

SPATIAL DISTRIBUTION OF 3 DAMSELFISH SPECIES

IN DISCOVERY BAY JAMAICA

Todd:
Good hypotheses,
organization, and
discussion. Data presentation
is a bit weak. Some tables + figures
are not clear, and you could have
included more observations (e.g. your
maps). Statistical analyses should have been
reported more fully; for each test conducted
you should give pertinent information --
G-value, df, P-value, etc. Writing/spelling
is a bit sloppy.

John

Todd Morrill

3/5/81

Abstract

The spatial distribution of five species of damselfish (Pomacentridae) are investigated. Eupomacentrus leucostictus, E. fuscus, E. planifrons, E. partitus, and Microspathodon chrysurus^{are} all territorial.
^
Two sampling methods were used: transects along the reef at a given depth, and maps of territories, ~~to~~ test four hypotheses. Species were found to replace each other as depth increased. The transect method was found to be a very poor method of sampling to determine territory size and density. Indications were found that the damsels are partitioning space by "specializing" on a particular substrate type. No intraspecific clumping was found on maps ^{of} ~~of~~ areas containing more than one species. The problems with the sampling methods ^{are} ~~is~~ discussed. Some speculations are made as to mechanisms and causes of species distribution changes after Hurricane Allan.

Introduction

Tropical ecosystems are known for their extremely high diversity, and among them, the coral reef is perhaps the most diverse. The high diversity occurs over several phyla, but perhaps the group most obviously diverse to the casual observer is the fishes. At One Tree Reef in the Great Barrier Reef, over 800 species of fishes have been observed (Talbot, Russell, and Anderson 1978). The Caribbean Sea is somewhat less species-rich, but still Randall's Caribbean Reef Fishes lists over 300 "common" species.

The question of how such high species diversity arose and is maintained has been under investigation in the terrestrial tropics for some time, but the seemingly related question of reef diversity has only recently been studied. Fish have sometimes been compared to birds in their role in their ecosystem; at first, the theories applied to bird diversity were applied to fishes. Specialization of fish species was suggested. In fact, there are some extreme specialists among the fish. For example, several species of goby are found only as inquiline mutualists in sponges (Sale 1978). Other fish may specialize by food particle size (Clarke 1977), and still others partition habitat space (Gosline 1965, Key 1973, Hobson 1974, Emery 1973, all in Clarke 1977; Brock, Lewis, and Wass 1979). But further investigation showed

that the majority of species were no^t specialists, or at least
were able to coexist with several species with very similar niches
(Sale 1977, Talbot et al. 1978, Clarke 1977, Luckhurst and Luckhurst,
1978). The bird analogy falls through for most fishes. Many
of the theories popular in terrestrial ecology fail when applied to
coral reefs, despite the seeming similarity of the two systems.

In place of specialization rose a theory of disturbance and
non-equilibrium. It became increasingly evident that coral reef
fish species diversity is maintained by frequent unpredictable
small scale disturbances, relatively short residence times for
individual fish, and random replacement and colonization of open
spaces (Connell 1978, Sale 1977, Sale 1979, Sale 1980, and many
others). The lottery theory as it has come to be called (Sale
1979), assumes that the species present are in constant flux with
locally extinct species. When an adult is removed from the system,
a juvenile more or less randomly selected from the planktonic
larval pool will fill the space. Predation is thought to play a
major role in opening niches for such colonization.

A large part of the support for the lottery theory has come
from work done on damselfish, the family Pomacentridae. The
genus Eupomacentrus (or Pomacentrus, depending on the source)
is a favorite subject because it has member species on reefs
around the world. Its members tend to be very common, highly visible,
territorial reef fish. Species closely related ecologically

often coexist, making comparison studies easy and relevant.

Why then another such study? Researchers with considerably more expertise, time, and equipment than I have published carefully thought-out, statistically sophisticated long-term studies. However, I feel that the published (and DFSP) papers have avoided or overlooked several aspects of Eupomacentrid territory distributions and behavior.

