Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density

Turesson, Håkan; Brönmark, Christer

Published in:
Journal of Fish Biology

DOI:
10.1111/j.0022-1112.2004.00455.x

2004

Journal of Fish Biology (2004) **65,** 363–375
doi:10.1111/j.1095-8649.2004.00455.x, available online at http://www.blackwell-synergy.com

Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density

H. Turesson* and C. Brönmark

Department of Ecology, Limnology, Ecology Building, Lund University, SE-223 62 Lund, Sweden

(Received 14 August 2003, Accepted 22 April 2004)

The effect of school size on capture success in three different piscivores, perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca* and pike *Esox lucius*, was investigated. Roach *Rutilus rutilus* were used as prey in a pool experiment where individual predators were presented prey at densities of one, two, four, eight and 16 prey, respectively. Treatments were replicated seven times for each predator species. Perch was at first virtually unable to capture a prey from a school and suffered a significant confusion effect with increasing prey density. The effect, however, was limited in the long run, as the perch was a very effective predator in its hunting strategy where it singled out and repeatedly attacked single prey irrespective of prey density or school size. Pikeperch and pike were able to attack and capture prey at any prey density equally successfully and thus did not suffer from a confusion effect. Neither did these predators receive any apparent advantages from increasing prey density.

Key words: confusion; consumption; escape; piscivory; predation; predator-prey.

INTRODUCTION

Prey of piscivorous fishes are very mobile and have a broad spectrum of behavioural predator defences that affect their escape capability or, from the predator's point of view, capture success (CS, number of captures per number of attacks). One such behaviour is schooling, which also may benefit prey fishes in other ways, including foraging benefits such as information sharing and social learning (Welty, 1934; Reader & Laland, 2000), improved food location, and increased time allocated to foraging. Antipredator benefits from schooling are vigilance sharing and improved predator detection (Godin *et al.*, 1988), and improved predator evasion (Magurran, 1990; Pitcher & Parrish, 1993). That schooling reduces mortality risk experienced by individual prey is well documented (Krause *et al.*, 2000; Krause & Ruxton, 2002), and could result from different mechanisms. Per capita survival chances upon attack increase with school size simply due to the increase of potential prey, the dilution effect (Godin, 1986), whereas the confusion effect operates when a predator is overloaded by numerous and conflicting nervous inputs when trying to single out

*Author to whom correspondence should be addressed. Tel.: +46 46 2228371; fax: +46 46 2224536; email: hakan.turesson@limnol.lu.se

and attack a single prey (Neill & Cullen, 1974; Milinski, 1984; Landeau & Terborgh, 1986; Krakauer, 1995; Krause & Godin, 1995). Studies on effects of school size for piscivore foraging have given contradicting results. Capture success has been found to be independent of prey school size in rock bass *Ambloplites rupestris* (Rafinesque) (Krause *et al.*, 1998) and negatively related to prey school size in blue acara cichlid *Aequidens pulcher* (Gill) (Krause & Godin, 1995), largemouth bass *Micropterus salmoides* (Lacepéde) (Landeau & Terborgh, 1986), *Perca fluviatilis* L., (Neill & Cullen, 1974) and pike *Esox lucius* L. (Neill & Cullen, 1974). Besides differences in experimental design and definitions of terms, the contrasting results may be explained by differences in foraging strategies among the piscivores, *i.e.* sit-and-wait predators might be expected to be less affected by confusion effects than predators that actively search for and pursue prey (Krause *et al.*, 1998). The three common temperate freshwater predators; perch, pikeperch *Stizostedion lucioperca* (L.) and pike, in this study, have very different foraging strategies. Pike is a sit-and-wait predator while both perch and pikeperch are actively searching predators (Neill & Cullen, 1974; Hart, 1997; Craig, 2000). Perch is a sight-dependent diurnal predator, pike is mostly diurnal but also has a well-developed lateral line system (Dobler, 1977, Skov *et al.*, 2002), while pikeperch is a nocturnal piscivore that prefer to hunt in dim light and is less dependent on sight than pike and perch (Popova & Sytina, 1977). Pike and pikeperch are solitary foragers, while perch is known to hunt co-operatively (Eklöv, 1992; Craig, 2000). In this study the effect of prey school size on capture success was compared among these piscivores. Mechanisms affecting foraging success in individual piscivores is essential in the understanding of the effects of piscivores at the population and community level.

