

Interactions between ophiuroids and beaugregory damselfish

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The interactions between beaugregory damselfish and ophiuroids, potential damselfish egg predators, were investigated using several field studies. A survey of back reef areas showed that the two most common ophiuroid species, *Ophiocoma echinata* and *Ophioderma appressum*, were significantly associated with the territories of beaugregory males within the coral rubble habitat where both ophiuroids and beaugregory's can be found. Feeding experiments showed that three ophiuroid species (*Ophiocoma echinata*, *Ophioderma appressum* and *Ophiocoma wendtii*) and *Echinometra viridis* consumed late development stage beaugregory eggs, whereas earlier stages were only consumed by *Ophioderma appressum* and *Echinometra viridis*. Manipulation of ophiuroid densities had no significant effect on the survival of beaugregory eggs and had no measurable impact on female mate choice. The aggressive response of male beaugregory damselfish towards three ophiuroid and one echinoid species showed significant differences among species but were lower than those shown to bluehead wrasse, *Thallasoma bifasciatum*; the principal daylight predator of eggs. The intensity of attacks by male beaugregory damselfish towards *Thallasoma bifasciatum* increased significantly if males were guarding eggs, but did not appear to change for the four echinoderm species. Male habitat selection was shown to be unaffected by the presence of ophiuroids.

INTRODUCTION

Male reproductive success in animals is highly variable among individuals (Mitton, 1997), and for the same individual among breeding attempts (Davies, 1992). In the beaugregory damselfish, *Stegastes leucostictus* Müller & Troschel, a small coral reef teleost fish with paternal care, variation in breeding success has been attributed to a variety of factors, including habitat quality (Itzkowitz, 1991) and male quality (Haley et al., 2002). The impact of egg predators can also be important in this species as it may affect female mate choice and spawning preferences (Knapp, 1993), as well as affecting the current reproductive success of an individual. Thus males must actively defend nests from predators (Haley & Müller, 2002), and select nest sites where predation rates are low.

Echinoderms are important coral reef organisms that occur at high densities on tropical reefs and which are often found inside or on the periphery of male damselfish territories (Albrecht, 1969; Sammarco & Williams, 1982; Itzkowitz & Koch, 1991). Echinoderms have been cited as potential predators of damselfish eggs (Albrecht, 1969; Itzkowitz & Koch, 1991; Knapp, 1993). Albrecht (1969) noted that *Diadema antillarum* (Philippi) would occupy sergeant-major, *Abudefduf saxatilis* L., nest sites if the guardian male was removed, suggesting that they may feed on the developing eggs. The ophiuroid *Ophiocoma echinata* (Lamarck) is a suspension and deposit feeder, with a diet that also includes detritus, algae, zoo- and phyto-plankton (Sides, 1981; Warner, 1982). This species has also been cited as a predator of damselfish eggs (Itzkowitz & Koch, 1991; Knapp, 1993). *Ophiocoma echinata* have often been found to occupy artificial beaugregory damselfish spawning sites

(Itzkowitz & Makie, 1986; Itzkowitz & Koch, 1991), and commonly occur in the same area of reef as the beaugregory damselfish (Itzkowitz, 1977; Kissling & Taylor, 1977; Sides, 1981; Itzkowitz & Koch, 1991). Itzkowitz & Koch (1991) caged *O. echinata* overnight in damselfish artificial spawning sites that contained either recently spawned or older eggs. The study demonstrated that *O. echinata* ate eggs that were present within the spawning site, and that all developmental stages were equally susceptible to predation.

Female bi-colour damselfish, *Stegastes partitus* Poey, are inhibited from spawning with males by egg loss and the presence of *O. echinata* odours (Knapp, 1993). Males with *O. echinata* odours in their nest received significantly fewer clutches than those without odours, even if those males already had eggs (Knapp, 1993). Thus predation may have direct effects on offspring survival, and may also affect male reproductive success by influencing female spawning decisions. As males only guard their nest during the day, nocturnal ophiuroids have an advantage because males may only harass or remove them during the day. Thus, male damselfish may base habitat selection on the presence or absence of echinoid predators as well as other factors, such as oxygen conditions (Payne et al., 2002) and site construction (Itzkowitz, 1991).

The principal daylight predators of beaugregory eggs are bluehead wrasse, *Thallasoma bifasciatum* Bloch (Randall, 1967; Itzkowitz & Makie, 1986). However, *T. bifasciatum* must form schools in order to overwhelm individual male damselfish defences and gain access to eggs (DeLoach, 1999), often allowing conspecific males, slippery dick wrasse, *Halichoeres bivittatus* (Bloch), and gobies (Gobiidae) to participate in egg predation (personal observation). These attacks can result in the loss of a male's entire

current reproductive effort in minutes (personal observation), but the overall frequency of such attacks is unknown. Conspecific intruders are rarely observed in most damselfish species (Bartels, 1984; Itzkowitz, 1985) and conspecifics do not appear to be a substantial cause of egg loss (Payne et al., 2002). Females may eat eggs when they enter a nest site to spawn, as has been shown for sticklebacks (Vickery et al., 1988), though no studies have demonstrated this behaviour in the beaugregory.

