The Effects of Damselfish Territoriality on Small Invertebrate Community Structure

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Abstract

Territorial ~~behavior~~ threespot damselfish (*Eupomacentrus planifrons* Cuvier) protect algal mats that act as a refuge for a variety and abundance of small invertebrates. Algal biomass, $CaCO_3$ concentration in algae, and small invertebrate size, density and diversity were calculated from samples of coral rubble within and without threespot territories. Manipulations were set up in order to isolate the effects of predation and algae on the invertebrate community. These involved moving rubble from territories to undefended rubble beds and sand channels, and moving rubble from undefended rubble beds to threespot territories. Decalcified dry algal biomass and small invertebrate size, density and diversity were recorded after five days.

where?

We found 1.9 times more algal dry biomass, 9.% times more $CaCO_3$ and 2.4 time more small invertebrates. Furthermore, when rubble was moved out of threespot territories, we found a dramatic decline in algal biomass and $CaCO_3$ and to a lesser extent, small invertebrate density. Rubble transferred from territories into sand and from undefended rubble beds into territories showed no significant differences in small invertebrate size density, diversity, algal biomass or $CaCO_3$ concentrations.

We conclude from these data that the threespot damselfish actively influence community structure by protecting filimentous algal lawns which catch sediment and detritus, increasing food for benthic invertebrates. Furthermore, threespot damselfish indirectly protect small invertebrates from predation by carnivorous and planktivorous fish.

what about algal lawns as shelter for the invertebrates?

INTRODUCTION

Like other Pomacentrid damselfish, the threespot damselfish (Eupomacentrus planifrons) agressively defends algal lawns against inter and intraspecific grazers and predators (Myrberg and Thresher 1974 cited in Williams 1979). Many studies have ~~x~~ investigated the microenvironment associated with these territories. Several have found that algal biomass is greater inside the territories and that this algae is primarily filamentous (DeRuyter Van Steeninck 1984, Vine 1974 in Brawley and Adey 1977, Brawley and Adey 1977). The effects of this increase in algal cover, coupled with reduced grazing within territories, has a profound effect on the invertebrate community within territories. This has been shown to affect survivorship (Potts 1977) and diversity (Sammarco 1982) ~~Sammarco 1983)~~ of corals. Risk + Sammarco (1982) look at bioerosion within damselfish territories and find that increased sedimentation may provide a rich environment for boring sponges on corals. ~~with~~

In this study we examine the effects of damselfish territoriality on the algal community and on a less obvious community, that of small marine invertebrates, ~~such as~~ planktonic and benthic, which we expect to be associated with algae. Territorial behavior of the damselfish and an increase in algal biomass within territories would increase small invertebrate density and diversity due to the following factors:

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(1) Decreased (or accidental?) ingestion by grazers. Damselfish keep out predators, and long filamentous algae provides cover from predators.

(2) Increased algal cover, increases sedimentation and capture of detritus, an important food supply for benthic invertebrates. Sedimentation also makes it more difficult for a predator to find prey.

(3) Filamentous algae within territories have a higher primary productivity ~~and~~ (Brawley + Adey 1977)

need to differentiate between $CaCO_3$ in calcareous algae and $CaCO_3$ sediment.

and thus may leak dissolved organic material to the invertebrates (locally).

Thus, we hypothesize that there will be a higher algal biomass within territories, although these algae will have less $CaCO_3$ sediment/algae. Furthermore, we expect to find a greater density of planktonic and bethic organisms within territories and these organisms will be larger within then without.

why?

To test this we examined the algal and invertebrate communities within + without damselfish territories. We also set up three manipulations to test each factor.

In the first manipulation, where coral rubble was moved from territories, we expected there to be a decrease in invertebrate numbers and diversity, and algal biomass, in the rubble outside the territories.

In the second manipulation, where coral rubble was moved from territories, into sand channels, we expected there to be an increase in grazing, but not as great an extent as the first manipulation.

why?