METHODS

EXPERIMENTAL FISH

Seven predators of each species were used in the experiments. Pike and perch were caught by electrofishing or hook and line in nearby lakes and ponds whereas the pikeperch were farmed in ponds. The size ranges (total length, L_T) were 190–235 mm for perch, 192–228 mm for pikeperch and 182–221 mm for pike. The predators were acclimatized to experimental conditions for a minimum of 3 weeks and all were consuming roach *Rutilus rutilus* (L.) for a minimum of 2 weeks prior to the experiments. The roach used as prey were wild fish caught from Lake Vombsjön where they are sympatric with perch, pikeperch and pike and constitute an important prey species for these predators. The roach were caught with a large hand-net and were used in the experiments 2 to 14 days after capture. Roach were fed dry flakes twice a day in the holding pools but were not fed during experiments. Unconsumed prey were reused in order to reduce the number of prey fish used. The prey were held in a pool of initially 300 fish and returned to this pool after each trial. The entire pool of prey, however, was exchanged between the perch and pikeperch experiments, and again between the pikeperch and pike experiments. This was to reduce differences in prey experience and the risk that the most escape capable prey would accumulate, as well as to avoid prey condition from decreasing due to long captivity times. Prey size was expressed as the ratio of prey L_T to predator L_T, (prey-to-predator size ratio, PPR; Hartman, 2000). For perch the prey size used were 0·27 PPR and for pikeperch and pike the prey size were 0·30 PPR. These sizes are well within the prey size range in nature for these predators. Prey fish were allowed to deviate up to 0·01 PPR from the length of its size class. For example, for a 200 mm predator, prey fish 58–62 mm L_T were used to get a PPR of 0·30. All prey were measured and examined for injuries or signs of illness at a minimum of 1 h prior to the experiments, after being anaesthetized with MS-222 (tricaine methane sulphonate).

EXPERIMENTAL POOLS

The experiments were carried out in a greenhouse under natural light conditions in southern Sweden. In summertime this means a day length of *c.* 17 h with extended dawn and dusk periods. Four circular test pools of 2·44 m diameter and a water depth of 350 mm were each equipped with a video camera mounted 3·4 m above the centre of the tank bottom. On the light blue pool bottom a black 200 mm grid net was drawn to be able to measure distances from the video recordings. The pools were bare except for a hide that consisted of two parallel bricks (length 250 and height 120 mm), positioned *c.* 75 mm apart and close to the pool centre. The hide was provided to give the predators, especially the pike, a chance to adopt the sit-and-wait predator strategy from a retreat and to give some structure. Otherwise the pools were kept bare to keep all fish visible on the video recordings and to be able to evaluate the effects of school size only, without other confounding factors affecting capture success. Oxygenated tap water was used and exchanged at a rate of 50% three times per week. The test pools were surrounded with a transparent plastic screen up to a height of 2·8 m to stop pike from jumping out of the pools (perch and pikeperch do not jump), without blocking light. A dark green tarpaulin was mounted to a height of 2·8 m between pools and along greenhouse walls to protect experimental fish from external disturbances.

EXPERIMENTS

In the experiments a single predator was used with prey densities of one, two, four, eight or 16 prey respectively. Each predator was used only once per prey density, in a randomized order, and prey densities were replicated seven times (once per predator). To reduce handling stress, an individual predator was not moved, but stayed in its experimental pool until it had experienced all prey densities. Individual predators were used for five consecutive days during the experiment and were fed one prey on the day preceding the first trial. In each trial, the video recording started before the prey were gently introduced to the predator with a small (1·5 l) bucket. In all replicates with more than one prey, the prey had time to form schools before being attacked by the predator. Due to the very different behaviours of the predator species, some differences in the duration of the experiments and time of day was needed. Perch and pike trials were performed under daylight conditions (*c.* 1000–5000 lx) at 1900–2100 hours. Perch trials were stopped after consumption of one to two prey to avoid satiation. Pike were allowed to feed for a maximum of 1 h. Due to the pikeperch's nocturnal behaviour, these experiments had to be performed at night. The experiments were started at 2130 hours (*c.* 500 lx), and video recordings continued until light levels were <1 lx, after *c.* 40 min, depending on weather conditions. Remaining prey were removed at 0800 hours the following morning. Only attacks preceding consumption were included in the analysis of capture success and only time to the consumption of the first prey was considered in the predator behaviour analysis. Satiation and motivation probably confounded the results for the later prey. Each experiment was recorded with VHS cameras that gave a good view of the behaviour of the fishes down to a light intensity of 1 lx. Temperature was measured in all replicates ($17{\cdot}6 \pm 1{\cdot}0°$ C for perch, $17{\cdot}2 \pm 1.1°$ C for pikeperch and $19.7 \pm 1.8°$ C for pike, mean ± S.D.). Swedish legislation concerning care and use of laboratory animals was followed and ethical permission for the experiments was given by Malmö/Lund's ethical committee (number M213-01).

VIDEO ANALYSIS AND STATISTICS

When analysing the video-tapes, data were collected on the following variables: (1) number of attacks preceding first capture (or number of attacks if no prey were captured); (2) attack type (sit-and-wait or pursuit attack); (3) attack outcome (capture or failure); (4) number of attacked prey (single or multiple). The attack was categorized as an attack towards multiple prey if there was one or more prey fish within two prey lengths from the prey closest to the attacking predator; (5) time to first foraging move (first move of the predator directed towards prey); (6) time from first foraging move to first attack.

