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The Diet of Pike in Irish Watercourses

Layman's Report

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Trophic flexibility and diet of pike (Esox lucius L.) in Ireland

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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*) in Ireland, a historically understudied species in the Irish context. This represents the second report from this project which deals with the diet and trophic ecology of pike in Ireland. The main aims of this investigation were to elucidate the variation in the diet of Irish pike between river, lake and canal habitats. Furthermore we aimed to quantify niche size and dietary specialisation and attempt to identify the timing of the switch to a piscivorous diet. A previous report on the genetics of pike in Ireland is available here: http://www.fisheriesireland.ie/Press-releases/new-study-reveals-pike-native-to-ireland.html; and a third and final report comparing life history and morphology (the study of form and structure in relation to function) of pike between these habitat types will follow shortly.

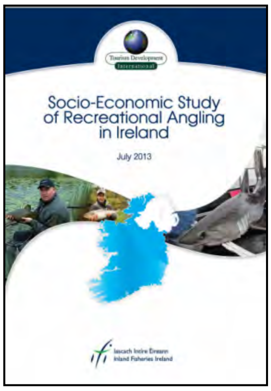
The field work and sampling for this project was carried out predominantly opportunistically in collaboration with Inland Fisheries Ireland. This study has been generously funded by Inland Fisheries Ireland, with contributions from the Irish Federation of Pike Angling Clubs.

INTRODUCTION

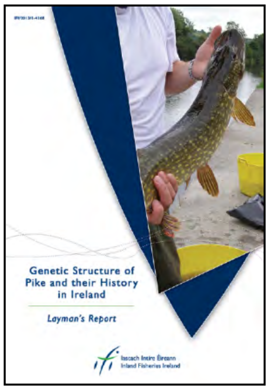
Northern pike *(Esox lucius*) are known for their voracious feeding behaviour, distinctive morphology (broad, flattened 'duck-billed' snout, large mouth, large teeth, heavy jaws)

and their sit-and-wait ambush predatory behaviour, seemingly specialised for capturing fish prey (Beaudoin *et al*. 1999; Venturelli & Tonn 2006). These observations have led to the assumption that pike are a specialist piscivore (fish-eater) with a low flexibility diet (Chapman *et al*. 1989; Grande *et al*. 2004). However, despite their morphology (shape) and the known advantages of piscivory for growth (piscivorous fish can grow bigger faster), multiple studies have shown that an opportunistic/generalist predator model suits this species best (e.g. Chapman *et al*. 1989; Adams 1991; Domínguez & Pena 2000; Paradis *et al*. 2008). This is further supported by the wide range of fish, macroinvertebrate, and even non-fish species such as waterfowl, snakes, frogs, mice, shrews, duck eggs, blackbirds, larval newts, and even bald eagle chicks that have been reported from the stomachs of pike worldwide. As such, pike present an interesting species in which to study dietary habits.

Historically, pike were thought to have been introduced to Ireland by man around the 1600s (Went 1950,1957; Kennedy 1969; Fitzmaurice 1984; King *et al*. 2011). This misconception, coupled with a reported dietary preference for the important angling species brown trout, *Salmo trutta* (IFT Annual Reports 1952-1980; King *et al*. 2011), led to management policies such as the removal of pike from lakes and rivers designated as 'trout waters' by Inland Fisheries Ireland (IFI; formerly Inland Fisheries Trust (IFT)), primarily in an attempt to protect brown trout from pike predation (IFT annual reports 1952-1980; Bracken 1973; O'Grady 1981, 1982; Minchin 2007; O'Grady & Delanty 2008). Beginning in the early 1950s, these operations removed approximately 36,000 pike from Irish lakes and rivers per annum (1952-1972; IFT Reports), however, these practices have been much



reduced in recent years. Today, pike angling is valued at €150 - €187 million to the Irish economy each year (IFI 2013). Recently, Pedreschi *et al.* (2013) concluded that pike may have colonised Ireland naturally after the last glaciation, calling into question many assumptions associated with this species.



Many studies from 1950-1970 (Healy 1956; Kennedy 1969; Bracken 1973) compare pike consumption of trout to their consumption of perch (*Perca fluviatilis,* L.). However, today we are dealing with very different systems to those of half a century ago; the recent introduction of multiple invasive species (e.g. *Lagarosiphon major*, *Dreissena polymorpha*, *Corbicula fluminea*) into waterbodies around Ireland, along with the continued expansion and proliferation of introduced fish species, such as roach (*Rutilus rutilus*), throughout Irish freshwater systems has likely contributed to altering food webs and hence the prey availability and preferences of predators such as pike. These changing systems highlight the need for continued monitoring and updated data in order to inform effective management strategies.

Freshwater systems are also subject to many anthropogenic pressures. These, coupled with anticipated impacts due to climate change (e.g. rising water temperatures, increased flooding events), make it imperative that we understand the capabilities of freshwater species to adapt, for instance to fluctuations in food availability, in order to predict how they may respond in the future (Graham & Harrod 2009).

Pike are a circumpolar species, found in freshwater systems ranging from small streams to major lakes, and even in

In ecology, **trophic** refers to anything that relates to feeding and nutrition. The **trophic level** of an organism is the position it occupies in a food chain. The term **trophic position** is used instead of trophic level when multiple measurements, such as those taken using stable isotope analysis are used to determine the location of a species in a food web.

