



Feeding Niche Separation in a Guild of Tropical Reef Fishes (Holocentridae)

William B. Gladfelter, William S. Johnson

Ecology, Volume 64, Issue 3 (Jun., 1983), 552-563.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Ecology

©1983 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

FEEDING NICHE SEPARATION IN A GUILD OF TROPICAL REEF FISHES (HOLOCENTRIDAE)¹

WILLIAM B. GLADFELTER

*West Indies Laboratory, Fairleigh Dickinson University,
Christiansted, St. Croix, 00820 United States Virgin Islands*

AND

WILLIAM S. JOHNSON

Department of Biology, Goucher College, Towson, Maryland 21204 USA

Abstract. To increase our understanding of how large numbers of similar species of reef fishes coexist, we have determined the components of feeding-niche separation among the members of a feeding guild of coral reef fishes. The seven West Indian species of shallow-water squirrelfishes (Holocentridae) comprised >99% of the nocturnally active, benthic-crustacean-feeding fishes at five sites off St. Croix, Virgin Islands. Resource utilization frequencies were determined for food and foraging habitat. Food was partitioned by taxon between the four species that consumed predominantly shrimps and the three species that ate mainly crabs. Food was secondarily partitioned by body size of prey items, particularly in the principal food category. Differences in foraging microhabitat (position within a reef zone) were as important as food differences in separating species. In all cases but one, overall feeding niche overlap was $\approx .25$ or less, with a mean value of $.13$. This low value contradicts statements that reef fishes are generalists with broadly overlapping resource utilization and, compared with overlap values in other guilds, suggests that the mechanisms permitting great local diversity within coral reef fish guilds are not basically different from those operating in other ecosystems. The mean overlap in food among the 6 commonest species was significantly different from the mean overlaps of 50 randomly generated competition-free communities (Sale 1974), suggesting that interspecific competition has played a role in the evolution of this assemblage.

Key words: *coexistence; coral reef; ecological separation; feeding niche; fish; foraging habitat; guild; Holocentridae; interspecific competition; overlap; resource partitioning; Virgin Islands.*

INTRODUCTION

Many of the recent studies of fish communities have been aimed ultimately at increasing our understanding of the mechanisms permitting the coexistence of large numbers of fish species in coral reef environments. Much of this work has involved either the statistical analysis of recruitment patterns on replicate small natural or artificial structures (Nolan 1975, Sale and Dybdahl 1975, Molles 1978, Talbot et al. 1978) or the analysis of similarity between the faunas of small or large patch reefs (Gladfelter and Gladfelter 1978, Smith 1978, Gladfelter et al. 1980, Ogden and Ebersole 1981). These studies have generated considerable discussion about the relative importance of stochastic or deterministic factors in structuring reef fish communities (Smith and Tyler 1975, Sale 1977, 1978, Smith, 1978) but in themselves have not really increased our understanding of the mechanisms permitting high local diversity.

At the root of this whole problem of how diversity is maintained in coral reef fish communities is really the implied question: how can the coexistence of large numbers of species be maintained in light of the competitive exclusion principle? More specifically, fish communities are composed of a relatively small number of subsets of species (guilds; Root 1967) whose

members have similar resource requirements. According to authors who have cataloged or described resource utilization (Hiatt and Strasburg 1960, Gosline 1965, Randall 1967, Smith and Tyler 1972, 1975, Vivien 1973, Hobson 1974, Hobson and Chess 1978), the members of such groups often show great similarity in resource utilization. However, it remains to be shown whether the members of such groups do in fact show sufficient ecological separation in the utilization of a resource category to permit coexistence under a given set of resource and consumer densities. The main resources potentially limiting to reef fishes are food and (sheltering) space. To date, only a few studies have quantified differences in resource utilization among similar species of reef fishes. In the most thorough of these, Clarke (1977) determined habitat overlaps among tropical Atlantic chaetodontids and pomacentrids; the magnitude of overlap was relatively high between most of these species, as suggested by earlier statements. However, as Schoener (1974) pointed out, in aquatic systems ecological separation is more often by food than by habitat, but quantitative analyses of ecological separation on the basis of food use among reef fishes are generally lacking. Roughgarden (1974) attempted to show that resource utilization curves in Atlantic serranids (roughly constructed from Randall's [1967] data) were relatively narrow and showed moderate separation, whereas among herbivorous fishes (also based on Randall [1967]) curves would be broader with

¹ Manuscript received 15 April 1980; revised 1 March 1982; accepted 6 May 1982.

greater overlap, but these statements were only weakly supported by the cited data.

In the present study we have therefore sought to demonstrate that the members of one feeding guild of tropical reef fishes do show substantial ecological separation in their utilization of food resources (food and foraging habitats) and to show the relative importance of the three main components of feeding niche separation (Schoener 1974): prey type, prey size, and foraging location.

Eight species of shallow-water squirrelfishes (Holocentridae) are found in reef habitats of the West Indies (Böhlke and Chaplin 1968). Seven of these (all in the Holocentrinae) feed primarily at night on benthic crustacea (Randall 1967): *Holocentrus rufus*, *H. ascensionis*, *Flammeo marianus*, *Adioryx vexillarius*, *A. coruscus*, *A. poco*, and *Plectrypops retrospinis*. The eighth species, *Myripristis jacobus*, is a water column forager and has been omitted from the present study. Studies in other parts of the world also indicate that squirrelfishes are typically nocturnally active feeders on benthic crustacea (Hiatt and Strasburg 1960: Marshall Islands, Hobson 1968: Gulf of California, Hobson 1974: Hawaii, Vivien and Peyrot-Clausade 1974: Madagascar). All seven species of bottom-foraging holocentrids coexist at some reef sites off St. Croix, Virgin Islands. In these environments they comprise >99% of the individual fishes foraging at night for benthic crustaceans, excluding the much smaller apogonids (Randall 1967, Gladfelter and Gladfelter 1978: Table 8), and thus comprise virtually the entire guild. In light of earlier comments about local species diversity this group was chosen for analysis because of the ostensibly great similarity in the diets and habitats of its members. Should the members of this group prove to show ecological separation, then it is also likely that other groups of reef fishes that have been considered to be composed of broad generalists may likewise show separation.

METHODS

Data collection

A total of 307 individuals of seven species of bottom-foraging holocentrids (squirrelfishes) was speared late at night during January and February 1979 at five sites off the north coast of St. Croix, Virgin Islands. From east to west the sites were: Patch Reef 16 (17°45'54"N, 64°35'06"W), Channel Rock (17°46'19"N, 64°35'18"W), Tague Bay Reef (17°47'33"N, 64°35'34"W), Buck Island Reef (17°47'33"N, 17°37'03"W), and Canebay (17°46'34"N, 64°48'49"W). At each site fishes were collected in several major reef zones (= macrohabitats), the characteristics of which are summarized in Table 1. Generally the deepest, most seaward zone was also the most structurally complex.

