Aggregation in juvenile pike (*Esox lucius*): interactions between habitat and density in early winter

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Summary

1. Juvenile pike (*Esox lucius*), a cannibalistic fish species, aggregates within habitat patches. The advantages to cannibals of aggregating in the absence of other predators and food constraints are not immediately obvious. In this study we explore the basis for this grouping by observing how spatial distributions of juvenile pike are mediated by the presence of conspecifics.

2. Solitary pike preferred shallow-water (0·17 m depth) habitats. When fish density was increased, the average time spent in alternative deep-water habitat (0·33 m) increased, consistent with a despotic type of distribution and suggesting that interference was occurring.

3. In pairs of fish, one pike, nominally the dominant individual, showed a habitat use similar to that of single fish. The second individual mostly occupied deep water, again consistent with a despotic distribution and apparently mediated by intimidation interference. However, dominant pike did on occasion enter deep water, at which times the subordinate pike remained with the dominant fish, appearing to aggregate in the pool.

4. We propose that habitat-specific risk could explain aggregations of pike in deep water. Although remaining in close proximity to dominant individuals in deep water would seemingly put subordinate fish at great risk, the alternative of moving to shallow water may increase risk still further by reducing the capacity to perceive and/or evade attacks.

Key-words: Competitive exclusion, dominance, grouping, ideal despotic distribution, intimidation

Introduction

Aggregating can provide benefits to individual animals in terms of predator defence, foraging, mate searching and energy efficiency (Pitcher & Parrish 1993; Lee 1994; Krause & Ruxton 2002). However, grouping may also incur costs, for example, from sharing resources (exploitation competition) (Krause & Ruxton 2002). In addition, high-density living often results in interference, whereby the presence of conspecifics impairs individuals from exploiting a resource effectively (Begon, Harper & Townsend 1996). Interference has been documented in many taxa, including insects (e.g. Whitehouse & Lubin 1999), birds (e.g. Goss-Custard *et al.* 2001), reptiles (e.g. James & M'Closkey 2004) and fish (e.g. Holbrook & Schmitt 2002).

Spatial distributions of animal populations that do not suffer interference can be modelled by the ideal free distribution (IFD; Fretwell & Lucas 1970), in which the proportion of a population in a given habitat patch relates to quality of the patch irrespective of total population density. This provides a good approximation of the distributions of some animals (e.g. Harper 1982; Kacelnik, Krebs & Bernstein 1992; Ohashi & Yahara 2002; Lin & Batzli 2004). However, most populations do not fit the IFD because interference commonly occurs (e.g. Yasukawa & Bick 1983; Nakano 1995; Whiteman & Côté 2004) and instead may approach an ideal despotic distribution (IDD; Fretwell 1972). Under the IDD, some individuals sequester and defend good quality patches of habitat, leaving poorer competitors to occupy remaining patches. The IDD may be modelled as a dynamic distribution in which individuals respond to temporal variations in the spatial distribution of resources and occupy the best quality of patch that is locally available (Ruxton, Armstrong & Humphries 1999). This dynamic IDD was developed on the basis that intrinsic quality of each patch was independent of total density of foragers and was diminished only by the presence of consuming animals within the patch.

Intensity of interference varies among species and in the extreme can take the form of cannibalism or fatal

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wounding from a single encounter. Northern Pike, *Esox lucius* L., can be considered to be a species in which interference intensity is very high. Juveniles can cannibalize individuals *c*. 50–75% of their own body length (Hunt & Carbine 1951; Craig & Kipling 1983; Giles, Wright & Nord 1986) and are particularly vulnerable to attack from conspecifics of similar size when handling prey (Nilsson & Brönmark 1999), as usual defence behaviours are presumably compromised.

In view of this high intensity of interference and the tendency for interference to promote dispersion, the earlier finding (Hawkins, Armstrong & Magurran 2003) that juvenile (age 0) pike form groups in deep water rather than dispersing to use shallow areas, seems surprising. There are some recorded examples of cannibalistic species grouping. Antlions, *Myrmeleon* spp., for example, aggregate when suitable microhabitats are rare (Gotelli 1993). Aggregations of pondskaters, e.g. *Gerris najas* Degeer, probably reflect a temporary high population density relative to carrying capacity prior to cannibalistic cropping (Brinkhurst 1966). The spider *Tegenaria atrica* C.L. Koch tolerates conspecifics under high-food conditions (Pourie & Trabalon 2001) when the presence of alternative food reduces risk of cannibalism and the abundant diet inhibits development of cuticular lipids used in pheromonal communication during aggressive interactions. These mechanisms did not appear to explain the grouping among pike, but Hawkins *et al*. (2003) suggested that antipredator benefits of shoaling might exceed risks of cannibalism from group living. Alternatively, the distribution may result from despotic occupation of shallow water with subordinate fishes clustering in more marginal deep-water habitat.