Beaugregory damselfish, *Stegastes leucostictus*, are common, sexually monomorphic damselfish, of between 38 and 73 mm standard length (SL) (Randall, 1967; Itzkowitz, 1985). Their distribution extends throughout the Caribbean, from Brazil to Florida where they inhabit back reef areas, in water depths of between 1 to 10 m, (Itzkowitz, 1977). *Stegastes leucostictus* is a benthic omnivore, feeding mainly on small invertebrates, such as worms, crabs and shrimps, with algae making up to 20% of its diet (Randall, 1967). Male *S. leucostictus* hold permanent territories between 0.3 and 3.5 m² that they use for both feeding and as a nest site (Itzkowitz, 1985; Itzkowitz et al., 1995). Spawning occurs throughout the year with a peak in the summer (Robertson et al., 1990). Once a female spawns in his nest the male protects the eggs from predators, but does not provide any direct parental care, such as fanning (Itzkowitz & Makie, 1986; Payne et al., 2002). Males are sequentially polygynous, with nests often containing more than one clutch, often at different stages of development (Fishelson, 1998). The eggs hatch after five or six days and the larvae join the plankton where they spend between 19 and 21 days (Robertson et al., 1990).

The objective of this study was to understand the interactions between *S. leucostictus* and ophiuroids and whether ophiuroid egg predation affected male reproductive success. Associations between beaugregory damselfish and ophiuroids were investigated, with rates of ophiuroid predation of beaugregory eggs quantified. The selectivity of different egg developmental stages by three ophiuroid and one echinoid species was also tested. Female choice of males at different ophiuroid densities was investigated, and the aggressive responses of male beaugregory damselfish towards ophiuroids, one echinoid and *Thalassoma bifasciatum* examined. Finally, male spawning site choice in the presence of ophiuroids was tested.

MATERIALS AND METHODS

Study site and artificial spawning sites

Field data were collected from two study sites, A and B, within the back-reef area of Discovery Bay, Jamaica. The sites were approximately 75 m from the reef crest in a water depth of 1–2 m. To study the aggressive response of beaugregory damselfish to ophiuroids, 60 five-entry artificial spawning sites called 'condos' (Itzkowitz & Makie, 1986) were placed haphazardly throughout Site A. Five-entry condos consisted of four PVC pipes, measuring 100 (length) × 70 mm (diameter), bolted to form a cross to a Plexiglass base of 30.5 × 30.5 cm (Figure 1). Male damselfish were able to enter the condos through the four tubes at either end, the entrances in the centre joining to form one entrance. For the ophiuroid predation experiments, single-entry condos were used. Single-entry condos had three

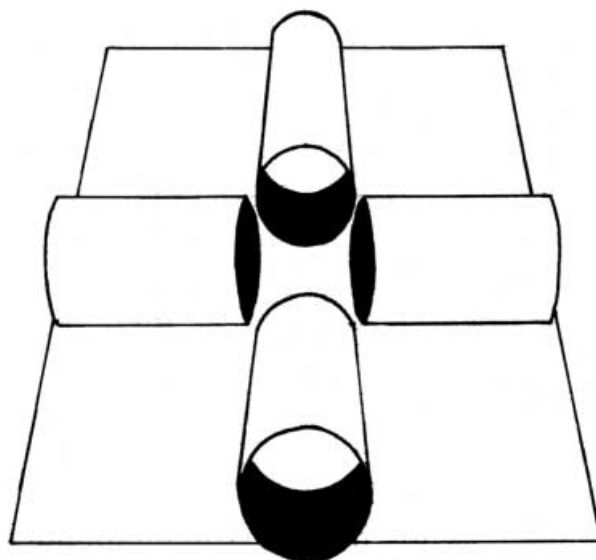


Figure 1. Diagrammatic representation of a five-entry condo.

of the four entrances and the central entrance blocked off using 8 × 8 cm Plexiglass squares, such that males could only enter the condo through the single tunnel that was unblocked. Previous observations demonstrated that ophiuroids were more likely to hide inside the dark corners of single-entry condos than the open tubes of five-entry condos. In order to collect developing eggs for the feeding experiment, acetate strips measuring 90 × 280 mm, on which a grid of 4 mm² squares had been photocopied, were rolled up and placed inside the tubes of several condos that were not used in experiments. The acetate strips allowed the collection and transport of egg masses and facilitated ready manipulation of egg clutches.

Association between ophiuroids and Stegastes leucostictus

At study Site A a 50 m² area was marked out on the substrate using four concrete blocks with floats attached to allow the corners to be easily located while snorkelling. Within the square a series of random co-ordinates was used to place 3 × 3 m quadrats (N=59). The number of beaugregory damselfish with the focus of their territory inside the quadrat was counted and each individual sexed. Any juveniles present were also recorded. All the coral rubble in the quadrat was then searched thoroughly and any ophiuroids present were captured. The ophiuroids were transported back to the laboratory for identification using Hendler et al. (1995).

