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Short-term effects of territoriality of a tropical damselfish and experimental exclusion of large fishes on invertebrates in algal turfs

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ABSTRACT: This study investigated the effects of territorial behaviour of the pomacentrid *Stegastes apicalis* and exclusion of fishes on the abundance and composition of small, mobile invertebrates associated with algal turfs on a fringing coral reef. The experiment tested for the effects of territoriality, caging, and large and small spatial scales of variability, utilizing standardized experimental substrata (plates of *Porites*). After 3 mo densities of invertebrates and algal biomass were greater on experimental plates inside territories than outside territories. Caging resulted in an increase in densities of mobile invertebrates, but was accompanied by a change in algal composition and a reduction (inside territories) or no change (outside territories) in algal biomass. The discrepancy between densities and algal abundance in caged treatments could have been caused by increased grazing intensity by the herbivorous components of the invertebrate fauna. This micrograzing (*sensu* Vadas 1986) is thought to account for the observed shift in species composition of algae.

INTRODUCTION

Multispecific assemblages of filamentous algae, generally termed algal turfs (Carpenter 1986), are thought to be the major source of primary production in coral reef systems (Hatcher 1983). Grazing is considered to have a major influence on the species composition, abundance and standing crop of algae on coral reefs (Hay 1985, Carpenter 1986, Lewis 1986). Considerable information exists on herbivorous grazers and their interaction with algae (reviews by Ogden & Lobel 1978, Hixon 1985). The most important grazers on coral reefs of the Great Barrier Reef are considered to be fishes (Hatcher 1983), and a significant increase in biomass of algae following exclusion of grazing fishes has frequently been reported (e.g. Day 1977, Lassuy 1980). Thus, much evidence suggests that grazing plays an important role in controlling the standing crop of algal turfs on coral reefs (Hatcher & Larkum 1983).

In contrast, little is known about small, mobile invertebrates that live associated with such algal turfs. Several lines of evidence suggest that these small invertebrates may be of substantial trophodynamic importance in coral reefs. First, many are likely to graze directly on the algal turfs, yet their contribution to total grazing pressure on coral reefs relative to the larger herbivorous grazers is almost totally unknown (Carpenter 1986). Second, these small, mobile invertebrates are likely to be a major source of food for fishes. This is supported strongly by the observation that communities of coral reef fishes are often dominated by fishes which feed on benthic invertebrates (e.g. Sale 1980, Harmelin-Vivien 1981).

It is possible that the abundance of these invertebrates is affected significantly by a complex relationship between the grazing activities of large herbivores, the standing crop of algal turfs, and the predatory feeding of fishes. Such a relationship has been demonstrated in other sublittoral systems of plant/herbivore interactions (e.g. Kennelly 1983).

Clearly, any factor which influences standing crop of algal turf may affect the abundance of small, mobile invertebrates. One of the most obvious influences on standing crop of algal turfs on coral reefs is the territorial behaviour of certain herbivorous fishes (Lassuy 1980). One such herbivore which is very common on

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inshore reefs of the Great Barrier Reef is the pomacentrid *Stegastes (= Eupomacentrus) apicalis* (De Vis) (Allen 1975), which defends its territory against other herbivorous fishes as well as against its conspecifics. By reducing the intensity of grazing by non-territorial fishes (such as scarids and acanthurids) on the algae, territorial fishes increase the standing crop of algal turfs inside territories (Brawley & Adey 1977, Lassuy 1980). Despite some recent reports (Lobel 1980, Carpenter 1986), little is known about the effects on the mobile invertebrate fauna of this increased standing crop of algal turfs inside territories.

The present study examined the effect of territoriality by *Stegastes apicalis*, and the effect of exclusion of large grazers and predators on the densities of small, mobile invertebrates associated with algal turfs.