A linear regression was used to analyse for effects of prey density on capture success, times from start to first move, and time from first move to attack. Prey densities were $\log_2$-transformed and time periods were $\log_{10}(x+1)$-transformed. When determining predator capture success for the different prey densities, the number of captures per number of attacks (CS) was calculated for each individual replicate and mean values of these individual replicates were then used for the regression. This allowed the inclusion of replicates that did not lead to prey capture. Excluding these replicates would have overestimated CS. SPSS 10.0 for Macintosh was used for all statistical analyses.

RESULTS

The three piscivore species behaved very differently in the experiments. The seven perch attacked and captured prey in all 35 trials while pike attacked prey in most trials and consumed prey in 25 trials. The activity of the nocturnal pikeperch increased as light level decreased and only 18 of the 35 trials resulted in prey captures before the 1 lx light limit was reached and prevented further filming. Prey were consumed during the night in another 13 trials (before 0800 hours), suggesting that pikeperch preferred to eat or were more capable of eating in the dark. Numbers of attacks and captures for the different species and an overview of the results are given in Table I. Perch typically hid in the refuge before the introduction of prey (27 of 35 trials) and so sometimes did pikeperch (16 of 35 trials), but both species always left the refuge to actively chase and attack prey with the exception of one sit-and-wait pikeperch attack (successful). Pike were immobile most of the time but, surprisingly, were the only species that did not use the refuge at all. Instead, pike were waiting motionless on the tank bottom, often close to the edge. Perch generally finished the entire predation cycle in a very short time compared to the other two species (Fig. 1). Roach formed schools in all trials with more than one prey, also during the lowest light levels for

TABLE I. Summary of the hunting behaviour of three piscivores. Density dependence, the number of captures per number of attacks (CS) was tested with linear regression on mean CS values per prey density

	Perch	Pikeperch	Pike
Number of attacks	199	211	166
Number of captured prey	35	18	25
Capture success	0·176	0·085	0·151
CS density dependent	Yes, $P = 0{\cdot}008$	No, $P = 0{\cdot}59$	No, $P = 0{\cdot}81$
Attack strategy	Pursuit	Pursuit	Sit-and-wait + pursuit

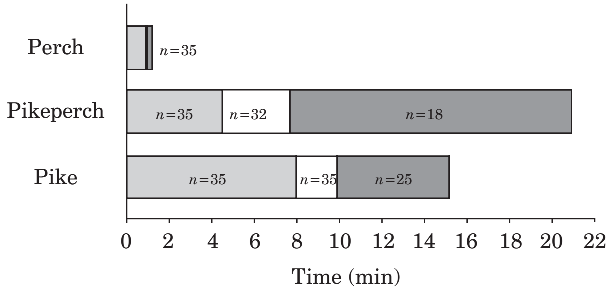

FIG. 1. Mean time spent in the different phases [time from: start to first move (▥), first move to first attack (□) and first attack to capture (▦)] of the predation cycle for the three piscivore species.

filming (pikeperch, 1 lx). They remained schooled on all occasions, except during direct attacks when schools split up.

CAPTURE SUCCESS

Number of attacks per replicate is shown in Fig. 2. These raw data are the basis for calculation of CS. For perch, capture success decreased with prey density (linear regression, $P = 0{\cdot}008$, $r^2 = 0{\cdot}93$). If individual values of attack number would have been used for the regression, the relationship would still have been significant ($P = 0{\cdot}044$, $r^2 = 0{\cdot}12$; Fig. 2). The CS for pikeperch ($P = 0{\cdot}59$) and pike ($P = 0{\cdot}81$) were not dependent on prey density. Here, also the replicates that did not end in prey captures were included in the calculations of mean CS for each prey density.

Attacks were further categorized as attacks towards single or multiple prey and CS for these different attacks were compared without regard to prey density (Fig. 3). When given multiple prey, perch were very skilled in splitting up the prey schools and then concentrated on single prey independent of prey number in the replicate. Thus, 168 of the totally 199 attacks were attacks towards single prey. Of these, 34 were successful, resulting in a capture success of $34/168 = 0{\cdot}20$ for attacks towards single prey. In contrast, of the 31 attacks towards schools of two or more prey, only one was successful (an attack towards two prey), which resulted in a CS of just $1/31 = 0{\cdot}03$. Clearly, perch were more effective in attacks towards single than multiple prey (likelihood ratio test, $P = 0{\cdot}008$). For pikeperch and pike, mean capture success was 0·09 and 0·15 respectively, and there were no differences in CS when attacking single or multiple prey (Fig. 3, likelihood ratio tests, $P = 0{\cdot}71$ and $P = 0{\cdot}45$). Pikeperch and pike were very capable of capturing one out of a school of prey, which further suggests that CS is independent of prey density in these two species.

