Ecological and recreational interactions of the native pike *Esox lucius* and the invasive pikeperch *Sander lucioperca* in England

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ABSTRACT

In England, freshwater angling is an important recreational pastime with substantial socio-economic benefits, but is also a major introduction pathway for non-native fishes. As recreational anglers often prefer targeting large-bodied fishes, introductions of non-native species have become an integral part of fisheries management practices to diversify angler opportunities and increase satisfaction. However, these introductions were often completed without full understanding of their ecological consequences, including their potential to develop invasive populations. To ensure management and policy measures improve the angling experience without resulting in negative ecological consequences, it is important to understand the ecological role of introduced non-native fishes and their interactions with native species. Of equal importance, however, is understanding angler motivations and behaviours in their choice of angling for non-native fishes, and their perceptions of the consequences of their activities, particularly when catch-and-release practices are widespread.

Pikeperch *Sander lucioperca* were introduced into open waters in England in the 1960s and subsequently established populations that dispersed through many river catchments. Due to their piscivory and correspondingly high trophic positions, their ecological impacts on prey fish populations are often considered, but their interactions with and potential impact upon native large-bodied piscivorous fish remain relatively poorly understood. Here, the ecological interactions of the native pike *Esox lucius* and the invasive pikeperch in England were quantified, including their life history traits, size-structured feeding relationships, and their trophic and spatial interactions. For anglers who exploit these species, their recreational interactions were assessed, including their behaviours in relation to their catch-and-release activity, and their motivations and perceptions in relation to their angling experience.

The results demonstrated that the expression of pikeperch life history traits vary spatially, and may be explained partially by latitude. Stable isotope analysis (SIA) revealed that tissues collected non-destructively can be reliably applied to diet assessments in piscivorous fish and are a useful tool in providing assessments of size structured feeding relationships between native and invasive piscivorous fishes. Assessments of ontogenetic dietary shifts on the trophic position and niche size of pike and pikeperch revealed a switch to piscivory at smaller body sizes in pikeperch and a partitioning of resources across both insectivorous and piscivorous life stages in both species. Additionally, the presence of marine resource pathways from angling baits and anadromous fishes to the diet of pike were revealed to be as a function of their spatial availability, pike body size, and individual trophic specialisations. A telemetry study revealed movement variability within species and that increased movement was associated with spawning for both pike and pikeperch, and highlighted the potential importance of limited off-channel habitat in a channelized lowland river which was important to pike all year and to pikeperch in winter and spring.

Qualitative interview and quantitative survey methods found that the invasive pikeperch is a valued fishery target species, with the experiences of anglers targeting non-native species influencing their perceptions on the ecological impact of introductions, such that they were seen as not causing adverse ecological impact. Additionally, angler conservation values towards native fishes were also reflected in their behavioural safeguarding of pikeperch populations, especially catch-and-release practices that are contrary to current regulations on pikeperch, such that 94% of surveyed predator anglers reported to always adopting catch-and-release practices for pikeperch despite it being illegal in England to release the species back into open waters after capture.

In conclusion, these results suggest that there remains a considerable disjuncture between the views of many recreational anglers and the underlying legislation governing the introduction and keeping of non-native fishes and that for species such as pikeperch, their integration into native fish communities and widespread dispersal requires management measures that consider their ecology, ecological impacts and angling value.

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Author’s declaration

I (ETN) confirm that the research presented within this thesis is my own.

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1 Introduction

1.1 Overview

The focus of this introduction chapter is to present the main concepts and to outline the rationale of the research, the study species, the study system and the aims and objectives. Following this, data chapters (Chapters 2 to Chapter 8) are presented and the thesis is concluded with Chapter 9 which discusses the implications of the research. The data chapters are presented according to an integrated thesis format whereby each chapter stands as an original and complete piece of research. They are presented as either the actual published peer-reviewed paper or as a manuscript suitable for submission to a journal. This format has been chosen as it provides flexibility around the types and numbers of papers that could be included in the thesis. Note, however, that the figures and tables are listed sequentially throughout the document and a reference list is only provided at the end of the thesis in order to improve the readability of the thesis and to avoid the repeated citing of some references.

1.2 Freshwater angling and sustainable fisheries management

Across industrialised countries, participation in recreational fishing is at approximately 10.5 % of the total population (Arlinghaus et al. 2015), where the definitions of recreational fishing cover any fishing of aquatic resources that are not sold or otherwise traded (Arlinghaus and Cooke 2009), are not essential for survival (Cooke, Arlinghaus, et al. 2016) and as a goal-orientated behaviour to meet individual satisfaction needs (Manfredo et al. 1996, Arlinghaus and Cooke 2009). Freshwater recreational, or ‘sport’ fishing is primarily by rod and line methods and is thus often referred to as angling, where a large proportion of the catch is released ‘catch-and-release' (Arlinghaus et al. 2007). Participation in freshwater angling can have considerable socio-economic benefits with, for example, it involving the licensing of over one million anglers per year in England and Wales who contribute approximately £1.2 billion to the economy (Mawle and Peirson 2009, Winfield 2016). Moreover, there are a range of social, cultural and health benefits derived from angling which make the activity important for human well-being (Hickley and Tompkins 1998, Arlinghaus and Cooke 2009, Parkilla et al. 2010).

Recreational freshwater fisheries are extensively managed to increase angler satisfaction and this management activity should also safeguard fish stocks and ensure sustainable exploitation (Cowx 1998, Arlinghaus et al. 2002, Post et al. 2002, Cowx and Gerdeaux 2004). However, recreational angling activities are responsible for substantial impacts on freshwater aquatic resources through, for example, the over-exploitation of fish stocks, habitat destruction and the introduction of non-native species (Post et al. 2002, Cooke and Cowx 2004, Cooke, Hogan, et al. 2016). Effective fisheries management thus require both the human and ecological dimensions of recreational fisheries to be considered as complex, coupled social-ecological systems (Fenichel et al. 2013, Hunt et al. 2013, Arlinghaus et al. 2016, Winfield 2016). A major obstacle is, however, a lack of consideration of angler dynamics in reconciling recreational fishing activities with their potential conservation consequences (Arlinghaus 2006a). This is surprising considering that the future of recreational angling is dependent upon sustainable management practices (Arlinghaus et al. 2016), which in turn is dependent on angler buy-in to issues of conservation concern (Cowx et al. 2010).

1.3 Introductions of non-native fish

A frequent management goal in freshwater fisheries is to diversify angling opportunities, with this often achieved through the movement or transfer of non-native fishes (Hickley and Chare 2004). Globally, enhancing angling with non-native fish has been responsible for approximately 12 % of all fish introductions (Gozlan, Britton, et al. 2010) and in England, a demand in the angling sector for capturing non-native fish has led to an increase in the frequency and occurrence of introductions (Copp et al. 2010). Introductions of non-native fishes are often made without full understanding or recognition of the risks they may pose (Cucherousset and Olden 2011) and their potential threat to native biodiversity (Gozlan, Britton, et al. 2010). Such introductions can, for example, result in the establishment of invasive populations (Britton, Cucherousset, et al. 2010, Gozlan, Britton, et al. 2010). Invasion is defined as a process in which an introduced species has established populations that spread rapidly and pose a risk to native species (Gozlan, Britton, et al. 2010). Although only a minority or introductions may become invasive, management measures to minimise their dispersal and impacts pose significant challenges (Britton et al. 2011, Oreska and Aldridge 2011).

A feature of many of these introduced fishes for angling enhancement is their large body size and relatively high trophic position that results from their piscivory (i.e. their predation upon other fishes) (Eby et al. 2006), which have the potential to cause substantial shifts in food-web structure via top-down mechanisms (Eby et al. 2006, Nowlin et al. 2006, Pelicice and Agostinho 2009). Angler preferences for catching fish of large body sizes to meet specific catch motivations (Beardmore et al. 2014) has resulted in both regulated and unregulated releases of large bodied, non-native predatory fishes (Hickley and Tompkins 1998, Elvira and Almodóvar 2001, Banha et al. 2017). Examples of species that have been moved specifically for angling enhancement globally include Peacock basses of the *Cichla* genus (Britton and Orsi 2012), European catfish *Silurus glanis* (Copp et al. 2009, Cucherousset et al. 2017) and largemouth bass *Micropterus salmoides* (Britton, Harper, et al. 2010). These introductions have been associated with the local extirpation of native species and changes to the functioning and structure of invaded freshwater ecosystems (Pelicice and Agostinho 2009, Juette et al. 2014, Pereira and Vitule 2019)

1.4 Pikeperch *Sander lucioperca*

In England, an example of a large-bodied, piscivorous non-native fish that has been introduced into a number of regions for angling enhancement is pikeperch *Sander lucioperca*. (referred to as zander by British anglers). Pikeperch has a native range extending throughout much of Europe, from Germany in the West to Central Russia in the East (Figure 1, Maitland 2004), with their invasive range now including France, Spain, Portugal and Great Britain Figure 1, Elvira and Almodóvar 2001, Kopp et al. 2009, Ribeiro et al. 2009). This species was first introduced into Britain in the late 19th Century, restricted to enclosed ponds (Sachs 1878) until they were released into the River Great Ouse relief channel in Eastern England in the 1960s (Figure 1, Wheeler and Maitland 1973). Here, their colonisation and dispersal through river systems was rapid (Linfield and Rickards 1979, Fickling and Lee 1983, Hickley 1986), with the resulting invasion of many river basins in central and southern England, including the Trent, Severn and Thames basins, and much of the canal network (Figure 1, Copp et al. 2003, Nunn et al. 2007).

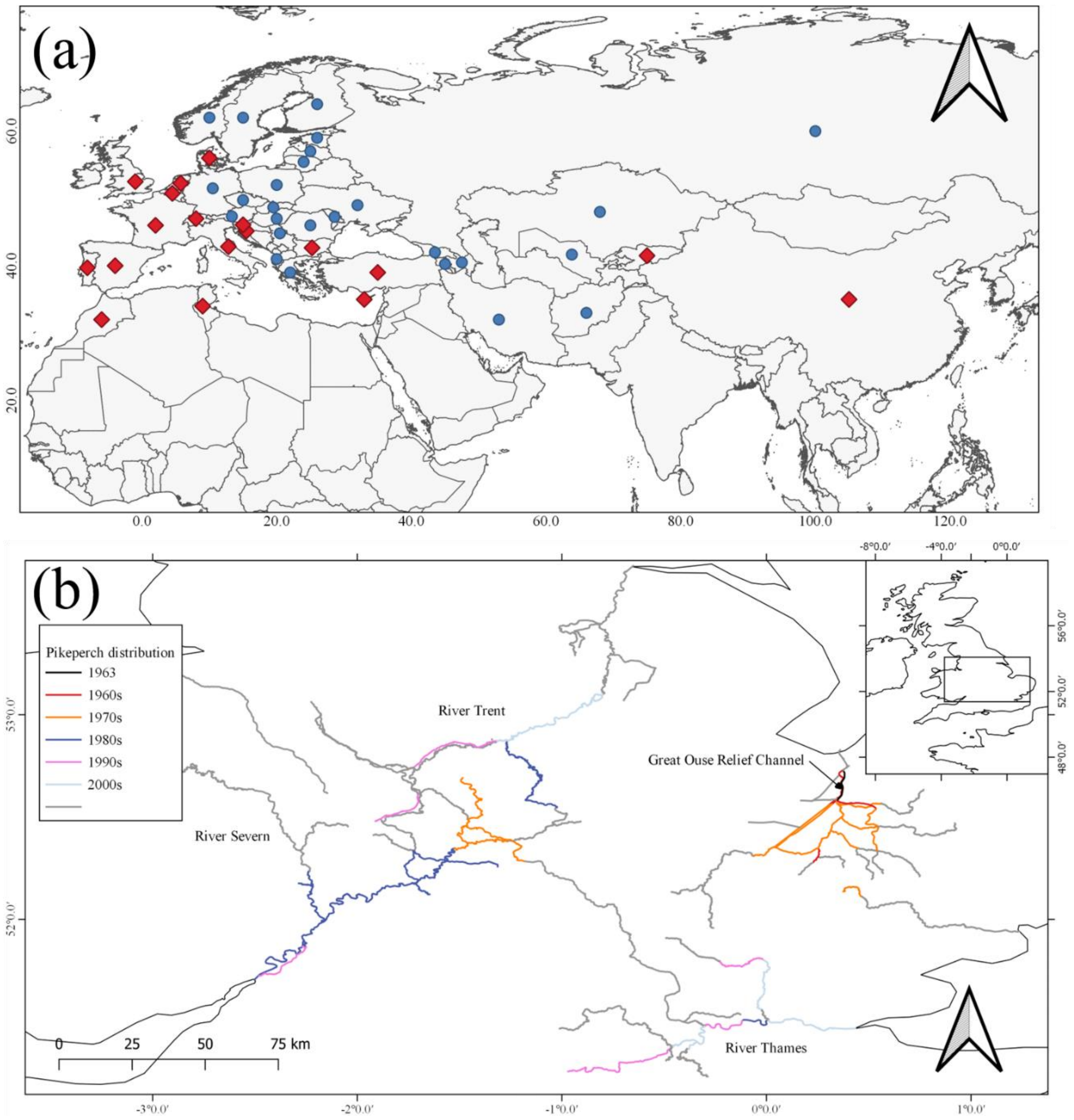

Figure 1. Distribution of pikeperch *Sander lucioperca* in (a) their native (blue circle) and non-native (red triangle) ranges across Eurasia, data from Fishbase.org (Froese and Pauly 2018), and (b) in English rivers and canals where colour corresponds to known dates of introduction (Wheeler and Maitland 1973, Linfield and Rickards 1979, Fickling and Lee 1983, Hickley 1986, Smith 1998, Copp et al. 2003, Nunn et al. 2007). It should be noted that the shown distribution of pikeperch in England is nonexhaustive and the extent of their distribution within the grey highlighted rivers and canals is unknown to the author.

During their colonisation period, studies tended to focus on the potential ecological impact of increased predation pressure to native fish communities (e.g. Linfield and Rickards 1979, Fickling and Lee 1983, Hickley 1986, Smith 1998, Smith et al. 1998). It was generally perceived that pikeperch posed a significant ecological risk due to their potential for deleterious impacts on the abundance and structure of prey populations, with anglers encouraged to kill any captured pikeperch, and removal operations by fisheries management agencies being common (Hickley 1986, Smith et al. 1997). However, given the propensity of anglers to enjoy angling for large-bodied piscivorous fish (Cowx 1994, Hickley and Chare 2004), then rather than assisting with their control, anglers were more likely to have facilitated pikeperch dispersal through illegal translocations (Hickley and Chare 2004).

Pikeperch are among the top predators in many freshwater systems and as a direct result of their predation can have major impacts on the population dynamics of prey (Persson et al. 1991, Dörner et al. 2007), with their introductions having the potential to have severe and long lasting effects (Nilsson 2001). In addition to these direct impacts, the responses of prey populations to pikeperch introduction include a variety of behavioural and phenotypic changes that result from the predator-induced modification of prey traits, including decreased foraging activity and a shift in habitat selection (Hölker and Mehner 2005, Hölker et al. 2007). In addition, the response of resident piscivorous fishes to pikeperch introduction can consist of complex interactions that include indirect effects of the trait mediation of prey species (Schulze et al. 2006).

1.5 Ecological interactions of native and invasive piscivorous fishes

Predictions that indicate whether an introduced species is likely to develop an invasion are fundamental to their risk-based management (Copp et al. 2014, 2016). For example, the expression of life history traits can help explain invasion patterns and processes (Vila-Gispert et al. 2005, Olden et al. 2006), while trophic interactions and activity patterns between native and invasive fishes can be important for predicting the ecological consequences of invasions (Guzzo et al. 2013, Britton et al. 2019) and in revealing the adaptability of sympatric native and invasive species to anthropogenic changes (Capra et al. 2018). In Britain, the only native large-bodied obligate piscivorous fish is the Northern pike *Esox lucius* ('pike' hereafter, Figure 2(b)). However, the extent of the interactions of native pike and invasive pikeperch is largely unknown.

Figure 2. (a) pikeperch *Sander lucioperca* and (b) pike *Esox lucius* caught from the lower River Severn, Western England. Pike image used with permission from Paul Thomas

Invasive fishes have a combination of characteristics that determine their success, including their life-history traits and adaptability (Ribeiro et al. 2008). Populations of species outside of their native range can show increased growth rates but smaller asymptotic sizes due to climatic conditions that are suboptimal for growth (Vilizzi and Copp 2017). The ability of native and non-native fishes to coexist is facilitated by trophic plasticity that enables their diets to become more specialised when in sympatry, thus avoiding competitive interactions via resource partitioning, including the segregation of food resources and/or habitat (Schulze et al. 2006, Comte et al. 2016, Guzzo et al. 2016). For pike and pikeperch, competitive interactions are more complex, given that their early life-stages are insectivorous before switching to piscivory (Mittelbach and Persson 1998) and that their predator-prey interactions are size-dependent (Nilsson and Brönmark 2000, Dörner et al. 2007). Additionally, individual trophic specialisation is a common feature of many piscivorous fishes, including pike, whereby the population trophic niche consists of smaller sub-sets of individuals specialising their diet on specific resources or energy pathways (Beaudoin et al. 1999, Bolnick et al. 2002), that can be independent of body size and growth (Nyqvist et al. 2012). The adaptability of invasive piscivores can also extend to their foraging and spawning behaviour such that they may be less likely to be affected by habitat degradation, increasing temperatures or fragmentation in comparison to native fishes (Capra et al. 2018).

1.6 Angler behaviour, perception, and management

As recreational angling is a key introduction pathway for non-native invasive fishes, it is important to understand the behaviours, motivations and perceptions of anglers that contribute to these introductions (Banha et al. 2017, Rees et al. 2017). In addition to angler releases of pikeperch into open waters in England (Hickley and Chare 2004), pikeperch fishing in England is also likely to be based on catch-and-release practices (i.e. fish are returned alive to the water following capture), despite a regulatory framework that makes it illegal to release captured pikeperch back into open waters (Hickley and Chare 2004). Motivated by different aspects of the angling experience, anglers can have divergent opinions relating to catch-and-release practices (Aas et al. 2002) with these differences often resulting in behavioural conflicts (e.g. Arlinghaus 2007). For example, anglers specialising on fishing for large-bodied predatory fishes can be defined as ‘specialist’ anglers, where their focus is on catching a particular species or on catching a large individual ‘specimen’ or ‘trophy’ fish (Eden and Bear 2011). For specialist anglers, catch motivations are considered among the most important drivers of angler behaviour (Beardmore et al. 2011) and are seen to be a significant determinant of angler satisfaction (Arlinghaus 2006b, Beardmore et al. 2014). When anglers are more generalist in their fishing behaviour, such as ‘match’ anglers, who compete against others in an attempt to catch the largest weight of fish in a given period or ‘pleasure’ anglers, where the overall fishing experience is important (Eden and Bear 2011), then releases of predatory species may be in conflict with their fishing motivations.

In addition, emerging research on perceptions can be used for assessing, informing, and gauging support for conservation initiatives and policy (Gelcich and O’Keeffe 2016). Indeed, assessments of angler perceptions relating to introductions have been successfully used for optimizing awareness campaigns (Lindgren 2006) and improving management and governance (Boone and Ryder 2017). In the UK, angler perceptions on the ecological threat of non-natives were found to be based on a perceived threat to their angling activity rather than on the greatest ecological threat (Gozlan et al. 2013). Therefore it is essential to further understandings on the behaviour of specialist predator anglers, particularly in relation to catch-and-release, to understand their values and motivations and their perceptions of the ecological consequences of pikeperch introduction.

1.7 River Severn basin, Western England

The River Severn basin in the west of England has been characterised by two major introductions of non-native fish in the last 60 years, European barbel *Barbus barbus* and pikeperch. The translocation of the non-indigenous barbel involved the release of 509 fish into the middle reaches of the Severn in 1956, with these fish taken from the River Kennet (Thames basin) (Antognazza et al. 2016). These fish subsequently established and have since dispersed throughout the basin (Gutmann Roberts et al. 2017). Pikeperch introduction into the River Severn basin was most likely a result of illegal stocking, and have been present in the River Severn for over 40 years (Hickley 1986). Thus, the Severn basin provides a strong model system for studying invasions of relatively large-bodied non-native fishes. The Severn basin catchment also provides natural variability in habitat typologies with tributaries (e.g. the Warwickshire Avon) and impounded/ non-impounded sections providing natural experimental scenarios (Amat Trigo et al. 2017). In the lower River Severn and Warwickshire Avon, both pike and pikeperch exist in sympatry, along with barbel, plus other cyprinid species including chub *Squalius cephalus*, roach *Rutilus rutilus*, common bream *Abramis brama* and perch *Perca fluviatilis*. The piscivorous pike and pikeperch are popular target species for angling, with the British rod caught record of pikeperch being caught from the lower Severn weighing approximately 10 kg (Angling Trust 2018). These river sections provide a novel opportunity to study the population dynamics and ecology of co-existing native and invasive predatory fish within a diverse fish community. In conjunction, the rivers as also provide access to an important pikeperch and pike fishery and the opportunity to understand the behaviours, motivations and perceptions of anglers who target for these fishes, providing fundamental insights into the social ecological dynamics of recreational freshwater fisheries.

1.8 Aims and Objectives

The research aim is to quantify aspects of the ecology of invasive pikeperch in England and their interactions with the native pike in both an ecological and recreational angling context. The objectives are to test differences in their ecological and behavioural traits, and their role in recreational fisheries. The invaded lower River Severn basin is used as the primary study area. The exceptions of this are in Chapter 2, where pikeperch populations are compared across their native and invasive ranges, Chapter 3, where the diet of pikeperch is quantified from the Grand Union Canal, and Chapter 8, where angler behaviours, motivations and perceptions are investigated across England. Each data chapter has its own set of aims and objectives, as follows:

Chapter 2: to determine the spatial patterns and drivers of pikeperch growth by synthesising data on their somatic growth rates from across their native and invasive ranges via a combination of field study and literature review.

Chapter 3: to develop non-destructive sampling techniques for dietary assessments of fishes that are important to recreational catch-and-release fisheries by comparing stable isotope signatures across multiple tissues and to stomach contents analysis.

Chapter 4: to assess the influence of ontogenetic dietary shifts on the trophic interactions of native and non-native freshwater piscivorous fishes by assessments of isotopic niche size and position across insectivorous and piscivorous life stages of both pike and pikeperch in an invaded river catchment.

Chapter 5: to predict the contributions of novel marine prey resources from angling and anadromy to the diet of pike across varying size classes and locations using stable isotope analysis

Chapter 6: to assess the activity patterns and habitat use of native and non-native piscivorous fish in a channelized lowland river by a telemetry study of pike and pikeperch in the lower River Severn.

Chapter 7: to evaluate angler behaviours and motivations and how they translate into behavioural practices and perceptions concerning the management and regulation of native and invasive predatory fish, particularly in relation to their catch-and-release activities by in-depth interviews with anglers of the River Severn catchment, Western England.

Chapter 8: for anglers that target native and invasive predatory fishes in England to evaluate their behaviours, motivations and perceptions of the ecological impact and management of pikeperch and in relation to different levels of angling commitment, experience and behaviour, assessed through targeted surveying techniques.

Chapter 9 then provides a synthesis of the main findings of Chapters 2 to 8.

2 Variability in the somatic growth of pikeperch *Sander lucioperca*, an invasive piscivorous fish

2.1 Abstract

Introduced fishes can develop invasive populations that impact native species and ecosystems. Understanding the population ecology of introduced species in their extended ranges and how this compares to their native ranges is therefore important for informing their management. Here, the age and somatic growth rates of the piscivorous freshwater fish pikeperch *Sander lucioperca* were analysed across their invasive and native ranges to determine their spatial patterns and drivers. Analyses were initially completed in their invaded range in central and western England with populations varying spatially in their growth rates being slowest for a population in a narrow and shallow canal and fastest in a large, impounded lowland river. A meta-analysis of parameters of the von Bertalanffy growth model then revealed that across their native and invasive ranges, their theoretical ultimate lengths ($L\infty$) and growth coefficients (K) were significantly related to latitude, but not longitude. Their relationships with latitude were non-linear, with higher values of $L\infty$ and lower values of K being evident towards their northerly and southerly range limits. Faster growth rates were evident in the middle of their range (45 to 55 °N), suggesting temperatures here were most optimal for growth, but were in a trade-off with reduced ultimate lengths. These spatial patterns suggest that whilst introduced pikeperch can colonise new waters across a wide area, the expression of their life history traits will vary spatially, with potential implications for how invasive populations establish and integrate into native fish communities.

2.2 Introduction

Introductions of non-native fishes can potentially result in the establishment of sustainable populations that naturally disperse and invade (Gozlan, Britton, et al. 2010, Cucherousset and Olden 2011). Whilst only a small proportion of introduced fishes develop invasions, these fishes can have substantial impacts on native species (Gozlan, Andreou, et al. 2010, Gozlan, Britton, et al. 2010). For piscivorous fishes, impacts tend to be via predation with, for example, invasive largemouth bass *Micropterus salmoides* and peacock basses of the *Cichla* genus having deleterious impacts on native species richness and fish abundance (Gratwicke and Marshall 2001, Pelicice and Agostinho 2009). Managing the impact of invasive fishes in open systems is challenging (Britton et al. 2011), so predictions that indicate whether an introduced species will develop an invasion are fundamental to their management (Copp et al. 2014, 2016). Spatial assessments of somatic growth rates assist these predictions (Britton, Harper, et al. 2010), especially as growth rates can be a strong proxy of other life history traits (Oyugi et al. 2011). The expression of life history traits can help to explain invasion patterns and processes for a number of non-native species (Vila-Gispert et al. 2005, Olden et al. 2006), particularly when related to abiotic parameters (Benejam et al. 2009). These patterns have also helped highlight the regions that are most vulnerable to invasion (Ribeiro et al. 2008, Cucherousset et al. 2009).

Pikeperch *Sander lucioperca* is a large-bodied piscivorous freshwater fish with a native range extending throughout much of Europe, from Germany in the West to Central Russia in the East (Maitland 2004). The major driver of pikeperch introductions and translocations has been the diversification of fish assemblages to increase sport angling opportunities (Hickley and Chare 2004). Their popularity for angling has resulted in a series of regulated and unregulated releases across Western Europe, with their invasive range now including France, Spain, Portugal and Great Britain (Elvira and Almodóvar 2001, Kopp et al. 2009, Ribeiro et al. 2009). In Britain, the first recorded pikeperch introduction was in 1878, when individuals of German origin were stocked into enclosed waters in the East of England (Hickley 1986). Subsequent translocations to Eastern England occurred during the 1960s (Wheeler and Maitland 1973), and it was these releases that lead to their establishment and invasion (Linfield and Rickards 1979, Hickley 1986, Copp et al. 2003). Reports of anglers capturing individuals from other catchments became widespread throughout the 1970s (Wheeler 1974, Hickley 1986), with self-sustaining populations now present throughout central and western England (Smith et al. 1998, Copp et al. 2003, Nunn et al. 2007).

Latitude can have a significant influence on the life history traits of freshwater fishes (Blanck and Lamouroux 2007), mostly via spatial differences in temperature and light intensity (Heibo et al. 2005, Rypel 2012). Consequently, latitude is often used as an explanatory variable in assessments of life history trait variation over large spatial scales.

This includes fishes in their European invasive range, where growth rates for invasive fishes tend to significantly decrease with increasing latitude (Benejam et al. 2009, Cucherousset et al. 2009). Although used less often, assessments of longitudinal variability in growth rates can also provide insights into how growth varies spatially (Britton et al. 2013). For pikeperch, many studies have been completed on their life history traits, including growth rates (e.g. Błaszczyk 2000, Copp et al. 2003, Ablak and Yilmaz 2004, Ložys 2004, Argillier et al. 2012). However, these studies have been primarily associated with stock assessment and aquaculture (e.g. Nyberg et al. 1996, Balik et al. 2004, Nyina-wamwiza et al. 2005, Özvarol and İkİz 2008). There has been much less focus on their spatial variability in growth parameters (Milardi et al. 2011, Pérez-Bote and Roso 2012), and how their age range and somatic growth rates might vary across their native and invasive distributions. This is despite the ecological and management utility of these data for assisting invasion risk assessments across their invasive range (Copp et al. 2014, 2016).

Consequently, the aim here was to synthesise data on pikeperch somatic growth rates from across their native and invasive ranges via a combination of field study and literature review. To initially test how invasive pikeperch growth rates vary between populations at small spatial scales, a field study focused on invasive populations in central and western England. To then test how pikeperch growth rates vary across their native and invasive European ranges, a meta-analysis tested spatial patterns in their somatic growth rate parameters across their entire range. As per patterns for other invasive fishes (e.g. Benejam et al. 2009, Cucherousset et al. 2009), it was predicted that latitude would be a significant predictor of pikeperch growth rates, with decreased growth rates with increased latitude.

2.3 Methods

2.3.1 Field study sites

The field study was mainly focused on the River Severn basin in central and western England. In this basin, the distribution of pikeperch is restricted to the Warwickshire Avon (52.0874 N, 1.9481 W), the lower River Severn, generally below the city of Worcester (52.3664 N, 2.3043 W), and the Gloucester-Sharpness Canal that is connected to the Severn estuary at its downstream end (51.7249 N, 2.4733 W). In addition, the Grand Union Canal has hydrological connection with the Warwickshire Avon and has invasive pikeperch present. An area of this canal close to its connection with Warwickshire Avon was thus also sampled (52.2287 N, 0.9159 W).

A common feature of these invaded waters is that they are heavily regulated for navigation; the Severn and Warwickshire Avon are impounded by navigation weirs, the Grand Union Canal comprises of series of locks to overcome changes in the gradient of the surrounding land and the Gloucester-Sharpness Canal was constructed specially for navigation of goods into Gloucester docks. However, the waters differ considerably in their other features. The lower River Severn is up to 40 m in width, with depths to 4 m and is subject to regular winter spates when levels can increase by 5 m. The Warwickshire Avon is generally of widths to 25 m and depths to 3 m, and although also prone to floods in winter, these tend to be much less severe than the Severn. The Grand Union Canal is generally no more than 15 m in width with depths rarely exceeding 2 m, and flood events are rare, whilst the Gloucester-Sharpness canal is unusually broad and deep for a British canal, being approximately 25 m wide with depths to over 5 m. Pikeperch were confirmed as present in the Warwickshire Avon in 1976, the lower River Severn in 1980 and the Grand Union Canal in 1984 (Hickley 1986, Nunn et al. 2007). There is no specific evidence over the timing of their introduction into the Gloucester-Sharpness Canal or whether it was from angler releases or, perhaps more unlikely, natural dispersal via the Severn estuary, although mixohaline waters have been suggested as a potential dispersal route for pikeperch (Brown et al. 2007).

Growth data on these populations was then supplemented by data on the age and growth rates of pikeperch from the River Great Ouse system (52.3276 N, 0.1769 W). With a catchment area of approx. 8600 km^2, the River Great Ouse is one of the largest river basins in England and, in the area of sampling, consists of a heavily modified, impounded and regulated river channel of 20 m width and depths to 2 m, with the flow regulated by numerous sluices for drainage and flood relief (Pinder et al. 1997). The rationale for including pikeperch from here was that the fish of the Severn and Great Ouse system all originated from the same original stock that was introduced into Eastern England in 1878 (Copp et al. 2003). Thus, the inclusion of the Great Ouse data utilised fish of the same genetic lineage to the Severn and represented another population from an impounded and regulated river channel.

2.3.2 Field sample collection

The age and growth analyses were completed on data obtained from scales collected from pikeperch, as scales provide a consistent and reliable method for age and growth rate analyses (Britton 2007). The habitat characteristics of the River Severn, Warwickshire Avon ('Lower Warwickshire Avon') and Gloucester Sharpness Canal meant their sampling for pikeperch using typical sampling methods were generally inefficient and/ or unfeasible (e.g. electric fishing, seine netting, fyke netting). Thus, scale sample collection was primarily via catch-and-release angling. This was facilitated by the Environment Agency, the inland fishery regulatory body of England, who established a network of anglers within the River Severn basin. Participating anglers recorded their catches and were trained in the collection of scale samples. Correspondingly, from 2014 to 2017, anglers collected scales (3 to 5 scales per fish from the area below the dorsal fin and above the lateral line) from captured pikeperch, with additional recording of the location, date of capture and fish fork length (FL, nearest mm). Additional scale samples were collected using seine netting techniques within off-channel boat marinas. For the Grand Union Canal, scales were collected from pikeperch in April 2017 where sampling used boat mounted electric fishing. In addition, some data were available for pikeperch from an upstream site on the Warwickshire Avon, where electric fishing was completed in May 2000 ('Middle Warwickshire Avon'; 52.1894 N, 1.7045 W). The Great Ouse fish were sampled by seine netting in August 2003 and 2005.

2.3.3 Age and growth determination from scales

Scales were aged on a projecting microscope (x10 to x48 magnification). Ages were determined by counting of annual growth marks ('annuli'), where an annulus was identified as the transition between two uninterrupted zones of closely and widely spaced circuli. In order to minimise error in age estimations, a confidence scoring system was utilised. In this system, the age estimate was assigned a score of 1 or 2, where 1 indicated relatively high confidence (e.g. scales with clearly defined annuli and high certainty in the age estimate) and 2 indicated reduced confidence (e.g. scales with poorly defined annuli and high age estimate uncertainty). Scales which were assigned a score of 2 were excluded from subsequent analyses to minimise the probability of using data based on low ageing accuracy. Following their ageing, scales were measured for their scale radius and the distances from the scale focus to the first, second and last annulus. These measurements were converted to back-calculated lengths using the Fraser-Lee back-calculation equation (Francis 1990):

$$L_i = c + (L_c - c)\ (\frac{S_i}{S_c})$$

Where *Lc* is the fish body length at capture, *Si* the mean scale length at annulus *i*, *Sc* the mean scale total length and *c* is the intercept from the regression of body length on mean scale length. Back calculated lengths enabled the growth increment between age 1 and 2 to be determined (interpreted as the 'juvenile growth rate') and the back calculated length at the last annulus (i.e. hatching date calculated as April according to Lappalainen et al. (2003) which provided a length at age that was not biased by sampling date).

2.3.4 Growth rate analyses of scale data

The age and growth data from the scales were analysed in two ways. First, length-at-age data were fitted, using non-linear, least-squares regression, to the von Bertalanffy growth model,

$$L_t = L_\infty (1 - e^{[-K(t-t_0)]})$$

here Lt is length at age t, $L\infty$ is the asymptotic length, K is the rate at which the curve approaches $L\infty$ and t_0 is the theoretical age of the fish at zero length. 95 % confidence limits for von Bertalanffy growth parameters were obtained by non-parametric bootstrap resampling over 10,000 iterations. This provided estimated values of $L\infty$, K and t_0.

Secondly, analysis of standardised growth residuals compared the pikeperch growth rates across the field sampling sites (other than the 'Middle Warwickshire Avon' where the juvenile growth data were not available). The analyses were completed using both lengths at the last annulus and the juvenile growth rate (Beardsley and Britton 2012, Amat Trigo et al. 2017). For the juvenile growth rate, the mean length increment (i.e. the back-calculated length difference between 1 and 2 years) across all populations was used to calculate the residuals, taken as the difference between the individual length increment of each fish and the mean length increment. For lengths at the last annulus, residuals were calculated using modelled length values, obtained by fitting the back-calculated length at last annulus to the von Bertalanffy growth model across all populations. The residual value of each individual fish was then calculated as the difference between its modelled and observed value. The standardized residual of each individual was determined and compared between populations using ANOVA, with type II sums of squares used to account for unbalanced data due to differences in sample sizes (Langsrud 2003); Tukey's post-hoc tests were used to determine the significance of differences between the populations.

2.3.5 Growth rate comparisons across the ranges of pikeperch

The von Bertalanffy growth model parameters of $L\infty$ and K for pikeperch within these field sites were then compared with data from other populations from across their native and invasive ranges, as gathered by literature review. This review was based on searches completed in Web of Science, and supplemented by Google Scholar, starting with search terms based on the species name ('pikeperch'; pike-perch'; 'zander'; '*Stizostedion lucioperca*'; '*Sander lucioperca*') in 'title' searches, and then using these within Boolean logic search terms with words including 'age', 'growth', 'von Bertalanffy', 'invasive', 'introduced', 'non-native', and their combinations. Searches were then completed using the same terms but searching for 'topic' to provide any additional material that would otherwise have been missed. These searches were then supplemented by data from Fishbase.org (Froese and Pauly 2018). Across these studies, data were omitted where the values were considered unreliable or were deemed to be not biologically relevant (see Appendix 1 for the rationale of each omitted study). These criteria were primarily where the value of $L\infty$ was considered very high or very low for the species in general, suggesting sampling had not been representative of the population (Živkov et al. 1999), or had been subject to high harvest rates (i.e. an additional pressure which other populations had not been exposed to). Where von Bertalanffy growth model parameters were calculated based on standard or total length, these were converted to fork length using linear models from Copp et al. (2003) to enable comparisons consistent across studies.

The relationship between the location of populations, as latitude and longitude, were then tested against $L\infty$ and K using linear and non-linear models, where regression statistics and the lowest value of Akaike's Information Criteria (AIC) were used in combination to select the best fitting model. All statistical analysis and graphical outputs were performed using R (Version 3.4.3; R Development Core Team 2017).

2.4 Results

2.4.1 Field study on growth parameters of invasive pikeperch

There were 625 pikeperch aged in the field study, of which 472 were retained for analyses based on a confidence score of 1. These retained fish ranged in length between 74 and 770 mm, with individuals aged to 11 years old (Table 1). However, populations from the Grand Union Canal, the Gloucester-Sharpness Canal and the 'Middle Warwickshire Avon', were only present in samples to 8 years old (Table 1). For the data combined across all populations $L\infty$ was 996 mm and K was 0.13. Among the populations, mean $L\infty$ ranged from 753 to 980 mm, and K between 0.12 and 0.22 (Table 1, Figure 3). However, there was considerable overlap in the 95 % confidence limits of these growth parameters across the populations, suggesting differences between these populations were not significant.

Table 1 Samples size, length and age range, and Von Bertalanffy growth parameters estimates for invasive pikeperch in England, values in parentheses represent the 95% the confidence limits of each parameter estimate.

River	N	Length (mm)	Age (years)	$L\infty$	K	$t0$
Gloucester-Sharpness Canal	18	345-660	2 - 8	980 (679, 2509)	0.13 (0.03, 0.36)	-1.10 (-3.94, 0.65)
Grand Union Canal	129	169-551	2 - 6	820 (598, 1726)	0.18 (0.05, 0.34)	-0.08 (-0.75, 0.46)
Lower Warwickshire Avon	26	90-695	0 - 11	870 (713, 1143)	0.16 (0.10, 0.25)	-0.82 (-1.23, -0.46)
Middle Warwickshire Avon	35	142-650	1 - 7	753 (676, 904))	0.22 (0.15, 0.30)	-0.08 (-0.54, 0.23)
Great Ouse	70	110-760	1 - 10	853 (725, 1138)	0.19 (0.11, 0.28)	-0.27 (-0.73, 0.03)
Severn	181	74-770	0 - 10	874 (806, 964)	0.18 (0.15, 0.21)	-0.43 (-0.62, -0.26)

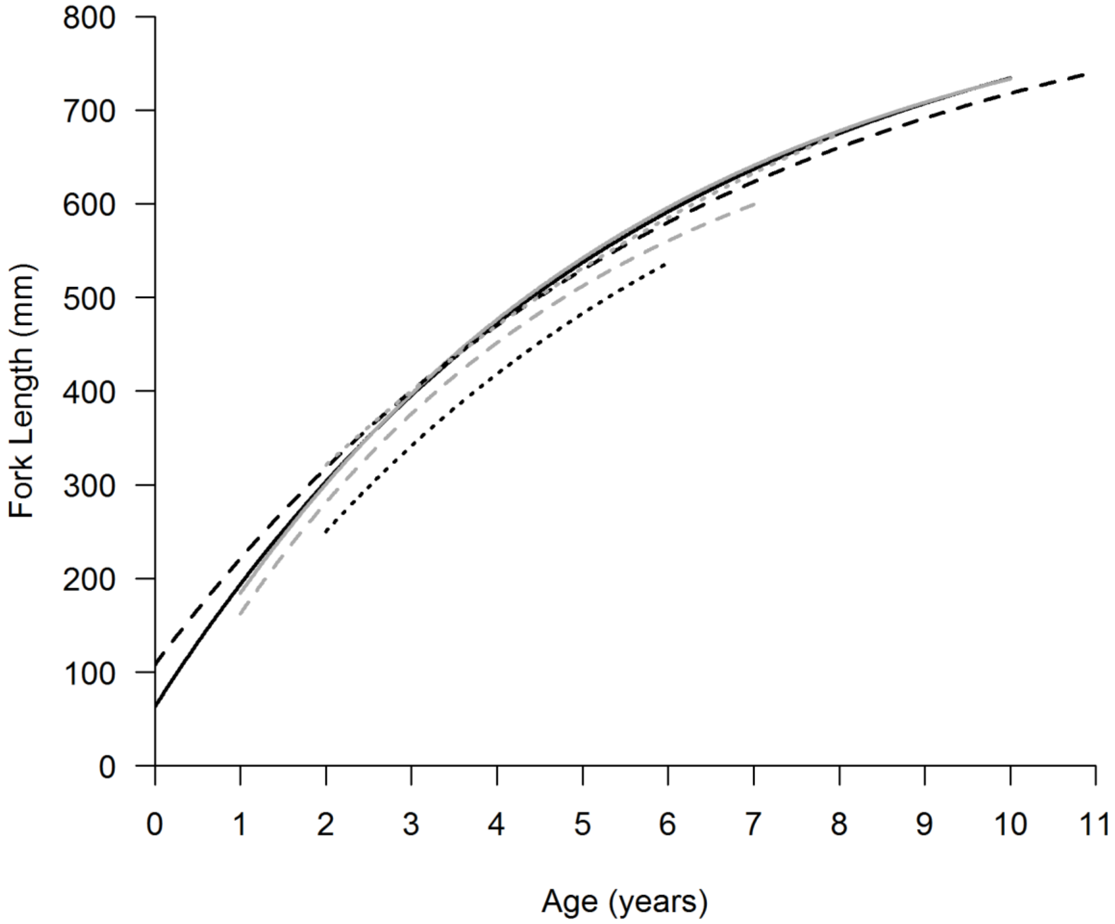

Figure 3. Fitted von Bertalanffy growth curve for populations of pikeperch at sites in England including the Gloucester-Sharpness canal (dotted grey line), the Grand Union canal (dotted black line), the lower Warwickshire Avon (dashed black line), the middle Warwickshire Avon (dashed grey line) the river Great Ouse (solid grey line) and the river Severn (solid black line).

Analysis of standardised growth residuals revealed significant differences between these populations in both their juvenile growth rates (ANOVA: $F_{4,347} = 45.01$, $P < 0.01$; Figure 4a) and lengths at the last annulus (ANOVA: $F_{5,434}= 16.97$, $P < 0.01$; Figure 4b). For juvenile growth rates, Tukey post-hoc tests revealed that significant differences were due to slower growth in the Grand Union Canal population compared to all other populations ($P < 0.01$) and faster growth in the River Great Ouse compared to all other populations (*P* < 0.01). For length at the last annulus, Tukey post-hoc tests showed that significant differences were due to faster growth in length at last annulus on the River Severn population to those of the Grand Union Canal, the River Great Ouse (*P* < 0.01) and the middle Warwickshire Avon (*P* < 0.05). The Grand Union Canal also showed slowest growth across all populations and significant differences with the Gloucester-Sharpness Canal, the River Severn (*P* < 0.01) and the River Great Ouse (*P* < 0.05).

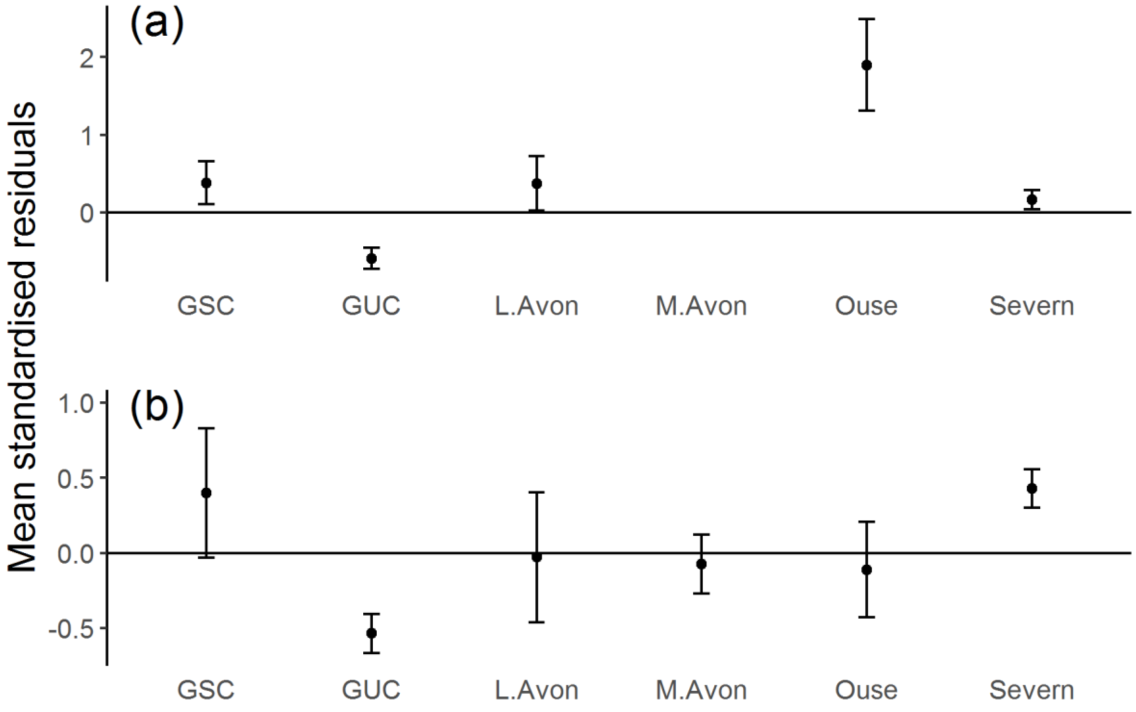

Figure 4. Mean standardised growth residuals for (a) juvenile growth rate; and (b) length at last annulus for the Gloucester-Sharpness canal (GSC), Grand Union Canal (GUC), the lower Warwickshire Avon (L. Avon), the middle Warwickshire Avon (M. Avon), the River Great Ouse (Ouse) and the River Severn (Severn). Error bars represent the upper and lower 95% confidence limits.

2.4.2 Spatial variability in pikeperch growth rates

Literature review provided 34 studies with data on the von Bertalanffy growth parameters of pikeperch, of which 22 were retained for further analysis (Appendix 1, Table A1.1). The analysis also included data from the 6 invasive populations from the field study. Across the 22 populations, $L\infty$ ranged between 709 and 1116 mm and K between 0.03 and 0.24 (Appendix 1, Table A1.1). The $L\infty$ and K parameters derived for the six invasive populations from England sat within these data, with their values towards the higher values of K and lower values of $L\infty$. However, von Bertalanffy growth parameter estimates were only retained from three of the populations within the field study based on the criteria outlined for the exclusion of data from meta-analysis, with subsequent analysis excluding data from the lower Warwickshire Avon, the Grand Union Canal and the Gloucester-Sharpness Canal. The relationship between $L\infty$ and K, estimated from a total of 25 populations, was significant, with decreasing values of K as $L\infty$ increased (linear regression: $R^2 = 0.19$, $F_{1,23} = 5.56$, $P = 0.02$, Figure 5). The relationships between latitude and both $L\infty$ and K were best described by non-linear regression (AIC; Table 2) and revealed significant U-shaped relationships ($P = 0.05$ and $P < 0.001$ respectively). There were higher values of $L\infty$ and lower values of K at either end of their latitudinal range (Figure 6). The relationships of longitude with both $L\infty$ and K were non-significant ($P > 0.05$; Table 2; Figure 6).

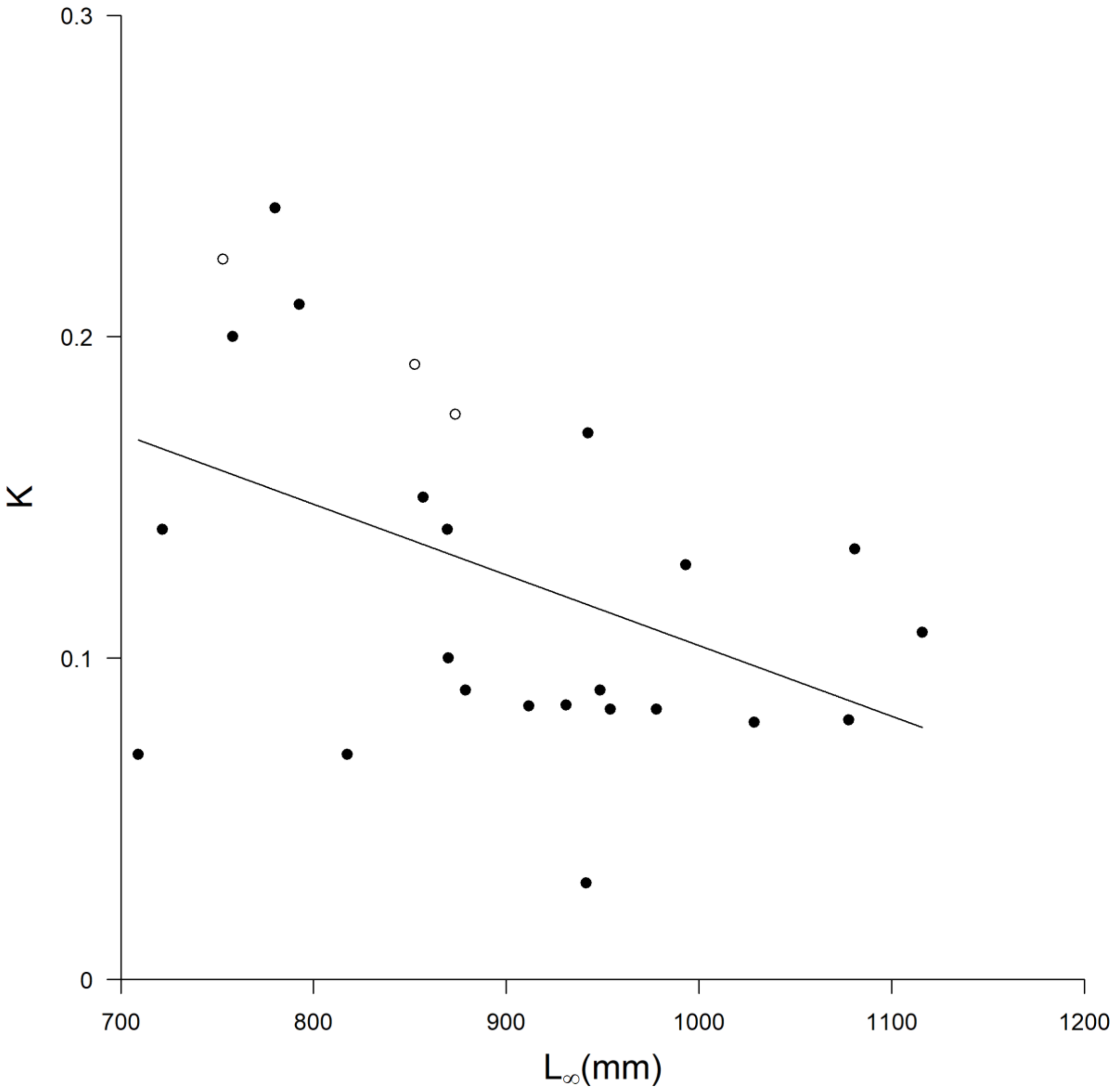

Figure 5. Relationship of *L*∞ (as fork length) and *K* of the von Bertalanffy growth model for populations of pikeperch, where the solid line is the significant relationship between the variables according to linear regression, filled circles represent values extracted from literature whilst open circles represent values from invasive populations in England derived in this study.

Table 2. Linear and non-linear (2nd order polynomial) regression statistics for the relationship between von Bertalanffy growth parameters $L\infty$ and K versus latitude and longitude.

Relationship	Model	R^2	F	P	AIC
Latitude *vs*. $L\infty$	Linear	0.01	$_{(1,23)}$ 1.23	0.28	310.61
	Non-linear	0.16	$_{(2, 22)}$ 3.36	0.05*	307.25
Longitude *vs*. $L\infty$	Linear	0.04	$_{(1,23)}$ 2.07	0.16	309.76
	Non-linear	0.08	$_{(2, 22)}$ 2.13	0.14	309.50
Latitude *vs*. K	Linear	0.29	$_{(1,23)}$ 10.71	0.01**	-77.85
	Non-linear	0.43	$_{(2, 22)}$ 10.06	< 0.001***	-82.84
Longitude *vs*. K	Linear	-0.01	$_{(1,23)}$ 0.99	0.33	-69.34
	Non-linear	0.07	$_{(2, 22)}$ 1.87	0.18	-70.24

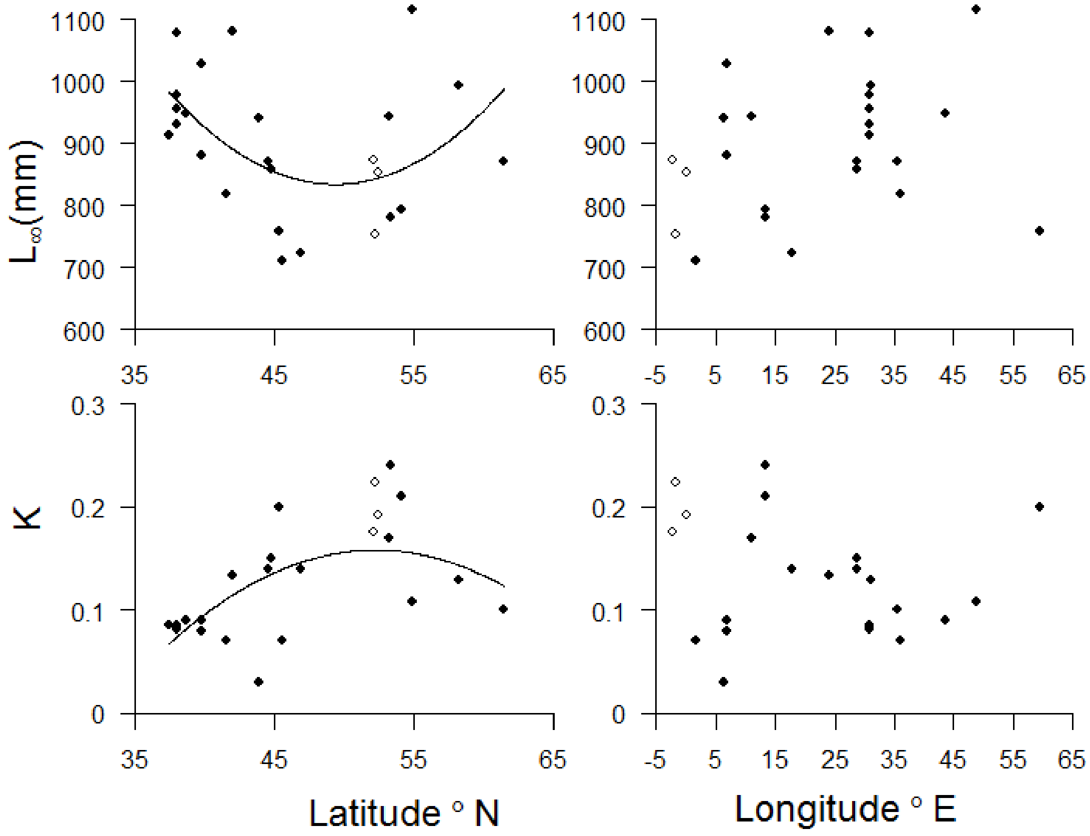

Figure 6. Relationships of latitude and longitude with *L*∞ (as fork length) and *K* of the von Bertalanffy growth model for pikeperch. The solid line represents the significant relationship between the variables according to polynomial regression (2nd order), filled circles represent values extracted from literature whilst open circles represent values from invasive populations in England derived in this study.

2.5 Discussion

Across their entire range, the results suggested pikeperch were rarely present in samples above the age of 10 years and $L\infty$ only exceeded 900 mm in a small number of populations. Spatially, there was variation in von Bertalanffy growth parameters across their entire range, with this at least partially explained by the influence of latitude. This spatial variation in von Bertalanffy growth parameters was less apparent in the field study that was completed at a smaller spatial scale. However, the standardized residuals of juvenile growth rates and length at the last annulus indicated some significant differences in growth rates between populations, even at this reduced spatial scale, suggesting factors other than latitude were also important determinants of pikeperch growth rates.

It was predicted that latitude would have a significant influence on the growth of pikeperch, with growth rates decreasing as latitude increases, given that this is a common spatial pattern for many freshwater fishes in the northern hemisphere (Heibo et al. 2005, Blanck and Lamouroux 2007, Cucherousset et al. 2009), and previous studies have shown fast growth rates in some southern pikeperch populations (Lappalainen et al. 2003). Whilst there was a significant relationship between both von Bertalanffy growth parameters and latitude, AIC values indicated that the best fitting models were both non-linear, with this contrary to the prediction. Instead, the models indicated U-shaped relationships between the parameters, whereby populations were comprised of individuals of larger body sizes with slower growth rates towards their northerly and southerly limits. These non-linear relationships were likely to have resulted from the population growth rates having a non-linear relationship with environmental factors (Lappalainen et al. 2008), especially water temperature. This is because water temperatures tend to strongly correlate with latitude, and the strong influence of temperature on fish growth rates is well established (Magnuson et al. 1979). Thus, the increases in K (growth coefficient) that were apparent from approximately 45 to 55 °N might be linked to water temperatures in these areas providing more optimum thermal conditions for faster and efficient growth rates. Indeed, some increases in water temperature have positive effects on pikeperch growth, with the number of degree days over 10 °C increasing their annual length increments (Buijse and Houthuijzen 1992, Ložys 2004, Lappalainen et al. 2005, 2009). However, faster growth rates tend to generally limit ultimate body sizes due to the influence of, for example, the earlier onset of sexual maturity that diverts energy from somatic growth to reproduction (Ložys 2004), so potentially explaining the trade-off of higher *K* values but lower ultimate lengths at 45 to 55 °N.

