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Long-term changes in the diet of pike (*Esox lucius*), the top aquatic predator in a changing Windermere

Ian J. Winfield, Janice M. Fletcher & J. Ben James

Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, U.K.

Correspondence: Ian J. Winfield, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, U.K. E-mail ijw@ceh.ac.uk.

Running head: Long-term changes in pike diet

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Summary

1. Pike (*Esox lucius*) is a key and flexible piscivore in many fresh waters of the northern temperate zone, but no previous studies have provided a continuous long-term perspective on its diet in response to changing environmental conditions. Here, we describe its winter diet from 1976 to 2009 in the North and South Basins of the lake of Windermere, U.K., where climate change, eutrophication and species introductions have combined to induce fundamental changes in the fish community.

2. A total of 6,637 adult pike (fork length 390 to 1090 mm) was examined and found to have consumed a total of 4,436 fish prey of which 98% of individuals identifiable to species comprised native Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), perch (*Perca fluviatilis*) and pike and non-native roach (*Rutilus rutilus*). Over the 34 year study period, the dietary importance of the salmonids Arctic charr and brown trout decreased, while that of the percid perch, the esocid pike and particularly the cyprinid roach increased. These changes were particularly marked in the more eutrophicated South Basin of the lake.

3. The above chronological trends in species-specific contributions to the diet composition of pike had considerable overall impacts. In the 1970s, pike diet composition was dominated by Arctic charr and brown trout which together comprised 94% of the diet. In contrast, in the 2000s these two species accounted for just 55% of the diet, with perch and roach now comprising 41%.

4. Recent changes observed in the Windermere fish community of a decrease in native salmonids and an increase in cyprinids are consistent with the generally expected effects of

climate change in the northern temperature zone. Here we have shown that they have led to corresponding changes in the diet composition of pike. In turn, this may have implications for lake food web structure through shortening food chain length from the primary producers to the top aquatic predator.

Introduction

The top aquatic predator in many fresh waters of the northern temperate zone is the pike (*Esox lucius* (L.)), which is frequently acknowledged to be a key species in the functioning of fish communities and entire lake ecosystems in both Europe (e.g. Sharma & Borgstrøm, 2008) and North America (e.g. Flinders & Bonar, 2008). In addition to this widespread ecological importance, this large-growing esocid piscivore is also frequently an important target species for recreational and commercial fisheries of considerable socio-economic value (Mann, 1996).

The principal mechanism through which pike exert an ecological impact is their feeding activities and so the lacustrine diet of this species has been extensively studied in the context of undisturbed fish communities (Frost, 1954; Diana, 1979; Sammons, Scalet & Neumann, 1994), as an introduced species (He & Wright, 1992; Flinders & Bonar, 2008; Dominguez & Pena, 2000) and to a lesser extent in response to introduced species (Adams, 1991). Other studies have shown that the pike is a remarkably flexible piscivore and is able to consume a diverse range of prey including salmonids, percids and cyprinids (Raat, 1988), to distribute itself within a lake in accordance with the ideal free distribution in response to changing conditions (Haugen *et al.*, 2006) and even to adapt rapidly to fishless conditions (Venturelli & Tonn, 2006). Conspicuous by its absence from such flexibility studies, and indeed from any other diet investigations, is a continuous long-term perspective on the diet of pike in response to changing environmental conditions such as eutrophication and climate change. Although a tolerance of relatively high temperatures with an upper incipient lethal temperature of approximately 29 °C means that directly lethal thermal effects of climate change are unlikely, pike growth could be affected by temperature shifts towards or away from lower optimum temperatures (Casselman, 1996). Furthermore, more indirect effects of such major environmental changes on pike could operate through long-term changes to their piscine prey populations, for which both eutrophication (Sarvala, Rask & Karjalainen, 2004) and climate (Casselman, 2002) effects are broadly taxon-specific.