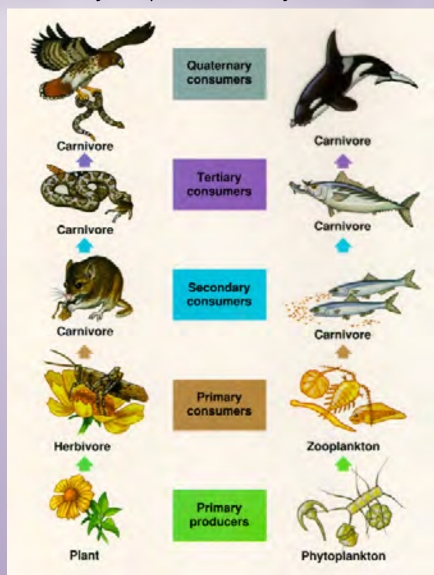


Image taken from http://belizesharks.org/2012/02/marine-trophic-levels-balance/

some brackish coastal waters (Chapman *et al*. 1989; Nilsson & Brönmark 1999; Venturelli & Tonn 2006). As a top down keystone predator, pike have had to adapt to a multitude of different environments and prey resources, and their feeding activity has been shown to alter the fish community, benthic (bottom dwelling) fauna and hence the entire ecosystem in which they reside (Chapman *et al*. 1989; Domínguez & Pena 2000; Sepulveda *et al*. 2013). As such, understanding dietary habits and **trophic** relationships is essential for effective fisheries management.

Stomach content analysis (SCA) is a useful tool that allows researchers to study species diets, enabling fine scale species identification that often is not possible from other methods. However, SCA results provide only a snapshot of what has been ingested directly before sampling, thus all prey types may not be observed. Investigating stomach contents can be problematic in piscivorous species, as it can be difficult to identify partially digested remains, and piscivorous species can often have empty stomachs which are uninformative.

This study investigates the diet and potential specialisations of pike by using **stable isotope analysis**, in order to determine its **trophic position**, and **stomach content analysis** to identify prey species and diet differentiation between three habitat types (lake, river, canal), something which has never before been investigated for this species. Furthermore we also address the degree of diet specialisation (invertivore vs. piscivore) both within and between populations, and aim to pinpoint the size and age of the ontogenetic switch to piscivory.

Elements can exist in multiple forms, known as **isotopes**. Isotopes vary in mass due to differences in their structure. These differences can be measured, resulting in **stable isotope analysis (SIA)**. Stable isotope analysis is based on the principle 'you are what you eat' as stable isotopes are incorporated into an animal's tissue throughout its life, through its diet. By tracing these isotopes, we can understand the links between species in food webs over time. Two main isotopes are used, those of **carbon** (^{13}C) and those of **nitrogen** (^{15}N). ^{13}C provides information on the source of carbon at the base of the food web [i.e. **littoral** (near shore) vs. **pelagic** (offshore) energy production] whereas ^{15}N is consistently enriched in organisms up through the food web, typically by 3.4‰ (+/−1‰) relative to its diet allowing us to view trophic position like the steps up a ladder. SIA provides information on the 'average' diet, over a longer term period than SCA, along with what is actually assimilated, rather than just ingested.

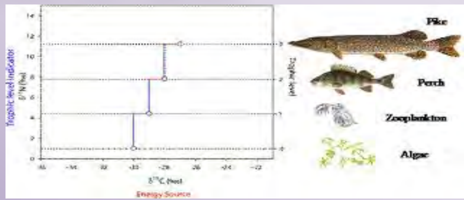


Image from: http://www.windermere-science.org.uk/use-stable-isotopes-within-project

METHODS

Sampling

Pike were sampled from 8 locations (3 rivers, 3 lakes and 2 canals; Table 1, Figure 1) between October 2010 and October 2012, using a combination of electrofishing (rivers and canals) and gill-netting (lakes) with one of each site type being resampled the following year. A range of habitat sizes were selected in order to characterise the diet across as wide a range as possible, and to encompass variations in site type within each category. Gill-netting and electrofishing were carried out opportunistically in collaboration with Inland Fisheries Ireland during their routine surveys. Fish were frozen upon return to the laboratory until analysis.

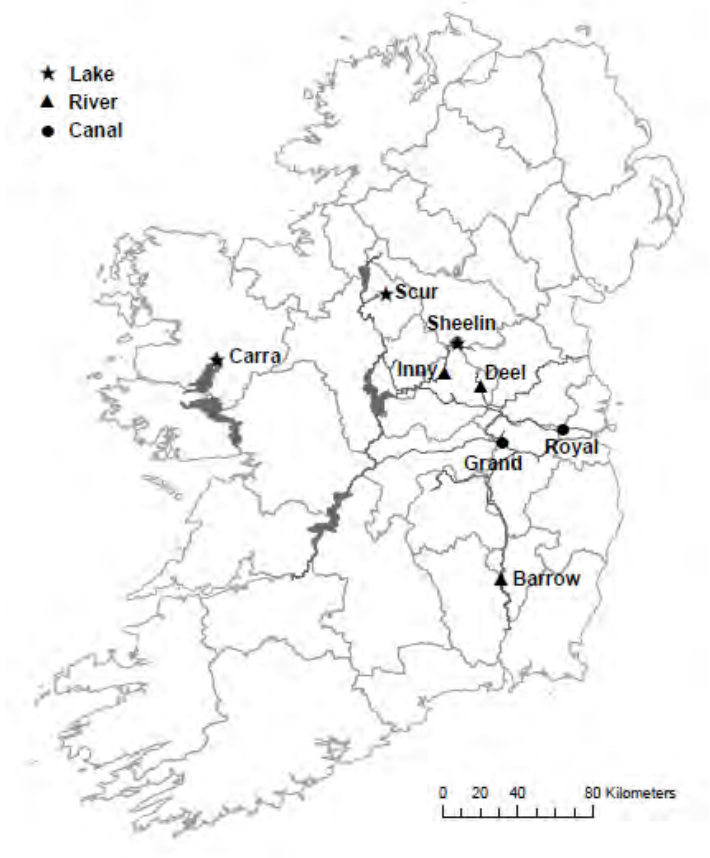


Figure 1. Pike sampling site locations around Ireland.

