

The Effect of Damselfish Territoriality
on the Abundance and Composition of
Algal Species

A nicely planned and very
ambitious study. You might have
tried to do too much.

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ABSTRACT :

We studied the effect of damselfish territoriality on the abundance and composition of algal species inside their territories. Algal abundance was significantly higher inside damselfish territories than outside, and differences in species composition inside and outside territories were noted, although neither of these trends was as striking as those found in the literature. Herbivory rates were ~~found~~ to be lower inside territories than outside territories based on ~~number~~ observations of fish bites, but examination of biomass decreases after 6 h. does not suggest lower grazing pressure inside territories.

Multispecific transplants of algal mats on natural substrate showed ~~significantly~~ higher herbivory outside territories than inside based on data of percent algal cover and number of bites by fish. Trends in biomass reduction suggest damselfish prefer algae taken from within territories, whereas nonterritorial fish prefer algae from outside territories. Monospecific transplants of algae on artificial substrate showed damselfish preference for Acanthophora over Liaogora, but this result was contradicted by data from the multispecific transplants.

Introduction:

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The effect of damselfish (Pomacentridae family) territoriality on the abundance and composition of algal species inside their territories has been the subject of numerous studies. Ruyter van Steveninck (1984) and Hatcher and Larkum (1983) have found algal density to be greater inside damselfish territories than outside. Differences in algal species composition inside as compared to outside territories have been quantified by many researchers (Vine 1974; Potts 1977; Brawley and Adrey 1977; Montgomery 1980 - all cited in Ruyter van Steveninck 1984; and Dartmouth 1987 FSP Lab No. 1).

The greater abundance of algal species within territories has been presumed to be the result of lower grazing pressure inside territories as compared to outside territories. Such an idea is supported by other studies noting inverse correlations between algal abundance and grazing pressure (Earle 1972), indicating that algae may be herbivore-limited, and by the fact that damselfish are successful defenders of their territory and excluders of other fish grazers (Foster 1985).

To explain the differences in species composition inside and outside territories, three mechanisms have been proposed. The first mechanism is that damselfish selectively remove certain undesirable algal species from their territories. Such "weeding" behavior has been observed by some researchers (Lassuy 1980 - cited in

Ruyter van Steveninck 1984) but not by others (Ruyter van Steveninck 1984). This proposal portrays the damselfish as a "farmer" cultivating an optimal algal "lawn" for its use.

The second possible mechanism is that damselfish selectively graze algae, eventually depressing or eliminating certain species and evoking a change in composition (Hay 1984). This proposal contrasts with the above concept of the damselfish as a prudent algal cultivator, and instead suggests that damselfish may exhaust favored foods and utilize their algal resources on a less-than-optimal manner.

A third mechanism by which algal composition inside territories may be altered is by non-selective damselfish grazing. Montgomery (1980 - cited in Ruyter van Steveninck 1984) and Hay (1987) have pointed out that even non-selective grazing can change competitive dominants by shifting the selective advantage of having a given growth rate. For example, if overall grazing inside territories is lower than outside, algal species that would not normally flourish because their growth rates are too low to make up for grazing, may flourish inside territories.

The purpose of this study was to quantify differences in grazing pressure and food preference

between damselfish and other, non-territorial fish, and to determine to what extent these differences can explain any differences in algal abundance and species composition inside and outside of damselfish territories.

In formulating our hypotheses, we invoked two axioms which are supported in the literature. While over the course of this study we will check their validity, we chose not to make these two points the focus of our study. The two axioms and the five hypotheses that we tested follow.

The Effect of Damselfish Territoriality on the Abundance and Composition of Algal Species

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Axioms:

1. There exist differences in algal composition inside and outside damselfish territories.
2. Algal abundance is greater inside than outside territories.

Hypotheses:

1. Algal mats placed inside territories will be grazed less than algal mats placed outside territories.

Rationale: Herbivory rates inside territories are lower than rates outside due to exclusion by damselfish of other, non-territorial species.

2. Algal mats taken from inside territory and placed inside territory, and mats taken from outside territory and placed outside territory will show no significant decrease in biomass. Mats taken from outside and placed inside will also show no change. Mats taken from inside and placed outside will show a decrease in biomass.

Rationale: These predictions are further extensions of the above hypothesis, additionally taking initial algal biomasses due to mat origin into account. * (see below)

3. Algal mats from inside territories will be eaten preferentially over mats from outside territories when

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Both are placed inside other damselfish territories.

