

Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory

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Nilsson, P. A. and Brönmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. – *Oikos* 88: 539–546.

The northern pike (*Esox lucius*) is a selective and important predator in lake ecosystems. Prey size in pike is limited by pike gape size, which is a linear function of pike body length. Here we show that the absolute gape-size limit in pike is greater than previously considered, and that maximum ingestible prey size is limited by prey body depth. Further, we experimentally show that pike prefer shallow-bodied roach before deeper-bodied common bream, and small prey sizes within each prey species. Handling time in pike increases with prey body depth, and since common bream are deeper-bodied than roach, handling time is longer for bream than for roach of the same length, but equal considering body depth. Prey handling time is suggested to be a major cost to the pike, since it increases the risk of losing the prey, as well as exposure to predation, kleptoparasitism and cannibalism. Consequently, prey vulnerability is determined by risk of predation and intraspecific interactions, and behavioural preferences in the pike, and not by pike gape-size limits. The consequences for natural populations is evaluated by analysing size structures of predator and prey fish populations in a eutrophic lake.

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Predation may have indirect or direct effects on prey, and prey defence strategies, in return, may affect foraging efficiency in the predator (e.g. Kerfoot and Sih 1987, Lima and Dill 1990, Fraser and Gilliam 1992). Thus, the life-time success of individual predators and prey depends on the characteristics of their opponents. Different predator and anti-predator strategies may therefore have different impacts on population and community dynamics (Fryxell and Lundberg 1998). Not only behavioural prey defence strategies affect predator efficiency, but also prey size. For instance, while large prey generally constitute large portions of food, they may also impose a cost on attacking predators, through e.g. being too fast, strong, costly or risky to capture (e.g. Dill and Fraser 1984, Hart and Hamrin 1990, Juanes and Conover 1994, Seed and Hughes 1995, Schatz et al. 1997). Prey selectivity in predators may thus not always be a matter of maximising energy

intake, but a balancing of different demands (Sih 1980, Cerri and Fraser 1983).

Predation by piscivorous fish is a major mortality source for fish populations in many freshwater systems. Piscivores may have direct effects on prey population density and size structure (e.g. Tonn and Paszkowski 1986, Brönmark et al. 1995, Persson et al. 1996) and indirect effects on prey growth rate, survival and fecundity through changes in behaviours associated with foraging, predator avoidance, or reproduction (e.g. Fraser and Cerri 1982, Fraser and Gilliam 1992, Tonn et al. 1992). As a result of this strong selection pressure, prey fish have evolved a number of adaptations to minimise the risk of being detected, caught and consumed, e.g. schooling, hiding in refuges, nocturnal activity, or toxicity (e.g. Ivlev 1961, Moody et al. 1983, Kerfoot and Sih 1987, Fraser et al. 1993). Further, it has been shown that a deep body may act as a morpho-

Accepted 23 June 1999

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ISSN 0030-1299

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logical defence against gape-limited piscivores (e.g. Webb 1986, Nilsson et al. 1995). Piscivores generally reorient their prey after catching it, to be able to swallow it head first and lying on its side (Hoyle and Keast 1987, Reimchen 1991). The body depth is therefore the greatest width of the prey fish during swallowing, and should be a relevant measure of prey size (Hambright 1991). If the body depth of the prey is larger than the gape size of the largest individual in the piscivore population, the prey fish is considered to enjoy an absolute size refuge from predation (Hambright 1991, Hambright et al. 1991). However, prey may also benefit from a deep body within the gape-size limits of the predator, since the body depth of the prey may affect piscivore predatory behaviour and efficiency (e.g. Hart and Hamrin 1988, Nilsson et al. 1995).

The cyprinid fishes common bream (*Abramis brama* L.) and roach (*Rutilus rutilus* L.) are widespread in temperate European freshwater systems (Maitland and Campbell 1992). The two species differ morphologically in that bream have dorso-ventrally deep and laterally compressed bodies, while roach have less deep, less compressed, and more fusiform body shapes (Maitland and Campbell 1992). They also differ in foraging habits and life history strategies, governing for a faster growth in bream (e.g. Lammens et al. 1987, 1992, Mooij et al. 1996). It is therefore plausible that bream would reach a size refuge from gape-limited predators, such as northern pike (*Esox lucius* L.), at shorter length and younger age, than roach.

