Carrying Capacity of
Chaetodontid and Pomacanthid
Fish Communities at St. Croix, U. S. Virgin Islands

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ABSTRACT

Whether local, coexisting populations of chaetodontid and pomacanthid fishes were at the carrying capacity of different reef areas was investigated with removal experiments at St. Croix, U.S.V.I. Estimates of population size were made by visual censusing of four transect areas in two habitats which differed in coral cover and structural complexity. On the average Chaetodon aculeatus, C. capistratus, and Holacanthus tricolor, accounted for more than 80% of these families at each site. These species were selectively removed in numbers approaching their relative abundances in the two habitats. Sites were recensused in 1980 and abundance and species composition before and after removals was compared.

The total abundance of these fishes per transect returned to preremoval levels after two years. Numerical differences in average total abundances were not significant ($P < 0.05$, t-test). Thus, local populations were probably at the carrying capacity of the sites. West wall sites had significantly greater coral coverage, much more structural complexity, and significantly more fishes than did east slope sites ($P < 0.05$, t-test).

While the average total abundance of the two families studied did not change significantly, and the three manipulated species were again the most abundant species two years after the removals, there were some changes in relative abundances and species numbers. Two species appeared on transects for the first time at the two sites, and another species went locally extinct at one site.

This experiment manipulated relatively large reef areas (400 m^3) and dealt with small regional species pools ($N = 9$). Nevertheless, there were changes in species composition but not total abundances. Chaetodontid and

pomacanthid fishes have broad food and habitat niches and within group overlap is present. While carrying capacity appears predictable because population levels are dependent on resource availability on the reef, species composition is probably more the result of chance related to space availability and recruitment. Consequently, local coexistence of these fishes, for the temporal and spatial scales considered, is probably more the result of chance associated with larval recruitment and space availability than fine niche partitioning.

INTRODUCTION

Processes which structure high-diversity communities, particularly assemblages of coral reef fishes with similar ecological requirements, have been debated for the past several years. Basically, the argument is divided into two competing schools of thought, one emphasizing the importance of environmental unpredictability and random colonization events, and the other emphasizing environmental stability and resource specialization. The stochastic school views coral reefs as unpredictable environments (sensu Slobodkin & Sanders 1969), where many species with similar patterns of resource utilization can coexist because of random changes in space availability and chance associated with larval recruitment (Sale 1974, 1976, 1977, 1978a, b, 1979; Sale & Dybdahl 1975; Russell et al. 1974). Determinists view reefs as stable and predictable environments where many species coexist in equilibrium that is the result of fine niche partitioning (Grassle 1973; Kohn 1968, 1971; Smith & Tyler 1972, 1973 a, b, 1975; Gladfelter et al. 1980). Another important parameter of equilibrium communities is resilience after disturbance which, after recovery, results in the same total and relative abundances of species (Connell 1978; Sousa 1979). As such, the deterministic model is an extension of a body of theory which attempts to explain community organization of terrestrial vertebrate communities (Cody 1968, 1974; MacArthur 1972; Schoener 1974; Diamond 1975).

Incorporated in the equilibrium view of community organization is the assumption that local populations are saturated in terms of numbers of individuals or biomass. However, there has been no experimental evidence to support that assumption. In fact, the only study which experimentally examined the carrying capacity of reef areas (Robertson, et al. 1981) found that when small reef areas (about $20m^2$) were manipulated in regards to resource availability, damselfish populations were not at the carrying capacity of the habitats tested. Robertson et al. (1981) reported that adult densities could be increased without apparent detriment to the existing adult population and without reducing juvenile recruitment. To explain their result, they speculated that juvenile recruitment is insufficent to maintain saturation and/or predation keeps densities below saturation levels.

This paper examines the carrying capacity and community organization of two guilds of coexisting coral reef fishes, chaetodontids and pomacanthids, through experimental manipulation of their population densities at two reef sites that differed in resource availability. Thus, populations and carrying capacity refer to those of the two feeding guilds rather than to single species populations. Both groups are most abundant on well-developed coral reefs where the fish species overlap completely in distribution but utilize different food resources. In the Caribbean, chaetodontids (butterflyfishes) eat corals, crustaceans, and polychaetes (Randall 1967; Birkeland & Neudecker 1981) whereas pomacanthids (angelfishes) feed primarily on sponges (Randall & Hartman 1968).