The last manipulation involved moving a peice of rubble from an undefended rubble bed to within a territory. We expected a migration of zooplankton and more mobile benthic organisms to the rubble within the territory assuming damselfish decrease small invertebrate predation.

Methods

The study took place from March 1 to March 7, 1985 at Discovery Bay Marine Laboratory, Discovery Bay, Jamaica. The field site was located below Mooring 1 on the west fore reef of Discovery Bay at a depth of 30 to 35 feet. It consists of small coral buttresses separated by sand channels. On the reef there is a large amount of fallen, dead *Acropora cervicornis* between living coral boulders.

With the aid of SCUBA we collected 3 pieces of coral rubble from within and 3 pieces from without three spot damsel fish territories. We placed each piece in a plastic bag and brought it back to the lab for analysis. We also did 3 sets of manipulations with 3 replicates in each:

1. Rubble from within territories was marked and placed outside of territories on rubble beds. Pieces from within the same territories were marked as controls.
2. Rubble from within territories was marked and placed outside of territories in a sand channel. A control was marked within each territory.
3. Pieces of rubble from outside territories were marked and moved to territories. Controls were marked in areas from which rubble was taken.

All marked pieces (except one control from the second manipulation which could not be relocated) were placed in separate plastic bags and brought back to the lab after five days.

We transfered the rubble and water from each bag to a plastic container and added enough formalin to each sample to make a ten percent or stronger solution. We shook each piece of rubble in the formalin solution to release the animals from the algae. We estimated the percent cover of the following growth forms: filamentous, encrusting, bulbous, Padina species and Dichtyota species. We scraped the algae from the rubble with razor blades and estimated the percent volume of the same growth forms of algae. We dried the algae at 60°C for 24 hours in preweighed weighing pans and recorded the dry weight of the algae. Then we added 10% HCl to the algae to decalcify it. After the reaction had ceased we decanted the liquid and repeated the drying and weighing process. We also calculated the percent of weight lost to aluminum dissolved by addition of HCl solution to an empty pan and readjusted the dry weights of the algae accordingly. We calculated $CaCO_3$ content from the differences of the calcified and decalcified algal dry weights. Because of time constraints we took the calcified weights for only half the samples.

We measured heights and diameters of the rubble pieces and estimated surface area by cylinderical surface areas. In one case where the rubble was irregular, foil was wrapped around the coral, dried and weighed. This weight was compared with that of a $4cm^2$ piece.

We strained the formalin and invertebrate solution to condense the volume to 100 ml. We counted, measured to 0.1 mm and identified to general taxa every animal in the first pair of samples (IN B and OUT B) but because of time constraints we examined only 20% of each remaining sample.

The most appropriate test for comparing the sets of data would be a matched pair analysis. But, since sample sizes are small we can not use this test. So, we compare data using the students t-test and means and standard deviations. Because of small samplesizes we consider both methods equally in the interpretation of results. We calculated a correlation coeficient between invertebrate density and $CaCO_3$ concentration and algal biomass.

How was invertebrate diversity measured?

Results

Invertebrate density and diversity and algal biomass inside and out side of the territories are summarized in Table 1. The invertebrate density inside the territory is higher than outside ($t = 2.135$, $p < .1$). The invertebrate diversity is higher outside the territories ($t = 2.19$, $p < .1$). Table 2 shows the invertebrate density and algal biomess of manipulated samples There is no significant difference amoung them.

The mean densities and percentages of taxa in the invertebrate community are shown in

SP Table 3. Polycheates, forminiferon and amphipods are significantly more dense within territories ($t = 2.410$, $p < .05$; $t = 2.695$, $p < .1$; $t = 5.58$, $p < .05$). Polycheates make up a larger proportion of the communities inside territories ($t = 2.25$, $p < .1$) and copeped harpaticoids are proportionally more numerous outside ($t = 2.22$, $p < .1$)

The mean size of animals in territories is $.94 \pm .77$ mm and outside is $.88 \pm .53$ mm.