The study presented here was designed to assess the behavioural mechanisms that underpin grouping behaviour among young-of-the-year pike. First, we established the preferred habitat of single fish. Then, using pairs and groups of four fish, we observed how density affected habitat use. Aggregation in preferred habitat would support the hypothesis that shoaling occurred. On the other hand, aggregation in more marginal habitat would be consistent with the hypothesis that interference excluded subordinate fish from favoured habitat, consistent with a despotic distribution. Finally, we compared time-space budgets of pairs of fish to determine whether subordinate fish used high-quality patches vacated by dominant fish, as predicted by Ruxton *et al*.'s (1999) dynamic IDD.

Materials and methods

FISH

Progeny of a single female and two male pike from Loch Freuchie (56°3′N, 3°5′W), stripped and fertilized in spring 2002, were reared at the Fisheries Research Services Almondbank field station, Perthshire, Scotland. Cannibalism occurred during fry stages (starting at a body length of *c*. 30 mm). As soon as this was noticed fish were size-graded in separate tanks. Some individuals quickly outgrew the other fry in the tanks and again attempted cannibalism, making size-segregation a continuous process during the first year. The fish used in these experiments were taken from three size-graded stock tanks supplied with water from the River Almond at ambient temperature. They were fed a diet of earthworms (*Dendrobaena* sp.) and dead Atlantic Salmon (*Salmo salar* L.) parr. Experiments were conducted in the first winter (18 November to 18 December 2002) when the length of the young-of-the-year fish used in the experiments was $145 \cdot 4 \pm 8 \cdot 7$ mm, 134–160 mm (L_T; mean $\pm$ SD, range). Individuals were chosen for experiments by first taking a stock tank randomly and then selecting an individual at random and ensuring this chosen fish was netted. In total, 45 pike were used and each individual was used once only. Test aquaria thus provided novel environments for all experiments and replicates. Each individual was identifiable by unique natural stripe markings on its lateral flanks. It was not possible to determine the sex of individuals.

For ethical reasons, groups of pike in each replicate had length differences of only 13–18% to prevent cannibalism. Furthermore, the fish were not fed, because it is known that this would make them particularly vulnerable to attack (Nilsson & Brönmark 1999). Therefore, the fish were provided with conditions in which they could exhibit the behaviours that reduced their vulnerability to attack.

EXPERIMENTS

We measured the habitat used by individual fish at three population densities – one, two and four fish per tank. Ten tanks ($0 \cdot 9 \times 0 \cdot 4 \times 0 \cdot 35$ m^3) were arranged along three sides of an observation arena, with water supplied as for the stock tanks. Three sides of each tank were covered with black polythene and the fourth side allowed the fish to be viewed by the observer in the centre of the arena. Each tank contained two habitat types – relatively shallow ($0 \cdot 17$ m depth) and deep ($0 \cdot 33$ m depth) water. The deep-water habitat (pool; $0 \cdot 3 \times 0 \cdot 4$ m^2) and the shallow habitat ($0 \cdot 6 \times 0 \cdot 4$ m^2) accounted for $0 \cdot 12$ m^2 (35·6%) and $0 \cdot 22$ m^2 (64·4%) of the total surface area, respectively (Fig. 1). The substrata of both habitats consisted of a layer of large gravel and were otherwise bare, which is a natural habitat type limited to the winter period. The pool occupied the left side of five of the aquaria and the right side of five of the aquaria. Replicates of each density treatment were distributed evenly throughout the time period and observation tanks. The mean daily average water temperature during the experiments was 5·0 °C (range: 0·3–7·5 °C). Fluorescent lighting provided illumination to the aquaria of 220 lux for 18 h per day (00.00–18.00 h).

