

# Alpha and Beta Diversity in Coral Reef Fish Communities

or

One Fish, Two Fish, Red Fish, Blue Fish!

by Elliott Gimble '84  
and Craige Williamson '85

March 6, 1984

Dartmouth College Biology FSP  
Discovery Bay, Jamaica

### Abstract:

Current theory regarding fish species diversity on coral reefs is divided into two camps: those who support Peter Sale's "Lottery" theory and those who support the conventional community theory.

Comparisons between alpha and beta diversity in four habitats in Discovery Bay, Jamaica showed a high degree of overlap between habitats (low beta diversity) and did not demonstrate niche partitioning. As a result Sale's hypothesis is inconclusively supported.

## Introduction:

Coral reefs support an incredibly diverse array of fish species consisting of over 500 different types in the Caribbean alone (Bohke and Chaplin, 1968). This complex fish community is the focus of recent studies and new theories are being developed and tested. Current debate addresses the controlling factors of fish species diversity on the coral reef and ecologists are divided in their approach.

One school of thought, generally centered around the ideas of Dr. Peter Sale, is based on the observation that fish larvae are pelagic and therefore widely dispersed, allowing for a stochastic distribution. This random distribution is maintained by a high degree of mixing and the large numbers of larvae released. Given that space availability is unpredictable to all larvae and adults, then a community's species composition should be influenced more by the randomly settling larvae than by the current residential community. In a resource rich environment, competition is expected to be insignificant according to Sale, and small deviations from the random species distribution may be the result of limited habitat preferences by the larvae. (Sale, 1980)

Others espouse a more conventional community theory (Anderson, et al, 1981) and maintain that coexistence of species can only occur through niche partitioning or competition. This competition for resources would exclude some species and might decrease diversity. Niche partitioning, however, allows for coexistence of species through mutual avoidance and this may be used to

explain the high diversity of the coral reef.

These two theories lead to two very different predictions of a fish community. Sale's theory would predict a high amount of species ~~diversity~~ overlap between habitats due to the randomly mixed gene pool. This would lead to a high  $\alpha$ -diversity (within habitats) and a low  $\beta$  diversity (between habitats) since every area would share species equally from a common pool. Further, there would be wide niche breadth and little specialization within such an area since competition for resources is considered insignificant. Sale explains any unique species found in a habitat as the result of limited habitat preferences by larvae, not due to niche partitioning. The conventional theory of community structure differs, however, in that it predicts heterogeneity between habitats due to niche partitioning. The expected results of this partitioning are spatial replacements by competitive species and higher species specialization. Beta diversity would be relatively high due to different species compositions, ~~if~~  $\alpha$  diversity would be relatively low due to highly successful or dominant species within a habitat.

In this paper, we compare these two opposing theories in regard to four habitats\* found at Discovery Bay, Jamaica. By censusing species types and abundances within four habitat areas, the amount of overlap between areas and the likelihood of niche partitioning can be determined. Because of the

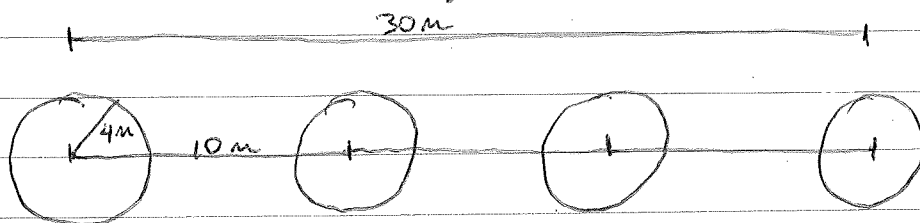
strengths and weaknesses of both diversity theories, we expect that neither can fully explain the diversities at Discovery Bay though certain aspects of Dale's argument make it more appealing (e.g. wide larval distribution should result in high overlap of species between habitat along the lines of his hypothesis). Even though we expect  $\beta$  diversity (between habitats) to be low and  $\alpha$  diversity (within habitats) to be high, weaknesses still exist within the Lottery (Dale's) theory. For example, we believe that unique species within habitats can still be explained by such factors as competition and resource partitioning equally <sup>as</sup> well as Dale's habitat-preference hypothesis. It is therefore hoped that this project will shed more light on the differing community theories and put them into context for Discovery Bay.

\* A clear, accepted definition of "habitat" eludes many studies and this one is no exception. Here, a habitat is defined as an area consisting of distinct geographic, structural and ~~per~~ perhaps biological make-up. While some vary more than others, each is different in at least one abiotic factor arbitrarily deemed significant.

## Methods:

Study sites were chosen to be representative of their respective habitats. Because of differing depths between sites, both SCUBA and snorkeling techniques were utilized to collect data; the former at 20' and 60' on the West Fore Reef and the latter on the East and West Back Reef. A standard visual census methodology similar to "point censusing" (Slotochkin and Fishelson, 1974) was used at each site. Censuses were conducted by one diver at a time and two replicates of four subsamples (see below) each were taken on separate days between February 28 - March 3, 1984.

Horizontal transects of 30 meters were chosen at each site and ten-minute censuses were conducted at 0, 10, 20, and 30 meters along the transect. These involved visually identifying all species of fish seen within an approximate radius of 4 meters and recording species type and abundance. After ten minutes in one area, the diver moved 10 meters to the next sampling point.



For comparison of different feeding types, a guide to Caribbean reef fishes was consulted (Randall, 1968).

### Study Site:

All fish censuses were taken in Discovery Bay, Jamaica at 4 sites chosen in an attempt to represent different reef habitats.

The East Back Reef (EBR) site was located on a large patch reef with numerous sea grass beds in depths ranging from 10 to 15 feet. Much of the bottom substrate was covered in sand and dotted with relatively small coral outcroppings. The site was located about 60 meters south (toward shore) of the reef crest.