It has been shown that once a territory has been colonized, its resident is very rarely ejected by a competitor (Sale 1979). Furthermore, residents don't tend to relocate, but rather live out their (often short) lives in place (Reese 1973, Dale pers. comm. in Clarke 1977). The only exception to this is if a particularly rich territory opens up nearby (Itzkowitz 1979). Yet despite all this, several sources have noted clumping of damselfish species. Clarke (1977) observed that Beaugregories (Eupomacentrus leucostictus) tended to hold territories in shallow water. He was unable to distinguish between several possible mechanisms: that this was E. leucostictus' preferred habitat, that they had been excluded from other habitats by specialists, or that they had been out-competed elsewhere by diffuse competition. Itzkowitz (1974) noted unspecific blocks of Dusky (Eupomacentrus fuscus) and Threespot (Eupomacentrus planifrons) damselfish, but offers no explanation for these clumpings, other than

that a block may be easier to defend. He also writes that Dusks are more common than Threespots, and both more common than Beau-gregories. Bicolor damselfish (Eupomacentrus partitus) follow a distant fourth. How is this pattern maintained, and how did it originate? So little is known of the egg production, hatching rates, and larval survivorship of reef fish that a researcher with the resources that I have can only look for the answers elsewhere.

Clumping

But the most interesting questions have been raised by DFSP papers, which not only concern Discovery Bay, but also tend to include more peripheral observations than published papers.

Dussourd (1979) writes that E. leucostictus occurs mainly in the lagoon area, E. fuscus in the back reef area, and E. planifrons in the Acropora palmata zone of the fore reef. He too notices clumping by species, and adds that E. planifrons seems to prefer habitats with vertical relief. In contrast, Luckhurst and Luckhurst (1978) found no such correlations of species with habitats.

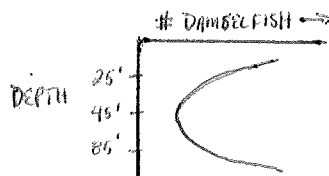
Besides that few^{of the} researchers have reported clumping, there seem to be several reasons to predict a nonclumped distribution. First, many damselfish are more agonistic toward conspecifics than toward other species (Myrberg 1974, Tlbot^a et al. 1978, Curry 1979).

This should tend to cause conspecifics to "spread out", away from established territories. Similarly, Ebersole (1977) has found a correlation between diet similarity and aggressive behavior; Beaugregories started threat displays and made active attacks at a greater distance against fish species that prefer the same algae as food. Social facilitation of colonization has yet to be shown an important factor in reef species makeup, although one study has suggested it (Talbot et al. 1978).

Space

Space partitioning patterns and mechanisms are often somewhat overlooked like clumping is. The Beaugregories are in the shallows, but how they got there isn't investigated. Baldwin and Carlsen (1980) describe several Eupomacentrid spatial patterns, but don't go into the mechanisms very deeply. They suggest a change in damselfish numbers with depth, described in figure 1.

FIGURE 1: Baldwin and Carlsen
model of damselfish numbers
as a function of depth



Carlsen, in unpublished data, found that E. planifrons was most common at 45 feet in the Acropora cervicornus zone, and decreased below that depth. He also observed that E. partitus was most successful in terms of numbers of individuals and algal mat composition at 85 feet. He makes no mention of either the Dusky damsel or the Beaugregory. Baldwin and Carlsen found that

generally, the mats held by damselfish decreased in quality with depth. This implies that the territories and mats should get bigger with depth, and therefore the density of fish should decrease. A question ^{that} arises is what are the Threespot damsels doing now that their preferred A. cervicornis regions have been destroyed by the hurricane?

In a DESP project report written ~~in~~ in 1979, Curry reports that Beaugregories are found in shallow water, Dusksies in deep water, and the back reef is ~~an~~ area where the two overlap. He also notes that Dusksies are found on Montastrea annularis heads, Threespots on A. cervicornis patches, and Beaugregories on flat coral rubble.

Hypotheses

I had four hypotheses ^{to} test in this study

- 1) Are the damsel fish partitioning a limiting resource substrate for territories, by depth? This is stated as a null hypothesis: the species composition at all depths is equivalent.
- 2) Is there a change in territory size or density of territories with depth?
- 3) Do the species of damsels partition the substrate in other ways?
- 4) Is there clumping of individuals in a species when in a multispecific group? The null hypothesis is that

in a multispecific group of territories, the individuals of a given species are randomly dispersed.

