

A short review of pike ecology

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Abstract A brief review is provided in some advances in understanding the ecology of pike *Esox lucius* Linnaeus over the last 10 years. Based on long-term studies and manipulative, often short-term experiments (laboratory, field and mesocosms) several established theories have been supported, as well as new concepts developed. Despite their wide distribution pike show low levels of polymorphism and divergence indicative of a recent common ancestral population. Recent genetic studies, however, indicate a single refugium in North America compared to several refugia in Europe. Pike are found in rivers, lakes and weakly saline waters. Variables such as growth and mortality are mainly affected by factors such as temperature, water transparency, productivity, availability of prey and density of pike and other predators. In choice of habitat pike have been shown to support the ideal free-distribution theory. The importance of macrophyte habitat in the life history of pike has been reconfirmed and pike have been shown to be flexible in response to water clarity. Pike are extremely ‘plastic’ in choice of prey

types, prey size and in response to prey behaviour (e.g. they are unaffected by shoal size). Predation by pike not only affects abundance and biomass of prey (including younger and smaller pike through cannibalism which plays a major role in population dynamics, other fishes and invertebrates) but also evolution and adaptation of their morphology (in particular body shape) and behaviours. There appears to be no relationship between stock and recruitment. Recruitment is influenced by several abiotic factors in lakes and rivers. Pike play a major role in structuring freshwater communities and have been used in stocking programmes to improve water quality (biomanipulation). Many new concepts have been developed in pike behaviour in maximizing these stocking programmes both in biomanipulation and fisheries management. Despite many recent advances in understanding the ecology of pike, particularly at the individual level, developments in quantifying and modelling the role of pike as a top predator in large ecosystems have been limited, probably due to the difficulties of sampling natural populations.

Keywords Ecology · *Esox lucius* · Freshwater fishes · Pike · Populations · Review

Introduction

In 1996 a multi-author book (Craig, 1996a) was published on the pike (Wheeler, 1992) (or northern

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pike as it is known in North America; Scott & Crossman, 1973) *Esox lucius* Linnaeus, a member of the Esocidae which is comprised only one genus *Esox*. The 1996 publication included other members of the genus, but concentrated mainly on *E. lucius*. Its purpose was to provide a synopsis and evaluation of what was known about pike biology at that time and indicate some future lines of research. The aim of the present paper is to briefly examine some advances in knowledge, in particular in pike ecology, since that publication. Pike populations like many other fish populations and communities have undergone considerable habitat changes (often human induced) and other perturbations including climate change (Casselman, 2002). It has long been known that pike are a keystone piscivore in cool-water habitats and can influence species composition, abundance and distribution of many species (including other pike, through cannibalism and competition) in a fish community. This has significant implications for the management and conservation of temperate freshwater fisheries and has resulted in a considerable number of publications on pike biology. These publications appear as the 'nuts and bolts' of understanding these freshwater systems.

Many investigations of pike ecology, in particular population dynamics and the role of pike in a community, have been based on long-term field studies, where extensive data have been collected. These studies of natural systems have a number of problems including lack of experimental controls, sampling limitations, monitoring in situ is often difficult in multi-species systems especially with long-lived species (where different life stages occupy dissimilar habitats), there is usually considerable variation in abiotic factors prior to recruitment, fish populations often show wide inter-annual fluctuations in numbers, and changes in variables such as growth and mortality can be offset by changes in subsequent life stages. In order to address some of these problems manipulative approaches have been taken including laboratory and field experiments and the use of mesocosms, where in experimental manipulations responses can be attributed to known causes. These experiments have their own drawbacks: they are often short-term and under contrived conditions and the findings are sometimes difficult to extrapolate to natural systems.