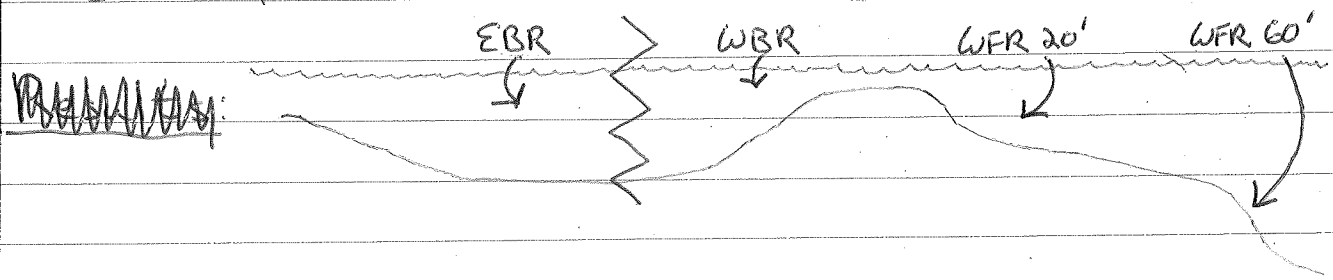
The West Back Reef (WBR) site was located in more substantial coral colonies at depths ranging from 3 to 6 feet. Algae growth was extensive covering in excess of 60% of the substrate. The site was about 5 meters from the reef crest and appeared to be subjected frequently to wave induced turbulence.

The West Fore Reef (WFR) was divided into two sampling sites, one at 20 ft. and one at 60 ft both near mooring 1.

The 20 foot site (WFR 20') was located about 30 meters from the reef crest and supported healthy and numerous coral colonies mostly comprised of *Acropora* and *Montastrea* genera. Algae coverage was not as extensive

on the fore reef as it was in either back reef site, Sea grasses were completely absent.

The 60 foot fore reef site (WFR 60') was also densely covered in coral and other invertebrates. At 60' the bottom slopes more rapidly forming a shallow wall. All 60' censuses were taken along this wall.



### Results:

A relatively high degree of overlap in species (irregardless of abundances of individuals) is shown by the low number of species unique to 1 habitat (Table 1) and the high proportion of species found to be common between habitats. (Table 2)

Beta diversities between pairs of habitats were determined using Euclidian distances which take relative abundances into account. Values were relatively close to zero implying a low degree of beta diversity. (Table 3)



To provide a comparison between alpha and beta diversities, Euclidian distances were also computed between subsamples within habitats. Distances were found to be very similar to beta diversity distances. (Table 4)

Mutual avoidance was used as a measure of niche partitioning and geographic replacement between habitats. Comparisons were first made within feeding types. (Fig. 1 a, b, c). No strong evidence for mutual avoidance was found.

Niche partitioning was also examined within families for Pomacentrids (Fig. 2a) and Scarids (Fig. 2b) <sup>each of</sup> since these families are very common ~~with~~ and incorporate numerous species with similar feeding habits, ~~in each~~. Mutual avoidance was noted between Chrysurus and Planifrons (Fig. 2a.) but no other trends were evident.

Feeding guild distributions were dominated by herbivores in every habit with planktivores and piscivores densities increasing with depth.

A comparison of abundances of the 3 most common fish families showed a non-random distribution between habitats. (g-test,  $\chi^2 = 26.4$ , d.f. = 6,  $p \leq .001$ )

Table 1 - Total species, abundances, and diversities of each habitat.

	E.B.R.	W.B.R.	W.F.R. (20')	W.F.R. (60')	Total
# of Species	35	29	44	35	63
# of Individuals	321	510	972	625	2428
$H'$	2.99	2.58	2.75	2.74	—
% Unique	11.4	10.3	18.2	20	34.9

% of total species found in all 4 habitats = 22.2%

Table 2 - Species overlap—expressed as the proportion of species in row habitat that are also present in column habitat. (Measure of beta diversity)\*

	EBR	WBR	WFR 20'	WFR 60'
EBR	—	62.8%	77.1%	52.1%
WBR	*75.9%	—	79.3%	62.0%
WFR 20'	61.3%	52.3%	—	59.0%
WFR 60'	56.7%	48.6%	70.3%	—

\* For example: 75.9% of all species found in the WBR ~~are~~ also found in the EBR.

### Table 3 - Euclidian distances between habits.

(A relative measure of beta diversity where distances closer to 0 represent more species overlap between habitats and distances closer to 1 represent less species overlap between habitats.

Derived from the equation:

$$\text{"Distance"} = \left[ \sum_{k=1}^S (P_{ik} - P_{jk})^2 \right]^{1/2} \text{ where}$$

S is total # of species considered,  $P_{ik}$  is the proportion of fish in sample i that are of the  $k^{\text{th}}$  species, and  $P_{jk}$  is the equivalent proportion of fish in sample j. " (Sale, 1978)

Habitats compared	Euclidian distance
EBR and WBR	.202
WFR 20' and WFR 60'	.302
WBR and WFR 60'	.310
EBR and WFR 20'	.321
EBR and WFR 60'	.325
WBR and WFR 20'	.339

Table 4- Euclidian distances between randomly selected subsamples within a habitat. (A measure of alpha diversity)

Habitat	Euclidian distance between samples within a habitat
EBR	.237
WBR	.246
WFR 20'	.241
WFR 60'	.242

