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The Foraging Specialisms, Movement and Migratory Behaviour of the European Eel

by

James Barry

BSc., National University of Ireland, Cork, 2009

MSc., University of Aberdeen, Scotland, 2010

Scottish Centre for Ecology & Natural Environment, Institute of
Biodiversity, Animal Health & Comparative Medicine, College of
Medical, Veterinary & Life Sciences

University of Glasgow

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"The mysterious eel"

Design by CaillicoCuts 2015

Abstract

The European eel is a mysterious animal and has a life cycle which has fascinated biologists for centuries. However many basic aspects of its life cycle and migrations remain unknown. European eels play a pivotal role in a balanced ecosystem both as a predator and prey species thus, understanding important ecological aspects of eel behaviour while resident in continental waters is vital in safeguarding and enhancing existing stocks.

In recent years we have witnessed declines in juvenile eel recruitment across Europe. Results from this thesis indicate a drastic decline in yellow eel abundance in a transitional water body in Northern Ireland between 1967 and 2013, with current levels at 3.38% of historical levels in the Foyle estuary. Many populations across Europe are thought to be reduced to approximately 10% of their size in the yellow eel growth phase of their life-cycle and juvenile recruitment to this phase is as low as 5% compared with 30 years ago. However, the continental phase in which eels spend up to 30 years before undertaking their spawning migration allows managers to direct effective conservation strategies.

The existence of two morphotypes “broad-headed” and “narrow-headed” in the European eel has been historically documented and this discrete head shape variation has interested biologists across Europe for a considerable amount of time. This phenotypic variation is widespread across the panmictic eel population. The findings presented in this thesis have highlighted the importance of understanding the ecology of alternative phenotypes which can exist in European eels co-occurring within the same habitat, and results suggest there may be potential consequences on life history as a result of foraging strategy undertaken in a growth habitat, with varying lipid stores and growth rates found between individuals. These alternative foraging strategies’ which manifest themselves in head shape variability corresponded to significant variation in space use and activity patterns in lacustrine growth habitat. This provides the first empirical evidence that observed morphological variation leads to significant differences in movement behaviour.

Feeding specialisations during the eel growth phase can have important consequences for population dynamics. Feeding strategies may incur greater risks from, for example, parasites. Intensity levels of the invasive nematode parasite *Anguillicola crassus* were associated with differences in ontogeny and trophic ecology. Infestation levels of parasites in affected fish revealed a significant

negative relationship between fish length and parasite intensity, with smaller individuals having higher parasite intensity than larger individuals. This study indicates that food intake and infection risk are linked in the host-parasite system.

The growth phase for eels in continental waters ends with a transition called “the silvering process” following which individuals begin migrating downstream towards marine waters to undertake their spawning migration to the Sargasso Sea. Understanding migration behaviour, life stage specific mortality and migration success at this important life stage, is critical to effective conservation management. The unimpeded downstream movement patterns and migration success of small female and male silver eels investigated during this study revealed a low success rate to open ocean. Only 26% of eels which initiated downstream migration were detected at the outermost end of an acoustic array located at the mouth of a sea lough. Telemetry equipment functioned efficiently at all locations, therefore this suggests high levels of mortality during sea lough migration, or less likely, long-term sea lough residence by silver eel emigrants.

The overall research approach employed in this study i.e the combination of morphometric, stable isotope analysis and telemetry has allowed vital information to be gathered. Managers can utilise this information to employ appropriate conservation strategies for *Anguilla anguilla* as well as guiding future research directions.

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APPENDIX TWO – Introduced parasite *Anguillicola crassus* infection significantly impedes swim-bladder function in the European eel *Anguilla anguilla* (L.) (Manuscript published: *Journal of Fish Diseases*)

APPENDIX THREE - Local scale, coastal currents influence recruitment to freshwater populations in the European eel *Anguilla anguilla*: A case study from the Isle of Man. (Manuscript published: *Journal of Fish Biology*)

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Author's Declaration

The material presented in this thesis is the result of original research, conducted between February 2012 and April 2015, under the supervision of Professor Colin E. Adams and Dr. Patrick Boylan. This work has not been submitted, in whole or in part towards the fulfilment of any other degree. This work is based solely on data collected and analysed by myself. Any published and unpublished material not of my own is acknowledged in the text.

Signature _____

Printed name: James Barry

Chapter One

An Introduction to the Biology of Eels, with Particular Reference to Resident Growth Phase and Migratory Silver Phase

1.1

GENERAL INTRODUCTION

Anguillid eels are distributed throughout the warm and temperate zones of the world (Tesch, 1977). As a group they are mostly marine but a number of species exhibit catadromous behaviour, migrating into fresh and transitional waters where they grow and then migrate to sea to spawn. The European eel (*Anguilla anguilla* L. 1758) falls within this category. The geographical distribution of the European eel, ranges from Northern Scandinavia to North Africa, and from the Eastern Mediterranean region to the Azores, the latter being the western limit of its distribution. In fact, no other fish stock within the ICES (International Council for the Exploration of Seas) area is as widespread as the European eel. *A.anguilla* has a complex multi stage life cycle encompassing two trans-Atlantic migrations. When resident in continental waterways the eel inhabits a wide range of habitat types covering fresh, brackish and saltwater (Moriarty & Dekker 1997; Harrod *et al.*, 2005).

1.1.1 CURRENT STATUS

The European eel population has been declining and major concerns have been raised over the long term viability of the species (Feunteun, 2002; Dekker, 2003; ICES, 2013). Recruitment has declined rapidly since the early 1980's (Fig. 1.1), and despite showing signs of recovery in recent years, remains at critically low levels (ICES, 2014). The European eel population is thought to be reduced to approximately 10% of its size in the freshwater (yellow eel) phase lifestage and juvenile recruitment to this phase is as low as 5% compared with 30 years ago (ICES, 2013). Despite showing signs of recovery in recent years, the stock remains at critically low levels (ICES, 2014). In an attempt to mitigate this rapid decline legislation within the EU encouraged member countries to reduce fishing pressure and take protective actions to increase silver eel output (spawning stock) from continental waters (EC Reg 1100/2007). In 1998 ICES recommended that all means should be taken to restore the depleted stocks, at all biological stages (Feunteun, 2002). The European eel is now heavily protected and has been added to Annex B of

the Convention on International Trade in Endangered Species (CITES) and to the International Union for the Conservation of Nature (IUCN) Red List as a critically endangered species (Freyhof & Kottelat 2010). Historically eels used to represent more than 50% of the standing fish biomass in most European watersheds (Moriarty & Dekker, 1997), playing a critical role in food webs and having a significant contribution to the functioning of inland hydrosystems, as both a predator and prey species (Laffaille *et al.*, 2003). Given the critical role the European eel plays in a balanced ecosystem it has become a species of high conservation value (Dekker, 2008).

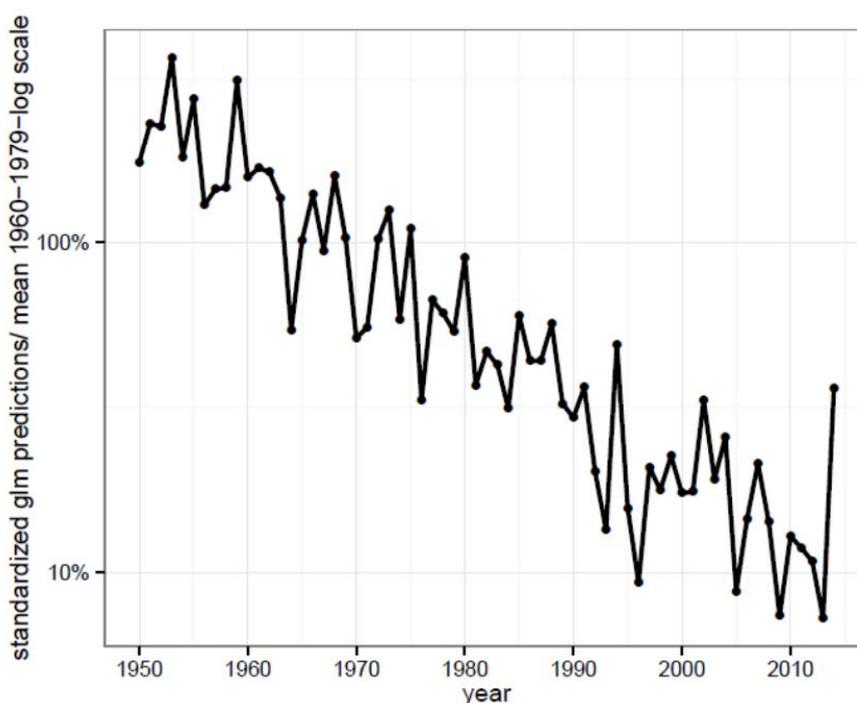


Fig.1.1 ICES eel working group (WGEEL) recruitment index; fitted to 12 yellow eel series and scaled to the 1960-1978 average (source: ICES, 2014)

What is most worrying about the observed decline in the European eel population is that the reasons for this collapse are not fully understood (Astrom & Dekker 2007). There is some evidence that the collapse in recruitment may have been caused by declining spawning stock leaving continental waters (Dekker, 2004), but other data suggests that inland catch declines have been less pronounced and could have been driven by climatic and economic factors (Knights *et al.*, 2003; Kettle *et al.*, 2011). Marine mortality, diminished natural food supplies (Svedäng & Wickstrom, 1997; Feunteun, 2002), infection by the swimbladder parasite *Anguillicola crassus* (Lefebvre *et al.*, 2012; Barry *et al.*, 2014), effects of pollutants

(Castonguay *et al.*, 1994; Geeraerts and Belpaire, 2010), viruses (van Ginneken & Meas, 2005), oceanographic and climatic changes (Knights, 2003; Miller *et al.* 2009; Kettle *et al.*, 2011), over exploitation (Dekker, 2004; Simon *et al.* 2011, Crook & Nakamura, 2013) obstacles to migration (Castonguay *et al.*, 1994; Winter *et al.*, 2006; Pederson *et al.*, 2011) have all been suggested as possible explanations. It is probable that none of these explanations are mutually exclusive and it is more likely interplay between human activities and oceanic fluctuations are responsible for impacting European eel populations.

Implementing conservation strategies for a fish species with various life stages established across a wide geographical area is challenging (ICES, 2009). Furthermore it is not clear which stage or stages of the life cycle have been affected (Feunteun, 2002; Kettle *et al.*, 2011), or whether the origin of the decline is the result of freshwater, inshore or oceanic influences (Dekker, 2008). The spatial variation in the age at which eels mature across Europe complicates population models (Vøllestad 1988; Poole *et al.*, 1990; Svedaung *et al.*, 1996), and the panmictic nature of the population means that local effects are not directly coupled to subsequent recruitment (Als *et al.*, 2011). Nevertheless, the decline in recruitment to continental populations on a European scale indicates that local populations may continue to decline even where human-induced mortality is reduced to zero (Astrom & Dekker 2007).

1.2 OCEANIC BEGINNINGS

Although spawning eels and their eggs have yet to be captured in the wild (Van Den Thillart *et al.*, 2009), the presence of newly hatched larvae in the Sargasso Sea in the western Atlantic implies this is the spawning area of the species (Schmit, 1923; Kleckner & McCleave 1988). Eel eggs develop into leaf-like, transparent leptocephalus larvae that drift with the ocean currents for a period of up to two years towards Europe and North Africa (Tesch, 2003; Friedland *et al.*, 2007; Miller *et al.*, 2014). Once they arrive in coastal waters, the leaf-like leptocephalus larvae metamorphose into typically eel shaped, transparent juveniles called glass eels (Tesch, 2003). These glass eels (unpigmented) gather in river estuaries utilizing currents and passive tidal transport to move upstream (McCleave, & Kleckner 1982; Gascuel 1986). Glass eels enter estuaries all year round, with migration peaks depending on latitude and oceanic factors (Desaunay & Guerault 1997; Knights,

2003; Barry *et al.*, 2015). For example, in southwest Spain, short-term (monthly) changes in glass eel density were reported to be partially driven by local environmental variables, such as turbidity, rainfall and temperature (Arribas *et al.*, 2012). However long-term (yearly) changes are associated with factors relating to recruitment success, such as the North Atlantic Oscillation (NAO) index and primary production at the spawning area (Bonhommeau *et al.*, 2009; Kettle *et al.*, 2011; Arribas *et al.*, 2012).

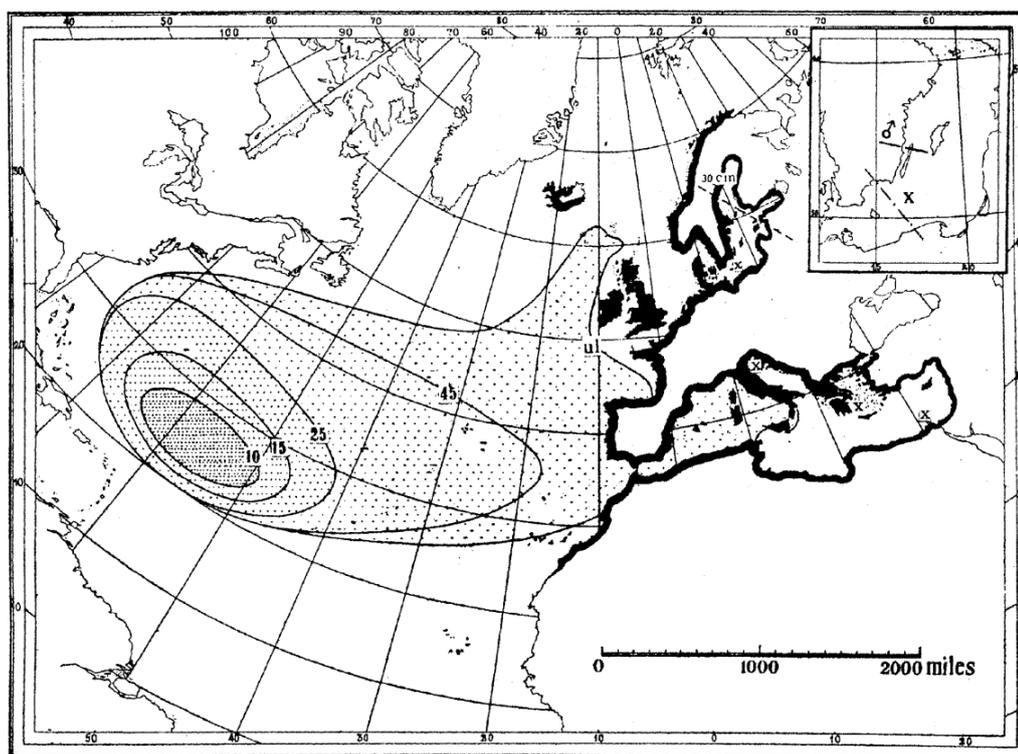


Fig.1.2. Distribution patterns of European eel larvae from spawning grounds in the Sargasso Sea, with the size of the larvae in mm on approach to continental Europe (source: Schmidt 1923)

The immigration of glass eels is commercially harvested across Europe. Originally this was for animal feed (Tesch, 2003), however at present the harvest of glass eels is mainly used for stocking purposes and natural seed for aquaculture (ICES, 2014). Glass eels entering coastal waters use tidal transport to migrate into river systems (Creutzberg, 1958; McCleave & Kleckner 1982; Gascuel 1986). This is an effective way to enter a catchment quickly, as little energy is required to reach the salt/fresh water interface (Harrison *et al.*, 2014). The European eel has an extremely well developed sense of smell (Tosi & Sola 1993) and it has been hypothesised that certain odours and environmental stimuli attract the eels to inland

waterways (Crnjar *et al.*, 1992; Briand *et al.*, 2002). Glass eels arriving straight from sea will not have had any previous experience of scents contained in freshwater, therefore the ability to distinguish these scents and odours within the sea water medium is believed to be instinctive (Tesch, 2003). Harrison *et al.* (2014) notes that during the short glass eel stage, movement is very directional towards inland waterways. However a recent study revealed that high current speed at the entry to river mouths may reduce the likelihood of freshwater entry to certain catchments (Barry *et al.*, 2015).

On entry to estuaries, settlement in habitat type has been related to the condition of glass eels on arrival (Edeline *et al.*, 2006). Plankton net surveys showed that lower condition fish initially settled out at lower estuary, brackish water sites, while better condition individuals continued up-river (Sullivan *et al.*, 2009). Freshwater habitats have traditionally been considered very important for juvenile eel (Ibbotson *et al.*, 2002; Laffaille *et al.*, 2003), however recent work has suggested that juvenile eels, may grow faster in brackish environments compensating for initial poor condition at settlement (Jessop *et al.*, 2007). When glass eels migrate towards transitional waters a decision appears to be made, possibly as a result of body condition, to either settle in brackish estuarine water or migrate to freshwater in search of suitable habitat (Edeline *et al.*, 2006). The evolution of multiple migratory strategies must be derived from environmental cues, i.e. a conditional Evolutionary Stable Strategy (Edeline, 2007, McCleave & Edeline, 2009). This is defined through evolutionary game theory, the conditional strategy describes sufficient plasticity through which an individual can express a range of differing phenotypes, i.e. freshwater, brackish, marine water or nomadic migratory types (Daverat *et al.*, 2006). Optimisation of individual fitness through the Evolutionary Stable Strategy (EES) has been implicated in habitat choice of eels. The strategy treats eel diadromy as a cost benefit analysis and suggests that when the cost/benefit ratio is low, migration upstream would be selected for (Edeline, 2007).

1.4 GROWTH PHASE – CONTINENTAL WATERS

The yellow eel phase has been described as the stage when juvenile eel's migratory period concludes and they attain body lengths >30cm, eels that have reached this part of their life are at the feeding or main growth stage (Tesch, 2003). The yellow eel growth stage can last between 3-30 years in which they grow and accumulate

sufficient fat reserves to complete this part of their life cycle before undertaking the spawning migration to the Sargasso Sea (Poole & Reynolds 1996; Tesch, 2003; Belpaire *et al.*, 2009).

Eels colonise continental waters as juveniles and search for adequate habitats. Feunteun *et al.* (2003) based yellow eel movement into three distinct behaviours which are; (i) "Founders" which colonise catchments until they settle in the first suitable habitat they encounter, (ii) "Pioneers" that migrate upstream to upper boundaries of the system, and, (iii) "Home range dwellers" that establish in a given area for several months or several years to grow. The last group consisting of "Nomads" or erratic eels that undertake a general upstream shift as they search for suitable areas to forage or settle. Generally, the mean age and size of eels increase in an upstream direction (Feunteun *et al.*, 1998; Ibbotson *et al.*, 2002).

Diversity of habitat use appears to be a common strategy of temperate eel species, and, as a life history tactic, is under environmental control (Daverat *et al.*, 2006; McCleave & Edeline 2009). There is an increasing amount of evidence available demonstrating considerable phenotypic plasticity of the European eel with regard to habitat choice (Harrod *et al.*, 2005). Otolith microchemistry studies (Strontium:Calcium ratios) have revealed that eel populations typically contain a mix of freshwater residents, saline water residents, and inter-habitat migrants (Arai *et al.*, 2006; Jessop *et al.*, 2008) termed by authors as facultative catadromy. As eels spend the majority of their lives in continental waterways (Tesch, 2003), understanding habitat use and habitat suitability is imperative in this important life stage. Laffaille *et al.* (2003) found that eel habitat preferences change with size, even if the species is spread over every type of microhabitat available. The lack of knowledge about precise relationships between densities, sizes and habitats make it very difficult to model eel habitat relationships and consequently to predict the size of eel stocks in a given watershed (Aprahamian *et al.*, 2007). Laffaille *et al.* (2003) found that density estimates are data poor and inaccurate as they do not account for the density of available habitats. It is therefore imperative to understand the relationship between key habitat requirements to aid conservation measures and the successful restoration of depleted stocks.

Tracking technologies have advanced recently allowing detailed studies of individual eel movements and habitat selection (Hedger *et al.*, 2010; Rosten *et al.*, 2013; Walker *et al.*, 2014). While the European eel is believed to be relatively

sedentary in freshwater (Riley *et al.*, 2011), studies have revealed that eels may utilise large areas and undertake regular movements in estuarine environments (Hedger *et al.*, 2010; Walker *et al.*, 2014; Béguyer -Pon *et al.*, 2015). The degree to which such movement translates to other habitats is poorly understood. *Anguilla* spp. establish a home range while resident during the continental stage of their life cycle (Parker, 1995; Morrision & Secor 2003). Studies have documented varying home range sizes for eels. Reported home ranges in small lakes, tidal creeks and estuaries have varied in size 0.0027 km² (Labar *et al.*, 1983), 0.01 km² (Bozeman *et al.*, 1985), 0.16 km² (Thibault *et al.*, 2007) and 3.25 km² (Parker, 1995). This variety highlights a lack of consensus of the factors that within species variation contributes in space use and home range size. Examples from previous studies suggest home range size may change depending on habitat type and individual eel characteristics. Given eels can spend more than 30 years in lakes (Tesch, 2003); the current lack of information about activity patterns and space use of eels in lacustrine habitat is hindering the development of effective conservation strategies.

1.4.2 FORAGING ECOLOGY

Eels are a remarkably plastic species. In addition to their wide ranging habitat selection, their diet is also diverse (Sinha & Jones 1967, Mann & Blackburn 1991). Primarily bottom-dwelling fish, eels rely on prey population that is present in such habitat (Tesch, 2003). Depending on the type of water body, these animals vary in abundance during annual cycles and therefore in eel diet. Foraging is seasonally dependant, with eels feeding much more in summer when food is abundant than in winter (Tesch, 2003). Stomach fullness has been found to increase from March peaking in May and then steadily decreases through to November (De Nie, 1987). Diel periodic differences are also observed in eels. Cairns (1942) found that a high percentage of eels in early evening catches had empty digestive tracts, but animals trapped overnight had food in their stomachs. The diet of eels in an English stream contained greater amounts of fish in springtime and at the beginning of the summer, than in later summer, autumn and winter. In this and other streams investigated, salmonids were only a minor component of the eel diet and any eels found with salmonids in their stomach were found in large eels (>40cm) (Mann & Blackburn 1991). Mussels, snails and crustaceans also appear but insect larvae were found to be significant component of invertebrate prey throughout the year (Sinha & Jones 1967, Mann & Blackburn 1991). There are few benthic taxa that eels do not eat.

An interesting relationship amongst eels is that of food choice and head width (Proman and Reynolds 2000; Ide *et al.*, 2011). Population panmixia (Als *et al.* 2011; Pujolar 2013) and random dispersal impair the possibility of local adaptation and favour the development of ontogenetic phenotypic plasticity. Phenotypic plasticity plays the most important role in the origin of alternative phenotypes (West-Eberhard 2005) and is defined as the expression of multiple alternative phenotypes resulting from exposure to different environmental (internal and external) conditions (West-Eberhard, 1989; Pigliucci 2005). The existence of two morphotypes, broad-headed and narrow-headed, in eels has been well documented among fishermen and eel biologists in Europe (Ide *et al.*, 2011). Phenotypic variation amongst traits has the potential to offer unique insights into individual behaviour and potential life history effects. A large number of the described alternative phenotypes are the result of foraging specialisation (Adams *et al.*, 2003). Diet is considered one of the most important factors that produce alternative phenotypes in a population (Mittelbach *et al.*, 1992). Several species have been shown to be highly plastic in their trophic ecology as a result to exposure to different prey items (Parsons & Robinson 2007; Walls *et al.*, 1993). Natural populations frequently contain a large degree of variation which can often be overlooked. Individual specialisation in foraging behaviour is believed to reduce intraspecific competition (Polis, 1984), however, in some cases, can be a result of sex or age related differences, ontogenetic foraging behaviour (Grey, 2001), discrete polymorphisms (Skulason & Smith 1995) and individual level variation (Bolnick *et al.*, 2003). Even though diet specialisation is widespread across populations there is a lack of knowledge about the life history consequences of discrete polymorphisms. Foraging specialisation in diet can manifest itself through changes in morphological characteristics, usually as a result of detection, capture and handling of varying prey items (Skulason & Smith 1995; Adams & Huntingford 2002). This discrete variation can be driven by resource availability, environmental exposure and the level of innate adaptability.

Anecdotal observations and circumstantial evidence have accumulated, indicating that eels become highly specialised within the habitats they reside foraging on specific food items resulting in head shape variation (Lammens & Visser, 1989; Proman & Reynolds, 2000). Variation in eel head shape has been noted in populations across Europe (Lammens & Visser, 1989; Proman & Reynolds, 2000; Ide *et al.*, 2011). These studies have shown that broad-headed specimens tend to be piscivorous and narrow-headed individuals feed predominately on benthic

invertebrates, independent of size (Cucherousset *et al.*, 2011). Findings from Ide *et al.* (2011) on European eels suggest bimodality in head shape with morphs being found across watersheds and occur sympatrically within the same habitat. An understanding of the life history consequences of such specialisations is crucial in the conservation management of this endangered species. On a very small spatial scale individuals with extreme head morphology have exhibited higher fitness than individuals with intermediate head morphology (Cucherousset *et al.*, 2011) suggesting that this observed individual specialisation demonstrates the existence of disruptive selection (Bolnick, 2004) and could possibly influence life history characteristics in freshwater.

These morphotypes, apparent in eels, highlight the morphological plasticity of the species and the ability of the species to adapt to their environment. The effect of this observed morphological adaptation to diet is poorly understood. The vast dietary spectrum of eels reflect their great adaptability with respect to the water body they inhabit (Tesch, 2003) and may explain why eels are readily found in a vast array of hydrosystems, with the species being able to adapt to food availability accordingly. Whether these differences are attributable to food selectivity or to habitat is questionable. The interplay between diet and acquisition of suitable energy reserves remains poorly understood and could play an important role in amount of time spent in growth habitats.

1.4.3 SEX DIFFERENTIATION

The eel is a secondary gonochoristic species, which is characterized by delayed sex differentiation (Devlin & Nagahama 2002). Eels enter catchments as sexually undifferentiated glass eels and develop into males and females (Davey & Jellyman 2005). Male and Female eels exhibit markedly different life history strategies. Generally eels that come from overpopulated habitats and exhibit rapid growth rate prior to gonad differentiation tend to become males (Tesch, 2003) whereas eels that grow slowly are more likely to become females (Davey & Jellyman 2005). Findings confirm that within a water body, males are generally a smaller size than females, as is typical in numerous fish species (Sinha & Jones 1967). Holmgren & Mosegaard (1996) showed from rearing studies that at a weight of 50-60g, males grew faster than females however when they reached 80-100g they gained weight more slowly than the females, and males almost stopped growing as they approached 150g. A study of eels in an Irish catchment which investigated growth rate in migrating silver

eels found that older females exhibited faster annual growth, as early as the first year in freshwater, and mean annual growth increments were much higher for females than for males (Poole & Reynolds 1996). Males mature at the smaller size and earlier age compared with females which generally attain a greater age and size before leaving rivers (Davey & Jellyman 2005). It has been hypothesised that an increased population density generally seen in the estuarine environment leads to the development of the male sex however recent results from aquaculture, have led to speculation that sex differentiation is due growth rate differences after the glass eel stage, with faster growth rates leading to the development of the male sex (Tesch, 2003). Highly skewed sex ratios in wild populations are most likely a result of local conditions rather than sex specific differences in dispersal (Davey & Jellyman 2005). The potential factors which have been identified as influencing sexual determination in eels include early growth rate, density, water temperature and habitat type, however it is difficult to isolate these factors as they are closely interrelated (Davey & Jellyman 2005). Sex differentiation appears to be determined principally by the environment but the intricacies influencing it are still unclear.

1.4.4 LIPID - ENERGY RESERVES

Lipid content or energy reserves are crucial for reproduction and successful migration to spawning grounds (Belpaire *et al.*, 2009). If a critical fat mass is not attained during the yellow stage, silvering may not be initiated (Larsson *et al.*, 1990). Eels are characteristically high in fat (Böetius & Böetius 1980, Belpaire *et al.*, 2009, EELREP, 2005) and variations in the total fat content of yellow eels can be attributed to diet (Otwell & Rickards 1981), temperature (Dosoretz & Degani 1987) and used as a general proxy for individual health (Belpaire *et al.*, 2009). Flume studies of silver eels have demonstrated the minimum lipid content a silver eel would require in order to: a) successfully migrate to respective spawning ground and, b) successfully reproduce upon arrival. Estimated minimum lipid thresholds required have been estimated at 28% (Larsson *et al.*, 1990), 20% (Böetius & Böetius 1980), 20.7% (van den Thillart 2007) and 13.5% (Palstra *et al.*, 2007). Fat content has been examined extensively in the silver phase of *Anguillid* eels, specifically in relation to measuring reproductive fitness, capacity and the ability to successfully complete migration to the spawning grounds, (Larsson *et al.*, 1990, EELREP, 2005, van den Thillart *et al.*, 2009). However the factors influencing lipid accumulation in yellow eels in the wild during the growth phase is poorly understood, and could potentially be influenced by diet (Otwell & Rickards 1981).

Once sufficient lipids (energy reserves) have been accumulated, eels will undergo a gradual morphological and physiological transition into migrant silver eels (Durif *et al.*, 2005). Silvering is a process that all eels go through before beginning their spawning migration. This metamorphosis marks the transition from the growth phase (yellow eel) to the onset of sexual maturation and beginning of spawning migration. During the silvering process eels undergo a number of physiological changes which prepare the eel for their migration to distant spawning grounds.

1.5.1 SILVERING

Unlike smoltification in salmonids, the silvering of eels is unpredictable and silver eels exhibit significant differences in age and length at migration (Poole & Reynolds 1996). With regard to external changes the most obvious is that of skin colour (Pankhurst & Lythgoe 1983). The underside turns silvery white, and the dorsal area turns a black colour. This dorsal-ventral grading in silvering colouration is most common in pelagic marine fish and is seen as preparation for the marine migration. Other distinctive features to note are elongated pectoral fins and increased thickness of the skin (Durif *et al.*, 2008). Sensory organs also start to develop during the silvering process. The eye begins to increase in size, and the number of rods increase while cones decrease (Pankhurst, 1982), a common trait in deep sea fish where colour is not necessary.

During silvering, eels cease feeding, a trait which is also seen in salmonids migrating to spawning grounds (Tesch, 2003). Modifications observed in the eel's swim bladder have been identified as an adaptation to life in the deep sea. Gonad weight increases during the silvering process (Durif *et al.*, 2008). Previously identification of silver eels was broadly based on skin colour however this identification was criticised and found to be unreliable and subjective (Pankhurst & Lythgoe 1983).

Durif *et al.* (2005) established a novel non-invasive method for classifying the developmental life stages and silvering of eels based on physiological and morphological characteristics. This involves a detailed description of the silvering process the silvering stage is broken down into seven classifications, five stages (F-I to F-V) for females and two stages for males based on four easy to measure external parameters (length, weight, eye diameter and pectoral fin length). This classification

yields a more realistic and complete image of the silvering process, rather than classifying eels into the restrictive yellow and silver stages.

1.5.2 DOWNSTREAM MIGRATION

Length and age at migration are highly variable in silver eels, and it is unclear why certain eels choose to maximise size while others opt for a time-minimizing strategy (Poole & Reynolds 1996; Davey & Jellyman 2005). Silver eels generally migrate in large groups during specific time periods. Forecasting silver eel runs is problematic, migrating eels in Dutch canals are most common in August whereas in Ireland and on the central Baltic Sea they occur in October. This is unexpected as Irish streams are over 1500 km closer to spawning grounds than the Baltic Sea (Tesch, 2003). Thus, trying to draw definitive conclusions about earlier or later onset of migration from water bodies separated by considerable distances is very difficult.

In a long-term study, the silver eel runs were monitored over a 29 year period in the Burrishoole system in Western Ireland (Poole *et al.*, 1990). This study gave some excellent insights into the timing of silver eel downstream migrations. The authors found that the main run of eels took place in September and October. It was also noted that there was a marked lunar effect on the eel migration pattern, particularly during the last quarter or "dark" phase. This long term data set demonstrates how intrinsically linked silver eels runs are to environmental conditions. Investigation from fishery data have also found that silver eels runs occur over a narrow time frame with the majority of the run peaking over 10-19 days (Durif *et al.*, 2003). Research information from experienced commercial fishermen indicates that silver eels are most active around the last lunar quarter (Poole *et al.*, 1990; Tesch, 2003). It is still unknown what effect moon phases exert on silver eels whether it triggers an internal rhythm or if it is simply a result of the dark nights associated with the last lunar quarter. Durif & Elie (2008) examined commercial data from the Loire River and found that runs of eels were higher during the last quarter (36%) and the new moon (29%), compared to the full moon (17%) and the first quarter (18%). Discharge is also broadly accepted as being a critical factor (Tesch, 1977; Durif & Elie 2008). During periods of high discharge it would be advantageous for eels to migrate due to the reduction in energy costs.

During downstream migration silver eels encounter many obstacles in the form of flood control dams, weirs, hydropower stations, sluices, pumping stations and fisheries, all of which are effecting downstream movement as well as survival

rates. The results of human activity on silver eel migration is significant and one that must be addressed to ensure healthy spawning stock leaving continental catchments. Several studies have revealed impacts of hydropower impoundment and fisheries on riverine survival of migrating silver eels (Winter *et al.*, 2006; Travade *et al.*, 2010). The freshwater -marine transition represents an important life history stage for diadromous fishes. In common with other diadromous fishes migrating silver eels pass through productive estuarine habitats which often have large numbers of avian, mammalian and fish predators. Knowledge of escapement success during the freshwater saltwater transition is crucial to our understanding of the natural dynamics of eel populations. Specifically, understanding migration behaviour, life stage specific mortality and ultimately migration success at this important life stage, is critical to effective conservation management. Recent work on downstream migration patterns has indicated low survival rates during migration to the open ocean (Verbiest *et al.*, 2012; Aarestrup *et al.*, 2010). However these studies were conducted in catchments impacted by hydropower and fisheries thus it is difficult to disentangle natural mortality from mortality arising from hydroelectric power generation or fishery pressure. Furthermore the migration of male eels, which migrate at a smaller size than females (Poole *et al.*, 1990), is particularly poorly understood. Previous studies have focused solely on the behaviour of larger females (which are preferred for tagging) and as a result, field data on the downstream migration of smaller sized female and male eels is lacking. Providing safe bypass for silver eels is vital to ensure healthy numbers of silver eels reach their spawning grounds and is an important component of the EU regulations. Silver eel migrations out of our freshwater systems are affected by anthropogenic impacts and potential bottlenecks need to be identified to safeguard downstream migrating eels.

1.6 *ANGUILLICOLA CRASSUS* - SWIMBLADDER PARASITE

The nematode parasite *Anguillicola crassus* originated from Eastern Asia and is now widespread throughout Asia, Europe, Africa and Eastern North America. The parasite was first described in cultured eels in 1974 in Japan and since then the nematode has spread across four continents in three decades and is known to infect at least six eel species (Lefebvre *et al.*, 2012). The origins of European eel infection and the parasite's subsequent trans-continental spread has been summarised by Kirk (2003) and is generally believed to have been introduced to European waters by the

importation of infected Japanese eels to Germany in 1980 (Koops & Hartmann, 1989). Incidences of *A. crassus* infection were first reported in Britain in 1987, with infected individuals found in the Rivers Thames, Welland and Trent (Kennedy & Fitch, 1990). The parasite is thought to have been introduced through eel trade imports and accidental contamination of local freshwater sources to refresh water containers which is common practice during the long-haul transport of individual eels.

A. crassus is a highly efficient parasite that has been able to rapidly exploit a naïve host (Kirk, 2003). Its capacity to spread throughout a catchment is a direct consequence of the organism's adaptability, high reproductive output and short life cycle (Lefebvre *et al.*, 2012). This success is ultimately contingent upon predator/prey interactions, with larval stages transmitted trophically through freshwater food-web interactions.

There are four larval stages and a terminal adult stage in the life cycle of the *A. crassus* nematode (Lefebvre *et al.*, 2012). Eggs are hatched in the eel's swimbladder and migrate out through the pneumatic duct and intestines before release into open water. These L2 larvae reach the benthos and attach themselves to the substratum, where they are preyed upon by intermediate copepod host or are directly ingested by eels. It has been hypothesised that the active movement of L2 larvae attracts copepod predation during this stage (Thomas & Ollevier 1992). Free living larvae can survive within the substratum in a dormant state for several days, particularly during periods of low water temperature (Kennedy & Fitch, 1990). Copepod ingested L2 larvae then burrow through the intestinal wall and spill out into the haemocoel (Thomas & Ollevier 1992). The continued success of the L3 larvae relies upon its host falling prey to a paratenic host fish or European eel.

The most direct route of transfer is therefore copepod to eel trophic transmission. In the natural environment, however, food webs are complex and a number of different species can play host to *A. crassus* (Thomas & Ollevier, 1992; Szekely, 1996). Infected individuals will either ultimately fall prey to eels, allowing the nematode to complete its life cycle, or will act as dead-end hosts. A vast number of diverse host species, covering multiple taxonomic groups, have been described. Lefebvre *et al.* (2012) compiled a list of those presented in literature and described 50 paratenic host fish species, spanning 20 families. Reported levels of infection within hosts vary between species and across sample sites (e.g. Haenen & Banning

1991; Szekely, 1993; Thomas & Ollevier 1992). Szekely (1996) detailed the successful infection of a secondary paratenic fish host, suggesting that transfer of *A. crassus* is possible by multiple trophic pathways, which has also been shown through the presence of viable L3 *A. crassus* larvae in the aquatic snail *Galba carvus*, and various adult and larval aquatic insects, tadpoles and newts (Moravec, 1992; Moravec & Skorikova 1998).

The parasite causes severe pathology in the host's swimbladder and it is unknown if affected silver eels can actually successfully complete their spawning migration (Pelster, 2015). According to Kennedy (2007), once introduced "it is here to stay" and following introduction, prevalence generally soon reach high values up to 100% in one year (Kennedy & Fitch 1990). However after a few years of high infection mean intensities and abundance start to decrease or level off (Audenaert *et al.*, 2003). This may resemble a phase stabilization due to the host immune response however Lefebvre *et al.* (2012) states, it reflects the fact that the infected organs are so badly damaged by repetitive infection events that they become unsuitable for further parasite establishment. The parasite is likely to affect the use of the swim bladder organ and impose substantial metabolic costs (Lefebvre *et al.*, 2012). The effect of the parasite on resident yellow eels has not been looked at in detail. Understanding the effects the parasite may be having on resident populations is vital to improve our understanding of how eels are being affected at the population level.

