

Quantitative evidence for assortative schooling in a coral reef fish

Anne C. Crook*

Department of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia

ABSTRACT: This study quantifies the schooling behaviour of a coral reef fish and, in particular, examines the stimuli that may motivate school formation. The focus of the study was the parrotfish *Chlorurus sordidus* (family Scaridae) which, in the juvenile phase, is able to undergo rapid physiological colour pattern ('PCP') changes. Juvenile *C. sordidus* frequently schools with other juvenile parrotfish species that share some PCPs. Solitary juveniles were followed in the field before and after joining a school to investigate whether their behaviour correlated with characteristics of the school joined. The variables recorded were size and PCP of focal juveniles, size and composition of schools and the feeding behaviour and PCPs displayed by the school members. Data were systematically collected and analysed using log-linear modelling to quantitatively examine the relationship between all possible combinations of the variables measured. The results of the study provide correlational evidence that juvenile *C. sordidus* display assortative schooling based on PCP and size characteristics of schools. In addition, the foraging behaviour of schools was influential in determining an individual's schooling behaviour. These data serve to highlight the complex and dynamic nature of schooling behaviour in this species.

KEY WORDS: Assortative schooling · Log-linear modelling · Coral reef · Parrotfish

INTRODUCTION

The adaptive significance of schooling behaviour has been studied extensively and the benefits of group formation, such as increased foraging efficiency, have been demonstrated for a number of fish species (Itzkowitz 1977, Pitcher et al. 1982, Pitcher & Magurran 1983). It is, however, generally believed that schooling has primarily evolved as a defence against predation (Magurran 1990). Owing to the 'confusion effect' created by schooling fishes, individuals have been shown to enjoy proportionately more protection in larger groups by making individual prey selection more difficult for predators (Radakov 1973, Neill & Cullen 1974, Curio 1976, Major 1978). This effect is likely to be most

effective if all the members within a school all look alike since 'odd' individuals are more easily selected by visually hunting predators (Hobson 1968, Mueller 1971, Landeau & Terborgh 1986, Theodorakis 1989). The phenotypic composition of a school relative to an individual's appearance is therefore likely to be important, particularly where predation pressures are intense (Ranta & Lindström 1990). Indeed, odd individuals within schools have been shown to be more likely to abandon schools following attacks by predators (Wolf 1985) and other aggressive (non-predatory) species (Crook unpubl.).

Because of the disadvantages associated with appearing different to their neighbours (Theodorakis 1989), it may seem counter-intuitive that many fish species, including those living on coral reefs, frequently form heterospecific schools (Ehrlich & Ehrlich 1973, Itzkowitz 1977). Heterospecific schools, however, often demonstrate the characteristics of monospecific schools, such as group cohesiveness and polarisation (parallel orientation) and are therefore

*Address for correspondence: Department of Zoology and Animal Ecology, University College, Lee Maltings, Prospect Row, Cork, Co. Cork, Ireland.
E-mail: anne.crook@bureau.ucc.ie

not simply aggregations of different species resulting from extrinsic environmental factors, such as a localised food source (Ehrlich & Ehrlich 1973). It is generally believed that heterospecific schools are important for providing protection from predators and improved foraging efficiency in the same way as monospecific schools (Theodorakis 1989). If the benefits of schooling for anti-predator purposes are to be realised within heterospecific schools then overcoming the problem of appearing odd, both behaviourally and phenotypically is likely to be particularly important. This will be most critical in habitats where predation pressures are intense, such as on coral reefs (Hixon 1991). Indeed, many fishes, including reef species, have been observed to form heterospecific schools with other species which are of similar colouration and size (Hobson 1963, 1969, Ehrlich & Ehrlich 1973, Alevizon 1976, Ranta et al. 1992). These are referred to as examples of 'assortative schooling' (Ranta & Lindström 1990).

