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SPATIAL AND TROPHIC INTERACTIONS IN WET AND DRY SEASONS BETWEEN *GAMBUSIA LUMA* AND *GAMBUSIA SEXRADIATA* (PISCES: POECILIIDAE) IN BELIZE, CENTRAL AMERICA

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ABSTRACT

Gambusia luma and *G. sexradiata* are sister species that are sympatric in the large rivers of northern Belize, but are also allopatric at various localities. The spatial and trophic interactions of these species were studied in both the wet and dry seasons at a locality where they occur together. Food for freshwater fishes is thought to be more abundant in the wet than in the dry season in the tropics, and thus, if lower food abundance results in more intense competition among fishes for food, the spatial and trophic partitioning between tropical river fishes should be greatest in the dry season. Field observations and feeding studies have demonstrated increased spatial separation (inshore-offshore) during the dry season for these two species when sympatric, and dietary differences support this separation: overlap coefficient ($C\lambda$) changed from .90 to .76 between the wet and dry seasons. No evidence for niche expansion was found for an allopatric population of *G. sexradiata*; however, where *G. luma* is allopatric, it will utilize all habitats occupied by both species while in sympatry. Therefore, it is suggested, in sympatric situations, the presence of *G. sexradiata* close to shore in the vegetation may prevent *G. luma* from utilizing that microhabitat during times of low water when potential competition for food may be greater. Although untested, the role of predation may be a factor in the ability of *G. luma* to live farther offshore than does *G. sexradiata* and in the failure of *G. sexradiata* to move offshore in the absence of *G. luma*.

INTRODUCTION

Northern Belize has distinct wet and dry seasons, resulting in large seasonal fluctuations in fish habitats and presumably also in the type and amounts of available food resources. Zaret & Rand (1971) reviewed the literature and presented their own evidence supporting the conclusion food was more abundant in the wet season in the tropics, as did Lowe-McConnell (1975). Assuming food is limiting in the dry season, competitive interactions should be greater, resulting in increased spatial and trophic partitioning. This corresponds with the findings of Zaret & Rand (1971) for a fish community in a small stream in Panamá.

Whereas Zaret & Rand (1971) compared various fish species belonging to different genera and families, our study compares two closely related (sister) species. Due to the similarities in morphology and general habitat utilization, potential competition should be greater between a pair of sister species than between species belonging to different genera or families (Dunham et al., 1979). Our study also differs from that of Zaret & Rand in that it compares the species in both allopatric and sympatric situations, thus providing information on

habitat utilization in wet and dry seasons for each species unaffected by potential competitive interactions with its sister species.

The closely related poeciliid fishes *Gambusia luma* and *G. sexradiata* each have distinctive distributions in Belize but are sympatric in several areas. *Gambusia luma* ranges from the southern border of Belize north to the Río Hondo and New River drainages, but is most abundant in southern Belize where it is often the only species of *Gambusia* present. *Gambusia sexradiata* occurs primarily in northern Belize away from coastal areas; south of the Sibun River it is rare (it was collected at only four localities) and is generally replaced by *G. luma* (Greenfield et al., 1982). Both species, however, are broadly sympatric in the large rivers of northern Belize.

MATERIALS AND METHODS

For stomach analysis, samples of both species were taken from Spanish Creek at Rancho Dolores (Belize District) during high water on April 1 and during low water on May 1, 1976. As this was the period of the most rapidly dropping water levels, it therefore provided samples from wet and dry periods separated by the least amount of time. In addition, an allopatric population of *G. sexradiata* was sampled on December 19, 1975 (wet season) from the Río Hondo at San Antonio (Orangewalk District) (fig. 1). All samples were taken between 0800 and 1100 hours, the predetermined period of peak feeding.

The April 1 Spanish Creek sample consisted of 29 *G. luma* (22.7–30.6 mm standard length [SL]) and 27 *G. sexradiata* (19.7–30.1 mm SL); the May sample consisted of 25 *G. luma* (20.6–31.6 mm SL) and 36 *G. sexradiata* (15.0–29.0 mm SL). The December 19 Río Hondo sample consisted of 45 *G. sexradiata* (15.2–30.8 mm SL). All individuals had food in their digestive tracts.

Observations on behavior and spatial preferences of sympatric *G. luma* and *G. sexradiata* were made on eight occasions (total of 14 hours) between March and June 1976 and on one day (three hours) in March 1977 at Rancho Dolores. (This locality cannot be reached prior to March due to extensive flooding of the dirt roads during the wet season.) *Gambusia luma* and *G. sexradiata* are easily separated in the field due to the visibility (from shore) of black falcate anal fin on *G. sexradiata*. Observations of allopatric *G. sexradiata* were made on two days (eight hours) in December 1975 at the Río Hondo. Allopatric *G. luma* were observed for two days (12 hours) in December 1975 and one day (two hours) in March 1976 at North Stann Creek at the Melinda Forestry Station.

At Rancho Dolores, Spanish Creek is relatively wide (48 m) and deep, and the shoreline is covered with heavy terrestrial vegetation that is completely submerged during periods of high water. The Río Hondo at San Antonio is also wide (80 m) and deep, with a shoreline similar to that at Spanish Creek. North Stann Creek at the Melinda Forestry Station is smaller than either Spanish Creek or the Río Hondo (15 m), shallower, and with a stronger current. The shoreline varies from sand bars lacking vegetation to areas with heavy terrestrial vegetation. Aquatic vegetation is lacking at all three localities.