The pike and other major fish populations of the lake of Windermere, U.K., have been studied extensively and continuously since 1944 as reviewed by Le Cren (2001). During this period, the lake's North and South Basins have experienced a significant increase and to some extent a recent decrease in eutrophication, particularly in the South Basin (Parker & Maberly, 2000). In addition, both basins have experienced a recent significant increase in water temperature (Winfield, Fletcher & James, 2008a). Towards the end of this same period, the abundance of the lake's native Arctic charr (*Salvelinus alpinus* (L.)) has declined while in contrast that of non-native roach (*Rutilus rutilus* (L.)) has increased, with both changes being greatest in the South Basin (Winfield *et al.*, 2008a). Concomitant with these changes in potential prey populations, there was an increase in pike catch-per-unit-effort in both basins during the mid 1980s in response to a lake-wide decrease in fishing pressure (Carlson *et al.*, 2007). From the late 1990s onwards, pike have been relatively more abundant and in relatively better individual condition in the North Basin than in the South

Basin, although since 2001 there has been an indication of a decline in both of these measurements in the North Basin (Winfield, James & Fletcher, 2008b). Prior to the present investigation, the only studies of the diet of pike in Windermere were conducted from 1933 to 1935 by Allen (1939) and from 1940 to 1953 by Frost (1954). Although these authors found that some pike fed to a limited extent on macroinvertebrates, fish dominated the diet and was composed primarily of Arctic charr, brown trout (*Salmo trutta* L.) and perch (*Perca fluviatilis* L.), with minnow (*Phoxinus phoxinus* (L.)) and three-spined stickleback (*Gasterosteus aculeatus* L.) taken to some extent and European eel (*Anguilla anguilla* (L.)) and pike very rarely consumed. Neither study found any roach in the diet, even though this cyprinid was first recorded in the lake in the late 1890s following its apparent introduction by anglers live-baiting for pike (Watson, 1899).

The objectives of the present study were to analyse pike diet data collected in both basins of Windermere during the early winter from 1976 to the present within the above long-term monitoring programme and to interpret these in relation to the contrasting basin-specific relative abundances of potential prey. Specifically, it was hypothesised that the importance of Arctic charr in the diet would decrease over the study period in both basins, particularly in the South Basin, while that of roach would increase, again particularly in the South Basin.

Methods

Study site

Windermere is situated (54° 22’ N, 2° 56’ W; altitude 39 m) in the English Lake District, U.K. It comprises a mesotrophic North Basin (surface area 8.1 km^2, maximum depth 64 m) and a eutrophic South Basin (surface area 6.7 km^2, maximum depth 44 m), although cultural eutrophication has impacted both parts of the lake (Parker & Maberly, 2000). The fish communities of the two basins are qualitatively similar and contain only seven species of numerical importance, i.e. Arctic charr, Atlantic salmon (*Salmo salar* L.), brown trout, European eel, perch, pike and in recent years roach, although at least a further nine minor species including common bream (*Abramis brama* (L.)), minnow and three-spined stickleback are also present (Pickering, 2001).

Pike diet

Pike have been monitored in the North and South Basins of Windermere by gill netting with significant variations in sampling sites and annual effort from 1944 to the present (see review by Le Cren (2001)). However, the gut contents of sampled individuals have only been consistently recorded from 1976 to the present and during this period the sampling methodology has been standardised as follows. Pike were sampled using 64 mm bar mesh multifilament gill nets, each 40 m in length and 3 m in height and set singly for 48 hours on the lake bottom between mid-October and late December of each year at depths of approximately 4-5 m at 10 sites in each of the North and South Basins (Fig. 1). Further sampling details are given in Winfield *et al.* (2008b). All pike taken in the nets were killed and taken to the laboratory for processing. Each individual was subjected to a number of measurements and observations not directly relevant to the present study and so not reported in full here (but for details see Winfield *et al.* (2008b)) before its gut contents were dissected, examined and all prey fish identified to species where possible. Non-fish prey were extremely rare and so are not considered further here. Due to the effects of digestion, the recording of prey length was not routinely possible and so these limited data are not presented here.