1.7

MOLECULAR ECOLOGY

It is broadly accepted that eels comprise a single randomly mating population, a panmictic population. However findings have indicated a potential genetic mosaic consisting of several isolated groups, indicating the hypothesis of complete homogeneity within the species may be false. An extensive genetic survey found that the geographical component of genetic structure lacked temporal stability (Van Ginneken & Maes 2005). Furthermore European and American eels have been found to hybridize, but hybrids have been observed almost exclusively in Iceland, suggesting hybridization in a specific region of the Sargasso Sea and subsequent nonrandom dispersal of larvae (Pujolar *et al.*, 2014). The mechanisms underlying the exact locations and timing of spawning remain poorly understood and a recent study by Baltazar-Soares *et al.* (2014) suggest female eels are philopatric within the Sargasso Sea, with males maintaining gene flow, questioning the assumption of a panmictic breeding system.

Although these studies suggest a level of spatial segregation, a very comprehensive study which genotyped over 1000 individuals at 21 microsatellite loci, showed a very low and non-significant genetic differentiation between geographical locations across Europe, and a lack of sub structuring among larvae collected in the Sargasso Sea (Als *et al.* 2011). Thus, providing very strong support for panmixia. Owing to the apparent panmixia and random larval dispersal across habitats, any signature of spatially varying selection in a given generation is expected to be lost in the subsequent generation (Gagnaire *et al.*, 2012). The hypothesis of panmixia in eels was again examined by Pujolar *et al.* (2014), a large SNP (Single Nucleotide Polymorphism) data set from 259 European eel individuals (glass eels) from eight locations covering the European eel range was examined and provided compelling support that the European eel is a panmictic species. All analyses of genetic diversity, genetic differentiation and isolation by distance are consistent with the interpretation of genomic panmixia, and thus European eels sampled along the coasts of Europe and northern Africa belong to a single spatially homogenous population. High gene flow associated with the particular life history characteristics of eels prevents local adaptation. Genomic panmixia suggests that larval dispersal is random and there is no larval homing to the parental original freshwater habitat (Pujolar *et al.*, 2014). As a consequence, the offspring of surviving individuals experiencing specific local conditions have no chance to return to the parental habitat in which the phenotype was originally advantageous and selected for.

These conclusive data from Als *et al.* (2011) & Pujolar *et al.* (2014) suggest that the species should be managed as a single unit involving coordinated conservation efforts across the panmictic population. However discrepancy between previous studies (Baltazar-Soares *et al.*, (2014) & Van Ginneken & Maes (2005) are unclear and cannot be discounted.

1.8 THESIS AIMS

Globally many freshwater fish face numerous threats including habitat degradation, migration barriers, fisheries exploitation, environmental climate change and the introduction of invasive species. Couple these threats with two trans-Atlantic migrations and a prolonged growth phase in contrasting continental waters and we can begin to realise the challenges facing the European eel in the successful

completion of its lifecycle. During the continental stage of the eel's life cycle which can last 3-30 years the species are faced with numerous anthropogenic impacts, however it is in this phase that effective management can have an influential bearing on the success of this critical life stage.

The main focus of this thesis is to investigate the diversity of ecology, movement and migration behaviour of the European eel utilising a suite of techniques, including: morphometrics, stable isotopes and telemetry. This will be achieved by investigating *A.anguilla* from sites in Ireland, Northern Ireland and Scotland, this thesis aims to deliver a greater understanding of European eel ecology during the important continental life stages based on the findings from the following outlined studies;

1) Ecomorphological variation in the European eel Anguilla anguilla, in a range of continental habitats; life history consequences

Phenotypic variation in head shape across the European eels range has resulted in a dichotomous description; however this distinction is debatable as the differences may actually represent continuous morphological variation (Ide *et al.*, 2011). An objective of this work was to examine the nature and extent of this phenotypic variation in head shape of female eels across habitat type's sampled. The effect of the known head shape polymorphism on growth is unclear, faster somatic growth has been noted for broad-headed individuals compared to narrow-headed individuals (Tesch 1977). Our aim was to examine how trophic ecology is related to growth and fat stores of female European eel while resident during their growth phase. The relationship between the environment in which individuals reside and phenotype (life history characteristic) highlights the importance for managers to take into account morphological variation within a habitat. The importance of understanding life history variations from a management perspective is discussed. In this chapter *A.anguilla* from five different locations were used to investigate; 1) the nature of the polymorphism and foraging specialisation (if any) across habitats types utilised by eels and, 2) the affect (if any) of foraging specialism on growth rates and lipid stores.

2) Foraging specialisms influence space use and movement patterns of European eels.

Effective fisheries management needs to consider spatial behaviour in addition to more traditional aspects of population dynamics. Understanding the movement and

habitat use of a threatened species is vital to implementing effective conservation strategies. Although eels can spend up to 30 years in lakes, there is little information on how eels utilise lacustrine environments and there are few data on home range size and activity patterns in lakes. The first objective of this study was to quantify the spatial distribution of European eel, in particular home range sizes and activity patterns, in a lacustrine habitat; Combining measures of individual head morphology with individual behavioural parameters obtained through acoustically tracking summer movements of individuals. Our second objective was to test the hypothesis that individual movement patterns and space use is correlated with differences in morphology and foraging specialisms.

The findings from this tracking are discussed in the context of designing more efficient survey programs in lake systems by improving our knowledge of spatial behaviour of European eels in freshwater habitats. Furthermore, home range areas are important to understand so as to allow managers to estimate potential production from large bodies of water.

*3) The effect of foraging and ontogeny on the prevalence and intensity of *Anguillicola crassus* in the European eel *Anguilla anguilla**

Studies of the early colonisation and infection dynamics of the invasive nematode parasite *A.crassus* are rare. However a rapid increase in prevalence over a short period of time can be observed when the parasite enters a new system, possibly due to the lack of immune adaptation and naivety of the European eel (Kennedy 1993; Lefebvre *et al.* 2012; Becerra-Jurado *et al.* 2014). Infection of eels by this parasite can occur through direct ingestion of infected copepods, and through eel predation in infected paratenic hosts (Kirk 2003). Thus variation in foraging ecology may influence the encounter rate and infection probability within the definitive host. The objectives of this work were to (i) document the recent invasion of the nematode parasite *A.crassus* to Loch Lomond Scotland, (ii) investigate the influence of trophic ecology on the intensity and prevalence of *A.crassus* in a previously naïve population of *A.anguilla*.

*4) Freshwater and coastal migration patterns of silver stage eels *Anguilla anguilla* (L.)*

Previous studies have focused solely on the behaviour of larger females (which are preferred for tagging) and as a result, field data on the downstream migration is

therefore skewed and information on smaller sized female and male eels is lacking. The objectives of this study were to (i) determine the progression rates and migration behaviour of small silver eel through sequential catchment compartments; (ii) elucidate cues to migration and how they may differ between catchment compartments; (iii) quantify escapement success of tagged individuals through freshwater and coastal sea lough habitats.

5) *Historical change in the European eel *Anguilla anguilla* (L.) population in the Foyle estuary, Northern Ireland.*

Although rapid declines have been witnessed across Europe, there is also good evidence from long term data that this decline has not occurred in catchments in North and Central Scotland. Two independent long term historical data sets suggest that eel populations are being maintained by regional processes directly related to the proximity to the North Atlantic drift and the continental shelf current (Adams *et al.* 2013). The Foyle catchment in Northern Ireland discharges north into the Atlantic and is situated very close to Scottish sites that appear to have stable eel populations. The objective of this work was to investigate long-term population change in the Foyle estuary.

Chapter Two

Ecomorphological Variation in the European Eel *Anguilla anguilla*, in a Range of Continental Habitats; Life History Consequences

2.1

ABSTRACT

European eels feed in continental habitats so as to accumulate sufficient energy reserves for their return spawning migration to the Sargasso Sea. Phenotypic variation in head shape across its range has resulted in dichotomous descriptions of broad-headed and narrow-headed morphs. Morphological variability is widespread in natural populations however linking potential life history consequences to this observed variation is difficult. This work presents results on phenotypic plasticity and specialisation in resource use among eels from five continental habitats and investigates the effects on lipid content and growth. Bayesian model groupings were used to identify morphs within habitat types based on ordination of geometric head shape. Broad-headed and narrow-headed groups were supported in the four lake sites but not in the estuarine site. Phenotypic traits were linked to feeding, individuals with broader heads displayed a significantly higher $\delta^{15}\text{N}$ and a higher proportion of prey fish in their diet compared to individuals with narrower heads that had a higher proportion of invertebrates in their diet. These findings corresponded significantly with a faster growth rate of broad-headed individuals in three of the four lake sites. Broad-headed individuals had significantly lower lipid content in comparison to narrow-headed individuals in locations that supported both morphs. This relationship between the environment in which individuals reside and phenotype highlights the importance for managers to take into account morphological variation within a population.

2.2

INTRODUCTION

The European eel (*Anguilla anguilla* L. 1878) is a catadromous species that spawns in the Sargasso Sea, in the western Atlantic, with larvae dispersing passively on the north eastern currents to continental habitats across Europe (Tesch, 2003; Friedland *et al.*, 2007; Miller *et al.*, 2009). Population panmixia (Als *et al.*, 2011; Pujolar *et al.*, 2014) and random dispersal impair the possibility

of selection for local adaptation in continental habitats during the feeding phase (yellow eel) of their life cycle, that is seen in other species (Taylor, 1991; Fraser *et al.*, 2011; Drouineau *et al.*, 2014).

Phenotypic plasticity is an organisms ability to express different phenotypes in response to exposure to different environmental conditions (both internally and externally) (West-Eberhard, 1989) and provides some capacity for an individual to match the expression of its phenotype to the environment to which it is exposed during a single lifetime (West-Eberhard, 2005; Pigliucci, 2005). In some species, phenotypic plasticity is known to be responsible for the expression of multiple alternative phenotypes in populations occupying the same ecosystem (Adams & Huntingford 2004; Garduno Paz & Adams 2010). The expression of multiple phenotypes in a species occupying the same habitat has the potential to offer unique insights in the relationship between expressed phenotype traits and ecological processes (Garduno Paz *et al.*, 2010).

Where discrete alternative phenotypes have been described living in sympatry, many are associated with some form of foraging specialisation (Adams *et al.*, 2003). Diet is considered one of the most important factors driving the emergence of alternative phenotypes in a population (Mittelbach *et al.*, 1992). Several species have been shown to be highly plastic in their trophic ecology as a result of exposure to different prey items (Parsons & Robinson 2007; Walls *et al.*, 1993). Natural populations often contain a high degree of variation which can often be overlooked (Bolnick *et al.*, 2003). Individual specialisation in foraging behaviour is believed to reduce intraspecific competition (Polis, 1984). Foraging specialisation in diet is often associated with differences in morphological characteristics that are involved in the detection, capture and handling of varying prey items (Skulason & Smith 1995; Adams & Huntingford 2002). Where such morphological characteristics are at least partly plastic then this discrete variation can be driven by resource availability, environmental exposure and the scope for plasticity an animal has.

It has long been known that in some places the European eel shows a pattern of discrete phenotypes (Sivertsen, 1938) which is at times found in sympatry (Cucherousset *et al.*, 2011; Ide *et al.*, 2011) and manifests itself in head shape variation (Lammens & Visser, 1989; Provan & Reynolds, 2000). This morphological variation seems to coincide with differences in foraging ecology

with individuals exhibiting large robust and broad heads tending to be piscivorous and those with more delicate narrow heads feeding predominately on benthic invertebrates, independent of size (Cucherousset *et al.*, 2011). Phenotypic variation in head shape among eels can be dichotomous in nature (Proman & Reynolds 2000; Ide *et al.*, 2011) and results suggest there may be fitness consequences of this observed trophic morphology (Cucherousset *et al.*, 2011). Population panmixia and random dispersal impair the possibility of local adaptation, thus any differences are likely to be the result of phenotypic plasticity in habitats during the growth phase of the lifecycle. Even though this phenotypic variation is widespread across the panmictic eel population (Ide *et al.*, 2011) we lack knowledge about the potential life history consequences of the reported polymorphisms.

An understanding of the life history effects of such specialisations is crucial in the conservation management of this endangered species. Eels feed in continental habitats so as to accumulate lipid reserves for their spawning migration. High lipid content is essential to cover the energetic requirements for this migration and successful reproduction (Belpaire *et al.*, 2009). The influence of foraging strategy on lipid content in eels is poorly understood, however it has been reported that an eel's lipid content can be influenced by the energy content of the food provided (Garcia-Gallego & Akharbach 1998). Thus dietary specialisation and growth habitat is likely to have significant consequences for life history and accumulation of sufficient energy reserves. Here we use *A. anguilla* from five different locations to investigate; 1) the nature of the polymorphism and foraging specialisation (if any) across habitats types utilised by eels and, 2) the effect (if any) of foraging specialism on growth rates and lipid stores.

2.3

METHODS

2.3.1 STUDY SITES & FIELD SAMPLING

The present study was conducted in four lake systems and an estuary site known to support *Anguilla anguilla*. The estuarine site was in the lower Foyle catchment. The lake sites, Lough Derg, Lough Finn and Baronscourt lakes were located in the Foyle catchment in Ireland and the fourth lake Loch Lomond was in Scotland (Fig. 2.1 & Table 2.1). Resident yellow eels were captured using fixed fyke nets,

consisting of five chains of five Dutch fykes fished for a period of 24 hours (leader length=8.5m, depth=55cm) in summer 2013 and 2014.

The total body length (mm), body weight (g), eye diameter (mm) and length of pectoral fin (mm) were recorded to determine their maturation stage according to Durif *et al.* (2005). Each eel was killed (using a schedule 1 method) and sex was determined by gonad examination following Colombo & Grandi (1996). Otoliths were removed for age examination and stomachs were removed and preserved in a 10% formalin solution for further analysis. Lipid content was measured on fresh individuals using a Distell FM 692 Fat Meter. The Distell Fat Meter measures the water content of a sample. The fat meter was calibrated to the fat - water relationship specific to European eel prior to taking measurements. Three measurements were taken along the body on both sides of the fish. The fat meter then calculates the average percent body fat for the individual based on the six readings.

Table 2.1 Study site characteristics, sampling dates and eel sample sizes. *Area obtained between outermost survey lines. Estuarine sample size in parenthesis as it did not support both types.

Site	Location	Surface area (ha)	Mean depth (m)	Collection dates	Sample size	
					B	N
Derg	54° 36'N, 7° 52'W	890	9	May 2014	31	15
Baronscourt	54° 42'N, 7° 26'W	60	5.4	May 2014	25	13
Finn	54° 51'N, 8° 07'W	115	11.5	May 2014	16	12
Lomond	56° 05'N, 4° 34'W	7100	37	May 2015	17	15
Estuary	55° 1'N, 7° 17'W	200*	4.8	Aug 2014	(26)	

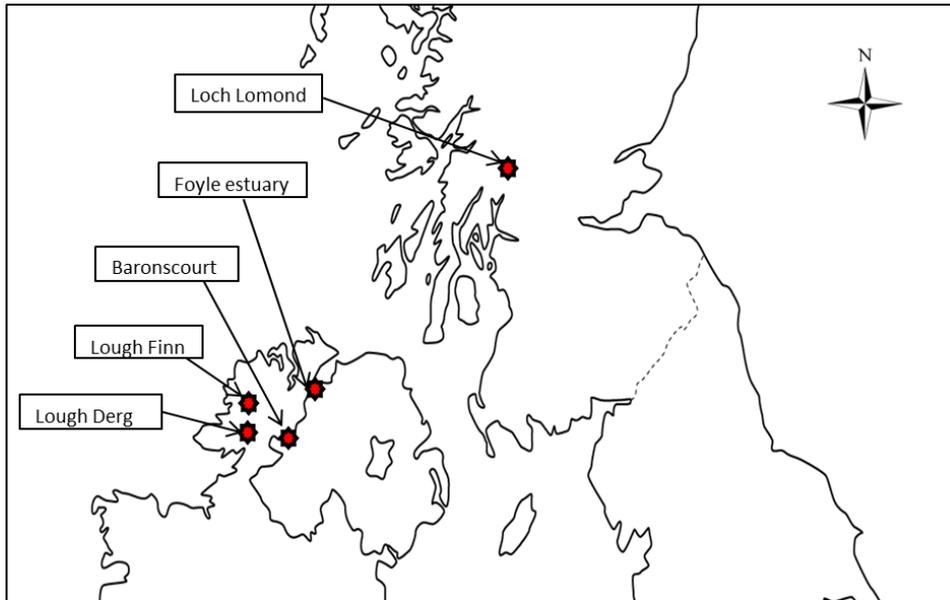


Fig. 2.1 Study site locations.

2.3.2 MORPHOMETRICS

Lateral view photographs of all fish were taken using a Cannon EOS 350D digital camera for geometric morphometric analysis. For each photograph a scale reference was added to allow the removal of shape change associated with size. Nine consistently identifiable landmarks (Fig. 2.2) were digitised in two dimensions (Rohlf 2006). Landmarks were carefully chosen to represent head morphology.

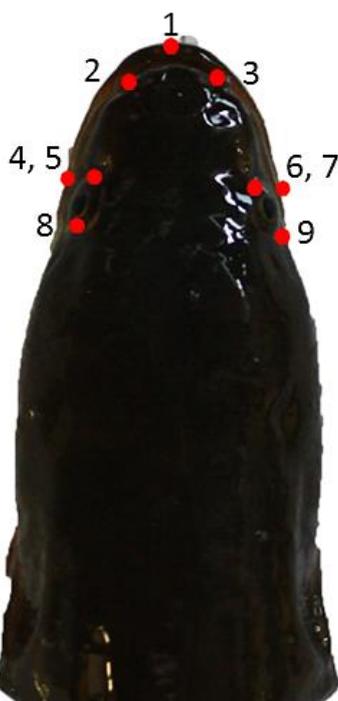


Fig. 2.2 Landmark placement for digitizing head shape. 1) most anterior point of the snout; 2) left rostral nostril; 3) right rostral nostril; 4) outermost jaw in line with rostral border of eye; 5) rostral border of eye (left); 6) outermost jaw in line with rostral border of eye (right); 6) rostral border of eye right; 8) caudal border of eye (left); 9) caudal border of eye right.

2.3.3 GUT CONTENT ANALYSIS

Stomachs were dissected and the contents identified to at least family level and where possible species level. Prey items and categories were quantified using frequency of occurrence (%).

2.3.4 STABLE ISOTOPES

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) provide an important complement to traditional stomach content analyses because they give a longer-term integrated signal of diet as opposed to the “snapshot” information from stomach contents. Stable isotope ratios from fish muscle tissue typically reflect assimilated food during the summer growth period (Perga & Gerdeaux 2005). Information about the temporal consistency of diets is especially important for assessing individual specialization (Bolnick *et al.*, 2002). Eel muscle tissue (1cm² white muscle tissue) and prey organisms were collected at each site for analyses of stable isotopes and dried for 72 hours in a drying oven. Dried tissue was ground to a fine powder using a pestle and mortar. Invertebrates were analysed as bulk samples of whole individuals. A subset of samples were analysed following lipid extraction; about 10–20 mg of ground tissue was soaked in a 2:1 chloroform:methanol (by volume) solvent mixture and the material suspended by stirring. After 15 min, the sample was centrifuged (3000 rpm for 5 min), the supernatant discarded (i.e., the analysis was not quantitative for lipids), and the pellet re-suspended in the solvent mixture. These steps were repeated at least three times or until the solvent ran clear. Finally, the sample was dried (60 °C). Analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were performed at the NERC Life Sciences Mass Spectrometry Facility, by continuous flow isotope ratio mass spectrometry (CF-IRMS), using a Costech ECS 4010 elemental analyser coupled to a ThermoFisher Scientific Delta XP-Plus IRMS. Given the large variation in lipid deposition between individual fish and the confounding effect on $\delta^{13}\text{C}$ values were corrected for tissue lipid concentration using a regression of the difference in $\delta^{13}\text{C}$ resulting from lipid extracted eels on their initial lipid concentration, for all tissue samples.

2.3.5 GROWTH

For age analysis one sagittal otolith from each pair was mounted onto a glass slide using 'Loctite' branded superglue. Otoliths were mounted concave side down and ground and polished on the sagittal plane using 1200 & 4000 grit silicon carbide grinding paper until the origin and all growth rings could be observed under an optical microscope. Age was determined following WKAREA (2009) and otolith measurements were made using Image Pro analysis software to allow back calculation of size at age. Following Lea (1910), growth was back calculated using the following formula;

$$l_n = \frac{S_n}{S} l;$$

Where l_n = length of fish when annulus 'n' was formed, l = length of fish at capture, S_n = radius of annulus 'n' and S = total otolith radius. This method assumes isometric growth.

2.3.6 STATISTICAL ANALYSIS

Shape Analysis & Bayesian model groupings

A Procrustes fit was performed on all landmark data to remove variation created by size, position and orientation (Rohlf & Slice, 1990; Mitteroecker & Gunz, 2009). The mean shape configuration was then computed and the variation around these means calculated (Dryden & Mardia, 1998). Shape change associated with size (allometry) was removed (size corrected) by performing a pooled within-group regression of the Procrustes coordinates on the log centroid size (a measure of fish size) (Klingenberg, 2008, 2011). The residuals derived from this regression were then used for all further analysis. Canonical variate analysis was used for between group comparisons and to test for significant differences in shape within sampling location. Procrustes distances (a measure of absolute shape deviations regardless of their direction) from group means were used to compare shape variance among locations. Mahalanobis distance (a measure of distance relative to the variation in each direction of the multivariate space) was used to investigate significant differences in shape variation between broad-headed and narrow-headed morphs within habitats. Geometric morphometric analysis was undertaken in MorphoJ v1.00k (Klingenberg, 2008; 2011).

A Bayesian clustering package implemented in R was used to test the hypothesis of the existence of two eel morphs within locations sampled (MCLUST; Fraley & Raftery 2009). Two MCLUST models (EII and VII; see Fraley & Raftery 2009 for model descriptors) were fitted to the first four principal components explaining head shape variation. The “best” models, representing the most likely number of groups on the basis of head shape, were identified using Bayesian Information Criterion (BIC). The BIC value is the maximised log-likelihood for the model, the data dimensions and the number of model components; the larger BIC, the stronger the support for the model that could, at a minimum, discriminate eels on the basis of head shape. The model with the highest BIC was selected to assign individuals to morphological groups and quantify uncertainty in model assignments. The best model, and the assignment to groups based on head shape, was selected based on the Bayesian Information Criterion (BIC, analogous to Akaike’s Information Criterion; (Fraley & Raftery 2002)). For each location we compared the best model with the next best model (e.g. support for one versus two groups) by calculating ΔBIC as the difference in the BIC-values between the best model and the next best model. Following Kass & Raftery (1995) we interpreted $\Delta\text{BIC}>10$ as very strong support for the best model, $6<\Delta\text{BIC}<10$ as strong support, $2<\Delta\text{BIC}<6$ as moderate support, and $\Delta\text{BIC}<2$ as equivalent support for the best and the next best model. Statistical analyses were conducted in the R statistical computing package (R Development Core Team, 2014). Thus this method provided a set of group assignments on the basis of head shape at each location sampled. Individuals were assigned into broad-headed and narrow-headed categories at each site and used in subsequent analysis.

Stable Isotope Analysis

The Bayesian mixing model Stable Isotope Analysis in R (SIAR) was used to assess the relative contribution of potential prey to the diet of individuals at each study site (Parnell *et al.*, 2010). Following the approach of Cucherousset *et al.*, (2011), averaged trophic fractionation factors with a large standard deviation were used in the mixing model (e.g. Post 2002). Fractionation of 1.0% (± 1.0 SD) and 3.3% (± 1.0 SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. The SIAR isotope mixing model uses a Bayesian approach to estimate relative dietary contributions and to

consider uncertainties related to isotopic variation in the consumer and in the food sources as well as in the trophic fractionation factors (Parnell *et al.*, 2010).

The SIBER method (Stable Isotope Bayesian Ellipses in R; Jackson *et al.*, 2011) was used in the SIAR package to investigate the isotopic niche width (measured as the SEAB standard ellipse areas in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space; accounting for small sample size). Pair-wise comparison between isotopic niche widths of broad-headed and narrow-headed individuals within the same location was based on 95% credibility limits. Carbon and Nitrogen stable isotope values were used to determine if there was a functional relationship between dietary intake and head shape within sites. Welch t-tests was used to investigate differences $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ between broad-headed and narrow-headed grouped eels in each habitat and ontogenetic variation was tested by investigating individual isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) relationship with fish length within sites.

Growth and Lipid analysis

Growth parameters from observed length-at-age data were obtained by using the nonlinear least-squares (nls) estimation package in R adapted by the fishmethods package for R (Nelson 2013). Likelihood ratio tests were used for comparison of two growth curves (broad-headed and narrow-headed growth curves from different habitat types; based on group allocation from Mclust) to make statistical comparison of the model parameters (K, Linf, T0) the vbrlt function in “fishmethods package” was used (Nelson, 2013). To identify the factors influencing lipid content of eels a linear model approach was used. Lipid content the primary response variable, was regressed with respect to four covariates; head shape, body length (log10 transformed), age and one fixed effect (four-level factor; maturation stage based on silver index). Model selection was carried out by starting with a full model and sequentially removing insignificant higher-order interactions until the final model with the lowest Akaike information criterion (AIC) was chosen (Zuur *et al.*, 2009). Diagnostic plots were used to check residual patterns before accepting the final model for each all analysis. All analyses were performed using R statistical software 3.1 (R Core Team 2014).

2.4

RESULTS

A total of 170 yellow eels were collected from the 5 sampling locations. The length of individuals ranged from 404mm to 676mm (mean +/- SD TL 509.7 +/- 67.8mm; Weight 221.05 +/- 110g), and gonad examination confirmed all eels were female.

2.4.1 SHAPE VARIATION AND HEAD SHAPE GROUP ASSIGNMENTS

Canonical variate analysis found head shape variation between sites to be significantly different. Pairwise comparisons revealed significant differences between sites in Procrustes distance (Table 2.2).

Table 2.2 Pairwise comparison of Procrustes distances between sites: Significant pairwise differences highlighted in bold.

	Baronscourt	Derg	Estuary	Finn
Derg	0.0352	x	x	x
Estuary	0.0537	0.0426	x	x
Finn	0.0339	0.0408	0.0648	x
Lomond	0.0545	0.0296	0.0355	0.0551

A model that used the first four principal components from an ordination of geometric head shape was used to discriminate head shape groups. The first four PC's accounted for 86% of the variation in head shape. Principal component 1 and 2 accounted for 58% and 18% of the variation in head shape respectively, whereby narrower, more delicate heads (i.e narrow heads) tended on the right side of the biplot and larger more robust heads tended on the left side of the biplot. The model supported the existence of two shape groups ($\Delta\text{BIC}>10$; very strong support) in the three lakes sites, Lough Finn, Loch Lomond and Lough Derg, the existence of two shapes had moderate support in Baronscourt lakes ($2<\Delta\text{BIC}<6$) and strong support ($\Delta\text{BIC}>10$) for one shape group in the estuarine site. The groups corresponded to classic descriptions of broad-headed and narrow-headed individuals. The group mean uncertainty in assignment suggests the presence of intermediate head shapes between extremes of both individuals.

Table 2.3 The number of principle components (PCs) from an ordination of head shape used to assign individual eels to morphological groups (PCs used), percentage of variation explained by those PCs (% variation explained), type of multivariate clustering model (MCLUST model), mean model uncertainty in group assignments (Mean uncertainty \pm SE); group assignments were only made using the best (highest Bayesian information criterion [BIC; indicated by bold italics]) of the two models in each model pair, and the associated BIC.

Location	PC's used (% variation explained)	No. of groups (Broad, Narrow)	McLust mode l	Mean uncertainty +/- SD	BIC
Finn	4 (86%)	1	EII	0.043 \pm - 0.106	608.2
		2 (16,12)	VII		629.4
Lomond	4 (86%)	1	VII	0.0126 \pm 0.033	728.6
		2 (17,15)	VII		742.8
Derg	4 (86%)	1	EII	0.0509 \pm 0.122	926.8
		2 (31,15)	EII		979.3
Baronscourt	4 (86%)	1	EII	0.072 \pm 0.118	811
		2 (25,13)	EII		820.6
Estuary	4 (86%)	1	EII	0.07 \pm .118	301.8
		2 (21,5)	EII		267.8

From group assignments Mahalanobis distance was used to investigate shape variation between broad-headed and narrow-headed morphs in habitats that supported both types. This analysis revealed significant differences between broad-headed and narrow-headed morphs in Baronscourt, Derg and Finn ($P < 0.05$ in all cases) and a marginally non-significant result ($P = 0.052$) in Loch Lomond.

Table 2.4 Mahalanobis distances among broad and narrow head individuals (assigned based on Mclust groupings) from different sites, P-values from permutation tests (10000 permutation rounds). Estuarine site not included as it did not support two forms.

Site	Mahalanobis distance between Broad and Narrow- headed individuals	P value
Baranscourt	1.2887	<0.05
Derg	1.7976	<0.001
Finn	1.4023	<0.001
Lomond	1.0466	0.052.

2.4.2 HABITAT & STOMACH CONTENT ANALYSIS

Eels exhibited a varied diet across locations sampled. The 170 eels sampled 64 had empty stomachs. Prey items were classified into six main categories namely; Fish, Chironomid, *Asellus aquaticus*, *Mollusc* sp. Invertebrate (unidentifiable), and *Crangon* sp. Stomach contents were analysed with respect to shape groups derived from Bayesian cluster analysis to draw comparisons between head shape and diet within habitat types. Eels fed mainly on benthic invertebrates and fishes in the study lakes and shrimp in the estuarine site (Fig. 2.3). Stomach contents analysed revealed an almost exclusively piscivorous diet by broad-headed individuals in Lough Finn, Loch Lomond and Lough Derg with relative frequency values of 100%, 100% and 92% respectively. Baronscourt broad-headed eels exhibited a 76% and 24% IRI for fish and benthic invertebrates respectively. Estuarine eels did not exhibit bimodality in head shape and thus were treated as one group for stomach content analysis. Eels sampled in the estuary exhibited almost exclusive feeding on *Crangon* sp. with an relative frequency value of 90%. Narrow-headed individuals had a more varied stomach contents than broad-headed conspecifics. Based frequency of occurrence (%), narrow-headed eels had diets dominated by benthic invertebrates with contrasting levels of bloodworms, *Asellus aquaticus* and molluscs depending on habitat location (Fig. 2.3).

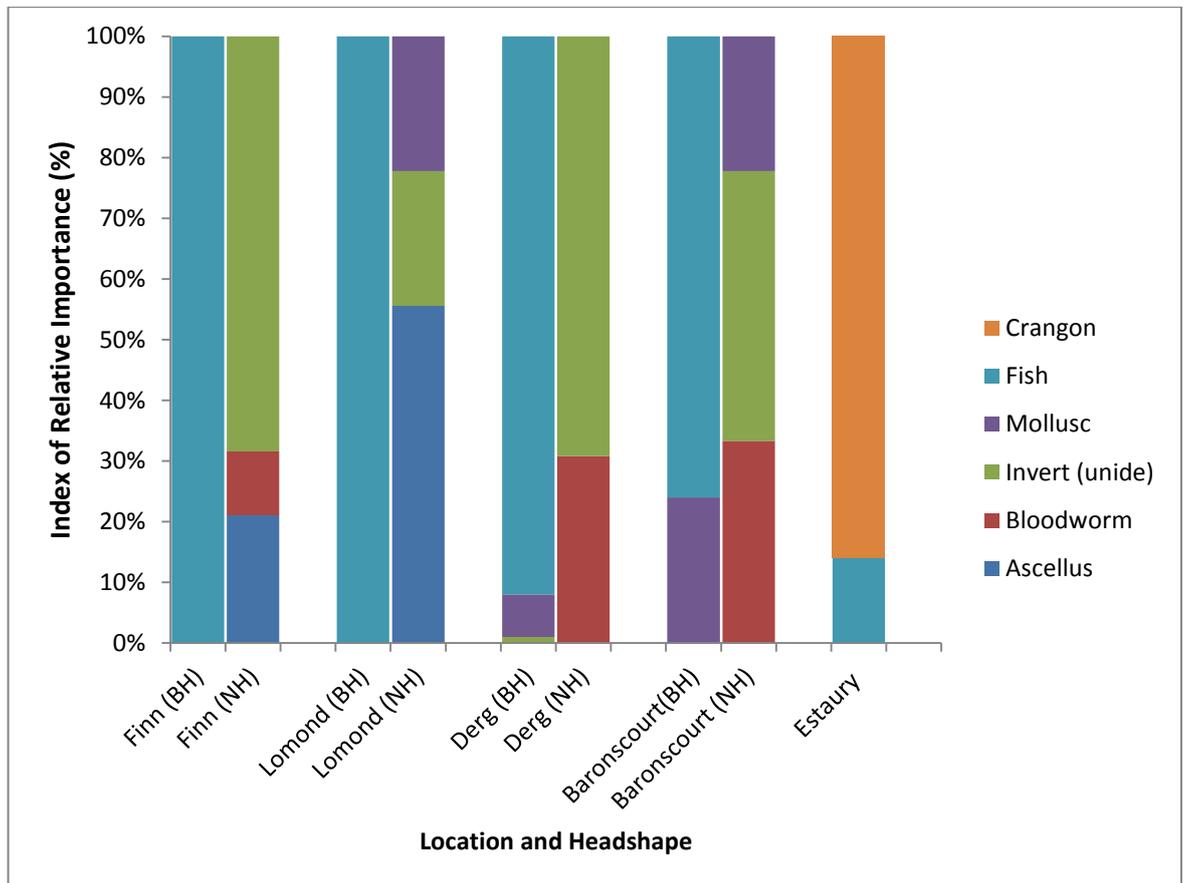


Fig. 2.3 Stomach content analysis of fish grouped according to Mclust grouping at each site. BH=broad-headed, NH=narrow-headed.

2.4.3 STABLE ISOTOPE ANALYSIS

Broad-headed and narrow-headed individuals had clearly separated $\delta^{15}\text{N}$ values in the four sites that supported the two shape groupings (Table 2.5). In Lough Derg, Lough Finn and Loch Lomond narrow-headed individuals were significantly more depleted in $\delta^{13}\text{C}$ in comparison to broad-head individuals (Table 2.5). Regression analysis was used to investigate ontogenetic changes in isotope signatures with respect to fish length (r^2 value reported in Table 2.5). The relationship between length and isotope values revealed a significant effect of increasing length on $\delta^{15}\text{N}$ in broad-headed individuals in Loch Lomond and narrow-headed individuals in Lough Finn and Loch Lomond, length was also observed to have a significant positive effect on $\delta^{15}\text{N}$ of estuarine fish. Length was not found to have a significant effect on $\delta^{13}\text{C}$ in eels sampled within sites (multiple r^2 value reported in Table 2.5).

Table 2.5 Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{S.D}$ in 5 study sites, minimum and maximum lengths for each type, significance of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between morphs in each habitat (P; significant in bold). Ontogenetic variation in isotope values (r^2) and isotopic niche width (Ec)

Location	Mclust grouping	L_T (mm)	n	Mean $\delta^{15}\text{N} \pm \text{S.D}$	t value & P value (difference in $\delta^{15}\text{N}$ values between morphs within site)	$r^2 \delta^{15}\text{N}$	$\delta^{13}\text{C} \pm \text{S.D}$	t value & P value (difference in $\delta^{13}\text{C}$ values between morphs within site)	$r^2 \delta^{13}\text{C}$	Ec (Niche width - SIBER)
Baronscourt	Broad	422-681	25	14.7996 \pm 0.305	-	0.05	- 33.72 \pm 0.663	-	0.05	11.67
	Narrow	416-617	13	13.5925 \pm 0.358	2.56 $P < 0.05$	0.01	- 35.03 \pm 0.758	1.29 $P > 0.05$	0.05	13.28
Lough Derg	Broad	415-660	31	8.2 \pm 0.09	-	0.00	-23.07 \pm 0.28	-	-0.03	2.72
	Narrow	428-559	15	7.9335 \pm 0.07	2.23 $P < 0.05$	0.04	- 25.66 \pm 0.36	5.61 $P < 0.001$	0.02	1.76
Lough Finn	Broad	429-725	16	10.57 \pm 0.17	-	0.09	- 23.86 \pm 0.31	-	0.05	2.52
	Narrow	425-520	12	9.89 \pm 0.12	3.17 $P < 0.001$	0.10*	-25.89 \pm 0.36	4.76 $P < 0.001$	0.00	1.75
Loch Lomond	Broad	420-661	17	11.42 \pm 0.19	-	0.236*	- 24.03 \pm 0.17	-	<0.00	2.96
	Narrow	430-600	15	10.44 \pm 0.27	2.92 $P < 0.05$	0.193*	- 25.76 \pm 0.2	6.3 $P < 0.001$	<0.00	3.1
Estuary	NA	425-570	26	14.95 \pm 0.14	-	0.11*	- 23.856 \pm 0.24	-	0.00	2.96

Isotopic niche width was quantified using the SIBER package by calculating SEA_B using Bayesian inference (Jackson *et al.*, 2011). Based on shape group assignment, niche width between morph types within locations sampled was compared. Narrow-headed individuals exhibited significantly larger niche width in comparison to broad-headed individuals in Lough Finn and Loch Lomond (95% credibility limits) however this was not significant in Baronscourt between types. Broad-headed individuals in Lough Derg had a larger but not significant niche width over narrow-headed individuals (Ec: Table 2.5 & Fig. 2.4). Relative contribution of different prey items to diet based on $\delta^{15}N$ and $\delta^{13}C$ the mixing model (SIAR) revealed that the mean contribution of fish in the broad-headed diet ranged from 49 to 84% (Table 2.S1; Supporting Information).