In this study, we evaluate gape-size limits and prey preference of northern pike when exposed to bream and roach, size selection within each species, and differences in handling time between sizes and species. We hypothesise that pike gape-size limits and prey size are determined by prey body depth, and that pike prefer shallow-bodied and small prey, in order to minimise handling time. This preference should in turn affect behavioural, functional limits of prey vulnerability to pike predation. The implications of our results on potential piscivore impact on prey populations and trophic interactions are discussed.

Materials and methods

Prey and pike morphology

Bream and roach morphology

The relationship between maximum body depth (BD; measured dorso-ventrally just anterior to the dorsal fin) and total body length (TL) was determined for common bream and roach. The fish were caught with sink and fyke nets in the Silvåkra stream during late autumn 1995 and 1996. Body depth and total body length were measured (to the nearest mm) on each fish (bream: $n = 161$; roach: $n = 256$).

Pike gape size

In order to establish a relationship between pike gape size and total body length we collected 49 pike from lakes and ponds in southern Sweden. The pike ranged in size from 128 to 685 mm total length. The increasing cross-sectional diameter of a plastic cone (height 215 mm: base diameter 95 mm) was marked along its side at 2-mm increments. The cone was inserted into the mouth of the pike, and the diameter of the gape at the corner of the mouth was registered (cf. DeMarco et al. 1985, Arts and Evans 1987).

Laboratory experiments

All experiments were conducted with individual pike kept in 200-l aerated aquaria. The bottom of each aquarium was covered with sand, and a stand of artificial vegetation (0.1 m^2 : 360 stems/ m^2), made of nylon string attached to a PVC plate, covered one end of each aquarium. Pike and prey were acclimatised to indoor conditions for two weeks before experiments. During the acclimatisation, pike were fed crucian carp, and bream and roach were fed frozen chironomids. Pike were starved for 48 h before all experiments.

Maximum prey size

To determine whether gape size, as measured above, is a good estimate of prey-size limitation in pike, maximum ingestible prey size was estimated for pike of different sizes. Eleven northern pike (size range: 134–590 mm TL) were individually held in 200-l aquaria. Each pike was given one bream or roach, which had been measured (TL and BD to the nearest mm) before the experiment. The fish were checked daily, and if a prey fish had been eaten, its size was considered within the limits of predation for that particular sized pike. The pike was then given a somewhat larger individual of the same prey species. If the prey had not been eaten within a fortnight, the prey was considered too large for the pike. Repeating this procedure, we were able to home in on and estimate the maximum ingestible prey size for both species of prey, as a function of pike size.

Species selectivity

Eight pike (254.6 ± 6.8 mm, TL \pm SD) were given sets of five bream and five roach of the same total length. All prey fish were measured before the experiment (total length and body depth, to the nearest mm). Average total length for both species pooled was 100 ± 0.02 mm, whereas the average body depth was 24.1 ± 2.2 and 20.0 ± 1.4 mm for bream and roach, respectively. Prey fish were introduced into the vegetation end of the aquaria and the pike were then allowed to choose and consume three to four individuals each.

The remaining fish of each species were recorded. Pike selectivity was evaluated using the Manly-Chesson α -index for prey preference (Manly 1974, Chesson 1983) and a t -test for difference from non-selectivity (i.e. $\alpha = 0.5$).

Size selectivity

Eight pike (249.0 ± 5.2 mm, TL \pm SD) were each given ten individuals of one prey species. The prey were selected to compose a size range with regards to body depth, from the smallest possible found in the field (bream: 9.9 ± 1.1 mm, roach: 10.4 ± 1.9 mm, BD \pm SD), to almost the largest this size of pike were able to ingest in the maximum prey size experiment (bream: 30.9 ± 1.5 mm, roach: 30.8 ± 0.5 mm, BD \pm SD). Prey sizes were sorted to form ten distinct prey size classes. Total body length and depth (nearest mm) of each prey fish were measured before they were introduced into the vegetation end of the experimental aquaria. Each pike was allowed to choose and consume three to five prey, and the remaining fish were remeasured to identify the size of the eaten individuals. This was done with both bream and roach as prey, in separate experiments, using the same pike.