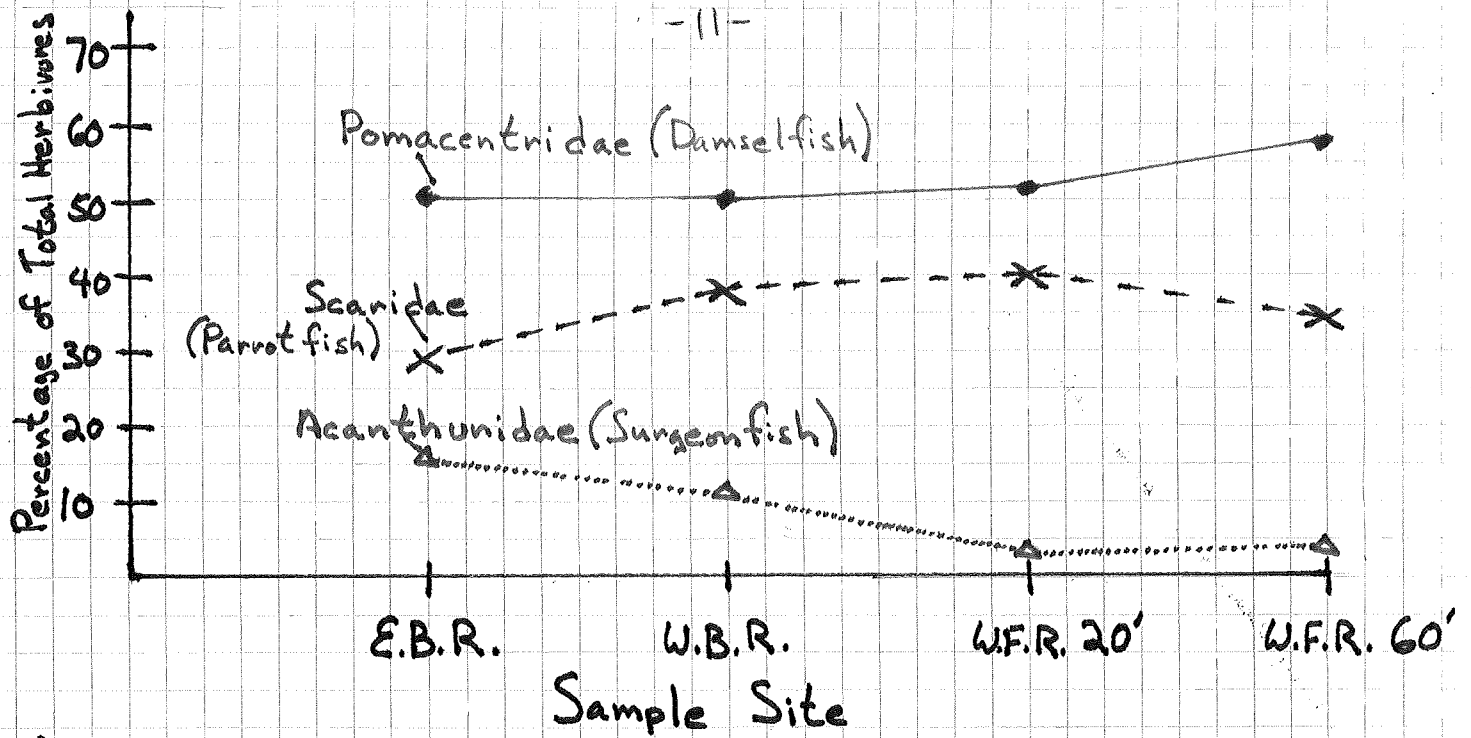


Fig. 1a- Relative abundances of herbivores within habitats.

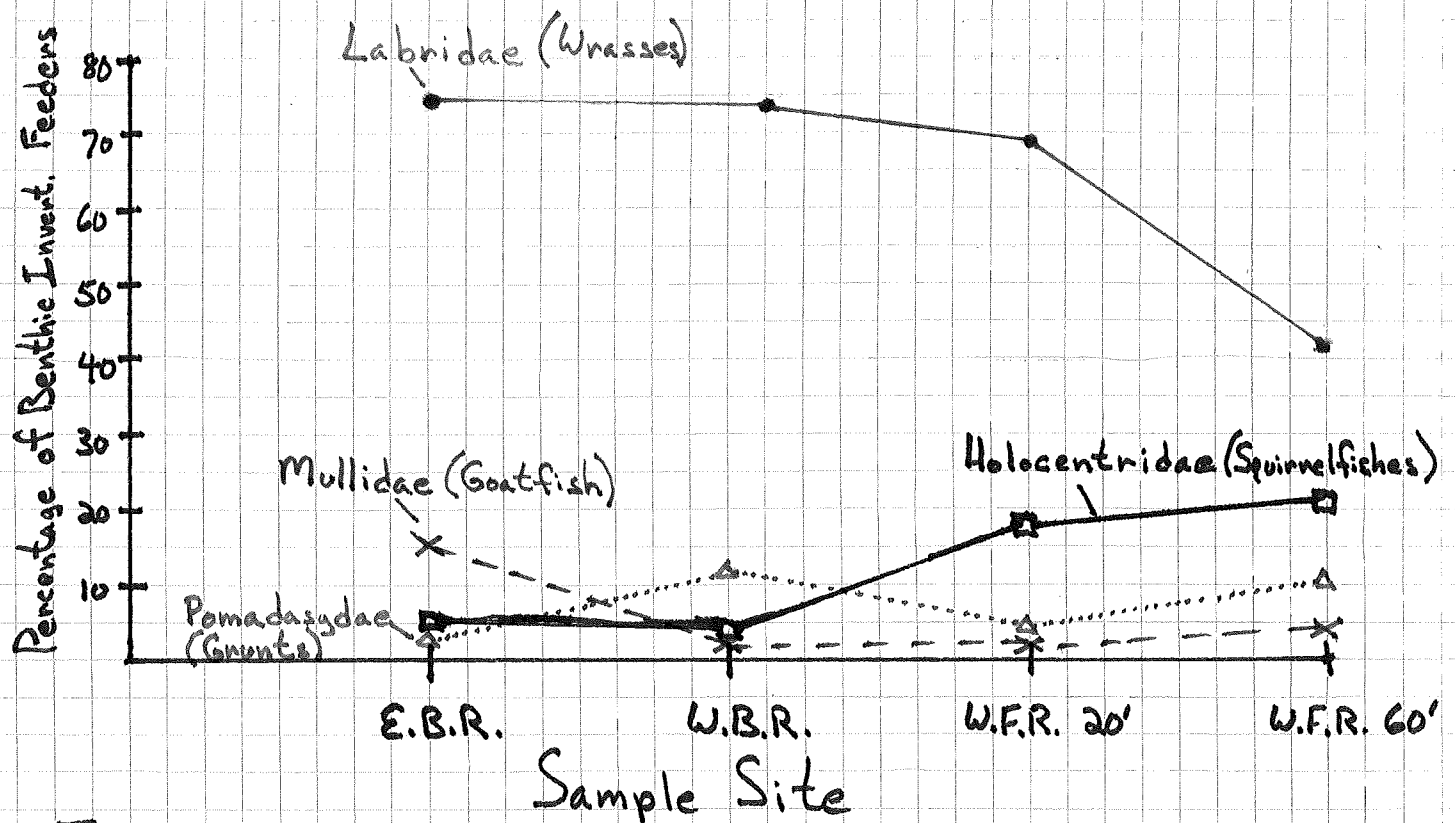


Fig. 1b- Relative abundances of benthic invertebrate feeders within habitats.