When analysing for effects of prey density on the number of attacks for perch, the increase in attacks with prey density depended on an increase in the number of attacks towards both single and multiple prey (Fig. 4, linear regression for pooled numbers of single prey attacks, $P = 0{\cdot}030$, $r^2 = 0{\cdot}84$; linear regression for pooled multiple prey attacks, $P = 0{\cdot}004$, $r^2 = 0{\cdot}99$, prey density of one was excluded). An ANCOVA revealed that the increase rate in single prey attacks

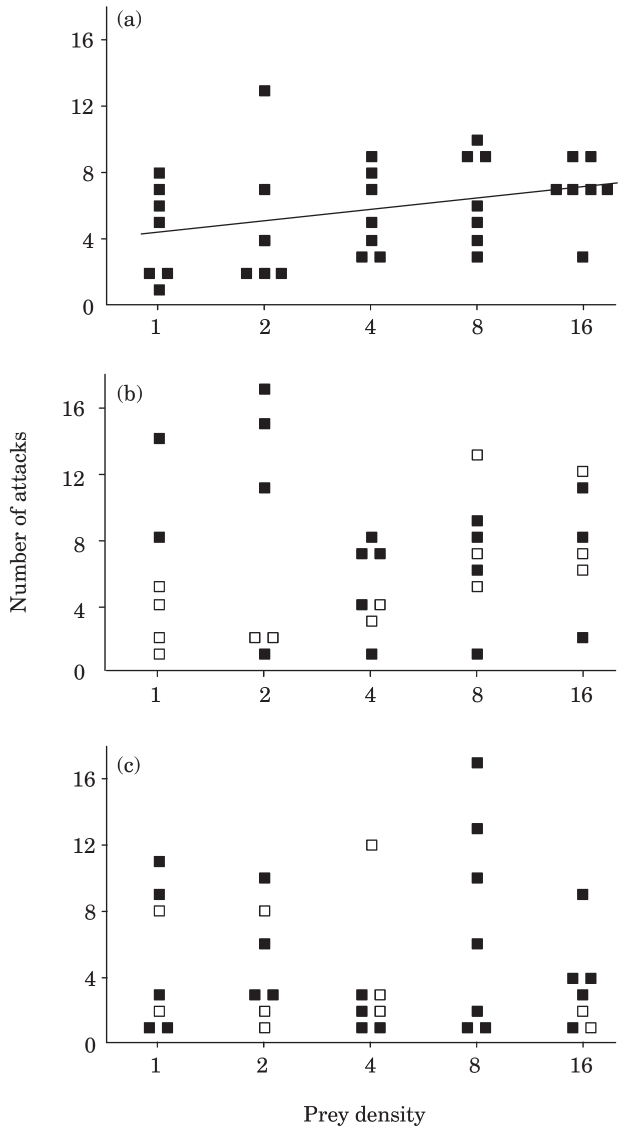

FIG. 2. Number of attacks that led to the first prey capture (■) or number of attacks in replicates that did not lead to prey capture (□) for (a) perch, (b) pikeperch and (c) pike. The line in the perch graph shows the best fit of a linear regression ($y = 4{\cdot}314 + 0{\cdot}686\log_2 x$; $P = 0{\cdot}008$). For pikeperch and perch, the regressions were non-significant ($P = 0{\cdot}59$ and $P = 0{\cdot}81$).

v. multiple prey attacks with prey density did not differ (interaction term, prey density × number of prey in attack, $P = 0{\cdot}28$).

Pike was the only species that undertook both sit-and-wait and pursuit attacks and therefore CS between these two attack strategies could be compared. Capture success was three times as high for sit-and-wait attacks than for pursuit attacks ($CS_{\text{sit-and-wait}} = 8/22 = 0{\cdot}36$, $CS_{\text{pursuit}} = 17/144 = 0{\cdot}12$, likelihood ratio test, $P = 0{\cdot}007$). The first attack in a trial was often a sit-and-wait attack where an

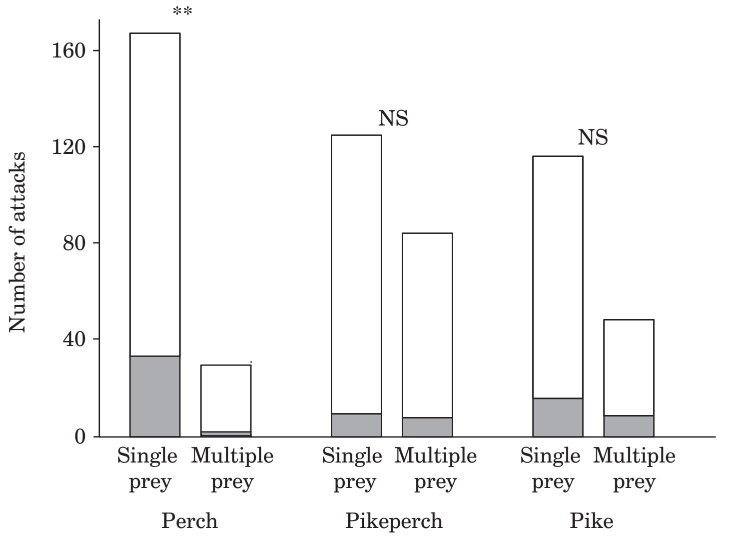

FIG. 3. Total number of successful (■) and unsuccessful (□) attacks towards single or multiple prey. The difference in proportions of successful attacks (CS) towards single or multiple prey was highly significant for perch (**, likelihood ratio test, $P = 0{\cdot}008$). For pikeperch and pike, CS was not different if the predator attacked single or multiple prey (likelihood ratio test, $P = 0{\cdot}71$ and $P = 0{\cdot}45$).

