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Effects of selective settlement and of aggression by residents on distribution of young recruits of two tropical damselfishes

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Abstract. The reef fishes that settled on an array of experimental corals at Lizard Island, Queensland, Australia, were counted during a pulse of recruitment in December 1986. Neither *Pomacentrus* sp. nor *P. amboinensis* showed any evidence that harassment by resident *Dascyllus aruanus* caused a decrease in persistence during the first day after settlement. Larval *Pomacentrus* sp. settled selectively on corals without resident *D. aruanus*. The results for *P. amboinensis* were ambiguous. Settlers of both species positioned themselves closer to the sand on corals with resident *D. aruanus* than on unoccupied corals. This could reduce access to planktonic food and increase the risk of predation. Adult aggression may be less important and active selection of settlement sites by larvae may be more important to the distribution of recruits than is suggested by the literature. The presence or absence of particular species should be included among the cues that larval reef fishes use to choose settlement sites.

Introduction

Coral reef fish larvae are assumed to disperse widely (and to some extent passively) from the habitat of their parents. One consequence of this is that local reproductive output may have little effect on local recruitment. For adult populations of such organisms to be at equilibrium, there must be density-dependent regulation of recruitment to the adult population rather than control of fecundity (Doherty 1983). Regulatory processes must act either at the time the larvae settle from the plankton, or between settlement and maturation. Proponents of equilibrium communities, whether single- or multispecies equilibria, would predict a negative relationship between density of superior competitors and recruitment to the adult population (Doherty and Williams 1988).

A number of investigators (e.g. Sale 1976, Talbot et al. 1978, Williams 1980, Doherty 1983, Jones 1987) have looked for a negative relationship between the density of resident fishes and the density of recruits as evidence of equilibrium communities maintained by competition for space. Only three such studies have found convincing evidence that the presence of certain species of reef fishes leads to decreased local recruitment of other species (Shulman et al. 1983, Sweatman 1985a, Jones 1987). In the first two cases, the reduction was evident within a few days of settlement.

This reduction could have come about because larvae avoid settling where certain species are present, or because prior residents actively repel or eat settlers. The two mechanisms are not mutually exclusive, but most authors implicitly or explicitly favour aggression by residents (e.g. Sale 1977, 1978a, Williams 1980, Shulman et al. 1983, Sweatman 1985a). This is supported by the results of an aquarium study (Sale et al. 1980) and by two anecdotal field observations: Nolan (1975) saw adult *Pomacentrus pavo* harass and drive off a *Chromis caerulea* settler that approached their home-patch reef and Sweatman (1985a) saw a planktivorous damselfish eat a newly-settled wrasse.

Estimates of daily mortality rates for new recruits are high initially but decline after a few days (Doherty and Sale 1986, Victor 1986, Sale and Ferrell 1988). Presumably this is because recruits are most vulnerable to predators immediately after settlement because of their weak swimming ability and unfamiliarity with the local topography. Their small size may also make them susceptible to predation by numerous small fishes, including a number of planktivorous and carnivorous species that are not normally considered to be piscivores. The same characteristics that make newly-settled fishes susceptible to predators will make them vulnerable to aggression by resident fishes. It has also been suggested that recruits can use their small size to elude territory holders ["topological deception" of Sale et al. (1980)], although this would require familiarity with the locality.

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The alternative mechanism, that larvae actively select settlement sites from which other species are absent, has received less attention. Historically, habitats of coral reef fishes have been defined in terms of substratum type and depth (e.g. Jones 1968, Sale 1969, 1974, Waldner and Robertson 1980, Bell and Galzin 1984, Ebersole 1985, Findley and Findley 1985). Studies of larval settlement sites (Williams 1979, Sale et al. 1984, Victor 1986) have also stressed substratum cues. Resident species can influence the choice of settlement sites. *Dascyllus aruanus* larvae settle preferentially where resident conspecifics occur (Sweatman 1985 b, 1988), while larvae of other species may avoid such sites (Sweatman 1988).