Table 1: Mean, maximum and minimum values for pike from each sampling site, including number of samples, length and age. N values reflect number of individual stomachs examined (SCA), or number from each population subject to stable isotope analysis (SIA).

Type	Site	Year	N		Fork Length			Age		
			SCA	SIA	Mean	Min	Max	Mean	Min	Max
Lake	Scur	2010	25	25	52.1	19	86.5	5.1	1	10
	Carra	2011	30	30	41.9	31.6	58	3.8	3	6
	Sheelin	2011	51	30	53.6	27.6	104.4	3.9	2	10
	Sheelin	2012	50	35	43.1	29.9	100	5	2	10
River	Barrow	2011	50	30	38.1	16.1	79.6	2.6	0	7
	Inny	2011	36	30	39.9	15.4	83.8	3	1	9
	Deel	2011	35	35	32.9	3.6	78	2.9	0	7
	Deel	2012	35	30	38.5	9.2	65.8	3.5	0	6
Canal	Grand	2010	31	30	33.9	12	74	3.6	0	6
	Royal	2011	33	31	25.7	9.7	69.8	1.9	0	6
	Royal	2012	40	30	35.4	10	78	2.6	0	7

Aging was performed through scale reading (Figure 2): annual checks were recorded as the point where circuli became discontinuous and irregular, sometimes forming a chaining pattern, usually followed by a hyaline area (Schneider 2001).

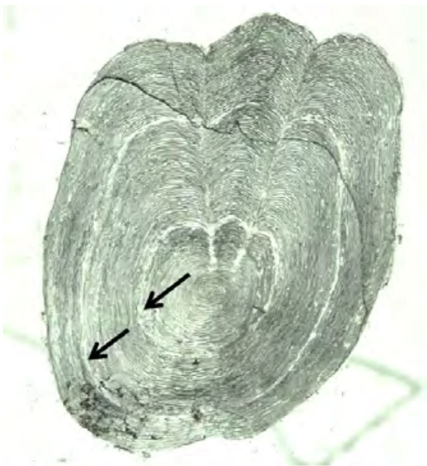


Figure 2. Pike scale or a 2+ fish showing annuli used for aging. Annual checks were recorded as the point where circuli became discontinuous/cut over and irregular, sometimes forming a chaining pattern, usually followed by a hyaline area (Schneider 2001).

Table 2: Fish sampled from each site.

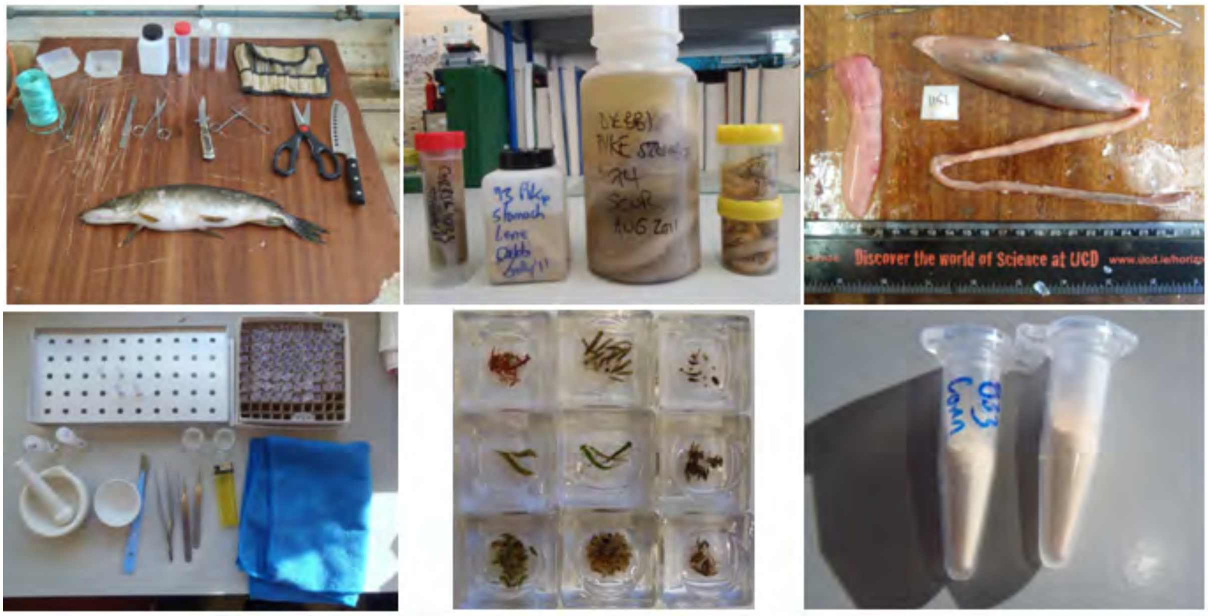
Type	Site	Year	Fish	
Lake	Scur	2010	Bream Perch Pike	Ro x Br Hybrid Roach
	Carra	2011	Perch Pike	3-spine stickleback 9-spine stickleback
	Sheelin	2011	Pike	
	Sheelin	2012	Hybrid Minnow Perch	Pike Roach Trout
River	Barrow	2011	Dace Eel Gudgeon Lamprey 3-spine stickleback	Perch Pike Roach Trout
	Inny	2011	Eel Hybrid Perch Pike	Roach Stone loach Trout Unidentified fish larvae
	Deel	2011	Perch Pike Roach	Trout 3-spine stickleback
	Deel	2012	Perch Pike	Roach 9-spine stickleback
Canal	Grand	2010	Pike Minnow	Perch Tench
	Royal	2011	Pike Minnow Perch	Roach Tench

The **benthic** zone is the ecological region at the lowest level of a body of water, including the sediment surface and some sub-surface layers. The **littoral zone** occurs on the edge of large lakes and rivers, where sunlight penetrates all the way to the sediment and allows aquatic plants (macrophytes) to grow. The pelagic zone is the open water area in which light does not penetrate to the bottom, hence food webs are dependent upon phytoplankton.