At higher latitudes, freshwater fish populations often show slower growth and larger asymptotic lengths (Blanck and Lamouroux 2007), and thus the results of the relationships of $L\infty$ and *K* with latitude outside of 45 to 55 °N were consistent with this. For example, the slower growth rates that were apparent towards the southerly limits of their range might relate to sub-optimal, warm summer temperatures that prevented their efficient growth, and thus depressed the values of *K* (Lappalainen et al. 2008). There might have also been a genetic component in the spatial growth patterns of pikeperch, given that significant population genetic variation has been detected across their range (Eschbach et al. 2014). This could not, however, be tested here.

Density dependent factors could also have been influencing the growth rates of these pikeperch populations, with this potentially related to differences in prey availability. In other piscivorous fishes, growth rates were 1.3 times faster at low population densities than high densities, for example in immature walleye *Sander vitreus* (Venturelli et al. 2010). However, Haugen et al. (2007) revealed conflicting interactions between density-dependent and density-independent factors affecting the growth of pike, *Esox lucius* a large-bodied piscivorous species. Variation in the annual growth rates of a 0+ pikeperch population has been explained by the higher availability of prey species in warmer years (Mooij et al. 1994). The onset of piscivory in pikeperch can also influence juvenile growth rates (Buijse and Houthuijzen 1992), with the realised lengths of piscivorous fishes early in life generally being an important determinant of their ultimate sizes (Mittelbach and Persson 1998). Additionally, pikeperch express faster growth rates in eutrophic waters (Argillier et al. 2012), with Keskinen and Marjomäki (2003) revealing pikeperch growth was positively correlated with total phosphorus and turbidity, and negatively with size of the water body. In our study, there were some significant differences apparent in juvenile growth rates in the field component. It can thus be hypothesised that differences in the growth rates between the Grand Union Canal and the River Great Ouse to all other populations were at least partially related to differences in prey availability, the physical characteristics of the water body and the onset of obligate piscivory between these populations. However, it was beyond the scope of this study to decouple the relative influences of these factors on pikeperch growth rates. It was also possible that sample year affected the juvenile growth rates of these populations via, for example, differences in prey availability and temperature. Additionally, these samples were obtained by different sampling methods, increasing the risk of some sampling bias in fish through selective sampling. Thus, the interpretation of these field data warrant some caution due to these issues.

In the field component of this study, the age and growth rate data were derived only from scales. This was because pikeperch is now considered a recreationally important fishery resource in most invaded waters in England (Hickley and Chare 2004), with catch-and-release angling most likely utilised by anglers. This is despite legislation that controls the distribution of the species in England (Hickley and Chare 2004), with evidence suggesting significant ecological impacts on native fish communities following their introduction (Fickling and Lee 1983, Hickley 1986, Smith et al. 1998). The use of scales in ageing studies can be problematic, especially in older fishes where the aggregation of annuli on the scale edge can result in ageing errors, with these usually being under-estimations of age (Britton et al. 2013, Amat Trigo et al. 2017). Nevertheless, in a comparative study on the use of calcified structures for age determination in pikeperch from Turkey, Bostanci (2008) found that scales were typically clear and straight forward to interpret, with the only exception being scales collected from large, long-lived individual fish. Scales were also used as a reliable ageing method for British populations of pikeperch by Copp et al. (2003) and Britton (2007). The use of the confidence scoring system in ageing the scales should have also increased the reliability of the data used in analyses, with those scales that were difficult to age with high certainty not being used. It should be noted that the scales aged with high uncertainty were not just those from large, slow growing fish, but include scales from smaller fish, where the annuli on the scales were too indistinct to enable a reliable age estimate. There was also no bias in the rejected scale data with respect to the population or the sampling method.

The use of literature review to compile a meta-analysis of pikeperch growth data enabled the study to look at growth patterns across a large spatial area. Similar approaches have been recently used for invasive fishes such as roach *Rutilus rutilus* (Tarkan and Vilizzi 2015) and carp *Cyprinus carpio* (Vilizzi and Copp 2017). Whilst effective at describing growth over environmental gradients and large spatial areas, differences in how data were collected and/ or analysed between the studies also potentially introduces some discrepancies into analyses. For example, in our study, standard, fork and total length were all used in the reporting of $L\infty$, and so all values were converted to fork length to enable reliable comparisons. In doing so, however, they might have slightly affected the relationship of $L\infty$ versus K, given K values could not be altered in same manner. However, the adjusted difference in lengths was relatively minor (generally < 20 mm) and so did not have a material effect of the relationship of $L\infty$ versus K. In addition, there are a number of analytical methods to derive von Bertalanffy growth parameters from length at age data, such as use of two or three parameter growth models that can result in different estimates (Pardo et al. 2013). However, these analytical issues could not be easily controlled in our meta-analysis and, thus, it was assumed that the published values were accurate for the sampled fish.

The increasing water temperatures that are generally predicted to occur via climate change will potentially have profound impacts on water resources and river ecosystems (Wilby et al. 2006, Johnson, Acreman, et al. 2009). As a result, there will be major changes in freshwater fish distribution and community structure (Graham and Harrod 2009, Ruiz-Navarro et al. 2016a). Ecological impacts of freshwater invaders are likely to be enhanced with this warming, such as through altered competitive interactions and increased predation pressure on native species (Rahel and Olden 2008). However, predicting the response of specific invaders to warming is inherently difficult due to these being influenced through complex direct and indirect effects (Britton, Cucherousset, et al. 2010, Kuczynski et al. 2018). For example, in temperate freshwaters, it is likely that all fishes (plus other taxa) will respond to warming by altering their distributions, life history traits and phenology (Comte and Grenouillet 2013, Ruiz-Navarro et al. 2016a, 2016b). This is likely to lead to range changes and altered population abundances (Ruiz-Navarro et al. 2016b). For pikeperch to invade temperate regions, low water temperatures are not considered a constraint due to them being primarily a cold-water species capable of reproducing at relatively low temperatures. Indeed, the temperate climate of England has not prevented population establishment and invasion in the last 50 years (Hickley 1986, Copp et al. 2003). Thus, it is unlikely that climate change will have a substantial influence on their ability to invade new temperate regions, unless the warming results in temperatures that are too high for their survival. However, given the significant relationships between latitude and their von Bertalanffy growth parameters, then it is likely that as warming proceeds then the impact for pikeperch is likely to be through altered growth rates. In England, for example, it is likely that their ultimate lengths will reduce, and growth rates increase, and potentially result in more abundant populations comprised of smaller individuals. This is in line with predictions for a number of native fishes (Ruiz-Navarro et al. 2016b).

In summary, this meta-analysis of the von Bertalanffy growth parameters of pikeperch suggested that whilst their introductions can result in invasive populations within a wide spatial area and in climates that range from temperate to Mediterranean, the expression of their life history traits will vary considerably. Growth rates will be faster in their mid-range (approximately 45 to 55 °N) than at their northerly and southerly range limits, most likely due to the influence of temperature, although it is acknowledged that other factors will influence their growth at the population level, such as prey availability. These results highlight the extent to which their growth data varies spatially and can be applied to their invasion management by providing a more robust basis for risk assessments that utilise data on their life history traits.

3 Diet of invasive pikeperch *Sander lucioperca*: developing non-destructive tissue sampling for stable isotope analysis with comparisons to stomach contents analysis

3.1 Abstract

Impact assessments of invasive piscivorous fishes usually rely on dietary analyses to quantify their predation pressure on prey communities. Stomach contents analysis (SCA), typically a destructive sampling method, is frequently used for this. However, many invasive piscivores are exploited by catch-and-release sport angling, with destructive sampling often not feasible. Stable isotope analysis (SIA) provides an alternative dietary analysis tool to SCA, with use of fin tissue, scales and/or epidermal mucus potentially enabling its non-destructive application. Here, the diet of a population of pikeperch *Sander lucioperca*, an invasive sport fish to Great Britain, was investigated by applying SIA to a range of tissues. Testing SI data of dorsal muscle (destructive sampling) versus fin, scale and mucus (non-destructive sampling) revealed highly significant relationships, indicating that the tissues collected non-destructively can be reliably applied to pikeperch diet assessments. Application of these SI data to Bayesian mixing models predicted that as pikeperch length increased, their diet shifted from macro-invertebrates to fish. Although similar ontogenetic patterns were evident in SCA, this was inhibited by 54% of fish having empty stomachs. Nevertheless, SCA revealed that as pikeperch length increased, their prey size significantly increased. However, the prey: predator length ratios ranged between 0.08 and 0.38, indicating most prey were relatively small. These results suggest that when non-destructive sampling is required for dietary analyses of sport fishes, SIA can be applied using fin, scales and/or mucus. However, where destructive sampling has been completed then SCA provides complementary dietary insights, especially in relation to prey size.

3.2 Introduction

Piscivorous fishes play an important role in regulating the structure of aquatic food-webs (Woodward and Hildrew 2002a). They can exert substantial top-down forces on prey communities, potentially initiating trophic cascades (Brett and Goldman 1996, Pace et al. 1999, Drenner and Hambright 2002). Invasive piscivorous fishes that are introduced to enhance sport angling, such as largemouth bass *Micropterus salmoides* and peacock bass *Cichla* spp., also exert substantial top-down forces on prey fish communities, resulting in impacts including reduced prey abundances and decreased species diversity (Gratwicke and Marshall 2001, Pelicice and Agostinho 2009). As the diets of piscivorous fishes tend to involve strong ontogenetic changes via increasing gape sizes (Zhao et al. 2014) then the strength of trophic cascades can be strongly influenced by the resultant dietary shifts (Sato and Watanabe 2014). Thus, an important step in the assessments of the ecological impacts of alien piscivores is analyses of their diet composition, including assessing ontogenetic shifts in their prey selection.

Dietary assessments of piscivorous fishes are often reliant on stomach contents analysis (SCA) (Sandlund et al. 2016). Whilst providing information on diet composition of individual fish, the method usually utilises relatively large numbers of fish to maximise statistical power and to assist understandings of dietary patterns over time and space (Cortés 1997). For piscivores such as the Northern pike *Esox lucius* and pikeperch *Sander lucioperca*, an inherent issue in stomach contents analysis is that many of the fish often have empty stomachs, resulting in a paucity of dietary data from the sampled population. Piscivorous fishes in general and particularly those that consume prey whole have higher proportions of empty stomachs compared to lower trophic level fishes (Arrington et al. 2002), with feeding frequency thought to decrease through the consumption of energy-rich food items (Bowen et al. 1995). These methodological issues can potentially be overcome by using complementary dietary assessment methods, such as stable isotope analysis (SIA) (Cucherousset et al. 2012, Jensen et al. 2012). Indeed, in a study where an average of 36 % of pike had empty stomachs across 16 populations, stable isotope analysis showed no trophic position differences between fish with and without prey items in their stomachs, or between piscovores and invertebrate feeders determined through stomach content analysis (Paradis et al. 2008), indicating opportunistic rather than specialist invertebrate feeding strategies. Therefore, integrative studies may often show that SCA and SIA provide contrasting dietary information due to, for example, differences in the temporal scales of the methods (i.e. short SCA versus long-term SIA diet assessments), (Locke et al. 2013, Busst and Britton 2017b), but these differences can provide insights where disintegrated studies cannot.

The issues of sacrificing relatively large numbers of piscivorous fish to satisfy the requirements needed for stomach contents analysis is also problematic when these fish have high values within sport angling. For example, catch-and-release angling (C&R) is increasingly applied to sport fishing for species such as largemouth bass, pikeperch and peacock bass. Mortalities associated with C&R can be minimised via use of best practice angling techniques and fish handling codes (Arlinghaus and Hallermann 2007, Siepker et al. 2007, Cook et al. 2015, Bower et al. 2016). Consequently, dietary assessments for piscivorous sport fishes based on destructive sampling are increasingly at odds with their fishery management and angling practises, even where the fishes are invasive (Hickley and Chare 2004). Indeed, the fishery value of invasive fishes are increasingly recognised (Gozlan 2008), especially when their populations are in large open systems in which their population management is inherently difficult (Britton et al. 2011, Britton and Orsi 2012).

Pikeperch is a large-bodied piscivorous freshwater fish whose native range in Europe extends from Germany in the West to Central Russia in the East (Maitland 2004). The species has been introduced outside of this range, into countries such as France, Spain and Great Britain (Elvira and Almodóvar 2001, Kopp et al. 2009), often with the primary purpose of increasing sport angling opportunities (Hickley and Chare 2004). Following their initial introduction into Britain in 1878, there was a series of translocations of pikeperch into waters in Eastern England during the 1960s (Wheeler and Maitland 1973). It was these releases that resulted in their invasion of river catchments across Eastern, Central and Southern England (Linfield and Rickards 1979, Hickley 1986, Copp et al. 2003). Whilst there were initial concerns on their impacts on prey populations, the species is now considered as an important angler target species in many fisheries (Hickley and Chare 2004). Consequently, whilst studies on their diet previously utilised stomach contents analyses (e.g. Smith et al. 1997, Schulze et al. 2006), methods based on stable isotope analysis might now be more preferable (Kopp et al. 2009), especially where tissues can be utilised that can be collected non-lethally (Britton and Busst 2018).

The diet of pikeperch has been well studied both within their native and non-native ranges (e.g. Campbell 1992, Keskinen and Marjomäki 2004, Pérez-Bote and Roso 2012, Didenko and Gurbyk 2016). They are generally considered to be piscivorous within their first year of life (Mittelbach and Persson 1998), although this switch to piscivory can become delayed if individuals do not reach a size advantage over prey (Persson and Brönmark 2002) or if suitable prey fish are unavailable (Ginter et al. 2011). Whilst pikeperch diet comprises of fish across a range of size classes, they can also be cannibalistic, with this acting as an important regulatory force (Mehner et al. 1996, Frankiewicz et al. 1999, Lappalainen et al. 2006). Individual pikeperch will also consume macro-invertebrates, with these prey items most frequently encountered in the diets of smaller individuals (Hansson et al. 1997a, Argillier et al. 2012).

The application of SIA using multiple tissues in conjunction with SCA enables the dietary habits of the target population to be assessed across difference timescales. SCA provides ‘snapshot’ dietary information (Cortés 1997). By contrast, SIA provides longer-term dietary perspectives, with the timescale dependent on the analysed tissue (Fry 2006, Newsome et al. 2007, Martínez del Rio et al. 2009). The aim of this study was thus to use pikeperch as a model fish exploited by C&R sport angling to assess how stable isotope analysis can be applied to assess their diet in relation to using tissues that are collected non-destructively. Objectives were to: (1) quantify the relationships of the stable isotopes of δ^{13}C and δ^{15}N between dorsal muscle and three tissues that can be collected non-lethally; (2) utilise the stable isotope data to predict the diet composition of a pikeperch population using Bayesian mixing models (Stock et al. 2018); and (3) complete stomach contents analyses on the pikeperch population and assess the results in the context of the dietary predictions from the mixing models.

3.3 Materials and Methods

3.3.1 Sample collection

The pikeperch population of the Grand Union Canal, Northamptonshire, in Central England was sampled by boat mounted electric fishing (‘boom-boat’, power supplied by a 2 kVA generator) in April 2017. This canal is generally of 15 m maximum width and depths rarely exceed 2 m. A series of locks overcome changes in the gradient of the surrounding land. Small-bodied cyprinid fishes are dominant in the fish community, especially roach *Rutilus rutilus*. Pikeperch have been present in the canal for at least 30 years (Hickley 1986). A total of 180 individuals were captured by the electric fishing that ranged in fork length (to nearest mm) between 169 and 551 mm (mean ± 95 % CI; 355 ±

14 mm) and weight between 48 and 1924 g (mean ± 95 % CI; 561 ± 71 g). Following their capture, the fish were euthanized and held on ice whilst being transferred to the laboratory where they were processed immediately.

3.3.2 *Stable Isotope analysis*

Of the 180 sampled pikeperch, a sub-sample of 19 were processed for stable isotope analysis using fish from across the length range (mean ± 95 % CI; 323 ± 54 mm). Following their measurement, the tissues that were sampled from each fish were dorsal muscle, pelvic fin tissue, scales and epidermal mucus. The epidermal mucus was collected by scraping the dorsal surface of each fish with a cover slip, with the sample then cleaned with forceps as per Maruyama et al. (2015) and transferred to a sample tube. This method was used in preference to the filtration method of Church et al. (2009), as it was demonstrated to result in reduced error (Maruyama et al. 2015). Scales were collected from the body area between the dorsal fin and the lateral line. Scale decalcification was not performed prior to isotopic analysis, since the removal of inorganic carbonates has been shown to have no significant effect on scale $\delta^{13}C$ and $\delta^{15}N$ values (Sinnatamby et al. 2007, Ventura and Jeppesen 2010, Woodcock and Walther 2014). Preparation thus focused on cleaning scales with distilled water prior to removing the outer portion of the scale for SIA, ensuring the tissue analysed was from recent growth only (~1 year) (Hutchinson and Trueman 2006, Bašić and Britton 2015). A selection of all prey fish species (dorsal muscle only) and macroinvertebrates (*cf.* Stomach contents analysis) were also prepared for stable isotope analysis recovered through dissection and removal of prey from the stomachs. These samples were based only on individual animals that were recovered in good condition, i.e. those very recently ingested, with negligible digestion and that were identifiable to species level. All samples were then dried at 60 °C for 48 h.

The samples were then analysed at the Cornell Isotope Laboratory, New York, U.S.A., where they were ground to powder, weighed precisely to approximately 1000 µg and analysed on a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, U.S.A.) interfaced to a NC2500 elemental analyser (CE Elantach Inc., U.S.A.). Verification of accuracy was against internationally known reference material and accuracy and precision of the sample runs was tested every 10 samples using a standard animal sample (mink). Delta (δ) isotope ratios were expressed as units per mil (‰). Analytical precision of the $\delta^{15}N$ and $\delta^{13}C$ sample runs was estimated at 0.42 and 0.15 ‰ respectively. Lipid correction was not necessary as C:N ratios indicated very low lipid content (Post et al. 2007).

3.3.3 Tissue comparisons

The significance of differences in the stable isotope ratios between the tissues were tested using pair-wise *t*-tests. Simple linear regression models tested the significance of the relationship between mucus and muscle, fin and muscle and scale and muscle for $\delta^{13}C$ and $\delta^{15}N$ isotope values. Models were run both with and without fish length. The best fitting model was chosen using regression statistics and the lowest value of Akaike's Information Criteria (AIC). Statistical analysis and graphical outputs were performed using R (Version 3.4.3; R Development Core Team 2017).

3.3.4 Bayesian mixing models

The stable isotope data were analysed to assess the effect of tissue type on fish diet predictions including after conversion of the stable isotope data of the non-lethal tissues to dorsal muscle (as the standard tissue used in fish isotope studies). The primary tool for this analyses was the use of Bayesian mixing models (Phillips et al. 2014) allowing for predictions of the relative proportions of the putative prey resources that contributed to the diet of pikeperch for each tissue both before and after their conversion to dorsal muscle values. The models were run in the package 'Mixing Models for Stable Isotope Analysis in R' (MixSIAR; Parnell et al. 2013, Stock et al. 2018). All models were run using normal run length (chain length: 100,000 iterations with burn-in of 50,000, with posterior thinning (thin: 50) and 3 chains). Model diagnostics were based on Gelman-Rubin and Geweke, with sufficient convergence to accept the results (Stock and Semmens 2016b).

Five mixing models were run that covered the use of pikeperch (as the consumer) stable isotope data from: (1) dorsal muscle; (2) epidermal mucus; (3) scales; (4) epidermal mucus data converted to dorsal muscle values (using the linear models for $\delta^{13}C$

and δ^{15}N mucus to muscle); and (5) scale data converted to dorsal muscle values (using the linear models for δ^{13}C and δ^{15}N scale to muscle). The putative prey (source) data used within the mixing models was constant across all models, except for model (3) where fish muscle isotope data were converted to scale data based on conversion factors in Busst et al. (2015) to ensure consistency in predictions by accounting for differences in isotope values between the tissues of source and consumer. Dietary contributions were predicted by splitting the fish into two size classes, < 350 mm and > 350 mm, with distinctions made between the two groupings based on: (1) the likelihood of sexual maturity at above approximately 350 mm (Lappalainen et al. 2003), and (2) based on differences in the contribution of prey items to the diet of individuals in each size class from stomach content analysis (*cf.* results).

In the mixing models, the isotopic fractionation values between the prey resources and pikeperch were varied according to the pikeperch tissue being used. For muscle and mucus, values were chosen based on standards proposed by Post (2002): δ^{15}N 3.4 ± 0.5 ‰; δ^{13}C 1 ± 0.5‰. For scales, the fractionation factors used were $\delta^{15}N = 2.58 \pm 1$ ‰ and $\delta^{13}C = 2.78 \pm 1$‰), based on the standards of Post (2002) but with correction for scales using the mean differences from three studies comparing fractionation between muscle and scale tissue (Δ^{15}N -0.82‰, Δ^{13}C 1.78‰) (Heady and Moore 2013, Busst and Britton 2015, Busst et al. 2015). Reported outputs of the models were overall estimated posterior density contributions to diet given as summary statistics; mean, standard deviation, and 95% confidence limits. Posterior density plots for each model are given in Appendix 2.

3.3.5 Stomach contents analysis

Pikeperch were measured (fork length, nearest mm) and weighed (nearest g), and then dissected and their stomach contents removed. Prey items from stomach contents were identified to their lowest possible taxonomic level, total stomach fullness (% in volume) was assessed, as was the contribution of each prey item to overall fullness. For subsequent analyses, stomach contents were categorised into three groupings consisting of: 1) 'Cyprinidae' including roach *Rutilis rutils*, common bream *Abramis brama* and gudgeon *Gobio gobio*; 2) 'Percidae' including perch *Perca fluviatilis* and ruffe '*Gymnocephalus cernua*' and; 3) 'Invertebrates' where macro-invertebrates were identified to family level, and included Gammaridae, Chironomidae and Mysidae.

The contribution of each diet category was expressed as percentages in terms of frequency of occurrence and prey-specific abundance. Frequency occurrence (% F_i) of a given prey type was defined as the number of stomachs in which that prey occurred, expressed as a frequency of the total number of stomachs in which prey were present (Costello 1990). For prey-specific abundance, prey type contribution was first estimated in proportion to overall stomach fullness (in volume). The proportional fullness contribution of each diet category was then expressed as percentage prey specific abundance (% P_i):

$$\%\, P_i = \left(\frac{\sum F_i}{\sum F_t}\right) \times 100$$

Where P_i was the prey-specific abundance of prey i, Fi was the stomach content fullness for diet category i and Ft was the total stomach fullness in only those predators with prey i in their stomach (Amundsen et al. 1996). In addition, the fork length (mm) of each prey item was also taken to assess changes in prey use patterns with increasing body length of pikeperch using regression analysis (as prey: predator length ratios). Dietary contribution was predicted for size classes < 350 mm and > 350 mm as per Bayesian mixing models.

3.4 Results

3.4.1 Relationship of δ^{13}C and δ^{15}N values between pikeperch tissues

There was a significant difference in the δ^{13}C values between scale and all other tissues (Table 3, Figure 7), where scale was significantly enriched in δ^{13}C relative to muscle (t-test, $t = 12.6$, $P < 0.001$), mucus (t-test, $t = 12.4$, $P < 0.001$) and fin (t-test, $t = 8.1$, $P < 0.001$). Although not significantly different, mucus was depleted in δ^{13}C relative to muscle (- 0.55 ‰; t-test, $t = -1.8$, $P = 0.07$), whilst fin was enriched in δ^{13}C relative to muscle (+ 0.53 ‰; (t-test, $t = 1.6$, $P = 0.10$). For δ^{15}N, significant differences were also evident between scale and all other tissues (Table 3, Figure 7), with scale depleted in δ^{15}N relative to muscle (-1.25 ‰; t-test, $t = -3.6$, $P < 0.001$), mucus (t-test, $t = -2.5$, $P < 0.001$) and fin (t-test, $t = -3.5$, $P < 0.001$). There was no significant difference in δ^{15}N between muscle and mucus (+ 0.38, t-test, $t = 1.1$, $P = 0.27$) or between muscle and fin (-0.01; t-test, $t = -0.1$, $P = 0.97$).

Significant relationships were found between pikeperch muscle isotope values (δ^{13}C and δ^{15}N*)* and all other tissue types (Table 4, Figure 8). Including length in the models improved their fit in all cases (according to AIC and regression statistics; Table 4). This is likely explained by the significant increase in δ^{13}C with increasing fish length (Figure 9; muscle, $R^2 = 0.68$; $F_{1,17} = 39.2$; $P < 0.001$; mucus, $R^2 = 0.52$; $F_{1,17} = 20.1$; $P < 0.001$; fin, $R^2 = 0.66$; $F_{1,17} = 35.4$; $P < 0.001$; scale, $R^2 = 0.70$; $F_{1,17} = 42.91$; $P < 0.001$). Consequently, length was retained in the regression analyses across all tissue/isotope conversions for consistency. There was no relationship between δ^{15}N and fish length (muscle, $R^2 = 0.06$; $F_{1,17} = 2.12$; $P = 0.16$; mucus, $R^2 = 0.01$; $F_{1,17} = 1.12$; $P = 0.31$; fin, $R^2 = 0.02$; $F_{1,17} = 1.32$; $P = 0.27$; scale, $R^2 = 0.01$; $F_{1,17} = 0.25$; $P = 0.62$).

Table 3. Number of individuals, tissue specific carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable-isotope ratios (Mean ±SD) indicating variation in isotope values between tissues

Tissue	n	$\delta^{13}C$ ‰	Range	δ15N ‰	Range
Muscle	19	-31.68 ± 0.77	-32.90 to -30.36	21.26 ± 1.03	19.15 to 22.94
Mucus	19	-32.23 ± 1.04	-34.15 to -30.84	20.88 ± 1.03	18.95 to 22.39
Fin	19	-31.15 ± 1.13	-33.38 to -29.13	21.27 ± 1.10	19.15 to 22.84
Scale	19	-28.67 ± 0.70	-29.68 to -27.37	19.99 ± 1.11	17.61 to 21.80

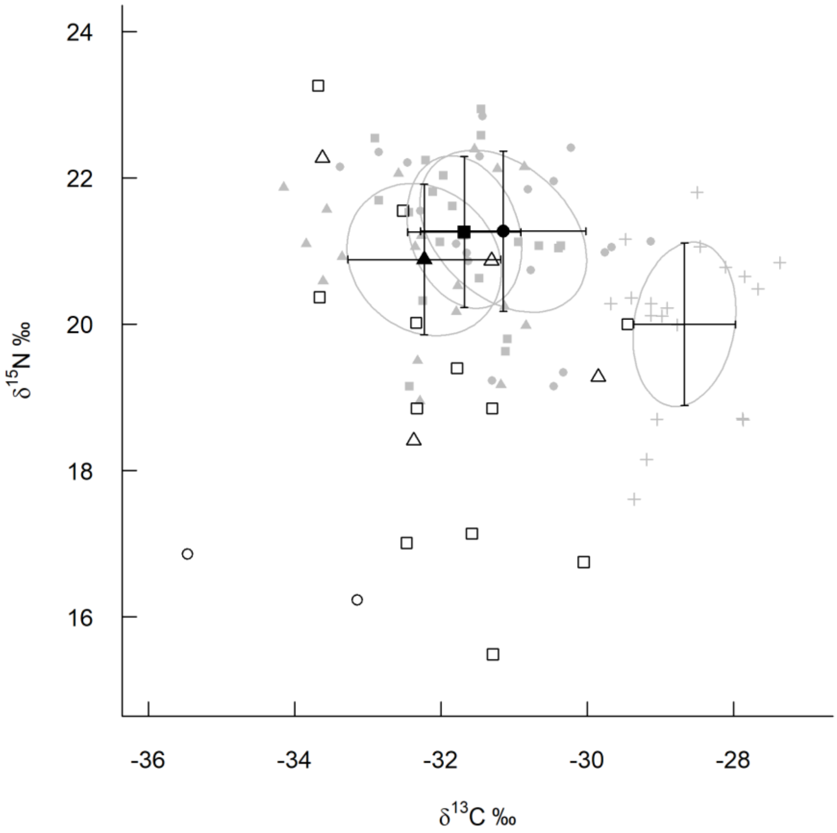

Figure 7. Stable isotope bi-plot of $\delta^{13}C$ versus $\delta^{15}N$ showing; individual (light grey) and mean (black) values for all tissue types (■ muscle; ▲mucus; ● fin; + scale), where error bars represent the standard deviation; and prey (□ Cyprinidae, ○ Invertebrates, Δ Percidae)

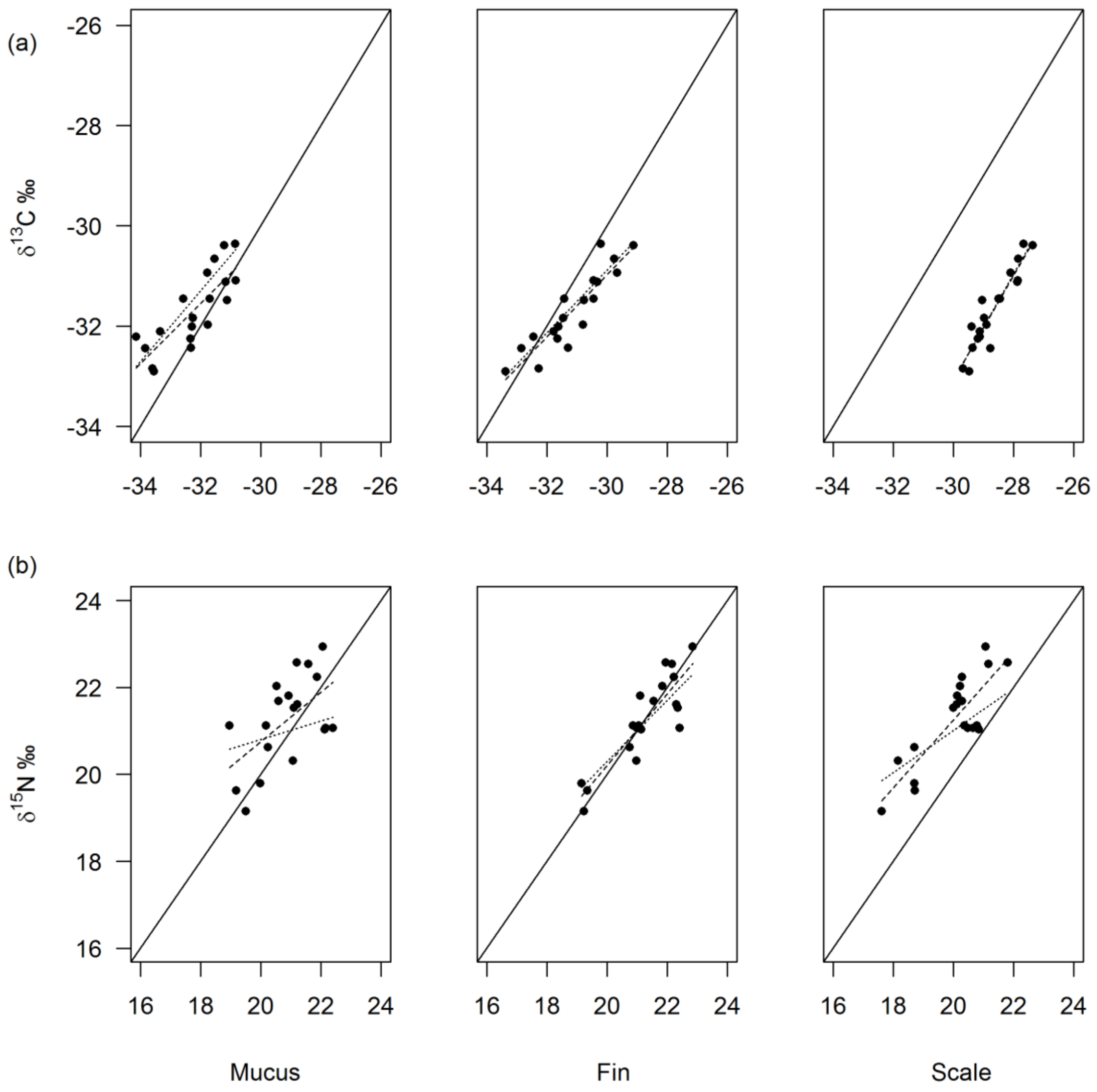

Figure 8. Linear relationships of (a) δ^{13}C and (b) δ^{15}N dorsal muscle versus epidermal mucus (‘mucus’), fin and scale, where the dotted line represents the relationship with length included in the model and the dashed line represents the relationship with length excluded.

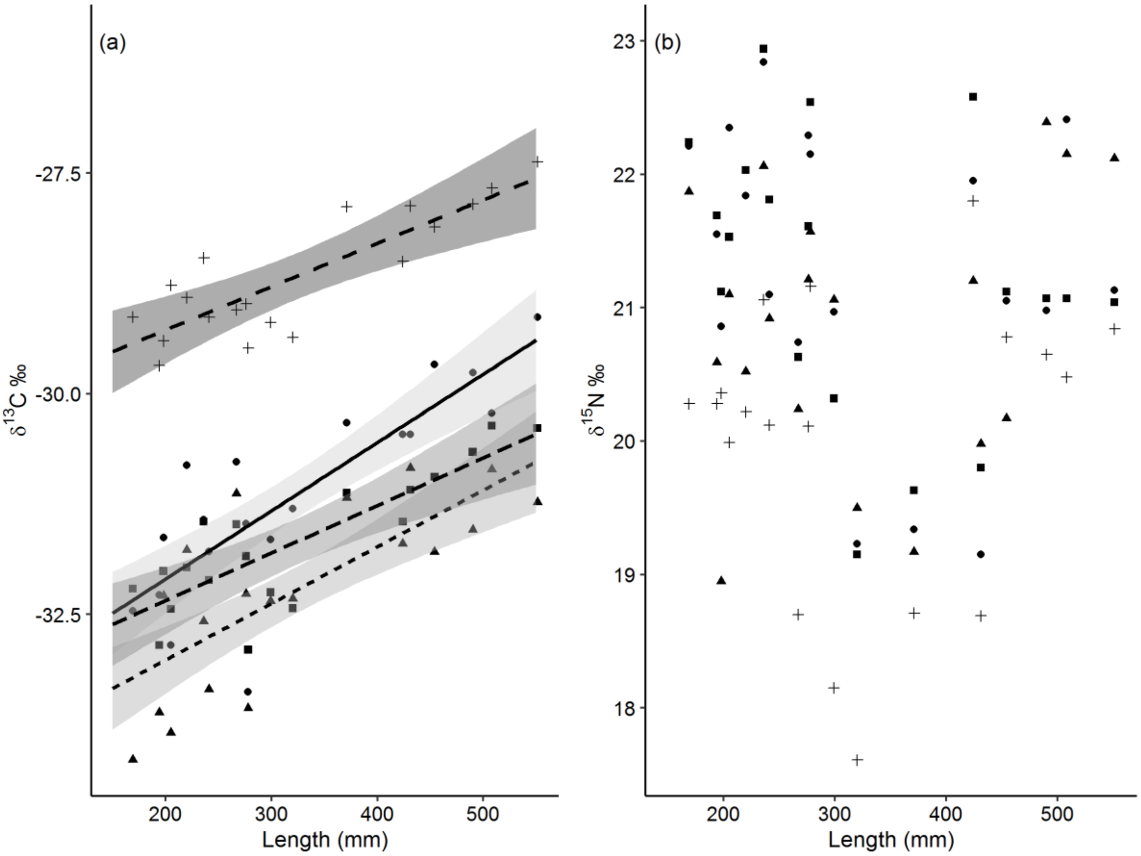

Figure 9. Linear relationships of (a) δ^{13}C and (b) δ^{15}N for muscle (■), mucus (▲), fin (●), and scale (+). Significant relationships are fitted with 95% confidence intervals around the line for muscle (long dashed line, light grey), mucus (short dashed line), fin (solid line) and scale (long dashed line, dark grey).

Table 4. Results showing the linear relationships of the stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of dorsal muscle with epidermal mucus, fin and scales.

Relationship	Isotope	R^2	F	P	a	b_1(95% CI)	b_2(95% CI)	AIC
Muscle/Mucus	$\delta^{13}C$	0.63	$_{(1,17)}$ 32.18	<0.001	-12.34	0.60 (0.37, 0.82)		29.02
Muscle/Mucus + length	$\delta^{13}C$	0.75	$_{(2,16)}$ 28.32	<0.001	-22.64	0.31(0.04, 0.58)	0.003 (0.001, 0.006)	22.45
Muscle/Mucus	$\delta^{15}N$	0.28	$_{(1,17)}$ 8.152	0.01	9.35	0.57 (0.15, 0.99)		52.60
Muscle/Mucus + length	$\delta^{15}N$	0.51	$_{(2,16)}$ 10.32	0.001	8.14	0.70 (0.33, 1.05)	-0.004 (-0.007, -0.001)	46.29
Muscle/Fin	$\delta^{13}C$	0.80	$_{(1,17)}$ 74.45	<0.001	-12.37	0.62 (0.47, 0.77)		17.23
Muscle/Fin + length	$\delta^{13}C$	0.82	$_{(2,17)}$ 42.34	<0.001	-18.04	0.46 (0.20, 0.71)	0.001 (-0.001, 0.004)	16.25
Muscle/Fin	$\delta^{15}N$	0.75	$_{(1,17)}$ 56.5	<0.001	3.71	0.83 (0.59, 1.06)		32.22
Muscle/Fin + length	$\delta^{15}N$	0.75	$_{(2,16)}$ 28.18	<0.001	4.57	0.79 (0.55, 1.04)	-0.001 (-0.003, 0.001)	33.36
Muscle/Scale	$\delta^{13}C$	0.86	$_{(1,17)}$ 111.9	<0.001	-1.90	1.04 (0.83, 1.25)		10.71
Muscle/ Scale + length	$\delta^{13}C$	0.86	$_{(2,16)}$ 56.4	<0.001	-6.69	0.88 (0.49, 1.27)	0.001 (-0.001, 0.003)	11.57
Muscle/Scale	$\delta^{15}N$	0.69	$_{(1,17)}$ 41.42	<0.001	5.65	0.78 (0.52, 1.04)		36.58
Muscle/ Scale + length	$\delta^{15}N$	0.88	$_{(2,16)}$ 72.21	<0.001	5.88	0.82 (0.67, 0.99)	-0.004 (-0.005, -0.002)	18.24

3.4.2 Stable isotope mixing models

The mixing models predicted the diet category ‘invertebrates’ to be the most important item to the diet of pikeperch < 350 mm, followed by Cyprinidae and then Percidae (Table 5). This result was consistent across all models (Table 5, Figure 10). For pikeperch > 350 mm, Cyprinidae had the greatest predicted contribution to pikeperch diet, followed by invertebrates and then Percidae (Table 5, Figure 10).

The difference in mean dietary contribution predictions across size classes between model 1 (muscle) and all other models was lowest for model 5 (scale data converted to dorsal muscle values) (Table 5, Figure 10). Differences were greatest between model 1 (muscle) and model 2 (mucus) for mean dietary contribution predictions in size class < 350 mm and for Percidae in size class > 350 mm, whereas differences were greatest between model 1 (muscle) and model 4 (epidermal mucus data converted to dorsal muscle values) for Cyprinidae and Invertebrates in size class > 350 mm (Table 5, Figure 10).

Table 5. Mean predicted dietary contributions from Bayesian mixing models of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of pikeperch by size class (< 350 mm & > 350 mm), showing standard deviation and 95% confidence limits. Mixing models were: 1) Consumer as muscle values; 2) Consumer as mucus values; 3) Consumer as scale values; 4) Consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ mucus to muscle; 5) Consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ scale to muscle

Resource		I < 350 mm				II > 350 mm			
	Model	Mean	SD	2.5% CI	95.7% CI	Mean	SD	2.5% CI	95.7% CI
Cyprinidae	1	0.32	0.13	0.07	0.552	0.47	0.22	0.04	0.83
	2	0.23	0.11	0.03	0.459	0.45	0.21	0.02	0.79
	3	0.28	0.11	0.07	0.499	0.40	0.18	0.05	0.73
	4	0.27	0.11	0.07	0.498	0.40	0.20	0.04	0.76
	5	0.31	0.12	0.07	0.535	0.46	0.21	0.04	0.81
Invertebrates	1	0.46	0.1	0.26	0.646	0.27	0.14	0.06	0.60
	2	0.63	0.11	0.4	0.811	0.33	0.13	0.11	0.59
	3	0.50	0.09	0.33	0.668	0.31	0.09	0.13	0.50
	4	0.49	0.09	0.31	0.648	0.38	0.17	0.10	0.76
	5	0.47	0.09	0.27	0.65	0.28	0.13	0.06	0.58
Percidae	1	0.23	0.12	0.03	0.475	0.26	0.19	0.01	0.68
	2	0.15	0.10	0.01	0.375	0.22	0.18	0.004	0.64
	3	0.22	0.10	0.04	0.439	0.29	0.16	0.02	0.62
	4	0.24	0.1	0.05	0.443	0.23	0.16	0.02	0.59
	5	0.23	0.11	0.04	0.454	0.27	0.18	0.02	0.68

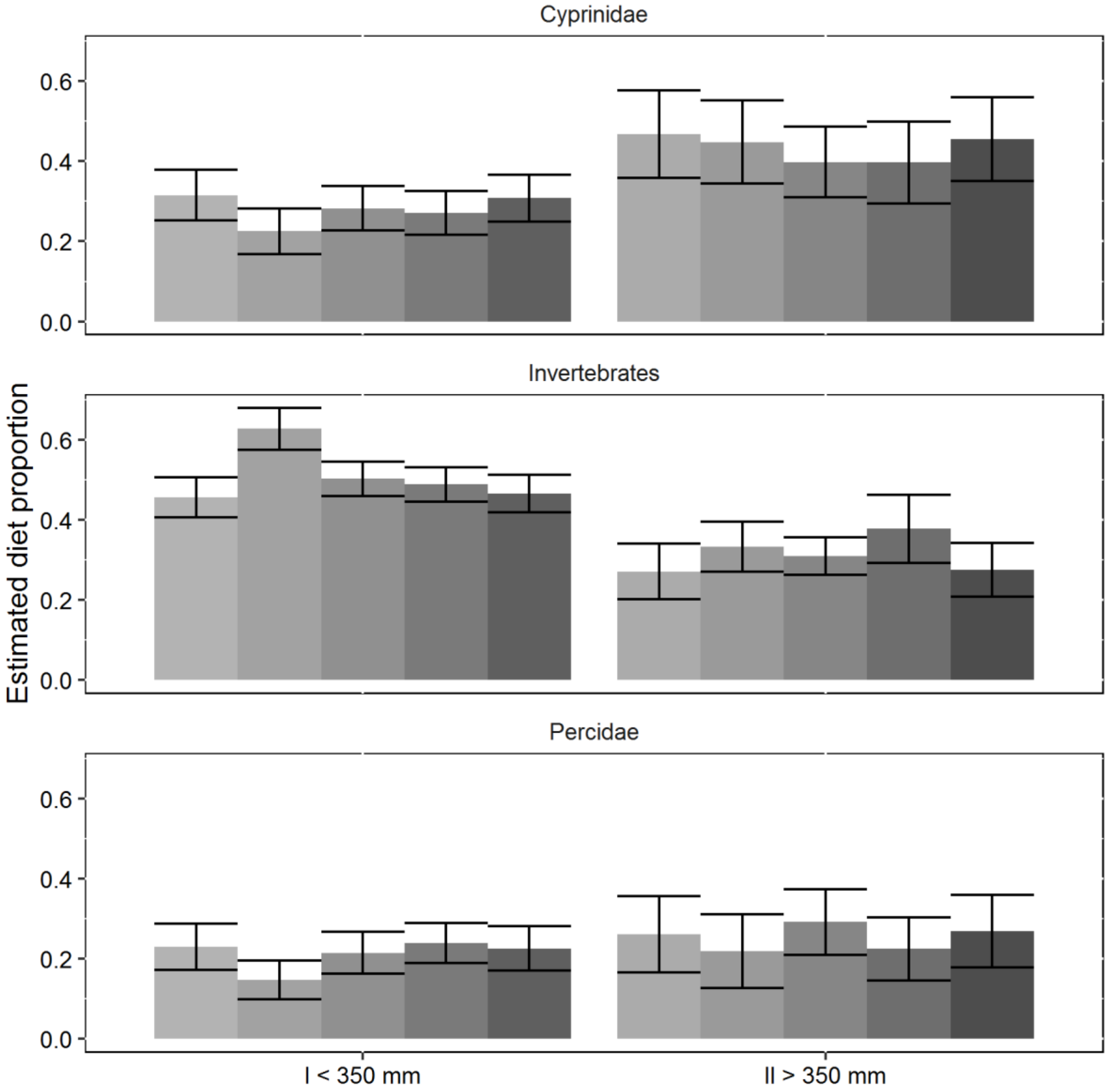

Figure 10. Mean predicted dietary contributions (0 – 1) of 'Cyprinidae', Invertebrates' and 'Percidae' to the diet of pikeperch by size class (< 350mm & > 350 mm) for each Bayesian mixing model. Models are represented by colour in sequence from light to dark, where model 1 is represented by light grey and model 5 by dark grey, and error bars represent the standard deviation. Mixing models were: 1) Consumer as muscle values; 2) Consumer as mucus values; 3) Consumer as scale values; 4) Consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ mucus to muscle; 5) Consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ scale to muscle.

3.4.3 Stomach contents analysis

Of the 180 sampled pikeperch, 98 had empty stomachs (54 %). Of the 82 fish with items in the stomach, analyses revealed that as pikeperch body size increased, the size of their prey significantly increased (Cyprinidae: $R^2 = 0.41$, $F_{1,65} = 46.48$, $P < 0.01$; Percidae: $R^2 = 0.43$, $F_{1,6} = 6.28$, $P = 0.05$) (Figure 11a). Between the two fish prey groups, there was no significant difference in their sizes (ANOVA $F_{1,72} = 0.35$, $P = 0.56$). Regarding prey: predator length ratios, these ratios generally decreased as pikeperch body size increased, although the relationships were not significant (Cyprinidae: $R^2 = 0.03$, $F_{1,6} = 2.23$, P = 0.14; Percidae: $R^2 = 0.09$, $F_{1,6} = 0.58$, $P = 0.47$; Figure 11b). The maximum prey length to predator length ratio was 0.38, whilst the minimum was 0.08 (mean ± SD; 0.22 ± 0.06), with the majority of pikeperch consuming small prey sizes relative to their body size (85% of prey < 0.3 prey length / predator length; Figure 11c).

The prey-specific abundance (% P_i) was highest for Cyprinidae at 79.8 %, followed by Percidae (13.1 %) and then invertebrates (7.11 %). Invertebrates were only represented in the diet of individuals up to 396 mm, whilst Cyprinidae were present in individuals from 204 to 532 mm and Percidae from 221 to 464 mm. Grouping pikeperch into the two size classes of < 350 mm (194 – 340 mm, n = 41) and > 351 mm (352 – 532 mm, n = 41) revealed the percentage prey abundance was higher for invertebrates in the smaller size category (< 350 mm = 15.8 %) than in the larger size class (> 350 mm = 0.5 %). For Percidae, the opposite pattern was evident, with higher % P_i for Percidae in the larger size class (> 350 mm = 20.3 %) than in the smaller size class (< 350 mm = 3.7 %). Percentage prey abundance remained similar for Cyprinidae in both size classes (< 350 mm = 80.5 %, > 350 mm = 79.3 %; Table 6).

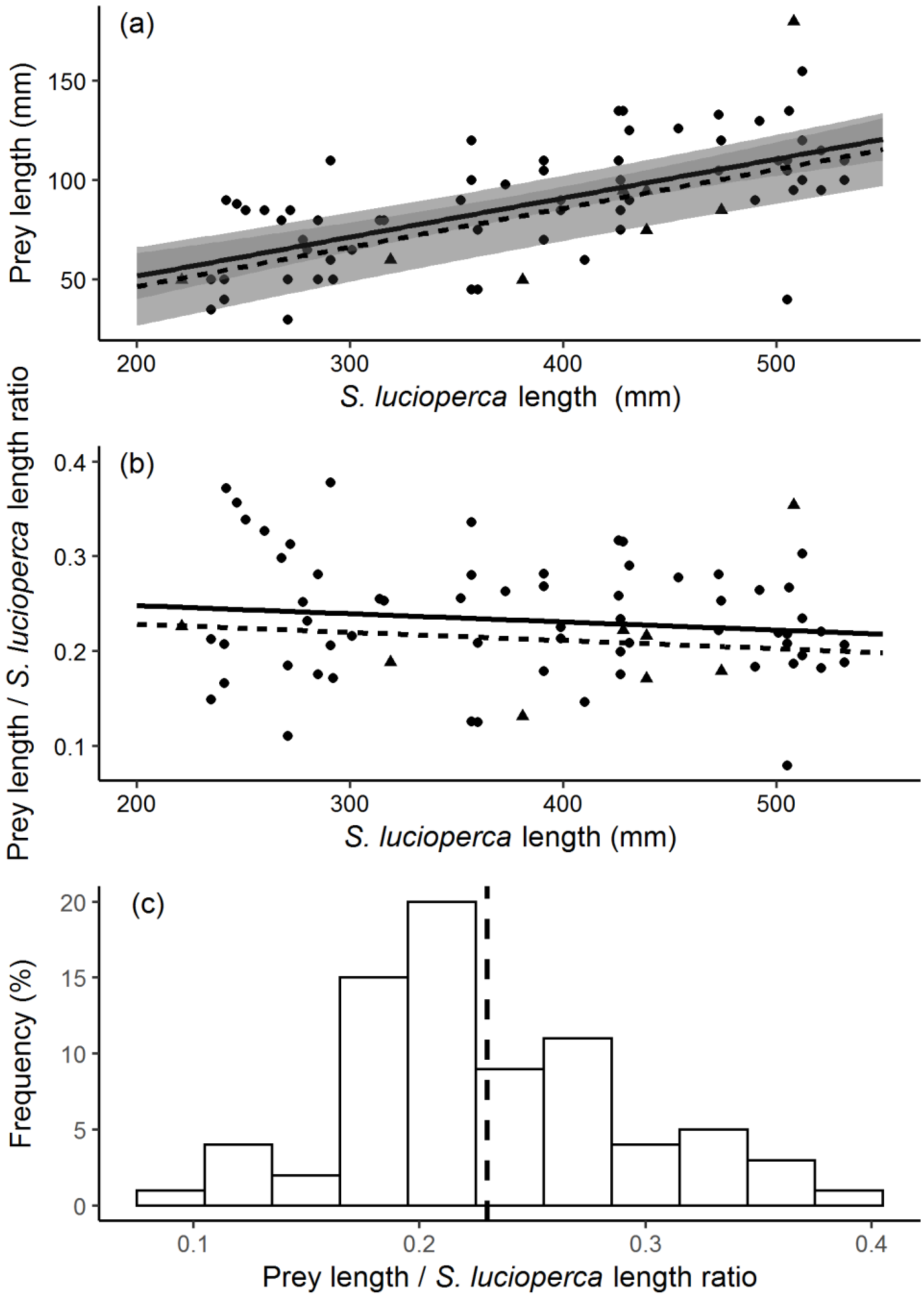

Figure 11. (a) Pikeperch size to prey size linear relationships (with 95% confidence intervals), (b) Prey: predator length ratios versus pikeperch body length, where lines represent relationships according to linear regression, and (c) Relative frequency distributions of prey: predator length ratios, where the mean prey size to predator size ratio is shown at 0.22. Relationships are shown for ‘Cyprinidae’ (closed circle, solid line) and ‘Percidae’ (closed triangle, dashed line)

Table 6. Frequency occurrence (% F_i) and prey specific abundance (% P_i) of diet by prey types ‘Cyprinidae’, ‘Percidae’ and ‘Invertebrate’ for pikeperch from the Grand Union Canal

Prey type	Size class	(% Fi)	(% Pi)
Cyprinidae	194 – 532 mm	70.2	79.8
	194 – 340 mm	73.2	80.5
	352 – 532 mm	67.9	79.3
Percidae	194 – 532 mm	21.3	13.1
	194 – 340 mm	9.8	3.7
	352 – 532 mm	30.2	20.3
Invertebrates	194 – 532 mm	8.5	7.1
	194 – 340 mm	17.1	15.8
	352 – 532 mm	1.9	0.5

3.5 Discussion

The predictable relationships between the SI data of dorsal muscle and from fins, scales and epidermal mucus revealed that tissues that can be collected by non-destructive methods can be used reliably within trophic studies on pikeperch, negating the collection of dorsal muscle samples. Mucus and fin showed no significant differences in isotope values compared to muscle, while scale was significantly depleted in δ^{15}N and enriched in δ^{13}C. Moreover, the data provided here enables the application of the SI data from these tissues to Bayesian mixing models for predicting diet composition from putative prey SI data (Parnell et al. 2013, Phillips et al. 2014, Stock et al. 2018). In this study, the diet composition predictions from Bayesian mixing model results were broadly similar to those from stomach contents analysis in assigning the importance of each prey type to the diet of pikeperch across size classes. The addition of stomach contents analysis, however, also provided data on the size-structured feeding relationships of these non-native piscivorous fish and their prey, revealing that these pikeperch were consuming small prey sizes relative to their body size. Finally, where diet assessments are being made in catch-and-release fisheries, the results suggest that tissue collection can successfully involve anglers, such as through scale collection (Kopp et al. 2009, Amat Trigo et al. 2017). In turn, this can help engage the public in research and build support for the conservation and management of aquatic resources (Cooke et al. 2013, Arlinghaus et al. 2017, Elmer et al. 2017).

The stomach contents analysis of this pikeperch population emphasised an inherent problem with the method; despite 180 fish being sampled, 98 had empty stomachs. Moreover, other studies that have utilised greater numbers of pikeperch have also reported this as an issue with, for example, over 20 % of 376 sampled individuals having empty stomachs in a sample from an Iberian reservoir (Pérez-Bote and Roso 2012), an average of 57.5 % of pikeperch stomachs reported to be empty across seasons and years in a German lake (Schulze et al. 2012) and 42 % of 591 sampled pikeperch from Lake Peipsi in Estonia with empty stomachs (Kangur and Kangur 1998). Additionally, high proportions of empty stomachs could be due to the sampling period, as data were collected during the spawning period (Lappalainen et al. 2003) which is known to be associated with reduced feeding in other piscivorous fishes (Dörner et al. 2003). Where this type of sampling regime is considered problematic, such as where it removes large numbers of fish from fisheries where pikeperch (or other piscivorous sport fishes) are an important target species for C&R (Hickley and Chare 2004), then stable isotope analysis clearly has high utility as a non-destructive dietary analysis tool.

Studies on the relationships of the SI values of fish dorsal muscle versus fin and scale tissues have shown that whilst differences in δ^{15}N are usually minor and often non-significant, there tends to be predictable shifts in δ^{13}C between the tissues (e.g. Pinnegar and Polunin 1999, Tronquart et al. 2012, Vašek et al. 2017). For example, in cyprinid fishes such as chub *Squalius cephalus*, barbel *Barbus barbus* and goldfish *Carassius auratus*, there was a predictable pattern of significant δ^{13}C enrichment from muscle to fin to scales (Busst et al. 2015, Busst and Britton 2016). This pattern of δ^{13}C enrichment between these tissues was also apparent here for pikeperch, although only significant from scales to muscle, mucus and fin. For epidermal mucus, however, studies have only recently started to determine how its SI values compares with other tissues, with limited differences in $\delta^{15}N$ but with more variability in $\delta^{13}C$ (e.g. Shigeta et al. 2017). Here, it was revealed that differences in $\delta^{13}C$ between mucus and muscle were primarily in mucus being depleted, a contrast to fin and scales. In a study of catfish *Silurus asotus*, there was also a general trend of depleted $\delta^{13}C$ values of mucus relative to muscle (Maruyama et al. 2017), and depleted relative to both muscle and fin in three freshwater cyprinid species (Shigeta et al. 2017). The tissues used in this study are also known to have considerable differences in their stable isotope turnover rates, with mucus generally having shorter half-lives when compared with fin and scale tissues (Church et al. 2009, Maruyama et al. 2017, Shigeta et al. 2017). The complementary use of these tissues in SIA could therefore provide insights into diet over different timescales, although this was not able to be assessed here. The use of mucus in fish isotope studies is still relatively new compared with tissues such as muscle and fin (Church et al. 2009, Maruyama et al. 2015, 2017). As such, further development work is needed, both specifically for pikeperch and for fishes more generally, with increased focus required on the isotopic relationship of mucus with other tissues, their turnover rates, and their fractionation factors with prey (Heady and Moore 2013). This work should then enable the wider application of epidermal mucus to fish stable isotope studies, with this potentially highly advantageous due to its ability to be collected by non-invasive sampling techniques from live fish.

The results of both dietary assessment methods here revealed that this pikeperch population was functioning as an obligate piscivore, but only in its larger sizes. Some ontogenetic dietary shifts were evident, with smaller individuals having diets that included macroinvertebrates. Whilst pikeperch tend to switch to piscivory during the first year of life (Mittelbach and Persson 1998), predictions from the Bayesian mixing models here suggested higher dietary contributions of invertebrates than fish for pikeperch < 350 mm, where all fish were greater than 1 year old (Nolan and Britton 2018a). This pattern was also reflected in stomach content analyses. Obligate piscivory in pikeperch has been reported in a number of studies (e.g. Campbell 1992, Kangur et al. 2007, Pérez-Bote and Roso 2012), and the benefits of becoming piscivorous early in life are well documented (Mehner et al. 1996, van Densen et al. 1996, Mittelbach and Persson 1998). However, in the absence of suitable sized prey fish, pikeperch will continue to consume invertebrates species (Ginter et al. 2011), but are likely to grow slower than those that are completely piscivorous (Persson and Brönmark 2008)

The stomach contents analysis of this pikeperch population also revealed that as pikeperch length increased, their prey fish size significantly increased, but that prey length to predator length ratios ranged between 0.08 and 0.38. These ratios were similar to those of (Keskinen and Marjomäki 2004) who also revealed that while lengths of pikeperch and their prey were positively correlated, their prey: predator size ratio were negatively correlated. Most prey were thus relatively small to the size of the predator, an outcome that cannot be explained by gape size limitations alone (Dörner et al. 2007). There was also no significant relationship between pikeperch length and $\delta^{15}N$ values, indicating that larger individuals were generally not feeding at higher trophic levels than smaller individuals (Post 2002). Active prey choice is thought to be more important in explaining diet patterns in pikeperch than passive selection mechanisms (Turesson et al. 2002). This behavioural trait could explain the trends seen here, indicating that in the absence of suitable-sized fish prey, pikeperch will utilise the resources available (i.e. invertebrates), but when fish prey are available, prey sizes are chosen which give the highest energy return per time spent foraging. These results on prey sizes highlight the value that SCA data can provide SIA studies, albeit with the caveat that its use is destructive or, if using non-lethal stomach evacuation techniques, are invasive to the individual fish.