The dryweight of calcified and decalcified algal samples are shown in Table 4. When control samples are merged we find 1.9 times more algae and 93 times more sediment in territories than outside. When rubble is placed outside of territories onto rubble algal biomass decreases by 79% and sediment by 98%. When rubble is moved from territories to sand or from outside territories to inside there is no significant trend.

Average percent cover and composition for encrusting, filamentous and other types of algae are given in table 5. We found no significant difference between encrusting algae inside and outside of territories but there is more filamentous algae cover and composition and less other algae cover and composition in than out ($t = 4.82$, $p < .05$; $t = -7.13$, $p < .05$; $t = 3.87$, $p < .1$; $t = 2.41 < .1$).

For the rest of the samples variences were too high to establish differences between samples.

sp We found no correllation between invertebrate density and algal biomass ($r = .395$) nor between invertebrate density and $CaCO_3$ concentration ($r = .213$).

A list of taxonomic groups of invertebrates found is presented in Appendix 1.

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	INSIDE TERRITORY			OUTSIDE TERRITORY		
	invertebrate density (individual/cm²)	invertebrate diversity (H)	algal biomass	invertebrate density	invertebrate diversity	algal biomass
A	8.33	-1.79	0.00242	5.33	-1.92	0.00946
B	6.12	-1.77	0.0145	2.93	-1.79	0.00728
C	6.90	-1.64	0.0139	3.22	-1.88	0.00521
$\bar{x}$	9.12 ± 3.46	-1.73 ± .081	0.0103 ± 0.00681	3.83 ± 1.31	-1.86 ± .067	0.00732 ± ± 0.00213

how can mean be higher than any of the replicates?

Table 1: Summary of Density and Diversity of Invertebrate Communities and Algal Biomass

		MANIPULATION		CONTROL	
		invertebrate density	algal biomass	invertebrate density	algal biomass
In → Rubble	A'	1.40	0.00251	8.33	0.982
	B	2.59	0.00154	2.40	0.00342
	C	7.09	0.00466	—	—
$\bar{x}$		4.69 ± 2.95	0.00290	5.37 ± 4.19	0.0140
In → Sand	D	4.06	0.00851	6.54	0.00558
	E	3.75	0.00252	4.25	0.0262
	F	2.51	0.0106	26.62	0.01106
$\bar{x}$		3.44 ± 0.82	0.00721	12.47 ± 12.31	0.0142
Out → In	G	5.84	0.0121	5.46	0.00592
	H	4.10	0.00272	4.10	0.00982
	I	—	—	4.87	0.00721
$\bar{x}$		4.97 ± 1.23	0.00741	4.81 ± 0.682	0.00765

Table 2: Summary of Invertebrate Density and Algal Biomass for Manipulations and Controls

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	INSIDE TERRITORY		OUTSIDE TERRITORY	
	$\bar{x}$ density	$\bar{x}$ % invertebrate community	$\bar{x}$ density	$\bar{x}$ % invertebrate community
forminiferan	3.24 ± 1.32	35.3 ± 0.9	1.16 ± 0.21	31.4 ± 4.46
polycheate	2.30 ± 0.74	25.7 ± 2.7	0.68 ± 0.36	17.4 ± 5.8
nematode	0.46 ± 0.29	5.6 ± 4.7	0.13 ± 0.10	3.1 ± 1.3
copepod, harpaticoid	1.28 ± 1.14	12.7 ± 6.8	0.78 ± 0.71	23.6 ± 5.7
copepod, cyclopoid	0.44 ± 0.33	3.1 ± 1.0	0.14 ± 0.11	6.2 ± 3.1
isopod	0.74 ± 0.46	8.1 ± 6.3	0.27 ± 0.28	9.1 ± 2.5
amphipod	0.26 ± 0.13	1.4 ± .1.3	0.05 ± 0.03	1.1 ± 0.5
ostracod	0.30 ± 0.26	3.4 ± 3.1	0.05 ± 0.04	2.8 ± 1.3

Table 3: Mean Densities and Diversities of Eight Most Common Taxa

TABLE 4 Dryweight of decalcified algae found in and out of Damselfish territories.