For all trials, fish were placed into the aquaria in the morning (10.00), and were distributed between the two
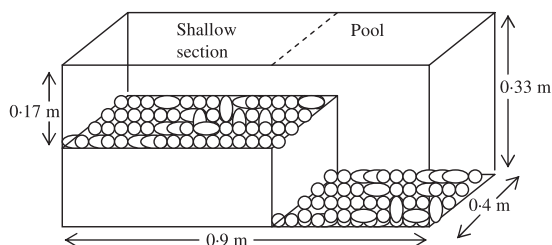
Fig. 1. Diagram of the tank design used in the experiments.

habitats (shallow- and deep-water) at random. Three days were allowed for fish to settle (Hawkins *et al.* 2003). Habitat use was recorded on day four as the proportion of observations that a fish was in each habitat. Observations were made every 30 min between 09.00 and 16.00 h. We conducted $n = 7$ trials with single fish (L_T: 140·7 ± 8·4 mm, weight: 20·5 ± 3·0 g, mean ± SD), $n = 7$ trials of density two (147·0 ± 7·6 mm, 23·2 ± 3·5 g) and $n = 6$ trials of density four (145·9 ± 9·3 mm, 23·1 ± 5·3 g). Size differences (mean ± SD, range) between individuals sharing an aquarium at density two were: L_T, 6·0 ± 5·1 mm, 1–16 mm; weight, 3·0 ± 2·1 g, 0·6–6·5 g. Size differences between the largest and smallest fish in density four replicates were 21·3 ± 2·7 mm, 18–24 mm, 10·7 ± 4·2 g, 7·7–18·8 g.

DATA ANALYSIS

Habitat preference and effects of density on habitat use

Habitat use was calculated as the proportion of observations in which a fish occupied each habitat. Data were normalized by square root arcsine transformation prior to analysis. Habitat preference of single fish was calculated as the proportion of the observations that an individual was in each habitat, and a mean value was calculated for the seven fish. We refer to these mean values as the expected time a fish would spend in a habitat with no interference (pool use = p and shallow habitat use = $1 - p$). Habitat preference was established by comparison of the habitat use of single fish with habitat availability. Comparisons of habitat use across densities used ANOVA followed by *post-hoc* Bonferroni testing.

Aggregation

A null estimate of proportions of time that fish in pairs would co-occur in each habitat if their individual distributions were independent of one another (i.e. no attraction or interference) was calculated from the data for habitat use by individual fish. The expected time for fish occurring in separate habitat is $2[p(1 - p)]$, for fish occurring together in pools is p^2 and fish occurring together in shallow habitat is $(1 - p)^2$. Actual frequencies of occurrence were compared with these null values to assess evidence for aggregation and segregation.
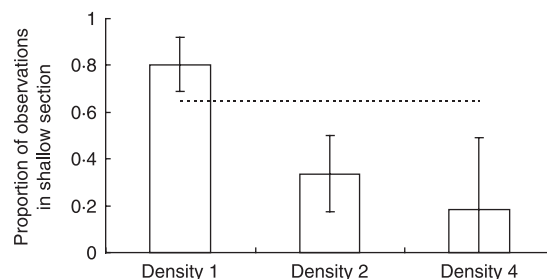
Fig. 2. Mean occupancy of the shallow section by fish at varying densities. Error bars indicate 95% CI. Dashed line represents shallow area as proportion of total area.

Results

### HABITAT PREFERENCE AND EFFECTS OF DENSITY ON HABITAT USE

There was a difference in mean habitat choice among fish densities ($F_{2,17} = 9.890$, $P = 0.001$; Fig. 2). Single fish occurred in the shallow habitat significantly more (shallow habitat occupied 80·3 ± 11·6% (mean ± 95% confidence interval, CI) of the time) than the average time that pairs (33·6 ± 16·2%, $P = 0.013$) or groups of four fish (18·2 ± 30·7%, $P = 0.02$) occupied shallow water. Pairs and groups of fish did not differ significantly in habitat use ($P = 0.926$). Single fish showed a significant tendency to use shallow water more than would be expected than if they were distributed at random (Fig. 2).

DOMINANCE AND AVOIDANCE IN PAIRS

Time spent in the preferred shallow section was asymmetric between individuals within pairs of fish (mean ± 95% CI; 62·8 ± 15·8% for one fish compared with 23·8 ± 12·9% for the other; Fig. 3). This suggested a dominance relationship, where the dominant individual is defined as the fish that occupied the preferred shallow section most of the time. Time spent in the shallow section by the dominant fish in the pair was not significantly different from single fish (*t*-test, $t_{12} = 0.669$, $P = 0.516$). By contrast the subordinate fish showed a significantly reduced use of the shallow habitat compared with single fish ($t_{12} = 6.023$, $P < 0.001$). Individuals within pairs occupied different habitats more often than would be expected if there was no interference (proportion of observations with fish in separate sections; mean ± 95% CI: 56·9 ± 9·6%; expected: 31·6 ± 11·9%; Fig. 4).

