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Threat-sensitive predator avoidance by pike larvae

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The threat-sensitive predator avoidance (TSPA) hypothesis was tested on hatchery-reared pike *Esox lucius* larvae. Larval swimming activity, food attacks upon zooplankton, escapes, immobility behaviour, vigilance, as well as time in vegetation under different predation risk were measured. Single larvae were video-filmed in aquaria allowing them to have visual contact with a small or a large perch *Perca fluviatilis* as predator. The odds of fleeing increased significantly if the larvae were exposed to a large predator instead of a small one. Swimming activity and foraging decreased significantly in the presence of a predator compared to the control. On the other hand, no significant effect was detected in time spent in the vegetation, and in vigilance of larvae, measured as time intervals between food attacks. The findings suggest that pike larvae primarily flee in the presence of a large predator, whereas they remain immobile, and forage, when possible, in the presence of a small predator. Sometimes a lack of response between the large and the small predator treatments was detected, which suggests that the antipredator response has a threshold, and when increasing the threat, the prey response does not increase. In the present paper it is demonstrated that hatchery-reared pike larvae respond to the level of threat, and thereby seem to be risk adjusting as predicted.

Key words: adaptive; *Esox lucius*; fleeing; risk-adjusting; trade-off.

INTRODUCTION

One strategy for juvenile fishes to decrease predation pressure is to grow as rapidly as possible (Milinski, 1986; Pedersen, 1997), and fast growth can be accomplished by energy maximization (Lima & Dill, 1990). Continuous feeding, however, is not usually adaptive because fish larvae must also avoid predators. On the other hand, minimization of risk, *i.e.* predator avoidance (Lima & Dill, 1990), is not adaptive either because prey may forgo too many feeding opportunities (Sih, 1987; Smith, 1997). Therefore, it is crucial to recognize different levels of predator threat correctly, so prey animals can allocate valuable time and energy to other activities (Sih, 1987; Lima & Dill, 1990; Mathis & Vincent, 2000; Chivers *et al.*, 2001).

The threat-sensitive predator avoidance (TSPA) hypothesis predicts that prey animals assess the magnitude of predator threat and adjust their behaviour accordingly (Helfman, 1989; Helfman & Winkelman, 1997). The ability to discriminate between different degrees of danger can have crucial effects on

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for example fitness and growth of the animal (Mathis & Vincent, 2000). Prey animals usually respond to predators by reducing the feeding rate or the efficiency of reproduction behaviour or other activities (Winkelman & Aho, 1993; Winkelman, 1996; Lima, 1998), and replace them with hiding, escaping or being immobile. The response of the prey animal should further reflect its level of vulnerability to a particular predator (Puttlitz *et al.*, 1999).

Threat-sensitivity has been studied in three-spined stickleback *Gasterosteus aculeatus* L., bicolour damselfish *Stegastes partitus* (Poey), the Pacific treefrog *Hyla regilla* (Baird & Girard), newt *Notophthalmus viridescens louisianensis* (*Wolterstorff*) and slimy sculpin *Cottus cognatus* Richardson (Bishop & Brown, 1992; Helfman & Winkelman, 1997; Puttlitz *et al.*, 1999; Mathis & Vincent, 2000; Chivers *et al.*, 2001). Slimy sculpins avoided areas where brook trout *Salvelinus fontinalis* (Mitchill) were big enough to pose a threat to them. Slimy sculpins further showed predator avoidance only when they were able to detect the predator visually (Chivers *et al.*, 2001). Three-spined stickleback larvae decreased feeding and spent little time close to large and medium-sized predators, whereas no change in behaviour could be detected in the presence of a small predator (Bishop & Brown, 1992).

The pike *Esox lucius* L. lays its eggs in shallow water with plants as the substratum (Casselman & Lewis, 1996). On these natural nursery grounds, pike juveniles may encounter strong predation pressure (Bry *et al.*, 1995). The pike is solitary and does not live in groups during any stage of its life (Casselman & Lewis, 1996) and the species exhibits a typical sit-and-wait foraging behaviour that is also reflected in the pike's responses to a predator (M. Lehtiniemi, unpubl. data). Hatchery-reared larvae that had no previous predator experience were used in the present study. Predator recognition, however, is considered to be an inherited character in pike (M. Lehtiniemi, unpubl. data).

In the present study the threat-sensitive predator avoidance hypothesis was tested on pike larvae. The main questions raised were: do pike larvae decrease their general activity level, *i.e.* swimming and feeding, and do they increase time in vegetation, as well as exhibit flight and freeze behaviour when exposed to a large-sized predator?