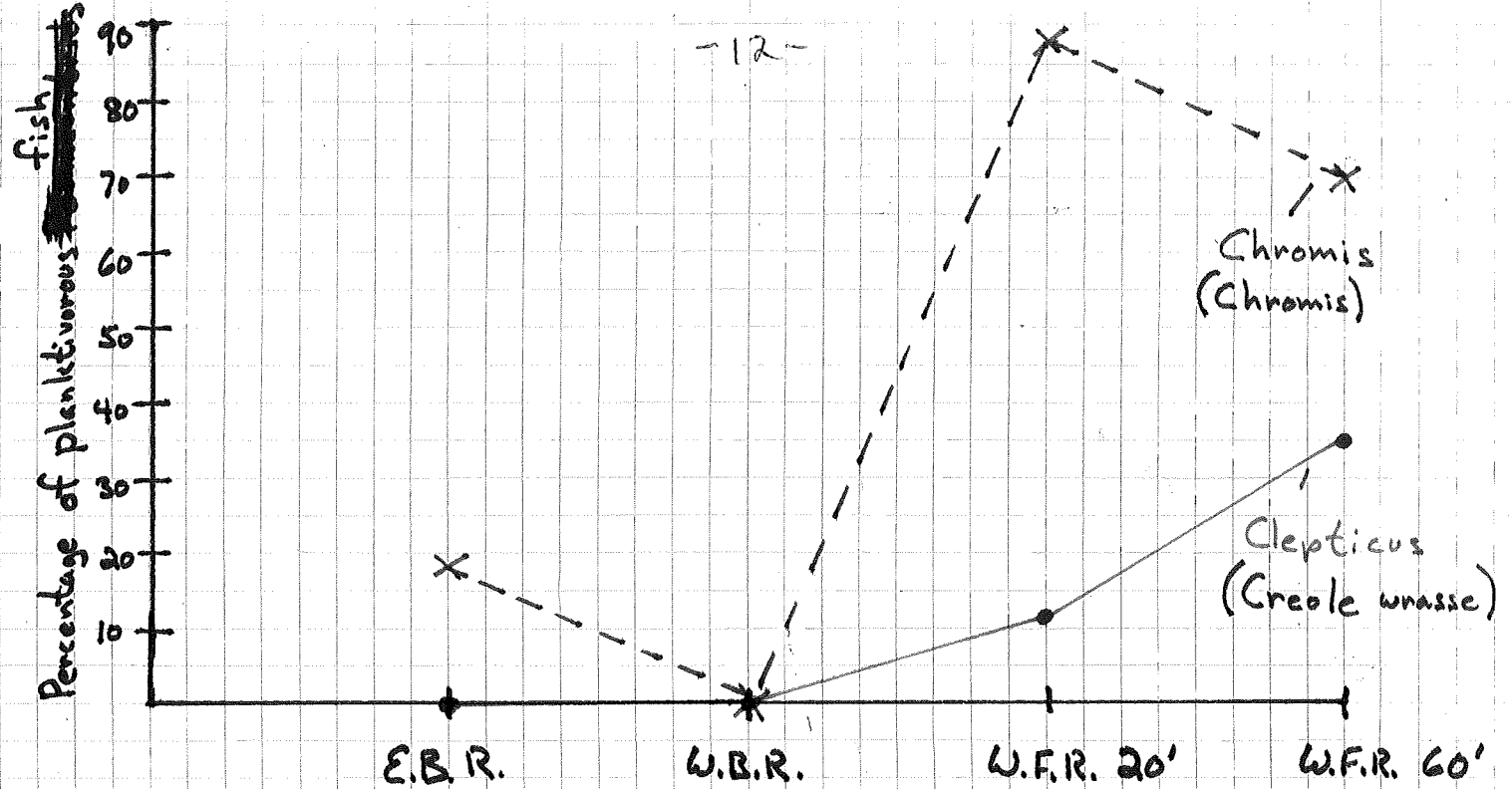


Fig. 1c - Relative abundances of planktivorous fish within habitats.