exposed but motionless pike suddenly moved towards one or several prey. Following attacks, however, were most often pursuit attacks and only 22 of the total 166 pike attacks (13%) were sit-and-wait attacks, despite the high efficiency of these.

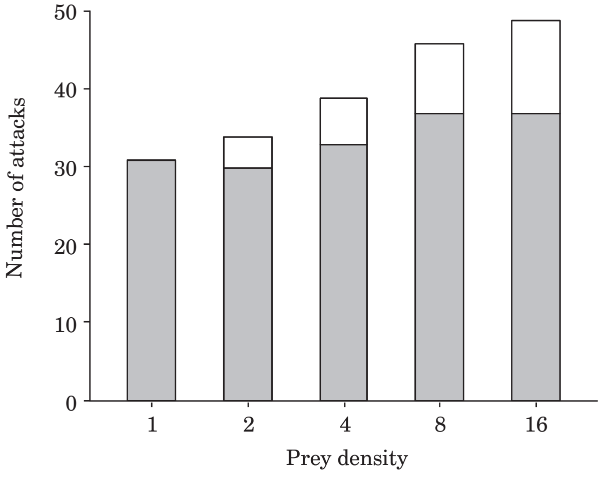

FIG. 4. Total number of perch attacks that were directed towards single (■) or multiple (□) prey. Both types of attacks increased with prey density (see text).

Number of attacks per attack sequence differed between the three species (Fig. 5). Perch did many attacks per attack sequence and were very successful, with 35/47 (74%) of attack sequences being successful. Pikeperch did rarely more than one attack per chase and pike only sometimes followed up the first attack (often sit-and-wait) with one or a few consequent pursuit attacks. Their success in attack sequences were 9·3 and 25% respectively.

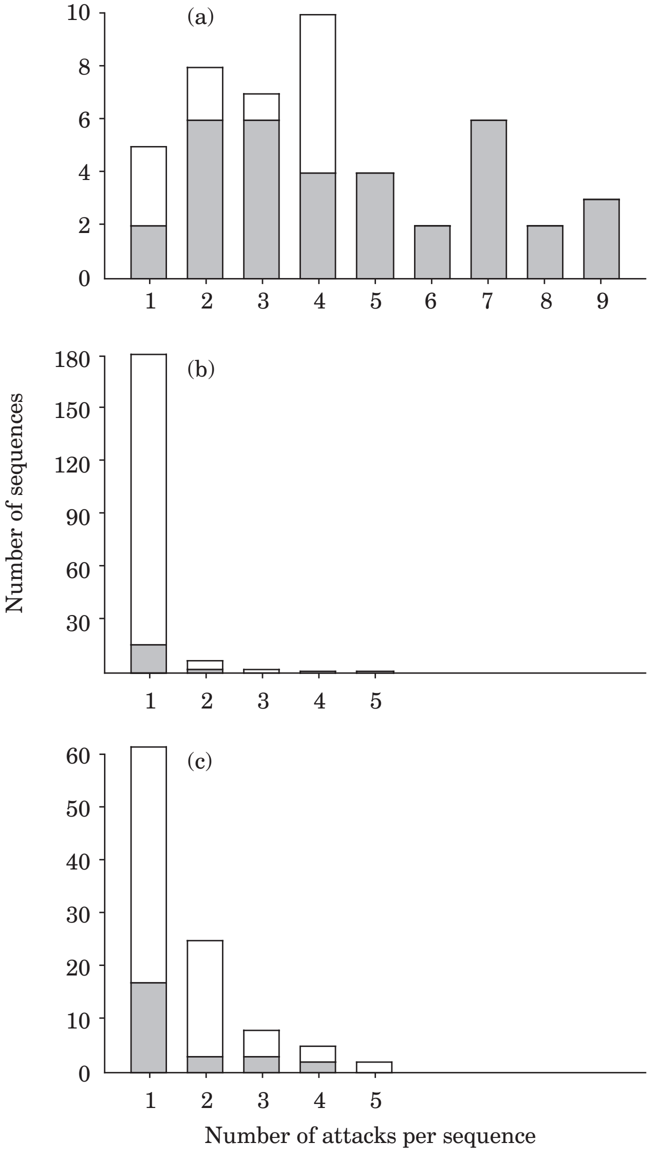

FIG. 5. Number of attacks per attack sequence for (a) perch, (b) pikeperch and (c) pike. Attack sequences led to prey capture (▨) or misses (□).