METHODS

Study sites. The study location was on a windward fringing reef on Orpheus Island (18° 135′ S, 146° 29′ E), a coastal island of the Palm group in the central Great Barrier Reef region. The crests of 2 coral patchreefs approximately 300 m apart on the upper reef slope were selected as study areas. The patchreefs were considered to be subjected to similar conditions of wave action and waterflow. The crest of each patchreef had 5 to 8 territories of adult-sized damselfish *Stegastes apicalis* (110 to 140 mm total length), 3 of which I selected as territorial sites. In each area 3 non-territorial sites, each approximately the same size as individual territories, were chosen between 5 and 15 m from the territorial sites. They were defined as not being part of an obviously defended territory of any pomacentrid, as determined during a 20 min observation period. The non-territorial status of these sites was confirmed during each subsequent visit. The depth of all sites was between 1.5 and 2.5 m below chart datum (port of Lucinda).

Experimental design. The experiment was designed as a 4-factor, mixed-model analysis of variance, comprising the following factors: (1) 'Area', i.e. large spatial scale represented by the 2 areas described above; (2) 'Territoriality', i.e. non-territorial and territorial treatments; (3) 'Sites', smaller spatial scale, i.e. individual territories or non-territorial habitats as described above; (4) 'Caging', caged and uncaged treatments, enabling the effect of exclusion of large grazers to be assessed. Factors 1, 2 and 4 were orthogonal and fixed in the analyses, while Factor 3, being nested within Factors 1 and 2, was a random factor. Throughout the following, the term 'sites nested within area and territoriality' will be referred to simply as 'sites'

Coral plates (made of dead *Porites*, approximately $8 \times 8 \times 2.5$ cm) were used as standardized substrata. Plates were attached directly to the natural substratum using stainless steel screws. Cages of size $12.5 \times 12.5 \times 6.5$ cm, made of galvanised welded mesh (mesh size 12.5 mm square, wire diameter 1.3 mm) were used to exclude grazers and predators larger than 12.5 mm minimum dimension. Each plate was caged separately. Replication consisted of 3 plates per treatment combination (i.e. 3 caged and 3 uncaged plates per site), resulting in a total of 72 plates.

Data collection. The experiment was done over a 3 mo period (February to May 1986) during which fouling organisms and accumulated detritus were cleared from cages by brushing the sides and replacing the lids every 3 wk. In May, all plates were collected during 1 wk, during daytime high tides. Plates were placed individually into a seal-top plastic bag immediately after removal from the substratum. A narcotizing technique of $MgCl_2 \cdot 6H_2O$ in solution isotonic to seawater (Steedman 1976, p. 92), was used to extract the mobile invertebrate fauna. Samples were rinsed out of the algal cover using filtered seawater, collected in a plankton mesh filter (mesh size 200 µm) and preserved in 10 % seawater-formalin. Staining with Eosin aided detection of the invertebrates amongst the detritus (Eleftheriou & Holme 1984). The invertebrate fauna in each sample was identified to the level of major taxonomic group (class, order) and their abundance determined. The specific surface area of each plate was determined using a 'BIOQUANT II' digitizing system (R & M Biometrics Inc.) in conjunction with an Apple IIe personal computer, thus allowing standardization of abundances to densities in individuals per 100 cm^2 (ind. $100cm^{-2}$). All algae on the plates were carefully removed, using scalpel and forceps, and dried to constant weight at 80 °C, allowing estimation of algal biomass as dry weight. Algae were not scraped from the plates, in order to minimize the content of calcium carbonate derived from the experimental substratum.

In order to establish possible influences of the use of experimental substrata on densities of invertebrates, natural and experimental substrata were compared. At the beginning and again at the end of the experiment samples of natural substrata (2 replicates each), approximately equal in size to the experimental plates, were taken from 1 territorial and 1 non-territorial site per area, and the invertebrate fauna were sampled as above ($n = 16$).

In February, 5 specimens of *Stegastes apicalis* living in close proximity to each experimental area were collected, while in May each fish occupying an experimental territory was collected to examine the stomach contents ($n = 10$ for February, $n = 6$ for May). A points method modified from Jones (1968) was used. The contents of each stomach was mixed with 10 % sea-

water-formalin and poured into a Petri dish. For each stomach sample 15 randomly-chosen subsamples were examined under a dissecting microscope with an ocular grid, on which 20 points were chosen randomly. The occurrence of 3 categories of material was determined for these 20 points in every subsample: 'algal fragments', 'invertebrate fragments' and 'empty or unidentifiable matter', thus allowing determination of percentage composition of identifiable stomach content.

