# REPORT

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# Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef

**Abstract** Adults of many closely related coral reef fish species are segregated along gradients of depth or habitat structure. Both habitat selection by new settlers and subsequent competitive interactions can potentially produce such patterns, but their relative importance is unclear. This study examines the potential roles of habitat selection and aggression in determining the spatial distribution of adults and juveniles of four highly aggressive damselfishes at Lizard Island, northern Great Barrier Reef. *Dischistodus perspicillatus*, *D. prosopotaenia*, *D. melanotus*, and *D. pseudochrysopoecilus* maintain almost non-overlapping distributions across reef zones, with adults of one species dominating each reef zone. Juveniles exhibit slightly broader distributional patterns suggesting that subsequent interactions reduce overlap among species. Although habitat choice experiments in aquaria suggest that associations between juveniles and substrata types in the field are partly due to habitat selection, large overlaps in the use of substrata by the different species were also found, suggesting that substratum selection alone is insufficient in explaining the discrete spatial distributions of adults. The strength of aggressive interactions among all four species was tested by a "bottle" experiment, in which an adult or juvenile of each species was placed in the territories of adult fish on the reef. The greatest levels of interspecific aggression were directed against adults and juveniles of neighbouring species. The highest levels of aggression were associated with species exhibiting the greatest levels of overlap in resource use. Evidently both habitat selection and interspecific aggression combine to determine the adult distributions of these species.

## Introduction

Species almost invariably exhibit restricted and unique distributions along gradients in the natural environment (e.g. Stevens 1989; Repasky and Schluter 1994; Connolly and Roughgarden 1998). Many ecologists seek understanding of the processes determining the extent of these distributions and the degree to which species overlap (Colwell and Futuyma 1971; Connell 1972; Abrams 1980). Habitat selection (Rosenzweig 1981, 1991; Morris 1996), competition (Diamond 1978; Connell 1983; Sih et al. 1985; Wilson 1991; Valone and Brown 1995; Robertson 1996), and predation (Sih et al. 1985; Hixon 1991; Wilson 1991) have been implicated at different life history stages to determine adult distributions. In marine organisms that have a dispersive larval stage these processes may act prior to settlement, at the time of recruitment into adult habitat, or throughout adult life (Jones 1991; Raimondi 1991; Olafsson et al. 1994; Caley et al. 1996), and the interactions amongst these are likely to be complex.

Coral reef fish assemblages, although unusually diverse, are not unusual in that species exhibit distinct patterns of distribution across a variety of spatial scales (Russ 1984a, 1984b; Roberts 1991; Williams 1991). Within reefs, species are often restricted to certain physiographic zones (Russ 1984b; Pitts 1991; Williams 1991). This may be particularly evident for fishes within guilds such as the territorial damselfishes (Williams 1991; Meekan et al. 1995), which are characterised by high site specificity and fidelity (Sale 1978a, 1978b). Populations of these fishes have been found to have non-overlapping spatial distributions by a number of studies (e.g. Itzkowitz 1977, 1985; Robertson and Lassig 1980; Waldner and Robertson 1980; Robertson et al.

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1981; Doherty 1983; Wellington 1992), but the factors causing and maintaining these patterns are poorly understood.

It has been suggested that patterns of larval supply and recruitment are primary determinants of the distribution of populations at a variety of spatial scales (Williams 1991; Caley et al. 1996; Jones 1997). Juvenile reef fishes commonly display strong habitat preferences at settlement (e.g. Wellington 1992; Danilowicz 1996; Ohman et al. 1998) and may recruit directly into adult habitat (Shulman et al. 1983; Sweatman 1983; Carr 1991; Levin 1991; Booth 1992; Wellington 1992; Danilowicz 1996; Ohman et al. 1998). This implies that patterns of adult distribution may be determined by juvenile habitat selection at settlement, but the extent to which juvenile habitat selection fully explains adult distributions has not been fully resolved.

Processes acting on juveniles after settlement may also affect spatial distributions (Jones 1991). Survival and migration of juveniles may alter distributional patterns established at settlement (Victor 1986; Jones 1987a, 1987b, 1988; Forrester 1990; Lewis 1997; Ault and Johnson 1998; Levin 1998; Nemeth 1998). Survival of juveniles may be affected by substratum characteristics (Shulman 1984; Jones 1988; Booth 1992; Wellington 1992; Nemeth 1998); predation (Booth and Beretta 1994; McGehee 1995); and intra- and interspecific density of juveniles (Jones 1987a, 1987b, 1988; Booth 1995; Schmitt and Holbrook 1999) as well as of adults (Sweatman 1983; Forrester 1990). Juveniles may also migrate post-settlement, thereby modifying distributional patterns established at settlement (Shulman 1985b; Shulman and Ogden 1987; Lewis 1997). These processes are often complex and highly species specific (e.g. Jones 1987a; Booth 1995), making generalisations regarding their effect on adult distributions hard to draw.

Behavioural interactions within and among species of mobile animals may be particularly important in determining the spatial distribution of adult populations. Aggressive interactions leading to habitat segregation have been found to structure the spatial distribution of territorial damselfishes (Robertson and Lassig 1980; Ebersole 1985; Robertson 1995, 1996). In addition, a number of these studies have found that the intensity of aggression determined the outcome of competitive interactions (Ebersole 1985; Shulman 1985a; Ormond et al. 1996; Robertson 1996). Non-overlapping distributions may be a result of discrete habitat preferences or interference in competitive interactions (Waldner and Robertson 1980). However, the roles of habitat selection and behavioural interactions at different life history stages are poorly understood.