A second study was conducted at Site A in which heaps of coral rubble were haphazardly selected and the circumference of the rubble area measured using a length of rope marked at 50 cm intervals. The rubble was then searched and all the ophiuroids located were captured and taken back to the laboratory for identification. Seventy-five heaps of rubble occupied by male beaugregory damselfish and 75 heaps of rubble unoccupied by damselfish were selected.

Predation of Stegastes leucostictus eggs by potential egg predators and female spawning choice

To investigate whether ophiuroids and *Echinometra viridis* A. Agassiz would eat *Stegastes leucostictus* eggs, and

to quantify their rates of predation, 36 acetate strips on which eggs had been laid were collected from condos. Within each clutch a 20×50 mm area of eggs was selected and the surrounding eggs scraped off using a scalpel blade. The clutches were assigned to developmental stages using Brinley (1939) and the strips of acetate labelled and placed inside cages made from 5×5 mm wire mesh, measuring 110 (width)×270 (length)×50 mm (depth). A single *Ophiocoma echinata*, *Ophioderma appressum* (Say), *Ophiocoma wendtii* (Müller & Troschel) or *E. viridis* was also placed inside the cage with the eggs. *Echinometra viridis* were tested as they have been observed consuming eggs (personal observation). The cages were placed inside the cavities of concrete blocks measuring 200 (width)×400 (length)×150 mm (depth), with cavities measuring 140 (width)×200 (length)×70 mm (depth). Placing the cages inside concrete blocks prevented other predators attacking the eggs and mimicked conditions inside a beaugregory nest. The blocks were placed in water of 1.5 m depth over a substrate of coral sand. The cages were collected after 24 h and the area of eggs that had been eaten was recorded.

To investigate the importance of ophiuroids as egg predators, the reproductive success of 72 males was monitored at different ophiuroid densities. Thus, 80 single-entry condos were placed haphazardly throughout Site B, and each male monitored every two days until they received their first spawning. The size of the clutch was estimated by measuring the length and width of the clutch to the nearest 1 mm. A net was then placed over the condo trapping the male inside, and both were transferred to an enclosure. The enclosure measured 100 (length)×100 (width)×20 cm (height) with 1 mm² on the base and 5×5 mm mesh on the walls. The enclosure had no top, so that males could court females, but ophiuroid movement was restricted. Four rocks were placed inside the enclosure to act as ophiuroid refuges and *Ophiocoma echinata* was added according to a predetermined treatment randomly assigned to each male. Each male was released from the net once the brittlestars had been placed in the enclosure. The treatments used were: zero, one, three and ten ophiuroids. The mean number of ophiuroids in the enclosures during the experiment for each treatment was 0.91 (SE 0.309), 2.66 (SE 0.645) and 8.96 (SE 1.421) respectively. These numbers mimicked natural variation in ophiuroid densities at the study site.

Each condo was visited three times daily for 14 days to detect changes in the size of egg clutches within the nest. Any egg losses or clutch losses (100% loss of one clutch of the same age) from the previous inspection were recorded and any new clutches laid were measured. The number of ophiuroids in the enclosure was checked each day so that any escaped ophiuroids could be replaced and any extras removed. All beaugregory males received the same amount of disturbance.

Beaugregory aggressive response to potential egg predators

The strength of response of males towards potential egg predators was measured using the bottle method of Myrberg & Thresher (1974) at Site A. During a test a male occupying a five-entry condo was presented with one of either *Ophiocoma echinata*, *Ophioderma appressum*, *Ophiocoma wendtii*, *Echinometra viridis* or bluehead wrasse, *Thalassoma*

bifasciatum, placed in a clear glass bottle measuring 350 (depth)×110 mm (diameter). An empty bottle and a bottle containing *Tripneustes ventricosus* (Lamarck) (a non egg predator (Hendler et al., 1995)) were also presented to males as controls. The bottles were placed 1 m from the condo and the observer moved at least another 1 m away. The behaviour of the male beaugregory was then observed for 1 min. The bottle was either moved away from the nest in 10 cm increments if a male attacked the bottle, or moved forward in 10 cm increments if no attacks were launched. The maximum distance at which attacks were initiated was recorded. Each male beaugregory was tested with each treatment in a randomly determined order, with at least one hour between tests to avoid habituation. The same test animals were not used with every test male beaugregory to avoid pseudoreplication. The presence of eggs in the condos of tested males was recorded.

A second experiment was used to measure the rate of aggression of the same group of beaugregory males to the same five test animals at a fixed distance. However, the bottle with the animal inside was placed directly on top of the condo and the number of bites directed towards each bottled animal in a 2 min period was recorded. Each male was again tested with each animal, in a randomly determined order, with at least one hour between observations. Only empty bottles were used as controls in this study as the previous study showed that *T. ventricosus* was never attacked.