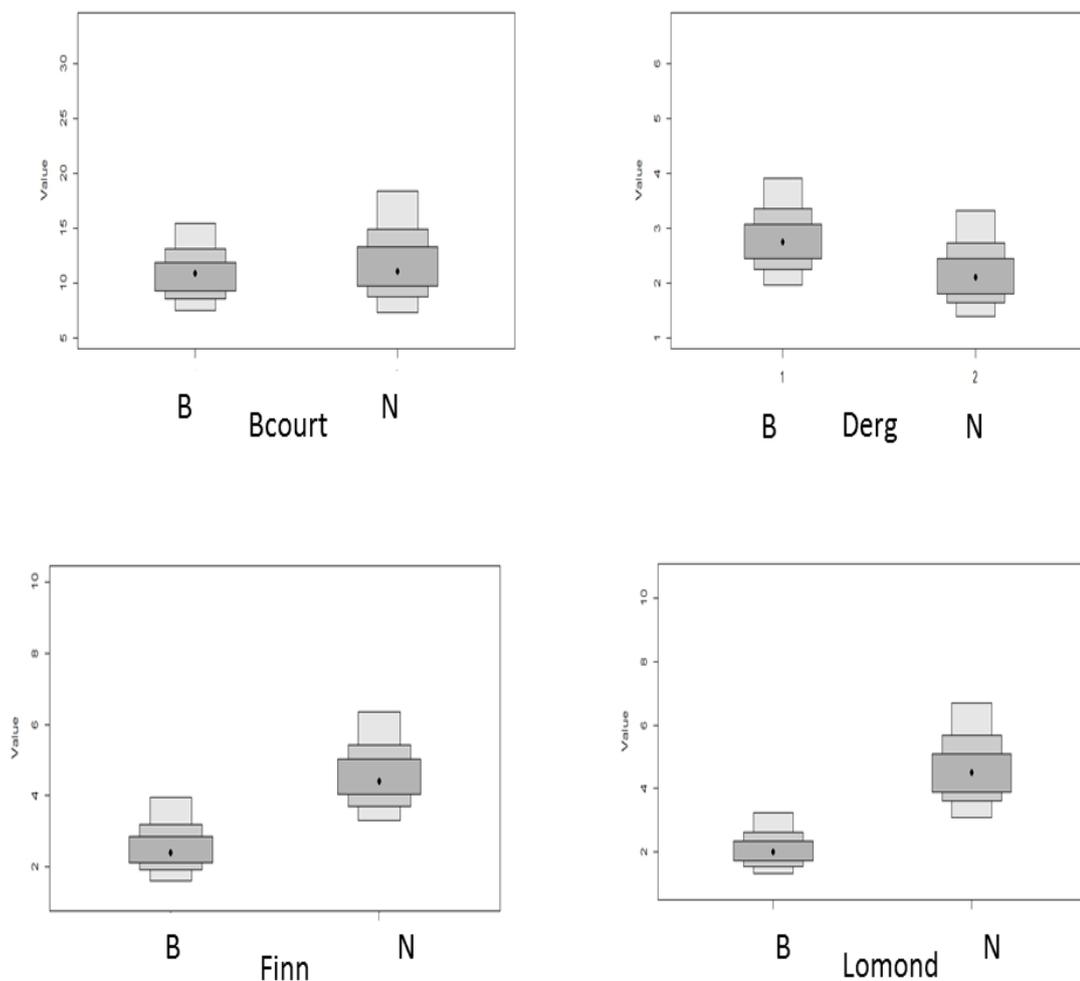


Fig. 2.4 Isotopic niche width variation ($SEAb$) between broad and narrow head individuals in study sites, The boxes indicate 95, 75 and 50% Bayesian credibility intervals for estimates based on SIAR isotopic mixing model. Grouping based on MCLUST shape allocation. Estuary fish not included as this site did not support two groups.

2.4.4 GROWTH & LIPID

To test the hypothesis that growth was influenced by head shape type von Bertalanffy growth parameters were examined using likelihood ratio tests in the “Fishmethods” package in R (Nelson, 2013). Broad-headed individuals exhibited a significantly faster growth rate (K) in Lough Derg, Baronscourt lakes and Loch Lomond, broad-headed individuals in these sites were also found to have significantly higher theoretical L -infinity (i.e maximum length) (Table 2.6 & Fig. 2.5).

Table 2.6 Likelihood ratio tests comparing growth curves parameters of broad and narrow headed individuals within each study site. L_{inf} = Theoretical maximum growth; K = Theoretical growth rate; T_0 = Theoretical minimum length from growth model. Estuary fish not included as this site did not support two groups.

Location	Parameter	Chi sq	df	P
Baronscourt	L_{inf}	15.17	1,37	<0.001
	K	10.94	1,37	<0.001
	T_0	0.14	1,37	>0.05
Lough Derg	L_{inf}	8.41	1,45	<0.05
	K	11.66	1,45	<0.05
	T_0	0.49	1,45	>0.05
Lough Finn	L_{inf}	1.11	1,27	>0.05
	K	1.35	1,27	>0.05
	T_0	0.22	1,27	>0.05
Loch Lomond	L_{inf}	9.99	1,32	<0.05
	K	8.83	1,32	<0.05
	T_0	0.02	1,32	>0.05

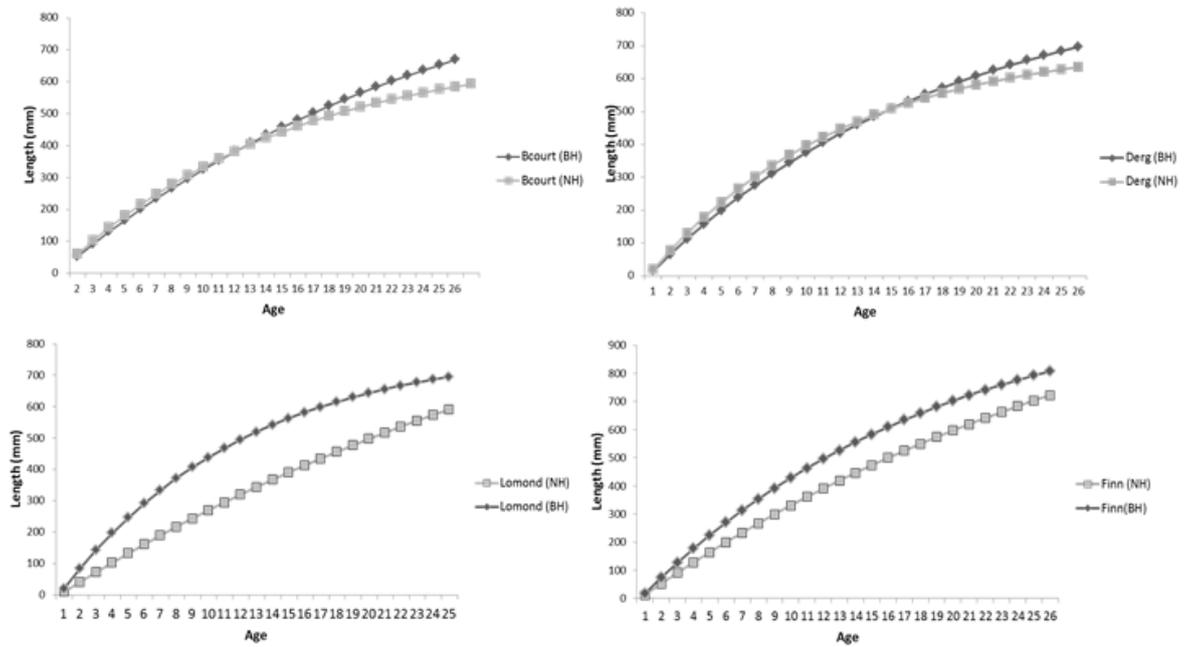


Fig. 2.5: Theoretical growth trajectories (Von Bertalanffy) for broad-headed (BH) and narrow-headed (NH) eels. Estuary fish not included as this site did not support two groups.

A linear model looking at the effect of lipid deposition in study sites revealed a significant effect of head shape. Broad-headed individuals had a significantly lower lipid content than individuals with narrower heads ($F=_{1,166} 42.5$, $P<0.0001$). No effect of the silver index ($F=_{4,162}$, 0.650 , $P>0.05$) or the length of individual ($F=_{1,166} -0.431$, $P>0.05$) or age at capture ($F=_{1,166} 0.035$, $P>0.05$) was observed on lipid levels of fish. Tukey pairwise comparison of broad-headed and narrow-headed lipid stores within sites revealed a narrow headed individuals exhibited significantly higher lipid content in four sites that supported both broad-headed and narrow-headed individuals (All sites $P<0.05$) (Fig. 2.6).

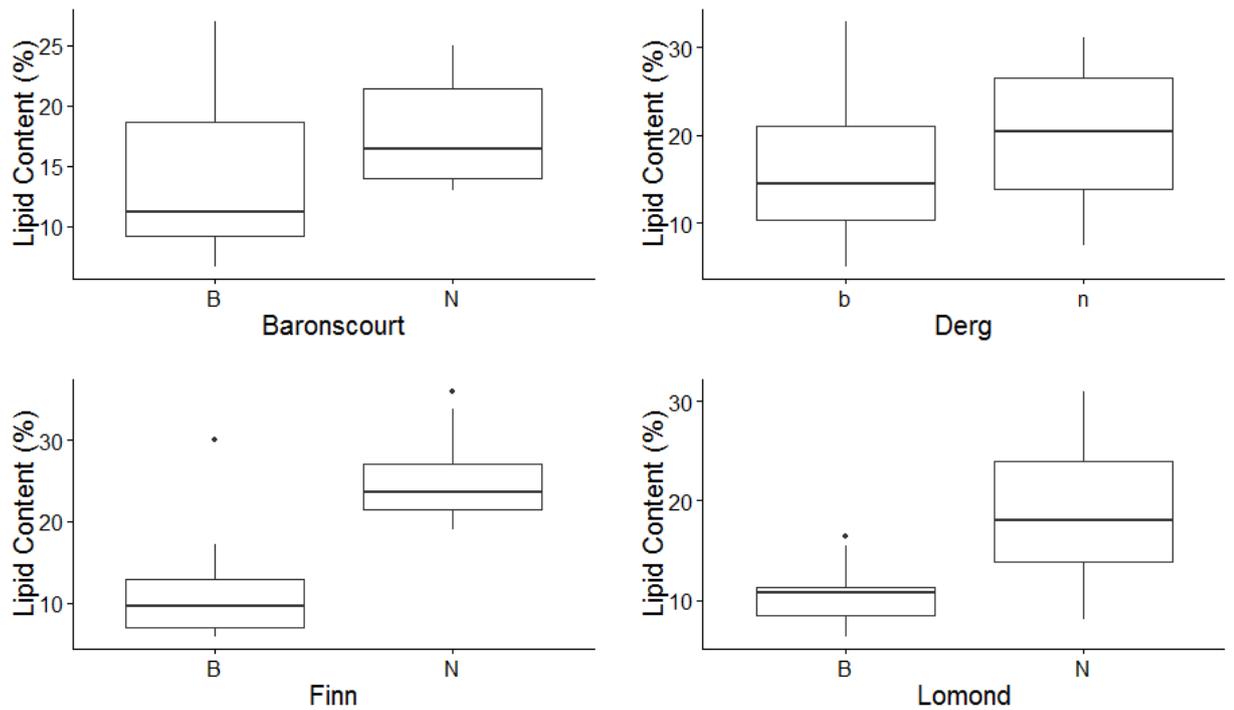


Fig. 2.6: Boxplot of lipid variation between broad-headed (B) and narrow-headed (N) individuals in study sites. Estuary fish not included as this site did not support two groups.

2.5

DISCUSSION

The aim of this study was to explore the interrelationships between trophic morphology, feeding ecology and potential life history consequences in *A. anguilla* in a range of continental habitats. Overall substantial differentiation was observed in the morphology and ecology between eels from the study sites investigated. Morphometric analysis revealed significant differences in head shape variation between sites and differentiation within sites between broad-headed and narrow-headed individuals (based on Bayesian group assignment). Interestingly the occurrence of both types was statistically supported in the four lake sites but not in the estuarine site. Population panmixa (Als *et al.*, 2011; Pujolar *et al.*, 2013) impairs the possibility of local adaptation favouring the emergence of phenotypic plasticity (Drouineau *et al.*, 2014). Thus, morphological variability between and within sites suggests that eels exhibit a plastic response to the environment in which it resides during the growth phase of its life cycle.

Stomach content analysis revealed eels residing in lake sites were found to utilise both fish and invertebrate resources and this corresponded to the support of

both broad-headed (fish feeders) and narrow-headed individuals (invertebrate feeders). A clear bimodality in estuarine head shape was not observed and this corresponded to a clear specialisation on a single prey *Crangon* sp. among all the eels sampled (stomach content analysis) with individuals specialising on one trophic resource and not multiple as was observed in lake systems. This provided evidence that there is a strong relationship between head shape and foraging ecology in different ecomorphs of European eels.

Stable isotope analysis provided clear evidence that the different foraging strategies were stable over time. Broad-headed individuals exhibited elevated $\delta^{15}\text{N}$ within study sites supporting the theory that the observed plasticity in eel head shape is a result of diet induced phenotype plasticity (Ide *et al.*, 2011, Lammens & Visser, 1989; Provan & Reynolds, 2000) with broad-headed individuals favouring a piscivorous diet and feeding at a higher trophic level than narrow-headed individuals within the same location. Interestingly, narrow-headed individuals were more depleted in $\delta^{13}\text{C}$ in comparison to broad-headed individuals in Lough Derg, Lough Finn and Loch Lomond. This is indicative of obtaining diet from different basal resources (March & Pringle 2003); this variation in $\delta^{13}\text{C}$ indicates a contribution of zooplankton to the diet (^{13}C depleted) of narrow-headed eels in comparison to a significantly higher signature from littoral resources ($\delta^{13}\text{C}$ enriched) in broad-headed individuals. Ontogenetic enrichment of $\delta^{15}\text{N}$ was observed in narrow-headed eels from Lough Finn and Loch Lomond, broad-headed eels in Loch Lomond and all eels in the estuarine site. An increase in $\delta^{15}\text{N}$ signature is common with increasing fish length (Grey 2001; Cucherousset *et al.*, 2011). Niche width was higher among narrow-headed individuals in three of the four sites which supported broad-headed and narrow-headed individuals, this can be explained by the higher diversity of prey species which was observed in the stomach contents of narrow-headed individuals. Narrow-headed individuals were selecting a more generalist invertebrate strategy in comparison to broad-headed individuals which had more specialised fish eating diet. It is important to note that broad-headed individuals in Lough Derg appeared to have a larger niche width. This cannot be easily explained; although there was statistically significant support for two morphs within the Lough. Interestingly stable isotope signatures did not correspond to stomach contents which exhibited clear differentiation; thus, we postulate that the discrimination power of stable isotope in Lough Derg may be lower

than expected and could potentially be influenced by environmental conditions (Davias *et al.*, 2014).

The data presented here reveal that broad-headed individuals in most sites exhibited faster growth and greater length at ages in comparison to narrow-headed individuals. Faster growth rates being observed for broad-headed individuals in three of the four study sites (Baronscourt lakes, Lough Derg and Loch Lomond). Faster somatic growth has been previously recorded for broad-headed individuals compared to narrow-headed eels (Rahn 1955; Tesch 1977). However in a recent study on the head shape polymorphism in the closely related Japanese eel (*Anguilla japonica*) slow growing fish became broad-headed while fast growing fish become narrow-headed (Kaifu *et al.*, 2013). Results also support the hypothesis that foraging strategy influences lipid reserves of individuals in study sites investigated and we found clear between-morph differences in fat content. Narrow-headed individuals exhibit a much higher lipid reserve than broad-headed individuals within the same habitat. This indicates that foraging strategy influences lipid accumulation in the growth phase.

Prey availability within the growth habitat indicates that it is playing an important role in the morphological variation. Resource use differences corresponded to the dichotomy in head morphology in the lake systems, however, when individuals specialised on a single resource, support for different shape groups was not seen. Given the unpredictable nature of prey availability and variability in space and time, individuals may specialise in a particular diet because it is the only one that they encounter (Pyke, 1984). Individuals within a species may occupy different geographic regions (e.g within large lakes) which may also lead to morphological adaptation to a particular diet/resource in that area (Hubbs, 1961). However capture of both broad-headed and narrow-headed individuals within the same fyke chain rules out spatial segregation within locations sampled. An individual's foraging strategy can also be determined by their size, and morphology (Schoener, 1974). Thus, juveniles may specialise on smaller and types of prey (e.g. invertebrates). However, interestingly a clear dichotomy in head shape independent of size is observed in the four lake sites investigated, with both broad-headed and narrow-headed eels occurring within the same size class and it is clear that “broadheadness” is not restricted to the largest specimens. So although ontogenetic shifts in diet can be observed in eels (Tesch, 2003), this does not explain the morphological variability independent of size co-occurring within the same habitat.

The physiological constraints of an individual may influence the foraging strategy employed (Hughes, 1980). Foraging strategies are based on maximising energy gain or potential reproductive success (Bergman *et al.*, 2001). Environmental variation may lead to the evolution of foraging strategies that benefit reproductive output, and adopted strategies within a habitat can have important consequences for population dynamics (Tyler & Rose 1994). Different feeding strategies may have different payoffs or outcomes, for example the results from this study suggest that broad-headed eels grow fast however lay lipid down at a slower rate in comparison to narrow-headed eels that grow slower but lay lipid down at faster rate.

All the eels sampled in this study were female. In comparison to fast growing male eels which adopt a time minimising strategy, female eels are assumed to adopt a time maximising strategy adapting to local environment conditions (growth habitat) (Davey & Jellyman 2005). Length and age-at-migration are extremely variable in female eels. A correlation has been reported between length at silvering and longitude (Vollestad 1992) however it is believed they certainly benefit from attaining a greater size in terms of fecundity (Drouineau *et al.*, 2014; MacNamara & McCarthy 2012). The time needed to reach maturity will inevitably be a result of habitat and growth conditions, therefore the foraging strategy while in freshwater may play an important factor on timing of silvering and the capacity to reproduce. Our results suggest a possible life history consequence between broad-headed and narrow-headed individuals co-existing in the same environment. Life history strategies undertaken by a species ultimately rely on how best to utilize resources in order to commence reproduction and complete life cycle. Thus, environments in which growth phase occurs will therefore play a pivotal role on how an animal adapts to available resources and may influence timing of reproductive events. For eels the trade-off for female eels revolves around whether resources should be used for reproduction now or invested in a larger body increasing fecundity in the future (Drouineau *et al.*, 2014) with female eels ultimately wanting to attain the greatest possible sizes, implying higher fecundity (MacNamara & McCarthy 2012).

It is extremely difficult to compare the payoffs from different feeding strategies. It is also probable that differences in head shape and resource use may be driven by physiological and morphological constraints of individuals (Metcalf & Monaghan 2003). For example fast growing individuals may adopt a piscivorous diet whereas slow growing individuals may adopt a generalist benthic invertebrate diet.

Most studies record the benefits, in terms of food intake, but very few can measure the costs of different diets or feeding without long term common garden experiments and investigating the nutritional value for example of an invertebrate versus fish diet.

Conclusion

This study suggests that eels exhibit a phenotypic response to available food resources within the habitat in which it resides. However, individuals of similar size adapt to different resources within the same habitat. Phenotypic plasticity best explains the observed variation, with both phenotypes having different prey preferences (Proman & Reynolds, 2000; Lammens & Visser, 1989). Changes in the ratio of phenotypes in a given population may have an impact on freshwater ecosystems. The relationship between phenotype and ecology suggests that efforts towards conservation may require the assessment of morphological variation within a population (Ide *et al.*, 2011)

One of the main concerns affecting freshwater fish is that of habitat loss or environmental change. If individuals specialise in different diets, they will be affected to a greater or lesser degree by subsequent change (Schoener, 1974). Individuals or groups that are unable to change foraging area, diet or feeding method for morphological reasons will be the most vulnerable to loss of prey in a growth habitat. Our findings indicate that morphological variability in eel head shape is linked to trophic ecology and generates varying growth rates and lipid deposition depending on the foraging tactic employed by individuals within growth habitat. The great variability in *A.anguilla* found in study sites indicates *A.anguilla* are extremely plastic in their nature. The adaptability to varying resources may be driven by internal as well as external cues and warrants further research through long-term common garden experiments. Resource availability and type seems to be playing an important role in morphological variability and influencing life history consequences.

The level of complexity observed in European eels in growth habitats make adopting a single population/demographic model a simplistic approach, and highlight the need to understand and appreciate the morphological variation of eels which can be observed in some locations. The mechanisms behind morphological variation in European eel's warrants future research and accounting for morphological variability should be incorporated into population monitoring.

2.6

SUPPLEMENTARY INFORMATION

Table S2.1 Relative contribution to diet

Location	Morph	%Littoral zoobenthos	%Chiromid	%Fish	%Crustaceans	Ec
Baronscourt	Broad	0.329±0.212	0.586±0.21	0.084±0.05	-	11.67
	Narrow	0.60±.13	0.096±.131	0.29±0.077	-	13.28
Derg	Broad	0.28±0.012	0.005±0.71	0.713±0.011	-	2.72
	Narrow	0.006±0.005	0.507±0.012	0.485±0.011	-	1.76
Finn	Broad	0.47±0.06	0.256±0.07	0.272±0.06	-	2.52
	Narrow	0.43±0.40	0.511±0.044	0.048±0.029	-	1.75
Lomond	Broad	0.42±0.014	-	0.575±0.014	-	2.96
	Narrow	0.601±0.01	-	0.38±0.245	-	3.1
Estuary	-	-	-	0.17±0.01	0.829±0.013	1.98

Table S2.2 Von Bertalanffy growth characteristics of broad and narrow headed *A. anguilla*. Growth rate (k), theoretical asymptotic (Linfinity) and theoretical age at length

Location	Headshpe	<i>Linfinity</i>	<i>K</i>	<i>To</i>
Baronscourt	Broad	1053.16	0.0398	0.350
	Narrow	712	0.068	-0.2364
Lough Derg	Broad	912	0.057	-0.190
	Narrow	714	0.087	-0.072
Lough Finn	Broad	1365	0.0298	-0.434
	Narrow	1085	0.054	-0.231
Loch Lomond	Broad	1300	0.025	0.409
	Narrow	791	0.087	0.342
Estuary	NA	912	0.054	-0.092

Chapter Three

Foraging Specialisms Influence Space Use and Movement Patterns of the European eel *Anguilla anguilla*.

*Note: This chapter has been published in *Hydrobiologia*.

3.1

ABSTRACT

A fixed receiver array was used to examine the movement patterns and space use of the European eel *Anguilla anguilla* in an oligotrophic Irish lake between July and September. We assessed home range size, temporal change in spatial behaviour and activity patterns of broad headed (n=11) and narrow headed (n=8) morphotypes. Broad-headed individuals displayed a larger home range (mean KUD₉₅ (km²):0.296 ± 0.04 S.E.) in comparison to narrow-headed individuals (mean KUD₉₅ (km²):0.143± 0.02 S.E.). Eel activity was strongly dependent on light conditions. Narrow-headed individuals' movement peaks occurred at dawn and dusk in comparison to broad-headed individuals which exhibited a more stable movement pattern throughout night and into dawn, suggesting that narrow-headed eels are more crepuscular in nature whereas broad-headed individuals are more nocturnal. Lunar phase period also influenced eel movement within the lake. These results provide valuable insights into the spatio-temporal distribution of yellow eels in a lake system, demonstrating that individuality in foraging behaviour has direct influence on spatial patterns.

3.2

INTRODUCTION

Understanding how animals utilise their habitat in both space and time provide insights into the ecological, competitive and environmental forces that shape their behaviour. Increasingly, telemetry is used to quantify spatial (e.g. home range) and temporal (e.g. diel phase) activity patterns to evaluate individual distribution (Lucas & Baras, 2001; Cooke *et al.*, 2012). These patterns encapsulate movement behaviours associated with fulfilling ecological needs (feeding, shelter etc.) and are regulated by predictable variation in the environment. Home range is an area over which an animal regularly travels (Burt, 1943; Powell & Mitchell 2012). A home range is considered to be a decision-making process shaped by natural selection, increasing the contribution of resources to fitness, which are spatially distributed in a habitat (Mitchell & Powell

2004). Thus home range represents interplay between the environment and an animal's understanding of that environment (Borger *et al.*, 2008; Powell, 2000).

Fish body size, and thus energetic demands, can markedly influence home range size (Jetz *et al.*, 2004; Killen *et al.*, 2007). Increased home range of larger individuals is associated with a behavioural response to optimise foraging for the elevated energy demands (Dahlgren & Eggleston 2000; Marshall *et al.*, 2011). Home range size and activity patterns can also be dependent on diet and the foraging tactic employed, for example carnivores typically occupy larger home ranges than herbivores (Peters, 1986).

An important driver of fish distribution is that of feeding opportunity, with fish responding to resource type and or availability within a given habitat (Clark & Levy 1988; Jackson *et al.*, 2011). Individual specialisation in diet is relatively common among wild populations of many species (Bolnick *et al.*, 2003). Individual feeding specialisations can be temporally stable and associated with the occurrence of discrete morphotypes (Skulason & Smith 1995). Such foraging specialisms seem to be particularly common in fishes found in post-glacial lakes (Garduno-Paz *et al.*, 2010; Siwertsson *et al.*, 2013). Interspecific differences in head morphology of fish are known to reflect differences in feeding behaviour (Adams *et al.*, 1998, Kristjansson *et al.*, 2002) and are generally a result of consistent individual differences in foraging and diet over time.

The European eel (*Anguilla anguilla* L.) occupies a wide range of aquatic systems and habitat types, including fresh, brackish and salt water (Moriarty & Dekker, 1997). If drainage basins have natural or artificial lakes with adequate passage for migrating juveniles and adults, they will represent important growth habitat (Laffaille *et al.*, 2004) producing high numbers of silver eels (Tesch, 2003). Determining space use by eels in lake systems is thus important for an understanding of their ecology and ultimately conservation management in such systems. The existence of foraging specialisms amongst individuals of eel in freshwater populations is reasonably well known (Lammens & Visser, 1989; Ide *et al.*, 2011) and such specialisms seem to be associated with the dichotomous description of "broad-headed" and "narrow-headed" individuals (Lammens & Visser, 1989; Provan & Reynolds, 2000; Ide *et al.*, 2011). These studies have shown that independent of body length, broad-headed specimens tend to be piscivorous and narrow-headed individuals feed predominately on benthic invertebrates with this discrete variation among individuals being evident in the same locality (Cucherousset *et al.*, 2011; Ide *et al.*, 2011). However, the extent to which the

observed morphological variation is associated with behavioural differences other than those linked with feeding is yet to be investigated.

Information about how they utilise lacustrine habitat is essential to help direct conservation strategies. Despite the length of time eel spend in lacustrine environments, there is little information about home range size and activity patterns in lakes. The first objective of this study was to quantify the spatial distribution of European eel, with a specific focus on home range sizes and activity patterns in a lacustrine habitat. Combining measures of individual head morphology with individual behavioural parameters obtained by tracking movements of individuals using acoustic telemetry, our second objective was to test the hypothesis that individual movement patterns and space use are correlated with differences in morphology and foraging specialisms.

3.3 METHODS

3.3.1 STUDY AREA & RECEIVER ARRAY

Lough Finn is an oligotrophic freshwater lake located adjacent to Fintown, Co. Donegal, Republic of Ireland (54 ° 51.7 N ' 008 ° 8.04' W). The lake is entirely natural, there are no obstructions in vicinity of the outflow so that eel are free to enter and leave the lake. Other fish species present in Lough Finn are, brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*), with no introduced species present. Lough Finn is approximately 1.15km² (115 ha) in size with a mean depth of 11.5m and a maximum depth of 21m. An echosounder linked to a GPS was used to record depths across a series of intersecting transects and these data were used to create a bathymetric map using Arcview GIS.

Preliminary tests were undertaken to determine the detection range of acoustic tags and receivers in Lough Finn. Based upon these preliminary detection range estimates, a fixed array of 20 omnidirectional acoustic receivers (69 KHz, Vemco VR2W) was deployed throughout the lake (Fig. 1). Receivers were attached (3 m from the bottom) to a rope riser on a moored anchor system, in 10-15 m depth of water. The receiver configuration allowed for range overlap (see below) and thus allowed tagged fish, that remained in the lake, to be continuously detected throughout the study.

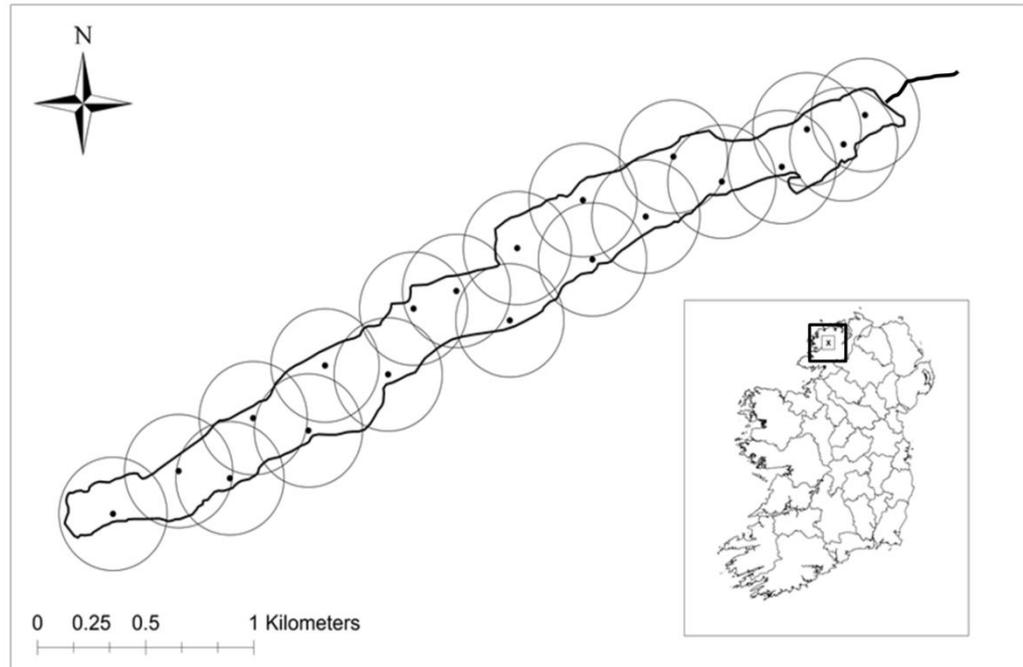


Fig. 3.1. Lough Finn and river finn outflow stream, receiver positions (black dots) and omnidirectional detection range from acoustic listening station (black circles).

3.3.2 FISH SAMPLING AND TAGGING

Yellow eels were captured using fyke nets on 27 June 2013 and again on 2 July 2013. Nets were set arbitrarily around the lake and fished for a period of 24 h. Each fish was classified using the silvering index of Durif *et al.* (2005) so as to ensure all individuals tagged were resident and in the growth phase of their life cycle. Individuals in stage I-III were considered suitable for tagging and individuals which were categorised as stage FIV and FV were rejected from the study due to the high possibility of them metamorphosing and beginning downstream spawning migration in the near future. Overall, twenty individuals were tagged with individually coded 69KHz acoustic transmitters (Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g weight in air, 139dB re 1 μ Pa power, Thelma Biotel AS, Trondheim, Norway 2013). Acoustic transmitters were programmed to each have an average acoustic transmission repeat cycle of 120s. The mean total length and mass of tagged fish was 498 ± 91.3 mm and 227 ± 141.1 g (range: 390-720mm, 90.3-602g). The mean tag to body mass ratio was $1.11 \pm 0.5\%$ (i.e. $< 2\%$ as recommended, *sensu* Lucas & Baras, 2000). For the tagging procedure, fish were anesthetized by immersion in a water clove oil solution (0.5mg per litre) until loss

of equilibrium. Fish were placed in a v-shaped support and an acoustic transmitter was surgically implanted through a 15mm incision into the peritoneal cavity, and the incision was closed with independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK). Fish were aspirated with 100% lake water throughout the procedure. The entire surgical process took less than 4 minutes. After complete recovery, defined as correct orientation and response to stimuli, fish were released in the location of initial capture. Recent work has demonstrated that this surgical procedure does not adversely affect behaviour of eels (Thorstad *et al.*, 2013).

3.3.3 DATA ANALYSIS

Head shape analysis

Where possible, an equal number of fish from broad and narrow-headed morphs were selected (*sensu* Proman & Reynolds 2000). Overall, twelve broad-headed individuals and eight narrow-headed individuals were tagged with individually coded acoustic transmitters. For each individual fish, head width (HW, to the nearest 0.1 mm) was measured between the outside of the jaw hinges, along with total body length (TL), the ratio HW:TL was calculated for each individual at tagging and subsequently used to assign tagged individuals to either broad (>0.33) or narrow (<0.33) according with previous studies (Lammens & Visser 1989; Proman & Reynolds 2000). To verify that this was an appropriate indicator of head shape we used a model-based clustering approach implemented in the package MCLUST for R (Fraley & Raftery 2009). Lateral view photographs of all fish were taken using a Cannon EOS 350D digital camera for geometric morphometric analysis. For each photograph a reference scale was included to allow the removal of shape change associated with size. Before comparing head shape of the groups a pooled within-group regression of Procrustes co-ordinates on log centroid size was performed. The residuals from this were derived thus providing a measure free from allometric scaling of shape associated with size (Klingenberg, 1998). Nine consistently identifiable landmarks were digitised in two dimensions. Land marks were carefully chosen to represent overall head shape. Principle component analysis was undertaken on Procrustes coordinates (2D coordinates that have been standardised for size and position) of the nine landmarks used to describe head shape. Principle component scores for each individual fish were clustered to allow an objective examination of head shape and assignment to ecological sub-group with clustering software. Two MCLUST models (EII and VII; see Fraley & Raftery 2006 for model descriptors) were fitted to the first four principal component scores of head shape data.

The “best” models, representing the most likely number of groups on the basis of head shape, were identified using Bayesian Information Criterion (BIC). The BIC value is the maximised log-likelihood for the model, the data dimensions and the number of model components; the larger BIC, the stronger the support for the model for head shape. The model that could at a minimum discriminate broad and narrow headed eels and had the highest BIC was selected to test accuracy of field classification method. For tagged fish, comparison between the best model with the next best model (resulting in a different number of groups) was undertaken by calculating ΔBIC as the difference in the BIC-values between the best model and the next best model. Following Kass & Raftery (1995) interpretation; $\Delta\text{BIC} > 10$ as very strong support, $6 < \Delta\text{BIC} < 10$ as strong support, $2 < \Delta\text{BIC} < 6$ as moderate support, and $\Delta\text{BIC} < 2$ as equivalent support for the best and the next best model. Statistical analyses were conducted in the R statistical computing package (R Development Core Team, 2014).

Acoustic position estimates

We estimated centres of activity (COA) for each fish for an allocated time bin using the mean position algorithm described by Simpfendorfer et al. (2002). R statistical computing language R development Core team (2014) was used to calculate mean latitude and longitude of all detections within each sequential time interval. The resulting set of estimated positions was used for the subsequent analysis. Fish position at each time was based on the averaged positions of the receivers that detected fish during the time interval and weighted by the number of detections at each receiver (Simpfendorfer et al., 2002; Hedger et al., 2008) to provide an estimated location for that time period. To test the assumption on which the centre of activity mean position algorithm is based; that the number of tag detections decreases with increasing distance from a receiver, a tag detection range test was undertaken. Transmitters (Model LP-7.3, 40-120s delay, 139dB re. 1 μPa , Thelma Biotel AS, Trondheim, Norway 2013) were moored at seven known distances from a receiver for 72 hours, and the number of receptions was determined each day for each distance. There was a significant negative linear relationship between the hourly number of receptions, relative to transmissions, and the distance from a receiver ($r^2 = 0.91$, $P < 0.001$). Thus the assumption of linearity that underlies this methodology was supported for the equipment within Lough Finn. Tag detection ranged from 50m-450m. Based on this range testing of equipment, the maximum distance at which a signal was detected at least 50% of the time was estimated at ~320 m and this distance was therefore used in array design to ensure

sufficient detection overlap between receivers. Following Villegas-Rios et al. (2013), to select the optimal time bin we calculated the mean number of receivers detecting signals from an individual tag (NR) and then we averaged the number of detections from this tag across all receivers (ND) during each time bin. The number of receivers (NR) detecting a tag is expected to increase asymptotically as time bin size increases, whereas the number of detections (ND) increases linearly with time bin size. Better position estimates are obtained when the fish is detected multiple times by multiple receivers. A suitable time bin was determined when the increase in NR was <10% between two consecutive values and ND remained >10 (Villegas-Rios et al., 2013). The resulting value was 60 minutes at which mean NR was 2.93 ± 0.4 and mean ND was 24.05 ± 14.2 . This ensured adequate spatial resolution of the data while maximising temporal resolution. In order to prevent bias of fish positions due to post tagging effects, all fish positions recorded until 4 days after release were excluded from analysis to allow the fish to recover sufficiently and resume normal movement behaviour.

Home range analysis

To avoid temporal autocorrelation and ensure independence of fish locations, Incremental Area Analysis (IAA) was conducted according to Hodder et al. (2007) to gauge the number of positions needed to represent maximum home range of individuals. From IAA a standardised sample of 108 positions per fish was used to examine monthly home range, this ensured a sufficient sample size and temporally stratified distributions of fish locations. Positions in the sample were chosen arbitrarily to represent the correct proportion of the number of hours in each time of day category (dawn, day, dusk, night; based on the NOAA sunrise/sunset calculator (NOAA, 2014) during each month.

Kernel Utilisation Distribution (KUD) was used as a home range estimator for eels. KUD estimates the intensity of area use of an animal's location over time (Worton, 1989). An animal's relative frequency of occurrence in a two-dimension plane was based on stratified locations throughout the study. To create 50% (core area) and 95% (home range) kernel estimates Geospatial Modelling Environment (GME) was used in conjunction with ArcGIS (v.10.1), KDE and isopleth tools were used to create 50% and 95% kernel distributions (KUD_{50} & KUD_{95}) for each individual fish in GME (Bandwidth = LSCV, cellsize=50m). Area calculations (km^2) of 50% and 95% kernel estimates were undertaken in ArcGIS. These polygons (containing 50% and

95% kernel estimates) were then clipped to the lake polygon (using the Intersection tool in ArcGIS) to exclude any portion of the calculated home range that occurred on land. To determine whether the location of monthly space use changed through time, the proportion of overlap between 50% and 95 % KUDs from month to month was calculated using the ArcGIS. Overlap was represented as the proportion (%) of the previous month's value and represented changes in month-to-month activity space. Finally depth preference was investigated for eels by employing the zonal statistics tool (ArcGIS) to obtain mean depth occupancy in KUD₅₀ assuming eels maintain a benthic lifestyle within their core range.

To investigate differences in home range size (KUD₅₀ and KUD₉₅) between morph type and month, a linear mixed effect model (LME) was constructed. A LME was also constructed to investigate the effects of mean water temperature and duration of night (minutes) on mean monthly KUD size between morphs. In all LMEs “individual” was treated as a random factor to account for repeated measures. Linear models were used to investigate; the effects of eel length and weight on mean KUD size; to test for differences in space use overlap (KUD₉₅ & KUD₅₀) for both morphs and; to investigate the influence of fish length and temperature on depth preference in (KUD₅₀). Differences in depth use in the core area (KUD₅₀) between morphs were compared using Welch's t-test. KUD data and KUD overlap data were transformed (log and arcsine transformed respectively) prior to analysis to improve normality. All model diagnostics were assessed graphically by examining the residuals for heterogeneity. For LME's *P* values were generated for fixed effects using the log likelihood method, by comparing models with and without the term(s) in question. All analysis was conducted using the R statistical computing package.