Rationale: Damselfish "farm" their algal "lawns," so the algae therin are more palatable and/or of higher nutritive value than are uncultivated algae. Damselfish will thus prefer to feed on within-territory algae. Otherwise, why would damselfish bother to defend their territories?

4. Algae taken from inside territories will be eaten preferentially over algae from outside territories when placed outside territories.

Rationale: Non-territorial fish prefer algae from inside territories because of its higher palatability and/or nutritive value. Otherwise, why would non-territorial fish bother invading territories?

5. Liagora will be eaten preferentially over Acanthophora when both are offered, both inside and outside territories.

Rationale: Based on previous studies, Liagora is more abundant inside and Acanthophora more abundant outside territories. Assuming this difference in composition is due to damselfish cultivation of Liagora and weeding of Acanthophora, it follows that Liagora is of higher palatability and/or nutritive value than Acanthophora. Liagora therefore should be preferred over Acanthophora by both damselfish and non-territorial fish, if the above reasoning is correct.

(Rationale, cont.)

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* We assumed algae ~~is~~ more abundant inside territory than outside. This second hypothesis makes predictions which would follow if overall herbivory is higher outside than inside territories. Algae taken from inside territory would be of a given cropped height and biomass due to damselfish action. This biomass per unit area should not change if placed on a (similar) damselfish territory. Algae taken from outside territory will have a second (lower) biomass per area ratio due to cropping by non-territorial fish. This ratio should not change much in another non-territory. Mats taken from outside should eventually show an overall increase in biomass in response to decreased herbivory when placed inside territory, but this increase will not be measurable in one day. On the other hand, the decrease in biomass due to increased herbivory when mats from inside territory are placed outside should be apparent after one day.

Site Description

Our experiment was run on the West Bank Reef of Discovery Bay, Jamaica, between 28/2/87 and 7/3/87. We chose Damsel fish territories within 15 meters of the reef crest so as to minimize differences between Damsel fish territories and between Damsel territories and non-territories due to factors other than territory; i.e. depth changes, salinity changes near mangrove areas and changes near the intertidal zone. All Damsel territories used in the experiment were Dusky Damsel territories and non-territories were classified as areas in which Damsel fish exhibited no territorial behavior. All territories and non-territories used in the experiment were within 0.5-1.5 meters of the surface, and ranged in size from 0.5-1.5 m².

Why choose dusky damselfish over 3D spot?

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I. Multispecific Transplants on Natural Rock Substrata:

A. Methods:

The outline for methods is as follows:

Day X-1.

- ① 6 samples of algae-covered rock from inside a Damsel fish territory and six samples from outside a territory were collected
 - ② For each of the 12 samples, we recorded
 - a - % algae cover on the rock by visual estimate
 - b - Total biomass of algal covers (= height of algal cover \times Area of cover.)
 - c - Algal biomass of each species (= Total algal biomass \times % of total algal biomass that each species percent represents)
 - d - Biomass / Unit area of algal cover.
- N.B., throughout this entire experiment, volume is used as a measure of biomass.

Day X:

③ 3 Damsel fish territories and 3 areas outside Damsel fish territories were identified.

- ④ In each of these 6 areas, one sample of algae covered rock from inside a territory and one sample from outside a territory were placed.
- ⑤ Each area was dosed for 15 minutes, and the # of bites made by fish [Damsel fish or multi-species school member] on each of the rocks recorded.

- ⑥ The areas were tagged and the samples retrieved after 6 hours.
- ⑦ Herbivory was quantified by repeating step ⑤ from day X-1.
- ⑧ Steps 1-7 were repeated for 2 subsequent trials.
- ⑨ The overall amount of algae removed from each rock was calculated as: Pre-grazing biomass - Post-grazing biomass.
- ⑩ The amount of each species of algae removed from each rock was calculated as: Pre-grazing biomass - Post-grazing, for each species of algae.

B- Analysis

① Biomass changes were standardized to the greatest initial ~~of all~~ of all biomass available on an individual rock.

② For each of the 4 treatments (see below), total algal biomass removed (the total of all changes) and total species-specific biomass removed (the total of all changes for each of the algal species) were calculated.

The four treatments were as follows:

- A rock from outside a territory placed inside a territory; beneath
"out:in"
- A rock from outside a territory placed outside a territory; beneath
"out:out"
- A rock from inside a territory placed inside a territory; beneath
"in:in"
- A rock from inside a territory placed outside a territory; beneath
"in:out"

③ To test for fish preferences, a Mann-Whitney U Test was run between total biomass removed from "out:in" and "in:in", and between total biomass removed from "in:out" and "out:out".

