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Ecomorphology of Pike in Irish Freshwaters

Layman's Report

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Ecomorphology of a top predator (*Esox lucius*) in freshwater habitats

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About

This research was carried out as part of a wider PhD research project conceived by Inland Fisheries Ireland and University College Dublin. The overall aim of the project is to update and inform managers as to the biology and ecology of pike (*Esox lucius* L.) in Ireland, a historically understudied species in the Irish context. This represents the third and final report from this project and deals with the morphology and condition of pike in Ireland. The main aims of this investigation were to elucidate the variation in the shape of Irish pike between river, lake and canal habitats, related to diet, condition, age and sex. The previous reports on the genetics of Irish pike, and the diet of pike in Ireland are available on the Inland Fisheries Ireland website (www.fisheriesireland.ie) The field work and sampling for this project was carried out opportunistically in collaboration with Inland Fisheries Ireland, and through attendance at many pike angling competitions. The authors would like to thank the many pike anglers that contributed to the study and allowed D. Pedreschi to sample their catch. This study has been generously funded by Inland Fisheries Ireland, with contributions from the Irish Federation of Pike Angling Clubs.

INTRODUCTION

Individual variation is key to allowing species to maximise their success in any one environment (Kekäläinen *et al*. 2010). All environments differ, particularly freshwater systems which have varying human-induced pressures such as damming, diversion and pollution, and are also subject to great variability naturally due to differences in nutrient load, underlying geology, and water levels due to variable rainfall. As such, many freshwater fish have had to adapt to variation in resource availability (e.g. food, shelter, spawning areas) by developing **polymorphisms**. Trophic polymorphisms are those related to food and feeding, and these can occur even within a single species, in the same location. For example, single species have been observed to segregate into littoral (near shore) and pelagic (off-shore) **ecotypes**. These ecotypes differ 'trophically' in that occupying these different habitats leads them to specialise in eating different things. The littoral individuals often eat benthically (from the bottom of the lake) in the shallow, well lit and productive near shore areas, whereas pelagic individuals tend to feed from the water column (e.g. on plankton). It follows that the different ecotypes may thus develop different 'equipment' (shape or structure) in order to deal with these different diets. These polymorphisms allow the same species to exploit multiple niches within the same lake/river/system and thus avoid intraspecific competition (competition with their own kind). Many habitat differences (e.g. flow regime, foraging opportunities, frequency of disturbance events) between and within lakes, rivers and canals can create selective pressures that result in the divergence of **morphological**, behavioural and life history traits, as individuals adapt to maximise their fitness (that is its ability to survive and reproduce within each environment) (Hjelm *et al*. 2001; Brinsmead & Fox 2002; Langerhans *et al*. 2003;

A **polymorphism** occurs when two or more clearly different forms or morphs exist in the same population of a species.

An **ecotype** is a distinct geographic variety, population or race within a species, which is adapted to specific environmental conditions.

Morphology is the study of the shape and structure of organisms, their specific structural features, form and function.

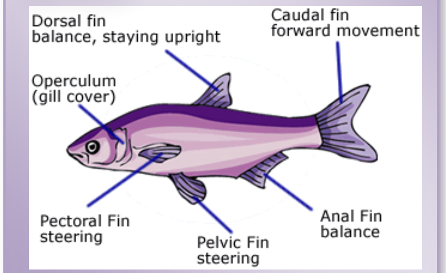


Image from:

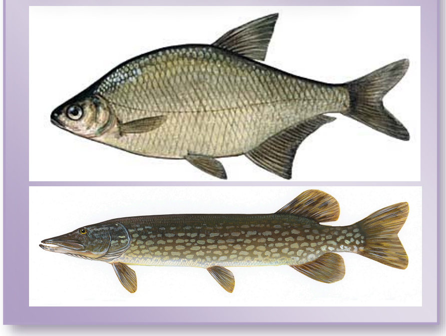
Bartels *et al.* 2012).