Gambusia specimens were collected with a 3-m seine. The body cavities were injected with 10% formalin immediately upon capture and the specimens preserved in 10% formalin; they were later washed in water and transferred to 40% isopropyl alcohol. Standard length and sex were recorded for each specimen. The digestive tract was severed at the esophagus and anus and teased from the

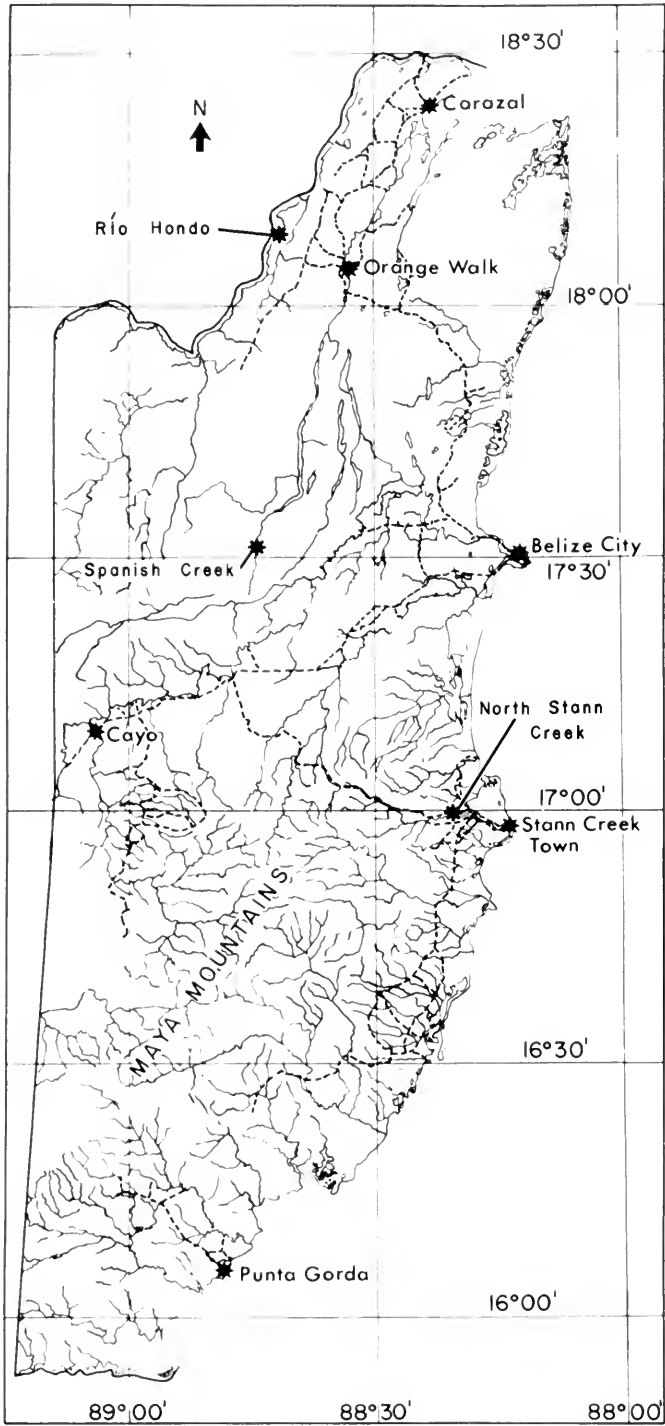


FIG. 1. Drainage map of Belize showing localities of study sites.

body cavity. All contents were removed from the digestive tract and the lining scraped, hydrated with a few drops of isopropyl alcohol in a petri dish, and the food items sorted and identified into taxonomic categories using a dissecting microscope. Depending upon the numerical importance of the food items, identifications were made to various levels ranging from family to order. Food category volume determinations were made using a squash-plate grid technique modified by Ross (1974, 1977) from Hellawell & Abel (1971). Although food items were not actually squashed, approximations were based on a measure of the calibrated two-dimensional area covered (volumes previously determined for squashed and unsquashed samples revealed that, due to the small size of the food items, the differences between the two methods were negligible). The number of food items in each category was counted.

Graphs were prepared of the number of prey taxa found in the digestive tracts vs. the cumulative number of *Gambusia* individuals (in the order in which they were examined) (Pontius & Parker, 1973); in all cases the curves became horizontal, indicating the sample sizes for the feeding study are adequate for description of prey taxa.

The overlap coefficient ($C\lambda$) of Horn (1966) was calculated for diet between the different species as:

$$C\lambda = \frac{2 \sum_{i=1}^s (X_i)(Y_i)}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

The proportional values used for this coefficient were calculated following Zaret & Rand (1971), where the proportional contribution (% volume) of each prey kind was determined for each stomach before summing and averaging for each prey category. The $C\lambda$ varies from 0, when two species have no food categories in common, to 1, when the proportions of each food category are identical; s = total number of food categories, X_i is the proportion of the total diet of species X , Y_i is the proportion of the total diet of species Y , for food category i .

The relative importance of each food category was determined using the index of relative importance (IRI) (Pinkas, 1971): $IRI = F(N + V)$, where N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage. This value integrates the measurements of numbers, volume, and frequency of occurrence usually used in evaluating fish stomach contents. In presenting proportions of particular food categories, the values refer to the percentage of total IRI for that category. To clarify feeding differences, prey organisms were designated, where possible, as allochthonous vs. autochthonous, aquatic vs. terrestrial, surface vs. submerged and/or shoreline, weedy vs. open, flowing. When making comparisons, qualitative category descriptions were considered independently, although strong correlations could exist between them.

RESULTS

SPATIAL INTERACTIONS IN SYMPATRY

During periods of high water (March–April), when much of the terrestrial vegetation along the shoreline was submerged, *G. sexradiata* and *G. luma* oc-

curred in the same general area at Spanish Creek and could be seen swimming together (i.e., they were syntopic); however, *G. sexradiata* was most abundant close to the shore in the vegetation (61% *G. sexradiata*, 39% *G. luma*). In May, when the water level was at its lowest just prior to the rains that would end the dry season, *G. luma* became more difficult to capture, and habitat differences became more pronounced. *Gambusia luma* occurred mostly in the open waters and, when pursued, moved out toward the middle of the river over deeper water. *Gambusia sexradiata*, however, occurred near the terrestrial vegetation close to shore and when pursued moved back into the vegetation; seine hauls made exclusively in the vegetation yielded 100% individuals of *G. sexradiata*, whereas seine hauls in open water yielded 100% individuals of *G. luma*. There was thus increased spatial segregation during periods of low water. During periods of high water, specimens of both *G. sexradiata* and *G. luma* were collected for feeding studies from all areas; during periods of low water, *G. sexradiata* was collected from areas with vegetation, and *G. luma*, from open water.

