 1.1. Mortality rates at Cliff HPS and Cathaleen's HPS, depending on station operation.

Operation	Cliff HPS	Cathaleen's Fall HPS
No flow	0%	0%
Generation & Spillage	7.9%	7.7% (one turbine) 15.4% (two turbines)
Generation only (no spillage)	26.7%	27.3%

1.8.2.3. Erne fishery

On the Erne, Matthews et al. (2001) noted that historic fisheries records are very incomplete and estimates of fishery yield have often been rather speculative. However, Matthews et al. (1999) found that overall there was a decline in silver eel fishing activity over time. For example, 11 silver eel weirs were fished in the 1970's but this had declined to just 4 in the 1990's. Reductions in fishing activity were attributed to declines in population size.

Establishment of a T&T programme required the gradual development of a conservation fishery. A number of sites are now fished throughout the catchment as part of T&T operations. Roscor Bridge (Site E1, Figure 1.9) is vital to monitoring silver eel population dynamics in the Erne. The site is located 750 metres downstream of the outflow point of lower Lough Erne and represents the last fishable site above Cliff hydropower station. Again, 99% of the cascade catchment is located above this point and provides a discrete river section from which to conduct mark-recapture experiments. Three coghill nets are fished from the downstream side of a road bridge (Figure 1.10). The nets are manually winched upwards during daylight hours and lowered from dusk until dawn to coincide with the nocturnal migrations of eels. Commercial fishing at the site suggested that efficiency was strongly affected by flow. This was confirmed in recent years based on replicated mark-recapture experiments and it was determined that at flows < 130 m^3s^{-1}, fishing efficiency is 9.78%, while when flow >130 m^3s^{-1}, efficiency is 18.43%.

Figure 1.10. Roscor Bridge eel weir. Fishing at the weir involves three nets which are hung from the bridge's arches. The nets are set in this photo but are lifted from above using hand-operated winches (Photo: Eamonn Lenihan).

1.9. Aims

Ireland has an obligation to reduce the anthropogenic mortality of silver eels through the operation of trap and transport programmes in hydropower-regulated rivers, and to monitor current levels of potential and actual silver eel escapement. In this context, this thesis had two primary goals. First, the contribution of T&T to eel conservation in Ireland was investigated and an alternative 'engineered solution' was investigated. Secondly, new monitoring protocols were investigated to address the current lack of quantitative tools available to assess silver eel production and escapement. The specific objectives of this thesis were:

- To review and evaluate Ireland's trap and transport programme as a conservation measure and as a source of data for the calculation of production and escapement in the Rivers Shannon and Erne (chapter 2).

- To evaluate the behavioural guidance of silver eel using underwater strobe lighting by reference to catch patterns at Killaloe eel weir. This study was a

case-study for potential long-term engineered solution to the eel passage problem at hydropower stations (chapter 3).

- To evaluate the ability of models (chapter 4) and an acoustic camera (chapter 5) to predict daily catches of silver eels at Roscor Bridge on the Erne and Killaloe on the Shannon and to facilitate the estimation of silver eel production.

- to assess the ability of an acoustic camera to determine silver eel route selection at a water regulating weir to facilitate the calculation of escapement (chapter 5).

- To investigate the ability of a net-based sampling protocol to provide robust, unbiased estimates of silver eel production based on catch records collected as part of T&T in the Shannon and Erne (chapter 6).

Chapter 2: A review and evaluation of silver-phase European Eel (*Anguilla anguilla*) Trap and Transport operations in Ireland.

2.1. Introduction

The European eel (*Anguilla anguilla*) is a catadromous fish species. As such, their lifecycle involves the migration of juveniles from oceanic to continental habitats, where they become the sedentary feeding and growth life-stage (yellow eels). Once sufficient energetic reserves have been accumulated, maturing eels undergo physiological, morphological and behavioural changes, transition to the migratory life-stage (i.e. silver eels) and begin seasonal seaward migrations to spawning grounds in the Sargasso Sea. Several studies have shown that silver eel escapement from rivers has declined throughout Europe (Andersson et al., 2012; Bevacqua et al., 2015). Although various factors are thought to have contributed to this decline (reviewed by Jacoby et al., 2015), hydropower barriers are recognised as having a significant impact on downstream migrating silver eels. Delays to migration (Besson et al., 2016), as well as injuries and mortality resulting from impingement against intake screens and turbine passage (Winter et al., 2006; Calles et al., 2010) reduces the number of individuals reaching the spawning grounds. Typical passage mortality rates range from 15 – 25 % (Bruijs and Durif, 2009) and passage through multiple dams can result in significant cumulative mortality. The European Union (EU) introduced a regulation (EC no. 1100/2007) requiring Member States to minimise anthropogenic mortality to enable escapement of at least 40% of the silver eel biomass relative to escapement if no anthropogenic factors had impacted the stock.

Unless an in-channel barrier can be removed, mitigation measures are required that reduce barrier related mortality and to restore river connectivity. Several solutions have been recommended that can enable safe passage for downstream migrating eels, including: bypasses (Travade et al., 2010), fish-friendly turbines (Hogan et al., 2014), deflection screens and the provision of safe alternative routes (Calles et al., 2013a) and flow management strategies (Teichert et al., 2020). However, in many older hydropower facilitates it is frequently not practical or cost-effective to retrofit structures and flow management strategies can incur significant losses to hydropower

companies. Trap and transport is considered as being a practical solution where viable alternatives are unavailable (Richkus and Dixon, 2003). Eels are captured above hydropower barriers and released at points downstream that have good seaward connectivity to continue their spawning migrations. At least six EU countries currently operate considerable silver eel T&T programmes (ICES, 2018a) in addition to similar programmes in New Zealand (e.g. Mitchell, 1996) for short-finned eels (*Anguilla australis*) and longfin eels (*A. dieffenbachii*), as well as North America (e.g. Stanley et al., 2014) for American eel (*A. rostrata*).

Hanel et al. (2019) suggested that T&T has considerable untapped potential and should be expanded to new rivers to enhance escapement. In this chapter, Ireland's silver eel T&T programme (2000 – 2019), the largest of its kind in the world, is reviewed. It is anticipated that a comprehensive review of this programme will help with the coordination and implementation of similar programmes in future. Until now no programmes have been post-evaluated to determine the efficiency of T&T as a mitigation measure, making it difficult to determine their conservation value. Therefore, to put Ireland's T&T in context, new analyses were conducted to assess the biomass of eels that would have been killed in the absence of T&T programmes and how this would have impacted compliance with conservation targets. We also assessed catch records collected as part of these programmes in order to determine their suitability for calculating production and escapement.

2.2. Background

2.2.1. Development of T&T in Ireland

Following the construction of hydropower stations, the Irish state-owned Electricity Supply Board (ESB) assumed the fishing rights to the Rivers Shannon and Lee, as well as fishing rights for the lower River Erne. The Erne is a trans-boundary river with portions in both Northern Ireland and the Republic of Ireland (chapter 1). ESB-authorised commercial fishing for yellow and silver eels occurred throughout the Shannon from 1937 until 2008, and management of the fishery was focused on the economic benefits possible. Declining silver eel catches became apparent in the late 1990's (McCarthy and Cullen, 2000) and resulted in a more conservation based management approach. Given the presence of an extensive fishery, the ESB decided

to establish a pilot-scale T&T programme in the lower Shannon catchment. During the early phase of this T&T programme (2000 - 2004), various proportions (32 – 65%; Figure 2.1) of commercial catches were released below hydropower structures as a conservation measure. From 2005 to 2008, all eels caught in the lower catchment were released. Of the 50.0 metric tonnes (t) caught over this period (2000 – 2008), 36.2 t of eels were released downstream of hydropower structures (72.4 %).

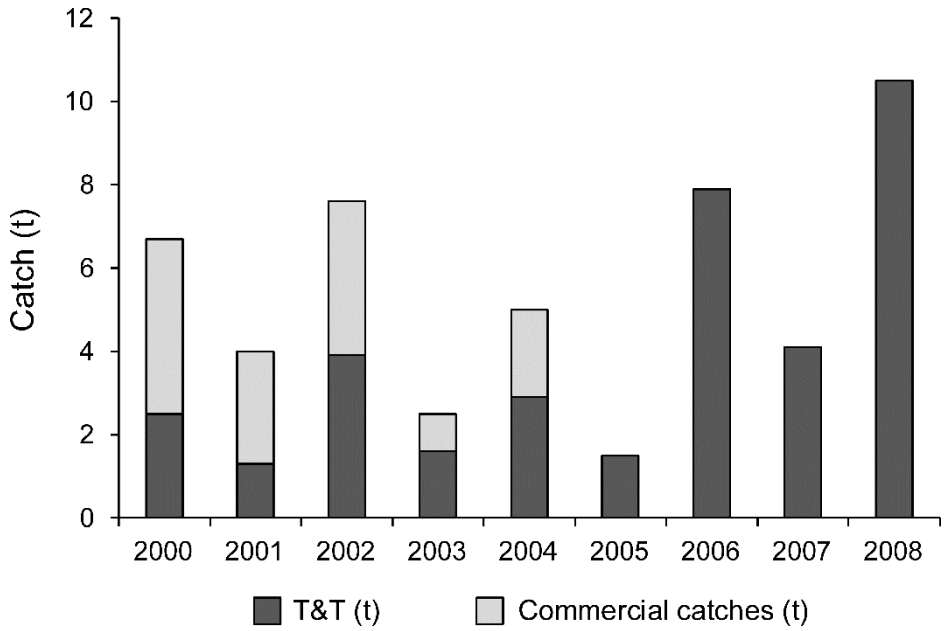

Figure 2.1. Catches recorded in the lower Shannon between 2000 and 2008. The quantities released for conservation and retained for commercial sale are indicated. Data supplied by the Electricity Supply Board (ESB).

2.2.2. T&T as part of Ireland's National Eel Management Plan

The EU regulation required each Member State to submit a National Eel Management plan (NEMP) that outlined strategies to reduce anthropogenic mortality in order to enhance silver eel escapement. Ireland's NEMP (DCENR, 2008) was accepted by the EU in 2009. A statutory body, the Standing Scientific Committee on Eel (SSCE), was established to oversee eel population monitoring, to facilitate research on eels and to report on compliance with the specified NEMP conservation measures. A complete closure of commercial fisheries for yellow and silver eels was specified by Ireland's NEMP. In combination with the 1959 Fisheries Act, which prohibited fisheries for

glass eels and elvers, fishing mortality in Ireland was reduced to zero. However, modelling suggested that closure of fisheries alone (and preventing illegal and unreported fishing) would be insufficient to reach the EU escapement target of 40% (DCENR, 2008). Almost 50% of freshwater habitat is located above major hydropower barriers in Ireland (DCENR, 2008). Therefore, the development of measures to mitigate against hydropower mortality in these regulated rivers was prioritised. Given the success of the pilot-scale T&T on the lower Shannon, it was decided that ESB should extend T&T operations to the remainder of the Shannon from 2009 with similar programmes to be established in the Erne and Lee catchments.

2.2.3. Fishing sites

Detailed descriptions of the Shannon and Erne catchments are presented in chapter 1, including details about the location of T&T fishing sites. Silver eels are trapped at specialised eel fishing weirs at Killaloe on the lower River Shannon and at Roscor Bridge on the lower River Erne. These weirs use either hydraulically (Killaloe) or manually (Roscor Bridge) lifted nets, which are attached to the downstream sides of bridges. Silver eels are also caught at various other upriver conservation fishing sites in these catchments using a variety of bespoke arrangements of winged river nets (e.g. MacNamara et al., 2017; McCarthy et al., 2019). From 2009, five sites were fished on the Shannon (Sites S1 – S5, chapter 1). On the Erne, a single site was fished in 2009 (Site E2; chapter 1). This increased to seven in 2010 (Sites E1 – E7). From 2016 onwards, fishing ceased at sites S4 and S5 on the Shannon and site E6 on the Erne. Small quantities (annual target of 500 kg) of eels are also captured and released past two dams on the River Lee. Given the relatively small quantities transported and general lack of scientific research, the Lee is not dealt with in detail here. The silver eel migration seasons in the Shannon and Erne typically extend from September until the following February (MacNamara and McCarthy, 2014; McCarthy et al., 2014), and are referred to by the year in which they began (e.g. September 2019 – February 2020 is referred to as the 2019 season). Former commercial crews are contracted by ESB to catch silver eels at designated conservation fishing sites.

2.2.4. Scientific monitoring and sampling

Nets are typically set at dusk and lifted at dawn at each site, to coincide with the nocturnal migrations of silver eels and to minimise the bycatch of non-target species. Crews report catches daily via text message and in written datasheets which are submitted weekly. Captured eels are transferred to storage nets or cages and kept in ambient water conditions. Eels are given sufficient time to recover in storage (at least 24 hours) prior to collection for transport and release. Eels are weighed (± 1 kg), under observation by fisheries inspectors, as they are loaded for transport. Eels are then transported in oxygenated tanks (usually 1000 litres) on trucks or trailers to designated release points below hydropower dams. All fishing, transport and release operations, are monitored by state agencies (Inland Fisheries Ireland [IFI] and the Department of Culture Art and Leisure Northern Ireland [DCAL]) and by research staff from the National University of Ireland, Galway (NUIG).

Catch records submitted by crews have revealed distinct seasonal migrations throughout the Shannon and Erne catchments. Migrations begin earlier in the middle and upper sections of these catchments and tend to reflect lunar phases, with more eels migrating during darker periods. Middle and upper catchment fishing sites contribute significantly to T&T, with 50% of catch reported in the upper Shannon (S2 – S5) and 54 % in the upper Erne (E3 – E7) on average. In the lower catchments, migrations tend to be more prolonged due to hydropower regulation and the impoundment of water obscuring the underlying lunar effect (Cullen and McCarthy, 2003). This combination of lower and upper catchment fishing sites was considered the most cost-effective way of ensuring that sufficient quantities of eels could be released in order to achieve the EU target. It also helped ensure that the majority of the eel migration period could be covered.

Representative samples of captured eels are taken annually in these catchments for scientific analyses. Size-frequency distributions are recorded and used to determine sex ratios of trapped silver eels. It was previously established that the vast majority of silver eels ≥ 440 mm in length in the Shannon and Erne were females based on macroscopic examinations of gonads (McCarthy et al., 2014). Size-frequency distributions revealed that most eels caught in the Rivers Erne (75%) and Shannon (92%) are female (Figure 2.2A). In both the Shannon and Erne catchments, population structure was shown to change with distance from the sea, with higher proportions of

female eels caught in the mid and upper catchments (Figure 2.2B). Large, female eels experience a higher turbine mortality rate. Given that fecundity of wild female eels increases with body length (MacNamara and McCarthy, 2012), these eels are considered to have a high reproductive value. Ensuring the escapement of these large eels is important for the conservation of the stock and further highlights the importance of multi-site T&T programmes. Eels sampled for length measurements are returned to storage and subsequently released with the other eels. Captured silver eels are also used for mark-recapture experiments. Eels are anaesthetised, tagged (with PIT or Floy tags) and released upstream of Killaloe (S1) and Roscor Bridge (E1) in order to determine fishing efficiencies.

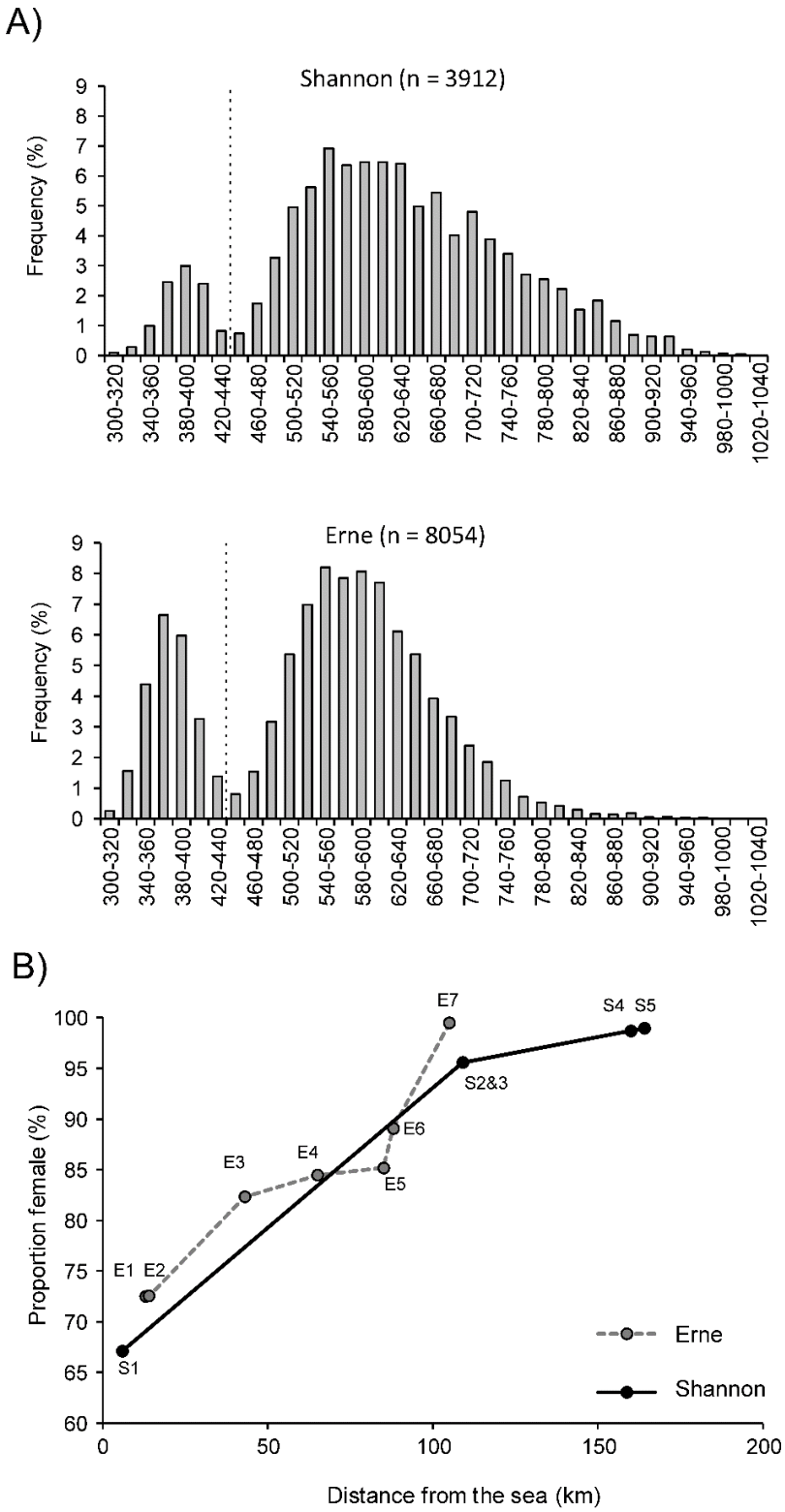

Figure 2.2. A) Size-frequency distributions for the Shannon and Erne. Dashed vertical line represents threshold between male (< 440 mm) and female eels (≥ 440 mm) B) The proportion of catch that is female at each site in the Shannon (Sites S1 – S5) and Erne (Sites E1 – E7) and how this changes with distance from the sea.

2.2.5. T&T quantities and catch targets

From 2009 to 2019, as part of Ireland's NEMP, T&T in Ireland involved the release of 630.7 t of silver eels. This included the capture and release of 226.3 t from the Shannon, 399.3 t from the Erne and 5.1 t from the Lee (Figure 2.3). It has been determined that this biomass corresponds to approximately 2.4 million eels (ICES, 2019).

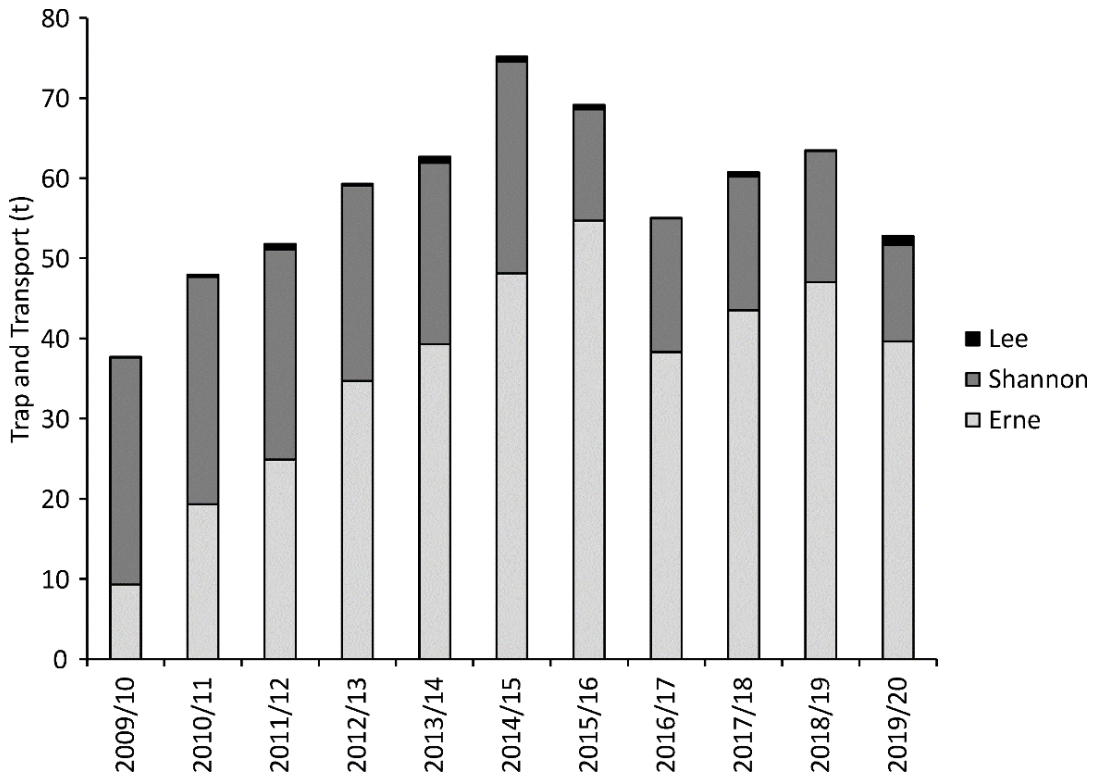

Figure 2.3. Quantities of silver eels transported downstream of hydropower dams in Ireland from 2009 to 2019. Data supplied by the Electricity Supply Board (ESB).

The SSCE set T&T catch targets that had to be achieved annually on the Shannon and Erne. These targets balanced practical considerations with maximising reductions to mortality and were set as a proportion of the silver eel 'run', or production, in each catchment. Detailed descriptions of the calculation of production are provided by MacNamara and McCarthy (2014) and McCarthy et al. (2014) for the Shannon and Erne respectively. Briefly, production is calculated in each catchment based on catch records from all T&T sites combined with an estimate of the biomass of eels not

captured. The uncaptured biomass is calculated at the lowermost fishing site in each catchment (Killaloe on the Shannon and Roscor Bridge on the Erne, chapter 1), based on mark-recapture experiments to determine fishing efficiency.

It was determined that on the Shannon, 30% of the silver eel 'run' should be transported annually. Production in the R. Shannon, which was stable between 2009 and 2014 (67.9 – 79.9 t; Table 2.1), declined dramatically in 2016 and has not recovered as of 2019 (32.6 – 38.0 t). Production could not be predicted in 2015 due to an extreme flooding event that meant the conservation fishery was closed for an extended period. The Shannon T&T programme exceeded the established target of 30% in all but one season (2013/14; Table 2.1), and on average, 39.3 % of silver eel production has been captured and released.

On the Erne, T&T targets were initially set as increasing biomasses (2009 = 22.5 t, 2010 = 33.75 t, 2011 = 39 t) to allow the gradual establishment of a conservation fishery. From 2012 onwards, a target of 50% of silver eel production was established to allow for inter-annual fluctuations in silver eel runs. Production could not be calculated in 2009 due to insufficient catch records but was estimated to be 41.2 t and 42.7 t in 2010 and 2011 respectively. From 2012 to 2019 production on the Erne increased and has remained relatively constant (62.9 – 83.3 t; Table 2.1). In the first three years (2009 – 2011), quantities transported failed to reach the biomass targets set. However, the 50% target has been exceeded in every year since, with on average 60.3% of the silver eel run captured and released (2012 – 2019).

Ireland's NEMP determined that poor juvenile recruitment in the recent past (2000 – present) will cause production in the Erne and Shannon to decline in the coming decade, making it difficult to comply with the EU target. Stock-assessments (e.g. Åström and Dekker, 2007) suggest that a recovery in recruitment can only be achieved by reducing total anthropogenic mortality to less than 15% of pre-NEMP levels. SSCE determined that achievement of T&T catch targets (i.e. 30% and 50% of Shannon and Erne production) would contribute to the EU escapement target while also reducing the mortality rate by an estimated 95 % on the Shannon and by 87.5 % in the Erne, compared to pre-NEMP levels (SSCE, 2012). Although catch targets have generally been achieved (Table 2.1), the actual reduction in mortality has never been determined for the Shannon and Erne.

Table 2.1. Summary of production, quantities released as part of T&T and compliance with targets set by SSCE.

Shannon					
	Production (t)	T&T Biomass (t)	% Production	Target	Target status
2009/10	74.3	23.7	31.9	30%	Achieved
2010/11	70.3	27.8	39.5	30%	Achieved
2011/12	67.0	25.7	38.4	30%	Achieved
2012/13	67.9	24.4	35.9	30%	Achieved
2013/14	79.9	22.6	28.3	30%	Not achieved
2014/15	70.7	26.4	37.3	30%	Achieved
2015/16	-	13.9	-	30%	-
2016/17	32.6	16.7	51.2	30%	Achieved
2017/18	34.1	16.7	49.0	30%	Achieved
2018/19	32.6	16.4	50.3	30%	Achieved
2019/20	38.0	12	31.6	30%	Achieved
Erne					
	Production (t)	T&T Biomass (t)	% Production	Target	Target status
2009/10	-	9.4	-	22.5 t	Not achieved
2010/11	41.2	19.3	46.8	33.8 t	Not achieved
2011/12	42.7	25.3	59.3	39 t	Not achieved
2012/13	67.7	34.7	51.3	50%	Achieved
2013/14	73.3	39.3	53.6	50%	Achieved
2014/15	72.5	48.1	66.3	50%	Achieved
2015/16	78.0	54.7	70.1	50%	Achieved
2016/17	62.9	38.3	60.9	50%	Achieved
2017/18	68.8	43.5	63.2	50%	Achieved
2018/19	83.0	47	56.6	50%	Achieved
2019/20	66.2	39.7	60.0	50%	Achieved

2.2.6. Silver eel escapement and EU target

Escapement, the biomass of eels that successfully circumnavigate all sources of anthropogenic mortality during downstream migrations, is a function of silver eel production and loss of silver eels through mortality. The ability to estimate escapement is vital to confirm compliance or otherwise with the EU escapement target. The 40% target is set relative to the best estimate of escapement if anthropogenic factors had never impacted the stock (termed pristine production). On the Shannon, it was not possible to directly estimate pristine production as construction of hydropower structures predates reliable catch records. Instead, pristine production was modelled based on habitat characteristics as well as estimates of productivity from other data

rich Irish catchments and was estimated to be 189.7 t (DCENR, 2008). Pristine production on the Erne has been estimated based on historic silver eel catches and fishing efficiency rates (SSCE, 2012). Yellow and silver eel catches from throughout the catchment and estimates of illegal and unreported catches were added and gave an estimate of 107.4 t. Therefore, the 40% escapement targets for the Shannon and Erne are 75.6 t and 43.0 t respectively.

Since the cessation of fisheries, hydropower mortality remains the main source of anthropogenic mortality to be accounted for when calculating escapement. Eels that are not captured as part of T&T (production minus T&T catch) must continue downstream towards hydropower structures. On the Shannon, a water regulating weir (chapter 1), diverts the main river flow to Ardnacrusha hydropower station (HPS). When the HPS reaches maximum capacity and water level continues to increase upstream of the regulating weir, excess water is released to the natural 'old river channel' (ORC) of the Shannon, providing eels with a second, safe migration route to the ocean. Eel route selection at the weir was previously established using acoustic telemetry (ICES, 2012). Although the analysis was limited, the results suggested that silver eel route selection was related to flow. Based on daily flow data and estimates of the biomass of uncaptured eels migrating downstream of Killaloe it is possible to determine the biomass of eels that migrate via the HPS and the ORC respectively (Table 2.2). At Ardnacrusha HPS, virtually all eels pass via the turbines and a fixed mortality rate 21.15 % was previously established (SSCE, 2012). Surviving eels pass to the tailrace, which connects with the natural river. Escapement is therefore calculated as the biomass of eels released as part of T&T, eels migrating via the ORC and eels surviving turbine passage. From total production of 567.4 t (2009 – 2019; excluding 2015), a total of 212.4 t were removed as part of T&T. Therefore, 355.0 t remained uncaptured. Of this biomass, it was estimated that 62.4 t migrated safely via the ORC. The remaining 292.6 t migrated via Ardnacrusha, of which 21.15% (61.9 t) suffered mortality. Therefore, 505.5 t successfully escaped. Since 2009, annual escapement from the Shannon has ranged from 29.5 t to 70.7 t (15.6 – 37.3% of pristine production) and as such, has never reached 40% escapement target (Table 2.2). Mean escapement (50.5 t) has represented just 26.7% of pristine production (189 t; DCENR, 2008).

All eels not captured as part of T&T on the Erne must pass via two hydropower stations located in the lower catchment (chapter 1), Cliff HPS and Cathaleen's Fall HPS. No bypass route exists on the Erne and all eels must pass these HPSs, either through turbines or spillways. Previous telemetry analyses revealed that mortality rates varied based on flow management for power generation (ICES, 2012). A daily mortality rate is applied depending on whether all flow is directed to turbines or whether excess water is released via spillgates (see chapter 1). Annual mortality rates are calculated at Cathaleen's Fall as the proportion of eels surviving passage through Cliff HPS which subsequently suffer mortality. Annual mortality rates for each dam can be seen in Table 2.2. Escapement is calculated as the biomass transported in combination with the biomass of eels surviving passage through both Cliff HPS and Cathaleen's HPS. From total production of 656.3 t (2010 – 2019), 389.9 t were released as part of T&T. Of the 266.4 t that remained uncaptured and migrated downstream, 45.6 t suffered mortality at Cliff HPS and a further 40.1 t were killed at Cathaleen's Fall HPS. Therefore, total escapement was 570.6 t. Escapement from the Erne has ranged from 38.1 t to 71.6 t (35.5 – 66.9 % of pristine production) and has exceeded the EU's 40% escapement target in every year since 2012 (Table 2.2). Mean annual escapement (57.1 t) has represented 53.3 % of pristine production (107 t; DCENR, 2008).