	Royal	**2012**	Pike Minnow Perch	Roach Tench

Between 25 and 50 individual pike were randomly sampled from each site, covering the full size range encountered (Table 1), along with up to three of each other fish species encountered where possible (Table 2). A variety of **benthic** invertebrates were sampled using kick netting in a range of habitat types (e.g. rocky, vegetated, sandy/silt) to provide average baseline ^{13}C & ^{15}N values that allow comparisons between sampling sites (Table 2). Gastropods (snails) and bivalves (filterers) have been found to be particularly useful to typify the differences in δ^{13}C and δ^{15}N between **littoral** and **pelagic** food webs (Vander Zanden & Rasmussen 1999; Post *et al*. 2000; Post 2002) and so were used here.

Stomachs were removed and preserved. Prey species from the stomachs were identified visually, and confirmed by microscopic examination (e.g. invertebrates, fish scales). White muscle tissue was removed from the flank of the fish species for stable isotope analysis.



RESULTS

STOMACH CONTENT ANALYSIS

A plethora of methods exist for the analysis of stomach contents (gravimetric, volumetric, frequency of occurrence, points, etc). Here, the compound % Index of Relative Importance (%IRI) (IRI=(Number+Weight)*Occurrence) was employed as a descriptive measure for each site (Table 3) to avoid individual method biases and provide an indication as to item importance (Cortés 1997). Overall, roach and *Asellus* were the most important items according to the Index of Relative Importance (Table 3). Roach and perch were eaten in all environments in which they occur (roach are not known to be present in Lough Carra), except for perch in the River Deel in 2011. Pike occurred in four stomach samples, but were only of any importance in the River Deel in 2012 (23% IRI). Trout were encountered in five sites (9 stomachs), and were only important in Lough Sheelin in 2011 (17% IRI), where despite a low occurrence rate of only 7%, their weight contribution to the diet was 48%. This was primarily due to two large relatively undigested trout, highlighting the bias when using only stomach contents. Minnow (*Phoxinus phoxinus*), and 9-spine sticklebacks (*Pungitius pungitius*), were important in some sites, but overall accounted for just 3% IRI each. Other fish species such as bream (*Abramis brama*), tench (*Tinca tinca*), stoneloach (*Barbatula barbatula*), gudgeon (*Gobio gobio*), eel (*Anguilla anguilla*) and lamprey (Petromyzonidae) appear to have been eaten only opportunistically. Together, the invertebrates accounted for 45.5% of all stomach contents. A wide range of invertebrates remained important in the diet throughout life at most sites, with the bulk being accounted for by *Asellus* (25%) and *Gammarus* (9%). In fact in all sites bar Lough Scur, River Inny and the Grand Canal, invertebrates accounted for over half of the diet (Table 3).

Table 3. Pike diet as reflected in the %IRI analysis of stomach contents. Percentages <1 are not shown for site data. Key: PIK =Pike, TRO=Trout, ROA=Roach, PER=Perch, 9SP=9-spine stickleback, 3SP=3-spine stickleback, MIN=Minnow, GUD=Gudgeon, STO=Stone Loach, BRE=Bream, TEN=Tench, DAC=Dace, LAM=Lamprey, ASE =Asellidae, GAM = Gammaridae; ANN=Annelid, ZYG=Zygoptera, TRI=Trichoptera, EPH=Ephemeridae, COR=Corixidae, SIA=Sialidae, CHI=Chironomidae; MOL=Mollusc, BIV=Bivalve, GYR=Gyrinidae, CRA=Crayfish, FR=Frog, UNID=Unidentified.

		Canal			River				Lake				Total
		Grand	Royal 11	Royal 12	Barrow	Inny	Deel 11	Deel 12	Scur	Carra	Sheelin 11	Sheelin 12	
Fish	PIK							23		1			2
	TRO						1				17		3
	ROA	61	29	33	4	92	1	2	86		2	20	25
	PER	17		9	16			12	4		13	5	10
	9SP								9		1	8	3
	3SP									1			0.4
	MIN	1	12		1			1					3
	GUD						1						0.1
	STO						2	2					1
	BRE												0.4
	TEN	5											0.4
	DAC				23								2
	LAM										1		0.1
Invertebrates	ASE	7	58	58	51	5	89	11		37	56	29	25
	GAM			1		1	3	34	1	45	4	34	9
	ANN							1		0			1
	ZYG	8						7		0			2
	TRI							5					1
	EPH						5				4		2
	COR												0.2
	SIA									0			1
	CHI									0			1
	MOL				1			1		1		3	2
	BIV												0.3
	GYR							1		1			1
Other	CRA				1			1					0.2
	FRO				4	2				13	2		4
	UNID						1	1					0.3

Stable Isotope Analysis

Invertivorous and piscivorous pike had differing isotopic values in both of the canals (Royal and Grand) and in the River Inny, possibly reflecting ontogenetic resource partitioning (see later). However, all other sites did not demonstrate a clear isotopic difference between pike with invertebrates and those with fish in their stomachs, likely reflecting opportunism in these habitats. Details of trophic positions and numbers of empty stomachs encountered can be found in Table 3.

Computer modelling methods were unable to pick out specific individual items as being of primary importance in the diet of pike. Instead, all resources appeared to be utilised to some degree, and individually important items were hard to identify.