In this paper we examine the potential roles of habitat selection and aggressive interactions in determining patterns of distribution and abundance in four species of damselfishes in Lizard Island lagoon, northern Great Barrier Reef. The four species of the genus *Dischistodus, D. perspicillatus, D. prosopotaenia,*

*D. melanotus,* and *D. pseudochrysopoecilus,* are common in lagoonal locations throughout the Great Barrier Reef. Adults are all highly aggressive and defend territories from a wide range of fishes including conspecific and congeneric individuals. We wished to examine whether reef zone and congeneric densities had an effect on habitat associations, and, if so, determine whether this changed with ontogeny. We documented the patterns of distribution and abundance of adults and juveniles of the four species of *Dischistodus* and determined the habitat use of adults and juveniles of the four species within and among reef zones. To test whether juvenile habitat use may be determined by habitat selection, a series of habitat choice experiments were conducted. We hypothesised that the distribution of juveniles was determined by the distribution of preferred habitats. Lastly, in order to test whether high levels of aggression may refine adult and juvenile distributions, a pair-wise comparison of the level of aggressiveness among species was carried out. Specifically, we hypothesised that greater levels of aggression are displayed among ecologically similar species. Aggression may therefore have the potential to modify juvenile and adult distributions.

## Materials and methods

### Patterns of distribution and abundance

Patterns of distribution and abundance of the four species of *Dischistodus* were examined at three sites in the eastern part of Lizard Island Lagoon (14°40′ S, 145°28′ E) in February 1997, and in February and April 1999. Each site was divided into four physiographic zones (reef base, reef gully, reef crest, and reef flat) based on depth and substratum (Table 1). Five randomly placed belt transects (4×20 m) were employed in each of the four zones at three sites (site 2 did not have a reef flat so only three zones were examined at this site). Along each transect, species identity, life stage, and total length of all individuals of *Dischistodus* spp. were recorded. In addition, the substratum beneath an individual when first observed was noted. Distribution and abundance of adults and juveniles among sites and reef zones were analysed by analysis of variance.

### Habitat availability and use

Patterns of habitat utilisation and availability were recorded along the same transects employed to document the distribution and abundance of the four species. Habitat availability was assessed by

Table 1 Definition of reef zones

| Zone | Depth (m) | Dominant substratum |
|---|---|---|
| Reef zone | 4–10 | Sand, *Porites cylindrica* |
| Gully | 2–7 | Sand, rubble, dead coral rock, little live and soft coral |
| Reef crest | 1–2 | Live, dead and soft coral, some rubble, little sand |
| Reef flat | 1–2 | Live, dead and soft coral, some rubble, some sand |

recording the substratum (dead coral, live coral, soft coral, rubble, and sand) under 100 random points along each transect. The degree of habitat specialisation for adults and juveniles was quantified by calculating resource selection ratios on pooled sites in reef zones with more than eight individuals (Manly et al. 1993). Selection ratios indicate the degree to which habitat use deviated from expectation based on the availability of the different habitats within each zone. Selection ratios (w) were calculated following Eq. (1):

$$\hat{w}_i = o_i/\pi_i \tag{1}$$

where $o_i$ is the proportion of individuals utilising resource units in the category i and $\pi_i$ is the proportion of resource units in category i. Bonferroni-corrected confidence intervals (adjusting for multiple tests) were calculated for each selection ratio (Eq. 2), where u denotes the total number of used resource units in the population:

$$se(\hat{w}_i) = \sqrt{\left\{o_i(1-o_i)/(u+\pi_i^2)\right\}} \tag{2}$$

The habitat was used in proportion to its abundance when the selection ratio encompassed "one". Where the selection ratio was larger than and did not encompass one, the habitat was used more than expected on the basis of availability. Conversely, when the ratio was smaller than one, the habitat was used less than it was available.

### Habitat preferences in juveniles

Selection trials were conducted in outdoor aquaria in order to test the strength of habitat preferences in juveniles under conditions of equal availability. Four habitats utilised by juveniles in the field were supplied at approximately equal availability (Fig. 1). The bottoms of the aquaria were covered with fresh beach sand and the tanks received a continuous supply of seawater. Between trials the sand was stirred and the habitats were rotated. The sand, water, rubble, and dead coral habitats were completely changed every 3 days and the live habitats were replaced every 2 days.

Juveniles of the four species were collected from the reef and transferred to holding tanks where fish spent a minimum of 24 and a maximum of 48 h. A total of 13 *D. perspicillatus*, 10 *D. prosopotaenia*, 13 *D. melanotus,* and 12 *D. pseudochrysopoecilus* juveniles were trialed, each individual participating only once. At the commencement of each trial, one juvenile was placed in a plastic tube positioned in the centre of the aquarium and allowed to acclimatise for 30 min (Fig. 1). The tube was then slowly lifted, thereby depositing the fish in the middle of the tank. The habitat selection was scored every 5 min for the next hour. Habitat choice was defined as the habitat upon which the individual had been observed most frequently during the trial period.

We tested whether juveniles made habitat choices in the tanks using binomial probability functions assuming that fish had an equal chance of selecting each of the four habitats (0.25). Binomial probabilities were then calculated from the observed proportional habitat selection, and a binomial probability of less than 0.05 was interpreted as statistically significant habitat selection.

### Factors affecting patterns of distribution and abundance

The role of aggressive behaviour in maintaining the spatial organisation of species was examined by presenting different intruders to territory holders. An adult or juvenile individual of each of the four species was enclosed in a transparent plastic bag and then introduced into the territories of the four species and the behaviour of the territory holder was recorded. We predicted that if resource overlap was important, greater levels of aggression would be expected amongst (1) conspecifics, (2) neighbouring species or species with higher resource overlap, and (3) individuals of the same life history stage.