Table 2.2. Summary of the biomass of eels not captured (production minus T&T biomass, details in Table 2.1), route selection and mortality rates. Escapement estimates are presented and compliance, or lack thereof, with the EU target is indicated. The EU target is 40 % of pristine production (i.e. 75.6 t for the Shannon and 43.0 t for the Erne)

Shannon	Uncaptured biomass(t)	% ORC*	Biomass ORC (t)	Biomass HPS (t)	Mortality (t) **	Escapement (t)	% of pristine production	Target status
2009/10	50.6	55	27.8	22.8	4.8	69.5	36.6	Not Achieved
2010/11	42.5	0.0	0.0	42.5	9	61.3	32.3	Not Achieved
2011/12	41.3	9.0	3.7	37.6	7.9	59.1	31.2	Not Achieved
2012/13	43.5	1.6	0.7	42.8	9.1	58.8	31.0	Not Achieved
2013/14	57.3	24.3	13.9	43.4	9.2	70.7	37.3	Not Achieved
2014/15	44.3	15.6	6.9	37.4	7.9	62.8	33.1	Not Achieved
2015/16	-	-	-	-	-	-	-	-
2016/17	15.9	8.5	1.4	14.5	3.1	29.5	15.6	Not Achieved
2017/18	17.4	19.9	3.5	13.9	2.9	31.2	16.4	Not Achieved
2018/19	16.2	13.2	2.1	14.1	3.0	29.6	15.6	Not Achieved
2019/20	26.0	9.4	2.4	23.6	5.0	33.0	17.4	Not Achieved
Erne	Uncaptured biomass (t)	Cliff mortality %	Mortality biomass (t)	Cathaleen's Fall mortality (%)	Mortality biomass (t)	Escapement (t)	% of pristine production	
2009/10	-	-	-	-	-	-	-	-
2010/11	21.9	6.9	1.5	7.7	1.6	38.1	35.6	Not achieved
2011/12	17.4	8.5	1.5	6.1	1.0	40.2	37.6	Not achieved
2012/13	33.0	25.0	8.3	8.0	2.0	57.4	53.6	Achieved
2013/14	34.0	8.9	3.0	18.9	5.9	64.4	60.2	Achieved
2014/15	24.4	12.0	2.9	13.8	3.0	66.6	62.2	Achieved
2015/16	23.3	8.9	2.1	20.1	4.3	71.6	66.9	Achieved
2016/17	24.6	26.7	6.6	27.3	4.9	51.4	48.0	Achieved
2017/18	25.3	23.1	5.8	22.7	4.4	58.6	54.8	Achieved
2018/19	36.0	19.6	7.1	26.8	7.8	68.1	63.6	Achieved
2019/20	26.5	25.5	6.8	26.3	5.2	54.2	50.7	Achieved

* average % of eels which migrated via the ORC based on telemetry model and daily hydrometric data.

**Mortality rate of 21.15% is applied to the biomass using the HPS.

2.3. Methods – Evaluating T&T programmes

2.3.1. Post evaluation of T&T biomasses

Given the large quantities of eels released by T&T programmes and the high proportion of total escapement they accounted for in the Shannon and Erne, it is tempting to presume that T&T is a highly efficient mitigation measure. However, acoustic telemetry assessments of hydropower mortality suggest that the majority of eels survive passage through Ardnacrusha on the Shannon, and Cliff and Cathaleen's Fall on the Erne (Table 2.2). It is important to quantitatively assess the proportion of migrating eels saved from mortality by these programmes to fully assess their conservation value. To do this, the biomass of silver eels present in the Shannon and Erne catchments each year (production; Table 2.1) was considered as if none had been caught and released downstream. Route selection and mortality rates calculated each season (Table 2.2) were applied to annual production in each catchment. Based on these calculations it was possible to determine what mortality and escapement would have been without T&T programmes. Escapement without T&T intervention was also considered in relation to the EU target of 40% to determine the importance of T&T for achieving management targets.

2.3.2. Assessment of anthropogenic mortality rates

Between 2003 and 2008, juvenile recruitment to the Shannon and Erne had declined to 4 % and 23 % of historic (1979 – 1984) levels respectively. It was recognised that, regardless of which management actions were taken, achieving the EU's 40% target in the long term would require a recovery of recruitment. A Stock-assessment relating recruitment recovery to anthropogenic mortality across all life stages (Åström and Dekker, 2007) found that mortality rates needed to be reduced below 15 % of pre-NEMP levels to allow recruitment to recover. SSCE estimated that if T&T capture targets (30% of Shannon and 50% of Erne production) were achieved, anthropogenic mortality in the Shannon would be reduced by 95 % and by 87.5 % in the Erne, compared to pre-NEMP levels (SSCE, 2012). However, whether this has been the case has never been determined.

Due to the closure of fisheries for all life-stages, the annual anthropogenic mortality rate (*A*) can be simplified to a function of annual silver eel production (Table 2.1) and

hydropower mortality, and is expressed as the negative of the logarithm of the percent surviving (Dekker et al., 2011):

$$A = -ln\ (((production) - Hydro_{mort})/(production)) \qquad \text{(Eq. 2.1)}$$

The biomass calculated to have suffered mortality during hydropower passage as well as production (Table 2.1) were inserted into Equation 2.1 to determine the anthropogenic mortality rate with and without T&T. Results were compared with pre-NEMP mortality rates to determine the importance of T&T in reducing mortality rates below 15% of pre-NEMP levels. On the Shannon, *A* was 1.95 in 2008, prior to Ireland's NEMP, while on the Erne is was 0.95 (ICES, 2018b). Therefore, mortality rate would have to be below 0.29 for the Shannon and 0.14 for the Erne to ensure that mortality is adequately reduced to enable recruitment to recover.

2.3.3. T&T as a data source

Quantitative estimates of annual silver eel production and escapement are required in order to confirm compliance with the EU target and T&T capture targets set by SSCE. Catch recorded at each site are added to an estimate of the biomass of eels not captured by T&T. Killaloe (S1, Shannon) and Roscor Bridge (E1, Erne) provide the ideal location from which to assess the biomass of eels that remains uncaptured in these catchments. Both sites provide discrete river sections where it is practical to conduct mark-recapture experiments to determine the efficiency of fishing. Additionally, 99% of these catchments are located above these sites meaning there is no significant production downstream. The use of catch data, whether from commercial or experimental fisheries, requires that the entire migration period is covered (Robinet et al., 2007). Therefore, it is vital that continuous catch records are available at these lower catchment sites each season. However, in regulated rivers fluctuations in discharge can disrupt fishing leading to periods of inactivity.

Weekly catch data sheets submitted by fishing crews at Killaloe and Roscor Bridge were inspected for discontinuities. The proportion of each season fished was calculated as the number of nights crews fished between the official start and end dates for the season. Crew reports also include notes on environmental conditions and the reasons provided on nights when fishing did not occur were noted. Catch records from

2009 – 2019 were assessed for Killaloe. On the Erne, the fishery developed gradually, and fishing seasons were truncated in 2009 and 2010. Therefore, catch records were assessed from 2011 – 2019 only.

2.4. Results

2.4.1. Post evaluation of T&T biomasses

Production in the Shannon catchment each year (567.4 t combined; 2009 – 2019, excluding 2015) was considered to have migrated downstream towards hydropower structures. Based on seasonal route selection rates (% ORC, Table 2.2) it was estimated that 471.5 t would have migrated via Ardnacrusha HPS, of which 21.15% would have suffered mortality (99.7 t), compared to a mortality of 61.9 t with T&T in place. Therefore, the capture and release of 212.4 t of eels as part of T&T saved 37.8 t of eels from mortality (17.8% of eels transported). The same protocol was applied to production in the Erne (656.3 t; 2010 - 2019). Of this biomass, it was estimated that 212.0 t of eels would have suffered mortality (111.4 t at Cliff HPS and 100.6 t at Cathaleen's Fall HPS). With T&T in place, mortality was recorded to have been 85.7 t (45.6 t at Cliff HPS and 40.1 t at Cathaleen's Fall HPS), meaning T&T of 389.9 t saved 126.3 t from mortality (32.4% of eels transported). The biomass suffering mortality annually with and without T&T are presented in Table 2.3.

Table 2.3. Estimates of the biomass of silver eel saved by T&T, calculated as the difference in mortality with and without T&T programmes in place on the Shannon and Erne.

	Shannon Mortality			Erne Mortality		
	With T&T	Without T&T	Biomass saved	With T&T	Without T&T	Biomass saved
2009/10	4.8	7.1	2.3	-	-	-
2010/11	9.0	14.9	5.9	3.1	5.8	2.7
2011/12	7.9	12.9	4.9	2.5	6.0	3.5
2012/13	9.1	14.1	5.0	10.3	21.0	10.7
2013/14	9.2	12.8	3.6	8.9	19.1	10.2
2014/15	7.9	12.6	4.7	5.9	17.5	11.6
2015/16	-	-	-	6.4	21.2	14.8
2016/17	3.1	6.3	3.2	11.5	29.4	17.9
2017/18	2.9	5.8	2.9	10.2	27.9	17.7
2018/19	3.0	6.0	3.0	14.9	34.2	19.3
2019/20	5.0	7.3	2.3	12.0	29.9	17.9

The biomass of eels saved each year (Table 2.3) was subtracted from escapement values (Table 2.2) to calculate escapement without T&T. On the Shannon, escapement would have dropped from 505.5 t to 467.7 t. Although the EU target was never reached on the Shannon (Table 2.2) T&T does reduce the amount by which the target is missed (Figure 2.4A). Overall mean escapement would have dropped to 24.7% of pristine production (compared to 26.7% with T&T). Escapement in the Erne would have decreased from 570.6 t to 444.3 t without T&T. The annual biomass saved from mortality (Table 2.3) on the Erne was found to have an important role in ensuring the EU target was reached (Figure 2.4B). From 2012, with T&T intervention, the EU target was exceeded every year. However, when the biomass saved by T&T annually was subtracted from escapement, three years would not have achieved the goal. Additionally, mean escapement would have dropped to 41.5% of pristine production compared to 53.3% with T&T intervention.

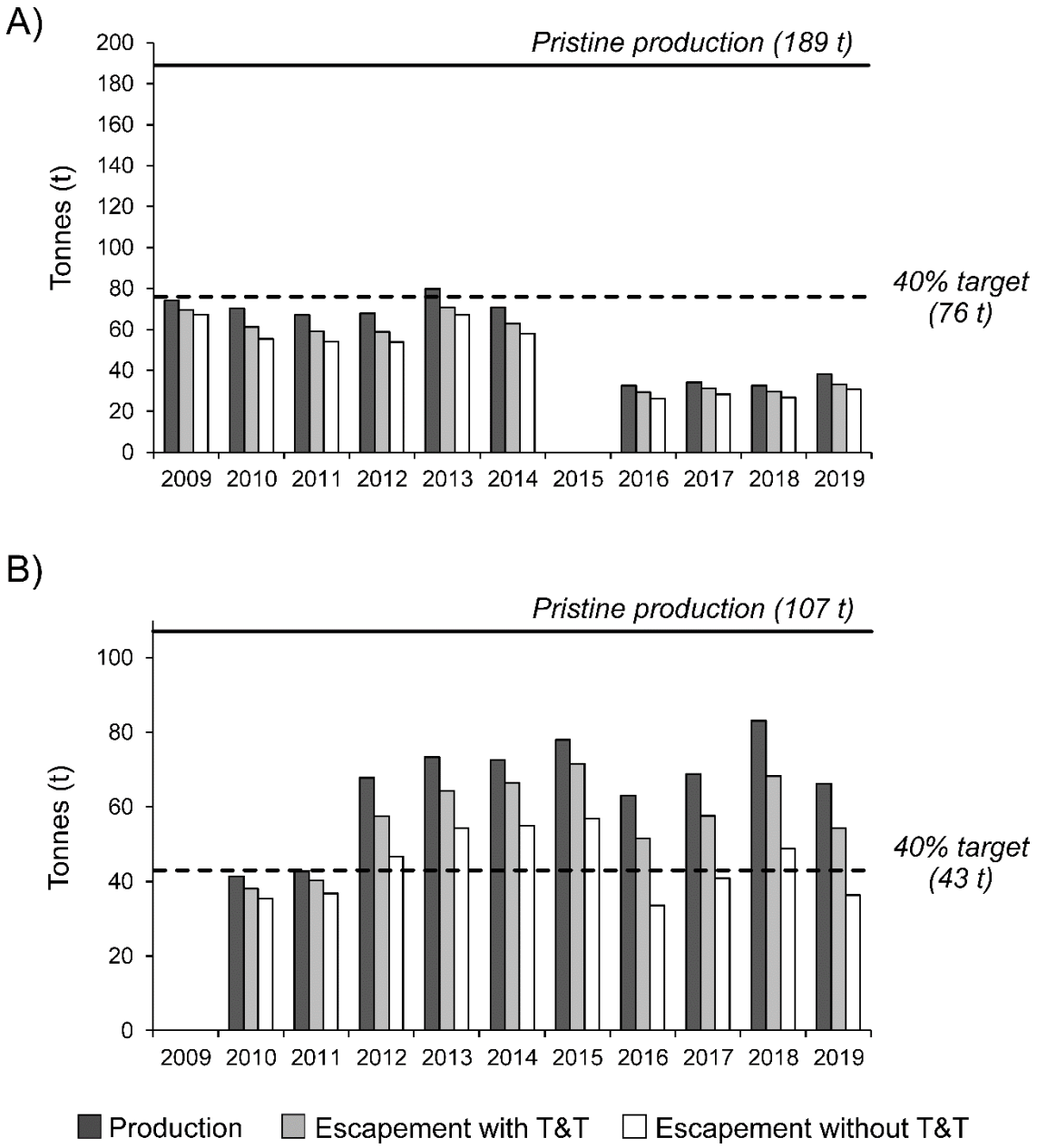

Figure 2.4. Production and escapement values with and without T&T intervention in relation to the EU target of escapement equivalent to 40% of historic levels for A) the Shannon and B) the Erne. Production represents the biomass of silver eels that currently exists within a catchment can potentially escape. Escapement represents the biomass that successfully circumvent anthropogenic obstacles and reach the ocean.

2.4.2. Assessment of anthropogenic mortality rates

Estimation of the annual mortality rates (Eq. 2.1) revealed that on the Shannon, rates (*A*) would have remained below 15% with (*A* = 0.11 or 5.8% of pre-NEMP levels; Figure 2.5A) or without T&T (*A* = 0.20; 9.2%). On the Erne, with T&T, five years were below the 15 % threshold, while five years were not. On average, mean mortality rate was 0.13 (14.3% of pre-NEMP levels). Without T&T, mortality rates would have been above the threshold in every year (mean = 0.39, or 40.5% of pre-NEMP levels; Figure 2.5B).

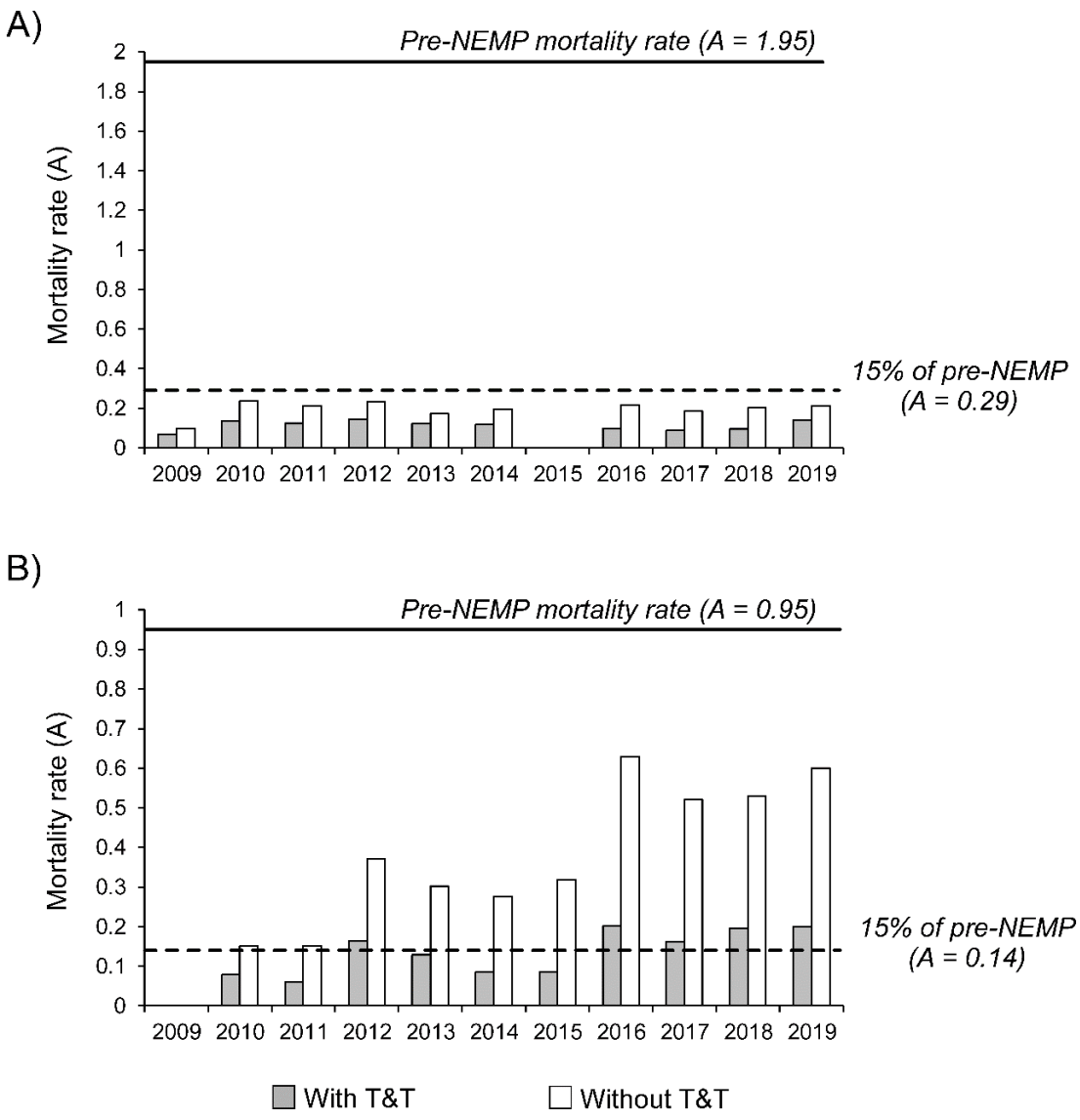

Figure 2.5. Estimated anthropogenic mortality rates (*A*, Eq. 2.1) for A) the Shannon and B) the Erne, with and without T&T intervention compared to pre-NEMP mortality rates and the 15% target.

2.4.3. T&T as a data source

It was found that there were considerable gaps in catch records (Table 2.4), with only 63.4% and 65.2% of possible nights fished at Killaloe (Shannon) and Roscor Bridge (Erne) respectively. At Killaloe, the most common reason for fishing ceasing was low flow conditions. When this occurred, fishing was deemed too inefficient and nets were not set until conditions improved. In one year (2015), fishing ceased due to exceptional flooding and associated safety considerations. At Roscor Bridge, the reasons for fishing not occurring included low flow conditions and reduced catches due to the lunar phase (i.e. full moon). The reason was also unspecified on several occasions. Fishing was not generally carried out early in the season at Roscor Bridge and tended to initiate in October. A fishing site located immediately upstream (< 1 km; site E2, chapter 1), does fish from the start of the season (generally early September) and caught considerable amounts of eels in the time between official start dates and the time when Roscor Bridge began (mean = 2,284 kg, range = 520 – 6,957 kg). This shows that significant eels runs were occurring in this time, meaning valuable data were potentially missed for the calculation of production.

Table 2.4. Summary of catch levels, fishing season length, number of nights fished, and proportion of total season fished at Killaloe on the Shannon and Roscor Bridge on the Erne. The biomass caught at site E2 on the Erne before Roscor Bridge (E1) began fishing is also indicated.

Killaloe					
Season	Catch (kg)	Season length (days)	Nights fished	%	
2009/10	11,951	84	53	63.1	
2010/11	12,311	152	74	48.7	
2011/12	9,704	82	49	59.8	
2012/13	12,657	114	97	85.1	
2013/14	12,738	128	85	66.4	
2014/15	12,808	99	78	78.8	
2015/16	8,549	95	49	51.6	
2016/17	6,398	153	89	58.2	
2017/18	10,873	166	115	69.3	
2018/19	7,362	132	89	67.4	
2019/20	6,667	143	71	49.7	
Roscor Bridge					
Season	Catch (kg)	Season length (days)	Nights fished	%	Catch upstream (Site E2; kg)
2011/12	4,303	168	121	72.7	520
2012/13	8,505	166	120	72.3	1,021
2013/14	7,138	192	136	70.8	1,455
2014/15	7,754	159	90	56.6	2,624
2015/16	5,805	133	67	50.4	1,667
2016/17	5,050	142	87	61.3	1,926
2017/18	3,487	94	49	52.1	6,957
2018/19	5,049	130	82	63.1	2,104
2019/20	4,613	84	74	88.1	1,625

2.5. Discussion

Ireland has been to the forefront in responding to the EU regulation for restoration of the European eel stock, through extensive eel surveys, eel focused research (e.g. McCarthy et al., 2008; Poole et al., 2018), full closure of eel fisheries and large-scale mitigation of hydropower. The biomass of silver eels transported under the Irish T&T programme is larger than all other countries in which it has been adopted (ICES, 2018a). Trap and transport represents a practical conservation strategy that can facilitate the escapement of large quantities of eels. However, the large quantities released belie the true biomasses saved by T&T intervention, particularly on the Shannon. This is an important consideration when determining the efficiency of T&T as a mitigation measure. For example, on the Shannon, only 17.8% of eels transported were saved from mortality, compared to 32.4% on the Erne. Trap and transport was found to be important on the Erne for reducing mortality rates and achieving EU targets, highlighting the site specific nature of these programmes.

The success of T&T to date has been measured against the EU escapement target and transport targets set by SSCE. On the Erne, where production has remained high (Table 2.1), the capture and release of at least 50% of production was sufficient to achieve the EU target in each year since 2012. An assessment of escapement without T&T intervention revealed that the EU target would not have been reached in three years, and mean escapement would have declined from 53.3% to 41.5% of pristine production. On the Shannon where production has decline dramatically, even if every eel available (i.e. 100% of production) escaped from the catchment, it would not be sufficient to reach the 40% target (except in 2013; Figure 2.4A). Without T&T, mean escapement would have dropped from 26.7% to 24.7%.

Although the situation on the Erne has appeared promising to date, a slower rate of decline in recruitment has allowed production to remain relatively high until now. As current cohorts of eels leave, low recruitment in the recent past (2000 – present) is expected to lead to a reduced stock of silver eel. Therefore, it appears unlikely that the 40% escapement target can be sustained into the near future. Similarly, declines in production for the Shannon were predicted by MacNamara and McCarthy (2014) and are the result of poor recruitment to the catchment. Between 1968 and 1986 an estimated 280 million elvers were stocked throughout the Shannon catchment

(Quigley and O'Brien, 1996). However, between 1987 and 2008, stocking involved only 40 million elvers. For both the Shannon and Erne to produce enough silver eels to reach the EU target in the future will require a significant improvement in natural recruitment. Recruitment in recent years to these catchments (2009 – 2017) has remained low, although improvement were observed in certain years (ICES, 2018b). Currently, recruitment remains the limiting factor to Ireland's ability to achieve the EU target in the long-term.

Like the Shannon, current silver eel escapement in many European catchments is substantially lower than the 40% target. As such, there is little chance of mitigation measures achieving this target and recovery is therefore a long-term goal by necessity. Åström and Dekker (2007) noted that anthropogenic morality rates needed to be reduced below 15% of pre-NEMP levels to allow juvenile recruitment to recover. This level of anthropogenic mortality should enable recruitment to recover within 90 years. This recovery in recruitment should subsequently enable the achievement of the EU silver eel escapement target (40%) within a similar, or shorter, timeframe. The SSCE set T&T capture targets for each catchment (as a percentage of production). If these targets were achieved it was determined that mortality should be reduced to approximately 5% of pre-NEMP levels on the Shannon and 12.5.% on the Erne. On the Erne, T&T dramatically reduced anthropogenic mortality rates (Figure 2.5B) and ensured that anthropogenic mortality, on average was 14.3% of pre-NEMP levels. Without T&T, this value would have been considerably higher (40.5%). On the Shannon, the anthropogenic mortality rate would have remained below 15% regardless of whether T&T was implemented or not. This suggests that pre-NEMP eel mortality in the Shannon was dominated by fisheries. Indeed, in 2008, 68 t of yellow and silver eels were captured in the Shannon's commercial fishery, while only 6 t suffered hydropower mortality (ICES, 2018b). Therefore, in both catchments, mortality rates are sufficiently low to contribute to the recovery of recruitment in the shortest time-frame possible in accordance with the stock assessment of Åström and Dekker (2007; < 100 years). This recovery depends on equal effort across the EU. However, ICES (2018a) reported that only six countries (out of 16 reporting) are currently achieving the EU escapement target.

There are clear differences between the Shannon and Erne T&T programmes, and this suggests that the efficiency of T&T programmes depends on several system specific

factors. For downstream migrating eels, the greatest problems lie in the successive construction of hydropower stations along their migratory axes. Successive dams result in high cumulative mortality rates, as seen on the Erne. By contrast, eels had to pass a single HPS on the lower Shannon, of which 78.85% of eels were expected to survive. Therefore, the effectiveness of T&T is directly linked to the number of hydropower stations bypassed. Additionally, the presence of an alternative migration route, which bypasses hydropower stations, can facilitate the escapement of large quantities of eels. On the lower Shannon, it was shown that 15.7% of silver eels escaped via the ORC (Table 2.2). By contrast no alternative migration routes existed on the Erne, exacerbating the issues associated with passage through multiple dams. Trap and transport programmes initiated in the future should consider the number of barriers eels would have to migrate through as a simple means of assessing the potential cost-effectiveness of the intervention.

In order to analyse mortality without T&T intervention it was necessary to assume that the biomass of eels estimated to have survived dam passage did not suffer any injuries. In reality eels, due to their elongate morphology, suffer a variety of injuries during passage through dams or pumping stations, including abrasion, bruising, lacerations, haemorrhage, crushing of body parts and damage to the jaws, eyes and skin (Bolland et al., 2019). Additionally, McCarthy et al. (2008) noted damage to internal organs and the spinal column following passage through Ardnacrusha HPS, even though eels did not display external wounds. Ceasing T&T would result in an increase in injuries which may or may not impact survival and spawning. In fact, Winter et al. (2006) estimated that more eels suffered from delayed mortality due to injuries than direct mortality during turbine passage. In addition to injury, turbine passage is associated with disorientation in fish and can result in increased predation, frequently by the great cormorant (*Phalacrocorax carbo*). Large winter roosts of several hundred great cormorants exist near Ardnacrusha HPS (McCarthy et al., 2008) and a previous analysis suggested that silver eels make up a large portion (41%) of their diet in winter months (Doherty and McCarthy, 1997). Increasing the number of injured and disorientated eels would result in a significant increase in predation risk. Therefore, if T&T on the Shannon ceases in the future, it is vital that alternative measures are initiated to reduce the biomass of eels passing turbines.

Although fishermen benefit from income and conservation agencies appreciate the data gathering value of the programme, it appears the adoption of alternative silver eel conservation measures should be considered for the Shannon. However, given the risks associated with turbine passage, it should be ensured that any alternative is at least as effective as T&T. The fact that 15.7% of eels, on average, migrated via the ORC highlights the potential of this channel as an alternative migration route. Physical or behavioural barriers could be used to guide eels towards the ORC. Physical barriers, such as bar racks and screens (Calles et al., 2013a; Økland et al., 2019) are often used to prevent fish entering intakes and guide them towards alternative routes. Behavioural guidance systems that exploit the sensory ecology of eels using visual, auditory or tactile stimuli are increasingly receiving interest as a mitigation measure (e.g. Kruitwagen, 2014; Piper et al., 2019; chapter 3). Sheridan et al. (2014) concluded that submerged low voltage LED strobe light arrays represent one of the most promising guidance technologies. Previous studies in the lower Shannon revealed that lights deployed above the water could greatly influence the catch pattern of eels (Cullen and McCarthy 2000). Further investigations using more advanced light arrays, such as strobe lighting, should be considered and could reduce or eliminate the need for extensive T&T by diverting eels towards alternative migration routes. Alternatively, lights could be used to direct eels towards nets, increasing the biomass of eels caught and transported. This would increase the benefit of T&T as a mitigation measure against hydropower mortality.

Estimating the biomass of downstream migration silver eels has traditionally relied on commercial fisheries data. As the closure of commercial fisheries was specified by Ireland's NEMP, T&T represents the only viable data source for these calculations. However, analyses of daily catch records from Killaloe and Roscor Bridge revealed that fishing was discontinuous, with 36.6% and 34.8% of designated fishing days not fished on average. Where fishing records do not cover the entire migration period, biases can be introduced in production calculations. Fishing stopped for a variety of reasons. At Killaloe, low flow conditions was the main cause, though extreme flooding also occurred in 2015. At Roscor Bridge, the crew cited low flow conditions and lunar effects as reasons for ceasing fishing. Despite this, fishing at site E2 early in the season showed that significant quantities of eels were migrating. As low flow and brighter lunar phases are associated with reduced catches at Roscor Bridge, it is possible that

very little would have been caught and this would have an insignificant impact on the calculation of production and escapement. However, new monitoring protocols capable of completing catch datasets are required to ensure this is the case and to facilitate the robust calculation of production and escapement in the future (e.g. chapters 4, 5 and 6).

Chapter 3: Evaluation of a strobing light system for deflecting downstream migrating silver-phase eels (*Anguilla anguilla*)

3.1. Introduction

The construction of anthropogenic structures for hydropower generation, flood control and navigation has resulted in a dramatic loss of river connectivity globally (Nilsson et al., 2005). Lack of fluvial connectivity hinders, and sometimes prevents entirely, the movement of fish between habitats. European eels (*Anguilla anguilla*, L.) are facultatively catadromous fish and obligate migrants, undergoing upstream riverine migrations as recruiting juveniles and downstream migrations as pre-spawning adults (silver eels). During their downstream spawning migrations silver eels are subjected to considerable interference from anthropogenic structures, including delays (Besson et al., 2016), injuries (Bolland et al., 2019), and mortality (Winter et al., 2007; Calles et al., 2010). As a result of their distinctive elongate morphology, eels are particularly vulnerable to impingement against intake screens, but also to blade strikes, cavitation and shear stress during hydropower passage (Bruijs and Durif, 2009). The biomass of silver eels escaping European rivers has dramatically declined since the 1980's (Bevacqua et al., 2015). As a result, the European Union implemented a stock recovery plan that requires Member States to enable spawner escapement of at least 40% of historic levels. In order to help achieve this target, Ireland established programmes capturing silver eels in hydropower regulated rivers and translocating them to river sections with good seaward connectivity. These 'trap and transport' (chapter 2) programmes were adopted as an interim solution while long-term solutions were researched. It was anticipated that longer-term management of eel escapement would include either physical or behavioural barriers (e.g. Cullen and McCarthy, 2000) to turbine entry.

Downstream migrating eels tend to 'go with the flow' (Jansen et al., 2007; chapter 5) and in most hydropower regulated rivers this results in eels being carried to turbine intakes. Although there are ongoing efforts to design 'fish friendly' turbines (e.g. Hogan et al., 2014), the general consensus remains that the entrance of fish to turbines should be minimised where possible (Fjeldstad et al., 2018). Physical barriers, such

as bar racks, screens and small spaced louver arrays (Gale et al., 2008; Calles et al., 2013a; Økland et al., 2019) are often used to prevent fish entering intakes. However, these screens can be costly to install and maintain, can results in reduced hydropower generation potential and can increase the risk of injury and mortality for fish species with poor swimming abilities. As a result, non-physical, behavioural barriers are receiving more attention. Behavioural barriers aim to exploit the sensory ecology of fish in order to divert them away from dangerous areas or attract them towards a safe route. Behavioural systems typically use visual, auditory and tactile stimuli to influence fish behaviour. Studies focusing on eels frequently involve the use of light and sound. Although several studies have shown sound to have a limited ability to guide eels (MacNamara, 2012; Piper et al., 2019), the use of light as a stimulus to guide eels has shown more promise.