Pikeperch also usually occupy higher trophic positions than other piscivorous fishes, with this apparent from across a range of habitat typologies (Campbell 1992, Kangur and Kangur 1998, Keskinen and Marjomäki 2004). This has been attributable to their piscivory of omnivorous cyprinid fishes (Keskinen and Marjomäki 2004) and, in larger pikeperch, on other piscivores such as perch *Perca fluviatilis* (Kopp et al. 2009). Other studies have also highlighted that cannibalism can be feature of pikeperch diet that tends to increase in importance with lengths over 250 mm (Campbell 1992, Didenko and Gurbyk 2016, Hempel et al. 2016), and so can help explain the high trophic position of larger individuals versus other piscivores (Kopp et al. 2009). The results here are generally consistent with these findings, with both roach and perch being the principal prey items encountered in stomachs. However, there was minimal evidence suggesting that these pikeperch were cannibalistic. This might be explained by the time of sampling, as young-of-the-year (YOY) pikeperch would not have been present in the population due to timing of spawning (Lappalainen et al. 2003). Both inter- and intra-cohort cannibalism in pikeperch has been shown to correlate with the density of juveniles in a population (Frankiewicz et al. 1999, Lappalainen et al. 2006). Indeed, cannibalism in pikeperch is seen as a key regulatory force in some populations (Mehner et al. 1996, Frankiewicz et al. 1999, Lappalainen et al. 2006)**.** This again points to the limitations of the stomach content analyses in providing accurate dietary assessments, as it was only completed at a single time of year.

In summary, this study has provided relationships on the stable isotope data of a range of tissues from pikeperch. The application of these data to Bayesian mixing models predicted strong ontogenetic dietary patterns, with shifts from macro-invertebrates/ fish to fish only as pikeperch length increased. These ontogenetic patterns were similarly evident in SCA, but with these data also highlighting that as pikeperch length increased, their prey size significantly increased, although prey items remained relatively small. In entirety, these results suggest that when non-destructive sampling is required for sport fishes such as pikeperch, SIA can be used to provide robust dietary assessments. However, if SCA can be completed then it can provide dietary data that are complementary to SIA and so help provide greater insights into their piscivory and predation pressure on native prey fishes.

4 Influences of ontogenetic dietary shifts on the trophic interactions of native and non-native freshwater piscivorous fishes in an invaded river catchment

4.1 Abstract

Introduced fishes for enhancing sport angling tend to be large bodied and of high trophic position, raising ecological concerns on both their impacts on prey communities and interactions with native fishes in the same functional guild. The piscivorous pikeperch *Sander lucioperca* is invasive in several European countries, including England where it occupies the same functional guild as the native Northern pike *Esox lucius*, with both fish undergoing an ontogenetic dietary shift from insectivory to piscivory during their juvenile life-stage. Here, the influence of this dietary shift on their trophic positions and niche sizes were assessed in three invaded sites in the lower Severn River Basin, Western England. Stable isotope metrics revealed that pikeperch switched their diet to piscivory at smaller body sizes than pike, with stomach contents analyses revealing piscivorous pikeperch from 31 mm. In both pike and pikeperch, there was low overlap in their trophic (isotopic) niches before and after their ontogenetic dietary switch to piscivory. The trophic niche of pike was significantly enlarged after switch to piscivory, but there were no significant differences in trophic niche sizes before and after switching for pikeperch. These results suggest some partitioning of prey resources between this invasive piscivore and native pike, irrespective of ontogenetic dietary shifts, suggesting that the ecological consequences of their invasion include predation pressure over a wider range of prey items than if the native pike was the only obligate piscivore present.

4.2 Introduction

Recreational angling acts as a major introduction pathway for non-native fishes, with large-bodied species often introduced to diversify sport angling experiences (Hickley and Chare 2004, Gozlan, Britton, et al. 2010). As these fish are of high trophic position (Eby et al. 2006), their invasions can result in substantial ecological impacts including increased predation pressure on native fish communities (Cucherousset and Olden 2011), potentially leading to trophic cascades (Drenner and Hambright 2002). For example, largemouth bass *Micropterus salmoides* which have been introduced globally for sport angling, exert strong top-down effects to native prey populations which can result in altered community structure (Pereira and Vitule 2019). In addition to these direct consumptive effects, indirect ecological impacts of non-native species introductions can also be incurred through both consumptive and non-consumptive effects (Sih et al. 2010). For instance, interactions with native species in the same trophic guild can result in behavioural alterations, trophic niche shifts, changes to food web structure and population declines (Cucherousset and Olden 2011, Ricciardi et al. 2013).

Understanding intra-guild trophic interactions between native and invasive fishes is thus important for predicting the ecological consequences of invasions (Guzzo et al. 2013, Britton et al. 2019). Resource partitioning is a key mechanism enabling the co-existence of functionally similar species (Guzzo et al. 2016, Butt et al. 2017, Britton et al. 2018), with studies suggesting that trophic niche divergence can be important in the structuring of invaded fish communities (Jackson and Britton 2014, Comte et al. 2016, Britton 2018). This divergence can occur when species minimise inter-specific competition by becoming more specialised in their diets, resulting in reduced population trophic niches that are divergent from competitors (Schulze et al. 2012, Jackson et al. 2016). Alternatively, increased competitive interactions can cause increased intraspecific resource variation and niche expansion through diets becoming more generalized (Svanbäck and Bolnick 2006).

Intra- and inter-specific trophic interactions can also be strongly influenced by ontogeny, where for predatory species, ontogenetic dietary shifts can be a key driver of dietary overlap that outweigh taxonomic differences (Woodward and Hildrew 2002b). For fishes in sympatry, these dietary switches influence the extent of intra- and inter-specific resource partitioning that facilitate their co-existence (Sánchez-Hernández et al. 2018). Ontogenetic dietary shifts in piscivorous fishes represent the period of development when individuals switch their diet to one primarily comprising of fish, with an early transition to piscivory potentially providing important fitness advantages (Mittelbach and Persson 1998). Ontogenetic dietary shifts can also influence the extent of individual movements and timing of natal departure from nursery areas (Cucherousset et al. 2013, Nyqvist et al. 2017). Predator-prey interactions in piscivorous fishes, particularly during ontogeny, are driven by morphological constraints, where maximum prey size is dependent on gape limitations (Mittelbach and Persson 1998, Lundvall et al.

1999). For freshwater, gape-size limited piscivorous fish, such as pike *Esox lucius* and pikeperch *Sander lucioperca*, these ontogenetic dietary switches generally occur in the first year of life, although the size at which this occurs can vary (Mittelbach and Persson 1998).

The pikeperch is a relatively large-bodied piscivorous fish that has been introduced for angling and aquaculture into countries including France, Spain and England (Hickley 1986, Elvira and Almodóvar 2001, Kopp et al. 2009). In England, where the native pike is the only other large-bodied piscivorous fish present, the first releases of non-native pikeperch for angling enhancement occurred in the 1960s (Hickley and Chare 2004), with invasive populations then developing in many river catchments in central and southern areas in the 1970s and 1980s (Hickley 1986). Described as a specialist piscivore (Kopp et al. 2009), ecological concerns on their invasion included both their predation of native fishes and their potential for adversely affecting native pike populations (Fickling and Lee 1983). Elsewhere, invasive pikeperch impacts on prey populations include predator-induced modification of prey behavioural traits (Hölker and Mehner 2005), and competitive interactions with native piscivores, but with their dietary overlap potentially being reduced due to differences in trophic positions and dietary specialisations that facilitate trophic niche partitioning (Kopp et al. 2009). There is, however, considerable uncertainty as to how these ecological interactions and mechanisms develop, especially in relation to ontogenetic dietary shifts.

The aim of this study was to therefore quantify the trophic interactions of sympatric native pike and invasive pikeperch populations, and in relation to their diet switch to piscivory, in the lower Severn River Basin, Western England. The approach was based on the application of stable isotope metrics using nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), given their utility for assessing the ecological interactions of native and invasive fishes (Cucherousset et al. 2012). The objectives were to quantify the body sizes at which ontogenetic dietary shifts to piscivory occurs in both species, assess how the ontogenetic dietary switches affect the size and position of their trophic niches, and assess the influence of the switch to piscivory on trophic niche overlaps within and between the species.

4.3 Methods

4.3.1 Sampling

The study areas were all within the lower reaches of the Severn River Basin, Western England (Figure 12a), and included sites within the lower River Severn between Diglis Weir (upstream) and Upper Lode Weir (downstream) (Figure 12a; 52.1819 N, -2.2241 W to 51.9943 N, 2.1735 W), and the lower Warwickshire Avon close to its confluence with the River Severn but separated from it by two weirs that were considered impassable to both species (Figure 12a; 51.9955 N, 2.1579 W to 52.1152 N, 2.0702 W). Pike and pikeperch populations have been present in sympatry in the study areas since the early 1980s (Hickley 1986). Both river sections have limited off-channel and littoral habitat, with river widths to 40 m and depths to 4 m. They are also popular locations for pike and pikeperch catch-and-release angling (Nolan, Curtin, et al. 2019). As a result of the characteristics of the main river channels, the application of traditional fish sampling techniques (e.g. electric fishing, seine netting, fyke netting) were largely ineffective. Sampling of pike and pikeperch was, therefore, primarily by catch-and-release angling in the main river channels and by seine netting in the limited off-channel areas provided by boat marinas located at Upton (Severn; Figure 12b) and at Tewkesbury, where one marina was connected to the River Severn and another was connected to the Warwickshire Avon (Figure 12c).

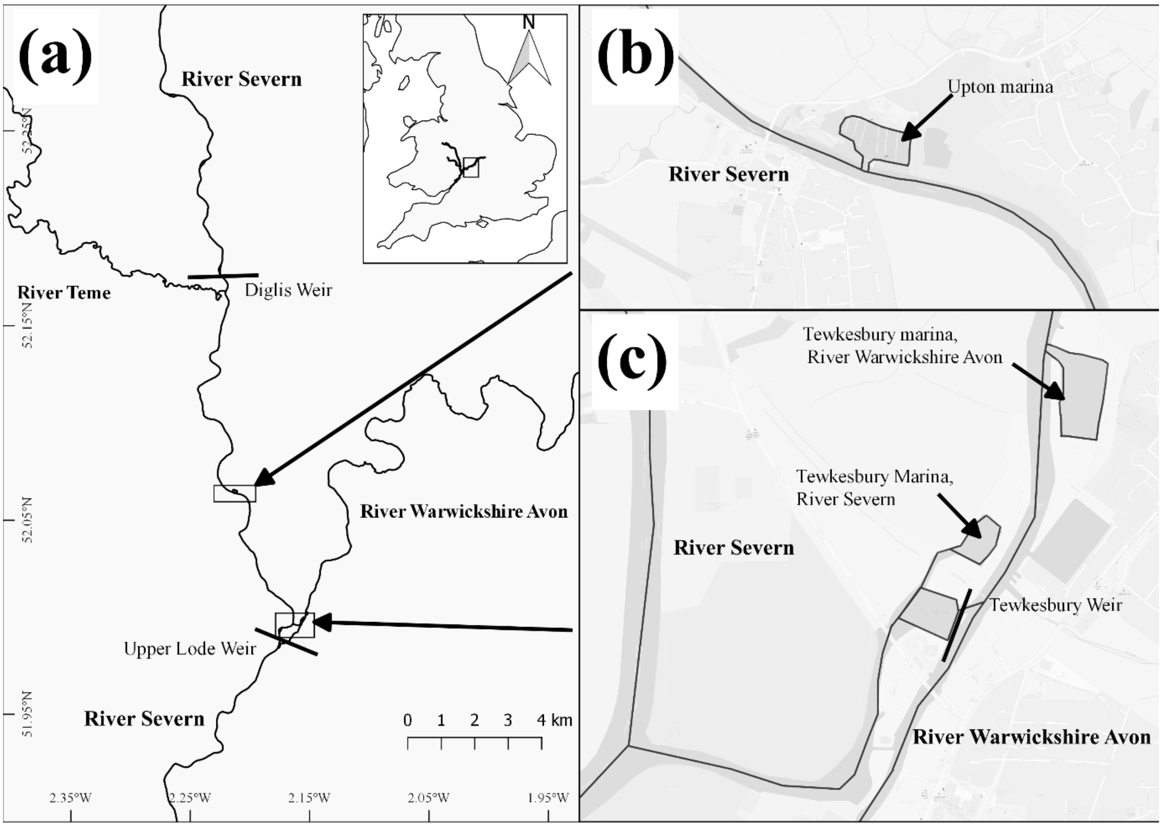

Figure 12. (a) Sampling locations on the Rivers Severn and Warwickshire Avon within the lower reaches of the River Severn basin in Western England (inset) and the position of off-channel sampling areas including (b) Upton Marina on the River Severn and (c) Tewkesbury marinas, one with connection to the River Severn and one with connection to the River Warwickshire Avon. Weirs are shown as solid lines.

Sampling by catch-and-release angling using specialist anglers occurred between June 2014 to December 2018; coordinated by the Environment Agency (the inland fishery regulatory body of England), who provided training in the collection of fish scales (from the body area between the dorsal fin and lateral line) and the recording of associated biometric and sampling data. While the purpose of scale sample collection was for fish age determination for management purposes, the scales also provided material suitable for stable isotope analysis (SIA) (Nolan, Gutmann Roberts, et al. 2019). Seine netting for fish and sweep-netting in the littoral zone for macro-invertebrates was completed every 6 weeks in off-channel areas between December 2016 and December 2018. During sampling, captured fish were identified to species, measured (nearest mm), and scale samples taken as per the angled fish. Pikeperch were then euthanised (overdose of anaesthetic, MS-222), and transported on ice to the laboratory for processing for stable isotope and stomach contents analysis. In contrast, all captured pike were returned alive due to their importance as the only native piscivore in the recreational fisheries of the rivers. Macro-invertebrate identification was to family level. Permission for sampling of fish was given by the Environment Agency. Regulated procedures on live fish were completed only by licenced individuals under UK Home Office licence 70/8063.

4.3.2 Stable isotope analysis

Fish scales are used regularly in stable isotope studies as a non-destructive sampling alternative in place of tissues such as muscle, with this particularly important for use in fisheries that operate on catch-and-release (Bašić and Britton 2015). Archived scale samples from both pike and pikeperch were thus available from angler caught fish in the River Severn basin which sustains an important catch-and-release fishery (Nolan, Curtin, et al. 2019). Scales tend to have a longer stable isotope half-life than muscle and fin tissue (Heady and Moore 2013, Busst and Britton 2017b), with predictable relationships for both pike and pikeperch between their scale stable isotope data and those from dorsal white muscle and fin tissue (Nolan and Britton 2018a, Winter et al. 2019). Processing of scale for isotope analysis was as per Trueman and Moore (2007), with scales cleaned with distilled water and the outer portion of the scale, which represents the most recent growth (generally the last full year), removed for analysis. Scale decalcification was not performed prior to analyses since the removal of inorganic carbonates has no significant effect on scale δ^{13}C and δ^{15}N values (Ventura and Jeppesen 2010).

One to three scales per individual were used for analyses (dependent on quantity of material). For macro-invertebrates, one to three individuals of the same family were used for analysis (dependent on body sizes); family groups were Asellidae (*Asellus aquaticus*), Chironomidae (non-biting midge larvae) and Gammaridae. For pikeperch < 100 mm, the small size of their scales prevented their effective use within SIA and so a portion of white dorsal muscle was used as an alternative tissue. All SIA samples were cleaned with distilled water and dried to constant mass at 60 °C prior to their analysis at the Cornell Isotope Laboratory, New York, U.S.A. The samples were then ground to powder, weighed to ~1,000 µg and analysed on a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, U.S.A.) interfaced to a NC2500 elemental analyser (CE Elantach Inc., U.S.A.). Verification of accuracy was against internationally known reference material and was tested every 10 runs. No lipid correction was performed as C:N ratios indicated low lipid content across all taxa (<3.5, Post et al. 2007).

4.3.3 Stomach content analysis

The pikeperch sampled from the boat marinas were analysed for their stomach contents in order to complement the SIA. Following estimation of total stomach fullness (% in volume), the prey items present in stomachs were identified to the lowest possible taxonomic level possible and their contribution to overall stomach fullness assessed. To quantify dietary shifts with body length, the prey items in stomachs were then categorised as either ‘macro-invertebrates’ or ‘fish’, and their contributions to diet expressed as percentages in terms of frequency of occurrence and prey-specific abundance. Frequency of occurrence (% F_i) of a given prey type was defined as the number of stomachs in which that prey occurred, expressed as a frequency of the total number of stomachs in which prey were present (Costello 1990). For prey-specific abundance, prey type contribution was first estimated in proportion to overall stomach fullness (in volume). The proportional fullness contribution of each diet category was then expressed as percentage prey specific abundance (% P_i):

$$\% P_i = \left(\frac{\sum F_i}{\sum F_t}\right) \times 100$$

Where P_i was the prey-specific abundance of prey *i*, *Fi* was the stomach content fullness for diet category *i* and *Ft* was the total stomach fullness in only those predators with prey *i* in their stomach (Amundsen et al. 1996). A binomial logistic regression was used to model the relationship between length and the binary response variables of diet (insectivorous vs. piscivorous), with fitted models used to estimate the length at which 50 % of individuals were predicted to be piscivorous.

4.3.4 Analyses of stable isotope data

Prior to analysing the stable isotope data, it was necessary to convert pikeperch muscle isotope values to scale values using pikeperch specific muscle to scale conversions, as there are inherent inter-tissue differences in their stable isotope values (Nolan and Britton 2018a). There was then a need to determine whether stable isotope data for pike, pikeperch and macro-invertebrates could be combined across sampling areas and years for the River Warwickshire Avon and the River Severn respectively (Appendix 3). For pike and pikeperch, this was completed using analysis of covariance (ANCOVA), testing for the independent and interactive effects on $\delta^{15}N$ and $\delta^{13}C$ of sampling area and year sampled (main effects), and fish length (covariate) (Appendix 3, Table A3.1). For macro-invertebrates, analysis of variance (ANOVA) tested for the independent and interactive effects on $\delta^{15}N$ and $\delta^{13}C$ of sampling area and year sampled (Appendix 3, Table A3.1). Temporal differences in $\delta^{15}N$ and $\delta^{13}C$ values were non-significant (Appendix 3, Table A3.2), but there were consistent, significant spatial differences for pikeperch $\delta^{15}N$ and $\delta^{13}C$ between the River Severn and Tewkesbury marina (River Severn side) (Appendix 3, Table A3.2). Consequently, all subsequent analyses were completed for three distinct areas (sites) in the study area: Site 1: the Warwickshire Avon, incorporating the River Warwickshire Avon and Tewkesbury marina (River Warwickshire Avon side); Site 2: the Severn, incorporating the River Severn and Upton marina; and Site 3: Tewkesbury marina (River Severn side) (Table 7; Figure 12).

The linear relationships of $\delta^{15}N$ and $\delta^{13}C$ versus body length were then tested for pike and pikeperch at each site using linear regression. To predict the body size at which a change in prey resource use occurred (i.e. the ontogenetic dietary shift to piscivory), regression models with segmented or piece-wise linear relationships were then fitted for $\delta^{15}N$ versus body length (Hammerschlag-Peyer et al. 2011); $\delta^{15}N$ was used in preference to $\delta^{13}C$ as it is more commonly used to estimate trophic position in animals due to its predictable enrichment with increasing trophic position (Post 2002). A segmented relationship is defined by the slope parameters and the breakpoints where the linear relation changes, and were determined using the package ‘segmented’ in R, implementing bootstrap restarting. Break-point estimates were reported, including standard error and regression coefficients (including the slope and intercept before and after breakpoints).

Table 7. Mean (± SD) carbon and nitrogen stable isotope ratios for pike and pikeperch from scale tissues and macro invertebrates by site, including the number of samples and their length range (mm). Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn.

Species	Site	n	Length range (mm)	Mean length (mm)	Range $\delta^{13}C$ (‰)	Mean δ13C (‰)	Range $\delta^{15}N$ (‰)	Mean $\delta^{15}N$ (‰)
Pikeperch	Site 1	54	40 to 870	206 ± 227	-32.99 to -25.19	-28.99 ± 1.93	13.19 to 21.72	18.30 ± 1.77
	Site 2	42	48 to 838	500 ± 234	-28.90 to -19.73	-24.94 ± 1.78	12.61 to 17.38	15.98 ± 0.85
	Site 3	67	29 to 331	76 ± 57.8	-32.79 to -27.43	-30.38 ± 1.43	13.20 to 20.82	17.65 ± 1.65
Pike	Site 1	35	101 to 1020	352 ± 283	-30.03 to -16.05	-26.46 ± 2.66	15.44 to 21.24	18.47 ± 1.33
	Site 2	78	114 to 1060	572 ± 295	-28.22 to -16.34	-23.54 ± 2.77	12.08 to 17.32	15.86 ± 1.00
Invertebrate	Site 1	25	NA	NA	-35.32 to -27.93	-30.16 ± 1.75	11.78 to 18.09	15.48 ± 1.79
	Site 2	17	NA	NA	-32.31 to -26.22	-29.46 ± 1.53	11.11 to 15.27	13.44 ± 1.23
	Site 3	18	NA	NA	-34.91 to -28.88	-32.15 ± 1.63	14.52 to 18.35	16.29 ± 1.04

The trophic positions (TP) of pike and pikeperch at distinct size classes within each population were then calculated through Bayesian estimation completed within the package ‘tRophicPosition’ in R (Quezada-Romegialli et al. 2017). Analysis were performed using the $\delta^{15}N$ and $\delta^{13}C$ values for the consumers pike and pikeperch and the baselines (macro-invertebrates) for each site. As such, a one baseline, two-trophic discrimination Bayesian model was run for each site with 5 parallel chains and 10,000 adaptive iterations which assumed a baseline trophic position of 2. The trophic discrimination factors used were 3.35 ± 0.5 ‰ for $\delta^{15}N$ and 3.49 ± 0.5 ‰ for $\delta^{13}C$, values which are suitable for piscivorous fish stable isotope data from scales (Nolan, Gutmann Roberts, et al. 2019). As ontogenetic dietary switches in pike and pikeperch are often apparent at lengths below 100 mm (Mittelbach and Persson 1998), this was tested in each species by estimating their posterior trophic positions at each 10 mm length increment for fish below 100 mm. For fish above this length, the grouping length increments were increased to 100 mm. Model outputs were reported as the means of all feasible solutions and the 5th-95th credible intervals of the distribution range.

The trophic niche of pike and pikeperch was calculated as the isotopic niche and was estimated at each site (population level) and for before and after the dietary shift to piscivory. For the latter, this was based on the predicted body sizes above and below the breakpoint from piecewise linear regression for each site). The isotopic niches were estimated using metrics based on stable isotope standard ellipse areas and completed within the package ‘Stable Isotope Bayesian Ellipses in R’ (SIBER; Jackson et al. 2011), with isotope niche metrics only calculated for sample sizes ≥ 5 (Table 10). Metrics included standard ellipse areas (SEA), this is a bivariate measure of the distribution of individuals in isotopic space and represents the typical resource use of a population (Jackson et al. 2011; Jackson et al. 2012). Additional calculations were the total area of the convex hull encompassing the data points (TA), the correction applied to SEA to account for small sample sizes (SEA_C), and the Bayesian estimated standard ellipse area (SEA_B) and their 95% credible intervals. Significant differences in the size of isotopic niches were identified when ≥ 95% of posterior draws from SEA_B for one area were smaller than the other. The area of niche overlap between ellipses was also calculated representing the area, in units of per mil squared, contained by the shape that lies within the overlapping ellipses. This was calculated both as the total proportional area of overlap and the proportional area of overlap for each ellipse. Prior to analyses, normality and homoscedasticity of data were assessed by visual inspection of the residual plots. Where error is expressed around the mean, it represents ± 95 % confidence limits unless otherwise stated. All statistical analysis and graphical outputs were performed using R (Version 3.5.3; R Development Core Team 2018).

4.4 Results

4.4.1 Stomach content analysis

At all sites, the most important prey item in pikeperch stomachs were fish, with piscivory evident at body lengths from 31 mm (Table 8, Appendix 3, Table A3.3). Macro-invertebrates were important as prey for individuals of lengths to 153 mm at site 1, but these prey items were only found in individuals below 31mm at Site 3. All analysed pikeperch at Site 2 were piscivorous, although the sample size was limited ($n = 7$; Table 8). Binomial logistic regression predicted the size at which 50 % of individuals were piscivorous as 69 ± 20 mm at Site 1 and 28 ± 8 mm at Site 3.

4.4.2 Stable isotope relationships with length

Regression analyses revealed significant enrichment in $\delta^{13}C$ and $\delta^{15}N$ with increasing length for both species and at all sites (Figure 13, Table 9), other than for length and $\delta^{15}N$ of pike at site 1 (Figure 13a; Table 9). Segmented relationships were significant for pike at Sites 1 and 2, and for pikeperch at Sites 1 and 3. Break-points for pike at Site 1 were 238 ± 36 mm and for Site 2 were 241 ± 14 mm (Figure 14a; Table 9). For pikeperch, break-points for Site 1 were 64 ± 7 mm and 148 ± 44 mm at Site 3 (Figure 14b, Table 9). There were no apparent breakpoints at Site 2 for pikeperch. Posterior trophic positions ranged from 2.07 to 2.96 for pike and from 2.02 to 3.21 for pikeperch. Trophic position increased with increasing body size in both species, with the lowest estimates in the smallest size class in pike (100 to 199 mm) and pikeperch (40-49 mm), while the highest estimates were for size classes 800 to 899 mm for pike and 600 to 699 mm for pikeperch (Figure 15).

Table 8 Frequency of occurrence (% F_i) and prey specific abundance (% P_i) of diet by prey types ‘macro-invertebrates’ and ‘fish’ for pikeperch from the River Severn basin Western England, by site, including the number of samples, number of empty stomachs and their length ranges (mm). Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn

Site	n	Empty stomachs (n)	Length range (mm)	Insectivorous length range (mm)	Piscivorous length range (mm)	% *F* (macro-invertebrates)	% *F* (fish)	% *Pi* (macro-invertebrates)	% *Pi* (fish)
Site 1	46	13	19 to 222	19 to 153	48 to 222	36.36	63.64	25.89	74.11
Site 2	7	3	48 to 490	-	77 to 100	0	100	0	100
Site 3	73	22	14 to 148	14 to 31	31 to 148	5.88	94.12	2.57	97.43

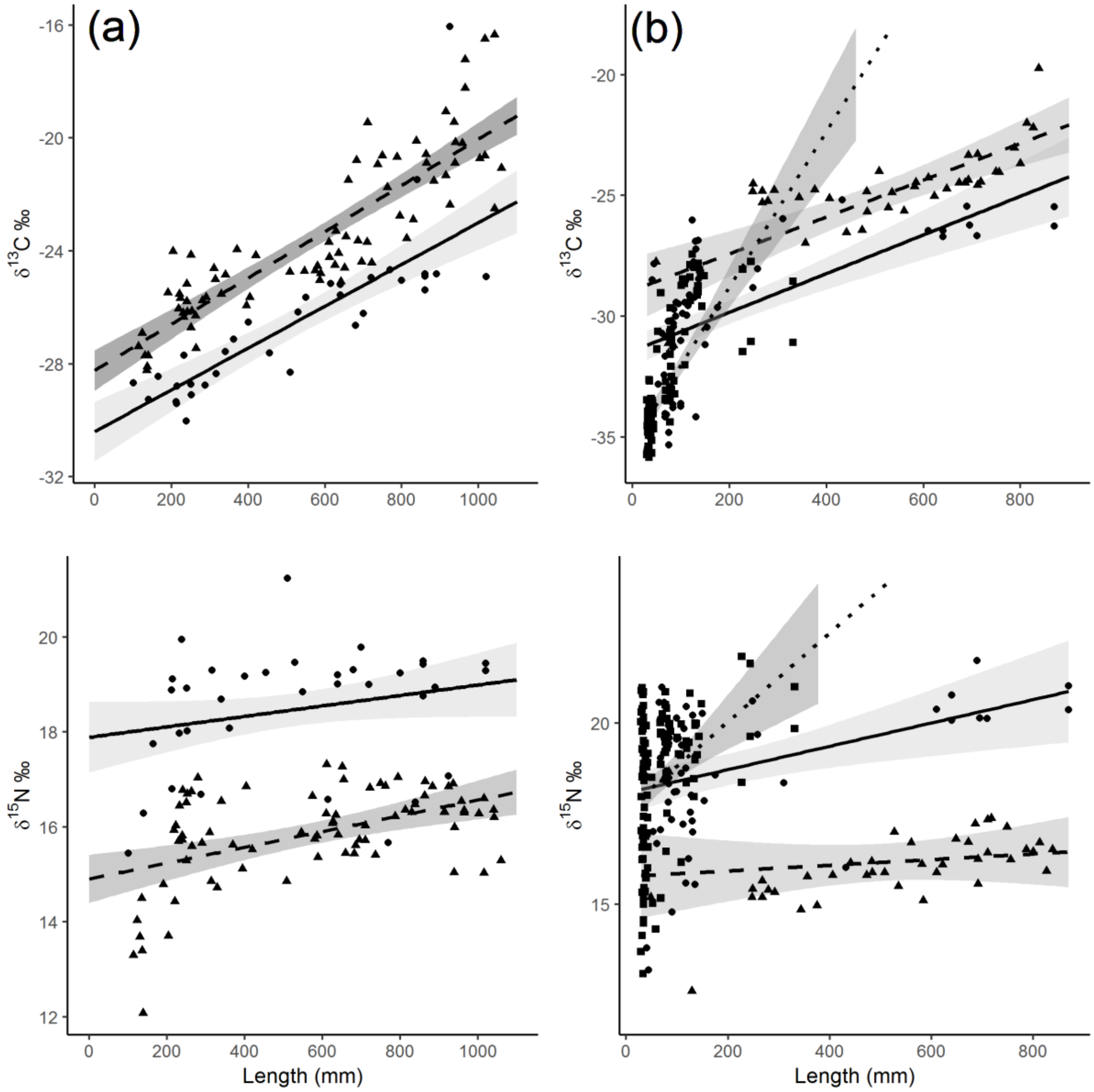

Figure 13. Linear relationships between pike (a) and pikeperch (b) length with $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) for site 1 (circle, solid line), site 2 (triangle, dashed line) and site 3 (square, dotted line) with 95% confidence intervals around the fitted values.

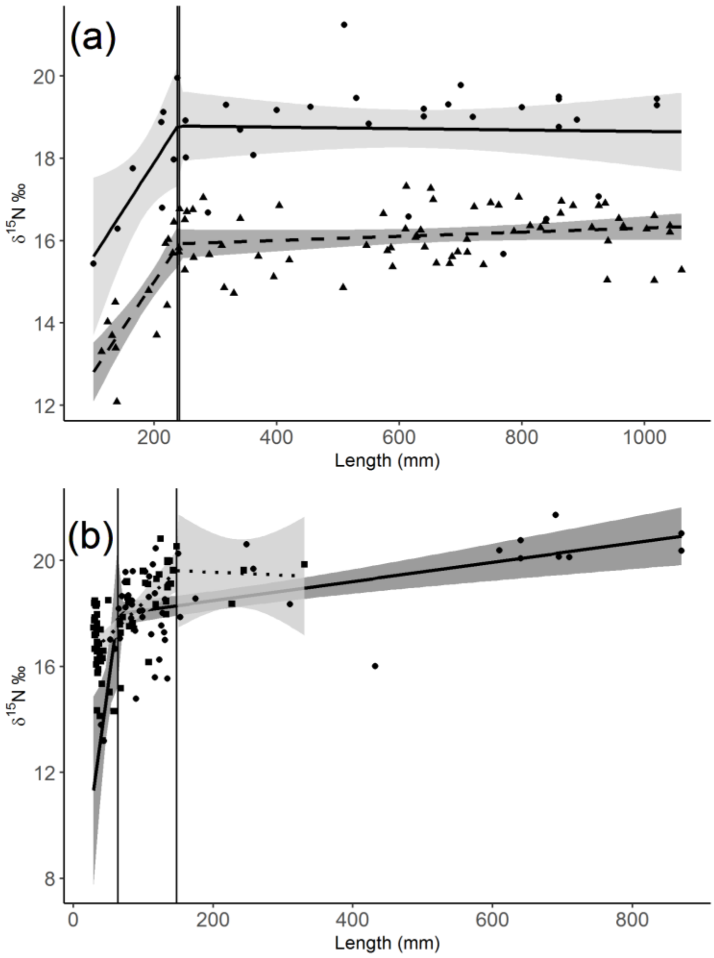

Figure 14. (a) pike and (b) pikeperch piecewise linear regression relationships between length (mm) and $\delta^{15}N$ stable isotope ratios from scale tissues, shown for (a) site 1 (circle, solid line) and site 2 (triangle, dashed line) and for (b) site 1 (circle, solid line) and site 3 (square, dotted line) with 95% confidence intervals around the fitted values. Breakpoints according to piecewise linear regression are highlighted for pike (a) (site 1: 238 mm: site 2: 241 mm) and pikeperch (b) (site 1: 64 mm: site 3: 148 mm).

Table 9. Relationships between pike and pikeperch length with $\delta^{13}C$ and $\delta^{15}N$ for each site according to linear and segmented regression. Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn.

Species	Site	Relationship	Statistics (*a* slope and *b* intercept.)
Pike	Site 1	$\delta^{13}C$	$R^2 = 0.61$, $F_{1,33} = 54.38$, $P < 0.001$, $a = 0.01$, $b = -30.40$
		$\delta^{15}N$	$R^2 = 0.03$, $F_{1,33} = 1.94$, $P = 0.17$, $a = 0.01$, $b = 17.89$
		Segmented $\delta^{15}N$	$R^2 = 0.19$, $P = 0.02$, $a1 = 0.02$, $b1 = 13.28$, $a2 = -0.01$, $b2 = 14.11$
	Site 2	$\delta^{13}C$	$R^2 = 0.76$, $F_{1,76} = 243.2$, $P < 0.001$, $a = 0.01$, $b = -28.23$
		$\delta^{15}N$	$R^2 = 0.23$, $F_{1,76} = 24.03$, $P < 0.001$, $a = 0.01$, $b = 14.91$
		Segmented $\delta^{15}N$	$R^2 = 0.54$, $P < 0.01$, $a1 = 0.02$, $b1 = 10.56$, $a2 = 0.01$, $b2 = 10.87$
Pikeperch	Site 1	$\delta^{13}C$	$R^2 = 0.50$, $F_{1,52} = 54.98$, $P < 0.001$, $a = 0.01$, $b = -30.24$
		$\delta^{15}N$	$R^2 = 0.29$, $F_{1,52} = 22.42$, $P < 0.001$, $a = 0.01$, $b = 17.42$
		Segmented $\delta^{15}N$	$R^2 = 0.48$, $P = 0.02$, $a1 = 0.19$, $b1 = 5.82$, $a2 = 0.01$, $b2 = 7.20$
	Site 2	$\delta^{13}C$	$R^2 = 0.65$, $F_{1,40} = 76.83$, $P < 0.001$, $a = 0.01$, $b = -28.02$
		$\delta^{15}N$	$R^2 = 0.35$, $F_{1,40} = 22.97$, $P < 0.001$, $a = 0.01$, $b = 14.89$
	Site 3	$\delta^{13}C$	$R^2 = 0.60$, $F_{1,65} = 99.26$, $P < 0.001$, $a = 0.02$, $b = -31.84$
		$\delta^{15}N$	$R^2 = 0.32$, $F_{1,65} = 32.22$, $P < 0.001$, $a = 0.02$, $b = 16.41$
		Segmented $\delta^{15}N$	$R^2 = 0.39$, $P < 0.01$, $a1 = 0.03$, $b1 = 15.88$, $a2 = -0.01$, $b2 = 17.03$

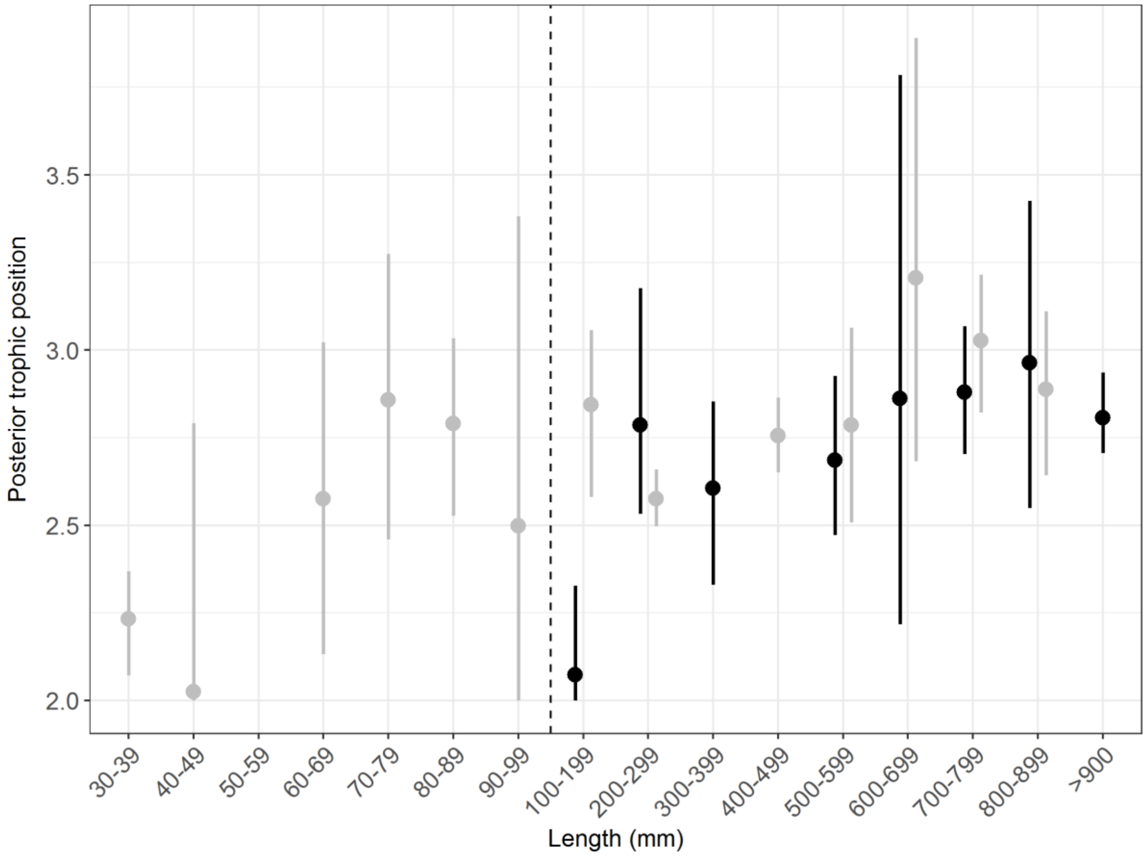

Figure 15. Posterior trophic position estimates (bars show 95% credible interval of each posterior trophic position) for pike (black) and pikeperch (grey) by size class within the Severn River Basin catchment, Western England. The dashed line represents a change in size class increments

4.4.3 Isotopic niche (as SEA$_B$)

The isotopic niches of pike and pikeperch were largest in Site 1 (Figure 16a; Table 10), with non-significant differences in niche size and near equal proportional niche overlap between species (pikeperch shared 34 % while pike shared 33 %). In contrast, the isotopic niches of pike and pikeperch were smallest at Site 2 (Figure 16b, Table 10), with pike having a significantly larger niche and sharing less niche space than pikeperch (42 % versus 75 %). The isotopic niche size of pikeperch at Site 3 was lower than at the other two sites (Figure 16c, Table 10).

Isotopic niche size could only be estimated pre- and post-ontogenetic dietary switch to piscivory for pike at Sites 1 and 2, and pikeperch at Site 1. The results revealed significant niche expansion post-switching to piscivory for pike but not for pikeperch, and with minimal niche overlap before and after the switch to piscivory within both species (Figure 16). Only at Site 1 could inter-specific differences be tested in isotopic niche overlap before and after the switch to piscivory. The results revealed that before the switch to piscivory, pike had a significantly smaller niche than pikeperch, and shared 14 % of their isotopic niche space, where pikeperch shared 4 % of their niche with pike, the total overlap was 3 %. Following the switches to piscivory in both species, there was no significant difference in their isotopic niche sizes and their niche overlap increased (total overlap 10 %, shared overlap at 19 % each)

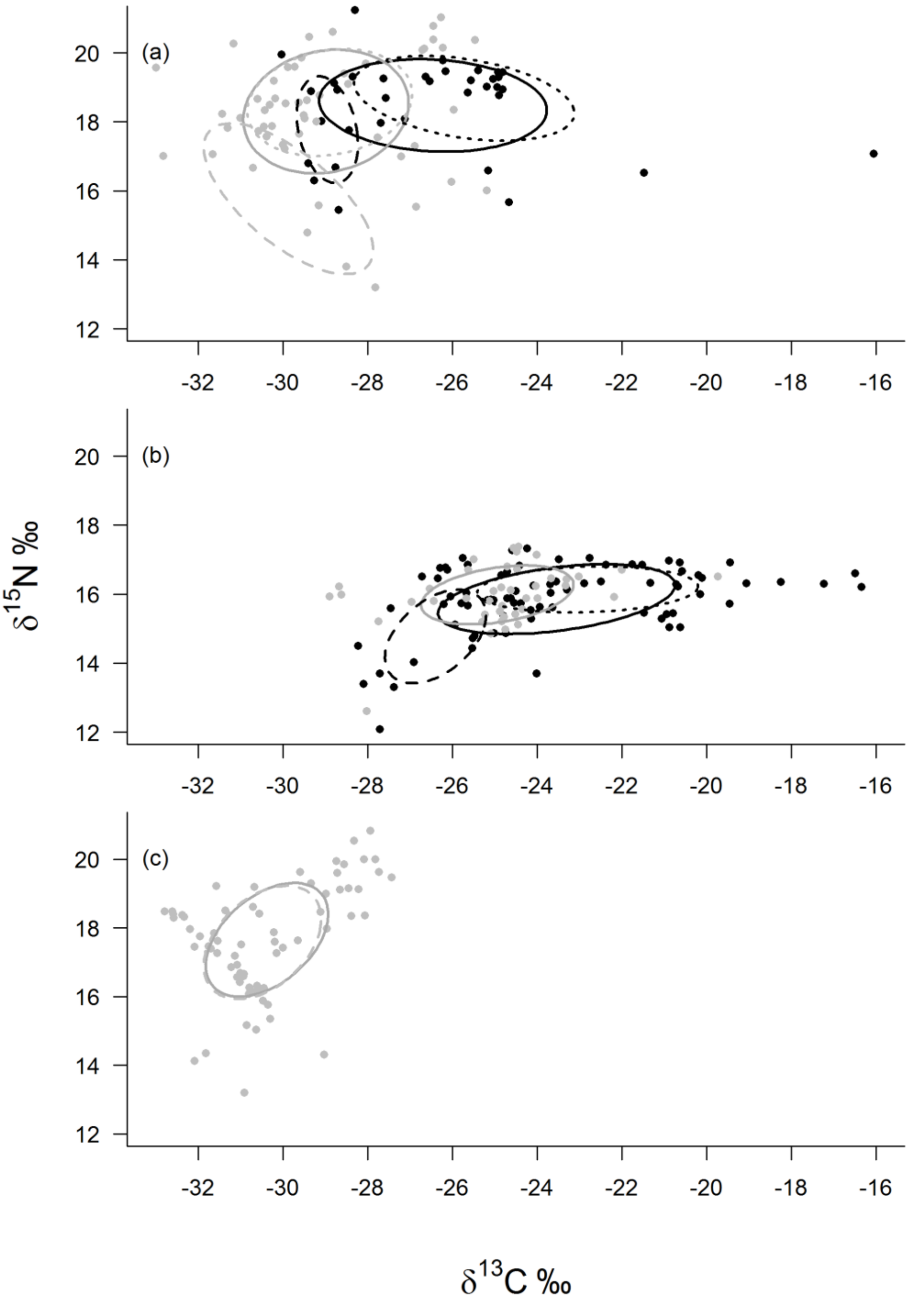

Figure 16. Stable isotope δ^{13}C and δ^{15}N bi-plots for pike (black) and pikeperch (grey). Bayesian standard ellipse area (40% SEA) are shown for whole population (solid line) and by species before ontogeny (dashed line) and after ontogeny (dotted line), determined by break-points from segmented linear regression. Plots are shown by location for (a) site 1, the Warwickshire Avon, (b) site 2, the Severn and (c) site 3, Tewkesbury marina, River Severn

Table 10. Isotopic niche metrics for pike and pikeperch by site and including groups before and after ontogeny, where TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area containing 40% of the data, SEA_C: Correction applied to SEA to account for small sample sizes, and the Bayesian estimate for SEA (SEA_B) with 95% credible intervals.

Site	Species	n	Length range (mm)	TA	SEA	SEA_C	SEA_B	SEA_B (95% CI)
1. Warwickshire Avon	Pikeperch	54	40 to 870	44.23	10.65	10.87	10.67	7.91, 13.92
	Pike	35	101 to 1020	43.71	11.02	11.35	11.16	7.61, 15.30
	Insectivorous Pikeperch	5	40 to 65	9.26	9.91	13.22	7.56	1.85, 17.46
	Insectivorous Pike	8	101 to 238	4.99	3.30	3.85	1.28	0.54, 2.55
	Piscivorous Pikeperch	49	67 to 870	36.09	9.12	9.32	8.59	6.61, 11.68
	Piscivorous Pike	27	251 to 1020	37.17	9.19	9.56	8.89	5.91, 12.56
2. River Severn	Pikeperch	42	48 to 838	21.31	4.43	4.54	4.48	3.15, 5.97
	Pike	78	114 to 1060	23.16	7.96	8.06	8.04	6.27, 9.89
	Insectivorous Pike	16	114 to 241	11.13	4.43	4.74	2.59	1.45, 4.10
	Piscivorous Pike	62	250 to 1060	19.02	5.28	5.37	4.53	3.45, 5.71
3. Tewkesbury marina	Pikeperch	67	29 to 331	25.47	6.57	6.67	6.65	5.11, 8.35
	Insectivorous Pikeperch	64	29 to 148	25.47	6.40	6.50	6.25	4.83, 7.88
	Piscivorous Pikeperch	3	227 to 331	NA	NA	NA	NA	NA

4.5 Discussion

Ontogenetic dietary shifts to piscivory are an important feature of the ecology of freshwater piscivorous fishes with body size an important determinant of predator-prey interactions. Here, break-points from piece-wise linear regressions and size class trophic position estimates revealed an ontogenetic dietary switch at smaller lengths for pikeperch compared to pike. Although there was spatial variability in the size at diet switching predicted from piece-wise linear regressing relationships for pikeperch (64 to 148 mm) compared to pike (238 to 241 mm), scale ageing revealed the diet switches to piscivory were during the first year of life for both species (unpublished data, the Authors, (Nolan and Britton 2018b)). These ontogenetic dietary shifts were also reflected in the trophic positions of both species, with increases in trophic position predicted at similar lengths to those indicated by the break-point analysis (50 to 70 mm for pikeperch, 200 to 300 mm for pike). The influence of these ontogenetic dietary shifts on the isotopic niches of the species was intra-specific isotopic niche segregation pre- and post-diet switching in both species, with some inter-specific niche partitioning evident, irrespective of the dietary switch to piscivory.

For pikeperch, a dietary switch to piscivory in the first growing season was supported through stomach contents analysis, where there was consistency in the size at which fish were the dominant prey item in stomachs across the sites. However, while break-points from segmented regression analysis for pikeperch produced a similar estimate of size at ontogenetic dietary switch at Site 1 (64 mm), the estimate was much higher at Site 3 (148 mm), although this was possibly an artefact of having fewer larger individuals in Site 3 rather than a delayed dietary switch. In a review of the dietary ontogeny of freshwater piscivorous fishes, pikeperch sizes at ontogenetic dietary switch to piscivory were found to range from 35 to 100 mm, which is usually within their first summer of life (Mittelbach and Persson 1998), with this trend well supported in other studies of ontogenetic dietary switch in pikeperch (Mehner et al. 1996, Persson and Brönmark 2002). For pike, the size at which their diet switched to being primarily piscivorous was consistent across the analytical methods and sites. These sizes were larger than reported for pike in Mittelbach and Persson (1998), where ontogenetic dietary switch to piscivory was found to be from 45 to 100 mm, although there can be considerable variation between individuals (Nyqvist et al. 2017) and high levels of dietary overlap between different ontogenetic stages in pike (Amundsen et al. 2003)

An early ontogenetic dietary shift towards piscivory has been linked to higher than average growth rates in the early life stages of piscivorous fishes with benefits including increased energy returns and growth which increase the long term survival and fecundity of individuals (Mittelbach and Persson 1998, Sánchez-Hernández et al. 2018). Although it is common for pike and pikeperch to switch to piscivory in their first growth season (Mittelbach and Persson 1998), this switch can be delayed in the absence of suitable prey species (Ginter et al. 2011). Indeed, synchronisation of ontogenetic diet shifts with fluctuations in resource availability, such as new cohorts of prey, has been observed for pikeperch (Persson and Brönmark 2002). Individual variability in the timing of dietary switch can result in intra-cohort variation in the size of juveniles where there are both fast-growing piscivorous and slow-growing insectivorous individuals (van Densen et al. 1996). Despite the differences in size at ontogenetic dietary switch found here between the two species, they do represent a switch to piscivory in their first year of life, where the average size of pike and pikeperch at age 1 from the sampled population was 281 and 188 mm respectively (unpublished data, the Authors).

Inter- and intra- specific interactions of pike and pikeperch were assessed at both the population and group level, where the latter was based on the pre- and post-diet switch to piscivory from break point analysis. When the isotopic niches pre- and post-diet switching were estimated, pike and pikeperch were largely partitioned, with between species piscivorous life stages displaying more convergence in isotopic niche space and being of similar sizes. Niche sizes pre- and post-diet switching also showed some intra-specific niche divergence and constriction. A moderate niche compression of pike in response to the introduction of pikeperch was observed in a whole lake experiment in Germany (Schulze et al. 2012), where the extent of pike niche modification was reduced and the overlap between niches was asymmetrical towards pike due to a less specialised diet composition. Pike populations were also resilient to adverse effects from invasive pikeperch in rivers in southwest France due to differences in their trophic positions that suggested some key dietary differences (pike: 3.7, pikeperch: 4.2) (Kopp et al. 2009). Here, the estimates of trophic positions (TP) for both pike and pikeperch were lower in the River Severn catchment than found for these sympatric populations in southwest France, with intra-species differences in trophic position generally more apparent than inter-specific differences.

In general, pike have broader prey preferences than pikeperch, and can take larger prey, with studies based on stomach contents analysis corroborating the importance of specialisation in partitioning resources when the two species are in sympatry (Schulze et al. 2012, Didenko and Gurbyk 2016). Levels of specialisation in pike can vary with prey availability, and whilst considered as an obligate piscivore that specialises on fish prey, individuals often continue to consume macro-invertebrates as adults, resulting in generalists dietary populations (Chapman et al. 1989, Beaudoin et al. 1999, Pedreschi et al. 2015). However, many generalist populations often comprise of sub-sets of specialised individuals (Araújo et al. 2011) and this could potentially provide some explanation for the intra-specific differences in isotope niche size and position for pike at Site 2. Intraspecific variability has also been shown for example in largemouth bass, where ontogenetic dietary shifts result in trophic niche differences, but with individual dietary specialisations on distinct resources (aquatic versus terrestrial) being important determinants of within niche variability (Zhao et al. 2014).

Constricted and divergent dietary trophic niches are often an important mechanism in facilitating the co-existence of invasive and native sympatric fish populations (Jackson and Britton 2014, Tran et al. 2015). Partitioning of resources during the first growing season is particularly important for reducing competitive interactions in closely related piscivores (Specziár 2005). For pike and pikeperch, however, their predator-prey dynamics can be also strongly influenced by morphological constraints related to gape limitations and prey, with pike capable of taking much larger prey (Nilsson and Brönmark 2000, Dörner et al. 2007). Despite this, pike often choose smaller prey than gape limitations allow or than is predicted by energy budgets due to increased handling time associated with large prey (Nilsson and Brönmark 1999). The impact of pikeperch invasion here might thus be in pike exploiting large-bodied prey where available, reducing competitive interactions as a result of morphologically differences between the species. However, this must remain speculative given the absence of data from before the period of pikeperch invasion.

Stable isotopes are an important tool when assessing the trophic interactions and ecological effects of non-native freshwater fish species (Cucherousset et al. 2012). In particular, $\delta^{15}N$ and $\delta^{13}C$ enable estimates of trophic positions and energy sources to be made (Fry 2006), and can be used to define isotopic niche space through advanced Bayesian techniques as a reliable proxy for ecological niche (Newsome et al. 2007, Jackson et al. 2011). However, when estimating ontogenetic dietary shifts using stable isotopes, it is also important to account for isotopic turnover (Hertz et al. 2016). Specifically, it should be recognised that there will be a time lag between dietary changes and the stable isotope values of the consumer tissue (Vander Zanden et al. 2015). This is important here, given that growth rates in the early life stages of pike and pikeperch can be extremely high (Rypel 2012, Nolan and Britton 2018b), and so dietary changes might have occurred at smaller sizes than detected by the stable isotope analyses. The combined use of SIA with stomach content analyses for pikeperch here enabled some corroboration on the body size at which the fish switched their diet to piscivory.

In summary, the application of stable isotope metrics here provided information on the differences on the size at which a native and an invasive fish switched their diet to piscivory, and the influence of this dietary switch on their trophic (isotopic) niches. Before and after switching to piscivory, the fishes were largely partitioned in their isotopic niches, suggesting some key differences in their exploitation of prey resources, with differences in their functional morphology potentially providing some explanation of this. These results suggest, however, that the influence of invasive pikeperch in these sites was potentially to increase predation pressure across a wider range of prey resources than would already be exploited by pike, although the ecological implications of this require further work.

5 Predicting the contributions of novel marine prey resources from angling and anadromy to the diet of a freshwater apex predator

5.1 Abstract

Anadromous fishes can be important prey resources for piscivorous fauna in lowland rivers. Freshwater anglers exploiting large-bodied cypriniform fishes use high quantities of pelletized marine fishmeal baits that can contribute substantially to fish diets. This marine-derived energy pathway also potentially provides a marine prey resource for freshwater piscivores. However, large-bodied cypriniform fishes are often in a size refuge against predation due to their large sizes. Stable isotope (δ^{15}N and δ^{13}C) analysis assessed how novel marine prey resources influenced the diet of a freshwater apex predator, Northern pike *Esox lucius*, in an impounded river basin (lower River Severn, Western England). Up to three groups of prey resources were present: anadromous European shad (*Alosa* spp.), cypriniform fishes with dietary specialisms based on marine fishmeal baits, and freshwater prey. The availability of these prey resources to pike varied according to river connectivity and levels of angling exploitation in different river reaches.

Where the three prey groups were present, pike were more enriched in δ^{13}C values (range: -24.74 to -16.34 ‰) compared to river reaches where aspects of the marine prey groups were absent. (range: -28.30 to -21.47) In all reaches, δ^{13}C increased as pike length increased. In the reach where all prey groups were present, the isotopic niches of three pike size categories were strongly partitioned; this was not apparent in reaches where the marine pathways were unavailable. Stable isotope mixing models suggested that freshwater prey were the most important prey item, contributing between 42 and 96 % to the diet of individual pike. However, where present, anadromous fishes and cypriniform fishes specialising on marine fishmeal baits were also important prey items, contributing substantially to the diet of larger pike (length > 650 mm). The total dietary contributions of the marine resources varied considerably among the individual larger fish (22 to 58 % of total diet). The presence of two marine resource pathways in a lowland river thus strongly influenced the diet of an apex predator, but with contributions being a function of their spatial

availability, pike body size, and individual trophic specialisations. These results emphasise how the anthropogenic activities of river engineering and human subsidies can affect the trophic dynamics of apex predators.

5.2 Introduction

Allochthonous resource subsidies can substantially alter food web and community dynamics of the receiving systems through, for example, increased primary and secondary productivity (Polis et al. 1997, Marcarelli et al. 2011). Although the response of food-webs to allochthonous subsidies can vary (Marczak et al. 2007), these subsidies are increasingly recognised as important drivers of the behaviour and abundance of many consumer species (Newsome et al. 2014, 2015). In freshwater ecosystems, the transfer of nutrients from allochthonous resource subsidies can play a primary role in food-web structuring (Takimoto et al. 2002, Samways et al. 2018). The benefits to freshwater nutrient budgets via marine derived nutrient (MDN) transfer from anadromous salmonid fishes (via excretion, gamete release and carcass decomposition) have been well established (e.g. Wipfli et al. 2003, Zhang et al. 2003, Schindler et al. 2005, Richardson et al. 2016). However, anadromous fishes can also play an important role in the transfer of MDN to freshwaters via their direct consumption by freshwater apex predators (MacAvoy et al. 2000, Guillerault et al. 2017). Where the upstream migration of anadromous fishes is impeded by blockages such as weirs and dams (Ovidio and Philippart 2002, Clavero et al. 2004), their downstream aggregations potentially provide important foraging opportunities for piscivorous fauna (Sorel et al. 2016).

Fishery management activities often enhance freshwater angling experiences by diversifying the species available through the release of large-bodied invasive species, such as carp *Cyprinus carpio* and European barbel *Barbus barbus* (Hickley and Chare 2004). To target these fishes, catch-and-release anglers can release large amounts of ‘groundbait’ to attract fish (Jackson et al. 2013), with the quantities used often exceeding 1 kg of bait per day (Niesar et al. 2004). These baits are increasingly based on marine fishmeal, with the intensive use of pelletised marine fishmeal now common in freshwater angling in Western Europe (Arlinghaus and Mehner 2003, Bašić et al. 2015, Gutmann Roberts et al. 2017). This MDN subsidy can alter the trophic interactions between consumers (Bašić et al. 2015), assist invasions (Jackson et al. 2013), and are increasingly recognised as an important dietary resource to benthivorous and omnivorous fishes (Gutmann Roberts et al. 2017, Mehner et al. 2018). Where high concentrations of marine fishmeal have been released into freshwaters, it can be traced through food webs using stable isotope analyses (SIA), with $\delta^{13}C$ differentiating between freshwater (depleted $\delta^{13}C$) and marine energy sources (enriched $\delta^{13}C$) (Grey et al. 2004, Jardine et al. 2005, Rasmussen et al. 2009).