Maximising its fitness is the key 'aim' for a species. Polymorphisms, such as the one described above are caused by divergent selection pressures due to environmental variation. However, they serve not just to reduce intraspecific competition; in fact they are extremely important as they represent different life history strategies that may become essential under environmental stress, and in some instances even lead to speciation events (Smith & Skulason 1996; Adams & Huntingford 2002a,b; Kekäläinen *et al.* 2010). Imagine a threat such as a pollution event that kills off the planktonic life in a lake. The pelagic ecotypes no longer have a food source. However, the species will continue, because the littoral type is able to survive on the benthos. In today's pressurised and modified systems, with the impacts of climate change becoming more obvious, and where environmental conditions are often unpredictable, these polymorphisms become increasingly important for species success and survival. Furthermore, these differing 'ecotypes' may eventually become so separately successful and specialised in their habits that they may become reproductively isolated from one another and eventually give rise to two species instead of one. For these reasons, the identification of differences in population morphotypes is a critical task to assess ecological **plasticity** and evolutionary potential.

Plasticity is the ability of an organism to change its **phenotype**, that is its observable characteristics or traits, in response to changes in the environment. Plasticity is one of the fundamental ways in which organisms cope with environmental variation.

In lotic systems (flowing water), water velocity can have a strong effect on individual growth, as the energy the fish expends in swimming or simply maintaining its position cannot be put into growth (Langerhans *et al.* 2003; Penczak 2007). However, as a result of constant movement, the fish may also be in a better physiological condition or have a higher metabolic rate, which may be reflected in their hepatosomatic index (HSI), an index designed to give an indication as to condition and is linked to liver energetic reserves and metabolic activity (Lenhardt *et al.* 2009). Stream fishes may be expected to be more **fusiform** than lake fish in order to reduce drag and hence energy expenditure when maintaining their position in the water (Brinsmead & Fox 2002; Langerhans *et al.* 2003); as well as to have a more robust caudal penduncle, suitable for thrust and sustained swimming, and more anteriorly positioned

Fusiform is a body shape common to many aquatic animals, characterized by being tapered at both the head and the tail (torpedo-shaped).



lateral fins for steady positioning in the current (Brinsmead & Fox 2002).

In lentic (still) waters, competitive interactions may stimulate active hunting as there is less passive dispersal of food by the current. Lower turbulence may also lead to increased visibility, hence increased predation threat (Abrahams & Kattenfeld 1997), and greater need to protect territories within the littoral zone.

Canals, a somewhat understudied habitat type (Arlinghaus *et al*. 2002), may in fact present an interesting intermediate habitat between lakes and rivers in relation to velocity, visibility and disturbance regimes but with their own set of challenges, particularly in relation to locks and weirs, which present barriers to dispersalLake and river habitats rarely experience the same dispersal barriers.

The quantitative analysis of the variation in shape of a species is known as morphometrics (Adams *et al*. 2004; Webster & Sheets 2010). **Geometric morphometrics** allow the rigorous quantification of the overall shape of an organism (Cadrin 2000; Webster & Sheets 2010). Here we use geometric morphometrics to investigate differences among river, lake and canal habitats. Morphological divergence in many species has been documented in *either* lake or stream environments; however, few studies have compared the morphology of lake *and* stream dwelling populations within a species (Brinsmead & Fox 2002). Those that have addressed the issue have found a high degree of divergence between lentic vs. lotic ecotype comparisons (e.g. Hendry *et al*. 2002; Langerhans *et al*. 2003).