Origins, distribution and habitats

Pike has a Holarctic (the ecozone covering much of Eurasia and North America and connected from time-to-time by the Bering land bridge) range. The wide distribution of pike and its occurrence in many different habitats give some indication of the influence it may have on freshwater communities. It is thought that pike and its relatives radiated in freshwater before Eurasia and North America became separated (Crossman, 1996). Pike have shown low levels of variation, as indicated by allozymes, mitochondrial DNA (mtDNA) and randomly amplified polymorphic DNA (Miller & Senanan, 2003). Maes et al. (2003) sampled pike from Belgium, The Netherlands, Norway, Estonia, Ireland, Finland, Denmark, Poland, Hungary and Canada to study mtDNA variation. They found an extremely low level of polymorphism and divergence at the mtDNA genome which they stated conforms to the small population sizes of predatory fishes such as pike, as pointed out by Healy & Mulcahy (1980), Nicod et al. (2004) and Launey et al. (2006). Small population size could lead to possible repeated bottlenecks (Miller & Senanan, 2003), e.g. in pike introduced into Lake Davis, California, U.S.A. (Aguilar et al., 2005), and subsequent effective size reductions and genetic drift; thus low levels of genetic variation are maintained. The data of Maes et al. (2003) could not identify the geographic origin of the present day variation, but suggest that the pike is an apparently young species that arose in the late Pleistocene and as indicated above expanded across the Holarctic. Nicod et al. (2004) found a genetic structuring in European pike based on a longer D-Loop fragment. Therefore, the proposal of a recent Holarctic expansion of pike in the late Pleistocene would need to be confirmed by studying a larger portion of mtDNA. Studies by Senanan & Kapuscinski (2000) and Launey et al. (2006) indicate that European populations of pike appear to be more variable than populations from North America and Siberia and suggest the possible existence of a single refuge area in North America compared to several such areas in Europe during the last period of glaciation (which ended c. 11 000 years ago). This is in contrast to the view held that postglacial repopulation of pike in North America came from at least two refugia (Mississippian and

Beringian) with a possible third (Missourian) (Crossman, 1996).

Miller & Senanan (2003) have indicated that in the north-central U.S.A. microsatellite analysis has been used to detect genetic differences among populations but detection of the structure or genetic relationships among populations has been inconsistent. They indicate that the lack of structure may be the result of 'repopulation from a common glacial refugium' but also from indiscriminate stocking. Thus in the future a wider range of populations need to be studied, additional polymorphic markers need to be identified (e.g. five new microsatellite markers were found in a population from France; Launey et al., 2003) and care must be taken in enhancement programmes, e.g. stocking, so that stocking conserves genetic diversity and maintains fitness of the individual populations.

As a predatory fish at the top of the food chain, pike populations are small in comparison to other fishes further down the food chain. It is extremely plastic in its life history traits, however, and is widely distributed in a variety of fluvial and lacustrine freshwater habitats. A study comparing growth and mortality of pike between a river and lake populations at the same latitude, however, did not show any differences (Griffiths et al., 2004), i.e. flow is probably unimportant compared to other abiotic factors. Studies in many lake types have shown that growth of pike is strongly affected by both abiotic and biotic factors, such as temperature, water transparency, productivity, prey type and abundance, pike density and other competitors (Margenau, 1995; Casselman & Lewis, 1996; Margenau et al., 1998; Pierce et al., 2003). Using 40 years of capture, mark and recapture data, Haugen et al. (2006) were able to demonstrate that pike were able to maximize their dispersal within a lake, supporting the ideal free distribution theory. In this way, pike chose 'habitat according to intrinsic fitness gradients' and distributed themselves in a way that equalized 'fitness across habitats'.

Pike are also found in weakly saline waters, such as the Baltic Sea. Westin & Limburgh (2002) found an interesting example of sympatry in two populations of pike in the Baltic Sea on the east coast of Sweden. One population was anadromous and an obligate freshwater spawner and the other reproduced in ambient salinities (<6.5) and appeared not to enter fresh water. Evidence for both spawning-site and

natal-site fidelity in pike has been shown both by mark and recapture experiments and by population genetics (Miller et al., 2001) which supports previous findings (Bry, 1996). Again this fidelity indicates the need for care in managing distinct stocks as mentioned above. Bosworth & Farrell (2006), however, found that the extent to which pike rely on natal spawning areas remained unclear, but significant genetic divergence was identified among sites in close proximity. Although the potential for natal homing existed, in general pike did not disperse widely and utilized the nearest suitable spawning site.