Movement patterns

The aim of the modelling process was to determine what factors were influencing eel movement within the array on an average hourly (diel patterns) and daily (environmental correlates) scale. Minimum displacement rates were obtained by calculating straight line distance between consecutive COA's (centre of activity), converted to body lengths / hour (BLh⁻¹) to standardise for body length effect. A general linear mixed effect model was used in both cases with a random intercept following Zuur *et al.* (2009) and Pinheiro & Bates (2000). Including fish ID as a random effect, the model accounted for potential correlation between repeated measures on each individual. Independent variables were interrogated for colinearity

and variance inflation scores were used to verify variable suitability. A LME was used to test the effects of average displacement rates per hour per month for individuals were used as the continuous response variable, fixed effects included; the individual's physical characteristics (length and head shape), month and hour of day. A second LME was constructed using average daily displacement (m) rates as the response variable with water temperature, duration of night and lunar phase as fixed effects. The lunar cycle was categorised into eight phases: new moon, waxing crescent, 1st quarter, waxing gibbous, full, waning gibbous, 3rd quarter, waning crescent based on the percent of the moon illuminated using R package "lunar" (Lazaridis, 2015). Duration of night was measured in minutes of darkness based on NOAA calculator (NOAA, 2014).

In both LME's the `glmulti` function, with a wrapper to enable use of a random effect (Calcagno & Mazancourt 2010) was used to allow model selection of the best set of independent variables up to two way interactions with minimum Akaike information criterion (AIC). For both LME's final models were generated with non-significant variables dropped. Model diagnostics were assessed graphically by examining the residuals for heterogeneity. *P* values were generated for interactions and fixed effects using the log likelihood method, by comparing models with and without the term(s) in question. All analysis was conducted using R statistical computing package.

3.4 RESULTS

3.4.1 FISH DETAILS

In total 20 (12-broad-headed, eight narrow-headed) European eel were individually tagged and tracked during this study (Table 3.1). On average, an individual fish was detected on 12.2 ± 0.76 receivers over the study period. The detection period for tagged fish ranged from 44-95 days (Table 3.1). Five of the 20 eels (broad headed individuals: 2315, 2329, 2335 and narrow head individuals: 2334, 2332) left the array within the lake system and were last detected at the receiver nearest to outflow stream. One broad headed individual (2318) exhibited behavioural movements between river and lake system and was removed from analysis due to the bias of this fish on home range estimates, The number of eels used in analysis per morph per month is presented in Table 3.S1 (supplementary information).

Table 3.1 Characteristics of the 20 individuals tagged and detection span. B=broad-headed, N=narrow-headed. 2318* excluded from analysis

Fish ID	Release Date	TL (mm)	Weight (g)	Detection Span (days)	MCLUST group	Morphotype	HW:TL
2318*	02/07/2013	390	90	26	1	B	0.038
2327	02/07/2013	398	101	91	1	B	0.048
2315	02/07/2013	421	117	53	1	B	0.036
2329	02/07/2013	455	154	59	1	B	0.044
2323	27/06/2013	459	154	95	1	B	0.048
2320	02/07/2013	476	160	91	1	B	0.040
2325	27/06/2013	521	320	95	1	B	0.047
2340	02/07/2013	521	306	91	1	B	0.046
2337	27/06/2013	533	243	95	1	B	0.043
2326	02/07/2013	584	371	90	1	B	0.050
2332	02/07/2013	660	540	91	1	B	0.048
2335	02/07/2013	720	602	44	1	B	0.046
2333	27/06/2013	399	130	91	2	N	0.028
2339	02/07/2013	408	102	91	2	N	0.025
2302	02/07/2013	409	94	90	2	N	0.022
2303	27/06/2013	465	218	95	2	N	0.026
2322	27/06/2013	498	201	95	2	N	0.029
2330	02/07/2013	500	214	91	2	N	0.032
2336	02/07/2013	500	224	90	2	N	0.024
2334	02/07/2013	523	216	52	2	N	0.027

3.4.2 MORPH CLASSIFICATION

A model that used the first four principal components from an ordination of geometric head shape, discriminated two shape groups in tagged fish. MCLUST model EII (Fraley & Raftery 2006) was used to discriminate groups, the best model based on BIC scores supported two clusters (1 group BIC=264.8; 2 groups BIC=304.21, Δ BIC>10 providing support for 2 groups). The assignment of individuals from cluster analysis matched exactly directly with broad and narrow heads based on HW:TL ratio assignment thus ensuring adequate morph categorisation.

3.4.3 HOME RANGE AREA ESTIMATES

Home range estimates are presented as the average KUD₅₀ (core area) and KUD₉₅ (home range area) (km²), per month for both broad-headed and narrow-headed morphs of eels (Tables 3.S1, 3.S2; Supplementary Information). Over the duration of the study period broad-headed individuals displayed a larger home range (mean KUD₉₅ :0.296 km² ± 0.04 S.E.) in comparison to narrow-headed individuals (mean KUD₉₅ :0.143 km² ± 0.02 S.E.) (Table 3.2). KUD₅₀ size was not significantly affected by month ($\chi^2=0.844, df=2, P=0.655$) or head shape ($\chi^2=1.87, df=1, P=0.17$). Month did not have a significant effect on KUD₉₅ area estimates ($\chi^2=4.11, df=2, P=0.127$) however the model revealed a significant effect of head shape ($\chi^2=11.169, df=1, P=0.0001$) indicating that broad-headed individuals had larger KUD₉₅ ranges in comparison to narrow-headed individuals. Mean water temperature per month had a significant positive effect on mean KUD₉₅ size for both broad-headed and narrow-headed individuals ($\chi^2=10.865, df=3, p=0.012$) however no effect of temperature was found on mean KUD₅₀ ($\chi^2=0.0996, df=1, P=0.565$). Mean duration of night per month (minutes between sunset and sunrise) did not significantly affect KUD₅₀ of eels ($\chi^2=2.40, df=1, P=0.122$). However the model revealed a significant interaction between month and morph ($\chi^2=8.2286, df=3, P=0.04$) this was explained by a negative effect of increasing night duration on KUD₉₅ size of narrow-headed individuals.

Table 3.2 Mean KUD₉₅ and KUD₅₀ per month and overall mean for the duration of tagging period.

Month	Broad KUD ₅₀	Broad KUD ₉₅	Narrow KUD ₅₀	Narrow KUD ₉₅
July	0.066	0.341	0.031	0.179
August	0.113	0.251	0.022	0.112
September	0.048	0.292	0.017	0.103
Overall mean (S.E)	0.076 (0.012)	0.295 (0.016)	0.023(0.003)	0.131(0.16)

Body length and mass had a positive effect on KUD₉₅ of all individuals (Length $t=2.486,_{2,16} P<0.05$; mass $t=3.455,_{2,16} P<0.001$). Controlling for length broad-headed individuals had a significantly larger KUD₉₅ than narrow-headed ($t=4.951,_{1,15}, P <0.05$) (Fig.3.2). KUD₅₀ size was significantly positively affected

by length of individuals ($t=3.069_{2,16}$, $P<0.001$) but no differences were observed on KUD_{50} size between morphs when controlling for length ($t=-0.349_{2,16}$ $P>0.05$).

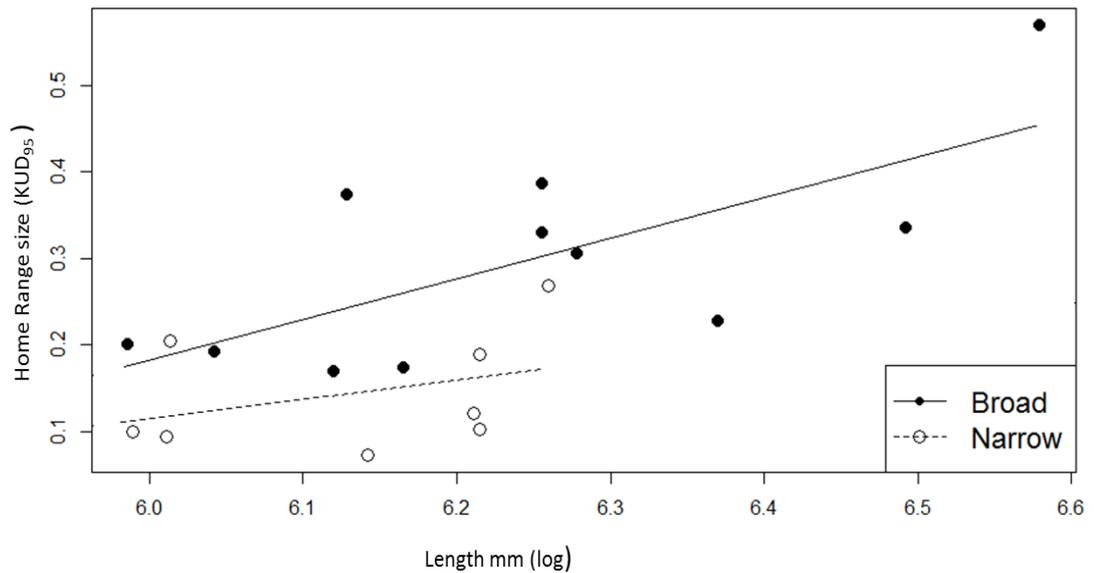


Fig.3.2 Relationship between home range size (KUD_{95}) and length of individuals (log transformed), broad heads black circles and associated trend line solid black line and narrow heads hollow circles and associated trend line dashed line

The amount of overlap in KUD area from month to month was used to define reuse of space through time as an indication of fidelity to home ranges. Average monthly overlap of 41% and 70% was observed for KUD_{50} and KUD_{95} respectively (Table 3.3). KUD_{95} overlap between consecutive months was similar in both morphs (Broad=69% Narrow = 70%). Mean overlap between consecutive months of individuals' KUD_{50} was significantly higher in broad-headed individuals ($t=2.453_{3,15}$, $P<0.05$) indicating higher site fidelity in this group. Further analysis revealed a significant interaction between length of individuals and head shape on KUD_{50} overlap between months ($t=-2.838_{3,15}$, $P<0.05$) indicating that small size narrow-headed individuals exhibit higher overlap between KUD_{50} compared with large size narrow-headed individuals, this contrasts with broad headed individuals which exhibit consistent overlap between core KUD's regardless of size. Differences in patterns between 50 and 95 % KUDs suggest individuals maintained a consistent KUD_{95} area that was reliably reused through time, but that the extent of movement in KUD_{50} varied in particular among larger narrow-headed individuals resulting in lower degree of overlap in core areas (Table 3.3).

The mean depth use of tagged eels at lake bed level in their estimated (KUD₅₀) was 9.0 meters. There was no relationship between mean depth in their KUD₅₀ and length of individuals ($F=0.384,_{1,17} P = 0.74, r^2 = 0.02$). Depth preference did not differ significantly between morphs (Welch t-test: $t=-0.216, d.f. = 14.03, P =0.68$). No relationship was found between mean depth in core area (KUD₅₀) and water temperature ($F=0.224,_{1,67} P = 0.604, r^2 = 0.004$) over the duration of the study.

3.4.4 MOVEMENT PATTERNS

The activity patterns of tagged fish and factors influencing average displacement between location fixes were monitored over the tagging period. Displacement between consecutive hourly centres of activities ranged from 0-2215m. In general, a distinct diel pattern was evident showing lowest activity during day light, and heightened activity during crepuscular periods and night (light categories based on NOAA sunrise/sunset calculator (NOAA, 2014)). The magnitude of effect was greater for broad-headed eels (average hourly displacement rates over duration of study: dawn: $196m \pm 9.2$, day: $123 m \pm 1.5$, dusk: $153m \pm 6.4$, night: $174m \pm 2.4$) than it was for narrow headed individuals (average hourly displacement rates over duration of study: dawn: $127m \pm 7.1$, day: $78 m \pm 1.5$, dusk: $125m \pm 5.6$, night: $99m \pm 1.7$

Diel movements

The minimal adequate linear mixed model for eel diel movement revealed a significant effect of hour of day on broad-headed ($\chi^2=21.013, df=1, P <0.001$) and narrow headed individuals ($\chi^2=5.14, df=1, P <0.05$) both morphs exhibited a clear nocturnal diel pattern with higher average BLh⁻¹ displacement observed during crepuscular and nocturnal periods (Fig.3.3 & 3.4). To explore the relationship between diel patterns and average displacement, hour of day was grouped into light categories based on NOAA calculator. Light category was found to have a significant effect on broad-headed ($\chi^2=223.17, df=7, P <0.001$) and narrow-headed individuals ($\chi^2=116.97, df=7, P <0.001$), broad-headed individuals average displacement peaked on dawn and night categories, in comparison to narrow-headed individuals which peaked on dawn and dusk light category.

Table 3.3 Temporal stability denoted by percentage home range overlap for home range KUD₉₅ and core range KUD₅₀ between months over the study period. (Refer to text for statistical analysis). B= broad-headed and N= narrow-headed.

I.D	TL	Morphotype	KUD ₅₀ (Jul-Aug)	KUD ₅₀ (Aug-Sep)	Mean monthly KUD ₅₀ overlap (50%)	KUD ₉₅ (Jul-Aug)	KUD ₉₅ (Aug-Sep)	Mean monthly KUD ₉₅ overlap (95%)
2315	421	B	62	-	62	62	-	62
2320	476	B	73	72	72.5	74	85	79.5
2323	459	B	29	49	39	36	53	44.5
2325	521	B	6	86	46	61	89	75
2326	584	B	29	64	46.5	73	86	79.5
2327	398	B	32	32	32	58	78	68
2329	455	B	64	-	64	74	-	74
2332	660	B	62	79	70.5	81	63	72
2335	720	B	28	-	28	59	-	59
2337	533	B	66	56	61	87	59	73
2340	521	B	50	76	63	75	86	80.5
2302	409	N	37	52	44.5	60	65	62.5
2303	465	N	52	68	60	88	71	79.5
2322	498	N	26	-	26	79	-	79
2330	500	N	0	19	9.5	54	61	57.5
2333	399	N	21	52	36.5	74	69	71.5
2334	523	N	10	-	10	65	-	65
2336	500	N	0	0	0	90	49	69.5
2339	408	N	61	58	59.5	84	80	82

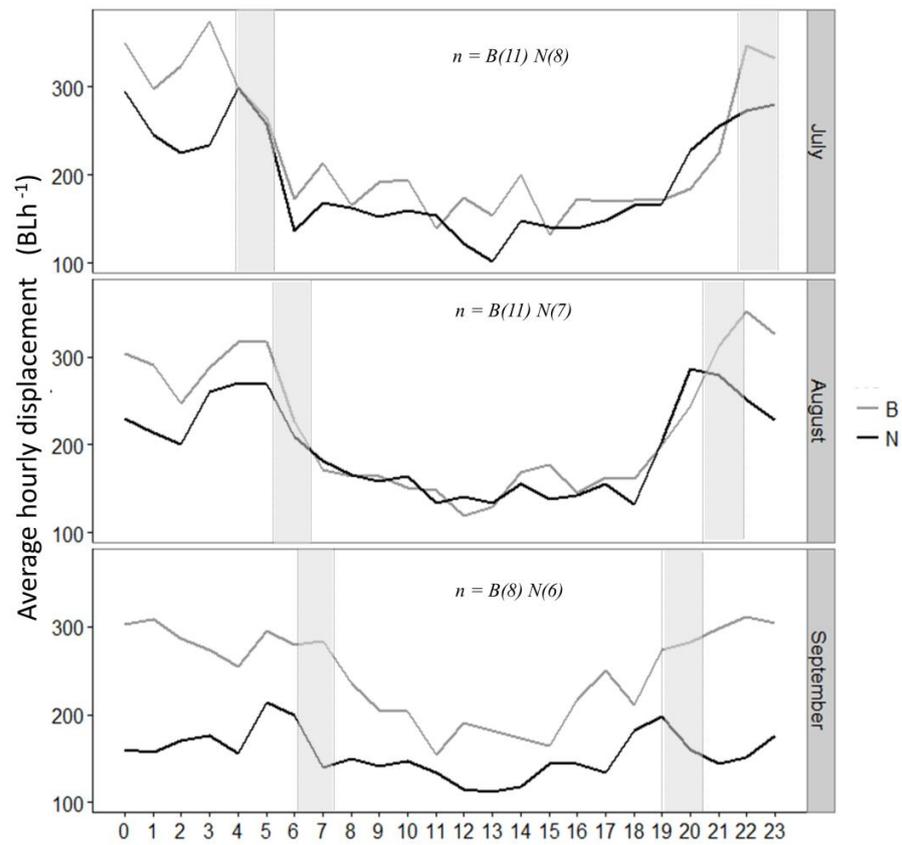


Fig. 3.3 The average displacement rate (BLh^{-1}) per hour (facet by month) for broad (B=grey line) and narrow-headed (N=black line) individuals. Crepuscular periods are represented by light shading (range = min and max sunrise/sunset for each month, NOAA 2014).

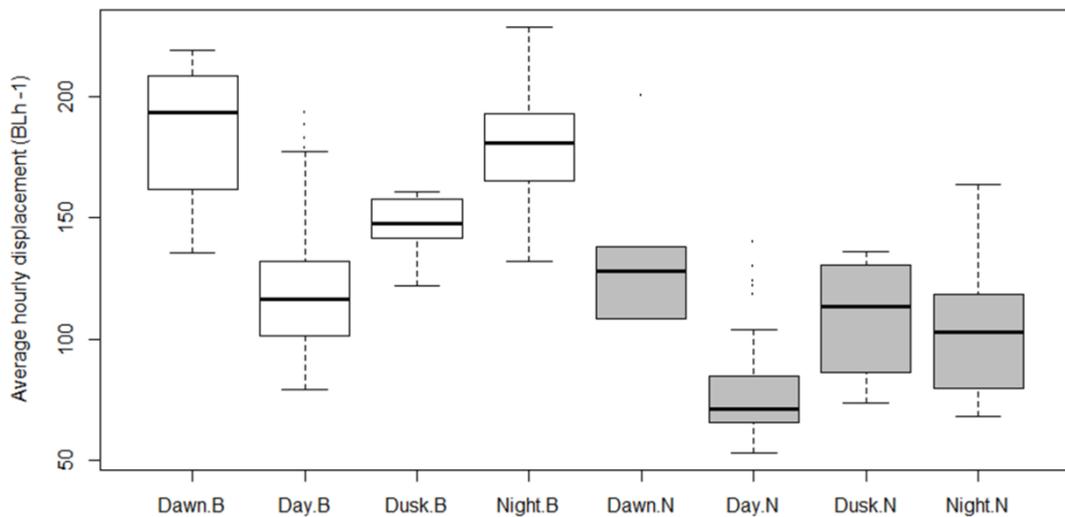


Fig. 3.4 The average hourly displacement rates (BLh^{-1}) for broad-headed (white box) and narrow-headed (grey box) individuals in different light categories. B = Broad-headed N= Narrow-headed.

Environmental correlates

The minimal adequate linear mixed model investigating the effects of environmental correlates revealed a significant effect of temperature ($\chi^2=8.16$, $df=1$, $P=0.004$) and lunar phase ($\chi^2=19.724$, $df=1$, $P=0.006$) on average daily displacement (BLh^{-1}) of broad-headed eels. Broad-headed individuals' average daily displacement was found to be higher during waxing lunar phases. Narrow-headed eels average displacement was not influenced by temperature ($\chi^2=1.469$, $df=1$, $P=0.225$), duration of night had a significant negative effect on narrow-headed individuals ($\chi^2=40.803$, $df=1$, $P=0.001$). Lunar cycle had a significant effect ($\chi^2=18.108$, $df=7$, $P=0.01$) with narrow-headed individuals' average daily displacement peaking on waning lunar phases (Fig 3.5).

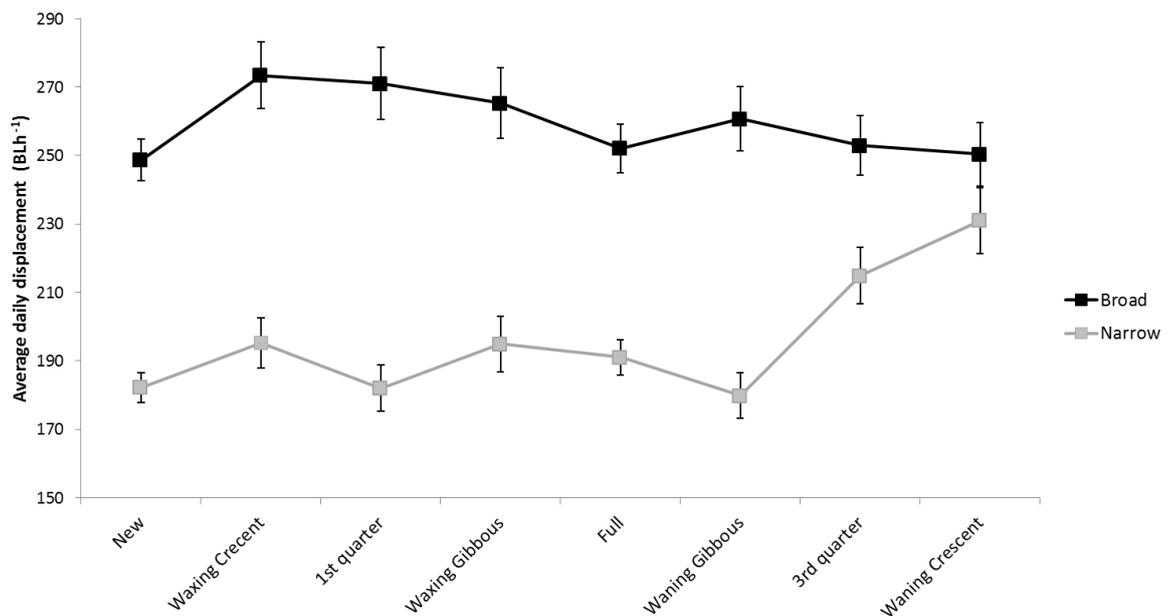


Fig. 3.5 Average daily displacement in meters with tagged individuals grouped by morph type during lunar phases. Error bars ± 1 standard error.

3.5

DISCUSSION

There are numerous studies detailing the extent of intra-population variation and individual specialisation in traits as a result of diet and foraging (Bolnick *et al.*, 2003; Araujo *et al.*, 2009). Detailed studies that link together spatial, temporal and individual level processes are however, rare. Here we report that yellow-phase lacustrine

European eels exhibit strong correlations between head morphology and spatial behaviour. This study is the first to provide an extensive account of home range size and movement patterns of European eel in a lake system. The lake system in which our study took place allowed for continuous observations of eel movements over the study period. While this study supports previous findings of extensive movement patterns of yellow eels (Thiabault *et al.*, 2007, *A.rostrata*; Walker *et al.*, 2014, *A.anguilla*) we add to the understanding of home range variation and activity among eels in lake systems, presenting evidence of movement patterns being influenced by diurnal and lunar drivers of activity as well as behavioural differences leading to variation in space use.

These findings support current evidence that *Anguilla* species establish a home range while resident during the continental stage of their lifecycle (Parker, 1995; Morrision & Secor 2003). Studies have documented varying home range sizes for eels in different habitat types. Reported home ranges in small lakes, tidal creeks and estuaries have varied in size 0.0027 km² (LeBar *et al.*, 1987), 0.01 km² (Bozeman *et al.*, 1985), 0.16 km² (Thiabault *et al.*, 2007) and 3.25 km² (Parker, 1995). Thus, the factors that drive within species variation in space use and home range size remain poorly understood and examples from previous studies suggest they may change depending on habitat type and individual eel characteristics.

Our findings suggest that total length and weight of individuals are important predictors of home range size. This finding is consistent with the allometric scaling relationship between body size and space requirements (Jetz *et al.*, 2004). Thiabault *et al.* (2007) observed an allometric relationship between total length and increased home range for American eels in tidal estuaries, comparable to results in the present study. The relationship between body size and home range size may result from the increased area required to provide the resources for a larger individual (Swihart *et al.*, 1988; Pearce *et al.*, al 2013). Kramer & Chapman (1999) proposed that allometric shifts in change of diet and decreased relative cost of swimming were potential drivers for this observed pattern. This expanding home range with size could also be a response to foraging optimization in association with reduced predation risk with increased body size (Dahlgren & Eggleston 2000).

Our findings also indicate that head morphology is a significant predictor of home range size in eels. Our study provides the first empirical evidence that this

observed morphological variation in eels leads to significant differences in home range size. Over the entire study period broad-headed individuals were found to have a significantly larger home range than that of narrow-headed individuals. Variation in space use as a result of different morph type has been observed for other predatory lacustrine fish (Kobler *et al.*, 2009). The increase in home range size could be in part, due to the higher mobility and greater space use requirements of fish prey that are targeted by broad headed individuals in comparison to more localised prey availability of insects for narrow head individuals. Overall home ranges remained stable over the study period for both morphs with monthly comparisons of range shift revealing mean home range overlap for broad-headed of 69% and 70% for narrow-headed individuals. The observed home range stability from this study supports findings of site fidelity within eels (Parker 1995 ; Baras *et al.*, 1998; Béguer -Pon *et al.*, 2015). Homing behaviour has been observed for both *A.anguilla* and *A.rostrata* respectively (Tesch, 1967, Lamoth *et al.* 2000). Tesch (2003) found that burrows and cavities were utilised as resting places and shelter for the eels, and may support the site fidelity findings from this study. The high level of site fidelity observed among eels may in turn contribute to maintenance of habitat associated phenotypic divergence.

Although home range remained relatively stable throughout the study period, significant variation in high-use core areas was observed between different morphs. Narrow-headed individuals exhibited a significantly higher core range overlap in comparison to broad-headed individuals. We hypothesize that the differences observed in core area space use is a direct result of foraging behaviour. Given the feeding strategy of broad-headed individuals as ambush feeders, they are likely to consume large meals and remain immobile for long periods while digesting (Fu *et al.*, 2009) and may have optimal feeding locations “ambush points” where an encounter with prey fish is high, therefore increasing spatial overlap and thus site fidelity to core areas. In comparison, lower overlap in core area use by narrow headed individuals may be a direct result of resource availability and the need to move will be higher for insect feeders due to patch depletion (Pyke, 1984).

In this study, mean depth zone occupancy by individual eels in a high intensity area (the most utilised area KUD₅₀) ranged from 1.5m – 22m but averaged 9m. This study could not identify drivers of depth occupancy in eels. Length, morphotype (broad narrow) and temperature did not significantly affect depth occupancy in the high intensity area of use. Studies on *A. anguilla* in lakes have shown that they are

common in the shallow regions near the shoreline. In summer they were observed to be most abundant at approximately 1 m depth along the edges of a small mesotrophic reservoir in Germany, with eel abundances decreasing down to 10 m (Schulze *et al.*, 2004). However Yokouchi *et al.*, (2009) found catches of eels in an Irish lake were lowest from 0.5 – 5m and greatest at the deepest depth range 22.5-25m, Anguillid eels are generally thought to adapt to the environment in which they reside therefore the depth distribution of *A.anguilla* in lakes may depend on the physical and biological characteristics of each lake. An issue to consider with regard to depth occupancy by fishes in deeper lakes is the occurrence of oxygen-depleted layers which may occur in thermally stratified lakes. Unfortunately, dissolved oxygen data were not available in this study, but since Lough Finn is oligotrophic and a cool climate, it is unlikely that oxygen depletion of deeper waters occurred.

While the European eel is believed to be relatively sedentary while in freshwater (Riley *et al.*, 2011), studies have revealed that eels also can utilise large areas and undertake regular movements in estuarine environments (Hedger *et al.*, 2010; Walker *et al.*, 2014; Béguer-Pon *et al.*, 2015). The substantial levels of movement and clear diel activity patterns found in the study reported here imply active foraging strategies within their stable home ranges. Rosten *et al.* (2013) found that in spring and summer yellow eel in a southern English chalk stream exited a side channel and returned at dawn, presumably foraging in the main channel by night and using the side channel as daytime refuge habitat. The strong influence of light conditions has been noted in other studies; telemetry studies of American eels in estuaries and salt marshes demonstrated increased activity at night (Helfman *et al.*, 1983, Thiabault *et al.*, 2007, Hedger *et al.*, 2010, Béguer -Pon *et al.*, 2015). European eels have also been found to be more active at night in estuarine environments with the start and end time of movements being strongly associated with sunset and sunrise respectively (Walker *et al.*, 2014). The results from this study further support this pattern of strongly nocturnal and crepuscular activity. Hedger *et al.* (2010) suggested nocturnal movements to be indicative of fish hiding in the substratum during the day and moving into the water column to forage under the cover of darkness. Regardless of morph types (broad/narrow) movement increased during low light conditions. However broad-headed individuals were found to maintain an active rate of movement under the cover of darkness in comparison to narrow-headed which exhibited a crepuscular nature with activity peaking at dawn and dusk. It is hard to interpret this as a direct

consequence of diet specialisation but we hypothesise that “searching effort” of broad-headed may lead to increased “activeness” as they seek a moving prey resource in comparison to narrow-headed individuals feeding on insects in a patch for a more protracted period. While our study confirmed that yellow eels are more active at night. Interestingly activity of narrow-headed individuals’ decreased with increasing night duration and the resulting lowering length of crepuscular periods. This indicates a strong relationship between dawn and dusk periods among tagged narrow-headed individuals.

Lunar phase was also shown to be a significant predictor of eel movement in this study. It has been well documented that there are intrinsic links between eel behaviour and lunar phase. Lunar periodicity has been thought to influence the onset of the spawning migration of anguillid eels (Durif & Elie 2008). The influence of lunar phase on fish movement is generally discussed in the context of marine species that show strong affinity to certain phases (Henderson *et al.* 2014). However given the strong relationship between tidal currents and lunar phase it is hard to tease apart the true effect of the lunar cycle in these cases, unlike in lake environments. Interestingly in this study morph activity peaked on different lunar phases in this lake (Fig.3.3), significantly increase rate of movement for broad-headed individuals was observed on waxing lunar phases in contrast to highest activity on waning phases for narrow headed individuals. However there is a paucity of data on yellow eel movement and the potential influence of lunar phases, Hedger *et al.* (2010) reported reduced areal ranges under high lunar illumination (full moon), but no effect was identified on absolute ground speed. Lamothe *et al.* (2000) identified homing during the new moon and Baras *et al.* (1998) observed higher yellow eel activity under full moon events. The synchronicity in movement of eels in relation to lunar events is similar to that observed for marine species (Henderson *et al.*, 2014). Lunar phase (new moon and waxing phase) has been linked with spawning event timing and the onset of migration. However, this study shows that there may also be links between foraging activity and lunar periodicity of freshwater eels. Our results also suggest that temperature has a positive effect on average home range size for both morphs and daily displacement of broad-headed eels but not narrow-headed individuals. The influence of temperature on eel movement has been noted by Hedger *et al.* (2010) who found that eels swam faster and covered larger areas when water was warm. Typically eels are more active at a higher water temperature (Tesch, 2003) and thus explain the results obtained from this

study. Interestingly the lack of an effect temperature on average displacement of narrow-headed eels over the study period may be as a result of the foraging tactic and the need for lowered displacement due to increased abundance of inveterate prey with increasing temperature.

In conclusion, the present study indicates that the movement patterns of lake dwelling European eels are complex and can be influenced by foraging behaviour as well as predictable environmental factors. Further studies of yellow eel behaviour and habitat use should take into account behavioural differences and whether the relationship between morphology and spatial patterns is observed in other ecosystems. Given the urgent need to design effective surveys of population size and distribution of eels, the information provided from these data can aid in survey design and the implementation of effective conservation strategies for this endangered freshwater

3.6

SUPPLEMENTARY INFORMATION

Table 3.S1 Fish locations (n=108) stratified proportionally in each time of day category over the three month study period. The number (*n*) of individual eels from each morph; Broad or Narrow for which home range was calculated for each month.

Month	Dawn	Day	Dusk	Night	Broad (<i>n</i>)	Narrow (<i>n</i>)
July	4	66	5	33	11	8
August	3	61	3	41	11	7
September	3	52	3	50	8	6

Table 3.S2 Summary of spatial utilisation information for *A.anguilla*. KUD₉₅= kernel utilisation distribution based on 95% of the positions (home range km²); KUD₅₀= kernel utilisation distribution based on 50% of the positions (core area km²). B= broad-headed and N= narrow-headed.

Code	Jul-50	Jul-95	Aug-50	Aug-95	Sep-50	Sep-95	Morph
2315	0.026	0.219	0.017	0.164	-	-	B
2320	0.058	0.164	0.032	0.165	0.035	0.193	B
2323	0.227	0.816	0.028	0.186	0.017	0.119	B
2325	0.079	0.52	0.067	0.315	0.065	0.325	B
2326	0.008	0.196	0.002	0.234	0.012	0.238	B
2327	0.053	0.251	0.008	0.166	0.064	0.185	B
2329	0.025	0.164	0.023	0.174	-	-	B
2332	0.068	0.4	0.057	0.228	0.045	0.377	B
2335	0.099	0.556	0.914	0.582	-	-	B
2337	0.032	0.214	0.027	0.186	0.079	0.517	B
2340	0.052	0.25	0.072	0.355	0.07	0.383	B
Mean (S.E)	0.066 (0.02)	0.341 (0.06)	0.113 (0.08)	0.251 (0.03)	0.048 (0.01)	0.292 (0.04)	
2302	0.065	0.369	0.027	0.157	0.02	0.086	N
2303	0.024	0.13	0.031	0.152	0.017	0.082	N
2322	0.001	0.088	0.002	0.058	-	-	N
2330	0.022	0.171	0.021	0.132	0.001	0.003	N
2333	0.027	0.122	0.03	0.09	0.018	0.087	N
2334	0.047	0.268	-	-	-	-	N
2336	0.033	0.186	0.025	0.106	0.035	0.274	N
2339	0.033	0.103	0.018	0.09	0.011	0.087	N
Mean (S.E)	0.031 (0.001)	0.179 (0.03)	0.022 (0.003)	0.112 (0.01)	0.017 (0.004)	0.103 (0.03)	

Chapter Four

The Effect of Foraging and Ontogeny on the Prevalence and Intensity of *Anguillicola crassus* in the European Eel *Anguilla anguilla*

4.1

ABSTRACT

Infection patterns of the invasive *Anguillicola crassus* nematode were investigated in a previously naïve population of the European eel *Anguilla anguilla* in Loch Lomond, Scotland. Intensity levels of the parasite were associated with differences in ontogeny and trophic ecology. Although eels foraged on both fish and invertebrates, individuals which were smaller and fed on invertebrates (>70% contribution to diet) were found to contain a greater number of parasites compared to larger eel with a predominance of fish in their diet (>60% contribution). Within affected fish a significant negative relationship was found between fish length and parasite intensity, with smaller individuals having higher parasite intensity than larger individuals. This study indicates that food intake and infection risk are linked in the host-parasite system. From a management perspective increasing our understanding of how infection intensity and repeated exposure is linked to resource use in an ecosystem is important with regard to selection of appropriate conservation stocking sites.

4.2

INTRODUCTION

The European eel (*Anguilla anguilla* L.) plays a pivotal role in a balanced aquatic ecosystem both as a predator and prey species. Since the 1970's a continuous decline has been observed in recruitment of glass eels to continental waters (ICES 2013), leading to growing concerns over the long term viability of the species (Dekker 2008). The factors underlying the collapse of this panmictic population (Als *et al.*, 2011; Pujolar *et al.*, 2013) are not fully understood. However since the 1980's a new threat to the European eel has emerged, the invasive parasitic nematode worm (*Anguillicola*

crassus Kuwahara, Niimi & Itagaki, 1974) (Lefebvre *et al.*, 2012). The parasite entered Europe through the transportation of its native host, the Japanese eel (*Anguilla japonica* Temminck & Schlegel, 1846) (Koops & Hartmann, 1989). Since its arrival it has spread rapidly across the continent (Kennedy, 1993; Lefebvre *et al.*, 2012) exploiting a naive host (Kirk, 2003).

In areas where the parasite has established it can rapidly reach a prevalence of over 90 per cent among eels within four years (Lefebvre *et al.*, 2002), in part because of its ability to infect a range of intermediate and paratenic hosts (Lefebvre *et al.*, 2012). Its capacity to spread within a catchment is a direct consequence of the organism's adaptability, high reproductive output and short life cycle (Kirk, 2003). The parasite relies upon predator/prey interactions, with larval stages transmitted trophically through freshwater food-web interactions (Lefebvre *et al.*, 2012). Eels have two routes of infection, either by direct consumption of copepods which act as the intermediate host or through ingestion of a paratenic host (Moravec, & Skorikova 1998). It is most likely, that crustacean intermediate hosts serve as the source of infection for smaller eels (<20 cm), whilst larger eels mainly acquire infection by preying on paratenic hosts (Thomas & Ollevier, 1992). Paratenic hosts are a very important part of the life cycle of *A. crassus* in Europe (Kirk, 2003). Studies have shown that a wide range of eel food organisms act as paratenic hosts (Moravec & Konecny, 1994). These include at least 37 species of fish, including freshwater (Thomas & Ollevier 1992), estuarine and marine species (Hoglund & Thomas 1992). Frogs and newt tadpoles, snails and insect larvae have also been noted as paratenic hosts, but the importance of these hosts in nature is unknown (Moravec & Skorikova, 1998).

The impact of *A. crassus* on European eels is well documented. In heavily infected eels, the swimbladder exhibits inflammation and thickening of the swimbladder wall (Molnar *et al.*, 1993; Molnar, 1994; Wurtz *et al.*, 1996) reduced elasticity of the organ (Barry *et al.*, 2014) and lowered resistance to environmental stressors (Gollock *et al.*, 2005). As a result of the physiological and physical changes to the structure of the swim bladder, reduced swimming speeds have also been recorded (Palstra *et al.*, 2007). This swim bladder parasite has been implicated as an

important factor impeding stock recovery (Van Banning & Haenen, 1991; Molnár *et al.*, 1993). In the European context, efforts are being made to collate *A. crassus* infection data as part of a European Eel Quality Database (Belpaire *et al.*, 2011) and to increase understanding of changing rates of infection in eels leaving continental waters.

Parasite infections typically vary among size classes of their fish hosts and can reflect the trophic ecology of the fish (Bertrand *et al.*, 2008; Knudsen *et al.*, 2014; Poulin & Leung 2011; Knudsen *et al.*, 2003; Amundsen *et al.*, 2013). Eel populations are known to display polymorphism, particularly in head shape and at least in some populations the variation in morphology is strongly associated with foraging specialisation (Lammens & Visser, 1989; Provan & Reynolds, 2000; Cucherousset *et al.*, 2011; Ide *et al.*, 2011). Studies have shown that individuals exhibiting large robust and broad heads tend to be piscivorous and those with more delicate narrow heads feeding predominately on benthic invertebrates. A recent scenario posed by Lefebvre *et al.*, (2013) suggested that individuals with high foraging rates i.e. those consuming more intermediate/paratenic hosts would have the higher probability of infection from the nematode parasite. Although the successful dispersal of *A. crassus* ultimately relies on predator prey interactions within a host-parasite system. the trophic transmission of *A. crassus* remains poorly understood .