TROPHIC INTERACTIONS IN SYMPATRY

Differences in spatial preference between these two closely related species are reflected in their feeding habits. For April's high-water period, Horn's $C\lambda$ gave a value of .90 (almost complete diet overlap); the diet of both species consisted mainly of insects, including various beetles, true bugs, flies, ants, and wasps (figs. 2-4; table 1). The two main resources, Hydraenidae and bryozoan floatoblasts, made up 59.4% and 69.3% of the total IRI values for *G. luma* and *G. sexradiata*, respectively. These prey are both autochthonous and constituted the greatest difference between the species: *Gambusia luma* utilized the Hydraenidae almost twice as much (42%/22%) as did *G. sexradiata*; however, *G. sexradiata* utilized a much greater proportion of the bryozoan floatoblasts

TABLE 1. Food categories by taxonomic groups presented in Figures 2-4 for *Gambusia sexradiata* and *G. luma* from Spanish Creek during April (IRI = index of relative importance).

Category	IRI	<i>G. luma</i>		<i>G. sexradiata</i>	
		IRI	% Total	IRI	% Total
A. Hydraenidae	3596	42.0	1993	22.0	
B. Bryozoan floatoblasts	1493	17.4	4284	47.3	
C. Acalyprate muscoids	923	10.7	772	8.5	
D. Apocrita (winged)	453	5.2	99	1.0	
E. Oligochaeta	430	5.0	27	0.2	
F. Corixidae	308	3.5	522	5.7	
G. Nematocera (adults)	297	3.4	176	1.9	
H. Gerridae	224	2.6	45	0.4	
I. Chrysomelidae	192	2.2	12	0.1	
J. Staphylinidae	144	1.6	2	0.02	
K. Labidognatha	113	1.3	61	0.6	
L. Hydrophilidae	106	1.2	51	0.5	
M. Hydracarina	76	0.8	131	1.4	
N. Noteridae	67	0.7	107	1.1	
O. Chironomidae (larvae)	68	0.7	491	5.4	
P. Coleoptera	36	0.4	261	2.8	
Q. Nematocera (larvae)	35	0.4	17	0.1	

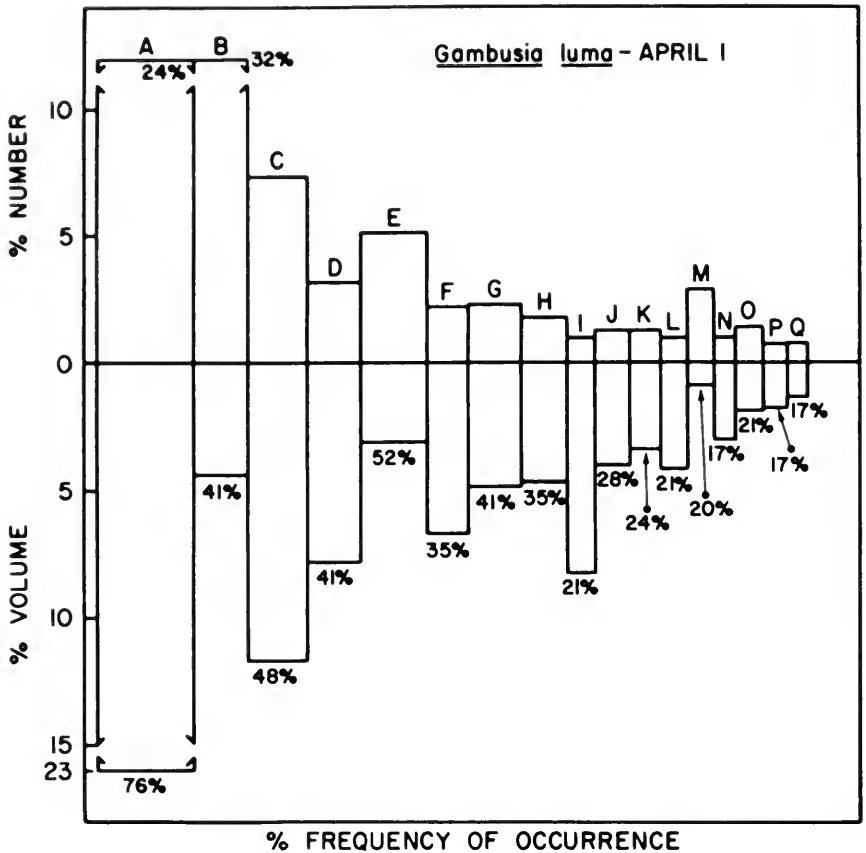


FIG. 2. Percent composition of food of *Gambusia luma* by taxonomic groups in number, volume, and frequency of occurrence at Spanish Creek during April (see Table 1 for abbreviations).

(47.3%/17.4%) than did *G. luma*. Allochthonous, terrestrial insects were also utilized to a greater extent by *G. luma* (22%/12%). Food resources considered allochthonous made up 25% of the diet of *G. luma* and 13% of the diet of *G. sexradiata*, whereas autochthonous resources made up 75% and 85% of these diets, respectively (percentages may not total 100 because it was not possible to assign all prey organisms to these categories).

Some major dietary shifts occurred between April 1 and May 1 (figs. 5-7; Table 2), resulting in a decrease in dietary overlap to .76 (Horn's CA). The proportions of hydraenid beetles and Acalyprate muscoids decreased. Some allochthonous terrestrial sources increased, especially Terebrantia (thrips) and Nematocera adults.