HABITAT-DEPENDENT AGGREGATIONS IN PAIRS

Occasions when both fish in a pair occupied the same habitat were mostly limited to the pool. Both fish occupied the pool concurrently more than was expected (observed: 28·2 ± 14·4%; expected: 3·9 ± 5·8%; Fig. 4);
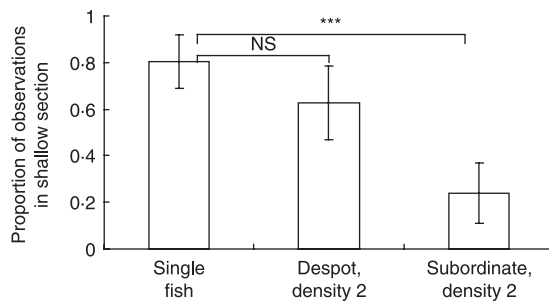
Fig. 3. Occupancy of shallow section by pairs of fish compared with single fish. Error bars indicate 95% CI. ***$P < 0.001$; NS = $P > 0.5$.
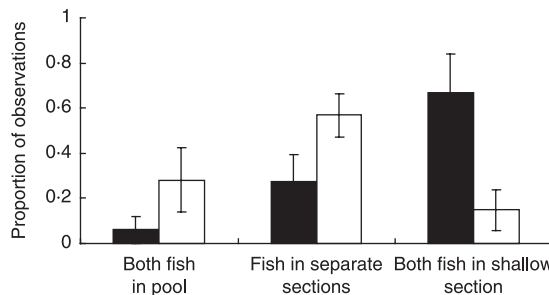
Fig. 4. Distribution of fish at density two per arena. Predicted values (filled bars) and observed values (open bars), with 95% confidence intervals.

in contrast, the two fish avoided simultaneously occupying the shallow section (observed: $14.9 \pm 9.2\%$; expected: $64.5 \pm 17.6\%$; Fig. 4).

SIZE-DEPENDENT EFFECTS

Body size (weight and L_T) did not affect habitat use of fish in any of the three density trials (Pearson; $r < 0.401$, $P > 0.170$). Neither was body size related to differences in habitat use between pairs of fish (paired t-test, with larger individual compared with smaller individual for each pair; L_T: $t_7 = 1.16$, $P = 0.291$; weight: $t_6 = 0.04$, $P = 0.973$) or within groups of four fish (individual size compared to mean size of the four fish; L_T: $r = 0.363$, df = 24, $P = 0.081$; weight: $r = 0.292$, df = 24, $P = 0.166$).

Discussion

The first aim of this study was to distinguish between the possibilities that aggregations of juvenile pike in the deepest water available (0·33 m) reflect shoaling in favoured habitat or grouping of those fish excluded from favoured habitat. The results showed that solitary pike had a preference for the shallow-water (0·17 m) habitat and that the overall time spent in the least preferred (deeper water) habitat increased with fish density. This indicates a despotic-type distribution with aggregation being a consequence of competitive exclusion. Similarly, a comparison of habitat use by

single and pairs of pike showed an overall tendency to disperse.

The second aim was to determine whether subordinate pike used those habitat patches that were preferred by dominant fish when they were vacant. On average, the fish in each pair that used shallow water the most exhibited habitat use indistinguishable from that of single fish, whereas the others tended to use the deeper water (which was deemed by single fish to be of relatively poor quality). This distribution is consistent with the pairs comprising a dominant despot whose habitat use is unaffected by density, and a subordinate fish that tends to be constrained to poor-quality habitat. However, it was not simply the case that the subordinate fish avoided the dominant, or used the best patch when it was available (Ruxton *et al.* 1999) because when dominant fish occupied deep water, subordinates tended to remain in the deep-water habitat, thus aggregating with the dominant fish. Although the present study was conducted in small arenas to facilitate the teasing out of mechanisms of interaction among fish, habitat-specific grouping has also been observed in juvenile pike in a large-scale laboratory canal (Hawkins *et al.* 2003) and among radio-tagged adult pike in the wild (Masters 2004).