Trend detection

Transient behaviours within time series of diet descriptors were detected using cumulative *z*-score plots in which *z*-scores (standardised anomalies produced by dividing deviations from the long-term mean of the series under investigation by the long-term standard deviation) were smoothed by calculating their cumulative sums. Such plots indicate periods with predominantly positive or negative anomalies and so can be used to determine the approximate date of trend initiation.

Results

A total of 6,637 adult pike (fork length 390 to 1090 mm) was examined over the 34 year study period, with samples sizes per year and basin ranging from 24 to 227 individuals. These pike had consumed a total of 4,436 fish prey including 2,246 Arctic charr, 1 Atlantic salmon, 191 brown trout, 1 chub (*Leuciscus cephalus* (L.)), 1 common bream, 11 European eel, 8 herring (*Clupea harengus* L.), 5 mackerel (*Scomber scombrus* L.), 14 minnow, 399 perch, 35 pike, 2 rainbow trout (*Oncorhynchus mykiss* (Walbaum)), 326 roach, 19 three-spined stickleback and 1,177 fish individuals which could not be identified to species. The five species Arctic charr, brown trout, perch, pike and roach constituted 98% of identifiable fish consumed.

The prevalence of fish of any species in the diet of pike is shown as both its frequency of occurrence in the diet of the population and as the number of individuals consumed per individual pike in Fig. 2. For the latter, 5 pike sampled from the South Basin between 2002 and 2004 were excluded from the analysis as extreme outliers because they each contained approximately an order of magnitude more fish than all other pike. This resulted from them having foraged unusually and exclusively on underyearling fish and consumed respectively 50 roach, 120 roach, 24 roach, 19 perch and 3 roach, and 20 roach.

Frequency of occurrence of fish in the diets of pike ranged from 31 to 81% in the North Basin and from 25 to 71% in the South Basin, with values being consistently higher in the North than South Basin since 2002. Overall frequency of occurrence was 55% in the North Basin and 45% in the South Basin. The numbers of individuals per pike showed a similar inter-basin difference, with mean values per year ranging from 0.3 to 1.4 individuals per pike in the North Basin and from 0.2 to 1.0 individuals per pike in the South Basin. Both frequency of occurrence and mean numbers of individuals per pike showed erratic but weakly increasing trends over time, with cumulative *z*-score plots indentifying 1994 in the North Basin and 1995 in the South Basin as the years in which values began to show a consistent increase for the frequency of occurrence. For mean numbers of individuals per pike, the corresponding years were 1996 in the North Basin and 1997 in the South Basin.

The long-term trends of Arctic charr in the diets of pike from the North and South Basins showed both similarities and dissimilarities (Fig. 3a). The mean number of Arctic charr per pike showed no consistent difference between basins up to 1995 (higher in the North and South Basins for 10 and 10 years, respectively), but since that time it has almost always been higher in the North Basin (higher in the North and South Basins for 13 and 1 years, respectively) due to a combination of North Basin values increasing and particularly South Basin values decreasing. Cumulative *z*-score plots indicate that North Basin values began to display an erratic increase in 1996, while South Basin values began to show a more consistent decrease in 1999. In the South Basin, the numbers of Arctic charr recorded from 2006 to 2009 have been the three lowest on record, while corresponding values from the North Basin have been within the range of long-term variation. The abundance of brown trout in pike diet has always been much lower than that of Arctic charr, particularly in the South Basin (Fig. 3b). Even so it has still declined in both the North and South Basins, with cumulative *z*-score plots indicating a decline in the former since 1991 and in the latter since 1995.

In contrast, in recent years relatively more perch have been consumed by pike in both the North and South Basins with cumulative *z*-score plots indentifying 2001 and 1997, respectively, as the years when the increases became consistent (Fig. 4a). Note that in this analysis of consumed perch, 1 pike sampled from the South Basin in 2004 was excluded from the analysis for the reason explained above. Although pike have always been consumed relatively infrequently, in recent years the level of cannibalism has increased in both basins and particularly so in the South Basin (Fig. 4b). Cumulative *z*-score plots indicate that these increases became pronounced, although not consistent, in the North Basin in 2002 and consistent in the South Basin in 2001. Most notably, roach first appeared in the diet of pike in the South Basin in 1996 followed by its first occurrence in the North Basin in 2000 (Fig. 5). Note that in this analysis of consumed roach, 4 pike sampled from the South Basin between 2002 and 2004 were excluded from the analysis for the reason explained above. Cumulative *z*-scores have identified 2004 and 1998 as the years in which these marked increases became consistent in the North and South Basins, respectively. Subsequently, roach has almost always been markedly more abundant in the diet of pike from the South Basin.