Studies of the early colonisation and infection dynamics of *A. crassus* are rare. However a rapid spread over a short period of time has been observed when it enters a new system, possibly because the European eel lacks immune adaptation for resistance and is naïve to the parasite (Kennedy, 1993; Lefebvre *et al.*, 2012; Becerra-Jurado *et al.*, 2014). Infection of eels by this parasite can occur through predator prey interactions (Kirk, 2003). Thus any variation in foraging ecology between individuals or groups may influence the encounter rate and thus infection rate within the definitive host. This study aimed to; (i) document the early stages of a recent invasion of the nematode parasite *A. crassus* to Loch Lomond Scotland; and (ii) investigate the influence of trophic ecology on the intensity and prevalence of *A. crassus* in a previously naïve population of *A. anguilla*.

4.3

METHODS

4.3.1 SAMPLE COLLECTION

Eels were collected from two sites in Loch Lomond 56° 05' N 4° 34' W (Fig.4.1) in June 2014. All fish were collected using fyke traps, (n = 64, 350–667 mm). Eels were killed (using a schedule 1 method), weighed and measured, and the abdominal cavity dissected to enable a measure of parasite loading (or to confirm its absence). Swimbladders were removed and all *A. crassus* present in the swim bladder lumen were counted macroscopically. Body condition of each eel was calculated as relative condition factor according to Froese (2006), which measures the deviation of an individual from average weight for a given length in a sample population. Fat content was measured on live individuals using a Distell FM 692 Fat Meter. This meter has a micro strip censor which measures the water content of a sample. The fat content of fish is correlated with the water content and thus the measurement of one can determine the other if the relationship between the two is known. The fat meter was calibrated (company calibration) to the fat /water relationship specific to European eel prior to taking measurements. Three measurements were taken along the body on both sides of the fish. The fat meter was then used to calculate the average percent body fat for the individual based on the six readings.

For age analysis one sagittal otolith from each pair was mounted onto a glass slide using 'Loctite' branded superglue. Otoliths were mounted concave side down and ground and polished on the sagittal plane using 1200 & 4000 grit silicon carbide grinding paper until the origin and all growth rings could be observed under an optical microscope. Age was determined following WKAREA (2009) and otolith measurements were recorded using Image Pro analysis software to allow back calculation of size at age.

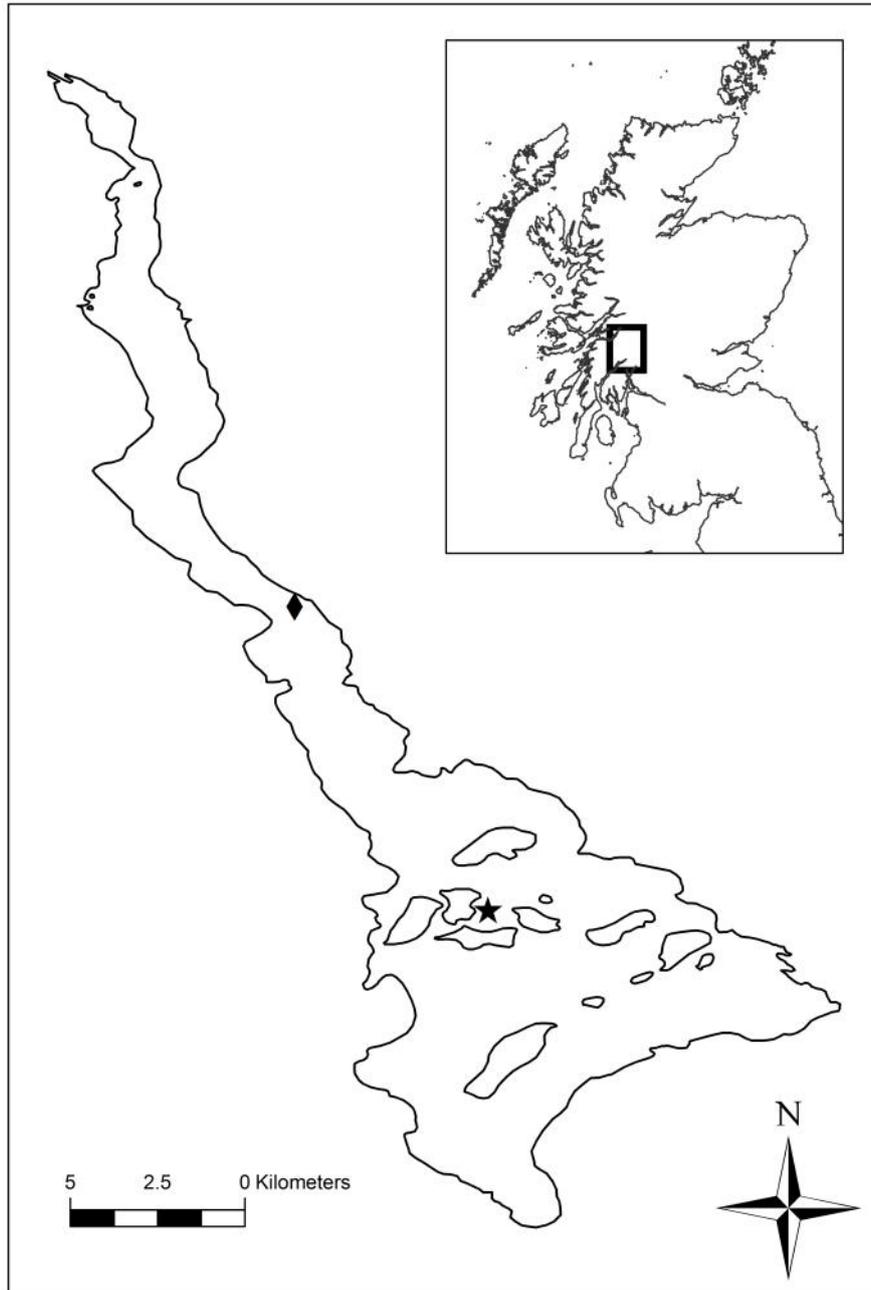


Fig. 4.1: The geographic location of Loch Lomond in Scotland and the location of the two sampling sites (★ ◆) in Loch Lomond

4.3.2 STABLE ISOTOPE ANALYSIS

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) provide a longer-term signal of diet compared with the “snapshot” information from stomach contents. Stable

isotope ratios from fish muscle tissue typically reflect assimilated food during the summer growth period (Perga & Gerdeaux, 2005). This information allows individual specialization in diet to be assessed (Bolnick *et al.*, 2002). Samples of muscle from eels and potential prey (invertebrates and fish fry) were dried for 72 hours in a drying oven. Dried tissue was ground in to a fine powder using a pestle and mortar. Invertebrates were analysed as bulk samples of whole individuals. High lipid concentration in muscle tissue can lead to particularly depleted $\delta^{13}\text{C}$ values (Post *et al.*, 2007). Thus a subset of eel tissue samples were lipid extracted to determine the effect of the lipid content on the stable isotope signature; 10–20 mg of ground tissue was soaked in a 2:1 chloroform: methanol (by volume) solvent mixture and the material suspended by stirring. After 15 minutes, the sample was centrifuged (3000 rpm for 5 min), the supernatant discarded (i.e. the analysis was not quantitative for lipids), and the sample re-suspended in the solvent mixture. These steps were repeated at least three times or until the solvent ran clear. Finally, the sample was dried (60 °C). Given the large variation in individual lipid deposition and the confounding effect on $\delta^{13}\text{C}$ values we undertook a correction for lipid level using a regression of the difference in $\delta^{13}\text{C}$ resulting from lipid extracted eels on their initial lipid concentration. Analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were performed at the NERC Life Sciences Mass Spectrometry Facility, by continuous flow isotope ratio mass spectrometry (CF-IRMS), using an elemental analyser (Costech ECS 4010) coupled to a ThermoFisher Scientific Delta XP-Plus IRMS.

To estimate the long term reliance of different prey to an individual's diet a Bayesian stable isotope mixing model was implemented through SIAR (Stable Isotope Analysis in R, version 4.1.3; Parnell *et al.*, 2010). Stomach content analysis (Fig. 4.S2; Supporting Information) confirmed benthic invertebrates and fish as the main food source for eels in Loch Lomond. Baseline samples of potential eel diet were gathered from Loch Lomond. Potential fish prey was captured in fykes nets and potential invertebrate prey were collected from the foreshore via kick sampling. For SIAR, the fish and invertebrate prey signature was calculated as the mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of ruffe (*Gymnocephalus cernus* Linnaeus, 1758) for fish, whereas the invertebrate signature was calculated from the isotopic values of snails and *Asellus*

aquaticus collected from the littoral zone. Following the approach of Cucherousset *et al.*, (2011) averaged trophic fractionation factors with a large standard deviation were used in the mixing model (e.g. Post, 2002). Fractionation of 1.0% (± 1.0 SD) and 3.3% (± 1.0 SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. The SIAR isotope mixing model uses a Bayesian approach to estimate relative dietary contributions and to consider uncertainties related to isotopic variation in the consumer and in the food sources as well as in the trophic fractionation factors (Parnell *et al.*, 2010). Where resource use (benthic invertebrates or fish) of one group (infected) was outside the 95% credibility limits of another group (uninfected), groups were deemed to be using significantly different levels of the particular resource.

4.3.3 DATA ANALYSIS

To identify the factors influencing the prevalence and intensity of *A. crassus* in the eel population we used a generalised linear model approach. Parasite presence and absence (Binomial response) among the eel population sampled and Parasite Intensity (parasite counts; Poisson response), the two primary response variables, were regressed with respect to five covariates (body length (log10 transformed), body condition, proportion of invertebrates in diet (arc-sine transformed), lipid content and one fixed effect (two-level factor; sampling sites x 2) in two separate GLM's for Binomial and Poisson distributed data respectively. Due to high collinearity between age and length (correlation factor; 0.9) age was dropped from the model. For parasite prevalence and intensity, maximal models including all covariates and fixed effects were fitted. A minimum adequate model was generated by significance testing between models and the sequential removal of non-significant terms. The final model for Parasite Presence/Absence and for Parasite Intensity contained only statistically significant terms. Inspection of diagnostic plots was used to ensure all model fit assumptions were satisfied. Minimum adequate models, with *P*-values and model parameter estimates are detailed in Tables 4.2 & 4.3. To test for differences between infected and un-infected fish, Welch t-tests were used to compare mean length, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. All analyses were performed using R statistical software 3.1 (R Core Team 2014).

4.4

RESULTS

Sixty-four eels were captured during the sampling period (size range: 350-661mm). *Anguillicola crassus* was found in 43.8% of the eels collected in Loch Lomond. Mean intensity was 0.85 (SE \pm 1.33) parasites per eel. The SIAR isotopic mixing model indicated that infected eels had a significantly higher reliance on invertebrates in their diet with only a small proportion of their diet being made up by fish (no overlap 95% Bayesian credibility interval; see Fig. 4.4) whereas uninfected eels had a significantly higher proportion of fish in their diet (no overlap in the 95% Bayesian credibility interval; see Fig. 4.4).

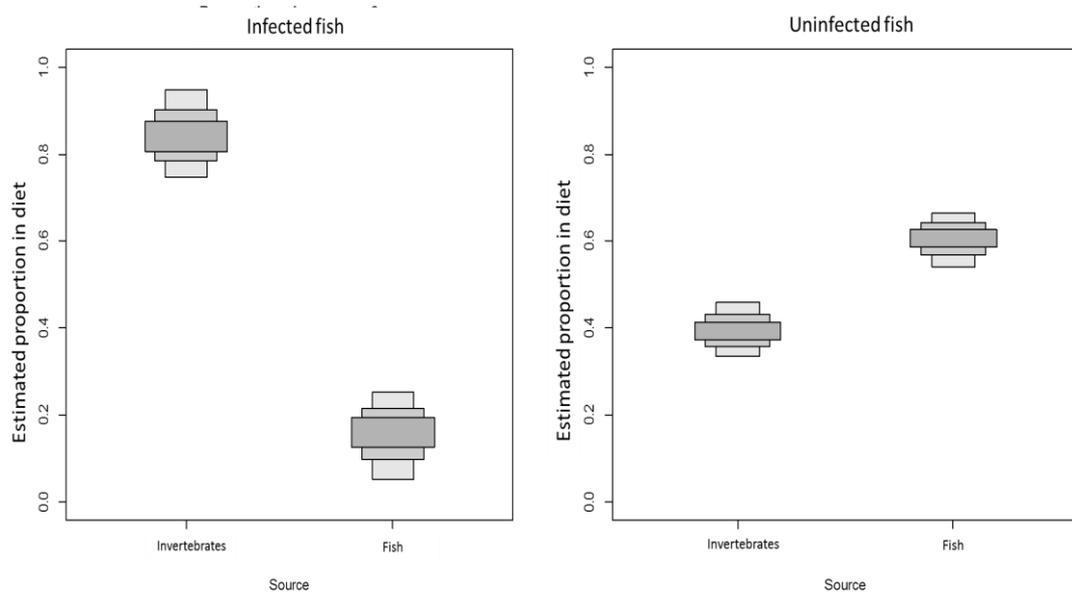


Figure 4.4: The relative proportion of each of the two food sources of infected and uninfected eels. Plots show 50%, 75% and 95% credibility intervals of the maximum likelihood values estimated using SIAR.

The minimum adequate model for prevalence among infected and uninfected fish revealed a significant effect of estimated proportion of invertebrates in diet (Table 4.2). The individuals with a higher estimated proportion of invertebrates in their diet exhibit higher probability of parasite infection ($Z=_{1.61} 3.728$, $P < 0.001$). The minimum adequate model for the factors influencing intensity of parasites in an infected fish revealed a significant negative relationship between fish length and parasite intensity

(Table 4.3), with smaller individuals having higher parasite intensity than larger individuals ($Z_{=1,26} - 2.192$ $P < 0.05$).

Table 4.1: Summary statistics of infected and uninfected eels.

	Mean $^{13}\text{N} \pm \text{S.D}$	Mean $^{13}\text{N} \pm \text{S.D}$	Mean Length (mm) $\pm \text{S.D}$
Infected	-24.584 \pm 1.03	11.53 \pm 1.05	518 \pm 95.9
Uninfected	-26.348 \pm 1.58	9.25 \pm 1.17	450.5 \pm 75.3

Table 4.2: Parameter estimates for the minimum adequate model describing parasite intensity.

Source	Estimate	SE	Z value	P
Intercept	2.7541	0.93593	2.943	-
Total length	-0.0474	0.02166	-2.192	<0.0001

Table 4.3: Parameter estimates for the minimum adequate model describing parasite prevalence.

Source	Estimate	SE	Z value	P
Intercept	-9.814	2.621	-3.744	-
Proportion of invertebrates in diet	15.390	4.128	3.728	<0.0002

Infected fish (n=28) were significantly smaller than uninfected individuals (n=36) ($t = -3.14$, $df = 60.88$, $P < 0.001$). Infected fish were significantly more depleted in $\delta\text{C}13$ ($t = -4.2672$, $df = 40.384$, $P < 0.001$) and $\delta\text{N}15$ ($t = -7.4061$, $df = 52.716$ $P < 0.001$) than uninfected fish (see Table 4.1 & Fig. 4.2).

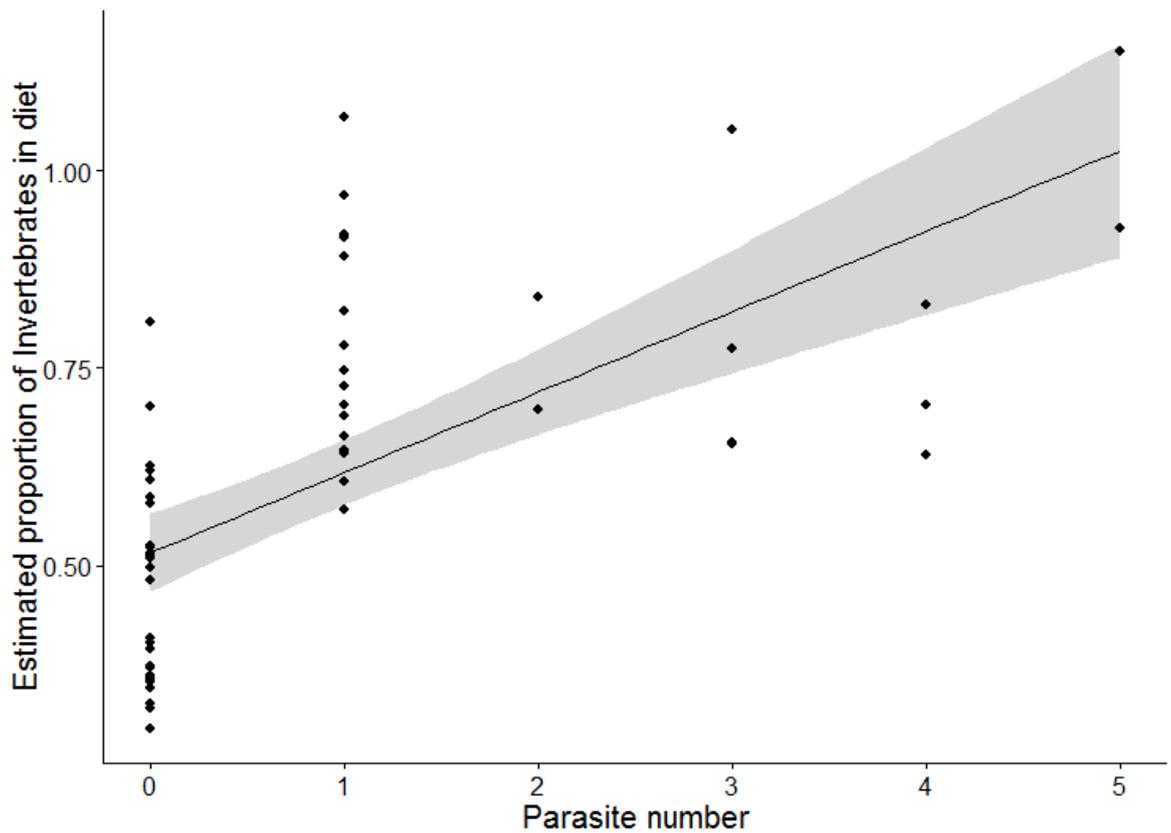


Fig 4.3: The relationship between estimated proportion of invertebrates in the diet and parasite number in swimbladder lumen. See text for significance.

4.5

DISCUSSION

The unpredictable nature of the invasion and establishment of non-native species means that information about mechanisms controlling the early stages of species invasions are only rarely studied. Given the difficulty in eradication of invasive species from aquatic environments (Clout & Veitch 2002), more information about the early stages of invasion has the potential to provide insights into the establishment process in a host–parasite system. This study uniquely addresses some of the ecological factors that impact on the transmission of an invasive parasite during the initial stages of parasite invasion.

The invasive nematode *A. crassus* has only recently invaded Loch Lomond. It was not detected on previous surveys (Barry *et al.*, 2014). Introduction of *A. crassus* through an intermediate host in ballast water or through the transportation

of live bait are possible routes of entry to Loch Lomond. Levels of recreational boating activity are high on the loch and increased human activity has been shown to increase the probability of invasion by non-native species (Gallardo & Aldridge, 2013) and Loch Lomond has been subject to invasion by a number of non-native species over the last few decades (Adams, 1991; Adams & Maitland 1998). This invasive parasite is likely to have a negative impact on the currently abundant eel population within Loch Lomond (Adams *et al.*, 2013). Studies have reported the effects of *A.crassus* on the condition of eels, and their ability to cope with environmental stressors infested with *A.crassus* (Gollock *et al.*, 2005). Loss of appetite and vitality has been reported in cultured eels (van Banning 1991). However the greatest effect may be the impact of the parasite on the swimming ability (Sjöberg *et al.*, 2009) and swimbladder function (Barry *et al.*, 2014). It is probably the silver eel stage, migrating to the open ocean that will be most impacted by these effects.

This study presented here shows patterning in the infection and transmission of the parasite in the eel population in the early stages of parasite establishment. Specifically the ontogenetic stage and individual foraging strategy of eels has an influence on the intensity of infection by the invasive nematode parasite *A.crassus*. Although eels foraged on both fish and invertebrates in Loch Lomond, the incidence of infection with *A.crassus* was higher in eels that specialised on invertebrates as a food resource (>70% contribution to diet). In addition, the severity of infection (number of parasites in the swimbladder lumen) increased with the relative contribution of invertebrates in an individual's diet. The most likely explanation for observed patterns of parasite infection among eels sampled in Loch Lomond is trophic ecology, mediated through foraging behaviour and a potential "encounter filter". Eels are known to show individual specialisation on available food resources (Lammens & Visser, 1989; Provan & Reynolds, 2000; Ide *et al.*, 2011). The drivers behind ecological specialisation and its consequences for individual fitness are poorly known. This study is among the first to demonstrate an effect of diet specialisation on parasite loading by *A.crassus*.

The intraspecific variation in isotope ratios (variability in C and N) in eels from Loch Lomond, suggest a level of dietary specialisation on potential paratenic

hosts as well as intermediate hosts. Exposure to parasites plays an important role in host vulnerability (Holmes, 1990), with diet as the encounter filter and the main factor determining the number of parasites present in trophically transmitted species (Poulin, 1995; Lafferty *et al.*, 2008). In this study smaller eels with a higher proportion of invertebrates in their diet and had higher infection levels than larger eels with a greater proportion of fish in their diet. These findings are contrary to those of Pegg *et al.* (2015) who reported increased probability of infection in larger piscivorous eels. Parasite infections typically vary among size classes of their fish hosts, and differences in transmission rates often reflect ontogenic trophic niche shifts (Knudsen *et al.*, 2003). In the literature, some authors have reported a decrease in the prevalence of *A. crassus* in the swimbladder lumen worms with increasing eel length (Möller *et al.*, 1991), while others have noted an increase (Thomas & Ollevier, 1992). When *A. crassus* larvae are consumed by an intermediate host (i.e a copepod), second-stage juveniles of *A. crassus* penetrate the digestive tract, enter the body cavity and moult into third-stage juveniles. Infected copepods move sluggishly and are more likely to occupy epibenthic zones in the water column than uninfected individuals (Kirk *et al.*, 2000). Thus we postulate that smaller and younger eels actively foraging in epibenthic zone on benthic invertebrates may have an increased chance of encounter, either directly through foraging on invertebrate paratenic hosts or feeding on infected copepods which may be occupying a similar epibenthic zone to invertebrate prey. Thus the invertebrate prey of smaller eels may act as an important paratenic host for *A. crassus*. Larger eels in this study were found to feed predominately on ruffe which may also act as a paratenic host (Pietroock, & Meinelt 2002) however our infection rate results suggest that larger fish eaters may not be encountering infected intermediate and paratenic hosts as regularly as smaller invertebrate feeders.

The existing literature presents conflicting results on the relationship between trophic ecology and infection levels. For example Morrissey & McCarthy (2007) reported lower *A. crassus* infection with increasing eel size in a marine environment, suggesting that larger eels typically do not feed directly on infected copepods and instead feed on larger crustaceans. In a naive host population of Lake Balaton, large eels (>100 g) acquired higher intensities of *A. crassus* than small eels (Barus & Prokes, 1996). This relationship was interpreted as the result of greater

consumption of infected intermediate and paratenic hosts by large eels. A recent study by Pegg *et al.*, (2015) reported that eels from riverine sites, with a higher proportion of fish in their diet, had a higher probability of infection.

The disparity in observed field observations may be the result of trophic transmission dynamics which may be site specific. Thus the trophic ecology of eels may act as a catalyst influencing encounter rate with *A. crassus* in certain systems and may also change as the parasite becomes more established in potential paratenic hosts within a system. A recent scenario posed by Lefebvre *et al.*, (2013) is that the most active foragers (those consuming more intermediate/paratenic hosts) have an increased probability of infection. It may be the case that in Loch Lomond the smaller eels feeding on invertebrates may be more active foragers (consuming more intermediate/paratenic hosts) than larger fish eaters with invertebrate feeders consuming a higher diversity (a little and often) of prey and thus increasing their chance of infection. Individuals will not only have different constraints, but also different priorities, for example, young animals may need to acquire extra nutrients for growth e.g an invertebrate diet whereas larger eels may need to acquire more nutrients offered by a piscivorous diet. Nonetheless our findings suggest that there is a link between infection and trophic parasite transmission in this host-parasite system. Seasonal variation in infection levels is an important factor to consider when examining prevalence and intensity in the definitive host. The majority of studies have failed to detect any seasonality in *A. crassus* prevalence (Kennedy & Fitch 1990, Möller *et al.*, 1991, Thomas & Ollevier 1992, Molnár *et al.*, 1994, Würtz *et al.*, 1996). However, one long term study noted a temporal pattern with maximum values of prevalence and mean intensity recorded each year in early summer and, to a lesser degree, in late winter (Lefebvre *et al.*, 2002). The timing of this survey in early summer would coincide with peak prevalence noted in the study above. It is also important to note that prevalence of infected paratenic hosts (potential prey) of eels could change seasonally and thus the prevalence and infection rate found in this study could be higher or lower at other times of the year.

Conclusion

Given that this study is of a relatively early establishment of *A.crassus* into a system it can be postulated that the observed patterns of Prevalence and Intensity may be temporally driven and will change as the parasite becomes more established in the loch. Nonetheless these results suggest that younger eels feeding on intermediate hosts and inveterate paratenic hosts could play an important role in the dispersal and establishment of *A.crassus* in this host-parasite system. Parasite infections have consequences on almost every aspect of fish behaviour. The behavioural consequences of *A.crassus* infection on eels is poorly understood during the continental stage (Lefbrave *et al.*, 2012). Therefore links in trophic transmission of *A.crassus* to host *A.anguilla* has significant importance. Factors relating to diet which may influence transmission of and repeat infections need to be investigated more robustly. The ability to identify potential mechanisms involved in the spread of *A.crassus* is imperative, given that conservation stocking has been identified as way of increasing numbers of eels (ICES, 2010). Trophic parasite transmission and the role of paratenic host warrant further research, and should be considered when choosing appropriate stocking locations.

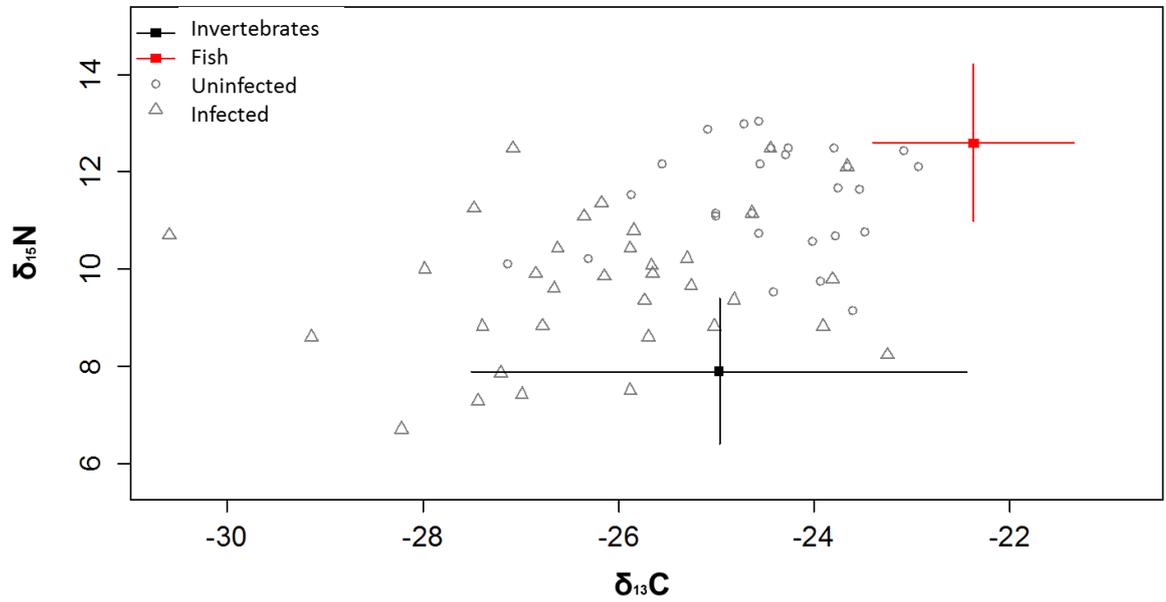


Fig. 4. S1: Stable isotope ratios of carbon and nitrogen in eels from Loch Lomond. O = Uninfected fish Δ = Infected fish. Mean \pm SD of carbon and nitrogen potential food sources, fish and benthic invertebrates.

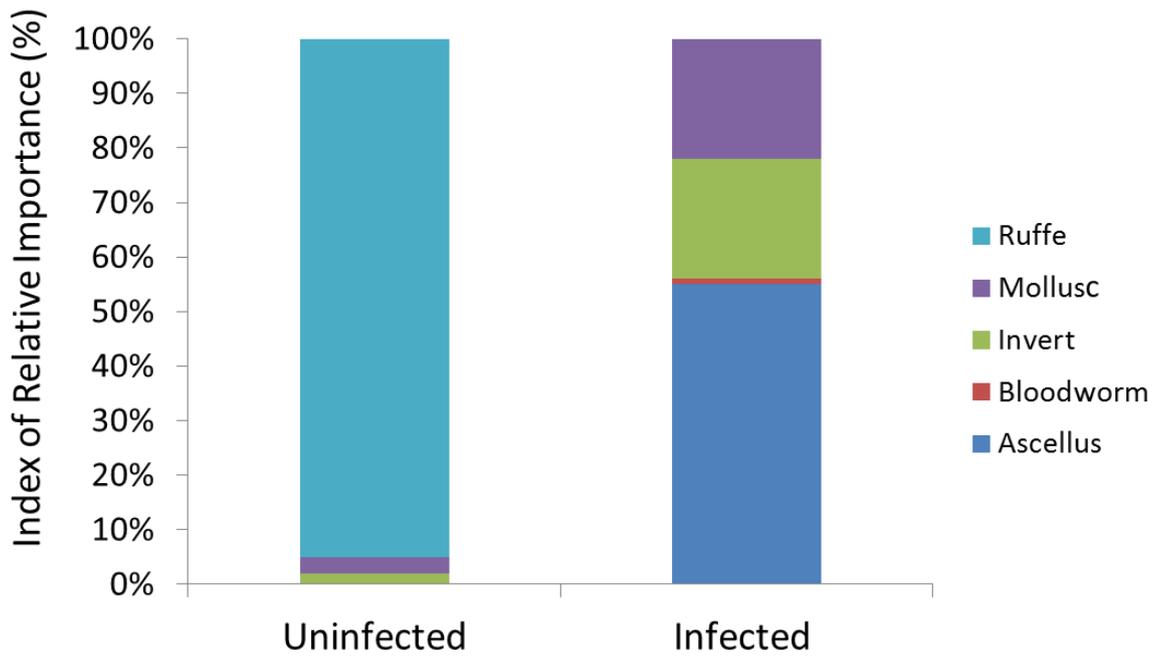


Fig. 4.S2: Stomach contents of Uninfected (n=8) and Infected (n=12) individuals

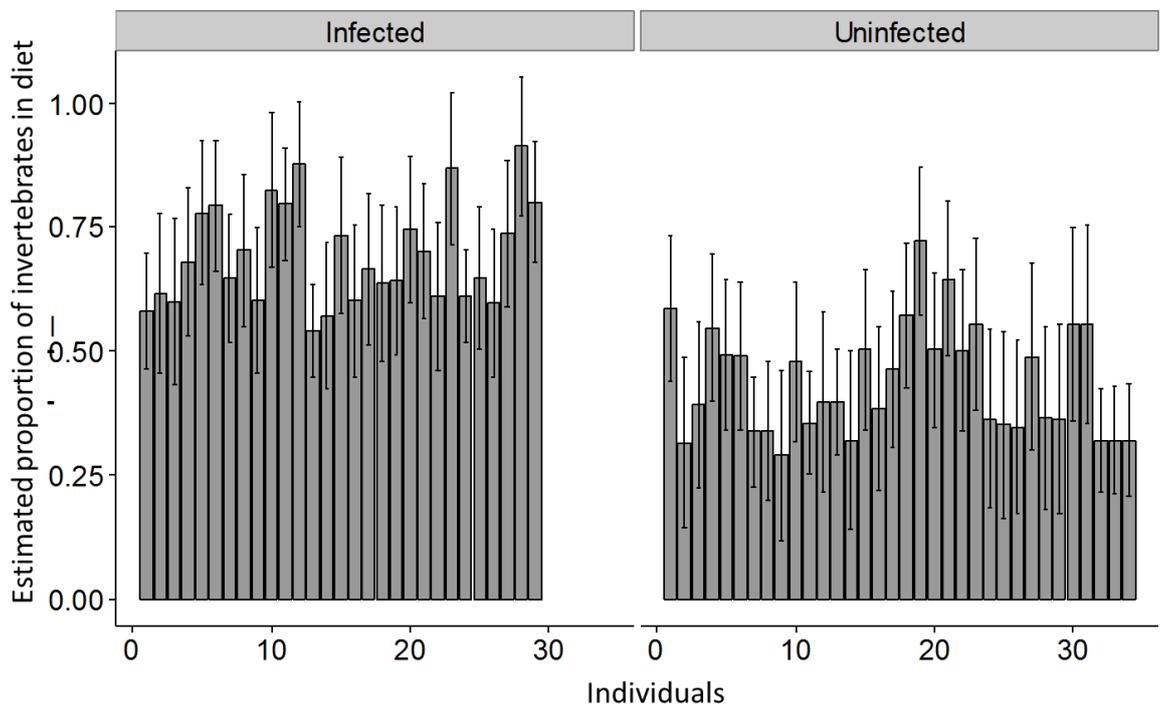


Fig. 4.S3: Estimated proportion of Invertebrates in the diet of infected and uninfected individuals. Bars show mean (+/- SD) of the maximum likelihood value estimated using SIAR.

Chapter Five

Freshwater and Coastal Migration Patterns in the Silver Stage Eel *Anguilla anguilla*

*Note: This chapter has been submitted as a manuscript to the *Journal of Fish Biology*.

5.1

ABSTRACT

The unimpeded downstream movement patterns and migration success of small female and male silver eels through a catchment in North West Europe was studied using an acoustic hydrophone array along the River Finn and into the Foyle estuary in Ireland. Twenty silver eels (L_t range: 332-520mm) were trapped 152 km upstream from a coastal marine sea lough outlet and internally tagged with acoustic transmitters. Migration speed was highly influenced by river flow within the freshwater compartment. Silver eel activity patterns were correlated with environmental influences; light, tidal direction and lunar phase all influenced initiation of migration of tagged individuals. Migration speed varied significantly between upstream and lower river compartments. Individuals migrated at a slower speed in transitional water and sea lough compartments compared with the freshwater compartment. While 89% survival was recorded during migration through the upper 121 km of the river and estuary, only 26% of eel which initiated downstream migration were detected at the outermost end of the acoustic array. Telemetry equipment functioned efficiently, including in the sea loch, so this suggests high levels of mortality during sea lough migration, or less likely, long-term sea lough residence by silver eel emigrants. This has important implications for Eel Management Plans (EMP's).

5.2

INTRODUCTION

In the last 30 years the panmictic European eel (*Anguilla anguilla*) population (Als *et al.*, 2011) has experienced unprecedented declines across its range (ICES, 2013), the causes of which are not fully understood (Kettle *et al.*, 2011). An important precursor

to any effective management of the existing population is to identify bottlenecks to critical life history stages. As a result of this decline, the European Union enacted legislation (EC Reg 1100/2007) to ensure increased eel escapement of the freshwater feeding lifecycle stage, the aim being to maximise the biomass of potential semelparous spawners leaving continental waters for the trans-Atlantic spawning migration. The growth phase for eels in continental waters ends with a transition called the silvering process (Tesch, 2003; Durif *et al.*, 2005), following which they begin migrating towards marine waters. The downstream migration pattern in eels is thought to vary across localities (Vollestad *et al.*, 1994; Breukelaar *et al.*, 2009). The majority of the information on silver eel migration comes from commercial fishing data (Durif & Eile 2008) and consequently details of silver eel behaviour as they transit from freshwater to saltwater are poorly understood.

Tracking technologies have advanced allowing detailed studies of individual eel migration behaviour in freshwater and inshore marine environments (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*, 2012). Several studies have revealed impacts of hydropower impoundment and fisheries on riverine survival of migrating silver eels (Winter *et al.*, 2006; Travade *et al.*, 2010). The freshwater -marine transition represents an important life history stage for diadromous fishes. During the transition they experience fundamental physiological challenges at the freshwater - saltwater interface and there is evidence of increased mortality risk from predators as migratory fish enter sea water (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Aarestrup *et al.*, 2014). In common with other diadromous fishes migrating silver eels pass through productive estuarine habitats which often have large numbers of avian, mammalian and fish predators. Predation pressures in such habitats may be high on migratory fishes, for example Keller (1995) reports that cormorants (*Phalacrocorax* spp.) a common species in estuarine habitats, feed heavily on smaller eels. Knowledge of escapement success during the freshwater saltwater transition is crucial to understanding of the natural dynamics of eel populations. Specifically, understanding migration behaviour, life stage specific mortality and ultimately migration success at this important life stage, is critical to effective conservation management. Recent work on downstream migration patterns has indicated low survival rates during migration to the open ocean (Verbiest *et al.*, 2012; Aarestrup *et al.*, 2010). However these studies

were conducted in catchments impacted by hydropower and fisheries thus it is difficult to disentangle natural mortality from anthropogenic mortality resulting from hydroelectric power generation or fishery pressure. Furthermore the migration of male eels, which migrate at a smaller size than females (Poole *et al.*, 1990), is particularly poorly understood. Previous studies have focused solely on the behaviour of larger females (which are large relative to tag size) and as a result, field data on the downstream migration of smaller sized female and male eels is lacking. The aims of this study were to (i) determine the progression rates and migration behaviour of small silver eel through sequential catchment compartments; (ii) elucidate influences to migration and how they may differ between catchment compartments; (iii) quantify escapement success of tagged individuals through freshwater and coastal sea lough habitats.

5.3

METHODS

5.3.1 STUDY AREA

The study was conducted in the Foyle catchment, Northern Ireland in 2013. The Foyle Catchment has an area of 4450 km² and drains into the Atlantic Ocean on the North coast of Ireland (55.01°N 7.08°W). The River Finn has no man-made barriers to migration and the hydrology retains high natural variability. The sea lough (Lough Foyle) located at the mouth of the River Foyle is typical of an enclosed broad, but shallow, productive estuary and the exit point to the open ocean at Magilligan Point is narrow (0.98km) (Fig. 5.1). The upper limit of tidal influence is located 60km from Magilligan Point and the salt wedge occurs approximately 40km upstream of Magilligan Point depending on the tide and river flow conditions. In this study, the catchment compartments were designated as follows: Freshwater (95km long), Transitional (26.8km long) and Sea Lough (30.2km long). Catchment characteristics are presented in Table 5.1.