Northern pike (*Esox lucius* L.) is a freshwater fish known for its large, duck-billed snout, elongated body, and voracious feeding behaviour (Grande *et al*. 2004). It exhibits a circumpolar distribution in the northern hemisphere (North America, Europe, and Asia) where it can be found in mesothermal freshwater systems, ranging from small streams to large rivers, and small ponds to major lakes, and even in some brackish coastal waters (Chapman *et al*. 1989; Grande *et al*. 2004; Venturelli & Tonn 2006). As a top down keystone predator feeding on a variety of species, they can potentially alter fish community structure, benthic fauna and hence the entire ecosystem in which they reside (Paukert & Willis 2003; Sepulveda *et al*. 2013; Pedreschi *et al*. 2014b). Pike are a sit-and-wait ambush predator, meaning that they are predominantly sedentary, tending to hover and snap at prey, occasionally leaving vegetative cover to pursue free-swimming prey in open water (Nilsson & Brönmark 1999; Lehtiniemi *et al*. 2005). Pike morphology is widely credited to exemplify the “ambushing predator” shape (Chapman & Mackay 1990; Venturelli & Tonn 2006). These morphological features include: a broad, flattened ‘duck-billed’ snout, large mouth, large teeth, heavy jaws, fusiform body, enlarged caudal fin, and a rear-positioned dorsal fin (Chapman *et al.* 1989; Eklöv & Diehl 1994; Grande *et al.* 2004). Nevertheless, studies have shown that pike are capable of eating a wide range of species of varying sizes, as well as, at times, preferring small, shallow-bodied, soft-rayed species over larger, deep-bodied, and spiny-finned prey (Hart & Hamrin 1988; Wahl & Stein 1988; Nilsson & Brönmark 1999, 2000; Venturelli & Tonn 2006; Pedreschi *et al.* 2014b), likely to reduce handling time, energy expenditure and risk of **kleptoparasitism** (Wahl & Stein 1988; Nilsson & Brönmark 1999). Pike have even been demonstrated to prey upon invertebrates during times of seasonal over-abundance of invertebrate prey, or simply opportunistically (Chapman & Mackay 1990; Beaudoin *et al.* 1999; Venturelli & Tonn 2006; Pedreschi *et al.* 2014b).

Trophic polymorphisms are the differences in morphological characteristics that are used in the detection, capture or handling of prey items (Smith & Skulason 1996; Adams & Huntingford 2002b; Bartels *et al.* 2012). The diet and trophic ecology of pike from Irish lakes, rivers and canals has been described by Pedreschi *et al.* (2014b), presenting an opportunity to examine the relationship between predatory preferences and anatomy of pike. Predators are thought to be limited in the prey that is available to them by the dimensions of their feeding apparatus (Hart & Hamrin 1988; Nilsson & Brönmark 2000). Thus, the morphological characteristics of pike may reflect the species they prey upon in different aquatic systems.

Kleptoparasitism is a form of feeding in which one animal takes prey from another that has caught, or collected, or otherwise expended energy obtaining.

Previous studies have indicated that stream and river pike populations are 'woefully understudied' (Rypel 2012), and that substantially more work is needed in order to inform management. Throughout the literature, pike are seen as a principally lake-adapted species with a preference for still or slow-moving water (Raat 1988; O’Grady & Delanty 2008). However, many lotic systems have been shown to support healthy pike populations (Lenhardt & Cakic 2002; Cooper *et al.* 2008; Sepulveda *et al.* 2013), and tracking studies have indicated that they can and do travel widely (Ovidio & Philippart 2005; Koed *et al.* 2006). This research compares and contrasts between lake, river and the often overlooked canal habitats to investigate variation in pike morphology driven by habitat and ecology.

METHODS

Sampling

Pike were sampled from 10 locations (3 rivers, 5 lakes and 2 canals; Table 1, Figure 1) between October 2010 and October 2012, using a combination of electrofishing (rivers and canals), gill-netting and angling (lakes). A range of habitat sizes were selected in order to encompass variations of site type within categories. Sampling was carried out opportunistically, in collaboration with Inland Fisheries Ireland during their routine surveys, and through attendance at pike angling competitions.