Sweatman (1985 a) showed that smaller numbers of several species recruited to corals with resident groups of 20 adult and subadult *Dascyllus aruanus* (or *D. reticulatus*) than recruited to corals with no resident fishes. In the present study we investigated the relative importance of two mechanisms, selective settlement and aggression by residents towards newly-settled individuals, that could produce the reduction in recruitment when *D. aruanus* was present. We concentrated on *Pomacentrus* sp. and *P. amboinensis* because they settle in reasonable numbers and have lower net recruitment where *D. aruanus* is present (Sweatman 1985 a).

"Settlers" refers to individuals that are in the process of settling from the plankton or have settled in the previous 24 h. "Juveniles" are fish that settled from 24 h to several months previously. "Recruits" are fish of any age that join the population under study.

Study area

The experimental area was a large (>6 ha) expanse of sand ca. 800 m southwest of Lizard Island Research Station, Lizard Island, Great Barrier Reef, North Queensland, Australia (14°38′S; 145°28′E). The depth was 3 to 4 m at high tide.

Background biology of species

Pomacentrus sp. (see description of this unnamed species, including meristics and colour plate, in Allen 1975), *P. amboinensis* and *Dascyllus aruanus* are planktivores and eat considerable amounts of drift algae (Williams 1979, Sano et al. 1984). *D. aruanus* live in groups in close association with colonies of branching corals (Sale 1971). *Pomacentrus* sp. and *P. amboinensis* usually inhabit small lagoonal patch reefs (Williams 1979).

Materials and methods

In November 1986, 24 "standard coral units" (SCUs; Sweatman 1983, 1985 a), each 0.5 m in diameter, were built by tying living colonies of the branching coral *Pocillopora damicornis* to steel stakes driven into the bottom. The SCUs were separated by 20 m of sand and were laid out in a 6 × 4 grid. Groups of about 20 *Dascyllus aruanus* were collected from pre-existing social groups using the anaesthetic quinaldine. Groups were released onto the SCUs allocated to treatments requiring resident fish at dusk. Twenty *D. aruanus* in a coral head the size of an SCU represents a high value within the natural density range (Sweatman 1985 a).

Recruitment experiment

The experiment followed a 2 × 2 factorial design. The first factor was the presence or absence of adult *Dascyllus aruanus*. The second factor was the time of day at which recruits were censused and collected: either at dawn or in the late afternoon. Six SCUs were allocated randomly to each combination of treatments.

Between 3 and 6 December 1986, we collected recruits of all species daily, using anaesthetic and handnets. The dawn collection proceeded as follows: Two divers entered the water at first light (around 05.20 hrs Eastern Australian Standard Time), just as the resident *Dascyllus aruanus* became active. Each diver counted the recruits on the SCUs designated for the dawn collection in one half of the grid. The SCUs in each half of the grid were censused in a set order, but the starting point was chosen randomly each day. When all the designated SCUs had been censused, each one was visited again to collect recruits. The SCUs were all censused before any recruits were collected so as to minimise the opportunities for *D. aruanus* to interact with settlers before we recorded their presence.

All recruits were counted and collected from SCUs allocated to the afternoon census between 15.00 and 18.00 hrs.

If settlement occurs at night, when *Dascyllus aruanus* are inactive and hiding in the coral, and it is indiscriminate with respect to residents, the numbers of settlers on SCUs both with and without resident *D. aruanus* should have been about equal at dawn. If settlers are less likely to persist when harassed by *D. aruanus* then, by the afternoon census, there should have been fewer settlers remaining on SCUs with resident *D. aruanus* than on SCUs without. This would result in a statistical interaction. Alternatively, if larvae actively choose sites without resident *D. aruanus*, then settlers would have been fewer where there were resident *D. aruanus* at both censuses (main effect of Factor 1 only).

Estimation of daytime and nighttime settlement rates

The recruitment experiment assumes that these species settle at night. Between 16 November and 2 December 1986 we counted recruits on twelve SCUs (that were later used in the recruitment experiment) twice each day – at dawn (starting at 05.20 hrs) and in the late afternoon. We collected recruits from four SCUs with resident adult *Dascyllus aruanus* only after the dawn census. We collected recruits from another four SCUs with resident adult *D. aruanus* after the afternoon census and from the remaining four SCUs (with no resident fishes) after both dawn and afternoon censuses. On the first day of the recruitment experiment we also censused recruits at dawn on all SCUs, including those that were not to be collected until the afternoon. Any increase in the number of recruits on a SCU between dawn and the afternoon could have been due to daytime settlement, although these values are maximum estimates because they also include any settlers we overlooked at the dawn census.