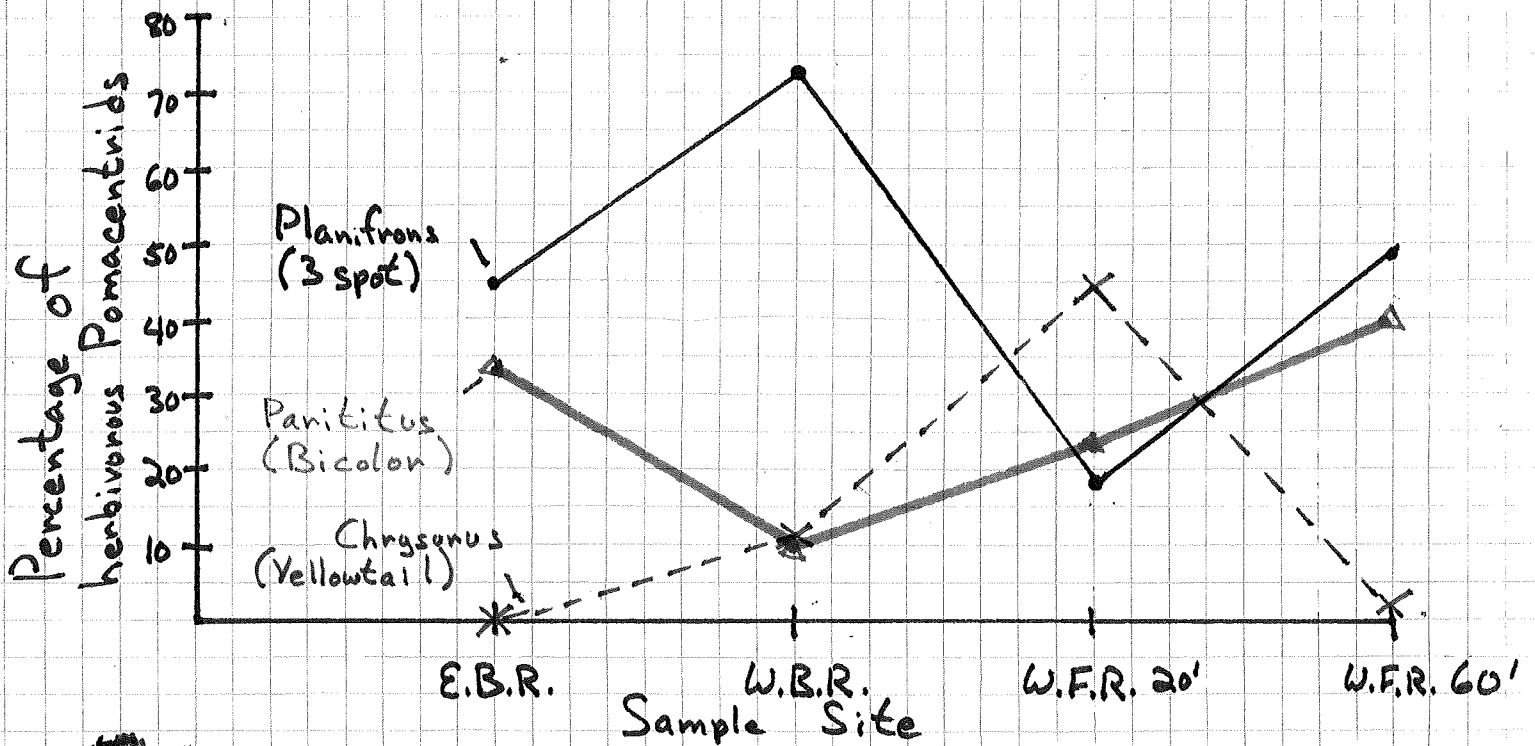


Fig. 2a - Relative abundances of herbivorous Pomacentrids (Damselfish)

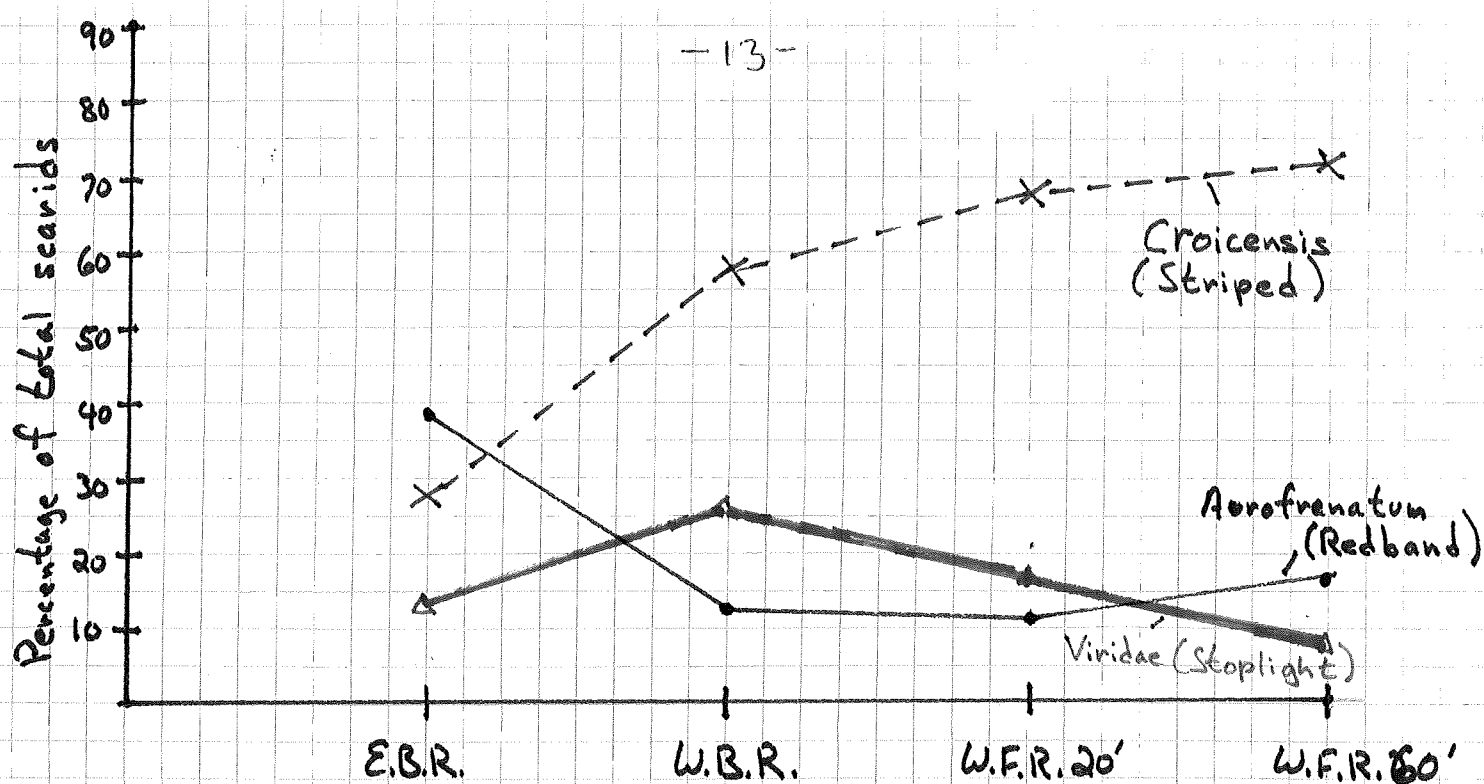


Fig. 2b - Relative abundances of Scanids (Parrot-fish) within habitats.