The herbivorous juvenile scarid *Chlorurus sordidus* frequently schools with other scarid species with which *C. sordidus* shares at least 2 rapidly interchangeable ('non-specific'), achromatic physiological colour patterns, or PCPs ('uniformly dark' and 'striped'; Bellwood 1986, Crook 1997a, b). Juvenile *C. sordidus* also display a unique, achromatic 'species-specific' PCP (referred to as the 'bullseye' PCP). The ability to undergo PCP changes provides these juveniles with a means of rapidly altering their phenotypic appearance. In addition, the schooling behaviour of juvenile *C. sordidus* is complex, primarily as a result of continual compositional changes arising from frequent interspecific encounters with territorial trophic competitors. Previous studies have shown important relationships between PCPs and schooling behaviour in this species (Crook 1997a, b) and a schooling juvenile's behavioural response to interspecific encounters has been demonstrated to be correlated with its PCP (Crook unpubl.). In particular, it is predicted that these juveniles will benefit from assortative schooling by displaying the PCP representative of the majority of school members. This would act to reduce individual oddity and therefore lower individual susceptibility to predatory attack.

This study extends previous work on the schooling behaviour of juvenile *Chlorurus sordidus* by investigating the relationship between focal juvenile PCPs and the characteristics of the schools they joined (PCPs displayed by members, group size and composition). The principal objective was to quantitatively determine whether juvenile *C. sordidus* exhibit assortative schooling in the field and, if so, to ascertain the relative importance of colouration (PCP) and body size as stimuli for this behaviour.

METHODS

Non-schooling juvenile *Chlorurus sordidus* ('focal' juveniles) were selected at random at 3 sites around Lizard Island on the northern section of the Great Barrier Reef, Australia, and followed (at a distance no closer than 2 m and following a period of acclimatisation to diver presence) until they were observed to join a school. The 3 sites used for data collection were selected because they are known to have relatively large and stable populations of these juveniles (Crook 1997a, b). Focal juveniles not observed to join a school within a 5 min period were not included in the final data analysis.

Schools were defined as 3 or more co-occurring fish (either conspecifics or heterospecifics); fish were said to be co-occurring if they demonstrated co-ordinated movements indicative of mutual attraction among all members (Helfman 1984). All data were recorded throughout November 1996 between 08:00 and 16:00 h by a single observer using SCUBA and snorkelling techniques. Methods to avoid repeat observations of the same focal juvenile within a single sampling session were conducted (Crook 1997a). The data recorded were as follows:

Juvenile size. Sizes (total length [TL], including tail fin) were estimated by comparing focal juveniles with the outlines of fishes of known lengths drawn on underwater slates. To monitor the accuracy of this method, juveniles whose size had been estimated were periodically caught at each of the 3 sites using barrier nets and placed within small polythene bags. Captured juveniles were measured underwater in their bags using callipers and their actual sizes (TL) recorded alongside the estimations. The accuracy of size estimations was then quantified using statistical correlation analysis. All captured juveniles were immediately returned to the reef following measurement. Focal juveniles were grouped into 2 size classes, small (25 to 50 mm TL) and large (>50 mm TL), for analysis using log-linear modelling.

Juvenile PCP upon joining a school. The achromatic PCPs displayed were classified according to categories identified in an earlier study (Crook 1997a). For log-linear analysis, data relating to only the 3 most common PCPs (the species-specific bullseye PCP and non-specific uniformly dark and striped PCPs) were used. The compression of variable categories in this way, as for focal juvenile size classes, is necessary to maintain the power of the log-linear modelling technique (Tabachnick & Fidell 1996, Crook 1997a, b).

Juvenile PCP and the school PCP ratio. Data were collected to record whether the PCP of the focal juvenile was the same as that of the majority (defined as $\geq 95\%$) of other school members upon joining the school. A record was also made of the focal juvenile's

PCP after 1 min within the school. This provided sufficient time for any subsequent PCP changes given their known rapid speed of interchange (Crook unpubl.). In addition, the school's species composition when a focal juvenile joined was recorded.

Number of school members. The total number of school members at the time the focal juvenile joined was recorded. Schools were divided into 3 size groups, small (3 to 5 members), medium (6 to 10 members) and large (≥ 11 members), for log-linear analysis.