Direct observations of behavioural changes in presence of resident *Dascyllus aruanus*

Between 6 and 8 December 1986 we studied the effect of the presence of *Dascyllus aruanus* on the positions of settlers on SCUs. *Pomacentrus* sp. and *P. amboinensis* settlers confine their movements to small areas, 0.2 to 0.3 m in diameter (Williams 1979, Sale et al. 1984). We recorded the heights of the centres of these areas above substratum for settlers on SCUs with and without resident

D. aruanus. We only considered settlers on the SCUs that were cleared daily, so no fish was recorded more than once. Data were collected during the afternoon. When we first approached a SCU, we recorded the position of every settler present. SCUs differed in the numbers of settlers that colonised them. Data were not collected from all SCUs each day, so different SCUs contributed different numbers of observations.

Analyses

Results were subjected to analysis of variance. When drawing biological conclusions from null results rather than significant differences, we checked null results for ambiguity by calculating the probability of Type II error (acceptance of a false null hypothesis). We estimated the power of tests folowing Cohen's (1977) procedures for factorial designs. We used the observed error mean square and overall mean number of recruits to calculate the probability of Type II error for hypothetical differences among sample means. These hypothetical differences were based on relative recruitment rates of the same species in a previous study (Sweatman 1985a).

Results

Pomacentrus sp. settlement

Of 46 *Pomacentrus* sp. which settled on the twelve SCUs censused between 16 November and 2 December 1986, 5 (10.9%) could have settled in daytime; 2 (15.4%) of the 13 *Pomacentrus* sp. that settled on the 12 "afternoon" SCUs on 3 December could have settled in daytime.

In the course of the recruitment experiment between 3 and 6 December, 131 *Pomacentrus* sp. settled on the experimental SCUs. The distribution of these settlers suggested that resident *Dascyllus aruanus* did not prey upon or aggressively exclude *Pomacentrus* sp. settlers in the course of their first day after settlement (Table 1, interaction term not significant). Tests for interactions in 2 × 2 designs are not powerful due to the low numbers of degrees of freedom (had resident *D. aruanus* reduced net recruitment of *Pomacentrus* sp. by 90% over the first day, the chance of rejecting the null hypothesis that residents have no effect would still only be 60%) but the lack of interaction as shown by the distribution of means (interaction mean square = 0.02, Table 1) is unambiguous.

Larval *Pomacentrus* sp. avoid settling where *Dascyllus aruanus* are present. At dawn, less than half as many *Pomacentrus* sp. settlers were collected from SCUs with resident *D. aruanus* (Table 1). This was also true in the afternoon collections.

Table 1. *Pomacentrus* sp. Settlement between 3 and 6 December 1986, showing mean numbers of recruits collected from "standard coral units" (SCUs) for each treatment combination and (95% confidence limits) based on pooled variance. Data were transformed by taking square root of $(x+0.5)$ before analysis; retransformed values are given here. SS: sum of squares; MS: mean square; **: $p<0.01$

Collection time	*Dascyllus aruanus* present (+)	*Dascyllus aruanus* absent (−)	Total
Dawn	2.2 (0.5–4.7)	5.5 (2.8– 9.0)	3.7 (2.1–5.7)
Afternoon	3.9 (1.6–6.9)	8.5 (5.1–12.6)	6.0 (3.9–8.4)
Total	3.0 (1.5–4.8)	6.9 (4.7– 9.5)	4.8 (3.4–6.3)

	DF	SS	MS	*F*
+/− *D. aruanus*	1	4.42	4.42	8.07**
Dawn/afternoon	1	1.47	1.47	2.68
Interaction	1	0.02	0.02	0.03
Error	20	10.93	0.55	
Total	23	16.82		

Table 2. *Pomacentrus amboinensis*. Settlement between 3 and 6 December 1986, showing mean numbers of recruits collected from "standard coral units" (SCUs) for each treatment combination and (95% confidence limits) based on pooled variance. Data were transformed by taking square root of $(x+0.5)$ before analysis; retransformed values are given here. SS: sum of squares; MS: mean square