Species composition and relative abundance of chaetodontid and pomacanthid fishes were sampled at four sample transects in two habitats differing in resource quality as expressed in terms of surface cover of corals, gorgonaceans, and sponges. The hypothesis that local populations of chaetodontid and ponacanthid fishes were at the spatial carrying capacity of two different habitats was tested by: 1) quantifying baseline species abundances by visual censusing, 2) selectively removing relatively large numbers of the three most abundant species, roughly in proportion to their relative abundances, and 3) recensusing the same sites after two years and comparing species abundance and composition.

If the carrying capacity of a particular reef area depends on availability of resources, such as food and/or shelter sites, then local population densities should vary consistantly betwen different areas before and after the removals. If local population densities are at the carrying capacity of the habitat, then densities of reestablished populations should not exceed those prior to the perturbation. If local populations are not saturated however, then densities should fluctuate above or below preremoval levels. If local populations are at equilibrium, they should be resilient after disturbance and given time to recover they should again exhibit the same total and relative abundances of species (Connell 1978; Sousa 1979). If habitat quality, in part, determines carrying capacity and community structure, species composition from two sites within each side of the canyon should be more similar than between the two different habitats.

A major criticism of the stochastic view of reef fish community organization regards the scale of past experiments (Gladfelter et al. 1980; Anderson et al. 1981), but this criticism also applies to experiments of Smith & Tyler (1972, 1973a, b, 1975) which emphasized deterministic patterns of community structure. Colonization of small artificial reefs and recolonization of denuded patch reefs has exhibited a high degree of variability in species composition between replicate samples leading to the conclusion that species composition results from chance factors (Russell et al. 1974; Sale & Dybdahl 1975; Sale 1978b, 1979; Talbot et al. 1978). However, those reef areas were so small in relation to the large available species pool that they could only accomodate a fraction of the available species, which resulted in low similarity of within-habitat diversity (Schoener 1974; Gladfelter et al. 1980). My experiments neutralized those criticisms by manipulating reef areas that are an order of magnitude larger (200 m^2) than most previous experiments, and two families of reef fishes with relatively small regional species pools (5 chaetodontids and 4 pomacanthids). Potential recruits, which were never observed in Salt River Canyon included *Chaetodon ocellatus* and *C. sedentarius* which are relatively rare at St. Croix, and the pomacanthid *Centropyge argi*.

MATERIALS AND METHODS

Data Base

Three sources of data comprise the basis for my analyses: 1) observations and removals made during 13 scuba excursions (38 hrs) from underwater habitat Hydrolab at St. Croix, U.S. Virgin Islands during National Undersea Laboratory System (NULS) Mission 78-1 (May and June 1978); 2) observations made during NULS Mission 80-1 (February - March 1980) in 13 excursions yielding an observation period of about 35 hrs; and 3) additional scuba dives made in Salt River Canyon after Mission 80-1.

Study Sites

Hydrolab is located on a sand bottom in 15.5 m of water about 30 m north of the barier reef fronting Salt River Estuary and about 5 m west of the east slope. Observations in Salt River Submarine Canyon were made along four 100 m transect lines established in 1978 (Birkeland & Neudecker 1981) along the 15 and 30 m isobaths on the east slope and west wall.

Both sides of Salt River Canyon support coral reef development but differ in submarine topography, species composition, and species abundance of benthic invertebrates and fishes. West wall transects covered a more structurally complex habitat than those on the east slope. Steep faces, cracks and overhangs resulting from slumping of large coral blocks from the canyon wall were characteristic of the west wall sites. Vertical grooves cut through the wall and their side tributaries serve as avenues of sediment transport (Adey et al. 1977). Among the anthozoans, scleractinian corals and antipatharians were far more abundant on both west wall transects than at either depth on the east slope (Birkeland & Neudecker 1981). Corals were more abundant at the 15 m isobaths, except for Agaricia which was more prevalent at 30 m depths (Birkeland & Neudecker 1981).

East slope transects had much less vertical relief and extended over a more gentle sloping bottom of 15 - 20 degrees. The substratum was more unconsolidated at east slope sites and contained many cobble-filled troughs (Adey et al. 1977). While scleractinian corals occupied less of the substratum, plexaurid gorgonaceans accounted for 80% of surface cover by anthozoans (Birkeland & Neudecker 1981).