Average size of school members. The school members appearing to be smallest and largest were captured and their sizes recorded using the technique previously outlined. From these data the average size of school members was calculated. Average sizes were divided into 2 groups, small (average size 25–50 mm TL) and large (average size >50 mm TL), for data analysis.

School foraging behaviour. Schools were defined as either feeding or non-feeding (swimming above the substratum without feeding) at the time of the focal juvenile joining the school.

RESULTS

No significant differences were found among sites and therefore data from all 3 were combined and are presented in a multiway contingency table (Table 1). Data were analysed using a saturated log-linear model, and the interactions between the variables measured were ranked using their corresponding standardised residual values (Table 2). Correlations underlying the identified significant interaction effects (where $p \equiv 0$) were then quantified using odds ratios generated from the appropriate subsets of the multiway contingency table; these ratios are presented in Table 3. The main variable effects are also described.

Main effects

Size of focal juvenile

The size distribution of small:large focal juvenile *Chlorurus sordidus* was 38:1027 which approximates

Table 1. Multiway contingency table showing the characteristics of focal juvenile parrotfish *Chlorurus sordidus* and of the schools they joined within a 5 min observation period ($n = 1065$). Foraging behaviour of the school was divided into feeding (F) and non-feeding (NF); average size of school members (and size class of focal juveniles) was either small, 25–50 mm TL (S), or large >50 mm TL (L); number of school members was either small, 3 to 5 members (S), medium, 6 to 10 members (M), or large ≥ 11 members (L); school PCP (physiological colour pattern) indicates that either the majority ($\geq 95\%$; MAJ) or minority (MIN) of members had the same PCP as the focal juvenile

Foraging behaviour of school	Characteristics of the school joined			Physiological colour pattern (PCP) of focal juvenile					
	Average size of school members	Number of school members	School PCP ratio	Bullseye		Uniformly dark		Striped	
				L	S	L	S	L	S
F	L	L	MAJ	1	0	11	0	0	0
F	L	L	MIN	16	0	15	0	0	0
F	L	M	MAJ	8	0	101	0	4	0
F	L	M	MIN	46	0	27	0	1	0
F	L	S	MAJ	135	0	348	0	9	1
F	L	S	MIN	87	0	38	0	1	0
F	S	L	MAJ	0	0	0	0	1	1
F	S	L	MIN	0	0	0	0	0	0
F	S	M	MAJ	0	0	2	0	9	5
F	S	M	MIN	1	0	3	0	0	0
F	S	S	MAJ	0	0	2	0	10	17
F	S	S	MIN	0	0	0	0	0	0
NF	L	L	MAJ	1	0	2	0	0	0
NF	L	L	MIN	3	0	1	0	0	0
NF	L	M	MAJ	5	0	9	0	1	0
NF	L	M	MIN	5	0	1	0	0	0
NF	L	S	MAJ	33	0	50	0	17	1
NF	L	S	MIN	9	0	3	0	0	0
NF	S	L	MAJ	0	0	0	0	1	0
NF	S	L	MIN	0	0	0	0	0	0
NF	S	M	MAJ	0	0	0	0	2	3
NF	S	M	MIN	0	0	0	0	0	0
NF	S	S	MAJ	0	0	0	0	8	10
NF	S	S	MIN	0	0	0	0	0	0

Table 2. Interactions from the saturated log-linear model where $p < 0.0000001$. Large standardised residual values correspond to the most important interaction effects

Interaction	Partial chi squared (χ^2)	Degrees of freedom (df)	Standardised residual (χ^2/df)
PCP of focal juvenile \times school PCP ratio	162.361	2	81.181
PCP of focal juvenile \times average size of school members	144.012	2	72.006
Average size of school members \times size of focal juvenile	29.199	1	29.199
Behaviour of school \times PCP of focal juvenile	42.885	2	21.443

to a 1:27 ratio. This clearly shows the higher proportion (96%) of larger juveniles (> 25 mm TL) observed during the study period.

