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ORIGINAL ARTICLE

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Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice

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Abstract The mechanisms and functions of mixed-species shoaling were investigated in two sympatric species of cyprinids, the chub and the European minnow, from the river Wharfe where they comprised approximately 70% of all year 0+ fish over a 20-year survey. Chub preferred conspecific shoals over heterospecific ones with olfactory cues being more important than visual ones for shoal choice. This preference was consistent with measurements of length:flank area ratios and length:weight ratios which suggest that both species are similar in appearance. When presented with mixed-species shoals, chub increased the percentage time spent with stimulus shoals with increasing proportions of conspecifics. Feeding experiments suggest that the preference for conspecific shoals is driven by interspecific competition (with minnows out-competing similar-sized chub) and the oddity effect. The importance of this work in the context of species assortment in free-ranging shoals is discussed.

Keywords Mixed-species shoaling · *Leuciscus cephalus* · *Phoxinus phoxinus* · River Wharfe

Introduction

Shoaling behaviour is estimated to occur in around 10,000 species of fish at some point in their lives (Shaw 1978) and has attracted significant attention from behavioural ecologists (e.g. Pitcher 1992). Shoaling provides a number of general benefits to individuals, such as a reduction of individual predation risk and increased foraging opportunities, as well as some costs, such as competition [see Pavlov and Kasumyan (2000) for a general review]. It is generally believed that shoal members benefit most when the shoal is phenotypically homogeneous. Such shoals are argued to reduce a predator's kills:attacks ratio (Landeau and Terborgh 1986) and may minimise competition costs to shoal members (Ranta et al. 1994). Because of this, shoals should show assortment with respect to size (Ward and Krause 2001), ectoparasite status (Krause and Godin 1996) and species (e.g. Allan and Pitcher 1986).

Despite this, mixed-species aggregations do occur where advantages accrue to individuals. For example, mixed-species avian flocks can benefit from increased vigilance with reduced competition costs, especially if the species involved exploit different resource niches (Sasvari 1992; see also Hino 2000). Similarly, Barnard et al. (1982) reported plovers (*Pluviaris apricaria*) actively joining lapwings (*Vanellus vanellus*), despite lapwings stealing food from them, because of the anti-predatory vigilance benefits. Fitzgibbon (1990) studied predation by cheetah (*Acinonyx jubatus*) on Grant's gazelle (*Gazella grantii*) and Thomson's gazelle (*Gazella thomsoni*), finding that cheetahs showed a preference for attacking single species herds over mixed species ones and were more successful against single species herds.

Mixed-species aggregations also occur amongst free-ranging shoaling fish. Overholtzer and Motta (2000) reported mixed-species aggregations amongst species of juvenile parrotfishes (Scaridae). Hobson (1963) provided anecdotal evidence of mixed-species shoaling between flatiron herring (*Harengula thrissina*) and juvenile anchovetas (*Cetengraulis mysticetus*). However, the author related some evidence of differential predation on shoal members, suggesting unequal benefits of shoaling between the respective species. Sweatman (1983) described species assortment in schools of damselfish (*Dascyllus aruanus* and *D. reticulatus*). Using the semi-natural conditions of a fluvarium, Allan and Pitcher (1986) reported mixed-species groups dividing and assorting according to species when under a predation threat (see also Wolf 1985). Krause et al. (1996) described the phenomenon in a Canadian freshwater lake which contained three different species of fish. Shoals

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collected in the littoral zone of the lake were observed to be strongly assorted by species.

Laboratory studies have investigated active choice as a mechanism promoting species segregation. Sensory mechanisms promoting the maintenance of shoaling behaviour have been well documented (e.g. Hemmings 1966 ; Pitcher et al. 1976 ; Hara 1992). Pitcher (1979) concluded that three prime sensory modalities – vision, olfaction and mechanoreception (via the lateral line) – were involved in maintaining fish grouping (shoaling) behaviour. Less clear is the relative role of the sensory modalities in the establishment of species-assorted shoals and in the choice of individuals as to which shoal to join.