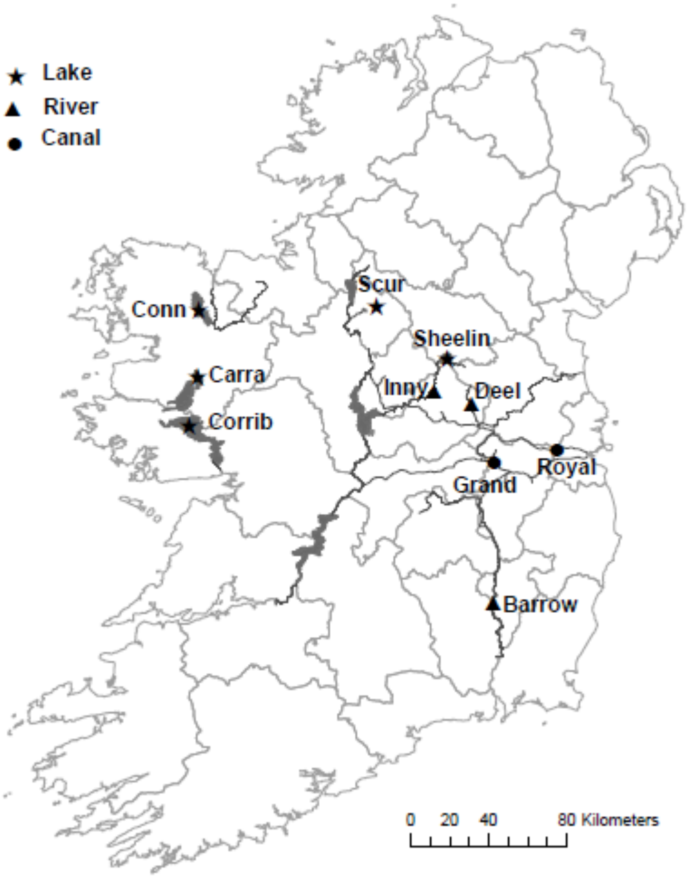


Figure 1. Pike sampling site locations around Ireland

Table 1: Sample size (n) for morphometric analysis and mean, maximum and minimum length and age per site. Diet N values reflect number of individuals examined; not all stomachs contained prey items. SIA: Stable isotope analysis.

Type	**Site**	**Morpho n**	**Fork Length**			**Age**			**Diet n**	**SIA n**
			Mean	Min	Max	Mean	Min	Max		
Lake	Scur	19	54.1	27.1	86.5	4.6	1	8	9	25
	Carra	20	43.0	31.6	67.1	3.9	3	6	19	30
	Sheelin	51	44.2	29.9	80.7	4.2	2	8	52	65
	Conn	10	69.2	51.5	83.4	6.6	5	8	0	0
	Corrib	22	33.1	10.6	66.6	-	-	-	0	0
	Total	122	46.3	10.6	86.5	4.5	1	8	80	120
River	Barrow	41	36.0	17.4	79.6	2.9	0	7	26	30
	Inny	38	37.9	13.5	83.8	4.0	1	9	24	30
	Deel	49	38.1	16.5	65.8	2.4	1	7	44	65
	Total	128	37.4	13.5	83.8	3.3	0	9	94	125
Canal	Grand	18	35.3	12.6	63.4	3.9	2	6	14	30
	Royal	45	35.9	12.5	77.7	2.8	0	7	38	61
	Total	63	35.7	12.5	77.7	2.9	0	7	52	91
Total		313	40.5	10.6	86.5	3.8	0	9	226	336

Morphometric Analysis

A total of 313 fish were photographed from the left lateral side on a white background with a ruler, and digital images were processed using 23 landmarks (Figure 2) and analysed using a range of statistical programs from TPS and MorphJ. The landmarks were converted to shape coordinates and standardised to a common size to remove the effect of size on the results.