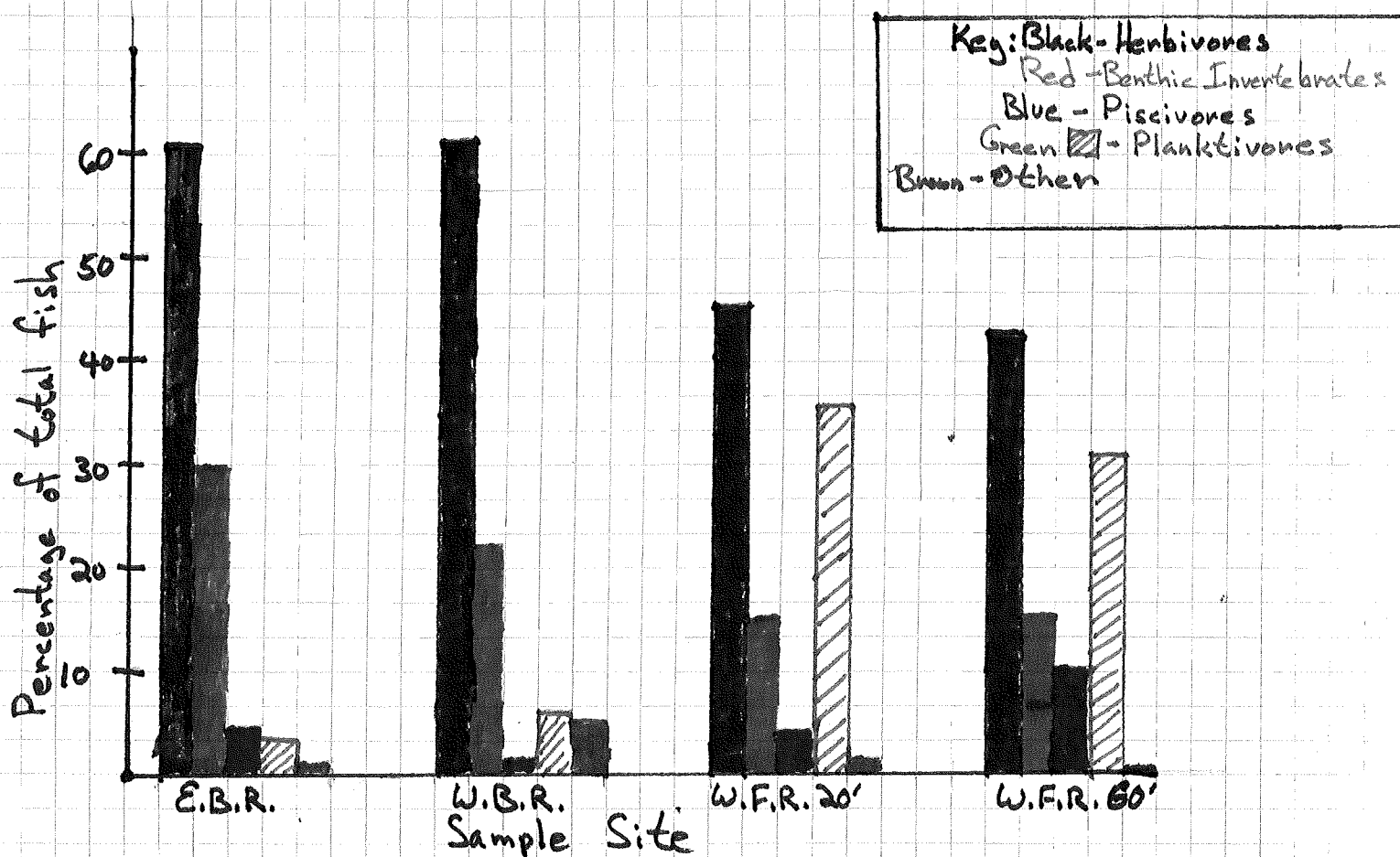


Fig. 3 - Relative proportions of feeding type & within habitats.

## Discussion:

Generally, there was an even distribution of species between habitat types (Table 1). Abundances, however, varied greatly and higher numbers were seen on the West Fore Reef indicating a higher density at that site.

Diversity in terms of Shannon-Wiener indices also appeared to be relatively similar between sites and no habitat had a particularly large percentage of unique species.

In examining the possibilities for niche partitioning presented by Anderson's hypothesis, relative abundances of different feeding guilds within habitats were calculated and graphed (Figures 1a-c, Fig. 2a, b). While some taxa are greatly separated in abundances throughout all habitats (e.g. the Pomacentridae and Acanthuridae, Fig. 1a) many times there seems to be no influence ~~on~~ by one taxa on the abundance of another (e.g. Pomacentridae and Mullidae, Fig. 1b).

This same relationship was considered within a family for damselfish and parrotfish and again ambiguous results appeared. Though the relative abundances of *Planifrons* and *Chrysonus* (Fig. 2a) might indicate niche partitioning using Anderson's approach, there does not seem to be full niche partitioning between *Parititus* and *Planifrons*. Even on the species level, niche partitioning (as according to Anderson, et al) is not clearly demonstrated in our results.

Sale points out the weakness of using the relative abundances to illustrate niche partitioning (Sale, 1982).

The differences in relative abundances between species or feeding guilds, he states, may be explained by non-competitive, non-niche partitioning factors and that competition is only



inferred by Anderson, et al in their use of these type graphs.