Eight different types of intruders (adults and juveniles of four species) were introduced into territories of adults of each species, yielding 32 types of encounters. Four replicate intruder individuals

(of each of the 8 combinations) were bagged, one of which was used at random in each encounter to minimise the effect of individual identity on the territory holder response. Each encounter was replicated randomly among territory holders ten times. In addition, empty plastic bags were introduced into ten territories of each of the species. The frequency of display of behaviours of the territory holder were recorded over a 4-min time period and these were later classified into three categories based on the severity of the response (Table 2). Territory holders very rarely reacted to the empty control bags, so this treatment was omitted from the analysis. Results were analysed separately for each of the four species using the T-method (Tukey's minimum significant difference intervals) for unplanned multiple comparisons. Tukey's confidence intervals were calculated from results of an analysis of variance (on the pooled frequency of category two and three aggressive responses) (Eq. 9.9
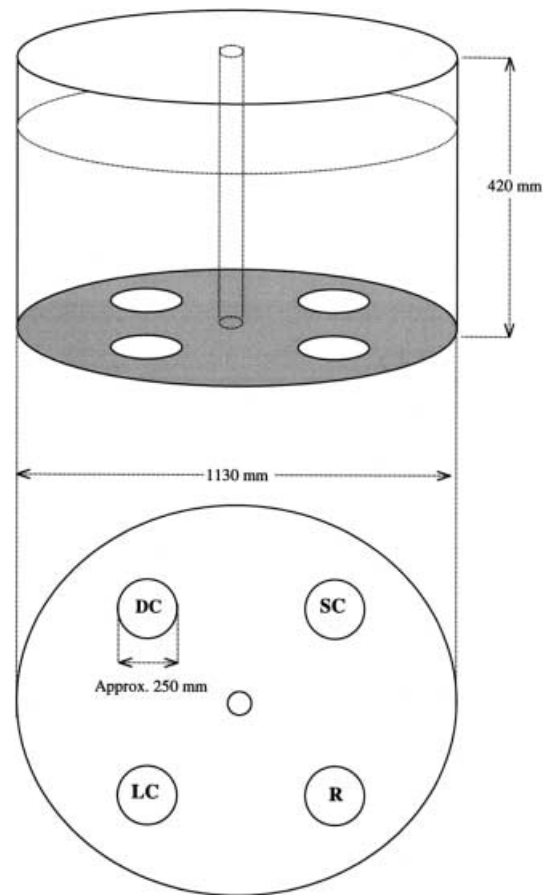


**Fig. 1** Design of the experimental aquaria used to examine habitat selectivity of juvenile *Dischistodus*. Four habitat types, dead coral (*DC*), live coral (*LC*), rubble (*R*), and soft coral (*SC*), were supplied in approximately equal availability, and the bottom of the aquaria was covered by sand

**Table 2** Behavioural categories used to quantify aggression within and between species

|  | Category 1 Investigation | Category 2 Lateral displays | Category 3 Attack |
|---|---|---|---|
| Behaviour | Ignore Inspect | Colour change Fin flare Tail fan Body flick/sound | Charge Bite |

in Sokal and Rohlf 1995). The confidence intervals were displayed on means plots of all encounter types. Non-overlapping confidence intervals indicate that the means are statistically different at the 0.05 level (Sokal and Rohlf 1995).

For each species an aggressive index for adults and juveniles of all four species was calculated. The number of aggressive interactions directed against each intruder type were expressed as a percentage of total aggression displayed by territory-holding adults of each of the four species. The overlap in habitat use (based on the substratum occupied) was calculated for each adult–adult and adult–juvenile combination following the percentage overlap index (Eq. 3: Krebs 1989).

$$P_{ik} = \left[ \sum^{n} \left( \text{minimum } P_{ij}, \ P_{ik} \right) \right] * 100 \qquad (3)$$

where $P_{ij}$ and $P_{ik}$ are the proportions of resource $i$ of the total resource use of species $j$ and $k$; and $n$ indicates the total number of resource states.

## Results

### Distribution and abundance of adult and juvenile *Dischistodus* spp.

The distribution and abundance of adult *Dischistodus* spp. differed markedly among the four reef zones (Table 3, Fig. 2). Each species preponderated one of the four reef zones and occurred relatively infrequently in other zones. *D. perspicillatus* was found in greatest abundance at the reef base, with only a few individuals in the adjacent gully zone. *D. prosopotaenia* preponderated the gully habitat at all three sites, but was more abundant at one site. *D. melanotus* numerically dominated the reef crest habitat, although was also common on the reef flat. *D. pseudochrysopoecilus* was mainly restricted to the reef flat habitat, but with a few individuals on the adjacent reef crest (Fig. 2).

The distribution of juvenile *Dischistodus* spp. also differed among reef zones (Fig. 3, Table 4). The distribution of juveniles generally coincided with that of conspecific adults, although in each case there was greater use of adjacent reef zones. *D. perspicillatus* was most abundant at the reef base, but was also found in the gully zone. *D. prosopotaenia* was mainly restricted to the gully zone, with only a few individuals being found at the reef base. *D. melanotus* was found at low abundances in both the reef crest and flat zones. Likewise, *D. pseudochrysopoecilus* juveniles were numerically dominant in both reef crest and flat zones across sites with higher abundances at one site than another (Fig. 3).

### Habitat availability and use

Adults of *D. perspicillatus* were primarily associated with sand in both the reef base and gully zones (Fig. 4a, b), using it in accordance with availability in the reef base zone where sand is by far the most common substrate, and selecting sand in the gully zone. Juveniles appeared broader than adults in their habitat use (Fig. 4a–d), and showed slightly different preferences. Juveniles were strongly associated with rubble at the reef base but dead coral in the gully zone. Habitat use in the gully, the zone of low adult conspecific abundance, was slightly broader than at the reef base (Fig. 4c, d).