Male beaugregory spawning site selection

To investigate whether beaugregory male habitat selection was affected by the presence of ophiuroids, males were presented with two spawning site choices; ophiuroids present or ophiuroids absent. Two of the enclosures from the predation study, containing a five-entry condo and four rocks, were placed on either side of a male occupying a natural nest site at Site B. Ten *Ophiocoma echinata* were added to one of the enclosures, while the other was left empty. The enclosure that males were occupying was recorded twice daily for 10 days and adjustments to ophiuroid numbers made if necessary. Each enclosure received the same disturbance to avoid bias.

Data analysis

All data were tested for normality using a Kolmogorov–Smirnov test and for equality of variance using a Bartlett's test. For the comparisons of ophiuroid density, number and development stages of clutches lost and the distance of attack, a Scheirer–Ray–Hare test was used as a non-parametric equivalent of the two-way ANOVA (Dytham, 1999). To determine if there was any association between beaugregory damselfish and ophiuroids a chi-squared contingency test was employed. A *G*-test was used to compare the developmental stages of embryos that the different species consumed. A one-way ANOVA was used to compare differences in embryo survival between males exposed to the four different ophiuroid densities and the mean number and size of clutches received by males exposed to the four ophiuroid densities. To compare the attack distances towards the controls and the two least

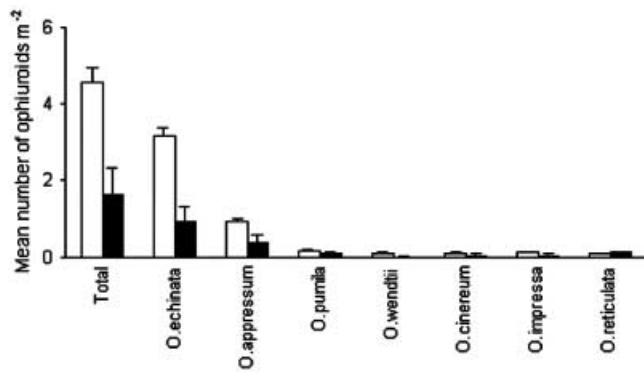


Figure 2. Mean (+1 SE) density of ophiuroids (m^{-2}) in quadrats in which beaugregory damselfish were either present (white bars) or absent (shaded bars).

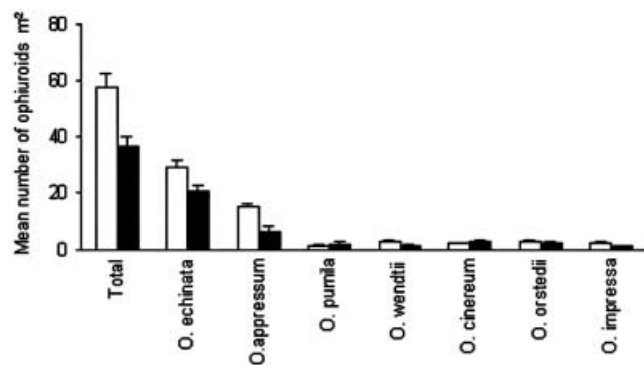


Figure 3. Mean (+1 SE) density of ophiuroids (m^{-2}) in samples of territories occupied by male beaugregory damselfish (white bars) or unoccupied rubble (shaded bars).

attacked species, a Mann–Whitney U -test was used. The mean bite rate of the two species attacked the least and the bottle were compared using a two-way ANOVA with Fisher's LSD for post-hoc comparisons. For the mean bite rate for all species without the control, a two-way ANOVA was used with Fisher's LSD (least significant difference method) for post-hoc comparisons. Male choice of condos was compared using a chi-squared test and, to compare the time males took to choose an enclosure, an unpaired t -test was used.

RESULTS

Association between ophiuroids and Stegastes leucostictus

The mean density of ophiuroids in quadrats with beaugregory damselfish present was 4.54 (SE 0.633) ophiuroids m^{-2} and absent 1.63 (SE 0.701) ophiuroids m^{-2} . This difference was significant (Scheirer–Ray–Hare test, $\chi^2=0.98$, $\text{df}=1$, $P=0.015$). There was also a significant difference in the mean densities of different ophiuroid species in all samples (Scheirer–Ray–Hare test, $\chi^2=1.00$, $\text{df}=11$, $P<0.001$) but there was no interaction between ophiuroid species and the presence or absence of damselfish (Scheirer–Ray–Hare test, $\chi^2=0.81$, $\text{df}=11$, $P=0.186$) (Figure 2). Despite *Ophiocoma echinata* being the most abundant ophiuroid in total and in beaugregory quadrats,

there was no significant association between *O. echinata* and beaugregory damselfish territories ($\chi^2=0.77$, $\text{df}=1$, $P=0.381$) or male territories ($\chi^2=0.03$, $\text{df}=1$, $P=0.860$). *Ophioderma appressum*, the next most abundant species, was not significantly associated with beaugregory territories ($\chi^2=1.32$, $\text{df}=1$, $P=0.251$), but was associated with male territories ($\chi^2=4.87$, $\text{df}=1$, $P=0.027$).