Methods

I collected data using two methods, a series of transects at given depths along the reef and at selected points in the bay, and ^Several sketch maps of coral configurations and damselfish territories at selected depths. All data were collected at Discovery Bay, Jamaica, although observations were made at the Rio Bueno and Pear Tree Bottom reefs. I used the Discovery Bay Marine Lab equipment and facilities throughout the study, as sponsored by Dartmouth College.

I sampled depths of one, four, 10, 15, and 20 meters by transect. Each transect was 18 meters long; a rope was stretched between coral projections to measure the distance. I sampled at least five transects at every depth, taking care to avoid passing over a spot more than once. I found that five ^was the most I could do on one tank of air at 20 meters. After the rope was stretched, I swam slowly along the transect, counting damselfish territories that were crossed by the rope. Each transect took about five minutes. The species of the residents, and major substrate features (such as corals, shapes, species, and predominant algae) I noted on a piece of roughened plexiglass with a pencil. Five resident damselfish were of interest: the Banggai, Dark, Threespot, Bicolor, and Yellowtail damselfish.

I used SCUBA for the 10, 15, and 20 meter transects, and skin-diving gear for the remaining samples. The data were transferred to a notebook kept in the library after each dive or snorkle.

Heavy seas and limited boat time prevented me from taking all the transects on the west fore^e reef. I had planned to sample from only the fore reef to reduce between-site variability in uncontrolled factors, for example siltation and disturbance levels. Instead, the one meter transects were performed on the west back reef, the four meter transects on the east back reef, and the deeper transects at LTS on the west fore reef.

Because there^e was some question as to how reproduceable my fish counts were, I took transects on the west back reef exactly duplicating those taken several days earlier. I found very little variation in the numbers and species of fish I found in the two transect sets and therefore decided the sam^{am}pling method was legitimate. However, only Beaugregories and Threespots lived along the test transects; these are the most aggressive of the damselfish, and hard to miss. Whether or not counts of the much shyer Dusky, Yellowtail, and Bicolor damselfish are as reproduceable is open to some debate. I made every effort to find the fish if they were there, but some may have slipped my notice.

My second sampling technique involved drawing maps of several adjacent damselfish territories. I mapped area in each of

the three areas in which I took transects. The transects and mapped areas probably did not overlap. The site to be mapped was effectively chosen at random; I followed my dive buddy to where he wanted to work. Since I buddied with people doing projects on schooling fish, sea urchins, nudibranchs, and anemones, it seems unlikely that any pattern should have developed. The randomness of my sample is important in assessing clumping of territories.

The major coral formations formed the background for each sketch. Next the territories of individual damselfish were carefully drawn in. I took special care to draw and note which fish were neighbors, that is, defended a common boundary. Territories separated by a coral ridge, so that the residents did not interact were not counted as neighboring. I took notes on the substrate of territory. I started with seven classifications of this substrate (flat, rough, open staghorn rubble, closed staghorn rubble, elkhorn, Montastrea, and Poritäs), but reduced it to four (flat, head corals, staghorn, vertical). A typical drawing of 20 territories took about an hour of observation time to complete.

Statistical analysis of the data was accomplished with large transfusions of aid from Jeff Foster, Chuck Levitan, and John Gilbert. Sokal and Rohlf helped out, too.

To determine whether or not the number of damselfish changed with depth in the transect data, I used a Student-Neumann-Keuls

Range test for variance among means. Although the theory that fish numbers would change was an a priori one, I failed to see that the Range test is an a posteriori test until well past my bedtime. Since a posteriori tests tend to be more stringent, any significance detected in the data would have certainly shown up if the more proper ANOVA test had been used. Regardless of absolute numbers, species contributions to the total number of fish may have changed with depth. This was tested ^with a log-transform G-test of frequency. The number of fish at each depth was plotted and a line fit using linear regression techniques.