In each zone (macrohabitat) visual censuses were carried out at night by swimming slowly using SCUBA

along a nonoverlapping zigzag pattern. Small (Super Q) lights were used to minimize disturbance of the foraging fishes. Census data were standardized to number of individuals counted per hour of census. Intra-zonal or microhabitat differences in distribution of the foraging fishes were clear-cut but seemed important only in one zone at the Canebay site and therefore were determined only at that site.

All individuals were speared between 2300 and 0100, 4–6 h after the onset of feeding. This time period yielded the maximum amount of identifiable gut contents; earlier in the evening the quantity of food was less, and gut contents of individuals speared later (just before dawn) were in a more advanced state of digestion and thus less amenable to analysis. Within 1 h of spearing, the abdominal cavity was injected with full-strength formalin. Within 12 h of collection, each individual was measured (standard length), and its stomach removed and placed in a vial of 80% ethanol.

Stomachs were subsequently dissected and the contents analyzed. Each item was identified to taxonomic group, and its body length (or greatest linear body dimension, exclusive of appendages) measured using a dissecting microscope with ocular micrometer. The proportional contributions by number of prey items in each of nine major taxonomic categories to the diets of each fish species was then determined. The proportion of the volume of each gut that was filled was estimated. The food items of these nine categories were combined for each holocentrid species at each of the five sites for volumetric analysis. Volume of food items was determined using a cylinder (hypodermic syringe tube) graduated to either 0.1 or 0.01 mL. Proportion of each prey category of total volume for each species was determined. Frequency of occurrence of items in each prey category among the individuals of each fish species was determined.

Data analysis

Niche breadth in the utilization of food resources was calculated using the Shannon-Wiener formula:

$$H' = -\sum_{i=1}^n p_i \log_2 p_i,$$

where p_i is the proportion by volume of a particular prey category, for n prey categories. Proportion in the diet by volume best reflected resource utilization (rather than proportion by number of items) because individual items varied in volume by about five orders of magnitude, and the contribution as food of small prey items could not be equated with that of large items. The above formula was also applied to the number of prey items in each prey category, thus yielding the standard measure of prey species diversity for each holocentrid species. A third measure of dietary breadth was the sum of proportional occurrences of all prey items in each holocentrid species (Table 2). Foraging habitat breadth was determined using the above for-

TABLE 1. Characteristics of habitats censused for holocentrid abundance.*

Site	Zone	Depth (m)	Relative substrate complexity	General oceanic setting	Habitat characteristics
PR 16		2-5	Medium	Lagoonal (semiexposed)	Reef flat and edge, interface with sea-grass bed; few caves, scattered <i>Acropora palmata</i> †
ChR	Base	11-15	Medium-high	Open bank	Coral heads, moderately diverse, some large and eroded with caves beneath; interface with sand
ChR	Palmata	3-7	Medium-high	Open bank	Monospecific stands of <i>A. palmata</i> with small corals and caves at base
TB	Forereef	3-9	Medium-high	Semiopen bank	Coral heads moderately diverse; old and broken <i>A. palmata</i> stands; large <i>Porites porites</i> ; few caves
TB	Backreef	2-3	Medium-high to low	Lagoonal	Broken <i>A. palmata</i> stands, coral heads, sand flats
BI	Forereef	3-8	High	Open bank	Porous reef framework mainly of fallen <i>A. palmata</i> ; stands of live <i>A. palmata</i> ; some coral heads
BI	Grottos	1-4	High	Lagoonal	Old large coral heads with caves; <i>A. palmata</i> stands; fields of dead and broken <i>A. palmata</i> ; caves of all sizes
BI	Lagoon	3	Very low	Lagoonal	Carbonate pavement with scattered small coral heads
CB	Buttresses	7-15	Very high	Shelf edge	Large-scale 3-dimensional reef structures 10 m wide separated by sand channels 5 m deep. Surface with high diversity of coral species; highly porous with variety of caves
CB	Gorgonians	3-7	Low	Bank	Flat carbonate pavement with moderate diversity of scattered coral heads, gorgonians and sponges
CB	Inshore	1-2	Low	Exposed shore	Flat pavement with some large cavities and a few <i>A. palmata</i> ; high turbulence and turbidity from breaking waves

* Arranged east to west and deep zones to shallow.

† Very large branched coral forming thicket-like growths.

mula where p_i was the proportional occurrence of each species in the i^{th} habitat.

Resource use overlaps between all holocentrid species pairs were calculated on the basis of prey type, prey size, and habitat distribution. Niche overlap on the basis of prey type was calculated as:

$$T = 1 - 0.5 \sum_{i=1}^n |p_{xi} - p_{yi}|,$$

where p_{xi} and p_{yi} are the proportions by volume of the i^{th} resource (prey category) for all fish species pairs x, y (Schoener 1968). This index theoretically ranges from 0 for species with no overlap to 1 for two species with all items present in the same proportions. Proportional overlap values for prey utilization based on prey size were determined independently for each of the major food categories. In the case of shrimp and crab utilization there were sufficient data to plot size frequency distributions of prey items and then to con-

struct curves to fit the data visually. The areas under the curves were adjusted to be approximately equal, and resource overlaps were then determined graphically as the proportional overlap of the areas under any two curves, i.e., $2A_o/(A_x + A_y)$, where A_o is area of overlap, and A_x and A_y are areas of prey size frequency curves for species x and y . Overlaps for other food categories with much-lower representation were estimated as the ratio of mean prey lengths between species x and y . This was found to be reasonably accurate in those cases where comparisons could be made with size frequencies (i.e., for crabs and shrimps). Overall prey use overlaps were then calculated:

$$\alpha_{x,y} = \alpha_T - \sum_{i=1}^n p_{xi}(1 - r_{xi,yi}),$$

where α_T is overlap by taxon as given above, p_{xi} is the proportional contribution (by volume) of the i^{th} food category to the diet of species x , which in species

TABLE 2. Occurrence of taxa of prey items in the guts of holocentrids: percent of individual fishes containing items of each taxon. Value for each major food category (e.g., shrimp) represents total percent occurrence of all items in that category in the guts of each species and need not equal the total occurrences of all the subcategories included in it.