MOTIVATION AND PREY DETECTION

Time from start of a trial (introduction of prey) to the first foraging move of the predator (Figs 1 and 6) were measured. Perch moved towards prey after a median time of just 10 s (mean ± S.D. 54 ± 165 s), independent of prey density (linear regression, $P = 0{\cdot}52$). Pikeperch was slower to initiate foraging activity

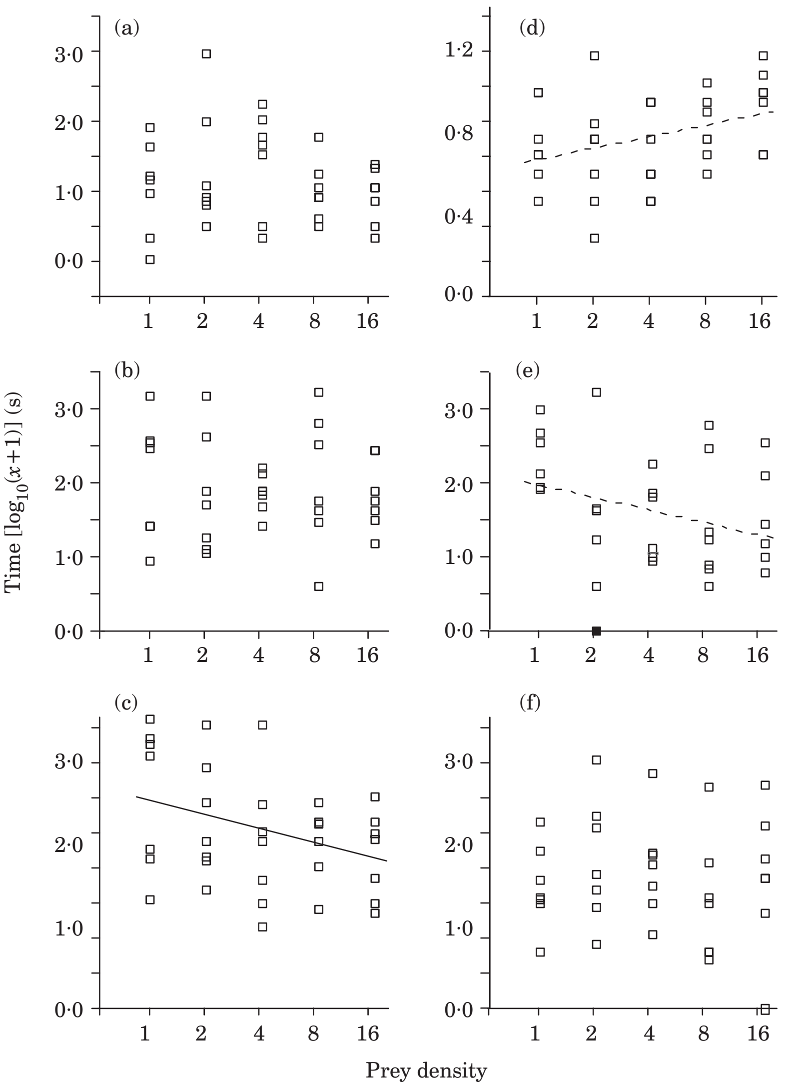

FIG. 6. Times from the start of the experiment to first foraging move [$\log_{10}(x+1)$-transformed] for (a) perch, (b) pikeperch and (c) pike. There was a negative relationship with prey density for pike (c) (linear regression, $y = 2{\cdot}481 - 0{\cdot}171\log_2 x$; $P = 0{\cdot}038$). For perch and pikeperch there were no relationships with prey density. Times from the first foraging move to the first attack [$\log_{10}(x+1)$-transformed] for (d) perch, (e) pikeperch and (f) pike. There was a positive trend for perch (d) (linear regression, $P = 0{\cdot}052$), and a negative trend for pikeperch (e) ($P = 0{\cdot}10$) [for pike (f), $P = 0{\cdot}70$].

(median time 72 s, mean time 271 ± 477 s) and this was also independent of prey density (linear regression, $P = 0{\cdot}69$). Time from introduction of prey to the first movement of the pike was long (median time 112 s, mean time 480 ± 835 s) but decreased with prey density (linear regression, $P = 0{\cdot}038$, $r^2 = 0{\cdot}12$, Fig. 6).

Time from first movement to attack was very short for perch (1–14 s) and showed a strong trend to increase with prey number (linear regression, $P = 0{\cdot}052$, $r^2 = 0{\cdot}11$, Figs 1 and 6). For pikeperch this time was much longer (Fig. 1) and tended to be weakly negatively related to prey number (linear regression, $P = 0{\cdot}101$, $r^2 = 0{\cdot}09$, Fig. 6). If the only sit-and-wait pikeperch attack is removed from the data, the regression becomes significant ($P = 0{\cdot}038$, $r^2 = 0{\cdot}14$). The data (Fig. 6) does not give an impression of a linear relationship, but rather that times in the lowest prey density (single prey) deviate from times in all the other prey densities. An independent group *t*-test between a prey density of one and all higher densities combined together give a *P*-value of 0·008. Time from first move to attack was independent of prey density in pike ($P = 0{\cdot}70$).