Macrophytes are of great importance in the life history of pike, i.e. their relevance is related to pike ontogeny (Bry, 1996; Grimm & Klinge, 1996). Loss of wetlands, reduction in shoreline cover and structure, eutrophication and siltation have negatively affected macrophyte cover (for example increased turbidity and eutrophication can reduce water transparency and thus macrophyte growth) and therefore suitable pike habitat (Casselman & Lewis, 1996). Pike have been shown, by radio tagging, to be highly flexible in their response to water clarity and differences in behaviour can be found within locations and populations (Jepson et al., 2001). Skov et al. (2002a) go on to suggest, based on pond experiments, that 0+ year pike (90–170 mm total length) can hunt equally well in clear and eutrophic ('chlorophyll') water.

It has long been known that vegetation is important as a spawning habitat and spawning success could be related to high water levels and increased inundated areas (Brodeur et al., in press) although in regulated systems a less variable water level regime was found to be more beneficial to the young stages of pike than natural fluctuations (Luz & Loucks, 2003). In a large and complex river system (St Lawrence River) physical and biological characteristics of spawning habitat were linked to spatial patterns of egg distribution (Farrell et al. 1996) and survival of young during the nursery period (Farrell 2001). Farrell et al. (2006) showed that the timing and distribution of pike spawning could affect young-of-the-year (YOY) production and influence year class strength (YCS). They identified three different spawning patterns along the entire littoral gradient starting from seasonally flooded emergent vegetation in tributaries to submerged aquatic vegetation in shallow bays and finally to spawning in deep water (up to 6 m). They

used a model with temperature as the driving variable to predict egg abundance, stage-specific development, growth, survival and relative YOY production. Early spawning as well as higher mean daily survival and growth in the tributaries yielded higher YOY production than in the shallow bays. The contribution of pike from the deep littoral habitat was almost insignificant. Farrell et al. (2006) termed this last habitat as ‘an ecological sink’ and emphasized the importance of the linkage between spawning and nursery habitat conditions. Casselman & Lewis (1996), however, indicate that spawning habitat requirements, particularly in lakes, may be less important than previously thought and that macrophyte cover is more critical as a nursery habitat as well as a habitat for pike juveniles and adults. In the early life stages, pike are highly dependant on vegetation (the depth of the nursery habitat also appears to be related to the size and age of the pike; Casselman & Lewis, 1996), and their behaviour and eventual survival may depend on the extent and form of the cover; complex structured habitats appear to be favoured (Lehtiniemi, 2005). There are several reasons for this including protection against cannibalism, cover against predators and trophic interactions (Skov & Koed, 2004). By using structured habitats in ponds, Skov & Koed (2004) were able to show that when the level of cannibalism was high the larger, potential cannibalistic pike occupied sheltered structural habitats while the smaller and more vulnerable (to predation) pike were found in unsheltered habitats outside the structures. Young pike are known to flee in the presence of a large predator but remain immobile and sometimes feed when a smaller predator is present (Engström-Öst & Lehtiniemi, 2004). In early winter, when vegetation is much reduced, pike have been found to congregate in pools and show no indication of territoriality; spacing between individuals appears to be based on social grouping rather than defence of territory (Hawkins et al., 2003). In the study of Hawkins et al. (2005) one member of a pair of pike, nominally the dominant individual, used a habitat similar to an individual fish (a shallow-water pool) while the other individual was mainly found in deeper water. On occasions the dominant pike did enter the deeper pool and the subordinate pike remained with the dominant fish. Hawkins et al. (2005) proposed that although this would put the subordinate pike at risk the alternative of moving into

shallower water would put this fish at greater risk by reducing the ability to perceive and avoid attacks. The conclusion that juvenile and adult pike require macrophyte cover that ranges in extent from 35 to 70 % (Casselman & Lewis, 1996) confirms the findings of previous studies.