Seven categories dropped from the diets of both species, but these constituted only a very minor portion of their total diets: 0.75% for *G. luma* and 0.5% for *G. sexradiata*. Both species experienced a reduction of April food resources (based on the summed percent reduction of IRI resource area for each

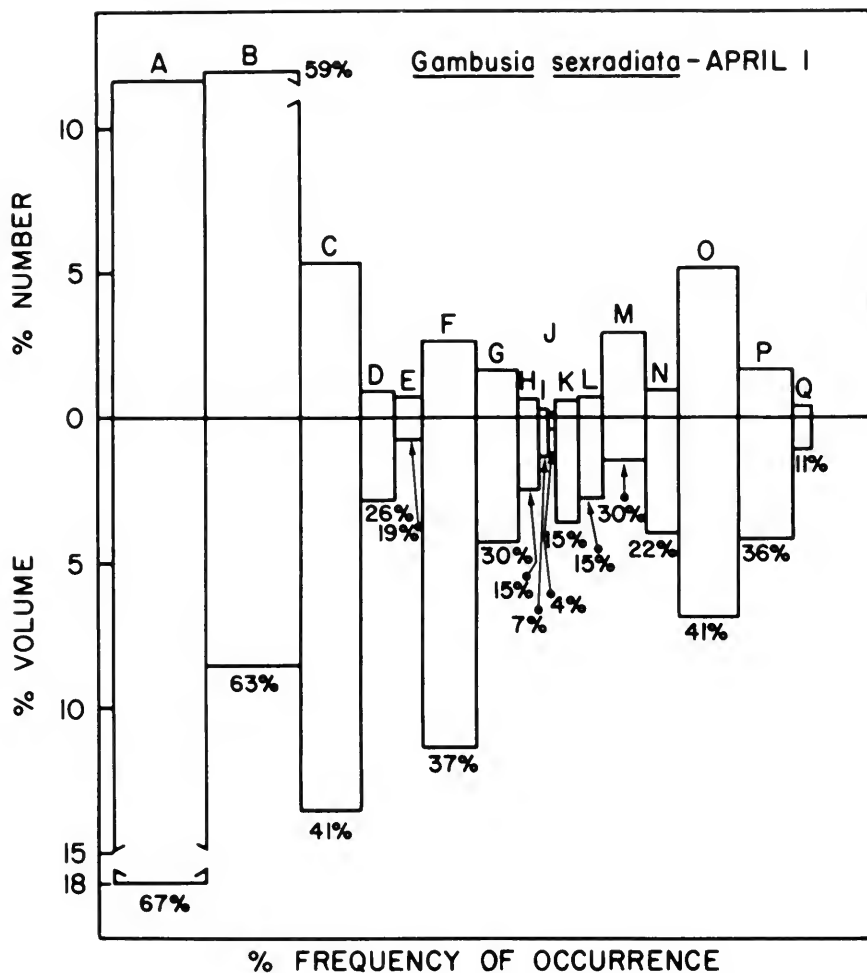


FIG. 3. Percent composition of food of *Gambusia sexradiata* by taxonomic groups in number, volume, and frequency of occurrence at Spanish Creek during April (see Table 1 for abbreviations).

prey item) that was much more dramatic for *G. luma* (67%) than for *G. sexradiata* (36%). Both species added proportionately to their diets from other categories present among the April food items: *G. luma* added 59% and *G. sexradiata* added 36%.

Ten new categories were added, including some important ones such as crustaceans, Collembola, and chironomid pupae: 16% of the diet of *G. sexradiata*, but only 8.5% of that of *G. luma*, came from new categories. The diet of *Gambusia luma* was expanded in the use of thrips, an allochthonous source that composed a large proportion of its diet in May (16% vs. 6% for *G. sexradiata*). Bryozoan floatoblasts were important elements of the diets in May as well as in April, but were more equalized in May, with only a 5% proportional difference