Adult *D. prosopotaenia* used dead coral more than it was available in the gully zone (Fig. 5a). Juveniles used rubble in excess of availability in the reef base and gully zones (Fig. 5b, c). Sand, the most abundant habitat category in both the base and gully zones, was used in accordance with availability by juveniles at the base and adults in the gully zones, but was avoided by juveniles in the gully zone.

**Table 3** ANOVA testing for differences in distribution and number of adult individuals of the four species across reef zones and sites. * Significance at $\alpha = 0.05$

| Source | Type III SS | df | MS | F | Significance of F |
|---|---|---|---|---|---|
| *D. perspicillatus* | | | | | |
| Zone | 7.811 | 1 | 7.811 | 27.736 | 0.034* |
| Site | 1.268 | 2 | 0.634 | 2.251 | 0.308 |
| Site×Zone | 0.563 | 2 | 0.282 | 2.971 | 0.070 |
| Residual | 2.275 | 24 | 9.47E-02 | | |
| *D. prosopotaenia* | | | | | |
| Zone | 17.439 | 1 | 17.439 | 5730.649 | 0.000* |
| Site | 1.485 | 2 | 0.742 | 243.994 | 0.004* |
| Site×Zone | 6.086E-03 | 2 | 3.04E-03 | 0.029 | 0.971 |
| Residual | 2.504 | 24 | 0.104 | | |
| *D. melanotus* | | | | | |
| Zone | 22.355 | 2 | 11.178 | 25.631 | 0.013* |
| Site | 0.348 | 2 | 0.174 | 0.399 | 0.702 |
| Site×Zone | 1.308 | 3 | 0.436 | 2.552 | 0.073 |
| Residual | 5.469 | 32 | 0.171 | | |
| *D. pseudochrysopoecilus* | | | | | |
| Zone | 21.111 | 2 | 10.556 | 47.631 | 0.005* |
| Site | 8.056E-03 | 2 | 4.02E-03 | 0.018 | 0.982 |
| Site×Zone | 0.665 | 3 | 0.222 | 3.085 | 0.041* |
| Residual | 2.299 | 32 | 7.18E-02 | | |
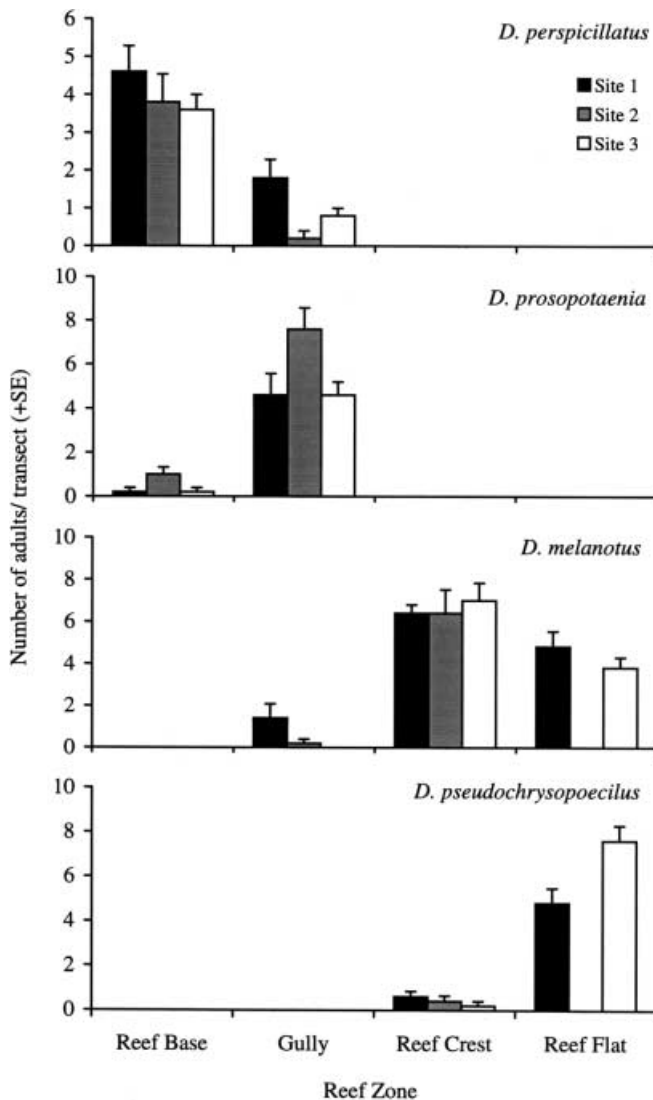
**Fig. 2** Distribution of adult *Dischistodus* spp. across reef zones and sites; *n* = 5 per zone
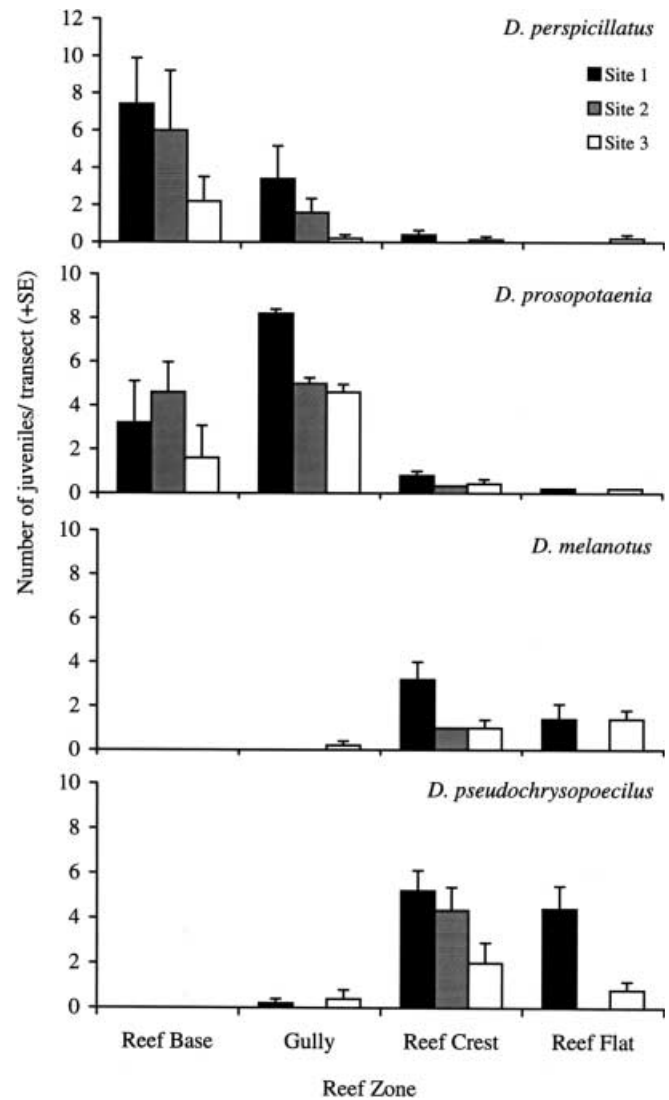