I used a Mann-Whitney U-test to test the difference between actual and expected numbers of conspecific neighbors (CSN) from the map data. The sum to total number of neighbors that the individuals of a species had were counted. In figure 2 this equal to 12 (3+3+5+1). Next, the actual number of CSN within that species were counted (8 in figure 2). Finally, the expected number of CSN was calculated from:

$$\text{Expected CSN} = \left(\frac{\# \text{ individ. within your species} - 1}{\text{total \# fish on the map} - 1} \right) (\text{total \# neighbors})$$

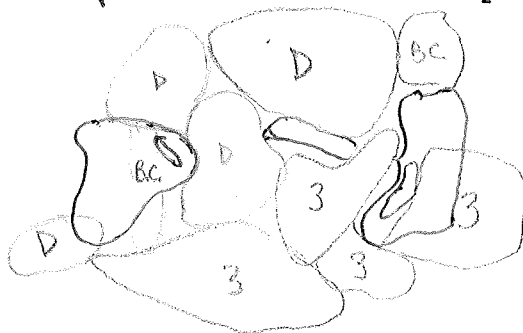


FIGURE 2 : Example map, simplified.
Pencil lines are territory boundaries.
Ink is coral heads.

	# INDIV	# NEIGHBORS	# CSN
SPOTS :	4	12	8
DUSKIES :	4	11	6

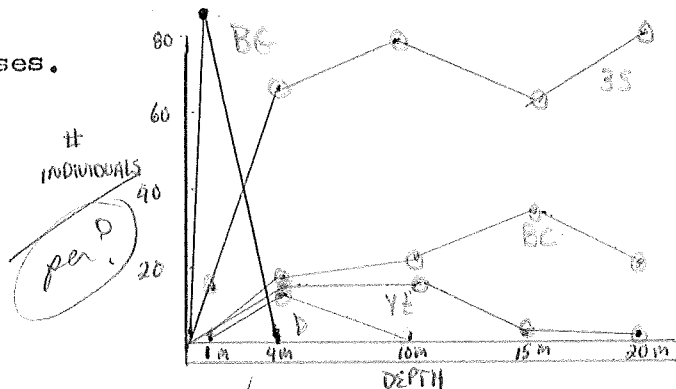
etc
 Expected CSN for SPOTS = $\left(\frac{4-1}{10-1} \right) (12) = 4$
 A > E, suggests clumping

Results

Transects

The data collected using the transect method show that there is a change in species composition of the Pomacentrids studied with a change in depth. The entire data set can be seen in Appendix I; figure 3 shows the change in absolute numbers of each species as depth increases.

FIGURE 3: NUMBERS OF INDIVIDUALS OF A SPECIES AT A DEPTH; GRAPH OF # VS DEPTH



I performed a Student-Neumann-Keuls Range Test to see if the means of numbers of individuals for a given species were significantly different at different depths. The results of this test are displayed diagrammatically in figure 4. The null hypothesis that species abundance are the same at all depths was disproven at the level $p < .05$.

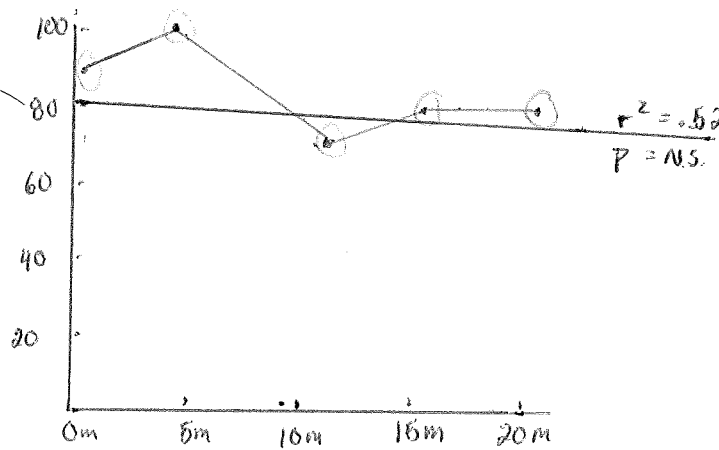
<u>Eupomacentrus leucostictus</u>	(6) 1 > 4 10 15 20 (5)	$p < .05$
<u>Eupomacentrus fuscus</u>	(5) 4 < 1 10 15 20 (6)	$p < .05$
<u>Microspathodon chrysurus</u>	(8) 20 1 15 < 4 < 10 (6)	$p < .05$
<u>Eupomacentrus partitus</u>	(6) 1 10 20 4 15 (5)	$p < .05$
<u>Eupomacentrus planifrons</u>	(5) 1 < 4 < 10 20 15 (6)	$p < .05$

FIGURE 4: Diagrammatic representation of S-N-K Range test. Note changing direction of greatest value to smallest as one goes down the list (clerical error)

Often in a data set like the one collected, there will be a large difference between the shape of a graph of absolute numbers, and one of relative numbers (abundance). To test this possibility, I used a log transformed G-test of frequency. Somewhat to my surprise, the results of this test closely paralleled those found using the Range test. That is, relative abundance and absolute numbers of fish changed in a similar manner. The only significant difference between results of the two tests I found was for mean numbers of Threespot damselfish at 15 and 20 meters. The Range test had showed no significant difference between these means, whereas the G-test showed significance at the 95% confidence level ($p < .05$).