	<i>Holocentrus rufus</i>	<i>H. ascensionis</i>	<i>Flammeo marianus</i>	<i>Adioryx vexillarius</i>	<i>A. coruscus</i>	<i>A. poco</i>	<i>Plectrypops retrospinis</i>
	Percent of fishes						
Fish	5.5	5.6	19.4	1.8	4.4	25.0	
Stomatopoda	12.3	11.1	17.7	5.5			
Shrimp	80.8	55.6	91.9	76.4	93.3	75.0	100.0
Stenopodidea			3.2				
Caridea (and Penaeidea)*	71.2	55.6	82.3	61.8	91.1	75.0	100.0
Alpheidae	17.8	5.6	16.1	29.1	8.9	12.5	
Callinassidae				3.6			
Scyllariidae			1.6				
Galatheidae						12.5	
Crab	76.7	77.8	41.9	78.2	48.9	25.0	
Paguridae			1.6	3.6			
Porcellanidae	1.4			1.8			
Brachyura*	76.7	72.2	41.9	78.2	48.9	25.0	
Portunidae		16.7	1.6				
Megalops larvae	9.6	5.6	6.5	7.3	2.2	12.5	
Other Crustacea	60.3	44.4	21.0	83.6	11.1	12.5	33.3
Ostracoda	13.7	11.1		1.8			
Calanoida	2.7						
Harpactacoidea				3.6			
Nebaliacea	1.4						
Mysidacea	13.7		4.8	3.6			
Cumacea			1.6	3.6			
Amphipoda (Gammaridea)	24.7	22.2	6.5	52.7	2.2	12.5	33.3
Tanaidacea	2.7	5.6	6.5	43.6	4.4		
Isopoda (Cirolanidae)	28.8	33.3	6.5	40.0	2.2		
Other	4.1	5.6		9.1		12.5	
Pycnogonida	1.4				2.2		
Polychaeta	13.7	5.6	9.7	58.2	11.1	12.5	
Sipuncula	24.7		22.6	70.9	13.3	25.0	
Ophiuroidea	8.2			16.4			
Mollusca (and Foraminifera)	57.5	5.6	17.7	50.9	2.2		
Foraminifera			1.6	1.8			
Polyplacophora				12.7			
Gastropoda*	54.8	5.6	17.7	30.9	2.2		
Keyhole limpets	4.1			1.8			
Limpets	1.4			12.7			
Opisthobranchia	1.4						
Bivalvia	1.4						

* Not including following subcategories.

pair x, y has the lower value, and $r_{xi, yi}$ is the proportional overlap by prey size of the I^{th} food category for species x and y , as determined above. The quantity $p_{xi}(1 - r_{xi, yi})$ is thus the geometric non-overlap by size within each prey taxon. Habitat overlaps were determined as:

$$\alpha_H = 1 - 0.5 \sum_{i=1}^n |p_{xi} - p_{yi}|,$$

where p_{xi} and p_{yi} are proportional occurrences of species x and y in the i^{th} habitat for n habitats (Fig. 4: solid bars). Overall niche overlaps were determined as the product of overlaps of prey and habitat utilization. Although independence of these two niche axes

was not demonstrated, we have assumed it since there are no data to suggest that availability of any type or size food is correlated with a particular reef habitat (although prey diversity is correlated with substrate complexity [Abele 1974]). Niche separation by various components was determined as $1 - \alpha$, where α is a particular component of overlap.

In order to determine if the overlap values thus determined were significantly different from random, the mean overlap with respect to food type and size of the six commonest species in this study (excluding *P. retrospinis* because of a paucity of data) was compared to the mean overlaps of 50 computer-generated competition-free communities, following the method of Sale

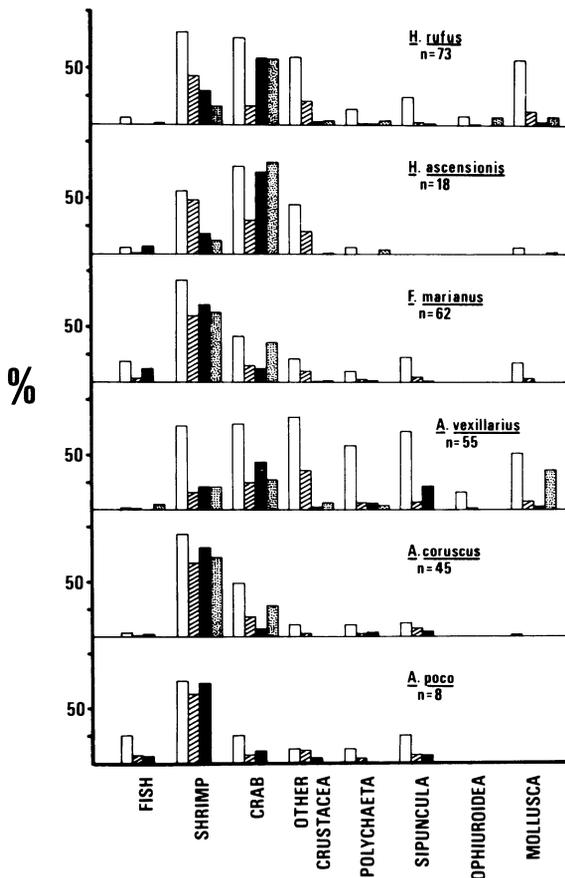


FIG. 1. Proportional representation of eight prey categories in the guts of holocentrids (*Stomatopoda included with shrimps here). White bars represent percentage of individuals of each holocentrid species in which prey category is present; hatched bars represent percentage of total number of prey items in each holocentrid species belonging to a particular prey category; black bars represent percentage of total prey volume in each holocentrid species belonging to a particular category; stippled bars are also percentages by volume, after Randall (1967). Based on total food volumes of: *Holocentrus rufus*: 23.4 mL; *H. ascensionis*: 22.6 mL; *Flammeo marianus*: 16.1 mL; *Adioryx vexillarius*: 17.9 mL; *A. coruscus*: 14.1 mL; *A. poco*: 1.2 mL; *Plectrypops retrospinis* has been omitted from the figure because of small sample size (0.3 mL).

(1974). For each species the principal food category was subdivided into size-categories (based on prey-size utilization frequency curves), 10 for crabs and 15 for shrimps, which were treated as distinct resources.

RESULTS

Benthic crustacea dominated the measured diets of all seven species of holocentrids (Fig. 1: solid bars). Shrimps and crabs (see Table 2 for taxa comprising these groups) constituted a mean of >83% by volume of measured stomach contents. In four species shrimps alone comprised a mean of 80% of the diets: *Flammeo*

TABLE 3. Variation in proportions by volume of principal gut content constituents among four species of squirrelfishes at four sites.*

	<i>Holo-</i> <i>centrus</i> <i>rufus</i>	<i>Flam-</i> <i>meo</i> <i>marianus</i>	<i>Adioryx</i> <i>vexil-</i> <i>larius</i>	<i>A. co-</i> <i>ruscus</i>	Mean
Shrimp					
Patch Reef 16	.26	.58	.18	.89	.48
Tague Bay Reef	.32	.95	.18	.89	.58
Buck Island	.30	.67	.17	.52	.42
Canebay	.42	.62	.32	.80	.53
(St. John†)	.15	.60	.21	.72	.42
Crab					
Patch Reef 16	.64	.35	.43	.11	.38
Tague Bay Reef	.54	.04	.43	.01	.26
Buck Island	.63	.01	.48	.07	.30
Canebay	.43	.12	.42	.07	.26
(St. John†)	.58	.35	.27	.28	.37

* No significant difference between sites. Friedman non-parametric "ANOVA" $\chi^2_{(shrimp)} = 5.4$; $\chi^2_{(crab)} = 5.1$; expected $\chi^2_{(0.05,4)} = 9.5$.