The rubble samples occupied by male damselfish had a mean of 58.0 (SE 5.15) ophiuroids m^{-2} whereas unoccupied rubble had a mean of 36.6 (SE 3.54) ophiuroids m^{-2} . There was a significant difference in the numbers of ophiuroids m^{-2} between rubble used as damselfish territories and unoccupied rubble (Scheirer–Ray–Hare test, $\chi^2=1.0$, $\text{df}=1$, $P=0.003$), density of different ophiuroid species in all samples (Scheirer–Ray–Hare test, $\chi^2=1.0$, $\text{df}=10$, $P<0.001$) and an interaction between the density of species and the presence or absence of damselfish (Scheirer–Ray–Hare test, $\chi^2=0.97$, $\text{df}=10$, $P=0.034$) (Figure 3). There was also a significant association between beaugregory damselfish and *Ophiocoma echinata* ($\chi^2=5.67$, $\text{df}=1$, $P=0.017$) and beaugregory damselfish and *Ophioderma appressum* ($\chi^2=7.73$, $\text{df}=1$, $P=0.005$).

Predation of Stegastes leucostictus eggs by ophiuroids

Of the 36 10 cm^2 patches of embryos presented to ophiuroids, evidence of embryo predation was clear for 12. Those that were eaten had a mean of 87.8% (SE 7.18) of the total clutch consumed. A G -test for association between predation by the different echinoderm species and the developmental stage of embryos eaten approached

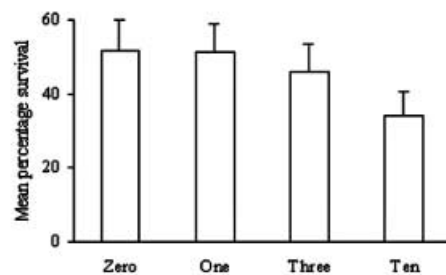


Figure 4. Mean (+1 SE) beaugregory damselfish egg survival over five days at four *Ophiocoma echinata* density treatments.

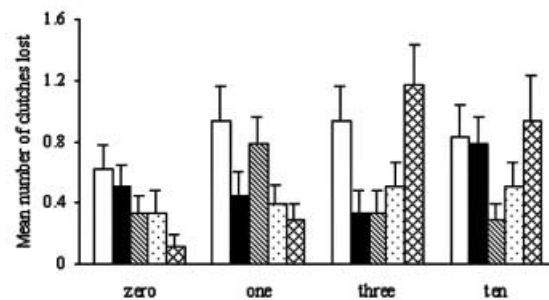


Figure 5. Mean (+1 SE) number of clutches lost at four *Ophiocoma echinata* density treatments after one day (white bars), two days (black bars), three days (hatched bars), four days (dotted bars) and five days (crossed bars).

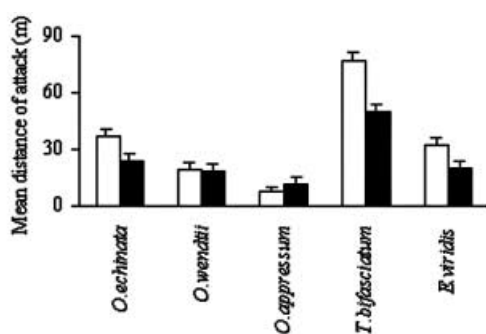


Figure 6. Mean (+1 SE) attack distance of male beaugregory damselfish for five test species when eggs were either present (white bars) or absent (black bars). An empty bottle served as control.

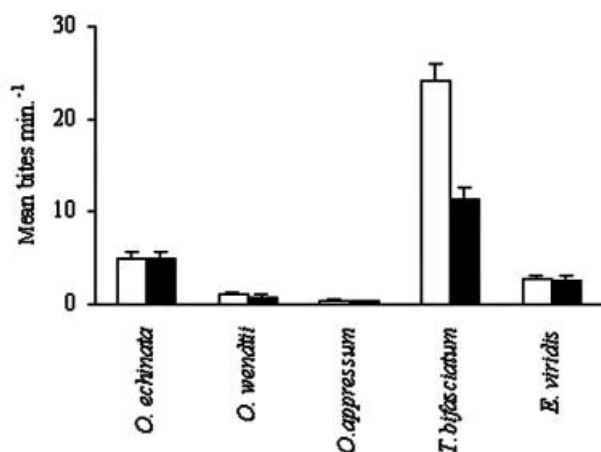


Figure 7. Mean (+1 SE) number of bites (min^{-1}) directed towards different test species when eggs were either present (white bars) or absent (black bars). An empty bottle served as control.

significance ($G=8.66$, $df=4$, $P=0.070$), with late stage embryos eaten at a higher than expected frequency by all species. Only *Echinometra viridis* and *Ophioderma appressum* consumed early stage embryos.