**Fig. 3** Distribution of juvenile *Dischistodus* spp. across reef zones and sites; *n* = 5 per zone

*D. melanotus* adults were positively associated with dead coral in both the reef crest and reef flat (Fig. 6a, b). Juveniles also used dead coral more than it was available at the reef crest; however, this habitat was used in accordance with availability at the reef flat, as was live coral and soft coral (Fig. 6c, d). There was a trend for juveniles to be slightly broader in their habitat use than adults in particular in the zone of low adult conspecific abundance (Fig. 6a–d).

Dead coral was used more than it was available by adult *D. pseudochrysopoecilus* in the reef flat zone (Fig. 7a). A large proportion of individuals was found on sand and this habitat was used in accordance with availability. Juveniles primarily occupied dead coral and rubble in both the reef crest and flat zones (Fig. 7b, c). Rubble was used in excess of availability and dead coral in accordance with availability in the crest zone. However, this was reversed on the reef flat.

## Habitat selection of juveniles in aquaria

Juveniles of *D. prosopotaenia* and *D. melanotus* chose mostly dead coral, while the majority of *D. perspicillatus* selected rubble, and *D. pseudochrysopoecilus* showed approximately equally frequent choice of dead coral and rubble (Fig. 8). These results from the habitat selection trials largely match the field observations of habitat utilisation. Rubble, the habitat occupied at the reef base, was selected more frequently than expected for *D. perspicillatus* (binomial probability test: $p = 0.000$). *D. prosopotaenia*, *D. melanotus*, and *D. pseudochrysopoecilus* all preferred dead coral in the experimental tanks ($p = 0.003$, 0.000, and 0.040, respectively) and this confirmed the choice of habitat in the field in the two latter species. The positive association of *D. pseudochrysopoecilus* with rubble observed in the field (Fig. 7b) was near significant ($p = 0.103$), while the field

**Table 4** ANOVA testing for differences in distribution and number of juvenile individuals of the four species across reef zones and sites. * Significance at $\alpha = 0.05$

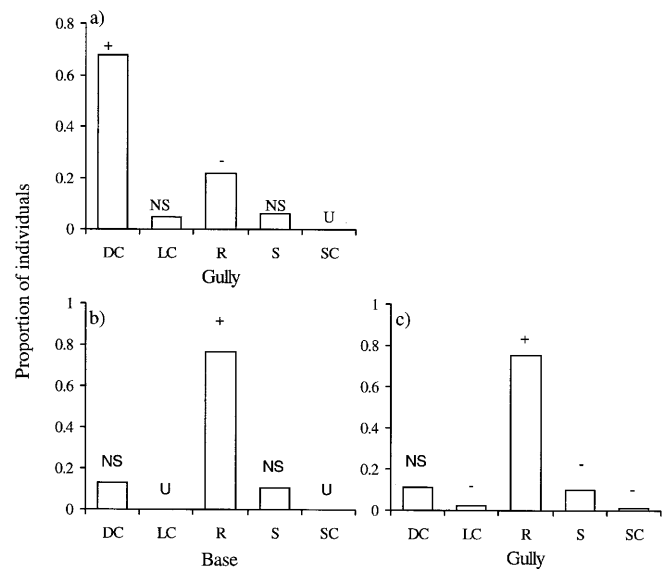| Source | Type III SS | df | MS | F | Significance of F |
|---|---|---|---|---|---|
| *D. perspicillatus* | | | | | |
| Zone | 14.776 | 3 | 4.925 | 8.194 | 0.022* |
| Site | 2.961 | 2 | 1.481 | 2.477 | 0.176 |
| Site×Zone | 3.010 | 5 | 0.602 | 1.449 | 0.226 |
| Residual | 18.283 | 44 | 0.416 | | |
| *D. prosopotaenia* | | | | | |
| Zone | 21.100 | 3 | 7.033 | 26.521 | 0.002* |
| Site | 1.329 | 2 | 0.664 | 2.503 | 0.172 |
| Site×Zone | 1.326 | 5 | 0.265 | 0.953 | 0.457 |
| Residual | 12.240 | 44 | 0.278 | | |
| *D. melanotus* | | | | | |
| Zone | 7.912 | 3 | 2.637 | 8.654 | 0.020* |
| Site | 0.280 | 2 | 0.140 | 0.465 | 0.653 |
| Site×Zone | 1.528 | 5 | 0.306 | 2.512 | 0.044* |
| Residual | 5.354 | 44 | 0.122 | | |
| *D. pseudochrysopoecilus* | | | | | |
| Zone | 19.476 | 3 | 6.492 | 10.905 | 0.012* |
| Site | 2.227 | 2 | 1.114 | 1.896 | 0.243 |
| Site×Zone | 2.988 | 5 | 0.598 | 3.913 | 0.005* |
| Residual | 6.720 | 44 | 0.153 | | |
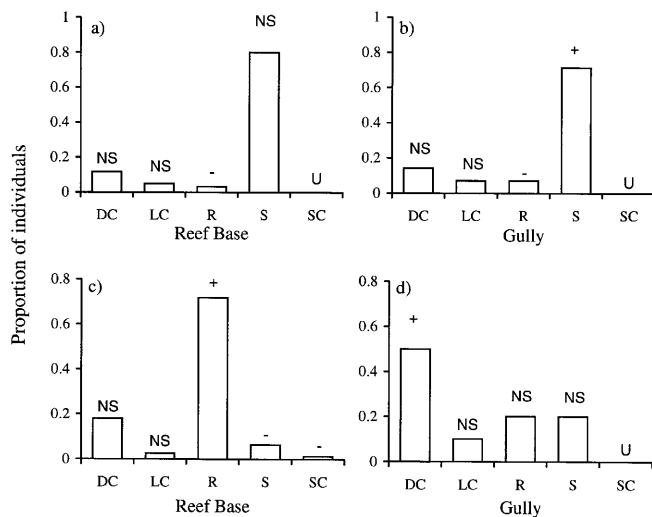