Data were not found to support the theory that territory size changes with depth, at least to the effect that the number of territories found along the transects did not change. Figure 5 is a graphical presentation of these data. A linear regression of the datapoints showed and $r^2 = .52$, but the slope proved not to differ significantly from zero. Figure 5 also shows a "connect the dots" approach to the graph. More data are needed to tell if the points actually fit some complex curve, for example the one proposed by Baldwin and Carlsen in figure 1. Numbers of territories didn't change with depth, and this implies that territory densities and sizes remained constant. However see the Discussion for a closer look at this relationship.

what are these numbers?
 FIGURE 5: LINEAR REGRESSION OF FISH VS. DEPTH. ALSO, "Connect the dots" method of graphing. See Fig. 1 for a similar shape



Should show maps of territories of your crew.

Mapping damselfish territories consumed the bulk of my field time. To get maps accurate, as much as an hour was spent sketching a small area. One of the actual maps appears in Appendix II. The data on clumping collected from each map appears in Appendix III. The actual and expected number of CSN were compared using the Mann-Whitney U-test. No significant clumping was found, although E. partitus was clumped at the level $.05 < p < .10$.

The damselfish showed a preference for various small scale substrate morphology types, for example flat areas, vertical surfaces, coral heads, and so on. Table 1 shows what these tendencies were. Note that the categories are not necessarily mutually exclusive for an individual fish. Unfortunately, I lost a considerable portion (~40%) of the microhabitat data, so I conducted no statistical tests. However, several trends

(heavily outlined boxes) appear:

TABLE 1: Microhabitats found by mapping of damselfish territories

TABLE 1

PREFERRED MICROHABITAT

Fish	FLAT	HEADS	VERTICAL	A. CEMENTOS
BG	.9	.6	.3	0
D	0	8.6	4.3	0
Ytail	1.4	4.4	0	0
BC	.7	2.0	6.0	3.3
35	.8	.9	.9	.9

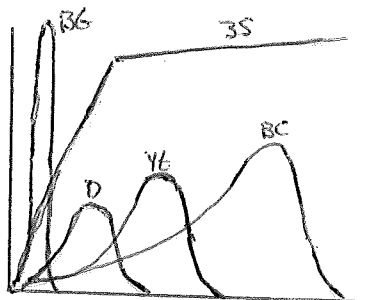
what are these numbers?

Discussion

Space

The data presented in figures 3 and 4 build a strong case for spatial partitioning among the Pomacentrids studied. Figure 6 below is simply a smoothed out and polished version of figure 3. The data look like the classical textbook resource and competitive exclusion curves, and it is difficult not to accept such a beautiful set up. Further support comes from anecdotal evidence (Dussourd 1979, Cairns and Baldwin 1980, and others).

FIGURE 6: FIGURE 3
MADE BETTER



The most telling support, in my opinion, comes from the Range test evaluation of the data. Four of the five species showed their most significant data at the peak of the curves in figure 6. Note that none of the species showed a split peak; numbers increased to a maximum, then fell off fairly evenly. I feel that Peter Sale notwithstanding, the damselfish are partitioning the limiting resources of substrate space by depth, at least in Discovery Bay. My data ~~are~~ insufficient to determine what the mechanism is: who's outcompeting whom, whether depth is the critical factor, and so on. But the ~~curves~~ ^{curves} remain.

Nevertheless, one shouldn't become too enamoured with these data, despite their beauty. Further study is definitely needed. I have failed to control for the different areas in the bay from which samples were taken; depth may not be the important factor, or even a factor at all in determining that Beaugregories live in the west back reef, ~~area~~, and dusgies in the east back reef.