④ To see whether algal grazing by *Damsel fish* differed from algal grazing by mixed species schools, a Mann-Whitney U Test was run between total biomass removed from "out:in" and "out:out", and between total biomass removed from "in:in" and "in:out".

⑤ To test for effects of algal origins, a Mann-Whitney U Test was run between the average of biomass removed from "in:out" & "in:in" and the average of biomass removed from "out:in" and "out:out".

⑥ For each of the 4 treatments; "in:in", "in:out", "out:out", "out:in", an average of biomass per unit area was calculated ~~before~~ when the rocks were initially collected, and again when the ~~rocks~~ were collected after grazing experiments.

⑦ To test for changes in biomass on rocks that were placed back into ~~the same~~ environment, a t-test was run between initial biomass per unit area and final biomass per unit area for "in:in", and another for "out:out".

⑧ To test for changes in biomass on rocks that were placed into the opposite environment than that which they originated in, a t-test was run between initial

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biomass per unit area and total biomass per unit area for "in-sit", and another between initial and final biomass for "out-in".

⑨ All data for Acanthophora and Liajora from all 36 codes were standardized to the greatest amount of algae initially available in an intended code.

⑩ A Mann-Whitney U Test was run to compare decreases in biomass of all Liajora with decreases in biomass of all Acanthophora for samples placed within Danskfjord territories.

⑪ A Mann-Whitney U Test was run to compare decreases in biomass of Liajora with decreases in biomass of all Acanthophora for samples placed outside Danskfjord territories.

⑫ A Mann-Whitney U Test was run to compare decreases in biomass of all Liajora placed inside territories with decreases in biomass of all Liajora placed outside territories.

⑬ A Mann-Whitney U Test was run to compare decreases in biomass of all Acanthophora placed inside territories with decreases in biomass of all Acanthophora placed outside territories.

Monogenetic Transplants on Artificial Substrates.

A Methods:

① Lagaria was collected from inside Damselfish territories, and Hanthophora was collected from outside Damselfish territories.

② Two samples of Lagaria and 10 of Hanthophora were prepared as follows:

- An amount of algae was superfused onto a 4 cm diameter inverted petri dish to give a natural appearance and so that $\frac{1}{3}$ - $\frac{1}{2}$ of the dish was covered with algae. The latter is done to eliminate visual cues from differing amounts of algae as a factor in herbivory.

b. A secondary dip, an extended gap dip was applied onto the petri-dish.

③ After removing all of the excess water from the samples with tweezers, each sample was weighed on a Mettler balance to determine initial total weight.

④ 6 Damselfish territories and 6 non-territories were identified, and into each, one sample of Hanthophora and one of Lagaria were placed.

⑤ Each area was observed for 10 minutes and # of bites [by either a Damselfish or a non-spawned adult member] made on each sample recorded.

⑥ Areas were bagged and samples retrieved after 6 hours.

⑦ Samples were dried and reweighed on Mettler balance to determine final total weight.

⑧ Water was scraped from petri-dish and weighed, for each sample to determine amount of water.

⑨ For each sample, weight change of the algae was calculated as: Initial Wt [Ngt] - Final Wt [Ngf].

⑩ For each sample, initial weight of algae sample + weight change of algae was calculated as: Wt. Change of Ngf Sample + weight of the algae scraped from the petri-dish.

B Analysis:

① All algal weight changes were standardized to the greatest amount of algae initially available on an individual scale.

② To test for fish preference, a ~~t-test~~ Mann-Whitney U Test was run between weight change in Lagaria and weight change in Hanthophora for samples placed inside a territory; and another Mann-Whitney U Test between weight change in Lagaria and Hanthophora for samples placed inside outside a territory.

③ To test for different behavior rates inside a territory versus outside a territory, a Mann-Whitney U Test was run between weight changes inside a territory and weight

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changes outside a territory for Lagopus, and a Mann-Whitney U Test was run between weight changes inside a territory and weight changes outside a territory for Neothophaea.

Results

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In preparing this study we began by accepting the previously supported axioms that algae would be more abundant inside damselfish territories than outside and that there would be a corresponding difference in composition of algal mats inside and outside territories. Our own data supported these suppositions. The total calculated algal biomass of rocks collected inside territories was 2311.6 cm^3 while that from outside territories was 1040.8 cm^3 . We showed that there was more algae per area of rock on those from inside territories than on those from outside (Table 1: t test, $0.001 < p < 0.01$) conclusively supporting the axiom.