Fish Censuses

Populations of all species of chaetodontid and pomacanthid fishes were quantified by visual, censuses taken repeatedly over about 25 days in 1978 and 1980. Abundance was determined by swimming along each transect line and counting all individuals seen within 1 m to either side and within 2 m above the line, yielding sample areas of 200 m^2. Counts were made during the day (0600-1800 hrs) when these fishes were actively foraging. Table 1 shows the mean total abundance of all chaetodontid and pomacanthid fishes before the 1978 removals. *Chaetodon capistratus*, *Holacanthus tricolor* and *C. aculeatus* were the most abundant species throughout the canyon when the removals were made accounting for more than 90% of all chaetodontid and pomacanthid fishes present.

Removal Experiment

Fishes were initially collected for stomach analyses at the end of observations in 1978. It was subsequently realized that the censuses and collections began a removal experiment that could compare spatial carrying capacity of the different reef areas (west and east) and their species compositions before and at some time after the removals. Because transects were repeatedly sampled over several days before the collections in 1978, some fish were known as individuals that lived at certain places along the transects. Fish were first located along a transect, pursued, and speared.

Fifteen individuals (6 *C. aculeatus*, 5 *C. capistratus*, and 4 *H. tricolor*) were removed between the west wall transects and 13 (6 *C. aculeatus*, 5 *C. capistratus*, and 2 *H. tricolor*) were collected from between the east slope transects. Numerically, these collections approximately represented total removal of these chaetodontid and pomacanthid fishes from the transect sites (Table 1). After the 1978 collections, no other was made at Salt River Canyon. These were no major environmental perturbations that could have caused noticeable changes in the chaetodontid and pomacanthid populations there.

Followup Censuses and Analyses

Transect areas were allowed two years to recover after the removals. Chaetodontid and pomacanthid fishes breed between January and May (Munro,

Table 1. Average total and relative abundance (%) of chaetodontid and pomacanthid fishes at Salt River Canyon, St. Croix before and at the time of the removal in 1978 and again two years later. The number of fish removed from the west and east transects are given (NR).

Species		West Wall					East Slope			
		15 m		30 m			15 m		30 m	
	West NR	1978	1980	1978	1980	East NR	1978	1980	1978	1980
Chaetodontidae										
Chaetondon aculeatus	6	1.14 (15)	1.17 (15)	2.25 (38)	1.33 (27)	6	0.33 (9)	0.33 (15)	1.0 (31)	0.83 (29)
C. capistratus	5	5.29 (67)	3.33 (42)	1.50 (26)	2.17 (43)	5	2.22 (63)	0.50 (23)	1.0 (31)	0.50 (13)
C. striatus								0.33 (15)		
Pomacanthidae										
Holacanthus ciliaris		0.48 (7)	0.67 (9)							
H. tricolor	4	0.71 (9)	2.67 (34)	1.75 (30)	1.33 (27)	2	0.33 (9)	0.83 (38)		1.0 (29)
Pomacanthus arcuatus		0.14 (2)		0.38 (6)	0.17 (3)		0.67 (19)	0.17 (9)	1.25 (38)	0.17 (5)
P. paru										1.0 (29)
Average Total Abundance		7.86	7.83	5.87	5.0		3.55	2.16	3.25	3.50
Relative abundance of *C. aculeatus*, *C. capistratus*, and *H. tricolor*		91%	91%	94%	97%		81%	76%	62%	66%
Number of species		5	4	4	4		4	5	3	5

Gant, Thompson and Reeson 1973 Neudecker and Lobel 1982) and consequently juvenile recruits are available roughly between February and July. Therefore, transects were probably exposed to two year classes of potential recruits before the comparative censuses in 1980. Transects were again sampled repeatedly and changes in species abundance were examined. Because I knew each population's species composition before the removals, it was possible to compare changes in each species' relative abundance. Statistical analyses were conducted with Biomedical Computer Programs P-Series (Brown 1977) and the Statistical Package for the Social Sciences (Nie et al. 1975); both run on the University of California, Davis, Burroughs 6700 computer.

RESULTS

Overall, there was a slight tendency for lower total abundances after the removals since all transects averaged 5.1 ± 2.2 fishes in 1978 and 4.6 ± 2.4 in 1980, but these differences are not significant (Table 1). *Chaetodon capistratus*, *tricolor*, and *C. aculeatus* were again the most abundant species at any transect and on the average accounted for 94% of all chaetodontid and pomacanthid fishes at the west wall and 71% at the east slope sites (Table 1). The single most abundant species was *C. capistratus*, exhibiting a mean relative abundance on all transects of 38.5% (range 13-67%).