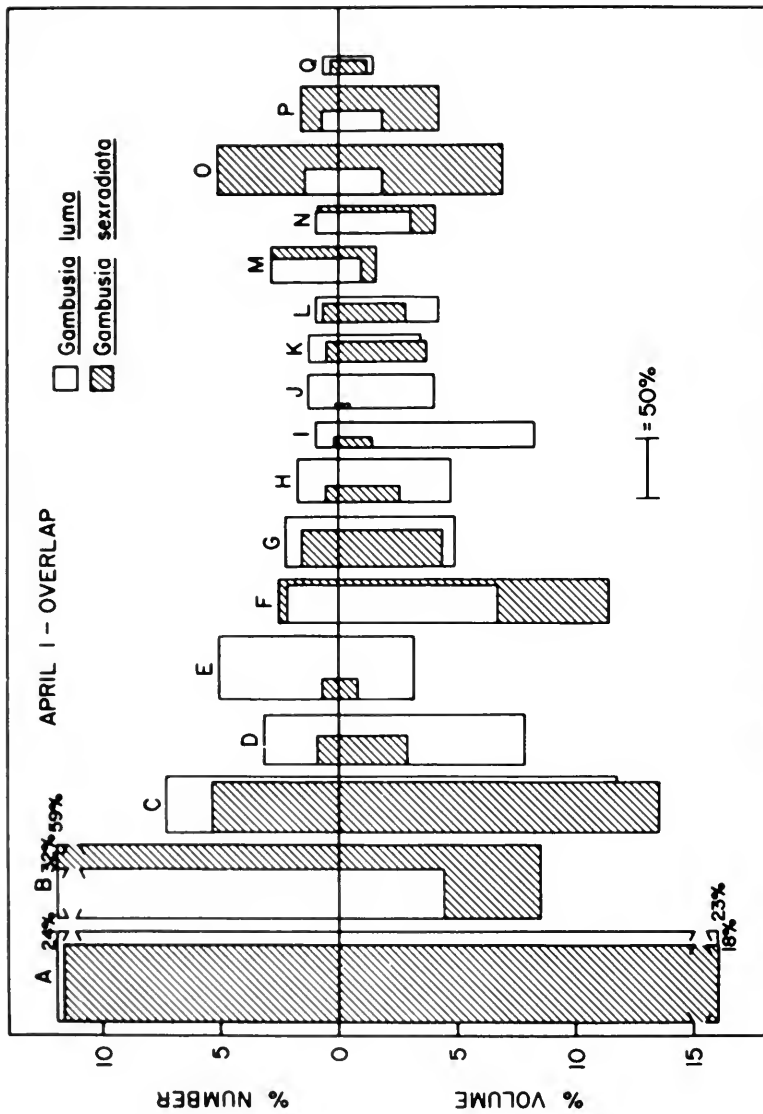


FIG. 4. Comparison of percent composition of food by taxonomic groups in number, volume, and frequency of occurrence for *Gambusia luma* and *G. sexradiata* at Spanish Creek during April (see Table 1 for abbreviations).

TABLE 2. Food categories by taxonomic groups presented in Figures 5-7 for *Gambusia sexradiata* and *G. luma* from Spanish Creek during May (IRI = index of relative importance).

Category	<i>G. luma</i>		<i>G. sexradiata</i>	
	IRI	% Total	IRI	% Total
A. Bryozoan floatoblasts	5693	49.9	4279	54.8
B. Terebrantia	1872	16.4	504	6.4
C. Nematocera (adult)	902	7.9	533	6.8
D. Chironomidae (pupae)	531	4.6	279	3.5
E. Oligochaeta	332	2.9	57	0.7
F. Coleoptera (minute)	307	2.6	37	0.4
G. Apocrita (winged)	296	2.5	23	0.2
H. Oribatei	238	2.0	30	0.3
I. Collembola	223	1.9	318	4.0
J. Hydracarina	211	1.8	247	3.1
K. Scolytidae	206	1.8	2	0.02
L. Formicidae	178	1.5	11	0.1
M. Hydraenidae	140	1.2	68	0.8
N. Staphylinidae	139	1.2	5	0.06
O. Chironomidae (larvae)	76	0.6	364	4.6
P. Noteridae	54	0.4	70	0.8
Q. Corixidae	4	0.03	300	3.8
R. Ostracoda	2	0.02	365	4.6
S. Cladocera	1	0.01	101	1.2
T. Copepoda	1	0.01	215	2.7

between the two species. Allochthonous food sources made up 32% and 14% of the total diets of *G. luma* and *G. sexradiata*, respectively, whereas autochthonous food sources provided 65% and 86%, respectively (percentages may not total 100 because it was not possible to assign all prey organisms to these categories).

ALLOPATRIC *GAMBUSIA* *SEXRADIATA*

The allopatric population of *G. sexradiata* at the Río Hondo during December 1975 (wet season) utilized food categories typical of *G. sexradiata* at Spanish Creek where it was sympatric with *G. luma* (fig. 8; table 3). Chironomid larvae, Collembola, Hydracarina, and crustaceans made up 82% of the diet. Categories typical of *G. luma*, including terrestrial insects such as ants, thrips, wasps, and flies, composed only 4% of the diet of *G. sexradiata*, and aquatic beetles, Hemiptera, and oligochaetes made up 1%. Visual observations showed *G. sexradiata* occurred close to shore (within 2 m). Seine hauls in open water more than 2 m from the shoreline did not yield any *G. sexradiata*.

ALLOPATRIC *GAMBUSIA* *LUMA*

The allopatric population of *G. luma* from North Stann Creek showed a shift in habitat utilization. In contrast to the open-water habitat of the sympatric population, it was most abundant close to shore. The greatest concentrations of fish were close to branches of bamboo or other terrestrial vegetation that extended into the water. *Gambusia luma* individuals were seen foraging in the open water several meters from the shoreline, but when pursued by a seine they moved toward the shoreline. In fact, the easiest method of collecting samples of *G. luma* from North Stann Creek was to seine toward the flooded terrestrial