Number of school members

The ratio of school sizes joined by focal juveniles was 779:233:53 for small (3 to 5 members), medium (6 to 10 members) and large (≥ 11 members) schools, respectively, which approximates to a 15:4:1 ratio. Juveniles therefore most frequently joined small-sized schools.

School PCP ratio

Most focal juvenile *Chlorurus sordidus* (76%) joined schools in which the majority of members were displaying the same PCP as the focal juvenile itself. Of those which joined schools but which displayed a different PCP to the majority of other school members, only 4% underwent a PCP change to match the majority colour pattern after 1 min of schooling (Fig. 1). Most

of the schools joined (74%) were heterospecific and composed of a number of different schooling juvenile scarid species which share non-specific (Bellwood 1986) PCPs with juvenile *C. sordidus*.

PCP of focal juvenile upon joining a school

The ratio of PCPs displayed by focal juveniles was 102:613:350 for the striped (non-specific), uniformly dark (non-specific) and bullseye (species-specific) PCPs, respectively, which approximates to a 1:6:3 ratio. The ratio of non-specific to species-specific PCPs was therefore 715:350 \approx 2:1.

Average size of school members

The majority of focal juveniles joined schools composed of small individuals (25–50 mm TL) compared to those comprising larger individuals. The corresponding ratio for this was 75:990, which approximates to a 1:13 ratio.

Table 3. Odds ratios associated with the correlations underlying the interaction effects given in Table 2. UD: uniformly dark; S: striped; B: bullseye

Interaction	Underlying correlation(s)	Associated odds ratio(s)
PCP of focal juvenile \times school PCP ratio	Focal juvenile displaying a 'UD' PCP and schools composed mainly of other 'UD' individuals	1.638
	Focal juvenile displaying a 'S' PCP and schools composed mainly of individuals also displaying 'S' PCPs	1.875
PCP of focal juvenile \times average size of school members	Schools containing small individuals and the 'S' PCP	57.52, 229.90
	Schools composed of large individuals and the 'UD' and 'B' PCPs	2.91, 2.88
Average size of school members \times size of focal juvenile	Large focal juveniles and schools in which the average size of individuals was large	18.278
	Small focal juveniles and schools in which the average size of individuals was small	24.947
Behaviour of school \times PCP of focal juvenile	Striped focal juveniles and non-feeding schools	3.915, 2.635

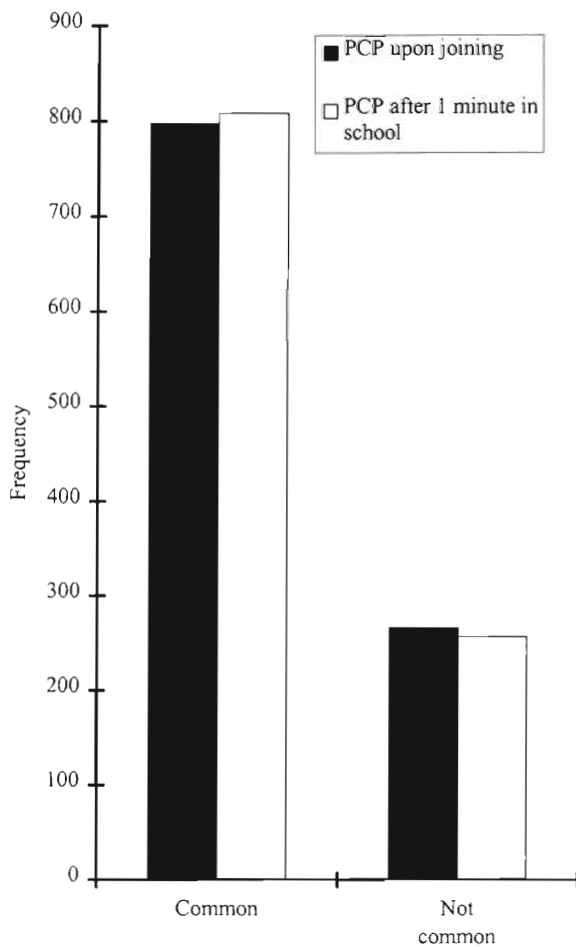


Fig. 1. The relationship between the physiological colour pattern (PCP) characteristics of focal juvenile *Chlorurus sordidus* and of the schools they were observed to join (immediately upon joining and after 1 min of schooling). Focal juvenile PCPs were referred to as either 'common' (representative of the majority [$\geq 95\%$] of other school members) or 'not common' (unlike the majority of other school members)