Handling time

Eight pike (249.0 ± 5.2 mm, TL \pm SD; the same as in the size selectivity experiment) were given individual bream or roach, and handling time, time elapsed between striking the prey until it had been completely swallowed, was measured from video recordings of the trials. A total of 20 bream and 20 roach of different total body lengths (48–121 mm and 47–144 mm respectively) and body depths (10–30 mm and 8–30 mm, respectively) were used.

Prey vulnerability

To illustrate the effects of pike gape-size limitation and prey preference in nature, we analysed a data set on size frequency distributions of pike, bream and roach from a biomanipulation program in Lake Finjasjön in southern Sweden. We estimated prey vulnerability using Hambright et al.'s (1991) vulnerability index, which gives an estimate of the proportion of the pike population that can feed on prey fish of increasing body depths. In our calculations we used the relation between pike total length and maximum ingestible prey size found in our experiment. We also calculated a behaviourally mediated, functional prey vulnerability, based on our findings in the size selectivity experiment. The resulting vulnerabilities were compared with the corresponding index in Hambright et al. (1991), since theirs has been customarily used in recent literature.

Results

Prey and pike morphology

Body depth (BD) increased linearly with total length (TL), for both bream and roach ($BD = 0.314TL - 4.523$, $r^2 = 0.993$, $P < 0.001$, $n = 161$; $BD = 0.265TL - 6.240$, $r^2 = 0.936$, $P < 0.001$, $n = 256$). However, for a given length, common bream were significantly deeper-bodied than roach (ANCOVA with TL as covariate: $P < 0.001$, $F_{1,414} = 2397$, $n = 417$). Pike gape size, as measured with the cone, was linearly related to total body length ($Gape = 0.098TL - 0.339$, $r^2 = 0.987$, $P < 0.001$, $n = 49$; Fig. 1). The relation is similar to the one in Hambright et al. (1991; $Gape = 0.087TL - 1.38$), but the slopes differ, and their relation gives relatively smaller gape sizes for pike larger than 300 mm TL.

Maximum prey size

The maximum size of prey ingested increased as a function of pike size. When considering body depth, there was no significant difference in maximum size ingested between bream and roach (bream: $Y = 0.127X + 1.427$, $r^2 = 0.967$, $P < 0.001$, $n = 8$; roach: $Y = 0.131X + 0.401$, $r^2 = 0.99$, $P = 0.0014$, $n = 6$; ANCOVA with TL as covariate: $P = 0.964$, $F_{1,11} = 0.0021$, $n = 14$; Fig. 1). However, since bream has a deeper body than roach for any given length, pike were able to ingest roach with a greater total length than bream (ANCOVA with BD as covariate: $P = 0.0059$, $F_{1,11} = 11.60$, $n = 14$). Furthermore, pike were able to take significantly deeper-bodied prey than estimated from our pike mouth diameter measurements (ANCOVA

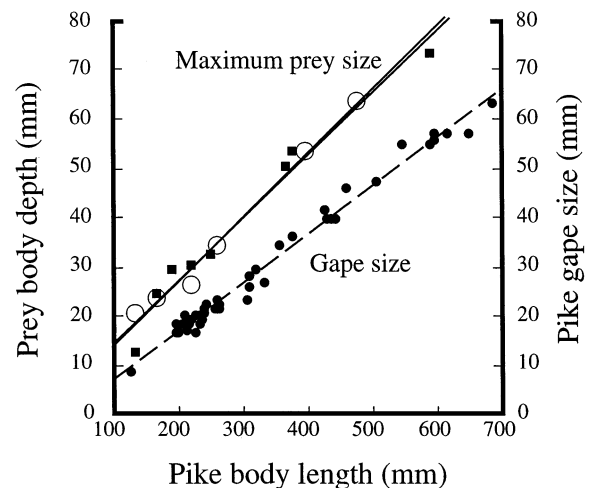


Fig. 1. Pike gape-size measurements (broken line, filled circles) and maximum ingestible prey size as a function of pike body length. Pike gape size was measured with a cone, whereas the maximum ingestible prey size (solid lines) was obtained as the body depth of the largest prey fish (common bream, filled squares, and roach, open circles) ingested in laboratory experiments.