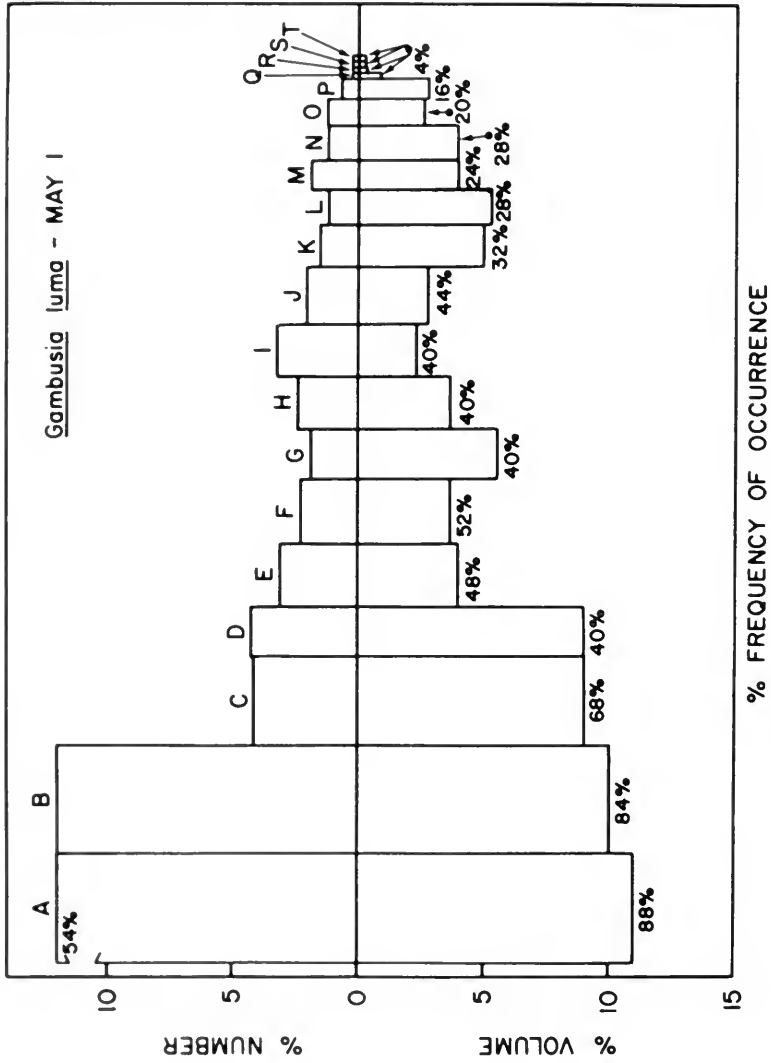


FIG. 5. Percent composition of food of *Gambusia luma* by taxonomic groups in number, volume, and frequency of occurrence at Spanish Creek during May (see Table 2 for abbreviations).

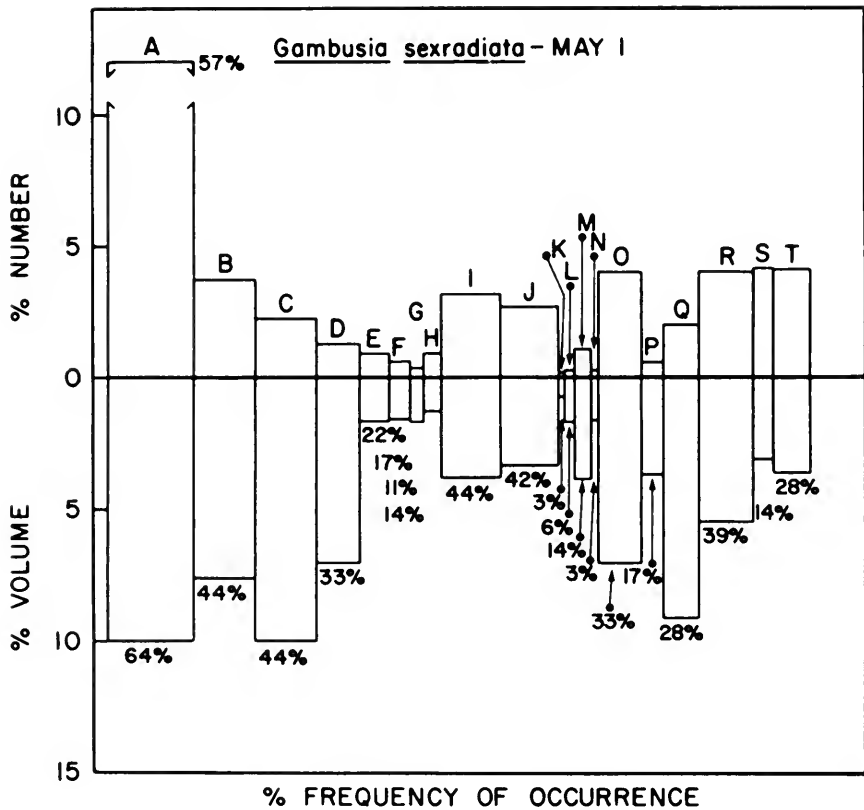


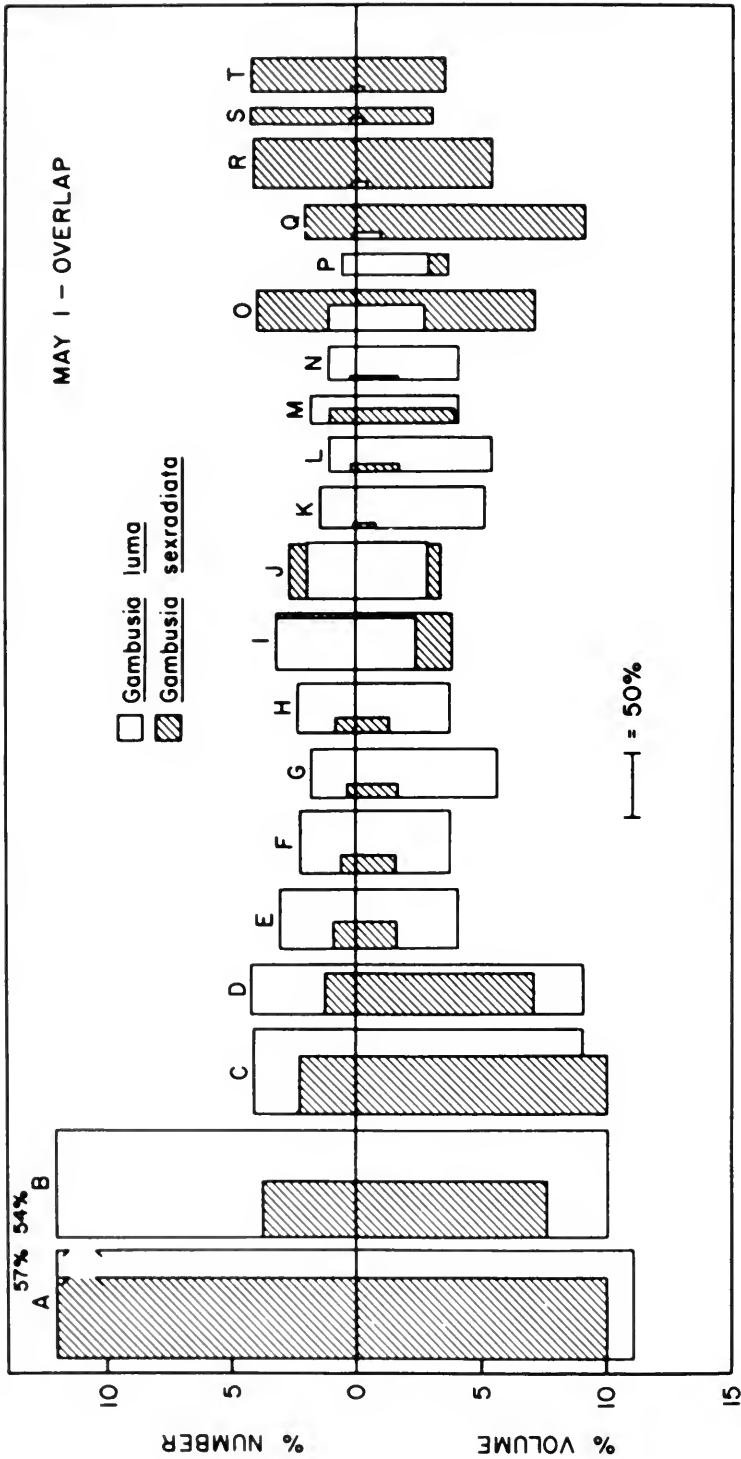
FIG. 6. Percent composition of food of *Gambusia sexradiata* by taxonomic groups in number, volume, and frequency of occurrence at Spanish Creek during May (see Table 2 for abbreviations).