Like other life stages, silver eels are negatively phototactic, with downstream spawning migrations typically occurring at night and during darker moon phases (Tesch, 2003; Bruijs and Durif, 2009). Prior to and during downstream migrations silver eels undergo a 'sensory reorientation' (Pankhurst, 1982) with eye size increasing and the ratio and spectral positioning of photoreceptors changing. These changes prepare silver eel eyes for efficient photon capture in the dark water of the deep ocean. Therefore, even before silver eels leave rivers, they have an increased sensitivity to light. The aversion of silver eels to light has been manipulated by humans for decades to increase fisheries yields by using basic over- and underwater lights to guide eels towards nets (e.g. Petersen, 1906; Lowe, 1952). With the decline of the eel stock in recent decades, the use of artificial light has undergone renewed interest in a conservation context (e.g. Hadderingh et al., 1992). These early attempts used constant illumination (fluorescent, incandescent, and mercury vapour bulbs) and highlighted the potential of artificial light to guide eels. Despite their success, these methods were inflexible, and this prevented their widespread adoption (Brown, 2000). Advances in technology, particularly the development of light-emitting diodes (LEDs), have led to new opportunities including experimentation with strobe lighting (Elvidge et al., 2018; Ford et al., 2018). Strobe lighting is considered to be more promising for eel guidance than constant illumination (Sheridan et al., 2014), possibly because the absolute sensitivity of fish eyes results in a greater avoidance to bright, strobing lights (Patrick et al., 1985). Given the urgent need to protect downstream migrating eels, there has

been a lack of experiments examining the effect of strobe lighting on silver eel behaviour.

In this chapter, a behavioural barrier was evaluated on the lower River Shannon. The response of downstream migrating silver eels to an underwater strobing light barrier was analysed by reference to the distribution of silver eel catches at an eel fishing weir when lights were powered on and off.

3.2. Methods

3.2.1. Killaloe eel fishing weir

Located in the lower River Shannon (chapter 1), Killaloe eel weir consists of a metal walkway which is attached to the downstream side of a road bridge and is secured to the riverbed using a series of steel girders. This walkway, which is entered from the western bank of the river extends across 90% of the river width (Figure 3.1). The bridge has 13 arches which vary in size, including five smaller arches (7 m wide) and eight larger arches (12.5 m) with one of these larger arches modified into a navigation channel. Six of the larger arches contain three nets each, while one of the smaller arches also contains a single net. Arches without nets are open and eels may pass via these routes undetected. All nets (stow nets) are identical and are composed of a rectangular steel frame (2.4 wide x 2.7 m high) with an opening of 6.75 m^2, from which an 8 m long net is attached. Mesh size (bar measure) was 11 mm in the cod-end, increasing progressively to 50 mm at the net opening. The net frames are mounted on the steel support girders and are lifted hydraulically. In all fished arches, except the navigation channel, steel rods (3 cm diameter, 2 cm spacing) extend from the riverbed to the water surface and are positioned diagonally from the road bridge to the steel frames to prevent eels from escaping to the side of the nets. Previous analyses of catch records suggested that one arch (arch 8) consistently yielded the highest proportion of the catch (MacNamara, 2012; 28.2%). The river bathymetry is uniform across the weir and is approximately 3 m deep.

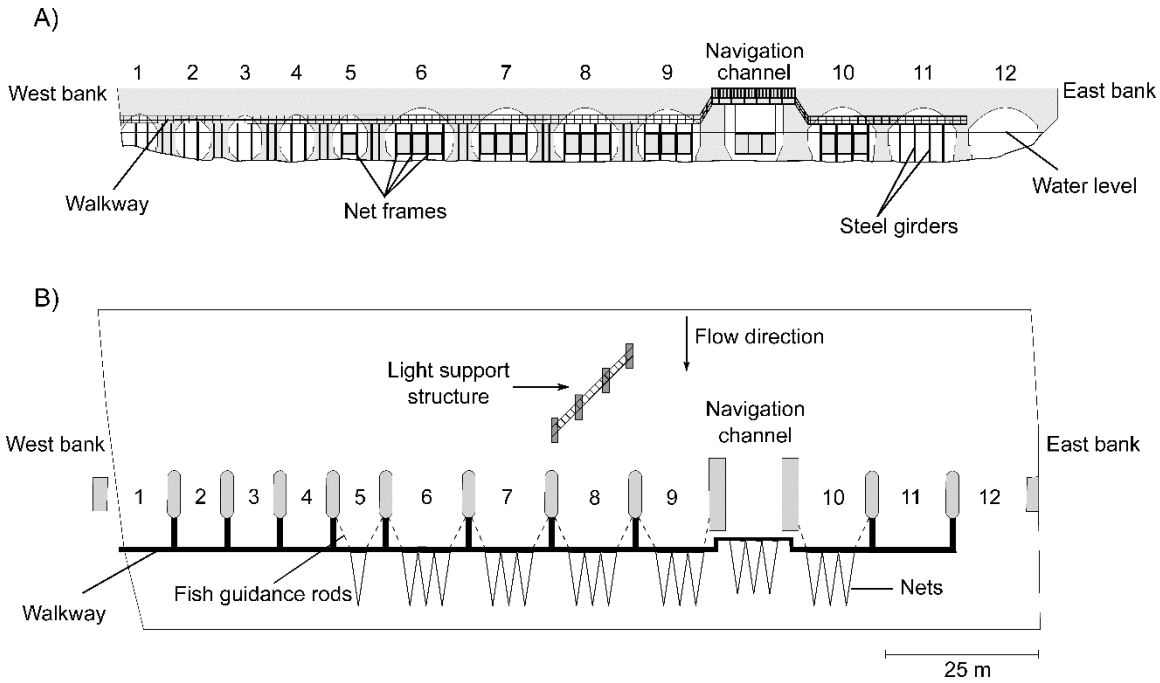

Figure 3.1. A) Killaloe eel weir as observed from downstream. Arch numbers are indicated, as well as the walkway and the supporting steel girders which hold frames and nets. B) Plan view of the weir showing the positions of nets and the light support structure from which lights were deployed upstream of arch 8.

3.2.2. Light system

In this study the High Intensity Light System (HIL, Fish Guidance Systems Ltd.) was assessed. This is a patented system which uses light emitting diodes (LEDs) that are capable of rapid flashing (strobing). The system is composed of individual light units, each approximately 100 cm long and containing 24 LEDs. In this study, 17 such light units were deployed from a custom made floating support structure which was anchored into position above arch 8 (Figure 3.1). Light units were hung from this structure using vertical bars that were either 1 or 2 m in length. Vertical bars of alternating length were spaced at regular intervals (1.08 m) (Figure 3.2). To prevent the lights from pivoting on the support bar, lengths of chain were hung from the bottom of each light unit. In total, the structure was 17.3 m long and was angled at 45° relative to the flow. Therefore, the structure was 12.24 m wide with a 0.76 m gap between lights as viewed from upstream, as migrating eels would perceive the structure. It was

anticipated that eels migrating downstream would sense the lights, and swim in the direction the light array was angled (towards arches 5, 6 and 7).

The strobe rate of the HIL system is proprietary but the LEDs emit a broad spectrum white light between 425 and 725 nm (EPRI, 2017), which coincides with the spectral sensitivities of many fish species. Pankhurst and Lythgoe (1983) showed that migrating silver eels have the highest retinal sensitivity to blue and green light (480nm and 520 nm respectively). Therefore, although light colour cannot be varied using the HIL system, the full-spectrum white light used was deemed appropriate as it encompassed the optimal range of values for silver eels.

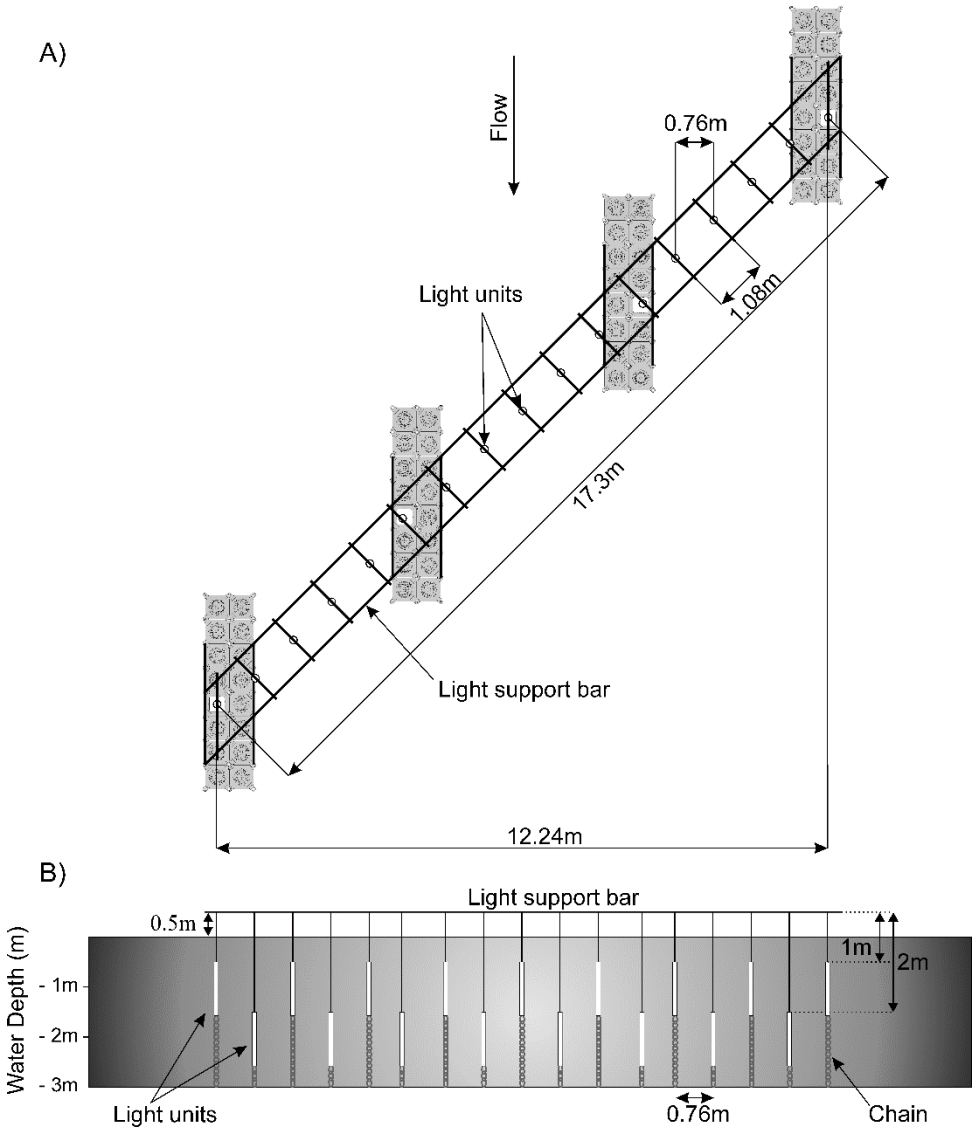

Figure 3.2. A plan view of the floating light support structure. B) the arrangement of the light array underwater.

3.2.3. Experimental trials

The total catch recorded in each arch (i.e. three nets combined for larger aches) across the weir was recorded on several nights with the lights off (control nights) and lights on (treatment nights) during the 2018/19 eel fishing season. Nets were set at dusk (18:00 hours) each night and lifted at dawn (06:00), to coincide with the nocturnal migrations of eels. During treatment periods, the lights were operated for the same duration that nets were set. The catch in each arch was converted to a proportion of total nightly catch to allow comparisons between periods of relatively low or high catches.

3.2.4. Estimation of light barrier efficiency

The efficiency of the light array above arch 8 was estimated from the mean proportion of eels caught in arch 8 during the treatment period (P_{on}) relative to the mean proportion caught during control periods (P_{off}). Deflection efficiency (E) of the light array was calculated as:

$$E = 100\% \cdot (1 - P)$$

Where $P = P_{on}/P_{off}$.

Following the methods of previous studies (Agresti 1996; Welton et al., 2002), standard formulae for calculating confidence intervals were modified to give approximate confidence intervals around the calculated efficiency:

$$100(1 - Pk) \text{ to } 100(1 - P / k)$$

Where $k = \exp(1.96 \sqrt{v})$, $v = ([1 - P_{on})/N_{on}] + [1 - P_{off})/N_{off}])$ and N_{on} and N_{off} are the total biomasses of silver eels caught in arch 8 with lights on and off respectively.

To investigate if the proportion of eels travelling via arch 8 during treatment periods was significantly lower than control periods, a one-tailed *z*-test for proportions was used. It was anticipated that the light array would result in a greater proportion of eels being caught in arches 5 – 7, while arches 9 – 10 would not change. Therefore, one-tailed z-tests were repeated for all arches to assess the impact of the light array on the dispersal of deflected eels.

3.2.5. Size-related response to light

To determine if light deflection was size-dependent, representative samples of eels captured in arch 8 were anaesthetised and measured (± 1 mm) during control (n = 199 eels) and treatment (n = 35) periods. Arch 9 was expected to remain unaffected by the light array. Therefore, eels were also measured from arch 9 during control (n = 189) and treatment (n = 155) periods to provide a baseline against which to determine the impact of lights on eels migrating via arch 8. The size of eels captured in each arch were compared with lights on and off using Mann-Whitney U-tests.

3.3. Results

During control periods (n = 16 nights), a total of 1,531 kg (Mean nightly catch, Range; 96 kg, 20 – 208 kg) were caught, while during treatment periods (n = 19 nights) 934 kg (49 kg, 8 – 187 kg) were recorded. Discharge did not differ significantly (Mann-Whitney, p = 0.341) between control (mean ± SD, range; 357 m^3s^{-1} ± 34, 295 - 420) and treatment (327 m^3s^{-1} ± 22, 309 - 398) periods.

Individual arches caught various proportion of the catch during the control period (Figure 3.3), however arch 8 consistently captured the highest proportion of the catch (Mean ± SE, Range; 0.28 ± 0.02, 0.15 – 0.5). During treatment periods, the proportion of eels caught in arch 8 was significantly reduced (0.05 ± 0.01, 0 – 0.2; z = 13.5, p < 0.001). The deflection efficiency (E) of the light array was calculated to be 80.6% (95% CL = 74.3 – 85.3 %).

The proportion of catch in arches 5 - 7 with lights on significantly increased (Arch 5, z = 5.36, p <0.001; Arch 6, z = 7.47, p < 0.001; and 7, z = 6.94, p < 0.001). When lights were off, arches 5 – 7 accounted for 0.21 of the catch on average. However, when the light array was on, arches 5 – 7 accounted for 0.45 of nightly catch, on average. Catch in the other nets (Arch 9, navigation and Arch 10) did not differ significantly (p > 0.05).

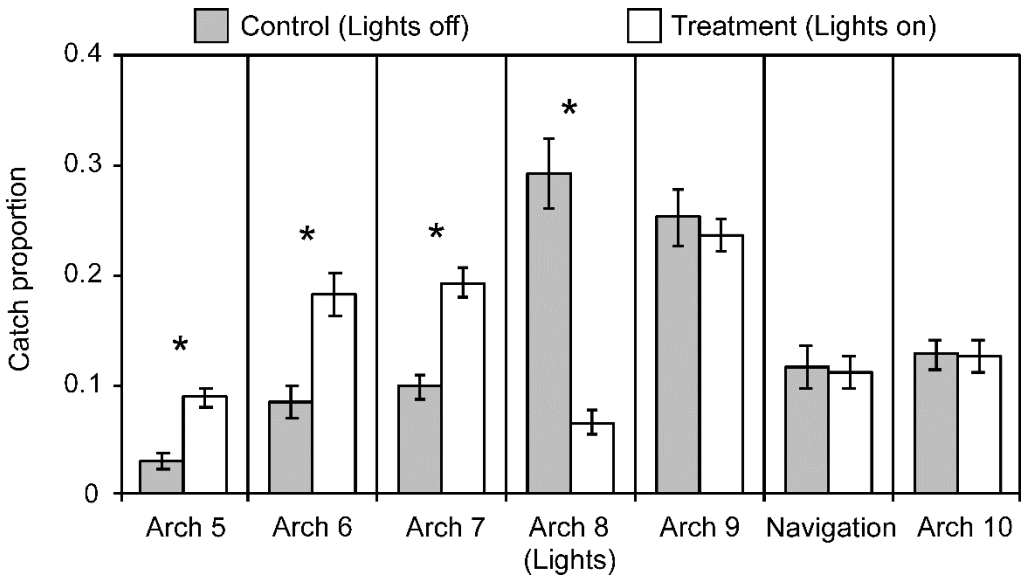

Figure 3.3. The proportion of catch (± 1 SE) in each arch with lights off and lights on. The proportion caught in each arch was compared for control and treatment periods using z-tests, with significant differences ($p < 0.05$) indicated (*).

Eels captured in arch 8 during treatment periods (Mean ± S.E.; 452 ± 11 mm) were significantly smaller (Mann-Whitney U test, $p < 0.001$; Figure 3.4) than control periods (538 ± 8 mm). However, eels measured from arch 9 during treatment (550 ± 9 mm) and control (532 ± 8 mm) periods did not differ significantly (Mann-Whitney U test, $p = 0.271$)

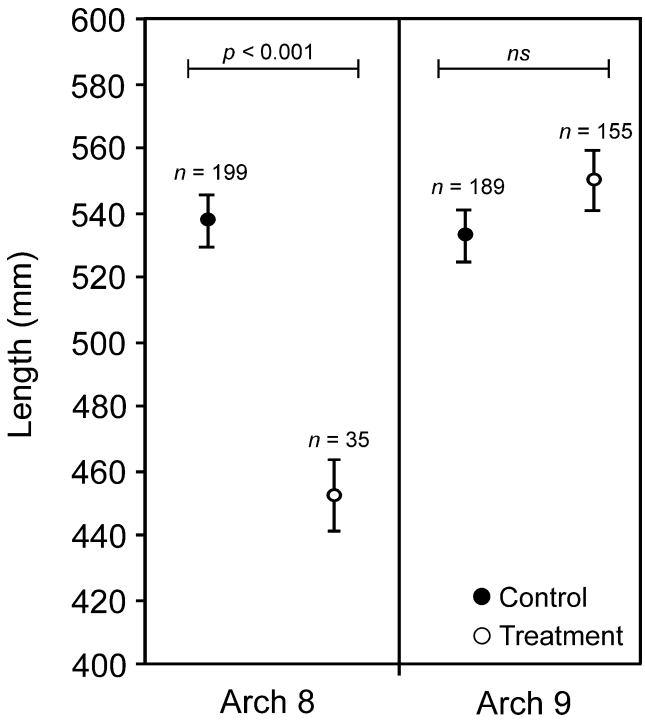

Figure 3.4. Length (mean ± S.E.) of eels captured in Arch 8 and Arch 9 during control (lights off) and treatment (lights on) periods. Numbers (*n*) are the number of eels measured in each arch for each period. ns = not significantly different.

3.4. Discussion

Based on the analysis of catch patterns at Killaloe eel weir, it was determined that silver eels demonstrated strong negative phototaxis in response to the HIL system. Comparisons between control and treatment periods revealed that the HIL system had a deflection efficiency of 80.6%. The confidence levels around calculated efficiency were 74.2 – 85.3%. Eels caught in arch 8 during treatment periods were significantly smaller than those caught during control periods and suggested that smaller eels (Mean length = 452 mm) were less capable of avoiding the light array. The ability of fish to swim upstream against water velocity is known to increase with body length (Videler, 1993), and this is reflected in the capture of smaller eels in this study when lights were on. Reducing flow may allow smaller eels to orientate themselves better and avoid lights. However, this is not always practical or economically feasible. It is thought that physical and behavioural barriers work best when fish do not have to alter their swimming trajectory greatly (Sand et al., 2000; Piper et al., 2019). The light array was angled at 45° relative to the flow, but it is generally agreed that for barriers to perform

optimally, a shallower angle (<20 degrees) is preferable to allow eels sufficient time to react (Russon et al., 2010; Sheridan et al., 2014). Deploying the light array at a sufficiently shallow angle might also serve to increase the deflection of smaller eels and represents a more viable option than reducing flow levels.

Most studies to date have focused on the use of constant illumination to deflect silver eels. Hadderingh et al. (1992), observed deflection efficiencies up to 66%, a value that was supported by subsequent laboratory experimentation (Hadderingh et al., 1999; 65%). Cullen and McCarthy (2000) also observed deflection efficiencies of approximately 66% at Killaloe eel weir using constant illumination. This was lower than the 80.3% deflection efficiency observed here using strobing lights. In addition to potentially lower deflection efficiencies, studies have also shown that fish, if not successfully deflected, can quickly become habituated to constant illumination. This is less likely to occur with strobe lighting (Patrick et al., 1985). There has been increasing interest in the use of strobe lights to deflect silver eels, with previous experiments highlighting their potential for juvenile (Patrick et al., 1982) and yellow eel (Elvidge et al., 2018).

The ubiquity of LEDs has led to new opportunities for experimentation with strobing lights and several studies have now been conducted which suggest that strobing light barriers are useful for deflecting silver eels. However, assessing the efficiency of these systems has proven difficult to date. Bowen (2014), who also assessed the HIL system, found it was capable deflection efficiencies as high as 95%. However, interpretation of results was limited by small sample sizes and limited statistical power (EPRI, 2017). The effect of an alternative strobe LED system (FishFlow Innovations Model FFI 012-I) on silver eel behaviour in front of a trash rack at a pumping station was assessed by Kruitwagen (2014). It was observed, based on acoustic camera observations, that fewer eels were observed when lights were powered on. However, the camera only viewed approximately 20% of the rack and based on concurrently collected catch data no statistically significant reduction in eel passage could be detected. At the Linne hydropower station, in the Netherlands, the same light array as Kruitwagen (2014) was deployed to deflect a variety of fish (including eel) away from the turbine intakes and guide them towards a fish-pass (EPRI, 2017). Although deflection efficiency was not estimated, through a combination of telemetry and netting it was determined that the strobe light system was not effective at guiding eels, with 0% of eels using the fish-

pass. Reasons suggested for this failure included high turbidity, turbulence near the fish-pass and loud noises from turbine operation (EPRI, 2017). Therefore, most studies to date have been limited by study design or sample sizes and the results of the present study are important for highlighting the potential of a strobe LED system to deflect silver eels in a fluvial setting.

In many cases, the ability to guide fish to a desired location is as important as the ability to deflect them from hazardous areas (Calles et al., 2013b). Økland et al. (2019) noted mortality could be as low as 0 – 8 % when eels were prevented from entering turbines and were simultaneously guided to a safe alternative route using a physical barrier. In this study, increases in the relative proportion of catch reported in adjacent arches (5 - 7) during treatment periods suggested that the HIL system was also capable of directing eels away from arch 8 in the direction the array was angled. The fact that there was no change in the proportion of catch recorded in other arches (Arch 9, navigation and 10) supports this. Therefore, it is possible that behavioural barriers, such as the HIL system tested here could drastically reduce mortality by both preventing entry to hazardous areas, but also accurately guiding them towards alternative safe routes.

On the lower R. Shannon, a water regulating weir diverts flow away from the natural river channel to Ardnacrusha hydropower station (HPS). Although several migration routes potentially exist at the HPS, in reality the vast majority of eels migrate via turbine intakes, where mortality of passing eels has been estimated at 21.15% (SSCE, 2012). When the dam is at maximum capacity but water level above the regulating weir continues to increase, the excess water is released to the natural river channel of the Shannon. This provides eels with a second migration route (chapter 1) that is free from sources of anthropogenic mortality and provides eels with a safe route to the Shannon estuary located 21 km downstream. The use of a behavioural barrier to prevent eels from entering the headrace might serve to force eels into the ORC, even if flow to this route is comparatively low. Current velocities in the headrace vary from 0 ms^{-1} in drought conditions, up to approximately 1.2 ms^{-1} when the dam is at full capacity. The burst swimming speed for a relatively small eel, 400 mm in length, is estimated to be approximately 1.25 ms^{-1} (Solomon and Beach, 2004). Most eels caught in the lower Shannon are larger than 400 mm (MacNamara and McCarthy, 2014), suggesting that the majority of eels should be able to avoid a behavioural deterrent

without simply being washed through. The use of baffles, which reduce water velocity, may serve to increase the efficiency of eel guidance (Schilt, 2007).

To date most field studies have deployed behavioural barriers directly in front of the intakes of hydropower stations. However, the operation of a trap and transport programme on the Shannon presents a unique opportunity to increase escapement using artificial lights. Several early studies increased fisheries yield by using lights to guide eels towards nets (e.g. Petersen, 1906; Lowe, 1952). The results of this study suggest that light arrays could be an effective means of improving fishing efficiency at this site. Killaloe is an important site in the Shannon trap and transport programme, capturing c. 50% of the eels released from the catchment annually. Nevertheless, capture efficiency at Killaloe is low, generally ranging from 20 – 30% (MacNamara and McCarthy, 2014), meaning significant quantities of eels migrating downstream towards the HPS. A number of arches at Killaloe are not fished (Figure 3.1) and potentially allow significant quantities of eels to escape downstream. For example, in the 1990's up to 34 nets were fished at the weir (Cullen and McCarthy 2000), with three nets also set in arches 2, 3, 4 and 11. In total, these arches accounted for approximately 18 % of nightly catch (Cullen and McCarthy, 2000). Following renovations to the weir in the 2000's, its capacity was reduced to its current configuration (19 nets). Therefore, it is known that considerable quantities of eels do escape downstream via arches without nets. Additionally, Lenihan et al. (2020) noted that fishing at Killaloe often ceases due to low flow conditions. In both these cases, artificial lights could be used to increase the biomass of eels captured by directing eels away from unfished arches and towards those containing nets. Any modifications that artificially increasing weir efficiency using lights and thereby increases the biomass of eels released as part of trap and transport represents an effective mitigation measure. This also effectively reduces the numbers migrating downstream and passing through Ardnacrusha HPS.

The primary barrier to the widespread adoption of strobe light arrays for eel guidance at present is the need to independently evaluate each novel application. Assuming a given barrier will be as effective in all locations would be inappropriate and would do a disservice to the fish, hydropower companies, fisheries managers and the technology (Brown, 2000). However, the results of the present study and Bowen (2014) revealed that the HIL strobe light barrier was capable of achieving high levels of deflection in

very different flow conditions, raising hopes that strobe lighting will be applicable to a variety of sites. Further efforts should be made to investigate the efficiency of strobe light arrays to deflect eels under various environmental conditions (e.g. high vs low turbidity). Additionally, efforts should be made to develop 'eel-specific' light arrays. Recent experimentation using narrow-spectrum blue light, which closely matches the spectral sensitivity of silver eels, has shown promise for fish deflection (Elvidge et al., 2018). The use of broad-spectrum white light in current light arrays means many non-target species could potentially be impacted by these lights. Lights do not exclusively deter fish and many species are positively phototactic, resulting in increased hydropower entrainment or by-catch in nets (e.g. Hadderingh, 1982). Furthermore, artificial light at night can interfere with the biological rhythms of non-target riverine fishes, with previous studies showing altered hormones production and gene expression in riverine fish due to artificial lights (Brüning et al., 2018). Blue light is less likely to be perceived by humans as a source of light pollution and is less likely to impact on the biological rhythms of fishes than white light (Brüning et al., 2016), likely due to non-target fish having different spectral sensitivities to eels.

Chapter 4: Modelling daily catches of silver-phase European eel (*Anguilla anguilla*) in two hydropower regulated rivers.

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4.1. Introduction

Recruitment levels and fisheries catch statistics have revealed that the European eel, *Anguilla anguilla* L., has undergone a dramatic decline since the 1980's (ICES, 2016a). As a result, the European eel is now classified as critically endangered (Jacoby & Gollock, 2014) and this has prompted the European Union (EU) to implement regulation EC no. 1100/2007. This regulation requires all Member States to contribute to the restoration of eel spawner biomass to enable escapement greater than or equal to 40% of historic levels. Escapement can be defined as the quantity of silver eels that successfully circumnavigate all sources of human-related mortality on their migrations from continental habitats to the ocean for spawning. Assessment of present day silver eel population size (i.e. production) is vital to confirm compliance with conservation targets and for the calculation of escapement. Implementation of the EU regulation is organised through Eel Management Plans (EMPs). In Ireland, the main conservation measures aimed at protecting silver eels included the cessation of commercial and recreational fishing and mitigating the negative effects of hydropower on these downstream migrating silver eels through "trap and transport" (T&T) programmes (DCENR, 2008). Silver eels are caught at several conservation fishing sites on the hydropower impacted Rivers Shannon and Erne and are released downstream of hydropower dams, close to the sea, in order to boost escapement. Monitoring and evaluation of the T&T programmes is undertaken annually and has presented a good opportunity for the analysis of silver eel production in these rivers. Due to the cessation of commercial fishing on the Rivers Shannon and Erne, T&T programmes provide the only data source for the calculation of eel production.

Although sampling protocols, analytic methodologies and models are constantly being refined (e.g. Aprahamian et al., 2007; Prigge et al., 2013), the overall objective of estimating silver eel production remains problematic. In a number of European catchments, including the Shannon and Erne, production is directly assessed using catch data in conjunction with estimates of fishing efficiency based on mark-recapture or removal sampling (Amilhat et al., 2008; Charrier et al., 2012; MacNamara and McCarthy, 2014; MacNamara et al., 2017). When complete daily catch records are available for the migration period, robust estimates of production are possible. However, where gaps in catch records occur, biases may be introduced in production estimates (Poole et al., 2018). Eels are caught at experimental eel fishing weirs on the lower most sections of the Rivers Erne and Shannon, at Roscor Bridge and Killaloe respectively, to aid with the calculation of production (MacNamara and McCarthy, 2014; McCarthy et al., 2014). Unfortunately, both of these fishing sites are prone to periods of low catch levels early in the season, and often, fishing crews cease fishing until more favourable conditions arrive. When this occurs, catch records required for the calculation of production are unavailable. Statistical analyses are increasingly used to investigate the relationship between fish abundance and causative factors (Hedger et al., 2004), however, the response of animal abundance to environmental factors is unlikely to be linear, monotonic or parametric (Oksanen and Minchin, 2002). Therefore, traditional linear modelling techniques might prove inadequate for describing the complexity of the interaction between silver eel catches and environmental factors.

Generalised Additive Models (GAMs; Hastie and Tibshirani, 1990) extend the power of traditional regression techniques by allowing the response variable (daily catch) to follow any distribution from the exponential family and allow explanatory variables to be modelled as nonparametric smoothing functions. GAMs provide an objective means of predicting animal abundance based on the known ecology of the species. When compared to other predictive models based on environmental variables, GAMs have been shown to perform as well, if not better that most methods (Guisan et al., 2002; Moisen and Frescino, 2002). Since their development, GAMs have been extensively used in ecological research for abundance estimation (Drexler and Ainsworth, 2013: Hedger et al., 2004), stream fish species distribution (Buisson et al., 2008), habitat characteristics of species (Jowett et al., 2008), as well as in research on

other eel life-stages such as elvers (Jellyman et al., 2009; Guo et al., 2016) and yellow eels (de Eyto et al., 2016).

The aim of this study was to facilitate more effective monitoring of silver eel production by developing models capable of accurately predicting daily catch levels in two hydropower rivers. The factors responsible were compared to assess the relative impact of each on catch and to determine the site specificity of variables affecting daily eel migrations.

4.2. Methods

4.2.1. Study area

The River Erne (chapter 1), located in the Northwestern International River Basin, drains an area of 4,375 km^2 and contains extensive lake habitat. It is a trans-boundary river located in the northwest of Ireland and drains areas of both the Republic of Ireland and Northern Ireland. The river has a total wetted area of 26,197 ha upstream of the two hydropower stations (HPS) (Cathleen's Fall HPS, 45MW; Cliff HPS, 20 MW) that are located in the lowermost section of the river system. Discharge varies from <10 m^3s^{-1} to a recorded maximum of 382 m^3s^{-1}, with a mean annual discharge of 92 m^3s^{-1}. Flow patterns, which affect the timing of silver eel migration in the lower part of the river system, are controlled at the hydropower dams. The experimental fishing weir on the lower River Erne is located at Roscor Bridge and is situated 750 m downstream of the outlet from Lower L. Erne. Another conservation fishing site (site E2; chapter 1) is located immediately upstream of this site at the outlet of the lake and is referred to as the Ferny Gap.