SAMPLE	IN: Live (Decalcified) Biomass Density (g/cm³)	IN: $CaCO_3$ density *	OUT: Live (Decalcified) Biomass density (g/cm³)	OUT: $CaCO_3$ density (g/cm³)	Proportion BIOMASS (IN/OUT)	Proportion $CaCO_3$ (IN/OUT)	PERCENT CHANG $\left(\frac{\text{Manipulation} - \text{Control}}{\text{Control}} \times 100\right)$ Biomass	PERCENT CHANG $CaCO_3$
A	0.00242	0.0673 (61%)	0.00916	0.00484 (34%)	0.26	1.4		
B	0.0145	0.0678 (35%)	0.00728	0.00552 (43%)	2.0	12.3		
C	0.0139	0.0093 (40%)	0.00521	0.00258 (33%)	2.7	3.6		
Avg	0.0103	0.0481	0.00733	0.00431	1.4	11.2		
Manipulation I	Control (IN)		IN → OUT (Rubble)					
a	0.0238	0.0982 (80%)	0.00251	0.00157 (38%)	9.5	62.5	-89%	-98%
b	0.00410	0.00342 (45%)	0.00159	0.00054 (26%)	2.7	6.3	-62%	-84%
c	—	—	0.00466	—	–	–	–	–
Avg	0.0140	0.0508	0.00290	0.00106	4.8	48.2	-79%	-98%
MANIPULATION II	CONTROL (IN)		IN → OUT (SAND)					
d	0.00558	0.00189 (25%)	0.00851	0.00519 (38%)	0.66	0.36	+53%	+175%
e	0.0265	0.0349 (57%)	0.00252	0.00101 (29%)	10.5	34.6	-90%	-97%
f	0.0106	—	0.0106	0.00150 (12%)	1.0		0%	
Avg	0.0142	0.0183	0.00721	0.00257	2.0	7.1	-49%	-86%
MANIPULATION III	OUT → IN		CONTROL (OUT)					
g	0.0121	–	0.00592	–	2.04		+104%	
h	0.00272	–	0.00982	–	0.28		-72%	
i	—	–	0.00721	–	–	–	–	–
Avg	0.00741	–	0.00765	–	0.97		-3%	

* Numbers in parentheses indicate percent of $CaCO_3$ in Algae dry weight (before decalcification).

NOTE: MANIPULATION I TAKE Rubble from in D.F. territory to undefended rubble patch.
MANIPULATION II TAKE Rubble from in D.F. territory to undefended sand patch.
MANIPULATION III TAKE Rubble from outside D.F. territory and place it within a territory.

		INSIDE TERRITORY		OUTSIDE TERRITORY	
		% cover	% composition	% cover	% composition
	encrusting algae & bare rubble	22.5 ± 10.6	0	41.0 ± 33.9	51.0 ± 62.2
	filamentous algae	67.5 ± 3.53	32.5 ± 3.53	17.5 ± 17.6	6.25 ± 5.3
	other algae	10.0 ± 7.07	60.0 ± 7.7	41.5 ± 16.2	42.8 ± 6.5
		MANIPULATION		CONTROL	
RUBBLE	encrusting algae & bare rubble	32.3 ± 20.4	4.5 ± 2.1	31.0 ± 19.8	0
	filamentous algae	55.0 ± 32.8	49.5 ± 67.11	29.0 ± 29.6	20 ± 21.2
	other algae	11.0 ± 16.5	3.5 ± 4.94	40.0 ± 9.9	80.0 ± 21.2
SAND	encrusting algae & bare rubble	28.3 ± 22.5	5.0 ± 7.07	31.6 ± 25.2	0
	filamentous algae	55.0 ± 32.8	41.7 ± 32.5	55.0 ± 35.0	53.3 ± 43.1
	other algae	12.6 ± 15.0	48.3 ± 38.2	13.3 ± 12.5	46.6 ± 43.1
IN → OUT	encrusting algae & bare rubble	67.0 ± 19.4	32.5 ± 46.0	32.3 ± 22.5	2.5 ± 3.5
	filamentous algae	11.7 ± 2.8	7.5 ± 3.5	36.7 ± 41.9	3.5 ± 2.1
	other algae	22.7 ± 20.4	55.0 ± 35.3	31.0 ± 21.2	94 ± 1.4