Analysis. Estimates of algal dry weight and densities of invertebrates from the experiment were analysed using *F*-ratios and degrees of freedom derived according to Winer (1971). Cochran's test was used to test for heteroscedasticity and data was log-transformed when necessary to homogenize variances. Where relevant means were ranked using the Student-Newman-Keuls procedure (Underwood 1981). Correlations between densities and algal dry weight were examined. The stomach contents of *Stegastes apicalis* were analysed for differences between areas and between February and May, using 2-factor analyses of variance (both factors fixed and orthogonal). Prior to the analyses the data was transformed to arcsine to normalize the distribution (Winer 1971). Samples from natural substrata collected during May were compared with experimental plates using 3-factor analyses of variance with 'Area', 'Territoriality' and 'Substratum' (all factors fixed and orthogonal). In order to maintain equal sample sizes, 2 experimental samples (from uncaged treatments) were chosen randomly from the same sites used for the collection of natural samples. Densities of invertebrates from natural substrata between February and May were compared in 3-factor analyses of variance with 'Area', 'Territoriality' and 'Month' as fixed and orthogonal factors.

RESULTS

Experimental investigation

The mobile invertebrate fauna on the experimental substrata was dominated by crustacean taxa. Harpacticoid copepods and gammarid amphipods were the most prominent groups, with overall mean densities of 97.5 and 66.2 ind. $100cm^{-2}$, respectively (see Table 1).

Table 1. List of taxonomic groups and their mean densities per 100 cm^2 (± SE) in decreasing order of abundance; $n = 72$ plates

Crustacea	Others	Ind. $100cm^{-2}$
Harpacticoida		97.6 (8.5)
Gammaroidea		66.2 (5.3)
	Polychaeta	58.7 (3.9)
Tanaidacea		58.0 (7.4)
Isopoda		39.5 (3.4)
Ostracoda		23.0 (2.3)
	Gastropoda	17.8 (5.3)
Cumacea		14.2 (5.9)
Caprellidea		10.7 (2.0)
Calanoida		9.5 (3.2)
	Platyhelminthes	2.3 (1.1)
	Pycnogonida	1.3 (0.5)
	Ophiuroidea	1.2 (0.4)

Differences in the densities of these 2 groups were analysed separately from the analyses of total density.

Total density of invertebrates did not vary between the 2 areas, but did differ between individual sites (Table 2); this small-scale variability was due to differences between territorial sites under uncaged conditions (Table 3). Territorial habitats were found to

Table 2. Four-factor, mixed-model analyses of variance for the 3 density parameters and algal dry weight. Indicated are: degrees of freedom (df), mean squares, *F*-values and significance thereof; $n = 72$. Data for Harpacticoida and total density were transformed to logarithms to stabilize the variances. In this and subsequent tables: NS, not significant ($p > 0.05$), $^{\bullet}0.05 > p > 0.01$, $^{\bullet\bullet}0.01 > p > 0.001$, $^{\bullet\bullet\bullet}p < 0.001$

Source of variation	df	Total density			Harpacticoida			Gammaroidea			Algal dry weight		
		Mean square	*F*	Sig.	Mean square	*F*	Sig.	Mean square	*F*	Sig.	Mean square	*F*	Sig.
Treatments:													
Area	1	0.092	2.788	NS	0.009	0.056	NS	2448.67	0.703	NS	0.018	0.304	NS
Caging	1	1.344	25.358	$^{\bullet\bullet}$	3.403	24.659	$^{\bullet\bullet}$	28171.11	8.835	$^{\bullet}$	0.268	20.489	$^{\bullet\bullet}$
Territoriality	1	0.685	20.758	$^{\bullet\bullet}$	1.581	10.006	$^{\bullet}$	7299.18	2.094	NS	0.725	12.066	$^{\bullet\bullet}$
Site (Area, Terr.)	8	0.033	2.750	$^{\bullet}$	0.158	2.078	NS	3484.84	3.362	$^{\bullet\bullet}$	0.060	4.140	$^{\bullet\bullet\bullet}$
Interactions:													
Area × Caging	1	0.067	1.264	NS	0.225	1.630	NS	3973.86	1.246	NS	0.002	0.171	NS
Area × Territoriality	1	0.091	2.758	NS	0.164	1.037	NS	137.99	0.039	NS	0.091	1.522	NS
Caging × Territoriality	1	0.374	7.057	$^{\bullet}$	0.662	4.797	NS	1696.39	0.532	NS	0.279	21.329	$^{\bullet\bullet}$
Caging × Site (Area, Terr.)	8	0.053	4.417	$^{\bullet\bullet\bullet}$	0.138	1.815	NS	3188.65	3.076	$^{\bullet\bullet}$	0.013	0.902	NS
Area × Caging × Territoriality	1	0.082	1.547	NS	0.002	0.014	NS	942.40	0.295	NS	0.014	1.049	NS
Residual	48	0.012			0.076			1036.53			0.014		