Preference for conspecifics has been recorded in a number of species (Brown et al. (1993): rainbow trout, *Oncorhynchus mykiss*; Krause and Godin (1994): banded killifish, *Fundulus diaphanus*; Barber et al. (1998): threespine stickleback, *Gasterosteus aculeatus*). Despite this, caution has to be exercised in the interpretation of such data. Keenleyside (1955), using the threespine stickleback as an experimental model in a two-way choice experiment, found a preference for conspecifics when the alternative was to shoal with bitterling (*Rhodeus sericeus*). However, an initial preference for conspecifics quickly disappeared when the alternative shoal comprised tenspine stickleback (*Pygosteus pungitius*) and test fish showed a preference for a shoal of roach (*Rutilus rutilus*) over a shoal of conspecifics. FitzGerald and Morrissette (1992) reported the absence of any preference for conspecifics in the threespine stickleback, *G. aculeatus*, where the alternative was the closely related blackspotted stickleback, *G. wheatlandi*. Warburton and Lees (1996) showed that juvenile Trinidadian guppies (*Poecilia reticulata*) actively preferred to associate with heterospecific swordtails (*Xiphophorus helleri*) when they had been raised with the latter.

The lack of consensus amongst laboratory studies could be due to a number of factors. Firstly, it is important that a sympatric species is used for the heterospecific shoal to provide a biologically meaningful alternative. In addition, laboratory studies reporting no preference for conspecifics were based on presentation methods that excluded, either partially or completely, one of the two main discriminatory communication channels (i.e. vision and olfaction).

Previous investigations into the costs and benefits of shoaling behaviour have predominantly concentrated on the interactions between members of the same species (although see Krause et al. 1998). Relatively little work has been carried out on the mechanisms that promote assortment by species in shoals (Pitcher and Parrish 1993). Similarly, little investigation has been made of the potential costs and benefits of mixed-species shoaling, or of the ways that such costs and benefits may shift according to a shoal’s species composition. This study investigated the mechanisms underlying active choice in the context of individuals being presented with a number of alternative shoal options. Furthermore, the functional significance of individual choice behaviour is addressed.

Based on previous studies (Ranta et al. 1994; Peuhkuri 1997) we predicted that test fish would prefer to shoal with conspecifics and that species discrimination by test fish would be most apparent when both olfactory and visual communication channels were available. In addition, we predicted that single individuals in a shoal of heterospecifics would pay a cost in terms of reduced feeding success.

Methods

Field population data

Population information on the year 0+ fish assemblage of the river Wharfe was taken from data published over a 20-year period, from 1980 to 2000, by the Environment Agency.

Morphometric analysis

Digital images were taken of 12 minnows and 12 chub at a size of 40±4 mm. These images were analysed, using Scion image analysis software, to determine the relationship between body length and flank area. This relationship was compared between the species. In addition, fish were weighed to provide a comparison of the length:weight ratio between species.

Fish and holding conditions

We used the chub (*Leuciscus cephalus*) and the European minnow (*Phoxinus phoxinus*) as model species because they are locally available in large numbers, adapt well to aquarium conditions, and their shoaling behaviour has been described in previous behavioural studies (e.g. Krause 1994). We caught ca. 1,000 non-breeding minnows and ca. 500 non-breeding chub using hand nets in the river Wharfe at Arthington in West Yorkshire, UK (grid reference SE26304550) during October 2000. At the study site, the river is ca. 20 m wide although in early autumn it is divided into a number of channels. Depth ranges from about 0.2 m in these channels to about 2 m in the main channel. Flow rate is also variable, ranging from zero in some of the cut-off inlets to ca. 0.5 m/s nearer the centre of the main channel. Minnows and juvenile chub were at their greatest densities in shallow water (0.2–0.6 m deep), with little or no flow.

The fish were housed separately according to species in vats (1 m×600 mm and 600 mm high) in a temperature-controlled room at 12°C on a 12:12 h light:dark cycle. They were fed live and frozen bloodworm and commercially available Aquarian flaked food ad libitum. The sex of each fish was not determined. Fish were not reproductively active during the period of the study.

All fish included in the study (both minnows and chub) measured 40±4 mm. Chub were used as focal fish throughout this study. After the laboratory work was finished the fish were released at the site of capture.