Table 4: Mean (and standard deviation) of trophic position values, and number and percent of empty stomachs encountered per site.

Type	Site	Year	Trophic Position (±SD)	Empty stomachs	
				No.	%
Lake	Scur	2010	3.6 (0.2)	13	52
	Carra	2011	3.7 (0.2)	7	23
	Sheelin	2011	3.8 (0.2)	17	33
	Sheelin	2012	3.9 (0.1)	7	14
River	Barrow	2011	3.8 (0.2)	10	20
	Inny	2011	4.0 (0.2)	10	28
	Deel	2011	3.8 (0.3)	8	23
	Deel	2012	3.5 (0.4)	6	17
Canal	Grand	2010	3.8 (0.2)	10	32
	Royal	2011	3.2 (0.3)	5	15
	Royal	2012	3.1 (0.3)	13	33

Habitat and Site Effects

Statistical analysis of SIA and SCA did not detect consistent differences between rivers, lakes and canal habitat types, instead variation among sites was too great. Differences in the degree of consumption of roach, *Asellus* and perch (in that order) were primarily responsible for diet differences between found between sites.

Inter-Annual Variation

Using SCA, Lough Sheelin and the River Deel were found to be different year on year, but the Royal Canal was not. This is unsurprising as stomach content data represent only a snapshot in time. Using stable isotope analysis, differences between years were also found, however, as illustrated in Figure 5 these differences were very small.

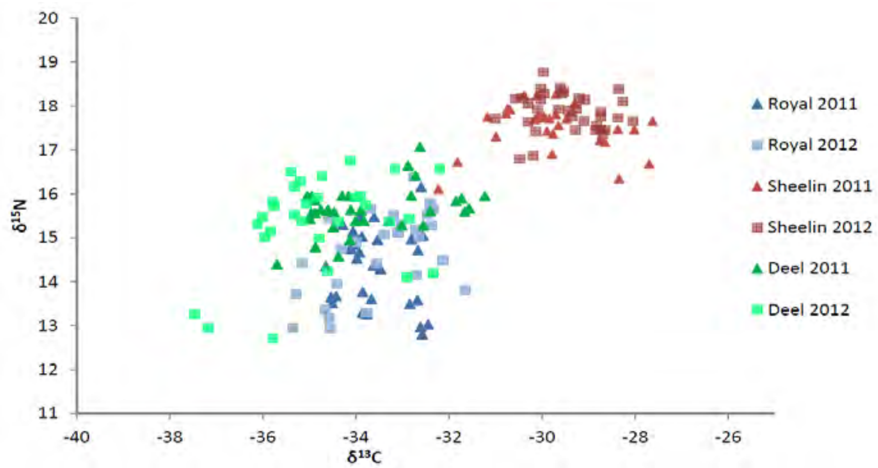


Figure 5: Scatterplot of $\delta^{15}N$ and $\delta^{13}C$ values for Lough Sheelin, River Deel and the Royal Canal for years 2011 and 2012.

Specialisation

Average individual specialisation (IS) values and dietary overlap values calculated from the stomach contents were low, indicating low dietary overlap, i.e. pike within each population were not eating the same things as one another.

Computer analysis using 'SIBER' created ellipses which revealed varying isotopic niche sizes between sites, which can be seen in Figure 6. Natural sites (rivers, lakes) presented a relatively wider range in carbon values (x-axis) than man-made canal sites. The Grand Canal and Lough Sheelin 2012 had significantly smaller dietary breadths than many of the other sites. The River Deel sample in 2012 had the largest isotopic niche, and was significantly different in size to all sites bar the River Inny and River Barrow, which had the next largest values. The Royal Canal niche size was not significantly different year on year, but the River Deel and Lough Sheelin niches were.

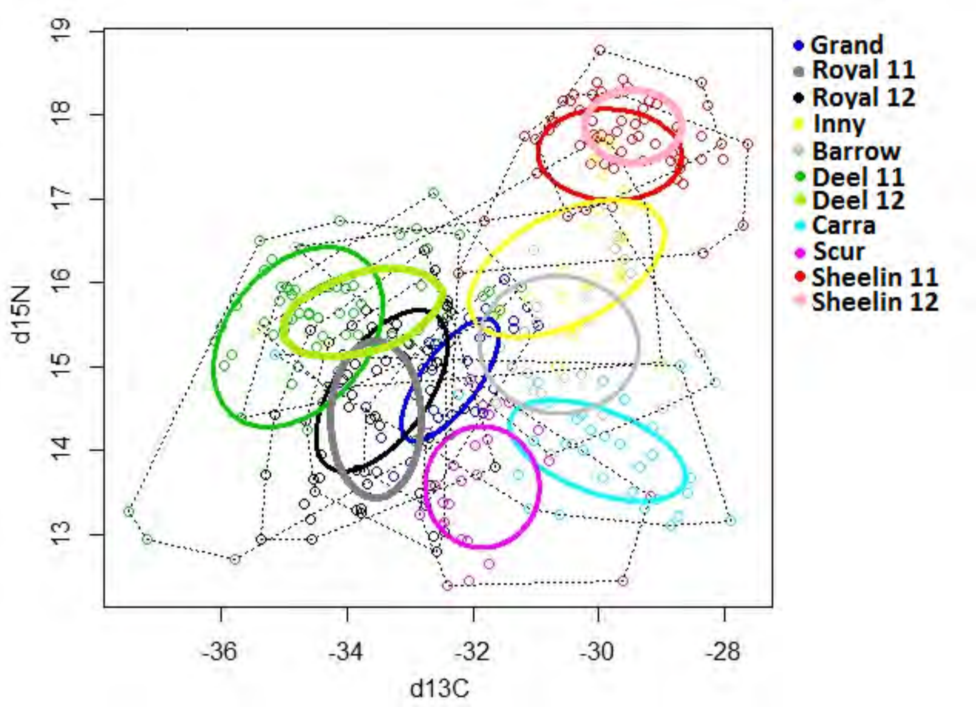


Figure 6: Isotopic niches: Bayesian standard ellipses (coloured circles) and traditional convex hulls (dotted lines) as calculated using SIBER (Jackson *et al.* 2011) for each population.