MATERIAL AND METHODS

TEST FISH

Pike larvae with yolk sacs (1 week post-hatch) were obtained from a fish hatchery in south-west Finland (Trollböle). The larvae originated from a wild, single female. They were transported to the laboratory in a covered plastic bag containing oxygen-enriched river-water. The larvae were acclimated to the temperature for 1 h and transferred to 30 l flow-through containers with brackish sea water (10 μm filtered, 12° C, salinity *c.* 5). *Fucus vesiculosus* L. and stones were added as protection. The larvae were fed with brackish-water zooplankton twice a day (0800 and 2000 hours). The light regime in the laboratory was 8L : 16D.

SAMPLING

Brackish-water zooplankton were collected by four hauls from 20 m depth to the surface with a 100 μm net.

Perch *Perca fluviatilis* L. were caught from a shallow bay with fish traps, which were emptied in the mornings and evenings. The perch were kept in a 30 l container with aerated sea water and they were fed with mysid shrimps caught from the littoral zone. The total length (L_T) of the fish was 21·0 cm (large) and 14·3 cm (small). The temperature was 15° C in the laboratory and the photoperiod was 8L : 16D.

EXPERIMENTAL PROTOCOL

Pike larvae were 18 days post-hatch (15·9 ± 0·8 mm, mean ± S.D.) when the experiment was conducted. Pike larvae were filmed with or without visual contact to a predator. Treatments consisted of a large and a small predator, and a control (no predator). The predator aquarium, the aquarium containing the perch, was placed next to the fish larval aquarium, the aquarium containing the pike, and the same predator (large or small), was used for all trials of a particular treatment. The fish larval aquarium was placed with its short side against the predator aquarium to be able to film the long side of the aquarium. The vegetation was always on the opposite side of the predator in the fish larval aquarium. The bottom of the fish larval aquarium was covered from underneath with black plastic, which imitated a dark bottom and prevented reflections. The video sessions were recorded at room temperature (*c.* 20° C) in 1·37 $\mu mol\ m^{-2}\ s^{-1}$ light. Two video cameras (JVC and Panasonic), filming one trial each, were used simultaneously side by side. The larvae were filmed in 2·1 l aquaria (15 × 7 × 20 cm). The predator was kept in an 8 l aquarium (20 × 20 × 20 cm). Vegetation was added to the aquaria and the plants consisted of green plastic strings pulled through perforations on a metal plate (13 strings per plate). Plastic plants were used to avoid potential compounds released from living vegetation. The metal plate covered half of the aquarium bottom, whereas the other half of the aquarium was an open water area. After the 'vegetation' had been put into the aquarium, filtered sea water (salinity *c.* 5) from the station's water filtration system (0·2 μm) was added. Finally a dense natural zooplankton community (*c.* 600 individuals l^{-1}) and the pike larva were added to the aquarium. By conducting all experimental trials during 1 day, it was assured that all fish encountered the same food concentration and food species. The zooplankton community was properly mixed before addition to the aquaria. The pike larva was tested singly with no conspecifics present. The fish were filmed for 10 min., *i.e.* one 10 min. session was considered one experimental unit in the experiment. Later during analysis of the video sessions, total swimming time, *i.e.* movement, of the pike larvae was measured. Time spent in the vegetation (hiding, *i.e.* searching for a refuge) was recognized when the fish larva was completely in the vegetation or on the border between vegetation and open water. The number of attacks upon zooplankton prey was counted in the open water and in vegetation. Other recorded behaviours were larva remained immobile after predator detection, by the surface or by the bottom ('freeze'), and the time intervals between food attacks ('vigilance'). Trials where larvae performed less than two attacks were excluded. Finally fleeing behaviour of larvae was recorded, indicating that they attempted to escape rapidly after detection of the predator. The 'flee' behaviour has been described by Helfman (1989) as rapid swimming toward the refuge site, often with erratic, zigzag motion. A record was made on whether predators behaved normally, *i.e.* showed interest in the prey and swimming was relaxed. There was no obvious difference in the characteristics of the predators (*e.g.* bold or shy). The total number of fish larvae used in the experiment was 30 (10 × 3, group size × treatments). The number of trials in the experiment was also 30, because only one fish was used per trial. Pike larvae were used once, in order to avoid learning.