Significance tests were not conducted on the species composition of algal mats inside and outside territories.

Species richness was similar; 11 species were present in the inside samples, 13 in the outside samples. Although Liaogora and Coleothrix comprised much of each sample, the abundances of other algae varied greatly, accounting for differences between algal mats inside and outside territories.

The study also relies on previous data collected from the West Back Reef that suggested Cosgora was more abundant inside territories than out, while Acanthophora was conversely more abundant outside. In our samples both Liaogora and Acanthophora were more frequent and abundant inside territories. When values were standardized to correct for differences in total biomass of the samples, values were more similar.

Data collected from all manipulated rocks was accumulated and summed in tables 7-10. When comparisons were made between algae from different treatments values were standardized to the greatest available biomass of any individual sample before exposure to herbivory.

We divided change in biomass of one algal sample by the amount of algae available before exposure to fish. We then multiplied by the greatest value of biomass before herbivory of any individual in the same treatment.

Overall grazing inside and outside territories:

The hypothesis that rocks placed outside territories would be more grazed than those placed inside was partially supported. Algal-covered rocks placed outside territories were bitten a significantly greater number of times while observed than those placed inside, regardless of origin (Table 2: Mann-Whitney U test; $p < 0.001$). Additionally rocks placed outside territories experienced a greater decrease in % cover than those placed inside territories (Table 3: Mann-Whitney U test $0.01 < p < 0.025$). There was, however, no significant difference in the decrease in biomass of rocks placed in territories as opposed to those placed outside territories (Table 4). Thus the hypothesis was not conclusively supported. Although non-territorial fish were seen grazing more on the rocks placed outside territories than did damselfish inside they did not reduce the biomass a significantly greater amount than did damselfish. [Most likely, non-territorial fish were able to enter territories and graze rocks there also.] It is also possible that the biomass data was only confounded, as well as explained below.

Individual treatment comparisons

Of the four transplants that we performed on algal covered rocks, none was shown to undergo a significant reduction in biomass per area (Table 1). We had only expected to see a significant change in the rocks collected from inside damselfish territories and placed outside. This treatment received average grazing, losing a mean

~~or inside or outside~~ of $118 \pm 76.7 \text{ cm}^3$ during the experiment. Rocks from outside placed outside were the most grazed, losing an average of $143.2 \pm 54.5 \text{ cm}^3$ biomass.

Fish did not graze any one treatment of biomass significantly more than any of the others. The only significant in the decreases of biomass data suggests that schooling fish prefer outside algal composition more than damselfish (Table 4 Mann-Whitney U test $0.025 < p < 0.05$). They consumed more biomass from outside rocks than did damselfish.

Preference for algae from damselfish territories:

The hypothesis is that both damselfish and non-territorial fish would prefer the algal composition from inside territories received mixed support. Biomass of rocks from territories was not reduced significantly inside or outside territories (Table 4). Nor was the % cover of rocks from inside herbivored more. Origin testing:

Comparing rocks from ~~inside~~ from outside regardless of placement never showed a significant difference in any tests (Tables 2, 3 and 4).

Non-territorial fish did demonstrate a slight preference for rocks from inside territories when presented with a choice between rocks from inside and outside. They bit the inside rocks a significantly (marginal) greater number of times (Table 2: Mann Whitney U test $0.05 < p < 0.1$) than they did the outside rocks. Damselfish were not shown to do this independently, but the significance was present when their data was compiled with that of non-territorial fishes.

Although the values were insignificant, there were trends in the biomass decrease and percent cover decrease data that suggest a preference for algae from inside territories. Damselfish reduced rocks from other damselfish territories

116.8 ± 80.9 cm while they reduced rocks from outside 87.8 ± 46.1 cm (Table 4). They reduced the % cover of rocks from inside $6.1 \pm 8.2\%$ and of those from outside $2.8 \pm 4.4\%$. Non-territorial fish reduced rocks from inside $12.8 \pm 17\%$ and rocks from outside $37 \pm 5.2\%$ (Table 3).