When the average number of fishes at any one transect was compared between 1978 and 1980, by the student's t-test, there were no significant differences between guild population densities before and after the removals ($p > 0.05$, Table 2). These differences were also compared simultaneously by a Hotellings T^2 test (BMDP-3D; Brown 1977) and were

Table 2. Comparison of mean total abundances (average total number) of chaetodontid and pomacanthid fishes at each transect between 1978 and 1980.

Site	Total Y Abundance ± SE (N) 1978	1980	t value	(df)	Two tailed Probability
West 15 m	7.86 ± 0.91 (7)	7.83 ± 0.70 (6)	0.02	(11)	0.984
West 30 m	5.87 ± 0.64 (8)	5.00 ± 0.26 (6)	1.13	(12)	0.282
East 15 m	3.55 ± 1.8 (9)	2.16 ± 0.8 (6)	1.76	(13)	0.101
East 30 m	3.25 ± 2.1 (4)	3.50 ± 1.4 (6)	-0.23	(8)	0.822

Table 3. Comparison of fish abundances on 15 and 30 m isobaths between the east and west sides of Salt River Canyon. Because censuses repeated over time were not independent samples and higher densities were expected at west wall sites, standard errors were corrected (SE) with an estimate of covariance between successive counts and the t-tests were adjusted (t_A) accordingly.

		Total Y Abundance ± SE (N)				
Depth	Year	West	East	t_A value	(df)	Two tailed Probability
15 m -	1978	7.86 ± 1.5 (7)	3.55 ± 0.4 (9)	3.59	(14)	$p < 0.01$
15 m -	1980	7.85 ± 1.2 (6)	2.16 ± 1.3 (6)	4.17	(10)	$p < 0.01$
30 m -	1978	5.87 ± 0.9 (8)	3.25 ± 1.1 (4)	2.83	(10)	$p < 0.02$
30 m -	1980	5.00 ± 1.0 (6)	3.50 ± 1.3 (6)	1.81	(10)	$p < 0.05$

again found not to be significantly different.

Counts at the west wall sampled a more structurally complex habitat with a greater surface cover of corals. Significantly more chaetodontid and pomacanthid fishes inhabited west sites compared with east slope sites both before and after the removals (Table 3). The relative relationship of overall mean total abundance at each transect was the same in 1978 and 1980 (Tables 1, 2, 3).

While overall average total abundances had nearly returned to pre-removal levels after two years, there were similarities and differences in species composition and relative abundance. The three most abundant species in 1978, *C. aculeatus*, *C. capistratus* and *H. tricolor*, were again the most prevalent species in 1980. However, *C. striatus* and *Pomacanthus paru* occurred on transects for the first time in 1980, while *P. arcuatus* became locally extinct at the 15 m west wall site.

I compared the mean relative abundance of each species at each transect between the baseline and resurveyed censuses. Of the 28 pairwise comparisons (7 species at 4 sites) in 9 cases a species was not present in 1978 or 1980, 1 species exhibited identical abundances at both times at one site, in 7 cases a relative increase in abundance occured, and 11 cases were of species which were less abundant in 1980. Of the 18 valid comparisons, only 3 were significantly different. *C. capistratus* was significantly less abundant (*P* = 0.05, t-test) at the west 15 m in 1980 whereas *H. tricolor* significantly increased in abundance (*P* = 0.04, t-test) at the same site. At the east slope 15 m site, *C. capistratus* was significantly less abundant (*P* = 0.04, t-test) in 1980, while *H. tricolor* made slight gains in abundance and *C. striatus* occurred for the first time.

Fish assemblages at each transect were examined for changes in species composition by calculating the percentage of species turnover (Talbot et al. 1978). There was a 20% species turnover at the 15 m west wall transect, a result of the local extinction of *Pomacanthus arcuatus* in 1980, but that species had comprised only 2% of the 1978 population (Table 1). The east slope 15 m transect also exhibited a 20% turnover because of the gain of *C. striatus*. Species composition did not change at the 30 m west site, but the relative abundances of *C. aculeatus* and *C. capistratus* inverted (Table 1). The most species turnover occurred at the 30 m east slope transect resulting from the addition of *H. tricolor* and *P. paru* with a concomitant 33% decrease in the relative abundance of *P. arcuatus*. However, it should be noted that the manipulated species were less abundant (66%) at the 30 m east transect at the time of removal than at the other transects.