† Based on Randall (1967).

marianus (67%), *Adioryx coruscus* (80%), *A. poco* (73%), and *Plectrypops retrospinis* ($\approx 100\%$). In the remaining species, crabs constituted a mean of nearly 60% of the diets: *Holocentrus rufus* (59%), *H. ascensionis* (73%), and *A. vexillarius* (44%). These two groups will be referred to subsequently as shrimp and crab specialists respectively. The differences in proportions of these major food categories were relatively consistent among the major study sites and were also consistent with Randall's (1967) data from the northern Virgin Islands (Fig. 1: stippled bars, Table 3).

The proportional contribution of number of prey items to holocentrid diets had a more even distribution than contribution by volume (Fig. 1: hatched bars). Crustacea other than shrimps or crabs made a greater contribution to the diets because of their generally smaller size (>10% by number of items but <1% by volume). In the cases of both shrimp and crab specialists, a relatively greater contribution was made by the other category by number of items (20%) than by volume (12.5%), again reflecting the smaller size of items not constituting the principal prey type. In two of the three crab specialists shrimps were actually more numerous in the diets than were crabs.

The frequency of occurrence of the various prey categories in the diets of the holocentrids was more evenly distributed than were proportions by volume or number of items (Fig. 1: open bars). Values of niche breadth for prey utilization (but not including foraging habitat) gave the same relative results by all three methods used (Table 4). *Adioryx vexillarius* had the greatest niche breadth, followed by *Holocentrus rufus*. In most cases *A. coruscus* had the least niche breadth.

The various holocentrid species differed in the size

TABLE 4. Niche breadth and prey diversity values among six species of holocentrids, arranged from greatest to least mean niche breadth. Data for *Plectrypops retrospinis* insufficient for inclusion.

	<i>Adioryx vexillarius</i>	<i>Holocentrus rufus</i>	<i>Flammeo marianus</i>	<i>Holocentrus ascensionis</i>	<i>Adioryx poco</i>	<i>A. coruscus</i>
H' (prey: % of volume)	2.15	1.72	1.60	1.33	1.35	0.98
H' (prey: % of items)	2.72	2.46	2.21	1.89	1.88	1.73
Total % occurrence	5.43	3.97	2.69	2.61	2.25	2.04
H' (habitat)	3.08	3.12	2.79	2.27	2.07	2.52

of prey items taken, especially in the principal food category, i.e., shrimps or crabs (Table 5). Among the shrimp specialists the largest shrimps (greatest mean body length) were eaten by *Adioryx coruscus* (12.4 mm), followed by *Plectrypops retrospinis* (10.1 mm), *Flammeo marianus* (9.7 mm), and *A. poco* (9.1 mm). Shrimps eaten by the remaining species all had smaller mean body size. The crab specialists also differentiated their principal prey type with respect to mean body size: *Holocentrus ascensionis* ate the largest (9.8 mm) items. Crabs eaten by shrimp specialists were generally small and had about the same mean body width as those eaten by *A. vexillarius*. Resource utilization curves based on body lengths (widths of some crabs) of the principal food category overlapped broadly (Fig. 2). The modes of these curves are less than the means because the curves are all skewed to the larger-sized food items. Thus, *P. retrospinis* probably had a greater proportional utilization of larger shrimps than indicated, because the small sample size omitted the larger forms that would have increased the mean.

Among the forms with adequate sample sizes however, *A. coruscus* ate the largest proportion of large shrimps. Among the other food categories eaten (Table 5), fishes and stomatopods were generally larger than other food items in all holocentrid species. The remaining items were generally small.

Among the holocentrid species that ate principally crabs, there was a general positive correlation between fish body length (hence jaw size) and principal prey length, both between and within species (Table 5, Fig. 3). On the other hand there was a total lack of correlation among or within shrimp-eating species except for *Adioryx coruscus*, which showed a nearly significant negative relation between body length and prey length (Fig. 3). The only species which showed a significant ($r^2 = .92$; $P < .01$) regression of food size as a function of body size was *Adioryx vexillarius* for crabs (Fig. 3). Thus, within the size-range of individuals examined individual body size was not an important consideration when comparing prey size in the various species. The principal overlap in mean food

TABLE 5. Mean overall body lengths of prey items from the guts of holocentrids (with mean standard length of all individuals of each fish species with gut contents).

Fish (standard species length)		Stomato-						Other		Total	
		Fish	poda	Shrimp	Crab	Isopoda	Crustacea	Mollusca	Crustacea	Total	
<i>Holocentrus rufus</i> (150 mm)	\bar{x}	7.7	13.1	6.7	6.3	5.5	3.1	3.0	6.1	5.6	
	<i>s</i>	2.9	8.1	11.8	3.6	4.8	2.2	1.9			
	<i>n</i>	3	13	240	96	33	87	74	469	546	
<i>H. ascensionis</i> (168 mm)	\bar{x}	50.0	20.3	7.7	9.8	4.1	3.4	10.0	7.9	8.2	
	<i>s</i>	...	14.6	6.1	4.3	1.3	2.1	...			
	<i>n</i>	1	6	56	39	15	12	1	128	130	
<i>Flammeo marianus</i> (115 mm)	\bar{x}	23.3	12.2	9.7	4.0	3.7	4.0	2.7	8.2	8.4	
	<i>s</i>	12.0	4.5	6.9	2.1	0.7	1.6	1.4			
	<i>n</i>	12	16	168	47	5	25	13	261	286	
<i>Adioryx vexillarius</i> (99 mm)	\bar{x}	14.0	14.0	8.1	4.4	2.8	2.9	3.7	4.5	4.4	
	<i>s</i>	...	2.2	5.1	2.1	1.6	1.6	1.9			
	<i>n</i>	1	4	92	151	46	171	49	464	514	
<i>A. coruscus</i> (93 mm)	\bar{x}	16.5	14.2	12.4	4.4	3.0	4.2	...	10.5	10.5	
	<i>s</i>	12.0	4.6	6.8	2.4	...	2.2	...			
	<i>n</i>	2	5	117	33	1	5	...	161	163	
<i>A. poco</i> (92 mm)	\bar{x}	11.0	...	9.1	4.5	5.0	6.5	...	8.3	8.5	
	<i>s</i>	5.4	0.7	...	2.1	...			
	<i>n</i>	2	...	17	2	1	2	...	22	25	
<i>Plectrypops retrospinis</i> (86 mm)	\bar{x}	10.1	2.0	...	9.2	9.2	
	<i>s</i>	4.0			
	<i>n</i>	8	1	...	9	9	