~~Non territorial fish results probably are not reliable because they did not exhibit any preference for rocks placed inside territories as it was not a preferred food. It may simply be that the water between two territories inside that attracts schooling fish to feed there. When rocks were placed side by side with each other they exhibited no preference.~~

Preference for Liagora over Acanthophora:

The hypothesis that all fish would prefer Liagora - an algae shown to be more abundant inside territories - over Acanthophora - an algae with a greater abundance outside territories was tested both directly, through observation, and indirectly, from the data provided by the algal rock transplantation experiment. Both methods demonstrated conflicting results in regard to damselfish preference for Liagora.

indicated in red on tables 5 and 6 The data, unfortunately, is marred by negative decreases that had to be included in order to obtain a sample size sufficient for statistical analysis. These increases in biomass were due to inconsistencies in our estimations of percent cover and areas of rocks, confounding individual algal biomasses before and after herbivory. Slight positive changes in biomass suggest the algae wasn't grazed. When an alga was shown to increase its biomass more than 50% the data was removed as noise.

In the petri dish experiment (Table 5) Liagora was untouched by damselfish (resulting in a slightly positive increase in biomass). They did graze the Acanthophora on

average of $0.18 \pm 0.19 \text{ cm}^3$ during the six hours. These values suggest a significant preference of damsel/fish for Acanthophora (Table 6: Mann Whitney U-test $0.025 < p < 0.05$).

Biomass changes for Lugora and Acanthophora were extracted from the data of the rock transplantation experiment and established as Table 6. This data suggests that damselfish prefer Lugora over Acanthophora (Table 6: Mann Whitney U-test $0.05 < p < 0.10$ marginally significant).

This supports the hypothesis that damselfish prefer ~~the perhaps more palatable algae than expected~~ the inside algae which is perhaps more palatable or has a higher nutritive value. Sample size of this data is greater and there is a lower proportion of extraneous negative decrease values than in the petri dish experiment. Nonetheless, from the results it would be difficult to conclude that Lugora was the preferred food. Non-territorial fish demonstrated no preference in either test.

Table 1:

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Comparisons of Biomass per Area Ratios of Manipulated Algal Rocks from All Four Treatments

(17)

	<u>$m \rightarrow m$</u>	<u>$out \rightarrow in$</u>		<u>$m \rightarrow out$</u>		<u>$out \rightarrow out$</u>		
	<u>Before</u>	<u>After</u>	<u>Before</u>	<u>After</u>	<u>Before</u>	<u>After</u>	<u>Before</u>	<u>After</u>
1.25	0.80	0.42	1.00	3.00	3.00	0.73	0.38	
2.22	2.20	0.38	1.00	2.06	2.44	1.00	0.70	
1.12	0.68	0.50	2.20	2.14	2.33	2.30	1.87	
2.70	1.50	1.00	1.00	2.51	2.09	1.13	0.45	
2.07	1.59	0.67	0.88	1.97	1.47	0.99	0.65	
1.00	1.00	1.00	0.80	1.60	0.79	3.00	2.00	
4.50	4.50	1.71	1.29	2.00	2.00	1.00	0.78	
1.00	1.00	1.00	1.00	4.00	3.00	<u>1.50</u>	<u>1.50</u>	
<u>1.94</u>	<u>3.50</u>	<u>1.00</u>	<u>1.00</u>	<u>1.92</u>	<u>1.67</u>			
$\bar{x} = 1.98 \pm 1.13$	1.86 ± 1.32	0.85 ± 0.42	1.35 ± 0.42	2.36 ± 0.73	2.01 ± 0.72	1.46 ± 0.79	1.09 ± 0.52	

Combined from outs ratio before: 1.14 ± 0.68 after: 1.09 ± 0.52 Combined from ms ratio before: 2.17 ± 0.94 after: 1.98 ± 1.04

T-tests comparing all ratios before and after:

 $m \rightarrow m$: $t = 0.21$ $v = 16$ N.S. $out \rightarrow in$: $t = -1.41$ $v = 16$ N.S. $m \rightarrow out$: $t = 0.79$ $v = 16$ N.S. $out \rightarrow out$: $t = 1.11$ $v = 14$ N.S.Combined from outs: $t = 0.56$ $v = 32$ N.S.Combined from ms: $t = 0.58$ $v = 34$ N.S.Combined placed out ratio before: 1.93 ± 0.87 $n = 17$ Combined placed in ratio before: 1.42 ± 1.01 $n = 18$

Combined from outs before vs combined from ms before:

 $t = 3.73$ $v = 33$ $0.001 < p < 0.01$

Combined placed out before vs combined placed in before:

 $t = 1.60$ $v = 33$ N.S.