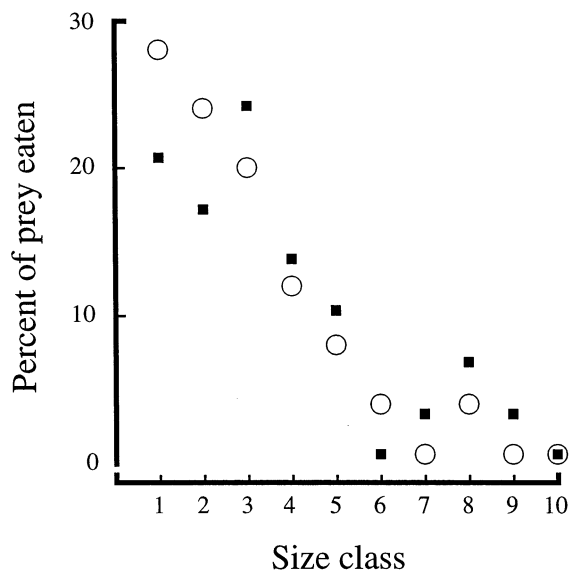


Fig. 2. Size selectivity in northern pike when feeding on common bream (filled squares) or roach (open circles) of ten size classes. Size classes range in size (i.e. body depth) from 9.9 ± 1.1 to 30.9 ± 1.5 , and 10.4 ± 1.9 to 30.8 ± 0.5 mm \pm SD (bream and roach, respectively).

with pike TL as covariate; bream: $P < 0.001$, $F_{1,54} = 195.2$, $n = 57$; roach: $P < 0.001$, $F_{1,52} = 198.0$, $n = 55$; Fig. 1).

Species and size selectivity

When given a choice between prey fish that were of equal length, pike preferred to feed on roach over bream (bream: $\alpha = 0.25 \pm 0.17$, roach: $\alpha = 0.75 \pm 0.17$ mean \pm SD; $P < 0.01$, $t = 4.079$, $df = 7$). In the size selectivity experiment, pike had a higher foraging rate on small prey and avoided the larger size classes (Fig. 2). The average body depth of the prey eaten by each pike was significantly shallower than the average depth of the surviving prey, considering both bream and roach (paired t -test: $P = 0.004$, $t = -4.17$, $df = 7$ and $P < 0.001$, $t = -9.74$, $df = 7$, respectively).

Handling time

The handling time increased with size for both of the prey species (Fig. 3). At the same body length, handling time was significantly longer for bream compared to roach (ANCOVA with TL as covariate: $P < 0.001$, $F_{1,37} = 16.78$, $n = 40$, Fig. 3). However, at the same body depth, there was no difference in handling time between the two prey species (ANCOVA with BD as covariate: $P = 0.751$, $F_{1,37} = 0.1024$, $n = 40$, Fig. 3). Thus, for bream and roach of equal length pike handling time was larger for bream, whereas there was no difference between species when body depth was identical.

Prey vulnerability

If the relative vulnerability is calculated on the basis of Hambright et al. (1991), the complete roach population in Lake Finjasjön is within the size range vulnerable to predation, while bream with a body depth > 80 mm (TL ≈ 260 mm) enjoy an absolute size refuge from pike predation (broken lines, Fig. 4). However, if the vulnerability index is based on the maximum ingestible prey sizes for pike found in our experiments, almost the complete bream population is also within risk of predation (solid lines, Fig. 4). When taking our prey size