The presence of both anadromous fishes and freshwater fishes with diets comprising mainly of marine fishmeal thus potentially provide apex predators in lowland rivers with additional prey resources to freshwater prey. However, the ability of these predators to exploit these marine derived resources will at least partially depend on their ability to consume large bodied prey. This is because anadromous fishes entering freshwater to spawn tend to be relatively large, with even the smallest *Alosa* spp. migrants to European rivers generally being above 300 mm body length (Aprahamian 1988). Cypriniform fishes that have diets specialising on pelletised fishmeal also tend to be relatively large (> 380 mm) (Amat Trigo et al. 2017, Gutmann Roberts et al. 2017). Given that freshwater apex fish predators, such as Northern pike *Esox lucius*, are gape-limited in their prey selection (Nilsson and Brönmark 2000, Craig 2008) then these marine derived resources might only be available to the larger individuals in their populations. This influence of predator body size on their prey sizes is important, as apex predator populations often couple multiple energetic pathways in aquatic food webs through their exploitation of a wide range of prey resources (e.g. Rooney et al. 2008). Thus, traits that influence prey size in apex predators will influence their ability to couple these energy pathways (Nilsson and Brönmark 2000, Rooney et al. 2008).

Correspondingly, the aim here was to quantify how spatial variation in the availability of marine prey resources (large bodied anadromous fish and cypriniform fishes consuming MDN angler baits) influenced the diet of a gape-limited apex predator in a lowland river. Where present, the exploitation of marine energy pathways by a freshwater apex predator should lead to enriched $\delta^{13}C$ values and distinct population dietary niches versus those fish that forage where the marine energy pathways are absent (MacAvoy et al. 2000, Samways et al. 2018). The apex predator was pike, with their populations studied in the River Severn basin, Western England (Figure 17(a,b)), where individuals grow to relatively large sizes (body lengths > 1 m; mass > 12 kg). In this basin, there is considerable spatial variation in the availability of marine prey resources. Impoundments affect the upstream access of migrating anadromous fishes (mainly *Alosa* spp.; Aprahamian 1988); inputs of MDN based angling bait are affected by spatial differences in fish community structure and varying levels of angling activity (Gutmann Roberts et al. 2017). Using SIA to test the influence of the presence/ absence of these MDN subsidies on pike diet, the objectives were to (1) assess the spatial variability in stable isotope data of the marine and non-marine prey resources; (2) quantify the relationships between pike body length (as a proxy of gape size) and their stable isotope data; (3) determine the influence of the marine prey resources on pike trophic niche sizes (as isotopic niches); and (4) assess how the diet composition of pike at individual and population levels are influenced by differences in the spatial availability of the marine prey resources.

5.3 Methods

5.3.1 Study area

The presence of impoundments (weirs, sluices) in the area of study in the lower River Severn basin enabled its split into three study reaches based on longitudinal connectivity (Figure 17c). These included two contiguous reaches of the River Severn (one immediately upstream of the other but separated by a weir), and a reach of the Warwickshire Avon. The lower River Severn reach (hereafter referred to as the downstream Severn reach) was located between Diglis Weir (upstream limit) and Upper Lode Weir (downstream limit) (52.1819°, -2.2241° to 51.9943°, -2.1735°; Figure 17c). Although a relatively long river reach (> 20 km), most of the pike were sampled within the initial 1 km downstream of Diglis Weir where river widths were to 40 m and depths to at least 5 m. The upstream River Severn reach was located on the River Severn above Diglis Weir, Worcester (52.1819°, 2.2241° to 52.3728°, -2.3086°; Figure 17c). In this reach, river widths were to 30 m and depths to 4 m. The lower reach of the Warwickshire Avon (‘Warwickshire Avon’; 51.9955°, -2.1579° to 52.1152°, -2.0702°; Figure 17c) was up to 20 m wide, with depths to 4 m and is separated from the Severn by the presence of flow regulation structures (two separate weirs).

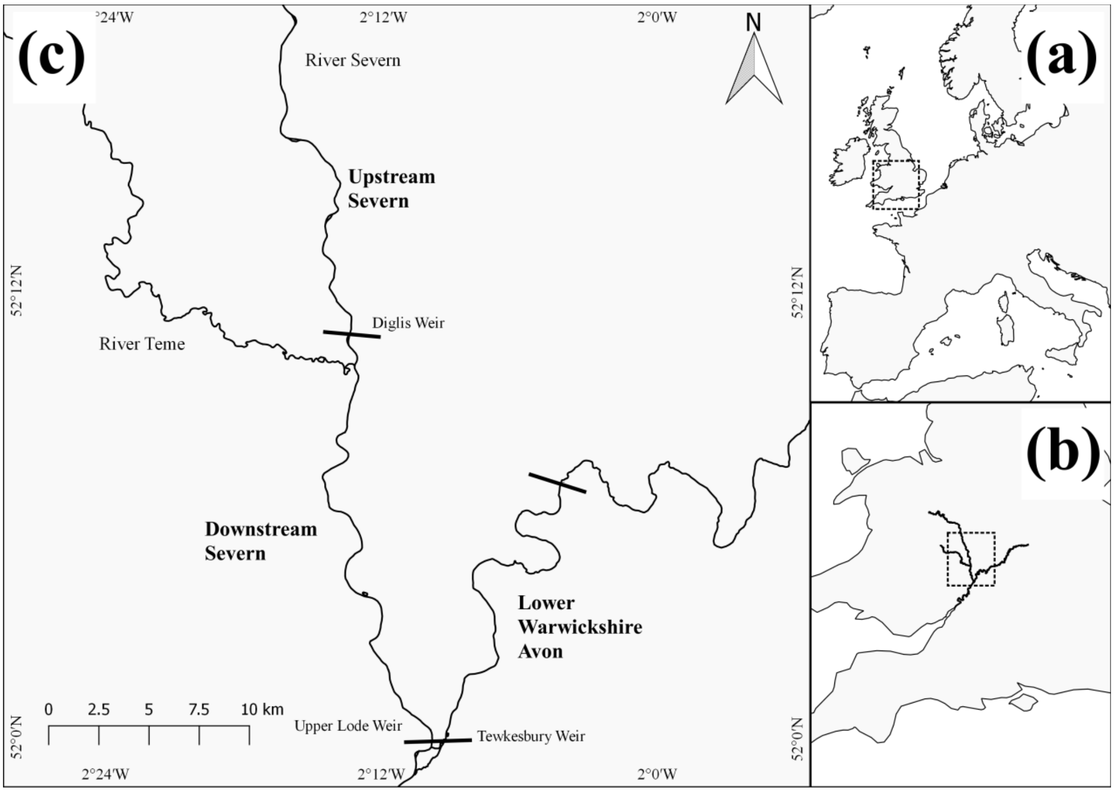

Figure 17. Western Europe showing the position (inset) of the study area (a), the location of the main rivers (inset) within the Severn River basin (b) and locations of the study reaches within the lower River Severn basin (c), where the areas of river covered by the reaches are represented as the areas between solid lines.

5.3.2 Sampling of pike

The habitat characteristics of the study reaches resulted in fish sampling by traditional methods (electric fishing, seine netting, fyke netting) being inefficient or unfeasible, other than within limited off-channel areas provided by boat marinas. Consequently, sample collection of pike was primarily via catch and release angling. This was facilitated by the Environment Agency, the inland fishery regulatory body of England, who established a pike angling network within the Severn catchment. Within this network, participating anglers recorded their catches and were trained in collecting scale samples. Whilst the primary purpose of scale collection was for fish age determination for management purposes, they concomitantly provided material suitable for stable isotope analysis in this study (Hutchinson and Trueman 2006, Bašić et al. 2015). Scales tend to have a longer stable isotope half-life than muscle and fin tissue (Busst and Britton 2017a). Consequently, between August 2014 and July 2017, anglers collected scales from captured pike and recorded the location and date of capture and fish fork length (Appendix 4, Table A4.1). Note, angling effort for pike was variable between reaches, being highest in the downstream Severn reach and lowest in the upstream Severn reach, resulting in spatial variation in pike sample sizes. Due to this method of sample collection, there was no opportunity for the collection of complementary data, such as stomach contents via stomach flushing or gape size measurements. Angling for pike is also not permitted on the river between mid-March and mid-June, a period covering the majority of the *Alosa* spawning season.

5.3.3 Spatial and temporal variation in the availability of putative prey of pike

Upper Lode weir is passable by anadromous *Alosa* spp. that enter the river each year to spawn between April and June, generally at lengths between 300 and 450 mm (Aprahamian 1988). Diglis weir and the weirs leading into the River Warwickshire Avon are, however, considered impassable to *Alosa* spp.. Therefore, the downstream Severn reach was considered as the only reach within the study where this anadromous energy pathway was present for pike. Although anadromous Atlantic salmon *Salmo salar* adults also enter the River Severn to spawn they are not resident in the study reaches or available as a prey resource as they can ascend all weirs on the main river during their upstream migration to spawning grounds located in the upper catchment. The Warwickshire Avon is inaccessible to migrating Atlantic salmon due to engineering structures in the lower river (Tewkesbury weir). Quantification of the levels of use of pelletized marine fishmeal baits by anglers within each reach could not be assessed directly (e.g. by creel census). However, large-bodied cypriniform fishes (mainly barbel, but also chub *Squalius cephalus*) in the downstream Severn reach have already been identified as specialising on pelletised fishmeal (Gutmann Roberts et al. 2017). Correspondingly, all reaches could potentially contain prey resources that include cypriniform fish specialising on marine fishmeal baits, but with the downstream Severn reach the only reach where both marine prey resource groups could be present (i.e. *Alosa* spp. and cypriniform fishes specialising on fishmeal baits). Note that throughout the catchment, whilst barbel populations were present and targeted by anglers, they were invasive, having been introduced in 1956 (Wheeler and Jordan 1990, Antognazza et al. 2016).

5.3.4 Sampling for putative prey species of pike

Samples for stable isotope analysis of the putative prey species of pike were collected throughout the study period from the downstream Severn and Warwickshire Avon reaches only, as logistical constraints prevented the collection of comparative putative prey species from the upstream Severn reach. The putative prey samples from the downstream Severn and Warwickshire Avon reaches were small cypriniform fishes (< 400 mm; roach *Rutilus rutilus*, chub and barbel), and macro-invertebrates (Gammaridae, Chironomidae and Asellidae), as macro-invertebrates can be important prey resources for pike, especially where individuals are less than 600 mm (Chapman et al. 1989, Venturelli and Tonn 2005, Pedreschi et al. 2015). Fish were sampled by angling in the main river channels and by seine netting in boat marinas, while macroinvertebrates were sampled by sweep netting in littoral areas. Samples of larger (> 400 mm) barbel and chub were collected via angling (Gutmann Roberts et al. 2017), ensuring that the putative prey resources of pike included larger cypriniform fish that can specialise on pelletised fishmeal (Gutmann Roberts et al. 2017). In addition, scale samples of *Alosa* spp. in the downstream Severn reach were collected opportunistically and non-invasively during their spawning periods (April to June), such as by collecting scales from carcasses from otter *Lutra lutra* predation. For all putative prey fish, identification was to species, with measurement (fork length, nearest mm) and the collection of 3 to 5 scales from the body area between the dorsal fin and lateral line. For macro-invertebrates, identification was to family.

5.3.5 Stable isotope analysis

For SIA, all captured pike from the upstream Severn reach were analysed (n = 8; lengths 420 to 901 mm). At the Warwickshire Avon reach, higher numbers of angler-captured fish enabled analysis of 19 pike across their length range (455 to 1020 mm). At the downstream Severn reach, 30 pike were analysed (508 to 1060 mm). Scale decalcification was not performed prior to their SIA. Whilst comparisons of acidified versus non-acidified scales have revealed significant differences in their isotopic data, the actual changes tend to be minor with, for example, Ventura and Jeppesen (2010) showing that the process produced mean changes in $\delta^{13}C$ (± SD) of 0.18 ± 0.12 and in $\delta^{15}N$ of -0.21 ± 0.24; conclusions were that these changes were not biologically relevant. Scale preparation for SIA thus focused on cleaning scales (distilled water) prior to the removal of the outer portion of the scale only. This process ensured the analysed tissue was only from the most recent growth of each fish (generally, the last full year of growth; (Hutchinson and Trueman 2006, Bašić and Britton 2015). For the majority of fish analysed, only one scale was used per individual, as this provided enough material for analysis. For smaller prey fishes (< 120 mm), up to three scales had to be used. For macro-invertebrates, three replicate samples were used per family, where a sample comprised of between one and three individuals (dependent on their body sizes). All samples were then dried to constant mass at 60 °C prior to their analysis at the Cornell Isotope Laboratory, New York, U.S.A. Stable isotope analytical details were as per Busst and Britton (2017a), with lipid correction not necessary as C:N ratios indicated very low lipid content (< 3.5; Post et al. 2007).

5.3.6 Data analyses

As samples were collected across years, data were first subject to analysis of variance (ANOVA) to test for differences in pike $\delta^{15}N$ and $\delta^{13}C$ values among years at each reach. As these results did not show consistent significant differences within reach (Appendix 4, Table A4.2), the stable isotope data were combined across all years without correction. The relationship between pike body length and $\delta^{15}N$ and $\delta^{13}C$ were determined for each reach using linear regression. Analysis of covariance (ANCOVA) was then used to test for independent and interactive effects of both reach and fish length on $\delta^{15}N$ and $\delta^{13}C$. Both models included reach as a factor (fixed, 3 levels: Warwickshire Avon, upstream Severn, downstream Severn) and fish length as a covariate, together with their interaction. Thus, a significant ($\alpha = 0.05$) interaction term would indicate that the relationship between the respective isotope value and body length varied according to reach. Where there was a significant main effect of reach, Tukey's post-hoc tests were used for pairwise comparisons between factor levels. In addition, differences in the SI data of all putative prey were tested between the downstream Severn and Warwickshire Avon reaches using t-tests. Prior to analyses, normality and homoscedasticity of data were assessed by visual inspection of the residual plots

The pike stable isotope data were then analysed in two ways. First, the isotopic niche of pike was estimated using metrics based on standard ellipses obtained by applying the data within a Bayesian framework, completed within the package 'Stable Isotope Bayesian Ellipses in R' (SIBER; Jackson et al. 2011). Niche metrics were first assessed for all pike at each reach and then, for the downstream Severn and Warwickshire Avon reaches where sample sizes were highest by three distinct size categories: ≥ 400 < 650 mm; ≥ 650 < 850 mm; and ≥ 850 mm. SIBER metrics were only calculated for sample sizes greater than or equal to five (Table 12). Isotopic niche sizes were calculated as standard ellipse areas (SEA), with these representing the core 40 % of the isotopic data (Jackson et al. 2011). This bivariate measure of the distribution of individuals in isotopic space thus is a representation of a population's typical resource use (Jackson et al. 2011; Jackson et al. 2012). Additional calculations were the total area of the convex hull encompassing the data points (TA), the correction applied to SEA to account for small sample sizes (SEA_C), and the Bayesian standard ellipse areas (SEA_B) and their 95% credible intervals. For SEA_B, significant differences in the size of isotopic niches were identified when ≥ 95% of posterior draws for one area were smaller than the other. The area of niche overlap between two or more ellipses was also calculated where appropriate.

Then, for pike at the downstream Severn and Warwickshire Avon reaches, their SI data were applied to Bayesian mixing models to predict the relative proportions (as posterior probability distributions) of the putative prey resources that contributed to their diet. This was not completed for the upstream Severn due to the low pike sample size (n < 5) and lack of SI data on their putative prey. The mixing models were completed in the package 'Mixing Models for Stable Isotope Analysis in R' (MixSIAR; Stock et al. 2018). MixSIAR was used to assess the proportional prey contributions to pike diet in the two reaches according to the three size categories outlined above for the niche metrics (to assess group level contributions), and then individually, by including individual as a covariate to explain variability in mixture proportions. This enabled assessment of differences in individual level contributions versus group level contributions. All models were run using 'normal' run length (chain length: 100,000 iterations with burn-in of 50,000, with posterior thinning (thin: 50) and 3 chains). Model diagnostics were based on Gelman-Rubin and Geweke, with sufficient convergence to accept the results (Stock and Semmens 2016a). The isotopic fractionation values between the prey resources and pike (δ^{15}N 3.35 ± 0.25 ‰; δ^{13}C 3.49 ± 0.25‰) were based on values obtained for other piscivorous fish through controlled feeding experiments (Barnes et al. 2007), with correction for scales from dorsal muscle (Heady and Moore 2013, Busst et al. 2015, Busst and Britton 2016). Mixing model outputs were reported as means of all feasible solutions with standard deviation and the 5th to 95th credible intervals of the distribution ranges.

Before the mixing models were run, there was consideration of how the putative prey data were entered. For the larger bodied (> 380 mm) cypriniform prey (barbel and chub), there was considerable range in their δ^{13}C isotope values (-28.4 to -19.4 ‰), with individuals with enriched δ^{13}C the result of their dietary specialisation on pelletised fishmeal released by anglers (Gutmann Roberts et al. 2017). Due to this considerable δ^{13}C range, this 'Cypriniform' prey resource was split into two groups ('marine' and 'freshwater'). This grouping was based on the Bayesian stable isotope mixing model results of Gutmann Roberts et al. (2017), where cypriniform prey resources with δ^{13}C of -22.90 to -19.40 ‰ had relatively high predicted proportions of MDN to their diet (predicted mean ± SE MDN contribution to diet: 0.50 ± 0.17; Appendix 4, Table A4.3). These fish were thus grouped as 'Cypriniform-marine' in the mixing models. Cypriniform prey resources with δ^{13}C of -28.04 to -23.04 ‰ had relatively low proportions of MDN in their diet (mean ± SE MDN contribution to diet: = 0.24 ± 0.11; Appendix 4, Table A4.3). These fish were then grouped as 'Cypriniform-freshwater' in the mixing models. The differences in MDN dietary contributions between the two groups were significant (t-test; $t = -5.66$, $P < 0.001$;

Table A3.3 Frequency of occurrence (% F_i) of prey types for pikeperch (*Sander lucioperca*) from stomach content analysis across three sites from the River Severn basin Western England. Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn

Prey	Frequency of Occurrence (% F*i*)		
	Site 1	Site 2	Site 3
Bleak	18.2	75	19.6
Roach	9.1	25	11.8
Common bream	3.0		1.0
Perch			2.0
Ruffe	3.0		
Unidentified fish	33.3		58.8
Daphniidae	21.2		3.9
Mysidae	18.2		1.9
Chrinomidae	3.0		1.9
Copepoda	18.2		
Odonata	3.0		
Simulidae	6.0		

Appendix 4Appendix 4, Table A4.3). Smaller bodied (< 380 mm) cypriniform fishes (roach, barbel and chub) were then all assigned to the appropriate group based on their isotope value and thus were incorporated within the 'Cypriniform-freshwater' group. This was due to the high similarity of their SI data with the larger non-MDN cypriniforms. Importantly, this also reduced the overall number of prey resources used in the mixing models, enhancing model performance and reducing prediction uncertainty (Phillips and Gregg 2003, Phillips et al. 2005).

The putative prey resources that could be entered into each mixing model were thus macro-invertebrates (combined data for Gammaridae, Chironomidae and Asellidae, due to similarity of SI data; *cf*. Results), *Alosa* spp., 'Cypriniform-freshwater' fish and 'Cypriniform-marine' fish, with the prey resources analysed separately for each reach. However, the use of all of these resources in the models for each pike size category was not appropriate. This was because of the pike size-specific gape limitations, where smaller individuals are limited in their ability to consume larger-bodied prey items (Nilsson and Brönmark 2000). The use of angler-captured fish meant the gape sizes of pike could not be measured directly. Therefore, for each individual pike analysed, their maximum ingestible prey size (MP) was estimated as a function of their fork length (FL) (MP = 0.13FL +0.40; Nilsson and Brönmark, 2000). To incorporate these maximum prey lengths into the analysis, mixing models were run for three size categories of pike outlined earlier. The mean MP was determined for each reach and size category, and only prey resources under the mean MP were entered into their mixing model (Table 11). Although this meant that the mixing models differed between the size categories, it ensured the final models were parsimonious and ecologically realistic. All statistical analysis and graphical outputs were performed using R (Version 3.5.2; R Development Core Team 2018). Where error is expressed around the mean, it represents ± 95% confidence limits unless otherwise stated.

5.4 Results

5.4.1 Stable isotope relationships with length in pike

There was a significant increase in $\delta^{13}C$ with increasing length for pike within reaches (Figure 18; Table 12; Warwickshire Avon: $R^2 = 0.34$, $F_{1,17} = 10.08$; $P < 0.01$, upstream

Severn: $R^2 = 0.71$, $F_{1.6}= 17.76$, $P < 0.01$; downstream Severn: $R^2 = 0.47$, $F_{1,28} = 24.75$, $P < 0.001$). This increase was also independent of reach (ANCOVA: $F_{1,51} = 75.21$, $P < 0.001$). The $\delta^{13}C$ values also differed significantly between reaches (ANCOVA: $F_{2,51} = 33.24$, $P < 0.001$), where pike from the Warwickshire Avon had depleted $\delta^{13}C$ versus both the downstream Severn (-3.49 ‰, $t = -7.87$, $P < 0.001$) and upstream Severn (-1.80 ‰, $t = -2.91$, $P = 0.01$). Fish from the downstream Severn reach also had significantly enriched $\delta^{13}C$ values versus the upstream Severn reach (+1.70 ‰, $t = 2.84$, $P = 0.02$). The interaction between length and reach was not significant (ANCOVA: $F_{2,51} = 2.86$, $P = 0.06$).

The relationship between $\delta^{15}N$ and fish length was not significant in the Warwickshire Avon ($R^2 = 0.04$, $F_{1,17} = 0.29$; $P = 0.60$) and downstream Severn ($R^2 = 0.01$, $F_{1,28} = 1.29$, $P = 0.28$) (Figure 18; Table 12). There was, however, a significant increase in $\delta^{15}N$ with fish length at upstream Severn (Figure 18; Table 12; $R^2 = 0.51$, $F_{1.6}= 6.12$, $P = 0.04$). The relationship between $\delta^{15}N$ and fish length was not significant independent of reach (ANCOVA: $F_{1,51} = 1.78$, $P = 0.19$), but $\delta^{15}N$ did differ significantly between reaches (ANCOVA: $F_{2,51} = 63.38$, $P < 0.001$). Fish in the Warwickshire Avon had significantly higher $\delta^{15}N$ than at the other reaches (downstream Severn +2.81 ‰, $t = 10.27$, $P < 0.01$; upstream Severn +3.06 ‰, $t = 8.04$, $P < 0.01$).

Table 11. Prey resources included in mixing models for each reach and pike size category, including their length range (mm) and carbon and nitrogen stable isotope ratios (‰).Cypriniform fishes as prey resources are separated to include those with a freshwater diet and those specialising on marine fishmeal bait

River reach	Pike size category	Prey resource	n	Prey Length range (mm)	Mean $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)
L. W. Avon	≥400 < 650 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	18	77 to 330	-26.69 ± 2.10	15.09 ± 1.69
	≥650 < 850 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	21	77 to 420	-26.50 ± 2.08	15.08 ± 1.85
	≥850 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	22	77 to 510	-26.45 ± 2.04	15.08 ± 1.81
Downstream Severn	≥400 < 650 mm	Macroinvertebrates	9		-29.67 ± 1.19	9.59 ± 0.81
		Cypriniforms – freshwater	15	60 to 316	-26.08 ± 1.38	12.49 ± 1.30
		Cypriniforms – marine	NA			
		Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90
	≥650 < 850 mm	Macroinvertebrates	9		-29.67 ± 1.19	9.59 ± 0.81
		Cypriniforms – freshwater	20	60 to 401	-25.94 ± 1.36	12.84 ± 1.37
		Cypriniforms – marine	5	380 to 450	-22.26 ± 0.19	11.88 ± 0.88
		Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90
	≥850 mm	Macroinvertebrates	9		--29.67 ± 1.19	9.59 ± 0.81
		Cypriniforms – freshwater	32	60 to 570	-25.56 ± 1.34	12.85 ± 1.21
		Cypriniforms – marine	21	380 to 565	-21.80 ± 0.98	11.73 ± 0.61
		Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90

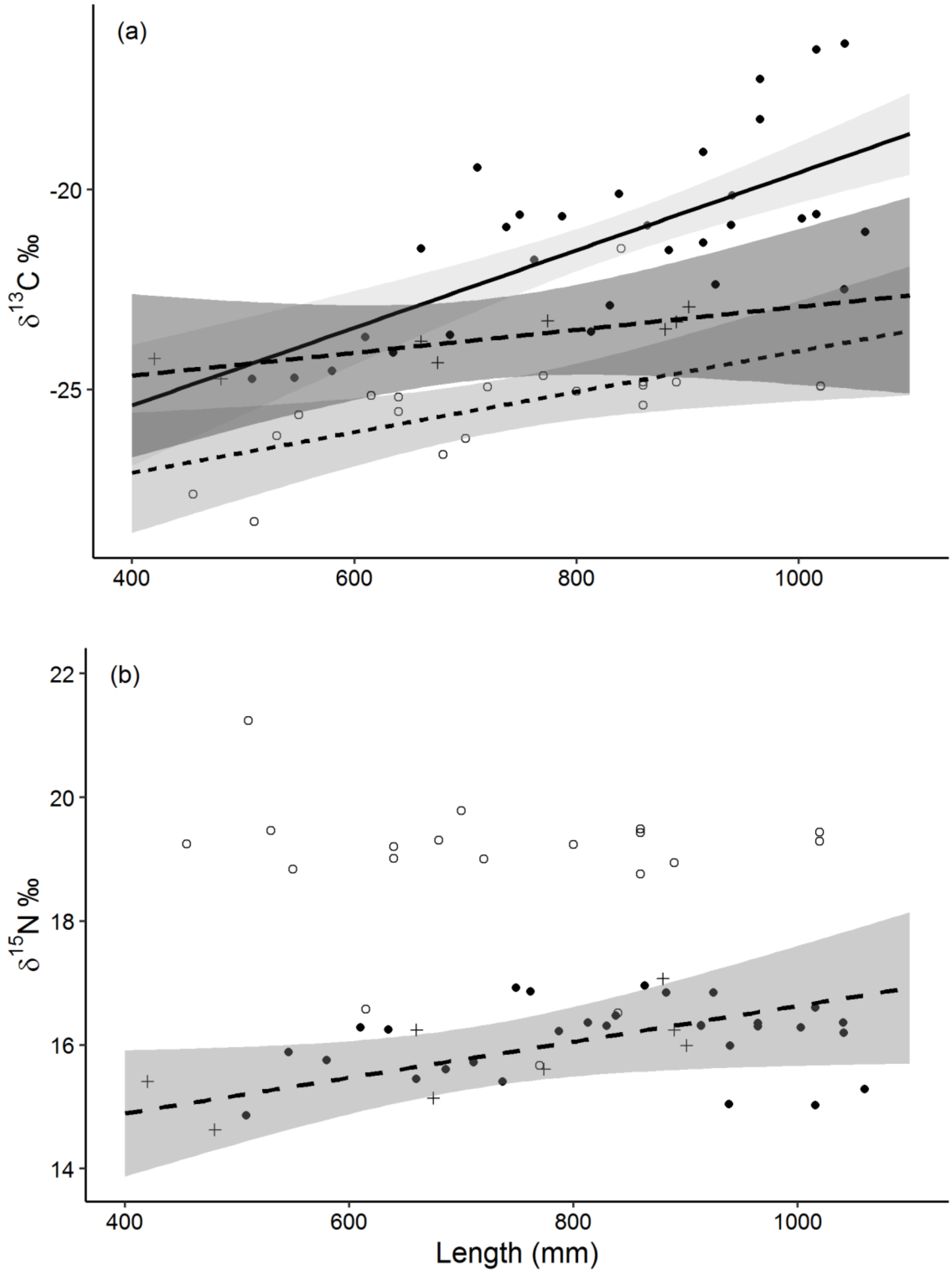

Figure 18. Relationship between length (mm) and (a) $\delta^{13}C$ and (b) $\delta^{15}N$ of pike from all reaches showing linear fit for the Warwickshire Avon (open circle, short- dashed line); Upstream Severn (cross, long-dashed line); Downstream Severn (solid circle, solid line) with 95% confidence intervals shown around the fitted values.

Table 12. Mean (± SD) carbon and nitrogen stable isotope ratios of pike by reach and size category, including the number of individuals analysed and their length range (mm).

River reach	Size category	Length range (mm)	n	Mean δ13C (‰)	Range δ^{13}C (‰)	Mean δ^{15}N (‰)	Range δ^{15}N (‰)
Warwickshire Avon	≥400 < 650	455 to 640	7	-26.23 ± 1.24	-28.30 to -25.15	19.08 ± 1.36	16.58 to 21.24
	≥651 < 850	680 to 840	6	-24.83 ± 1.82	-26.63 to -21.47	18.25 ± 1.71	15.67 to 19.78
	≥850	860 to- 1020	6	-24.96 ± 0.22	-25.39 to -24.81	19.23 ± 0.30	18.76 to 19.49
Upstream Severn	≥400 < 650	420 to 480	2	-24.48 ± 0.35	-24.73 to -24.23	15.02 ± 0.55	14.63 to 15.41
	≥651 < 850	660 to 774	3	-23.80 ± 0.53	-24.33 to -23.28	15.66 ± 0.55	15.14 to 16.24
	≥850	880 to 901	3	--23.24 ± 0.29	-23.49 to -22.93	16.43 ± 0.57	15.99 to 17.07
Downstream Severn	≥400 < 650	508 to 635	5	-24.35 ± 0.46	-24.74 to -23.69	15.80 ± 0.58	14.86 to 16.28
	≥651 < 850	660 to 838	10	-21.51 ± 1.44	-23.64 to -19.45	16.13 ± 0.56	15.41 to 16.92
	≥850	864 to 1060	15	-19.96 ± 2.02	-22.49 to -16.34	16.18 ± 0.61	15.03 to 16.96

5.4.2 Isotopic niche of pike

The isotopic niche size (as SEA_B) of pike was largest for the Warwickshire Avon, followed by downstream Severn and was smallest at upstream Severn (Table 13). The position, size and location of the ellipses varied in niche space, where pike isotopic niche from the Warwickshire Avon occupied more space on the $\delta^{15}N$ axis and less space on the $\delta^{13}C$ axis compared with the downstream Severn reach that showed the opposite pattern (Figure 19).

Isotopic niche sizes (as SEA_B) by the three size categories of pike revealed that in the Warwickshire Avon, the largest niche was in fish of 651 to 850 mm and the smallest niche for fish > 850 mm (Table 13; Figure 20). These niches also showed a high degree of overlap across all size categories with, for example, the niche of the largest size category (> 850 mm) sitting entirely within the niche for fish of 651 to 850 mm (Fig. 4). By contrast, the isotopic niches by size category in the downstream Severn reach had greater separation along the $\delta^{13}C$ axis (Table 13; Figure 20). The niche size for fish of 400 to 650 mm was relatively small compared to the two larger size categories and did not overlap (Table 13; Figure 20). The isotopic niche for fish of > 850 mm was the largest within the downstream Severn reach and was considerably $\delta^{13}C$ enriched, resulting in it sharing only 40 % of its niche space with that for fish of 651 to 850 mm (Table 13; Figure 20).

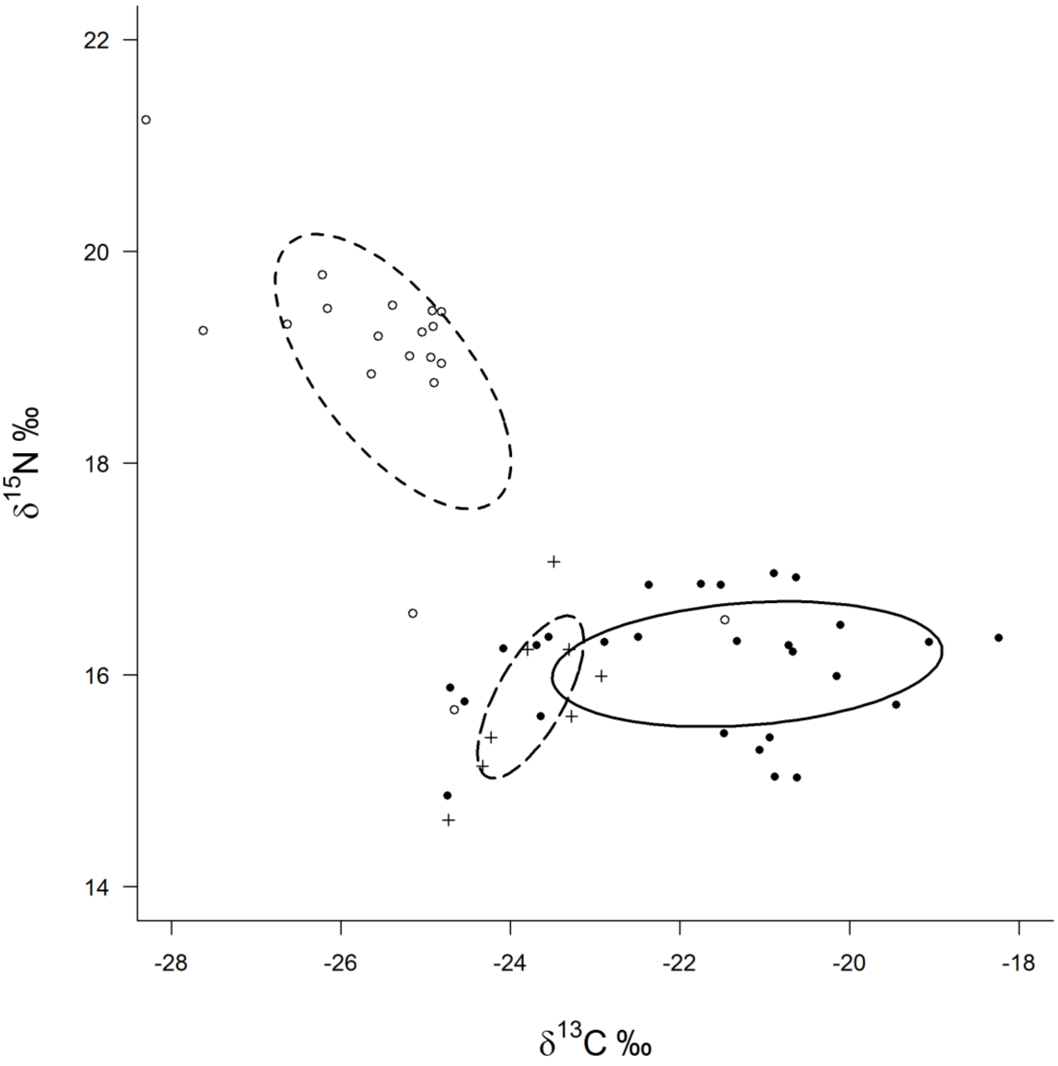

Figure 19. Pike $\delta^{13}C$ and $\delta^{15}N$ stable isotope bi-plots and the 40% standard ellipse area (SEAc) for the Warwickshire Avon (open circle, short- dashed line), Upstream Severn (cross, long-dashed line) and Downstream Severn (solid circle, solid line).

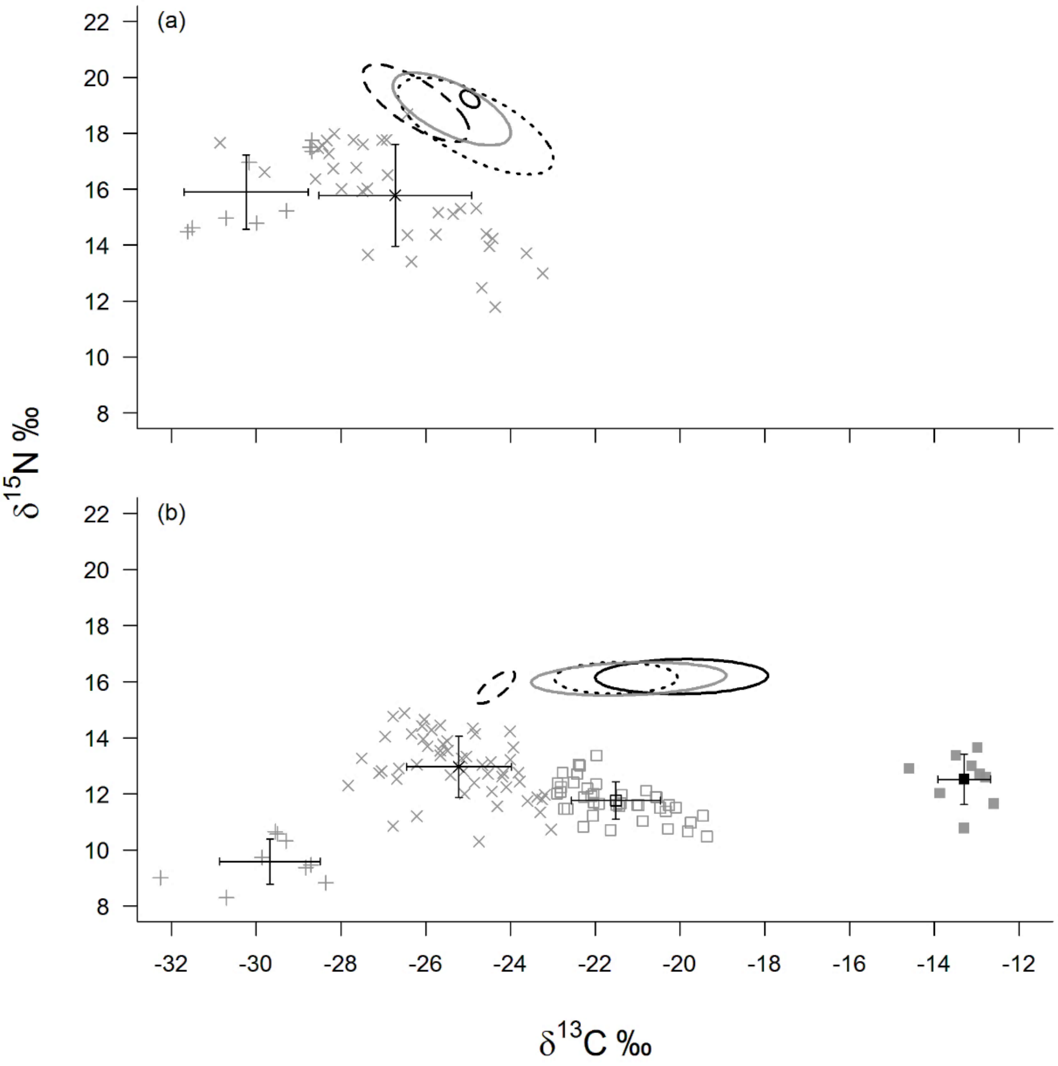

Figure 20. Stable isotope bi-plots for (a) the Warwickshire Avon and (b) Downstream Severn showing prey resources as invertebrates (cross), cypriniforms with freshwater diet (x), cypriniforms with marine diet (open square) and *Alosa* spp. (solid square). Pike isotopic niche for the sample population (solid grey line) and by size categories (400 - 650 mm (dashed line), 651 - 850 mm (dotted line) and > 850 mm (solid line) enclosing the 40% standard ellipse area (SEA) are also shown. Mean ± SD of resource points are displayed with symbols corresponding as above.

Table 13. Isotopic niche metrics for pike by reach and size categories, where TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area containing 40% of the data, SEA_C: Correction applied to SEA to account for small sample sizes, SEA_B: The Bayesian estimate and 95% credible intervals.

Groupings	TA	SEA	SEA_C	SEA_B	95% CI
Warwickshire Avon	14.21	4.21	4.45	4.21	2.63, 6.85
Upstream Severn	1.45	1.06	1.24	1.03	0.51, 2.35
Downstream Severn	11.79	4.09	4.23	3.96	2.77, 5.82
Warwickshire Avon ≥400 < 650 mm	5.28	3.59	4.31	3.57	1.59, 8.68
Warwickshire Avon ≥650 <850 mm	9.07	7.18	8.98	5.41	1.76, 13.93
Warwickshire Avon ≥850 mm	0.22	0.19	0.23	0.11	0.05, 0.31
Downstream Severn ≥400 < 650 mm	0.58	0.54	0.72	0.29	0.11, 0.89
Downstream Severn ≥650 <850 mm	4.49	2.52	2.83	2.18	1.09, 4.31
Downstream Severn ≥850 mm	7.29	3.87	4.17	3.07	2.01, 5.88

5.4.3 *Spatial and temporal variation in $\delta^{13}C$ and $\delta^{15}N$ of putative prey resources*

The δ^{13}C values of macro-invertebrates did not differ between reaches (Warwickshire Avon: -30.23 ± 0.46 ‰; downstream Severn: -29.67 ± 0.39 ‰; *t-test*: $t = -0.92$, $df = 17$, $P = 0.37$; Table 11; Fig. 4). There was, however, significant δ^{13}C enrichment in the putative prey resources between the reaches (*t-test*: $t = 7.82$, $df = 168.67$, $P < 0.001$; Table 11; Figure 20). This significant δ^{13}C enrichment was thus due to significant differences in the fish prey resources (Warwickshire Avon: -26.48 ± 0.31; downstream Severn: -22.78 ± 0.34; *t-test*: $t = -8.01$, $df = 145.62$, $P < 0.001$; Table 11; Figure 20).

The putative prey resources were significantly enriched in δ^{15}N in the Warwickshire Avon (16.02 ± 0.24 ‰) versus the Severn (12.28 ± 0.13 ‰) reaches (*t-test*: $t = -7.81$, $df = 168.67$, $P < 0.001$; Table 11; Figure 20). Differences were in both macroinvertebrates and fish prey resources (macroinvertebrates: *t-test*: $t = 12.64$, $df = 15.10$, $P < 0.001$; prey fish: *t-test*: $t = -8.0$, $df = 145.62$, $P < 0.001$; Table 1; Figure 20).

5.4.4 Stable isotope mixing model predictions of pike diet composition

At both the Warwickshire Avon and downstream Severn reaches, pike isotopic niches across all size categories were positioned between the putative prey resources (Figure 20). At the Warwickshire Avon, whilst the cypriniform fishes specialising on marine fishmeal baits were present, the gape limitations in the size range of the analysed pike meant none were considered as available prey in mixing models. Thus, all dietary contributions in this reach were of freshwater origin (Table 11), with predictions that macro-invertebrate prey resources were contributing substantially to the diet of pike < 650 mm (Table 14). Freshwater fishes and macroinvertebrates were then important prey items at sizes > 650 mm (Table 14).

In the downstream Severn reach, whilst freshwater fish were predicted as the most important prey resource in all size categories, the two marine prey resources were increasingly important prey items as pike body length increased. Overall, the proportions dietary contributions of *Alosa* spp. increased from 0.05 ± 0.04 in fish < 650 mm to 0.13 ± 0.06 in fish of length > 850 mm (Table 14). Whilst gape limitations precluded cypriniform fishes specialising on marine fishmeal bait from diet predictions for pike < 650 mm, in the larger size categories, the predicted contributions were 0.24 ± 0.13 for 650 to 850 mm and 0.20 ± 0.14 for fish > 850 mm (Table 14).

When predicted at the individual level, there was less dietary variability in pike in the Warwickshire Avon than in the downstream Severn reach (Table 14; Figure 21). At the downstream Severn reach, individual variability in diet increased with increasing gape size, with the highest individual variability apparent for fish > 850 mm (Table 14). For these fish, the ‘Cypriniform-freshwater’ prey had an estimated range of between 0.37 and 0.71 contribution to individual diet, *Alosa* spp. between 0.06 and 0.25 and cypriniform fishes specialising on marine fishmeal bait between 0.18 and 0.33 (Table 14; Figure 21b). The highest mean proportional contribution of marine resources to the diet of an individual fish was 58 % (Figure 21b).

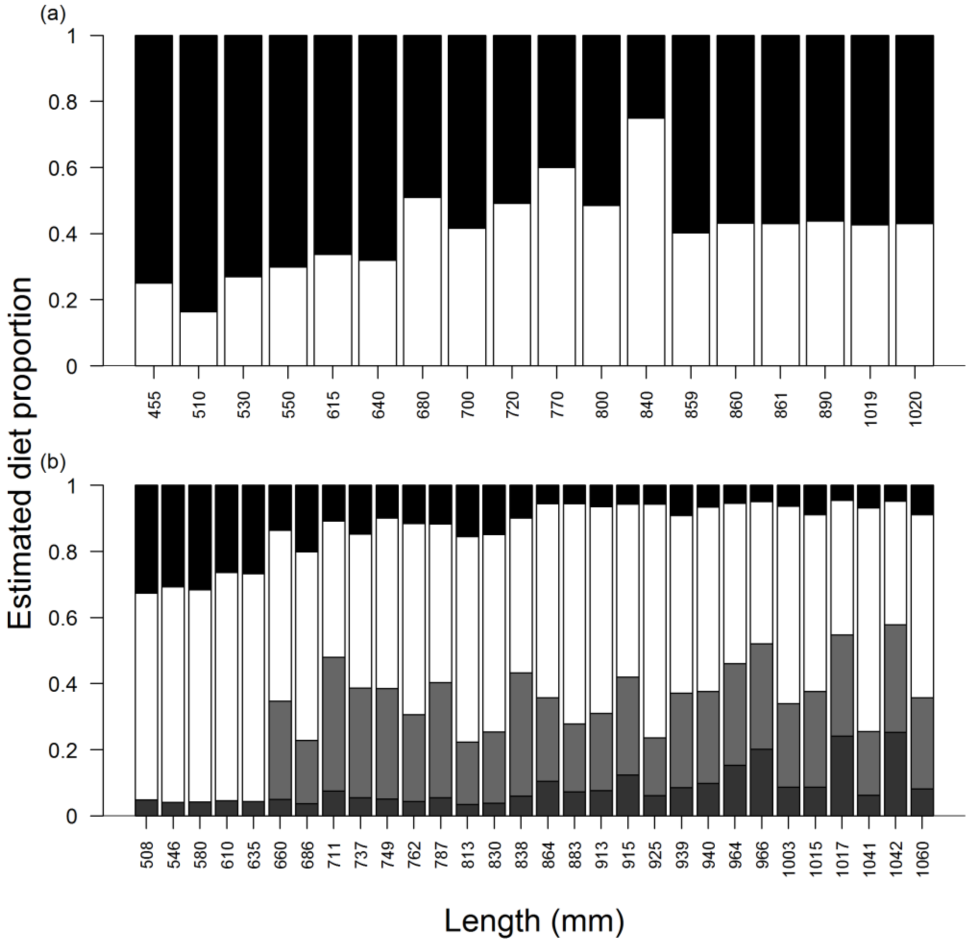

Figure 21. Estimated dietary prey contributions (0 – 1) from MixSIAR models to the diet of individual pike by body length at (a) the Warwickshire Avon and (b) downstream Severn. Prey resources are represented as overall means in a stacked bar plot for *Alosa* spp (dark grey), ‘Cypriniform-marine’ (light grey), ‘Cypriniform-freshwater’ (white) and Invertebrates (black).

Table 14. Estimated dietary prey contributions from MixSIAR models to pike by reach and size category, group mean % ± SD with 5% and 95% Bayesian credible intervals in parentheses and individual mean % ± SD with predicted proportional contribution range in parentheses. Cypriniform fishes as prey resources are separated to include those with a freshwater diet and those specialising on marine fishmeal bait

River reach	MixSIAR	Resource	≥400 < 650 mm	≥650 < 850 mm	≥850 mm
Warwickshire Avon	*Group*	Macroinvertebrates	0.73 ± 0.14 (0.47, 0.95)	0.43 ± 0.20 (0.13, 0.78)	0.57 ± 0.13 (0.35, 0.78)
		Cypriniforms – freshwater	0.27 ± 0.14 (0.05, 0.52)	0.57 ± 0.20 (0.22, 0.88)	0.43 ± 0.13 (0.22, 0.65)
	Individual	Macroinvertebrates	0.73 ± 0.02 (0.66 to 0.84)	0.45 ± 0.05 (0.25 to 0.58)	0.58 ± 0.01 (0.56 to 0.59)
		Cypriniforms – freshwater	0.27 ± 0.02 (0.16 to 0.33)	0.54 ± 0.05 (0.42 to 0.75)	0.42 ± 0.01 (0.40 to 0.44)
Downstream Severn	*Group*	Macroinvertebrates	0.33 ± 0.13 (0.11, 0.53)	0.15 ± 0.13 (0.04, 0.44)	0.06 ± 0.05 (0.01, 0.15)
		Cypriniforms – freshwater	0.62 ± 0.14 (0.39, 0.85)	0.54 ± 0.11 (0.36, 0.71)	0.61 ± 0.09 (0.46, 0.75)
		Cypriniforms – marine	NA	0.24 ± 0.13 (0.04, 0.44)	0.20 ± 0.14 (0.02, 0.46)
		Alosa spp.	0.05 ± 0.04 (0.01, 0.13)	0.07 ± 0.05 (0.01, 0.17)	0.13 ± 0.06 (0.03, 0.23)
	Individual	Macroinvertebrates	0.29 ± 0.01 (0.26 to 0.33)	0.13 ± 0.01 (0.09 to 0.20)	0.06 ± 0.01 (0.04 to 0.09)
		Cypriniforms – freshwater	0.66 ± 0.01 (0.63 to 0.69)	0.52 ± 0.02 (0.41 to 0.62)	0.55 ±0.03 (0.37 to 0.71)
		Cypriniforms – marine	NA	0.29 ± 0.02 (0.19 to 0.41)	0.27 ± 0.01 (0.18 to 0.33)
		Alosa spp.	0.04 ± 0.01 (0.04 to 0.04)	0.05 ± 0.01 (0.03 to 0.07)	0.12 ± 0.02 (0.06 to 0.25)

5.5 Discussion

Stable isotope analysis revealed the presence of marine subsidies within an impounded lowland river resulted in their substantial contribution to the assimilated diet of large-bodied pike. Results showed considerable dietary niche partitioning between pike size categories when anadromous *Alosa* spp. and cypriniform fish specialising on marine fishmeal bait were available as prey. Where these resources were not available, this niche partitioning was not evident. Stable isotope mixing models revealed that in the downstream Severn reach, up to 33 % of pike population diet could be attributed to the marine subsidies at the population level, with the greatest proportion of this marine resource contributed by cypriniform fishes (20 % of total population diet). There was, however, considerable variation among individuals, with between 22 and 58 % of individual diets consisting of the two marine resources.

These results are consistent with studies on individual specialisation that suggest long term differences in the diet of consumers can result in considerable variation of $\delta^{13}C$ within populations (Matthews and Mazumder 2004). Other apex predators have also been reported to couple distinct energetic pathways within complex food webs. For example, Matich et al. (2011) revealed that two pelagic shark species coupled distinct food webs through dietary variations resulting from one species being dietary specialists and the other being generalists. Individual specialisation in pike has also been previously documented (Beaudoin et al. 1999, Kobler et al. 2009). It has been hypothesised as a potentially important mechanism in reducing intraspecific competition, with Kobler et al. (2009) showing substantial behavioural diversification in individual pike that helped to reduce intra-specific competitive interactions. Here, the diet diversification in the larger pike was through their specialisation on the marine prey subsidies that were all lengths >280 mm. Although it could not be tested whether the fish specialising on these subsidies had different behavioural traits to those that primarily consumed freshwater prey, they did require functional traits that enabled the capture and handling of large prey. Whilst it could also not be tested whether the consumption of these larger prey was a response to intra-specific competition, the exploitation of marine subsidies by these individuals resulted in higher intrapopulation variation and individual specialisation, as has been shown elsewhere (e.g. Beaudoin et al. 1999, Bolnick et al. 2002, Araújo et al. 2011). In doing so, the two marine energy pathways present in the downstream Severn reach were coupled with those from non-marine sources at the apex of this riverine food web.

The $\delta^{13}C$ of pike differed significantly between the reaches, but with the effect of the interaction of reach and fish length on $\delta^{13}C$ not being significant. There was, however, high variability in $\delta^{13}C$ of larger pike in the downstream Severn reach that could potentially have strongly influenced this non-significant result. There was also considerable variability in the contribution of marine resources to the diet of the larger fish in the downstream Severn reach. Nevertheless, within this reach, the dietary contributions of the two marine subsidies did increase with pike body length, explained by their prey selection being dependent on gape size, with this a function of their body length. This finding is important, as in the dietary analyses of pike, individual diets tend to primarily consist of smaller prey (e.g. < 200 mm length), irrespective of whether that fish can consume larger prey (Craig 2008, Sandlund et al. 2016). This results from both a limited availability of larger prey and larger prey having higher handling times that incurs an increased risk of kleptoparasitism (Nilsson and Brönmark 2000, Craig 2008). Here, the stable isotope data suggested that individual pike over 650 mm could consume relatively large fishes, with, for example, the approximate sizes of *Alosa* spp. in the River Severn during their spawning period being > 300 mm (Aprahamian 1988). Moreover, the MDN prey resource from angling bait comprised of fishes of only above 380 mm length. The presence of anadromous *Alosa* spp. in diet was also interesting given they are only available for a relatively short period each year, generally April to June, a period coincident with the post-spawning period of pike (Craig 2008). Utilisation of these gape dependent resources resulted in isotopic niche differences between populations with and without MDN pathways. This finding is also consistent with Samways et al. (2018), who found that whilst the total ecological niche space did not always increase in river communities following spawning of anadromous fishes, this niche space did show consistent movement toward the marine-nutrient source.

Apex predators are often associated with exerting top-down forces that can initiate trophic cascades within food webs (Brett and Goldman 1996, McIntosh and Townsend 1996, Ritchie et al. 2012). However, bottom-up forces, such as prey availability, can also influence predator behaviour and dietary preferences, resulting in prey switching and altering predator-prey relationships (Newsome et al. 2014, 2015). For example, human-influenced food subsidies have altered natural predator-prey relationships in terrestrial systems via bottom-up processes (Ripple et al. 2013, Newsome et al. 2014, 2015). These anthropogenic subsidies have been sufficient to maintain the abundance and richness of numerous terrestrial predators, including species of birds, mammals and reptiles (Ripple et al. 2014, Newsome et al. 2015). Here, the provision of an anthropogenic prey subsidy in an aquatic system was via the release of large amounts of angling baits that contained high proportions of MDN. The population benefits of this subsidy for pike might have been limited, as it can only be exploited at relatively large sizes. It was beyond this study to determine if there were reproductive and fitness benefits for individuals exploiting these marine prey resources. Nevertheless, the relatively distinct $\delta^{13}C$ signal of the angler bait subsidy, located between the freshwater and anadromous prey $\delta^{13}C$ signal, enabled these nutrients to be traced through successive trophic levels in the food web. Previously, MDN subsidies from aquaculture and angling have only been detected as being assimilated directly by freshwater fishes (Jackson et al. 2013, Bašić et al. 2015, Gutmann Roberts et al. 2017). Thus, a novel outcome of this study was the demonstration that this anthropogenic marine subsidy was transferred to higher trophic levels in the freshwater food web via piscivory. Notwithstanding, this result was detected in only one river reach. Given the characteristics of the study system, this was unavoidable, as the two marine prey pathways were only present in the downstream Severn reach. Although sample sizes were often small in some reaches, these were not considered to have been a major impediment to data analysis and interpretation due to some of the considerable differences in the stable isotope data of both prey and pike. However, it would be beneficial to identify whether this transfer of angling MDN though riverine food webs is apparent elsewhere, especially in reaches where they are released in high quantities.

Angling baits have been argued as acting as a very strong allochthonous subsidy compared to inputs of, for example, terrestrial invertebrates (Busst et al. 2015, Mehner et al. 2018). Here, their use in the River Severn basin created a novel MDN energy pathway involving cypriniform consumers and the piscivorous pike. The dietary contribution of this MDN pathway was generally predicted to be higher than that of the anadromous MDN pathway. This anadromous prey resource was, however, still an important dietary component. Its presence was also consistent with a large body of research that demonstrates the importance of anadromous fishes for maintaining the productivity, diversity, and community structure of many freshwater systems (e.g. Schindler et al. 2005, Richardson et al. 2016). Indeed, apex predatory fishes have been shown to regularly predate upon anadromous fishes when they enter freshwaters to spawn (MacAvoy et al. 2000, Guillerault et al. 2017).

In summary, the diet composition and isotopic niches of pike populations was influenced by the spatial variation of novel marine prey resources. Whilst body size had a strong influence on the ability of pike to exploit these marine prey resources, there was considerable variability in the MDN dietary contributions to larger fish. Notwithstanding, that angling bait based on marine resources could be traced through successive trophic levels is a novel finding and highlights how human subsidies can affect the trophic dynamics of apex predators.

6 Activity patterns and habitat use of native and non-native piscivorous fish in a channelized lowland river

6.1 Abstract

To understand the temporal and spatial movement patterns of co-existing large-bodied native and non-native piscivorous fishes, passive acoustic telemetry techniques were used to track 16 native pike *Esox lucius* and 8 invasive pikeperch *Sander lucioperca* for 12 months in the lower River Severn, Western England. The River Severn supports an important fishery for both species but is a heavily impounded, channelized lowland river with limited areas of off-channel habitat. For management of their populations and fisheries, understanding of the spatial ecology of these co-existing native and non-native predatory fishes is needed. There was considerable variability in the movement patterns within and between the species. Pike and pikeperch increased their total daily distance moved during spring, with this likely to relate to spawning migrations in pike and increased foraging behaviours in post-spawned pikeperch. Elevated water temperatures increased the frequency of movements of both species up to a threshold of 15 °C, with decreased movements at higher temperatures. In pike there was a reduction in the frequency of movements in winter and an increase during twilight periods in summer and autumn. The limited off-channel habitat available was important to pike all year round, whereas pikeperch primarily used it in winter and spring. These results highlight the importance of off-channel habitat and the potential for such areas to be used as spawning locations for non-native pikeperch and as important foraging areas for native pike.

6.2 Introduction

In lowland rivers, engineering structures, such as weirs and dams, can result in reduced aquatic biodiversity (Clavero et al. 2004, Dudgeon et al. 2006). This occurs as a result of decreased longitudinal connectivity that inhibits access to or alters key habitats for spawning and foraging in potamodromous freshwater fishes (Ovidio and Philippart 2002, Ziv et al. 2012, Benitez et al. 2018), coupled with a deterioration or destruction of complex habitats as a result of increased channelization (Allan and Flecker 1993). These changes can thus disrupt patterns of native biodiversity, as there may be a general shift away from lotic to more lentic conditions (Johnson et al. 2008), whilst often creating favourable conditions for the successful establishment of invasive species, for example by providing stable conditions all year round (Corbacho and Sánchez 2001, Clavero et al. 2004, Johnson et al. 2008). However, lotic habitats can also be beneficial to the establishment of non-native fishes as they provide access to a greater variety of food resources (Garcia et al. 2018).

