Species-specific antipredatory behaviours: effects on prey choice in different habitats

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Summary. Prey species may use many different behaviours to avoid predation. In this study, the antipredator behaviours of juvenile roach (Rutilus rutilus) and juvenile perch (Perca fluviatilis) were studied in wading pools with three kinds of structural complexity: no structure, structure simulating vegetation and structure simulating bottom crevices. Predation experiments with piscivorous perch and habitat choice experiments with the prey were performed, and the foraging success and prey choice of the predators were related to the type of structure. Predator foraging success was lower in the vegetation than in the other treatments. In the absence of structure and with vegetation structure, predators preferred perch over roach, while the preference was reversed in the crevice treatment. Roach and perch differed in their antipredatory behaviours. Roach responded to the presence of predators by schooling, moving fast and remaining at the surface, and escaped from attacks by jumping out of the water. In contrast, perch moved more slowly, dispersed after attacks and tried to hide at the bottom. Perch always preferred the vegetation structure to the non-structured part of the pool, while roach showed preference for the vegetation structure only when predators were present. Roach never occurred in crevices, whereas perch used crevices when predators were present. Predator pursuit speed was lower in the vegetation structure than in the non-structured treatment, but prey escape speed was unaffected. The results suggest that both the quantity and quality of structural complexity interacting with species-specific antipredator behaviours are important for predator-prey dynamics. It is also suggested that the presence of structure can have substantial effects on the structure of North Eurasian fish communities, by affecting relative and absolute predation pressures from piscivorous perch on prey species.

Introduction

The impact of predators on prey populations can be direct as a result of harvesting of prey, or indirect as a result of the effect that predators have on the behaviour of prey. Traditionally, it has been thought that harvesting of prey individuals may reduce the resource limitation for the remaining individuals (Wilbur 1988). In contrast, behavioural responses of prey to predators may lead to increased resource limitation as a result of competition in refuges or a reduction in prey activity decreasing foraging rate and growth rate (Stein 1977; Milinski and Heller 1978; Werner et al. 1983; Holmes 1984; Caldwell 1986; Holomuzki 1986; Gilliam and Fraser 1987; Rahel and Stein 1988; Nonacs and Dill 1990). Prey-species-specific antipredator behaviours may also affect the predator’s diet (Sih and Moore 1990). When the competitive abilities of different species are habitat-specific, predator-mediated habitat shifts may, in addition to intensifying competition, also lead to changes in the outcome of competition (Persson 1991a; Werner 1991).

In the ecological literature, predator-dependent habitat use by prey is generally expressed in the context of refuge use by the prey (Paine 1974; Jeffries and Lawton 1984; Sih 1987; Ives and Dobson 1987). Experimental studies on prey refuge use have most often concentrated on the effects of different levels of structural complexity. In aquatic systems, structured environments have been shown to reduce predation rates by restricting movement of the larger predators more than that of the smaller prey, and by decreasing predator vision, thereby affecting encounter rate (Savino and Stein 1982; Savino and Stein 1989a, b). Studies on refuge use by prey in aquatic systems have focused on the effect of structural complexity on predator foraging success per se (Glass 1971; Savino and Stein 1982; Crowder and Cooper 1982; Schramm and Zale 1985), but there have also been some studies of the mechanisms behind the effect of the structural complexity (Anderson 1984; Winfield 1986; Savino and Stein 1989a, b). Generally, these studies have shown
that structural complexity is negatively correlated with predator foraging success, and this relationship also appears to be valid for fish foraging on invertebrates (Coull and Wells 1983; Gilinsky 1984; Diehl 1988; but see Winfield 1986). It is important to note that the foraging behaviours of different predator species are likely to be influenced in various ways by an increase in structural complexity, and different prey species are expected to use structural complexity in different ways to evade predators (Rahel and Stein 1988). The effects of structural complexity are thus expected to depend on the species involved. Eklöv and Hamrin (1989) found that the overall foraging success of pike (Esox lucius) on two prey species, Eurasian perch (Perca fluviatilis) and rudd (Scardinus erythrophthalmus), declined with increasing structural complexity. They also found that both the relative (i.e. the frequencies with which perch were caught relative to rudd) as well as the absolute (i.e. frequencies with which perch were caught) foraging success on perch increased with increasing complexity, indicating that a shift in predator preference took place as the degree of complexity increased.