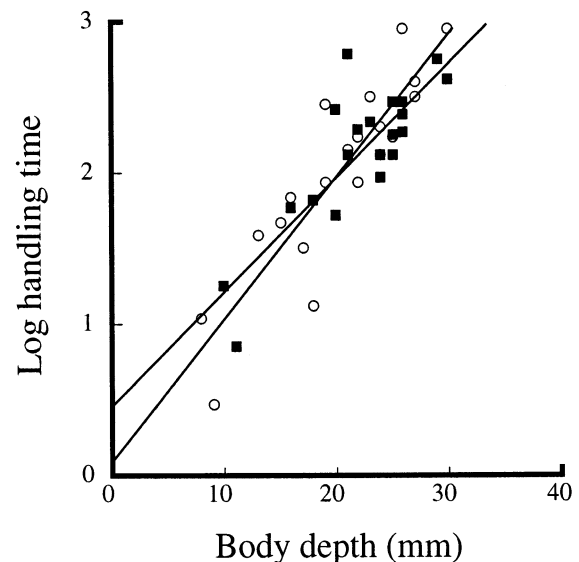
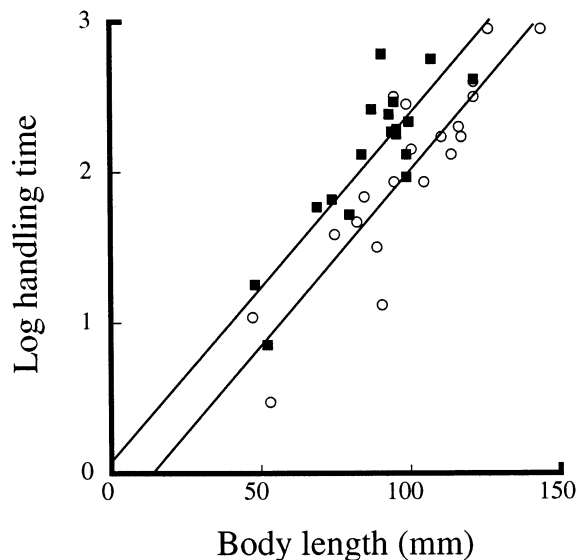
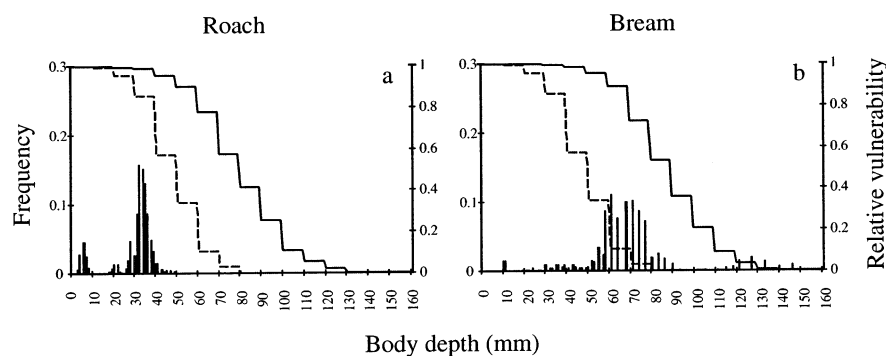


Fig. 3. Handling time in northern pike as a function of prey (bream, filled squares, and roach, open circles) total body length and body depth.

Fig. 4. Distributions of body depths of the common bream and roach populations in Lake Finjasjön, Sweden, and their relative vulnerabilities to pike predation. The relative vulnerability indices are based on gape size measurements (Hambricht et al. 1991; broken line) and on estimates of maximum ingestible prey size (solid line; cf. Fig. 1).



preference results into consideration, functional prey vulnerabilities agree with the gape-size based vulnerabilities in Hambricht et al. (1991).

Discussion

Body morphology and size

For the pike in our experiments, the maximum ingestible prey body depths are the same for bream and roach, while maximum body lengths differ between species. Therefore, body depth, and not body length, determines prey size refuge against predation. This corroborates previous suggestions, i.e. that the body depth of a prey fish is a crucial measure of morphological defence against gape-size limited piscivores (e.g. Hambricht 1991, Hambricht et al. 1991, Nilsson et al. 1995). The vulnerability to pike piscivory differs between species (Mauck and Coble 1971), and we suggest that prey morphology and size contribute to this difference, since a deep body substantially decreases vulnerability to pike predation.

Hambricht et al. (1991) measured jaw dimensions of pike preserved in alcohol and established a body length to jaw width relation. Since we in previous experiments have shown that pike are able to take larger prey than estimated from such gape size to body length relations (Nilsson et al. 1995), we decided to measure live individual pike, using a slightly different method. There was no major difference between the methods considering the relation between pike body length and mouth size for small pike, while the estimated gape sizes of larger pike from Hambricht et al. (1991) deviate out of the 95% confidence interval of our measures. Further, our experiments on maximum prey size show that northern pike are able to swallow larger prey than suggested from gape measurements. Direct measures of pike gapes thus result in underestimates of gape-size limits, and the relation between body length and experimentally measured maximum ingestible prey depth should be used to estimate absolute gape-size limits.