Large-bodied non-native fishes of high trophic position are often introduced to enhance recreational freshwater angling (Hickley and Chare 2004). However, their introductions and subsequent invasions can have substantial negative effects on native fish diversity through both their consumptive effects on prey species and non-consumptive effects on native analogues (Eby et al. 2006, Sih et al. 2010, Menezes et al. 2012). In many lowland rivers in England, the native large-bodied piscivorous fish, pike *Esox lucius*, is increasingly existing in sympatry with the non-native pikeperch *Sander lucioperca*, which was released specifically for angling enhancement into the Great Ouse catchment in Eastern England in the 1960s (Hickley and Chare 2004). Following its release, the species established and subsequently dispersed throughout river catchments in central and southern England (Hickley 1986).

The extent of interactions between non-native pikeperch and native pike remain uncertain. In pike, submerged vegetation and macrophyte growth are extremely important as spawning substrate (McCarraher and Thomas 1972) and nursery habitats (Craig 2008), and are directly correlated with adult abundance (Casselman and Lewis 1996). In river basins affected by anthropogenic activities where natural vegetation is limited, laterally connected off-channel habitats can provide important habitats for refugia and foraging (Pauwels et al. 2016). During foraging, pike are generally considered stationary, due to their sit-and-wait predator ambush behaviour but may actually shift positions regularly to enhance predation success and avoid conspecifics (Nilsson et al. 2006, Knight et al. 2008). In contrast, pikeperch, spawn in nests constructed by the males, which may be made on sandy, silty or muddy substrates, and on which females deposit eggs (Lappalainen et al. 2003). The males then nest guard, remaining in position for between 2 and 6 weeks (Jepsen et al. 1999). In rivers, spawning movement is thought to be towards habitats with low water velocity (Koed et al. 2002), as this can minimise the risk of larvae being displaced downstream by elevated flows (Koed 2000). In contrast to pike, pikeperch foraging consists of active searching (Turesson and Brönmark 2004), with relatively small bodied prey taken when compared to pike (Turesson et al. 2002).

Whilst there are some clear differences in the foraging strategies and spawning behaviours of pike and pikeperch (e.g. Turesson and Brönmark 2004, Nilsson et al. 2006), studies assessing their movement patterns in riverine environments, suggest some context dependencies in the results. For example, pikeperch activity rates can increase during twilight periods (Poulet, Arzel, et al. 2005, Horký et al. 2008), with seasonal activity differences related to their spawning behaviours (Koed 2000, Koed et al. 2002, Horký et al. 2008). However, in other studies such as on Dutch river systems, these patterns were not observed and swimming activity was highest at night (Aarts and Breukelaar 2017). Pike spatial behaviours tend to vary considerably between individuals, with some being almost exclusively sedentary through to others being highly active, coupled with high individual variability in activity and habitat use (Masters et al. 2005, Kobler et al. 2009, Skov and Nilsson 2018). Most studies on riverine pike movements reveal spawning migrations in spring (Ovidio and Philippart 2005, Koed et al. 2006, Pauwels et al. 2014). These spawning migrations include instances where all individuals move considerable distance upstream (Ovidio and Philippart 2005), and others where movements are much shorter and in both upstream and downstream directions (Pauwels et al. 2014). Similar to some pikeperch studies, a peak in movement activity at twilight periods has also been observed for pike (Kobler et al. 2008, Baktoft et al. 2012). If the movements of both native pike and non-native pikeperch are tracked simultaneously in the same system, then issues around context dependent behaviours can potentially be overcome enabling their response to environmental changes to be compared directly.

The aim of this study was therefore to assess the temporal and spatial movement patterns of co-existing large-bodied piscivorous fishes, the native pike and the non-native pikeperch, over twelve months in an impounded lowland river, the lower River Severn, Western England. Objectives were to determine the spatial and temporal movement patterns and diel activity behaviours for both species, the influence of water flow and temperature on these patterns of behaviour, and the importance of the limited off-channel habitat considering the homogenous nature of the main channel of the River Severn.

6.3 Materials and Methods

6.3.1 Study area

The study area was a section of the lower River Severn, Western England (Figure 22a) between Diglis Weir (upstream) and Upper Lode Weir (downstream) (Figure 22b; 52.1819, -2.2241 to 51.9943, -2.1735) and encompassing the lower section of the River Teme tributary. The weirs at the up- and downstream limits of the area provided a closed area of 28 km, as neither of the species were assumed to be capable of traversing these weirs. The weirs were constructed for navigation and have resulted in the river being highly impounded, with heavy boat traffic in summer. The study area is characterised by widths to 40 m, depth to over 4 m (C-MAP 2019) with minimal in stream vegetation and off-channel areas, the only exception being a boat marina located at Upton-upon-Severn (Figure 22).

An acoustic receiver array was established in the study area prior to fish tagging, comprising a total of 11 acoustic receivers (VR2, Vemco Ltd) in fixed locations (Table 15; Figure 22b). These receivers remained in place throughout the study period, with the exception of receiver #3 which was deployed on 24/04/18. Range testing revealed a maximum detection range of approximately 100 m across the study area (Gutmann Roberts et al. 2019); this exceeded the river width in all locations and thus the receivers functioned as a gated array. Receiver positions were selected to provide equidistance coverage between the upstream and downstream range of the study area, whilst also enabling detection of movements in and out of the boat marina at Upton-Upon-Severn, and the residency of the fish in this marina (Figure 22c). Receivers were removed and replaced periodically allowing the stored data to be downloaded for analysis. A temperature logger (Tinytag) was deployed at the site of receiver number 6 and recorded temperature (to 0.1 °C) every three hours. Flow data (m^3/s) were acquired from the flow gauging station operated by the Environment Agency at Saxons Lode (52.0495, -2.2005, Fig. 1b) with records of flow every 15 minutes.

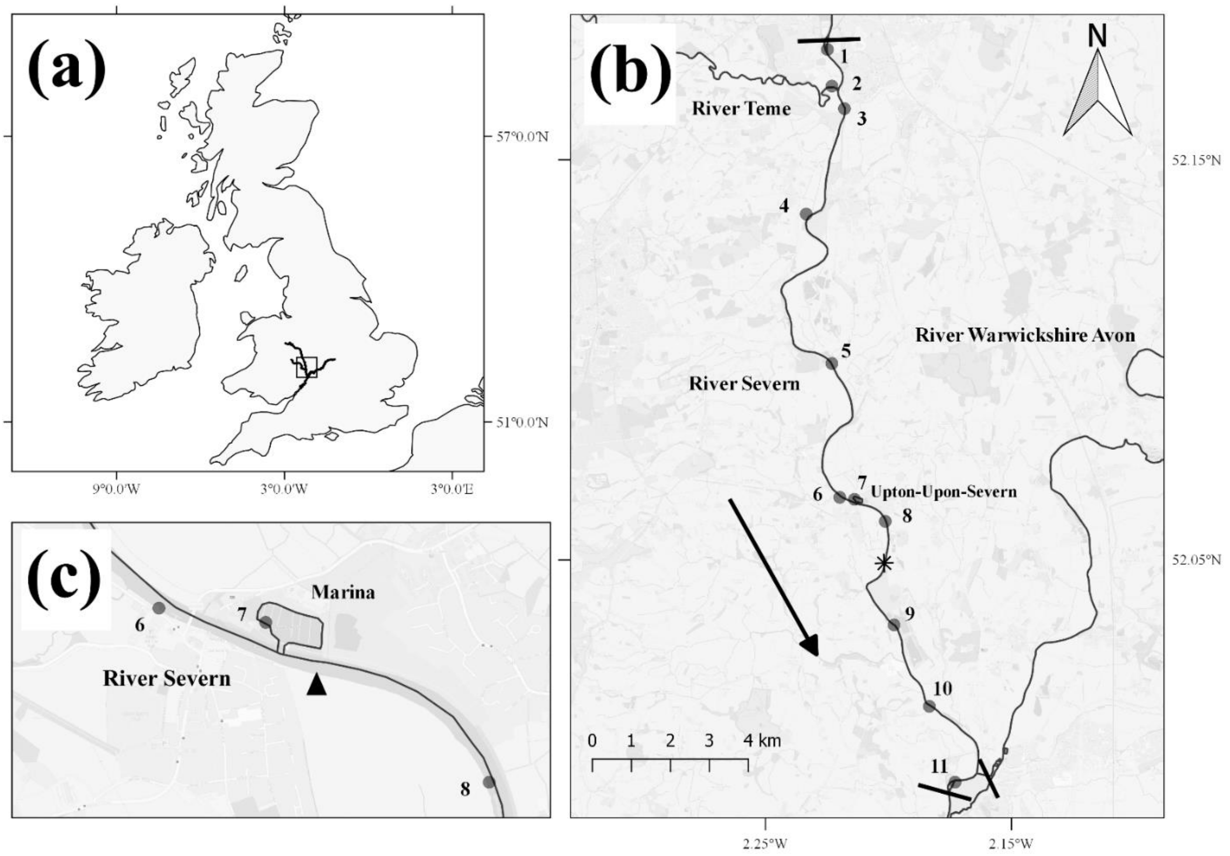

Figure 22. Map showing a) the position of the study area within the UK; b) the study area within the River Severn with the receiver locations shown by circles and the position of the flow gauging station (star) c) the off-channel habitat provided by Upton-Upon-Severn marina showing the receiver locations (circles) and the sampling location (triangle). The arrow indicates the direction of water flow, solid lines show the position of weirs.

Table 15. Receiver identification, name and location coordinates (decimal degrees), the total number of detections recorded by each receiver within the study period, and the time and date of first and last detections

Receiver number	Receiver name	Latitude	Longitude	Detections	First detection	Last detection
1	Diglis	52.17755	-2.22481	468	28/01/2018 09:11	17/09/2018 20:15
2	Teme confluence	52.16841	-2.22301	1526	06/05/2018 23:04	27/05/2018 04:38
3	Carrington Bridge	52.16278	-2.21790	738	06/05/2018 21:50	16/10/2018 15:45
4	Pixham	52.13644	-2.23344	34480	27/10/2017 20:45	26/10/2018 23:48
5	Severn Stoke	52.0991	-2.22302	6956	01/11/2017 18:18	26/10/2018 02:44
6	Upper Upton	52.06562	-2.2198	130455	27/10/2017 00:41	26/10/2018 17:18
7	Upton marina	52.06513	-2.21382	969494	27/10/2017 00:00	26/10/2018 23:59
8	Lower Upton	52.05664	-2.20039	122986	27/10/2017 00:00	17/10/2018 08:43
9	Ripple	52.03369	-2.19773	139	08/03/2018 13:58	04/07/2018 22:27
10	Yeandley farm	52.01329	-2.18339	160	09/03/2018 13:04	30/03/2018 08:38
11	Upper lode	51.99431	-2.17293	0	NA	NA

6.3.2 Fish sampling and tagging

Fish sampling and tagging was completed over one day on 27/09/17 in the river and marina at Upton-Upon-Severn (Figure 22c), selected due to its centrality within the study area. Fish were captured using electric fishing from a boat and rod and line angling. Following their capture, fish were transferred to an aerated tank. Tagging involved general anaesthesia (tricaine methanesulfonate; MS-222) before an acoustic transmitter (69 KHz V9 or V13; Vemco Ltd) was inserted into the peritoneal cavity through a small incision (less than 2 cm wide) which was then closed with a single suture and the application of surgical adhesive. V9 acoustic transmitters were 9 x 21 mm and 1.6 g, whilst V13 transmitters were 16 x 36 mm and 6 g, with V13s only used on fish above 500 mm fork length. All transmitters were set to transmit randomly every 60 to 180 s providing an overall battery life of 22 months (V9) and 36 months (V13). Random repeat pulse rates allowed multiple individuals to be monitored simultaneously within a given area via fixed receivers with reduced risk of continuous signal overlap and interference. Tag identification numbers were recorded, fish measured (fork length, nearest mm) and then transferred to an aerated recovery tank where they were held until normal swimming behaviour resumed. The fish were then released close to their location of capture. All surgical procedures were completed following ethical approval, were licenced under UK legislation for animal research (project licence number: PPL 70/8063), and were undertaken by a licensed, competent and experienced practitioner. A total of 17 pike and 8 pikeperch were tagged, pike ranged in size from 574 to 958 mm and pikeperch from 356 to 692 mm (Table 16).

Table 16. Summary data for each transmitter, including species, fork length at tagging (mm), the date of last detection, the number of days from first to last detection, the number of days detected, the number of detections, upstream and downstream distance (m), total distance (m), mean daily distance (m) and marina residency index.

ID	Sp	Length (mm)	Last detected	Days from first to last detection	Days detected	Detections	Downstream distance (m)	Upstream distance (m)	Total distance (m)	Mean daily distance (m)	Marina residency index
43258	Pike	574	26/10/18	364	223	42099	0	1374	26112	72	0.22
43259	Pike	586	12/5/18	197	134	31491	-2949	6359	36582	186	0.27
43260	Pike	628	24/9/18	332	226	50434	0	1374	28861	87	0.25
43261	Pike	682	20/10/18	358	324	71707	-5483	16542	288674	806	0.32
43264	Pike	651	26/10/18	364	342	71490	-2949	1374	25138	69	0.37
43267	Pike	710	26/10/18	364	224	56036	0	1374	41230	113	0.28
51147	Pike	611	26/10/18	364	363	109726	0	1374	5497	15	0.54
51148	Pike	641	15/4/18	170	116	28236	-2949	6359	75118	442	0.00
51149	Pike	589	26/10/18	364	363	140649	-2949	1374	44032	121	0.33
51152	Pike	936	26/10/18	364	358	69495	0	1374	140182	385	0.29
51153	Pike	863	26/10/18	364	323	60308	0	2006	145499	400	0.20
51154	Pike	958	3/8/18	280	272	83509	-2949	15696	69975	250	0.48
51155	Pike	626	9/11/17	NA	NA	NA	NA	NA	NA	NA	NA
51156	Pike	655	17/10/18	355	263	44575	-2949	1374	14144	40	0.25

51158	Pike	722	26/10/18	364	340	58743	-8759	2006	202542	556	0.25
51159	Pike	795	26/10/18	364	323	74077	-8759	6359	100850	277	0.32
51160	Pike	695	26/10/18	364	276	85111	-8759	12341	35141	97	0.30
43262	Pikeperch	441	19/9/18	327	166	18018	0	1374	9620	29	0.00
43263	Pikeperch	473	4/7/18	250	216	33201	-2949	1374	57449	230	0.26
43266	Pikeperch	484	25/4/18	178	54	4219	-2949	1374	10452	59	0.04
51146	Pikeperch	356	26/10/18	354	150	22713	0	2006	14807	42	0.05
51150	Pikeperch	692	25/10/18	355	210	39215	-2949	16542	128468	362	0.20
51151	Pikeperch	692	22/10/18	359	187	23229	0	12341	58831	164	0.09
51157	Pikeperch	581	25/10/18	361	207	27373	-2949	2006	41809	116	0.14
51161	Pikeperch	535	4/7/18	250	149	20042	-2949	1374	243235	973	0.02

6.3.3 Data analysis

Fish movement data was analysed from 27/10/17 to 26/10/18, providing 365 continual days. Data from the period between tagging and 27/10/17 were not include to avoid movement that might have been subject to behavioural changes caused by the tagging procedure (Pauwels et al. 2014). Pike ID 51155 was not detected after 09/11/17 and was removed from further analysis. At the end of the tracking period, the detection data (comprising of over 1.6 million individual detections) were initially analysed in the package 'Vtrack' in R (Campbell et al. 2012) for residency and non-residency events for each individual. A residency event was defined when a transmitter was detected by a receiver (minimum of 2 detections) and terminated when the transmitter was detected at another receiver, or if the transmitter was not detected by the same receiver within a defined timeout window of 10 minutes. This time was chosen as a conservative estimate of the time it would take an individual pike or pikeperch to move away from the detection range of a receiver (~100 m) based on pike mean swimming speed of 0.23 m s^{-1} (0.45 body length s^{-1}) (Diana 1980). No data exists for absolute swimming speed in pikeperch although swimming speed has been recorded to 1.6 body length s^{-1} (Poulet, Arzel, et al. 2005). A non-residency event was defined as the movement between the detection fields of two receivers and incorporated measurements of the circuitous distance (river distance) between receivers, river distance was used in all subsequent distance calculations.

Individual maximum upstream and downstream distance moved was calculated from the central position of Upton-Upon-Severn marina ('0'; Figure 22) to the most upstream and downstream receivers with detections. Individual total distance moved was calculated for the 12-month study period as the sum of all movements between receivers. Individual mean daily distance was then calculated for the 12-month study period as the total distance travelled by each individual divided by the length of the study period (i.e. the time between first and last detections for each individual). Although such movement rates are likely to be an underestimate of total activity, they can provide useful insight (Cooke et al. 2001) and are an attempt to reduce the error associated with differences in the number of days individuals were detected. Spearman's rank correlation coefficient was used to initially test for a correlation between individual total distance moved and mean daily distance moved across the analytical period; as there was significant correlation for both pike (Spearman's rho (*r*) = 0.97, *P* < 0.01) and pikeperch (*r* = 0.95, *P* < 0.01), then following testing for normality and homoscedasticity (Shapiro-Wilks and Levene's tests respectively), differences in mean daily distances moved during the 12 month study period were tested using a Mann-Whitney test. The mean total daily distance moved for pike and pikeperch across all individuals was calculated and differences across seasons were tested using a generalised linear model (GLM) with a quasi-Poisson distribution to account for over-dispersion, and the significance of the model was tested using a likelihood ratio test, pike and pikeperch were analysed separately.

To assess movement activity in relation to time of year, water flow and temperature for pike and pikeperch, it was first necessary to ensure data were comparable across the study period. For pike this meant removing individuals that were not detected for the entire 12 month study period, resulting in the exclusion of 4 fish (Table 16). For pikeperch, due to a lower tagged sample number, the removal of fish with a full 12 months data would have excluded half of them. Consequently, only pikeperch ID 43266 was removed, with the analysis of movement activity for the remaining 7 individuals completed only for months when all individuals were present (to 04/07/18; Table 16). Then, a mixed effects logistic regression model tested the binary response of daily movement (as a detected daily movement vs. no detected daily movement) against daily mean water temperature and river flow for both species, with season as a fixed effect and individual as a random effect in the model. Individual was included as a random effect to mitigate autocorrelation from repeated measures from the same individual (Harrison et al. 2018). Water temperature and flow were entered as quadratic terms to account for potential non-linear relationships and data were scaled for continuous variables before analyses. Season was defined according to the Northern meteorological season and so summer and autumn did not retain complete data in the pikeperch model.

As range testing revealed that the receiver located within the boat marina could only detect transmitters within the marina and not the river, then the proportion of time spent in the marina by each fish was assessed as its 'marina residency'. This was calculated as the total time of individual residency events within the marina for both the length of the study period (i.e. the time between first and last detection for each individual) and weekly with the latter enabling testing of differences in the weekly marina residency between the species and by season using a generalised linear model (GLM; with a quasi-Poisson distribution to account for over-dispersion in the data) where the independent variables were mean weekly water temperature and water flow, and season was a fixed effect.

Daily timings of dawn, day, dusk and night were retrieved for each day in the study period obtained using the package maptools with civil twilight definitions (Bivand and Lewin-Koh 2019). Movements within each diel period were counted and standardised to counts per hour for both pike and pikeperch. These measurements were calculated for the entire 12-month study period, by season and by month for individuals with 12 months of data only. A Kruskal-Wallis rank sum test then tested the overall differences in number of movements over the 12-month study period across diel periods, and a chi-squared (χ^2) contingency table analysis was used to test for an association between dawn, day, dusk and night movements with season. Monthly movement within each diel period was used for graphical purposes only. Tests were completed for pike and pikeperch separately.

All analysis and graphical outputs were completed in R (Version 3.6.1; R Development Core Team, 2018). Logistic regression and generalised linear models were analysed for pike and pikeperch separately and were completed using the package lme4 (Bates et al. 2014). Where error is expressed around the mean, it represents the mean ± 95 % confidence intervals, unless otherwise stated.

6.4 Results

6.4.1 Tag detections and general movements of tagged fish

Across the tracking period, there was a greater total number of detections on receivers around Upton-Upon-Severn (location of fish capture and tagging) than elsewhere in the array (Table 15), with the majority of detected movements for both species being in this area (Figure 23). All pikeperch and all but one pike showed some level of residency within the off-channel habitat of the marina at Upton-Upon-Severn (Table 16), with pike having a significantly higher mean marina residency index across the tracking period than pikeperch (0.29 ± 0.06 vs. 0.10 ± 0.06; t test: $t = 3.88$, $P < 0.01$; Table 16).

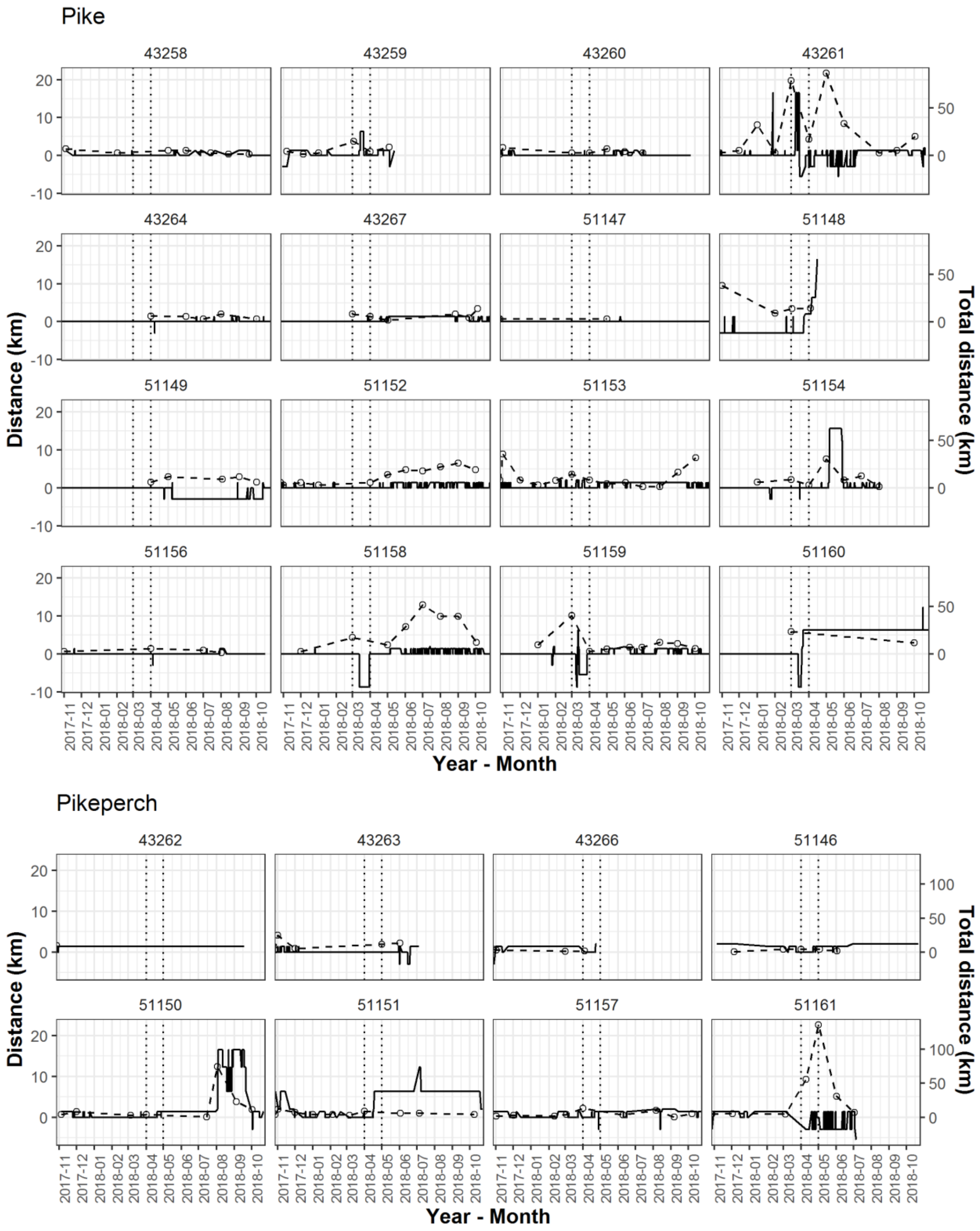

Figure 23. Continuous upstream and downstream movements (km) of pike and pikeperch from 0 (r representing the marina at Upton-Upon-Severn) on the primary axis (solid line), and the total monthly distance moved (km) on the secondary axis (open circle, dashed line); spawning month is represented by the area between the dotted lines and individuals

are identified according to transmitter ID (Table 2). Note the difference in scale between the primary and secondary axis.

Pike detections beyond the Upton-Upon-Severn receivers included three pike that were detected 8.8 km downstream of the marina between 08/03/18 and 16/03/18 and returned back upstream between 10/03/18 and 11/04/18 (ID 51158, 51159 and 51160; Figure 23). Pike ID 43261 was also detected 5.5 km downstream in March and May 2018 (Figure 23). Pike detections upstream of Upton-Upon-Severn included two pike (ID 43261 and 51148) that moved 16.5 km to the upper limit of the array, where they were detected between 28/01/18 and 15/04/18 (Figure 23). Pike ID 51154 and 51160 moved upstream a distance of 12.3 km in May and October 2018 respectively (Figure 23), with pike ID 51154 being detected on receiver #2 between 06/05/18 and 27/05/18; this fish was the only one detected within the River Teme tributary throughout the study period.

There were three of tagged pikeperch that were detected beyond the Upton-Upon-Severn receivers. This included pikeperch ID 51150 that was detected on receiver #1 at the upper limit of the array on 15 separate dates between 03/08/18 and 17/09/18 (Figure 23). Pikeperch ID 51151 was first detected at receiver #5, then moved 6.4 km downstream to Upton-Upon-Severn in October, and upstream in April; it was also detected upstream at receiver #4 on 05/05/18 and 07/05/18 after which it was consistently detected at receiver #5 (Figure 23). Only one pikeperch (ID 51161) moved downstream a distance of 5.5 km, where it was detected at receiver #10 on 04/07/18, after which it was not detected (Figure 23).

6.4.2 Mean daily distances, marina residency and diel activity

Across all individuals, differences in mean daily distance moved between species across the tracking period were not significant (pike: 245 ± 108 m; pikeperch: 247 ± 217 m; Mann-Whitney $U = 57$, $P = 0.97$). There was a significant difference in mean total daily movement across seasons for both pike (GLM; $F = 20.57$, $df = 3$, $P < 0.01$) and pikeperch (GLM; $F = 14.59$, $df = 3$, $P < 0.01$) with both species showing higher mean total daily movements in spring (Table 17, Figure 24). Assessment of daily movement behaviour (binary response of detected movement vs. no detected movement) for pike and pikeperch separately, revealed that up to a threshold of 15 °C, higher temperatures increased the probability of a detected movement, while at temperatures >15 °C, this probability was significantly reduced (Table 18, Figure 25). There was also an increase in the probability of a predicted movement with increasing fork length for pike, but not for pikeperch (Table 18, Figure 25). Seasonally, the probability of a detected movement for pike in winter was significantly reduced ($P < 0.05$; Table 18), but with no significant seasonal differences in the probability of a detected movement in pikeperch ($P > 0.05$; Table 18). For both species, whilst increasing water temperatures significantly reduced their marina residency ($P \leq 0.02$; Table 19; Figure 26), the effect of increasing river flow was not significant ($P > 0.05$; Table 19).

Table 17. Coefficient estimates, standard errors, *t* values and their significance from results of generalised linear models testing mean total daily distant moved for pike and pikeperch (analysed separately) versus season.

Species	Coefficients	Estimate	SE	*t* value	*P*
Pike	Intercept	-0.10	0.09	-11.47	< 0.01
Pike	Summer	-0.40	0.15	-2.67	< 0.01
Pike	Autumn	0.30	0.15	-2.06	0.04
Pike	Winter	-1.55	0.23	-6.72	< 0.01
Pikeperch	Intercept	-1.05	0.13	-8.25	< 0.01
Pikeperch	Summer	-0.53	0.21	-2.52	0.01
Pikeperch	Autumn	-0.80	0.23	-3.48	< 0.01
Pikeperch	Winter	-1.87	0.35	-5.32	< 0.01

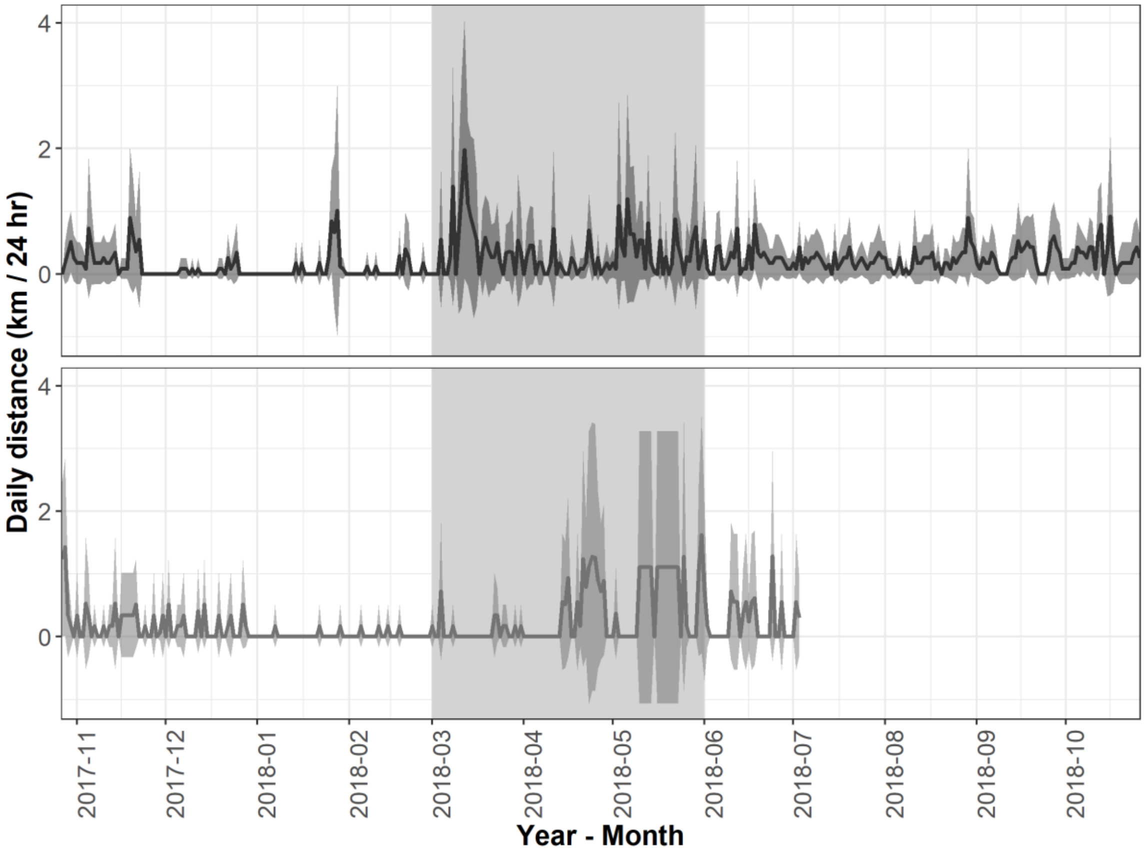

Figure 24. Mean daily distance moved for pike (*N* = 12, length 574 to 936 mm, black line, dark grey shade) and pikeperch (*N* = 7, length 356 to 692 mm, grey line, light grey shade) from 27/10/17 to 26/11/18. Mean (solid line) ± 95% confidence intervals (shaded areas)

Table 18. Scaled coefficient estimates, standard errors, z scores and their significance from results of mixed effects logistic regressions for pike and pikeperch (analysed separately) to test for the binary response of detected daily movement (detected movement vs. no detected movement) versus daily mean water temperature and water flow, and fish length (mm) with season as a fixed effect. Individual was used as a random effect in the model. Where temperature and flow are represented by two coefficients it represents their quadratic terms

Species	Coefficients	Estimate	SE	*Z* value	*P*
Pike	Intercept	-2.38	0.28	-8.56	< 0.01
	Temperature 1	0.46	0.12	3.87	< 0.01
	Temperature 2	-0.48	0.11	-4.41	< 0.01
	Flow 1	-0.01	0.09	-0.15	0.88
	Flow 2	-0.10	0.07	-1.50	0.13
	Summer	0.34	0.23	1.43	0.15
	Autumn	0.14	0.15	0.92	0.36
	Winter	-0.57	0.27	-2.14	0.03
	Length	0.84	0.25	3.43	< 0.01
Pikeperch	Intercept	-2.53	0.31	-8.25	< 0.01
	Temperature 1	0.60	0.22	2.74	0.01
	Temperature 2	-0.44	0.21	-2.05	0.04
	Flow 1	0.01	0.14	0.05	0.96
	Flow 2	0.12	0.11	1.15	0.25
	Summer	-0.66	0.50	-1.31	0.19
	Autumn	0.26	0.29	0.92	0.36
	Winter	-0.26	0.35	-0.75	0.46
	Length	0.17	0.25	0.70	0.49

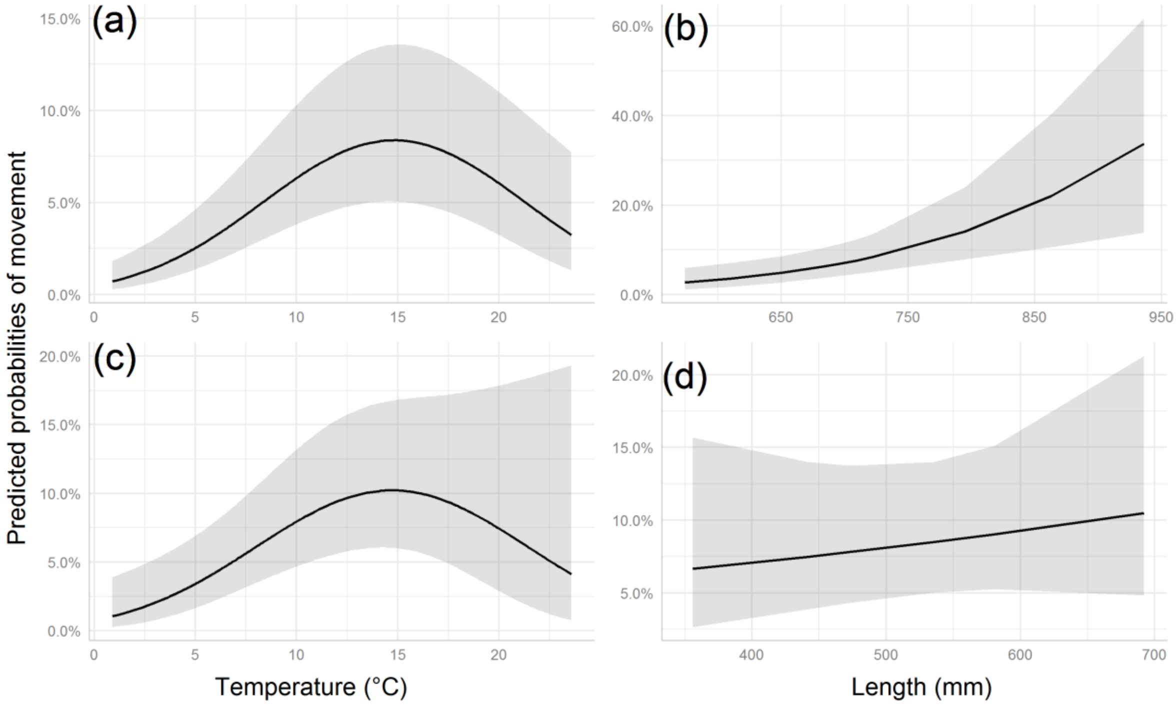

Figure 25. Predicted probabilities of daily movement with mean daily water temperature (°C) for (a) pike and (c) pikeperch, and with fish length (mm) for (b) pike and (d) pikeperch for the lower River Severn during the 12 month study period as predicted from a mixed effects logistic regression where the binary response was daily movement (detected movement vs. no detected movement). Shaded regions represent the 95 % confidence intervals.

Table 19. Coefficient estimates, standard errors, *t* scores and their significance from results of generalised linear models testing weekly marina residency of pike and pikeperch (analysed separately) versus weekly mean water temperature and water flow with season as a fixed effect.

Species	Coefficients	Estimate	SE	*t* value	*P*
Pike	Intercept	-0.45	0.25	-1.83	0.07
Pike	Temperature	-0.07	0.02	-3.73	< 0.01
Pike	Flow	0.01	0.01	0.75	0.46
Pike	Summer	0.17	0.28	0.60	0.55
Pike	Autumn	-0.05	0.17	-0.32	0.75
Pike	Winter	0.09	0.15	0.63	0.53
Pikeperch	Intercept	0.21	0.48	0.44	0.66
Pikeperch	Temperature	-0.11	0.05	-2.42	0.02
Pikeperch	Flow	-0.01	0.01	-1.88	0.07
Pikeperch	Summer	-2.31	1.15	-2.02	0.04
Pikeperch	Autumn	-1.15	0.50	-2.32	0.02
Pikeperch	Winter	-0.48	0.29	-1.66	0.10

The diel activity of both species revealed no significant differences in the number of movements per hour within each dawn, day, dusk and night period over the 12 months (pike: Kruskal-Wallis χ^2 = 7.26, *P* = 0.06; pikeperch: Kruskal-Wallis χ^2 = 6.27, *P* = 0.09; Figure 27). However, when analysed seasonally, pike movement within each diel period were not equally distributed across seasons (χ^2 = 24.46, *df* = 9, *P* < 0.01; Figure 27), with increased movements during dawn and dusk in summer and autumn (Figure 27). This was not apparent in pikeperch, where movements at dawn, day, dusk and night were equally distributed across seasons (χ^2 = 6.27, *df* = 9, *P* = 0.44) (Figure 27).

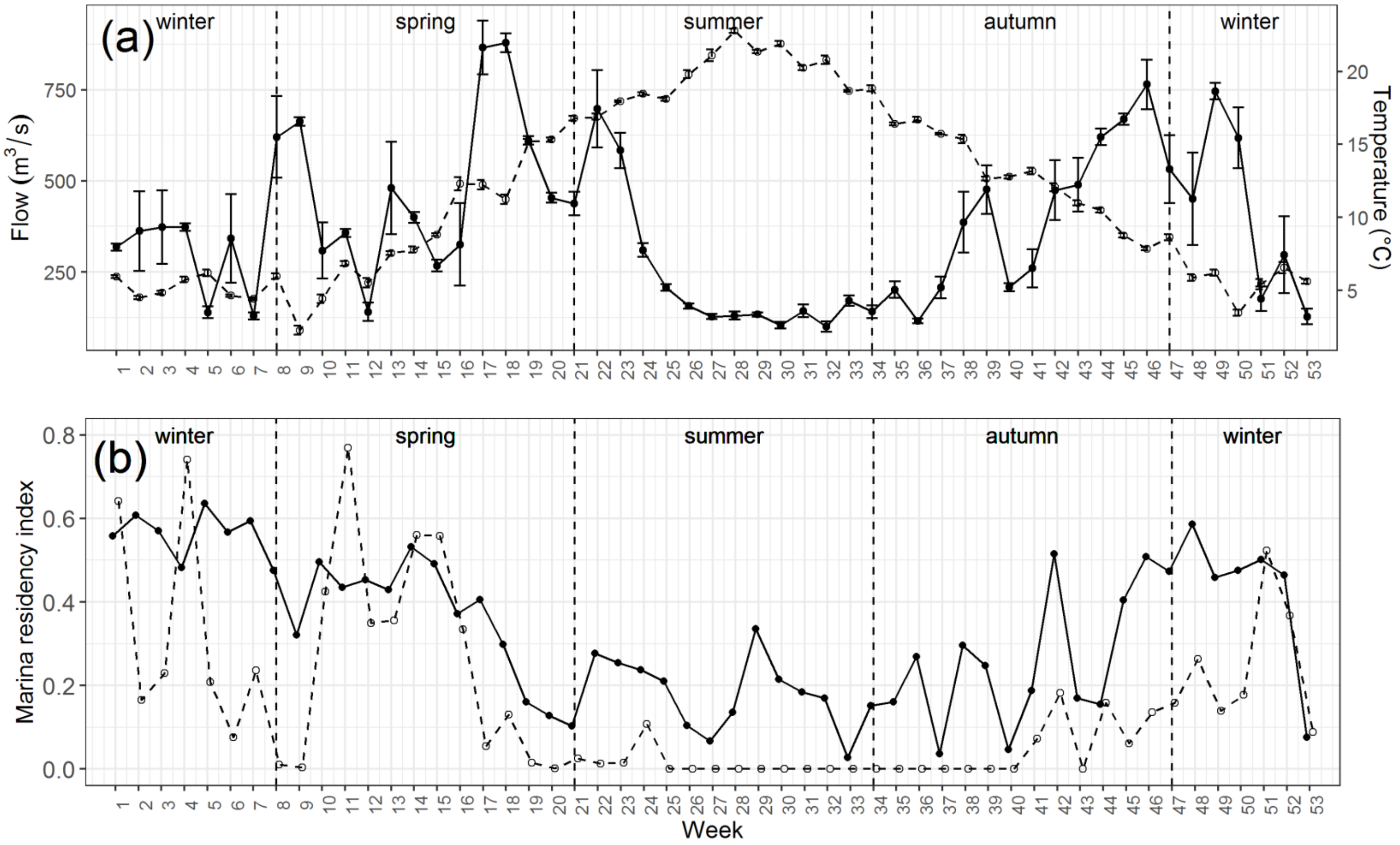

Figure 26. (a) Weekly mean water temperature (°C) (open circle, dashed line) and water flow (m^3/s) (closed circle, solid line) with 95% confidence intervals across the study period; and (b) weekly mean marina residency index for pike (closed circle, solid line) and pikeperch (open circle, dashed line) for the lower River Severn during the 12 month study period

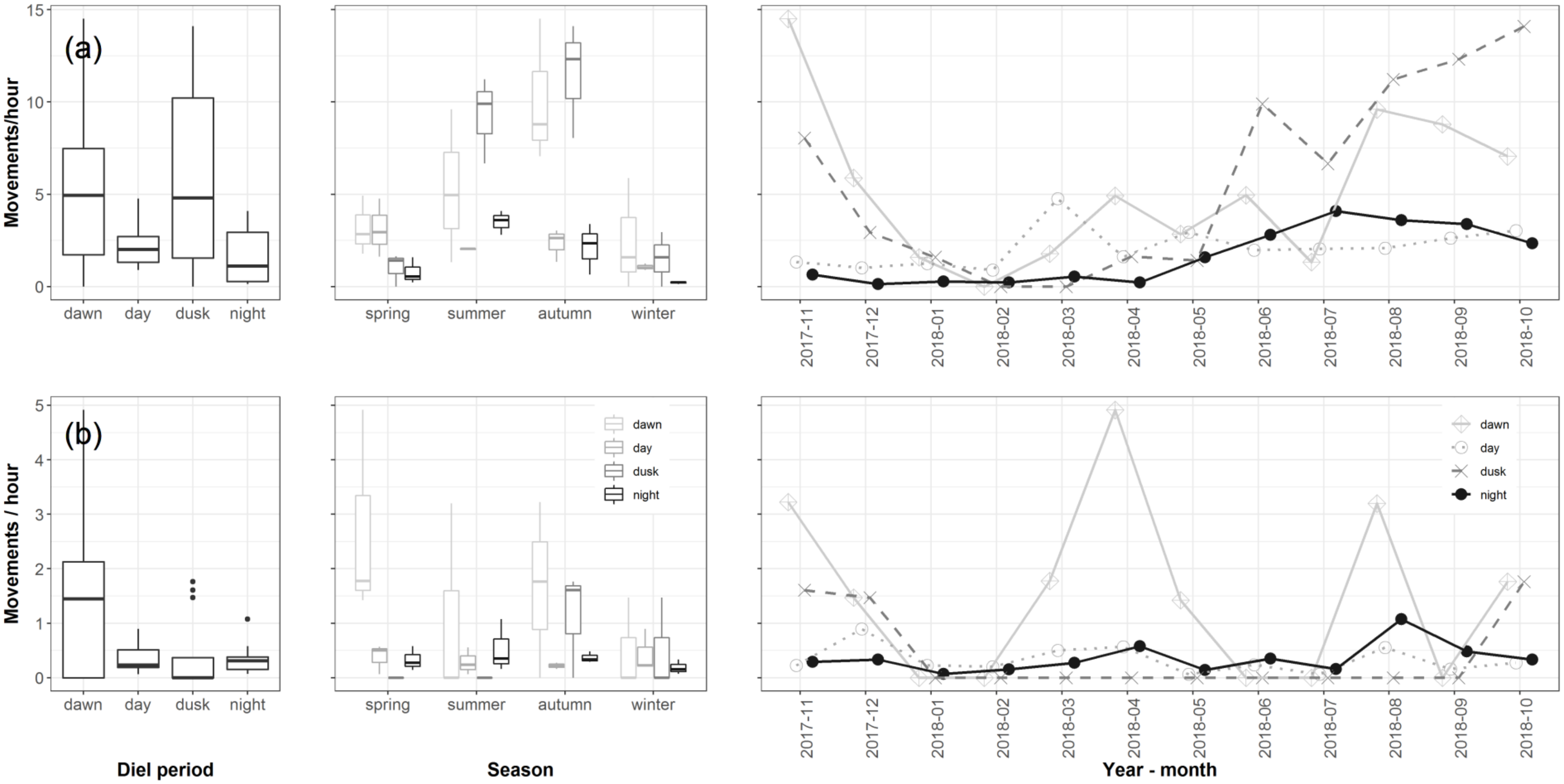

Figure 27. Number of detected movements per hour for (a) pike and (b) pikeperch for dawn, day, dusk and night across the tracking period, seasonally, and for each month of the study. Boxplots show the first, median and third quartiles and 95% confidence intervals are shown by the whiskers, and outliers as filled circles

6.5 Discussion

The movement and behaviour of the native pike and non-native pikeperch was characterised by within species variability in spatial and temporal space use, but with an overall increase in the total daily distance moved during spring, increased movement activity up to 15 °C for both species and with fish fork length for pike, and seasonal variation between species in the use of limited off-channel habitat. Relatively long-distance movements were detected in pike in spring, assumed to be spawning migrations, but with these movements not detected for pikeperch. Off-channel habitat was important for pikeperch in winter and spring, and could represent an important spawning location, while this habitat was important to pike all year round.

Spatial utilisation of the river for both pike and pikeperch across the 12-month study period was focused to an area of less than 5 km upstream and downstream of the sampling location. Movement activity could be characterised as long stationary periods followed by movements that were either infrequent or frequent but across short distances. In pike, long distance movements of greater than 5 km tended to be abrupt and primarily occurred during the spawning season. For pike, it has been suggested that populations are made up of different behavioural types including those that are primarily sedentary and those that move more frequently (Vehanen et al. 2006, Sandlund et al. 2016), although others have suggested that pike are represented by a continuum of behavioural types (Masters et al. 2005). They have also been categorised across three broad behavioural groups, including individuals that stay in restricted areas, those that move between favoured areas and those that are more opportunistic and exploratory in their resource use (Jepsen et al. 2001, Kobler et al. 2009). For pikeperch, individual variability in resource use has rarely been reported, with synchronised movements most often associated with spawning activity or foraging (Koed 2000, Koed et al. 2002), although evidence exists to suggest they may be represented by two distinct behavioural types, active and sedentary (Fickling and Lee 1985). Distinct differences in movement patterns within species were apparent in this study, but the combination of a relatively limited sample size and the intermittent distribution of receivers preventing the measurement of fine-scale movements, inhibits the classification of individuals into distinct behavioural groupings.

The timing of onset of spawning for pike in rivers in England tends to be in March (Mann 1976, Masters et al. 2005) with optimum spawning temperatures of between 6 to 14°C (Frost and Kipling 1967). For pikeperch, spawning takes place at temperatures of between 8 to 16 °C and is expected to occur predictably across latitudes, suggesting it will commence in mid-April in central England in most years (Lappalainen et al. 2003). In mature individuals, pike activity increases around the spawning period (Koed et al. 2006, Baktoft et al. 2012), with migratory spawning movements in spring accounting for differences in seasonal movement patterns (Ovidio and Philippart 2005, Koed et al. 2006, Pauwels et al. 2014). Indeed, evidence of seasonal differences in movement activity beyond migratory spawning behaviour is rare (Kobler et al. 2008). Temperature usually triggers migration in both sexes (Pauwels et al. 2014), and pike can show homing to natal spawning sites (Engstedt et al. 2014, Sandlund et al. 2016), although where homing behaviour has been observed it may not be evident across the entire population (Vehanen et al. 2006). It is therefore possible that pike making the relatively long-distance movements in spring in this study were homing to specific spawning locations that are suitable for spawning, such as over vegetation in shallow water (Casselman and Lewis 1996).

Increased activity of pikeperch in spring is also associated with reproductive behaviour and spawning migrations (Lappalainen et al. 2003), although this can vary between sexes, as male movements can be reduced due to their nest guarding behaviours (Jepsen et al. 1999, Poulet, Lek, et al. 2005). However, it is also common to see seasonal activity peaks in pikeperch that are unrelated to spawning migrations, such as peaks in autumn, summer or winter activity that are linked to feeding migrations, particularly in systems where prey are a limiting resource (Jepsen et al. 1999, Koed 2000, Horkỳ et al. 2006). These seasonal migration patterns have been linked to seasonal changes in prey availability, with corresponding dietary shifts (Huuskonen et al. 2019). Pikeperch prefer to spawn in still or slow flowing waters (Lappalainen et al. 2003) and if spawning takes place in unsuitable high-water velocity conditions then larvae and juveniles can be displaced downstream (Koed 2000). The higher residency index of pikeperch in the marina in spring may in part be due to the use of this area as a spawning location, exposed pikeperch nests were observed in the marina during a receding flood in April 2018 (personal observations, the authors).

Temperature is an important factor in explaining increased activity for both pike and pikeperch. For example, relative changes in temperature can stimulate movement in pikeperch during the pre-spawning and spawning season, with the extent of temperature changes potentially a more important predictor of movement than the actual water temperature (Saulamo and Lappalainen 2007). However, decreased activity with decreasing temperature, and increased activity with increasing temperature, has also been observed for pikeperch (Jepsen et al. 1999). In pike, elevated winter temperatures of up to 5 °C can also trigger increased movements (Jepsen et al. 2001, Koed et al. 2006), although both high and low temperatures can decrease movement rates overall (Kobler et al. 2008). For example, in a study of riverine pike in Finland, movement decreased when summer water temperatures reached 20 °C compared to higher levels of movement when summer water temperature reached a maximum of 15 °C (Vehanen et al. 2006). These findings are consistent with those found in this study over both species.

Many piscivorous fishes have activity peaks at dawn and dusk due to the potential for higher foraging success during these periods (Helfman 1986). Here, pike were detected to have activity peaks during twilight periods in summer and autumn, whereas no significant activity differences across diel periods were detected in pikeperch, although more movements were generally observed at dawn, these were not significantly different to other periods, perhaps at least in part due to the relatively small sample size. For pike, results were similar to those of Kobler et al. (2008), who suggested that increased activity in summer twilight periods was a shortterm behavioural response to maximise food intake during this period. For pikeperch, a measured increase in activity in twilight periods was shown by Horký et al. (2008), with water temperature, individual behaviour and sex influencing the extent of diel activity patterns (Poulet, Arzel, et al. 2005).

In summary, these results suggested that whilst there was some individual variation in the spatial behaviour and activity of both pike and pikeperch in the river, there were also some important differences between the species. In particular, the limited off-channel habitat available was important to pike all year round, whereas pikeperch primarily used it in winter and spring, and whilst pike reduced the frequency of their movements in winter, this was not evident in pikeperch. These results thus provide important insights on the spatial ecology of these co-existing native and non-native predatory fishes, and can be applied to the management of their populations and fisheries, especially in relation to the consideration of increasing the provision of off-channel habitats, given their apparent importance for both species.

7 Angler behaviours and motivations for exploiting invasive and native predatory fishes by catch-and-release: A case study on the River Severn catchment, Western England

7.1 Abstract

Catch-and-release sport angling for large-bodied fishes is a popular recreational pastime, but is also a major introduction source of invasive fishes that can impact native biodiversity. Introductions of large non-native fishes are often part of fisheries management practices to diversify angler opportunities and increase satisfaction. Interviews with sport anglers (*n* = 12) targeting native pike *Esox lucius* and invasive pikeperch *Sander lucioperca* in the River Severn, Western England, were conducted to determine angler motivations, behaviours and perceptions. While motivations were catch orientated, they also related to catching wild fish in natural surroundings. Conservation values were reflected in the behavioural safeguarding of pikeperch populations, including catch-and-release practices that are contrary to current fisheries policy. Anglers perceived pikeperch as enhancing the fishery without causing long-term ecological impacts and were opposed to current management practices and policy. These results suggest considerable disjuncture between angler motivations and behaviours, and non-native fish policy and management.

7.2 Introduction

It is generally agreed that recreational fishing is a goal-orientated behavioural process driven by psychological desires (Fedler and Ditton 1994, Manfredo et al. 1996). However, there are many reasons why people fish, including both catch and non-catch aspects of the fishing experience (Arlinghaus 2006b, Young et al. 2016). Activity general, non-catch related motivations include relaxation, getting away from the daily routine (‘escaping’), and being outdoors, whereas activity specific, catch motivations include catching specific species, sizes, and numbers of fish; the challenge and experience; developing skills; and testing equipment (Fedler and Ditton 1994). Non-catch related motivations tend to be more ubiquitous among angler groups than catch motivations that can vary widely depending on angler type (Chipman and Helfrich 1988, Fedler and Ditton 1994).

Understanding how activity specific motivations translate into actual angling behaviours is important for managing fisheries (Fedler and Ditton 1994, Arlinghaus 2006b, Beardmore et al. 2014). For example, a preference for fish attributes that meet trophy motivations has resulted in unregulated releases of large bodied, non-native predatory fishes by anglers (Elvira and Almodóvar 2001, Banha et al. 2017). Indeed, sport angling has been responsible for approximately 12% of global fish introductions (Gozlan, Britton, et al. 2010). Participatory fishery management approaches such as these are common and can exert a strong influence on management agencies (Eden and Bear 2012). Species that have been introduced around the world for angling include Peacock basses of the *Cichla* genus (Britton and Orsi 2012), European catfish *Silurus glanis* (Cucherousset et al. 2017) and largemouth bass *Micropterus salmoides* (Britton, Harper, et al. 2010). A common feature of these fish species is their generally high trophic position that results from their piscivory (i.e. their predation upon other fishes, herein referred to as ‘predator’) (Eby et al. 2006). The aim of this study was to understand how the motivations and preferences of anglers who target large-bodied native and invasive predatory fish translate into actual behavioural practices and perceptions.

The pikeperch *Sander lucioperca* (commonly referred to as zander by the angling community of England) were first introduced into Britain in the late 19th Century (Sachs 1878), but became more widespread following translocations in the 1960s to the River Great Ouse Relief Channel in Eastern England (Wheeler and Maitland 1973). From there, their colonization and dispersal through river and canal systems was rapid, aided by unregulated movements by anglers (Hickley and Chare 2004). The result was their subsequent invasion of many river basins in central and southern England (Copp et al. 2003, Nunn et al. 2007). Associated with these introductions were reported deleterious impacts on the native fish community (Linfield and Rickards 1979, Fickling and Lee 1983, Hickley 1986, Smith et al. 1998), although evidence remains equivocal.

The majority of British recreational freshwater anglers practice catch-and-release (i.e., returning the fish alive after capture; (North 2002) North 2002), including anglers targeting pikeperch. Mandatory catch-and-release practices for species such as Atlantic salmon *Salmo salar* are commonly used as a conservation tool (Aprahamian et al. 2010), although these activities can generate conflict within angling communities. For example, in Germany, conflict arises between specialist anglers practicing voluntary catch-and-release and those who see these practices as cruel, illegal (despite not being so), or contrary to consumptive fishing practices (Arlinghaus 2007). Despite the apparent popularity of pikeperch for sport angling in British rivers such as the River Severn, and the propensity for anglers to practice catch-and-release, it is an offence for an angler to release a pikeperch that has been caught (Schedule 9, Section 14(1), Wildlife and Countryside Act 1981). Conversely, under different legislation, the species can be legally stocked into enclosed waters [Import of Live Fish (England and Wales) Act 1980, (ILFA); Keeping and Introduction of Fish (England and River Esk catchment Area) Regulations 2015, (KIF)]. These contradictory policies and practices could be heightening conflicts between anglers of opposing motivational drivers.

In England, freshwater anglers tend to be classified as either ‘coarse’ or ‘game’ by management agencies (Environment Agency 2018a). Game anglers target species such as salmon, trout *Salmo trutta*, and grayling *Thymallus thymallus*, whereas coarse anglers, who represent the majority of freshwater recreational anglers in England (Environment Agency 2018b) tend to target cyprinid species including carp *Cyprinus carpio*, barbel *Barbus barbus*, and chub *Squalius cephalus*. However, coarse anglers also include those that target large-bodied predator species, such as Northern pike *Esox lucius* and pikeperch. Nevertheless, anglers are a heterogeneous ‘public’ (Eden and Bear 2011) and, according to their own descriptions, coarse anglers in England can be categorized into three groups: (a) ‘match’ anglers, who compete against others in an attempt to catch the largest weight of fish in a given period; (b) ‘pleasure’ anglers, where the overall fishing experience is important; and (c) ‘specialist’ anglers, who focus on a particular species or on catching a large individual ‘specimen’ or ‘trophy’ fish (Eden and Bear 2011).

Here, specialist predator anglers are defined as those whose primary fishing activity is involved in the targeting of large-bodied obligate predatory fishes such as pike and pikeperch. Sophisticated rod and line techniques, including lures, as well as live- and dead-bait angling are used to target these species. Where species coexist, targeting of one species over the other can be difficult, although size selectivity is possible. This definition of specialization follows that of Scott and Shafer (2001) where there is a focusing of behaviour, skill development, commitment, and the acquisition of knowledge. For the specialist predator angler, catch orientated motivations are known to be important drivers of behaviour (Chipman and

Helfrich 1988, Beardmore et al. 2011), with ‘trophy seeking’ among their most important motivations (Beardmore et al. 2011).