DISCUSSION

Chaetodontid and pomacanthid fishes overlapped completely in distribution and no cases of interspecific aggression were observed. Clarke (1977) reported broad habitat niches and high overlap by Caribbean chaetodontids such that any one habitat could support various combinations of species. *Chaetodon capistratus* is an active generalist that browses on anthozoans (Birkeland & Neudecker 1981) and was the most abundant species of the two families on most transects and throughout the canyon. *C. aculeatus*, another particularly abundant species, exhibits different foraging patterns because it is a predator but overlaps with *C. capistratus* on preferred prey such as fish eggs and some crustaceans (Birkeland & Neudecker 1981). The pomacanthid species primarily eat sponges and also overlap with each other in some of the species they take (Randall 1967; Randall & Hartman 1968).

Although the transects showed a slight tendency towards lower average total abundances, these changes were not significant (Table 2). This resiliency in total numbers suggests a finite carrying capacity for these fishes at the study sites and that local populations were saturated with respect to number of individuals. Consequently, when viewed at the guild or family level, the number of individuals present seems to be determined by the resource availability at that site. This conclusion is supported by the fact that relative differences in total abundances between west and east transects were the same after the removals as before (Tables 1, 2, 3).

That fish assemblages could be organized in a deterministic manner at the guild but not the species level has been suggested before (Sale & Dybdahl 1975; Bradbury 1977). Bradbury & Goeden (1974) suggested that in complex reef fish communities the guilds of species functioned as single species do in less complex system.

One of the factors that may determine the number of individuals present at a site is the amount of structural complexity. While it has been shown that local species diversity is a function of small scale spatial heterogeneity (Risk 1972; Luckhurst & Luckhurst 1978; Gladfelter et al. 1980), in this study the less complex habitats contained one more species (6) than did the more complex sites (5; Table 1). However, the structurally more diverse sites had significantly greater absolute abundances (Table 3); and therefore differences in species number are mainly the result of additions or deletions of relatively rare species.

While average total abundances returned to predisturbance levels, there were some changes in species composition and relative abundance of some species within transects. East slope sites were of lower quality than those on the west wall because of lower coral cover and diversity (Birkeland & Neudecker 1981) and less structural complexity. Removals had the greatest effect on species turnover and diversity at the 30 m east slope site (Table 1, 2) which is partly a result of the lower initial abundances of the three manipulated species.

At St. Croix, the total species pool of chaetodontid and pomacanthid fishes is relatively small. Three of five chaetodontid species occurred on sample transects while the remaining two, Chaetodon ocellatus and C. striatus, are uncommon at most reefs at St. Croix. Four of the five pomacanthid species were observed and the remaining one, Centroypge argi, is a habitat specialist (Clarke 1977). Therefore, in this case, random patterns of species composition is not the result of small local samples from a large regional species pool. It should also be noted that both of the "new" species in 1980, C. striatus and Pomacanthus paru, were occasionally observed in Salt River Canyon in 1978 but did not occur on sample transects until after the removals.

Although we have observed breeding by all of the three manipulated species in Salt River Canyon (Neudecker & Lobel in press), we have no data on their fecundity, larval survivorship, or recruitment and can not say whether these local populations were self sustaining or not. However, the lack of significant difference in total abundance at each site (Table 2) indicates that space was probably occupied by new recruits rather than by range extensions of remaining adults. This conclusion is supported by the fact that recruits colonizing artificial and defaunated natural reefs are almost always recently- metamorphosed juveniles (Randall 1963; Gunderman &

Popper 1975; Talbot et al. 1978). Chaetodontid and pomacanthid fishes are known to be site-attached and adults probably remain at a particular site for life (Reese 1973, 1975; Allen 1980). However, the conclusion that recolonization, after two years, came from new recruits does not preclude the possibility that range extensions of resident adults could have initially occurred as suggested by Sale (1979).

Talbot et al. (1978) experimentally supported the stochastic view of community organization and suggested that predation was the random disturbance factor which promoted high within-habitat diversity. At the level of species, my results support that view. However, it must be mentioned that adult chaetodontids and pomacanthids are widely believed to be relatively immune from predators (Ehrlich 1975; Clarke 1975; Allen 1980). This opinion is based on their absence from the stomachs of predators (Hiatt & Strasburg 1960; Randall 1967; Hobson 1974) and the fact that individual chaetodontids have been known to remain at specific sites for as long as 10 years (Reese 1973, 1975; pers. comm.). This situation contrasts sharply with the average individual longevities of all reef fishes together, of less than one year reported by Talbot et al. (1978). Therefore, when time between disturbances (e.g. predation) is long, one or a few species may become locally predominant while others go extinct. This may explain the high relative abundances of _C. capistratus_ at both 15 sites in 1978 (Table 1).