There are several plausible explanations for this behaviour. Pike may be more secure when they can observe conspecifics and monitor their behaviour closely to acquire information on their readiness to attack, akin to predator inspection in minnows (Pitcher, Green & Magurran 1986; Pitcher 1992). Pike are generally sit-and-wait predators (Raat 1988) that ambush unsuspecting prey (Casselman & Lewis 1996). Vigilance on the part of subordinate pike may discourage a prospective cannibal from attacking because a successful ambush is less likely (Webb 1982; FitzGibbon 1989).

Subordinate fish may also have a preference for deeper water because it would allow greater manoeuvrability (in three dimensions) to escape from a predatory attack, compared with shallow water. Furthermore, the structural complexity typical of many shallow-water habitats (although not in this experiment) may offer more opportunities for pike to set up ambushes. Shallow water may therefore constitute a favoured habitat for a predator (single or dominant pike) and more dangerous habitat for a potential prey (subordinate pike).

In the present study, there was no observation of overt aggression, which occurs in many species of fish (e.g. Mikheev *et al.* 1994; Adams & Huntingford 1996; Whiteman & Côté 2004), and no individuals had any signs of injury. Instead, interference probably operated through intimidation, in which the mere presence (or possibility of imminent presence) of a dominant individual impairs behaviour of a subordinate pike. Subordinates would presumably have used visual cues to avoid dominants. However, odour cues may have played a role. Areas of the tank consistently inhabited by dominant fish may have become labelled with scent, similar to substrate marking in salmon (Stabell 1987).

Subordinates could then use these odour cues to avoid areas preferred by the dominant fish (Griffiths & Armstrong 2002).

Other studies of pike have recorded threat posturing (Raat 1988), movements of individuals towards one another without aggressive encounter (Eklöv & Diehl 1994) and behavioural displays of mouth opening and gill flaring (Nilsson, Nilsson & Nyström 2000), which may all be associated with intimidation. None of these behaviours was observed in the present study, which suggests that more subtle forms of intimidation occurred. We cannot rule out the possibility that aggressive interactions occurred but were sufficiently infrequent that our observations did not detect them. However, as even single acts of overt aggression in pike are likely to cause serious damage, they likely pose high risks to both dominant and subordinate fish, such that all individuals may attempt to avoid them. It is also possible that overt aggression observed in previous studies was part of a process of establishing dominance relationships, which had probably already been established in our individuals. Nevertheless, as these pike showed highly skewed spatial distributions, it appeared that dominant individuals used intimidation tactics to control access to resources (space), and the risk of a confrontation escalating was probably very low.

Despite of a difference up to 64% in body weight within groups of four pike, neither body weight nor length was related to behavioural interactions. By contrast, Eklöv & Diehl (1994) found evidence of size-dependent interference in groups of three wild pike (age 1; 194–315 g), despite similar size variation within groups (weight difference up to 62%). However, the occurrence of interference may have been influenced by hunger levels, as the pike in Eklöv & Diehl's (1994) study lost weight during the experiment. It is also possible that initial dominance relationships in our pike may have been size-dependent and remained unchanged even if lower-ranked individuals subsequently grew faster than dominant fish (e.g. Abbott, Dunbrack & Orr 1985; Huntingford *et al*. 1990; Stamps & Krishnan 1994). In some instances, kinship or familiarity may affect the use of overt aggression (Brown & Brown 1992, 1993; Chivers, Brown & Smith 1995). However, the only study of kinship effects in pike found that fry did not cannibalize non-siblings more than siblings, once growth variations between families were accounted for (Bry & Gillett 1980).

Avoidance by subordinate animals of vacant patches preferred by dominant individuals (Griffiths & Armstrong 2002; this study) can be expected to increase the influence of despots across geographical space, particularly when dominant individuals use a network of patches (Armstrong, Braithwaite & Huntingford 1997; Maclean *et al*. 2005). Risk of damage and mortality may override considerations of energy gain (Ruxton *et al*. 1999) in defining patch quality, although these two parameters should be integrated (Gilliam & Fraser 1987). From the perspective of defining habitat quality,

it is interesting that habitat preference of fish in isolation may be quite different from those in groups. For young-of-the-year pike, the availability of shallow habitat that is preferred in isolation and by dominant individuals may be less important than that of deep water that is preferred by subordinates in determining carrying capacity, provided that there is sufficient recruitment of juveniles to use the space fully.

Acknowledgements

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