Shoal choice experiments

The test tank measured 900×300 mm and 300 mm high. This was filled to a depth of 150 mm. Two separate compartments, measuring 120×294 mm and 300 mm high, were inserted towards either end of the test tank such that they were 400 mm apart. The front panel of each compartment was made of clear PennPlax perforated plastic (perforation diameter ca. 1 mm, 5±1 perforations/cm^2). The use of clear perforated plastic allows for olfactory, as well as visual, stimulation of a test fish. A substrate of standard 5 mm aquarium gravel was added to a depth of 10 mm throughout both the test tank and the two compartments. We drew lines on the outside of

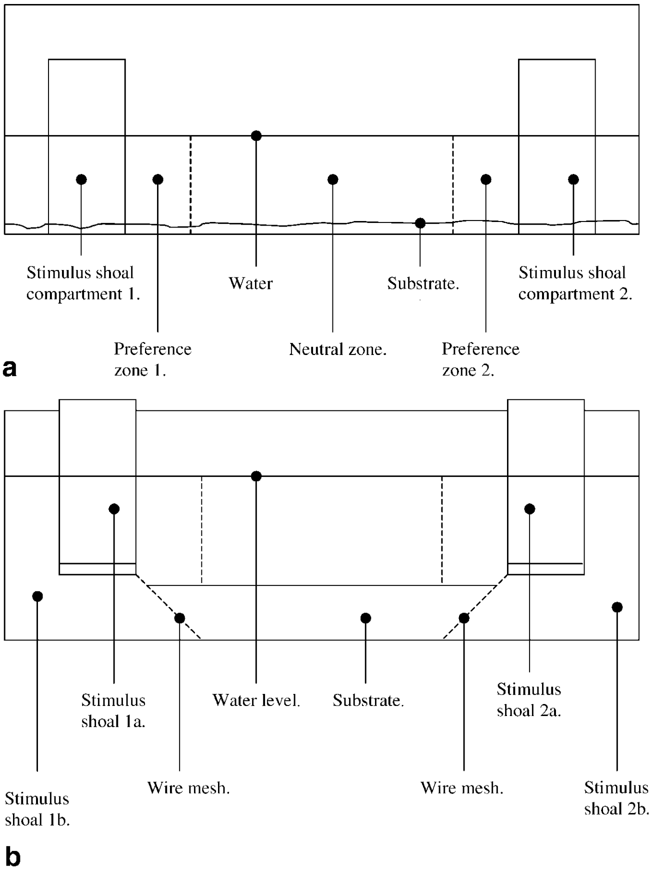

Fig. 1a, b Side elevation of presentation apparatus. **a** Standard experimental set-up. **b** Set-up allowing accommodation of additional concealed stimulus shoals to provide olfactory cues

the glass demarcating two 120 mm preference zones at either end of the central compartment. This distance represents three body lengths of a 40±4 mm focal fish which falls within the range of interindividual distances observed in free-ranging shoals (Pitcher and Parrish 1993) (see Fig. 1a).

Single species shoals – preference for conspecifics

Two stimulus shoals, each consisting of eight size-matched individuals, were assembled. One stimulus shoal was composed of minnows, the other was composed of chub. The shoal of eight chub was randomly allocated to one of the compartments and the shoal of eight minnows was introduced to the remaining compartment. Both stimulus shoals were allowed to acclimatise for 1 h before each trial commenced. After this time had elapsed, the focal fish was allowed to swim freely throughout the test area.

Single species shoals – the roles of sensory modalities in conspecific preference

Stimulus shoals were assembled and allocated to compartments as in the first experiment. The clear, perforated interface between the stimulus shoals and the focal fish were replaced with (1) clear, unperforated plastic to allow visual but not olfactory communication and then with (2) opaque, perforated plastic (perforation diameter ca. 1 mm, 5±1 perforations/cm^2) to allow olfactory but not visual communication.

Single species shoals – juxtaposition of heterospecific olfactory and visual cues

Each stimulus shoal compartment was placed on top of an inverted glass beaker such that they were each raised by 120 mm. Two pieces of galvanised wire mesh were cut to size and one was attached to the base of each stimulus shoal compartment and to the base of the test tank. The mesh was fitted such that it ran diagonally away from the base of the stimulus shoal compartment. The gap was filled with standard 5 mm aquarium gravel to a depth of 120 mm in order to obscure the mesh. The water level was filled to a depth of 150 mm above the surface of the gravel to maintain consistency of depth with previous experiments The interface between the stimulus shoal was composed of clear, unperforated plastic to allow visual but not olfactory communication. A stimulus shoal of 8 chub was allocated to one of the stimulus shoal compartments at random. A stimulus shoal of eight minnows was added to the area adjacent to this. Another shoal of eight minnows was added to the compartment opposite and a further stimulus shoal, composed of eight chub, was added to the area adjacent to this. This arrangement allowed for focal fish to simultaneously perceive conspecific olfactory cues with heterospecific visual cues, and conspecific visual cues with heterospecific olfactory cues (see Fig. 1b).