DISCUSSION

Perch was an active and efficient predator that usually finished its entire predation cycle in *c.* 2 min. It was the only species where prey density had an effect on the capability to catch prey. A confusion effect was evident as it took more attacks to catch prey at higher prey densities, resulting in a decreasing capture success (captures per attacks) with increasing prey density. Perch directed a large part of their attacks towards single prey even when multiple prey were present, which might be interpreted as a strategy to circumvent the confusion effect. When perch attacked a school, the first attack was almost always unsuccessful, but the unsuccessful multiple prey attacks broke up the school and the perch then followed with a sequence of more successful attacks towards single prey. Therefore, it may be more relevant to measure hunting success as the proportion of successful attack sequences. It then becomes apparent that perch, despite being regarded more of a generalist than a specialist piscivore, is a very efficient fish predator. The effective strategy of repeated attacks towards single prey may be a reason for the confusion effect being relatively moderate in perch. In comparison, the confusion effect is much more important in largemouth bass, which is effective in catching single prey or one out of two prey, but virtually unable to take prey from a school of eight or 15 prey (Landeau & Terborgh, 1986). Similarly the blue acara cichlid experiences a stronger reduction in capture success when attacking larger schools of prey (Krause & Godin, 1995). Perch is known to be a piscivore that often hunts in groups in nature, and its low success in first attacks when attacking multiple prey may be an important reason for co-operation (Eklöv, 1992). Several predators may then share these costly, but ineffective, attacks that are needed to split up a prey school for further attacks on single prey.

Pikeperch had a different hunting strategy. It was active most of the time and chased prey at low speed, sometimes interrupted by single attacks on prey, but these had low success and were rarely followed by an immediate second attack. Capture success was independent of prey number and pikeperch were able to capture a single prey from a school. There was no difference in capture success between single and multiple prey attacks, which further suggests that pikeperch do not suffer from a confusion effect. The capture success for pikeperch attacking roach (8·5%) was lower than for the other two piscivore species, which may in part be due to the experimental situation suiting pikeperch poorly. Pikeperch is known to be a nocturnal predator and is less dependent on sight than perch and pike. Pikeperch can use its lateral line system to track the hydrodynamic trail of prey in complete darkness (W. Hanke, pers. comm.). It can be noted that prey were consumed during the night in 13 of the 17 trials when prey were not consumed during filming under dusk conditions.

The mean capture success of pike was 15%, and did not depend on prey density. Attacks towards multiple prey were as successful as single prey attacks and, thus, pike did not suffer from a confusion effect. This result contrasts with the result of Neill & Cullen (1974), who found pike to suffer from confusion when attacking multiple prey. In their study, however, attack success was measured as captures per contacts, which differs from the method (captures per attacks) used in this study. Moreover, when attacking more than one prey in an approach, Neill & Cullen (1974) registered multiple contacts, possibly leading to the lower success rate of attacks towards schools of prey. It is interesting that pike, generally known as a sit-and-wait predator (Eklöv, 1992), was using the sit-and-wait foraging strategy in only 13·3% of the attacks, even though the sit-and-wait attacks were three times as effective (CS = 36%) as the pursuit attacks (CS = 12%). It may be that the sit-and-wait attack generally has a higher success rate than the pursuit attack in piscivores, since sit-and-wait predators mostly attack unaware prey. Despite the low proportion of sit-and-wait attacks, pike was a sit-and-wait predator in the sense that it was immobile or stalking and waiting for prey for most of the time. It may be that pike under natural condition spend a lot of time waiting for prey, immobile or stalking, *i.e.* adopts a sit-and-wait strategy when it comes to encountering prey, but is more active in the pursuit and attack phase of the prey cycle than generally acknowledged.

After the detection of prey and the initiation of foraging behaviour, the time to first attack was positively related to the density of prey for perch. This may be an effect of predator confusion where the perch needs more time for the attack decision. For pikeperch, the trend in time between first foraging move and first attack was negative. This trend is significant if the only sit-and-wait pikeperch attack is excluded from the data. The reason for the time delay, especially the longer times involved with single prey, is unknown. Normally pikeperch chased the prey at a slow pace during this time, irrespective of prey number. The delay in attacking single prey may be a result of weaker predator motivation. For pike, time from initiation of foraging behaviour to first attack did not depend on prey density.

A confusion effect was not apparent in pikeperch and pike, while perch suffered a significant but weak confusion effect. Therefore, confusion does not seem to be an important factor limiting predation on roach in the experiments. On the other hand, none of the predator species seemed to benefit from higher prey density. Thus, from the prey perspective, the roach clearly had an antipredator advantage of schooling by lowering its per capita predation risk through the dilution effect.