The River Shannon, the longest river in Ireland, is located in the Shannon International River Basin District, drains an area of about 18,000 km^2 and discharges to a 97 km long, 5,002 km^2 estuary. The total water surface area is approximately 4,100 km^2 with ten larger lakes representing about 90% of the total lake area. Ardnacrusha generating station (86 MW) is located 3km upstream of the tidal limit of the river and it harnesses 10,400 km^2 of the catchment area upstream. The total wetted area of the cascade catchment is 42,466 ha and this includes 38,771 ha of lake habitat and 3695 ha of fluvial habitat (DCENR, 2008). Discharge on the Shannon varies from 10 m^3s^{-1} to in excess of 700 m^3s^{-1} in major winter floods. The mean annual flow of the River

Shannon is 186 m^3s^{-1}. The experimental fishing weir on the lower Shannon is located at Killaloe (chapter 1).

4.2.2. Catch data

Commercial fishing occurred throughout the Erne and Shannon catchments until 2008, before the closure was specified by Ireland's EMP. Following the cessation of commercial fishing, the trap and transport conservation programme was established on the Erne in 2009 as a mitigation measure against the adverse effects of hydropower on spawner escapement. The experimental weir at Roscor Bridge is fished using three coghill nets attached to the weir. Nets are set at dusk (18:00 hr) and lifted at dawn (08:00 hr) to coincide with the nocturnal migrations of silver eel. The downstream migration of silver eel in the River Erne generally begins in late August or early September and extends until January (Matthews et al., 1999; McCarthy et al., 2014).

A trap and transport programme was initiated on the Shannon at Killaloe in 2000 on a trial basis, with various proportions (32-65%) of the catch released (McCarthy et al., 2008) and continued until the adoption of Ireland's EMP. Since 2006 all eels captured at Killaloe have been released to boost escapement. On the Shannon, the migration period extends from September/October until January/February, though may extend to March in very dry years. Nets are set from 18:00 until 06:00 hr. For this study, silver eel migration seasons are named for the year in which they begin (e.g. October 2017 until February 2018 is referred to as the 2017 season).

Roscor Bridge and Killaloe eel weirs have been used in the calculation of production and escapement since 2009. Both sites provide discrete sections of river in which fishing efficiency can more easily be established for production calculation. This study included catch data from the 2011 to 2016 (n = 582 fishing nights) eel fishing season for the Erne and from 2011 to 2017 (n = 504 fishing nights) for the Shannon. For the Shannon, the 2015 eel season was excluded due to an extreme flooding event that meant catch data were unavailable.

4.2.3. Explanatory variables

Daily catch at Killaloe and Roscor Bridge was modelled using a variety of environmental factors as explanatory variables (Table 4.1), to give a 'Shannon

environmental model' and an 'Erne environmental model' for each fishing site respectively. The transition from yellow eel, the sedentary growth phase, to migratory silver phase is marked by a series of morphological and physiological transformations, which make eels more perceptive to environmental changes that encourage migration. Therefore, a number of environmental factors were considered (Table 4.1). Average daily discharge and water temperature data were obtained from Cliff HPS on the Erne and Ardnacrusha HPS on the Shannon. Water level data for the Erne were obtained from Department for Infrastructure, Northern Ireland, while on the Shannon it was supplied by the Electricity Supply Board (ESB). The biomass of eels migrating on a given day may be influenced by events prior to that day. Therefore, the change in discharge and water level over the previous one, three, five and seven days were tested. All climatic variables (Table 4.1) were obtained from Ireland's national weather service, Met Eireann. Day number was considered a proxy for photoperiod.

On the Erne, another conservation fishing site is located immediately upstream of Roscor Bridge at the Ferny Gap. Because of its proximity to Roscor Bridge (<1 km), it was expected that catch patterns at this site would be reflective of daily catch at Roscor Bridge. Additionally, while gaps tend to occur in Roscor Bridge catch records early in the season, fishing at the Ferny Gap is more continuous during this time. Therefore a 'combined Erne model' was also developed, which incorporated catch from the Ferny Gap site, as well as environmental variables. When available, local data, such as Ferny Gap catch, has the potential to increase the accuracy of model predictions. However, it cannot be guaranteed that data from this upstream site will always be available, either as a result of small gaps in catch records due to extreme weather conditions or in the complete cessation of fishing at the site. As a result, reliance on the availability of this catch data may limit the applicability of the model. This provided a means of comparing the more flexible 'Erne environmental model' with a potentially more accurate, though limited, 'combined Erne model'. On the R. Shannon, the nearest fishing site to Killaloe is located 94 km upstream and as such fishing catches at each site do not overlap temporally. Therefore, only the 'Shannon environmental model' was developed.

Table 4.1. List of explanatory variables included in this study. The 'Shannon environmental model' and 'Erne environmental model' were developed to explain daily catch at Killaloe and Roscor Bridge based solely on environmental variables. A second, 'combined Erne model' was developed for Roscor Bridge, incorporating catch from an upstream fishing site (Ferny Gap).

Variable Name	**Meaning**
Environmental variables	All models
Day number	Number of days since start of year in which seasonal eel migration began
Discharge	Mean daily discharge (m^3s^{-1}) obtained from Cliff HPS (Erne) and Ardnacrusha (Shannon)
δDischarge	Change in discharge (change over 1, 3, 5 and 7 days tested)
Water Level	Water level (m) recorded at Roscor Bridge and Killaloe eel weirs
δWaterLevel	Change in water level from previous day (change over 1,3, 5 and 7 days tested)
Lunar	Continuous index from 0 (new moon) to 100 (full moon) indicating the proportion of the moon being illuminated.
Temperature	Water temperature (^oC) recorded at 8 am at the Cliff HPS (Erne) and Ardnacrusha HPS (Shannon).
Wind Direction	Wind direction (^{o})
Pressure	Atmospheric pressure (mbar)
Wind speed (kt)	Wind speed (kn)
Precipitation	Daily rainfall (mm)
Fisheries variable	**'combined Erne model' only**
Ferny Gap catch	Daily catch from site E2 on the Erne

4.2.4. Model description

Daily catch was modelled for each river separately. Catch data were assumed to have a Poisson distribution (Dalgaard, 2008, Sandlund et al., 2017). However, when using GAMs with a Poisson distribution it is important overdispersion is not occurring. To prevent overdispersion, a quasi-Poisson distribution was used (Crawley, 2007). Variance Inflation Factor (VIF) and Spearman's correlation analyses were used to check for collinearity between predictor variables, which increases the risk of type-I error. Daily silver eel catch was expressed as:

$$Catch\ (kg) = \alpha + \sum s\left(x_{1,2....i}\right) + \varepsilon \text{ (Eq. 4.1)}$$

Where catch data were modelled with a log link function, α is the intercept, *s* is a cubic regression spline fit given to each explanatory variable x_i, ε is random error and the maximum effective degrees of freedom (edf) was limited to 5 to prevent over-fitting (Zuur et al., 2009; Xue et al., 2018).

Prior to model fitting, the datasets for each river were randomly divided into a training dataset (3/4 of the data) and a test dataset (1/4). Starting with initial models that included all explanatory variables, a stepwise backward selection procedure was implemented to select the best fitting models based on the minimisation of Akaike's Information Criterion (AIC; Akaike, 1974). By this method, the variable with the highest p-value was dropped if its removal decreased AIC. This was continued until removal of variables no longer reduced AIC. Because quasi-Poisson distributions do not return true likelihood values, quasi-Akaike's Information Criterion (qAIC) was used instead. The relative contribution of retained variables to the final models was assessed by withdrawing each individual variable and calculating the change in total deviance explained between the full final model and the model with the variable dropped. Deviance explained is a pseudo-R^2 value for model fit and ranges from 0 – 100%, with higher values more desirable. All GAM analyses were conducted in the 'mgcv' package of R (R Core Team, Version 3.5.1, 2018).

4.2.5. Model validation

The fit of the final models for each river, based on the training datasets, were evaluated by analysing the total deviance explained in catch. Following this, model performances were evaluated by predicting daily catches in the test datasets. Predictions of daily catches were compared to observed catches using Spearman's correlation. Predictions were made using the 'predict.gam()' function of the 'mgcv' package in R.

4.2.6. Estimation of Production

In the 2017 Erne eel fishing season, the eel fishing season began on 06/09/17, however fishing at the experimental weir was delayed until 13/10/17. This represented a significant challenge in calculating production. Similarly, in 2018 on the River Shannon, the fishing season began officially on the 29/09/18, however fishing at Killaloe did not begin until 18/11/18 due to low discharge conditions. In both of these scenarios, valuable catch data were absent for the calculation of production.

If predictions of daily catches in the test datasets based on the fitted models were deemed acceptable, the final models were used to predict the entire season's daily catch for the 2017 Erne eel season and the 2018 Shannon season. This acted as further validation of these models' abilities to predict catches accurately. The calculation of production for the Erne system is described by McCarthy et al. (2014), while the Shannon is described by MacNamara and McCarthy (2014). Briefly, production is based on catches from other sites (sites E2 – 7 in the Erne and S2-3 in the Shannon (chapter 1)) combined with an estimate of the remaining biomass of silver eels migrating to Roscor Bridge and Killaloe eel weirs, which is calculated based on results from mark-recapture experiments.

Commercial fishing at the Roscor Bridge site in previous decades indicated that catch levels were low when regulated discharge was below $130m^3s^{-1}$ (McCarthy et al., 2014), and increased thereafter. Weir efficiency was previously calculated as 9.78% in low flow conditions ($<130m^3s^{-1}$) and 18.43% in high discharge conditions ($>130m^3s^{-1}$: McCarthy et al., 2014). On the Shannon, several mark-recapture

experiments are conducted annually. Based on these, an average fishing efficiency is assigned to the eel weir. In the 2018/19 eel season this was calculated at 31.0%.

4.3. Results

4.3.1. Final models

Water level and discharge were collinear for each model (VIF>2, Pearson's correlation >0.5) and thus discharge was retained as it had the greater impact on catch. All remaining variables were included in the analyses. With regards change in discharge, only change from the previous day was significant for each model. Change from the previous three, five and seven days were tested and rejected.

Following backward, stepwise removal of variables, the same six variables significantly contributed to the final 'Shannon environmental model' and 'Erne environmental model' (Table 4.2). Both models had the following formulation:

$$\text{Catch} = s(\text{Discharge}) + s(\delta\ \text{Discharge}) + s(\text{Day number}) + s(\text{Temperature}) + s(\text{Lunar luminosity}) + s(\text{Atmospheric pressure}) \quad \text{(Eq. 4.2)}$$

When Ferny Gap catch was incorporated in the 'combined Erne model', a final model was reached with the following formulation:

$$\text{Catch} = s(\text{Discharge}) + s(\delta\ \text{Discharge}) + s(\text{Day number}) + s(\text{Temperature}) + s(\text{Lunar luminosity}) + s(\text{Atmospheric pressure}) + s(\text{Ferny Gap}_{catch}) \quad \text{(Eq. 4.3)}$$

The 'Shannon environmental model' and 'Erne environmental model' explained 83.7% and 78.8% of the total deviance in Killaloe and Roscor Bridge catches respectively. The same environmental variables were important in both river systems. The 'combined Erne model' explained 91.7% of the total deviance in Roscor Bridge catch. The retained variables and their relative contribution to final models is shown in table 4.2. Although the same environmental variables contributed to the Shannon and Erne environmental models, their relative contributions varied (Table 4.2).

Table 4.2. The relative contribution (%) of retained variables to total deviance explained was assessed by withdrawing individual variables and calculating the change in total deviance explained between the full final model and the model with the variable dropped.

	Shannon - Killaloe	Erne – Roscor Bridge	
Variables	Environmental model	Environmental model	Combined model
Discharge	45.6	45.7	23.3
Lunar luminosity	1	23.8	11.5
Atmospheric pressure	6	3.8	3.8
δ discharge	1.7	2.4	2
Temperature	4.1	1.8	1.9
Day number	25.3	1.3	0.9
Ferny Gap catch	-	-	47.6
Total	83.7%	78.8%	91.7%

Smoothed response curves from GAM analysis (Figure 4.1) show the effect of the retained explanatory variables on daily catch of silver eel at Roscor Bridge and Killaloe, where positive and negative values on the *y*-axis indicate increasing and decreasing influence on daily catch respectively. In both the 'Erne environmental model' and the 'combined Erne model', the environmental variables had positive and negative values with the same range (x-axis), though the magnitude of the effect varied (*y*-axis) (Figure 4.1). Discharge had a consistently negative effect on Roscor Bridge catch before becoming positive at 100 m^3s^{-1} and increased until 150 m^3s^{-1} and remained stable thereafter. Discharge on the Shannon had a negative effect at values < 360 m^3s^{-1}, but this rapidly became positive after this point and remained stable at values above 500 m^3s^{-1}. For both systems, an increase in discharge from the previous day positively affected catch. Day number had a positive effect on Roscor Bridge catch from day 280 until day 380. On the Shannon, day number had a positive effect from day 290 until 385, after which it briefly had a negative effect. A strongly positive effect is observed after day 430 and reflects late eel runs in dry seasons. Lunar luminosity had a positive effect on catch in both rivers when closer to zero and had a negative effect on catch when luminosity reached approximately 40% for the Erne, and 50% for the Shannon. This corresponds approximately to the illumination between the last and first quarter. On the Erne, lunar luminosity greater than 80% had a strongly negative effect on daily catch. Temperature had a positive effect on catch from 6.5 –

13 ºC in the Erne and 6 –13 ºC at Killaloe. Low atmospheric pressure had a positive effect on catch levels, becoming negative at approximately 1010 mbar in both systems. When catch at the fishing site upstream of Roscor Bridge (Ferny Gap) was greater than 200 kg, there was a positive effect on Roscor Bridge catch.

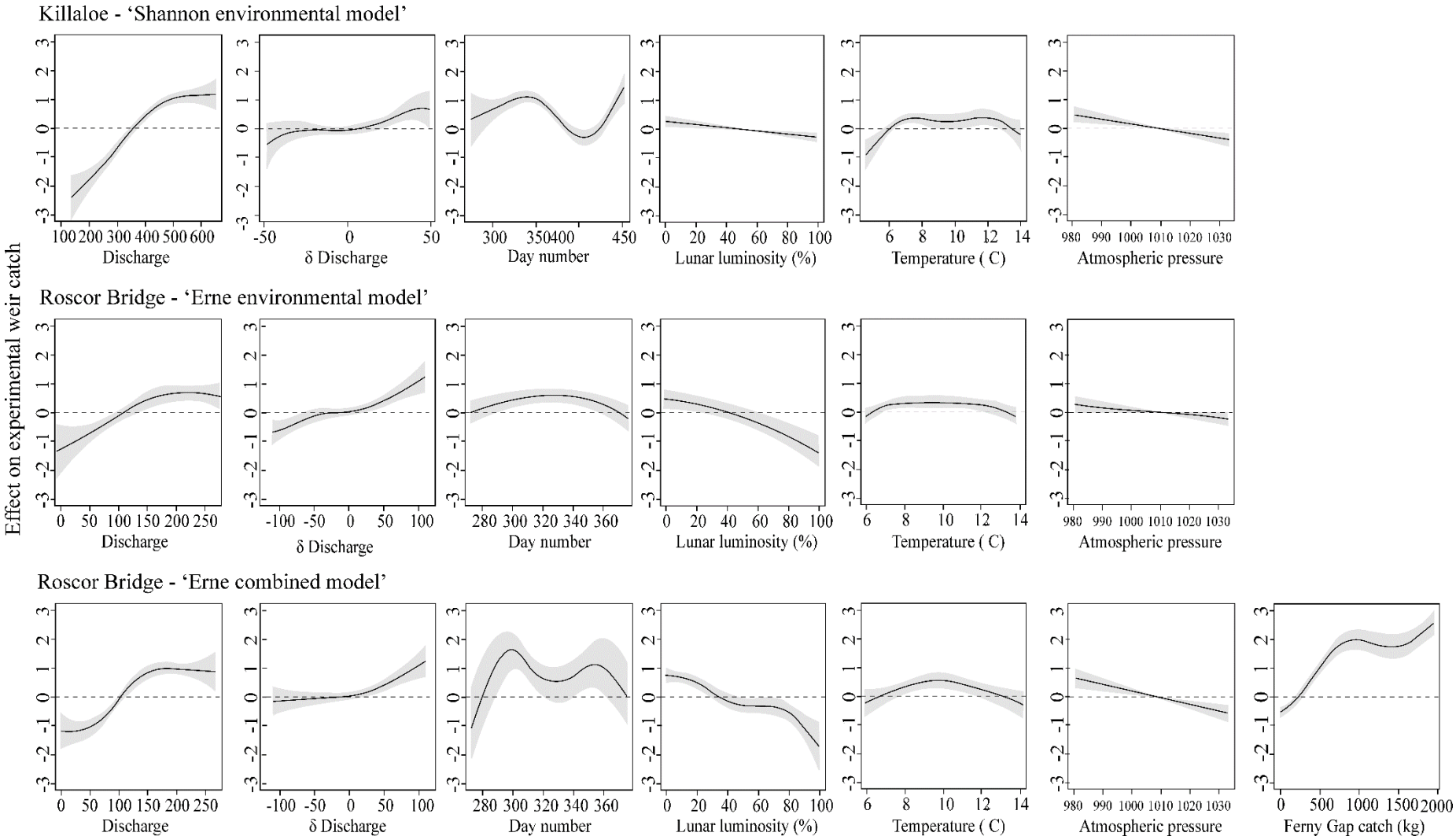

Figure 4.1. GAM response curves for the Erne and Shannon models.

4.3.2 Estimation of production

At Killaloe, the final 'Shannon environmental model' was used to predict daily catch in the test dataset. Predicted and observed catch were significantly correlated (rS = 0.81, $p < 0.001$). As such, the 'Shannon environmental model' was deemed appropriate for the calculation of production. Daily catches for the entire 2018 eel season were predicted. On days when fishing occurred, a total of 7,362 kg were captured. For these days, the model estimated that 7,669 kg would be caught (Figure 4.2). In total, fishing did not occur on 93 nights during the fishing season due to poor flow conditions, during which the model estimated that an additional 952 kg would have been caught. Therefore, daily catch combined with model predictions of daily catch for unfished days gave 8,314 kg. Based on the results of mark-recapture experiments at Killaloe, an average fishing efficiency of 31% was established. This value was applied to daily catch values to estimate the biomass of eels approaching the weir (26,819 kg). Combined with catches from Athlone (sites S2-S3; 9,391 kg), this gave an estimate of production (36,210 kg; 0.85 kg/ha). Based on catch alone, the biomass of eels estimated approaching the weir would have been 23,748 kg, and production would have totalled 33,139 kg (0.78 kg/ha). Therefore, the estimation of production incorporating modelling represented an increase of 9.3% (Table 4.3).

The final models for Roscor Bridge were used to predict the observed catch in the test dataset based on environmental and upstream catch data. Predicted and observed catch were significantly correlated for both models ('Erne environmental model', rS = 0.76, $p < 0.001$; 'combined Erne model', rS = 0.86, $p < 0.001$). Based on total deviances explained and strong correlations between predicted and observed catches in the test data set, it was decided that both the 'Erne environmental model' and 'combined Erne model' were appropriate for estimating production. During the 2017 season, 3,553 kg of eels were caught at the site. The 'Erne environmental model' predicted that, on the same days, 3,826 kg of silver eels would have been caught (Figure 4.2). However, a number of days were not fished (n = 53) during the designated fishing season. Corresponding environmental factors were available on these days, making model predictions possible. The model predicted that an additional 310 kg of silver eels would have been caught on these days. Therefore, daily catch combined with model predictions for unfished nights gave a total of 3,863 kg. Discharge dependent (low vs

high discharge) weir efficiencies established from previous mark-recapture experiments were applied to daily model predictions of catch in order to predict the biomass of eels approaching Roscor Bridge (26,983 kg). This value was added to catch from other conservation fishing sites (site E2 – E7; 39,916 kg) to give an estimate of production (66,899 kg; 2.55 kg/ha). If production had been based on catch alone, a lower biomass of eels would have been expected to approach the weir (25,181 kg) and therefore a lower estimate of production (65, 097 kg, 2.48 kg/ha). Estimates based on GAM predictions of daily catch represent an increase of 2.8 % in the estimate of production (Table 4.3).

Although fishing did not occur on a number of days at Roscor Bridge (*n* = 53), Ferny Gap catch was available for the entire season meaning predictions with the 'combined Erne Model' were possible. This model predicted that 3,687 kg of eels would be caught on fished nights (Figure 4.2), with an additional 561 kg caught on the 53 unfished nights. Therefore, daily catch combined with model predictions for unfished nights gave a total of 4,114 kg. Again, discharge dependent weir efficiencies were applied and predicted a biomass of 27, 131 kg approaching Roscor Bridge. Therefore, production was estimated at: 67,047 kg (2.56 kg/ha), which represents an increase in production of 3.0% (Table 4.3).

Table 4.3. Summary of the use of actual and modelled daily catch to calculated production for the Shannon and Erne catchments.

	Shannon model	Erne models	
	Environmental model	Environmental model	Combined model
Catch on days fished (kg)	7,362	3,553	3,553
Model prediction of fished days (kg)	7,669	3,863	3,687
Difference (kg)	307	310	134
Number of days without catch data	93	53	53
Model predictions on unfished days (kg)	952	310	561
Daily catch + model predictions (kg)	8,314	3,863	4,114
Upstream population estimate (kg)	26,819	26,983	27,131
Catch from other T&T sites (kg)	9,391	39,916	39,916
Production based on daily catch only (kg)	33,139	65,097	65,097
Production with catch and model prediction	36,210	66,899	67,047
Percentage change (%)	+9.3	+2.8	+3.0

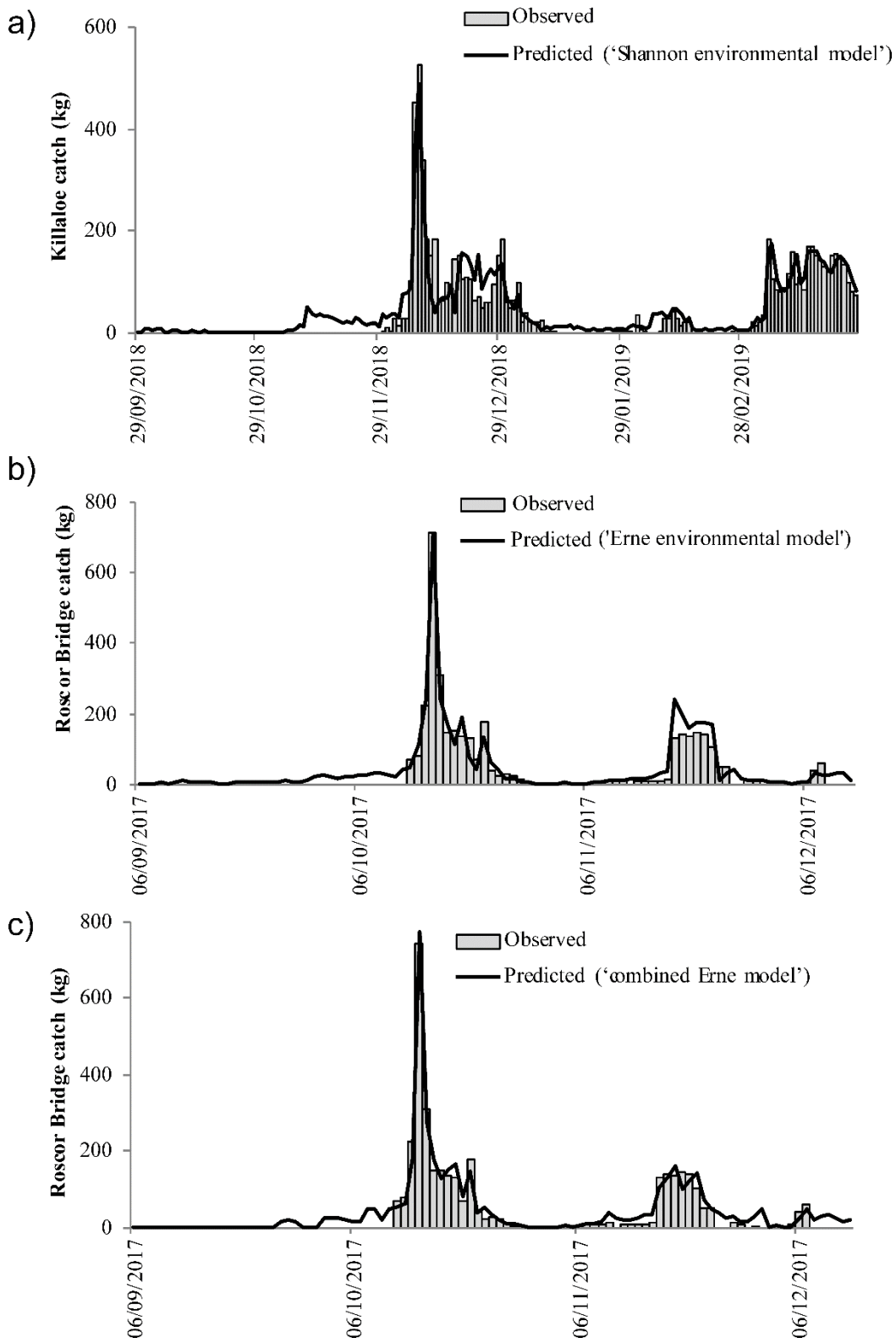

Figure 4.2. Observed (grey bars) and GAM predicted (black line) daily catches at a) Killaloe ('Shannon environmental model') b) Roscor Bridge ('Erne environmental model'), c) Roscor Bridge ('combined Erne model').

4.3.3 Comparison between Erne and Shannon models

As the 'Shannon environmental model' and 'Erne environmental model' used the same variables, we attempted to develop a common model for the two rivers. This involved cross-validating the two models by applying the Erne model to predict the Shannon test dataset and vice versa. The predictive abilities were poor with the Erne model poorly predicting the Shannon test data set (rS = 0.21), while the Shannon model fared almost as poorly predicting the Erne test data set (rS = 0.27).

4.4 Discussion

Robust annual estimates of silver eel production are essential for assessing the efficacy of EMPs at local, regional, national and EU scales. Traditionally, the analysis of downstream migrating eel populations has relied on the use of fisheries catch records from sites where mark-recapture experiments have been used to establish capture efficiency of the operation. The establishment of experimental fishing weirs at Roscor Bridge and Killaloe for analysis of silver eel migrations was critical to silver eel production and escapement research on the Rivers Erne and Shannon (MacNamara and McCarthy, 2014; McCarthy et al., 2014). At these sites mark–recapture experiments are undertaken in discrete river sections that favour the analysis of eel migration and are used to estimate population size upstream based on daily catch records from T&T programmes. However, both Roscor Bridge and Killaloe have limitations as monitoring sites. Early in the season, low discharge and catch levels often lead to fishing crew inactivity. This can clearly be seen in the present study where a number of days were missed early in the season on both rivers. This resulted in gaps in catch records. However, both sites remain crucial as they represent the only fishable points below Lower Lough Erne and L. Derg on the Shannon, from which to assess the number of eels migrating downstream. Therefore, improved monitoring protocols are required to ensure the continuation of robust assessment of production and escapement at these sites (e.g. Lenihan et al., 2019). In this study, we developed models capable of predicting daily catch at two sites in different hydrosystems based on environmental variables, and also catch from an upstream fishing site. When combined with estimates of fishing efficiencies, model predictions of daily catch provided estimates of production. When compared to production based on catch

records alone, an increase in the production estimate was observed (2.8 - 3.0% on the Erne, 9.3% on the Shannon), which reflects the impact of gaps in catch records. From these estimates of production, escapement can be calculated based on dam mortality rates and data from T&T programmes, which represent contributions to spawner biomass escapement (McCarthy et al., 2014).

Lack of resources often limits the ability of countries to directly assess escapement and production. In the absence of basic quantitative silver eel data on many European rivers, modelling rather than field data has been used to estimate escapement. There is now an array of models used in the study of eels (e.g. Bevacqua et al., 2007; Fenske et al., 2011). Walker et al. (2011) reviewed the main models used in Europe's EMPs. These models require various input variables based on eel biology, which can be estimated directly or sourced in the literature. In Ireland, the Eel Density Analysis (EDA, 2.0; e.g. de Eyto et al., 2016) model has been used to calculate production based on extensive electrofishing surveys. However, rivers such as the Erne and Shannon have extensive lake habitat meaning that validation of such a model is difficult. Aprahamian et al. (2007) discussed the Scenario-based Model of Eel Production, which was developed for and tested on large rivers. Again, such rivers lack the extensive lake habitat observed in Ireland's larger rivers. Most common fish population models have been developed for iteroparous species with well-defined population structures, something the European eel lacks. Models estimating population dynamics in eel often attempt to assess large geographical regions and therefore depend on input data compiled from literature sources (e.g. Aprahamian et al., 2007). Therefore, when catchment-specific input data is unavailable, it is often necessary to generalise vital population information at a larger scale and simplify the model assumptions (Aprahamian et al., 2007; Åström and Dekker, 2007). It has been shown, however, that key eel population characteristics are system specific (e.g. Poole and Reynolds, 1998; Sandlund et al., 2017), meaning simplification can have significant impacts on model outcomes. GAMs are said to be "data-driven" rather than "model-driven" because the data determines the relationship between the response variable and the explanatory variables, rather than assuming some form of parametric relationship (Guisan et al., 2002). This feature makes GAMs suitable for describing complex local effects, a feature that suits their application to predicting catch based on site specific interactions with environmental variables. However, it also means GAMs

tend to extrapolate poorly when applied to another site, as was observed in the present study. Although the same environmental factors were used in both the Shannon and Erne models, predicting Killaloe catch with the Roscor Bridge model and vice versa gave poor results. This is due to environmental variables having different relative contributions in each catchment (Table 4.2). For example, lunar luminosity had a greater relative contribution to the Erne models than the Shannon model. This also highlights the site specificity of factors affecting eel migrations.

The flexibility of GAMs makes them suitable for predicting fish abundance. In this study, catch from a nearby site (Ferny Gap) was included in the 'combined Erne model'. This increased the accuracy of the model, explaining 91.7% of the total deviance in Roscor Bridge catch (versus 78.8% without upstream catch). Although the addition of local data such as this can increase accuracy, it reduces the applicability of the model, which could only be used when this upstream data source was available. In extreme weather conditions or if the fishing site ceased operating entirely, the model could no longer be used. Although the model based only on environmental data explained less deviance and wasn't quite as accurate in predicting daily catch in the test dataset (rS = 0.76 vs rS = 0.86), its performance was still impressive and is in many ways more useful. The flexibility of GAMs is one of their advantages and the explanatory variables included will depend on the research objective. Both the Erne and Shannon models based on environmental variables have uses beyond predicting daily catch. For example, the dates within which fishing is permitted varies each year and does not necessarily cover the entire migration period, which can have significant impacts on the calculation of production (Poole et al., 2018). These models based on environmental data can provide data on the biomass of eels migrating outside of fishing periods, which would contribute to more robust calculations of production and escapement. This study showed that certain thresholds existed after which variables had a positive impact on eel migrations and can be used to advise when fishing should begin and cease. For example, this study showed that day number has a positive effect on catch from day 280 to 380 on the Erne and 290 to 385 on the Shannon. It is likely that the biomass of eels migrating before and after these dates are negligible and fishing dates could be set accordingly.

Following the transition from the yellow to silver life-phase, eels are more preceptive to environmental changes that encourage migration. The daily catch of eels is likely

to be impacted by local, site specific variables and will therefore be different from the variables triggering the initial migration of eels. All of the explanatory variables used to explain catch in this study were environmental with the exception of catch data from a conservation fishing site located upstream of Roscor Bridge on the Erne. The effects of various environmental factors on the downstream migration of eels is well established with most of what is known about the dynamics of downstream migrating eels coming from fisheries catch data (Bruijs and Durif, 2009). Eel migratory patterns in many smaller rivers can often be linked to one or two environmental variables (e.g. rain; Boubée et al., 2001). However, the results of this study show that the overall effect of environmental factors in these relatively large, hydropower impact rivers is complex.