Predation, cannibalism and behaviour

Although pike will consume a wide variety of food items from invertebrates to fishes, they are extremely well-adapted piscivores for most of their lives. Their ability, as predators, to capture and consume prey is determined by both their size and that of the prey, the prey-to-predator size ratio. The size ranges within which predator and prey interactions take place has been termed by Claessen et al. (2000, 2002) as the ‘predation window’. Although very plastic in the size of prey they consume, in laboratory experiments pike have been shown to be size-selective predators (Nilsson & Brönmark, 2000). This size selection or ‘predation window’ was clearly illustrated by Hyvärinen & Vehanen (2004) for pike preying on brown trout *Salmo trutta* Linnaeus stocked into a regulated river. The brown trout were hatchery-reared fish and naïve to predators. Age 3 year brown trout were subjected to predation by pike whereas 4 year-old fish appeared to have ‘an almost size refuge from predation’. Nilsson & Brönmark (2000), however, showed that pike could eat larger prey (deeper body) than their gape size would indicate: another indication of their plasticity. The success of prey capture is also affected by the behaviour of the prey. There are several examples of anti-predatory behaviour by prey fishes (Kelley & Magurran, 2003; Skov et al., 2003a) including pike themselves in the presence of pike. The response can result from visual (for instance turbidity can play a key role; Skov et al., 2002a, 2007; Lehtiniemi et al., 2005), olfactory (e.g. chemical; Brown, 2003) tactile and auditory detection (Kelley & Magurran, 2003).

The role of cannibalism, a special form of predation, in pike has been well documented (Craig, 1996a) and the importance of habitat is illustrated above. In cases of cannibal and victim interactions, both the victim and cannibal usually share the same resources and thus are also involved in competitive interactions (Polis, 1988).

Pike appear not to be affected by shoal size of the prey, i.e. do not show a confusion effect, as demonstrated with roach *Rutilus rutilus* (Linnaeus) in experimental circular pools (Turesson & Brönmark, 2004). They were able to attack and capture prey at any of the densities presented with equal success.

Although feeding habits of pike usually show ontogenetic shifts, i.e. they change with growth, a study by Soupier et al. (2000) of several lakes in Minnesota showed no consistent change of any particular food (aquatic insects, fishes or other prey) in terms of mean per cent mass and total length of pike. Soupier et al. (2000) did state that this lack of ontogenetic shift may have been attributed to the simplicity of the lake communities. The pike is an opportunistic feeder and prey consumed will depend on prey availability (including behaviour) and abundance. For example in the Minnesota lakes investigated by Soupier et al. (2000), aquatic insects were more commonly ingested by pike in spring when prey fish abundance was low. In a whole lake experiment, pike were introduced into a fishless lake (Venturelli & Tonn, 2006). The adults preyed mainly on 'energy-rich leeches', while the juveniles fed on a wider range of invertebrates. Although pike were able to adapt to a fishless diet it was with a penalty. A comparison in growth with nearby lakes containing prey fishes showed that adult pike growth was 'compromised' while that of juveniles was high. Pike were shown to switch from powan *Coregonus lavaretus* (Linnaeus) to introduced ruffe *Gymnocephalus cernuus* (Linnaeus) in Loch Lomond, Scotland (Adams, 1991) and to feed on introduced crayfish *Procambarus clarkia* in the Ruidera Lakes, Spain (Elvira et al., 1996). In the St Louis River estuary, western Lake Superior, ruffe were accidentally introduced. Five predatory fishes, 'managed predators' (i.e. they were heavily stocked), including pike fed on up to 47% of the ruffe biomass in 1 year, however, they did not constrain the increase in ruffe biomass (Mayo et al., 1998). Of the total ruffe consumed by the five predators, pike consumed the most from 62 to 90% over the 4 year study. The predators in this case appeared to select native prey in preference to ruffe.

The above examples show the extensive plasticity of pike to food availability both temporally and spatially.