Table 2:

Comparisons of Numbers of Bites Counted on Manipulated Alegal
Rocks During 15 Minutes Observation

(18)

inside territories			
rocks from inside	rocks from outside	rocks from inside	rocks from outside
0	0	6	0
0	0	7	1
0	0	20	10
1	0	53	16
7	0.	60	20
10	2	70	24
13	4	85	50
20	5	120	66
22	<u>16</u>	<u>370</u>	<u>75</u>
$\bar{x}=8.1 \pm 8.7$	3 ± 5.2	87.9 ± 112.2	29.1 ± 27.8

Mann-Whitney U-tests (comparisons of #s of bites) $n_1, n_2 = 9$

Comparison of rocks from inside vs rocks from outside placed inside territories
 $U=48.5$ N.S.

Comparison of rocks from inside vs rocks from outside placed outside territories
 $U=57.5$ $0.05 < p < 0.10$

Comparison of rocks from inside territories placed inside vs placed outside terrs.
 $U=70.0$ $0.005 < p < 0.01$

Comparison of rocks from outside territories placed inside vs placed outside terrs.
 $U=67.0$ $0.01 < p < 0.025$

Comparison of combined rocks from inside vs rocks from outside
regardless of placement

$U=203.5$ N.S.

Comparison of combined rocks placed inside vs placed outside regardless of origin
 $U=275$ $p < 0.001$

Table 3:

Decreases in % Cover of Manipulated Algal Rocks

(19)

Put inside Territories	Put outside Territories	Both inside Territories	Both outside Territories
Rocks from inside	Rocks from outside	Rocks from inside	Rocks from outside
0	0	0	0
0	0	0	0
0	0	0	0
0	0	5	0
5	0	5	5
5	0	10	5
10	5	15	5
10	10	30	<u>15</u>
<u>25</u>	<u>10</u>	<u>50</u>	
$\bar{x} = 61 \pm 8.2$	28 ± 4.4	12.8 ± 7.0	5.7 ± 5.2

Mann Whitney U tests comparing decreases in % cover:

Comparison of rocks from inside to from outside, ^{placed} inside terrs.
 $U=42$ N.S. $n_1, n_2 = 9$ Comparison of rocks from inside to from outside, ^{placed} outside terrs.
 $U=41$ N.S. $n_1 = 9, n_2 = 8$ Comparison of rocks from inside, ^{placed} inside and outside terrs
 $U=41$ N.S. $n_1, n_2 = 9$ Comparison of rocks from outside placed inside and placed outside terrs.
 $U=42$ N.S. $n_1 = 9, n_2 = 8$ Comparison of combined rocks from inside and from outside regardless of where placed
 $U=156.5$ N.S. $n_1 = 18, n_2 = 17$ Comparison of combined rocks placed inside and outside territories regardless of origin
 $U=215.5$ $0.01 < p < 0.025$ $n_1 = 18, n_2 = 17$

Table 4:

Comparisons of Decreases in Total Algal Biomass
of Manipulated Algal Rocks (Standardized to 336 Before) (20)

Rocks Placed Inside		Rocks Placed Outside	
Rocks from Inside	Rocks from outside	Rocks from inside	Rocks from outside
0	28.2	0	63.1
40.3	39.7	40.3	100.8
64.9	64.6	88.4	105
66.6	67.2	89.5	118.4
131.9	83.8	98.9	156
140	100.8	138	186.1
150	105.6	158.5	205.1
209.2	120	207.2	<u>211.5</u>
<u>248.1</u>	<u>180.8</u>	<u>240.9</u>	
$\bar{x} = 116.8 \pm 80.9$	87.8 ± 46.1	118.0 ± 76.7	143.2 ± 54.5

* Comparison of rocks from inside vs rocks from outside placed inside terrs.
 $U=50$ NS $n_1, n_2 = 9$

Comparison of rocks from inside vs rocks from outside placed outside terrs.
 $U=45$ NS $n_1 = 9$ $n_2 = 8$

Comparison of rocks from inside territories placed inside vs placed outside terrs.
 $U=41$ NS $n_1, n_2 = 9$

Comparison of rocks from outside territories placed inside vs placed outside terrs.
 $U=55.5$ $0.025 < p < 0.05$ $n_1 = 9$ $n_2 = 8$

Comparison of combined rocks from inside vs combined rocks from outside regardless of placement
 $U=157$ NS $n_1 = 18$ $n_2 = 17$

* All are Mann-Whitney U-tests comparing total algal biomass decreases from individual rocks of each type.

Comparison of combined rocks placed inside vs rocks placed outside regardless of origin
 $U=190.5$ $n_1 = 18$ $n_2 = 17$ N.S.