The role of river discharge in stimulating silver eel poised for downstream migrations is well established (Vøllestad et al., 1986; Boubée et al., 2001; Haro, 2003), with larger catches frequently observed during increased discharge (Tesch, 2003). The findings of this study agree with this, with discharge > 100 m^3s^{-1} having a positive effect on daily catch levels on the Erne and > 360 m^3s^{-1} on the Shannon. Eels are considered to use semi-passive swimming, utilising active swimming and passive drift, during their downstream migrations. Therefore, migration during high discharge conditions is clearly going to be advantageous to silver eels as it requires less energy. A number of studies have observed a positive relationship between water level and eel migrations (Trancart et al., 2013). Migration during higher water conditions can be considered an anti-predator behaviour, but also reduces energetic costs of migration as it is associated with higher water discharge (Barry et al., 2016), however because it was closely associated with river discharge it was omitted from this study. Day number, which can be considered as a proxy for photoperiod (Durif and Elie, 2008), had a positive influence on catch from mid-October until mid-January. This time range corresponds to a period of relatively shorter day length, allowing eels, which are photophobic, more time to migrate. Vøllestad et al. (1994) observed that tagged eels migrated downstream faster as daylight decreased. On the Shannon there is a further positive effect observed from early to late March and this corresponded to years in which the fishing season was extended due to prolonged periods of low generation levels at the hydropower stations caused by drought conditions in the preceding months. The effect of lunar luminosity on eel catch is well established. Tesch (2003) noted that silver eels tend to

be most active around the last quarter, while a full moon caused a reduction in eel activity (Bruijs and Durif 2009). On both the Erne and Shannon, a positive effect on catch was observed from the last to the first quarter of the moon. However, on the Shannon, lunar luminosity had a much weaker effect on catch (Figure 4.1) and contributed the least to the final model, whereas on the Erne, it was far more important. This compares well with the findings of Cullen and McCarthy (2003) who argued that the higher discharge levels on the lower Shannon obscure an underlying lunar pattern. Some authors state that it is lunar phase which is the influence (Jens, 1953). However, the results of this study agree with others (e.g. Vøllestad et al., 1986; Sandlund et al., 2017) that that the effect of lunar luminosity is related to light conditions rather than the moon phase itself. Eels photophobic behaviour is likely an anti-predator behaviour (Lennox et al., 2018), and on the Erne, where discharge levels are lower and the river is shallower at Roscor Bridge, eels are likely to be more perceptive of light from the moon than in the Shannon. The role of water temperature is unclear, with migrations occurring over a wide range of temperatures and varying from river basin to river basin (Vøllestad et al., 1986; Bruijs and Durif, 2009). The effect of temperature on eel migrations also appears to be temporally variable, changing from autumn to winter in some rivers (Stein et al., 2016). It is therefore difficult to set a threshold value, however our results suggest temperatures ranging from 6 – 13 ^{o}C positively influence migrations in both catchments, which falls within ranges previously recorded (Vøllestad et al., 1986; Bruijs and Durif, 2009). Cullen and McCarthy (2003) noted that temperatures below 10°C coincided with peaks in silver eel migrations in the Shannon, and this falls within the temperature range described here. Several studies (e.g. Hvidsten, 1985; Okamura et al., 2002) have suggested that atmospheric pressure is strongly linked to eel runs, with atmospheric depressions associated with storms triggering downstream silver eel migrations. This study also showed that low pressure (< 1010 mbar) was associated with increased catch at Killaloe and Roscor.

In this study, silver eel production was successfully calculated in two relatively large rivers by combining modelled daily catches with mark-recapture experiments. Over 99% of the cascade catchment for the Shannon and Erne are located above the experimental sites located at Killaloe and Roscor Bridge. In order to simplify comparisons with other waterways, production values were also expressed in terms of wetted area for the Shannon (0.85 kg/ha) and Erne (2.55 - 2.56 kg/ha). Production on

the Shannon appears to be undergoing a further decline, with production values in recent years almost half of what they were only a decade ago (1.45 - 1.62 kg/ha; MacNamara and McCarthy, 2014). This appears to be the result of the continuing collapse of recruitment to the Shannon (MacNamara and McCarthy, 2014). Conversely, production on the Erne has increased in recent years (1.62 - 1.70 kg/ha; McCarthy et al., 2014). This increase was anticipated based on good recruitment to the fishery in recent times (e.g. Matthews et al., 2003). McCarthy et al. (2019) observed that the production estimate in the upper catchment was similar to that of the entire catchment, meaning stocking appears to be allowing elvers to exploit suitable habitat throughout the catchment. Production estimates from this study are comparable with those from other Irish rivers like the Burishoole (Poole et al., 2018). Production on the Shannon and Erne is low in comparison to some of areas of Europe (e.g. Bages-Sigean (30-34 kg/ha)): Amilhat et al., 2008), however due to low densities, many Irish catchments tend to produce a high proportion of large, female eels (MacNamara and McCarthy, 2014; Rosell et al., 2005). MacNamara and McCarthy (2012) observed that female silver eel fecundity is related to size. Therefore, the Erne and Shannon are likely to have high population fecundities, and compare well with the more productive waterbodies, such as the Bages-Sigean, which is dominated by males (97%; Amilhat et al., 2008). It is therefore important that improved monitoring protocols, such as those described in this study, are developed to ensure that robust estimation of silver eel production continues in such important rivers.

Chapter 5: Monitoring downstream migrating silver-phase eels with an acoustic camera

Part of this chapter has been published as: Lenihan, E.S., McCarthy, T.K., & Lawton, C. (2019). Use of an acoustic camera to monitor seaward migrating silver-phase eels (Anguilla anguilla) in a regulated river. Ecohydrology & Hydrobiology, 19(2), 289-295.

A second manuscript has been submitted to Marine and Freshwater Research and is in review: Lenihan, E. S., McCarthy, T. K., & Lawton, C. Route selection by silver eels (Anguilla anguilla) in a regulated river.

5.1. Introduction

The European eel (*Anguilla anguilla*, L.) is a catadromous fish species with a life cycle characterised by long distance, transatlantic larval and spawner migrations (Tesch 2003). During their downstream spawning migrations from rivers and lakes to the ocean, silver eels are exposed to considerable interference from in-channel structures and the biomass of eels escaping from European waters has greatly diminished (Bevacqua et al., 2015; Aalto et al., 2016). The importance of protecting silver eels was recognised by the European Union in the form of regulation EC no. 1100/2007. This regulation requires Member States to develop eel management plans (EMPs) that aim to reduce anthropogenic mortality in order to permit silver eel escapement greater than or equal to 40 % of historic levels. Assessment of present day silver eel population size (i.e. production) is required to evaluate compliance with conservation targets and to calculate escapement. Production has traditionally been calculated using catch data from experimental (McCarthy et al., 2014) or commercial fisheries (Amilhat et al., 2008). However, the use of catch data requires that fishing is more or less continuous during the eel migration period. In the hydropower regulated Rivers Shannon and Erne, eels are caught as part of trap and transport programmes and provide an important data source for the calculation of production. Unfortunately, fishing is frequently interrupted due to low flow conditions (chapter 2) and can result in discontinuities in catch records. Therefore, new methods of quantify silver eel production are required.

New monitoring protocols are also required to assist with the estimation of silver eel escapement. Eels undertaking seaward migrations are considered to migrate by relatively passive means, following the main current (Jonsson, 1991; Porcher, 2002). As such, in-channel structures present silver eels with multiple migration routes during downstream migrations. The route an eel takes can have significant implications with mortality varying between paths. This is most obvious at hydropower dams where eels may migrate via safe routes such as fish passes or spillways, or may migrate via turbines, resulting in injuries or mortality. Alternatively, navigation channels or sections of natural river may provide eels with safe alternative routes around these structures. Several studies have shown that river flow is an important determinant of silver eel route selection. Jansen et al. (2007) found that eel route selection through turbines and via spillways was proportional to the amount of flow through each. Breukelaar et al. (2009) noted that at bifurcation points in larger rivers, the majority of eels tend to migrate in the channel receiving the greater volume of water but do so in quantities far exceeding the amount predicted by flow alone. Therefore, while it is clear that flow plays an important role in eel route selection, there appears to be no exact ratio between flow and the route taken by silver eels (Økland et al., 2019), with local geometry and hydrology playing an active role in eel migration behaviour (Piper et al., 2013). Knowledge of the relative importance of potential migration routes can assist in identification of migration barriers, detection of mortality hotspots and development of appropriate eel conservation measures. Therefore, a clear understanding of eel migration routes is critical for the estimation of spawner escapement and the overall management of eel stocks at river, regional, national and European levels. As it appears that route selection is site specific, new monitoring protocols are required to facilitate the widespread monitoring of eel route selection.

Acoustic cameras, such as dual-frequency identification sonar (DIDSON), are increasingly being used for fisheries research as they are quantitative and non-invasive (Foote, 2009; Martignac et al., 2015). Acoustic cameras use sound to form an image, meaning they can be used in any ambient light conditions, including both day and night as well as high and low turbidity. This feature makes them ideally suited to studying silver eels, which are photophobic and have largely nocturnal migrations. While species identification is a known limitation of acoustic cameras, eels are easily identifiable from their sinusoidal movement and elongate morphology (Webb, 1982).

As well as providing quantitative data on eel abundance, acoustic cameras can provide qualitative information on eel behaviour, such as swimming direction or speed (Martignac et al., 2015). This chapter aimed to: (1) establish the relationship between the number of eels counted using a DIDSON acoustic camera and nightly catches at a fishing weir and to evaluate the potential of acoustic camera surveys in future monitoring of silver eel production and (2) to determine the ability of an acoustic camera to assess silver eel route selection at a hydropower structure, assess the role of flow in eel route choice behaviour and determine the consequences of route selection on silver eel escapement.

5.2. Methods

5.2.1. Dual-frequency identification sonar (DIDSON)

Traditional acoustic monitoring techniques (single-, dual- and split-beam echosounders) have been used in inland fisheries assessments since the 1960's (e.g. Davis, 1968). These echosounders use sound waves to detect underwater targets, such as fish. However, the interpretation and analysis of collected data is complex and often requires extensive training (Jech and Michaels., 2006). Additionally, the effectiveness of these methods is reduced by high turbidity, interactions of acoustic beams with river boundaries, and signal attenuation (Boswell et al., 2007). Multi-beam sonars, also known as acoustic cameras, represent the latest advance in acoustic monitoring devices and overcome the limitations of traditional acoustic systems. The dual-frequency identification sonar (DIDSON) is one such multi-beam echosounder. Initially developed for naval use in harbour surveillance and underwater mine detection (Belcher et al., 2002), DIDSONs have now been widely used in fish monitoring studies (Martignac et al., 2015).

DIDSONs utilise proprietary acoustic lenses to form, transmit and receive acoustic beams and have two operating modes, high frequency model (1.8 MHz) and low frequency mode (1.1 MHz). The overall field of view is 29° horizontally and 14° vertically with high frequency mode divided in 96 beams (0.3^{o} x 14° with beam spacing of 0.3^{o}) and low frequency divided into 48 beams (0.6^{o} x 14° with spacing of 0.6^{o}; Figure 5.1A). High frequency mode produces better quality images but only has a maximum range of 15 m while low frequency mode can extend up to 40 m, at a

lower resolution. Fish that enter the insonified field of view reflect sound back to the DIDSON where the control software transforms it into a pixel value to form an image on an attached laptop computer. DIDSON images resemble pixilated video footage recorded from a vantage point above the fish, looking down at their dorsal surface (Figure 5.1B). This data can be viewed in real time or exported to a hard-drive for later review. Although efforts are being made, there is currently no method for automatically processing data and all collected records must be manually reviewed.

Species identification is a known limitation of all hydroacoustic echosounders. Fortunately, eels are easily distinguished based on their swimming behaviour and distinctive morphology, even in low-frequency mode. Parasite echoes, for example from drifting debris, often superficially resemble eels. However, the distinctive non-linear movement of eels differs from that of debris which is constant in velocity and direction (Martignac et al., 2015).

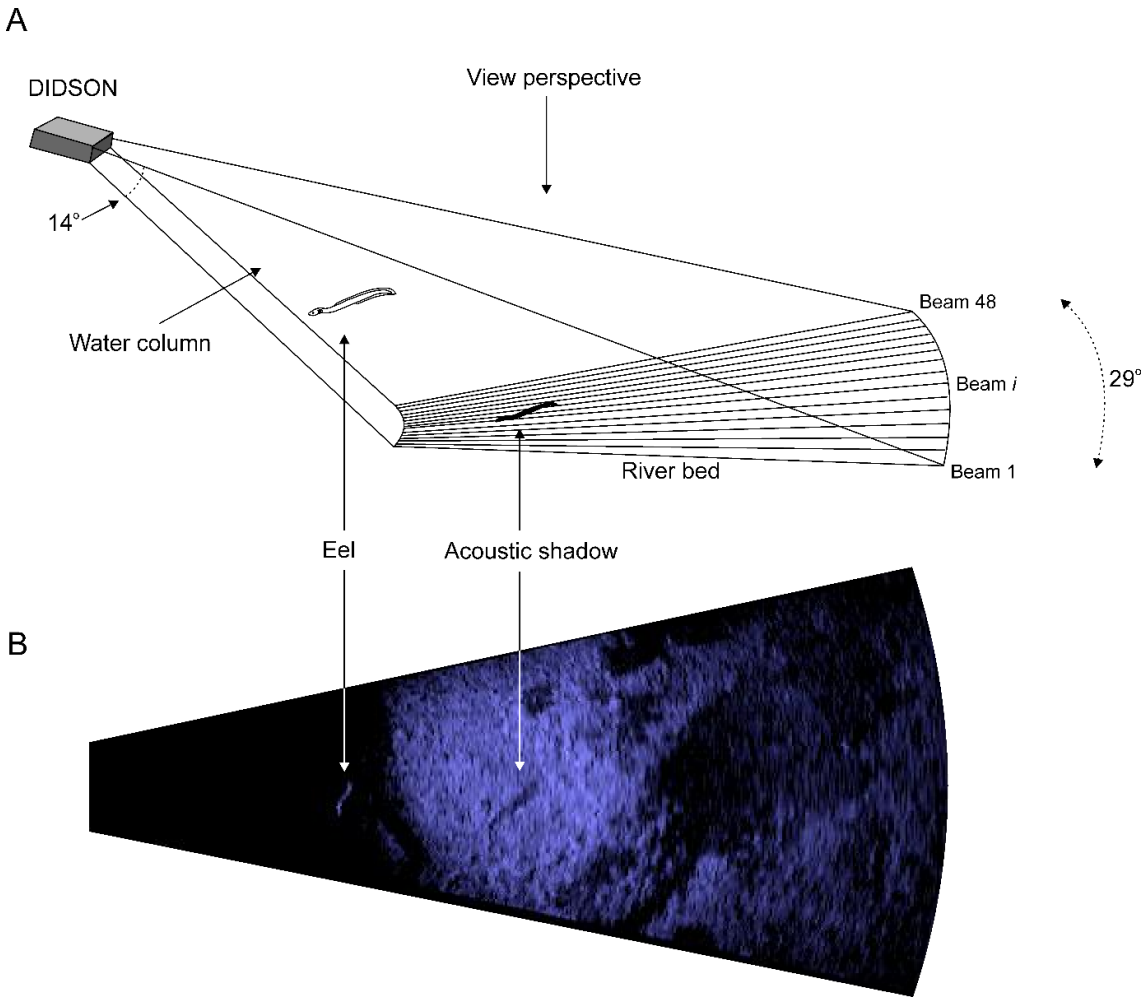

Figure 5.1. A) Schematic drawing showing the DIDSON field of view, generated from 48 beams (low frequency mode). B) Low frequency DIDSON image of a silver eel and its acoustic shadow.

5.2.2. DIDSON field sites

Detailed descriptions of the Erne and Shannon catchments are provided in chapter 1. During the 2016 eel fishing season, a DIDSON was deployed in the lower River Erne, 5 km downstream of the Roscor Bridge fishing site (Figure 5.2A). The river is 48 m wide at this point. The acoustic camera was attached to a floating pontoon which was secured to the riverbed and bank with anchored chains. In 2017, the DIDSON was deployed in the lower R. Shannon on the headrace canal to Ardnacrusha HPS, 7.5 km downstream of Parteen weir (Figure 5.2B). The river is 35 m wide at this point. The camera was held on a custom-made frame which could be lowered in and out of the water on a sliding track.

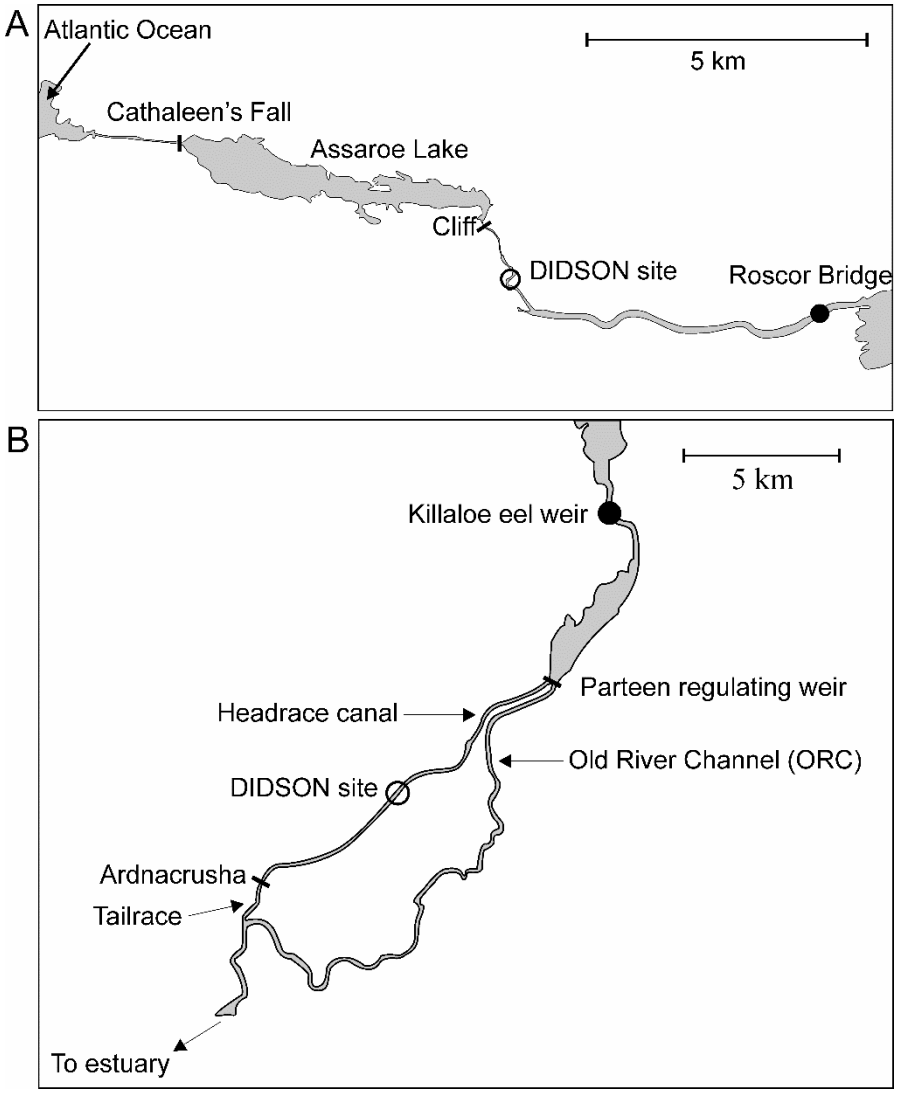

Figure 5.2. Maps of the A) lower Erne and B) lower Shannon highlighting DIDSON deployment sites, hydropower structures and fishing sites.

At both sites, the DIDSON was deployed at a fixed nearshore location. When submerged, the camera faced perpendicular to the flow of the river. The camera was tilted down until the riverbed was visible to ensure that the entire depth of the water column was sampled. The camera was operated in low frequency mode and the insonified field of view was programmed to start at 6 m from the DIDSON and extend a further 20 m. It was possible that eels could pass downstream beyond, above or below the acoustic beams undetected (Figure 5.3). However, as the primary goal of these deployments was for the acoustic camera to provide reliable indices of eel

numbers, absolute counts of downstream migrating eels were not necessary. DIDSON data were automatically exported to hard-drives for later processing. A standard protocol was adopted for reviewing data. First, recorded data were viewed up to 10 times faster than the real-time recorded rate. When a fish was detected, playback was stopped, and images were slowly reviewed to confirm the identity of the fish. Finally, the swimming speeds of downstream migrating eels were calculated (m s^{-1}). Only nocturnal hours were analysed to correspond to periods of peak silver eel activity between dusk and dawn (1800 hr to 0600 hr).

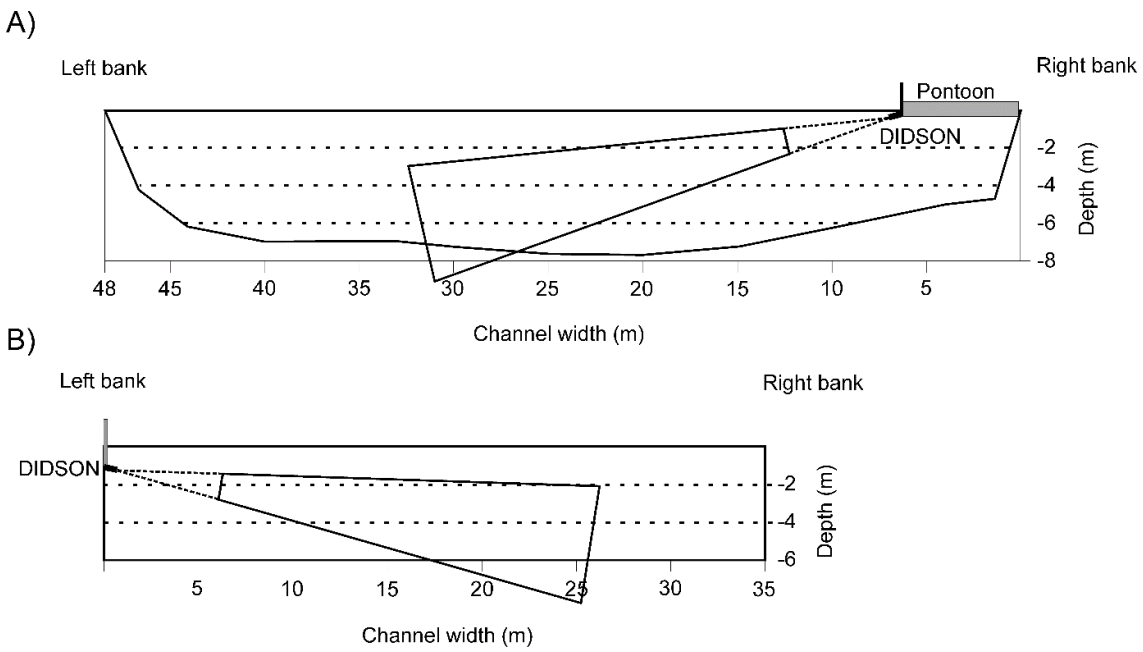

Figure 5.3. Cross-sections and bathymetric profiles of A) the lower Erne DIDSON site and B) the lower Shannon DIDSON site. The extent of the DIDSON beam, which was programmed to start 6 m from the DIDSON and extend a further 20 m, is shown.

5.2.3. Application 1: Predicting catch at Roscor Bridge (River Erne)

5.2.3.1. Relationship between DIDSON counts and silver eel catches

Due to water regulation at Cliff hydropower station (Figure 5.2A), interruptions to flow are common in the lower R. Erne. This frequently results in discontinuities in catch records at Roscor Bridge (chapter 2). During the 2016 fishing season, downstream migrating silver eels were caught at Roscor Bridge by a fishing crew as

part of trap and transport operations. Nets were set from dusk to dawn (1800 hr to 0600 hr). The DIDSON was simultaneously used to count eels migrating downstream of the fishing site. Linear regression analysis was used to investigate the relationship between nightly acoustic camera eel counts (D_c) and reported catch at Roscor Bridge (RB_{catch}). The relationship was described as:

$$D_c = \beta_0 + \beta_1(RB_{catch}) + \varepsilon_i \text{ (Eq. 5.1)}$$

where β_0 is the intercept, β_1 is the gradient and ε_i is random error.

5.2.3.2. Flow alteration and eels swimming behaviour

Previous studies have also shown that alteration of flow at dams can interrupt the downstream migrations of eels (Besson et al., 2016). As the acoustic camera was deployed upstream of Cliff hydropower station (< 1 km; Figure 5.2A), the impact of various flow conditions on silver eel swimming behaviour was also observed. Nightly flow data for the sampling period was recorded at Cliff dam and was assigned to three distinct categories: continuous, interrupted and no flow. Continuous flow remains reasonably constant throughout the night while interrupted flow was characterized by continuous flow for a portion of the night followed by a rapid drop to near zero m^3s^{-1}. The mean number of eels observed moving upstream and downstream were compared for each of the three flow categories using independent-samples t-tests.

5.2.4. Application 2: Silver eel route selection in the lower River Shannon

Understanding the conditions that dictate silver eel route selection is important for the assessment of spawner escapement rates. In the lower reaches of the catchment, the River Shannon is regulated for hydropower generation at Ardnacrusha HPS and its associated water regulating weir at Parteen (Figure 5.2B). A 12.8 km artificial headrace canal supplies Ardnacrusha with up to 380 m^3s^{-1} of water, which is required for maximum generation. Parteen weir is located at the start of the headrace canal and serves to divert the main flow away from the River Shannon to the headrace canal (Figure 5.4A). In times of high flow, when Ardnacrusha has reached its maximum load (380 $m^3 s^{-1}$) and the water level above Parteen weir continues to increase, excess

water is allowed down the natural "old river channel" (ORC) of the River Shannon through any or all of the set of three undershot sluice gates located at Parteen weir (Figure 5.4B). This process is referred to as "spillage". Therefore, seaward migrating silver eels have two routes available to them depending on flow conditions. The ORC has no barriers to migration and provides a safe migration route to the Shannon estuary, 21 km downstream, while eels which migrate via the headrace must pass via Ardnacrusha and risk injury and mortality during turbine passage.

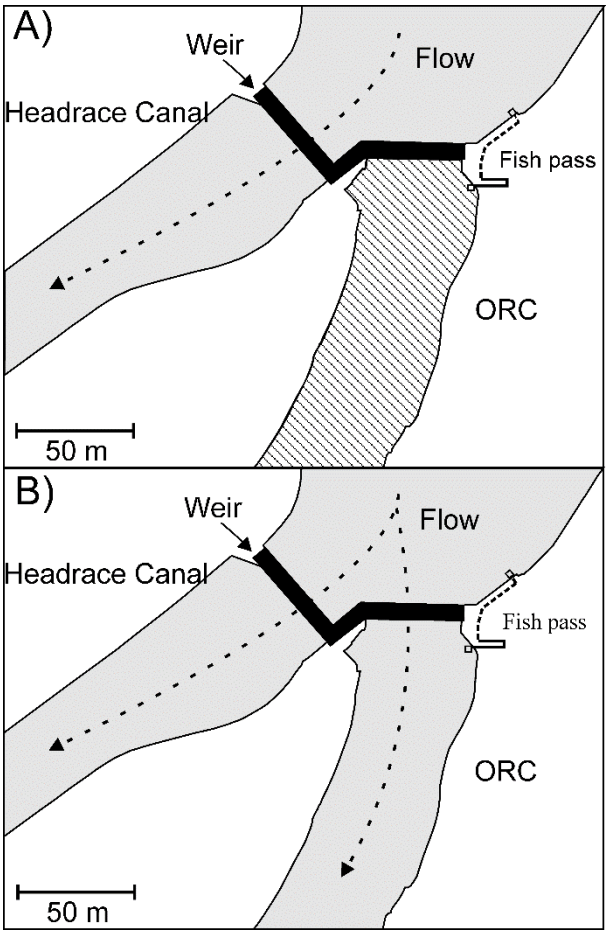

Figure 5.4. Parteen weir serves to divert the main river flow to the HPS via the headrace canal. A) When flow is < 380 m^3s^{-1} all water is directed to the headrace canal and eels must migrate via Ardnacrusha HPS. B)When the HPS is drawing its full load (380 m^3s^{-1}) but water level about Parteen continues to increase, excess water is released to the old river channel (ORC), providing eels with an alternative migration route

5.2.4.1 Biomass of migrating eels

In late 2017 and early 2018, eels were caught at Killaloe eel weir (Figure 5.2B) as part of the Shannon trap and transport programme (chapter 2). Fishing efficiency at Killaloe is generally considered to be quite low (MacNamara and McCarthy, 2014) allowing large proportions of migrating eels to continue downstream to Parteen weir where the river splits. Replicated mark-recapture experiments were conducted to provide an estimate of fishing efficiency. Silver eels were selected from the catch, anaesthetised, measured and tagged using external Floy tags (FD-68B; Floy Tag & Mfg. Inc., Seattle, WA, USA), following the protocols of MacNamara and McCarthy (2014). All tagged eels were allowed to recover sufficiently prior to release. Tagged eels were released from a boat 200 m upstream of the eel weir, with all releases occurring after dark. Subsequent catches were screened for the presence of Floy tags. Fishing efficiency was calculated as the percentage of tagged eels recaptured. Based on daily catches and calculated weir efficiency, the biomass of eels migrating downstream of Killaloe towards Parteen weir each night was calculated. Negligible quantities of eels are caught during daylight hours at Killaloe. Therefore, nets were set at dusk (1800 hr) and lifted at dawn (0600hr) to coincide with the nocturnal migrations of eels.

5.2.4.2 Route selection

Route selection at Parteen weir was established by reference to the biomass of eels approaching Parteen weir and DIDSON eel counts on the headrace each night. During lower flow conditions (i.e. flow < 380 $m^3 s^{-1}$), all water was directed to the headrace and this channel and the river above Parteen weir constituted a single continuous waterway. It was assumed that the biomass (B) of eels migrating downstream of Killaloe to Parteen weir each night would therefore be related to nightly DIDSON counts (D_c), as all eels had to pass via this route. The relationship was investigated using linear regression:

$$D_c = \beta_0 + \beta_1(B) + \varepsilon_i \text{ (Eq. 5.2)}$$

When the HPS reached its maximum capacity, sluice gates to the ORC were opened at Parteen weir to release excess water. Spillage tended to occur in discrete categories,

initially being increased in increments of 50 $m^3 s^{-1}$ as required. When spillage exceeded 150 $m^3 s^{-1}$, increments of increase tended to be less well defined and varied as required to balance increasing water level above Parteen weir. Therefore, in the present study three approximate spillage categories were recognised: 1) 50 $m^3 s^{-1}$ 2) 100 $m^3 s^{-1}$ 3) 150 - 250 $m^3 s^{-1}$. Spillage presented eels with a second migration route. Nightly DIDSON counts on the headrace were again compared to biomass approaching Parteen weir using linear regression for each spillage category. To provide a baseline for comparison with periods of no spillage, analysis of covariance (ANCOVA) was used to investigate whether scaling relationships (i.e. gradient) of regressions changed for each spillage category. If gradients were significantly lower with each increasing spillage category, this would suggest that fewer eels were passing via the headrace for a given migrating biomass, as spillage to the ORC increased.