Animal welfare was respected during all stages of the study. Permission (number 347) was granted by the ethical committee at the University of Helsinki, Finland. All larvae were released after the experiment.

STATISTICAL ANALYSES

All data were tested for normality and homoscedasticity. Swimming, food attacks and time in the vegetation were analysed with the multivariate analysis of variance (MANOVA).

Pillai's trace was used as a MANOVA test-statistic because it is considered the most robust concerning slight deviances from the usual test assumptions (Zar, 1999). Tamhanes' *post-hoc* test was used due to the same reasons. Vigilance, *i.e.* time intervals measured between food attacks, was analysed using one-way ANOVA, by comparing mean slopes of food attack curves, the mean slope calculated separately for each treatment. The 'flee' and 'freeze' data were bivariate, and therefore analysed with a logistic regression. Controls were excluded from the logistic regressions. In the 'freeze' analysis, fish 'freezing' by the surface were scored 1, and the ones 'freezing' by the bottom or not 'freezing', were scored 0. The food attacks in the vegetation were analysed with Spearman's rank correlation. The hypothesis test was performed by meta-analysis (Sokal & Rohlf, 1995).

RESULTS

GENERAL ACTIVITY LEVEL

Larval swimming time was significantly different between treatments: no predator, the small and the large predator (MANOVA, univariate tests, d.f. = 2 and 27, $P < 0{\cdot}01$) and was significantly lower in the presence of a large predator than in the control (Tamhane's T2 *post-hoc* test, $P < 0{\cdot}001$) [Fig. 1(a)].

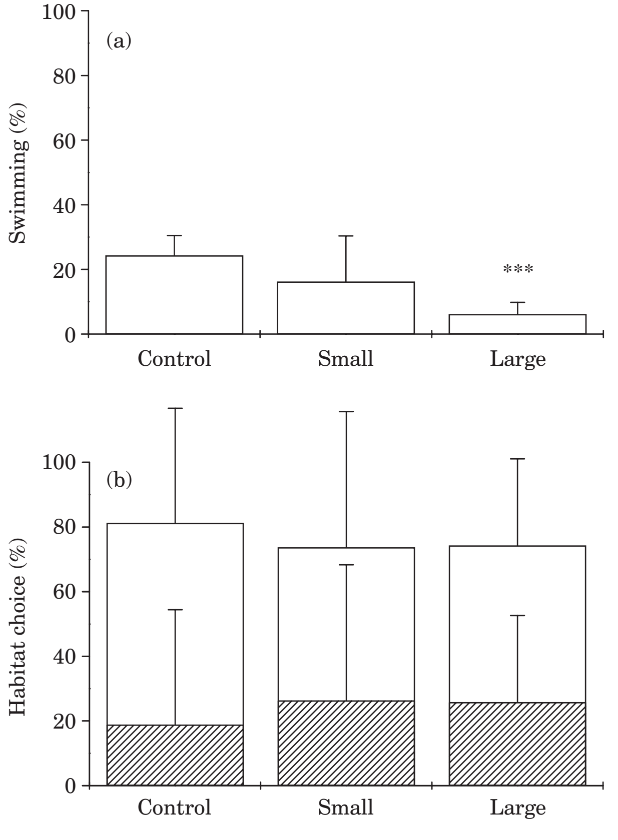

FIG. 1. Mean + S.D. (a) swimming time and (b) time spent in the open water (□) and the vegetation (▨) as percentages of the total session time (10 min), by larval *Esox lucius* exposed to a small or large *Perca fluviatilis* (predator) or no predator (control). ***, $P < 0{\cdot}001$.

Total time spent hiding by pike larvae in the vegetation was not significantly higher when they had visual contact with the perch (MANOVA, univariate tests, d.f. = 2 and 27, $P > 0{\cdot}05$) [Fig. 1(b)].

Larvae often performed 'flee' behaviour in the presence of a predator, whereas this behaviour was never observed in the control. The odds of 'fleeing' in the presence of a large predator were 94·6% higher, or two-fold, than in the presence of a small predator (logistic regression, Wald = 5·185, d.f. = 1, $P < 0{\cdot}05$, Odds ratio = 0·056, 95% CI = 0·005–0·669) [Fig. 2(a)]. The odds of 'freezing' close to the surface, in the presence of a large perch, were not significantly different between the large and the small predator treatment (logistic regression, Wald = 0·534, d.f. = 1, $P > 0{\cdot}05$, Odds ratio = 0·500, 95% CI = 0·078–3·210) [Fig. 2(b)].