Recreational fisheries have been defined as complex adaptive socio-economic systems and it is argued that equal recognition should be given to both the human and ecological dimensions for effective management (Cooke et al. 2013, Hunt et al. 2013, Arlinghaus et al. 2017). In the last decade, interdisciplinary methods have been used for integrating recreational fishing practices with conservation (Cooke et al. 2006). Emerging research on perceptions can also be used for assessing, informing, and gauging support for conservation initiatives and policy (Gelcich and O’Keeffe 2016), and assessments of angler perceptions relating to introductions have been successfully used for optimizing awareness campaigns and understanding risk behaviour (Lindgren 2006, Gozlan et al. 2013). Although such assessments can improve management and governance (Boone and Ryder 2017), they often rely on quantitative analyses of social data that might not fully consider the complexities of managing fisheries as social adaptive systems (Fenichel et al. 2013, Barclay et al. 2017). In contrast, qualitative methods such as interviews can provide greater insight into the perceptions and behavioural processes of recreational anglers (Barclay et al. 2017).

Consequently, the objectives of this study were to use in-depth interviews with specialist anglers of the Severn basin in Western England who exploit pike and / or pikeperch, to understand the motivations and preferences of these specialist anglers and how they translate into behavioural practices and perceptions concerning the management and regulation of native and invasive predatory fish, particularly in relation to their catch-and-release activities.

7.3 Methods

7.3.1 Study River

The River Severn basin covers an area spanning central and western England, and parts of Wales (

Figure 28). The River Severn is an important fishery in England, where freshwater angling contributes £1.5 billion per year to the economy (Environment Agency, 2018a). Pikeperch were first reported in the catchment in 1976, with reports of captures by anglers from the lower River Severn in 1980 (Hickley 1986). Pikeperch are now established throughout much of the canal and river network in Central and Southern England, and in the Severn are considered an important fishery resource. The British rod-caught record pikeperch weighing 9.67 kg was caught from the lower River Severn at Tewkesbury (British Record (Rod Caught) Fish Committee, 2016). Some of the interviewed anglers also fish on the River Wye for pike, where pikeperch are absent.

7.3.2 Data Collection

Semi-structured interviews with specialist predator anglers within the River Severn catchment were conducted (*n* = 12). Anglers were chosen based on the criteria that: (a) their primary fishing activity was centred on freshwater predator species including pike and/or the non-native pikeperch, and (b) the majority of their angling activity occurred within the Severn catchment. These criteria were determined by means of a survey prior to these interviews, and were essential to ensuring that the views expressed represented specialist freshwater predator anglers practicing catch-and-release from lotic environments where pikeperch were present. All anglers either identified as ‘dedicated predator anglers’ where they only target predator species or ‘dedicated predator anglers, but also target non-predator species’ (Table 20). The initial survey also provided an opportunity to collect angler demographic information. Candidates for interviews were originally identified through facilitation with the Environment Agency, the inland fishery regulatory body of England, who had established a predator angling network within the River Severn catchment. As the interviews progressed, interviewees would sometimes refer the interviewer to other potential candidates for interviews as appropriate (snowball sampling). To maintain anonymity, anglers are identified here as angler #1 through to #12.

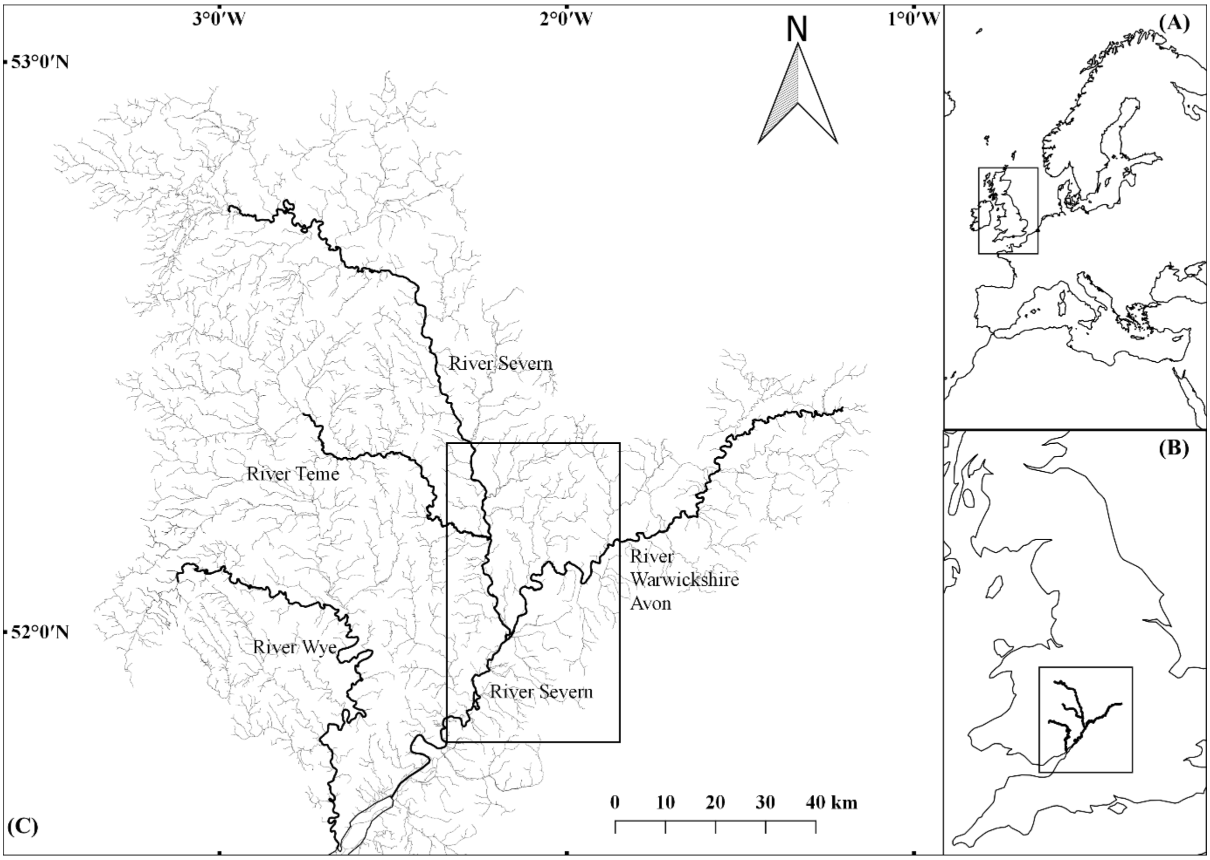

Figure 28. Maps of: (A) Western Europe showing the position (inset) of Great Britain, (B) the main rivers shown within the Severn River basin (inset) within England, and (C) a detailed outline of the Severn River basin showing the main rivers and their tributaries within which the approximate limits of pikeperch fishing are shown (inset).

The interviews followed a semi-structured, open-ended approach (Gall et al. 2003, Jennings 2005) and included five main topics: (a) the development of their angling interest, (b) their predator angling participation, (c) their fishing preferences, (d) their views on management and conservation, and (e) their experience with pikeperch. Within these themes, questions were developed and designed to be used as a conversational guide. The aim of the interview was to be informal, with topics introduced in a non-rigid manner to encourage reflection and self-expression (Turner III 2010). Interviews followed the ethical code of conduct for social research with anglers assured anonymity and given information relating to the study prior to their interview. Interviews were recorded and transcribed verbatim to written text by the interviewer immediately after each interview, allowing for reflection by the interviewer on the emergent themes. Sampling continued until the interviews yielded consistent themes (i.e., data saturation; Jennings 2005).

7.3.3 Data Analyses

A thematic analysis framework was used for identifying, analysing, and reporting themes within the data generated by the interviews and was conducted using NVIVO qualitative analysis software (QSR International 2012). Thematic analysis was used for developing categories of meaning within the data through a six-step approach. The data were initially assigned to non-hierarchical open codes that identified interesting features of the data (Miles et al. 1994). Then, codes that showed commonality were grouped and re-focused, enabling collation into identified themes (Graneheim and Lundman 2004). This was followed by reviewing the themes to ensure clear and identifiable distinctions that offered clearer insight into the meanings contained within. Finally, the themes were refined and named before producing an analytical narrative around the data (Braun and Clarke 2006). It should be noted that in Britain, pikeperch are commonly referred to as zander by the angling community and this is reflected in the interview data.

7.4 Results

7.4.1 Interviewees and Main Themes from Interviews

All of the interviewed anglers identified themselves as dedicated predator anglers, with only two anglers also targeting non-predator species (Table 20). The 12 interviewees were predominantly male (*n* = 10), and the majority had been recreationally angling for more than 40 years (*n* = 7). Of the remaining anglers, three had been fishing for predator species for more than 20 years, one for more than 10 years, and one for more than five years. Ages ranged between 25 and 74 years. All of the anglers interviewed practiced catch-and-release angling for both pike and pikeperch.

The analyses revealed six main themes: (a) the predator angler identity; (b) angler led management; (c) catch orientated motivations; (d) angling preferences; (e) angler reconciliation on the introduction, establishment and exploitation of pikeperch; and (f) current views on the management of pikeperch.

Table 20. Participant profile including age, sex, years of experience, predator angling activity, preferred target species, and specialization. Anglers are identified by number from 1 to 12, those described as ‘dedicated predator anglers’ only fish for pike and/or pikeperch and do not target other species.

Angler ID	Predator angling specialization	Preferred target species	Predator angling activity (days per year)	Years fishing	Years predator fishing	Age category	Sex	Interview duration (minutes)
1	Dedicated predator angler	Pike	13 to 35	> 40	> 40	55 - 64	M	59
2	Dedicated predator angler	Pike and pikeperch	> 35	> 40	> 40	55 - 64	M	35
3	Dedicated predator angler	Pike	2 to 5	< 10	< 10	45 - 54	F	56
4	Dedicated predator angler	Pike and pikeperch	13 to 35	> 30	> 30	25 - 34	F	47
5	Dedicated predator angler, also targets non-predatory species	Pike and pikeperch	> 35	> 40	> 20	35 - 44	M	53
6	Dedicated predator angler	Pikeperch	> 35	> 40	< 5	45 - 54	M	38
7	Dedicated predator angler	Pikeperch	> 35	> 40	> 20	55 - 64	M	53
8	Dedicated predator angler, also targets non-predatory species	Pike and pikeperch	> 35	> 30	> 20	45 - 54	M	62
9	Dedicated predator angler	Pike	13 to 35	> 40	< 10	65 - 74	M	63
10	Dedicated predator angler	Pike	13 to 35	> 20	> 20	25 - 34	M	68
11	Dedicated predator angler	Pike and pikeperch	> 35	< 5	< 5	65 - 74	M	33
12	Dedicated predator angler	Pikeperch	> 35	> 40	> 40	55 - 64	M	53

7.4.2 The predator angler identity

The interviewed anglers often reflected that their desire to fish was a way of life, with wording such as: "*it's in my blood,*" "*it gets under your skin,*" and "*the gene*" used regularly to reflect their feelings toward fishing generally. There was also a strong sense of the predator angler identity, which in part had been formed out of pike angler conflict with other angling groups: "*we saw pike fishing and being a pike angler as being a bit elite, I suppose, compared to round here - they were all either match anglers or salmon anglers*" (angler #1). The majority of interviewed anglers spoke about this conflict and separation between angler groups, which seemed to arise from the historical practice by 'coarse' anglers of killing captured pike as a way to reduce predation pressure on non-piscivorous fish population: "*in those days, this is the early 1970s, match anglers threw all the pike up the bank, they weren't kept, no pike were returned and they weren't kept for the table - they were just thrown up the bank"* (angler #2).

Most anglers in this study still referred to the opposition of some modern day 'coarse' anglers to predatory fish species: "*there are still many clubs which are very anti-predators*" (angler #10); "*some of them they hate predators because they think they are eating my fish, the coarse fish*" (angler #4). For the pike angler, a commonly displayed trait was the fostering of a conservation attitude toward pike. This attitude was reflected in their fishing practices: "*it's a natural resource that needs to be looked after; there are other anglers coming up behind us and hopefully there will be a few decent fish for them to enjoy*" (angler #9). This conservation attitude was apparent in their education and influences on other anglers regarding the ecological role of predator species in maintaining a healthy and balanced fishery: "*it is very important to promote the understanding of these magnificent creatures which preform a role in nature, they are not the voracious pirates that they have been made out to be in years past*" (angler #1).

7.4.3 Angler led management

The interviewed anglers often revealed a feeling of ownership toward their target species, and employed a variety of measures that they see as vital for protecting the species and for sustainable resource use: "*you do have to protect the fish as well as your own fishing interests*" (angler #5). The most commonly used 'management' tool among all interviewed anglers was secrecy, and it seemed to be a well-established rule among specialist predator anglers that favorite fishing locations are never or rarely shared, even among friends: "*they don't tell me where they fish and I don't tell them where I fish*" (angler #1); '*it's anti-social and secretive generally speaking and it's different to most types of fishing, that's the thing*' (angler #3), *"the pike fishers are quite secretive and they don't like giving their positions away"* (angler #12). Secrecy is perceived as a means of reducing the fishing pressure to a particular area or even to individual fish: "*many people just want to protect the fishery, they think if it is just my spot I will catch this fish and no one else*" (angler #4), *"you do have to protect the fish as well as your own fishing interests*" (angler #5).

These anglers had very defined views on the care that should be taken throughout the catch-and-release process, with good handling techniques an important part of being a respected predator angler: "*I like to pride myself on it, I think I have a certain level of skill in handling a fish and putting it back in excellent condition*" (angler #5). There was also contempt shown toward other predator anglers with inadequate handing methods: "*When you see a pike, it's like I said before, it is a delicate fish and when you see it in a picture covered in crap so you can tell they haven't used a mat and you can guess it's been thrashing around and you just think for God's sake, that's the kind of thing that really annoys me, it's just totally undermining everything that proper anglers are trying to do*" (angler #10).

7.4.4 Catch orientated motivations

The chance of catching a large 'trophy' fish was mentioned by all of these anglers as an important motivation for targeting predatory species: "*we were all brought up 'biggest is best' and that's what we have always been about, trying to catch the biggest fish"* (angler #1). However, it was not necessarily about beating national records, as these anglers also often spoke about the size in weight of their biggest predator captures and their aspirations to beat their own personal best (pb) record: "*ultimately if I am doing it then what I want is a pb*" [angler #7); "*It's competing with yourself, challenging to catch your personal best, so I think the most beautiful thing is when you catch that fish*" (angler #4). Thus, personal challenge motivations were important.

As national record catches of pike in Britain now usually come from managed lake fisheries (British Record (Rod Caught) Fish Committee, 2016), river angling is less likely to achieve a record pike. Correspondingly, the anglers revealed their motivations were to catch what they considered as a natural river fish: "*A river pike is a wild fish, so much more appealing, to me, than the artificially fed giants of trout reservoirs, which are of no interest to me"* (angler #10]; "*if you are talking a 30 lb trout water fish, as nice as it is, and a great achievement it still doesn't scratch a 30 lb wild Wye river fish, not at all, and that's my sort of fishing*" (angler #9). This motivation to fish for large river fish exists despite low catch returns in relation to effort expenditure, with the anglers often reflecting on this: "*if you expected to catch every time you went you would probably give up quite quickly"* (angler #3). However, for the anglers specifically fishing on the River Severn for pikeperch, catching a record fish is an important motivation: "*The chance of a record fish would be the zander. So, it's always at the back of your mind the Severn will produce a 20lb zander and the chance that there is a record there, I think that's probably what keeps me going*" (angler #12).

Activity general motivations to fish rivers were also important with interviewed anglers mentioning a main motivation to fish rivers as an opportunity to enjoy nature and to be in a natural setting: "*I enjoy being out, the bird life the fresh air and that and just chilling*" (angler #7); "*the way the trees are with the way the sun sets and the light through them, you just find a pleasant spot to be, it's away from the crowds and stuff*" (angler #8). Rivers also provided an angling opportunity that was distinct, compelling, and related to the catch uncertainty: "*like you go up the lake and you know you are going to catch, you go on a river and you could catch anything*" (angler #11). This ties into the acknowledgement by these anglers that the anticipation of catching provided nearly as much pleasure as the act of catching itself: "*it's always nice to catch fish, but even if you are getting takes the anticipation is there*" (angler #12). It was particularly apparent that not knowing which species might be caught added an additional element of excitement to the fishing experience: "*my favourite species are pike; always have been, but every time the float dips and we strike into a fish and it feels like a good one, we both say, please be a zander*" (angler #2). These anglers acknowledged that if they fish for pike in a water that also supports populations of pikeperch, they are likely to catch both: "*caught it* [pikeperch] *by accident my first one, I was float ledgering a dead roach for pike and one* *took and that was just over 4lb and that was the first one I ever caught*" (angler #5). To some degree, predator fishing in England has thus become non-selective in terms of target species.

7.4.5 Angling preference

The preferences of interviewees in catching pike and pikeperch seemed to be toward a diversification in fishing styles: "*there is that many different methods for catching them, we are sitting here legering now, but we can paternoster a live bait, dropshot, dead-bait, lure fish, vertical jig, you know, so there are that many different methods*" (angler #7). Specifically, lure fishing was often acknowledged as helping to increase the popularity of predator fishing: "*the one thing that is turning people into predator anglers is lure fishing, that is the massive deal these days*" (angler #1). It was also the opinion of the interviewed predator anglers that lure fishing is more popular when targeting pikeperch than for pike: "*there a significant proportion of the lure angler population that fishes canals that don't want to catch a pike, it's more like a bycatch*" (angler #6), and more popular among the younger generation: "*kids are getting into it, chucking their lures, you know, catching little zander, brilliant. You know I see it as a huge benefit"* (angler #10), whereas another angler commented: "*there are lot more younger people in the lure angling side of things. Now we're not talking teens, we are talking people in their 20s and 30s*" (angler #6). All of the anglers interviewed used lures in their fishing to some degree, even if they had a preference for using baits, and all of these anglers talked about lure fishing and its importance to angling generally, making it the most talked about topic overall: "*it's probably the biggest growing sport now, I think carp fishing has levelled out and lure fishing is taking its place*" (angler #7). The popularity of lure fishing was attributed to its success as a method for catching predatory species and as a more convenient and accessible method compared to bait fishing: "*It's a good way of getting a few hours fishing in, or an hours fishing in if you are pushed for time, most lure gear will fit in the boot of your car quite easily*" (angler #5).

7.4.6 Reconciliation

One angler's opinion on the introduction of pikeperch to the Severn nicely summarised the opinion of many of those interviewed: "*we knew the pike weren't a problem because* *the pike perform a function of natural fishery management and I think we thought the pike would sort them* [pikeperch] *out anyway, and those that did get through the pike gauntlet would be big enough to be worth catching so it didn't really bother us*" (angler #1). However, many interviewed anglers who had experience of fishing the river during the time of pikeperch introduction also recognized an impact to their fishing at the time: "*it was really the zander round about that time that took me away from the river because we were struggling to catch the pike, we were just getting hit by little zander all the time"* (angler #2). The same recollection was given by an angler who fishes the adjoining canal systems: "*when people introduced zander to the canal it changed the structure of the fishery completely, if you went to catch a roach it was impossible to catch a small roach, the only thing you could catch was 8 to 10 oz because the zander had them* [the smaller roach]" (angler #7).

Angler knowledge and experience with the introduction and subsequent establishment of pikeperch, a conservation attitude toward piscivorous species, and unique catch orientated motivations and preferences appear to foster a favorable understanding toward pikeperch: "*I actually think it's better than it's ever been and I think that's down to the zander being there because the zander are a food source for the pike - they are benefiting if anything, pike are eating them up, they are controlling other fish and it's balanced out*" (angler #10). The use of the word 'balance' was common among these anglers when asked about pikeperch introduction and establishment. However, for something to be in balance suggests a perception of imbalance; when anglers were asked to clarify this dichotomy they said things such as: "*I think the zander population has maybe stabilized a bit and pike have come back because I guess they do compete in some way*" (angler #7). When asked specifically about the view that pikeperch can have a negative impact to native species, the anglers then recollected that it is only in recent years that they have seen an improvement in pike fishing since the introduction of pikeperch: "*I think 30 years on from when zander came into our rivers, the pike are the dominant predator again, it's taken that time for them to get back to where they are now*" (angler #2).

7.4.7 Current views on management of pikeperch (perceptions)

It was apparent that the interviewed anglers saw major potential in pikeperch as a species in providing new angling opportunities and commented on a perceived increase in popularity from pike to pikeperch fishing within the predator angling community: "*a lot of my friends who were pike anglers, they now go for zander, I think they find it more exciting*" (angler #4). The anglers also highlighted fishing for pikeperch as a means to help promote angling more generally: "*my perception is that fishing is more on the decrease than the increase as a sport and having another species that is going to encourage people to go fishing, like zander, that can only be a good thing really*" (angler #3), and these anglers often talked about the economic importance of the fishing resource: "*You only have to think about it in economic terms, a lot of people are coming to fish for these zander"* (angler #1).

Interviewed anglers were opposed to the culling of pikeperch and had a pragmatic view on the subject: "*they are in there now, we are never going to eradicate them*" (angler #8). Well-developed opinions were also expressed on the validity of pikeperch removal operations: "*by actually not removing them, you end up with a situation where they self-regulate and it doesn't take a very long time to get the zander population in control. They are widespread, you can't eradicate them and I'm not sure what the rationale is for doing it"* (angler #6). With these anglers speaking of their distress at seeing a culling operation, where pikeperch were removed from a section of canal and dispatched via electric-fishing: "*for me I think it's awful. It was maybe 3 tonne of zander from maybe 4 km of the river, so that's a lot and I don't understand why they do it, why they remove fish*" (angler #4).

The practice of catch and release was never defended, or questioned by the interviewed anglers and it was apparent that it was seen as the moral thing to do and that it was their right. In fact, one particular angler had even successfully lobbied for an angling club to change their rules in relation to the catch-and-release of pikeperch: "*about 3 years ago I persuaded the* [club name removed for anonymity] *to do away with their archaic rule of killing zander on site*" (angler #1). Interviewed anglers also recognized the current legislation: "*legally and technically, zander are still on the alien species register*" (angler #1), and would like to see them having some sort of legal protection: "*they are naturalized I would class them as now and deserve some kind of protection*" (angler #8). However, these same anglers were opposed to the introduction of pikeperch to an important pike river fishery in an adjacent river basin: "*I'm happy enough they are not in the Wye; I'd be on absolute tenterhooks if they turned up in the Wye*" (angler #9); "*the great thing for me is that when I go pike fishing on the Wye if I get a take it's going to be a pike, it's not going to be a zander so that's great*" (angler #1).

7.5 Discussion

Motivations of these predator anglers to the voluntarily catch-and-release of an invasive species were revealed here to be connected to an underlying conservation attitude that has developed out of cultural norms, an awareness of the consequences of their activity and unique motivations and preferences. Findings revealed a lack of support for current management and policy relating to pikeperch in England, with the perception by these anglers that the practice of catch-and-release for pikeperch does not cause adverse ecological impacts and that culling is an ineffective management tool. For this group of anglers, catch orientated motivations to fish (e.g., size, anticipation, challenge) were important, but so too were motivations related to catching wild fish in natural surroundings. These anglers saw pikeperch as providing angling opportunities and as contributing to a growing sport with economic importance, but they also showed support for maintaining pristine wild populations of pike, unconstrained by pikeperch, and so some opposing perceptions relating to the ecological impact of pikeperch were apparent.

The behavioural intentions of these anglers to practice voluntary catch-and-release are influenced by angling norms and an awareness of their consequences, where aspects such as ecological or stock status, setting, species and social factors are all considered (Stensland et al. 2013). Development of angling specialization through angling style and/or species preferences can also cause divergent experience-quality norms and motivations (Arlinghaus and Mehner 2003). For this group of anglers, voluntary catch-and-release behaviour of a non-native species seemed to be connected to inherent conservation values and unique motivations and perceptions of the ecological consequences of pikeperch to native populations. These predator anglers often invoked a model of nature as normally being in equilibrium (i.e., 'the balance of nature,' Eden and Bear 2011) to make sense of their fishing experience and behaviours.

Catch-and-release angling is practiced widely in recreational fishing (Arlinghaus et al. 2007) and has become a useful tool for resource conservation (Cooke and Schramm 2007, Brownscombe et al. 2017). However, it can also generate conflict both within the angling community and between anglers and managers due to opposing cultural, institutional, and emotional drivers; divergent motivation and ethics; and varying expectations and tolerance (Arlinghaus 2007). This group of anglers spoke of conflict within the predator angling community that resulted in angler-led management responses with the aim of protecting personal fishing motivations. These indirect responses were most apparent with the adoption of secretive fishing behaviours, seen as protecting individual fish from over-exploitation. Management measures often develop out of angler led initiatives and include best practice guidance relating to appropriate fish handling techniques, fishing gear restrictions, size and catch regulations, and the implementation of catch-and-release policies (Eden and Bear 2012). This is especially true of the interviewed anglers who demonstrated instances of peer influence to, for example, change club rules relating to the catch-and-release of pikeperch. Sanctioning actions carried out by and within the angling communities can be used for promoting and maintaining best practices in relation to catch-and-release angling (Guckian et al. 2018), and could be explored further in relation to pikeperch in England.

Interviewed anglers also described their experience of conflict with other angling groups and managers that was generated from their catch-and-release behaviour toward pikeperch. In England, most freshwater recreational anglers target cyprinid species (Environment Agency 2018a), and pikeperch introduction has been linked to perceived declines to cyprinid populations (Smith et al. 1996). Specialist predator anglers may also have experienced similar declines to pike populations or at least impact to fishing experiences as a result of pikeperch introduction. However, findings here suggest that if these declines existed, fishing motivations were being altered to incorporate the introduced species. Removal of pikeperch (culling) as a management measure after their initial introduction was widely employed, with the desired outcome of reducing pikeperch biomass and maintaining native cyprinid populations (Smith et al. 1996, 1997). The practice of culling is still employed by fisheries managers in the hope of controlling the spread and establishment of pikeperch, despite them also becoming a popular and valuable target species for some anglers (Hickley and Chare 2004). The effectiveness of removal operations is often debated and, indeed, it has been demonstrated that removals of low intensity could increase the predation pressure of pikeperch on prey populations, thus exacerbating their potential deleterious impact on native cyprinid prey species (Smith et al. 1996, 1997).

Anglers are known to be one of the main drivers of non-native introductions (Gozlan, Britton, et al. 2010) due to their catch specific motivations and preferences for certain fish attributes, such as large body size (Elvira and Almodóvar 2001, Banha et al. 2017). Illegal non-native introductions to enhance sport fishing are often more common in regions with fewer native sport fish (Johnson, Arlinghaus, et al. 2009). For example, introductions of species with high trophic positions, such as largemouth and smallmouth bass *Micropterus dolomieu*, can have significant ecological impact (Jackson 2002, Eby et al. 2006), but can also provide substantial benefits for angling (Carey et al. 2011). Additionally, anglers are not only drivers of introductions of non-native species, but they can also increase the rate of their spread (García-Llorente et al. 2008). A major management goal in freshwater fisheries is to diversify angling opportunities for increased angler satisfaction, such as through the permitted movement or transplantation of non-native fishes into waters that minimize their potential of developing invasive populations (Cowx 1994, 1998, Cowx and Gerdeaux 2004, Hickley and Chare 2004). Different stakeholder groups will, however, have unique perceptions about the impacts or benefits of non-native introductions and diverse attitudes regarding their management (García-Llorente et al. 2008). Recognition of angler perceptions and motivations of invasive species is, therefore, important when trying to discourage the deliberate spread or introduction of these species through angling activity.

In this study, catch orientated motivational drivers leading to overall satisfaction were complex, with catch expectation in relation to a natural wild fish being an important factor. Gaining these types of data on the characteristics, preferences and behaviours of recreational anglers can enable managers to gauge the effectiveness of management decisions and policies (Brooks et al. 2015). Preferences of anglers for different target species can change with time, with national surveys in England showing a shift in preferences of target species from roach *Rutilus rutilus* and pike in the 1960s to carp, roach, bream *Abramis brama*, and tench *Tinca tinca* since the 1990s (Simpson and Mawle

2001, Aprahamian et al. 2010). The ability of anglers to constantly evolve and adapt is an important mechanism for the sustainability of recreational fishing (Aprahamian et al. 2010), especially under current climate projections that will likely drive fish assemblage reorganizations that could favour non-native species (Ruiz-Navarro et al. 2016a, Kuczynski et al. 2018).

7.6 Conclusions

The catch-orientated motivations and preferences of these anglers to target large-bodied native and invasive predatory fish in natural surroundings translate to the behavioural practice of catch-and-release for an invasive predatory fish and a perception that pikeperch do not cause adverse ecological impact. It is important that these angling groups are not further marginalized by current policies and management practices. Engagement between management organizations and anglers to improve knowledge relating to the effectiveness of pikeperch policies, and promoting practices to limit the species' further spread, could help facilitate more effective relationships among all parties, and enhance management outcomes. Further support could also be gained if the motivational characteristics of predator anglers in England were aligned to maintaining pristine wild populations of fish. Understanding how the motivations and the perceived impacts of pikeperch to native fish populations vary within the wider angling community could assist determination of more effective management programs and regulation. There is a need for clarity regarding the current legislation relating to pikeperch in England, given they can be stocked into waters under permitted regulations, yet where it is also illegal to release captured individuals back into the wild, which includes all open water (rivers and canals). Moreover, this clarity is important, as results highlight considerable disjuncture between angler motivations and behaviours, and current non-native fish policy and management.

8 Behaviours, motivations and perceptions of anglers targeting native and non-native predatory fishes in freshwater fisheries in England

8.1 Abstract

Recreational angling is a major introduction pathway for large-bodied invasive fishes that are released to enhance angling experiences. To ensure management and policy measures improve angling experience but do not result in invasions, it is important to understand angler behaviours and motivations for targeting invasive fishes, the value attributed to them and their perceptions of the impact of angling for them. Here, anglers were surveyed on their behaviours, motivations, and perceptions of piscivorous (‘predator’) freshwater fishes in England. This included the native predators (pike *Esox lucius* and perch *Perca fluviatilis*) and the invasive predator pikeperch *Sander lucioperca*, a recreationally important fish species in England. Commitment to predator angling (measured as proportional income expenditure) increased with increased angling activity, experience and specialisation but was also higher for pikeperch anglers. Despite it being illegal in England to release captured pikeperch back into open waters after capture, 94% of respondents reported to always adopting catch-and-release practices for pikeperch. There was more agreement on the motive to relax and enjoy nature among respondents than for any other motive, whereas agreement to species specific motives increased with increasing specialisation. Groups differing in the extent of their specialisation were also revealed to have different perceptions relating to the ecological impact and management of pikeperch. These results suggest that the invasive pikeperch is viewed as a valued target species with anglers’ experience influencing their perceptions of the ecological impact of pikeperch but not their decision to practice catch-and-release.

8.2 Introduction

Biological invasions are a global driver of biodiversity loss (McGeoch et al. 2010), with relatively large-bodied invasive fishes of high trophic position being a recognised threat to native fish diversity (Eby et al. 2006, Menezes et al. 2012). The introduction pathways of large-bodied invasive fishes include recreational angling (Gozlan, Britton, et al. 2010, Britton and Orsi 2012), with these fishes introduced to diversify angling experiences, especially in regions with relatively restricted fish faunas (Hickley and Chare 2004). As recreational angling in inland waters has a high number of participants globally, mostly in industrialised countries but with increasing participation rates now in developing regions (Cooke, Arlinghaus, et al. 2016), then there is potential for this pathway to have a substantial influence on the introduction rates of non-native fishes (Copp et al. 2010, Gozlan, Britton, et al. 2010).

As recreational angling is a key introduction pathway for non-native invasive fishes, it is important to understand the behaviours, motivations and perceptions of anglers that contribute to these introductions (Banha et al. 2017, Rees et al. 2017). While this knowledge should help fishery managers implement measures that aim to enhance angler satisfaction (Beardmore et al. 2014), it should also help to reduce the ecological impacts of non-native species through effective policy implementation and management (Arlinghaus et al. 2016, Banha et al. 2017). This is especially important given that management options for managing fish invasions in open waters are extremely limited (Britton et al. 2011, Rytwinski et al. 2018).

In England, there has been an increase in popularity of ‘big game’ type sport freshwater angling in recent decades (Hickley and Chare 2004), with the development of lake fisheries where large-bodied non-native fishes, such as European catfish *Silurus glanis*, are introduced to provide new and challenging angling experiences (Copp et al. 2009, Rees et al. 2017). Pikeperch (or zander) *Sander lucioperca* are now invasive in England following their release into a river catchment in Eastern England in the 1960s to create a new angling opportunity (Hickley 1986). This relatively large, obligate piscivore from eastern and central Europe rapidly established populations that quickly dispersed through river catchments in central and southern England (Fickling and Lee 1983, Smith et al. 1998, Copp et al. 2003, Nunn et al. 2007). Associated with these introductions were reported ecological impacts to native fish communities (Fickling and Lee 1983, Smith et al. 1998) although evidence on this remains equivocal. Hereafter, anglers targeting freshwater piscivorous fishes (‘predators’) are referred to as ‘predator anglers’ (that engage in ‘predator angling’).

Pikeperch now support important sport fisheries in English rivers (Nolan, Curtin, et al. 2019), with evidence suggesting that anglers increasingly perceive pikeperch to be an acceptable target species, and with their angling behaviours informed by their practices for targeting native predatory fishes (Nolan, Curtin, et al. 2019). These fisheries are thus likely to be based on catch-and-release practices (i.e. fish are returned alive to the water following capture), despite a regulatory framework that makes it illegal to release captured pikeperch back into open waters (Hickley and Chare 2004). If catch-and-release angling behaviours result from angler perceptions that pikeperch no longer pose an ecological threat to native fishes, at least in invaded catchments, this would represent a considerable disjuncture between anglers and regulators and fishery managers who aim to improve angling experiences while also protecting native fish communities.

Freshwater angling comprises of a diverse group of users that vary according to differences in, for example, their preferences for target species and angling methods (Eden and Bear 2011). Indeed, sport anglers often have a preference for attributes such as large body sizes that are often associated with invasive fish from sport angling (Banha et al. 2017). Motivated by different aspects of the angling experience, anglers can then have divergent opinions relating to catch-and-release practices (Aas et al. 2002), with these differences often resulting in behavioural conflicts (e.g. Arlinghaus 2007). Differences in value orientation between groups are often the basis of social conflicts in relation to wildlife conservation (Manfredo et al. 2016). Anglers’ value orientations are defined as the patterns of basic beliefs governing their interactions with the resource (i.e. how they use, treat, value, manage or otherwise affect; Bruskotter and Fulton 2008). Anglers that are more specialist in their practices are thought to be more catch orientated (Beardmore et al. 2011) and place a higher value on their fishing trips compared to more generalist anglers (Oh et al. 2005). Correspondingly, there could be considerable heterogeneity in the behaviour, value, motivation and perception of predator anglers to native and invasive predatory fishes, with these varying according to differences in their experiences and behaviour.

The aim of this study was therefore to evaluate the behaviours, motivations and perceptions of anglers in England that target native and invasive predatory fishes. Using a questionnaire survey, the objectives were to quantify predator angler expenditure; determine the extent of catch-and-release behaviours of freshwater anglers targeting predatory fishes; determine the motivations and perceptions of anglers that target these fishes; and quantify differences in expenditure, catch-and-release activity, and motivations and perceptions in relation to different levels of angling commitment, experience and behaviour, particularly in relation to the ecological impact and management of pikeperch. The results are discussed in relation to assisting the development of management and regulatory measures that enhance levels of angling satisfaction whilst protecting native biodiversity.

8.3 Methods

8.3.1 Questionnaire survey

The data for the study were generated through responses to a questionnaire designed using ‘Jisc Online Surveys’ (formerly ‘Bristol Online Survey’). The questionnaire targeted recreational freshwater predator anglers in the UK and was first developed and pre-tested on a small group (n = 11) of experienced predator anglers, to assess structure and clarity. It was then distributed online from December 13th 2018 to January 25th 2019 and was promoted via social media forums (Facebook and Twitter), and posted to pages and groups based on an associations with freshwater predator fishing in England. This approach relied on ‘snowball’ sampling to reach the target audience. While it is recognised that there are a number of biases and limitations associated with this type of nonprobability sampling (Coughlan et al. 2009), it did allow for the selective targeting of respondents who participate directly in and have considerable experience of predator angling. Moreover, this approach has been used widely to understand human dimensions within social sciences fisheries literature (Peterson and Carothers 2013, French et al. 2019) and Facebook has been shown to be particularly successful for targeting elusive sub-populations (Brickman Bhutta 2012).

8.3.2 Questionnaire Design

The questionnaire comprised of four main sections that related to generating data on the extent of angler specialisation and behaviour, their catch-and-release practices, their fishing motivations and their perceptions toward pikeperch and pikeperch angling. Basic demographic information was collected for each respondent including age, gender, region of residence, education and employment status and average monthly income categories. A full list of questions and responses is provided in Appendix 5.

8.3.3 Section 1: Fishing behaviour

Here, the fishing behaviour of respondents was explored to determine angling activity commitment (devotion of time and resources to an activity) and experience (Sutton and Ditton 2001). The term angler/ angling specialisation refers to the focusing of angler behaviour, skill development and the acquisition of knowledge and commitment processes on a particular type of angling (Scott and Shafer 2001). Respondents were asked to estimate the total number of years they had been predator fishing and the total number of days spent predator fishing in the last year. They were also asked to select the description that best defined their predator fishing habits along a specialisation gradient that was developed from in-depth interview analysis (Nolan, Curtin, et al. 2019). This self-classification measure of specialisation was similar to that used by (Needham et al. 2009), which had comparable performance rates to multivariate measures of specialisation. Four definitions were presented; ‘1) I am a predator angler and don’t fish for any other species’, 2) ‘I am a predator angler but also target other species’, 3) ‘I fish for predators but wouldn’t consider myself just a predator angler as I also target other species’ and 4) ‘I fish for predators rarely and my main angling activity is targeting other species’. Thus, an angler whose angling activities primarily targets the capture of predatory fishes in preference to other groups of fishes (e.g. ‘coarse fish’ (primarily cyprinid fishes) and ‘game fish’ (salmonid fishes)) is considered more specialised. General assessments of fishing behaviours included asking their preferred predator target species and all freshwater species routinely fished for, with an open-ended option available to ensure all species were included in the list but the primary purpose was to determine predator species targets. Respondents were then asked to estimate their annual expenditure (GBP) in relation to three aspects of their predator fishing activity: membership fees and day tickets, equipment and bait, and travel (including fuel, food and accommodation), all on a six point scale (< £100, £100 to £300, £300 to 500, £500 to £1000, £1000 to £2000 and > £2000).

8.3.4 Section 2: Catch-and-release practices and fishing motivations

The catch-and-release behaviour of anglers was assessed by asking for a response to the questions ‘I practice the catch-and-release of pike’, ‘I practice the catch-and-release of perch’, and ‘I practice the catch-and-release of pikeperch’. Responses to the three questions were given on a five point scale, where 1 = Always (without exception), 2 = Always (unless it looks as if it won't survive i.e. deep hooking), 3 = Usually, 4 = Occasionally, and 5 = Never; an option of 'Non-Applicable (I do not fish for this species)' was also provided.

8.3.5 Section 3: Fishing motivations

To examine the motivational drivers of predator anglers, respondents were given 14 motivational statements and asked to rate their agreement along a six-point likert scale where 1 = strongly disagree and 6 = strongly agree. An emphasis was placed on catch orientated motives (Appendix 5), as these activity-specific drivers are known to be more important to specialised anglers than activity-general motives (Beardmore et al. 2011). These 10 motivational drivers were developed from in depth interview analysis with predator anglers (Nolan, Curtin, et al. 2019) and incorporated both catch (Sutton 2007) and challenge seeking (Beardmore et al. 2011) items. An item relating to angler's proximity to predator fishing locations was also provided as a motivational driver. Additionally, three of the most significant non-catch related motives were also included covering socialising, enjoying nature and relaxing (derived from Sutton (2007); Appendix 5).

8.3.6 Section 4: Perceptions of anglers to pikeperch

This section focused on assessing the anglers awareness and perceptions to the invasive pikeperch, respondents were asked to rank their agreement to statements along a six-point likert scale (1 = strongly disagree and 6 = strongly agree). Statements were used to assess angler conservation awareness, their perceptions of the ecological impact of pikeperch and their views on the legislation and management of pikeperch in England. (Appendix 5).

8.3.7 Data analysis

Following descriptive reporting on the demographics of respondents, the initial analyses were to estimate annual expenditure on predator angling as a function of angler annual income. Individual mean annual expenditure was calculated based on the mean value of the annual expenditure category chosen and added across the three aspects of expenditure.

Individual mean annual income was calculated based on the mean value of monthly income category chosen. Kruskal-Wallis (one way Anova by rank) tests were used to assess differences in expenditure across income groupings, with the significance of differences between groupings determined using pairwise comparisons (Dunn's test with Bonferroni adjustment for unequal sample sizes). Kruskal Wallace chi squared statistics were reported. Expenditure in relation to different levels of angling commitment (specialisation/days spent predator angling in the last year), experience (years spent predator fishing) and behaviour (fishing for pikeperch or native predators) was assessed in the same manner.

Exploratory factor analysis (EFA) was used to provide a clear conceptual understanding of the underlying constructs of the measured variables (Fabrigar et al. 1999) for predator angler motivation and perceptions data. The result of EFA is to group items (variables/statements) into domains by determining the number and nature of common factors (groups) which account for the pattern of correlation among the measured variables. This analysis was necessary as the survey data introduced new items in motivational and perception scales when compared to other studies on angler motivational research, and so helps to create links of meaning between the statements. Where items had negative wording (in the case of some of the perceptions data), the scores were reversed before analyses. Analysis was completed using the 'psych' package in R (R Development Core Team 2018) and following standard guidelines (Velicer and Jackson 1990, Osborne et al. 2008). Factor analysis used minres (ordinal least squares) with oblimin rotation, as factors could not be assumed to be completely uncorrelated or normally distributed. The number of factors to be extracted was determined through parallel analysis. Factors were combined into domains where factor loadings were greater than 0.5, where there was an overall Tucker Lewis index of factor reliability of greater than 0.9, and there was a root mean square error of approximation of less than 0.05.

Domains were named and median values from within each domain were used to provide an index of individual angler motivational drivers and perceptions. To compare levels of agreement across angler motive and perception domains, pairwise comparisons were conducted using Bonferroni-Holm-adjusted Wilcoxon signed rank tests for dependent samples. Likert statistics were reported as median values with 1st and 3rd quartiles. Then, to test motivational and perception group differences in relation to different levels of angling commitment (specialisation), experience (years spent predator fishing) and behaviour (fishing for pikeperch), Pearson's chi-squared tests were used. Here, agreement statistics were based on 3 levels of agreement (disagree, neutral and agree), modified from the original six-point scale (where 1 = strongly disagree and 6 = strongly agree). Agreements of 1 and 2 were assigned 'disagree', 3 and 4 were assigned 'neutral', and 5 and 6 were assigned 'agree'. The significance of differences between groupings were determined using pairwise comparisons (chi squared test of association with Bonferroni adjustment for unequal sample sizes). Statements which did not fit into an underlying domain were not subject to these analyses.

8.4 Results

There were 823 survey responses received. Of these, 80 were excluded as the reported fishing activity was outside England and 12 were excluded due to completion errors. Of the 731 remaining respondents, the majority were male (n = 721, 99 %) of over 35 years of age (n = 577, 79 %) and that had at least 10 years' experience fishing for predatory species (n = 603, 82%), of which 31 % had more than 30 years experience (n = 227). Regarding fishing effort, 33 % of respondents (n = 238) fished for predators between 30 and 60 days per year, whilst 29 % (n = 212) of anglers fished for predators for more than 60 days per annum. Whilst most anglers fished for pike (n = 678, 93 %) and perch (n = 632, 86 %), over half of all anglers fished for pikeperch (n = 372, 51 %), and most anglers routinely targeted more than one predator species, with 324 anglers (44 %) fishing for all three species. Over half of all respondents identified as predator anglers as per specialisation definition 1 and 2 (n = 378, 52%). However, a large proportion of respondents (n = 318, 43.5%) defined their fishing habits according to definition 3 'I fish for predators but wouldn't consider myself just a predator angler as I also target other species'. The preferred predator species was pike (n = 430, 63 % of pike anglers), followed by pikeperch (n =136, 37 % of pikeperch anglers) and perch (n = 165, 26 % of perch anglers).

8.4.1 Income and expenditure

The highest expenditure by respondents was on equipment and bait, with 48 % spending more than £300 annually (Figure 29a). This was followed by travel (including fuel, food and accommodation), with 43 % of respondents spending more than £300 annually (Fig. 1a). Survey questions relating to income were not mandatory and as such were not answered by 77 participants. Of those responding, almost half earned less than £24,000 annually (n = 284, 44 %). Expenditure was significantly lower for those who earned less than £18,000 compared to those who earned above £30,000 (chi squared = 23.8, $P < 0.001$, df = 5, Figure 29b). However, the proportion of annual income spending on predator angling was significantly higher for anglers with reported earnings of below £12,000 compared to all other income groupings (chi squared = 66.8, $p < 0.001$, df = 5, Figure 29c). Total annual expenditure on predator angling increased with increasing levels of predator angling specialisation (chi squared = 147.9, $P < 0.001$, df = 3), increasing number of years fished (chi squared = 11.12, $P = 0.04$), and increasing number of predator fishing days per annum (chi squared = 181.1, $P < 0.001$, df = 5). In general, anglers who fished for pikeperch also spent more than those who fished only for native predators (chi squared = 71.9, $P < 0.001$, df = 1), where average annual spend for the native predator angler was £879 compared to £1503 for anglers who fished for pikeperch.

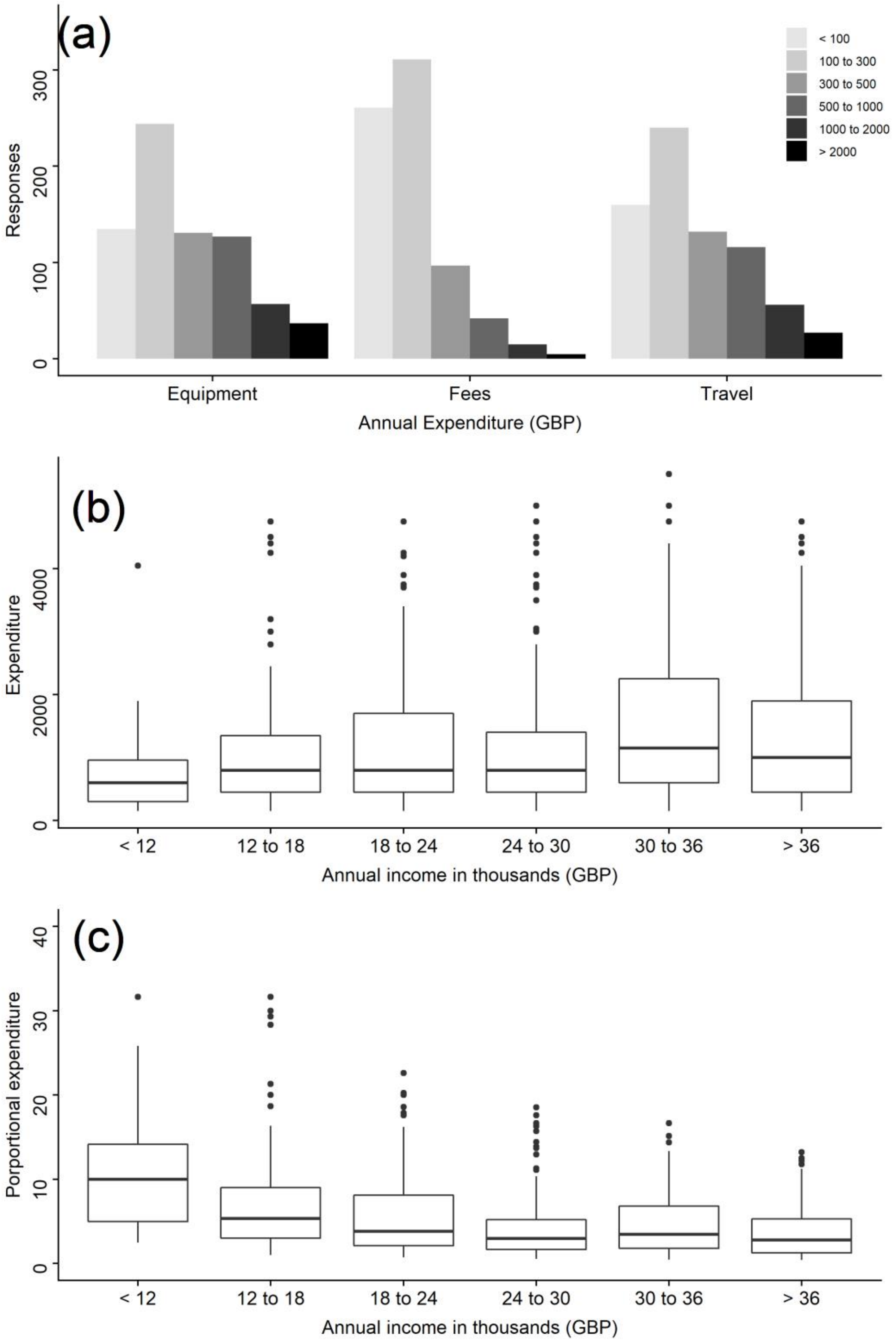

Figure 29. (a) Reported annual predator angling related expenditure for "Equipment and bait", "Membership fees and day tickets" and "Travel (including food, fuel and accommodation", (b) mean annual expenditure by income category and (c) proportion of income spent on predator angling by income category.

8.4.2 Catch-and-release practices

The majority of survey respondents adopted catch-and-release in their angling for predatory fishes. For anglers who targeted the native pike and perch, 95 % (n = 645) and 94 % (n = 595) respectively always practice catch-and-release. The exceptions were respondents who reported they always practice catch-and-release, unless there was substantial damage caused by deep hooking. For anglers who targeted pikeperch, the adoption of catch-and-release practices was at similar levels to the native species, with 90 % (n = 336) always practicing catch-and-release. Again, the exception were anglers reporting to always practice the catch-and-release of pikeperch unless there was substantial damage caused by deep hooking 7 % (n = 26). Only 4 respondents reported to never practice the catch-and-release of pikeperch.

8.4.3 Angler motivations and perceptions

Exploratory factor analysis revealed four general domains within the responses to motivational statements that explain their angling for predatory fishes: (i) species specific motivations (e.g. ‘predators are more exciting to catch’); (ii) challenge related motivations (e.g. ‘predators are more of a challenge to catch’); (iii) relaxing and enjoying nature (e.g. ‘to relax and escape from everyday life’); and (iv) anticipation of catch (Table 21). Significant differences were found in respondent’s agreement across all motivational domains (Table 21), with distribution frequencies of agreement showing more consistency of agreement among respondents within the domain ‘relaxing and enjoying nature’ than within any other domain (median = 5.5 (5 - 6)). Agreement within the challenge related motivational domain was also high (median = 5 (5 - 6)), however inconsistencies in agreement to species-specific motives (median = 4 (3 - 5)), and in ‘anticipation of species catch’ (median = 4 (3 - 5)) were more apparent (Figure 30).

Exploratory factor analysis of respondents agreement to statements on perceptions of the ecology and management of pikeperch in England also revealed four general domains: i) pikeperch as an ecological and angling enhancement (e.g. ‘the positive role of zander in a fishery’); ii) angler awareness of pikeperch ecology and legislation (‘well informed of the ecological concerns of zander’ and ‘awareness of legislation relating to zander’); iii) non-native species (‘the impact of non-native species and non-native fish to the environment') and iv) fishery management (e.g. 'culling of zander' and 'zander should be considered as a native species) (Table 22). Significant differences were found in respondent's agreement across all perception domains (Table 22). Within domains, fishery management perceptions showed most consistency of agreement among respondents (median = 5 (4 – 6)), followed by awareness (median = 5 (3.5 – 6)) and pikeperch as an enhancement (median = 4.5 (3 – 6)) (Figure 31). Overall, there was disagreement within the domain concerning the perception that non-native species and fish were positive (median = 3 (2 – 4)) (Figure 31).

Table 21. Factor loadings (EFA) for predator angler motivations in England based on levels of agreement with comparative statistics

Factors	Item	Wording in survey [a]	Factor loadings [b,c,d]				Wilcoxon’s rank-sum test (z score)		
Activity general motivational measures			***Species***	***Challenge***	***Nature***	***Anticipation***	***Species***	***Challenge***	***Anticipation***
Relaxing and enjoying nature	Relaxation	I fish for predators because it’s relaxing, an escape from everyday life	0.02	-0.01	***0.83***	0.05	-16.97**	-2.24*	-17.70**
	Enjoyment of nature	I fish for predators because I like to be in wild natural places, enjoying nature	-0.01	0.27	***0.60***	-0.04			
n/a	Socialising	I fish for predators because I can do it socially with friends and/or family	0.11	0.16	0.18	0.24			
Activity Specific motivational measures									
Species specific	Sense of accomplishment	I fish for predators because it gives me a greater sense of accomplishment compared to catching other species	***0.87***	0.01	-0.05	0.03		-15.93**	-2.57**
	Excitement	I fish for predators because they more exciting to catch compared to other species	***0.84***	0.17	-0.07	-0.07			
	Fascination with species	I fish for predators because they are fascinating, more intelligent than other species	***0.72***	-0.10	0.05	0.19			
	Fishing style	I fish for predators because I prefer the fishing style over other types of fishing	***0.6***	-0.01	0.23	-0.13			
	A natural way to fish	I fish for predators because it’s a more natural way to fish than other types of fishing	***0.54***	-0.11	0.22	0.06			
Challenge	Challenge	I fish for predators because it’s more of a challenge compared to catching other species	0.09	***0.74***	0.12	-0.07			-16.88**
	Catching a big fish	I fish for predators because there is a chance of catching a big fish	0.02	***0.54***	0.05	0.11			

	Experience of a good fight	I fish for predators because they are good fighting fish	0.06	***0.52***	-0.02	0.32
Anticipation	Anticipation of catch	I fish for predators because I like the anticipation of not knowing what species I might catch	0.01	0.12	0.11	***0.59***
n/a	Using different angling techniques and styles	I fish for predators because I can use different angling techniques and styles	0.04	0.48	0.10	0.23
n/a	Proximity to good predator fishing venues	I fish or predators because there are good predator fishing venues close to me	-0.14	0.21	0.09	0.24

[a] Items were ranked according to agreement to statements along a six-point likert scale where 1 = strongly disagree and 6 = strongly agree

[b] Cumulative variance explained = 0.52

[c] Tucker Lewis Index of factoring reliability = 0.98

[d] Root mean square error of approximation = 0.01

[*] Indicates statistically significant differences at $P < 0.05$ (Bonferroni-Holm corrected)

[**] Indicates statistically significant differences at $P < 0.001$ (Bonferroni-Holm corrected)

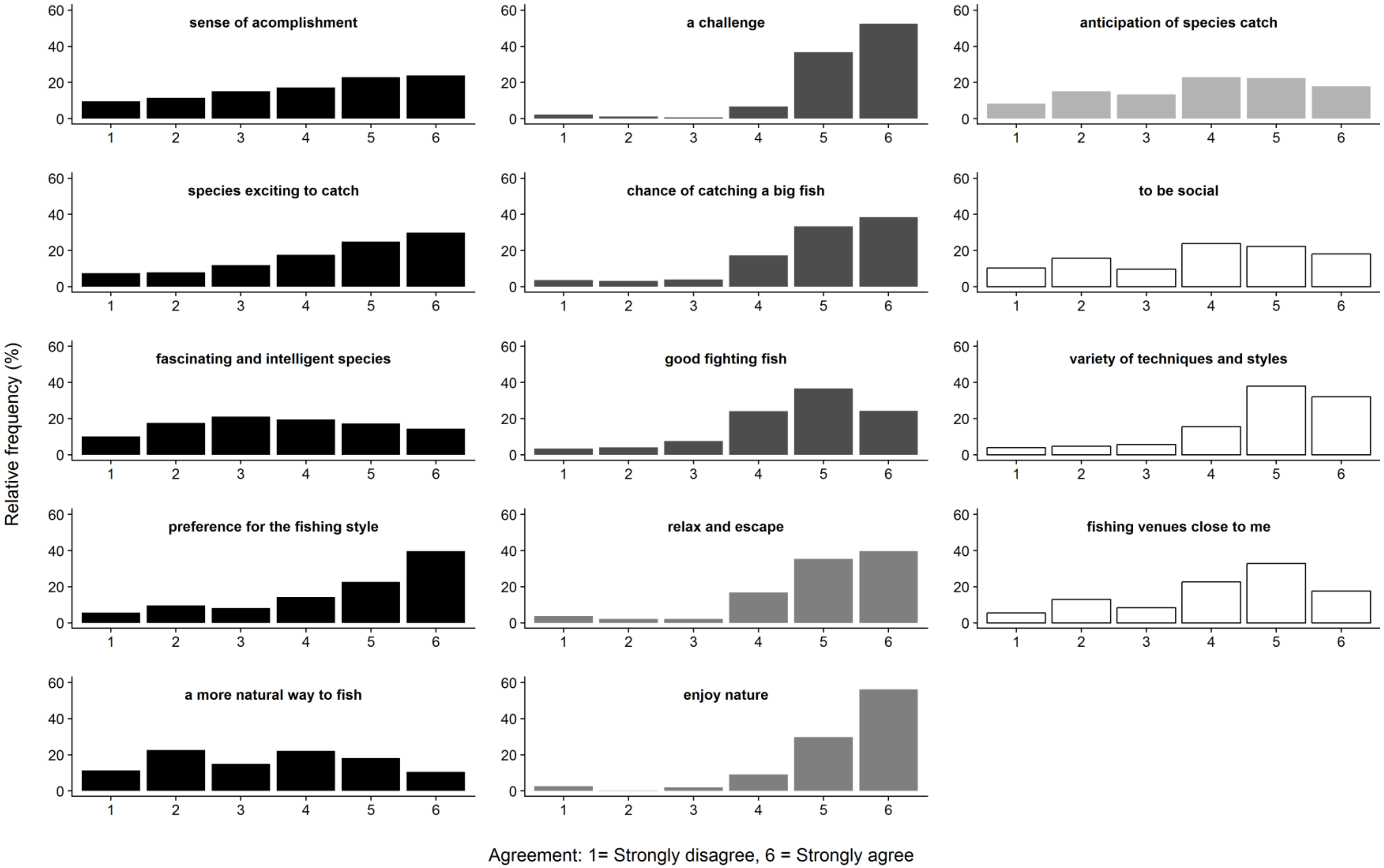

Figure 30. Frequency distribution of agreement to motivational statements for predator anglers in England. Motivations are grouped into domains by colour based on exploratory factor analyses, those without a colour did not group to a domain.