**Fig. 4** Habitat use of *D. perspicillatus*. **a**, **b** Adults; **c**, **d** juveniles. Habitats: *DC* dead coral, *LC* live coral, *R* rubble, *S* sand, and *SC* soft coral. Resource selection: + habitat used more than available, – habitat used less than available, *NS* habitat used in proportion to availability, *U* habitat never used



**Fig. 5** Habitat use of *D. prosopotaenia*. **a** Adults; **b**, **c** juveniles. Habitats and resource selection as in Fig. 4

choice of *D. perspicillatus* juveniles of dead coral in the gully zone (Fig. 4d) was not reflected in the habitat preference in tanks ($p = 0.206$).

## Potential role of aggression in determining the distribution and habitat use of the four species

*D. perspicillatus* displayed significantly more aggressive behaviour towards adult conspecifics than other intruders, but were in general less aggressive than the other species (Fig. 9). *D. prosopotaenia* displayed highly variable levels of aggression among species and life stages. The greatest levels of aggression were displayed
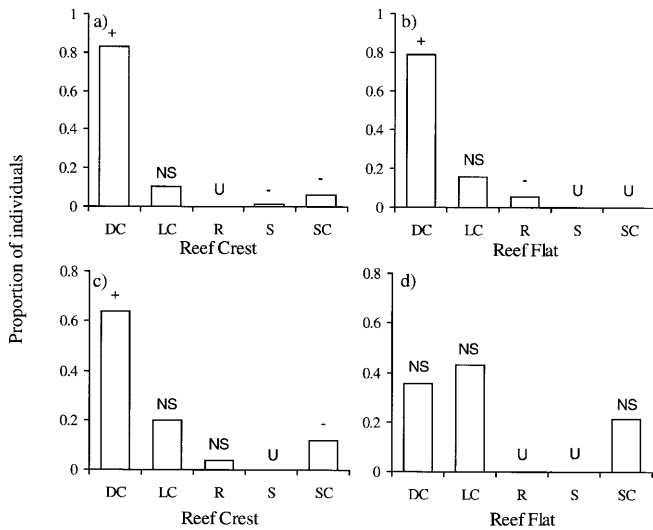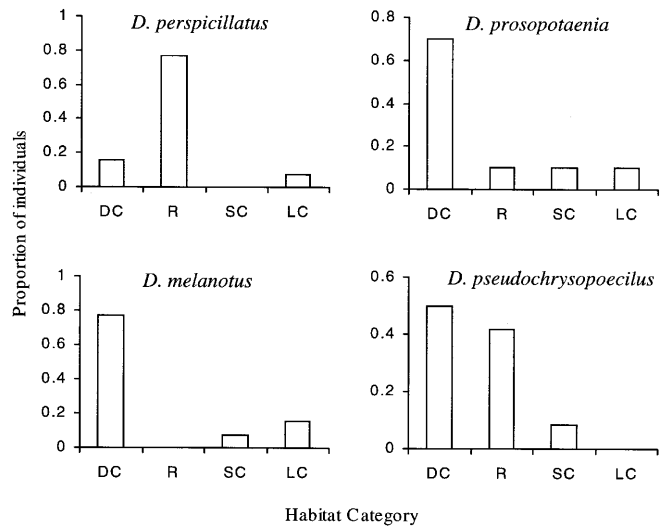
towards conspecific juveniles and adults of the neighbouring *D. melanotus* (Fig. 9). Interestingly, adult conspecifics elicited significantly less aggressive behaviours than adults of the other three species.