Table 5.1. Environmental variables in compartments through catchments. Salinity range – PSU, Dissolved oxygen – mgL ± S.D and Depth – metres ± S.D.

Variable	Freshwater	Transitional	Sea Lough
Salinity	-	0.14- 28.41	29.63- 32.20
Dissolved oxygen	-	8.10±0.65	8.04 ± 0.15
Mean Depth	-	2.58±086	3.12±1.49
Length	95km	26.88km	30.22km

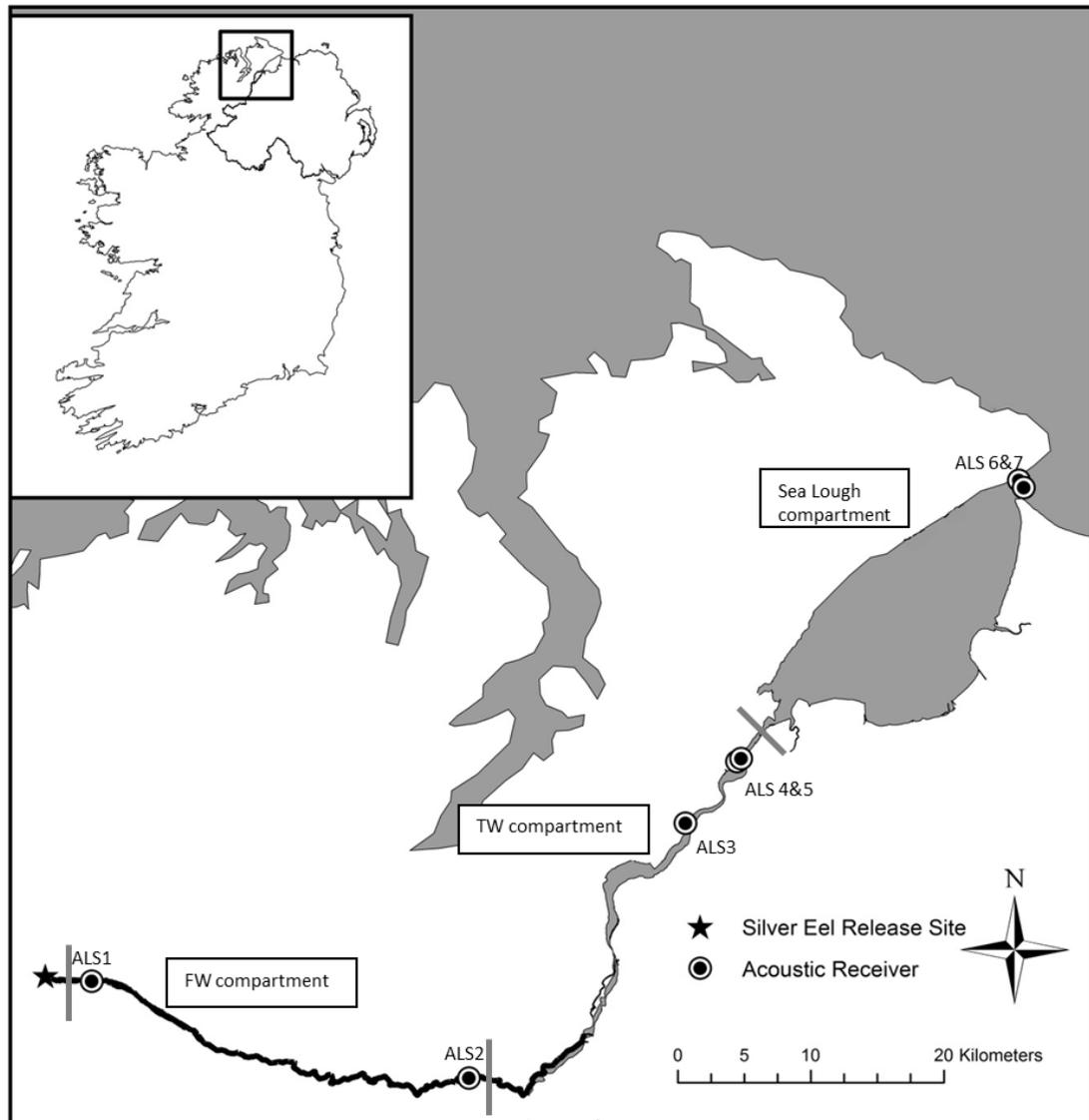


Fig. 5.1 Map of study site, compartment types marked with grey boundary line, and Acoustic Listening Stations (ALS's) are black dots which outline receivers, FW=freshwater and TW=transitional zones.

5.3.2 FISH CAPTURE AND TAGGING

Migrating silver eels were captured using a fixed fyke net in the outflow stream from Lough Finn at the source of the River Finn (54.50°N 8.05°W) between 29 September and 28 October 2013. Prior to measuring and tagging, fish were placed in a holding tank and anaesthetised with clove oil (0.5mg per litre). After anaesthetisation, the total body length (L_t mm), mass (g), eye diameter (mm) and length of the pectoral fin (mm) were recorded to determine their maturation stage and sex according to Durif *et al.* (2005) (Table 5.2). According to this classification, 17 fish were deemed mature male eels and three mature females (Table 5.2). Fat content was measured on live individuals using a Distell FM 692 Fat Meter. This meter has a micro strip sensor which measures the water content of a sample. The fat content of fish is correlated with the water content and thus the measurement of one can determine the other if the relationship between the two is known. The fat meter was calibrated (company calibration) to the fat /water relationship specific to European eel prior to taking measurements. Three measurements were taken along the body on both sides of the fish. The fat meter was then used to calculate the average percent body fat for the individual based on the six readings.

A total of 20 silver European eels, 17 males and 3 females (L_t range:332-520mm, mass range: 83-384g) were tagged with individually coded acoustic transmitters (Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g mass in air, 139dB re 1 μ Pa power, Thelma Biotel AS, Trondheim, Norway 2013). For each fish, an acoustic transmitter was surgically implanted through a 15mm incision into the peritoneal cavity, and the incision closed with independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK). The mean tag to body mass ratio was $1.53 \pm 0.5\%$ (<2% recommended, *sensu* Lucas & Baras, 2000). Fish were aspirated with 100% river water throughout the procedure. Tags were programmed to have an acoustic transmission repeat cycle of $30s \pm 50\%$, giving a tag life span in excess of 110 days. This surgical procedure does not adversely affect behaviour of tagged eels (Thorstad *et al.*, 2013). Once the tagging procedure was complete, the fish were returned to a recovery tank filled with highly aerated water. The entire surgical process

took less than four minutes. After complete recovery, defined as; orientation regained and response to stimuli, fish were released.

Table 5.2. Characteristics of tagged individuals. **Successful migrants detected passing final array. Silver Index (*sensu* Durif *et al.*, 2005) MII = mature males, FV = mature female. ALS 1 refers to Acoustic listening station 1.

I.D	Length (mm)	Mass (g)	Fat (%)	Silver Index	Release date	Detection span from ALS 1 (days)
2585	354	72	29.8	MII	06/10/2013	5.14
2577	365	79	30	MII	05/10/2013	8.14
2575	354	82	22.9	MII	05/10/2013	80.14**
2592	332	83	28.4	MII	08/10/2013	5.15
2583	360	84	22.9	MII	06/10/2013	5.06
2581	360	86	30.6	MII	08/10/2013	5.97
2586	365	92	26.6	MII	28/10/2013	11.27**
2593	365	96	21.9	MII	04/10/2013	2.91
2576	350	97	26.3	MII	08/10/2013	43.15**
2578	384	99	23.6	MII	08/10/2013	62.87
2579	400	100	28	MII	28/10/2013	16.59
2588	394	105	26	MII	28/10/2013	3.01
2582	401	110	28	MII	29/09/2013	3.95
2587	395	115	30	MII	05/10/2013	19.69
2589	410	126	22.6	MII	08/10/2013	22.93**
2584	435	129	26.8	MII	05/10/2013	-
2580	442	249	29.6	MII	28/10/2013	10.17
2590	530	280	21.7	FV	29/09/2013	36.43
2591	520	320	22	FV	29/09/2013	2.99
2574	515	384	24.5	FV	02/10/2013	48.9**

5.3.3 ACOUSTIC TRACKING

The passage of tagged eels was recorded using seven acoustic listening stations (ALS: VEMCO VR2 W; Fig. 5.1.) deployed prior to tagging (August 2013) and recovered in February 2014. ALS 1 & 2 were positioned in the River Finn to record movement in freshwater compartment, ALS 3,4 and 5 monitored movement in the transitional compartment and entry to the sea lough. ALS 6 and 7 were positioned at the exit point of the sea lough and this location was considered as the entrance to the open ocean (Fig. 5.1). Detection ranges were tested for all ALS's to ensure all tagged fish passing ALS sites would be recorded. Range testing was conducted in freshwater and

transitional compartments with varying hydromorphological conditions. No fish were recorded on a downstream ALS which had not been previously recorded at inward ALS's higher in the catchment. Extensive range tests were undertaken for ALS6 and ALS7 (the sea lough sites; Fig.5.1) to ensure coverage at these points was adequate to determine escapement success. To test for acoustic breaches at the final ALS an acoustic transmitter (Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g weight in air, 139dB re 1 μ Pa power, Thelma Biotel AS, Trondheim, Norway 2013) was immersed at 3 m depth and trolled (~1500m x 4; ebbing and flooding tide) by a drifting boat (engine off). Range tests revealed an acoustic range of 450m ensuring overlap between the two final ALS (6&7), no acoustic breaches were recorded during range tests.

5.3.4 MIGRATION DESCRIPTORS

The ALS array was used to examine behavioural differences in migration patterns of silver eels during their downstream migration. Nineteen out of the 20 silver eel transmitters were detected at ALS1 (0.5km from release), it is assumed that these fish had initiated downstream migration. Freshwater compartment (FW) migration is defined as movement of tagged fish from the most upstream receiver ALS 1 downstream to ALS 2 at the point of tidal interface. It is assumed that fish which were detected at the first upstream receiver (ALS 1) but not detected entering the estuary (ALS 2) either terminated their migration or suffered mortality or tag failure in the freshwater compartment. Transitional water compartment (TW) migration is defined as the movement of fish between ALS 2 and ALS 4&5. Similarly fish which were detected at ALS 2 but not at ALS 4 and 5 are assumed to have terminated their migration, suffered mortality or tag failure in transitional compartment. Sea lough compartment (SL) migration is defined as movement between ALS 4 and 5 and the lough exit at ALS 6 and 7. Tagged individuals were deemed successful migrants (i.e successful transit between the freshwater, transitional and sea lough compartments) if they were detected passing ALS 6 or 7 and thus entering the open ocean. For migrating eels, transit time and travel speed between ALS's were calculated. The transit time corresponds to the time elapsed between the departure from an ALS, that is, the last detection at that ALS, and arrival at the next, that is, the first detection at the successive downstream ALS. Distance travelled between detection sites was

calculated using the centre line of the river using ARC GIS software and was expressed in km per day.

5.3.5 ENVIRONMENTAL DATA

River discharge data were provided by the Office of Public Works, Ireland. Mean daily discharge from the River Finn was used to assess flow conditions for the study period in 2013. Tidal range data were obtained from published data (www.tidetimes.org.uk). Light level was defined as “day” or “night”, based on the times of sunrise and sunset, these were calculated using the NOAA sunrise/sunset calculator (NOAA, 2014). The lunar cycle was categorised into eight phases: new moon, waxing crescent, 1st quarter, waxing gibbous, full, waning gibbous, 3rd quarter, waning crescent based on the percentage of the moon illuminated using the R package “lunar” (Lazaridis, 2015).

5.3.6 DATA ANALYSIS

Differences in the number of successful migrants moving through successive compartments were tested using a Pearson chi-square test. Migration speed was \log_{10} transformed to reduce heterogeneity of variances. Differences in migration speed through compartments were tested by ANOVA. To investigate the potential factors influencing migration speed of individuals through the catchment a general linear model approach was taken. Migration speed ($\log_{10} \text{ km d}^{-1}$) in freshwater, transitional water and sea lough compartments was modelled using fish body length, body fat and water discharge as predictor variables. Final models were generated with non-significant variables being dropped. Model diagnostics were assessed graphically by examining the residuals for heterogeneity. A *t*-test was used to test for significant differences between migration speeds of successful and unsuccessful migrants. Pearson chi square tests were used to test for differences in diurnal, lunar phases and tidal cycle (ebb or flood) effects on movement activity. Movement activity times were defined as the difference between detection time when entering receiver range and the time of the last detection before leaving receiver range. All analyses were performed using R statistical software 3.1 (R Core Team 2014).

5.4

RESULTS

5.4.1 MIGRATION SUCCESS

The nineteen tagged fish which initiated downstream migration (detection at ALS 1) were all detected at the lower end of the FW compartment (ALS 2), thus 100% of migrants made successful passage through the FW compartment (Fig. 5.2, and Fig. 5.3). Of these, a further 17 (89%) were detected at the lower end of the TW compartment (ALS4-5) and thus successfully moved through the TW zone. Seventeen fish entered the sea lough compartment, of which five (29%) were detected at ALS6-7 indicating successful passage through this zone (Fig. 5.2).

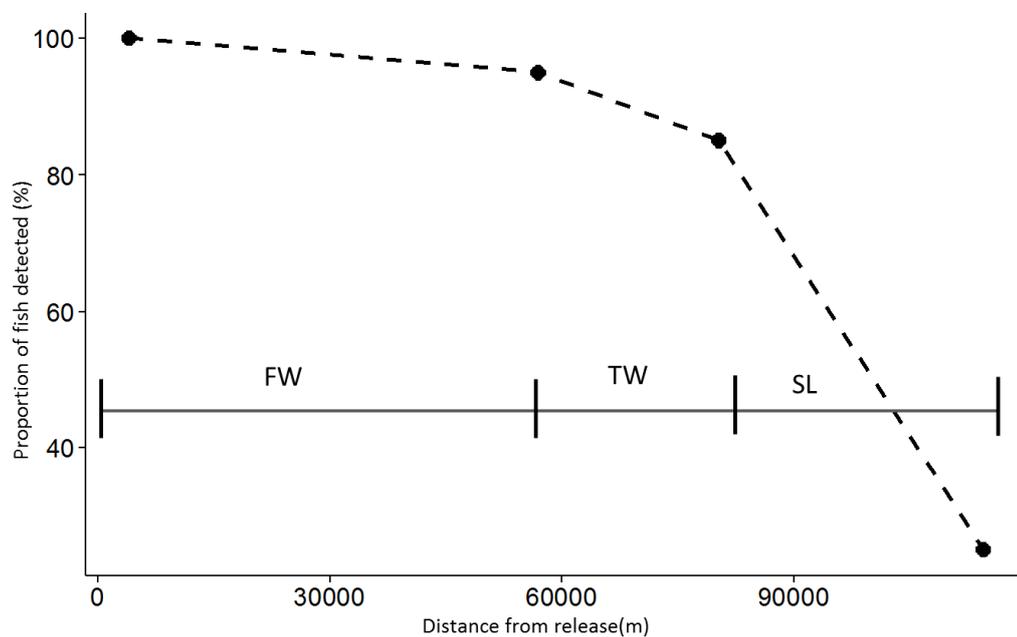


Fig. 5.2 Proportion of tagged fish detected through catchment compartments defined as freshwater (FW), transitional water (TW), and sea lough (SL) Distance 0 is the release point.

Thus, overall there was 26% escapement of tagged silver eels to the open sea. There was a non-significant difference in migration success (assuming that non-detected tags at downstream loggers represent successful passage of tagged fish) between Freshwater and Transitional water compartments ($\chi^2= 0.054$, $df=1$, $P >0.05$).

Estimated survival rates of tagged individuals were significantly lower in the sea lough compartment compared to the transitional compartment ($\chi^2 = 10.31$, $df=1$, $P < 0.001$).

5.4.2 MIGRATION INFLUENCES

Migration patterns of individuals were significantly related to environmental factors, in some compartments. A general linear model revealed a significant relationship between discharge and migration speed in freshwater ($F_{1,17}=8.761$, $r^2=0.35$, $P < 0.05$) and transitional water ($F_{1,15}=5.058$, $r^2=0.26$, $P < 0.05$) but not through the sea lough compartment ($F_{1,4}=8.761$, $r^2=0.02$, $P > 0.05$). The number of downstream movements was also significantly higher at night than during the day through all compartments (Table 5.S1. Supplementary information); freshwater compartment ($\chi^2= 35.103$, $df=1$, $P < 0.001$) Transitional compartment ($\chi^2= 36.250$, $df=1$, $P < 0.0001$) and sea lough compartment ($\chi^2= 5$, $df=1$, $P < 0.05$). The number of downstream movements was significantly different between tidal cycles, a higher proportion of movements occurred during ebb tides (92.3%) in comparison to flood tide (7.6%) ($\chi^2= 32.362$, $df=1$, $P < 0.001$) (Table 5.S2 Supplementary information). A significantly higher number of eel movements (77.7%) were observed in the three moon phases which represent the least illumination during the lunar phase, waning crescent, new moon and waxing crescent compared with higher illuminated phases ($\chi^2= 135.067$, $df=7$, $P < 0.001$) (Table 5.S3, Supplementary information).

5.4.3 MIGRATION SPEEDS

Of the 19 tagged eels for which directional migration was recorded, all progressed downstream, no individuals detected at ALS 1 were recorded moving back upstream. Time spent from release to last detection on the outermost receivers ranged from 11 to 80 days for successful migrants ($n=5$). Overall the mean migration speed (km.d^{-1}) of individuals was not found to be significantly influenced by length ($F_{3,37}=1.905$, $P > 0.05$). Mean migration speeds (km.d^{-1}) decreased significantly between successive compartments (ANOVA; $F_{2,38}=13.77$, $P < 0.001$), specifically, slower migration speeds were observed in the Transitional compartment compared with the Freshwater compartment (Tukey HSD $P < 0.001$) and between the sea lough compartment and the freshwater compartment (Tukey HSD $P < 0.001$). However there was no difference in

migration speeds between transitional and sea lough compartments (Tukey HSD $P>0.05$) (Fig. 5.3).

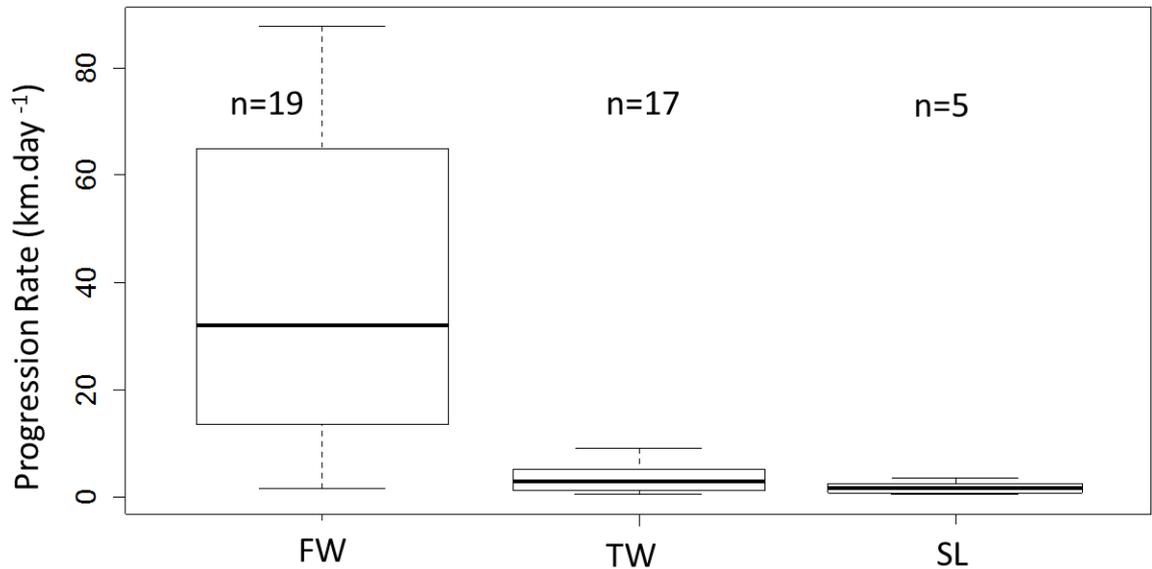


Fig. 5.3 Migration speed (kmd⁻¹) through catchment compartments. FW= freshwater, TW= Transitional compartment, SL=Sea lough.

Mean migration speed of migrants successfully reaching the open sea was not significantly different from unsuccessful migrants in the transitional compartment, freshwater compartments or sea lough ($P>0.05$ in all cases). Overall the level of fat deposition did not significantly influence migration speed through the catchment ($F=0.842_{,1,18}$, $P>0.05$). The level of fat deposition was found to have a significant positive effect on migration speed of successful migrants through the sea lough of ($F=5.204_{,1,3}$, $P<0.001$).

Table 5.3. Mean migration speed (mean \pm S.D; parentheses: range) in compartment types, n = number of eels monitored in a given compartment.

	n	Distance (km)	m/s ⁻¹	km/day ⁻¹
Freshwater	19	95	0.45 \pm 0.36 (0.01-1.01)	39.18 \pm 31.84 (1.58-87.7)
Transitional	17	26.88	0.04 \pm 0.03 (0.005-0.11)	3.42 \pm 2.68 (0.42-9.21)
Sea Lough	5	30.22	0.019 \pm 0.015 (0.006-0.04)	1.64 \pm 1.34 (0.55-3.48)
Total			0.19 \pm 0.27 (0.005-1.01)	16.68 \pm 23.97 (0.42-87.74)

5.5

DISCUSSION

This study details differences in migration success and behaviour of small silver eels as they migrate down a freshwater river reach, through a transitional zone and into a coastal marine sea lough. The eels in this study (L_t range: 332-520mm) exhibit a marked decline in migratory speed in the lower reaches of the catchment. Also shown is substantially higher losses of migrating eel in the sea lough compartment compared with freshwater and transitional water zones. While high mortality has been reported for downstream migrating larger female silver eels (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011), they have not been recorded for male and smaller female eels, nor in a catchment exhibiting a natural hydrology and free of anthropogenic influences (e.g. hydropower facilities and fisheries). These results strongly suggest that passage through a coastal marine sea lough imposes a high mortality rate on the seaward escapement of smaller eels, which has not been reported.

5.5.1 MIGRATION SUCCESS

Of the seventeen individuals that entered the sea lough only five were detected reaching the open sea successfully. The detection of 26% of the tagged individuals which initiated downstream migration at the final array is a minimum estimate of

successful escapement of tagged individuals. There are three possible explanations for the very low rate of detection of tagged eels.

Acoustic equipment failure or tag loss by fish

It is plausible that low detection efficiency resulting from poor receiver performance and or tag failure / performance may have resulted in low detection of tagged fish that reached ALS 6 or 7. This is highly unlikely as no acoustic breaches were recorded during range tests at the outer ALS array ruling out the likelihood of potential miss detection at the final listening stations. Additionally all receiver detections of individual fish were detected were recorded as more than one signal. All eel transmitters had an estimated battery end life in late February and given that eels are estimated to arrive at spawning grounds in mid-April (Aaerstrup *et al.*, 2009) it is expected that any successful migrants would have passed before February. Manufactures' reported tag failure rate in tests are <1% and studies using the same tags, over the same period, have reported control tag failure rates in field environments of 0% (Gauld *et al.*, 2013). There was no evidence of impaired migration related to tagging with ~90% of tagged fish successfully migrating through the freshwater compartment and transitional compartments. Silver eels have been successfully surgically tagged in numerous other studies (Aaerstrup *et al.*, 2008, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*, 2012; Bultel *et al.*, 2014) and surgical tagging of European eel in a similar manner to our study was not deemed to significantly affect eel behaviour and or survival over a 6 month period (Thorstad *et al.*, 2013).

Settlement

A possible interpretation of migration patterns shown here, which has been raised by other studies is that sea migration could be a two-step migration process (Durif *et al.*, 2005; Aaerstrup *et al.*, 2008; Béguyer -Pon *et al.*, 2015; Stein *et al.*, 2015). It has been reported that eel maturation may be more flexible than originally thought (Svedäng & Wickström, 1997) and that individuals may have the ability to interrupt migration and begin feeding again. Crook *et al.* (2014) demonstrated extended estuarine residence time for *Anguilla australis*, highlighting the possibility of more complex migration behaviour instead of the rapid and direct seaward migration originally assumed. Stein

et al. (2015) also highlighted the possibility that *A.anguilla* may need more than one migratory season to reach the sea and may temporally revert to a non-migratory stage. Therefore it is possible that a proportion of the tagged eels in this study ceased their migration in the lower Foyle and began feeding again to commence migration at a later date.

Mortality

The most probable explanation is that eels in this study experienced high mortality in the sea lough and the low escapement rate observed in this study represents true escapement of migrating eels (or a combination of the above factors). Thus, the results from this study strongly suggest substantial mortality of silver eels during the period they are in coastal marine habitat, even in the absence of a fishery. These findings are similar to those of Aarestrup *et al.* (2010) who also reported significant losses of tagged female European eels, interpreted as mortality during early marine phase. Due to the high fat content (van Ginneken *et al.*, 2000) and their relative abundance, eels are a very profitable prey source for avian, fish and mammalian predators (Keller, 1995; Knoesche, 2003; Britton *et al.*, 2006; Lundström *et al.*, 2010; Béguer-Pon *et al.*, 2012). Productive estuarine habitats are home to numerous potential fish predators, and such predators could represent an important and unappreciated source of eel mortality which has important management implications.

5.5.2 MIGRATION INFLUENCES

An important environmental cue initiating migration in both freshwater and transitional compartments was increased water discharge. Increased discharge has been identified as initiating downstream movement in European eels (Vollestad *et al.*, 1986; Feunteun *et al.*, 2000). In the study presented here, this effect was clearer for eels migrating through the freshwater reaches and although evident also in the estuary (transitional compartment) the effect was considerably less pronounced. In the sea lough, the effect of water discharge on movement disappeared. Aarestrup *et al.* (2010) noted a similar effect of declining migration responses to river discharges with passage downstream of the silver eels suggesting that tidal currents may possibly buffer the effect and this is consistent with the pattern in the current study. Selective tidal stream

transport (STST) has been proposed as a mechanism influencing eel migration (McCleave & Arnold 1999) which allows eels to quickly move through areas utilising tidal currents. The study presented here indicates that European eels may exploit outgoing tidal currents while migrating in the transitional and sea lough compartments with 92% of migration initiations occurring at these times. This concurs with findings by Béguer-Pon *et al.* (2015) who reported that American silver eels (*Anguilla rostrata*) use nocturnal ebb tide transport to migrate out of the St. Lawrence estuary. The eels in the present study also exhibited increased movement activity on phases around a new moon, with the majority of movements occurring in the lead up to a new moon, suggesting that migration is preferred on nights of the lowest lunar illumination.

In this study, most (94%) migratory movements of tagged eels occurred during the night, even when moving through the relatively turbid lower reaches of the river and estuary. Resident yellow eel tracking studies have also shown activity peaks at night (Hedger *et al.*, 2010, Walker *et al.*, 2014). This pattern for smaller females and male eels has been found in other studies in freshwater (Vollestad *et al.*, 1986; Tesch, 2003) and for coastal marine habitats on large female eels (Davidsen *et al.*, 2011; Aarestrup *et al.*, 2008, 2010). Predation has long been implicated as a major selective force in the evolution of several behavioural characteristics of animals (Lima & Dill 1990). The migration influences noted in this study are likely an evolutionary response to predation pressures. *A. anguilla* are important food source for predators (Keller, 1995; Knoesche 2003; Britton *et al.*, 2006; Lundstrom *et al.*, 2010; Béguer -Pon *et al.*, 2012). One such noted predator, cormorants (*Phalacrocrax* spp.) are visual foragers, feeding during daylight and twilight hours (Siegfried *et al.*, 1975) and nocturnal eel movements and higher eel movements on nights with reduced lunar illumination observed in this study are probably indicative of predator avoidance behaviour, which reduces the likelihood of encountering predators when undertaking their downstream migration (Fuiman & Magurran 1994).

5.5.3 MIGRATION SPEED

The migration speed of individuals through the catchment was not influenced by body length. This contrasts with findings by Verbiest *et al.* (2012) and Bultel *et al.* (2014) who reported faster migration progression of larger individuals. Inter-individual

variability in migration speeds was apparent across compartment types, however ultimate migration success was not affected by individual migration speed through the catchment. Overall migration speed was found to be significantly higher in the upper reaches in comparison to the lower reaches of the study catchment. This contrasts with the findings of Aaerstrup *et al.* (2010) who found slower progression rates upstream in comparison to downstream reaches in large female European eels. Given that tagged fish in this study ranged from 332-520mm in comparison to Aaerstrup's study (560-840mm), the contrasting results may be due to size or sex differences of tagged fish. Thus, the fresh-saltwater transition may possibly take longer for smaller sized eels. Bultel *et al.* (2014) also noted a slower migration speed in the downstream catchment compartments and suggested reduced progression may be a result of very strong salinity gradients. Such gradient transfers can be found in large estuaries similar to that in this study. The salinity gradient changes quickly in the lower Foyle ranging from 0.14- 25.50 PSU over 20km, this may explain the reduced migration speed. Thus one can postulate that reduced migration speed in lower compartments could be related to an acclimatization process due to increased salinity levels, and potential physiological size related factors.

5.5.4 CONCLUSIONS

This study strongly suggests previously unreported poor survival through coastal marine habitat of small female and male silver eels (340-520mm), though with the possibility that low recorded escapement could reflect long-term sea lough residency by a high proportion of small silver eel emigrants. More detailed research is needed to differentiate and quantify between these possibilities. If the low level of recorded escapement is due to mortality coastal sea loughs may be a potential bottleneck to eel escapement and potential mortality through such zones should be considered in models estimating production from a system. Given the smaller size of tagged eel in this study we hypothesise that predation pressure may be high on this size component and thus significantly influence escapement success. The study suggests that eels adopt migration strategies to reduce predation from visual predators which forage in marine-freshwater interface. Given the likely scale of the effects identified here,

estuarine and coastal migration processes may be having very significant effects on the long-term dynamics of eel populations if this pattern is replicated elsewhere. More information is urgently needed.

5.6

SUPPLEMENTARY INFORMATION

Table 5.S1. Number of movements on ebb and flood tides in transitional and Sea Lough compartments.

	Transitional	Sea lough
Total	47	5
Ebb	43	5
Flood	4	0
<i>P</i> -value	<0.001	<0.001

Table 5.S2. Number of movements during day and night tides in compartments.

	Freshwater	Transitional	Sea lough
Total	38	51	5
Night	37	47	0
Day	1	4	5
<i>P</i> -value	<0.001	<0.001	<0.001

Table 5.S3. Number of movements during lunar phases. FW=freshwater, TW= transitional water, SL= Sea Lough. *n*= number movements

Compartment	<i>n</i>	Waning Crescent	New Moon	Waxing Crescent	First Quarter	Waxing Gibbous	Full Moon	Waning Gibbous	Last Quarter
FW	38	22	1	10	2	0	0	1	2
TW	47	23	5	9	2	6	0	0	2
SL	5	0	0	0	0	0	0	2	3

Chapter Six

Historical Change in the European Eel *Anguilla anguilla* Population in the Foyle Estuary, Northern Ireland

*Note: This chapter has been published in *Biology and Environment: Proceedings of the Royal Irish Academy*

6.1

ABSTRACT

This study presents evidence of the decline in European eel abundance in a transitional water body in the Northern Ireland from 1967-2013. The available historical data is from important period; representative of the baseline abundance of eels in a transitional water body before recruitment collapse. The results from this study indicate the current eel population in the Foyle estuary is 3.38% of historical levels.

6.2

INTRODUCTION

The European eel *Anguilla anguilla* (L. 1758) is an important component of freshwater and coastal ecosystems across Europe. It is a facultative catadromous fish, found in fresh water, estuaries, lagoons and coastal waters from North Africa to northern Norway and throughout the Baltic and Mediterranean regions (Tesch, 2003). Long term index sites in Europe have shown that recruitment to catchments has declined rapidly since the early 1980's, as low as 5% compared with 30 years ago (ICES, 2013). Despite showing signs of recovery in recent years, the species remains at critically low levels (ICES, 2014). The mechanisms underlying the collapse of the European eel population remain uncertain and the panmictic nature of the species with no innate homing ability mean local effects are not directly linked to subsequent recruitment (Als *et al.*, 2011; Pujolar *et al.*, 2013; Adams *et al.*, 2013). Possible explanations of the species decline include over-exploitation (Simon *et al.*, 2011, Crook & Nakamura 2013), oceanographic and

climate changes (Miller *et al.*, 2009; Kettle *et al.*, 2011), habitat degradation (Feunteun 2002), barriers to migration (Acou *et al.*, 2008; Winter *et al.*, 2006; Pederson *et al.*, 2011), a non-native nematode parasite (Barry *et al.*, 2014) and contaminants (Geeraerts & Belpaire, 2010)

As a result of the decline in recruitment the International Council for the Exploration of the Seas (ICES) declared the stock as ‘outside safe biological limits’ (ICES, 2006) leading to the establishment of EC Regulation 1100/2007 (European Council, 2007) in an attempt to safeguard existing stocks.

The EU regulation requires Member States to assess the escapement of eel from ‘natural eel habitats’ in their territories and compare these with the potential production at historic levels. Historic estimates are biased towards production from fresh waters (ICES, 2009; Knights *et al.*, 2001). It has also been shown that some eels never migrate into freshwater and spend their entire growth phase at sea or within brackish waters (Daverat *et al.*, 2006). However, in European assessments, eel conservation during the continental phase is mainly focused towards freshwater habitats (ICES, 2014), however in recent times studies have exhibited that saline and brackish waters are highly productive growth habitat for eels (Harrod *et al.*, 2005 Daverat & Thomas, 2006, Jessop *et al.*, 2007). Recruitment upstream to fresh waters is considered to be density driven (Ibbotson *et al.*, 2002), and therefore estuarine populations may be most resilient to recent declines in recruitment, as a result of current declines recruiting eels may be more inclined to settle in estuaries as a result of the lowered density driven effects. Hence, there is an urgent requirement to assess eel production from estuaries, lagoons and coastal waters (SGAESAW, 2009). There is, however a paucity of published historical data on yellow eel populations from transitional waters increasing the need to retrieve and analyse any available data.

Although rapid declines in recruitment have been witnessed across Europe, there is also good evidence from long term data that observed declines have not occurred in catchments in north and central Scotland. Two independent long term historical data sets suggest that eel populations are being maintained by regional processes directly related to the proximity to the North Atlantic drift and the continental shelf current (Adams *et al.*, 2013). The Foyle catchment in Northern Ireland discharges north from

the island into the Atlantic and is situated very close to Scottish sites that appear to have stable eel populations. It is thus reasonable to expect that the eel population in the Foyle might also be stable over time. To investigate long term population change in the Foyle estuary a survey of eel populations from 1967 was repeated in 2013.

6.3

METHODS

The Foyle Catchment has an area of 4450 km² and drains into the Atlantic Ocean on the North coast of Ireland. The sea lough located at the mouth of the River Foyle is typical of an enclosed broad but shallow productive estuary and the exits to open ocean at Magilligan Point. The upper limit of tidal influence is located 60km upstream with a full salinity salt wedge occurring 40km upstream depending on the tide and flow conditions. The survey sites were undertaken 37.8 km from Magilligan point and 22.2 km downstream from the tidal limit (Fig. 1), site characteristics can be seen in Table 1. The primary objective of this study was to replicate the original survey in 1967, 46 years later to examine possible change in European eel populations. Physio-chemical data was available for 1973, and these data were used to investigate if there was long term change in physio-chemical characteristics in the study area. Historical salinity profiles were not available for the exact location of survey area however to investigate potential long term change in salinity profile in the Foyle estuary a reference site from 1973 (3 miles below survey sites) were compared with present day data.

In 1967 eels were sampled for a period of four nights using a string of 10 experimental fyke nets with 10mm mesh. The main hoops and leaders of nets were 610cm deep, the leaders being 7.3 metres long. The survey in autumn 2013 used comparable net specifications (leader length=8.8m, depth=56cm). Sites outlined in the 1967 report were re-fished using the same effort at the same time of year. Collected eels were euthanised (using a schedule 1 method) and body size parameters were collected: total length (mm) and mass (g), sex was determined by gonad examination following Colombo & Grandi (1996).

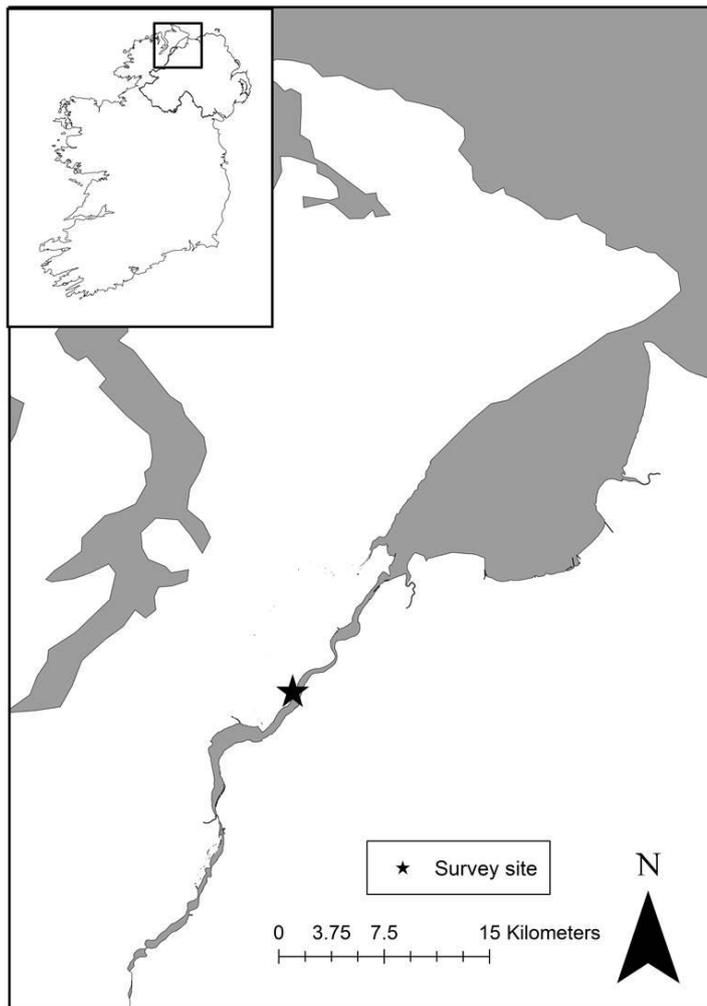


Fig. 6.1: Locations of survey sites within the river Foyle estuary.