Table 22. Factor loadings (EFA) for predator angler perceptions to the ecology and management of pikeperch in England based on levels of agreement with comparative statistics

Factors	Item	Wording in survey ^{a}	Wilcoxon's rank-sum test (z score)						
Perceptions			***Enhancement***	***Awareness***	***Non-native***	***Management***	***Awareness***	***Non-native***	***Management***
Enhancement	Pikeperch ecology	I think zander provide an important ecological function in a fishery	**0.88**	0.05	-0.05	0.03	-3.95*	-16.90*	-12.76*
	Pikeperch spread	I would like to see zander introduced to additional waterbodies other than where they are currently found	**0.85**	-0.03	0.06	-0.10			
	Pikeperch and growth of angling	I think zander are important to the growth of angling in the UK	**0.84**	0.05	0.02	0.10			
	Pikeperch enhances angling	I am happy that zander are in the UK as it provides another angling opportunity, we otherwise would not have	**0.57**	-0.01	0.08	0.40			
Awareness	Aware of ecology of pikeperch	I am well informed of the ecological concerns of zander in the UK	0.10	**0.93**	-0.01	-0.04		-17.01*	-6.73*
	Aware of legislation	I am aware of the legislation relating to zander in the UK	0.05	**0.73**	0.11	0.01			
Non-native	Non-native species positive	Non-native species generally have a negative impact to the environment$^{\#}$	-0.07	0.02	**0.80**	0.05			-20.39*
	Non-native fish positive	Non-native fishes generally have a positive impact to the environment	0.15	0.12	**0.57**	0.04			
Management	Opposed to culling of pikeperch	I am opposed to the culling of zander in the UK	0.15	-0.02	0.08	**0.59**			
	Pikeperch considered native	I believe zander should be considered as a native species to the UK	0.28	0.02	0.29	**0.52**			
	Imbalance	When zander are first introduced	-0.09	0.15	-0.09	**0.50**			

	associated with pikeperch	they negatively impact the quality of the fishing where they are found but, if left alone they find a balance				
n/a	Ecologically aware	I consider myself to be aware of the conservation issues facing freshwater environments	-0.11	0.43	-0.25	0.20
n/a	Opposed to illegal stocking of pikeperch	I am opposed to the illegal stocking of zander in the UK	-0.34	0.07	-0.37	0.21
n/a	Pikeperch positive for fishery ecology	Pikeperch negatively impact the quality of fishing where they are found[#]	0.23	-0.06	0.30	0.04

[a] Items were ranked according to agreement to statements along a six-point likert scale where 1 = strongly disagree and 6 = strongly agree

[b] Cumulative variance explained = 0.60

[c] Tucker Lewis Index of factoring reliability = 0.98

[d] Root mean square error of approximation = 0.04

[*] Indicates statistically significant differences at $P < 0.001$ (Bonferroni-Holm corrected)

[#] Negatively worded item scores were reversed before analyses

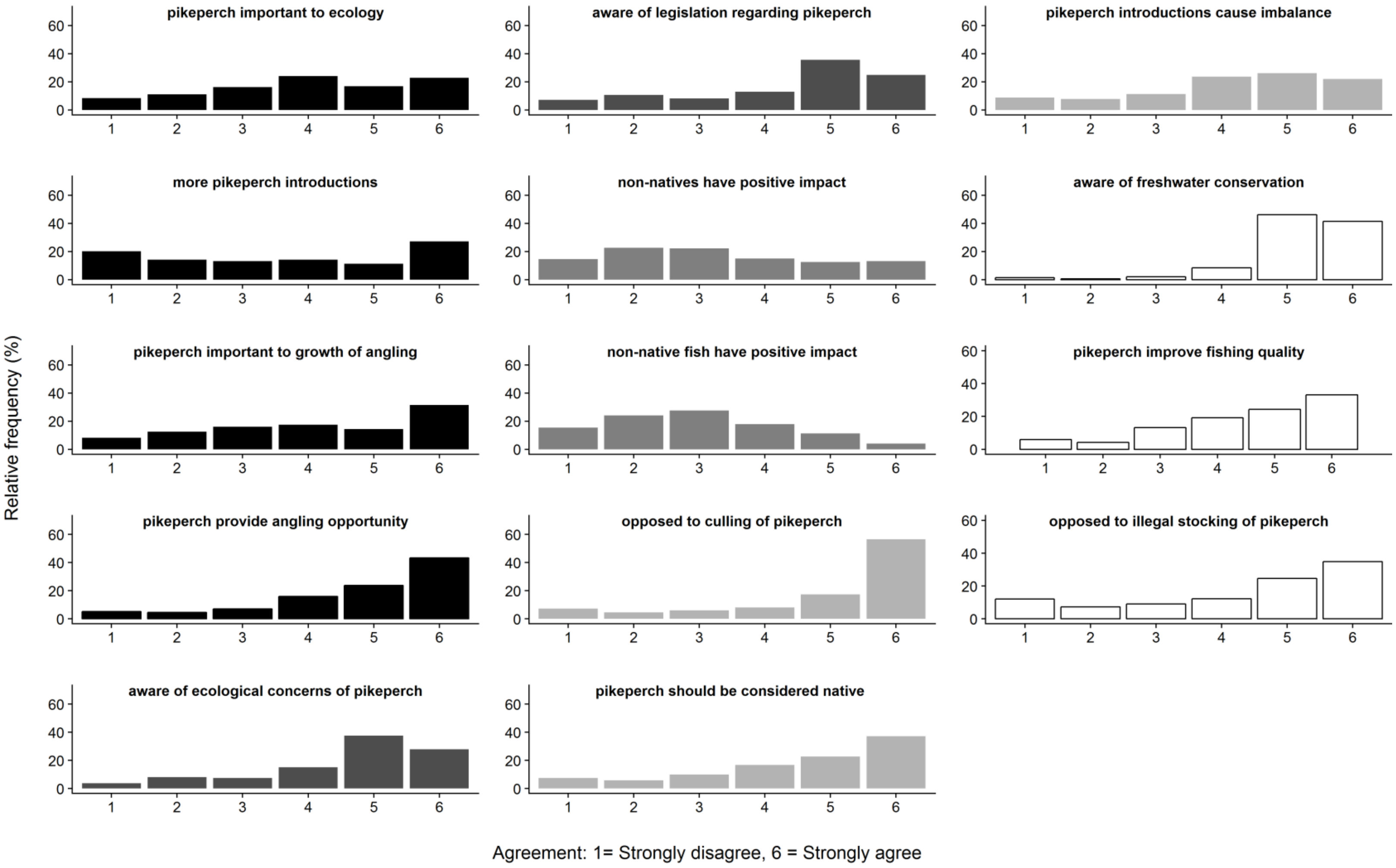

Figure 31. Frequency distribution of agreement to statements on perceptions of the ecology and management of pikeperch in England. Perceptions are grouped into domains by colour based on exploratory factor analyses, those without a colour did not group to a domain.

Motivational and perception group differences in relation to different levels of angling commitment (specialisation), experience (years spent predator fishing) and behaviour (fishing for pikeperch) revealed that more specialised anglers showed increasing agreement across all motivational domains, with the exception of anticipation of species catch (Figure 32, Table 23). While respondents who fished for pikeperch and those who fished for less than 30 years showed increased agreement to species specific and to anticipation of species catch motivations only (Figure 32, Table 23). Across all perception domains, angling commitment (specialisation), behaviour (fishes for pikeperch) and experience (years predator fishing) influenced levels of agreement, with the exception that years predator fishing did not change agreement to management perceptions, and specialisation did not change agreement to awareness perceptions (Figure 33, Table 23). Agreement across all other perception domains increased with increasing levels of angler specialisation and if anglers targeted pikeperch (Figure 33, Table 23), although significantly more specialist anglers fished for pikeperch compared to generalist anglers (chi squared = 31.75, $P < 0.001$, $df = 3$). Agreement to perception statements based on the number of year spent predator fishing was more complex to interpret, with increasing agreement to awareness perceptions with more than 30 years predator fishing experience, but decreasing agreement to the perceptions that pikeperch are positive for ecology and that non-native species are positive as number of years fishing increased (Figure 33, Table 23). No differences in specialisation were seen across years spent predator fishing (chi squared = 10.47, $P = 0.06$, $df = 5$).

Table 23. Pearson’s chi-squared statistics for assessments of motivational and perception group differences in relation to different levels of angling commitment (specialisation), experience (years predator fishing) and behaviour (targets pikeperch or native predatory species) for predator anglers in England.

	Domain	Angler category	*Chi-squared*	*df*	*P*
Motivations	Species specific motivations	Specialisation	107.63	6	< 0.001
		Target pikeperch	13.27	2	0.001
		Years predator fishing	19.52	4	< 0.001
	Challenge related motivations	Specialisation	17.22	6	0.01
		Target pikeperch	0.09	2	0.96
		Years predator fishing	1.55	4	0.82
	To relax and enjoy nature	Specialisation	13.32	6	0.04
		Target pikeperch	5.21	2	0.07
		Years predator fishing	4.25	4	0.37
	Anticipation of species catch	Specialisation	6.31	6	0.39
		Target pikeperch	31.43	2	< 0.001
		Years predator fishing	22.85	4	< 0.001
Perceptions	Pikeperch as an enhancement	Specialisation	73.78	6	< 0.001
		Target pikeperch	122.80	2	< 0.001
		Years predator fishing	23.71	4	< 0.001
	Awareness	Specialisation	10.99	6	0.09
		Target pikeperch	37.44	2	< 0.001
		Years predator fishing	22.85	4	< 0.001
	Non-native species	Specialisation	41.45	6	< 0.001
		Target pikeperch	56.82	2	< 0.001
		Years predator fishing	26.67	4	< 0.001
	Fishery management	Specialisation	62.68	6	< 0.001
		Target pikeperch	89.85	2	< 0.001
		Years predator fishing	6.43	4	0.17

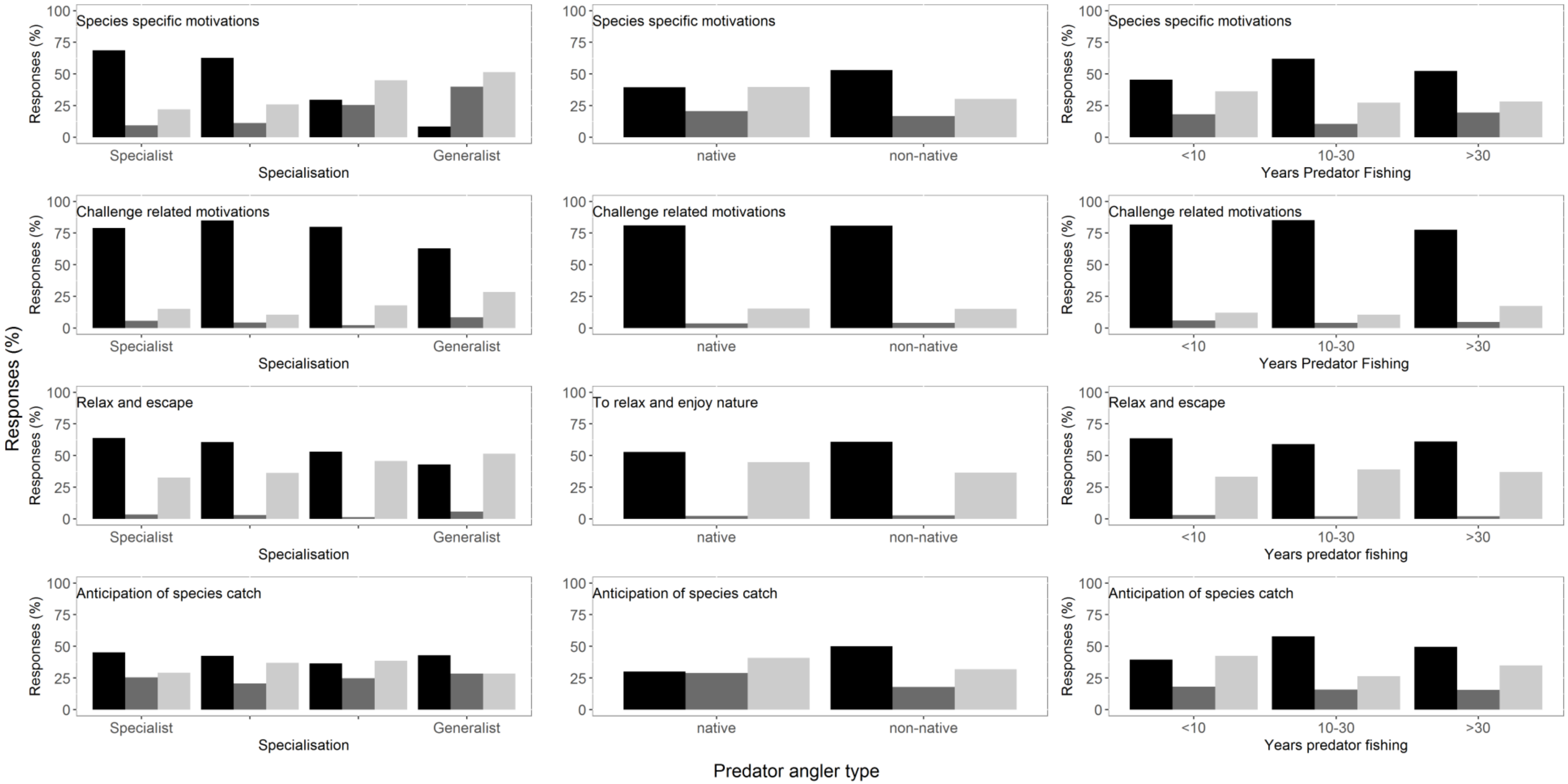

Figure 32. Percentage of agreement (black – agree, dark grey- disagree, and light grey – neutral) to motivational domains in relation to different levels of angling commitment (specialisation), behaviour (targets pikeperch or native predatory species) and experience (years predator fishing) for predator anglers in England. Motivational domains from exploratory factor analysis were i) species specific motivations, ii) challenge related motivations, iii) relaxing and enjoying nature and iv) anticipation of species catch.

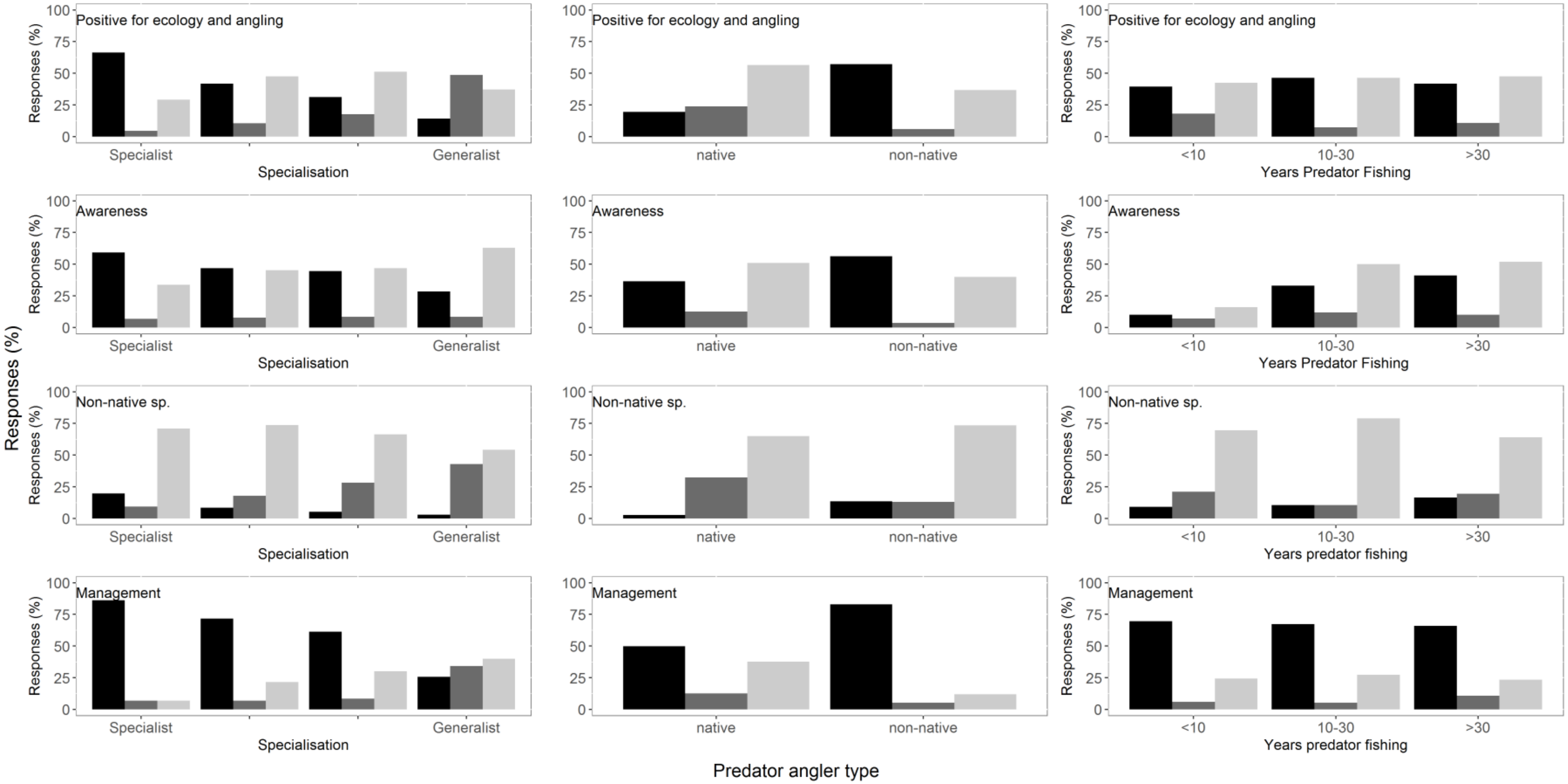

Figure 33. Percentage of agreement (black – agree, dark grey- disagree, and light grey – neutral) to perception domains in relation to different levels of angling commitment (specialisation), behaviour (targets pikeperch or native predatory species) and experience (years predator fishing) for predator anglers in England. Perception domains from exploratory factor analysis were i) pikeperch as an ecological and angling enhancement, ii) aware of pikeperch ecology and legislation, iii) non-native species and non-native fish have a positive impact to the environment) and iv) management of pikeperch (e.g. ‘opposed to culling’ and ‘should be considered native’).

8.5 Discussion

Respondents to the survey reported to overwhelmingly practice catch-and-release angling towards predatory fishes, irrespective of the native versus non-native status of the captured species. Angling expenditure was found not to be related to the annual income of respondents but to the degree to which predatory fishes were targeted (i.e. specialisation). To relax and enjoy nature was an important motivation across all respondents followed by challenge related motives (i.e. catching a big fish and catching a good fighting fish). Other important catch-related motivations included species specific aspects of the fishing experience, such that they provided a greater sense of accomplishment and excitement, and there was a preference for the fishing style. However, agreement to these species specific motives varied depending on the degree to which predatory fishes were targeted (specialisation, number of years spent predator angling and if the respondent targeted pikeperch). Perceptions on the ecology and management of pikeperch also changed with the degree to which predatory fishes were targeted by respondents. However, respondents showed general consistency of agreement in relation to management perceptions, with the majority opposed to culling of pikeperch, that pikeperch should be considered native, and that when first introduced they negatively impact the quality of fishing, but if left alone they find a (ecological) balance.

An important finding from the survey was the prevalence of the use of catch-and-release practices of anglers targeting pikeperch. The regulatory framework for non-native fish in England makes it an offence for captured pikeperch to be released back into open waters (i.e. rivers, canals etc.). Therefore, if the behaviour of the surveyed predator anglers is reflective of the predator angling community more widely, this regulatory framework is being largely ignored. The same regulatory framework also makes it a requirement for releases of European catfish to be permitted by regulatory authorities (Hickley and Chare 2004), yet many releases are unregulated due to the motivations of catfish anglers to catch this large bodied species (Rees et al. 2017). A consequence of this unregulated practice is the stocking of European catfish into unsuitable waters that enable their escape to open systems (e.g. ponds in the floodplain), resulting in their wider dispersal in freshwater environments (Britton, Cucherousset, et al. 2010). There seems here to be similar motivational drivers in the catch-and-release behaviour of pikeperch anglers. However, there was also disagreement in the respondents desire for pikeperch to disperse more widely in England and the majority were opposed to illegal stockings, a view echoed in more in-depth interviews by predator anglers in the River Severn basin of Western England (Nolan, Curtin, et al. 2019).

Social norms and an awareness of consequences are thought to influence an anglers behavioural intention to release fish (Stensland et al. 2013, French et al. 2019), as is increased commitment to fishing (Sutton and Ditton 2001). However, the catch-and-release behaviours outlined here were not associated with an angler’s commitment or perceptions on the ecological impact of their activity, given it was ubiquitous among respondents. Catch-and-release practices in the UK are commonly used as a conservation tool for species such as Atlantic salmon *Salmo salar* (Aprahamian et al. 2010) and, as a fishery management tool, it is a well-established practice among recreational anglers (Cooke and Schramm 2007). Voluntary catch-and-release angler considerations include aspects of the ecology, setting, species, stock status and social norms (Stensland et al. 2013). These social norms can be defined as informal rules shared by groups that guide behaviour (Heywood 2011). Homogenous catch-and-release practices as reported by respondents here are likely to be a result of such social norms; indeed, anglers are well known for their management of water environments via practices, including stocking and habitat management, that are often underpinned by their norms, ideals and value orientations (Bruskotter and Fulton 2008, Eden and Bear 2011).

Angler specialisation has been shown to be an important explanatory factor for preference and behavioural variation between anglers, especially when centrality-to-lifestyle indicators are used (Beardmore et al. 2013, Arlinghaus et al. 2019). The self-classification measure of specialisation used here reflects that of (Needham et al. 2009) and was used to minimise respondent burden while also being comparable to multivariate centrality-to-lifestyle indicators of specialisation (Scott et al. 2005). More highly specialised predator anglers, as a function of increasing commitment and experience (including the self-classification measure of specialisation, number of years spent predator fishing, and number of days per annum spent predator fishing) spent more on their predator angling activity. Interestingly, spending was also higher for pikeperch anglers, although this may have been related to the fact that more specialist anglers also fished for pikeperch. The results reported here reflect the findings of other studies where, for example, more specialised anglers have been shown to attribute more value to their fishing trips than less specialised anglers (Oh et al. 2005). This is in part due to an increased dependence by the specialist angler on their fishing activity that ensures they are willing to pay more for their fishing activity to exist into the future. Sport anglers are also known to show a preference for invasive fish attributes, such as large body size (Banha et al. 2017), with non-native species introduced for sport angling often providing substantial economic benefits. For example, common carp *Cyprinus carpio*, a non-native fish to the UK, is now the most commonly fished for species in England (Environment Agency 2018a). Thus, a combination of specialisation and invasive attributes could be contributing in combination to increased expenditure here.

Angling specialisations can also be closely related to activity-specific motivations (Oh and Ditton 2006). Among surveyed respondents, agreement to the activity-specific motivations included challenge, and species aspects of the fishing experience were higher for the more specialised angler. However, there was also more agreement to the activity-general motivations to relax and escape for the more specialist angler. Indeed, it should be acknowledged that catch motives associated with trophy fishing have been shown to be a key motivation for specialist anglers targeting species such as pike and pikeperch, and that trophy-seeking anglers and nature-oriented anglers can be closely related in terms of motivational orientation (Beardmore et al. 2011), which is consistent with the results here. Motivational heterogeneity can be an important indicator of the value assigned to sport fishes and can influence behavioural decision-making processes. For example, French et al. (2019) revealed motivational differences in the value that recreational anglers attribute to the shortfin mako shark *Isurus oxyrinchus* as a sport fish, which in turn influences their decisions to practice catch-and-release. Generalist anglers in this survey may be motivated by other aspects of the fishing experience that were not explored here, or simply that they were motivated by many aspects and as such no clear dominant motive could be discerned.

The management preferences of anglers can also vary based on levels of angler specialisation, such that more specialised anglers have been found to be more likely to be supportive of restrictive management regulations (Oh and Ditton 2006). Results here are in contrast to this, as higher agreement to more lenient management of pikeperch populations in England was detected in more specialised anglers. However, catch-orientation is a primary driver of angler satisfaction, so much so that catch-orientated anglers are among the least satisfied, regardless of actual catch or harvest rates (Arlinghaus 2006b), a result of their very specific catch-orientated goals. Perhaps opposition to current management and policy of pikeperch is therefore explained by their desire to meet catch motivations and improve satisfaction.

Different stakeholder groups are likely to have opposing perceptions in relation to the benefit, impact and management of non-native invasive species (García-Llorente et al. 2008), and this is particularly true for anglers with opposing motivations (Arlinghaus 2007). Managing angler perceptions of fishing success can be important in managing angler expectations (Schramm et al. 1998) and could play an important role here in ensuring angler satisfaction without sacrificing the ecological integrity of native species. For example, improving access to angling opportunity such that predatory anglers can fulfil both catch and nature orientated motivations when fishing for pikeperch within regulated waters.

8.6 Conclusion

Most respondents reported to practice catch-and-release of pikeperch and perceived that current policy and management measures are unwarranted, highlighting that the regulatory framework for pikeperch in England is increasingly ineffective within their current range. Challenge related motives were important to specialist predator anglers, however, all anglers agreed that to relax and enjoy nature was among the most important motivational driver to fish. These catch-and-release behaviours and perceptions driven by catch motives could be inhibiting the ability of authorities to control pikeperch populations. Therefore, to improve support for management policies we recommend promoting practices that limit the species further spread while also relaxing legislation in waters where the species have been established for a long time. This could help to facilitate a more effective relationship between all parties provided they incorporate clear objectives that aim to maintain and improve the status of populations of wild fish and are not contrary to the catch-orientated motivational drivers of these anglers.

9 Discussion

9.1 Invasive attributes of pikeperch

Pikeperch *Sander lucioperca* have been successfully introduced outside of their native range throughout much of Europe, mainly for recreational sport fishing (Elvira and Almodóvar 2001, Hickley and Chare 2004, Kopp et al. 2009), but also for their commercial harvest value (Hansson et al. 1997b). Pikeperch have been identified as a ‘globally’ high risk invasive species due to their invasive attributes and their potential to cause negative impacts to native species and ecosystems (Vilizzi et al. 2019). For pikeperch, the attributes that contribute to its success as an invasive species include their ability to maintain a high level of genetic variation (Poulet et al. 2009), their ability to thrive in highly turbid and eutrophic systems (Sandström and Karas 2002, Argillier et al. 2012) and their role as an aquatic top-predator (Kopp et al. 2009). In addition to these attributes, a combination of life-history traits also contribute to their success as an invasive species, these include aspects of their spawning behaviour which allow them to spawn in poorly oxygenated silted and muddy substrates (Lappalainen et al. 2003), their early switch from an insectivorous to a piscivorous diet (Mittelbach and Persson 1998) and as has been explored here, variability in their growth rates allowing them to adapt to sub-optimal growing conditions (Chapter 2). These traits have some consistency with those that Liu et al. (2017) identified as being predictors of invasion success in freshwater fishes, including relatively large body size, longevity, delayed maturation, high fecundity and the ability to display a high degree of trait variability.

The expression of pikeperch growth rates was found to vary across their native and invasive ranges (Chapter 2) but had a predictable relationship with latitude, where they increased in their mid-latitudinal ranges and decreased at their northerly and southerly range limits. Growth rates for pike *Esox lucius* across native and invasive populations show a weak relationship with latitude in their Eurasian range but a strong relationship with latitude in their North American range (Rypel 2012). The lack of correlation between growth and latitude for pike in Eurasia was thought to reflect the more prominent role of local drivers to growth, such as productivity, density and prey availability (Rypel 2012). Notwithstanding, these results can assist the formulation of invasion risk assessments for pikeperch by providing information on how aspects of their life-history traits are likely to be expressed to different regions but local factors should also be considered important when determining growth characteristics in invasive pikeperch populations, including the environmental characteristics of the receiving water and prey availability (Poulet et al. 2004). For example, juvenile growth rates for populations of pikeperch across England were found to be slower in a canal network compared to riverine populations, with the canal population in turn showing reduced maximum ultimate lengths (Chapter 2). In pikeperch, juvenile growth rates can be highly variable and positively correlated with the early onset of piscivory, and this dietary switch can be delayed when suitable prey are absent (Persson and Brönmark 2002), with this also having potentially important consequences on the survival and fecundity of individuals (Mittelbach and Persson 1998, Sánchez-Hernández et al. 2018). Although not explicitly tested for, variability in the life-history characteristics of pikeperch in England, particularly in relation to juvenile growth rates, could potentially be explained by the ontogenetic dietary interactions between pikeperch and their prey.

For the Grand Union Canal population investigated in Chapter 3, although the size at switch to piscivory could not be determined due to a lack of individuals below 100mm, macro-invertebrates were identified as an important prey item in individuals from 194 to 396 mm, as determined by the combination of stable isotope and stomach contents analyses (Chapter 3). In contrast, in the River Severn and the lower River Warwickshire Avon, the size at which this ontogenetic shift occurred was predicted at 28 and 69 mm respectively, with this influencing the position of their isotopic niches such that individuals above these sizes occupied a distinct niche space that were more reflective of a piscivorous diet (Chapter 4). Moreover, stomach contents analysis revealed an absence of invertebrates in pikeperch stomachs for individuals that were greater than 31 mm from the River Severn and 153 mm from the River Warwickshire Avon. These trends might be explained by the differences in prey abundances across water body types which can influence the interactions between invasive predators and their prey. For example, in other invasive piscivorous fishes, such as introduced populations of largemouth bass *Micropterus salmoides* in Italy, have been found to vary in their degree of piscivory due to resource availability, with populations in northern Italy having a higher trophic position due to their piscivory compared to primarily insectivorous populations in the south of the country (Costantini et al. 2018). Invasive largemouth bass populations in South Africa also show diet variability and opportunisms across populations, linked to prey abundance and availability, with one population switching to piscivory at lengths below 200 mm where small prey fish were available, compared to a population which were still primarily reliant on macro-invertebrates at lengths above 400 mm (Taylor et al. 2019). Improved understandings of these predator-prey interactions across waters of varying prey diversity and abundance could therefore help to explain variability in pikeperch invasion dynamics, and could be considered in future research on the impact of pikeperch establishment in England. However, the primary purpose of Chapter 3 was to assess the application of non-destructively sampled tissue to the dietary analysis of recreationally important fish species and for Chapter 4 to determine the influence of ontogenetic diet shifts to piscivory on the trophic interactions between sympatric populations of native pike *Esox lucius* and invasive pikeperch populations (Chapter 4).

9.2 Ecological interactions between native and invasive piscivorous fishes

In the application of stable isotope analysis to fish ecology, the majority of studies are based on the analysis of muscle tissue (Vander Zanden et al. 2015), and as such usually involve lethal or invasive sampling methods. Non-lethally sampled fish tissues can provide an alternative for fishes of conservation concern, or where they are important for catch-and-release fisheries (Tronquart et al. 2012, Hayden et al. 2017). However, when these tissues are used for predicting the dietary composition of putative prey, it is important to determine their tissue and species specific relationships, as subtle isotopic differences as a result of tissue turnover rates can confuse their interpretation (Pinnegar and Polunin 1999, Jardine et al. 2005, Busst et al. 2015). For pikeperch, $\delta^{13}C$ and $\delta^{15}N$ stable isotopes from scale and muscle tissue had a predictable relationship, with results from Bayesian mixing models demonstrating that they can be used reliable in predicting dietary composition (Chapter 3). Consequently, the application of scale tissue to stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ provides a non-destructive dietary analysis method that can be used in preference to more lethal and invasive methods such as stomach contents analysis. Although fin tissue has been used previously as a surrogate for muscle to determine trophic position in a pikeperch fishery that practices catch-and-release (Kopp et al. 2009), this is the first time pikeperch scale tissue has been used in the application of dietary assessment, although it has been used in other fishes (e.g. Bašić and Britton 2015, Gutmann Roberts et al. 2017). Indeed, in recent years, there has been a considerable increase in using non-destructively sampled tissue such as fin and scale for the stable isotope analysis of both recreationally important fishes and fishes of conservation concern (Kelly et al. 2006, Hanisch et al. 2010, Busst et al. 2015, Cano-Rocabayera et al. 2015, Vašek et al. 2017). This includes for pike, where the isotopic relationships between muscle and fin, scale and mucus were also found to vary predictably, with increasing $\delta^{13}C$ enrichment from muscle to scale (Winter et al. 2019). Stable isotope values from pikeperch scales were also found to be enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$ relative to muscle, with this trend also seen in other species, including walleye *Sander vitreus* (Fincel et al. 2012), where the stable isotope signatures from scale tissue were also found to be most closely matched to muscle in showing variability across populations, and were determined to be a suitable surrogate of muscle for assessments of dietary niche partitioning.

9.2.1 Trophic interactions

In Chapter 4, stable isotope analysis of scale samples revealed isotopic niche partitioning in sympatric populations of pike and pikeperch in the River Severn and Avon; whilst their populations occupied similar trophic positions, there was strong isotopic niche partitioning evident at both their insectivorous and piscivorous life stages (Chapter 4). Competitive interactions can be reduced as a result of interspecific niche segregation, for example, gut content analysis and stable isotope analysis of muscle tissue showed significant dietary niche partitioning across insectivorous and piscvirorous life-stages of sympatric populations of piscivorous asp *Leuciscus aspius* and pikeperch within two reservoirs in the Czech Republic (Vašek et al. 2018). These results suggest that the introduction and subsequent invasion of non-native pikeperch is to increase predation pressure across a wider range of prey resources than would already be exploited by native pike. Trophic niche partitioning is an important mechanism for explaining the structure of invaded freshwater fish communities (Guzzo et al. 2013, Comte et al. 2016) and has been observed between pike and invading pikeperch populations through stomach contents analysis from a semi-natural lake experiment in Germany, where pike responded to pikeperch stocking through a moderate dietary niche compression (Schulze et al. 2012).

In addition, there was a level of dietary overlap between pike and pikeperch reported by Schulze et al. (2012) but this overlap was asymmetrical towards pike, such that pike shared less dietary niche space with pikeperch than pikeperch did with pike. This asymmetrical niche sharing in favour of pike was also evident for River Severn pike and pikeperch, with these pike also having a larger trophic niche than pikeperch, reflecting a more variable or generalist diet.

Many generalist populations often comprise of sub-sets of specialised individuals (Araújo et al. 2011) and in Chapter 5, stable isotope analysis revealed that the presence of marine subsidies from the River Severn contributed substantially to the diet of large-bodied pike, but with considerable variation among individuals. Pike in the lower River Severn were thus identified as being composed of sub-sets of individual specialists, some of which exploit energy pathways based on large prey items containing marine derived nutrients (MDN), with other individuals primarily exploiting freshwater energy pathways. Increased dietary niche variation can be as a result of increased resource competition, as species add alternative prey items to their diets in order to maintain their energy requirements (Svanbäck and Bolnick 2006). While it could not be tested whether the consumption of these larger prey was a response to increased competition with pikeperch, specialist feeding behaviours were not evident from the lower River Warwickshire Avon where pike also exist with pikeperch, and so it would suggest that this is not the case, although it is also the case that novel MDN pathways were largely unavailable to pike in the lower River Warwickshire Avon. However, specialisation in feeding behaviour in pike has been demonstrated previously through a stable isotope approach, where individual specialists within Canadian lake populations were feeding either on invertebrates or fish (Beaudoin et al. 1999), and so it might be expected that this invertebrate specialisation would be evident in the lower Warwickshire Avon if there was a significant competitive interaction with pikeperch.

Specialisation as a result of individual dietary variation can however have many ecological causes, including intra and interspecific competition, the exploitation of new ecological opportunities, and predation risk (Araújo et al. 2011). In addition, trophic niche partitioning between native and invasive fishes may occur as a result of the behavioural or physiological characteristics of the competing species such that they occupy distinct habitats as a result of temperature requirements or foraging tactics (Raby et al. 2019). For example, pike and co-occurring piscivorous fishes, burbot *Lota lota* and lake trout *Salvelinus namaycush* in Canadian sub-Artic lakes were shown to partition resources according to habitat and diet, resulting in the spatial core areas and habitat use across the fishes having minimal overlap (Guzzo et al. 2016). In addition, pike can display a wide range of behavioural flexibility, with opportunistic foraging strategies employed as a possible way to reduce intraspecific competition (Kobler et al. 2009). Understanding the activity patterns of fishes can thus be useful in revealing behavioural variability within populations.

9.2.2 Spatial interactions

The movement patterns of co-existing pike and pikeperch were tracked over twelve months in the lower River Severn, revealing within species variability in spatial and temporal space use (Chapter 6). It would be interesting to determine if $\delta^{13}C$ and $\delta^{15}N$ stable isotopes could help to explain this variability, and if it relates to differences in dietary specialisations both within and between species. Although not explored here, primarily due to the low sample sizes of tagged fish, such studies are capable of showing a connection between dietary specialisation and behavioural variation in individuals with, for example, Harrison et al. (2017) revealing that in a group of tagged burbot, there were individual specialisations on pelagic versus littoral resources that helped explain between-individual variance in their mean movement rates. Consequently, the lower River Severn could represent an important study system for understanding the role of behavioural specialisations in the partitioning of resources between invasive and native fishes. However, freshwater riverine fishes are known for being heterogeneous in their movement patterns (Radinger and Wolter 2014) and there are many reasons for potential variation in movement, including life-history characteristics, habitat use, foraging strategies and the physical and environmental characteristics of their habitats (Lucas and Baras 2008). In both the tagged pike and pikeperch of Chapter 6, there was substantial within species variability in their movement activity. However, there were also between species differences in the importance of the off-channel habitat, with it being important to pike all year round, but only important for pikeperch in winter and spring. There was also an increase in movement activity for both species in spring and in relation to water temperature.

Pikeperch are a highly effective predator that actively searches for prey in open water (Turesson and Brönmark 2004) and usually at low light intensity (Horký et al. 2008). They are well adapted to foraging in highly eutrophic and turbid conditions (Ranaaker et al. 2014) and are able to establish and thrive when introduced to disturbed aquatic environments (Clavero et al. 2004). The lower River Severn has a relatively high suspended sediment load and flow velocity when compared to many lowland rivers in Britain, particularly in winter (Manning et al. 2010). As a result, it is likely to be provide a foraging habitat of very low light conditions which could thus be more favourable for pikeperch than pike. In addition, areas of high vegetation can be important for pike foraging success, but might also reduce foraging success in pikeperch (Greenberg et al. 1995). Pike can also show greater behavioural variation in response to turbid conditions, as they need to search for more favourable foraging conditions (Andersen et al. 2008). These factors could help explain the importance of the limited off-channel habitat to pike all year round as it was likely to provide more complex and favourable foraging habit than the main river channel. Understanding the spatial ecology of fishes in their natural environments is important for their management and conservation (Cooke, Martins, et al. 2016), with these results highlighting the importance of habitat complexity to the management of both pike and pikeperch.

9.3 Angler behaviours

As pike and pikeperch are important recreational fisheries in England, another important consideration in their management is managing human behaviour (Arlinghaus 2006a, Cowx et al. 2010), particularly as influencing these behavioural patterns is key to promoting conservation practices (Schultz 2011). Preventing the illegal introduction of non-native freshwater fishes is a primary conservation concern due to their potential to cause irreversible ecological impacts (Gozlan, Britton, et al. 2010, Cucherousset and Olden 2011, Ricciardi et al. 2013, Liu et al. 2019) and angling continues to be a major source of non-native introductions (Carpio et al. 2019). Indeed, the role of anglers and angling as an introduction pathway for freshwater non-native fish can be important with, for example, the state of Wyoming in the United States of America, having 27 % of all freshwater fish introductions since 1961 being the result of deliberate and illegal releases of sport fish for angling (Rahel and Smith 2018). Estimates in Europe are similar, with 24 % of all non-native fish introduced into Europe during the last century being released for the purpose of angling (Carpio et al. 2019), while non-native freshwater fish introductions for the purpose of angling in South Africa account for 55 % of the total number of invasive species (Ellender and Weyl 2014). In addition to preventing further introductions, there is also a management need to prevent illegal translocations of non-native fishes between water bodies, as they can be a major contributor to their establishment and spread (Ellender and Weyl 2014, Carpio et al. 2019).

The impact of pikperch introduction are generally thought to include increased predation to native prey populations (Fickling and Lee 1983). For example, pikeperch introductions in Turkey resulted in the decimation of native prey species (Yerli et al. 2013), while introductions of pikeperch to Norway changed fish community structure and habitat use (Brabrand and Faafeng 1993) and in France their interactions with native pike showed that pikeperch occupy higher trophic positions (Kopp et al. 2009). Introductions of similar piscivorous species such as walleye *Sander vitreus* and pike outside of their native range in North America are also common for the purpose of angling enhancement, particularly in the northwestern United States (McMahon and Bennett 2012). The effects of these introductions are comparable to those reported from pikeperch introductions in Europe, including native fish depletions and large shifts in community composition and structure (reviewed in McMahon and Bennett 2012). Walleye for example caused a shift in community structure to large numbers of prey-limited piscivores and resulted in the collapse of many salmonid fisheries (reviewed in McMahon and Bennett 2012) while pike introductions in Alaska also had direct top-down impacts to native salmonid populations (Dunker et al. 2018), with habitat heterogeneity and spatial overlap between native salmonids and pike thought to increase the predation risk (Sepulveda et al. 2013). These examples serve to highlight the need to balance the potential recreational and economic benefits of such introductions with their potential to cause substantial harm to naive native populations.

Despite the ecological impact of non-native invasive fishes, they can provide substantial economic benefits (Arismendi and Nahuelhual 2007, Britton and Orsi 2012, Hickley et al. 2015). Indeed, non-native species play a key role in the sustainable development of sports fishing in developed countries (Vilizzi 2012, Carpio et al. 2019) and increased sports fishing opportunities can provide sustainable economic alternatives in developing countries (Barnett et al. 2016), although such fisheries require careful consideration, regulation and management. In England, a regulatory framework prevents the unauthorised introduction of pikeperch into open waters, including their catch-and-release, although they can be stocked into enclosed waters under permitted conditions for the purpose of creating and/ or supporting recreational catch-and-release fisheries (Hickley and Chare 2004). This framework is designed to promote angling opportunities while also protecting native species and fisheries, with the objective of containing the species to licensed waters thus limiting their spread (Hickley and Chare 2004). However, the results of Chapters 7 and 8 highlight that there is increasing demand for catching these species in natural surroundings, outside of enclosed water permitted settings, with a common held view of these anglers that pikeperch do not cause significant ecological impact. This view has most likely developed due to a combination of factors, such as the long term integration of pikeperch into native fish communities and their widespread distribution, in combination with specific predator angler catch motivations and specialisations.

The findings here also highlight that the regulatory framework for pikeperch in England can be considered as somewhat ineffective, given that the majority of surveyed predator anglers reported the application of catch-and-release practices to pikeperch, regardless of the water bodies in which they fish (Chapter 8). There was however disagreement with illegal introductions of pikeperch and a general desire to prevent pikeperch from entering waters that support fisheries based on native piscivorous fishes. Therefore, although there is considerable disjuncture between the perceptions, motivations and behaviours of predator anglers, and the conservation aims and objectives of management and regulatory bodies in regard to pikeperch in England, there is the potential to reconcile these groups based on protecting native species and fisheries from pikeperch population spread.

9.4 Conclusions

The increasing popularity of sport fishing in England has meant that the catch-and release behaviours of pikeperch anglers are conflicting with the conservation priorities of other angling factions. For example, canal networks in England are an important fisheries resource for both cyprinid and predator anglers, particularly with the growing popularity of lure fishing. However, the Canal and Rivers Trust who are responsible for managing these water bodies are under increasing pressure from cyprinid anglers to continue to control pikeperch populations through removals by electric fishing, particularly in areas where pikeperch are thought to be actively invading (John Ellis, pers. comm.). This is despite the effectiveness of such removal operations being uncertain (Smith et al. 1997) and their growing popularity as a recreationally important sport fish (Chapter 8). It is therefore recommended that future research should consider the ecological impact of pikeperch in England along its invasive gradient, such that the ecological impact of actively invading versus established populations is differentiated. However, it is acknowledged that decoupling the ecological impacts of invading species from other environmental factors across multiple and complex water bodies is extremely difficult. It is also worth considering socio-ecological factors in the management of pikeperch. For example, an economic cost-benefit analysis guided by ecological predictors could help to identify waters most at risk from the spread of pikeperch and thus help to concentrate management efforts to areas where they are likely to be most effective and where there is an economic and ecological rationale to do so (Keller et al. 2008). An economic assessment of pikeperch fishing in England would also be beneficial to management agencies, as there is a lack of evidence relating to the true value of these fisheries.

In summary, despite pikeperch having been introduced to open waters in England since the 1960s, there has been limited understanding of their ecology and their interactions with native piscivorous fishes. This has at least been partially overcome here through studies on their growth and diet and their trophic and behavioural interactions with native pike, and by revealing insight into how anglers view and exploit pikeperch populations. Across these studies, it was nevertheless apparent that if non-native pikeperch populations are to be managed more effectively, there remains a series of ecological and recreational research questions to be answered.

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Appendices

Appendix 1: Spatial variability in the somatic growth of pikeperch Sander lucioperca, an invasive piscivorous fish

Table A1.1. The von Bertalanffy growth parameter estimates for populations of *Sander lucioperca* throughout their range from published studies, including coordinates for latitude and longitude, Country and reference. *L*∞ estimates are converted to fork length for comparative purposes

L∞	K	t0	Latitude	Longitude	Country	Reference	Included
1257	0.13		36.16	2.56	Algeria	Bouamra, Belaifa, Chaoui, Kara, & Arab (2017)	No
1360	0.07		37	35.2	Turkey	İkİz (1985) in Özvarol & İkİz (2008)	No
576	0.29		37.1	29.6	Turkey	Alp (1996) in Özvarol & İkİz (2008)	No
551	0.15	-2.59	37.2	51.5	Iran	Abdolmalaki & Psuty (2007)	No
912	0.08	-2.7	37.37	30.83	Turkey	Özvarol & İkİz (2008)	Yes
931	0.08	1.62	37.9	30.8	Turkey	Balik, Çubuk, Özkök, & Uysal, 2004	Yes
954	0.08	-1.56	37.9	30.8	Turkey	Balik et al. (2004)	Yes
978	0.08	-1.52	37.9	30.8	Turkey	Balik et al. (2004)	Yes
931	0.08	1.62	37.9	30.8	Turkey	Balik et al. (2004)	Yes
1078	0.08		37.9	30.8	Turkey	Özvarol & İkİz (2008)	Yes
614	0.43		38.6	28.3	Turkey	Sari (1995) in Özvarol & İkİz (2008)	No
949	0.09	-1.31	38.6	43.6	Turkey	Becer and Ikiz (1999) in Milardi et al. (2011)	Yes
879	0.09	-1.05	39.7	6.8	Spain	Pérez-Bote & Roso (2012)	Yes
1029	0.08	-1.16	39.7	6.8	Spain	Pérez-Bote & Roso (2012)	Yes
818	0.07		41.5	36.07	Turkey	Özvarol & İkİz (2008)	Yes

1080	0.13	0.01	41.97	24.19	Bulgaria	Raikova-Petrova & Živkov (1998)	Yes
742	0.61	0.3	42.14	25.9	Bulgaria	Raikova-Petrova & Živkov (1998)	No
941	0.03		43.9	6.5	France	Argillier et al. (2012)	Yes
869	0.14		44.5	28.8	Romania	Cernisencu and Staras (1992) in Pérez-Bote & Roso (2012)	Yes
379	0.33		44.6	47.5	Russia	Pauly (1978)	No
857	0.15		44.8	28.9	Romania	Staras et al. (1993) in Pérez-Bote & Roso (2012)	Yes
758	0.2		45.3	59.6	Kazakhstan	Pauly (1978)	Yes
709	0.07		45.5	1.8	France	Argillier, Barral, & Irz (2012)	Yes
722	0.14	-0.91	46.82	17.7217	Hungary	Wysujack et al. (2002)	Yes
942	0.17	-0.88	53.19	10.967	Germany	Wysujack et al. (2002)	Yes
780	0.24	-0.01	53.34	13.4423	Germany	Wysujack, Kasprzak, Laude, & Mehner (2002)	Yes
704	0.3	0.05	53.4	14.6	Poland	Błaszczyk (2000)	No
793	0.21	0.21	54.09	13.4656	Germany	Wysujack et al. (2002)	Yes
1351	0.09	-1.35	54.2	13.5	Germany	Hahlbeck & Müller (2003)	No
1115	0.11	-0.45	54.9	48.8	Russia	Berg (1965)	Yes
993	0.13		58.2	31.2	Russia	Pauly (1978)	Yes
474	0.34	0.063	59	17.4	Sweden	Hansson, Arrhenius, & Nellbring (1997)	No
621	0.11	-0.12	60.7	25.4	Finland	Milardi, Lappalainen, Malinen, Vinni, & Ruuhijärvi (2011)	No
663	0.1	-0.12	60.7	25.4	Finland	Milardi et al (2011)	No

Rational for omission of von Bertalanffy parameters in order of appearance in supplementary material table S1

1. Boumara et al (2017) omitted due to L∞ values that were considerable higher than the largest captured individual; FL L∞ = 1257 mm, FL of largest individual = 882 mm.
2. İkİz (1985) omitted due to very high L∞ estimation and thus considered to not be biological relevant, L∞ = 1422 mm
3. Alp (1996) omitted due to very low L∞ estimation and thus considered to not be biological relevant L∞ = 605 mm
4. Abdolmalaki & Psuty (2007) omitted as samples based on commercial fishery catches where more than 90% of the pikeperch caught were smaller than 330 mm.
5. Sari (1995) omitted due to very low L∞ estimation and thus considered to not be biological relevant L∞ = 645 mm
6. Raikova-Petrova & Živkov (1998) omitted as L∞ was found to be lower than largest individual captured and hence seen as unreliable, SL L∞ = 678, SL of the largest individual = 780 mm
7. Pauly (1978) omitted due to very low L∞ estimation and thus considered to not be biological relevant, L∞ = 379 mm
8. Hahlbeck & Müller (2003) omitted based on L∞ values that were considerable higher than the largest captured individual; TL L∞ = 1413 mm, TL of largest individual = 945 mm.
9. Hansson, Arrhenius, & Nellbring (1997) omitted as L∞ was acknowledged by the authors to be too low as larger fish had occured in the area (TL L∞ = 500).
10. Milardi et al (2011) Omitted as based on a population subject to heavy commercial fishing pressure

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Appendix 2: Diet of invasive pikeperch *Sander lucioperca*: developing non-destructive tissue sampling for stable isotope analysis, with comparisons to stomach contents analysis

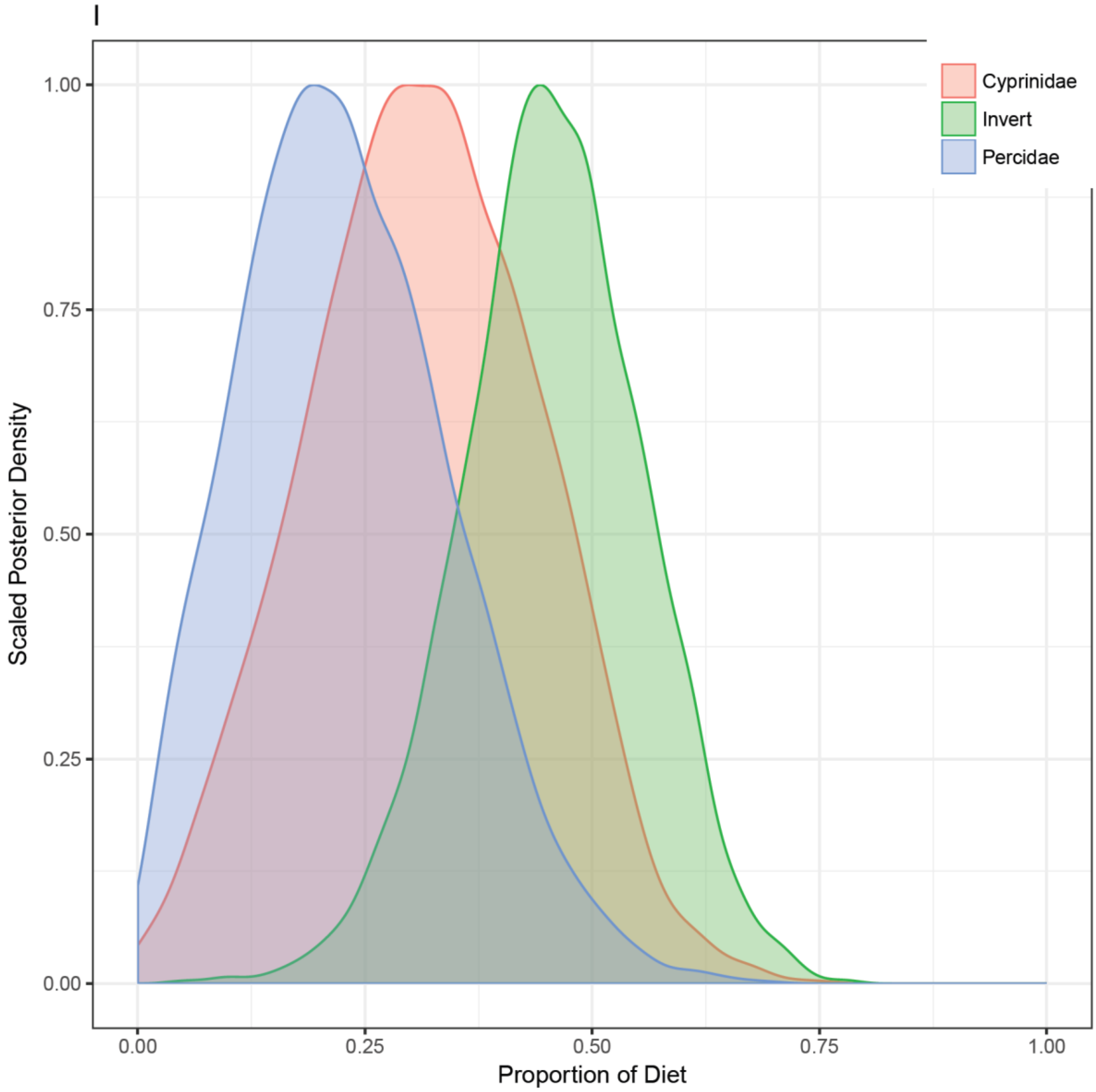

Fig A2.1. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class < 350 mm for model 1, consumer as stable isotope muscle values

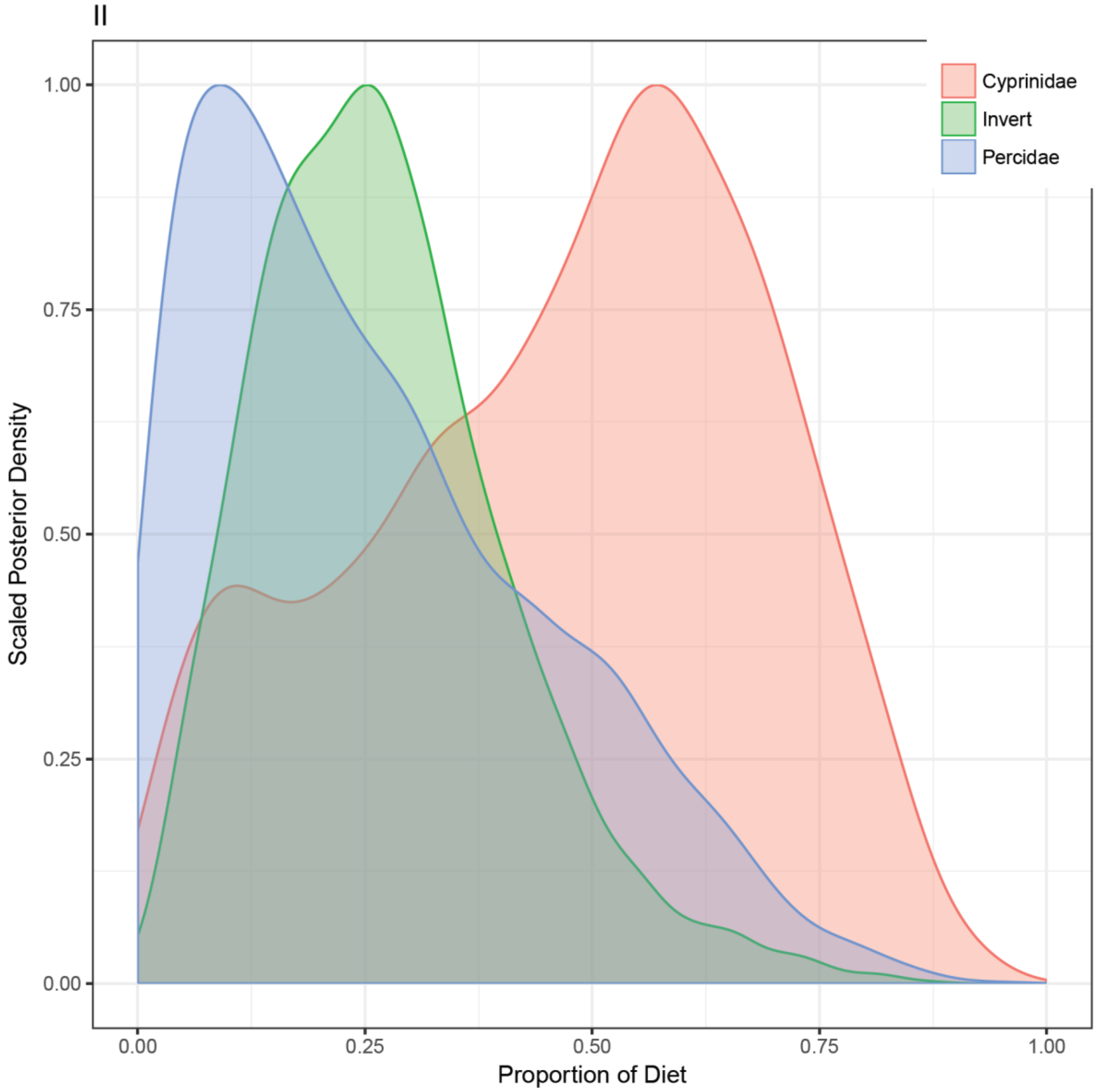

Fig A2.2. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class > 350 mm for model 1, consumer as stable isotope muscle values