Collection time	*Dascyllus aruanus* present (+)	*Dascyllus aruanus* absent (−)	Total
Dawn	31.6 (18.2–48.5)	42.7 (26.2–62.09)	36.9 (26.2–49.4)
Afternoon	34.9 (20.8–52.6)	47.3 (30.6–67.6)	40.9 (29.6–53.9)
Total	33.2 (23.1–45.1)	45.0 (33.1–58.6)	38.9 (30.9–47.7)

	DF	SS	MS	*F*
+/− *D. aruanus*	1	5.29	5.29	2.15
Dawn/afternoon	1	0.59	0.59	0.24
Interaction	1	0.00	0.00	0.00
Error	20	49.13	2.46	
Total	23	55.02		

Pomacentrus amboinensis settlement

Of 168 *Pomacentrus amboinensis* that settled on twelve SCUs between 16 November and 2 December, 35 (17.2%) could have settled in the daytime. Of the 170 *P. amboinensis* that were found on the 12 "afternoon" SCUs on 3 December, 7 (4.0%) could have settled in the daytime.

During the recruitment experiment between 3 and 6 December, 988 *Pomacentrus amboinensis* settled on the 24 SCUs. As with *Pomacentrus* sp., there was no evidence that resident *Dascyllus aruanus* reduced the persistence of *P. amboinensis* settlers during their first day after settlement (interaction mean square = 0.00; Table 2).

There was no statistical evidence that *Pomacentrus amboinensis* settlers avoided settling where there were resident *Dascyllus aruanus* (no significant main effect of presence of *D. aruanus*, Table 2) but this test was inconclusive. In 1981, 3.2 times as many *P. amboinensis* were collected from SCUs with 20 resident *D. aruanus* than from control SCUs (Sweatman 1985a). In 1982/1983, the

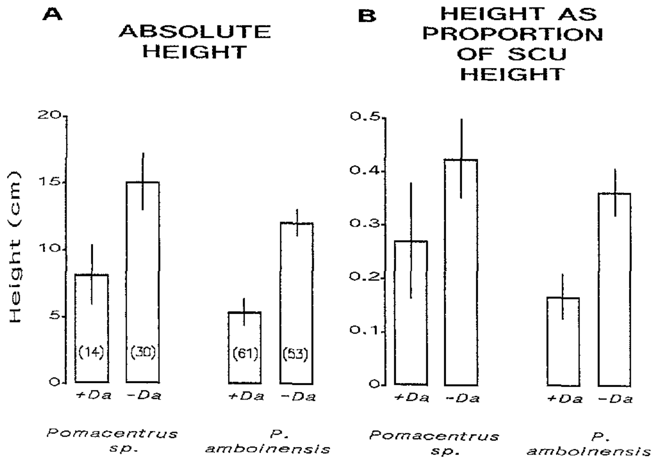

Fig. 1. *Pomacentrus* sp. and *P. amboinensis*. Position of newly-settled individuals on "standard coral units" (SCUs) with (+*Da*) and without (−*Da*) resident *Dascyllus aruanus*. Open bars represent mean height above sand, vertical lines are confidence intervals based on pooled variance. Numbers in parentheses are sample sizes. One-way ANOVAs for (A) absolute height (cm) and (B) height expressed as proportion of total height of SCU were as follows – *Pomacentrus* sp.: (A) $F_{(1,42)}=10.7$, $p<0.01$; (B) $F_{(1,42)}=5.94$, $p<0.05$. *P. amboinensis*: (A) $F_{(1,112)}=52.1, p<0.001$; (B) $F_{(1,112)}=43.24$ $p<0.001$

ratio was 1:1.4 (Sweatman 1985a). *P. amboinensis* recruited in the same proportions to SCUs with and without residents in this experiment (ratio of treatment means was also 1:1.4, censuses from both times of day combined), but the difference was not statistically significant because great variation in the numbers of *P. amboinensis* settlers on SCUs of the same treatment group made the test weak. Even if the means of the statistical populations had differed by the higher ratio (1 : 3.2) the probability of making a Type II error would still have been greater than 65%.