Mixed species shoals

One stimulus shoal, composed of eight conspecifics, was allocated randomly to a stimulus shoal compartment. The other stimulus shoal was composed of four different combinations of conspecific and heterospecifics to make a total of eight individuals. These combinations were as follows: one chub, seven minnows; two chub, six minnows; four chub, four minnows; two chub, six minnows (a total of four separate treatments). The interface between the focal fish and stimulus shoal was composed of clear, perforated plastic, as described previously.

In all shoal choice experiments, the time spent by the focal fish within each of two preference zones over a 10 min period was recorded as a measure of shoaling preference (cf. Krause and Godin 1994) by an observer behind a blind. Each focal fish was used only once, and the fish used as members of stimulus shoals were taken at random from a stock of around 250 fish of each species. Focal fish and stimulus fish originated from separate holding tanks to avoid the potentially confounding effects of familiarity, whereby fish opt for shoalmates of whom they have prior experience (Griffiths 1997). Twenty replicates were carried out for each presentation treatment.

Feeding experiments

A test tank (450×300 mm and 300 mm high) was filled to a depth of 150 mm with water. A gravel substrate was added and a small artificial plant was placed in the centre of each test tank. One focal fish and eight stimulus fish were introduced to each aquarium. In the first treatment, all eight stimulus fish were heterospecific to the focal fish. In the second treatment, four stimulus fish were conspecific and four were heterospecific.

On the day following the addition of the fish, a series of 27 bloodworms (size range 6–8 mm) was added to each test tank one at a time at 20 s intervals using a hand-held pump which injected each bloodworm and ca. 10 ml of water. Three bloodworms were allocated for each individual fish. We recorded (1) the number of the first bloodworm taken by the focal fish in the sequence of worms (i.e. the 1st/5th/9th) and (2) the total number of bloodworms taken by the focal fish over the period of the trial.

Both focal fish and stimulus fish were used only once. Each were housed separately to avoid the potentially confounding influence of familiarity. Twenty-five replicates were carried out for each treatment.

Results

Field population data

Minnows and chub were the most numerous species in the sample making up 47±29% (mean±SD) and 22±19%, respectively. Two other cyprinid species, roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) were the next most abundant species. Predatory species known to occur at the site include pike (*Esox lucius*), perch (*Perca fluviatilis*) and trout (*Salmo trutta*).

Morphometric analysis

There was no difference between chub and minnows in terms of body length:flank area (Mann Whitney U-test: $Z_{12,12}=1.04$, $P=0.32$) or body length:weight (Mann-Whitney U-test: Z12,12=1.27, $P=0.22$).

Shoal choice experiments

In all trials, test fish visited both preference zones and thus had the opportunity to assess each stimulus shoal.

Single species stimulus

Focal fish showed a significant preference for a stimulus shoal composed of 8 conspecifics over a same-sized heterospecifics one when both visual and olfactory stimuli were present (Wilcoxon signed ranks: $Z=2.6$, $n=20$, $P=0.01$). Olfactory stimuli alone were sufficient to elicit a preference for conspecifics (Wilcoxon signed ranks: $Z=3$, $n=20$, $P=0.003$). However, focal fish showed no preference for conspecifics when only visual communication was possible (Wilcoxon signed ranks: $Z=0.34$, $n=20$, $P=0.7$). When conflicting visual and olfactory information was provided, focal fish associated with the shoal where conspecific olfactory cues were provided (Wilcoxon signed ranks: $Z=3.1$, $n=20$, $P=0.002$) (see Fig. 2).