Sex

There were no significant differences observed between male and female diets. Stage of maturation was found however to have an effect on stable isotope values with significant differences between mature and immature individuals being observed at all river and canal sites. These differences were not observed in the lake populations, most likely due to the bias caused by using gill nets in lakes (fewer immature individuals are caught).

Environmental Factors

Analysis was carried out to investigate if the species found in the stomachs were related to the species abundances in the environment. The species abundance information was only available for the River Barrow, Lough Scur, and the Grand & Royal Canals, and so analyses were only carried out for these sites. A strong relationship was found for all sites (River Barrow, Grand & Royal Canals) except Lough Scur (Figure 7).

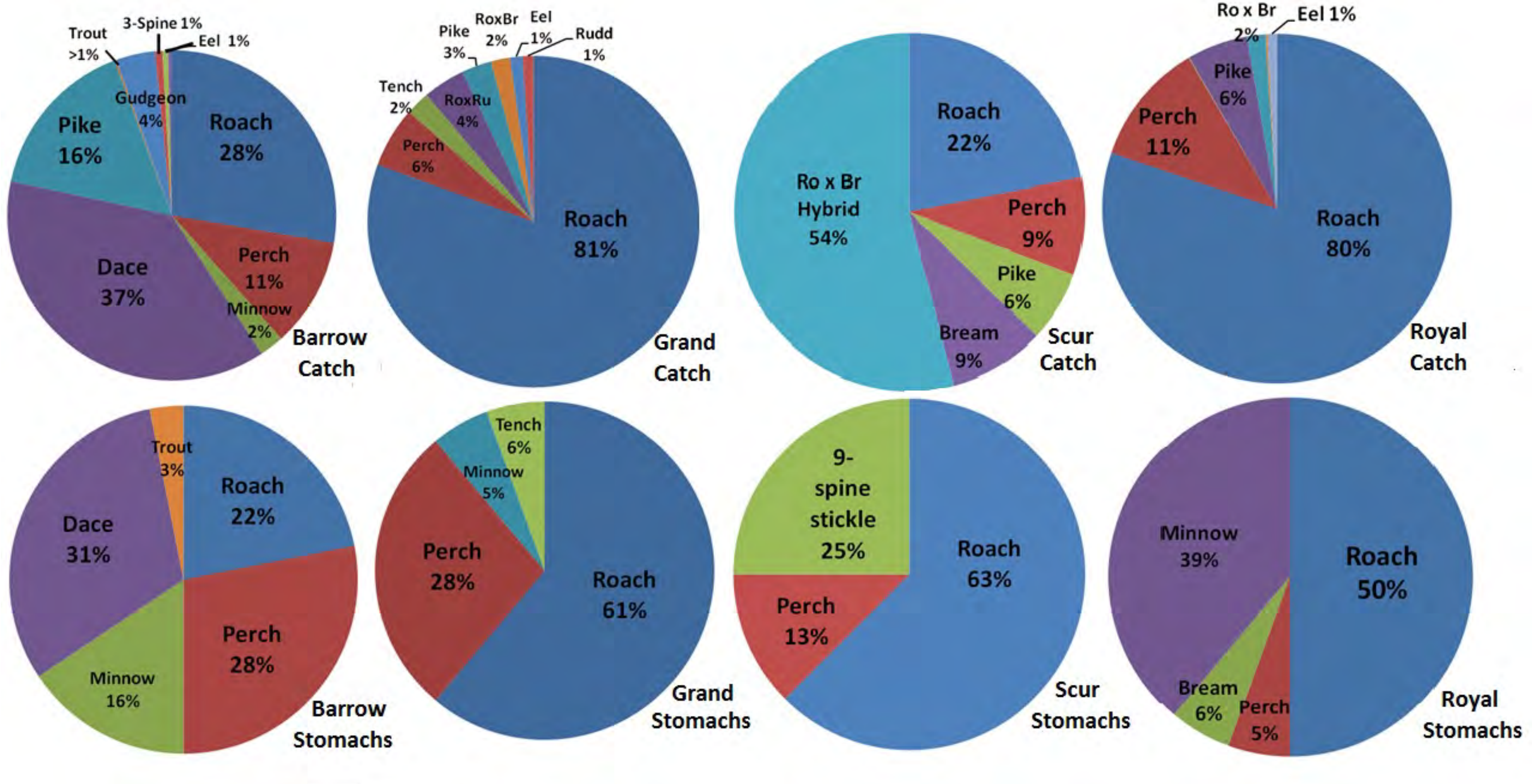


Figure 7. Prey species percent relative abundance from catch data (upper) and pike diet stomach content data (lower). Overall diet proportions follow the general trends found in the environment. Exceptions occur in relation to species such as sticklebacks and minnow that are generally under sampled due to their small size. Differences occur in Lough Scur in relation to Bream and Roach x Bream Hybrids, likely related to differences in morphology (see Discussion).

ONTOGENETIC SWITCH

Ontogeny refers to the origin and the development of an organism. When used in relation to diet we mean the natural shift in diet from smaller, easier to catch organisms to larger, more profitable prey as the fish grows and develops.

