

Comparative ecology of eleotrid fishes in Central American coastal streams

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Synopsis

The population structure, abundance, reproductive status, and feeding interrelationships of eleotrid fishes from two freshwater streams of the Caribbean coast of Costa Rica were investigated over 10 continuous months. *Eleotris amblyopsis* was abundant in both streams. *Dormitator maculatus*, *Eleotris pisonis*, and *Gobiomorus dormitor* were present in both streams but common only in the larger stream that contained dense growth of floating aquatic macrophytes. *Dormitator maculatus* is a detritivore and overlaps with the other three eleotrids, all of which had diets dominated by shrimp and fishes. Intraguild predation and cannibalism was documented with *E. amblyopsis* as the prey. Except for the benthic *G. dormitor*, eleotrids were associated with dense mats of floating macrophytes in the large stream, and leaf peaks in the small stream. Diet similarity among the three carnivorous eleotrids declined during the wet seasons, the period when their prey disperse at lower per-unit-area densities within the flooded forests that surround the streams. Analysis of population size distributions and gonadal maturation indicated that at least some reproduction occurs on a nearly year-round basis within these eleotrid populations. The spring dry period may be associated with migration of ripe eleotrids to estuarine habitats for spawning. Juvenile *Eleotris* are the dominant fishes in the 'tismiche', mass migrations of juvenile shrimp and fish larvae and juveniles that enter and ascend the estuary, especially during the summer wet season.

Introduction

Because coastal rivers and wetlands are ecotones that encompass numerous physical gradients, their inhabitants must respond to a great deal of physical and biological complexity. Many fishes of coastal environments are diadromous or euryhaline and hence deal with the full complement of ecological factors associated with transitions between freshwater and marine habitats during various intervals of their life cycles. Compared with the considerable attention received by diadromous and euryhaline fishes of temperate coastal regions, the life histories

and ecology of most tropical coastal diadromous and euryhaline species remain poorly documented. Tropical euryhaline and diadromous fishes inhabit coastal ecosystems with environmental gradients that often are strongly heterogeneous and temporally variable. Sleepers, fishes of the gobioid family Eleotridae, are common inhabitants of tropical coastal habitats throughout the world. In the Neotropics, several eleotrid species are sympatric and frequently syntopic in a variety of habitats ranging from small forest streams to river estuaries.

Myers (1938) classified Central American freshwater fishes as either primary division (fishes hav-

ing almost no salinity tolerance), secondary division (fishes having limited or sometimes substantial salinity tolerance), or peripheral division (freshwater representatives from families dominated by marine species). Eleotrids correspond to the peripheral division, and most species seem to be physiologically and ecologically adapted to live either all or a portion of their life cycle in freshwater habitats (Myers 1966, Miller 1966, Bussing 1976). For example the bigmouth sleeper, *Gobiomorus dormitor*, completes its entire life cycle in freshwater Lake Nicaragua (McKaye et al. 1979), although normally spawning takes place in estuaries (Nordlie 1981), and the bighead gudgeon, *Philypnodon grandiceps*, spawns and develops in floodplain lagoons at inland locations of Australia (Gehrke 1992). However, most eleotrids appear to spawn in coastal freshwater habitats or estuaries from which their eggs are transported to the outer estuary or beyond (McDowall 1965, Todd 1975, Nordlie 1981). Juveniles of these species then migrate back into coastal freshwater systems where they feed, grow, and mature (Gilbert & Kelso 1971, Nordlie 1981).

Several studies have examined aspects of eleotrid ecology in the Central American nation of Costa Rica. Bussing (1987) described the taxonomic status and geographic distributions of Costa Rican freshwater fishes, including eleotrids common to freshwater habitats. Caldwell et al. (1959), Gilbert & Kelso (1971), and Winemiller & Leslie (1991) described the spatial distribution and abundance patterns of eleotrids based on fish community samples from the Tortuguero region of Costa Rica's Caribbean coast. Nordlie (1979, 1981) examined the abundance patterns and feeding interrelationships of eleotrids in the Laguna Tortuguero (estuary). Winemiller (1982) and Winemiller & Morales (1989) investigated spatial distributions, habitat associations, and diets of eleotrids and other fishes in streams of the Osa Peninsula on Costa Rica's Pacific coast.