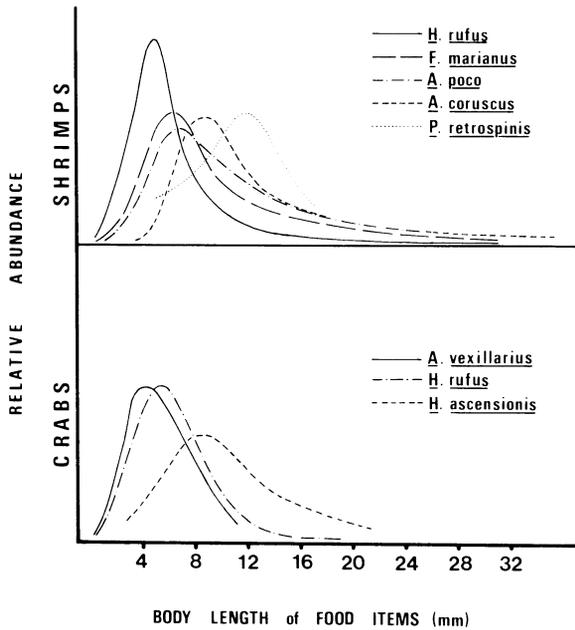


FIG. 2. Size-frequency distribution of principal food categories (shrimps or crabs) in the guts of seven species of holocentrids. Curves have been fitted by eye to the data points, which have been omitted for clarity. Areas beneath the curves have been adjusted to equality for comparison: proportion of area shared by two curves represents proportion of overlap in food size utilization for each food category.

size was between larger *A. vexillarius* and *H. rufus* for crabs. There was also little correlation between the maximum-sized prey items eaten and fish standard length. For all five species with large sample sizes the maximum length of shrimps eaten was ≈ 30 mm (except for one 50-mm stomatopod eaten by *H. ascensionis*). In all cases the largest items were eaten by fishes of about mean standard length.

Although the diets of most individuals in each species did not vary greatly from the proportions shown in Fig. 1, one or a few individuals of even the most specialized species had somewhat atypical gut contents. In all such cases the gut was relatively empty suggesting that such variations occurred primarily when food was scarce. Examples of the dietary extremes found in the most specialized shrimp and crab eaters were:

Adioryx coruscus

Typical: full: 2 large shrimps (24.0 ± 4.2 mm)
Atypical: 15% full: 8 small crabs (4.4 ± 1.4 mm)

Holocentrus ascensionis

Typical: full: 7 large crabs (10.4 ± 4.5 mm)
Atypical: 15% full: 28 small shrimps and peracarids (4.5 ± 1.8 mm)

By 45 min after sunset all individuals appeared to be foraging. By the time of collection (5–7 h after sun-

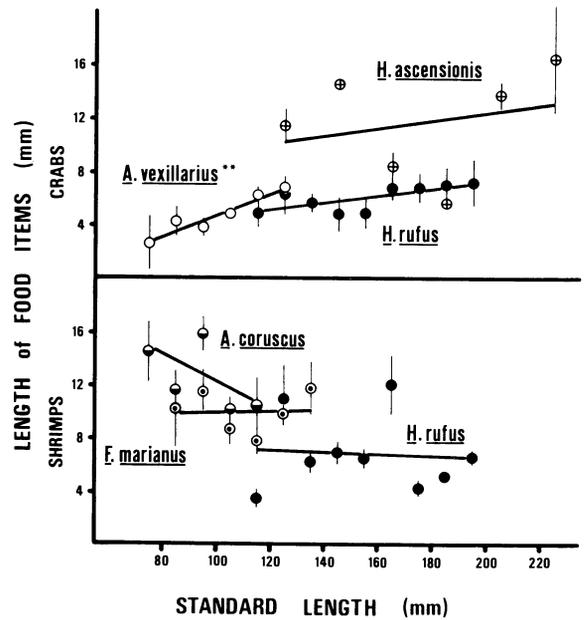


FIG. 3. Prey size as a function of predator size (body lengths) for shrimps and crabs. Regression equations, coefficients of determination, and significance levels of the regressions are:

crabs: *H. ascensionis*: $y = 0.029x + 6.6$;
 $r^2 = .074$; $.2 < P < .4$
A. vexillarius: $y = 0.081x - 3.4$;
 $r^2 = .92$; $.001 < P < .01^{**}$
H. rufus: $y = 0.027x + 1.8$;
 $r^2 = .53$; $.05 < P < .1$

shrimps: *A. coruscus*: $y = -0.097x + 21.7$;
 $r^2 = .36$; $.05 < P < .1$
F. marianus: $y = 0.007x + 9.2$;
 $r^2 = .007$; $.5 < P$
H. rufus: $y = -0.006x + 7.8$;
 $r^2 = .003$; $.5 < P$

A significant relationship between predator and prey body lengths exists only for *A. vexillarius* feeding on crabs; within other species food size is not a function of predator length.

set) the guts of most individuals of most species were $>10\%$ full. The guts of all species were $\approx 40\%$ full (overall mean), except for *Holocentrus rufus*, in which guts were $\approx 20\%$ full. The guts of fishes collected at Patch Reef 16 were more full ($\approx 50\%$ full), and those from Tague Bay Reef were less full ($\approx 25\%$ full), than those at the other sites.

Although most of the holocentrid species foraged in most of the reef zones, similarity in macrohabitat distribution was relatively high only for *Holocentrus rufus* and *Adioryx vexillarius*; both species had a broad habitat distribution and were common in many reef zones (Fig. 4). *Holocentrus ascensionis* overlapped with both of these to a moderate extent, tending to be most common in inshore zones, and particularly where topographically flat areas were adjacent to reefs. Among shrimp specialists, *A. coruscus* was clearly