Statistical examination revealed an increase in the number of fish in the diet, and a decrease in the number of invertebrates consumed with increasing fish size in the canals, and in all of the rivers, with the exception of the River Barrow, which had a missing size class (no individuals were obtained between 43.8cm and 52.5cm fork length). This effect was not observed in Lough Scur or Lough Sheelin in either year - likely due to the use of gill-nets for sampling in lakes, which generally miss smaller individuals (≤35cm). However, a decrease in the importance of invertebrates was observed in Lough Sheelin in both years, indicating that the smallest size ranges sampled here were in the process of switching and progressively eating fewer invertebrates. Lough Carra reflected the trends seen in the rivers and canals, likely due to the fact that despite gill-netting size bias, pike in this lake continue to eat a high proportion of invertebrates and other resources such as frogs throughout life, as the fish biodiversity in this lake is particularly depauperate (Kelly *et al*. 2012), likely leading to a situation where only very large individuals are able to eat a high proportion of fish. This is also illustrated by the fact that invertebrates account for over 97% of the diet according to IRI (Table 3), however, it should be noted that these pike were sampled during spawning season and were making use of the seasonal abundance of frogs.

No consistent increases in the number of empty stomachs with fork length were found (Table 4). This is interesting as the number of empty stomachs are thought to be correlated with piscivory (a piscivorous fish needs to eat less often and so stomachs are empty more often).

Isotopic values were also investigated in relation to length, to detect ontogenetic changes in trophic position. Both carbon and nitrogen values varied with length, generally illustrating an increase in values with size.

DISCUSSION

HABITAT EFFECTS

Both stomach content analysis and stable isotope analysis revealed that *among site* differences were responsible for a much greater proportion of the variability observed than any differences dictated by habitat type. In fact, there were no consistent patterns discerned between any of the habitat types examined. SCA analysis seemed to indicate that canals are somewhat of a more 'consistent' habitat type as they were not significantly differentiated using stomach content analysis, nor was the Royal Canal found to be different across years. However, this was not supported by SIA analysis. Essentially, comparisons between waterbodies revealed that inherent local variation overrides habitat differences.

DIET & TROPHIC VARIATION

As expected, pike do engage in piscivory, with roach and perch being by far the most important prey species across all sites, and within each site, with the exception of Lough Sheelin in 2011 and the River Deel in 2012, where trout and pike respectively, constituted the largest fish proportion of the diet. Contrary to the expected (Kennedy 1969; O'Grady & Delanty 2008), trout made up a small proportion of the overall diet, with predation levels being similar to pike cannibalism levels. This likely reflects the relatively low numbers of trout captured in the sites sampled.

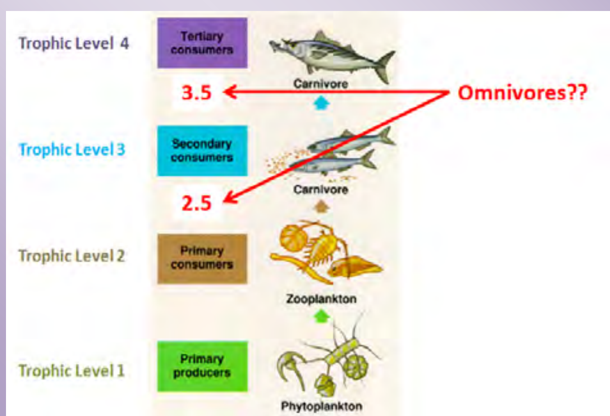
It is generally acknowledged in the scientific literature that pike prey primarily upon fish once a length of **>10cm** has been attained (Frost 1954; Mittelback & Persson 1998; Beaudoin *et al.* 1999). In Ireland however, Healy (1956) stated that pike have a preference for fish when **>55cm** length, and noted that in two of the three lakes she examined, pike ate more trout than perch. This may have been due to the greater natural defences of perch (i.e. tough skin and hard spiny fin rays). More recently, O'Grady & Delanty (2008) have also highlighted the piscivorous habits of pike **>60cm**, which is further supported here, and described a preference of pike for eating trout in Lough Sheelin. As a 60cm fish in Ireland is estimated to be 5-6 years old (O'Grady and Delanty 2008), and as relatively few fish have been found to live beyond 6 years in Irish waters (Healy 1956; O'Grady & Delanty 2008), the impact of pike on brown trout may not be as drastic as previously feared, as it seems few individuals reach an age / size suitable for predating primarily on trout. The present study suggests that since the invasion of roach throughout Irish waterways, particularly since the 1970s (IFT Reports; King *et al*. 2011), a certain amount of predation pressure on trout in may have been alleviated. However, continued monitoring is essential for management purposes, as pike may predate more heavily on trout if roach stocks collapse, which can happen with the introduction of invasive mussels and clams.

A much higher degree of invertivory was found than expected from the literature. A division between invertivorous and piscivorous individuals such as that seen by Beaudoin *et al*. (1999) was observed in some sites (canals and River Inny), but here was attributed to size effects (ontogenetic switch). In other sites, individuals were observed with both invertebrates and fish in their stomachs, this, in conjunction with the isotopic values indicates opportunism rather than consistent differing dietary strategies. It is possible that the canals, being artificial habitats, present a more limited environment in which competition within the species may be higher, and as such, size related competition is stronger (bigger fish can access more profitable prey as they can out-compete smaller individuals).

Invertivory was observed at all sites with >50% of the diet accounted for by invertebrates in five out of the eight sites examined, consistent across years. It has previously been suggested that eating invertebrates is purely a survival strategy to deal with suboptimal conditions, however substantial impacts were not apparent at the study sites and prey items appeared plentiful. Other studies have also found invertivory to occur even when fish prey are seemingly plentiful (Chapman *et al*. 1989; Venturelli & Tonn 2005, 2006; Paradis *et al*. 2008). It may be that the high success rate of foraging on slow-moving benthic insects compensates for the greater number of prey items required (Chapman & Mackay 1990).