Size and density

The transect data describe numbers of fish seen, but don't really tell much about territory densities or sizes. If sizes increased and/or densities decreased, the number of fish on a transect might change. A changing species composition with depth, and territory size differences among species will confuse the issue. Since both these factors are found in this system, the transects are not good density or size data collection techniques. Directly measuring territory sizes and densities (frequencies) is a better method. A direct approach was used by Curry and also Carlsen and Baldwin. The latter found territory sizes to significantly increase with depth. They suggested that lower light levels and higher grazing pressure may be the causes.

A larger territory would take more time and energy to patrol. In addition, a damselfish living some distance from the reef crest is more likely to encounter pelagic and deep water predators. It would be interesting to see if these factors promote lower rese-

dence times of territorial Pomacentridae in deep water.

Specialization

The notes I took concerning substrate types while doing the transects further support my contention that the damselfish partition living space. Figure 7 shows a cross section of the reef at each of the places I laid out transects. Above each cross section is the name of the damselfish that reached its peak abundance at that depth. These habitat preferences are occasionally noted in the literature (Clarke 1977, Sale and Dybdahl 1975, Risk 1972 in Luckhurst and Luckhurst 1978, and Itzkowitz 1974). However, several researchers have found no habitat structure selection for other Pomacentrids in the Pacific (Sale 1977, Talbot et al. 1978).

Clumping

I was surprised at how little clumping I found using the territory map data. I was unable to disprove the null hypothesis that individuals within a species are arranged randomly over the substrate (in multispecific groups). Only the Bicolor came close to statistical clumping ($p < .10$). I think that part of my failure to find clumping was a function of the method of mapping I used. Rather than many small maps, I should have drawn a few big ones. Fish with territories on the map's edge are "cheated" out of neighbors by the map boundaries, and should be discarded from the analysis. Since this would have left me with effectively no data,