The long-term impacts of the above chronological trends in species-specific contributions to the overall diet composition of pike are illustrated in Fig. 6, in which overall diet data are contrasted between the 1970s and the 2000s. In the 1970s, pike diet composition was dominated by Arctic charr and brown trout which together comprised 94% of the diet. In contrast, in the 2000s these two species accounted for just 55% of the diet, with perch and roach now comprising 41%. The three cyprinids roach, chub and common bream were recorded for the first time in the diet of pike in 1996, 2006 and 2007, respectively. The marine species herring and mackerel were not observed in the diet of pike during the 1970s, but single individuals of each species were first observed in 1999 followed by a further 7 herring and 4 mackerel from 2002 onwards.

Discussion

The diet of adult pike in Windermere has remained very consistent from the early part of the previous century (Allen, 1939), through its mid part (Frost, 1954), to the late 1970s of the present study. During this time, diet was composed primarily of Arctic charr, brown trout and perch, with minnow and three-spined stickleback of much lower prevalence and European eel and pike very rarely eaten. However, from the 1990s onwards a number of significant changes have occurred in the diets of pike in both basins of Windermere and have supported the hypothesis that the importance of Arctic charr in the diet would decrease over the study period in both basins, particularly in the South Basin, while that of roach would increase, again particularly in the South Basin, as a result of changes in population abundances.

The present more extensive diet examination has also recorded an additional seven fish species in the diet of pike in Windermere over the seven species previously noted by Allen (1939) and Frost (1954). Of these new records, the marine species herring and mackerel must have been taken as anglers' dead baits and the North American rainbow trout may also have originated from this source or from the stocking activities of a fishery in the nearby and connected lake of Esthwaite Water. The recent increase in the still very rare consumption of herring and mackerel probably resulted from the 2002 introduction of a local ban on the use of freshwater fish as live or dead bait (Winfield & Durie, 2004), which has presumably increased the use of marine baits. The remaining newly consumed species of Atlantic salmon, chub, common bream and roach were, in contrast, likely taken from reproducing populations within the Windermere fish community. The Atlantic salmon has probably been present in Windermere since the lake's formation and its previous absence from the recorded diet of pike is probably due to its relative scarcity and the more limited sampling efforts of the earlier studies. However, the three new cyprinid dietary records probably reflect true increases in environmental abundance and thus consumption by pike. Brief historical notes on cyprinid species in the lake reviewed by Le Cren, Kipling & McCormack (1972) document, in addition to an abundant and assumed native minnow population, very rare and localised populations of roach, rudd (*Scardinius erythrophthalmus* (L.)) and tench (*Tinca tinca* (L.)) which were concluded not to be native to the lake but to have resulted from live-baiting by anglers. The common bream and chub recorded in the present study thus appear to be more recent additions to the Windermere fish community. In addition to the general development of the roach population documented by Winfield *et al.* (2008a), increases in the abundance of large individuals of this species and common bream, particularly in the South Basin, were observed by Winfield, Fletcher & James (2011).

Detailed comparisons of the present level of feeding intensity by pike with those shown during the earlier studies are hampered by methodological differences and reporting limitations. For example, Allen (1935) sampled primarily using a seine net during various months of the year and although the sampling by Frost (1954) was reported separately for different net types and gill netting was concentrated during a similar seasonal window to that of the present analysis, neither earlier investigation gave basin-specific values. Furthermore, both earlier studies only presented prey frequencies of occurrence and not mean prey numbers per pike. As a result, the present overall frequencies of pike having consumed fish of 55% in the North Basin and 45% in the South Basin for the period from 1976 to 2009 can only be compared in the most general terms with the equivalent measures of 68% reported by Allen (1935) and 52% reported for gill-netted pike by Frost (1954). The comparison with Frost (1954) is the more robust of the two and indicates no great change in this crude measurement, but within the present study it is clear that in recent years pike in the North Basin have been consuming relatively more fish than their conspecifics in the South Basin.