Population dynamics

Changes in pike population size and structure are caused by a complex variety of factors affecting individuals, which has influenced recruitment, growth and mortality (Craig, 1996b). The abundance and availability of forage fishes (including conspecifics) is probably crucial in influencing the density and size distribution of the predator. Kipling & Frost (1970) concluded that cannibalism could be a major factor in determining YCS and the density-dependent mortality of pike fry due to cannibalism can potentially regulate the population density (Treasurer et al., 1992). Persson et al. (2006) have suggested that cannibalistic population dynamics may be predicted from individual life-history characteristics such as minimum and maximum victim:cannibal size ratios. The cannibal-driven population dynamics they observed in pike appeared to be robust to variation in environmental conditions, but their environmental conditions were simplistic. The minimum ratio can be used to predict population dynamics of this cannibalistic species which in the populations studied by Persson et al. (2006) had a little variation in size distribution with time. Persson & De Roos (2006) suggest that the cannibals prevent negative competitive impacts from strong cohorts by killing individuals at an early age.

As stated above, there are several factors that influence YCS of pike. Although Craig (1996b) found temperature was important, there appeared to be no relationship between the adult spawning stock and YCS. The factors which influence variation in reproduction include fecundity, growth, mortality, age of maturity and biomass of the spawning stock (Craig & Kipling, 1983). For example, in Windermere, England, pike were unable to produce the maximum number of recruits at the minimum stock biomass. Changes in these factors, however, were not compensatory, i.e. there were wide fluctuations in recruitment (Craig & Kipling, 1983). Recent analysis of Windermere pike data (1940s–1990s) showed that there were no significant stock and recruitment relationships (C. G. M. Paxton, I. J. Winfield, J. M. Fletcher, D. G. George & D. P. Hewitt, pers. comm.). General additive models, however, showed that autumnal water temperature, strength and direction of the North Atlantic Oscillation displacement (related to different winter

climatic conditions), zooplankton abundance and, in particular, late-summer water temperature were important explanatory variables over the time period. In another long-term study of pike year class formation in a river system (the upper St Lawrence River), Smith et al. (2007) suggested that the environmental variables, water level and temperature, regulated pike YCS index cycles and dampening in the magnitude of the YCS index was probably related to a combination of variables (e.g. wetland habitat changes, reduced nutrient loading and predation by double-crested cormorants *Phalacrocorax auritus*).

Both density-dependent (compensatory) and density-independent factors affect recruitment. An important review of compensatory density dependence in fish populations has been given by Rose et al. (2001). They suggest that density dependent processes (e.g. growth, reproduction, mortality and movements) are compensatory if their rates change in response to variations in population density. Although this concept is simple it has led to a great deal of controversy in population dynamics. The theory may be straightforward but extrapolating to the field situation may be difficult due to imprecise field measurements. There are several examples where reducing predation has resulted in increased size and numbers of juveniles (Post et al., 1999). The effects of density and productivity on growth and size structure of natural pike populations have been limited by the need to obtain accurate estimates of population size. This has been achieved by Pierce & Tomcko (2003) and Pierce et al. (2003) for some lakes in Minnesota. They clearly showed that size structure was negatively and non-linearly related to density and this relationship was maintained when data from some Wisconsin lakes were added. Although lake productivity was only a marginally important variable in the relationship between density and growth for the Minnesota lakes data, it became more significant in the pooled data. In a survey of the literature Allen et al. (1998) found exploitation may be compensatory for pike less than 40 cm total length (cannibalism was reduced; natural mortality decreased to compensate for the exploitation and total mortality remained near constant) but became additive (i.e. total mortality increased) in larger fish. Therefore if large pike are fished this leads to increased density.

Although several insect species have been shown to prey on pike fry from 3 to 30 days of age (Le Louarn & Cloarec, 1997), the significance of this predation is not apparent. At the yolk sac stage pike inhabit the same shallow areas as predatory insects so the mortality could be severe.

Emigration and immigration can play an important role in population dynamics. The concept that pike are mainly but not exclusively sedentary and do not move far from a home range (Craig, 1996b) has been supported by studies in rivers (Rosell & Macoscar, 2002; Vehanen et al., 2006). Those undertaking migrations exhibited homing behaviour as they returned to the same spawning area the following year. Koed et al. (2006) also studying movements in a river found that females rather than males moved greater distances. Evidence for both spawning-site and natal-site fidelity in pike have already been discussed.