FORAGING AND HIDING

The behaviour of pike larvae was significantly altered when fish were exposed to predators (MANOVA, Pillai's trace = 0·503, d.f. = 6 and 52, $P < 0{\cdot}05$). Foraging by larvae was significantly different between the treatments, *i.e.* small, large or no predator (MANOVA, univariate tests, d.f. = 2 and 27, $P < 0{\cdot}01$), *i.e.* foraging was significantly lower in the presence of a large predator than in the control lacking a predator (Tamhane's T2 *post-hoc* test, $P < 0{\cdot}001$) (Fig. 3).

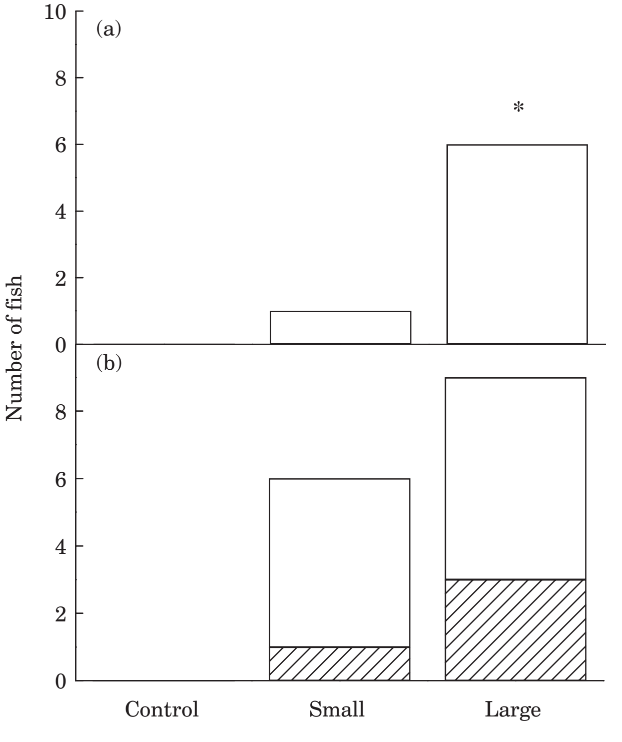

FIG. 2. (a) 'Flee' and (b) 'freeze' behaviour by *Esox lucius* larvae exposed to a small or large *Perca fluviatilis* (predator) or no predator (control). 'Freeze' behaviour was measured as immobility close to the surface (□) or the bottom (▨) during the video session. Group size = 10. *, $P < 0{\cdot}05$.

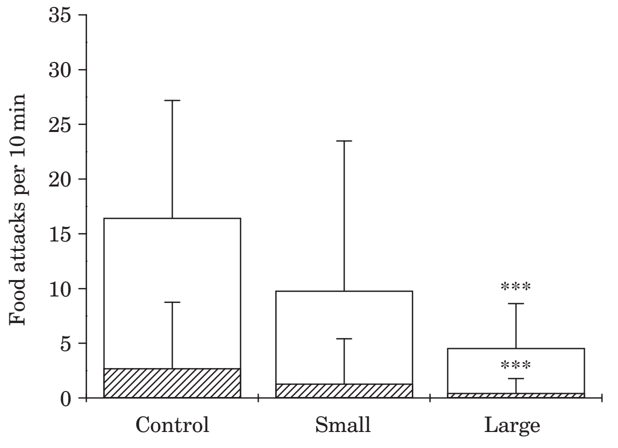

FIG. 3. Mean + S.D. number of food attacks upon zooplankton in the open water (□) and in the vegetation (▨) per 10 min session by larval *Esox lucius* exposed to a small or large *Perca fluviatilis* (predator) or no predator (control). ***, $P < 0.001$.

Vigilance was analysed by comparing the slopes of the food attacks over time. The result showed that the mean time interval between attacks in the different treatments did not differ from each other (one-way ANOVA, d.f. = 2 and 25, $P > 0.05$) (Fig. 4), although the number of attacks varied significantly.

The number of attacks performed in the vegetation did not correlate with food attacks in the open water (Spearman's rank correlation, $r_s = -0.211$, $n = 30$, $P > 0.05$). Time spent by larvae in the vegetation, however, was significantly correlated with number of food attacks upon zooplankton, performed in the vegetation (Spearman's rank correlation, $r_s = 0.622$, $n = 30$, $P < 0.001$).