*D. melanotus* were highly aggressive against conspecific adults, displaying on average nearly 30 aggressive interactions during the trial (Fig. 9). Adult neighbouring species elicited significantly less aggressive displays and significantly more were directed at *D. pseudochrysopoecilus* than *D. prosopotaenia*. Conspecific juveniles and *D. pseudochrysopoecilus* juveniles prompted intermediate levels of aggression.
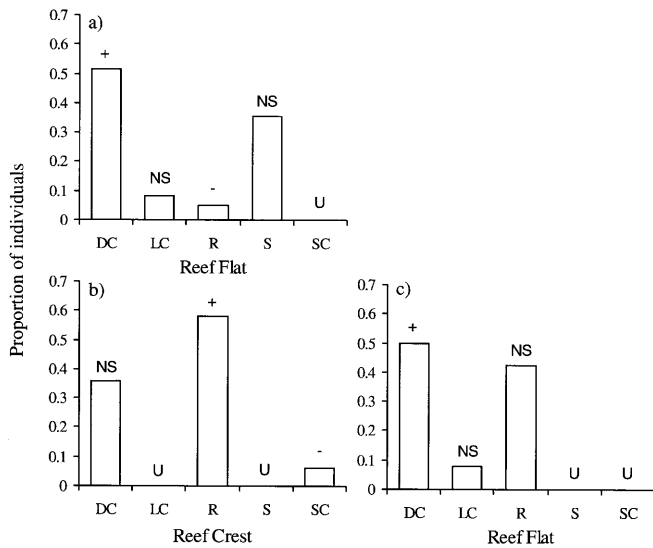
Adult *D. pseudochrysopoecilus* displayed the greatest levels of aggression against conspecific adults and sig-

**Fig. 6** Habitat use of *D. melanotus*. **a**, **b** Adults; **c**, **d** juveniles. Habitats and resource selection as in Fig. 4



**Fig. 8** Habitat choice of juvenile *Dischistodus* spp. in outdoor aquaria. For habitat codes see Fig. 1



**Fig. 7** Habitat use of *D. pseudochrysopoecilus*. **a** Adults; **b**, **c** juveniles. Habitats and resource selection as in Fig. 4

individuals with high overlap, and high levels of aggression were never displayed where the overlap in habitat use was low.

## Discussion

This study confirms the widely documented pattern of distinct non-overlapping spatial distributions of territorial damselfishes (e.g. Itzkowitz 1977; Robertson and Lassig 1980; Waldner and Robertson 1980; Robertson et al. 1981). Adults of the four species of *Dischistodus* displayed distinct distributional patterns across the reef zones. Each species numerically dominated one of the reef zones and this pattern was largely consistent across sites in the Lizard Island lagoon.

While adult distributional patterns may arise as a direct result of habitat selection of juveniles at the time of settlement (Shulman et al. 1983; Sweatman 1983; Carr 1991; Levin 1991; Booth 1992; Wellington 1992; Danilowicz 1996; Ohman et al. 1998), they may also be modified by ontogenetic habitat shifts (e.g. Shulman 1985b). Although generally in the same zone, the distribution of juvenile *Dischistodus* was found to be broader than that of the adults, with juveniles typically being abundant in two reef zones. Also, for two species, juveniles and adults were associated with different microhabitat within reefs. Juveniles of *D. perspicillatus* and *D. prosopotaenia* were associated with rubble, whereas adults were associated with sand and dead coral, respectively. Thus, there appear to be substantial ontogenetic shifts in both the distribution of juveniles and the use of habitats. Differences between patterns of adult distributions may have been underestimated since juveniles may have been on the reef for up to 100 days (based on their body size). It is possible that initial settlement patterns were altered by differential growth,

nificantly less against *D. melanotus* adults, but low levels of agonism against *D. perspicillatus* and *D. prosopotaenia* (Fig. 9). Juveniles of all four species were virtually ignored by *D. pseudochrysopoecilus*.

Consequently, in three out of four species, conspecific adults elicited significantly greater levels of aggression than any other encounter type. Neighbouring adults prompted more aggression than non-neighbouring species in four of six instances and this tended to be directed towards the reef crest neighbour (*D. melanotus*) rather than reef edge neighbour.
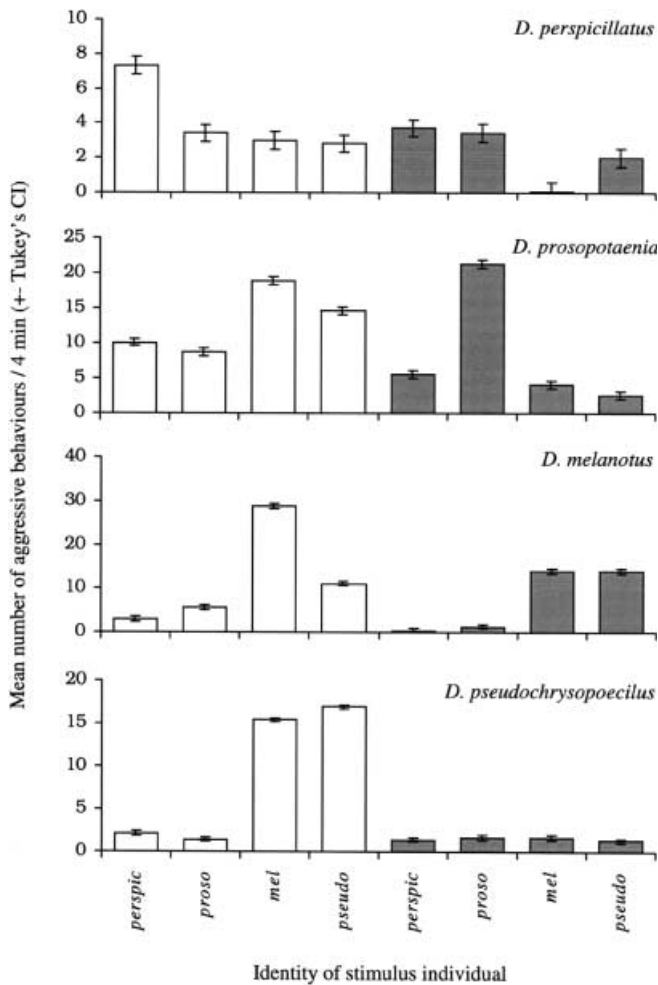
The levels of aggression displayed against species and ontogenetic stages appear to be partially related to overlap in habitat use (Fig. 10). Although aggression was variable, the greatest levels were recorded between