Feeding behaviour of school

Most focal juveniles joined feeding schools compared to non-feeding (swimming) schools with an associated ratio of 900:165, which approximates to a 5:1 ratio.

Interaction effects

PCP of focal juvenile \times school PCP ratio

An association between the PCPs of focal juvenile *Chlorurus sordidus* and the PCPs displayed by members of schools joined was shown and was found to be the most significant of all the interaction effects (having the highest standardised residual value, $\chi^2/df =$

81.181). More specifically, focal juveniles displaying the uniformly dark PCP were shown to be 0.63 times more likely than focal juveniles displaying the bullseye PCP to join a school where the majority of members displayed uniformly dark PCPs (Table 3). Furthermore, striped focal juveniles were almost twice as likely as a bullseye coloured juvenile to join a school in which the majority of members were also displaying striped PCPs (Table 3).

PCP of focal juvenile \times average size of school members

Striped juvenile *Chlorurus sordidus* were shown to be over 57 and 229 times more likely than juveniles displaying either the uniformly dark or bullseye PCPs, respectively, to join a school in which the average size of members was small (Table 3). Moreover, juveniles displaying either the bullseye or uniformly dark PCPs were both approximately 3 times more likely than a striped juvenile to join schools in which the average size of members was large (Table 3).

Average size of school members \times size of focal juvenile

Large focal juvenile *Chlorurus sordidus* were over 18 times more likely than small juveniles to join a school where the average size of individuals was large (Table 3). In addition, small focal juveniles were approximately 25 times more likely than large juveniles to join a school in which the average size of individuals was small (Table 3).

Feeding behaviour of school \times PCP of focal juvenile

A striped focal juvenile *Chlorurus sordidus* was shown to be approximately 3 and 4 times more likely than either a bullseye or uniformly dark coloured juvenile, respectively, to join a non-feeding school (Table 3).

DISCUSSION

Focal juvenile *Chlorurus sordidus* most frequently joined heterospecific schools composed of other juvenile scarid species which share non-specific PCPs. The data presented provide quantitative evidence for assortative schooling in this species based on both the PCPs and size (total length) of school members. An association was also shown between these juveniles and feeding schools, highlighting the potential foraging benefits associated with schooling. The data

demonstrate the multifunctional nature of juvenile scarid schools and suggest that these functions most likely change throughout the day in response to changes in their immediate environment. This is particularly relevant for reef fishes, such as *C. sordidus*, living in complex social and physical environments.

In this study a significant difference in the size distributions of juvenile *Chlorurus sordidus* was observed, with small juveniles being rarely recorded. This may have been the result of extensive predator related mortality of small, newly settled juveniles since this is known to be particularly high during the summer period (Bellwood 1986). Interestingly, most juvenile *C. sordidus* joined schools composed of few members (3 to 5), which is surprising because individuals have been shown to enjoy proportionately more protection (through the 'dilution effect') and increased foraging efficiency in larger groups (Neill & Cullen 1974, Itzkowitz 1977, Major 1978). Large schools of juvenile scarids, however, are commonly fragmented as a result of the aggressive behaviour of territorial trophic competitors (Crook unpubl.). Such fragmentation results in numerous smaller schooling units. Indeed, schools of between 3 and 5 members were the most common group sizes observed so that joining small schools probably represents a compromise given their relative availability.