Table 3. Results of Student-Newman-Keuls (SNK) tests indicating only significant difference between individual sites. Numbers in main body of table indicate the identity of the sites in question; significant differences at the 5% level are represented by '>' T: territorial; NT: non-territorial; C: caged; U: uncaged

	Area 1				Area 2			
	T		NT		T		NT	
	C	U	C	U	C	U	C	U
Total density		1>2				7,9>8		
Gammaroidea		1>2,3			7,9>8		12>11	
Algal dry weight						7,9>8		

support greater densities than did non-territorial habitats, with mean densities of 470.1 and 327.6 ind. $100cm^{-2}$, respectively (Fig. 1). Caging resulted in an increase in total density, predominantly outside territories, as indicated by the Caging × Territoriality interaction (Table 2; Fig. 1), while in some cases a reduction in density was observed in territorial sites (Sites 1, 3 and 7; Fig. 1), as indicated by the Caging × Site interaction (Table 2).

Caged substrata contained larger densities of harpacticoids than did uncaged substrata, and territories included larger densities than found in non-territorial habitats (Fig. 2). The analysis indicated no differences at either the large or small spatial scale (Table 2).

The analysis of gammarid density illustrated significant variability between sites (Table 2), under caged and uncaged conditions, inside and outside of territories (Table 3). Thus, gammarids appeared very variable in their distribution (Fig. 3). Caging resulted in an increase in density in all but one case (Site 1; Fig. 3), but the extent of the change in density varied considerably between sites, as evidenced by the significant Caging × Site interaction (Table 2; Fig. 3).

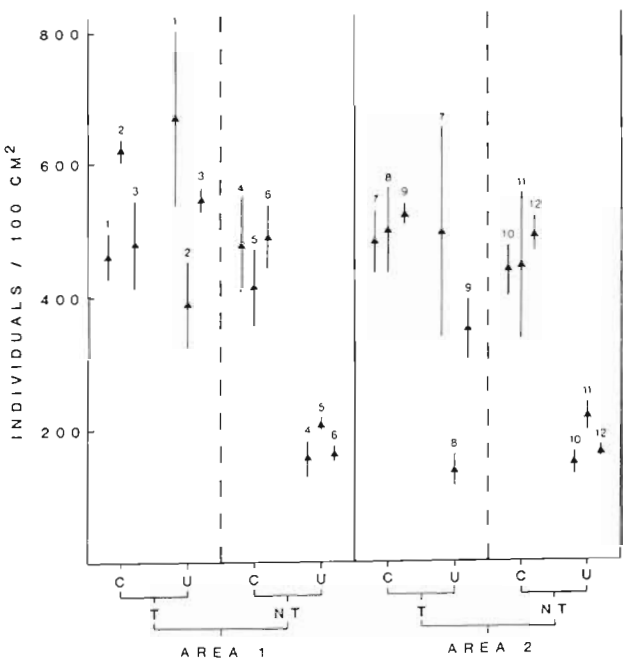

Fig. 1. Mean total density (± SE) of invertebrates per 100 cm^2, separated by the 3 orthogonal factors 'Area', 'Territoriality' and 'Caging'. Numbers identify individual sites; n = 72 replicates. T: territorial; NT: non-territorial; C: caged; U: uncaged