Mixed species stimulus shoals

The response of focal fish to mixed-species stimulus shoals varied according to the number of conspecifics present in the mixed-species shoal (Kruskal-Wallis ANOVA: $\chi^2_{4,95}=10.7$; $P=0.03$; Fig. 3). A conspecific stimulus shoal was significantly preferred by the test fish if the alternative stimulus shoal consisted of seven heterospecifics and one conspecific (Wilcoxon test: $Z=2.7$, $n=20$, $P=0.007$) but not if the alternative shoal consisted of six heterospecifics and two conspecifics (Wilcoxon signed ranks test: $Z=0.7$, $n=20$, $P=0.5$). Test results generated using Wilcoxon test, comparing (% time spent with matched) – (% time spent with unmatched) against zero; α levels adjusted according to Bonferroni method [$\alpha'=\alpha/k$] (Fig. 3).

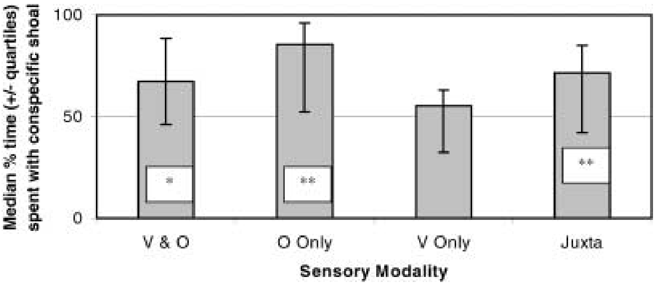

Fig. 2 The median time ± quartiles spent by focal fish shoaling with the conspecific shoal is shown as a percentage of overall time spent shoaling in relation to the communication channels available to the focal fish. *O* Olfactory; *V* visual; *Juxta* juxtaposition of stimuli (see Methods). Significant differences in percentage shoaling allocation by focal fish between the two choice shoals are shown: * $P<0.05$; ** $P<0.01$ [α levels adjusted according to Bonferroni method ($\alpha=\alpha/k$)]. Test results generated with Wilcoxon signed ranks test, comparing (% time spent with conspecific shoal) – (% time spent with heterospecific shoal) against zero. $n=20$ for each treatment

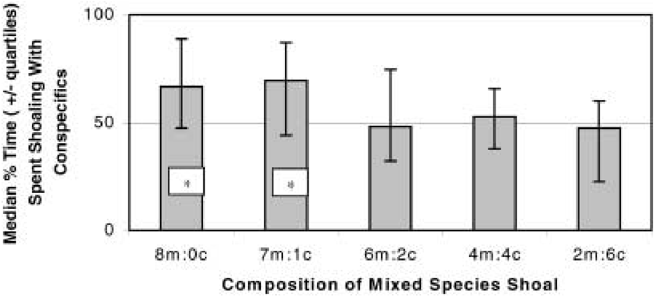

Fig. 3 The median time ± quartiles spent by focal fish shoaling with the conspecific shoal is shown as a percentage of overall time spent shoaling in relation to the species composition of the mixed-species shoal. Data from the experiment using single species shoals are included (8m:0c) for comparison. Significant differences in percentage shoaling allocation by focal fish between the two choice shoals are shown: * $P<0.05$; ** $P<0.01$ [α levels adjusted according to Bonferroni method ($\alpha=\alpha/k$)]. Test results generated with Wilcoxon signed ranks test, comparing (% time spent with conspecific shoal) – (% time spent with heterospecific shoal) against zero. $n=20$ for each treatment

Feeding experiments

A total of 27 bloodworms per trial were introduced to the test tank which gives an expected average intake of three prey items per fish. Chub consumed less than the expected number of prey items per trial when grouped with four conspecifics and four heterospecifics (Wilcoxon test: $Z=2.2$, $n=25$, $P=0.03$) as well as when grouped with eight heterospecifics (Wilcoxon test: $Z=3.7$, $n=25$, $P<0.001$). Chub captured significantly more food items when grouped with four conspecifics and four minnows than when grouped with eight minnows (Mann-Whitney U-test: $Z_{25,25}=2.6$, $P=0.01$).

Discussion

Our experiments demonstrate the relative roles of visual and olfactory cues in promoting species homogeneity in shoals of chub. Chub were able to recognise and respond to changes in species composition between groups, becoming progressively less likely to associate with a shoal as the proportion of conspecifics within it decreased. The preference for conspecific shoals is potentially driven by competition costs associated with mixed-species shoaling.