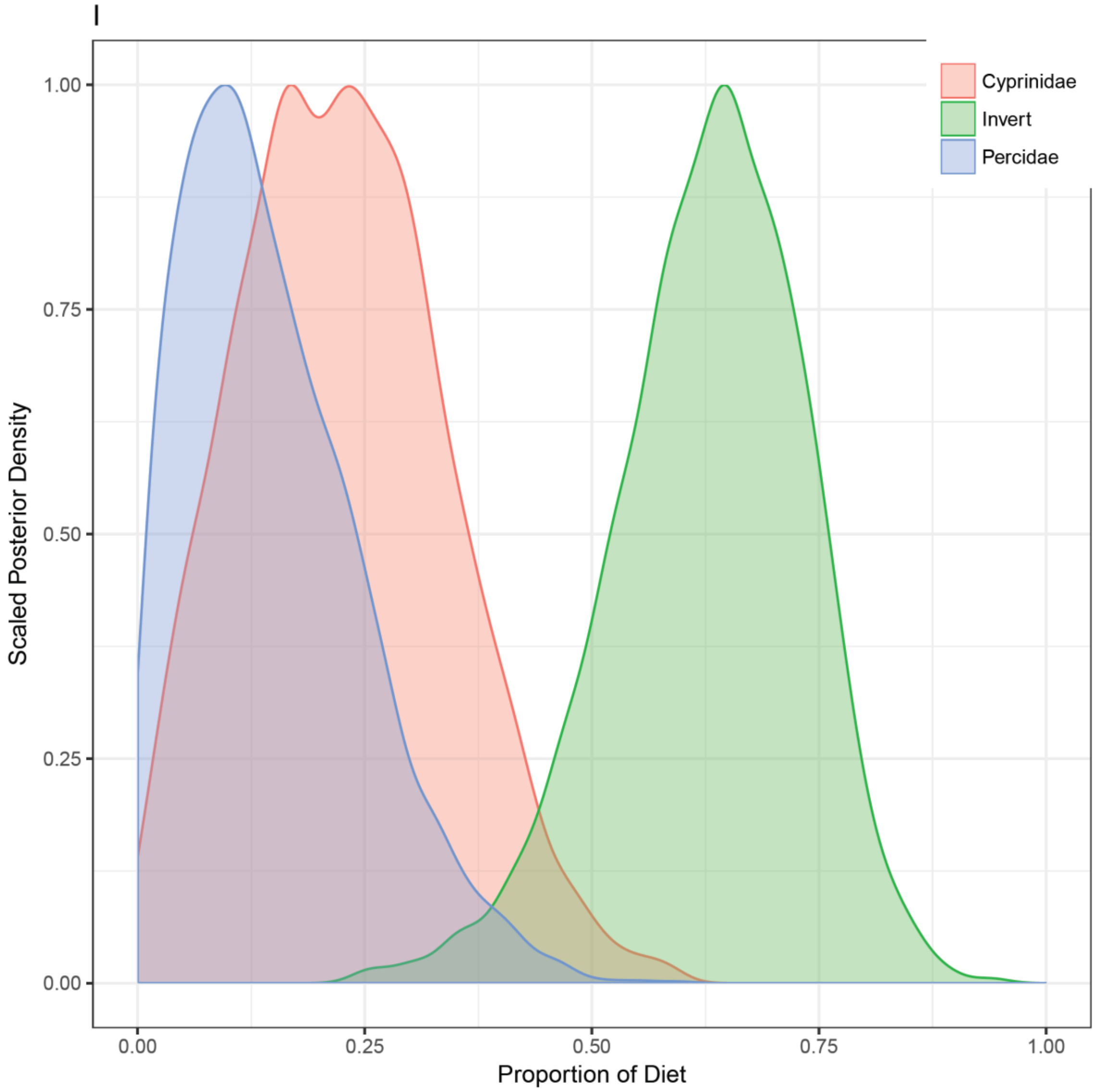

Fig A2.3. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class < 350 mm for model 2, consumer as stable isotope mucus values

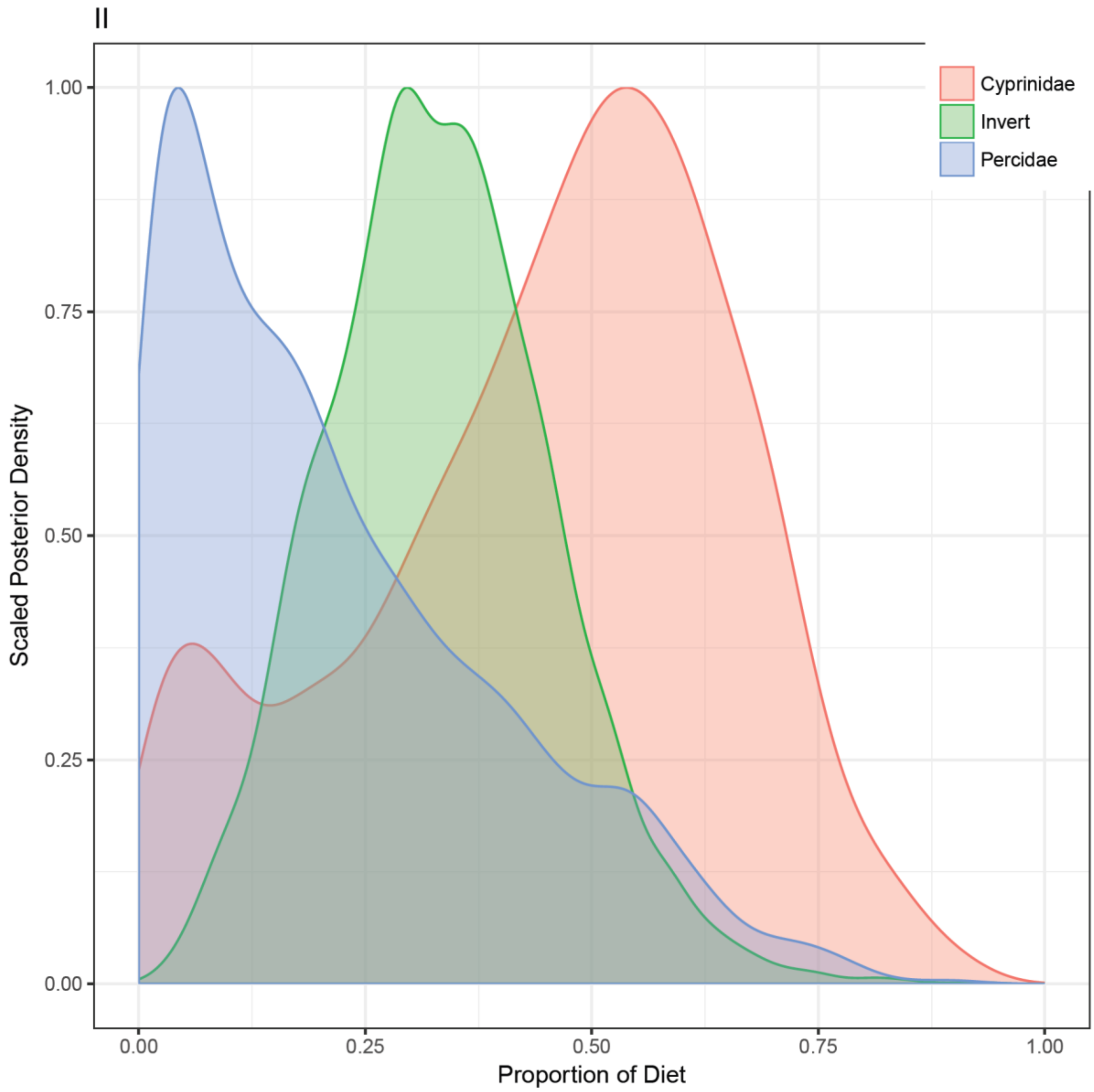

Fig A2.4. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class > 350 mm for model 2, consumer as stable isotope mucus values

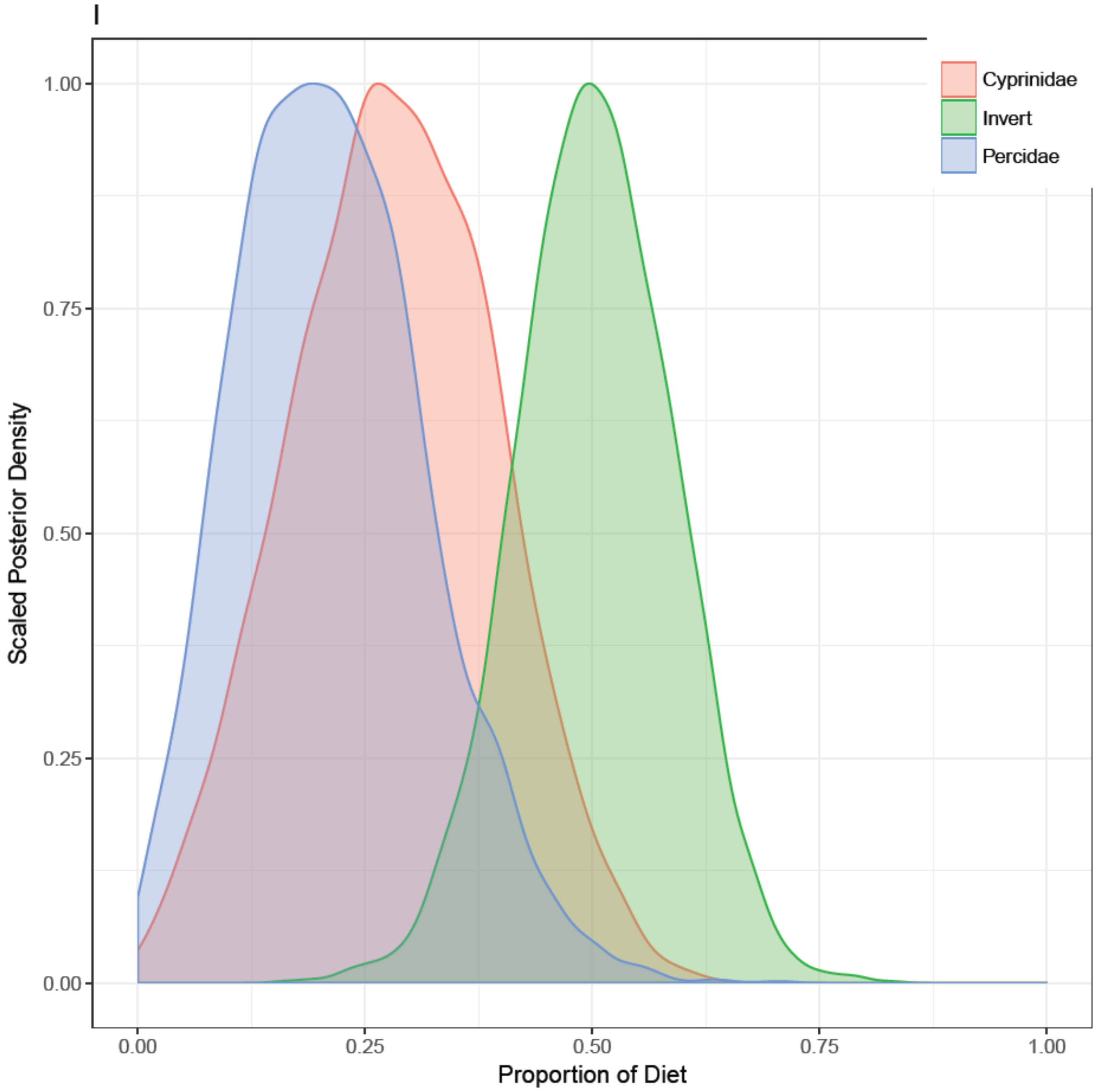

Fig A2.5. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class < 350 mm for model 3, consumer as stable isotope scale values

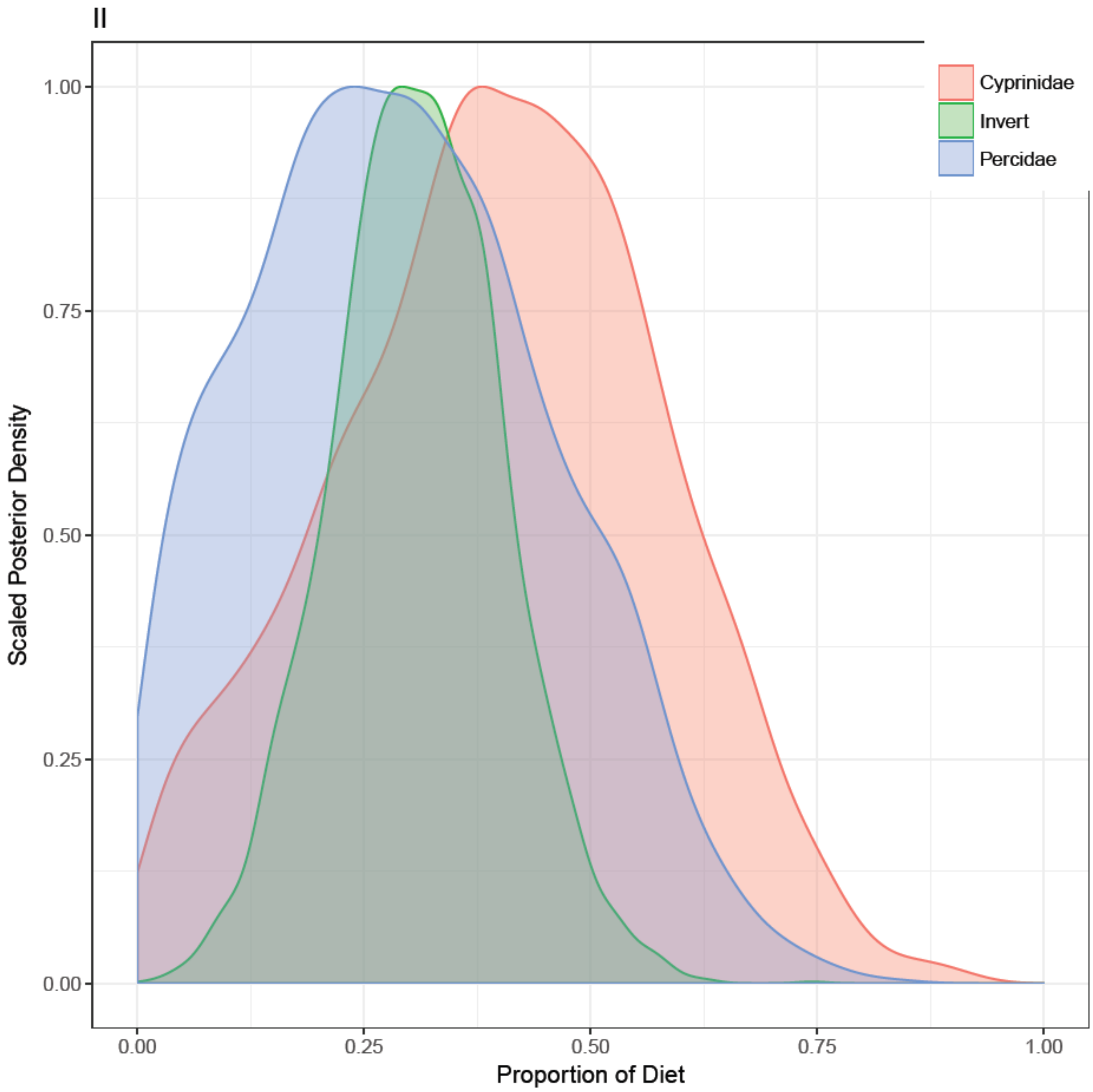

Fig A2.6. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class > 350 mm for model 3, consumer as stable isotope scale values

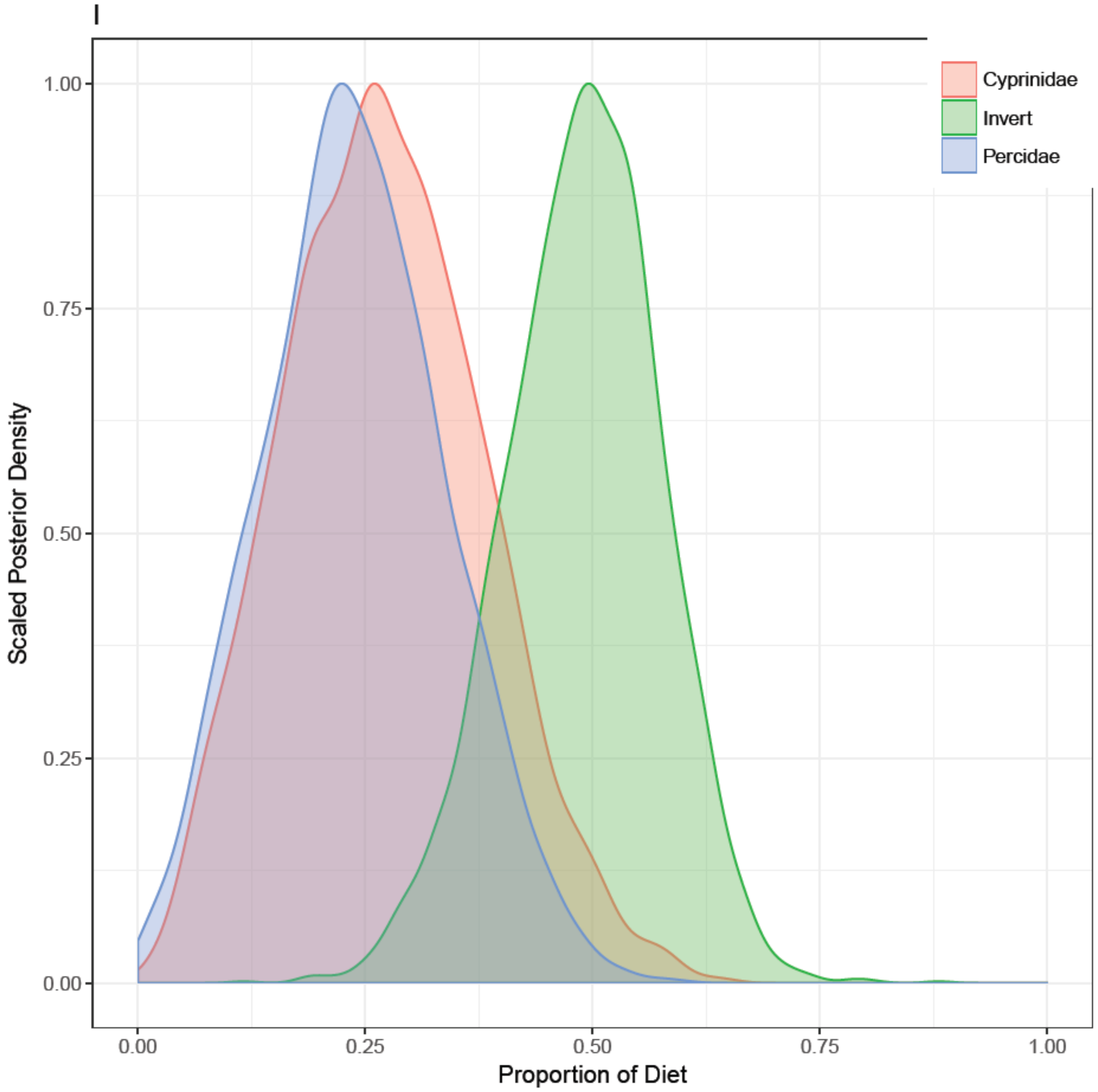

Fig A2.7. Mean predicted dietary contributions of 'Cyprinidae', Invertebrates' and 'Percidae' to the diet of *Sander lucioperca* by size class < 350 mm for model 4, consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ mucus to muscle scale values

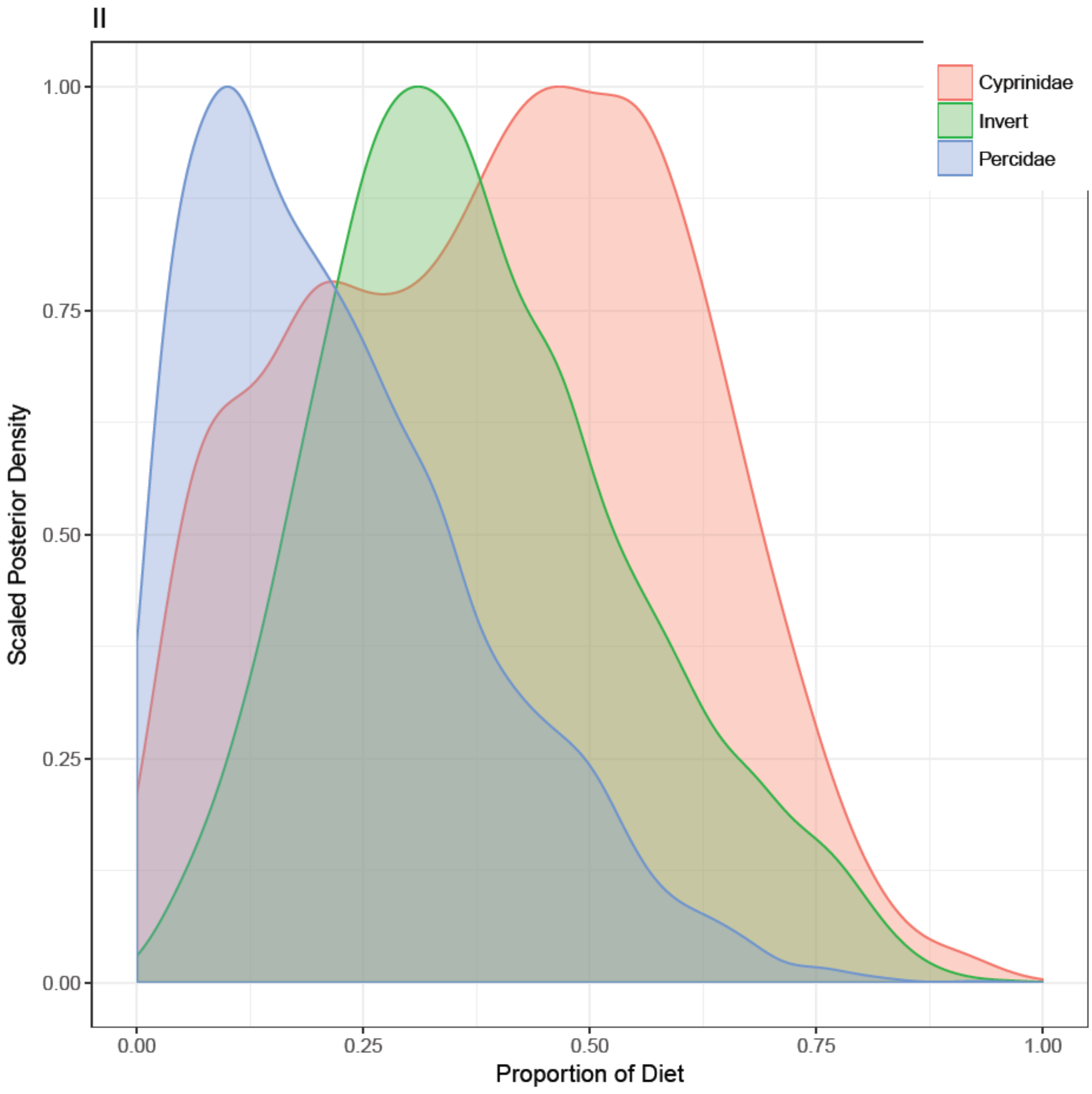

Fig A2.8. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class > 350 mm for model 4, consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ mucus to muscle scale values

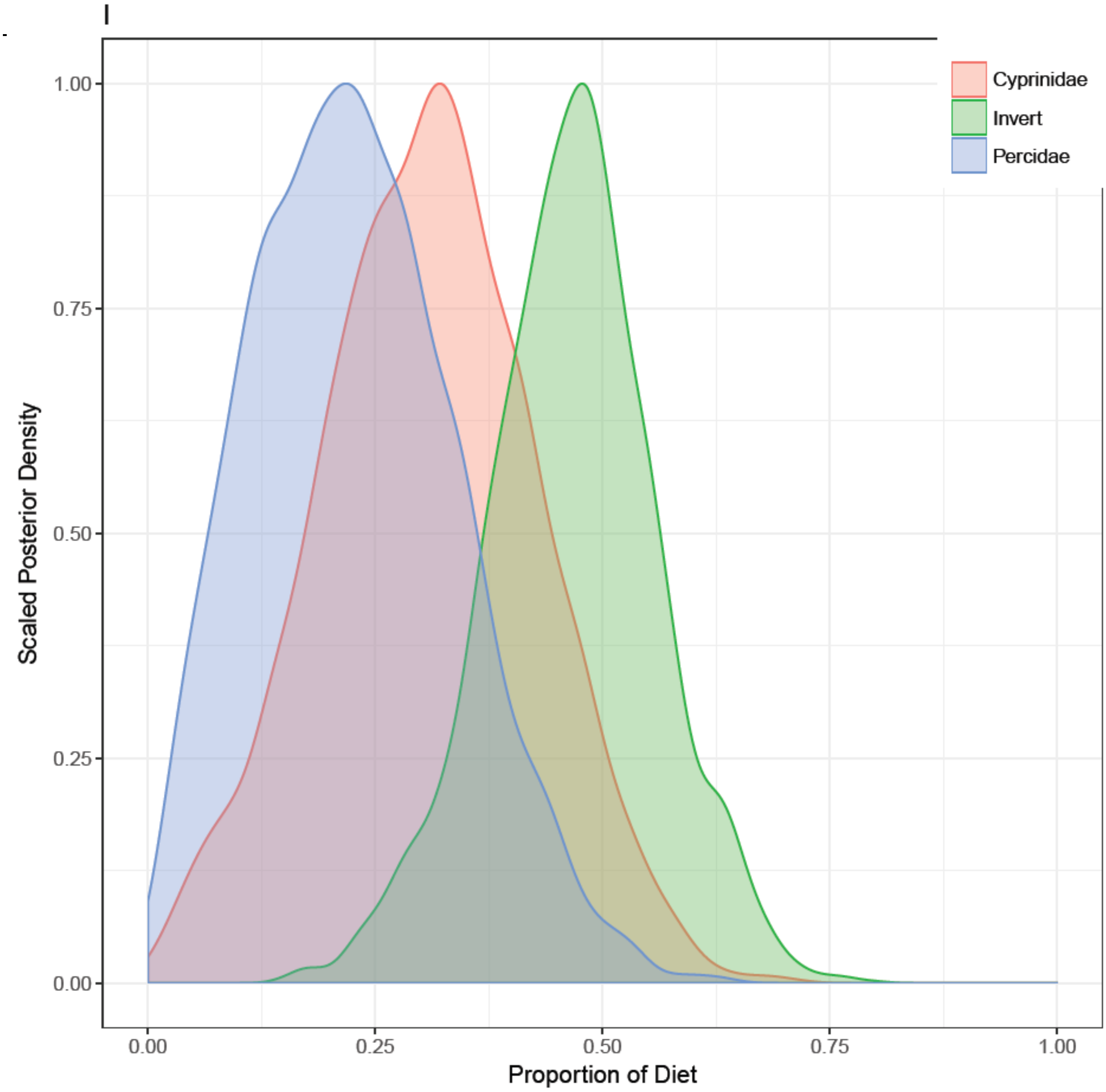

Fig A2.9. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class < 350 mm for model 5, consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ scale to muscle

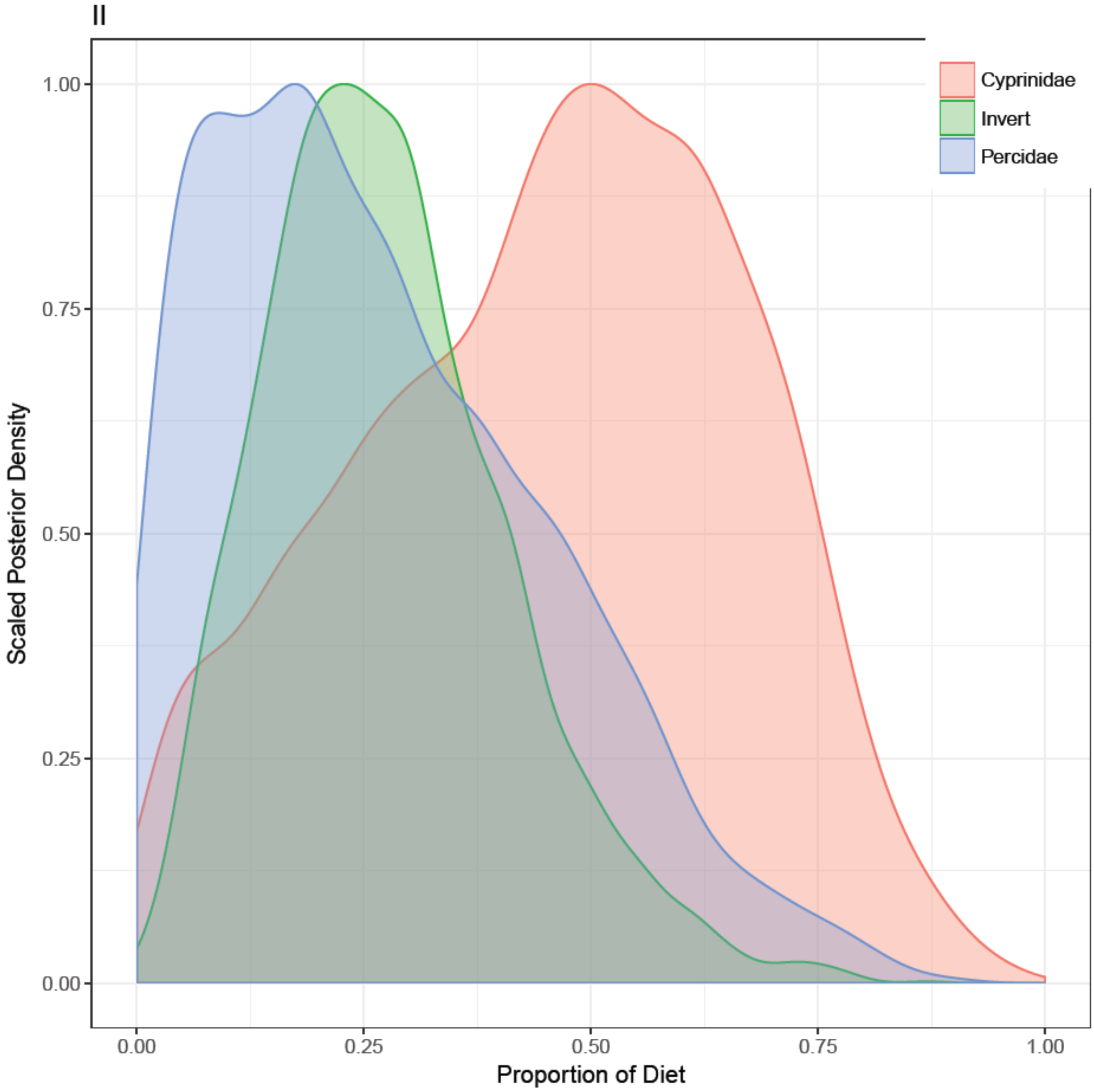

Fig A2.10. Mean predicted dietary contributions of ‘Cyprinidae’, Invertebrates’ and ‘Percidae’ to the diet of *Sander lucioperca* by size class > 350 mm for model 5, consumer as muscle values based on conversion using the linear models for $\delta^{13}C$ and $\delta^{15}N$ scale to muscle

Appendix 3: Influences of ontogenetic dietary shifts on the trophic interactions of native and non-native freshwater piscivorous fishes in an invaded river catchment

To determine if stable isotope data for *E. lucius*, *S. lucioperca* and macro-invertebrates could be combined across sampling areas and years for the River Warwickshire Avon and the River Severn respectively (Table A3.1). Analysis of covariance (ANCOVA) was used to test for the independent and interactive effects of sampling area, year sampled and fish length on *E. lucius* and *S. lucioperca* δ^{15}N and δ^{13}C. Analysis of variance (ANOVA) was used to test for the independent and interactive effects of sampling area and year sampled on macro-invertebrate δ^{15}N and δ^{13}C. Models included the effect of sampling area and sampling year as factors (main effects, fixed, levels changing according to species) and length as a covariate (excluding for macro invertebrates), together with their interactions (Table A3.2). Thus, for *E. lucius* and *S. lucioperca* a significant ($\alpha = 0.05$) interaction term would indicate that the relationship between the respective isotope value and body length varied according to sampling area. Whilst for macro invertebrates a significant ($\alpha = 0.05$) interaction term would indicate that the relationship between the respective isotope value and sampling area varied according to sampling year. Where there was a significant interaction, post-hoc tests were used for pairwise comparisons between factor levels. If there was a significant interaction on both δ^{15}N and δ^{13}C, sites were analysed separately. Prior to analyses, normality and homoscedasticity of data were assessed by visual inspection of the residual plots.

Table A3.1. Carbon and nitrogen stable isotope ratios (mean ‰ ± SD) for *E. lucius* and *S. lucioperca* and macro invertebrates and fish length range (mm) for each sampling area and year, n denotes sample size

Sp.	Sampling area	Year	n	Length range (mm)	Mean $\delta^{13}C$ (‰) ± SD	Mean $\delta^{15}N$ (‰) ± SD
Macro invertebrate	Tewkesbury Marina, Avon	2017	14	NA	-29.90 ± 1.40	15.93 ± 1.31
Macro invertebrate	Tewkesbury Marina, Avon	2018	15	NA	-31.02 ± 2.09	15.80 ± 2.41
Macro invertebrate	Tewkesbury marina, Severn	2017	9	NA	-32.43 ± 1.35	16.13 ± 0.93
Macro invertebrate	Tewkesbury marina, Severn	2018	13	NA	-32.51 ± 2.03	16.31 ± 1.19
Macro invertebrate	Upton marina, Severn	2017	7	NA	-29.65 ± 1.49	13.19 ± 1.32
Macro invertebrate	Upton marina, Severn	2018	14	NA	-29.54 ± 1.42	13.60 ± 1.13
Esox lucius	Avon	2015	14	530 to 1020	-24.66 ± 2.55	18.82 ± 1.11
Esox lucius	Avon	2016	3	510 to 840	-24.97 ± 3.42	18.11 ± 2.71
Esox lucius	Avon	2017	4	340 to 800	-26.18 ± 1.12	19.08 ± 0.26
Esox lucius	Tewkesbury Marina, Avon	2017	9	101 to 455	-28.89 ± 0.69	18.14 ± 1.51
Esox lucius	Tewkesbury Marina, Avon	2018	5	140 to 362	-28.26 ± 0.86	17.84 ± 1.02
Esox lucius	Severn	2014	4	737 to 925	-21.58 ± 1.28	16.26 ± 0.61
Esox lucius	Severn	2015	20	508 to 1060	-21.53 ± 2.41	15.91 ± 0.55
Esox lucius	Severn	2016	8	340 to 1016	-21.02 ± 2.74	16.50 ± 0.43
Esox lucius	Severn	2017	4	310 to 420	-25.06 ± 0.81	15.31 ± 0.50
Esox lucius	Upton marina, Severn	2016	2	230 to 240	-25.99 ± 0.30	15.72 ± 0.02
Esox lucius	Upton marina, Severn	2017	37	114 to 958	-24.92 ± 2.15	15.68 ± 1.27
Esox lucius	Upton marina, Severn	2018	3	263 to 314	-25.68 ± 0.64	16.22 ± 1.18
Sander lucioperca	Avon	2014	2	432 to 610	-25.82 ± 0.89	18.20 ± 3.09
Sander lucioperca	Avon	2015	8	310 to 870	-26.15 ± 0.49	20.32 ± 0.98
Sander lucioperca	Tewkesbury Marina, Avon	2017	20	65 to 136	-30.23 ± 1.06	18.00 ± 0.97
Sander lucioperca	Tewkesbury Marina, Avon	2018	24	40 to 258	-29.16 ± 1.58	17.89 ± 2.02
Sander lucioperca	Severn	2014	5	267 to 813	-24.51 ± 1.46	16.16 ± 1.08
Sander lucioperca	Severn	2015	19	247 to 826	-24.35 ± 0.73	16.05 ± 0.63
Sander lucioperca	Severn	2016	4	375 to 787	-24.43 ± 1.04	16.47 ± 1.06
Sander lucioperca	Severn	2018	1	838	-19.73	16.51
Sander lucioperca	Tewkesbury marina, Severn	2017	56	29 to 331	-30.67 ± 1.31	17.48 ± 1.50
Sander lucioperca	Tewkesbury marina, Severn	2018	11	50 to 140	-28.91 ± 1.13	18.56 ± 2.08
Sander lucioperca	Upton marina, Severn	2017	12	74 to 692	-26.42 ± 1.88	15.65 ± 0.99
Sander lucioperca	Upton marina, Severn	2018	1	48	-27.74	15.20

Table A3.2 Analysis of covariance (ANCOVA) and analysis of variance (ANOVA) test results for independent and interactive effects of sampling area, year sampled and fish length (mm) on δ^{15}N and δ^{13}C for pike, pikeperch and macro-invertebrates from the River Warwickshire Avon and the River Severn. Models included effect of sampling area and the effect of year as factors (main effects) and length as a covariate, together with the interactions for length and area. Post-hoc test statistics are reported as pairwise comparisons between factor levels.

Species	River	δ^{13}C (‰) ANCOVA statistics	δ^{15}N (‰) ANCOVA statistics	δ^{13}C (‰) Tukey post-hoc statistics	δ^{15}N (‰) Tukey post-hoc statistics
Macro-invertebrates	-	area $F_{(2,66)}$, 16.65, **P < 0.001***	area $F_{(2,66)}$, 21.15, **P < 0.001***	TMS – TMA t = -3.48, **P = 0.01***	UM – TMA t = -3.86, **P < 0.001***
		year $F_{(1,66)}$, 1.28, P = 0.26	year $F_{(1,66)}$, 0.08, P = 0.77	UM – TMS t = 3.25, **P = 0.01***	UM – TMS t = -3.86, **P < 0.001***
		area:year $F_{(2,66)}$, 0.93, P = 0.40	area:year $F_{(2,66)}$, 0.19, P = 0.83		
Pike	Avon	δ^{13}C (‰) length $F_{(1,28)}$, 48.40, **P < 0.001***	δ^{15}N (‰) length $F_{(1,28)}$, 2.03, P = 0.17	Avon-TMA t = -0.30, P = 0.77	Avon-TMA t = 2.14, **P = 0.04***
		δ^{13}C (‰) area $F_{(1,28)}$, 0.19, P = 0.67	δ^{15}N (‰) area $F_{(1,28)}$, 0.76, P = 0.39		
		δ^{13}C (‰) year $F_{(3,28)}$, 0.36, P = 0.78	δ^{15}N (‰) year $F_{(3,28)}$, 0.40, P = 0.75		
		δ^{13}C (‰) length:area $F_{(1,28)}$, 0.09, P = 0.77	δ^{15}N (‰) length:area $F_{(1,28)}$, 4.59, **P = 0.04***		
	Severn	δ^{13}C (‰) length $F_{(1,70)}$, 251.8, **P < 0.001***	δ^{15}N (‰) length $F_{(1,70)}$, 27.79, **P < 0.001***	Severn-UM t = -1.34, P = 0.19	Severn-UM t = 2.64, **P = 0.01***
		δ^{13}C (‰) area $F_{(1,70)}$, 3.42, P = 0.07	δ^{15}N (‰) area $F_{(1,70)}$, 3.03, P = 0.09		
		δ^{13}C (‰) year $F_{(4,70)}$, 0.87, P = 0.49	δ^{15}N (‰) year $F_{(4,70)}$, 1.98, P = 0.11		

		δ^{13}C (‰) length:area $F_{(1,70)}$, 1.79, *P* = 0.19	δ^{15}N (‰) length:area $F_{(1,70)}$ = 6.95, **_P_ = 0.01***		
Pikeperch	Avon	δ^{13}C (‰) length $F_{(1,48)}$, 67.03, **_P_ < 0.001***	δ^{15}N (‰) length $F_{(1,48)}$, 24.47, **_P_ < 0.001***	Avon-TMA *t* = 2.08, **_P_ = 0.04***	Avon-TMA *t* = 1.94, *P* = 0.06
		δ^{13}C (‰) area $F_{(1,48)}$, 3.05, *P* = 0.09	δ^{15}N (‰) area $F_{(1,48)}$, 3.96, *P* = 0.05		
		δ^{13}C (‰) year $F_{(2,48)}$, 4.01, **_P_ = 0.03***	δ^{15}N (‰) year $F_{(2,48)}$, 0.50, *P* = 0.61		
		δ^{13}C (‰) length:area $F_{(1,48)}$, 4.33, **_P_ = 0.04***	δ^{15}N (‰) length:area $F_{(1,48)}$, 3.77, *P* = 0.06		
	Severn	δ^{13}C (‰) length $F_{(1,99)}$, 1480.27, **_P_ < 0.001***	δ^{15}N (‰) length $F_{(1,99)}$, 10.17, **_P_ = 0.01***	Severn-TMS *t* = 7.97, **_P_ < 0.001***	Severn-TMS *t* = 4.61, **_P_ < 0.001***
		δ^{13}C (‰) area $F_{(2,99)}$, 48.04, , **_P_ < 0.001***	δ^{15}N (‰) area $F_{(2,99)}$, 32.81, , **_P_ < 0.001***	Severn-UM *t* = 4.01, **_P_ < 0.001***	Severn-UM *t* = -0.79, *P* = 0.43
		δ^{13}C (‰) year $F_{(4,99)}$, 12.94, , **_P_ < 0.001***	δ^{15}N (‰) year $F_{(4,99)}$, 1.72, , *P* = 0.15		
		δ^{13}C (‰) length:area $F_{(2,99)}$, 34.13, , **_P_ < 0.001***	δ^{15}N (‰) length:area $F_{(2,99)}$, 12.55, , **_P_ < 0.001***		

Table A3.3 Frequency of occurrence (% F_i) of prey types for pikeperch (*Sander lucioperca*) from stomach content analysis across three sites from the River Severn basin Western England. Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn

Prey	Frequency of Occurrence (% F*i*)		
	Site 1	Site 2	Site 3
Bleak	18.2	75	19.6
Roach	9.1	25	11.8
Common bream	3.0		1.0
Perch			2.0
Ruffe	3.0		
Unidentified fish	33.3		58.8
Daphniidae	21.2		3.9
Mysidae	18.2		1.9
Chrinomidae	3.0		1.9
Copepoda	18.2		
Odonata	3.0		
Simulidae	6.0		

Appendix 4: Predicting the contributions of novel marine prey resources from angling and anadromy to the diet of a freshwater apex predator

Table A4.1. Individual *E. lucius* sample data including date sampled, location, fork length (mm), weight (g) and carbon and nitrogen stable isotope ratios (‰)

Date Sampled	Location	Length (mm)	Weight (g)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
27/01/2015	Warwickshire Avon	890	7730	18.94	-24.81
06/02/2015	Warwickshire Avon	700	2320	19.78	-26.22
02/03/2015	Warwickshire Avon	1020	9090	19.44	-24.92
04/03/2015	Warwickshire Avon	770	5200	15.67	-24.66
11/03/2015	Warwickshire Avon	1020	9099	19.29	-24.91
03/07/2015	Warwickshire Avon	860	4750	19.43	-24.81
14/07/2015	Warwickshire Avon	720	3300	19	-24.94
20/07/2015	Warwickshire Avon	640	1400	19.01	-25.19
22/07/2015	Warwickshire Avon	550	960	18.84	-25.64
24/07/2015	Warwickshire Avon	860	5500	19.49	-25.39
22/08/2015	Warwickshire Avon	680	1525	19.31	-26.63
24/08/2015	Warwickshire Avon	530	960	19.46	-26.16
14/11/2015	Warwickshire Avon	860	7260	18.76	-24.9
20/02/2016	Warwickshire Avon	510	1400	21.24	-28.3
20/02/2016	Warwickshire Avon	840	5950	16.52	-21.47
27/02/2016	Warwickshire Avon	615	1632	16.58	-25.15
22/06/2017	Warwickshire Avon	455	NA	19.25	-27.62
20/07/2017	Warwickshire Avon	640	NA	19.2	-25.56
25/07/2017	Warwickshire Avon	800	NA	19.24	-25.04
20/09/2014	Downstream Severn	925	5981.7	16.85	-22.37
30/10/2014	Downstream Severn	838	5103	16.47	-20.11
28/11/2014	Downstream Severn	830	5900	16.31	-22.89
05/12/2014	Downstream Severn	737	2948.4	15.41	-20.94
24/01/2015	Downstream Severn	864	6577	16.96	-20.89
24/01/2015	Downstream Severn	940	8278	15.99	-20.15
24/01/2015	Downstream Severn	965	8165	16.3	-17.23
15/02/2015	Downstream Severn	508	1247	14.86	-24.74
15/02/2015	Downstream Severn	711	4649	15.72	-19.45
05/03/2015	Downstream Severn	686	3430.3	15.61	-23.64

05/03/2015	Downstream Severn	914	6463.7	16.31	-19.06
06/03/2015	Downstream Severn	635	1899.4	16.25	-24.08
06/03/2015	Downstream Severn	939	6633.8	15.04	-20.88
10/03/2015	Downstream Severn	660	3459	15.45	-21.48
12/03/2015	Downstream Severn	610	3345.2	16.28	-23.69
12/03/2015	Downstream Severn	1060	9043.5	15.29	-21.06
02/08/2015	Downstream Severn	787	4876	16.22	-20.67
07/09/2015	Downstream Severn	813	3799	16.36	-23.55
04/10/2015	Downstream Severn	546	1247	15.88	-24.71
05/10/2015	Downstream Severn	914	7711	16.32	-21.33
31/10/2015	Downstream Severn	1016	9072	15.03	-20.62
31/10/2015	Downstream Severn	1041.4	9724	16.2	-16.34
05/11/2015	Downstream Severn	1041	12105	16.36	-22.49
13/11/2015	Downstream Severn	580	2070	15.75	-24.54
23/01/2016	Downstream Severn	965	7541	16.35	-18.24
22/02/2016	Downstream Severn	762	3742	16.86	-21.75
01/03/2016	Downstream Severn	1016	9525	16.6	-16.49
02/03/2016	Downstream Severn	749	3515	16.92	-20.63
17/03/2016	Downstream Severn	883	6861	16.85	-21.52
13/11/2016	Downstream Severn	1003	8391.5	16.28	-20.72
31/08/2014	Upstream Severn	774	3160	15.61	-23.28
16/09/2014	Upstream Severn	480	880	14.63	-24.73
29/11/2014	Upstream Severn	420	460	15.41	-24.23
29/11/2014	Upstream Severn	880	5750	17.07	-23.49
29/11/2014	Upstream Severn	901	4280	15.99	-22.93
03/12/2014	Upstream Severn	660	3650	16.24	-23.8
20/12/2014	Upstream Severn	890	3680	16.24	-23.31
24/02/2015	Upstream Severn	675	2420	15.14	-24.33

Table A4.2. Carbon and nitrogen stable isotope ratios (mean ‰ ± SD) for *E. lucius* at each reach and year showing analysis of variance statistics

River reach	Year	n	Mean $\delta^{13}C$ (‰) ± SD	Mean $\delta^{15}N$ (‰) ± SD	ANOVA
L. W. Avon	2015	13	-25.32 ± 0.17	18.95 ± 0.29	$\delta^{13}C$ (‰) $F_{(2,16)} = 0.49$, $P = 0.61$
	2016	3	-24.97 ± 1.97	18.11 ± 1.56	$\delta^{15}N$ (‰) $F_{(2,16)} = 0.64$, $P = 0.54$
	2017	3	-26.07 ± 0.79	19.23 ± 0.02	
Downstream Severn	2014	4	-21.58 ± 0.64	16.26 ± 0.31	$\delta^{13}C$ (‰) $F_{(2,27)} = 1.28$, $P = 0.29$
	2015	20	-21.53 ± 0.54	15.91 ± 0.12	$\delta^{15}N$ (‰) $F_{(2,27)} = 4.81$, $P = 0.02$*
	2016	6	-19.89 ± 0.85	16.64 ± 0.11	
Upstream Severn	2014	7	-23.68 ± 0.23	15.88 ± 0.29	$\delta^{13}C$ (‰) $F_{(1, 6)} = 0.95$, $P = 0.37$
	2015	1	-24.33	15.14	$\delta^{15}N$ (‰) $F_{(1, 6)} = 0.82$, $P = 0.40$

Rationale of putative prey resources in mixing models

At the upstream and downstream Severn reaches, the SI data for *S. cephalus* and invasive *B. barbus* were highly similar and so they were combined as a single prey resource in mixing models ('Cypriniforms'). However, in their combined data, $\delta^{13}C$ had high variation (-19.37 to -27.04 ‰) resulting from some individuals specialising on MDN baits and others on macro-invertebrates (Gutmann Roberts et al., 2017). Thus, this 'Cypriniform' prey resource was split into two groups based on their $\delta^{13}C$ data: (1) -19.37 to -22.9 ‰; where diets comprised of a relatively high proportion of MDN ('Cypriniform marine'; mixing model: mean ± SE = 0.50 ± 0.17; Table S3); and (2) -23.04 to -27.04 ‰; where diets were relatively low in MDN ('Cypriniform-freshwater'; mean ± SE = 0.25 ± 0.11; Supplementary material, Table S3). The two groups were entered as separate prey resources in the mixing models. The differences in MDN dietary contributions between these two groups were significant (t-test; $t = -5.66$, $P < 0.001$).

Table A4.3. Individual carbon and nitrogen stable isotope ratios, lengths and marine derived nutrient contributions for cypriniform fish *S. cephalus* and *B. barbus* used as resources 'Cypriniform freshwater' and 'Cypriniform marine' in Bayesian mixing models as derived from Gutmann-Roberts et al. (2017)

Cypriniform Freshwater					Cypriniform Marine				
Species	δ^{13}C (‰)	δ^{15}N (‰)	Length (mm)	MDN (%)	Species	δ^{13}C (‰)	δ^{15}N (‰)	Length (mm)	MDN (%)
B. barbus	-27.04	12.82	510	0.089	*B. barbus*	-22.89	12.37	740	0.359
B. barbus	-26.5	14.88	397	0.11	*B. barbus*	-22.81	12.24	690	0.396
B. barbus	-26.09	14.42	364	0.151	*B. barbus*	-22.74	11.47	520	0.514
B. barbus	-26.03	14.65	660	0.094	*B. barbus*	-22.43	12.71	680	0.411
B. barbus	-25.66	13.54	520	0.375	*B. barbus*	-22.27	11.89	529	0.285
B. barbus	-25.65	13.38	800	0.148	*B. barbus*	-22.04	12	520	0.583
B. barbus	-25.49	13.89	401	0.169	*B. barbus*	-21.98	12.35	670	0.457
B. barbus	-25.41	12.67	580	0.185	*B. barbus*	-21.91	11.65	591	0.607
B. barbus	-25.11	12.81	660	0.231	*B. barbus*	-21.5	11.61	520	0.1
B. barbus	-25.04	13.34	580	0.212	*B. barbus*	-21.4	11.67	630	0.582
B. barbus	-24.85	12.4	770	0.275	*B. barbus*	-21.02	11.61	565	0.584
B. barbus	-24.66	13.03	750	0.215	*B. barbus*	-20.88	11.03	557	0.614
B. barbus	-24.46	13.14	620	0.241	*B. barbus*	-20.55	11.88	800	0.535
B. barbus	-24.31	11.56	530	0.177	*B. barbus*	-20.29	10.75	800	0.671
B. barbus	-24.1	12.24	630	0.328	*B. barbus*	-20.1	11.51	602	0.835
B. barbus	-24	13.22	593	0.335	*B. barbus*	-19.37	10.48	790	0.776
B. barbus	-23.81	12.76	480	0.226	*B. barbus*	-22.36	13.01	450	0.339
B. barbus	-23.37	11.89	698	0.371	*S. cephalus*	-22.09	11.92	400	0.422
B. barbus	-23.25	11.81	545	0.329	*S. cephalus*	-20.8	12.12	540	0.378
S. cephalus	-24.74	10.3	104	0.463	*S. cephalus*	-19.82	10.66	510	0.655
S. cephalus	-23.6	11.75	300	0.333					
S. cephalus	-23.04	10.73	190	0.417					
Mean ± SE	-24.83 ± 1.09	12.78 ± 1.17		0.25 ± 0.11	Mean ± SE	-21.46 ± 1.06	11.75 ± 0.66		0.50 ± 0.17

Appendix 5: Behaviours, motivations and perceptions of anglers targeting native and non-native predatory fishes in freshwater fisheries in England

Participation

1. In order to proceed, please confirm that you fish for the predatory freshwater species (pike (Esox lucius) / perch (Perca fluviatilis) and/or zander (Sander lucioperca) by rod and line (angling)

Yes, I fish for these species
No, I do not fish for these species

2. For how many years in total have you been fishing?

fewer than 2 years
2 to 5 years
6 to 10 years
11 to 20 years
21 to 30 years
more than 30 years

2a Of those years, of how many have you been predator fishing?

3. How many days do you go on predator fishing sessions in a year?

fewer than 10 days
10 to 30 days
31 to 60 days
61 to 180 days
181 to 240 days
More than 240 days

4. How many hours do you spend on an average predatory fishing session?

less than 2 hours
2 to 6 hours
7 to 12 hours
13 to 24 hours
more than 24 hours

5. How far do you travel ON AVERAGE from your home to a predatory fishing ‘venue’?

fewer than 5 miles
5 to 10 miles
11 to 20 miles
21 to 50 miles
51 to 100 miles
more than 100 miles

6. How many occasions would you travel more than 100 miles to a predatory fishing ‘venue’ in a year?

Never
Fewer than 10

11 to 20
21 to 30
31 to 40
more than 40

7. How much do you spend on predator angling annually for membership fees and day tickets?

less than £100
£100 to £300
£301 to £500
£501 to £1000
£1001 to £2000
more than £2000

8. How much do you spend on predator angling annually for equipment and bait (including boat moorings etc.)? (answers are given in euro)

less than £100
£100 to £300
£301 to £500
£501 to £1000
£1001 to £2000
more than £2000

9. How much do you spend on predator angling annually for travel (including fuel, food and accommodation)? (answers are given in euro)

less than £100
£100 to £300
£301 to £500
£501 to £1000
£1001 to £2000
more than £2000

Behaviour

10. Which of the following BEST describes your predator fishing habits?

I am a predator angler and don't fish for any other species
I am a predator angler but also target other species
I fish for predators but wouldn't consider myself just a predator angler as I also target other species
I fish for predators rarely and my main angling activity is targeting other species

11. Which species do you target routinely? Please tick ALL that apply.

If you selected Other, please specify:
List of all British freshwater fishes was available

12. Which predator species is your preferred target?

pike (Esox lucius) / perch (Perca fluviatilis) / zander (Sander lucioperca)

13. Which predator species do you catch most often?

pike (Esox lucius) / perch (Perca fluviatilis) / zander (Sander lucioperca)

14. When predator fishing, what proportion of your time is spent targeting the following species (even if you catch other species unintentionally)? please give your answer as a % where the total should equal 100%

pike (Esox lucius) / perch (Perca fluviatilis) / zander (Sander lucioperca)

15. Which of the following best describes your seasonal predator fishing habits?

I fish for predators throughout the fishing season
I only fish for predators in winter
I only fish for predators in summer

16 Please describe the importance of each of these predator fishing 'venues' to you

Canal
River
Lake
Other
Not at all important
Slightly important
Moderately important
Fairly important
Very important
Extremely important
If you selected Other, please specify:

17 Which fishing method do you use most often on a typical predator fishing session?

Dead fish bait
Live fish bait
Lure (including fly)
Non-fish bait (worm etc.)
Other
If you selected Other, please specify:

18 Which of the following BEST describes your predatory angling catch and release behaviour

I practice catch and release of perch
I practice catch and release of pike
I practice catch and release of zander
  Always (without exception)
  Always (unless it looks as if it won't survive/ i.e. deep hooking)
  Usually
  Occasionally
  Never
  Non-Applicable (I don't fish for this species)

Motivations

19 Please rank your agreement to each of the following statements

I fish for predators because there are good predator fishing venues close to me
I fish for predators because I prefer the fishing style over other types of fishing
I fish for predators because it's a more natural way to fish than other types of fishing

I fish for predators because it's relaxing, an escape from everyday life
I fish for predators because I like to be in wild natural places, enjoying nature and tranquillity
I fish for predators because I can do it socially with friends and/or family
I fish for predators because it's a challenge and exciting
I fish for predators because I can use different angling techniques and styles
I fish for predators because there is a chance of catching a big fish
I fish for predators because I like the anticipation of not knowing what species I might catch
I fish for predators because they are a good fighting fish
I fish for predators because they are more exciting to catch compared to other species
I fish for predators because it gives me a greater sense of accomplishment compared to catching other species
I fish for predators because they are fascinating more intelligent than other species

Strongly disagree
Disagree
Disagree slightly
Agree slightly
Agree
Strongly agree

Perceptions

20 . Please rank your agreement to each of the following statements
Non-native SPECIES generally have a negative impact to the environment
I consider myself to be aware of the conservation issues facing freshwater environments
Non-native FISHES generally have a positive impact to the environment
I am well informed of the ecological concerns of zander in the country where I fish (e.g. through media, angling forums, environmental organisation)
I believe zander should be considered as a native species in England
I am opposed to the culling of zander in England
Zander negatively impact the quality of the fishing where they are found
When zander are first introduced they negatively impact the quality of the fishing to that place, but if left alone they find a balance
I am opposed to the illegal stocking of zander
I am happy that zander where I fish as it is provides another angling opportunity we otherwise would not have
I think zander are really important to the growth of angling
I think zander provide an important ecological function in England
I would like to see zander introduced to additional waterbodies other than where they are currently found

Strongly disagree
Disagree
Disagree slightly
Agree slightly
Agree
Strongly agree

Demographics

21 What is your gender
Male
Female
Other

21 What is your age category?
Younger than 16
17 to 18
18 to 24
25 to 34
35 to 44
45 to 54
55 to 64
65 to 74
Older than 75

23. In which country do you live? (if not listed please select 'Other')
England
Scotland
Wales
Northern Ireland
Other

24 What is the highest level of education you have achieved?
Less than high school degree (Pre – 16 education no qualification)
High school degree or equivalent (Post – 16 education with qualification)
College / University but no degree
Bachelor Degree
Graduate Degree

25. What is your employment status?
Unemployed
Employed - Full time
Employed - Part time
Self employed
Student
Apprentice
Retired

26. What is your monthly income?
less than £1000
£1000 to £1500
£1500to £2000
£2000 to £2500
£2500 to £3000
more than £3000