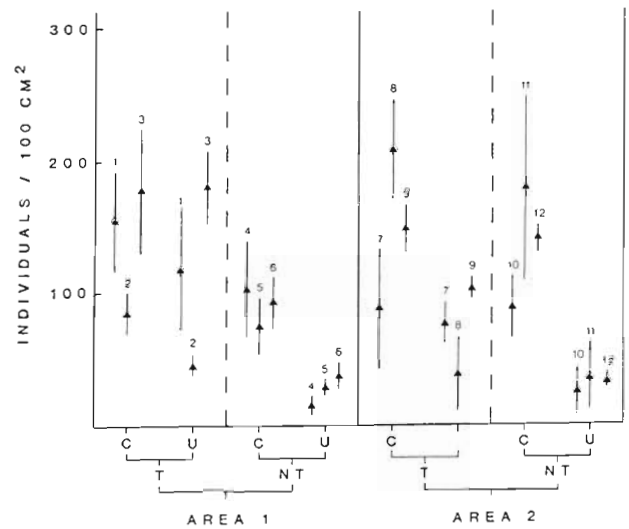

Fig. 2. Mean density (± SE) of harpacticoid copepods per 100 cm^2, separated by the 3 factors 'Area', 'Territoriality' and 'Caging'. Numbers identify individual sites; n = 72 replicates. T: territorial; NT: non-territorial; C: caged; U: uncaged

Algal dry weight showed variability on the small spatial scale, i.e. between individual sites (Table 2; Fig. 4). This was the case particularly for Site 8 under uncaged conditions, as indicated by the SNK test (Table 3). Territories contained greater algal biomasses than did non-territorial habitats (Table 2; Fig. 4). The effect observed for caging was, however, different from the pattern found for the invertebrates. Caging resulted either in a decrease (inside territories), or in no change in algal dry weight (outside territories) (as indicated by the Caging × Territoriality interaction in Table 2). A change in the algal composition was apparent on caged plates. A dense, filamentous algal cover, visually similar to uncaged plates, developed inside the cages during the first 2 mo. At the end of the experiment,

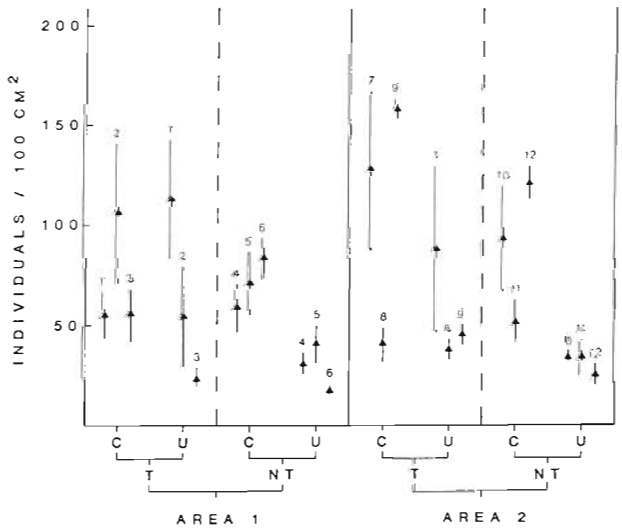

Fig. 3. Mean density (± SE) of gammarid amphipods per 100 cm^2, separated by the 3 orthogonal factors 'Area', 'Territoriality' and 'Caging' Numbers identify individual sites; n = 72 replicates. T: territorial; NT: non-territorial; C: caged; U: uncaged