Focal fish showed a clear preference for shoaling with conspecifics over the option to shoal with heterospecifics where they could both see and smell the stimulus shoals. Once the olfactory stimulus was removed, focal fish showed no preference for the conspecific shoal. In contrast, focal fish that were deprived of visual stimulation but were still able to smell the stimulus shoals spent a significantly greater amount of time in the choice zone proximate to conspecifics. Furthermore, when smell and sight were juxtaposed, focal fish preferred to associate with a stimulus comprising visual communication with a shoal of heterospecifics and olfactory communication with conspecifics. From these observations it appears that olfaction is the primary sensory modality promoting specific assortedness in shoals of chub, particularly when, as in this case, both species have similar shapes. The significance of chemical cues in mediating general shoaling decisions has been recognised in a number of recent papers (Olsen and Winberg 1996; Steck et al. 1999; see also Penn and Potts 1999). Kotrschal et al. (1998) described the ecomorphology of cyprinid brain structure. Leuciscines are generally mid-water species, hunting a range of invertebrate prey primarily by sight. Their brains are well adapted to both visual and olfactory communication. The relative importance of the olfactory sense increases at night and in turbid conditions, as when a river is in spate (see Hartman and Abrahams 2000). Similarly, as convergent evolution has produced a number of species of similar general appearance amongst temperate, lotic cyprinids, the olfactory sense allows individuals an additional way of distinguishing conspecifics from heterospecifics. The ability to discriminate conspecifics is generally considered adaptive as conspecifics share the same requirements in terms of diet and habitat.

Chub were out-competed for food items by minnows in shoals containing approximately equal proportions of each species. This suggests that there is a competition cost for chub in shoals containing minnows. Single chub in shoals of minnows performed worse still. This may be as a result of the ‘oddity effect’ (Landeau and Terborgh 1986) whereby individuals whose phenotype does not match the general pattern of the shoal suffer a greater per capita risk of predation and appear to adopt a more risk-averse approach to foraging. These costs potentially explain the observed preference for conspecifics.

The feeding experiments revealed a competition cost to chub joining shoals of minnows, but that this cost decreased with increasing proportions of the shoal being composed of conspecifics. Focal fish only avoided shoals where the oddity effect or competition costs would be extreme. Evidence exists from field studies of mixed-species shoals containing majorities of one species (e.g. Krause et al. 2000). Such behaviour may be adopted especially when the one shoaling species exists at a lower relative density than another and would otherwise be able only to form sub-optimally sized groups.

Whilst active choice is shown to be important in this study, other mechanisms may operate in addition to promote the kind of species segregation so often observed in the field (Debrot and Myrberg 1988; Ward and Krause 2001). According to the ‘activity synchrony’ theory of Conradt and Roper (2000), species segregation could occurs as a result of differential time budget priorities between species. Similarly, species segregation could arise as a result of differences in habitat preference (possibly mediated via diet preferences) – chub tend to occupy deeper water than do minnows (Ward, personal observation). This mechanism is likely to be temporally variable.

Despite the costs, mixed species groups do occur in the wild (Nikolsky 1974; Pavlov and Kasumyan 2000). Such shoals are likely to occur when the anti-predator benefits of being in a large shoal outweigh the competition costs (Landeau and Terborgh 1986). A model constructed by Ranta et al. (1994) predicted that both shoal size and commuting costs would effect shoal assortment: small shoals should be assorted when commuting costs are high but not when they are low. Larger shoals tend to be assorted when commuting costs are low and become increasingly mixed as commuting costs rise. This generally agrees with qualitative observations made by the authors on shoals of chub and minnows in the river Wharfe system.

The likelihood of an individual chub associating with a stimulus shoal increased with the number of conspecifics contained within that shoal. Once the proportion of conspecifics in a mixed-species shoal reached 25%, the preference of focal fish for an alternative, entirely conspecific shoal broke down. This may reflect some advantages to mixed-species shoals, for example any slight variation in dietary preferences between species (i.e. resource partitioning) could promote coexistence with minimal competition costs and benefits in terms of ‘safety in numbers’ (Ehrlich and Ehrlich 1973; Wolf 1987), although it has been shown that mixed-species shoals segregate along species divisions at the approach of danger (Wolf 1985; Allan and Pitcher 1986).

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