Furthermore, these recent changes in this overall measure of feeding intensity have enveloped marked species-specific differences in predation patterns.

As hypothesised, the contribution of Arctic charr to the diet of pike in Windermere has decreased appreciably in recent years. However, it is notable that this overall decrease is driven primarily by changes in the South Basin, where Arctic charr now form only a very small component of the diet. To a large extent these dietary changes have mirrored those known to have occurred in the availability of Arctic charr in the two basins, with deteriorating environmental conditions in the South Basin having apparently driven fish to the North Basin (Winfield *et al*, 2008a) in a reverse of a 're-colonisation' to a previously improving South Basin observed by Elliott *et al.* (1996). The principal driver for this movement of Arctic charr is probably seasonally poor oxygen availability at depth in the South Basin (Jones, Winfield & Carse, 2008), although the consequences of a competitive interaction with the increasing roach population may also be involved because Arctic charr have recently shifted from being primarily zooplanktivorous to feeding much more on benthic macroinvertebrates (Corrigan *et al.*, 2011).

The contribution of brown trout, the only other salmonid of numerical importance in Windermere, to the diet of pike has also generally decreased in recent times but in most years this species has been relatively more important in the South Basin. Little is known about the local lacustrine abundance of the brown trout, although over a similar study period Winfield *et al.* (2011) found no significant difference in the abundance of larger brown trout in the lake's two basins. The generally higher consumption of this species in the South Basin may thus reflect not its own abundance, but the generally lower availability of Arctic charr in this part of the lake. The late 1990s decrease in Arctic charr availability in the South Basin may also explain the relative increase in perch and pike consumption by pike in this area which began at approximately the same time.

As hypothesised, the contribution of the non-native roach to the diet of pike in Windermere has increased appreciably in recent years, with this development occurring earlier and to a larger extent in the South Basin of the lake. As for Arctic charr, these dietary changes can be readily explained by the spatio-temporal pattern of development of the roach population, which first increased in the 1990s in the South Basin (Winfield *et al.*, 2008a) where larger individuals are still more common than in the North Basin (Winfield *et al.*, 2011). It is remarkable that although first documented in Windermere in the late 1890s (Watson, 1899), for many decades including a period of substantial eutrophication (Parker & Maberly, 2000) which often benefits this species, roach remained extremely scarce such that it went unrecorded by extensive and continuous long-term fish monitoring programmes and also failed to appear in the diet of pike. Rather, this cyprinid only increased in importance in the lake's fish community and in the diet of its top predator in the mid 1990s after water temperature had shown a significant long-term increase (Winfield *et al.*, 2008a).

The pike population of Windermere has thus recently experienced a number of major changes in the availability of its prey populations (Winfield *et al.*, 2008a; Winfield *et al.*, 2008b; Winfield *et al.*, 2010; Winfield *et al.*, 2011) which may be summarised overall as a probable decrease in feeding opportunities in the South Basin of the lake, leaving the North Basin as a relatively more profitable habitat in terms of foraging conditions. Note that although the abundance of roach has increased more in the South than in the North Basin, this species is still only a relatively small component of the local fish community (Winfield *et al.*, 2008a) and as the present study has shown it is only now contributing as much as the Arctic charr to the diet of pike in the South Basin. In the North Basin, pike diet remains dominated by Arctic charr. The great behavioural flexibility of pike (Adams, 1991; Raat, 1988; Venturelli & Tonn, 2006) has enabled it to adapt rapidly to these changes in prey availabilities. In particular, its ability to move between the two basins of Windermere in response to local conditions (Kipling & Le Cren, 1984; Haugen *et al.*, 2006) provides a plausible explanation for its abundance and individual condition becoming relatively higher in the North Basin than in the South Basin when the abundance of Arctic charr in the latter area declined markedly in the late 1990s (Winfield *et al.*, 2008b). Long-term shifts in the size structure of pike could also potentially induce changes in their diet composition (Sammons *et al.*, 1994) although this issue was not specifically addressed in the present analysis. However, the length range of individuals sampled over the study was consistent from year to year (authors, unpublished data) and so is highly unlikely to be a significant contributory factor to the observed dietary trends.