HYPOTHESIS TEST

The result of the meta-analysis showed that the null hypothesis of TSPA, stating that there is no difference in predator avoidance in the presence of different levels of threat, can be rejected with confidence (d.f. = 12, $P < 0.001$) (Table I).

DISCUSSION

The present study demonstrated that hatchery-reared pike larvae are able to discriminate between different levels of threat. The ability of larvae to distinguish between magnitudes of threat was most clearly observed in the large increase in the probability of fleeing. Swimming activity and foraging decreased significantly with increased degree of threat. These findings are in agreement with previous research (Lima & Dill, 1990; Williams & Brown, 1991; Bishop & Brown, 1992; Stauffer & Semlitsch, 1993; Cieri & Stearns, 1999; Brown & Dreier, 2002).

GENERAL ACTIVITY

Animals usually reduce their activity level in the presence of predators (Lima & Dill, 1990). In the large predator treatment, less swimming was observed,

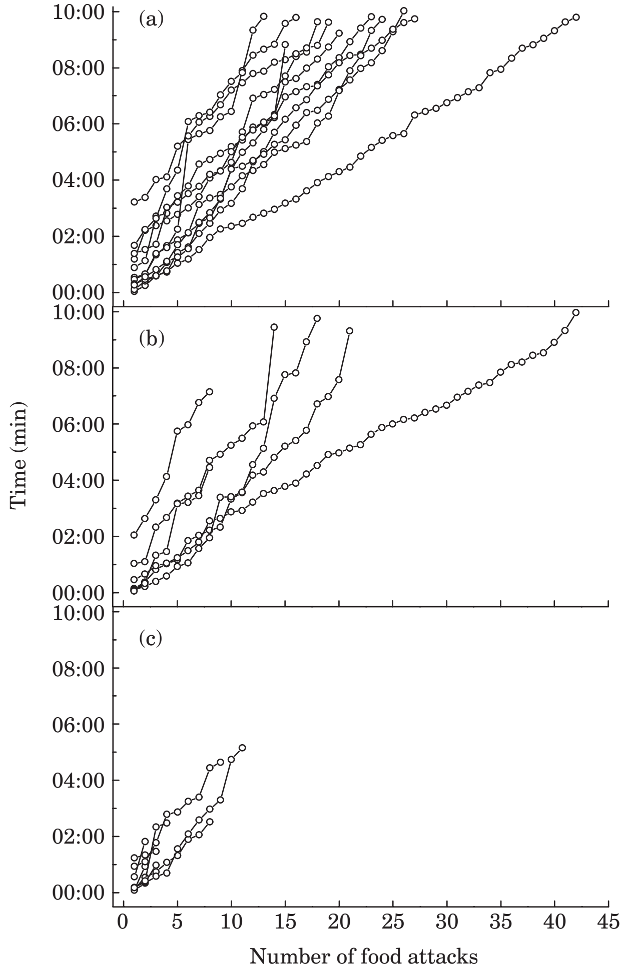

FIG. 4. Number of food attacks plotted on a 10 min timescale separately for each experimental unit, *i.e.* fish larva. The *Esox lucius* larvae were filmed (a) without a predator (control), and with visual contact with a (b) small or (c) large *Perca fluviatilis* (predator).

TABLE I. Summary of P values included in the meta-analysis. The analysis combines probabilities from independent tests of significance as follows $-2\Sigma \ln P$ (Sokal & Rohlf, 1995)

Analysis	P
MANOVA	0·016
Spearman rank correlation	0·001
Spearman rank correlation	0·264
Logistic regression	0·023
Logistic regression	0·465
One-way ANOVA	0·544

which is adaptive and in agreement with the TSPA-hypothesis (Helfman, 1989). Blaxter & Fuiman (1990) suggested that reduced movement or activity decreases the number of attacks on small pelagic larvae by fish predators and Werner *et al.* (1983) showed how prey decrease activity or shift to safer habitats in the presence of predators. Fishes, such as slimy sculpins, have been reported threat-sensitive when exposed to visual cues, and not chemical cues (Chivers *et al.*, 2001).