6.4

RESULTS

To account for long term changes in environmental conditions in the survey area in the Foyle estuary data on physio-chemical variables from August 1973 were used. Parameter values observed in 2013 were not considered to be significantly elevated or decreased from values obtained by the Northern Ireland Water Council in 1973 (Northern Ireland Water Council 1974, Table 1). A reference site in the Foyle estuary provided long term salinity data, no significant change was observed between 1973 levels and present day (Table 1).

Table 6.1: Mean (\pm SE) physio-chemical parameters of survey site. Variable measurements taken in August 2013 and August 1973 for sampling area. Parenthesis contains reference site salinity levels in lower Foyle estuary between 1973-2013.

Variable	Sampling site 2013	Sampling site 1973
Salinity (psu)	4.3 \pm 2.4	-
Dissolved oxygen (mg/l)	7.3 \pm 0.85	6.7 \pm 0.54
Depth (m)	1.53 \pm -0.45	-
pH	7.8 \pm 0.1	8.1 \pm 0.0
Temperature ($^{\circ}$ C)	16.2 \pm 0.06	16.8 \pm 0.02
	Foyle estuary (2013)	Foyle estuary (1973)
Salinity (psu)	19.17 \pm 0.8	19.33 \pm 0.3

The results from this study indicate that there has been a significant decline in eel populations in the lower Foyle between the years 1967-2013 ($t=2.975_{,6}$, $P<0.05$, Fig. 2). A total of 1568 eels were captured during the survey period in 1967, compared to 53 eels captured during the repeat survey in 2013, revealing a population decline of 96.6%. The mean catch rate of eels in 1967 was 39.2 eels per net per night; in 2013 the study recorded a catch rate of only 1.3 per net per night.

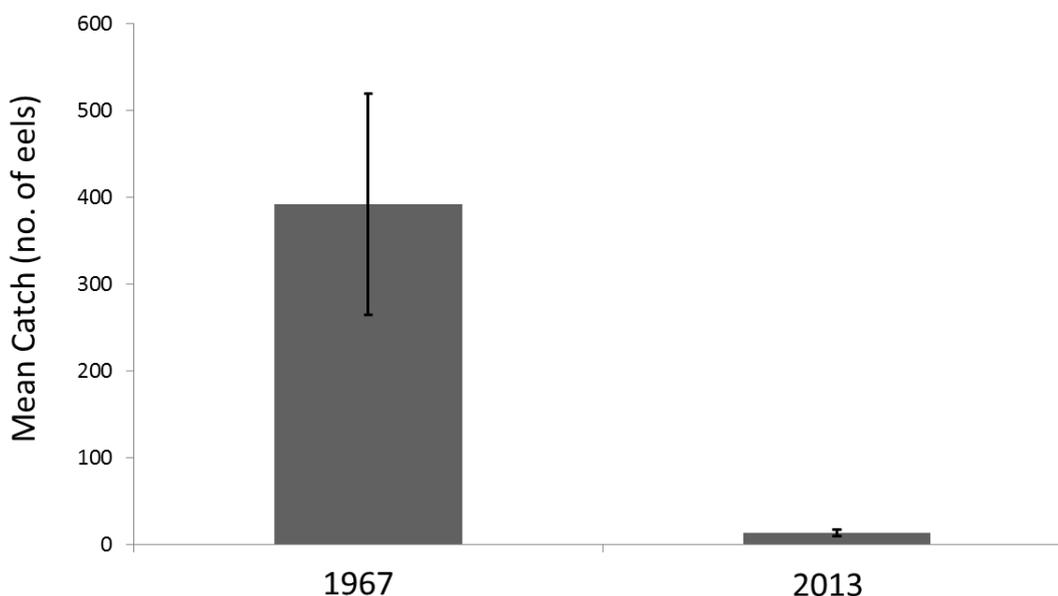


Fig. 6.2: Mean catch of eels from the lower Foyle; 1967 survey and re-survey 2013 \pm standard error.

Analysis of length frequency distributions of captured eels showed no difference in mean size of individuals between 1967 (37.7cm) and 2013 (39.1cm) ($t=-1.150$, $_{56.14}$, $P>0.05$, Fig. 3). The 1967 survey reports from a random sample of 58 eels, six were found to be males and the remaining 52 females. Extrapolating from length frequency data (Female eels classed as ≥ 40 cm) suggests that 57% of the 1967 catch were females. The sex ratio from the 2013 survey was 35 females, 8 males and 12 immature individuals, indicating 66% of the catch were females. Chi square analysis revealed a significantly higher proportion of female eels in 2013 catch in comparison to 1967 ($\chi^2=8.22$, $df=1$, $P <0.001$).

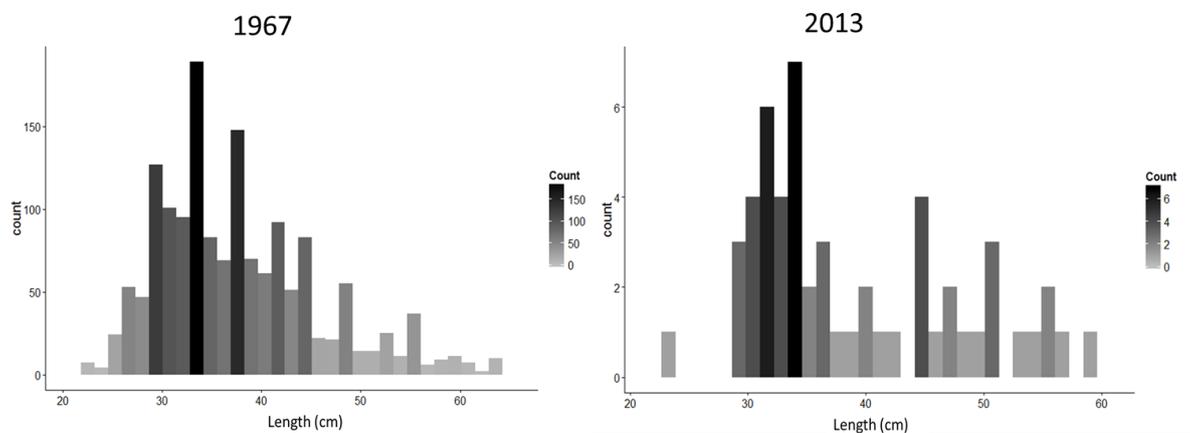


Fig.6.3: Length–frequency of eels caught at Foyle estuary 1967 & 2013. Data allocated into 10 cm size-classes. Number of eels is identified through count colour ramp increasing from grey-black indicating higher numbers.

6.5

DISCUSSION

This study indicates that current population size is 3.38% of that recorded in 1967. This is a major decline, but one that is consistent with main index sites in central Europe (ICES, 2013). Evidence from a range of independent data sources point towards the conclusion that eel numbers have declined rapidly and is generally widespread across Europe (Dekker, 2008). The similarity in size structure of the population (Fig. 2.) indicates that the methodology is consistent with gear selectivity (sample bias) being reduced. Therefore the differences observed here are most likely representative of the

population decline which has occurred in the Foyle estuary. There are of course other factors which must be considered when comparing eel numbers from two surveys over a 46 year period. An experimental fishery was active in the lower Foyle during the early 70's, however was halted due to low catches. Even if populations of eels were unsustainably overfished during this period, it is reasonable to expect that the lower Foyle eel numbers would have recovered in subsequent "pristine years" before the recruitment collapse. Additionally estuaries are changeable environments and what was a good habitat for eels in the 1960's may not be suitable in current day. During the time period of the original survey and resurvey there was no obvious evidence of environmental change or human-induced alterations at the scale of the study site which would adversely affect eel populations. Eels are known to be highly migratory within brackish water environments (Harrod *et al.*, 2005) and movement is considered to correlate positively with temperature (Riley *et al.*, 2011), to account for seasonal variation and potential seasonal habitat shifts the re-survey was undertaken during the exact same time period as the 1967 survey. Mean water temperature was not observed to change significantly between August 1973 and August 2013 in the sampling site accounting for potential confounding temperature changes over time. Whilst comparable physio-chemical data were unavailable for the 1967 survey, none of the parameters observed in 2013 were considered to be significantly elevated or decreased from 1973 levels (Table 1.)

A comparison of size distribution between years revealed no significant difference in mean size (Fig. 2). Similar observations by Henderson *et al.*, (2012) suggest that in the River Severn size structure stability over a long period, indicative of a long term poor recruitment to growth habitat. It is highly unlikely that the decline observed here is a natural cyclic process; such effects would be buffered due to slow growth of yellow eels (312-570mm; 6-16 years) in the Foyle estuary (K. Bodles, pers. comm.). It is also possible but unlikely that the size structure of the yellow eel in the Foyle has remained stable but the age structure has changed reflecting fish reaching larger size at smaller age, however no historical age data exists in this case.

Over the time period of the study presented here, the European eel population has undergone rapid declines across its range, numerous studies have reported decline in

recruitment of up to 90% (ICES, 2013) and a long term study of eels entrained in a power station cooling water intake on the Severn estuary revealed a decline of 15% per annum between 1981- 2009 (Henderson *et al.*, 2012). Despite the marked decline in the recruitment of glass eels and the general view that yellow eel stocks are declining throughout Europe, Bark *et al.* (2007) have shown that continental stage yellow eel have remained stable in some UK river systems. The study concluded that, despite declining levels of recruitment, many west coast rivers were still at, or near their respective carrying capacity. This finding was also supported by Adams *et al.* (2013) who found evidence of long term stability of yellow phase eels in western Scotland relating catchment population stability to the favourable geographic position of western Scotland to the North Atlantic current and winds. Although the Foyle is located geographically close to western Scotland (~150km) and thus within close proximity of favourable currents and winds for arriving eel larvae, the yellow eels, at least in the lower Foyle, show no signs of the long term stability as seen in western Scotland yellow eels. In another long term study, eels were monitored in the Rio Esva over a 15 year period. A decline in abundance of yellow eels within the estuary tracked more clearly with the decline in glass eel recruitment however freshwater yellow eels appeared to remain stable, potentially, buffered by density dependant factors (Lobon-Cervia and Iglesias 2008). Thus freshwater yellow eels and estuarine yellow eels from the same catchment may show differential responses to changes in recruitment.

The paucity of historical production from estuarine habitats across Europe highlights a current gap in knowledge. Given panmixia, the potential contribution of eels residing in estuaries and saline habitats to recruitment cannot be overlooked. Previous studies have reported longitudinal segregations of the eels over the length of the rivers with more abundant smaller (male) individuals in the lower reaches and less abundant larger (females) in the upper reaches (Feunteun *et al.*, 1998; Laffaille *et al.*, 2003 Domingos *et al.*, 2006). This study suggests that productive estuarine habitats form an important component to the European eel population and indicate that estuarine habitats can and in the case of the Foyle support a high proportion (>55%) of females and are not always dominated by males which has been reported in the literature elsewhere (Ibbotson *et al.*, 2002).

Overall the present study gives support to the view that we are presently witnessing a general collapse in European eel population and also highlights the importance of transitional waters in the production of eels in the continental life stage. Further long-term monitoring of the Foyle eels and inland watercourses would contribute substantially to our understanding of this species particularly in light of current increase in recruitment trends in recent years (ICES, 2014).

Chapter Seven

GENERAL DISCUSSION

7.1 SYNTHESIS

In this thesis five studies are addressed that have implications for the direction of conservation strategies for the European eel (*Anguilla anguilla*). In recent years we have witnessed unprecedented declines of this important fish species across Europe. Results from this thesis indicate significant declines in a transitional water body in Northern Ireland from 1967-2013, with current population levels at 3.38% of historical levels in the Foyle estuary (Chapter 6). The focus of this thesis was on resident populations (eels in their growth phase) Chapter 2, 3 & 4 and Chapter 5 focus on the downstream migration of silver eels leaving freshwater after completing this important life stage.

The findings presented in this thesis have highlighted the importance of alternative phenotypes exhibited in sympatric European eel populations. These data suggest there may be potential fitness consequences associated with an adopted foraging strategy (Chapter 2). These alternative foraging strategies which manifest themselves in head shape variability corresponded to significant variation in space use and activity patterns of individuals in important growth habitat, providing the first empirical evidence that this observed morphological variation leads to significant differences in space use (Chapter 3). The existence of foraging specialisation among individuals highlighted in Chapter 2 dovetails with the work undertaken in Chapter 4 which provides evidence that ontogeny and foraging significantly influences infection risk of the invasive nematode parasite *A. crassus* in the host-parasite system.

In the following discussion the relevance of the results obtained are discussed from a management perspective highlighting how an increased understanding of European eel ecology can help direct conservation strategies for this endangered species.

7.2 FORAGING ECOLOGY AND CONSERVATION IMPLICATIONS

The existence of two morphotypes “broad-headed” and “narrow-headed” in the European eel has long been known (Sivertsen, 1938) and this discrete head shape variation has interested biologists across Europe for a considerable amount of time (Lammens & Visser, 1989; Provan & Reynolds, 2000; Cucherousset *et al.*, 2011; Ide *et al.*, 2011). The observed phenotypic variation in head shape among eels can be dichotomous in nature and results suggest there are potential life history effects of this trophic morphology (Chapter 2). This phenotypic variation is widespread across the panmictic eel population (Ide *et al.*, 2011) therefore it is crucial to understand the potential life history effects of this variation.

As discussed in chapter 2, eels can specialise on food resources within a given habitat. Such individual variations have important implications not only on individuals but also at the population level. The interrelationships between diet, morphology and life history are indicative that different strategies adopted by eels in the same location will not necessarily have equal payoffs (measured in terms of lipid deposition). An individual's choice of strategy will be conditional upon its limitations in terms of, for example, size, foraging ability or physiology. Thus, feeding specialisations may be frequency dependent, but the optimum strategy for a given individual in a given location at a given time will ultimately be conditional upon its specific priorities and constraints. One of the main concerns affecting freshwater fish is that of habitat loss or environmental change. If individuals specialise in different diets, they will be affected to a greater or lesser degree by any change (Schoener, 1974). Individuals or groups that are unable to change foraging area, diet or feeding method for morphological reasons will be the most vulnerable to loss of prey in a growth habitat. Our findings indicate that morphological variability in eel head shape is linked to trophic ecology and generates varying growth rates and lipid deposition depending on the foraging tactic employed by individuals within the growth habitat. The great variability in *A.anguilla* found in the study sites investigated indicates *A.anguilla* are extremely plastic in their nature. The adaptability to varying resources may be driven by internal as well as external cues and warrants further research through long-term common garden experiments.

Feeding specialisations can have important consequences for population dynamics. Different feeding strategies may incur greater risks from, for example, parasites (Chapter 4). The study presented in Chapter 4 exhibits that diet specialisation is playing an important role in the transmission success or increased chance of encounter with infectious *A.crassus* larvae. The potential dispersal of this invasive nematode in Scotland is of great importance given the majority of lake systems are pristine eel habitat and produce high quality silver eels. Although this study only provides a snapshot of potential limiting factors of *A.crassus* and dispersal within a newly infected site, it does however, highlight the potential importance of diet specialisation in eels and how it can be linked to parasite intensity. Future monitoring is required for evaluation of potential changes in trophic interactions between eels and *A.crassus* as the parasite becomes more established within the Loch. Individuals will not only have different constraints, but also different priorities: for example, young animals may need to acquire extra nutrients for growth, larger eels may need to acquire more nutrients offered by a piscivorous diet. Linking trophic transmission dynamics to potential infection risk or repeated infection risk of *A.crassus* may be an important factor to consider when choosing potential conservation stocking sites.

The level of complexity observed in European eels in growth habitats make adopting a single population model a simplistic approach, and highlight the need to understand and appreciate the morphological variation of eels which can be observed in some locations. The mechanisms behind morphological variation in European eels warrants future research. The clear links between morphology, resource availability and life history consequence highlight the importance of accounting for morphological variability in current sampling programs so as to account for this important variation.

7.3 THE VALUE OF TELEMETRY AS A MANAGEMENT TOOL

The complex ways in which animals move within and interact with the environment are fundamental to understanding both basic and applied aspects of their biology. While researchers were once limited to making inferences on movement and ecosystem interactions by observing animals visually or through mark–recapture studies, advances in telemetry provide near continuous, automated tracking of

individuals across large spatial scales (Robinson *et al.*, 2009). Fish behaviour in aquatic ecosystems is particularly difficult to observe, however chapter 3 and 5 demonstrate how telemetry-based research has helped to reveal important aspects of eel behaviour which otherwise would be extremely difficult to elucidate.

The telemetry studies outlined in chapters 3 and 5 aid in informing management both directly (eg survival estimates & potential migration bottlenecks) and indirectly (eg effective survey design from home range estimates). The management of a highly migratory and mobile species such as the European eel is difficult. An understanding of the general ecology of endangered species such as identifying home range size and activity patterns (Chapter 3) and quantifying survival during challenging life history stages such as migration (Chapter 5) can inform managers of potential avenues to direct and aid conservation strategies. Chapter 3 identifies discrete variation between eels in a lacustrine habitat (broad-headed and narrow-headed) using acoustic tracking, thus, increasing our understanding of ecology of the species in this important growth habitat. From a conservation viewpoint the findings from Chapter 3 can be utilised by managers through aiding in the design of effective surveys. The results on distance travelled during regular and nocturnal periods provide valuable insights into the spatial and temporal behaviour of eels in a lacustrine environment. From a survey design perspective, this is valuable information on when eels move within lakes and what the main drivers of these movements are and thus gear deployment at these times will increase likelihood of capture. Survey programmes within lacustrine habitat are urgently required so as to estimate production from large lake systems. Knowledge of the distances over which eels move and size of home range can aid in informing the spatial dimensions of a survey. In addition, with behaviour of eels relating to environmental factors in a predictable manner (diel patterns and lunar phase) then the efficiency of a trapping programme can be improved by targeting specific environmental conditions.

Given the considerable variation in home range of eels, and differences between morphs, it is recommended that survey programmes that aim to quantify local eel populations should be designed to encompass as wide an area of the target lake as possible to ensure that the whole local population is sampled. Failure to survey

throughout the range of the sampled local population risks introducing sampling biases into the assessment procedure. This of course has a resource cost, both in time and equipment. However, the nocturnal activity patterns of the eels mean that traps should be set over the period of darkness and fishing during daylight is not necessary. Despite the intensive resources required to survey eels in the open waters lakes, the data these surveys will provide are essential to national and international efforts to conserve the European eel and a greater understanding of populations and production from lacustrine environments.

The study presented in Chapter 5 presents vital information on the migration success of male and small female silver eels during the downstream passage through a catchment. The results from this study identify a potential bottleneck to silver eel migration in the lower part of the catchment through the sea lough compartment. Further study is warranted and in particular employing manual tracking throughout the sea lough to test the hypothesis of settlement in the lower estuary. Fisheries and hydropower entrainment are two anthropogenic factors that may have a significant impact silver eel escapement and results suggest that mortality through potential predation could also be having a significant effect on the successful migration through the lower catchment. While survivorship is based on extrapolations from telemetry data, exploring measures to allow or enhance safe passage through the lower estuary is warranted.

The identification of discrete population structure using this technology could have important implications for vulnerable species. Acoustic monitoring can help to prioritize areas of interest so they can receive conservation efforts, for example important habitat or potential migration bottlenecks. The studies in chapters three and five which use this technology have highlighted novel research topics, provided key examples and highlighted areas that warrant future research. With the advancement of acoustic technology answering demanding hypothesis driven questions will aid in the advancement of fisheries research in the area of spatial and migratory ecology.

7.4 RECOMMENDATIONS FOR FUTURE RESEARCH

In this thesis five studies addressed fundamental ecological questions on European eels during the continental stage of their life cycle and have resulted in several recommendations for conservation and management and potential avenues for future research of this keystone species.

In chapter 2, 3 & 4 the importance of foraging specialisms within eels is explored. These studies have highlighted that there is intrinsic links between phenotype and environment. From a management perspective this has important implications. If indeed phenotypic variation is driven by environment and resource availability, then unbalance or change in an ecosystem as a result of man-made anthropogenic effects (e.g habitat loss), ecological changes (e.g establishment of invasive species) or climate change may induce shifts in the trophic which in hand may influence the fitness of the different phenotypes within habitat. Thus the relationship between phenotype and environment means that population assessment should account for morphological variation. For example if habitat loss or change occurs, some sections of the population could be affected more than others and the effects on population size might be very different from that predicted by models based on individual uniformity. It is critical to acknowledge such biodiversity in management decisions and or population modelling.

Although this thesis has highlighted some important aspects of head shape dimorphism and potential life history consequences, some aspects warrant further research. A genetic component of head shape dimorphism cannot be ruled out and this is an area which should be investigated. Common garden experiments would allow questions such as the role of ontogeny and feeding and the relationship between morphological diversification and potential phenotypic trajectories to be answered.

The telemetry work undertaken in this thesis has provided an intriguing insight to movement and migratory behaviour of European eels while resident in continental waters. Managers should give consideration to the findings in chapter 3 with regards space use and activity patterns as these data can be used in effective survey design in

large lakes. This thesis has demonstrated that tracking technology can answer some fundamental ecological questions and future research should aim at incorporating some level of physiological knowledge and ecological understanding to better understand variation in movement and migratory behaviour. The suite of techniques used in this thesis can be used to answer important fundamental ecological questions which can aid in the conservation of fish species in fresh brackish and saline waters.

Appendix ONE

A.1 Population Size and Movement of European Eel *Anguilla anguilla* (L.) in an Interconnected Lake System

A.1.1

ABSTRACT

A mark recapture study was undertaken in Baronscourt lakes system in 2012 so as to quantify eel population size within the lakes. Yellow eels were individually PIT tagged. Recapture rates of 34% and 27% were obtained within the two lakes investigated. Population estimates based on mark recapture experiment were 19 eels ha⁻¹ in Lough Catherine and 11.3 eels ha⁻¹ in Lough Fanny. The movement of individuals between successive recaptures revealed mean minimum straight line distance of 493.86 ± 18.72 (range: 18.8m-3679), movement rates between successive recaptures were significantly higher in larger size classes. Results from historical catches indicate CPUE figures have remained stable in the lakes between 1971 and 2012, with a significant decrease in weight being observed between 1999 and 2012. A total of 119 silver eels were captured at the outflow trapping station at Baronscourt lakes. The silver eel run was dominated by male eels (n=110) with only nine female eels being captured. Of the 388 yellow stage eels tagged during summer sampling, five were recaptured as silver eels. Peak silver runs were found to occur during high water flow events, coinciding with dark moon phases.

A.1.2

INTRODUCTION

In response to advice from the International Council for the Exploration of the Sea (ICES) that the European eel (*Anguilla anguilla* L.) is outside safe biological limits, an EC regulation was enacted to aid recovery of the European eel stock (Council Regulation 11000/2007). The regulation for the recovery of the eel stock identifies a number of monitoring objectives, including; creating baseline data sets for monitoring changes in yellow eel populations over time, and comparison with historical surveys. In light of current population declines, yellow-eel stock monitoring is thus integral to

gaining an understanding of the current status of local stocks, and for informing models of escapement (Arahamian *et al.*, 2007). Such monitoring also provides a means of evaluating post-management changes. The size of a population is a very important ecological variable. However estimating fish population size can be quite difficult for the following reasons; sampling gear can be selective for certain size classes (O'Neill *et al.*, 2009), populations are often quite abundant meaning large sample sizes are needed to get adequately estimate population size; fish may actively avoid some monitoring methods in deep water. One highly effective population size estimation method is to combine trapping with mark and recapture techniques over several closely spaced time intervals (Borchers & Efford 2008; Efford *et al.*, 2009). In this study a “Mark-Recapture” approach was undertaken to determine the population size and movement of resident eels within Baronscourt lakes. In addition the effectiveness of yellow eel sampling at predicting silver eel out migration was investigated.

A1.3

METHODS

A1.2.1 STUDY AREA

The study was conducted in Baronscourt lakes; Lough Catherine (N54° 701' W-7° 434') and Lough Fanny (N54° 692' W-7° 442'), Northern Ireland in 2012. The combined surface area of these 2 connected lakes is 60 ha with a maximum depth of 6 metres. Eel, roach (*Rutilus rutilus*), bream (*Abramis brama*), pike (*Esox Lucius*) and perch (*Perca fluviatilis*) compose the ichthyofauna within the lakes.

A1.2.2 FISH CAPTURE AND TAGGING

In summer 2012 resident yellow eels were captured using fixed fyke nets comprising 5 chains of five double ended Dutch fyke nets (leader length=8.5m, depth=55cm). Fish were placed in a holding tank and anaesthetised with Clove oil (0.5mg per litre) prior to measuring and tagging. The total body length (mm), body weight (g), eye diameter (mm) and length of pectoral fin (mm) were recorded to determine their maturation stage according to Durif *et al.* (2005).

Over the duration of the study, a total of 388 yellow stage European eels (L_t 300-749mm, W 24-796g) were tagged with individually coded Passive Integrated Transponders (PIT tags; Model FDX-B, 7 x 1.35mm: Loligosystems). PIT tags were inserted into the abdominal cavity with a syringe. Each tag has a unique code to allow identification of recaptured tagged eels, using a portable PIT tag reader.

A1.2.3 POPULATION ESTIMATION

A maximum likelihood spatially explicit capture recapture (ML-SECR) analysis was conducted on Baronscourt lake system data during 2012. The “Density” programme V4.4 (Efford *et al.*, 2009) estimates the density of animal populations from capture – recapture data collected using an array of detectors. In this study detectors are live capture traps with animals uniquely marked with PIT tags. The density values reported here are representative of the gear-dependent proportion of the population. In this study it was decided to tag only eels that were >300 mm (due to the effect of tagging on eels). Fyke nets were set in grids at a 90 degree angle from shore. Nets were not set on consecutive nights as the anaesthetic suppresses appetite and therefore tagged eels are unlikely to forage directly after release impacting on their recapture rate. Existing data indicates that eels feed every 2-3 days (Tesch, 1977; Moriarty, 1978). Fyke nets were not baited to avoid attracting eels into the study area (Morrison & Secor, 2004). ANOVA was used to investigate differences in distance moved (m) and movement rate (distance/time) between successive recaptures of yellow stage eels within the lake system. A TUKEY HSD post-hoc test was used for pairwise comparisons. A Welsh t test was used to test for differences between the length of marked fish and the length of recaptured fish.

A1.2.4 LONG TERM CHANGE IN THE EEL POPULATION

Historical survey work was carried out on eels in Baronscourt lakes in 1971 and in 1999. Dutch fyke nets and length and weight data were \log_{10} transformed to reduce heterogeneity of variances and an ANOVA was used to investigate differences in length and weight of captures across the three studies. For the historical data, only worked up CPUE's are available for comparison with recent survey. As there can be a

lot of variation in the catch of eels per fyke net group per night as this variation is not available, no statistics was performed on CPUE's.

A1.2.5 SILVER EEL

Silver eels migrating out of the Baronscourt lakes were trapped at sluice gates on the exit stream providing a unique opportunity to examine silver eel migrations and to collect migrating eels previously marked as yellow eels. The silver eel run was monitored in relation to water flow (flood events) and moon phase from August through to December 2012. Using the Durif *et al.*, (2005) classification method, a percentage of tagged yellow eels (marked population) were classified as potential migrants and migrant activity was monitored via silver eel traps.

A1.4

RESULTS

A1.3.1 MARK RECAPTURE & POPULATION ESTIMATION

Overall a total of 388 yellow stage eels were captured over the study period. Of these, 110 fish were recaptured and identified. Recapture rates were 27.2% in Lough Catherine and 34.2% in Lough Fanny. The mark recapture estimates of population size based on these catches was estimated at 683 +/- 59.7 and 132 +/- 19.1 in Lough Catherine and Lough Fanny respectively. This represents density estimates of 19 eels.ha⁻¹ in Lough Catherine and 11.3 eels.ha⁻¹ in Lough Fanny (Summary of mark-recapture results can be seen Table A.1, A.2 & A.3). There was a significant difference in the length of marked versus recaptured eels (Fig. A.2). The mean length of the recaptured eels was significantly longer than overall marked individuals ($t=-3.12$, 99.014, $P=0.002$).

A1.3.2 LONG TERM CHANGES IN EEL POPULATION

ANOVA revealed a significant difference in eel weight between the years 1971, 1999 and 2013 ($F=5.331, 2, 137$, $P<0.001$). A post-hoc Tukey HSD test showed a significant difference in weight, between the years 1999 and 2013 (Bonferroni correction, $P<0.05$). There was no significant difference in length between years $F=2, 137, 1.155$, $P=>0.05$). A slight negative trend in CPUE was observed 1971 to 2013, however

catches between 1999 and 2013 have remained stable over time. The summary CPUE data are presented in Table A.6 the value obtained in current study is lower than the CPUE in 1971 however comparable catches were recorded between 1999 and 2012.

A1.3.3 MOVEMENT

The minimum straight line distance moved between recapture events ranged from 18.8 to 3679m. ANOVA revealed no significant differences in distance moved between size classes (30-40; 41-50; 51-60; 61-70, unit (cm)), ($F=3,105$ 0.866, $P=0.43$). To calculate minimum movement speed, distance moved was divided by time between recaptures. Significant difference were observed between size classes ($F=9.876$, $3,105$, $P=0.002$). Tukey HSD revealed significant differences between Bonferroni corrected pairwise comparisons (Table A.7; Fig. A.3).

A1.3.4 SILVER EEL RUN & RECAPTURES

A total of 119 silver eels were captured at the outflow trapping station at Baronscourt lakes. Mature male eels (n=110) made the majority of the silver eel catch with only eight female eels being caught during the sampling period. Of the 388 yellow stage eels marked during summer sampling, only five were recaptured as silver eels, these data can be seen in summary Table A.5. Peak silver runs were found to occur during peak water flows coinciding with dark moon phases (new moon) Fig. A.4.

Applying the Silver Index (Durif *et al.*, 2009) to all yellow eels captured in 2012 indicated that 3.8% (n=15) of the tagged yellow stage eels in Baronscourt should have migrated in 2012 (life stage FIV, FV, MII). Five eels representing 1.28% of the tagged population were successfully recaptured as silver eels. Of the five tagged individuals, the two mature male eels were classed as immature when caught during the summer sampling. Of the three females eels captured, two were classed as mature during summer sampling in the remaining female eel was classed as FIII and changed status to FIV in a 72 day period (individual summary can be seen in Table A.5).

A1.5

DISCUSSION

In the mark recapture study carried out in Baronscourt lake system in 2012 the rate of recapture varied slightly between location, (Lough Fanny; 34.2% in comparison to

Lough Catherine which had a recapture rate of 27.2%) but in general, recapture rate was very high. Sampling the density of eel populations is fraught with difficulties and comparative sampling is also difficult however, mark recapture techniques yield reasonably accurate estimates of population size in small closed waters (Naismith & Knights 1990). The density values reported here are representative of the gear dependent proportion of the population (O'Neill *et al.*, 2009). In this study, the density of eels was estimated at 19 eel's ha⁻¹ in Lough Catherine and 11.3 eel's ha⁻¹ in Lough Fanny. Numerous studies have attempted to quantify eel numbers and reported densities in estuaries, rivers and lakes vary greatly. For example; 1-30 eels.ha⁻¹ (Morrison & Secor 2004), 4-13.8 eels.ha⁻¹ (Hightower & Nesnow 2006), 50-518 eels.ha⁻¹ (Barak & Mason 1992), 232-636 eels.ha⁻¹ (Labar & Facey 1987). Poole *et al.* (1994) quantified eel densities using techniques similar to those of this study, densities ranged from 2-28.3 eels.ha⁻¹ in freshwater lakes. Making comparisons with other sites is difficult given the number of factors which may be influencing density estimates such as distance from sea and water chemistry (Feunteun *et al.* 2003). The homing and territorial habits of eels (Tesch, 2003) make it difficult to achieve a random distribution of marked eels throughout a population and also make it difficult to sample with the same effort the total unmarked and marked populations. It is also been hypothesised that marked eels may be more active and therefore more catchable (Naismith and Knights 1990). Despite this, mark recapture techniques for population studies are regarded effective in closed sites where a high proportion of the population can be marked and subsequently recaptured (Naismith & Knights 1990).

The historical survey work undertaken in Baronscourt lakes in 1971 and 1999 used Dutch fyke nets, the same net specification were used in the current study and allow comparison. In this study there was no difference observed in eel length over time however mean weight of individuals was found to decrease significantly between 1999 and 2013. This may be due to resource availability at the time, competition or possibly sampling bias (time of year). The trend in CPUE, over this period is that of a decline in the yellow eel population. This is generally in line with European recruitment trends, however the same magnitude of change is considerably lower than reported elsewhere. CPUE over this period has remained stable between 1999 and 2013 this contrasts markedly with drastic declines in eel recruitment observed across Europe and

indeed in the lower part of the same catchment (Chapter 6). Stability in yellow eel populations has been observed elsewhere and population size is believed to be regulated by in-stream density-dependence (Lobón-Cerviá & Iglesias 2008). This occurs when high recruitment results in an over-saturation of suitable habitats within a catchment. Subsequent years of reduced recruitment causes less competition and a lower rate of mortality, thus the population remains stable (Feunteun *et al.* 2003). This has shown to be the case in a long-term study in Spain, where despite the decline in abundance of yellow eels within the estuary following a decline of glass eel recruitment, freshwater population numbers have increased (Lobon-Cervia & Iglesias, 2008).

Smaller size classes were observed to move a significantly shorter distances between recaptures when compared to larger size classes (Fig. A.3). The significantly higher movement distance between successive recaptures of larger individuals may be explained by the size of a fish. Larger individuals have been shown to expand their range as a behavioural response to foraging optimization in association with reduced predation risk due to increased body size (Marshall *et al.*, 2011). This may explain the observed trend in higher movement rates of larger individuals. This is also an important factor to take into consideration when small scale sampling is undertaken. One consequence is that smaller size classes may be under represented due to gear bias and lower activity levels which reduce the likelihood of encountering nets.

The downstream trapping facilities provided a unique opportunity to monitor migrating eels previously tagged as yellow eels in the lakes upstream. In this study, eels were recaptured that had been tagged in Lough Fanny and Lough Catherine. It is not always possible to monitor the silver eel catch escaping from a catchment so there is a need to accurately predict how many yellow stage eels sampled will migrate as silver eels. Summer sampling took place in June 2012, of the 388 eels classified using the silver index 96.2% classified as resident yellow eels with 3.8% assigned to potential migrant stages. Three silver eel recaptures were classed as yellow eels in summer sampling matured to silver eel stage. Of the individuals classed as potential migrants during yellow eel sampling (FIV, FV) two were recaptured as silver eels. The remaining migrant classified eels did not appear in silver eel traps. It may be that

during one flood event when a net was displaced a number of tagged fish may have gone undetected. During resident eel surveys yellow eels >30cm were pit tagged. Fyke nets are known to under represent male eels, our results suggest that only 1.8% of the male silver eel run were successfully captured during intensive yellow eel surveys within the lake system. This highlights the importance of including this missing component during resident eel sampling so as to get a true picture of silver eel runs. Fyke nets can be deemed successful for estimating female numbers however the underrepresentation of male eels makes estimating production from certain systems very difficult. Future work will aid in better understanding of the maturation process of yellow eels and in accounting for the male component of eel biomass within a lake system.

A1.6

FIGURES & TABLES

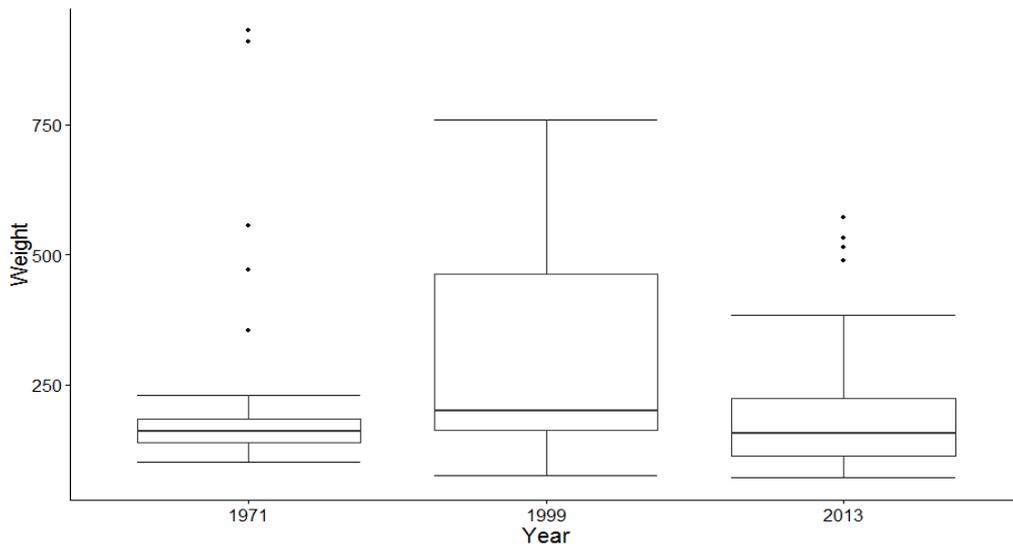


Fig. A.1.1 Weight (g) differences between the years 1971, 1999 and 2013. (1999-2013 $p < 0.05$)

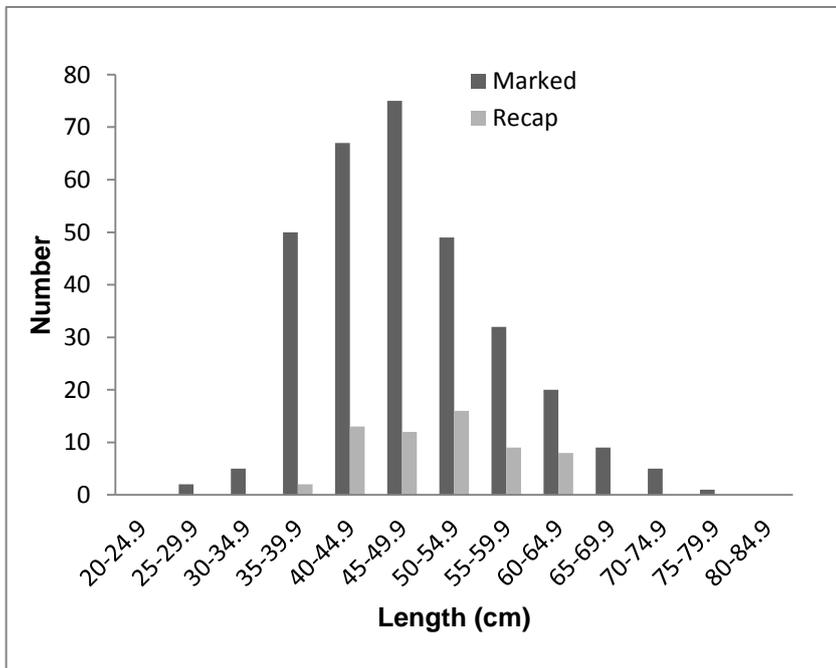


Fig. A1.2: Length-frequency distribution for marked (n=385) and recaptured (n=110) yellow eels in Baronscourt lakes.