Overall overlap between habitats was consistently high (over 50% and into the 60-70% range, Table 2) but these calculations do not consider relative species abundances, only overall species numbers. Because of this weakness, Euclidian distances were calculated (Tables 3, 4 - These are useful in comparing  $\alpha$  +  $\beta$  diversities). This "distance" calculation is an indication of how similar two habitats are to one another in terms of species diversity and abundance. Values close to 1.0 indicate low overlap and therefore high diversity between habitats; values closer to 0 indicate high overlap and lower diversity between habitats.

The results indicated that within each habitat ( $\alpha$  diversity), there was consistently high overlap between samples (.2 is relatively low) and all habitats were similar in their diversity compared to one another (all values are approximately the same,  $\approx .24$ ), Table 4). When habitats were compared to each other, consistently high overlap and similarities of comparisons between habitats indicated low  $\beta$  diversity (Table 3). Because  $\alpha$  diversity distances are similar to each other and to  $\beta$ -diversity distances, it is implied that the reef is relatively homogeneous in ~~the~~ terms of species distribution. (If the species distributions were completely homogeneous within and between habitats, then distances would all be the same).

This apparent uniform distribution supports Sale's point that fish larvae are distributed randomly within and between different habitats. The G-test of the abundances of

The three most common species, however, prevents this from being a conclusive result. Because there is a significant difference in the distribution of these three species, it ~~cannot~~ cannot be concluded that distribution is totally random and other factors must be considered. ~~(Theory, Lottery Theory is not a perfect model)~~

It appears that neither the conventional community theory nor the Lottery Theory is sufficient to explain the results of these censuses. Though Sale's random distribution hypothesis seems to hold, his theory is not without fault. One criticism relates to the question of scale; that is, how large a habitat should be sampled in order to properly address the question of niche partitioning and varying diversities? Sale uses smaller sites in his studies; others use very large ( $50 \text{ km}^2$ ) transects - which are more useful in determining diversity and the factors that influence it? There is no answer to this question and this study may itself lack some validity if the habitats studied were effectively part of only one large habitat.

Another weak point in Sale's theory is his explanation of possible heterogeneity within a habitat. He maintains that larvae may show habitat preferences, but does not suggest which factors might create those preferences. While they need not be restricted to competition and/or predation, these factors must be present in order to ~~cause a preference~~ influence a preference and Sale lacks ideas in terms of possible

suggestions (Aale, 1980 p 409, 1982 p 122). Until more weight can be added to his habitat preference hypothesis, the Lottery Theory will be incomplete.

Research is vitally needed in the areas of larval ~~dispersal~~ dispersal, ~~and~~ limiting resources, and factors limiting dispersal if they exist. Visual censusing techniques are never complete but provide a somewhat effective and convenient way of sampling and newer methodologies might enhance the old. Further studies in regard to fish diversities in coral reef communities include: addition of nocturnal censusing, correlation of interhabitat distance and overlap in species, comparisons of specialization (e.g. feeding habits) which may indicate niche partitioning, documentation of competitive interactions (i.e. territorial fish effects on other species and on diversity), substrate or spatial utilization as a factor in niche partitioning, etc.

Though this study does not provide a basis for accepting one fish diversity theory over another, that was not its purpose. Both Theories are strong in some respects but at present, neither is strong enough alone to <sup>fully</sup> explain fish diversity on the coral reef. The future acceptance or rejection of these theories or the creation of a totally new one remains the challenge for future research in this area.

Appendix 1 - Species abundances at each habitat.  
Names in parentheses are families that contain the species listed below them.

Species (Common Name)	Latin name	EBR	WBR	WFR20'	WFR60'	Total
(Damselfish)	(Pomacentridae)	103	170	526	282	1081
Dusky Damselfish	<i>Eupomacentrus fuscus</i>	11	2	7	1	21
Cocoa Damselfish	" <i>variabilis</i>	4	7	20	14	45
Bicolor Damselfish	" <i>parititus</i>	35	13	55	64	167
Yellowtail Damselfish	<i>Microspathodon chrysurus</i>	-	18	100	2	120
3-spot Damselfish	<i>Eupomacentrus planifrons</i>	45	115	41	77	278
Honey Damselfish	"	1	4	-	-	5
Beau Gregory	" <i>leucostictus</i>	5	-	-	-	5
Sargent Major	<i>Abudefduf saxatilis</i>	-	11	-	-	11
Brown Chromis	<i>Chromis multilineata</i>	-	-	220	-	220
Blue Chromis	<i>Chromis cyanea</i>	2	-	83	124	209
(Wrasses)	(Labridae)	72	84	134	110	400
Slippery Dick	<i>Halichoeres bivittatus</i>	3	-	-	-	3
Yellowheaded Wrasse	" <i>garroti</i>	11	-	15	13	39
Blueheaded Wrasse	<i>Thalassoma bifasciatum</i>	42	80	79	30	231
Clown Wrasse	<i>Halichoeres maculipinna</i>	14	4	1	-	19
Black-ear Wrasse	" <i>poeyi</i>	2	-	-	-	2
Creole Wrasse	<i>Clepticus parrae</i>	-	-	39	67	106
(Parrotfish)	(Scaridae)	58	122	180	92	452
Yellowtail Parrotfish	<i>Sparimosa rubripinna</i>	2	-	-	-	2
Stoplight	" <i>viridae</i>	8	32	31	9	80
Redband	" <i>aurofrenatum</i>	23	16	22	15	76
Striped	<i>Scarus croicensis</i>	16	70	122	67	275
Princess	" <i>taeniopterus</i>	9	4	5	1	19
(Blennies)	(Blennidae)	-	1	-	-	1
Redlip Blenny	<i>Ophioblennius atlanticus</i>	-	1	-	-	1