vegetation, trapping the fish along the shoreline. Because the concentrations were so obvious, counts of individuals taken in seines at various distances from the shoreline were not made. Numerous collections made throughout the southern portion of the country, where *G. luma* is usually the only species of *Gambusia* present (Greenfield et al., 1982), supported these observations.

In southern Belize, where *G. luma* is the dominant species of *Gambusia*, *G. sexradiata* was taken four times and then in low numbers and in marginal habitats. For example, at the Swasey Branch of the Monkey River, *G. luma* was abundant in the main river and *G. sexradiata* was found only in an isolated overflow pond alongside the river. These southern populations of *G. sexradiata* are believed to be related to populations in southern Guatemala and probably have had a much longer history of interaction with *G. luma* (Greenfield et al., 1982).

DISCUSSION

In sympatry, *Gambusia sexradiata* and *G. luma* utilized different microhabitats, with *G. luma* increasing in abundance away from shore. Spatial separation is



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Fig. 7. Comparison of percent composition of food by taxonomic group in number, volume, and frequency of occurrence for *Gambusia luma* and *G. sexradiata* at Spanish Creek during May (see Table 2 for abbreviations).

TABLE 3. Food categories by taxonomic groups presented in Figure 8 for *Gambusia sexradiata* from the Río Hondo during December (IRI = index of relative importance).

Category	IRI	% Total
A. Cyclopoida	3833	34.1
B. Cladocera	2821	25.1
C. Chironomidae (larvae)	1392	12.3
D. Chironomidae (pupae)	837	7.4
E. Collembola	584	5.1
F. Hydracarina	556	4.9
G. Nematocera (adult)	374	3.3
H. Oligochaeta	183	1.6
I. Protozoa (tested)	134	1.1
J. Apocrita (winged)	84	0.7
K. Homoptera	70	0.6
L. Helodidae (larvae)	69	0.6
M. Ephemeroptera (larvae)	67	0.5
N. Amphipoda	65	0.5
O. Harpacticoida	59	0.5
P. Staphylinidae	31	0.2
Q. Noteridae	25	0.2
R. Conchostraca	19	0.1
S. Formicidae	14	0.1
T. Oribatei	8	0.07
U. Ostracoda	4	0.03
V. Insect eggs	1	0.01
W. Veliidae	1	0.01

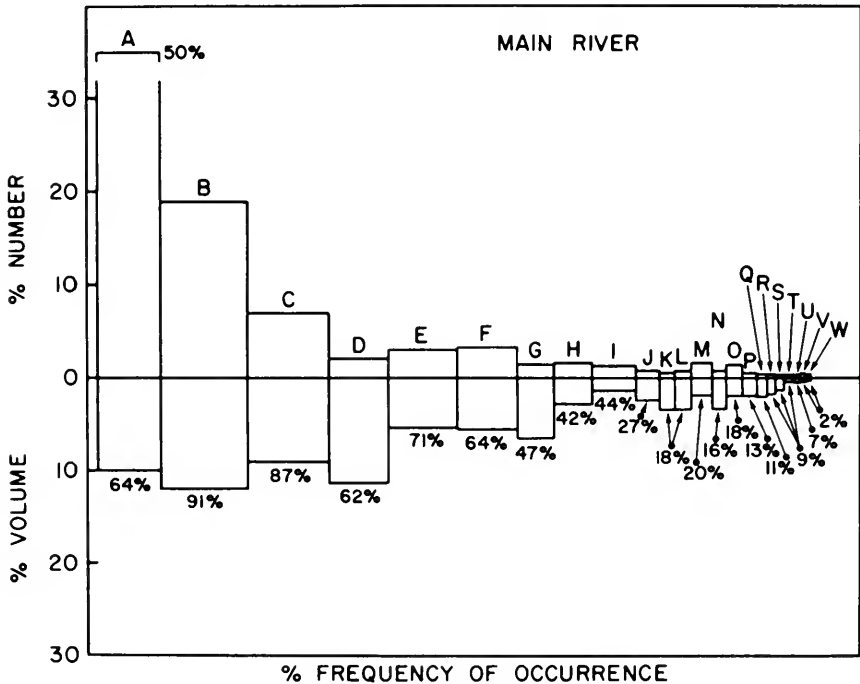


FIG. 8. Percent composition of food of *Gambusia sexradiata* by taxonomic groups in number, volume, and frequency of occurrence at the Río Hondo during December (see Table 3 for abbreviations).

supported by dietary differences: *G. luma* contained 87.5% surface-terrestrial organisms and only 12.5% shoreline and cover-inhabiting organisms, whereas *G. sexradiata* contained 37.5% surface-terrestrial organisms and 62.5% shoreline and cover-inhabiting organisms. Segregation increased as the water level dropped: $C\lambda$ changed from .90 to .76. These results are similar to those of Zaret & Rand (1971) for stream fishes in Panamá.