Behavioural changes in the presence of *Dascyllus aruanus*

The presence of *Dascyllus aruanus* affected settlers of both *Pomacentrus* sp. and *P. amboinensis*. Settlers of both species were found closer to the sand on SCUs where there were resident *D. aruanus*. This was true whether position above the sand was expressed in absolute units or as a proportion of the maximum height of the SCU (Fig. 1).

Discussion

Several species of fishes recruit in smaller numbers on SCUs with high densities of resident *Dascyllus aruanus* than on unoccupied SCUs (Sweatman 1985a, Jones 1987). In the present study we were concerned with the relative importance of resident aggression and selective settlement in determining this pattern in two damselfishes. We found no evidence that aggression by resident *D. aruanus* reduced the persistence of either species of damselfish over the first day, the time when settlers are likely to be most vulnerable to being driven away, wounded or eaten.

Reduced recruitment of *Pomacentrus* sp. is largely due to active choice by the larvae: *Pomacentrus* sp. settlers avoid settling where *Dascyllus aruanus* are present. The larvae can detect residents by dissolved chemical cues (Sweatman 1988). The data for *P. amboinensis* were inconclusive.

The distributions of settlers of the two species at dawn show differences of magnitude similar to differences in previous experiments (Sweatman 1985a, Jones 1987). In previous studies, recruits were counted at weekly (Sweatman 1985a) or monthly (Jones 1987) intervals. Several days of aggression from resident *Dascyllus aruanus* may make new recruits smaller or weaker and more vulnerable to predation than fishes of similar age on corals without residents, or it may drive them to emigrate. We saw little overt aggression between *D. aruanus* and *Pomacentrus* sp. or *P. amboinensis* settlers. We saw much more between the residents and *P. pavo* and *Lutjanus gibbus* settlers that swam above the coral, close to the feeding *D. aruanus*. Both *Pomacentrus* sp. and *P. amboinensis* settlers were found closer to the sand when *D. aruanus* was present, presumably in order to avoid such aggression. This change in position could restrict access to food in the water column, slowing a recruit's growth. It could also increase the rate of encounters with predators such as *Pseudochromis fuscus* that hide in the bases of corals, or with lizardfishes that live on the surrounding sand. In this way, resident *D. aruanus* may have some indirect, adverse influence on survival over a period of days following settlement, which would amplify differences in net recruitment.

This interpretation of the results of the recruitment experiment assumes that the larvae settle at night when adult *Dascyllus aruanus* are inactive. There are anecdotal accounts of larvae settling in daytime (Nolan 1975, Sale et al. 1980), and Robertson et al. (1988) found that ≤7.5% of fishes settling on a small artificial reef in the Caribbean appeared in the day, although the estimate for Pomacentridae considered alone was ≤20%. Each SCU was cleared only once per day during the recruitment experiment, so collections at both times of day could include daytime settlers. Any daytime settlers on SCUs with resident *D. aruanus* could have been subject to harassment. Substantial daytime settlement combined with harassment by residents would lower the number of settlers on SCUs with resident *D. aruanus* at the dawn collection compared with that on SCUs without residents. This would exaggerate the main effect of presence of *D. aruanus*, which we would interpret as evidence of selective larval settlement, and reduce the apparent interaction which is our indicator of adult aggression.

We argue that daytime settlement does not affect our conclusions. First, our maximum estimates of daytime settlement are <20% of the total settlement of either species. As visual censuses of juvenile and adult reef fishes lack precision and accuracy (e.g. Sale and Douglas 1981), these estimates are certainly inflated because they include nighttime settlers that were not seen at the dawn census. Even so, the difference in mean number of settlers at the dawn census between SCUs with and without residents was much greater than 20% for either species. Second, the interaction term for each species was minimal and only a very large increase would make it equivocal. Third, there is other evidence for selective settlement by *Pomacentrus* sp (Sweatman 1988).