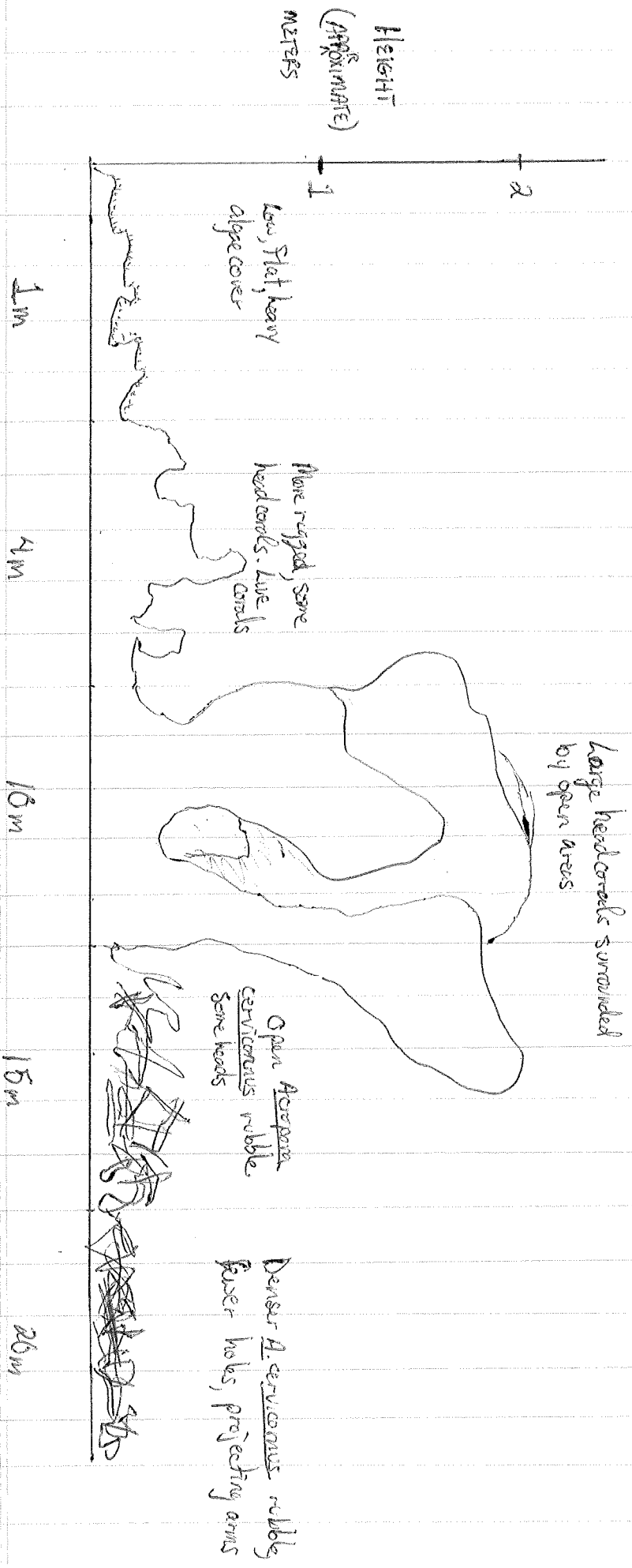


FIGURE 7: SUBSTRATE MORPHOLOGY (CROSS)

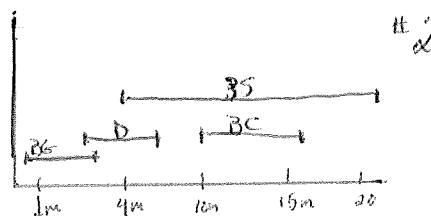
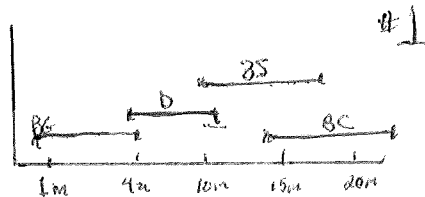
I didn't throw them out, in my analysis.

This method should only be used when sufficient time^m is available. Drawing the maps carefully takes a long time; for their final value, the maps were grossly overrepresented in the field time allotted for this study. I also suggest that a grid system be used when making the map. This simplifies mapping and allows several more statistical tests to be performed.

The map data failed to show clumping, and therefore lends support to Sale's lottery theory of colonization and territoriality.

It would be interesting to see previous species-depth diagrams. I have tried to construct one from the literature, and it appears as figure 8, followed by a comparable diagram using my data. Exactly how accurate the historical diagram may be can only be guessed at. I feel that it quite possibly is fairly accurate.

FIGURE 8: The approximate ranges of 4 species of damselfish. #1 reconstructed from the literature; #2 taken from my data.



note the
source(s)!

Beaugrories have remained more or less the same over the

time between the two profiles. Hurricane Allan, which may have affected the other damselfish and their territories greatly, seems to have passed by E. leucostictus. The reef front bore the brunt of the heavy seas during the storm, leaving the lagoon relatively calm. The low coral and rubble habitats are not very susceptible to waves, so Beaugregory substrate remained relatively unaffected. Whether E. leucostictus has been forced into the shallow lagoon, ^{whether} on that's their preferred territory, they "lucked out", and seem not to have been affected too much by Allan.

aggregations | The Threespot damsel, on the other hand, had its preferred habitat, the Acropora cervicornus zone completely destroyed. But comparing the profiles shows that they have become more cosmopolitan than before. Perhaps the Threespot is the opportunist of its guild, able to respond most quickly to available territories opened by catastrophe. It is also possible, however, that they are simply the most aggressive species, and when large numbers of the species had their home ranges destroyed, they just forced other species out of their territories. Most researchers would agree ^{that} ~~anta~~ damselfish are rarely successful in evicting established territory holders; but here we are dealing with a possibly tremendous catastrophic event. Unusual behaviors may ~~ab~~ve been forced on the Threespots or their competitors.

The dusky damselfish may have been the most common territor-

ial Pomacentrid on the reef prior to the hurricane. But I found very few. What happened? It's certainly possible that the population change is unrelated to the hurricane, but such a catastrophe must have some effect. I suggest that the Dusks were in some way less able to respond to the changed environment. Perhaps they were specialists on some parameter or resource as yet undiscovered, and since removed by the hurricane. ^Maybe they are simply not good territory holders, and were pushed out by invaders (Threespots?). Previous studies would not predict this, but the recovery of the damselfish community from such a disaster hasn't been observed (to the best of my knowledge and the library's resources).