Assuming fewer eels were observed on the headrace when spillage occurred, route selection was estimated with a two-step process. Firstly, the number of eels expected to be counted with the DIDSON ($E(D_c)$) each night for a given biomass level was estimated based on equation 5.2. This tells us how many eels were expected to be counted if all the biomass of migrating eels had passed via the headrace canal. Secondly, this was compared to the observed DIDSON count (D_c) for this biomass level with spillage occurring. This relationship was used to quantify the proportion of eels using the headrace canal (P_h):

$$P_h = D_c / E(D_c) \quad \text{(Eq. 5.3)}$$

Conversely:

$$1 - P_h = P_{orc} \quad \text{(Eq. 5.4)}$$

describes the proportion of eels migrating down the ORC (P_{orc}). Once the proportion of eels choosing each route was known, we assessed the biomass migrating to the headrace (B_h) and ORC (B_{orc}) respectively:

$$B_h = B \times P_h \quad \text{(Eq. 5.5)}$$

And:

$$B_{orc} = B \times P_{orc} \quad \text{(Eq. 5.6)}$$

5.2.4.3. Mortality and escapement

With route selection established, the consequences of this choice were assessed. Turbine passage mortality for silver eels entering Ardnacrusha HPS was previously determined by means of acoustic telemetry, using protocols described in several reports (e.g. SSCE, 2012). This study revealed an average mortality of 21.15 % (range 16.6 – 25 %, n = 103 eels). This mortality rate was applied to the biomass of eels calculated migrating down the headrace (B_{hr}). The quantity of eels which survive turbine passage, combined with the biomass choosing the ORC (B_{orc}) and eels transported as part of the trap and transport programme provided an estimate of escapement.

5.2.4.4. Flow to alternative routes

Mean hourly flow data were available for the headrace and ORC each day during the study period and were provided by the Electricity Supply Board. The flow for each hour from 1800 until 0600 hrs was averaged to derive a nocturnal flow figure. For each night the proportion of total flow to the headrace canal and ORC respectively was calculated. The proportion of eels migrating down the headrace (P_h) was compared to the proportion of flow to the headrace using linear regression.

Currently, route selection on the Shannon is based on the results of a telemetry study (McCarthy, unpublished data) undertaken to assess the proportion of eels that used the old river channel to bypass Ardnacrusha. The ability of an acoustic camera to assess route selection was assessed by comparison with the results based on this more traditional telemetry method.

5.3. Results

5.3.1. Application 1: Predicting catch at Roscor Bridge (R. Erne)

5.3.1.1 Relationship between DIDSON counts and catch

Fishing at Roscor Bridge occurred from 29/09/2016 until 03/02/2017 with 5,050 kg of eels captured (Figure 5.5). The acoustic camera recorded continuously from the 21/11/2016 until 03/02/2017 ($n = 74$ nights), with 612 eels observed. During the DIDSON deployment period, corresponding catch data were available on 42 nights. On these nights, 4,249 kg were captured at Roscor Bridge and 587 eels were recorded with the acoustic camera.

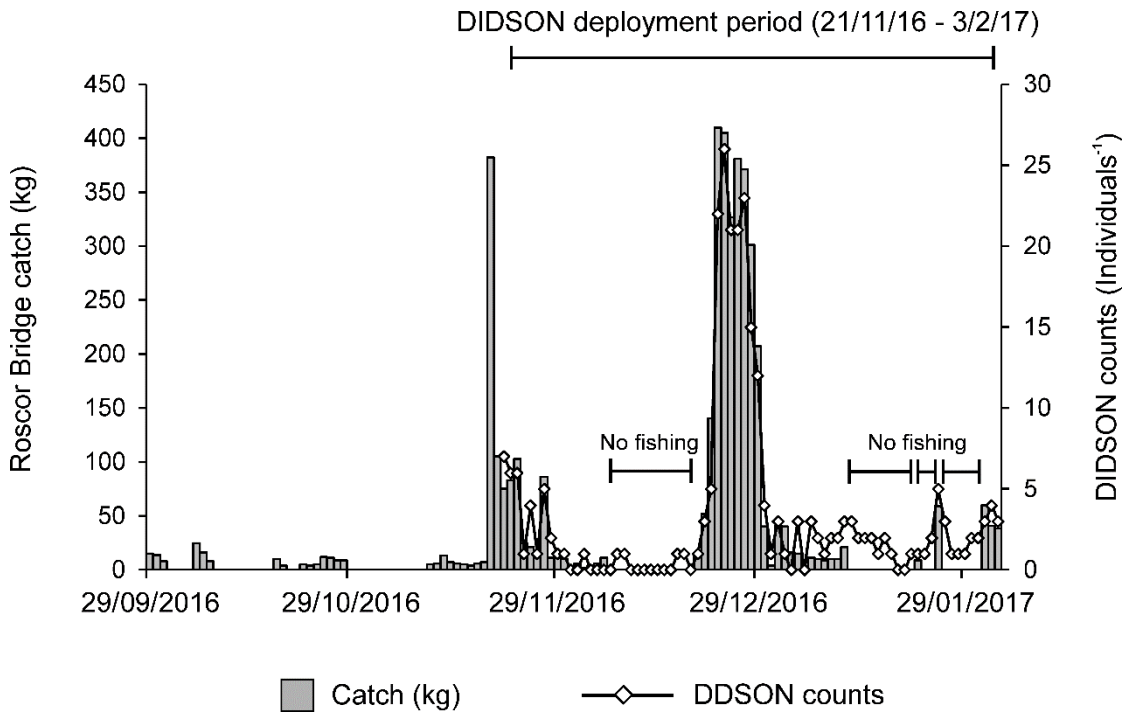

Figure 5.5. Seasonal pattern of silver eels catches at Roscor Bridge and eels counted with the DIDSON. The fishing crew did not operate on a number of nights during the DIDSON deployment periods (n = 32 days).

Of these eels, 303 (52%) were observed swimming downstream, and 284 (48%) were observed swimming upstream. Only eels observed swimming downstream (n =303) (from Roscor Bridge) were used in the linear regression analysis. A strong relationship was established between Roscor Bridge catch and DIDSON counts each night (R^2 = 0.968, $p < 0.001$, $n = 42$, Figure 5.6), and was described by the following equation:

$$D_c = 0.0607(RB_{catch}) + 0.3318 \text{ (Eq. 5.7)}$$

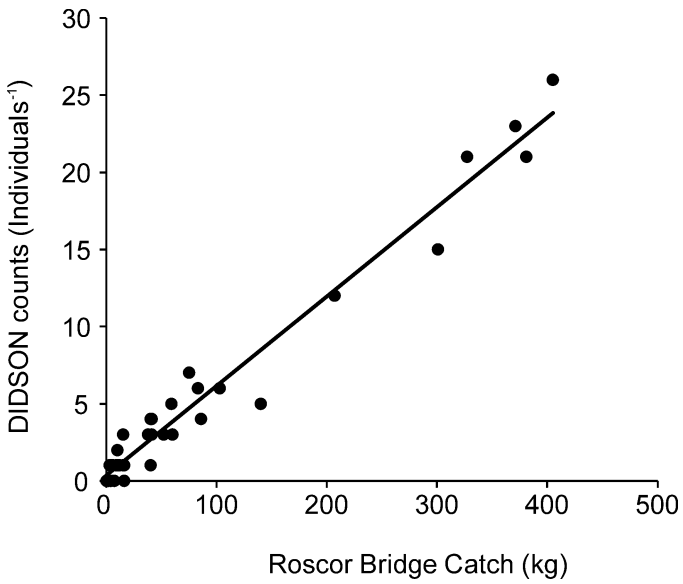

Figure 5.6. The relationship between number of silver eels counted using the DIDSON and the biomass of eels captured at Roscor Bridge each night (R^2 = 0.968, $p < 0.001$, $n = 42$).

Production during the 2016 eel season was estimated to be 62,871 t for the Erne (chapter 2). However, it was noted that 32 night were not fished during the DIDSON deployment (Figure 5.5), with the crew citing low flow conditions. An additional 25 eels were counted on these nights from recorded DIDSON data and based on the relationship established between catch and DIDSON counts (Eq. 5.7), it was predicted that an additional 410 kg would have been caught during this time, had fishing occurred. This biomass was combined with the known fishing efficiency rate for low flow conditions (9.78 %; chapter 1) and suggested that an additional 4,192 kg of eels migrated to Roscor on nights when no fishing occurred. Therefore, the estimate of production would have increased to 67,063 kg (an increase of 6.7%).

5.3.1.2. Flow alteration and eels swimming behaviour

The swimming direction of eels was shown to differ with flow conditions (Table 5.1; Fisher's exact test, $p < 0.001$). Significantly more eels moved downstream during continuous flow than upstream (independent-samples *t*-test: $p < 0.05$; Figure 5.7). When flow was interrupted, there was no significant difference in the mean number of eels moving downstream or upstream ($p > 0.05$). However, during nights with no flow, the mean number of eels moving upstream was significantly higher compared to the mean number moving downstream ($p < 0.05$). It was also repeatedly observed when comparing the number of downstream migrating eels on nights with interrupted flow and continuous flow that eels stopped migrating downstream as soon as flow dropped to zero, while eels continued to move downstream throughout the night during continuous flow (Figure 5.8).

Table 5.1. Summary of the number of eels observed swimming downstream ($n = 303$) and upstream ($n = 284$) with the DIDSON during different flow conditions.

	Swimming direction	
Flow condition	Downstream	Upstream
Continuous	280	91
Interrupted	20	57
No flow	3	136

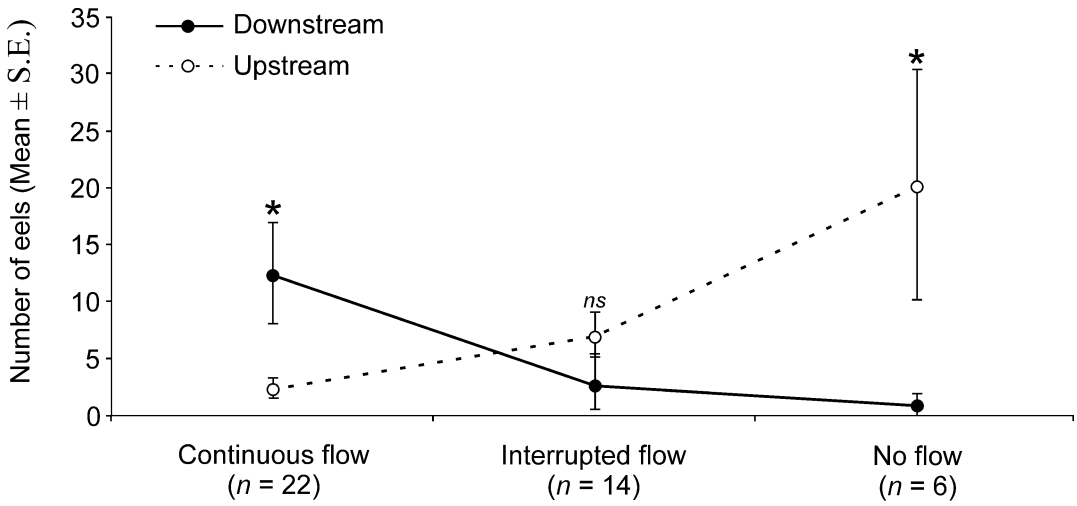

Figure 5.7. The mean number of eels (± standard error) observed passing downstream and upstream each night with the DIDSON for each of the flow categories respectively. * = significant at the $p < 0.05$ level and ns = not significant.

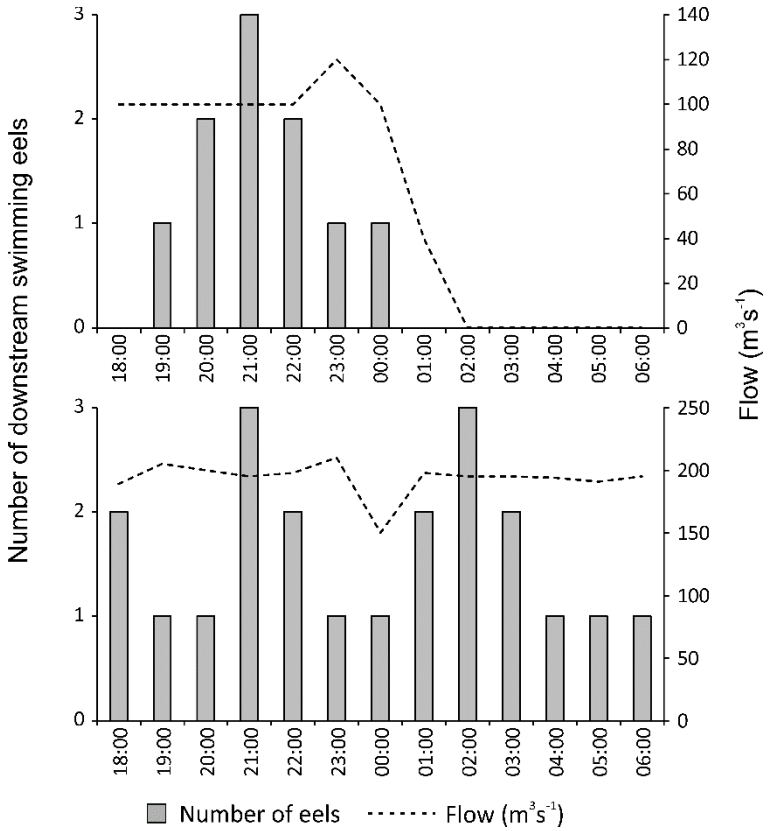

Figure 5.8. Two examples of night-time numbers (per hour) of eels moving downstream in (A) interrupted flow conditions (08/12/16) and (B) continuous flow conditions (26/12/16).

5.3.2. Application 2: Silver eel route selection in the lower River Shannon

5.3.2.1 Biomass of migrating eels

During the 2017/18 Shannon eel season, fishing was undertaken at Killaloe eel weir on 120 nights between 26/09/17 and 13/02/18 with a total catch of 10,873 kg recorded. All these eels were released to freshwater habitat, downstream of the hydropower structures. Early in the season, a clear lunar pattern was observed (Figure 5.9). This pattern was obscured once spillage to the ORC began, with high catches recorded even when the moon luminosity was at 100 %. Five mark-recapture experiments (n = 653 eels) were conducted and an average efficiency of 38.6 % was calculated. Based on daily catch and average efficiency, a total of 17,295 kg of silver eels were estimated to have migrated downstream of Killaloe towards Parteen weir.

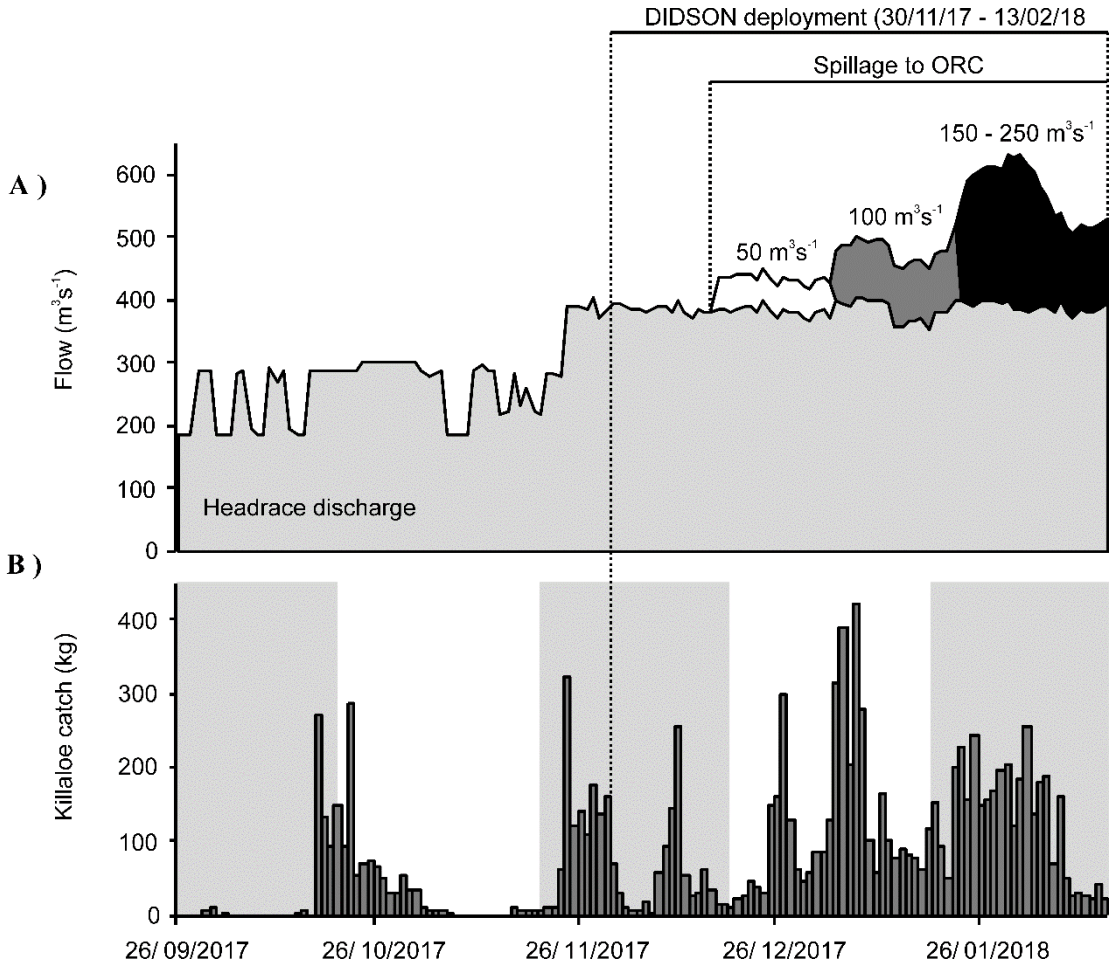

Figure 5.9. A) The pattern of flow discharged to the headrace headrace and spillage to the ORC during the 2017/18 eel migration season. The duration of DIDSON deployment is indicated. B) Record of silver eel catches recorded at Killaloe eel weir and lunar period. Grey areas highlight the lunar dark period from the start of the last lunar quarter to the start of the first lunar quarter.

5.3.2.2. DIDSON survey

The DIDSON acoustic camera was deployed on the headrace to Ardnacrusha from 30/11/17 until 13/02/18 (*n* = 75 days) and covered all days when spillage to the ORC occurred (Figure 5.9). Corresponding catch data were available each day, with 8,326 kg caught during this deployment (77 % of season's catch). Applying the catch efficiency rate of 38.6 % indicated 13,246 kg of silver eels continued migrating downstream beyond Killaloe eel weir during this period. In total 1,437 eels were counted migrating downstream via the headrace.

Water velocity in the headrace during maximum generation was 1.2 m s^{-1} and subtracting this value from calculated eel swimming speeds gave the active swimming speed of eels. The median active swimming speed of eels (in excess of water velocity) was 0.16 m s^{-1} (interquartile range = 0.18 m s^{-1}), with values ranging from 0.01 to 0.66 m s^{-1}. Swimming speeds were highly skewed with most eels (n = 969, 67 %) observed migrating at speeds < 0.2 m s^{-1} (Figure 5.10).

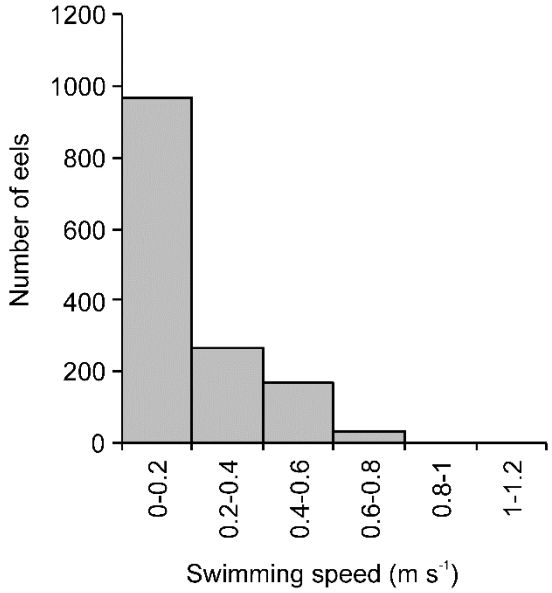

Figure 5.10. Frequency distribution of the swimming speeds of eels in excess of water velocity.

5.3.2.3.Route selection

For the first 16 days of the DIDSON deployment all flow at Parteen weir was diverted to the headrace canal (Figure 5.9) making it the only route available for eels migrating downstream. The catch during this time was 896 kg, corresponding to a downstream migrating biomass of 1,425 kg, with 219 eels observed with the DIDSON. A strong relationship was established between the biomass downstream of Killaloe (B) and DIDSON counts (D_c) each night (R^2 = 0.955, p < 0.001, n = 16, Figure 5.11), and was described by the following equation:

$$D_c = 0.1358(B) - 1.4963 \text{ (Eq. 5.8)}$$

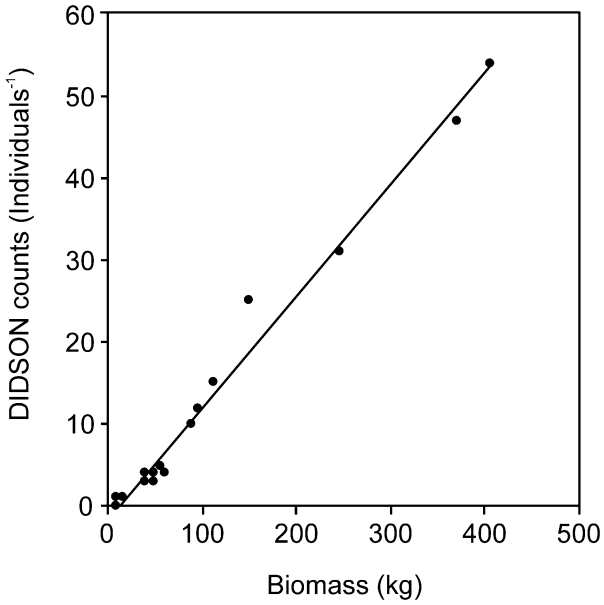

Figure 5.11. The relationship between numbers of silver eels counted using the DIDSON and the biomass of eels migrating downstream of Killaloe each night (R^2 = 0.955, $p < 0.001$, $n = 16$).

Following this period, flow to the headrace approached its capacity threshold of 380 $m^3 s^{-1}$ and excess water was spilled to the ORC. Spillage to the ORC occurred in the following approximate categories: 50 $m^3 s^{-1}$ (n = 18 days), 100 $m^3 s^{-1}$ (n = 19) and 150-250 $m^3 s^{-1}$ (n = 22) (Figure 5.9). The number of eels observed with the DIDSON for a given biomass level decreased with each spillage category (Figure 5.12; Table 5.2). ANCOVA results showed that the intercepts of each regression line were similar ($p > 0.05$), while the gradients differed significantly ($p < 0.001$), meaning fewer eels were counted with the DIDSON for a given biomass level with each increasing spillage category (Figure 5.12). This suggested that as spillage to the ORC increased, more eels migrated via this route.

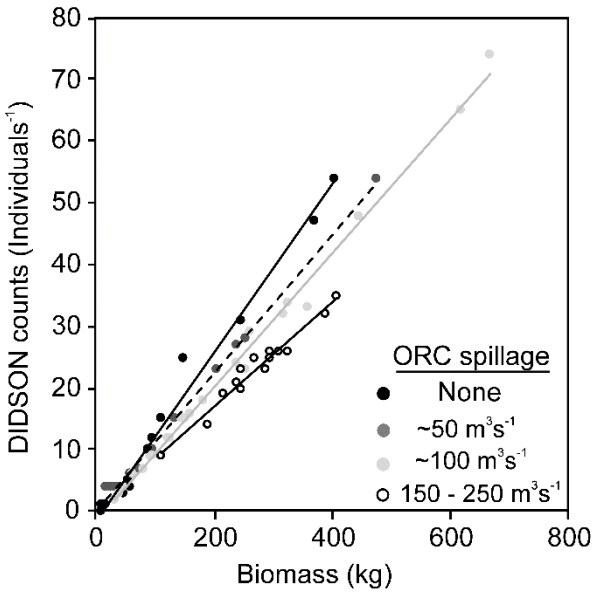

Figure 5.12. Relationship between DIDSON counts and biomass of eels migrating downstream of Killaloe during various spillage levels.

Table 5.2. Summary of the results of DIDSON deployment, exploring route selection of silver phase eel at Parteen Regulating Weir. Expected DIDSON count (E(Dc)) calculated based on counts when all flow was directed through the headrace canal (Eq. 5.8).

	Spillage category			
	None	50 m^{3}s^{-1}	100 m^{3}s^{-1}	150 - 200 m^{3}s^{-1}
Number of nights	16	18	19	22
Total catch (kg)	896	1,714	3,307	2,409
Total biomass (kg) downstream of Killaloe	1,425	2,726	5,260	3,832
DIDSON counts (Dc)	219	325	557	336
Expected DIDSON count (E(Dc))	-	358	678	503
Average nightly P_h (Dc/E(Dc))	1.0	0.91	0.82	0.67

Equation 5.8 was used to calculate the expected number of eels that would be observed each night with the DIDSON, if all flow was directed down the headrace, based on the biomass approaching Parteen. The ratio between expected and observed eel counts was used to quantify the proportion of eels utilising the headrace each night (P_h) under varying spillage conditions. Because all spillage events were observed in this study, it was possible to extrapolate for the entire season (downstream migrating biomass, B = 17,295 kg). Based on nightly calculations of B_h and B_{orc}, 14,077 kg and 3,217 kg of eels were estimated to have migrated down the headrace and ORC respectively. These results closely matched route selection, mortality and escapement values based on the established telemetry method, which predicted that 13,830 kg would migrate via the headrace and 3,465 kg of eels would migrate via the ORC.

5.3.2.4. Mortality and escapement

Mortality (21.15 %) was applied to B_h and calculated as 2,977 kg and therefore the biomass migrating downstream of Ardnacrusha HPS to the estuary was estimated to be 11,100 kg. When combined with the biomass migrating down the ORC this gives 14,317 kg. The trap and transport programme released 16,737 kg (chapter 2), meaning the total escapement was 31,054 kg.

5.3.2.5. Effect of flow on route selection

The proportion of eels migrating down the headrace canal was strongly associated with the proportion of flow directed to the headrace ($R^2 = 0.827$, $p < 0.001$; Figure 5.13), suggesting that eel route selection was passive at this site. As a result, in future, if information on the biomass of eels migrating downstream of Killaloe is available, it will be possible to predict route selection on the R. Shannon without an acoustic camera, based on the flow proportionality, as described by:

$$P_h = 0.9122 * (\text{Proportion flow to headrace}) + 0.058 \quad \text{(Eq. 5.9)}$$

For example, during the 2018/19 eel season 16,169 kg were estimated to have migrated downstream of Killaloe to Parteen. Based on the proportion of flow to alternative routes each night (equation 5.9), it was estimated that 14,270 kg used the headrace,

1,899 kg used the ORC. Subsequently, 3,018 kg were calculated to have perished at Ardnacrusha generating station. Based on the established telemetry model, a total of 14,029 kg were estimated to have migrated down the headrace, while 2,141 kg of eels escaped to the ORC and 2,967 kg perished at the generating station.

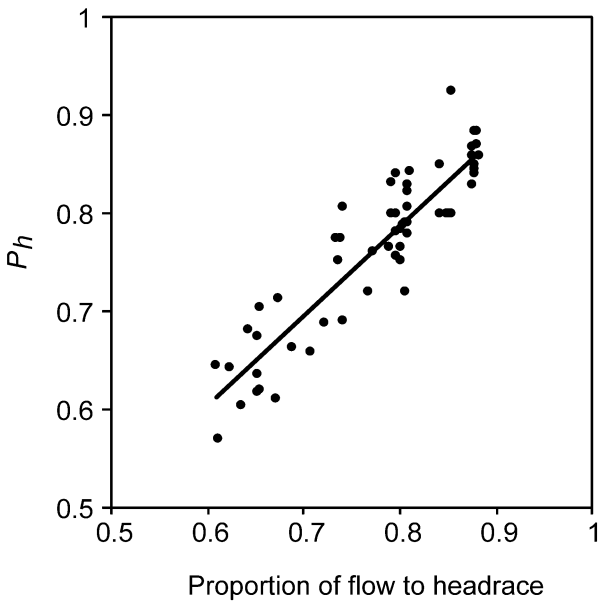

Figure 5.13. The relationship between the proportions of flow diverted to the headrace and the eels choosing the headrace (Ph; $R^2 = 0.827$, $p < 0.001$).

5.4. Discussion

The finding of these studies add to a growing body of literature investigating silver eel migrations with acoustic cameras (e.g. Egg et al., 2017; van Keeken et al., 2020). Acoustic cameras are non-invasive and quantitative, giving them a real advantage over more traditional sampling methods (Bilotta et al. 2011). Although requiring significant initial investment (up to $ 100,000 for certain DIDSON models), the use of acoustic cameras for fisheries monitoring purposes has steadily increased in recent years, meaning there is a greater availability of these devices. Therefore, the method developed in this study could be replicated in other areas and for other species that are readily identifiable from acoustic data, especially other species of Anguillid eels. A means of quantifying the biomass of migrating fish is initially required to calibrate the method. While this will not be an issue in areas with existing commercial or

experimental fisheries, in areas lacking quantitative catch data, short term experimental fishery may need to be established.

Perhaps the greatest challenge to the use of DIDSON at present is the lack of automated fish counting (Rakowitz et al., 2009). This means that manually processing the data is the only viable option available at present. In this study data were collected on 149 days (74 days on the Erne and 75 days on the Shannon). Reviewing a single night of data took approximately 2.5 hours meaning, in total, approximately 372 hours were spent manually reviewing DIDSON files. In many applications, manually reviewing the data will not be feasible. However, it is hoped that the process could become partially or wholly automated in future (Jing et al., 2017). Additionally, suitable sub-sampling approaches can also yield sufficient data to detect population dynamics (e.g. Petreman et al., 2014; McCann et al., 2018). Acoustic cameras enable continuous monitoring over prolonged periods allowing the observation of discrete eel migration events and potentially reduced the need for larger research teams to carry out more traditional, labour-intensive survey methods (Bilotta et al., 2011).

5.4.1. Use of an acoustic camera to predict eel weir catch

The ability to robustly estimate silver eel production is vital for assessing the effectiveness of conservation measures adopted as part of eel management plans. Traditionally, the analysis of downstream migrating eels has relied on fisheries data from sites where mark-recapture experiments can be conducted to established fishing efficiency (e.g. Charrier et al., 2012). However, fishing can stop for a number of reasons, and it is vital that alternative monitoring protocols are available to quantify eel migrations in the absence of continuous catch data. In the present study, it was demonstrated that acoustic camera counts of downstream migrating silver eels were significantly related to catches recorded at Roscor Bridge in the lower R. Erne (R^2 = 0.968, $p < 0.001$). On a number of nights when fishing did not occur, silver eel counts collected with the DIDSON estimated that an additional 410 kg would have been caught. When combined with an estimate of fishing efficiency, model predictions increased the estimate of silver eel production by 6.7%, reflecting the bias introduced by gaps in fishing records.

In many European countries, a complete lack of basic data on silver eel migrations means that silver eel production and escapement are estimated based on catchment characteristics or using demographic models (reviewed by Walker et al., 2011). This means it is necessary to extrapolate from data rich catchments to unmonitored catchments (Walker et al., 2011). This process often necessitates that vital eel population characteristics (e.g. growth rate and density) are assumed to be the same in all rivers. In reality, eel stocks vary widely, even within small geographical areas. The method developed here for quantifying spawner biomass should provide a versatile, portable means of gathering catchment specific data to ground-truth model assumptions about eel productivity.