An interesting component of the equilibrium view of community organization is that along with population densities at carrying capacity, it assumes that local populations are at competitive equilibrium. If they were not, there would be no need to invoke fine niche partitioning and specialization to allow coexistence. This removal experiment has shown that local populations are probably saturated in numbers of individuals. Since food resources are partitioned to some extent but also overlap (Birkeland and Neudecker 1981) species composition over time appears to be unpredictable. Species composition after perturbation may be more the result of chance events than of evolved differences in resource utilization. Whether local coexistence results from chance associated with recruitment and/or the availability of space, species composition is not definitely predictable from a knowledge of preremoval species composition alone.

ACKNOWLEDGEMENTS

This research was supported by a NOAA (NULS 80-1) grant to Steve Neudecker and by a grant to William J. Hamilton III, Steve Neudecker and Peter Ward from the Institute of Ecology, University of California, Davis.

My studies would not have been possible without the help of many persons to which I am grateful. I thank Bill and Joann Schane, Barry Walden, Rod Catanach and Joe Langersdorf for execution of perfect missions and their operation of the Hydrolab. I appreciate the long hours and sleepless nights Scott Grace and Don Morris gave as our surface support team. Bob and Sonia Dill, Dennis Hubbard, and the staff of the West Indies Laboratory provided additional support. Hal Grade gave much help with the computerized analyses. Bill Hamilton served as a mentor, fellow aquanaut, and reviewed drafts of this paper. Russ Davis, Keith Hopper, Peter Moyle, Matt Rowe, Steve Smith and Charles van Riper III criticized the paper and gave many helpful suggestions.

LITERATURE CITED

Adey, W., W. Gladfelter, J. Ogden & R. Dill. 1977. *Field guidebook to the reefs and reef communities of St. Croix, Virgin Islands. Third Intl. Coral Reef Symp.*, Atlantic Reef Committee, University of Miami, 52 pp.

Allen, G.R. 1980. *Butterfly and angelfishes of the world*, Vol. 2. New York, Wiley-Interspace, 352 pp.

Anderson, G.R.V., A.H. Ehrlich, P.R. Ehrlich, J.D. Roughgarden, B.C. Russell & F.H. Talbot. 1981. The community structure of coral reef fishes. *Am. Nat.*, Vol. 117, pp. 476-495.

Birkeland, C. & S. Neudecker. 1981. Foraging behavior of two Caribbean cheatodontids: *Chaetodon capistratus* and *C. aculeatus*. *Copiea*, Vol. 1, pp. 169-178.

Bradbury, R.H. 1977. Independent lies and holistic truths: towards a theory of coral reef communities as complex systems. *Proc. Third Int. Coral Reef Symp.*, Vol. 1, pp. 2-9.

Bradbury, R.H. & G.B. Goeden. 1974. The partitioning of the reef slope environment by resident fishes. *Proc. Second Int. Coral Reef Symp.*, Vol. 1, pp. 167-178.

Brown, M.B., ed. 1977. *BMDP-77 biomedical computer programs P-Series*. University of California Press, Berkeley, 880 pp.

Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.*, Vol. 40, pp. 277-289.

Cody, M.L. 1968. On the methods of resource division in grassland bird communities. *Am. Nat.*, Vol. 102, pp. 107-148.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science, Vol. 199, pp. 1302-1310.

Diamond, J.M. 1975. Assembly of species communities. In, Ecology and evon of communities, edited by M.L. Cody & J.M. Diamond, Belknap, Cambridge, Mass, pp. 342-444.

Ehrlich, P.R. 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst., Vol. 6, pp. 211-247.

Gladfelter, W.B., J.C. Ogden & E.H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology, Vol. 61, pp. 1156-1168.

Gundermann, N. & D. Popper. 1975. Some aspects of recolonization of coral rocks in Eilat (Gulf of Aqaba) by fish populations after poisoning. Mar. Biol., Vol. 33, pp. 109-117.