The mean survivorship of embryo clutches was 51.6% (SE 8.55), 51.3% (SE 7.25), 46.2% (SE 7.35) and 34.2% (SE 6.63) for the zero, one, three and ten ophiuroid treatments respectively. Despite a decrease in survivorship of clutches with increasing density of ophiuroids (Figure 4), there was no significant difference between treatments (ANOVA, $F_{3,68}=1.184$, $P=0.322$). There was also no significant difference in the mean number of clutches lost in each treatment (Scheirer–Ray–Hare test, $\chi^2=0.89$, $df=3$, $P=0.105$). However, there was a significant difference in the number of clutches lost at each developmental stage (Scheirer–Ray–Hare test, $\chi^2=0.98$, $df=4$, $P=0.016$), and a significant interaction between the treatment and the developmental stage eaten (Scheirer–Ray–Hare test, $\chi^2=0.97$, $df=4$, $P=0.028$). Overall more clutches were lost after one day of development (all treatments combined) but for the two highest densities more were lost on day five of development than at any other developmental stage (Figure 5). There were no significant differences in the mean number (ANOVA, $F_{3,68}=1.647$, $df=3$, $P=0.187$) or mean size of clutches received by males (square root transformation, ANOVA, $F_{3,68}=1.374$, $df=3$, $P=0.258$).

Beaugregory aggressive response to potential egg predators

Male beaugregory damselfish attacked all five species tested. The attack distances towards the bottle were significantly lower when compared with *Ophiocoma wendtii* (Mann–Whitney U -test, $U=1166$, $N=84$, $P<0.001$) and *Ophioderma appressum* (Mann–Whitney U -test, $U=2303$, $N=84$, $P<0.001$), which had the two lowest attack distances. Both *Ophiocoma wendtii* (Mann–Whitney U -test, $U=241$, $N_1=15$, $N_2=42$, $P<0.001$) and *Ophioderma appressum* (Mann–Whitney U -test, $U=1374$, $N=84$, $P=0.003$) also had significantly different attack rates from *Triptoneustes ventricosus*. Thus the bottle and *T. ventricosus* were excluded from any further analysis. The mean distances of attack were 19.05 (SE 2.583) for *Ophiocoma wendtii*, 9.43 (SE 1.675) for *Ophioderma appressum*, 0.67 (SE 0.337) for the bottle and 3.07 (SE 2.032) for *T. ventricosus*.

There was a significant difference in the mean distance of attack among species (Scheirer–Ray–Hare, $\chi^2=1.00$, $df=4$, $P<0.001$) (Figure 6). However, differences among attack distances when eggs were either present or absent approached significance (Scheirer–Ray–Hare, $\chi^2=0.94$, $df=1$, $P=0.057$), with males attacking test animals at greater distances if they had eggs in their nest. There was no interaction between the presence or absence of eggs and the species that was attacked (Scheirer–Ray–Hare, $\chi^2=0.57$, $df=4$, $P=0.434$).

There was a significant difference between the attack distances for the bottle and for the two species with the lowest attack rate *Ophiocoma wendtii* and *Ophioderma appressum* (\log_{10} transformation, ANOVA, $F_{2,66}=16.63$, $P<0.001$). Post-hoc analysis demonstrated that both *Ophiocoma wendtii* (Fisher's LSD, $P<0.001$) and *Ophioderma appressum* (Fisher's LSD, $P=0.023$) differed significantly from the bottle. Thus the bottle was removed from any further analysis. The mean bite rates were 2.00 (SE 0.341) bites min^{-1} for *Ophiocoma wendtii*, 0.792 (SE 0.233) bites min^{-1} for *Ophioderma appressum*, and 0.125 (SE 0.069) bites min^{-1} for the bottle.

There was a significant difference in the rate of attack among species (square root transformation, ANOVA, $F_{4,110}=139.72$, $P<0.001$). Males that had eggs in their nest attacked at a significantly higher rate than those that did not (square root transformation, ANOVA, $F_{1,110}=9.60$, $P=0.003$), and there was an interaction between species and the presence or absence of eggs (square root transformation, ANOVA, $F_{4,110}=7.60$, $P<0.001$). Post-hoc analysis demonstrated that each species was attacked at a significantly different rate to every other species; with *Thalassoma bifasciatum* attacked at the highest rate, followed by *Ophiocoma echinata*, *Echinometra viridis*, *Ophiocoma wendtii* with *Ophioderma appressum* attacked at the lowest rate (Figure 7).

Male beaugregory spawning site selection

Of the 28 males tested, 14 chose the condo in the ophiuroid absent enclosure, seven chose the ophiuroid present enclosure and seven remained on their original site. There was no significant difference in choice ($\chi^2=3.50$, $df=2$, $P=0.174$) between treatments. Males that chose the enclosures without ophiuroids did so after a mean of 4.0

(SE 0.78) d^{-1} , the same as males that chose enclosures with ophiuroids, for which the mean was also 4.0 (SE 1.11) d^{-1} and this was not a significant difference (unpaired *t*-test, $t = 0.00$, $df = 19$, $P = 1.000$).