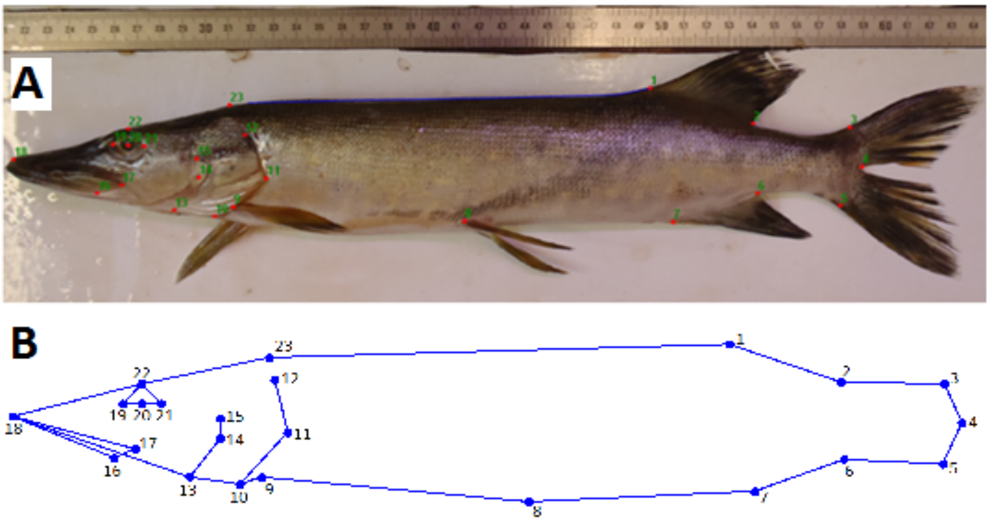


Figure 2: Illustration of landmarks selected for geometric morphometric analysis A) landmarks numbered and visible on an individual pike; B) illustrates how these landmarks capture the overall shape of the fish.

Diet and Stable Isotope Analysis

As many of the individuals examined were also subject to stomach content and stable isotope analysis (SIA) to investigate feeding habits (Pedreschi *et al.* 2014b), relationships between feeding habits and morphology were also examined.

Age, Growth & Condition

Individuals were measured (fork length) and weighed and a sample of scales (taken between the dorsal fin and the lateral line) were removed for ageing. Scales were dried, cleaned to remove dried mucus and skin cells and photographed. Annual checks were recorded as the point where circuli became discontinuous and irregular, sometimes forming a chaining pattern, usually followed by a hyaline area (Figure 3; Schneider 2001). Care was taken to avoid counting false annuli. At least three scales were read for each fish to confirm the age, and 30% of scales were cross-checked by a second analyst, with an agreement of 82%. Where discrepancies occurred, differences were of a single year, and usually of older age fish. In these cases, conservatively, the younger age was taken.

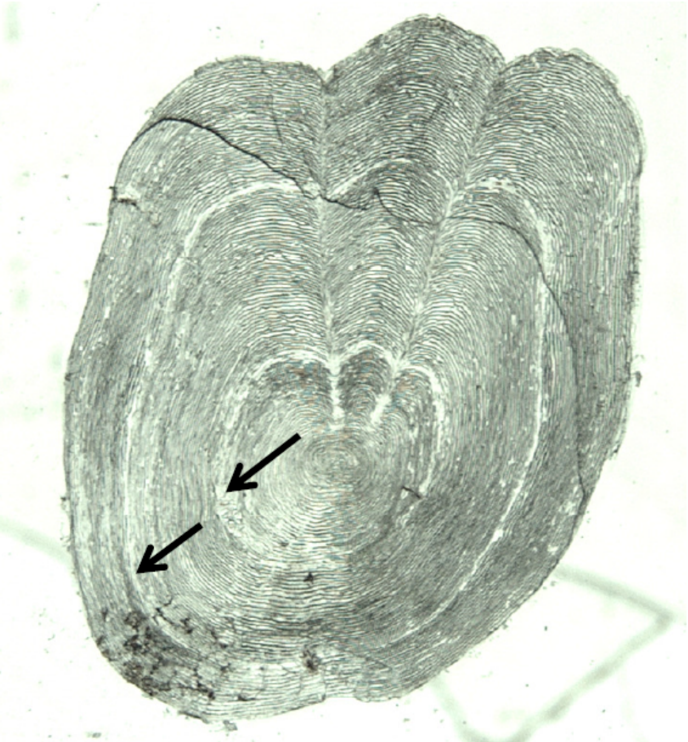


Figure 3. Pike scale or a 2+ fish showing annuli used for aging.