FOOD ATTACKS

The risk of starvation and predation is much larger in larval fishes (Hunter, 1981; Fuiman, 1989) and the ability to recognize predatory threat is important, so that larvae can assess trade-offs and reduce costs associated with predator avoidance. The energetic status of fishes, *i.e.* 'the hunger level', may indicate that the fishes take more risk and are more prone to predation (Hossain *et al.*, 2002). Fraser & Huntingford (1986) have classified different predator avoidance behaviours. Risk adjusters reduce foraging proportionally to the level of threat and this classification can be applied to pike in the present study. The present results showed that the difference in number of food attacks was considerable between control and large predator treatment, whereas the difference between the small and the large predator treatments were not always that clear. A plausible reason for the lack of difference between predator treatments is that the antipredator response has a threshold value and when threat increases, the prey response does not necessarily increase (Miklósi & Csányi, 1999). It has further been shown that young fishes either show low responsiveness to predators, or show few graded responses and might respond strongly to predators, independent of threat intensity (Blaxter & Fuiman, 1990; Helfman & Winkelman, 1997).

Vigilance can be detected by decreased feeding efficiency (Fraser & Huntingford, 1986; Milinski, 1986) and in the current study it was measured by comparing the slopes of time intervals between food attacks, which did not differ between each other. Although all larvae were siblings and had the same growth history, they exhibited individual behaviour, resulting in variation in the data. A variable response to predation would have been expected if larvae varied in size (Bishop & Brown, 1992), but this was not the case in the present study. Grand (2002) showed that individual fish varied considerably in their responses to predators, depending on their competitive abilities. Brick & Jakobsson (2002) also showed individual differences in predatory response among fishes, with some individuals more prone to inspect and fight with a model predator.

SEARCH FOR REFUGE

The total time spent in vegetation did not indicate that larvae preferred to stay in a refuge in the presence of a predator [Fig. 1(b)]. In this study pike larvae chose to 'freeze' instead of searching for a refuge. 'Freezing' is probably less risky than swimming to a shelter (Blaxter & Fuiman, 1990). The trade-off between lost food opportunities and predator avoidance in refuges (Krause *et al.*, 2000), may have affected the behaviour of the larvae.

The more time larvae spent in vegetation the more food they ingested. This result suggests that larvae 'felt safe' in the refuge, when they decided to enter it. Studies suggest that many animals prefer feeding close to cover (Lima & Dill, 1990). On the other hand, feeding in the open water did not correlate with feeding in the vegetation, which indicates that larvae fed more in the open water than in the vegetation. It is an expected outcome, because foraging of fishes decrease with increasing habitat complexity, as submerged vegetation impedes swimming and obstructs sight for the feeding fishes (Manatunge *et al.*, 2000). The result clearly shows that although larvae had to spend part of their time in the vegetation, to survive, they were able to feed there, although not as much as in the open water.

'FLEE' AND 'FREEZE' BEHAVIOUR

In the present study, pike larvae fled in the large predator treatment. This behaviour suggests that fish larvae considered the predator dangerous. Miklósi & Csányi (1999) found that paradise fish *Macropodus opercularis* (L.) larvae fled more in the presence of larger predator models and the models with large threatening eyespots. The cost of predator avoidance can also be higher when larvae have to stay vigilant and are unable to feed. If larvae decide to flee, this could also be risky. Risk in a predator-prey encounter depends, among other things, on the time it would take for prey to reach safety, and fishes farther from safety, such as rock or seaweed, should flee sooner than those closer to cover (Lima & Dill, 1990). It suggests that the pike larvae fled soon and rapidly, because they were quite close to the predator (the aquaria placed next to each other). The result was clearly not affected by the short distance to cover (maximum 7·5 cm).

During a predatory encounter, larvae reduced swimming activity and exhibited 'freeze' behaviour. In this study 'freezing' is interpreted as an adaptation to reduce the larva's probability of detection (Bishop & Brown, 1992). 'Freezing' is a useful antipredator defence because the predator's mechanoreceptors detect movement of potential prey, and because fish larvae often lack pigmentation; they blend with the environment (Blaxter & Fuiman, 1990; Williams & Brown, 1991). Although pike use a sit-and-wait strategy during foraging, time spent on swimming decreased considerably in the presence of a predator.

Hatchery-reared pike larvae, with no previous predator-experience, were able to respond sensitively to different magnitudes of hazard, and behaved predictably. The strongest proof for the threat-sensitive predator avoidance hypothesis was observed in the larvae's escape behaviour. The larger the predator was, the greater the probability of escape. In general, the findings suggested that pike larvae primarily flee in the presence of a large predator, whereas they remain immobile, and forage, when possible, in the presence of a smaller predator. Further, pike larvae also showed individual variation in behaviour, although they were offspring from the same female, were of the same age, and had the same growth history. Although the pike larvae had no previous predator experience, they seem to develop the ability to assess risk at an early age.

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