Species (Common name)	Latin name	EBR	WBR	WFR 20'	WFR 60'	Total
(Groupers + Sea Bass)	(Serranidae)	14	6	24	57	101
Red Hind	<i>Epinephelus guttatus</i>	-	-	2	9	11
Barned Hamlet	<i>Hypoplectrus puella</i>	-	-	-	11	11
Butter Hamlet	" <i>unicolor</i>	-	1	2	1	4
Indigo Hamlet	" <i>indigo</i>	4	4	9	22	39
Golden Hamlet	" <i>gummigutta</i>	-	-	2	-	2
Shy Hamlet	" <i>guttavarius</i>	-	-	1	2	3
Harlequin Bass	<i>Serranus tigrinus</i>	10	1	7	5	23
Tobacco Fish	<i>Serranus tabacarius</i>	-	-	-	7	7
Coney	-	-	-	1	-	1
(Fairy Basslet)	(Grammidae)	-	-	-	8	8
Fairy Basslet	<i>Gramma loreto</i>	-	-	-	8	8
(Hawkfish)	(Cirrhitidae)	1	-	2	-	3
Redspotted Hawkfish	<i>Amblycirrhitis pinos</i>	1	-	2	-	3
(Mackerels)	(Scombridae)	-	-	1	1	2
Cero	<i>Scomberomorus regalis</i>	-	-	1	1	2
(Snappers)	(Lutjanidae)	-	-	-	1	1
Lane Snapper	<i>Lutjanus synagris</i>	-	-	-	1	1
(Grunts)	(Pomadasysidae)	2	15	6	13	36
French Grunt	<i>Haemulon flavolineatum</i>	1	15	6	13	35
White Grunt	" <i>plumieri</i>	1	-	-	-	1
(Goatfish)	(Mullidae)	15	3	3	7	28
Yellow Goatfish	<i>Mullusichthys martinicus</i>	-	-	2	4	6
Spotted Goatfish	<i>Pseudopomacentrus maculatus</i>	15	3	1	3	22
(Drums)	(Sciaenidae)	-	-	2	-	2
Spotted Drum	<i>Equetus punctatus</i>	-	-	2	-	2
(Sweepers)	(Pempheridae)	-	1	-	-	1
Copper Sweeper	<i>Pempheris shomburgkii</i>	-	1	-	-	1

Species (Common Name)	Latin name	EBR	WBR	WFR 20'	WFR 60'	Total
(Gobies)	(Gobiosoma evelynae)	11	60	18	-	89
Sharknose Goby	Gobiosoma evelynae	9	33	6	-	48
Cleaning Goby	" sp.	2	27	12	-	41
(Surgefish)	(Acanthuridae)	32	35	18	13	98
Blue Tang	Acanthurus coeruleus	7	24	15	13	59
Ocean Surgeon	" bahianus	10	-	2	-	12
Doctorfish	" chirurgus	15	11	1	-	27
(Triggerfish)	(Balistidae)	-	-	1	-	1
Black Durgon	Melichthys niger	-	-	1	-	1
(Filefish)	(Monacanthidae)	1	-	2	-	3
Tail-light Filefish	Canthenehines pullus	1	-	2	-	3
(Trunkfish)	(Ostraciontidae)	-	1	-	1	2
Smooth Trunkfish	Lactophrys triquetus	-	1	-	1	2
(Puffers)	(Tetraodontidae)	5	1	11	13	30
Bandtailed Puffer	Sphaeroides splengleri	2	-	-	6	8
Sharnose Puffer	Centrigaster rostrata	3	1	11	7	22
(Squinnelfishes)	(Holocentridae)	4	4	27	22	56
Squinnelfish	Holocentrus rufus	1	4	2	1	7
Longspine squinnelfish	Flammeo marianus	-	-	13	19	32
Blackbar Soldierfish	Mynipristis jacobus	3	-	12	2	17
(Jacks)	(Carangidae)	2	-	3	4	9
Bar Jack	Caranx huber	2	-	3	4	9

Species (Common Name)	Latin name	EBR	WBR	WFR 20'	WFR 60'	Total
(Butterfly and Angelfish)	(Chaetodontidae)	-	1	3	3	7
4 eye Butterflyfish	Chaetodon capistratus	-	1	3	-	4
Rock Beauty	Holocanthus tricolor	-	-	-	2	2
French Angelfish	Pomacanthus paru	-	-	-	1	1
(Lizardfish)	(Synodontidae)	-	-	-	1	1
Sand Diver	Synodus intermedius	-	-	-	1	1
(Morays)	(Muraenidae)	-	-	1	-	1
Spotted Moray	Gymnothorax moringa	-	-	1	-	1
(Trumpetfish)	(Aulostomidae)	-	-	9	-	9
Trumpetfish	Aulostomus maculatus	-	-	9	-	9
(Stingrays)	-	1	6	-	-	7
Yellow Stingray	Urolophus harrisi	1	6	-	-	7
(Eagle Rays)	-	-	-	1	-	1
Spotted Eagle Ray	Aetobatis narinari	-	-	1	-	1

## Literature Cited:

Anderson, G.R.V., Ehrllich, A.H., Ehrllich, P.R., Roughgarden, J.D., Russell, B.C., and Talbot, F.H. (1981). The Community Structure of Coral Reef Fishes. *Am. Natur.* 117(4): 476-493.

Bohlke, J.E., and Chaplin, C.C.C. (1968). "Fishes of the Bahamas and Adjacent Tropical Waters." Livingston Publ. Co., Pennsylvania.

Sale, P.F. (1980). The Ecology of Fishes on Coral Reefs. *Oceanogr. Mar. Biol. Ann. Rev.*, 18: 367-421.

Sale, P.F. and Dybdahl, R. (1978). Determinants of Community Structure for Coral Reef Fishes in Isolated Coral Heads at Lagoonal and Reef Slope Sites. *Oecologia* 34: 57-74.

Sale, P.F. and Williams, D.M. (1982). Community Structure of Coral Reef Fishes: Are the Patterns more than those Expected by Chance. *Am. Natur.* 120: 121-127.

Slobodkin, L.B. and Fishelson, L. (1974). The Effect of the Cleaner Fish *Labroides dimidiatus* on the Point Diversity of Fishes on the Reef Front at Eilat. *Am. Natur.* 108: 369-76.

Excellent study and write up.