Differences in growth between males and females and between habitat types and sites were examined. The hepatosomatic index (HSI) is thought to be indicative of energy reserves as the liver acts as a major energy store (Chellappa *et al.* 1995), especially in non-fatty fish such as pike. As such the HSI was calculated for 568 fish. Stomach and gonad weights were removed in order to avoid variability due to feeding and reproductive status.

RESULTS & DISCUSSION

Morphometric analysis indicates that a continuum exists between individuals with short, deep heads, smaller eyes and deeper bodies located in lakes, to more stream-lined individuals, with more tapered heads and larger eyes in rivers and canals (Figure 4). Discrete categories do not exist (i.e. a lentic morph and a lotic morph as described in the introduction), similar to findings for pumpkinseed and rock bass (Brinsmead & Fox 2002), however the differences between river, canal and lake groups were significant ($P<0.01$). The observed differences were also in line with our predictions of a more streamlined, fusiform body shape in lotic habitats. The variation in eye size is hypothesised to be related to differences in turbulence and disturbance regimes which may affect visibility. Higher flow rates may lead to higher amounts of suspended particles, along with turbulence, which may affect vision by reducing light penetration and increasing scatter, both of which affect vision in fish (Aksnes & Giske 1993; Utne-Palm 2002). Additionally, larger eyes may be favoured in riverine systems due to a higher presence of predatory birds because of the larger riparian zones along rivers than lakes proportionally (Gregory *et al.* 1991). However, this requires further investigation.