DISCUSSION

Association between ophiuroids and Stegastes leucostictus

Ophiuroids are common inhabitants of all areas of the reef, but are particularly abundant in rubble areas of the back reef (Kissling & Taylor 1977; Hendler et al., 1995). The beaugregory damselfish occupies a similar area of the reef (Itzkowitz, 1977, 1985; Itzkowitz & Koch, 1991). The results demonstrated that within the back reef, ophiuroids were more numerous where beaugregory damselfish were present than where beaugregory damselfish were absent. There were also differences in the abundance of the different species that occupied these areas. *Ophiocoma echinata* and *Ophioderma appressum* were the most numerous in both damselfish and non-damselfish areas, whereas the other five species showed much lower abundances. However, no association was found between *Ophiocoma echinata* and *Ophioderma appressum* and beaugregory damselfish of all ages and sexes within the sampled area. This result suggests that beaugregory damselfish occupy a specific area whereas ophiuroids, while being most numerous where damselfish occur, also occur in other parts of the back reef (Kissling & Taylor, 1977; Sides, 1981). However, *O. appressum* was found to be significantly associated with male beaugregory damselfish whereas *Ophiocoma echinata* was not. *Ophioderma appressum* is a predatory and carrion feeding species, unlike *Ophiocoma echinata*, which is primarily a suspension and deposit feeder (Warner, 1982). Predatory ophiuroids are likely to be better able to seek out sites where males with embryos are present (Reimer & Reimer, 1975) and this may explain the association. Alternatively, *Ophioderma appressum* may share the habitat preferences of male beaugregory damselfish.

The data from the rubble sampling demonstrated a similar pattern; ophiuroids were significantly more abundant under rubble that was occupied by male beaugregory damselfish. However, in the rubble samples *Ophiocoma echinata* and *Ophioderma appressum* were both significantly associated with males and this appears to contradict the results of the quadrat study. However, the rubble samples were collected on a smaller spatial scale, suggesting that within the rubble area of a reef ophiuroids may associate with beaugregory nest sites, either as a consequence of shared habitat preferences, for protection (see Lobel, 1980), or to feed on beaugregory embryos.

Predation of Stegastes leucostictus eggs by potential egg predators and female spawning choice

Clear evidence of embryo predation by three species of ophiuroid, *Ophioderma appressum*, *Ophiocoma echinata* and *Ophiocoma wendtii*, and one echinoid species, *Echinometra viridis*, was detected, all eating some or all of the embryos with which they were presented. Itzkowitz & Koch (1991) suggested that *O. echinata* was mostly responsible for beaugregory damselfish embryo losses and that both recently spawned and older embryos were equally susceptible to

predation. However, the data show that late developmental stage embryos are most susceptible to predation by *O. echinata*, with earlier stages only eaten by *E. viridis* and *Ophioderma appressum*. The results from the study of the effect of different ophiuroid densities agree with the premise that *Ophiocoma echinata* eats beaugregory embryos, but not with the evidence that *O. echinata* is the major cause of embryo losses or that they are unselective in the stages they eat. The results demonstrated that only on the fifth day of embryo development did the number of clutches eaten differ between the two low and high *O. echinata* densities. As echinoderms use chemoreception to detect food (Reimer & Reimer, 1975; Sloan & Campbell, 1982) it may be that *O. echinata* can only detect the later stages, whereas *Ophioderma appressum* and *E. viridis* have better developed chemoreception and can also detect the earlier stages. The later stage embryos may also be more palatable. Further studies will be needed to investigate the proximate reasons for embryo stage selectivity by *Ophiocoma echinata* and other echinoderms.

It is possible that other forms of predation, and even cannibalism, are responsible for the majority of embryo losses experienced by parental males. Predation by *Thalassoma bifasciatum* can cause the loss of a male's entire current reproductive effort in minutes, with far reaching effects for a male's lifetime reproductive success if he is more susceptible to attacks, or less able to defend his embryos, than his neighbours. However, Emslie & Jones (2001) demonstrated that variation in densities of the embryo predator *Thalassoma lunare* (L.) (Labridae) did not explain differences in embryo mortality rates for *Pomacentrus amboinensis* (Bleeker), but suggested that predation prior to hatching could affect individual males' reproductive success. Further work is needed to assess the importance of mobile fish predators on male reproductive success.