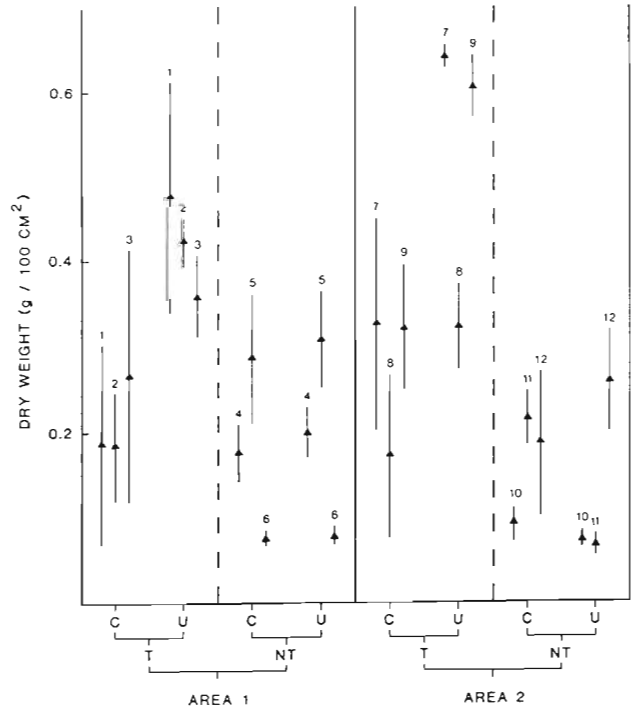

Fig. 4. Mean algal dry weight per 100 cm^2 (± SE), separated by the 3 orthogonal factors 'Area', 'Territoriality' and 'Caging' Numbers identify individual sites; n = 72 replicates. T: territorial; NT: non-territorial; C: caged; U: uncaged

however, the plates were dominated by larger, more fleshy species such as *Spyridia filamentosa, Jania* spp. and *Hypnea* spp.

Correlation analyses between invertebrate densities and algal dry weight were limited to uncaged treatments, since the above analyses indicated a distinct discrepancy between these variates for caged treatments. Thus, factors other than algal biomass appeared to influence density of invertebrates in caged samples. Densities of all 3 taxal groups showed significant positive correlations with algal biomass under uncaged conditions (total density of invertebrates: r = 0.57, $p<0.001$; Harpacticoida: $r=0.51$, $p<0.001$; Gammaroidea: $r=0.37$, $0.05>p>0.01$).

Natural samples

No differences in densities of harpacticoid, gammarid or total invertebrates were detected between natural and experimental substrata (Table 4). Similarly, there were no differences in densities on natural substrata between February and May (Table 5).

Table 4. Results of 3-factor analyses of variance testing for differences in densities of invertebrates between natural and uncaged experimental substrata. Indicated are: degrees of freedom (df), mean squares, F-values and significance thereof; n = 16. Data for Gammaroidea and total density were transformed to logarithms to stabilize the variances

Source of variation	df	Total density			Harpacticoida			Gammaroidea		
		Mean square	F	Sig.	Mean square	F	Sig.	Mean square	F	Sig.
Treatments:										
Area	1	0.0272	1.346	NS	92.55	0.099	NS	0.000393	0.008	NS
Territoriality	1	0.632	31.351	•••	26266	28.228	•••	0.577	11.069	•
Substrata	1	0.0169	0.843	NS	1035.52	1.113	NS	0.000221	0.004	NS
Interactions:										
Area × Territoriality	1	0.00419	0.208	NS	41.70	0.045	NS	0.0272	0.522	NS
Area × Substrata	1	0.0255	1.268	NS	4581.15	4.923	NS	0.0576	1.104	NS
Terr. × Substrata	1	0.00351	0.174	NS	1670.78	1.795	NS	0.0533	1.021	NS
Area × Territoriality × Substrata	1	0.000175	0.008	NS	1856.73	1.795	NS	0.0649	1.246	NS
Residual	8	0.0202			930.51			0.0522		

Table 5. Three-factor analyses of variance of densities of invertebrates on natural substrata collected at the beginning and end of the experimental period. Indicated are: degrees of freedom (df), mean squares, *F*-values and significance thereof; $n = 16$. Data for Gammaroidea were transformed to logarithms to stabilize the variances

Source of variation	df	Total density			Harpacticoida			Gammaroidea		
		Mean square	*F*	Sig.	Mean square	*F*	Sig.	Mean square	*F*	Sig.
Treatments:										
Area	1	22666	2.009	NS	1789	1.642	NS	0.00453	0.053	NS
Territoriality	1	440269	39.018	•••	30800	28.270	•••	2.124	24.577	•••
Month	1	12769	1.132	NS	65	0.060	NS	0.00682	0.079	NS
Interactions:										
Area × Territoriality	1	8562	0.759	NS	1066	0.978	NS	0.0452	0.522	NS
Area × Month	1	8986	0.796	NS	490	0.450	NS	0.0232	0.268	NS
Terr. × Month	1	10502	0.931	NS	753	0.692	NS	0.00104	0.012	NS
Area × Territoriality × Month	1	3412	0.302	NS	285	0.262	NS	0.0431	0.498	NS
Residual	8	11280			1089			0.0864		