All trophic values calculated fell between 3.1-4.0 – effectively indicating the same trophic level, with some degree of omnivory (Post

Trophic levels are rarely as nice and neat as depicted graphically. As many species are omnivores, they often don't fit into the strict categories as they are described conceptually. Instead, a continuum between trophic levels exists.



2002; Vander Zanden *et al*. 1997, 1999). Furthermore, trophic level values for all sites with the exception of the Royal Canal fell between 3.5-4.0, lower than expected for a top predator if it eats only fish, but consistent with other studies of the species (Vander Zanden *et al*. 1997). The Royal Canal had a consistently high proportion of *Asellus* in the diet each year (SCA: 58% IRI), which may illustrate a local adaptation, as this was also reflected in the lower trophic position (TP= 3.1-3.2).

Ontogenetic switch

All parameters investigated with length gave support to an ontogenetic dietary change. An increase in the proportion of fish, and a decrease in the amount of invertebrates was indicated by SCA. Similarly, an increase in $\delta^{15}N$ with length was found in all sites except Lough Sheelin in 2011. There was no increase in the proportion of empty stomachs, which may be due to the tendency of these populations to increase the amount of fish in the diet, but not to the exclusion of invertebrates. Significant differences related to the onset of maturity (circa age 2; Healy 1956; Roche *et al*. 1999; O'Grady & Delanty 2008) lend support to years 2-3 as the age where the diet makes its most dramatic change.

Specialisation

The degree of dietary specialisation within a species will vary according to a range of factors such as abundance, size and behaviour of prey, along with preference and phenotype of the predator (Gurtin 1996). Within this study $\delta^{15}N$ values often ranged across nearly a full trophic level within each population, indicating a that a wide prey base is used.

Specialisation and niche overlap values were low, further reflecting that individuals often ate different things from one another. Overall the data indicates a generalist population, and the marked opportunistic nature of individuals that appear to be utilising resources in proportion to their availability in the surrounding environment. The only site that did not present a strong correlation was Lough Scur, probably due to the high proportion of roach x bream hybrids present, which do not seem to be utilised as a food source by pike. This is likely due to the fact that roach x bream hybrids often have a deeper and more flattened body in comparison to roach (Nilsson & Brönmark 2000). Despite their predatory capabilities, pike are generally cautious in the type of prey they pursue, usually selecting the least risky option rather than the most profitable prey (Hart & Hamrin 1988; Nilsson &

Brönmark 1999, 2000). Handling time is very important to them as the risk of cannibalism can be high and as such pike tend to choose prey that are the easiest to manipulate and swallow, such as those with a more fusiform shape (e.g. roach instead of bream or hybrids) (Wahl & Stein 1988; Abrahams & Kattenfeld 1997; Robinson and Wilson 1998; Nilsson & Brönmark 1999).

CONCLUSIONS

An opportunistic feeding strategy is particularly advantageous in prey-limited temperate lakes (Chapman & Mackay 1990; Beaudoin *et al*. 1999; Domínguez & Pena 2000; Venturelli & Tonn 2005; 2006; Paradis *et al*. 2008). The present study has confirmed previous findings that pike are highly plastic in what they can utilise as a food source. This is important, as when conditions are limited in some way, they can ensure their survival through dietary flexibility (Frost 1954; Inskip 1982; Chapman *et al*. 1989). This flexibility is likely to have been a major factor in enabling them to adapt to a wide range of environments globally, and also enables them to adapt to perturbations through prey switching as certain species become more or less available throughout the year, or as species introductions occur (Frost 1954; Adams 1991; King *et al*. 2011); an extremely important attribute during these times of changing climate.

Overall it appears that, as a thoroughly efficient predator capable of dispatching any prey within its gape width, pike are inherently opportunistic, selecting only for more fusiform prey to minimise their own exposure risks when predating upon fish (Wahl & Stein 1988; Nilsson & Brönmark 1999; Domínguez & Pena 2000). This study has highlighted an unusual phenomenon in the delay of the ontogenetic dietary switch, widely reported to occur at lengths of 10-12cm (Frost 1954; Raat 1988 and references therein; Mittelback & Persson 1998). Within Ireland, stomach content data indicate that fish are more important in the diet from 40cm, and the primary food item after 60cm, however this is not clearly reflected in stable isotope values, instead a general increase in isotopic values is seen throughout life. It seems likely that as a consequence of the somewhat depaupaurate freshwater fish biodiversity, coupled with large numbers of invertebrate prey, Irish pike continue to prey on invertebrates (predominantly *Asellus* and *Gammarus*) throughout their lifetime.

This study has provided important baseline SIA information for this species in Ireland, and updated SCA data. Combined, these findings are particularly relevant in relation to the ongoing management activities, and the data from this study will contribute to policy management and plans. This research also serves to highlight the change in diet of a top predator with the introduction of an invasive species, in this case roach.

Research should continue to investigate stomach contents on a longer term sampling plan to see if they better reflect SIA values, and to build stronger estimates of individual specialisation and diet overlap. Sampling using a dedicated plan rather than opportunistic sampling would also facilitate a wider range of analyses and hypothesis testing, including for example, comparisons between seasonal variations in diet.

Managers need data on feeding habits, interactions and competition in order to gain a better insight into community dynamics and manage waterways as ecosystems rather than separate components. This study for the first time provides this information across lake, river and canal habitats, representing a cross-section freshwater ecosystem diversity, and inputting directly into the better conservation and management of this economically and ecologically important species.

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