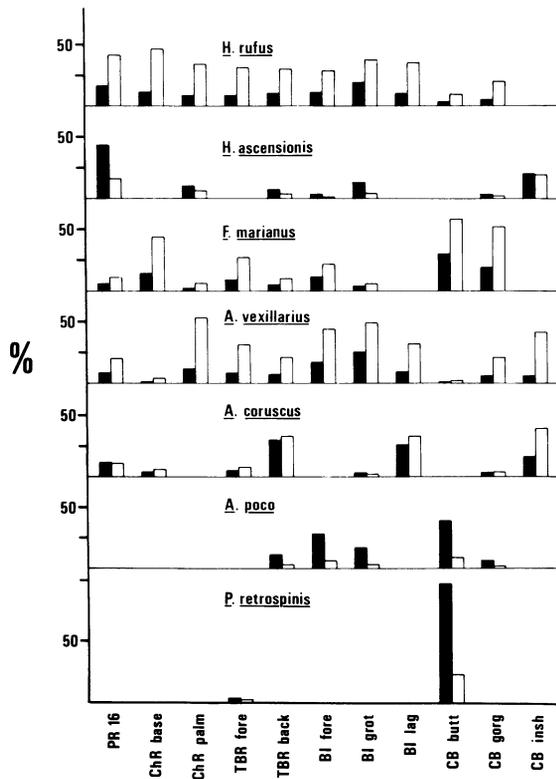


FIG. 4. Proportional representation of holocentrids censused at night in 11 habitats. Solid bars represent percentage of individuals of a given species found in a particular habitat and total 100% for each species (row). Open bars represent percentage of individuals in a given habitat that belong to a particular species; they total 100% for each habitat (column). The number of fish censused per hour at each site is: PR 16: 79; ChR base: 48; ChR palm: 47; TBR fore: 51; TBR back: 67; BI fore: 80; BI grot: 103; BI lag: 57; CB butt: 78; CB gorg: 56; CB insh: 31. (See Table 1 for abbreviation expansion.)

separated by microhabitat from the others, occurring primarily in low-profile zones of sand bottom or flat carbonate pavement (Table 1). The remaining three species were separated primarily by microhabitat differences, especially at Canebay, the site with greatest densities of all three. *Flammeo marianus* was the most conspicuously abundant bottom-foraging holocentrid in the buttress zone at Canebay. It foraged in the open just above the reef surface, primarily over the tops of the buttresses. *Adioryx poco* was seen only near the buttress-sand channel boundary (a situation similar to that where it occurred at other locations). *Plectrypops retrospinis* was observed only within the small interconnected cavities in the buttress framework. The two latter species seemed to be common in their respective habitats, but both were very shy and difficult to census or collect. Breadth of habitat utilization was greatest for *Holocentrus rufus* and *Adioryx vexillarius* (Table 4). *Flammeo marianus*, *A. coruscus*, *A. ascensionis*,

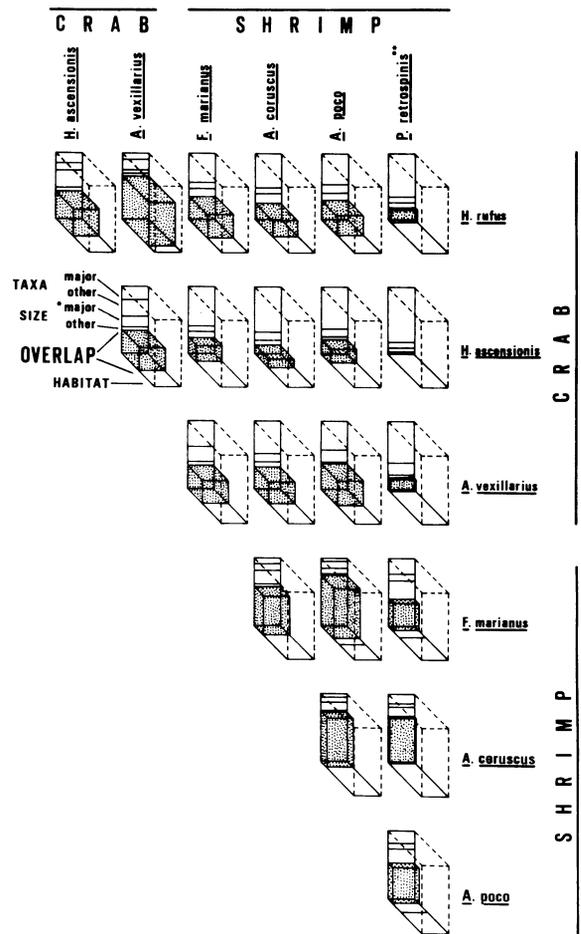


FIG. 5. Components of niche separation and overall resource use overlaps (shaded boxes) along food and foraging habitat axes (independence assumed between food and habitat but not between food type and size). Holocentrid species are arranged as crab and shrimp specialists. Proportional contributions of the components of niche separation along the food (vertical) axis are indicated by horizontal lines along that axis. These are: principal taxon (e.g., shrimps for shrimp specialists), other taxa, size within principal taxon (*not a component of separation across categories; therefore, in the group of shrimp \times crab specialists there are only three components represented along the vertical axis), and size in other taxa. (** Separation by size in other taxa is 0.0 between *P. retrospinis* and the three other shrimp specialists; thus, there are only three components of niche separation along the vertical axis there.) Separation by habitat is presented along the horizontal axis; there is additional separation by microhabitat among *F. marianus*, *A. poco*, and *P. retrospinis*, indicated by a line on the horizontal axis in each of those cases.

and *A. poco* all had lower values. *Plectrypops retrospinis* had a very restricted habitat range.

The various components of feeding-niche separation and overall feeding-niche overlaps are summarized in Fig. 5. Separation by principal food taxon was most important between crab and shrimp specialists with a

mean separation of .56 between all pairs of the two groups. Among shrimp specialists and among crab specialists separation due to differences in the primary food taxon was much less (.16 and .12, respectively). Differences between taxa other than the major one contributed only moderately to niche separation (.09 among shrimp specialists and .17 among crab specialists). Separation by food size in the principal category was of moderate importance among both shrimp and crab specialists (.17 and .16, respectively). Size differences in prey items in other categories were of slight importance in niche separation (.06 for all pairs of species). Differences in foraging habitat were important among shrimp specialists (.71) and between shrimp and crab specialists (.68) and were of less importance among the other species (.38). Microhabitat differences were important only in the separation of the three shrimp specialists: *F. marianus*, *A. poco*, and *P. retrospinis*. Proportional contributions by food (type and size) and foraging habitat (macro- and micro-) to niche separation were similar (.62 and .71, respectively). Overall niche overlap was generally low (mean = .13), with the only real exception being between the two most generalized species, *Holocentrus rufus* and *Adioryx vexillarius* (.53). There was no correlation, positive or negative, between food and foraging-habitat overlap value when plotted for all species pairs.

The mean overlap of the six commonest species by the method of Sale (1974) modified to take into account size-categories of food items of the major prey taxon (i.e., either crabs or shrimps) was .46. This value was significantly less than the mean of the overlaps in 50 synthetic competition-free assemblages: .51, standard deviation = 0.26; $t = 1.92$, $P < 0.05$, one-tailed t test.

Five groups of reef zones were distinguished on the basis of similarities of their holocentrid faunas (Fig. 6). These similarities coincided with similarities in substrate structure, depth, and general oceanic conditions. The most distinctive fauna was that of the Canebay buttress zone, the only shelf-edge site and the site with by far the greatest substrate complexity and diversity. The next most distinctive site was the Canebay inshore zone characterized by barren pavement as well as greater wave action and turbidity than all other sites. The next most distinctive group of sites all were moderately exposed, moderately deep, and with similar substrate complexity. Of the remaining two groups, one included the shallow exposed forereef sites with relatively high substrate complexity, and the other included the only three lagoonal sites. In all cases, proximity of the reef zones to one another seemed to have little effect on similarity of the communities of these zones.