Prey density and school size has been used interchangeably when describing and discussing the results. This is no problem for the experimental set-up, where number of prey was controlled and the prey almost constantly formed one school, except when attacked. In a more natural situation it is possible that prey density and school sizes are not directly related. To fully understand the implications of the results of this study for prey consumption in nature, it would be essential to know how school sizes and size distribution relate to prey density and environmental variables such as predation risk, light, turbidity and habitat complexity. A few studies on how school sizes relate to population density, *e.g.* guppies *Poecilia reticulata* (Peters) (Seghers, 1981) and tunas *Thunnus albacares* (Bonnaterre), *Thunnus obesus* (Lowe) and *Katsuwonus pelamis* (L.) (Bonabeau & Dagorn, 1995), suggest that there is a positive relationship between density and school sizes. To better be able to predict piscivore consumption rates under natural conditions, the present result points to the need for a better understanding of how prey school sizes and school size distributions depend on prey density, and how predator capture success depends on prey school sizes in nature. Only prey density, without information on schooling behaviour, however, may not be a good predictor of predation rates.

Thanks to G. Linde for considerable help with the experiments and to the local fishermen in Vomb, for allowing collection of roach in their lake. Financial support was received from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (to C.B.).

References

Bonabeau, E. & Dagorn, L. (1995). Possible universality in the size distribution of fish schools. *Physical Review E* **51,** R5220–R5223.

Craig, J. F. (2000). *Percid Fishes*. Oxford: Blackwell Science.

Dobler, E. (1977). Correlation between the feeding time of the pike (*Esox lucius*) and the dispersal of a school of *Leucaspius delineatus*. *Oecologia* **27,** 93–96.

Eklöv, P. (1992). Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*. *Animal Behaviour* **44,** 313–326.

Godin, J.-G. J. (1986). Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). *Canadian Journal of Zoology* **64,** 1675–1678.

Godin, J.-G. J., Classon, L. J. & Abrams, M. V. (1988). Group vigilance and shoal size in a small characin fish. *Behaviour* **104,** 29–40.

Hart, P. J. B. (1997). Foraging tactics. In *Behavioural Ecology in Teleost Fishes* (Godin, J.-G. J., ed.), pp. 104–133. New York: Oxford University Press.

Hartman, K. J. (2000). The influence of size on striped bass foraging. *Marine Ecology Progress Series* **194,** 263–268.

Krakauer, D. C. (1995). Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behavioural Ecology and Sociobiology* **36,** 421–429.

Krause, J. & Godin, J.-G. J. (1995). Preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Animal Behaviour* **50,** 465–473.

Krause, J. & Ruxton, G. R. (2002). *Living in Groups*. Oxford: Oxford University Press.

Krause, J., Ruxton, G. J. & Rubenstein, D. (1998). Is there always an influence of shoal size on predator hunting success? *Journal of Fish Biology* **52,** 494–501.

Krause, J., Hoare, D. J., Croft, D., Lawrence, J., Ward, A., Ruxton, G. D., Godin, J.-G. J. & James, R. (2000). Fish shoal composition: mechanisms and constraints. *Proceedings of the Royal Society of London series B* **267,** 2011–2017.

Landeau, L. & Terborgh, J. (1986). Oddity and confusion effect in predation. *Animal Behaviour* **34,** 1372–1380.

Magurran, A. E. (1990). The inheritance and development of minnow anti-predator behaviour. *Animal Behaviour* **39,** 834–842.

Milinski, M. (1984). A predators costs of overcoming the confusion-effect of swarming prey. *Animal Behaviour* **32,** 1157–1162.

Neill, S. R. St R. & Cullen, J. M. (1974). Experiments on whether schooling by their prey affects hunting behaviour of cephalopods and fish predators. *Journal of Zoology. London* **172,** 549–569.

Pitcher, T. J. & Parrish, J. K. (1993). Functions of shoaling behaviour in teleosts. In *Behaviour of Teleost Fishes*, 2nd edn (Pitcher, T. J., ed.), pp. 369–439. London: Chapman & Hall.

Popova, O. A. & Sytina, L. A. (1977). Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. *Journal of the Fisheries Research Board of Canada* **34,** 1559–1570.

Reader, S. & Laland, K. (2000). Diffusion of foraging innovations in the guppy. *Animal Behaviour* **60,** 175–180.

Seghers, B. H. (1981). Facultative schooling in the spottail shiner (*Notropis hudsonius*): possible costs and benefits. *Environmental Biology of Fishes* **6,** 21–24.

Skov, C., Berg, S., Jacobsen, L. & Jepsen, N. (2002). Habitat use and foraging success of 0+ pike (*Esox lucius* L.) in experimental ponds related to prey fish, water transparency and light intensity. *Ecology of Freshwater Fish* **11,** 65–73.

Welty, C. (1934). Experiments in group behaviour of fishes. *Physiological Zoology* **7,** 85–128.