The study reported here examined the population structure and abundance, temporal and size-based variation in reproductive state, and feeding interrelationships of four common eleotrid fishes in two freshwater streams that flow through a rainforest landscape to a coastal lagoon of the Caribbean

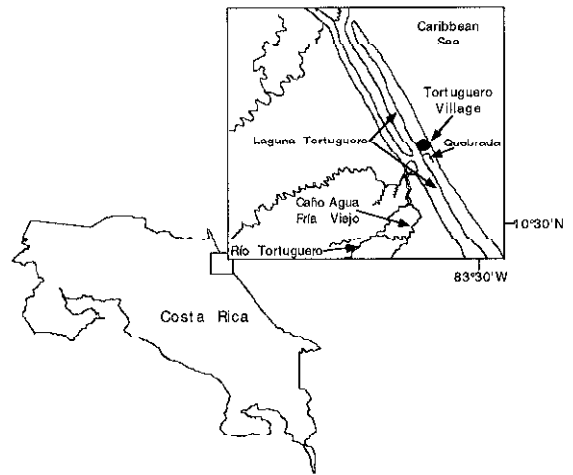


Figure 1. Map showing the location of the Quebrada and Caño Agua Fria Viejo study systems in Tortuguero region of Costa Rica.

coast of Costa Rica. This coastal lagoon, Laguna Tortuguero, is the same estuarine system investigated by Nordlie (1979, 1981) and Nordlie & Kelso (1975). Therefore, our analysis complements and expands the scope of ecological knowledge for this important group of fishes within this heterogeneous freshwater-marine ecotone.

Methods

Study region

The research was conducted in two streams (Quebrada & Caño Agua Fria Viejo) in Tortuguero National Park within the Caribbean coastal lowlands of Costa Rica's Limón province (Figure 1). Most of the western area of the park is covered by pristine, lowland tropical rainforest. However, other vegetative communities occur within the reserve (for further descriptions see Winemiller & Leslie 1992). Apart from the Lomas de Sierpe hills in the interior of the park, most of the area is coastal plain a few meters above sea level. A network of narrow lagoons lies parallel to the coast. One of these, Laguna Tortuguero, averages approximately 7.5 m depth at midchannel between Tortuguero village and its mouth (Nordlie & Kelso 1975). Nordlie & Kelso (1975) observed a tongue of saline water (8.7–10.5 ppt) near the bottom (depths > 5 m) and sur-

face salinities < 0.7 ppt throughout the year in the upper Laguna Tortuguero. During 1985, salinity never reached 0.1 ppt in our two study systems. Regional rainfall averages about 5.0 m annually with two major rainy seasons from July through August and November through January. Rainfall 7.0 m can occur during exceptional years, and no month receives < 50 mm. Temperature averages 23–26°C annually with little seasonal variation (Hirth 1963).

Caño Agua Fría Viejo (AFV hereafter) is a sluggish side channel of the Río Tortuguero (Figure 1). Some pools of Caño AFV exceed 3.0 m depth, but most stream reaches range between 0.5 and 2.0 m. The stream has little or no water current during dry periods. The substrate consisted of sand and patches of coarse detritus, the latter being most common near the channel margins under floating sedges and associated aquatic plants. Dense mats of floating aquatic plants (*Eichhornia*, *Hydrocotyl*, *Salvinia*, *Azolla*) sometimes cover the surface of stream segments during dry periods and are removed by faster currents during wet periods. During extended wet periods (e.g., June–August), large areas of the forest bordering Caño AFV become flooded with standing water and are colonized by fishes.

Quebrada is a narrow (< 3.5 m), shallow (< 0.5 m) creek at the national park's northern boundary on the barrier island that separates the sea and the Laguna Tortuguero (Figure 1). Because Quebrada has negligible gradient and drains directly into the lagoon, its lower section is under tidal influence during much of the year. The substrate was sand and leaf litter, and water current velocity was 0–0.20 m s⁻¹. Like Caño AFV, the forest surrounding QB contains extensive pools of standing water < 0.5 m deep during wet periods. Further descriptions of habitats at both sites appear in Winemiller (1990, 1993).

Field samples

The two sites were intensively sampled during each month from February–December 1985 using seines (6.2 \geq 1.9 m, 4.7 mm mesh; 2.5 \geq 1.9 m, 3.2 mm mesh) and dipnets (3.2 mm mesh). A few specimens of *G. dormitor* were captured by hook and line. All

aquatic habitats were collected to obtain a sample representing all species in relative proportions approximating those of the local fish community (further details given in Winemiller 1990). Monthly sampling efforts lasted approximately 0.5 day at Quebrada and 5 days at Caño AFV, and the effort was continued until 1 h of collecting produced no additional species for the sample. The sampling methods were effective for adult and larger immature size classes of all eleotrid species, but the smallest immature size classes were underrepresented. The relative effort and effectiveness of collecting methods did not differ greatly between sampling periods, such that relative abundances can be compared between time periods for a site.

To obtain estimates for fish biomass per unit area, subsamples were obtained from two different habitats (open channel and marginal vegetation) using the 2.5 \geq 1.9 m seine at Caño AFV during May (dry season) and December (wet season). For each of the hauls that contributed to these subsamples, area surveyed was computed as the length of the seine \geq the distance of the haul. The total area surveyed was the sum of the areas of individual seine hauls. Seine hauls in dense vegetation involved moving the leadline under the floating vegetation mass, then quickly raising the trapped vegetation and fishes above the water and removal of materials from the net at the shore or in a boat. In these cases, the area of the haul was the area of the seine net.