Behaviour and prey selectivity

All the prey individuals in our selectivity experiments were within the prey size limits, but the present study demonstrates that pike show preference for shallow-bodied roach over deeper-bodied common bream (see also Webb 1986, Wahl and Stein 1988, Hambricht 1991). Further, a larger prey item should contribute a greater foraging return than would a small (Nursall 1973, Hart and Connellan 1984). In spite of this, our pike fed on the smaller individuals within each prey species. This is consistent with other studies that have shown that pike prefer prey far smaller than ingestible, and even smaller than predicted from optimal foraging theory (Beyerle and Williams 1968, Hart and Connellan 1984, Hart and Hamrin 1988, 1990, Juanes 1994; but see Einfalt and Wahl 1997). Potentially, this preference for shallow and small prey could be a result of differences in behavioural characteristics among the prey (cf. Einfalt and Wahl 1997). However, in this experiment, the experimental arena was relatively small, which restrains anti-predator behavioural differences between species and sizes of prey fish (e.g. schooling, habitat choice or evasive behaviour; cf. Christensen 1996, Jacobsen and Perrow 1997, Dettmers et al. 1998). The "sit-and-wait" or "ambush" (Webb and Skadsen 1980) predatory behaviour of the pike, on the other hand, is hardly affected by the small size of the arena. Recently, we have shown that predator-induced, deep-bodied crucian carp are avoided by pike, and that shallow crucians are preferred (Nilsson et al. 1995). Since pike prefer shallow-bodied prey also within a species, it is feasible to presume that the species and morph selectivity is not due to differences in prey behaviour. Further, prey escape probability is likely to increase with prey size, thereby potentially affecting our results. However, remaining prey from the selectivity experiments had no marks or injuries, indicating no differences in escape rate between prey categories. Thus, any preference for prey exhibited in this experiment should be due to behavioural characteristics of the pike.

The hunting procedure in pike is characterised by localisation of the prey, decision to strike, a short distance attack, and the subsequent manipulation, swallowing, and digestion of the prey (e.g. Webb and Skadsen 1980, Moody et al. 1983, Wahl and Stein 1988, Hart and Hamrin 1990, Nilsson et al. 1995). The foraging behaviour of pike could potentially be altered at each of these stages as an effect of prey size/species. However, since the northern pike is a sit-and-wait predator, pre-attack events should not be as important to pike as it would be to mobile predators, such as perch (Christensen 1996). Experimental studies in fact show that pre-attack behaviours in pike are not affected by prey size (Nilsson and Brönmark 1999). Thus, the answer to prey-size preference in pike should be sought for in post-attack events, such as handling time. However, it may be argued that the handling time in northern pike rarely becomes long enough to seriously affect the pike regarding energetic costs and gain from the predatory event, since pike spend little time foraging (e.g. Breck 1993). For example, if 40-cm pike eat prey 40 mm deep instead of 20 mm, they increase their handling time with over 600%. However, this would only increase handling time from 17 to 103 s (recalculated from Nilsson et al. 1995). In the total time budget of a pike that forages maybe only once every or second day, 17 or 103 s would not make a major difference. However, handling time may have important effects on other traits than the time budget. During handling, pike may be exposed and vulnerable to attacks from other fish. Pike may be preyed upon by other species (e.g. largemouth bass, Wahl and Stein 1988, Szendrey and Wahl 1995) or by conspecifics (e.g. Giles et al. 1986, Bry et al. 1995, Grimm and Klinge 1996). It has been shown that prey fish that excrete alarm substances when attacked by piscivores attract other predators (Mathis et al. 1995). Secondary pike, or other piscivores, that are attracted to a pike that has captured a prey may interfere with the first pike and increase the opportunity for the prey to escape (Chivers et al. 1996). The intruder may even take over the prey, or feed on both the pike and the prey (Grimm and Klinge 1996, Nilsson and Brönmark 1999). Since pike are attracted to prey by visual, chemical and mechanical cues (e.g. Raat 1988), a long handling time that emits such signals should be avoided. As handling time increases with prey size, i.e. body depth (Hoyle and Keast 1987, Nilsson et al. 1995), the risk of losing the prey, and/or exposure to eventual predators, cannibals or kleptoparasites, should increase along with it. Consequently, risk of kleptoparasitism and predation increases with handling time and prey size, as has been shown by Nilsson and Brönmark (1999). Thus, given a choice, pike should prefer to eat shallow-bodied and small prey to minimise risk, as they indeed did in our experiments.