The recent changes observed at Windermere of a decrease in native salmonids and an increase in cyprinids are consistent with the expected effects of climate change promulgated in a large body of fish and fisheries literature reviewed by Magnuson & DeStasio (1997). Specifically, there is a common expectation that salmonid distributions will shift northwards and/or show decreases in local productivity. In this context, it is notable that within the U.K. Winfield *et al.* (2010) have recently found a widespread decline in Arctic charr populations with the exception of one site in northern Scotland where a population increase was recorded.

In addition, Lehtonen (1996) anticipated a shift towards cyprinid and percid dominance at the expense of salmonids and Power (1990) has specifically suggested that climate change is likely to benefit non-salmonid introduced species. Again, the local increase of roach in Windermere is consistent with these generic expectations. Although pike have the ability to predate members of all of these taxonomic groups (Raat, 1988), it is to be expected that they will differ in their relative profitabilities and thus changes in their relative abundances are likely to have significant consequences for foraging pike. In addition, the replacement or displacement of native carnivorous salmonids such as Arctic charr and brown trout by omnivorous cyprinids such as roach and common bream is likely to have implications for lake food web structure through shortening food chain length from the primary producers to top aquatic predators such as pike. Quantifying and understanding such changes will have important lessons for our wise protection and use of increasingly stressed lake environments (Olden & Poff, 2004; Strayer *et al.*, 2006).

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Figure legends

Fig. 1. Sampling sites for pike in the North (closed circles, 10 sites) and South (open circles, 10 sites) Basins of Windermere.

Fig. 2. The prevalence of fish in the diet of pike from 1976 to 2009 in the North (closed circles) and South (open circles) Basins of Windermere expressed as (a) frequency of occurrence and (b) number of individuals per pike (mean ± 1 S.E.). Corresponding cumulative z-score plots are given to the right of each graph. For the analysis of the number of individuals consumed per individual pike, 5 pike sampled from the South Basin between 2002 and 2004 were excluded from the analyses as extreme outliers because having foraged unusually and exclusively on underyearling fish they each contained approximately an order of magnitude more fish than all other pike (see text for details).

Fig. 3. The native salmonids (a) Arctic charr and (b) brown trout in the diet of pike from 1976 to 2009 in the North (closed circles) and South (open circles) Basins of Windermere expressed as the number of individuals per pike (mean ± 1 S.E.). Corresponding cumulative z-score plots are given to the right of each graph.

Fig. 4. The native (a) perch and (b) pike in the diet of pike from 1976 to 2009 in the North (closed circles) and South (open circles) Basins of Windermere expressed as the number of individuals per pike (mean ± 1 S.E.). Corresponding cumulative z-score plots are given to the right of each graph. For the analysis of the number of perch individuals consumed per individual pike, 1 pike sampled from the South Basin in 2004 was excluded from the analysis as an extreme outlier because having foraged unusually and exclusively on underyearling fish it contained approximately an order of magnitude more fish than all other pike (see text for details).

Fig. 5. The introduced roach in the diet of pike from 1976 to 2009 in the North (closed circles) and South (open circles) Basins of Windermere expressed as the number of individuals per pike (mean ± 1 S.E.). Corresponding cumulative z-score plots are given to the right of each graph. For the analysis of the number of individuals consumed per individual pike, 4 pike sampled from the South Basin between 2002 and 2004 were excluded from the analyses as extreme outliers because having foraged unusually and exclusively on underyearling fish they each contained approximately an order of magnitude more fish than all other pike (see text for details).

Fig. 6. The overall diet composition by prey numbers of pike in Windermere in the 1970s (open bars) and 2000s (closed bars).