Table 5:

Comparisons of Decreases in Biomass of Algae Stocked
Petri Dish Samples (Standardized to 0.66 Before)

(21)

Acanthophora		Lagora	
placed inside	placed outside	placed inside	placed outside
0.07	0.06	0.13	0.10
0.07	0.13	0.07	0.07
0.10	0.17	0.02	0.10
0.14	0.20	0.03	0.49
<u>0.51</u>	<u>0.53</u>	<u>0.11</u>	<u>0.59</u>
$\bar{x} = 0.18 \pm 0.19$	0.22 ± 0.18	0.02 ± 0.09	0.23 ± 0.30

Mann-Whitney U tests comparing decreases in algae biomass
from petri dishes: $n_1, n_2 = 5$

Comparison of Acanthophora and Lagora placed inside territories.
 $U=22$ $0.025 < p < 0.05$

Comparison of Acanthophora and Lagora placed outside territories
 $U=14$ N.S.

Comparison of Acanthophora placed inside and outside territories
 $U=16$ N.S.

Comparison of Lagora placed inside and outside territories
 $U=19$ N.S.

Table 6:

(22)

Comparisons of Decreases in Biomasses of Acanthophora
and Liagora on Manipulated Algal Rocks (Standardized to 20.6 Before)

Liagora

$m \rightarrow m$	$out \rightarrow m$	$m \rightarrow out$	$out \rightarrow out$
164.7	80.6	20.6	73.9
92.9	73.0	127.4	122.4
160.8	148.6	147.8	122.9
43.9	8.1	103.3	<u>46.1</u>
18.7	<u>90.6</u>	0	
109.1		117	
<u>163.4</u>		<u>162.1</u>	

Acanthophora

$m \rightarrow m$	$out \rightarrow m$	$m \rightarrow out$	$out \rightarrow out$
68.5	<u>23.2</u>	96.6	146.4
43.1		113.8	74.6
21		11.6	<u>158.5</u>
80.6		46.9	
24.3		<u>173.4</u>	
<u>0</u>			

$$\bar{x} = 102.3 \pm 69.8 \quad 80.2 \pm 50.1 \quad 122.7 \pm 63.1 \quad 91.3 \pm 37.9 \quad 18.2 \pm 49.2 \quad 23.2 \quad 88.5 \pm 62.4 \quad 126.5 \pm 45.4$$

Mann-Whitney U-tests:

Decreases in biomass of all Liagora compared to decreases in biomass of all Acanthophora placed within Damselfish territories ($m \rightarrow m$ and $out \rightarrow m$ combined: columns 1+2 vs 5+6)

$$U=59.5 \quad 0.05 < p < 0.10 \quad n_1=12 \quad n_2=7$$

Decreases in biomass of all Liagora compared to decreases in biomass of all Acanthophora placed outside Damselfish territories ($m \rightarrow out$ and $out \rightarrow out$ combined: columns 3+4 vs 7+8)

$$U=49 \quad \text{N.S.} \quad n_1=11 \quad n_2=8$$

Decreases in biomass of all Liagora placed inside territories compared to all that placed outside ($m \rightarrow m$ and $out \rightarrow m$ combined, $m \rightarrow out$ and $out \rightarrow out$ combined: columns 1+2 vs 3+4)

$$U=77 \quad \text{N.S.} \quad n_1=12 \quad n_2=11$$

Decreases in biomass of all Acanthophora placed inside territories compared to all placed outside ($m \rightarrow m$ and $out \rightarrow m$ combined, $m \rightarrow out$ + $out \rightarrow out$ combined: columns 5+6 vs 7+8)

$$U=48 \quad 0.01 < p < 0.025 \quad n_1=8 \quad n_2=7$$

Table 7: Summary of Rocks from Inside Placed Inside

Table 8: Summary of Rocks from Inside Placed Outside

Table 9: Summary of Rocks from Outside Placed Inside

Table 10: Summary of Rocks from Outside Glacial Outside.

Discussion:

SCW/EC+CM

In terms of the 2 axioms that algal abundance will be higher inside a territory and that species composition will be different inside a territory than outside, both were supported either by statistical tests or observations.

The first hypothesis that algal mats placed inside territories will be grazed less than algal mats placed outside territories was not conclusively supported. While bites per minute data and % cover data suggested the hypothesis, decreases in biomass data did not. As an explanation of this contradiction, it is possible that errors of changes in biomass and % cover were highly imprecise due to inconsistencies in our estimations of % cover and areas of each confounding individual algal biomass before and after herbivory. It is also possible that mixed species schools were able to enter territories quite successfully during the course of our experiment, thus reducing biomasses inside and outside of territories by equivalent amounts.