Stomach contents

Filamentous algae clearly dominated the identifiable contents in terms of percentage occurrence, with algal fragments comprising on average 83.82 % (SE = 4.41 %) and the rest being invertebrates. No difference was detected between areas or between February and May in the abundance of either algal or invertebrate fragments (Table 6).

DISCUSSION

Territories of *Stegastes apicalis* contained larger densities of mobile invertebrates than found in non-territorial habitats. Caging led to an increase in densities of harpacticoids, gammarids and the total assemblage of invertebrates. While densities outside territories showed relatively little variation between areas and between sites, territorial habitats displayed a larger variability in densities between individual sites, often resulting in significant interactions between the factors 'Territoriality', 'Caging' and 'Site'.

Effect of territoriality

In the following discussion emphasis is placed on the effect of territoriality. Nevertheless, one should remember that it is entirely possible that differences between territorial and non-territorial treatments could also be the result of differences in the places where damselfishes like to place their territories, such as in areas where plants are more productive. It does not seem possible to design an experiment that removes this problem.

It has been stated frequently in the literature that differences in abundance of small, mobile invertebrates depend upon the size (Edgar 1983, Gunnill 1983), as well as the availability of algae per unit area (e. g. Lobel 1980). Thus, one would expect the greater densities of invertebrates on territorial than on non-

Table 6. Results of the 2-factor analyses of variance testing for differences in stomach contents (algal and invertebrate fragments) between the 2 areas and between February and May. Indicated are: degrees of freedom (df), mean squares, *F*-values and significance thereof; $n = 16$. Data was transformed to arcsine to normalize the distributions

Source of variation	df	Algae			Invertebrates		
		Mean square	*F*	Sig.	Mean square	*F*	Sig.
Treatments:							
Area	1	0.00007	0.015	NS	0.0053	1.709	NS
Months	1	0.01902	4.226	NS	0.0001	0.032	NS
Interaction:							
Area × Months	1	0.0101	2.244	NS	0.0002	0.065	NS
Residual	12	0.0045			0.0031		

territorial plates to be paralleled by a change in algal dry weight. This was the case for uncaged samples, with greater algal biomass inside territories than outside. The analyses of uncaged samples indicated that densities showed significant, positive correlations with algal biomass. The low correlation coefficients obtained suggest 2 things. First, there was a great variability in densities on the 'Site' scale, especially for territorial habitats. Such highly variable densities have been reported also by Lobel (1980) for mobile invertebrates inside territories. Second, factors other than algal biomass are important in influencing the abundance of the invertebrates inside territories. Coull & Wells (1983) examined the phytal meiofauna on a temperate rocky shore and found that structural complexity of algae (i.e. surface to volume ratios) rather than biomass gave the best correlations with faunal abundances. Thus, structural complexity of habitats may significantly influence population density. No quantitative measure of complexity of the algal cover was collected in the present study, and thus this hypothesis could not be tested. Nevertheless, from the distinct differences in dry weight of algal turf observed between territorial and non-territorial treatments, one would predict that cover of algae inside territories should be of greater structural complexity than cover outside territories. Thus, the greater biomass and perhaps greater structural complexity of algal cover inside territories appeared to provide a refuge for the invertebrate fauna. The algal mats might provide increased availability of food, either in terms of filamentous algae, or increased amount of particulate organic matter and detritus that is deposited in these mats (Hicks 1980). Complex environments may also permit a moderation of or protection from predation by the provision of spatial refuges (Coull & Wells 1983). Territorial pomacentrids aggressively exclude other herbivorous fishes such as scarids, acanthurids and siganids (Lassuy 1980, Hixon 1985), while a number of small predators are consistently ignored (Itzkowitz 1974). Thus, mortality of invertebrates due to the activities of large grazers (as reported by Brock 1979), could be reduced inside territories because of the behavioural patterns of *Stegastes apicalis*.