Grassle, J.F. 1973. Variety in coral reef communities. In, Biology and Geology of Coral Reefs, edited by O.A. Jones and R. Endean, Academic Press, New York, Vol. 2. Biology, pp. 247-270.

Hiatt, R.W. & D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr., Vol. 30, pp. 65-127.

Hobson, E.S. 1974. Feeding relationships of teleostian fishes on coral reefs in Kona, Hawaii. Fisheries Bull., Vol. 72, pp. 915-1031.

Kohn, A.J. 1968. Microhabitats, abundance, and food of Conus on atoll reefs in the Maldive and Chagos Islands. Ecology, Vol. 49, pp. 1046-1061.

Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow water marine invertebrates of tropical oceanic islands. Limnol. Oceanogr., Vol. 16, pp. 332-348.

Luckhurst, B.E. & K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol., Vol. 49, pp. 317-323.

MacArthur, R.H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, N.Y.

Munro, J., V. Gant, R. Thompson and P. Reeson. The spawning seasons of Caribbean Reef Fishes. J. Fish. Biol. 5:69-84.

Neudecker, S. & P.S. Lobel. In press. Mating systems of chaetodontid and pomacanthid fishes at St. Croix. Z. Tierpsychol.

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner & D.H. Bent. 1975. SPSS Statistical Package for the Social Sciences. McGraw-Hill, New York, 675 pp.

Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3:31-47.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami), Vol. 5, pp. 665-847.

Randall, J.E. & W.D. Hartman. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol.. Vol. 1, pp. 216-225.

Reese, E.S. 1973. Duration of residence by coral reef fishes on "home" reefs. Copiea, Vol. 1, pp. 145-149.

Reese, E.S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family chaetodontidae. *Z. Tierpsychol.*, Vol. 37, pp. 37-61.

Risk, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bull.*, Vol. 153, pp. 1-4.

Robertson, D. R., S. G. Hofman, and J. M. Sheldon. 1981. Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. Ecology 62(5): 1162-1169.

Russell, B.C., F.H. Talbot & S. Domm. 1974. Patterns of colonization of artificial reefs by coral reef fishes. *Proc. Second Int. Coral Reef Symp.*, Vol. 1, pp. 207-215.

Sale, P.F. 1974. Mechanisms of co-existence in a guild of territorial fishes at Heron Island. *Proc. Second Int. Coral Reef Symp.*, Vol. 1, pp. 193-206.

Sale, P.F. 1976. The effects of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. *J. Exp. Mar. Biol. Ecol.*, Vol. 24, pp. 297-306.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.*, Vol. 111, pp. 337-359.

Sale, P.F. 1978a. Coexistence of coral reef fishes: a lottery for living spaces. *Environ. Biol. Fish.*, Vol. 3. pp. 85-102.

Sale, P.F. 1978b. Chance patterns of demographic change in populations of territorial fish in coral rubble patches of Heron Reef. *J. Exp. Mar. Biol. Ecol.*, Vol. 34, pp. 233-243.

Sale, P.F. 1979. Recruitment, loss and coexistence in a guild of territorial coral reef fishes. *Oecologia*, Vol. 42, pp. 159-177.

Sale, P.F. & R. Dybdahl. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology*, Vol. 56, pp. 1343-1355.

Schoener, A. 1974. Colonization curves for planar marine islands. *Ecology*, Vol. 55, pp. 818-827.

Slobodkin, L.B. & H.L. Sanders. 1968. On the contribution of environmental predictability to species diversity. *Brookhaven Symp. in Biol.*, Vol. 22, pp. 82-93.

Smith, C.L. & J.C. Tyler. 1972. Space resource sharing in a coral reef fish community. *L.A. County Nat. Hist. Museum Sci. Bull.*, Vol. 14, pp. 125-170.

Smith, C.L. & J.C. Tyler. 1973a. Direct observations of resource sharing in coral reef fishes. *Helgolander Wiss Meersunt*, Vol. 24, pp. 264-275.

Smith, C.L. & J.C. Tyler. 1973b. Population ecology of a Bahamian suprabenthic shore fish assemblage. *Am. Museum Novitates*, Vol. 2528, pp. 1-38.

Smith, C.L. & J.C. Tyler. 1975. Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. *Am. Museum Novitates*, Vol. 2572, pp. 1-18.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, Vol. 60, pp. 1225-1239.

Talbot, F.H., B.C. Russell, & G.R.V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? *Ecol. Monogr.*, Vol. 48, pp. 425-440.