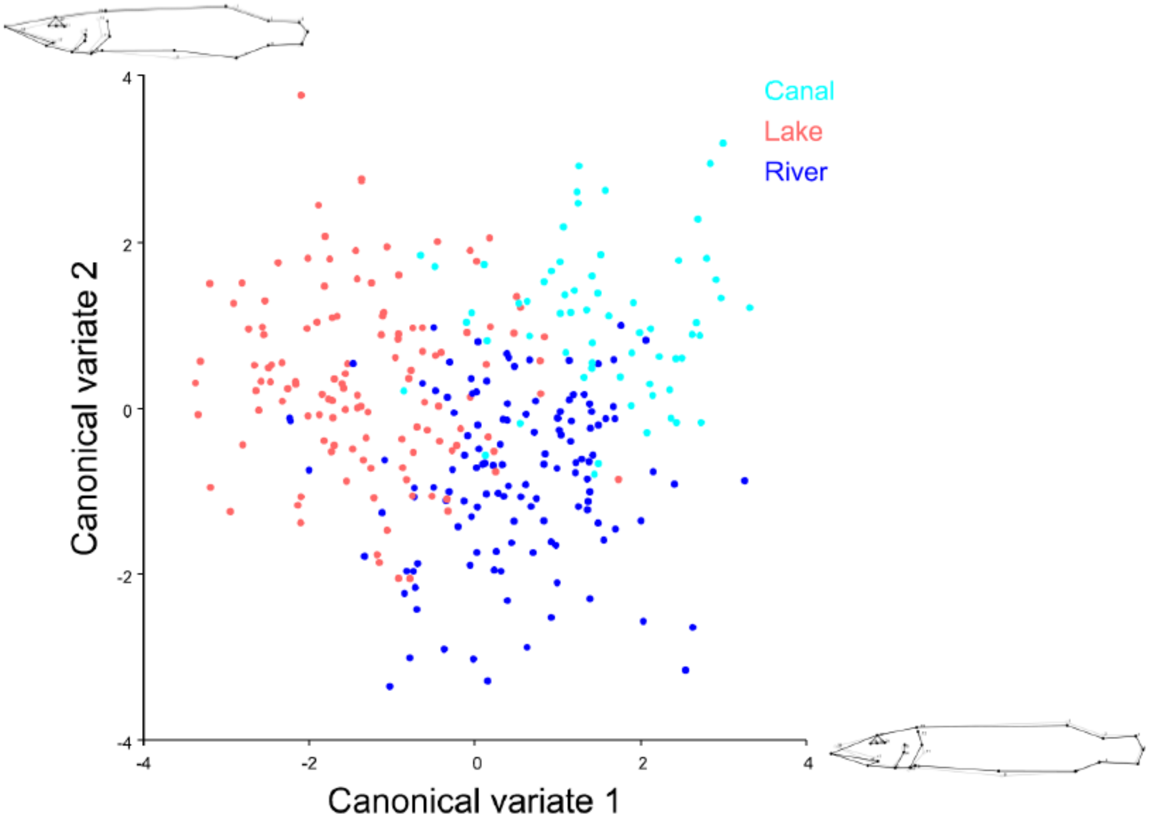


Figure 4. Delineation of habitat groupings using canonical variate analysis (CVA). CVA is used to find the shape features that best distinguish among multiple groups of specimens. Wireframe diagrams indicated the change along each axis (black) from the average shape (grey). CV1 accounts for 70% of the variance observed and indicates a change in body depth and eye size, with those in lotic environments being more streamlined, with longer heads and bigger eyes than those in lentic waters. CV2 accounts for only 30% of the variation, indicates relatively little morphological difference between lake and canal individuals, only contributing to slightly separating river individuals through variation in body depth.

Interestingly, hepatosomatic index (HSI) values were also significantly related to habitat type, but contrary to our hypothesis, lotic (flowing water) habitats demonstrated lower HSI values than lentic (still water) habitats. This may reflect the increased energy expenditure in lotic habitats where more constant swimming is required; thus, although the fish may be in good physical condition, there are higher energetic costs to life in lotic environments than lentic littoral habitats. This may be due to the fact that for pike in lakes, benthic ambush predation allows for less movement, and thus an increased ability to store lipids. In contrast to Brinsmead & Fox (2002), changes in the depth of the caudal peduncle were not found nor in fin placement. Pike exhibit a characteristic long slender form which enables its classic 'fast-start' performance, a behavioural adaptation which enables a higher prey capture success rate, and efficient escape from threats (Harper & Blake 1991; Frith & Blake 1995). The overall morphology of pike has remained largely unchanged since its Cretaceous ancestors (Grande 1999), and thus likely represents a highly efficient and conserved evolutionary state. As such, it is unsurprising that this region may be morphologically constrained, as any alterations may result in a decrease in predation and escape efficiency, factors that are essential for survival.

In keeping with other studies (Griffiths *et al.* 2004; Rypel 2012), no growth differences were found between habitat types. Longevity (lifespan) was found to be 10 years, as predicted for our latitude (Rypel 2012), however older fish have been found in Irish waters (12 years; Rosell & MacOscar 2002).

Sex was shown to be a somewhat significant factor in determining morphology, however the differences between males and females were minor, centring around landmark 8 (pelvic fin insertion), the only non-skeletally fixed landmark (Figure 2). This landmark indicated the deeper body of females, likely relating to the large size of female gonads. Immature individuals seemingly represent an intermediate morphotype between males and females as miss-classification rates were 49% for immature individuals. The hepatosomatic index also demonstrated an effect of sex, as in all sites females were found to have a higher HSI, possibly indicating different lipid storage pathways between the sexes, or bigger organs overall (liver and gonads; Lloret *et al.*2002). Growth rates were however significantly higher ($P<0.05$) in females than in males in Lough Scur only, likely due to a highly skewed sex ratio (15 females to 8 males). In his cross-continental meta-analysis, Rypel (2012) concluded that sexual differences in pike growth were not significant, a conclusion that is supported here.