Community structuring and biomanipulation

It is well known that pike can have significant effects on the structuring of fish communities, for example size and condition, abundance and longevity of both prey (which can be species specific) and other predators (Hinch et al., 1991; Bertolo & Magnan, 2005). As pointed out by Craig (1996b) these effects have been mainly observed when pike have been accidentally or intentionally introduced into a community. An analysis by Colby et al. (1987) not cited by Craig (1996b) illustrated the effects of pike stocking in two Minnesota lakes, in particular the decline in yellow perch *Perca flavescens* (Mitchill) abundance 2 years after the initial pike stocking. Changes in other fish species were also noted. In the Experimental Lakes Area (ELA, Ontario, Canada) similar reductions in the yellow perch population were noted when pike were introduced into an experimental lake and there were subsequent changes in the invertebrate and phytoplankton communities (Findlay et al., 1994). In other lakes at ELA, cyprinids which had been dominant were reduced by the introduction of pike (Kidd et al., 1999). Due to constraints in field sampling and the difficulty in inter-calibrating different sampling gears, the effects of natural populations of pike on the community are difficult to quantify (Hinch et al., 1991; Kahilainen & Lehtonen, 2003; Bertolo & Magnan, 2005).

Although pike prey on percid where they occur together, a recent analysis of long-term data from Windermere, indicated that pike had no influence on perch *Perca fluviatilis* Linnaeus recruitment (Paxton et al., 2004). Paukert et al. (2003) showed that pike could substantially reduce introduced yellow perch abundance although they had no effect on introduced bluegill *Lepomis macrochirus* Rafinesque abundance. Pike have been shown to interact through predation and competition with walleye *Sander vitreum* (Mitchill) (Craig, 1996b), an important sport and food fish in North America (Craig, 2000), which is stocked yearly in many water bodies.

Adaptive and evolutionary morphological changes can occur as a result of pike predation. In 1 year-old perch and roach exposed to pike predation, perch increased their body depth whereas roach responded by displacement of the dorsal and pelvic fins and width of the anal fin (Eklöv & Jonsson, 2007). The variation in response was related to differences in anti-predator strategies. Body depth and fin ray length in YOY perch were found to be correlated with predation risk by pike (Magnhagen & Heibo, 2004) when compared across five lakes in northern Sweden. In the same way crucian carp *Carassius carassius* (Linnaeus) were found to become deeper bodied and thus reduce predation risk when pike were introduced into small ponds occupied by the crucian carp (Brönmark & Miner, 1992). Before these morphological changes took place, crucian carp exhibited a substantial decrease in activity. Prey fishes that have not come into contact with pike before can take some time to exhibit anti-predator behaviour (Chivers & Smith, 1995). The effect of chemical cues from pike on the prey fishes can have a long-term effect on their activity (Pettersson et al., 2001). This in turn could affect prey vulnerability, predation rate and the food web.

Using a combination of a whole-lake experiment (without fish prey), mesocosms, to allow for replication and controls, and nearby lakes containing fish prey, Venturelli & Tonn (2005) were able to show the direct effects of pike predation (invertivory) on the littoral macroinvertebrate community: there were significant changes in the fishless lake from 'large conspicuous taxa' to 'less-conspicuous taxa'. In the boreal lakes studied there are large fluctuations in fish densities due to winterkill, and pike, which is less sensitive to these winterkills can directly affect non-fish littoral food webs.