Eklöv and Hamrin (1989) interpreted the shift in predator preference as a consequence of species-specific microhabitat choice by the prey. However, structural complexity may affect other antipredator behaviours directly, and, as a consequence, alter prey vulnerability. Such effects should be most pronounced in species with different antipredator tactics. In addition to habitat selection, prey are known to use a range of behaviours which lower the risk of predation. Group living, which has been described as an antipredatory behaviour in a range of prey organisms (Crook 1965; Berger 1978; Pulliam and Caraco 1984; Pitcher 1986; Magurran 1990), has been hypothesized to reduce the risk of predation by reducing predator encounter rate (Helfman 1986; Pitcher 1986), increasing distance at which predators are detected (Kenward 1978; Caraco 1979a, b; Bertram 1980; Caraco et al. 1980), reducing the probability that a particular individual will be caught in a given attack (Duncan and Vigne 1979; Foster and Treherne 1981), and confusing predators by presenting predators with multiple targets (Neill and Cullen 1974; Milinski 1979). Other obvious antipredatory behaviours are escape through speed, and disappearance from the predators' search fields (Pitcher 1986). Finally, a more subtle behaviour such as prey fish location in the water column has also been suggested as an important antipredatory behaviour (George 1960, quoted in Magurran 1990).

Eurasian perch and roach are the numerically dominant fish species in many North European lakes and co-occur in many waters (Persson 1991b). When piscivores are present, both suffer heavy predation among juvenile stages. The perch is a perciform, high-bodied fish with spiny rays, while the roach is a cyprinid with an elongated body and soft rays. These differences in morphology suggest that the two species might use different antipredator behaviours. If structural complexity is used in species-specific ways by the prey, it is also possible that, in addition to changing absolute predator foraging success (i.e. predator success in terms of intake per time or energy unit), structural complexity could also change relative capture probabilities with which the different species are captured, and thus promote a shift in the predators' choice of prey. Shifts in both predator efficiencies and choice of prey may in turn have important consequences for population and community dynamics.

The objectives of this study were: (1) to determine if structural complexity affected absolute predator foraging success; (2) to determine if structural complexity affected relative predator foraging success; (3) to determine if the relative number of the two prey species affected predator choice, and (4) if such effects could be related to the effects of structural complexity on predator and prey behaviours.

**Methods**

Piscivorous perch, juvenile perch and roach were caught by electrofishing in lakes in the vicinity of Umeå, Sweden. The fish were acclimatized to indoor conditions for at least 1.5 months before the start of the experiments. 0+ perch (6.4±0.3 cm, 1.9±0.3 g wet weight) and 1+ roach (6.0±0.5 cm, 1.5±0.2 g wet weight) (means±1 SD) were used as prey. Similar sized piscivorous perch were used as predators (22.3±0.3 cm, 122.5±1.6 g wet weight). Between trials, fish were held in 500-l tanks with similar temperature, light regime and type of structure as in the experimental pools. Prey fish were fed daily with live zooplankton (mainly Daphnia), chironomids and commercial flake food. The piscivores were fed with earthworms and pieces of vendace (Coregonus albula). A total of 100 juvenile roach, 80 juvenile perch, and 8 predators were used in the experiments.

The experiments were conducted in two indoor wading pools (radius 135 cm, height 50 cm) with a water depth of 40 cm from September 1989 to April 1990. The bottoms of the pools were marked with a 1-m 2 grid. The water temperature during the trials was 18°C (range ±1°C); 20% of the water was replaced every week and an aeration pump circulated the water during the trial period. The experimental room was illuminated by fluorescent lamps 4x40 W over each pool) on a 12L/12D light cycle. Three different trial series were used: (1) no structural complexity in the pools, (2) simulated vegetation in the pools (in the following called vegetation structure) and (3) simulated crevices at the bottom (in the following called bottom structure). The vegetation structure consisted of floating, 50 cm long, white polypropylene strings tied to plastic plates, placed at the bottom of the pools. The plates were covered with sand to ensure that prey fish could not escape by hiding under the plates. String density was 200 strings/m 2, which is equivalent to vegetation densities commonly found in the littoral zone of lakes (Winfield 1986). The strings soon became covered with periphyton, which gave the strings a close resemblance to natural vegetation. The trial series involving vegetation structure was not initiated before strings were covered by the periphyton. The vegetation structure covered 66% of the pool area and 75% of the edge of the pools. The bottom structure consisted of 15 cm long PVC-pipes (radius 5 cm) which were cut in half lengthwise, and placed with the convex part facing the surface. Pipe density was 5.6 pipes/m 2. The predators were chosen at random from the eight in the stocking tank in advance of each treatment. They were exposed to a random sequence of prey species proportions. Two predators were used in each run. In both pools, each predator pair was replaced by a new pair after approximately half of the runs had been carried out in each treatment, to ensure that all predators participated in a similar number of runs per treatment. Before runs, predators were trained until they foraged willingly. To minimize disturbance, predators were left in the pools during the whole period they took part in the treatment. A pair of predators was