The role of increasing flow in stimulating silver eels to migrate is well established (Cullen and McCarthy, 2003; chapter 4). In the lower Erne, regulated variation in flow impacted on the swimming behaviour eels and may have implications for timing of eel migration from the river system. Under continuous flow conditions, the majority of eels migrated downstream. This is the most natural behaviour associated with seaward migrating eels. However, a number of eels were observed swimming upstream during continuous flow conditions. Piper et al. (2015) noted that eels encountering constricted flow and velocity gradients (common near the entrance to turbines), often tended to retreat rapidly upstream. Therefore, the upstream movement of eels during high flow may reflect the failure of individuals to successfully pass the dam located 750 m downstream. On nights with interrupted flow, eels were observed swimming downstream until flow ceased (Figure 5.8). When flow dropped to near zero m^3s^{-1}, eels began to move upstream with very few individuals observed swimming downstream. Some eels were observed swimming into the acoustic camera's field of view, hesitating and swimming back in the direction they came. This recurrence behaviour seems to reflect exploratory searching activity (Calles et al., 2010; Piper et al., 2015). Van den Thillart et al. (2009) estimated that eels swim 4–6 times more efficiently than salmonids. Given their remarkably low levels of energy use, it seems likely that eels swimming in no flow conditions, while making no progress towards the sea, are wasting little energy. However, it has been shown that delays at dams tend to cause fish to congregate upstream of structures, which attracts predators (Enders, 2012). In future, efforts should be made to directly assess silver eel interactions with hydropower structures using acoustic cameras. Eel behaviour in front

of a pumping station intake trash rack was recently investigated using a DIDSON (van Keeken et al., 2020) and observed a number of approach behaviours, including hesitation, retreating upstream and alteration of vertical position in the water column. Detailed information on the interactions of eels with structures, under differing flow conditions, could be used to improve the efficiency of behavioural guidance technology (e.g lights, chapter 3) and physical screens, and to minimise delays.

5.4.2. Silver eel route selection – River Shannon

Based on DIDSON observations and replicated mark-recapture experiments, it was determined that there was a direct relationship between the proportion of flow to alternative channels and eel route selection at Parteen weir, in the lower R. Shannon. This supports the hypothesis that seaward migrating eels utilise passive drift (Porcher, 2002). The swimming speeds of eels in the headrace were broadly similar to results from other large European rivers (Klein Breteler et al., 2007; Breukelaar et al., 2009), and did not greatly exceed flow velocity, further suggesting that eels were largely carried by the current. This may be due to natural hesitation on the part of eels migrating in high flow conditions and their need to have a capacity to avoid potential in-stream hazards. Additionally, migrating with the main current is clearly advantageous for silver eels as it requires less energy. The approach to Parteen Weir is large and uniform which means eels, utilising passive drift, were likely to be evenly spread across migration routes (McCarthy et al., 2008).

Fish are highly sensitive to minute water velocity changes caused by river obstacles and it was thought this might affect route selection at Parteen weir. However, the observed relationship between route selection and flow to each channel appears to suggest that sluice gates situated at the entrance to the headrace canal and ORC did not impede eel migrations. Approaches to more complex structures, such as dams, are likely to result in more variable movement patterns than those observed, including: hesitation, recurrence, alteration of position in water column, and searching behaviours (Behrmann-Godel and Eckmann, 2003; Trancart et al., 2020).

The Shannon eel stock has greatly diminished in recent years (ICES, 2018b). Silver eel production was *c*.71 tonnes in 2014 but dropped to as little as *c*.34 t by the time of this study in 2017/18. Bevacqua et al. (2015) forecasted eel dynamics until the end of

the 21st century and noted that conservation policies that aim to increase spawner escapement can result in stock recovery. By assessing route selection, we were able to calculate the biomass of silver eels vulnerable to mortality and ultimately, the biomass successfully reaching the sea. In some European rivers, no quantitative data on silver eel migrations is available, while in other areas eel dynamics are estimated based on catchment wide modelling approaches (e.g. Aprahamian et al., 2007). In the absence of quantitative data, new monitoring protocols, such as those described here, will be of use for confirming compliance with escapement goals, or lack thereof. Also, purpose-collected quantitative data will be useful for the calibration of models. Knowledge of the relative importance of alternative migration routes can assist in the identification of mortality hotspots and in the identification of safe migration routes. For example, given the lack of viable by-pass options at Ardnacrusha HPS, the results of this study were important in highlighting the fact that silver eels used the safer ORC when flow was released to this route.

Spillage of excess water to the ORC provided eels with an alternative migration route and in total 19% (3,217 kg) of downstream migrating eels were estimated to have migrated via this route. This suggests that flow management practices already in use are helping to increase silver eel escapement rates (Cullen and McCarthy, 2006). Although natural spillage rates are too sporadic to represent a reliable means of enhancing silver eel escapement, it does highlight the potential to manage flow rates to maximize the benefit to eels (e.g. Watene and Boubée, 2005; Durif and Elie, 2008). Therefore, flow management strategies could be adopted that aim to maximise spillage to the ORC during peak eel migration periods, indicated from Killaloe catches, while reducing night-time power generation at the HPS. To expedite this process on a European scale, some authors are attempting to establish decision frameworks to help stakeholders and fisheries managers find a balance between the benefits of maximising eel escapement while minimising losses to hydropower generation (e.g. Teichert et al., 2020).

Alternatively, previous analyses on the lower Shannon have shown the potential of behavioural deterrents (artificial lights; chapter 3) to guide significant proportion of eels to desired locations. If a greater proportion of flow could not be redirected to the ORC as part of a flow management strategy, the use of light deflection technology at the entrance to the headrace canal may help to discourage eels from passing via this

route. Although the hydropower mitigation measure currently being applied on the Shannon is trapping and transporting, it is anticipated that longer-term management of migrating eels on the Shannon will involve controlled spillage and/or guidance towards by-pass routes.

Chapter 6: Evaluation of removal sampling for estimating silver-phase eel population size

6.1. Introduction

The European eel (*Anguilla anguilla*) stock has been in decline for several decades and is now listed as critically endangered (Jacoby and Gollock, 2014). Various measures have been adopted at local, regional and international scales in an attempt to restore the stock in line with the European Union regulation EC No. 1100/2007. Assessment of present day silver eel population size (i.e. production) is vital to confirm compliance with conservation targets and for the calculation of escapement. However, eels are often regarded as difficult to sample quantitatively, and consequently, analyses of silver eel populations have generally relied on the use of catch records from commercial or experimental fishing sites where mark-recapture experiments are used to provide information on the capture efficiency of the fishing operations (Amilhat et al., 2008; MacNamara and McCarthy, 2014; McCarthy et al., 2014). Acoustic camera (DIDSON) surveys have been used in support of this work in several Irish rivers (MacNamara and McCarthy, 2014; chapter 5). However, at many fishing sites it is frequently not possible, or cost-effective, to undertake replicated tagging experiments and the use of acoustic cameras may not be technically possible. In many European river systems quantitative data is absent entirely and models are frequently used to estimate population parameters. However, such models still require purpose collected quantitative data for calibration. New quantitative sampling techniques are required to facilitate the widespread estimation of silver eel production from a variety of habitat types.

Removal sampling (also known as depletion sampling) is based on the concept that the repeated removal of fish, using equal effort, will cause catches to decline at a rate that is indicative of the starting population size (Kelso and Shuter, 1989). Removal sampling is appealing because it is intuitively and practically simple to implement. Although initially developed for the study of small mammals, removal sampling has now been widely used for analysing fish populations (e.g. Sweka et al., 2006; Poos et al., 2012). This technique has been used to estimate the abundance of juvenile eels

(Jessop, 2000) and is used, in Ireland and elsewhere, in electric fishing surveys to assess the sedentary eel life-stage (i.e. yellow eels). This routinely involves double- and triple-pass sampling over a defined stretch of lotic or lake shore habitat (Callaghan and McCarthy 1993; de Eyto et al., 2016). However, to date, removal sampling has rarely been used to quantify silver eel abundance. Silver eels migrate downstream in large numbers and as a result they are relatively easy to intercept using nets. Two recent studies (MacNamara et al., 2017; McCarthy et al., 2019) conducted experiments, which involved deploying a second net directly behind a primary fishing net, repeatedly removing fish and estimating silver eel abundance based on the rate of decline in catches. Both studies were conducted in small rivers (<15m wide) where sequential nets could remove the majority of migrating eels. The ability of net-based removal sampling to provide silver eel abundance estimates from larger river has not been investigated. Additionally, the migrations of eels through lakes are still poorly understood in comparison to rivers (Trancart et al., 2018). Removal sampling using sequentially deployed nets may be capable of characterising the migrations of eels through lake sites. This will assist with the widespread estimation of production, but also for calibrating population models, which frequently extrapolate riverine data to lakes due to a lack of quantitative sampling techniques.

In the hydropower regulated Rivers Shannon and Erne, eels are captured as part of trap and transport programmes (chapter 2). Monitoring of these programmes is undertaken annually and provides valuable data on the seaward migrations of eels and for the development of novel monitoring protocols. At several sites within these catchments, nets are deployed sequentially, with a second net deployed immediately downstream of the first. These sites could enable the estimation of production and escapement based on removal sampling. The aim of this study was to evaluate catches from sequential nets fished at a riverine site on the River Shannon and a lake site in the Erne catchment, in order to generate population estimates and to determine the usefulness of this method for the estimation of silver eel production in the future.

6.2. Methods

6.2.1. Sampling locations

Eels were captured below the outlet of Lough Ree, in the town of Athlone (hereafter referred to as the Athlone site), as part of the Shannon trap and transport programme (Site S2; chapter 1). This is a riverine fishing site with a channel width of 100 m. Although the river is up to 6 m deep upstream of the site, the river bathymetry forms a natural bottleneck within a narrow navigation channel (Figure 6.1A). A single net was set in this channel. It was possible for a second net to be deployed 60 m downstream. Both nets fished at this site were coghill nets, which are similar to single chambered fyke nets with net leaders (20 m in length) configured in a "V" shape away from the mouth of the net (Figure 6.1B). When these leaders were fully extended, each nets covered 25 m of the river width. The nets were set on the riverbed and were 2 m tall, in water approximately 2.5 m deep.

As part of the Erne trap and transport programme, eels were captured in the last wide section of Lower Lough Erne (Site E2; chapter 1). This basin (Figure 6.1C) is an enclosed area with one entrance from the main lake and one outlet via the River Erne (the fishing site is referred to as 'Ferny Gap' hereafter). Much of the basin is shallow (1 – 2 m), however, a deep channel (3 – 4 m) leads northwest from the inlet to the outlet and is used for navigation. Several nets were deployed at Ferny gap, the 'removal nets' were those set in the navigation channel. All nets were coghill nets, equipped with 20 m long wings, which extend from the net opening to the shore on each side. Several islands are located within the basin and present downstream migrating eels with several potential migration routes. Nets were also fished in these channels and were used to determine what proportion of eels migrated via the navigation channel. In the 'Southern nets', each net was connected to the next by their leaders with the first and last net tied to the shore. A single net was fished in the northern most channel ('Northern net').

Both sites were fished by former commercial fishing crews. Two nets were set in the removal series at each site when large catches were anticipated based on environmental conditions (increasing flow and lunar phase). Nets were set from 14:00 to 11:00 at the Ferny Gap and from dusk (18:00) until dawn (06:00) at Athlone. All

eels caught were removed from these sites as part of the trap and transport programmes and released below hydropower stations in the lower sections of these catchments.

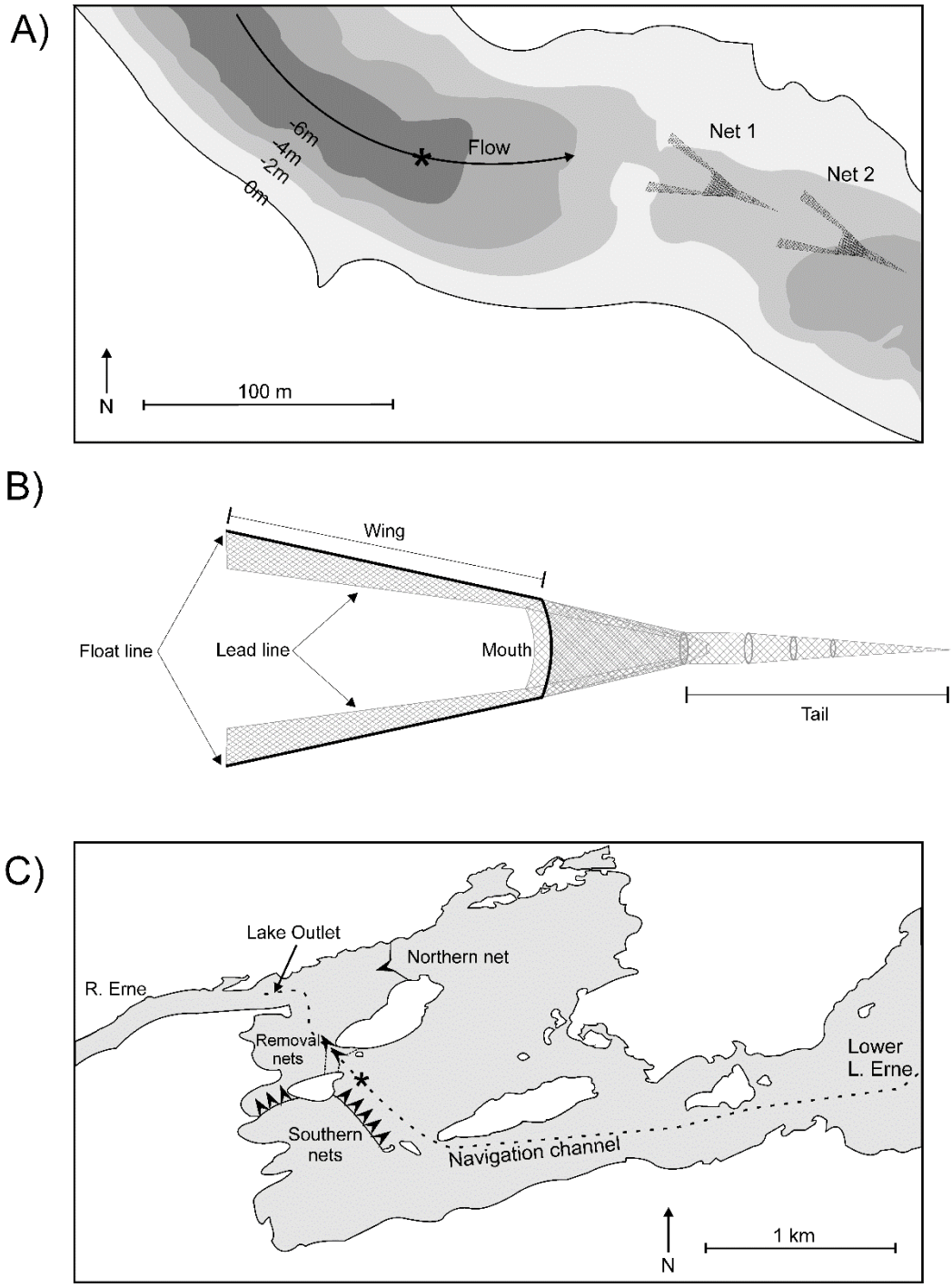

Figure 6.1. A) The experimental site in Athlone showing details of net deployment and river bathymetry. B) Generalised design of coghill nets used at both fishing sites. Exact dimensions and configuration varies based on local site characteristics C) The Ferny Gap fishing site. The removal nets were set in the navigation channel. The release point for mark-recapture experiments for both sites are indicated (*).

6.2.2. Removal sampling

With removal sampling, a population is sampled at least two times, using equal effort (identical nets), and the individuals captured are removed from the population. The decline between catches can determine what proportion of the population abundance the removal represented. There are a number of prominent methods for estimating population size using removal sampling, including the maximum-likelihood methods proposed by Zippin (1958) and Seber and LeCren (1967). In the present study, the weighted maximum-likelihood method of Carle and Strub (1978) was used to estimate population size from paired nets as it is often considered the most robust method (Cowx, 1983; Hedger et al., 2013). The Carle and Strub model uses an iterative process for estimating population size (N), whereby the value of N is repeatedly substituted until the smallest value $N \geq T$ solves the following inequality:

$$\left(\frac{N+1}{N-T+1}\right)\prod_{i=1}^{k}\left(\frac{kN-X-T+\beta+k-i}{kN-X+\alpha+\beta+k-i}\right) \leq 1 \qquad \text{(Eq. 6.1)}$$

Where N = population estimate, T = total catch in all nets, k = number of nets, X = an intermediate statistic ($\Sigma(k - i)C_i$), C_i = biomass captured in net i. Both α and β are parameters of the prior distribution and are used to weight the equation. Where no prior information is available, α and β are both set to a value of 1 (uniform distribution). All Carle and Strub analyses were carried out in R (Version 3.5.1) using the FSA package (Ogle, 2016).

Data sheets completed by crews for the 2018/2019 eel fishing seasons at Athlone and the Ferny Gap were assessed and divided into nights when two nets were set and night when only one was set in removal net series. Nights when two nets were set were used to generate population estimates using the Carle and Strub model (Eq. 6.1). This calculated the biomass of eels vulnerable to capture each night. Capture efficiency of the removal series was defined as the proportion of the estimated population size (N) captured in both nets (C) of the removal series:

$$\textit{Capture efficiency (\%)} = (C / N) \times 100 \qquad \text{(Eq 6.2)}$$

The relationships between the catch in the first net of the removal series and the resulting Carle and Strub population estimates were analysed using linear regression. If sufficiently strong relationships were established then nights when only one net was

set could be extrapolated to a Carle and Strub population estimate based on the linear regression model (Arnason et al., 2005; Hanks et al., 2018; McCarthy et al., 2019).

6.2.3. Evaluation of removal estimates

Removal sampling is considered an attractive option for fisheries biologists for its simplicity and ease of implementation (Meyer and High 2011). However, removal estimates of population size are frequently reported as being negatively biased (Peterson et al., 2004; Sweka et al., 2006; Hedger et al., 2018). Therefore, it is important to assess population size using an alternative method to assess the accuracy of removal estimates. Although not without issues, mark-recapture is often regarded as the most accurate means of assessing population size where the entire population cannot be sampled (Rosenberger and Dunham, 2005). Therefore, replicated mark-recapture experiments were also conducted at both fishing sites to assess removal sampling.

Eels captured as part of trap and transport operations were kept in storage nets (Athlone) or cages (Ferny Gap) in ambient river water while awaiting collection and release. Eels were selected from catches, anaesthetised, and tagged using Floy tags (FD-68B; Floy Tag & Mfg. Inc., Seattle, WA, USA). Following a period of recovery (approximately 8 hours), these eels were released. At Athlone, releases occurred 100 m upstream of the nets (Figure 6.1A). At Ferny Gap, eels were released 100 m upstream of the removal nets in the navigation channel (Figure 6.1C). All releases occurred after dark. Subsequent catches were carefully screened for the presence of tagged eels. Fishing efficiencies were calculated as the proportion of marked eels recaptured and daily estimates of population size (N_{mr}) were subsequently calculated as:

$$N_{mr} = (Catch \times 100) / (Efficiency\ \%) \qquad \text{(Eq. 6.3)}$$

Based on visual assessment of their colouration, in addition to fin and eye indices (Pankhurst, 1982; Durif et al., 2005), all eels used in mark-recapture experiments were deemed to be at an advanced stage of maturation. In addition to adequate recovery times, it was not anticipated that tagging eels for release would bias estimates of fishing efficiency and subsequent population size. Additionally, tagging is one of the

most widely used method for estimating silver eel population size (Rosell et al., 2005; Amilhat et al., 2008; MacNamara and McCarthy., 2014; McCarthy et al., 2014). The accuracy of removal sampling estimates was expressed as the percentage difference between the population size calculated using removal sampling (N) compared to that estimated from mark-recapture (N_{mr}):

$$Accuracy = ((N \times 100)/ N_{mr}) - 100 \quad \text{(Eq. 6.4)}$$

6.3. Results

6.3.1. Athlone

In total 6,023 kg (median nightly catch = 30 kg, range = 5 – 290 kg) of silver eels were caught at the site during the 2018/2019 fishing season, with fishing occurring on 117 days between 07/09/18 and 15/01/19. Two nets were set on 30 nights (Figure 6.2; 26% of nights fished) with 3,650 kg caught (61% of season's catch, median = 95 kg, range = 50 – 290 kg). Single net fishing occurred on the remaining 87 nights, with 2,373 kg caught (median = 25 kg, range = 5 – 125 kg).

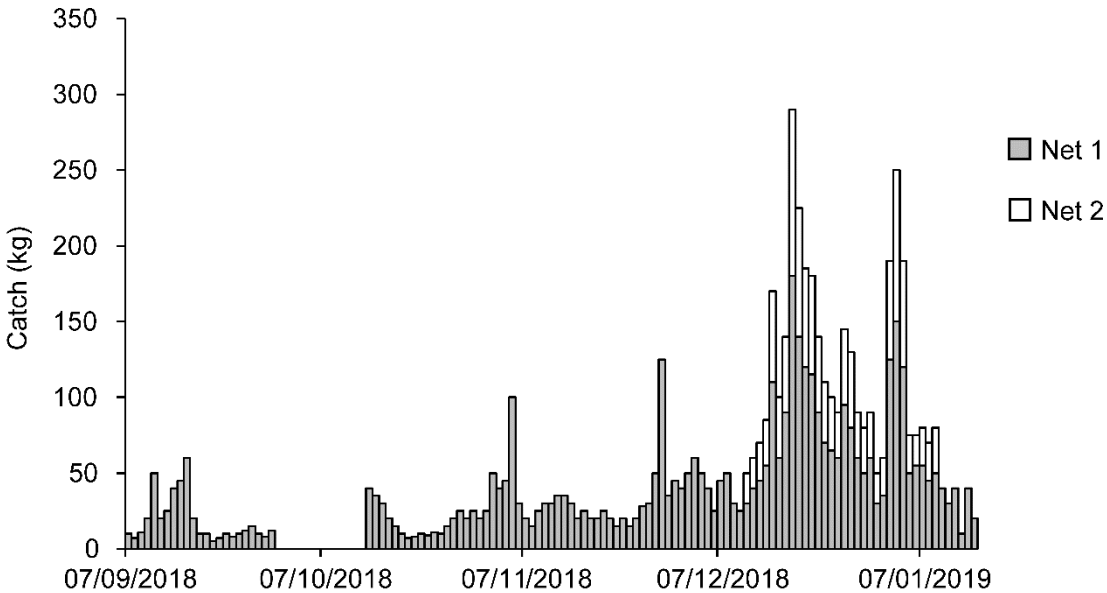

Figure 6.2. Seasonal catch pattern at the experimental fishing site in Athlone. The catch in net 1 and net 2 is indicated, with removal fishing occurring between 11/12/18 and 09/01/19.

Summation of nightly estimates of *N* suggested that 5,710 kg of eels were migrating towards the nets on these nights. Capture efficiency (Eq. 6.2) was therefore estimated to be 63.9%. Catch in the first net of the removal series was strongly related to nightly Carle and Strub population estimates (*N*) (R^2 = 0.94, n = 30, $p < 0.001$; Figure 6.3). Based on this relationship, catches from single nets on 87 nights were used to produce Carle and Strub estimates. This suggested that an additional 4,501 kg of eels were upstream of the site on single net nights. Therefore, based on both double net and extrapolated single net nights, a population estimate of 10,211 kg was obtained.

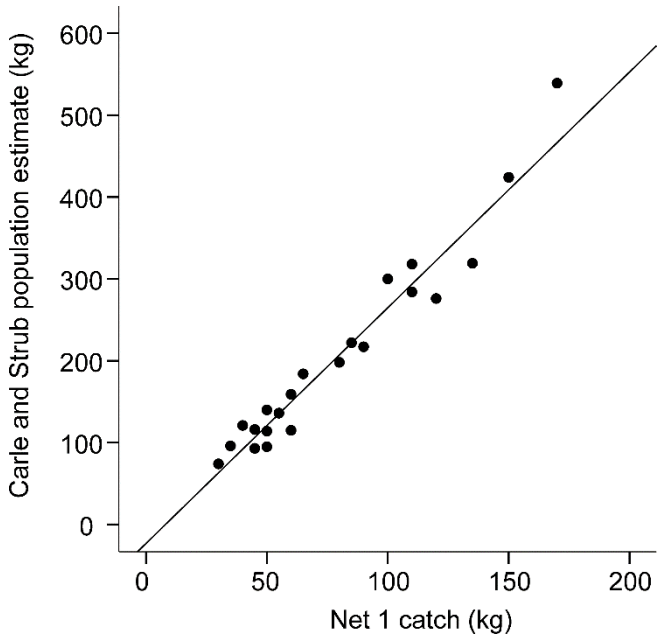

Figure 6.3. The relationship between catch in net 1 of the Athlone removal series (n =30) and Carle and Strub population estimates.

The results of two mark-recapture experiments (n = 50 eels each) showed that mean capture efficiency was 57 % and this was also used to calculate daily population sizes (N_{mr}; Eq. 6.3). Analysis of accuracy (Eq. 6.4) revealed that removal estimates of silver eel abundance were consistently negatively biased compared to mark-recapture estimates (Mean = -14.1%; range, -29.1 – +4.1 %). Despite being negatively biased on all but one night, removal and mark-recapture estimates were strongly related (R^2 = 0.96, $p < 0.001$; Figure 6.4). Additionally, nightly estimates of population size for each method did not differ significantly (Mann-Whitney *U*-test, p = 0.169). This

suggests that the removal model estimates were sufficiently similar to mark-recapture estimates and could provide a robust method of calculating eel population size. The estimate of population size based on double and extrapolated single net nights (10,211 kg) was combined with catch from an upstream fishing site (1,519 kg; T&T catch from site S3, chapter 1) to give an estimate of production in the upper catchment of 11,730 kg. To facilitate comparisons with other studies these values was converted to $kg.ha^{-1}$ (upper catchment = 18,685 ha; 0.63 $kg.ha^{-1}$).

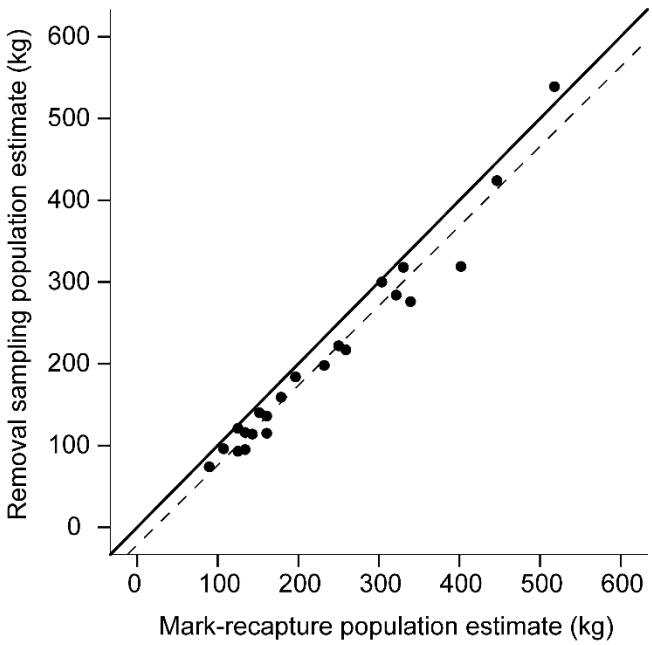

Figure 6.4. Relationship between population estimates from mark-recapture and removal sampling from Athlone. Solid line represents 1:1 relationship, while dashed line represents the regression line ($R^2 = 0.96$, $n = 30$, $p < 0.001$).

6.3.2. Ferny Gap

In total 15,091 kg of eels (median = 62 kg, range = 0 – 1,780 kg) were caught at the Ferny Gap site, with fishing occurring on 94 days between 1/09/18 and 7/12/18. Two nets were fishing in the navigation channel on 20 nights (Figure 6.5A). On these nights, a total of 7,375 kg caught in all nets at the site (49 % of seasons catch), but only 1,259 kg were captured in the removal nets (Figure 6.5B). Nights when two nets were fished in the main channel were used to generate population estimates (Eq. 6.2)

and it was estimated that 1,435 kg were upstream of the removal nets. Based on this estimate, capture efficiency (Eq. 6.2) of the removal series was calculated as 87.7%. Catch from the first net in the removal series was significantly related to Carle and Strub population estimates ($R^2 = 0.748$, $p < 0.001$). Based on this relationship, catches from single net nights (n = 74) were used to produce population estimates and suggested that an additional 2,249 kg of eels were upstream during single net deployments, meaning that 3,684 kg were estimated to have been upstream over the entire season.

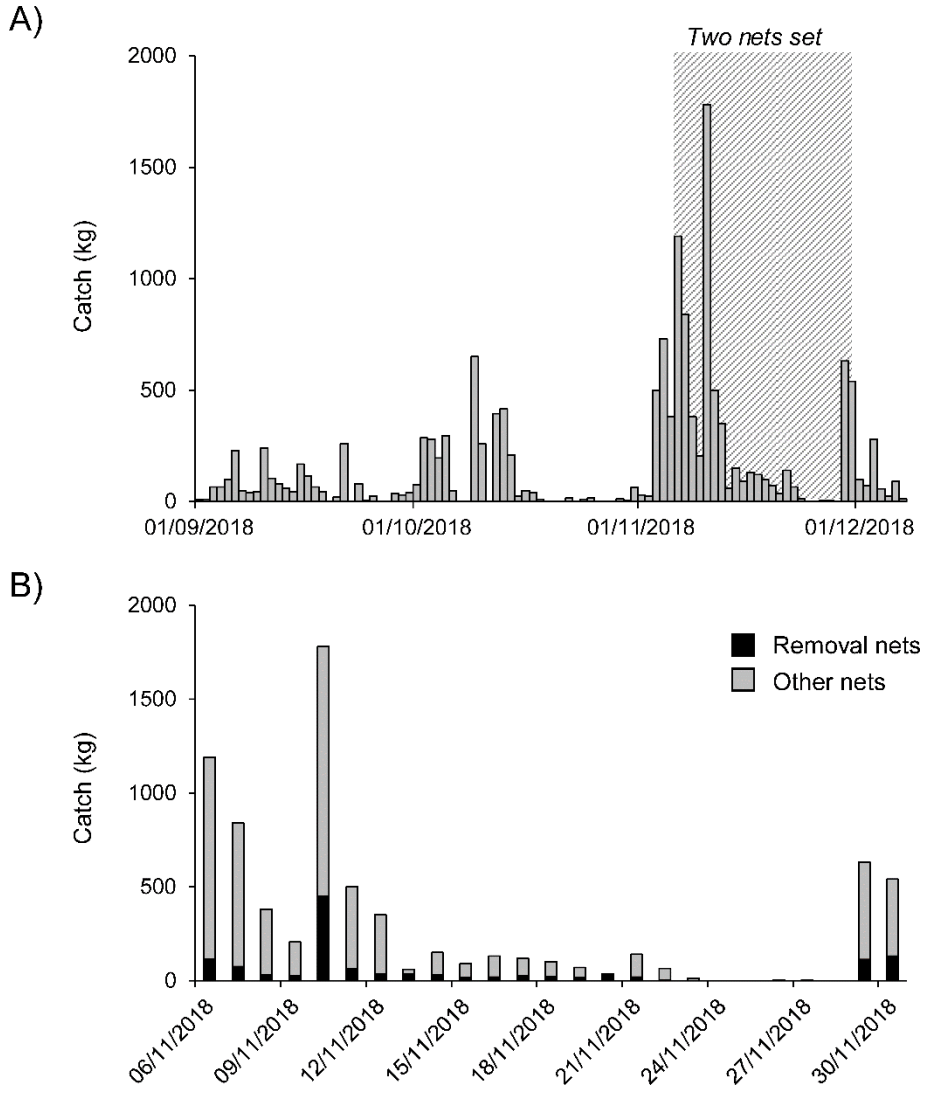

Figure 6.5. A) The seasonal catch pattern at the Ferny Gap fishing site. The period of time when two nets were set in the navigation channel is indicated. B) The proportion of total catch caught in removal nets compared other nets during this period. (northern net and southern nets combined).