Like *Pomacentrus* sp., larvae of some sedentary invertebrates avoid settling near potential competitors (e.g. Grosberg 1981, Young and Chia 1981, Petersen 1984). That such behaviour has evolved and is maintained by *Pomacentrus* sp. suggests a predictable cost to settling near *Dascyllus aruanus*. We found that residents restricted settlers' movements in ways that might reduce feeding and increase risk of predation. Damselfishes are often site-attached (Sale 1978b). Moving between sites involves both the risk of predation while crossing unfamiliar territory and the need to re-establish in a new site. Avoiding potential competitors at settlement will reduce the likelihood of having to emigrate later. This avoidance of sites with resident *D. aruanus*, is unlikely to limit the *Pomacentrus* sp. populations. Because *D. aruanus* require living coral colonies (Sale 1971), only a very small proportion of the potential habitat of *Pomacentrus* sp. at Lizard Island is occupied by *D. aruanus* or *D. reticulatus*. Settlers are likely to find alternative sites nearby.

The significant differences in recruitment of *Pomacentrus amboinensis* among the experimental SCUs in previous years (Sweatman 1985a) are more difficult to explain. The present study, in 1986, suggests that aggression or predation by *Dascyllus aruanus* over the first 24 h cannot explain the reduced recruitment because of the lack of a statistical interaction in the recruitment experiment. We found fewer settlers on SCUs with resident *D. aruanus*, and the proportions settling on SCUs with and without residents was the same as in 1982/1983; however, in 1986 the difference was not significant because the variation in settlement among SCUs of the same treatment group was much higher. We cannot exclude the possibility that settling *P. amboinensis* avoid resident *D. aruanus*, although Sweatman (1988) found no evidence that they responded to chemical cues.

It is not clear why this error variance was greater in 1986 than in previous years. Similar SCUs were built in substantially the same place and experimental procedures were similar. 1986 differed from previous years in that settlement of *Pomacentrus amboinensis* was much more intense. An average of 45.0 *P. amboinensis* settled on each SCU without resident *Dascyllus aruanus* in the 4 d of the recruitment experiment. In 1981 and 1982/1983 the equivalent values, recorded over periods of more than 8 wk (and more than one settlement pulse), were 22.3 and 59.6. *P. amboinensis* settlers favoured certain locations on each SCU: individuals were removed daily, but particular sites would be occupied by new settlers each day. This was probably a response to particular conformations of coral; for instance, *P. amboinensis* settlers seemed to prefer sites where the tips of the *Pocillopora damicornis* reached down to the level of the sand. If the numbers of such sites differed among SCUs, this difference would not have been evident if only one or two larvae settled per SCU per night (or interval between censuses). When ten or more larvae settled per SCU per night, all the sites on some SCUs may have been saturated. The differences among SCUs would become more evident as settlement increased, up to the point when all the sites on all SCUs were saturated. In this way, error variance could be positively correlated with settlement intensity.

Although *Pomacentrus* sp. and *P. amboinensis* are closely related and have been considered members of a planktivorous guild (e.g. Williams 1980), Sweatman (1985b) found indirect evidence that their larvae behaved differently at settlement. We observed that *Pomacentrus* sp. settlers were already in their daytime positions on the SCUs at first light. In contrast, the majority of *P. amboinensis* settlers hovered close to the sand 0.2 to 0.3 m from the bases of the SCUs and did not move closer when approached by a diver. On several occasions we saw settlers swim away from SCUs and we also encountered faintly-pigmented larvae swimming 0.5 m above the bottom and several metres from any substantial cover. Many *P. amboinensis* seemed to be in the process of settling at first light, although they had assumed their daytime positions within an hour.

We conclude that the distribution of recruits of these two species after 24 h owes less to the activities of prior residents and (in the case of *Pomacentrus* sp. at least) more to selective settlement than the literature suggests. Second, if the mere presence of potential competitors causes larvae not to settle at a site, then reduced recruitment does not necessarily indicate that any resource, such as space, is in short supply locally. Third, the avoidance behaviour of *Pomacentrus* sp. together with the evidence for gregarious settlement by *Dascyllus aruanus*, *D. reticulatus* and *Chromis caerulea* (Sweatman 1985a), show that larval pomacentrids are capable of sophisticated discrimination when choosing settlement sites. Studies that only distinguish broad habitat categories and emphasise substratum characteristics while ignoring the possibility of negative and positive effects of the presence of resident fishes, are likely to underestimate the influence that active choice has on the distribution of recruits.

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