Table 5 : Percent Cover and Composition of Algal Types In and Out of Territories and in Manipulations and Controls

What is percent composition and how was it calculated?

Discussion

Rubble in damselfish territories contains more algal biomass per square centimeter of substrate than rubble outside of territories and when rubble from inside territories is moved outside it loses a significant amount of biomass. This suggests that the presence of the damselfish directly affects the algal biomass within the territories. Territories do not just happen to fall around areas with high algal biomasses. This finding is further supported by Brawly and Adey (1977) who found a drastic decrease ~~in~~ within one day in the algal biomass in territories from which damselfish were removed. Algal biomass loss in rubble moved to sand was less than that of rubble moved to rubble beds. Fish predation on this algae should be low because potential predators would be more vulnerable because they would be far from the protection of the reef and because the algae was covered by the sand and thus less accessable. We would expect algal biomass to increase on rubble brought from outside into the territories since predation would be decreased, but it is not surprising that there is no measurable increase after only six days.

As expected there is more filamentous algae inside damselfish territories. Its high primary productivity, low $CaCO_3$ concentration and low toughness make it a rich food source. The pieces that were moved out of territories into rubble beds lost a significant amount of filamentous

algae showing that damselfish are effective at defending this algae from other herbivores. There was no significant difference between encrusting algae within and with out. These algae are not a food source and do not seem to hamper growth of other types of algae. De Ruyter van Stevenick (1984) found similar proportions of algae. We found more other types of algae with out than within. These algae types include padina and dichtyota species bulbous and highly calcarious algae, most of which we assume to be preferred less by the damselfish because of of their toughness and high $CaCO_3$ content. Algal percent composition and cover of manipulated rubble, except in the case mentioned above, were not significantly different from those of the controls probably because of small sample sizes and our method of determining percent cover and composition. We should have distinguished between percent cover on the top and the bottom of the rubble pieces because the collected rubble had varying amounts of area exposed for algal colonization.
SP Rubble lying parrellel to the ocean floor had algal growth concentrated on the top side and rubble pieces which were sticking out of the rubble bed had fairly evenly distributed algae. Percent composition should have been determined by a more exact method such as finding volumes or weights of algae separated into groups.

We found 9.3 times more $CaCO_3$ inside territories than out. This high concentration of

$CaCO_3$ is more likely an indication of the amount of sediment trapped with in the fine filamentous algae than an indication of the amount of calcarious algae as it was intended to be. That the rubble moved out of territories to rubble beds lost an average of 98% $CaCO_3$ and that rubble moved into territories neither gained nor lost $CaCO_3$ supports this hypothesis. The $CaCO_3$ concentration in algae on rubble moved to the sand did not change because less algae was lost and the algae was exposed to more sedimentation.

Contrary to our expectations we found more diversity in the invertebrate community, outside damselfish territories than in. It could be that damselfish exclude predators which control the population of an otherwise superior small invertebrate competitor But it is more likely that forminiferon and polycheates, two taxa which are significantly more dense inside territories, being filter feeders, are associated with sediment and are therefore more abundant within territories, lowering diversity. Harpaticoid copepods make up a significantly higher proportion of the community outside the territories perhaps reflecting an intolerance for sediment. Amphipods may make up a significantly higher proportion of the community inside the territory possibly because these large bodied animals are ~~more~~ highly susceptable

SP

to predation.