A significant correlation was found between focal juvenile PCPs and school PCP ratios in that most juveniles joined schools in which their PCP was the same as that of the majority of the other school members. The apparent preference of juveniles to join schools of similarly coloured individuals provides quantitative evidence for assortative schooling using PCPs as a discriminatory stimulus. This may function to reduce individual oddity within schools and therefore lower individual susceptibility to predation (Ehrlich & Ehrlich 1973, Alevizon 1976). Moreover, the interaction between a focal juvenile's PCP and the PCP ratio of the school joined was the most significant (having the highest standardised residual value; Table 2), demonstrating a relationship between both uniformly dark and striped juvenile *Chlorurus sordidus* and schools of the same respective colouration. Interestingly, the majority of those juveniles that joined schools but displayed odd PCPs were observed to remain distinctly coloured throughout the observation period. In fact, after 1 min of schooling, only 4% of these odd juveniles underwent a PCP change to match that of the majority of other school members. Given that PCP changes occur in a matter of seconds (Crook unpubl.) it is surprising that juvenile *C. sordidus* are ever oddly coloured when schooling. It can perhaps be explained by the fact that the benefits of schooling are likely to be constantly changing in response to changes in the immediate environment and

that being part of a school for other benefits, such as foraging or hydrodynamic gains, may be more relevant than for anti-predator purposes at certain times.

Most of the schools joined were composed of a number of different juvenile scarid species which share non-specific PCPs. Schooling with other individuals capable of appearing alike provides further evidence that increasing the likelihood of school colour pattern uniformity is important. Indeed, the most common PCPs displayed by focal schooling juvenile *Chlorurus sordidus* were of the non-specific variety (uniformly dark or striped).

A significant relationship between a focal juvenile's size and the average size of school members was also shown. Large juveniles were associated with schools of large members and small juveniles most frequently joined schools composed of small individuals. This provides yet further evidence of assortative schooling with body size as another important motivating stimulus. This probably functions to reduce individual oddity in the same way as for juveniles joining schools of similar colouration and/or pattern.

The majority of juvenile *Chlorurus sordidus* were observed to join schools of large-sized individuals, probably because schools of small individuals were relatively rare. Furthermore, most focal juveniles were shown to join feeding schools, possibly because this provides an immediate increased foraging efficiency and/or access to high quality algal resources, many of which are defended by aggressive territorial trophic competitors. Since these territory holders have been shown to be especially aggressive towards solitary juvenile *C. sordidus* (Crook unpubl.), it seems particularly advantageous for juveniles to join feeding schools to increase the likelihood of them successfully gaining access to these defended areas.

An association between the PCP of focal juvenile *Chlorurus sordidus* and the average size of school members was also demonstrated: striped juveniles were shown to be more likely than either uniformly dark or bullseye-coloured juveniles to join schools composed of small-sized individuals. Schools of small individuals were mainly observed in open areas (low percentage of coral cover) where opportunistic and diurnally active predators are abundant (pers. obs.). In these areas the striped PCP probably has anti-predator functions (Crook 1997a, b) and will be most effective if the majority of individuals in schools are also striped and if the schools are highly mobile (Barlow 1972). Indeed, the data collected substantiate this since displaying a striped PCP was correlated with joining schools of striped individuals and also with joining swimming (non-feeding) schools (Table 3).

Display of either the bullseye or uniformly dark PCP in focal juvenile *Chlorurus sordidus* was shown to be

correlated with joining schools of large-sized individuals. Juvenile scarids above 60 mm TL rarely display the striped PCP (Crook 1997a), and therefore it is more likely that bullseye or uniformly dark juveniles will gain the benefits of school colour pattern uniformity if they join groups composed of predominantly larger individuals.

It appears that pressures for maintaining school uniformity exist in this species and that they are most likely driven by the opportunistic behaviour of diurnally hunting predators known to be present within the same reef locations (pers. obs.). Given that coral reefs represent dynamic and complex social environments it seems likely that the functions of schooling will be constantly changing. The ability of juvenile *Chlorurus sordidus* to undergo rapid PCP alterations, combined with their assortative schooling behaviour, is therefore likely to be important for enabling them to adjust to these changes and thus maximise their survival chances.

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