In the reasoning above, handling time includes the time between a successful strike and complete swallow-

ing of a prey item. It has been suggested that handling time should also include digestion time (Hart and Hamrin 1990, Hart and Gill 1992). A small prey item constitutes a larger surface to body mass ratio, and should be digested faster per prey mass (e.g. Jobling 1981, Bromley 1994). A reduced digestion time could potentially explain pike prey-size preference, but some facts argue against this. First of all, the surface of both small and large prey is comprised of scales that should be hard to digest (e.g. Bromley 1994). Therefore, an increased surface to mass ratio would potentially decrease prey profitability. Also, recent experiments have shown that pike digest equal-mass rations of small or large prey at the same rate (P. A. Nilsson and C. Brönmark unpubl.). Thus, neither pre-attack behaviour nor gastric evacuation rate could explain pike prey selectivity. Instead, we suggest that costs associated with post-attack manipulation events, e.g. risk of predation or kleptoparasitic interactions, determine prey selectivity in pike.

Effects in natural ecosystems

Piscivory may have profound effects down food chains (e.g. Carpenter and Kitchell 1993, Ramcharan et al. 1995), and may e.g. skew prey size and species distributions away from normal, subsequently affecting lower trophic levels and ultimately community structure. However, most piscivores are gape-size limited, and the effect of their predation on prey populations and food chains should be determined by the size ratio between predators and prey (Hirvonen and Ranta 1996, Persson et al. 1996). Therefore, a gape-size limit creates an upper limit of the food window for the predator, and narrows its potential impact on prey stock. Consequently, a limited impact on the prey population, through for instance gape-size limits, may decouple the effects of predation down the food chain, and thus also community dynamics (e.g. Hambright et al. 1991, Hambright 1994, Brönmark and Weisner 1996). For example, predation by piscivores may result in prey fish populations dominated by deep-bodied and/or large-sized individuals (Brönmark and Miner 1992, Hambright 1994, Brönmark et al. 1995). These large, deep-bodied fish, such as bream, may then continue feeding on lower trophic levels and, further, producing new recruits, resulting in a decoupling of trophic cascades. The data from Lake Finjasjön show that only a minority of the largest bream are in an absolute size refuge from predation, i.e. there is no definite decoupling of cascading trophic interactions in this lake. However, the effective vulnerability of the larger size classes of bream is very low, due to the low densities of large pike and their selectivity against large and deep-bodied prey. Also, pike prefer to feed on smaller prey than they can actually ingest ($<$ maximum prey size).

As an example, in our selectivity experiments a substantial part of the prey that had been eaten, 76% of the bream and 72% of the roach, were less than half as deep as the maximum prey size for the pike (Fig. 2). If preference for prey this small is a general pattern (cf. Beyerle and Williams 1968, Maitland and Campbell 1992), this behaviour would result in a functional size refuge for prey fishes, resembling the size refuge found by Hambright et al. (1991) (Fig. 4). Therefore, at normal bream and roach population densities and size structures, there are probably sufficient numbers of small prey to put the larger bream in an effective, functional size refuge through size and morph selectivity by pike, although pike are morphologically capable of taking them. Subsequently, since pike feed on small sizes of prey, and avoid feeding on deep-bodied individuals and species, bream, to a larger extent than roach, may well have the decoupling effects on trophic interactions and ecosystem appearance suggested above. Thus, the balancing of different demands in prey size selectivity in pike, i.e. maximising energy intake rate and minimising post-attack risk, may affect behavioural size refuges for prey, and subsequently affect dynamics and composition of populations and communities in lake ecosystems.

Acknowledgements – We thank Peter Eklöv, Thomas Madsen and Mikael Svensson for constructive comments on earlier manuscripts, Henrik Smith for advice on the statistics, and Anders Persson and Rikard Aagren for data from Lake Finjasjön. Financial support was received from the Swedish Board for Agriculture and Forestry Research, the Royal Swedish Academy of Science, and Göte Borgströms Fond.

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