There is no correlation between invertebrate density and algal biomass nor between invertebrate density and $CaCO_3$ concentration. Therefore the high invertebrate density within territories is not due solely to the high algal biomass nor to the high $CaCO_3$ concentration with in those territories. It could be due to the type of algae growing in the territories or the protection against predators afforded by the damselfish. Invertebrate density does not increase on rubble moved into territories from non territory areas. So, protection against predators is not the determining factor in high invertebrate density within territories either. Probably it is a combination of all four factors; algal biomass, abundance of filamentous algae, sediment concentration and protection from predators.

graphs of these relationships would be nice

This would take time!

I don't think this is a justifiable conclusion

The densities of invertebrates ~~zooplankton~~ on rubble moved out of territories to sand and rubble beds are lower, but because of small sample size and high varience, the differences are not significant. We expect invertebrate density to decrease because of increased predation both on algae and animals.

The benthic community associated with algae, especially with algae inside damselfish territories has been found to be complex and extremely rich and varied.

The high number of animals may constitute a rich food source for the carnivorous fish which inhabit the reef. These fish such as goatfish have been observed to root through algae (LaChance and McCleod pers. comm.) and we noticed blueheaded wrasses pecking at algae inside territories once damsel fish were displaced. By excluding intruders damsel fish ~~[illegible]~~ protect algae and invertebrates from predation and allow the algal biomass and percent of filamentous algae within territories to increase, greatly increasing the primary productivity of the reef and providing more living spaces for invertebrates. The abundance of filamentous algae directly affects the amount of sediment ~~captured~~ and detritus captured. These factors working together tend to increase the amount of benthic invertebrates associated with algae especially within threespot damsel fish territories.

A very good, initial study on this new relationships between damselfish, algae, and small invertebrates associated with the algae.
Report could be more clearly written in places.

Appendix I
List of Taxa seen in samples.

Amphipoda *
Chitin
Cnidarian larvae
Copepod
  Calanoid *
  cyclopoid *
  harpacticoid *
Cumacea
Echinodermata - brittlestars + urchins
foraminifera *
Gastropoda
Holothurian
Isopoda *
Lamillibranch ~~mollusc~~
larvacea
Nauplii
Nematoda
Ostracoda *
Pictnogonids
polychaete worms (Annelida) (+ Spirorbid) *
Tanaid

* = Most common Taxa seen

References

Brawley S.H., Adey W.H., 1977, Territorial Behavior of threespot damselfish (Eupomacentrus planifrons) increases ~~#~~ reef algal biomass and productivity. Env. Biol. Fish 2(1): 45-51

De Ruyter Van Steveninck, E. 1984, The composition of algal vegetation in and outside damselfish territories on a Florida reef. Aquatic Botany 20: 11-19

Myrberg A.A, Thresher, R.E. 1974 Interspecific agression and its relevance to the concept of territoriality in reef fishes. Am. Zool. 14(1): 81-96.

Potts, D.C. 1977, Suppression of coral populations by filamentous algae within damselfish territories. J. exp. Mar. Biol. Ecol. 28: 207-216.

Risk MJ, Sammarco PW, 1982, Bioerosion of corals and the influence of damselfish territoriality: A preliminary study. Oecologia 52: 376-380.

Sammarco PW, Williams AH, 1982, Damselfish territoriality: Influence on Diadema distribution and implications for coral community structure. Mar. Ecol. Prog. Ser. 8: 53-59.

Vine PJ, 1974, Effects of Algal grazing and aggressive behavior of fishes Pomacentrus lividus and Acanthurus sohal on coral reef ecology. Mar. Biol. 24: 131-136.

Williams, HA, 1979, Interference behavior and ecology of threespot damselfish (Eupomacentrus planifrons). Oecologia 38: 223-230.