In the second hypothesis, not examining the reduction in biomass of the four treatments: "in" "in/out" "out/in" and "out/out", we expected significant biomass reduction in only one treatment: "in/out". However, no change in any treatment ~~was observed~~ was observed because biomass loss did not decrease significantly for any treatment. Thus, even if they had existed, no trends could have been seen. This suggests that we did not leave the samples out in the field long enough to observe any significant biomass decreases; and that samples should be left out for longer periods in order to observe biomass reductions in future studies. An interesting finding that came up while investigating this second hypothesis was that non-territorial fish prefer algal mats originating outside territories more than territorial do. This could be due to the fact that each type of fish is more used to and thus more willing to eat algae originating in its respective habitat. This finding also lends support to the idea that plantability conditions alone are not different between territories and non-territories.

In regard to the third and fourth hypotheses, preference for algae from inside territories was not conclusively suggested. Although bites/min results suggested the idea, only insignificant trends were present in the biomass changes. One explanation for this is that, as with the first hypothesis, errors of change in biomass and % cover were highly imprecise due to inconsistencies in our estimations of % cover and areas of each confounding individual algal biomass before and after herbivory. Another explanation is that it was wrong to

assume higher nutritive value and palatability of deer originating inside Dausset's territories. The *Red Fox* reacted to the Dausset's territory sinks because of the higher biomass areas inside these territories; which makes their foraging more efficient, seeing that they do not have to expend energy to move very far while feeding on a dense patch. However, if the inside and outside of territories are placed side by side, as they were in our experiment, the *Red Fox* can move between the two sinks without significantly increasing his net energy expenditure and thus can forage on the two sinks as if they were one, removing equal biomass from each. This equal biomass removed from the 2 sinks would have resulted in the insignificant biomass change that we found.

In examining preference for Lingua over Acanthophora, the petridish transplants and the rock transplants produced contrasting results. While the petri-dish transplants revealed that Acanthophora was preferred over Lingua by Damarfjord, the rock transplants showed that Damarfjord prefers Lingua over Acanthophora. These differences may have been due to migratory movements concerning individual shellfishes before and after testing, yet the rock transplants and to the artificial nature of the petri-dish and superflue methods in the petri-dish transplants. This, for those reasons, we are unable to conclude that either species is preferred over the other. The fact that non-territorial Sit exhibited no preference in either case can possibly be explained by the fact that the gill-disks were much smaller in comparison to the non-territorial Sit in the territories, and thus non-preference may simply have been due to the gill-disks not being visually isolated, or presented as good sources in the large non-territories.

Some of the reasons why our data do not support our hypotheses are as follows:

- D-W may have allowed insufficient time for each experiment to end, not exposing the algae to darkness long enough to observe any substantial decreases in biomass. However, initially, we did not want to leave the samples out overnight because Daphnia do not hunt at night and thus other organisms would have grazed on the samples placed inside the tanks/tubs, skewing the results.

- 2) - The coast of Discovery Bay has been under intense fishing pressure for many years, and as a result is considered to be fished out, biologically.

overall low fish populations. In addition, the recent Diadema die-off in '83 drastically reduced the Diadema numbers. As a result, it is quite possible that resources have become more abundant as the number of herbivores has decreased. With fewer herbivores the overall biomass ~~was~~ removed over time has decreased, and as a result the chance that the samples that we placed outside territories will be consumed is lower. The ^{lower chance for feeding} samples may be live for Damselfish territories if Damselfish have expanded the size of their territories as resources have become abundant. Thus, on the basis of these differences between a normal reef community and the reef community at Discovery Bay, comparisons of relative herbivory patterns may not be valid between these two sites.

3)- Attraction to the rocks and petri-dishes, in terms of the fact that fish may have been wary of the novel presence of algae and took interactions with what naturally present, may have resulted in lower biomass reductions than expected. Thus, it is quite possible that the introduced algae was grazed at a lower rate than the algae naturally grazed in the area.

4)- In precise biomass measurements may have confused individual algal biomasses before and after herbivory. This error was observed as algal biomasses that apparently increased after herbivory.

As methodologies for future studies are planned, future researchers should keep these sources of error and uncertainty in mind.

Future research could well focus on differential herbivory on individual algal species to a greater extent, and avoid generalizing between normal reef communities and those such as Discovery Bay that exhibit untested, unique and low populations. Future research will also examine herbivory rates of Damselfish species other than Dusty Damselfish on algae placed inside territories, and should attempt to find a more consistent, accurate measure of biomass.

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E.C.

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