The analysis of stomach contents of *Stegastes apicalis* indicated a predominance of filamentous algal fragments. This agreed with findings by Lassuy (1980), Lobel (1980) and Robertson & Polunin (1981) for other *Stegastes* species. In the present study, invertebrates made up only a small component (16.18%) of the overall diet, which is comparable to the 14% by volume recorded for *S. planifrons* (Lobel 1980). Other herbivorous pomacentrids have also been found to contain invertebrates in their stomachs (e.g. Hobson 1974). This could indicate that invertebrates are either taken incidentally or as a dietary supplement. It has been suggested that such animal matter, despite low occurrence, forms an important dietary component, to satisfy the need for nitrogen, which is rare in plants (Lobel 1980).

Feeding by the moon wrasse *Thalassoma lunare* and other predatory, benthic feeding fishes was observed inside territories of *Stegastes apicalis* throughout the study, and such feeding did not elicit any aggressive response from the pomacentrid. The access permitted to many predatory fishes could result in considerable predation on the invertebrate fauna inside territories. The increased algal cover inside territories may, however, provide increased refuge from the visual predation by these fishes. In areas unaffected by territorial pomacentrids the cover of algae was considerably reduced by grazing (Miller 1982).

Effect of caging

Caging resulted in an increase in faunal densities, and algal biomass changed in composition and either underwent a reduction (inside territories) or no change in biomass (outside territories). A shift in species composition inside cages, favouring a few prominent macroalgae, has been reported previously (e.g. Lassuy 1980). Caging experiments are known to be affected by various confounding effects which have been addressed repeatedly (e.g. Choat & Kingett 1982, Kennelly 1983). Russ (1987) and Scott & Russ (1987) used similar types and sizes of cages and plates to test for possible caging effects using the method proposed by Kennelly (1983), and reported no significant artefactual effects on algal biomass over a 1 mo period.

Alternatively, the exclusion of large grazers and predators may have led to an increase in the densities of small, herbivorous invertebrates. Intense grazing pressure by micrograzers (*sensu* Vadas 1986) could thus have produced the observed reduction in algal biomass to levels equal to or below uncaged treatments. Similar results were obtained by Brawley & Adey (1981) and Kennelly (1983). Brawley & Adey reported increases in densities and feeding intensity of micrograzers upon exclusion of fishes from their experimental reef system, resulting in drastic changes in algal cover, with preference to algal species that were consumed rarely or not at all by the invertebrates. The caged plates in the present experiment were dominated by *Spyridia filamentosa, Jania* spp. (which is lightly calcified) and *Hypnea* spp. Considering the evidence put forward by Brawley & Adey, it seems quite likely that none of these algae were fed upon preferentially by micrograzers, but their abundance might be the direct result of the high densities of micrograzers.

Detailed knowledge of feeding requirements and consumption rates of small, tropical invertebrates is lacking. Nevertheless, the effect of micrograzers on the algal cover, in addition to the effect of predation on the invertebrates, would have to be taken into account in future caging experiments longer than 1 mo in duration. The selective territorial defence by pomacentrids, allowing access of small predatory fishes, might therefore have the indirect effect of maintaining the mobile invertebrate fauna at a level low enough to avoid those changes that were observed under caged conditions inside territories. Invertebrate densities in uncaged conditions might, however, be high enough to explain partially the contradictory findings of fast rates of algal removal inside territories despite apparently smaller bite rates of grazing fishes (Russ 1987).

CONCLUSIONS

The major findings of this study are:

(1) Densities of small invertebrates were significantly greater in algal turfs inside territories than outside territories of *Stegastes apicalis*. Increased availability of food and/or refuges from predators due to increased structural heterogeneity of the environment are possible explanations for this.

(2) An increase in densities of invertebrates, accompanied by a change in algal composition and reduction in algal biomass were observed in caged treatments. The reduction in algal biomass may have been caused by temporally delayed cage effects and/or by increased intensity of grazing by the herbivorous species in the invertebrate community.

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