Bicolor damselfish no longer exist mainly as a deep water species it seems. My counts found them at several depths on the reef, although other researchers had found them mainly below 50 feet. If they were deep living, the hurricane should have had a less pronounced effect on them than on the reef crest dwelling species. From their "safe" zone they may have colonized other parts of the reef. Data taken from my maps hint that they are poor competitors for space. I found them most often on nearly vertical territories. If deep water was a niche refuge, one would expect to find them being outcompeted elsewhere; for example holding vertical territories that are less able to grow algae (assuming that Bicolors have algae farms). Why I didn't ~~still~~ find them

still dominating in deep water isn't clear.

I found no references to where Yellowtails held territories.

The previous five paragraphs are based on questionable historical data, and are highly speculative. They aren't meant to be so much serious theories of the mechanisms of recovery as they are suggestions for further study and experimentation.

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Shire, M. (1978). Unpublished (DESP project).

Talbot, F.H., B.C.Russell, G.P.V. Anderson (1978). Ecological Monographs pp425-480.

Further background information was taken from the plethora of articles in J.J.Gilbert's folder "Reef Fish" used on the DESP.

The following articles were read:

Barlow 1975a

Rnadall 1974

Barlow 1975b

Randall and Hartman 1968

Goreau 1959

Robertson, Sweatman 1976

Hobson 1972

Sale 1978

Hobson 1978

Sale and Dybdahl 1975

Molles 1978

Sale and Dybdahl 1978

Myrberg and Thresher 1974

Targett 1978

APPENDIX I: TRANSECT DATA

WBR (lagoon)	BG	3S	Ytail	Dusky	Bicolor
~1m	12	-	-	-	-
	13	-	1	-	-
	4	-	-	-	-
	15	5	-	-	-
	11	6	-	-	-
EBR (lagoon)	-	10	1	-	-
4m	-	12	2	-	1
	-	7	2	2	6
	-	14	2	1	3
	-	10	3	3	3
	-	14	1	4	2
WFR	-	9	3	-	-
10m	-	8	3	-	1
	-	4	2	-	5
	-	3	1	-	3
	-	13	-	-	5
	-	10	1	-	2
WFR	-	12	-	-	3
15m	-	2	-	-	9
	-	6	-	-	7
	-	8	1	-	5
	-	13	-	-	3
	-	15	1	-	3
WFR	-	9	-	-	6
20m	-	12	-	-	2
	-	9	-	-	1
	-	9	-	-	4
	-	15	-	-	1

APPENDIX II: MAP DATA

species	total #	#neighbors	actual SSN	expected SSN
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35	3	13	2	1.9
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D	0	0	0	0
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I = WBR

BC	11	32	20	24.6
----	----	----	----	------

YE	0	0	0	0
----	---	---	---	---

35	3	13	4	2.4
----	---	----	---	-----

D	0	0	0	0
---	---	---	---	---

II = WBR

BC	9	29	20	21.1
----	---	----	----	------

YE	0	0	0	0
----	---	---	---	---

35	4	14	6	6
----	---	----	---	---

D	0	0	0	0
---	---	---	---	---

III = WBR

BC	4	14	6	6
----	---	----	---	---

YE	0	0	0	0
----	---	---	---	---

35	9	33	12	17.6
----	---	----	----	------

D	3	12	0	1.6
---	---	----	---	-----

IV = EBR

BC	3	17	4	1.1
----	---	----	---	-----

YE	2	13	2	0.8
----	---	----	---	-----

35	13	47	34	35.2
----	----	----	----	------

D	0	0	0	0
---	---	---	---	---

V = EBR

BC	4	14	4	2.6
----	---	----	---	-----

YE	0	0	0	0
----	---	---	---	---

APPENDIX II (cont)

species	total #	# neighbors	actual CSN	expected CSN	
35	8	12	10	9.2	
D	0	0	0	0	VI = EBR
BC	0	0	0	0	
YE	2	5	2	6	
35	15	48	32	31.3 30.5	
D	0	6	0	0	VII = WFR
BC	7	28	10	7.4	
Y	1	2	0	0	
35	9	24	12	11.3	
D	5	17	6	4	VIII = WFR
BC	2	8	2	0.5	
Y	2	7	0	0.4	
<u>TOTALS</u>					
35	64	204	112	117.4	
D	7	29	6	2.0	
BC	15	67	20	11.0	<u>TOTALS</u>
BG	24	75	46	52.3	
Y	7	27	4	1.7	