DISCUSSION

The main points we have tried to make in this paper are that tropical reef fishes are not necessarily the broadly overlapping generalists they have been claimed

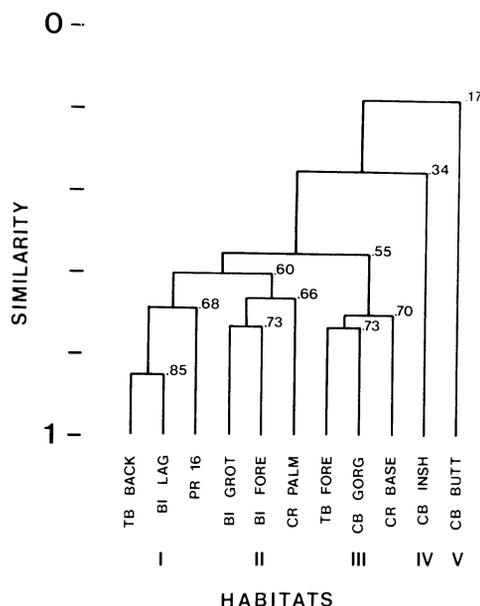


FIG. 6. Similarity of holocentrid assemblages in 11 habitats. These fall into five groups based more on environmental similarities of the habitats than on their proximity (see text).

to be in the past, that they do partition resources on a scale comparable to that in other communities, and therefore that the complex of mechanisms regulating their diversity is not fundamentally different from that of other such systems, as has been suggested (Sale 1977, 1978). Sale (1977) has stated "... current data indicate that many reef fishes do not finely partition resources of food or living space ..." and further that "... among the food specialists it is common for two or three sympatric species to show nearly identical specialization, thus overlapping greatly in the foods they consume ..." The studies these statements were based on (e.g., Hiatt and Strasburg 1960, Reese 1973) were either catalogs of gut contents or behavioral studies, and their findings do not justify Sale's statements. We believe the demonstration of generally low niche overlaps among the ostensibly very similar species in the present study invalidates such generalizations that reef fishes are broad generalists with respect to food and habitat utilization.

The few data available on food resource partitioning among reef fishes are too general to permit quantitative comparison with our data (e.g., Roughgarden 1974). Birkeland and Neudecker (1981) have compared the dietary preferences of two coexisting species of chaetodontid and found that they do utilize largely different food sources. Clarke (1977) has presented values for habitat overlaps among 22 species of pomacentrid and chaetodontid reef fishes. From his data the mean habitat overlap within the six multispecies genera was .40 or very close to our value of .37 for foraging habitat overlap. Unfortunately, diet similarity

was not investigated by Clarke. Among other coral reef organisms only the gastropod *Conus* has been analyzed in detail with respect to niche overlap and resource partitioning (Kohn 1959, 1968, Kohn and Nybakken 1975, Leviten 1978). Using data from Kohn (1959) on eight species of *Conus* coexisting on subtidal Hawaiian reefs, we calculated overlaps for resource utilization as we did in the present study. The mean values of .23 for mean food overlap (by taxon only) and .76 for habitat overlap and a value of .17 for total overlap compare to our values of .37 for food and .35 for foraging-habitat overlap, with a mean total overlap of .13. Other studies of *Conus* have shown similar trends (Kohn and Nybakken 1975). Among terrestrial systems Pianka (1974) has summarized niche overlaps among species in a broad spectrum of desert lizard communities. Among his North American lizard faunas (with a mean of about seven species) the average overall overlap along the three niche dimensions of food, place, and time was .16 by the multiplicative method used here (and greater by the additive method). Among birds overlap values were higher in examples of slightly smaller guilds. Overlap values of .64 for food and .64 for habitat (.41 total) were derived from Lack's (1971) data four species of tits (*Parus* spp.). In Mac Arthur's (1958) classic study of the separation of five species of wood warblers (*Dendroica* spp.), calculated mean niche overlap was .58 for spatial separation alone. Food differences among those warblers were believed to be solely due to differences in foraging space and technique. May and Mac Arthur (1972) have theorized that under a given set of circumstances as the number of species (in a guild) increases, niche separation should generally increase, but making comparisons across communities, this is not necessarily so (Mac Arthur 1971). This has been borne out in a number of communities (Schoener 1974), including desert lizards (Pianka 1974), nectivorous hummingbirds (Feinsinger 1976), and *Conus* (Leviten 1978). Thus, it is difficult to make generalizations by comparing the magnitude of overlaps in our system with others except that our values are comparable to or lower than those in many other systems of comparable size.

The principal exception to the generally low overlap values among all species of holocentrids was the high overlap between *Holocentrus rufus* and *Adioryx vexillarius*. The high overlap between these two species was due to similarity in prey type, prey size, and foraging habitat. In many of the habitats censused these were also the two most-abundant species (Fig. 4: open bars). This apparent paradox can be reconciled with our previous comments because they are the two most-generalized species (Table 4), both in food and foraging-habitat use. In addition, *H. rufus*, whose overall feeding niche breadth is probably slightly less than that of *A. vexillarius* (by all criteria, Table a) was found generally to have proportionally less food in its gut

than the other species (20% full as compared to 40%), suggesting that perhaps competition may be operating between these two species.

The general correlation between fish size and food size among crab-eating species is as expected according to theory (Hutchinson 1959) and as seen among many taxa from birds (Hespenheide 1971) to snails (Leviten 1978). However, the lack of correlation among shrimp-eating species between body length and prey length can be explained partly by the relatively great degree of microhabitat specialization between them. Thus, *Adioryx coruscus*, one of the smallest species, consumed shrimps of the greatest mean size, possibly because it foraged in the simplest, most-open microhabitat where it could be more effective in catching the larger, faster shrimps. Such differences in foraging effectiveness could also explain the almost significant negative correlation between fish length and prey length for *A. coruscus*; within the limits of the food-catching apparatus (jaws) to catch prey effectively, other factors may control the frequency of success in catching larger prey, such as maneuverability or closer approach distance of smaller fish.

Mac Arthur (1958), Kohn (1959), Root (1967), Pianka (1974), and numerous other authors have pointed out that coexistence among closely related or ecologically similar species is permitted by niche separation or the partitioning of resources along one or more niche axes. More recently Mac Arthur (1972), Roughgarden (1974), Cody (1974), and Schoener (1974) have tried to place such evidence of niche separation in the context of competition (theory); in other words, they have tried to set the theoretical limits of niche separation necessary to permit coexistence under a given set of available resources. It has been pointed out by Sale (1974), Abrams (1980), and Connell (1980) that the mere demonstration of such ecological differences between similar species does not imply that competition is operating or has operated in the community to produce these differences and that other criteria must be considered before such a conclusion can be reached. Finally Sale (1974) and Strong et al. (1979) have shown that when such systems are tested against null hypotheses that they frequently show no differences from randomly generated assemblages (e.g., of prey organisms [Sale 1974] or character displacement [Strong et al. 1979]), and thus many of the assemblages showing niche separation may not be structured by competitive interactions (Strong et al. 1979).