No evidence for niche expansion was found for an allopatric *G. sexradiata* population. Data from the population at the Río Hondo indicate *G. sexradiata* occupied essentially the same microhabitat and fed on the same major food categories as it did in sympatry with *G. luma*; however, in southern Belize, where *G. luma* was often the only *Gambusia* species in a river, it occurred from the shoreline (with vegetation) out into the river during periods of both high and low water. Unfortunately, information on feeding habits of *G. luma* from these allopatric situations is not available.

Gambusia luma is typically a river and stream species, seldom occurring in ponds or standing water, whereas *G. sexradiata* is typically found in ponds throughout Belize and is most abundant in ponds with a heavy cover of sedges and rushes (Greenfield et al., in press). The adaptation of *G. luma* to river environments is supported by its streamlined body and by the tendency of individuals to school and remain very close to the surface. Additional evidence suggesting an adaptation to rapidly flowing waters is provided by the gonopodial structure of *G. luma* which, in contrast to that of *G. sexradiata*, has large terminal hooks (Greenfield et al., 1982). Studies of other genera within the family Poeciliidae, particularly the swordtails in the genus *Xiphophorus*, showed that species with larger holdfasts inhabit more swiftly flowing waters (Rosen, 1960). The ability of *G. luma* to utilize more open surface waters with a greater current may be a consequence of the fish having evolved in the rapidly flowing streams of the emergent mountainous areas of southern Belize when higher sea levels covered the coastal plain (Greenfield et al., 1982).

Although conclusive evidence for microhabitat exclusion has not been presented, our field observations show that where *G. luma* is allopatric it will utilize all habitats from the shoreline vegetation out into the more open water during both high- and low-water periods; *Gambusia sexradiata*, however, utilizes the near-shore, vegetation habitat regardless of whether *G. luma* is present. Therefore, in sympatric situations, the presence of *G. sexradiata* close to shore in the vegetation may prevent *G. luma* from utilizing that habitat during times of low water when potential competition for food may be greater. Possibility of exclusion from shoreline vegetation obviously did not prevent *G. luma* from moving northward into the range of *G. sexradiata* in northern Belize after that area became emergent. If one assumes that the environment is near saturation (in regard to mosquitofishes), because the May sample was taken at a time of lowest water level and presumably greatest habitat separation, then the overlap values for May at Spanish Creek ($C\lambda = .76$) may represent a reasonable estimate of maximal overlap along the gradient of prey kind for two sister species of *Gambusia* in a large open river.

Although untested, the role of predation may be a factor in the ability of *G. luma* to live farther offshore than does *G. sexradiata* and in the failure of *G. sexradiata* to move offshore in the absence of *G. luma*. Anderson (1980) showed

that there are two major predators of *Gambusia* species in Belize, the cichlid *Petenia splendida* and the poeciliid *Belonesox belizanus*, both of which are relatively abundant at Spanish Creek. Thus, in the large northern rivers where *G. luma* and *G. sexradiata* are sympatric and where *G. luma* is found farther out from shore where predators tend to be more abundant, it is tempting to speculate that *G. luma* is more successful at escaping predation than is *G. sexradiata*, which remains near cover along the shoreline. The more streamlined body shape and schooling behavior of *Gambusia luma* may aid in escaping predation. Charnov et al. (1976) demonstrated the presence of a predator can result in changes in the microhabitat and behavior of the prey, perhaps explaining the failure of *G. sexradiata* to utilize the more offshore, open waters occupied by *G. luma*. If *G. sexradiata* is indeed limited to the shoreline microhabitat by predators, then one would expect selection to have favored behavioral adaptations in feeding methods that maximize efficiency in taking shoreline and cover-inhabiting organisms. Observations in the field and also in aquaria have shown *G. sexradiata* will feed from the bottom as well as throughout the water column. Conversely, *G. luma* is a schooling species that tends to remain near the surface and seldom feeds from the bottom.

Werner's (1977) ideas on the importance of differences between morphologically similar species in foraging efficiency as it relates to microhabitat utilization can be illustrated by these two species. *Gambusia sexradiata* generally eats smaller organisms than *G. luma* does during both periods of high and low water, mainly due to the greater numbers of bryozoan floatoblasts, crustaceans, and insect eggs in its diet. This is inferred by comparative average values of 6.875×10^{-4} ml/organism for *G. luma* vs. 5.079×10^{-4} ml/org. for *G. sexradiata* feeding in April, and 5.212×10^{-4} ml/org. for *G. luma* vs. 3.339×10^{-4} ml/org. for *G. sexradiata* in May. The ability to utilize smaller prey would seem to be a more appropriate feeding method in vegetation; however, *G. luma* could be a more efficient predator, forcing *G. sexradiata* to feed more frequently on smaller organisms. If *G. sexradiata* is more efficient at foraging in the covered vegetative portion of the shoreline area, it may be excluding *G. luma* from this area (during periods of low water), or *G. luma* may simply be more efficient at taking open-water submerged and surface-terrestrial organisms.

Obviously this is a very dynamic system, as evidenced by the dramatic major shifts demonstrated in the diets of these species over just one month between the wet and dry seasons. These shifts presumably involve either changes in the abundance (i.e., availability) of prey organisms and/or are the result of increased habitat separation. Distinct differences between these species in the extent of utilization of few resources such as corixids, chironomid larvae, ostracods, cladocera, and copepods (fig. 7) point to a latent potential for increased nonoverlap at other times, such as the Terebrantia (thrips) provided between April and May. It has been recently emphasized that tropical environments and their insect populations are no more stable than are temperate ones (Wolda, 1978). The nature of this dynamic system may involve either regular (cyclical) or erratic fluctuations of the prey populations. These predators are adjusted to each other in a finely tuned manner through complementary differences in the use of most of the same food resources. This kind of system may be particularly characteristic of a tropical community, such as this one, allowing for better species-packing potential.

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