A single mark-recapture experiment was conducted at the Ferny Gap fishing site to determine the efficiency of fishing (n = 100 eels). Despite being released directly upstream of the removal nets, eels used all available routes with 5 eels caught in the removal nets, 8 in the northern net 3 in the southern nets. Therefore, out of 100 released eel, 16 were recaptured. The efficiency for the removal nets (5%) and daily catches were used to calculate daily population sizes (N_{mr}; Eq. 6.3). Analysis of accuracy (Eq. 6.4) suggested that removal estimates were highly negatively biased compared to mark-recapture estimates (mean = -95.9%, range = -93.4 to -96.2 %). Given the level of bias associated with removal sampling and the disparity between mark-recapture (5%) and removal sampling (87.7%) estimates of capture efficiencies in the removal nets, it was deemed inappropriate to use the removal method to estimate production.

6.4. Discussion

Sampling methodologies, models and analytical methods are constantly being refined (e.g. Aprahamian et al., 2007; Prigge et al., 2013). However, the overall objective of quantifying silver eel production has remained difficult. The results of this study provide evidence that removal sampling can assist with the estimation of silver eel abundance in certain circumstances. Although population estimates generated at the lake sampling site were highly biased, the same protocol applied to the riverine site fared much better. At the riverine site removal sampling gave robust population size estimates, comparable to those calculated from mark-recapture experiments. As removal sampling has been calibrated against mark-recapture results, production can be estimated in future based on catch data sheets submitted by the fishing crew as part of trap and transport.

At the Ferny Gap fishing site, catch data and tagging revealed that eels used all available migration routes despite the prior expectation that most eels would migrate via the deeper navigation channel. As such, many eels left the basin without ever passing the removal nets. This represented a major challenge as removal sampling requires that a large proportion of the population is captured in order to generate precise estimates of population size (Zippin, 1958). Sequential nets would need to be deployed in each potential migration route to fully assess the population size vulnerable to capture. However, site characteristics mean that this is not a viable

solution at present. Kelso and Shuter (1989) also noted that there were serious issues associated with the application of removal sampling to lake sites and found that sampling efficiency could remain constant, increase or decrease between trappings. When this occurs, population abundance can be severely underestimated (van Poorten et al., 2017). For these reasons, the removal sampling method was deemed inappropriate for this lake site and was not used to produce estimates of production. In less complex lake sites, where eels are limited to a single migration route, the removal sampling method might perform better.

The Athlone site was far less complex with all eels migrating within a single channel. As such, capture efficiency based on removal sampling (63.9%) was much closer to that estimated from mark-recapture (57%). Despite being negatively biased (mean = -14.1%), population estimates from removal sampling were strongly related to those based on tagging ($R^2 = 0.96$, $p < 0.001$; Figure 6.4) and suggest that removal sampling provided reliable estimates of population size above Athlone. These results are of particular interest as production in the Shannon has undergone a significant decline from *c.*170 t in 1986 to *c.*38 t in 2019. Production in the upper catchment (11,730 kg in 18,685 ha^{-1}; 0.63 $kg.ha^{-1}$) was lower than the catchment overall (32,580 kg in 42,466 ha^{-1} [0.77 $kg.ha^{-1}$]; chapter 2). By removing the upper catchment from total production, the lower catchment was estimated to have produced 0.88 $kg.ha^{-1}$ (20,850 kg in 23,781 ha^{-1}). The difference in production is likely due to stocking practices and a legacy of poor recruitment. The presence of hydropower facilities in the lower catchment means that recruitment relies on the capture of eels at barriers for stocking upstream. Detailed data on the stocking of juvenile eels to the Shannon can be found in Quigley and O'Brien (1997). From 1968 to 1986 approximately 91 million elvers were stocked to the upper catchment, with an additional 103 million stocked to the lower catchment. However, recruitment decreased dramatically from the mid-1980's and stocking between 1987 and 2008 involved only 40 million elvers, all of which were released immediately above hydropower structures in the lower catchment. Age data for eels from lakes in the mid and upper Shannon catchment (Arai et al., 2006; Yokouchi et al., 2009) shows that eels stocked to the upper catchment (i.e. prior to 1987) have long since matured and emigrated from the catchment. This study revealed differential production within the Shannon catchment and suggests that natural dispersion of eels

stocked in the lower catchment is insufficient to allow juvenile eels colonise all available habitat in the upper catchment.

Although useful for assessing compliance with the EU eel regulation, the removal sampling method developed here will be useful for other Regulations. The Habitats Directive (92/43/EEC) requires Member States to maintain and restore habitats and ensure the conservation status of species. Similarly, the Water Framework Direct (2000/6/EC) requires that waterbodies have good ecological status or potential. Assessing compliance with both of these Regulations requires that fish populations trends are monitored. In most rivers, this is achieved through the use of removal sampling applied to data collected as part of electric fishing surveys for eels, salmonids and coarse fish (Baldwin and Aprahamian, 2012). Monitoring fish populations as part of the Habitats Directive requires that all habitats occupied by a species during its life are sampled. However, it has been noted that removal methods are less successful in large rivers (Knights et al., 2001; Cowx et al., 2009), with electric fishing being limited to shallow water (< 0.5 m). The results of this study revealed that sequential paired nets were capable of producing reliable estimates of silver eel abundance, extending the power of removal sampling to large, mainstem rivers.

Chapter 7: General Discussion

Eel management plans initiated in response to the EU regulation have been in place for more than a decade. Analyses of linear trends suggest that there has been a slight increase in glass eel recruitment to European water (ICES, 2018a) and raises hopes that management actions adopted to date are having the desired effect. However, only six out of 16 countries reporting in 2018 were achieving the EU's escapement target (ICES, 2018a) and actively contributing to the restoration of the stock. As such, information on effective mitigation measures to restore river connectivity is needed to enhance silver eel escapement levels (chapters 2 and 3). Similarly, it became clear through the review chapter (chapter 2) that a reliance on catch data in most areas represents a limiting factor to the robust estimation of escapement. Therefore, additional monitoring protocols developed in this thesis are needed to supplement existing monitoring programmes (chapters 4, 5 and 6).

7.1. Hydropower mitigation measures

The impacts of anthropogenic structures on diadromous fish migrations are well documented, with fishes injured, killed and partially or wholly prevented from accessing habitat essential for the completion of their life-cycles (Limburg and Waldman, 2009). A range of indirect effects associated with dam passage have also been noted and can impact the ability of fishes to complete spawning migration (Drouineau et al., 2017). With many of Europe's and North America's large dams built in the early 20th century and fast approaching the end of their functional lifespan due to structural degradation (Stanley and Doyle, 2003), the complete removal of barriers is increasingly viewed as a panacea for issues related to fish passage. The benefits of dam removal for diadromous fish populations have been well documented, with the rapid recovery of populations possible (Roni et al., 2002), including for eels (Turner et al., 2018). However, the removal of barriers is not always feasible for social, economic or practical reasons (Doyle et al., 2003). For example, although dams on the Rivers Shannon and Erne no longer play a key role in hydropower generation, they are still important for flood control (OPW, 2012), and efforts will be made to prolong the life-span of these dams. Additionally, the demand for clean, carbon free energy is increasing globally, and legislation is prioritising sources of renewable energy. For

example, the EU Renewable Energy Directive 2009 (2009/28/EC) requires that 20% of Europe's gross energy consumption be sourced from renewable sources and it is anticipated that hydropower will represent the second largest contributor to this, after wind-power. Interestingly, this places the EU Renewable Energy Directive at odds with the EU Water Framework Directive (2000/60/EC), which seeks to ensure the sustainable management of EU waters and restoration of aquatic habitat to good quality. Most opportunities for large hydropower facilities in European rivers have been utilised, meaning further expansion of hydropower capacity will involve the construction of low-head dams. These dams are difficult to mitigate as physical barriers and bypasses can significantly reduce generation potential, meaning most options for mitigation are financially unviable.

Where effective diversion of fish to alternative migration routes is not possible, trap and transport (T&T) is recognised as a practical solution (chapter 2; Richkus and Dixon, 2003). Therefore, it appears likely that T&T will continue to be an important conservation tool in future. Indeed, Hanel et al. (2019) recommend that T&T be expanded to more European river systems, even if only in the short-term, to enhance silver eel escapement. To mitigate against hydropower mortality on the Rivers Shannon and Erne, catchment-wide T&T programmes were initiated in 2009. Capture targets, set by the Standing Scientific Committee on Eel, were generally achieved and proved important for reducing anthropogenic mortality to a level that should allow recruitment to recover in the future (assuming equal effort among Member States; chapter 2). In total, more that 2 million eels have been released with the majority being female eels. This represents a significant local contribution to the spawning stock. However, clear differences exist between the Shannon and Erne T&T programmes. It appeared that the efficiency of a T&T depends on system specific factors, primarily the number of dams and the presence of alternative migration routes. As seen on the Erne, successive dams resulted in a cumulative mortality rate. However, in the lower Shannon, 21.15% of eels migrating via Ardnacrusha dam are expected to suffer mortality, meaning that in the absence of T&T, the majority of eels would still survive turbine passage. Therefore, the effectiveness of T&T is directly linked to the number of hydropower stations bypassed and suggests that new T&T programmes initiated throughout Europe should first target rivers with multiple dams. Conversely, rivers

with only one dam, or alternative migration routes should consider other mitigation measures prior to T&T.

As a mitigation measure for silver eels, T&T has been adopted in six European countries in an attempt to reduce mortality (ICES, 2019). To date, in excess of five million eels have been released from European rivers and Ireland has represented the greatest contributor to this quantity (2.4 million; Figure 7.1). Most of these programmes were established to protect eels from hydropower dam turbine mortality. However, in some areas of Europe, pumping stations, rather than hydropower dams, represent the primary source of mortality for downstream migrating eels. Mortality rates as high as 97% have been recorded at these stations (Buysse et al., 2014) and it appears likely that expansion of T&T programmes to new rivers will increasingly focus on mitigating against pumping stations. In the Dutch polders alone, in excess of 3,000 pumping stations are used for drainage. Although efforts have been made to develop pumping station specific fish passes (Kroes et al., 2006), the sheer quantity of stations that would require retrofitting to allow effective eel passage means that T&T is currently considered the most cost effective means of restoring river connectivity (van der Meer, 2012).

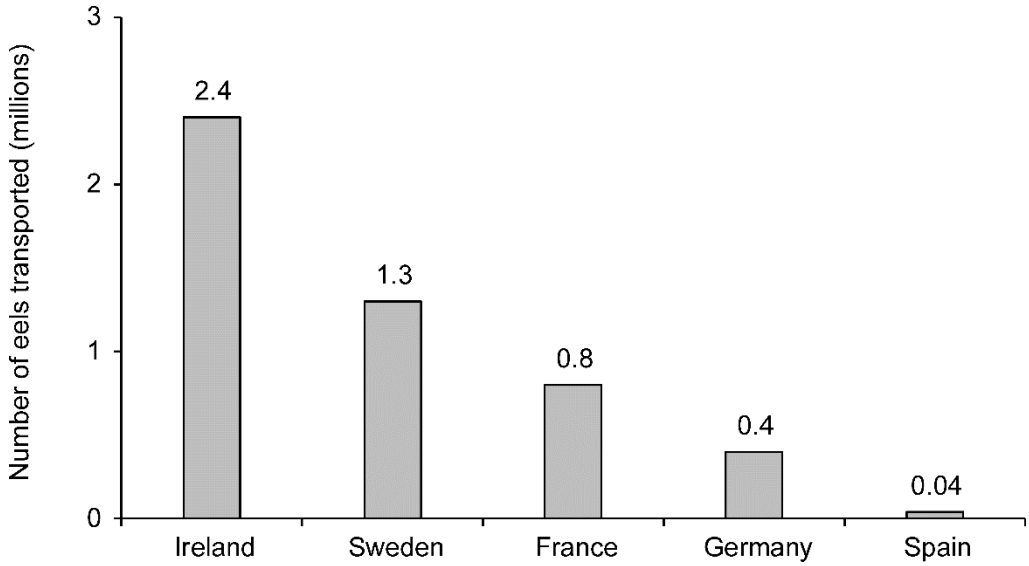

Figure 7.1. The number of eels (in millions) estimated to have been captured and released downstream of anthropogenic structures in five European countries (data from ICES, 2019).

Although most silver eel T&T involves the capture of eels upstream of structures and release to river sections with good seaward connectivity, less conventional forms of T&T also occur in Europe and globally. For example, an initiative was introduced whereby approximately 200,000 eels so far have been captured in commercial fisheries in France's Mediterranean lagoons. These eels are then released beyond the lagoons to protect them from further capture and to continue their migrations (PGA, 2018). On the St. Lawrence in North America, American eels (*Anguilla rostrata*) caught as bycatch in multi-species fisheries are released downstream of hydropower structures (Béguer-Pon et al., 2018). A now discontinued practice in Taiwan saw Japanese eel (*A. japonica*), artificially matured and transported for release in rivers or at sea near supposed spawning grounds (Tzeng, 2011). These alternative forms highlight the versatility of T&T as a conservation measure and the various ways programmes can be implemented in future.

Trap and transport in Ireland was only intended as an interim solution while long-term alternatives were researched (DCENR, 2008). To help facilitate escapement in the lower Shannon, an assessment of a strobe light array (chapter 3) showed considerable promise as a mitigation measure. On average, 80.3% of eel migrating towards Killaloe eel weir were prevented from entering a selected arch and were successfully guided towards a desired location. Sheridan et al. (2014) concluded that submerged low voltage LED strobe light arrays represent one of the most promising guidance technologies available for use at turbine intakes. Studies have shown that when fish are prevented from entering turbines and are simultaneously guided to a safe alternative route, mortality rates as low at zero can be achieved (Økland et al., 2019). In the lower Shannon, the river is split in two by a water regulating weir. One route leads to a hydropower station, where all eels must pass via turbines. The other route represents the natural river channel. Eels were found to be capable of escaping via the natural river route when sluice gates to this river section were open. This highlights the potential of this channel to enhance eel escapement. Releasing spill water to this route and simultaneously using strobe lighting to guide eels towards the channel could ameliorate passage issues and reduce or eliminate the need for extensive T&T programmes. However, spillage can result in significant economic losses to hydropower generation and, at present, there is a clear duality between hydropower

production and eel conservation. The management of these resources should be assessed as interconnected processes. Efforts are being made to develop decision frameworks to help hydropower stakeholders and fisheries managers make informed decisions on the conservation of eel and water resources (e.g. Teichert et al., 2020).

At present, it appears that the results of the light deflection experiment could be most usefully applied to increase the efficiency of T&T operations. Several early studies increased fisheries yields by using lights to guide silver eels towards nets (e.g. Petersen, 1906; Lowe, 1952). Previous studies have highlighted that high capture effort is required for a T&T programme to successfully safeguard sufficient quantities of eels (Piper et al., 2020). In many countries with T&T programmes, the proportion of migrating eels captured and transported is too low. For example, in Germany, 12 t of eels were transported annually between 2013 and 2016 from three river basins (Hanel et al., 2019). However, when it is considered that production in these three catchments was estimated to be approximately 2,500 t (ICES, 2016b), the quantities transported were negligible (<1% of migrating eels). By comparison, between 2009 and 2019, 39% and 53% of eels migrating in the Shannon and Erne respectively were captured and released safely downstream of hydropower structure. Future work should be directed towards optimising the efficiency of eel T&T through the use of artificial light.

7.2 New approaches to meet monitoring needs

In this thesis a number of candidate protocols for quantifying silver eel dynamics were developed. Chapter 4 describes the use of generalised additive models (GAMs) to assess the role of various environmental factors on silver eel catches and how they can facilitate the assessment of production and escapement. In chapter 5, an acoustic camera (DIDSON) was used to predict catch at an eel fishing weir. The acoustic camera was also used to assess silver eel route selection and can assist in the identification of migration barriers, detection of mortality hotspots, development of appropriate eel conservation measures and the calculation of escapement. Removal sampling is widely used in inland fisheries to quantify absolute population size. However, it has been noted that problems arise when removal sampling is applied to estimate fish abundance in large rivers. The net-based method of estimating silver eel

production developed in chapter 6 extends the power of removal sampling to large, mainstem rivers.

EU Member States are required to provide information on silver eel production (i.e. potential escapement) and actual escapement annually. This information is used to confirm compliance with the EU escapement target, or lack thereof. While evaluating Ireland's T&T programmes, it became clear that there were substantial discontinuities in catch records used to assess silver eel production and escapement in the Shannon and Erne. Catch data is only considered robust where fishing covers the entire migration period (Robinet et al., 2007). Unfortunately, gaps frequently occur due to unfavourable environmental conditions (chapter 2) or the implementation of fisheries regulations aiming to decrease fishing effort and rates of exploitation. For example, implementation of the Total Allowable Catch (TAC) quota system in France lead to dramatic shifts in fishing strategies, with crews preferentially targeting nights when the largest catches were expected. Examples such as this represent a significant challenge to the calculation of population parameters based on commercial catch data. ICES (2019) has noted that 68% of silver eel escapement estimates reported from European catchments are based on commercial fisheries data. Although the Data Collection Regulation (EC no. 199/2008) provides a framework for the collection, management and use of fisheries data relating to the European eel, uncertainties remain over issues relating to data quality, availability and gaps in methodology. This framework requires Member States to provide detailed data on fisheries effort and capacity. However, sampling the various life stages of eels involves active (e.g. dipnets) and passive (fyke-nets, pots and traps) methods and a lack of a standardised reporting of fishing effort to accompany landings data has affected interpretation. Since 2017, the EU Multi-Annual Plan (EU MAP; EC 2016/1251) has sought to standardise monitoring methodologies for all life stages of eels. However, coordinating the collection and sharing of comparable datasets between countries remains a significant challenge. Additionally, at present there is no requirement for sampling to continue in the case of fisheries closure. Given that efforts are being made to reduce anthropogenic mortality as close as possible to zero, it is likely that fisheries will continue to cease in future. Therefore, until EU MAP harmonizes data collection, it is important that data collection embraces both fisheries and non-fisheries data

sources in the interim to help close gaps in datasets used to assess silver eel production and escapement.

While gaps in catch records represent a major problem for stock assessments, many European catchments completely lack quantitative data on silver eel migrations. The paucity of data has been acknowledged and has resulted in a variety of habitat and demographic models to predict silver eel production and escapement (see Walker et al., 2011). These models seek to extrapolate from monitored, 'data rich' catchments, to data poor catchments, which are unmonitored. For example, in Ireland, five catchments (including the Shannon and Erne) are considered to be 'data rich' in relation to eel biological reference points, 17 are listed as poor and 242 have little to no data (Walker et al., 2011). When extrapolating to data poor catchments, it is necessary to assume that eel characteristics are the same in all rivers. In reality, eel stock characteristics vary widely, even within small geographical areas, and extrapolation can lead to major under- or over-estimations of production for rivers without data. Several studies have highlighted that silver eel migrations have site specific characteristics (chapter 4; Sandlund et al., 2017). The monitoring methods developed in this thesis could provide versatile means of gathering catchment specific data to ground-truth model assumptions about eel productivity.

In establishing a possible monitoring framework for eels, it was appreciated that the methods developed here will be applicable to other life stages and species of eels, as well as other diadromous fish. Along with the European eel, the Japanese eel and the American eel represent the most commercially valuable Anguillid species. Both of these species are listed as endangered (Jacoby et al., 2015). Like the European eel, information on silver eel escapement is the most relevant metric for American and Japanese eel population assessments and, again, assessments tend to rely on fisheries data (De Lafontaine et al., 2010; Kaifu and Yokouchi, 2019). Therefore, the methods developed here will be of interest to eel researchers globally. Additionally, 39% of Europe's freshwater fish species are currently listed as threatened (Freyhof and Brooks, 2011), one of the highest rates among major taxonomic groups. As such, a number of diadromous fish are listed as species of interest in the Habitats Directive (92/43/EEC) and the Convention on Migratory Species, including shad (*Alosa alosa*) and sea lamprey (*Petromyzon marinus*). Similarly, Atlantic salmon (*Salmo salar*) are the target of protection or recommendations under the North Atlantic Salmon

Conservation Organisation. Confirming compliance with goals set out by these various organisations and regulations will require accurate information on their abundance. Hydroacoustic techniques have successfully been applied to assess aspects of shad (Grote et al., 2014), lamprey (McCann et al., 2018) and salmonid life-cycles (e.g. Burwen et al., 2010). The methods developed in this study could be applied to provide quantitative information on migrations in these species. In addition to assessing abundance, GAMs have previously been used extensively in ecological research to monitoring fish distributions and preferred habitat characteristics (Buisson et al., 2008; Lankowicz et al., 2020). Understanding fish occurrence and habitat needs are vital for the development of adequate monitoring programmes and to enable the sampling of representative sites of discrete populations.

Several rivers throughout Ireland and the UK have been designated as Special Areas of Conservation (SACs) as part of the Habitats Directive. Within these SACs, fish monitoring seeks to detect changes in populations abundance and demographic structure in order to inform management decisions (Cowx et al., 2009). These assessment criteria are complementary to those recommended for fish assessment under the Water Framework Directive (2000/60/EC) which considers fish as biological quality elements (BQEs) which help to determine the ecological status of water bodies (rivers, lakes and transitional waters). Electric fishing, using removal models, is often considered the best method for monitoring fish populations as part of these Directives. This is because the results of electric fishing surveys can provide a good measure of the distribution and abundance of species, as well as an assessment of their demographic structure. However, electric fishing is restricted to shallow water (<0.5 m) and problems arise with the reliable assessment of fish populations in large, mainstem rivers. This is an issue as sampling must incorporate information on all habitats populated by a species. The method developed in chapter 6, repeatedly sampling migrating eels with sequentially deployed nets, extends the power of removal sampling to deeper rivers. However, this method is currently only useful for eels and when designing monitoring programmes, it is important that sampling is representative of range of fish species in the target river. In addition to eels, removal sampling is commonly used for salmonids and coarse fish and the method developed in chapter 6 will be compatible with existing monitoring programmes for these species. Other species designated for protection in Ireland as part of the Habitats

Directive, such as lamprey species and shad (*Alosa fallax*) are frequenctly sampled with nets (fyke and gill respectively; King and Linnane , 2004) and efforts should be made in future to determine if the results presented in chapter 6 are applicable to other net types. If possible, it will be possible to sample all fish protected as part of the Habitats Directive using comparable removal sampling methodologies.

7.3. Future research needs: silver eel quality

This thesis evaluated mitigation measures that seek to enhance eel escapement and developed novel monitoring protocols to accurately quantify this biomass. However, not all eels successfully leaving a river will be physiologically capable of reaching spawning grounds due to the adverse effects of infection with viruses or parasites and insufficient fat reserves. Silver eels monitoring programmes should aim to establish the proportion of escapees that are of sufficient quality to reach the spawning grounds, breed and produce viable larvae. Estimation of this 'effective' spawner biomass should be undertaken in all countries in order to assess the actual contribution made by particular rivers.

A standardised approach would be adopted across Member States and should request that a sub-sample of representative eels are sacrificed and examined for fat content, pathogens and levels of contamination from metals and organic chemicals. Several laboratory experiments using swim-tanks to simulate the oceanic migrations of eels have revealed that a fat content in the region of 12% is required to fuel trans-Atlantic migrations, while an additional 8% is thought to be necessary to allow successful reproduction following arrival at spawning grounds (van den Thillart et al., 2007; Palstra and van den Thillart, 2010). Among pathogens, the invasive nematode *Anguillicola crassus* (Figure 7.2) is considered the most damaging to the eel stock. The parasite was introduced to Europe through the importation of its original host, the Japanese eel. First recorded in Ireland in the 1990's (Evans et al., 1999), the parasite is now found in at least 75% of Ireland's wetted area (Becerra-Jurado et al., 2014), with prevalence ranging from 60 – 80% in both yellow and silver eels. The parasite damages the swimbladder of European eel, impacting their oceanic swimming performance (Palstra et al., 2007). The Eel Quality Database (e.g. Belpaire et al., 2011) suggest that further impacts should be measured, including contamination levels (e.g.

Capoccioni et al., 2020). Very little is known about contamination in Irish eels, beyond reports for the Burishoole and Corrib catchments (Bourillon et al., 2020). However, chemical contaminants can accumulate in the lipid, muscle and organs of eels during their residential life-phase and can remobilise during migration and be redirected to the developing gonads and eggs. This is thought to result in a range of disruptions to biological functions (Geeraerts and Belpaire, 2010) and result in embryotoxicology in future eggs, further damaging the stock.

Figure 7.2. Two Anguillacola crassus nematodes in the swim bladder of an eel captured at Killaloe (Photo: Eamonn Lenihan).

An initial attempt to estimate effective spawner escapement was conducted by Conneely (2011) and raised serious concerns about the quality of Irish eels. Analyses between 2009 – 2011 found that only 10.5% of Shannon (82 out of 780) and 23.3% of Erne (100 out of 430) silver eels assessed were considered of sufficient quality to reach spawning grounds, based on fat content (>12%) and the absence of *A. crassus*. At present, the calculation of escapement from Irish rivers does not include information on eel quality. Therefore, escapement values reported for the Shannon and Erne (chapter 2) may drastically overestimate the contribution these rivers make to effective eel spawner biomass.

The analyses of Conneely (2011) were overly simplistic in their treatment of *A. crassus* infections. It was assumed that any eel infected could not successfully reach spawning grounds and contribute to spawning, though this is not necessarily accurate. Instead, it is now considered more appropriate to measure the damage done to the swimbladder, using a measure called the 'swimbladder degenerative index' developed by Lefebvre et al. (2002). Eels scoring a zero on this index are considered to have normal, healthy swim bladders exhibiting no damage or evidence of infection, past or present, with *A. crassus*. Eels with a low score on this index have moderate damage to the swimbladder but are still likely to be capable of successfully migrating. Those scoring higher will have profoundly damaged swimbladders with limited capacity to regulate gas exchange and buoyancy. The parasite burden an eel has can also impact migration success, with the cost of migration estimated to be far higher in heavily burdened eels, often leaving eels with insufficient reserves to spawn (Clevestam et al., 2011). Therefore, new analyses that consider parasite burden and the extent of swimbladder damage need to be conducted and incorporated into assessments of Irish eel escapement in future.

The latest introductions of eel pathogens to Ireland are viral diseases, (e.g. EVE and EVEX, McConville et al., 2018), and these are likely to have arrived via importations of live glass eels from continental Europe for stocking the commercial fishery in Lough Neagh, Northern Ireland. The impact of these pathogens on Irish eel stocks and the extent to which they affect spawner biomass escapement from major Irish rivers remains to be determined. Although migrating silver eels sampled from the Shannon in 2018 were free from viruses (Lenihan et al., unpublished data), it is important that biosecurity protocols adopted by conservation agencies involved in eel research are continued to avoid the spread of invasive species or pathogens, especially where this involves movement between Lough Neagh and the Erne catchment.

A further concern to the accurate estimation of escapement, is delayed mortality and sub-lethal effects resulting from dam passage. Due to their elongate morphology, eels suffer a variety of injuries during dam passage, including abrasions, bruising, lacerations, haemorrhage, crushing of body parts and damage to the jaws, eyes and skin (Bolland et al., 2019). However, most assessments of mortality focus on direct mortality stemming from the impacts of turbines, while the delayed mortality of eels following passage receives little attention. Eels with and without visible injuries often

display abnormal behaviour following passage through anthropogenic structures (Bolland et al.,2019) and the potential energetic costs and stress associated with this can result in considerable sub-lethal effects including reduced body condition and reduced spawning success (Pankhurst and van der Kraak, 1997). Efforts should be made to study delayed mortality following dam passage. For example, eels could be captured downstream of hydropower structures using nets and transferred to a suitable storage site for monitoring over a period of 48 – 72 hours following turbine passage (e.g. Buysse et al., 2015).

The problems associated with injury and abnormal behaviour can be exacerbated by predators. The greater cormorant, *Phalacrocorax carbo*, has been a source of both real and perceived conflict with humans in relation to fisheries exploitation. Interestingly, Östman et al. (2013) noted that the impact of cormorants on silver eel escapement from two Swedish catchments was of the same magnitude as commercial fisheries, a finding supported elsewhere in the Baltic by Hansson et al. (2017). Given that considerable roosts of cormorants exist downstream of Ardnacrusha on the Shannon, new efforts to assess their impact on eel escapement is required. The EU Regulation lists reducing predation as a possible conservation option to help achieve the escapement target of 40%. However, predation is not currently included in the assessment of escapement from Irish catchments. Ireland's national eel management plan submitted that predation on eels is a major, but relatively unknown, factor in the population dynamics of eels, and represents natural mortality. However, where increased predation rates occur due to injuries suffered during dam passage, mortality should be considered as an anthropogenic factors impacting escapement.

Although the results of this thesis revealed that Ireland's T&T facilitated the escapement of large quantities of silver eels (chapter 2), little is known about the physiological toll of this process on eels. T&T necessitates the storage of fish while awaiting release. In Ireland's trap and transport programmes, eels are given at least 24 hours to recover prior to collection, with collections subsequently scheduled every two to five days depending on catch levels. In some systems, where catches are smaller, eels are often held for longer. Piper et al. (2020) held captured eels for up to eight days before releasing them. While not ideal, holding fish for prolonged periods of time is often necessary in smaller operations, as the frequent release of small quantities of eels may not be economically viable. Although silver eels can tolerate storage for

prolonged periods of time as they are non-feeding (Tesch, 2003), it has been observed in other species that stress associated with the cumulative effects of capture, handling and storage can dramatically reduce disease resistance, osmoregulatory ability and swimming performance (Maule et al., 1988). To date, no studies on silver eel trap and transport (e.g. Béguer-Pon et al., 2018; Piper et al., 2020) have considered the physiological effects of T&T on eels. Therefore, for a complete assessment of trap and transport's value as a conservation strategy, an assessment of the delayed effects of the process is required.

7.4. Conclusions

The EU Regulation EC No. 1100/2007 requires Member States to reduce anthropogenic mortality rates in order to enhance the escapement of silver eels. However, it is acknowledged that our knowledge of appropriate mitigation measures is hindering Member States abilities to achieve management goals. Policy makers require accurate scientific information on appropriate mitigation measures. This thesis provided new insights into two mitigation measures aiming to reduce hydropower mortality rates. It was observed that trap and transport programmes can provide a robust means of enhancing escapement. However, the effectiveness of these programmes appears to depend on the number of dams present in a river and whether alternative migration routes are present. The expansion of trap and transport to new rivers should preferentially target heavily regulated rivers to maximise the benefits of these costly programmes. In rivers where the provision of a safe migration route around dams is possible, behavioural barriers (such as light arrays) could prove a valuable method of guiding eels to desired locations. Although most applications will target eels directly at structures, at present light arrays could most usefully be deployed to artificially increase the efficiency of conservation fisheries. For example, light arrays could be used to guide eels away from unfished river sections towards areas containing nets. Any modifications that artificially increasing weir efficiency using lights and thereby increases the biomass of eels released as part of trap and transport represents an effective mitigation measure. This also effectively reduces the numbers migrating downstream and passing through hydropower structures.

The ability to quantitatively assess the biomass of eels produced in and escaping from rivers is vital to assessing the effectiveness of conservation programmes and to confirm compliance with targets. Although traditionally reliant on fisheries catch data, alternative methods developed in chapters 4, 5 and 6 will help ensure that the continuous monitoring of eel migrations is possible, enabling the robust estimation of production and escapement. The use of acoustic cameras, models and net-based removal sampling represent flexible methodologies that will be applicable to eel populations across Europe but also to other Anguillid species, many of which are listed as threatened or near-threatened.

Although these new monitoring protocols will help ensure estimates of spawner escapement are accurate, it is important to recognise that not all eels that leave rivers are capable of reaching spawning grounds and reproducing. In future, efforts should be made to incorporate details on pathogens, contamination, body condition and injuries into estimates of escapement. Estimation of this ‘effective’ spawner biomass should be undertaken in all countries in order to assess the actual contribution made by particular rivers.

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