We have shown herein that overlap in food utilization among the six commonest species of holocentrids is significantly less than in random, or competition-free, assemblages with respect to food items taken (ignoring the minor contribution to niche separation made by prey size differences in categories other than the major one). This suggests that competitive interactions have played a role in the evolution of this assemblage. This is also supported by the dietary consistency of

major food items at different sites in this study and in the northern Virgin Islands (Table 3 herein; Randall 1967). This is not to say, however, that competition is occurring at present or that competitive interactions are playing a role in structuring the community. In fact the differences in food utilization shown herein permit competition-free coexistence over a spectrum of holocentrid and resource (prey) densities (or availabilities) whose limits are set by a lower limit of prey availability and an upper limit of holocentrid density. It can be expected that under some conditions competition between these species is not occurring and that population limits are set by other factors.

ACKNOWLEDGMENTS

We are grateful to the following individuals for their contributions to this study: Dr. R. F. Dill, former Director of the West Indies Laboratory; Mr. Marvin Madre, former Superintendent, Buck Island Reef National Monument; Ms. June Baumer, Biology Department, UCLA, for writing and setting up the computer program for the simulated competition-free communities; E. H. Gladfelter for numerous helpful tasks, including providing references, assisting in running the computer simulation, and reading the manuscript; anonymous reviewers of the manuscript who provided useful suggestions for the subsequent development of this paper; and Dr. J. B. C. Jackson for his perseverance and encouragement in getting this manuscript to press. This is Contribution No. 66 of the West Indies Laboratory, Fairleigh Dickinson University.

LITERATURE CITED

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44-49.
- Birkeland, C., and S. Neudecker. 1981. Foraging behavior of two Caribbean chaetodontids: *Chaetodon capistratus* and *C. aculeatus*. *Copeia* 1981:169-178.
- Böhlke, J., and C. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical regions. Livingston, Wynnewood, Pennsylvania, USA.
- Clarke, R. D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Marine Biology* 40:277-289.
- Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.
- Connell, J. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131-138.
- Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecological Monographs* 46:257-291.
- Gladfelter, W. B., and E. H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Revista de Biología Tropical (Supplement No. 1)* 26:65-84.
- Gladfelter, W. B., J. C. Ogden, and 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* 61:1156-1168.
- Gosline, W. A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology* 46:823-831.
- Hespenheide, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds with special reference to the Tyrannidae. *Ibis* 113:59-72.
- Hiatt, R. W., and D. W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* 30:65-127.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. United States Fish and Wildlife Service Research Reports 72:1-92.
- . 1974. Feeding relationships of Teleostean fishes on coral reefs in Kona, Hawaii. United States National Marine Service Fishery Bulletin 72:915-1031.
- Hobson, E. S., and J. R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. United States National Marine Fisheries Service Fishery Bulletin 76:133-153.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93:145-159.
- Kohn, A. J. 1959. The ecology of *Conus* in Hawaii. *Ecological Monographs* 29:47-90.
- . 1968. Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. *Ecology* 49:1046-1062.
- Kohn, A. J., and J. W. Nybakken. 1975. Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resource utilization. *Marine Biology* 29:211-234.
- Lack, D. 1971. Ecological isolation in birds. Blackwell, Oxford, England.
- Levitin, J. 1978. Resource partitioning by predatory gastropods of the genus *Conus* on subtidal Indo-Pacific coral reefs: the significance of prey size. *Ecology* 59:619-631.
- Mac Arthur, R. H. 1958. Population ecology of some warblers of northern coniferous forests. *Ecology* 39:599-619.
- . 1971. Patterns of terrestrial bird communities. Pages 189-221 in D. S. Farner and J. R. King, editors. *Avian biology*. Volume I. Academic Press, New York, New York, USA.
- . 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York, New York, USA.
- May, R., and R. H. Mac Arthur. 1972. Niche overlap as a function of environmental variation. *Proceedings National Academy Sciences (USA)* 69:1109-1113.
- Molles, M. C., Jr. 1978. Fish species diversity on model artificial and natural patch reefs: experimental insular biogeography. *Ecological Monographs* 48:289-305.
- Nolan, R. S. 1975. The ecology of patch reef fishes. Dissertation. University of California, San Diego, California, USA.
- Ogden, J. C., and J. P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. *Marine Ecology Progress Series* 4: 97-103.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences (USA)* 71:2141-2145.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography (Miami)* 5:665-847.
- Reese, E. S. 1973. Duration of residence by coral reef fishes on "home" reefs. *Copeia* 1973:145-149.
- Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37:317-350.
- Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. *Theoretical Population Biology* 5:163-186.
- Sale, P. F. 1974. Overlap in resource use and interspecific competition. *Oecologia (Berlin)* 17:245-256.
- . 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* 111:337-359.
- . 1978. Coexistence of coral reef fishes: a lottery for living space. *Environmental Biology of Fishes* 3:85-102.
- Sale, P. F., and R. Dybdahl. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56:1343-1355.
- Schoener, T. W. 1968. The anolis lizards of Bimini: re-

- source partitioning in a complex fauna. *Ecology* **49**:704–726.
- . 1974. Resource partitioning in ecological communities. *Science* **185**:27–39.
- Smith, C. L. 1978. Coral reef fish communities: a compromise view. *Environmental Biology of Fishes* **3**:109–128.
- Smith, C. L., and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Los Angeles County Natural History Museum Science Bulletin* **14**:125–170.
- Smith, C. L., and J. C. Tyler. 1975. Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. *American Museum Novitates* **2572**:1–18.
- Strong, D. R., L. A. Szyska, and D. S. Simberloff. 1979. Tests of community-wide character displacement against null hypotheses. *Evolution* **33**:897–913.
- Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high diversity systems? *Ecological Monographs* **48**:425–440.
- Vivien, M. L. 1973. Contribution a la connaissance de l'ethologie alimentaire de l'ichthyofaune du platier interne des recifs coralliens de Tulear (Madagascar). *Tethys Supplement* **5**:221–308.
- Vivien, M. L., and M. Peyrot-Clausade. 1974. A comparative study of the feeding behavior of three coral reef fishes (Holocentridae), with special reference to the polychaetes of the reef cryptofauna as prey. Pages 179–192 in *Proceedings of the Second International Coral Reef Symposium*. Great Barrier Reef Committee, Brisbane, Australia.