The alteration of food web structure by reducing external nutrient loading in standing water, in particular shallow lakes, has often accompanied by biomanipulation, to improve water quality (Shapiro et al., 1975) and to sustain fisheries (Kitchell, 1992; Mehner et al., 2004). These methods of phytoplankton control have been the subject of intense worldwide interest in recent years in temperate zones (Jeppesen et al., 2007). The idea behind biomanipulation is to remove and thus reduce planktivores to allow zooplankton to increase in size and numbers. This results in increased grazing on the phytoplankton and clearer water. One way of reducing planktivores is to enhance piscivores such as pike in the system, e.g. by stocking 0+ year pike at $>1000 \text{ ha}^{-1}$ to control newly hatched roach and bream *Abramis brama* (Linnaeus) (Prejs et al., 1994; Berg et al., 1997). There have been extensive experimental studies conducted to determine the optimal conditions for maximizing the impact of these pike stockings, in particular in small eutrophic lakes, for example in Denmark (Skov & Berg, 1999; Skov et al., 2002b, 2003a; Jacobsen et al., 2004). Many of the in-depth studies on habitat requirements and predator and prey behaviours, as described above, have been carried out as part of these biomanipulation programmes. For example Grønkjær et al. (2004) showed the importance of the time of stocking: those stocked early in the season had higher survival than those stocked later in the season, the latter being more susceptible to cannibalism from native 0+ year recruits. Skov et al. (2003b) also indicated that post-stocking mortality by cannibalism of 0+ year pike was reduced if alternate prey were available and that the initial size heterogeneity was kept as low as possible.

Modelling

The wide range and complexity of communities and the very large diversity of ecosystem types which pike inhabit make it difficult to model the effects of pike predation in large natural systems. Models to estimate food consumption as a function of mortality, food type, morphometrics, temperature and salinity have been derived for a variety of species including pike (Palomares & Pauly, 1998). Since Kitchell et al. (1977) published a paper on a bioenergetics model for

yellow perch and walleye, there have been numerous papers which have applied the model to many species including pike to further understanding in fish ecology and management. The model is based on an energy balance equation which equates energy consumed with energy gained and expended and the parameters used in running it are based on a mix of field and laboratory estimates. This has led to considerable controversy although studies described above used to determine the value of management practices such as stocking (Fayram et al., 2005) and control of unwanted exotics (Mayo et al., 1998) have been applied. The application of bioenergetics models and requirements for improvement in their predictive power was assessed by Hansen et al. (1993). For the latter they identified the need for improved estimates of mass-dependent consumption, metabolic costs of activity, thermal habitats occupied by fishes, population sizes and survival rates. There is also a requirement to understand differences between juveniles and adults in the parameter values. Detailed studies on energy budgets and metabolism in pike have been carried out by Diana (1983, 1996), Armstrong (1986, 1998), Armstrong et al. (2004), Lucas & Armstrong (1991) and Lucas et al. (1991) and the use of telemetry has been instrumental in the improvement of estimates of metabolism in the field. There has been a little progress, however, in the development of the other factors and users of the bioenergetics model have usually extrapolated from other species.

As far as it is known, there is no published study on Ecopath–Ecosim modelling (Walters et al., 1997, 2000; Walters & Christensen, 2004) with pike as the top predator although the models have been applied to a simple system comprised of two freshwater predatory fishes (Taylor, 2006). Ecopath is a practical trophic mass-balance model (Christensen & Pauly, 1992, 1993) where estimated total biomass loss rates for each modelled biomass group are portioned among assumed static predation rate components and unaccounted losses. In Ecosim these static flows are turned into dynamic, time varying predictions by assuming that flows from prey to predator groups are mediated by vulnerability exchange rates between vulnerable and non-vulnerable prey pools (Walters et al., 2000). Despite the problems of collecting quantitative estimates in the field, there is no doubt that the use of ecosystem models has considerable

potential in defining management practices in whole lake and river systems in particular in the manipulation of top predators like pike. In the present form, however, they are not able to provide the information required for single species as, generally, many species are combined into one ‘box’.

Conclusions

Studies in the last 10 years appear to support established theories, e.g. predation by pike not only affects abundance and biomass of prey (including younger and smaller pike through cannibalism, other fishes and invertebrates) but also induces adaptive and evolutionary changes in prey morphology (in particular their body shape) and prey behaviour and that pike can rapidly switch their prey preferences such as when an alien species is introduced. In the same way the effect of abiotic variables, including temperature and vegetation, on the population dynamics of pike has been reconfirmed. There have been significant advances in understanding interactions at the individual level by carrying out detailed short-term experiments. The effect of pike in communities especially in lakes has been well defined and the use of pike by stocking in biomanipulation refined. Despite these studies, advances in quantifying and modelling the role of pike as a top predator in large ecosystems have been problematic.

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