**Fig. 10** Relationship between percentage overlap in habitat use and level of aggression displayed between adults and juveniles of the four species of *Dischistodus*. Each point represents a single interaction. Each point represents 1 of the 32 possible adult–adult or adult–juvenile combinations of the 4 species
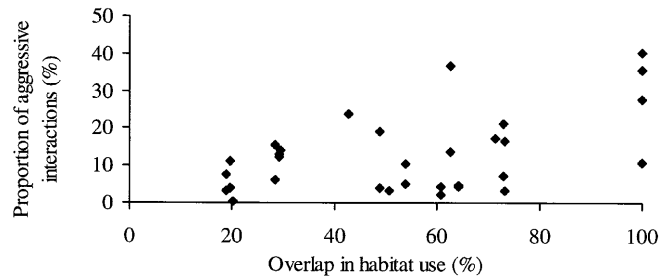
**Fig. 9** Levels of aggression displayed within and among *Dischistodus* spp. *n* 10 per encounter. *White bars* represent adult and *shaded bars* represent juvenile stimuli individuals

survival, and/or migration within and amongst habitats (e.g. Shulman 1985b; Jones 1987a, 1987b, 1988; Forrester 1990; Nemeth 1998).

A variety of factors may explain the distribution of juveniles and the association with particular habitats. Juveniles of a range of species have been found to have distinct habitat preferences at the time of settlement (Sweatman 1983, 1985; Danilowicz 1996; Ohman et al. 1998). Consequently, patterns in the distribution of juvenile *Dischistodus* spp. may be a function of habitat preference at settlement. Substratum preference experiments on juveniles of the four species in aquaria largely confirmed that patterns of habitat choice in the field were the result of actual preference. Although we examined habitat selection of juveniles with prior exposure to the reef environment, other studies have found that field-caught juveniles made habitat choices very similar to naive juveniles (Danilowicz 1996; Ohman et al. 1998).

Discrete distributional patterns may arise as a function of the dispersion of preferred substrata (Ebersole 1985; Tolimieri 1995). *D. perspicillatus* primarily used sandy substrata and showed strong selection for this substratum type when it was found in low abundance. The distribution of this species coincided with that of the preferred substratum type. However, adults of *D. prosopotaenia*, *D. melanotus,* and *D. pseudochrysopoecilus* showed great overlap in their habitat use, all using dead coral significantly more than it was available. This habitat was relatively abundant across the reef zones. Habitat segregation based on preference alone therefore appears insufficient in explaining the distributional pattern in three of the four *Dischistodus* species.

Extensive overlap in resource preference has previously been observed in spatially segregated species (Ebersole 1985; Robertson 1996). Resource partitioning in these species was the result of interference competition where differential levels of aggression resulted in the spatial segregation of species (Ebersole 1985; Robertson 1996). Our results may indicate that species compete for a preferred reef zone, resulting in a competitive hierarchy. However, it is equally probable that species are competitively dominant in their respective reef zones as a result of historical processes leading to zone-specific competitive reversals. Carefully maintained removal experiments (such as Robertson 1996) are clearly needed to resolve the ecological significance of the zones and the nature of the interactions among species.

There was a general trend for species to display significantly higher levels of aggression against conspecific adults and high to intermediate levels against neighbouring species. The highest levels of aggression generally coincided with the highest levels of overlap in habitat use. This may indicate that adult *Dischistodus* are competing for this resource. It is possible that *D. melanotus* by virtue of its highly aggressive nature maintains use of the reef crest zone where dead coral is abundant. Both *D. pseudochrysopoecilus* and *D. prosopotaenia* need to display high levels of aggression against adults of *D. melanotus* in order to maintain dominance in their respective zones. Furthermore, the more aggressive nature of *D. prosopotaenia* relative to *D. pseudochrysopoecilus* may be the reason that *D. melanotus* are found on the reef flat but not in the gully, despite the presence of dead coral in both zones. Adults of *D. perspicillatus* do not share habitat choice with either adults or juveniles of any of the other species

and were observed to show relatively low levels of aggression against all but conspecific adults.

The presence of conspecific adults may significantly affect the distributional patterns of juveniles, although at this stage this does not appear to be a general rule. Adults have been found to increase (Sweatman 1983, 1985; Jones 1987b; Booth 1992), decrease (Shulman et al. 1983; Jones 1988), or have no effect (Jones 1987b) on the recruitment, growth, and survival of juveniles. Adult *Dischistodus* were generally found to display relatively high levels of aggression against conspecific and some congeneric juveniles, and juveniles were never observed to live inside adult territories. Juvenile *Dischistodus* were generally broader in their habitat use in the zone of low adult abundance, suggesting that adults may affect habitat association. Since habitat characteristics may affect the growth and survival of juveniles (Jones 1988; Booth 1992; Wellington 1992), it is likely that aggression may affect the patterns of distribution established at settlement. This may take place by the enhancement of distributional patterns in preferred habitats or by the disruption of patterns by aggression of adult *Dischistodus*.

In conclusion, the distribution of adults and juvenile *Dischistodus* species appears to be the result of a number of processes, including habitat preference at settlement, ontogenetic changes in habitat choice, and aggressive interactions among individuals with similar habitat requirements. Further experiments are required to measure the relative contribution of these different processes.

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