Knapp (1993) suggested that female bi-colour damselfish, *Stegastes partitus*, avoided males whose nests contained ophiuroid odours. However, the different densities of *O. echinata* had no significant effect on female *Stegastes leucostictus* mate choice. The bi-colour may be influenced more than the beaugregory by the presence of ophiuroids, possibly due to a more pronounced affect of ophiuroids on male reproductive success. *Stegastes partitus* are much smaller than *S. leucostictus* and so may not be able to remove *O. echinata* as readily, thereby allowing the ophiuroids to gain easy access to embryos. However, in the present study, differences in beaugregory male quality may have influenced the decisions of females to spawn with specific males (Haley et al., 2002) and this may have confounded any differences in choice caused by the presence of ophiuroids. Female beaugregory damselfish have been shown to base mate choice on male characteristics (Haley et al., 2002), the construction (Itzkowitz & Makie, 1986) and prevailing oxygen conditions of the habitat that males occupy (Payne et al., 2002), and the quality of the resources held within the territory (Itzkowitz et al., 1995; Itzkowitz & Slocum, 1995). These factors combined may override the presence of a relatively insignificant embryo predator that does not pose a serious threat to a male's reproductive success.

Beaugregory aggressive response to potential egg predators

There were clear differences in the distance and intensity of attacks directed towards the five test species in the

aggressive response experiments. The results demonstrate that despite the echinoderms' cryptic and nocturnal behaviour, the beaugregory males perceive them as a potential threat to the resources held within their territory. This study is the first to demonstrate both that *Ophiocoma wendtii*, *Ophioderma appressum*, and *Echinometra viridis* eat beaugregory embryos and that they are perceived as a potential threat to embryos by parental male beaugregory damselfish.

The differences in attack rates and attack distances among species may reflect the relative vulnerability of the male to the intruder he is confronted with (Haley & Müller, 2002). *Thalassoma bifasciatum* are mobile, highly visible embryo predators that pose a serious threat to a male's current reproductive output and hence elicit a strong defensive response from parental males. The ophiuroids and *E. viridis* are less mobile, cryptic and relatively slow moving, and may pose less of a threat to the current reproductive effort of a male, thereby eliciting a weaker defensive response. *Echinometra viridis* may additionally represent a threat to algal resources held within a male's territory (Sammarco & Williams, 1982). Itzkowitz & Slocum (1995) imply that female choice of oviposition sites may be influenced by the species of algae present within a male's territory. Thus the removal of *E. viridis* from a male's territory would be advantageous. However, *E. viridis* is easily removed by a male (Sammarco & Williams, 1982), perhaps explaining why this species was attacked less than *Ophiocoma echinata*. Males dealt with *O. echinata* by repeatedly attacking them and only grabbed them if they stopped moving, which only occurs when they receive a sustained attack (personal observation). *Ophiocoma wendtii* were rarely seen at the study site (Figures 1 & 2) and males may not encounter them frequently, and consequently may attack them less vigorously. The lower attack rate directed towards *Ophioderma appressum* may reflect their small body size, ease of removal (personal observation) and lack of large defensive spines like those possessed by *Ophiocoma echinata* (Sides, 1981; Hendler et al., 1995).

Males change their defensive behaviour according to both external and internal cues (Haley & Müller, 2002). However, Figure 7 demonstrates that the difference in attack rates when embryos are present or absent in this study was driven largely by the difference in the attack rates on *T. bifasciatum*. The escalation in attack rate towards *T. bifasciatum* may be caused by a change in a male's vulnerability to attack (i.e. the possible loss of embryos) to which the male responds by increasing the level of 'high-cost/high-threat' territorial behaviour (Haley & Müller, 2002). However, for the ophiuroids and the one echinoid there appears to be no change in threat, possibly because the ophiuroids and *E. viridis* do not pose a serious threat to the embryos and can be easily removed. Beaugregory males can assess the degree of threat that each type of intruder poses and their own vulnerability to that threat (i.e. the presence of embryos) and alter their defensive strategy accordingly (Haley & Müller, 2002).

Male beaugregory spawning site selection

The habitat selection experiment reiterates the lack of a pronounced effect of ophiuroids on male reproductive success. Male damselfish select territories that maximize their reproductive success (Bartels, 1984; Itzkowitz &

Makie, 1986; Itzkowitz, 1991). In the present study, male habitat choice was unaffected by the presence of ophiuroids and had no measurable effect on female mate choice. It is possible that the males did not detect the ophiuroids in the experimental design used and thus the males did not perceive them as a threat to their reproductive success. However, other features of nest sites may have been more important, such as the quality of the spawning site (Itzkowitz et al., 1995), quality of the territory (Itzkowitz & Slocum, 1995) or nest oxygen levels (Payne et al., 2002). Males will only move to a new site if it is unoccupied and where they can greatly improve their reproductive success (Bartels, 1984; Itzkowitz, 1991; Itzkowitz et al., 1995). Thus, as ophiuroid predation does not appear to greatly affect male reproductive success, males would not be expected to show strong preferences for sites with ophiuroids either present or absent. Female choice was similarly unaffected by the presence of ophiuroids. Female choice may be more strongly influenced by other factors, such as male quality (Haley et al., 2002), spawning site quality (Itzkowitz, 1991; Itzkowitz et al., 1995), territory quality (Itzkowitz & Slocum, 1995) and oxygen conditions within the nest (Payne et al., 2002).

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