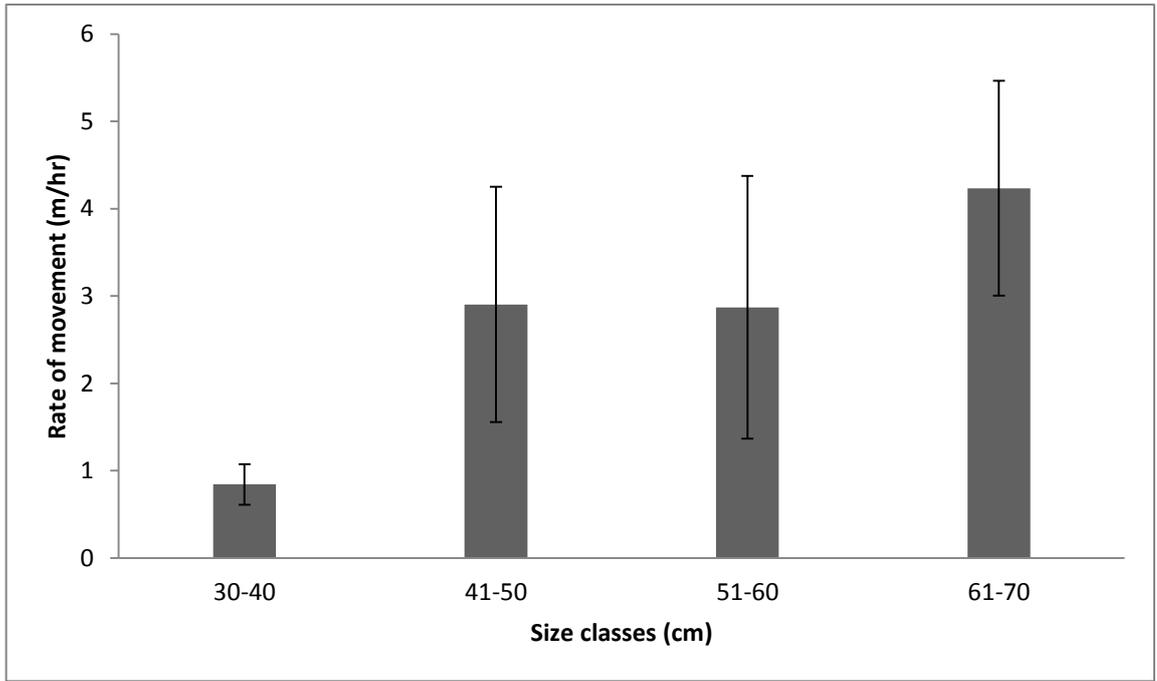


Fig. A1.3: Rate of movement differences between successive recaptures based on size classes. Refer to Table 7 for pairwise comparisons.

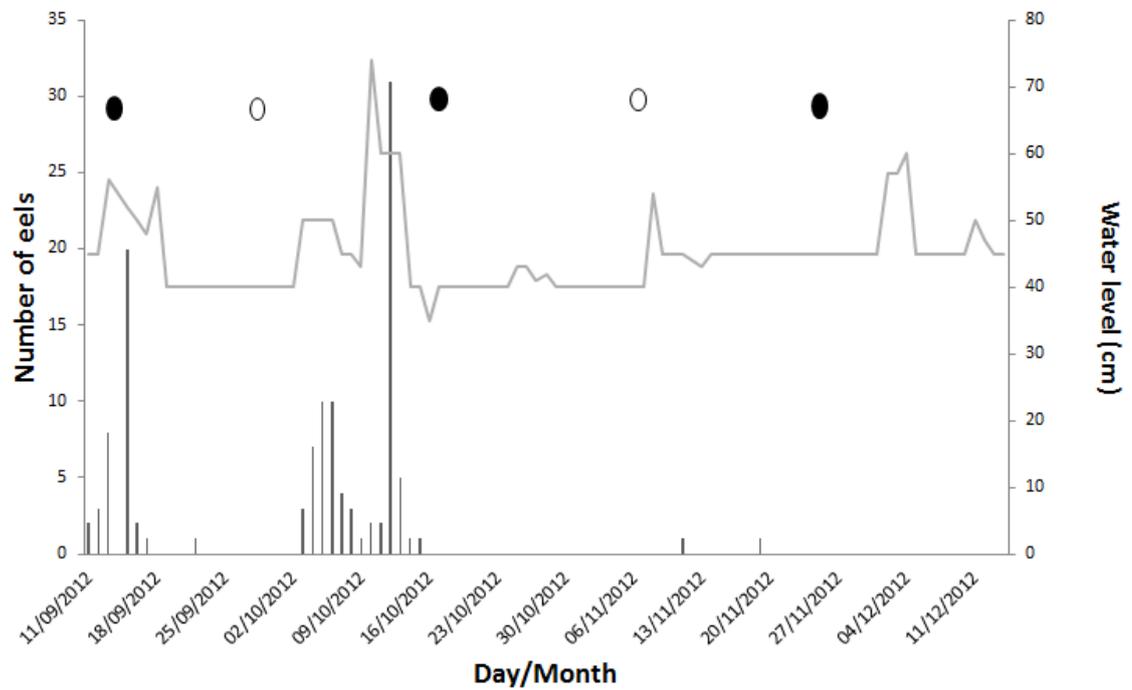


Fig. A1.4: Relationship between silver eel run from Baronscourt 2012 in relation to water flow and lunar phase.

Table A.1: Summary statistics of multiple census mark recapture.

Site	Total Marked (captured)	Recaptures	Recapture rate (%)	Population size	Eel/ha
L.Catherine	309(393)	84	27.20%	683 +/- 59.7	19 eel/ha
L.Fanny	76(102)	26	34.20%	132 +/- 19.1	11.3 eel/ha

Table A.2: L.Catherine Multiple census

Occasion i	1	2	3	4	5	6	Total
Caught at time i	76	64	59	67	59	68	393
First caught at time i	76	55	45	51	44	38	309
Caught exactly i times	227	62	15	5	0	0	309
Marked eels at i+1	76	131	176	227	271	309	

Table A.3: L.Fanny Multiple census

Occasion i	1	2	3	4	5	6	Total
Caught at time i	8	32	24	21	0	17	102
First caught at time i	8	25	18	16	0	9	76
Caught exactly i times	55	18	2	0	1	0	76
Marked eels at i+1	8	40	64	85	85	102	

Table A.4: Proportion of yellow eel catch according to silver index

Lake	I	FII	FIII	FIV	FV	MII
Catherine	156	134	14	2	3	2
Fanny	37	28	4	1	5	2

Table A.5: Silver eel recapture data. Morphometric statistics from yellow eels stage to silver stage

Date		Length		Weight		Silver index		Lake of Origin	Time elapsed
Yellow	Silver	Yellow	Silver	Yellow	Silver	Yellow	Silver	Yellow	Silver
4.8.12	15.9.12	365	368	102	120	I	MII	Fanny	42
4.7.12	15.9.12	609	615	438	456	FIII	FIV	Catherine	72
5.7.12	5.10.12	371	376	98	102	I	MII	Catherine	92
29.7.12	12.10.12	689	692	627	636	FIV	FIV	Catherine	75
2.8.12	12.10.12	676	685	644	654	FIV	FIV	Fanny	71

Table A.6: Trend in CPUE figures from 1969-2012

	Net*Night	No.Eels	CPUE
1969	24	35	1.452
1999	30	34	1.133
2012	70	71	1.014

Table A.7: Pairwise comparison of rate of movement (metres per hour) between successive recaptures between size classes (bonferroni correction applied).

Size class (cm)	30-40	41-50	51-60	61-70
30-40	-	<0.05*	<0.05*	<0.05*
41-50	<0.05*	-	>0.05	<0.05*
51-60	<0.05*	>0.05	-	<0.05*
61-70	<0.05*	<0.05*	<0.05*	-

Appendix TWO

A.2.1 Introduced Parasite *Anguillicola crassus* Infection Significantly Impedes Swim-Bladder Function in the European Eel *Anguilla anguilla* (L.).

J. Barry¹, J. McLeish¹, J.A. Dodd¹, J. F. Turnbull², P. Boylan³ AND C. E. Adams¹.

¹*Scottish Centre for Ecology & the Natural Environment, IBAHCM, University of Glasgow, Rowardennan, Glasgow, G63 0AW UK.* ²*Institute of Aquaculture, University of Stirling, Stirling, FK9 4LA, UK.* ³*Loughs Agency, 22 Victoria Road, Derry, Northern Ireland, BT47 2AB, UK*

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Infection with the nematode parasite *Anguillicola crassus* has been implicated as one possible cause initiating or maintaining the collapse of European eel populations across its range. This study compared the structural stability of infected and uninfected eel swim-bladders. Infected swim-bladders exhibited lowered elasticity and required increased pressure to rupture swim-bladder walls. These findings indicate impairment of buoyancy regulation arising from *A. crassus* infection. It is thus highly reasonable to suggest that this will impact on the success of the spawning migration of infected individuals to the Sargasso Sea.

Key words: European eel; Swim-bladder function; *Anguillicola crassus*; elasticity; pressure

The European eel *Anguilla anguilla* (L. 1758) is an important component of freshwater ecosystems across Europe. In recent years, populations have declined rapidly with many populations thought to be around 10% of their size in the freshwater (yellow eel) phase of their life-cycle and juvenile recruitment to this phase as low as 5% compared with 30 years ago (Feunteun, 2002; Freyhof & Kottelat 2010; FAO, 2011). This has raised concerns over the long term viability of the species (Dekker, 2003). The mechanisms underlying the collapse of populations in freshwater remain uncertain. Possible explanations include over-exploitation, oceanographic and climate changes, habitat degradation, barriers to migration and diseases (Dekker, 2003). Another possibility is the impact of the non-native nematode parasite of the swim-bladder, *Anguillicola crassus* (Kirk, 2003). This parasite was accidentally introduced to Europe in the late 1980's through imports of its native host, the Japanese eel, *Anguilla japonica* (Koops & Hartmann, 1989) and since then it has rapidly spread across the continent (Moravec, 1992; Székely, 1993; Evans & Matthews, 1999; Kirk, 2003; Lefebvre *et al.*, 2012). Its arrival has posed a new threat for freshwater eel populations (Lefebvre *et al.*, 2012). It appears that European eels have not evolved an appropriate immunological response to this parasite, and thus infection has been identified as a potential source of eel mortality (Molnar *et al.*, 1991).

Both physiological and physical changes to the structure of the swim-bladder as a result of *A. crassus* infection have been reported previously. Long-term exposure has been shown to result in inflammation and increased thickness of the swim-bladder

wall (Molnar *et al.*, 1993; Molnar, 1994; Würtz *et al.*, 1996). These morphological changes imply a potential loss of swim-bladder function with possible long term effects on individual fitness. The study presented here examines the effect of *A. crassus* infection on the function of the swim-bladder in the European eel, specifically testing the effect of infection on elasticity and pressure required to rupture the swim-bladder.

Female eels were collected from three populations: Loch Lomond (56° 7' 30 " N, 4° 36' 48) and the Dubh Loch (56° 7' 50.9" N, 4° 37' 1.22" W) in Scotland and Lough Neagh (54° 43' 23" N, 6° 29' 20 " W) from Northern Ireland. The eel population from the Dubh Loch and Lough Neagh are known to be infected by *A. crassus*, the Loch Lomond population has no record of the parasite (unpublished surveys 2008, 2009, 2010, 2012 and 2013 Glasgow University).

All fish were collected in June and July 2012. Fyke traps were used in Loch Lomond and Dubh Loch and fish were temporarily held in aquaria (Lomond n=11, length range 391-710mm; Dubh Loch n=8, 390-670mm). Eels from Lough Neagh were obtained from the Lough Neagh eel fishery (n=7, 434-625mm).

Each eel was killed (using a schedule 1 method) weighed and measured and its abdominal cavity dissected to enable a count of parasite loading (or to confirm its absence). The swim-bladder was then dissected from the abdominal cavity measured and tested for structural properties. The pneumatic duct was connected via a ligature to a plastic pipe connected to a peristaltic air pump connected in series with a manometer to measure pressure. The swim-bladder was slowly inflated and continuous pressure measures taken by recording manometer pressure readings with a video recorder. The pressure was slowly increased until catastrophic rupturing of the swim-bladder membrane. Boyle's law was used to calculate the absolute pressure in the swim-bladder lumen at failure. A proxy for swim-bladder elasticity was also calculated using:

$$E = \frac{P \times V}{\Delta v}$$

E= Elasticity (Pa)

P= Pressure

V= Volume

Δv = Change in Volume

Elasticity and the absolute pressure required to rupture the swim-bladders from infected and uninfected fish was tested with Welch's t- test with d.f. adjusted for unequal variances (Satterthwaite, 1946). Statistical analysis was performed using R (R Development Core Team, 2010).

There was no significant difference in length between infected and uninfected eels ($df=21.209$, $t= 1.09$, $p>0.05$), ensuring size homogeneity when comparing specimens. Prevalence of *A. crassus* in study sites was 0% in Loch Lomond, 72% in Lough Neagh and 100% in Dubh Loch. Mean intensity within lakes infected with *A. crassus* were 6.9 ± 1.8 and 2.5 ± 1.1 in Dubh Loch and Loch Neagh respectively.

The absolute lumen pressure needed to rupture the swim-bladder was significantly higher in infected fish compared with uninfected fish. ($df= 24.78$, $t= 4.2$, $p <0.05$, Fig 1). In addition the swim-bladders from infected fish showed significantly lower elasticity than uninfected swim-bladders ($df=22.04$, $t= 4.09$, $p <0.05$, Fig.2). No between site differences were evident in the infected populations (Dubh Lochan and Lough Neagh in either swim-bladder elasticity ($df=13.34$, $t= 0.54$, $p>0.05$) or rupture pressure ($df=9.34$, $t= -1.367$, $p>0.05$). In addition, there was no significant correlation between individual parasite load (parasite number) and either rupture pressure ($r=0.382$, $p>0.05$) or elasticity ($r=-0.08$, $p>0.05$).

The function of the swim-bladder rests on its ability to maintain space inside a fish and to vary the amount of gas according to changing hydrostatic demands (Hoar & Randall, 1971) For a fish, such as the eel, with reduced paired fins and thus only minimal ability to modify depth by forward motion, this function is of critical importance for the maintenance of position in the water column (Palstra *et al.*, 2007).

Elasticity of the swim-bladder wall is an essential element of its function and the importance of its elastic properties has been discussed in detail for cyprinids (see Alexander, 1959). The speed of expansion and contraction of the swim-bladder is closely related to the speed at which a teleost fish may modify its depth and still remain neutrally buoyant (Jones & Scholes 1984). The reduced elasticity and related to this the higher rupture pressure of swim-bladders from infected eels shown here is most likely the result of swim-bladder wall thickening resulting from scar tissue formation following perforation of the swim-bladder wall by the parasite and tissue scarring due to infection (Molnar *et al.*, 1993). The lack of correlation between parasite intensity and swim-bladder function suggests that even small parasite numbers may result in function loss. This might occur if for example scar tissue response to a migrating parasite moving laterally through swim bladder was as greater than one moving transversely through the swim-bladder wall. Recent telemetry studies on European eels during their oceanic migration to the spawning sites have reported dramatic diel vertical movements from 200-1000m in a 24 hour period (Aarestrup *et al.*, 2009). The reason for these vertical movements is not known but the importance of being able to regulate buoyancy efficiently is obvious, Marshall (1960) noted that swim-bladders of vertical migrants were highly elastic to aid such movements. The effect of reduced function of the swim-bladder reported here may impact the ability of infected eels to maintain buoyancy due to loss of elastic properties. Alexander (1966) noted that the less extensible the swim bladder, the lower the rate of change of buoyancy with depth of the fish. In the freshwater environment where the species is primarily benthic-living, swim-bladder function impairment may arguably have only minimal effect. During oceanic migration however it is very likely that migration may be inhibited due to swim bladder dysfunction (Palstra *et al.*, 2007) and loss of elasticity in the swim-bladder reported here may explain these previous findings. The results from this study coupled with documented reduced swimming performance in infected eel (Palstra *et al.*, 2007) points to the very real possibility that successful return migration to spawning sites in Sargasso Sea may be significantly compromised.

A.2.2 FIGURES & TABLES

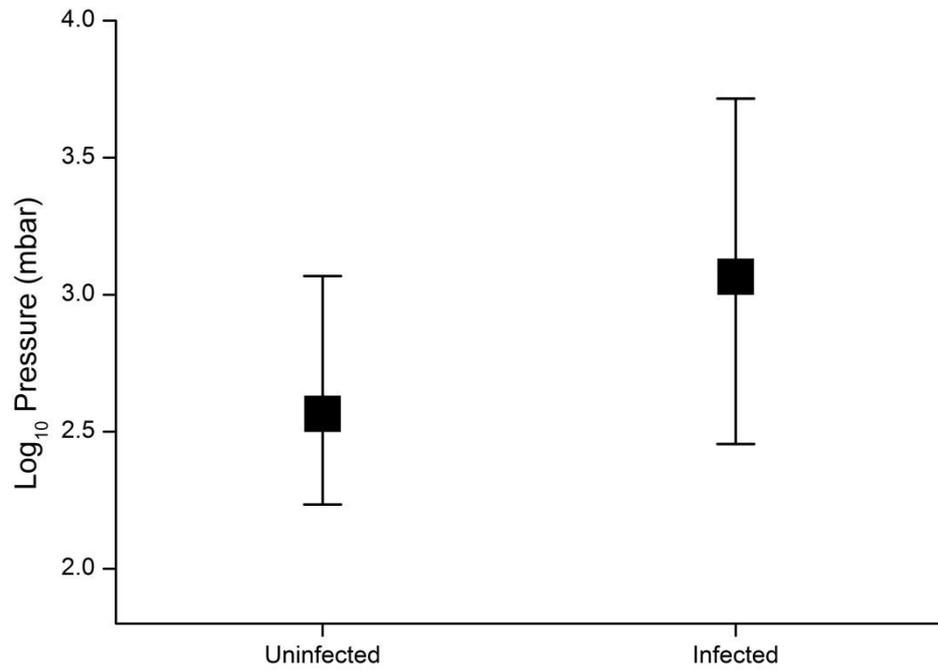


Fig. A2.1 The mean pressure (log transformed) at rupture of swim-bladder in eels, error bars show 95% confidence limit.

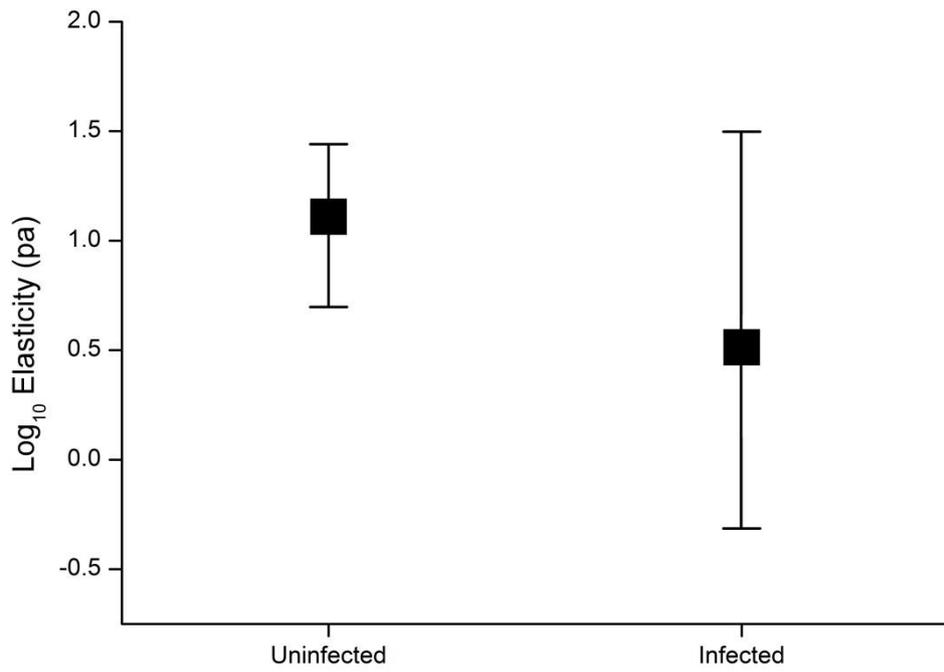


Fig. A2.2 The mean (error bars = 95% confidence limits) Elasticity (log transformed) in swim-bladders from eels; infected and uninfected

Appendix THREE

A.3.1 Local Scale, Coastal Currents Influence Recruitment to Freshwater Populations in the European Eel *Anguilla anguilla*: A Case Study from the Isle of Man.

J. Barry*, K. Mcharg[†], J.A. Dodd*, AND C. E. Adams*.

**Scottish Centre for Ecology & the Natural Environment, IBAHCM, University of Glasgow, Rowardennan, Glasgow, G63 0AW UK. † Department of Environment Food and Agriculture St John's Isle of Man IM4 3AS.*

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This study examines juvenile eel (<300mm) abundance in five study catchments on the Isle of Man. Fish abundance in similar growth habitat differed substantially between sites. Preliminary results suggest juvenile eel abundance is negatively correlated with increasing coastal current speed at river mouth entry ($t=-3.39$, $df=7$, $p<0.05$). These findings indicate that at least under some circumstances, tidally driven coastal currents may influence recruitment to freshwater habitats. It is presumed that high coastal current speed at the entry to river mouths may reduce the likelihood of freshwater entry.

Key words: European eel; coastal currents; abundance; recruitment

Major declines in recruitment of the European eel (*Anguilla anguilla* L.) glass eel life stage have been observed since the late 1970's and have led to growing concerns about long term viability of populations (Dekker, 2003). Recruitment trends have seen levels drop as much as 98% over three decades (ICES, 2013). Freshwater phase populations still remain at a critical level, with many thought to be around 10% of their size (yellow eel phase of their life cycle) compared to 30 years ago (Henderson *et al.*, 2012; Åström & Dekker 2007). The mechanisms underlying the collapse of populations in freshwater are not fully understood. Possible explanations include over-exploitation, climate change, habitat degradation, barriers to migration and diseases (Dekker, 2003). However in recent years there has been an increase in eel recruitment returning to continental waters, heightening the need for an increased understanding of the processes which may be affecting eel recruitment (ICES 2014). Oceanographic influences on eel recruitment are also poorly understood. Ocean current dynamics have been implicated in the recruitment collapse of eels (Baltazar-Soares *et al.*, 2014), but have also been linked with sustaining freshwater phase of eel populations in some locations (Adams *et al.*, 2013). Considerable variation in the density of eels in the freshwaters has been reported over relatively small geographic areas (Bark *et al.*, 2007), suggesting that local-scale processes (natural and anthropogenic) may influence local freshwater population recruitment. One potential factor which may influence recruitment to freshwater on a local catchment scale is the pattern of near-shore coastal currents, the strength of which is strongly affected by tidal influence (Ciccotti *et al.*, 1993; Gasceul 1986; Mcleave 1980). A recent review by Harrison *et al.*, (2014)

highlighted that although the general behaviour of juvenile eels in estuaries is reasonably well understood site specific factors are likely to play a significant role in determining finer scale distribution patterns. In this study we test the influence of the coastal currents and stream characteristics on juvenile eel abundance in freshwater populations.

The Isle of Man is a 572 km² island in the Irish Sea, it presents a relatively pristine habitat for eels (Isle of Man Government River Water Quality 2010; Isle of Man Government Water Quality Report 2005). The region has not suffered from widespread habitat disruption or changes in accessibility to freshwater nor any commercial exploitation of eel populations. The island is however subject to a relatively complex pattern of tidally induced local coastal currents (Wolf *et al.*, 2009) and rivers discharge into coastal areas with significantly different current speeds. This study collected data on the abundance of juvenile eel (<300mm; juvenile migratory stage sensu Tesch 2003) across the Isle of Man from catchments that differed in their exposure to coastal currents (see Table 1, Figure 1). Eel densities were calculated from data on eels of <300mm to exclude potential bias in density estimates arising from older eels (greater than 300mm) entering the freshwater system from saline or estuarine environments (Bark *et al.*, 2007; Arai *et al.*, 2006; Harrod *et al.*, 2005). Eels were collected from five catchment sites, the River Sulby, River Neb, Lhen trench Silverburn and River Dhoo (Figure 1. Table 1) Fish were collected in May and June 2010 by electric fishing. Eel specific electric fishing methods (as outlined by Knights *et al.*, 2001) were followed, particularly including a minimum of three passes per site and slow progression up the survey stretch. To ensure that small eels were sampled adequately, 3mm stop nets were deployed at the upper and lower extent of sample site. Electric fishing sites comprised 100m of linear river length that contained juvenile habitat features outlined by Laffaille *et al.* (2003) & Domingos *et al.* (2006), particularly areas with gravel/pebble substrate with a large amount of riparian cover and channel vegetation. In each catchment, two survey sites were sampled and the density of juvenile eels per m² was estimated from 3 pass sampling in each site using the Zippin removal method (Zippin, 1958). Considerable care was taken to ensure similar juvenile habitat was sampled to avoid potential habitat specific bias and to allow valid comparison of density estimates between rivers. Elevation profile of study

sites and distance to sea were calculated using elevation and path tools in Google Earth software (Google Earth, 2014; Potere, 2008; Gorokhovich & Voustianiouk 2006). Current speed information was obtained through publicly available resources. The data obtained from DTI Atlas of UK Marine Renewable Energy Resource (Atlas of UK Marine Renewable Energy Resources 2015) has been developed by the UK Department for Business, Enterprise and Regulatory Reform (BERR), the underlying Marine Atlas providing very high quality current data is now available through web interface. The Geographic Information System (GIS) data layers downloadable from the web interface were interrogated in ArcGIS and current speeds mapped (Figure 1). The Atlas provides mean spring and neap tide velocity magnitude and water depth, the Marine Atlas data was interrogated at the specific cells of interest to obtain a mean tidal flow over neap and spring tides. Although tides are highly variable, the methodology presented represents a consistent means of obtaining current flow data at the sites of interest. Current speed results were then compared with manipulated admiralty chart data (Isle of Man Government; Tidal Streams 2014) and the openly available, Norwegian Meteorological Resource which utilises Regional Ocean Modelling System (Meteorological Institute 2014) to ensure accuracy of these data.

To investigate the potential factors affecting juvenile eel recruitment to Isle of Man rivers eel density was examined with respect to five variables; catchment size (the area of land conveying water to the water course within which the site was located), sampling site (two sites per river), elevation, distance of sampling site from estuarine entry, depth at discharge point and mean current speed (mean over spring and neap tides) at discharge point. Sampling site was nested within catchment as random variables to account for pseudo-replication and spatial autocorrelation respectively in a linear mixed model. To investigate the potential factors affecting mean population length, a similar model was investigated using the same five variables. All analyses were performed using R statistical software 3.1 (R Core Team 2014) and the associated package “*nlme*” (Pinheiro *et al.*, 2014) provided the platform for model analysis.

A minimum adequate model was generated by process of significance testing between models (using Akaike Information Criterion method), and sequential

backward elimination of non-significant terms namely elevation profile ($p=0.7186$) distance to sea ($p=0.5191$) and depth at discharge point ($p=0.7660$). The minimum model contained only a significant negative effect of current speed at discharge point on measured eel density ($t=-3.39$, $df=7$, $p=0.0115$) indicating that as current speed at the mouth of the river increased the density of eels recorded in that catchment decreased (Figure 2). Using the same analytical procedure, population mean fish length at each site showed no significant relationship with any of the explanatory variables used in the model ($t=-0.512$, $df=7$, $p=0.624$).

Glass eels have been noted to sustain swimming for only very short periods in water velocities greater than 30 cm s^{-1} (Adam *et al.*, 2008) in addition glass eels are believed to drift in the water column making them potentially vulnerable to near shore coastal currents (McCleave & Kleckner 1982). Glass eels entering coastal waters from the north Atlantic are thought to use tidal currents as a low energy passive migration mechanism to reach the marine/freshwater interface (Creutzberg, 1958). It is generally accepted that eels utilise “Selective Tidal Stream Transport” described by various authors to aid movement through estuarine systems (McCleave and Kleckner 1982; Gascuel 1986). However the mechanisms and behaviour of juvenile eels utilising tidal currents on approach to estuaries are poorly understood.

The catchments investigated in this study (Figure 1) are characteristic of small to medium watersheds (Isle of Man Government River Water Quality 2010, see Table 1). To test for an effect of the reported decline in eel density with increasing elevation and distance from the tidal limit (Aprahamian *et al.*, 2007) these variables were used to predict eel density. Neither showed a significant effect (elevation: $p<0.05$; distance from tidal limit $p<0.05$). The European eel has an extremely well developed sense of smell and it has been hypothesised that certain odours and environmental stimuli attract eels to freshwater systems (Tesch 2003). Glass eels arriving from the open ocean will not have any previous experience of scents contained in freshwater and therefore the ability to distinguish these scents and odours within the sea water medium must be instinctive. However the mechanisms through which odours affect eel behaviour are unclear. Given that scent is thought to be an important factor in determining freshwater entry (Tosi & Sola 1993; Tesch, 2003), the correlation

between catchment size and freshwater discharge implies that larger catchments could potentially attract more eels through the larger plume of freshwater odour stimuli. This study has shown no significant effect of either catchment size or depth at discharge point on juvenile eel density. In contrast the results of this study show that coastal current speed is an important factor and one possible mechanism influencing the recruitment of juvenile eels to freshwater. Here higher recruitment to freshwater was predicted by with lower coastal current velocities in the vicinity of the river discharge point. Recent studies have highlighted the site specific nature of migratory behaviour in glass eels (Harrison *et al.*, 2014) strongly suggesting the importance of local scale features in determining eel entry to freshwater.

The results from this case study suggest that tidally driven coastal currents in close proximity to marine/freshwater interface may at least at some sites have a significant role in determining eel recruitment to, and therefore abundance in freshwater. A better understanding of how local coastal current speed may be influencing migratory behaviour is needed to improve models of glass eel recruitment across different estuaries (Harrison *et al.*, 2014). This study shows that coastal currents, a catchment level factor have the potential to affect fine scale distribution patterns of eels in freshwater. From a management perspective, the development of stock recruitment models rely on estimating key population parameters of each life history stage and the factors which affect each stage. A fundamental understanding of the factors influencing juvenile eel abundance is therefore essential to inform management decisions. This study indicates that the influence of coastal currents should be considered in management programmes for this endangered species.

A.3.2 FIGURES & TABLES

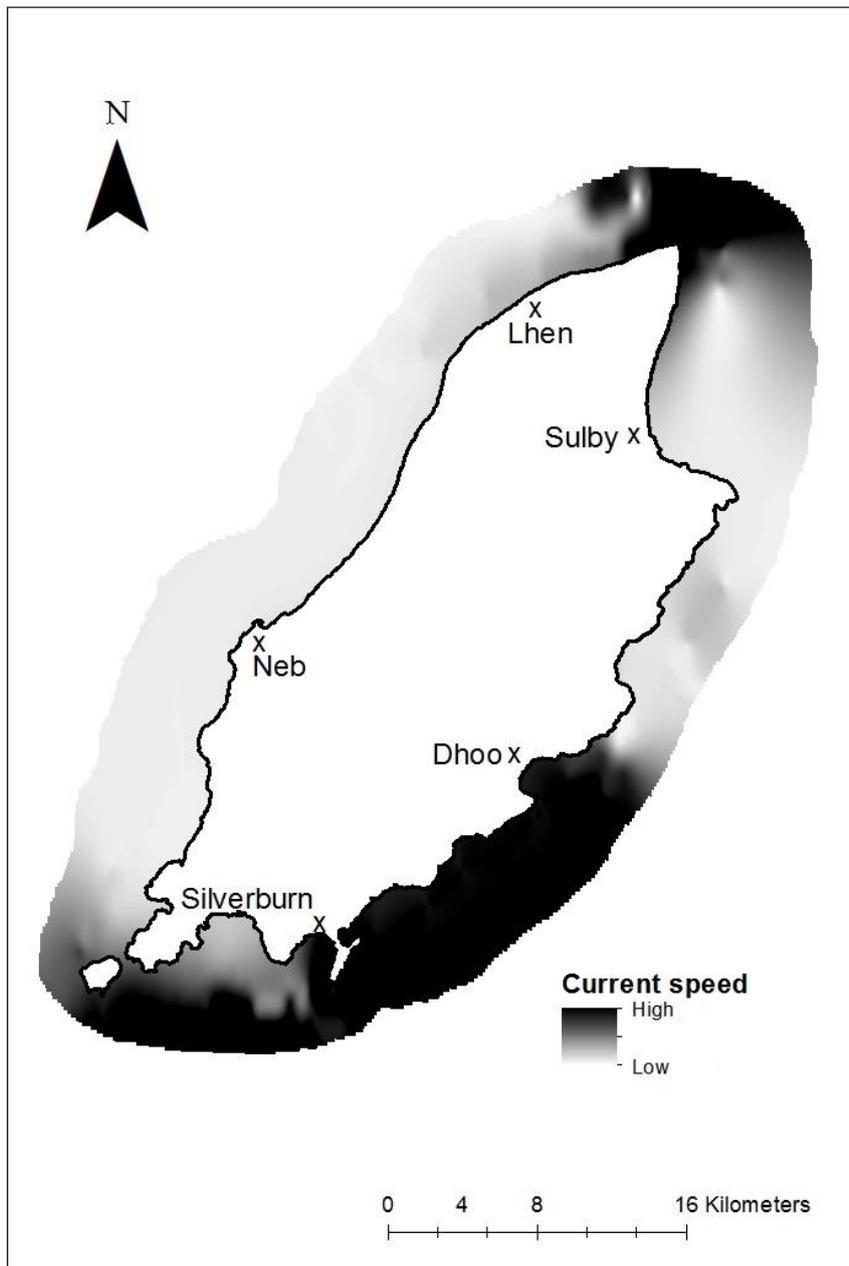


Fig.A3.1: Location of test catchment in the Isle of Man, currents strength denoted by coloured gradient ramp, derived from Atlas of UK marine renewable energy resources (2014).

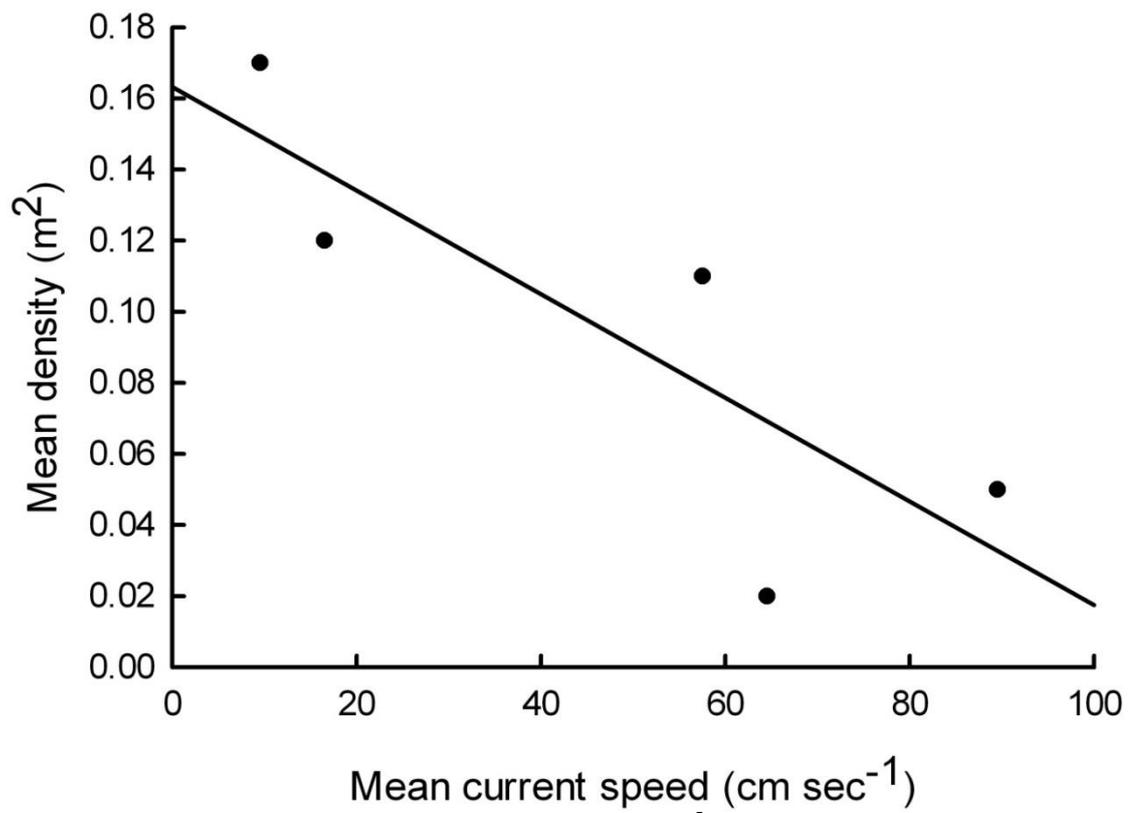


Fig. A.3.2: Relationship between mean density per m² of juvenile eel in test catchments and mean current speed encountered at river mouth entry. ($p < 0.05$)

Table A3.1: Physical variables in test catchments.

River Catchment	Geographical location (Lat (N) Long (W))	Elevation (m) Site 1,2	Distance from Sea Site 1,2	Current speed (cm/s \pm S.E)	Depth (m) (1km from sea entry)	Mean Length (cm \pm S.E)	Mean Density (number/m ² \pm S.E)
Sulby	54°19' 4° 22'	1)20 2)10.9	1)3200 2)2012	9.5 \pm 4.5	15	15.65 \pm 0.69	0.17 \pm 0.00
Neb	54° 13' 4° 41'	1)33.5 2)37.7	1)1600 2)2130	16.5 \pm 12.5	18	20.43 \pm 1.23	0.12 \pm 0.04
Dhoo	54° 08' 4° 28'	1)30 2)27.2	1)2360 2)1780	64.5 \pm 19.5	15	19.70 \pm 0.85	0.02 \pm 0.00
Lhen trench	54° 23' 4° 29'	1)7.29 2)10.6	1)1300 2)2200	57.5 \pm 2.5	17	16.95 \pm 2.66	0.11 \pm 0.01
Silverburn	54° 04' 4° 38'	1)13.8 2)25.9	1)1004 2)2750	89.5 \pm 27.5	18	20.11 \pm 1.54	0.05 \pm 0.05

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