HSI was found to increase throughout the lifetime of the fish, indicating that these populations are healthy and do not seem to have been subject to major impacts affecting their ability to grow and/or store lipids. Comparisons of the rate of increase in HSI with length illustrated that lotic habitats such as rivers and canals did not differ from one another, however lakes values were not only significantly different from rivers and canals, but also often significantly different from one another. Essentially, lakes are more variable in their structure (size, depth, available habitat, water retention times, geology, etc) and thus a wider range of behaviours, including predation and activity levels may be required in order to deal with such variation. In fact, the site with the lowest average HSI level, and the only lake value that fell below the lotic values, was the smallest of the studied lakes (Lough Scur), perhaps reflecting that pike have to expend more energy being competitive in this smaller, potentially resource-limited habitat.

Trophic polymorphism was not indicated using stomach content data, as shape variation was uncorrelated with prey choice. However, both $\delta^{15}N$ and $\delta^{13}C$ stable isotope values were significantly correlated with morphology, illustrating that those with differing isotopic values are also likely to differ morphologically. This may indicate that increasing isotopic ratios, which represent an increased propensity for piscivory, are reflected in concomitant changes in predator shape.

Stable isotope values for these populations were previously demonstrated to increase with length (Pedreschi *et al.* 2014b), illustrating an ontogenetic change in pike feeding as they move from eating invertebrates to fish. However, as both SIA and HSI values continue to increase throughout their lifetime, this may indicate that as they grow they are able to become more choosy, to select prey with a higher reward / return on investment, as bigger fish are more competitive as they are less likely to become prey themselves, and the risk of having their prey stolen by competitors becomes greatly reduced (Robinson and Wilson 1998). Morphology also strongly correlated with both of these indices, indicating that as pike grow and diet changes, the equipment used to deal with it also changes.

To the best of our knowledge, this study represents the first investigation using geometric morphometric analysis to investigate ecologically influenced polymorphisms in this species. Despite research focussing on pike gape width and prey morphology, little attention has been paid to questions relating to variation and potential ecological determinants of pike overall shape. This research indicates that for pike, certainly within the Irish setting, environment is more of a determinant of morphology than prey choice. Significant differences were not found in the feeding habits of pike in Irish lake, river and canal habitats (Pedreschi *et al.* 2014b), a finding that sits well with many previous studies that have similarly found that, despite the specialised predatory morphology of pike, an opportunistic - generalist model suits best (e.g. Chapman *et al.* 1989; Adams 1991; Skov *et al.* 2003; Paradis *et al.* 2008). However, pike jaw and gape widths are perhaps the most likely candidates to be correlated with prey size or type (Hart & Hamrin 1988; Adams & Huntingford 2002b). Accurate measurements of gape width are difficult, which has led to the use of experimentally derived maximum ingestible prey depths to estimate gape-size limits (Nilsson & Brönmark 2000). The traditional lateral view morphometrics used here did not detect variation related to gape size, despite the inclusion of many head-based landmarks, however it is hypothesised that due to the duck-billed nature of pike, modern morphometric approaches examining pike heads in 3-dimensions may be more informative.

CONCLUSION

In contrast to the vast majority of studies that focus on either lentic or lotic habitats, or divisions within them, the present study has compared and contrasted *between* them. Rypel (2012) highlighted the low representation of riverine studies in the pike literature, and called for more research. This study has addressed morphology, longevity, growth and condition, along with their inter-relationships and compared across lake, river and canal habitats. These data should prove informative to managers, particularly in relation to translocation operations; pike adapted to lotic waters may not fare so well if relocated to lake habitats, and vice versa. Furthermore, this project has addressed research gaps in the understudied lotic pike populations and succeeded in identifying key ecological polymorphisms that may become important under stressed conditions. In the face of uncertainty due to global climate change, increased extreme weather events and continued anthropogenic impacts and extraction, these differences may reflect underlying plasticity essential to the adaptability and survival of the species.

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