Fishes were preserved in 10% formalin and later transferred to 45% isopropanol. Species were identified based on characters described in Bussing (1987). Voucher specimens and records of sample sites and dates are on file at the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas.

Measurements and analysis

Most preserved specimens were examined at the Tortuguero Park station, but the final two samples were examined in the laboratory at the University of Texas. All specimens were identified and measured for standard length (SL) using vernier calipers. For each monthly sample and each of the two

study sites, 30 to 50 individual specimens were selected for dissection and examination of gonads and stomach contents. The selection of specimens for dissection subsamples was based on size and aimed at representing the approximate size distribution in the larger sample. Whenever fewer than 30 specimens were collected during a particular month at a site, all specimens were dissected. An electronic balance was not available at Tortuguero, therefore, the condition of male and female gonads was coded based on the relative size, texture (smooth, fine grainy, coarse granular), and color (translucent, opaque, white, yellow) criteria of Winemiller (1989). Immature and completely regressed gonads (e.g., tiny, translucent ovaries) were recorded as 1.0 and ripe gonads (e.g., large ovaries with large, fully-yolked oocytes) were coded as 4.0, with intermediate stages sequenced by 0.5 unit increments to yield 7 levels of development. Using a dissecting microscope and ocular micrometer, the diameter of the largest oocyte in gonads at levels 3.5 and 4.0 were measured to the nearest 0.05 mm.

Diet was investigated by means of stomach contents analysis and the methodology and criteria reported in Winemiller (1990). Except for fishes, which were identified to species whenever possible, most animal food items were identified to order, and plant and detritus categories were usually grouped according to broader taxonomic and functional categories (e.g., small seeds, vegetative detritus, diatoms). Contents from the anterior half of the gut were identified, sorted, and quantified volumetrically by water immersion in appropriately sized graduated cylinders. Diets were compared as percent volumes of items consumed. Diet breadth was calculated using Simpson's (1949) index, and diet similarity was calculated using Pianka's (1973) symmetrical measure of niche overlap. Dietary overlap and diet breadth were compared for aggregate samples representing dry (Apr–May, Oct) and wet (Feb–Mar, Jun–Sep, Nov–Dec) seasons. Because some species' monthly samples contained fewer than 30 individuals and the two sites exhibit very similar temporal changes in habitat conditions (relative to rainfall), some data analyses were performed on combined AFV and QB monthly samples. Temporal change in the state of gonad maturation,

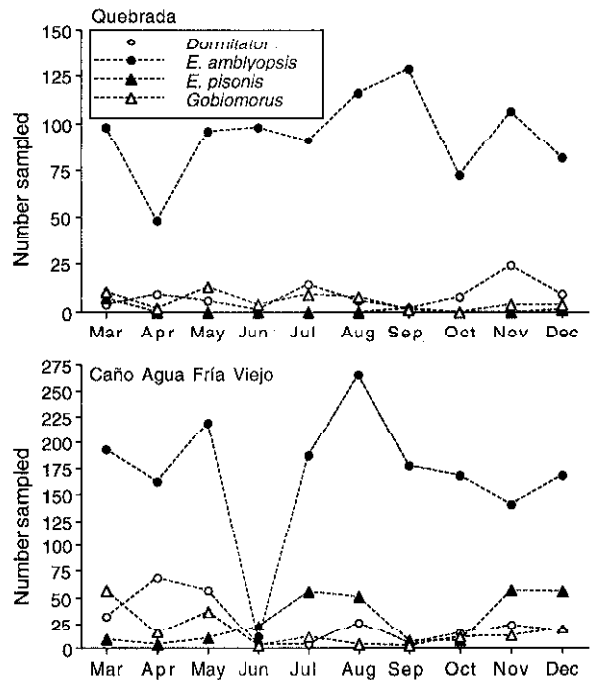


Figure 2. Monthly changes in the relative abundances of eleotrid fishes at Quebrada and Caño AFV over the 10 month study.

and diet variation was examined in relation to body length and mouth gape.

We also report observations of the 'tismiche', massive aggregations of juvenile shrimp and fishes that periodically migrate into the Laguna Tortuguero from the sea (Gilbert & Kelso 1971, Nordlie 1981). Most 'tismiches' are dominated by palaemonid shrimp (mostly of the genus *Macrobrachium* ca. 10 mm) or atyid shrimp (ca. 5 mm), but the major fish component tends to be juvenile eleotrid fishes of the genus *Eleotris* (probably a combination of *E. amblyopsis* and *E. pisonis*, however species verification is difficult at these small sizes).

Results

Population abundance and structure

Four eleotrids (*Dormitator maculatus*, *Eleotris amblyopsis*, *Eleotris pisonis*, and *Gobiomorus dormitor*) were common (mean monthly abundance ranged from 17.4 for *G. dormitor* to 65.6 for *E. amblyopsis*) in samples from Caño AFV (Figure 2). *Gobio-*

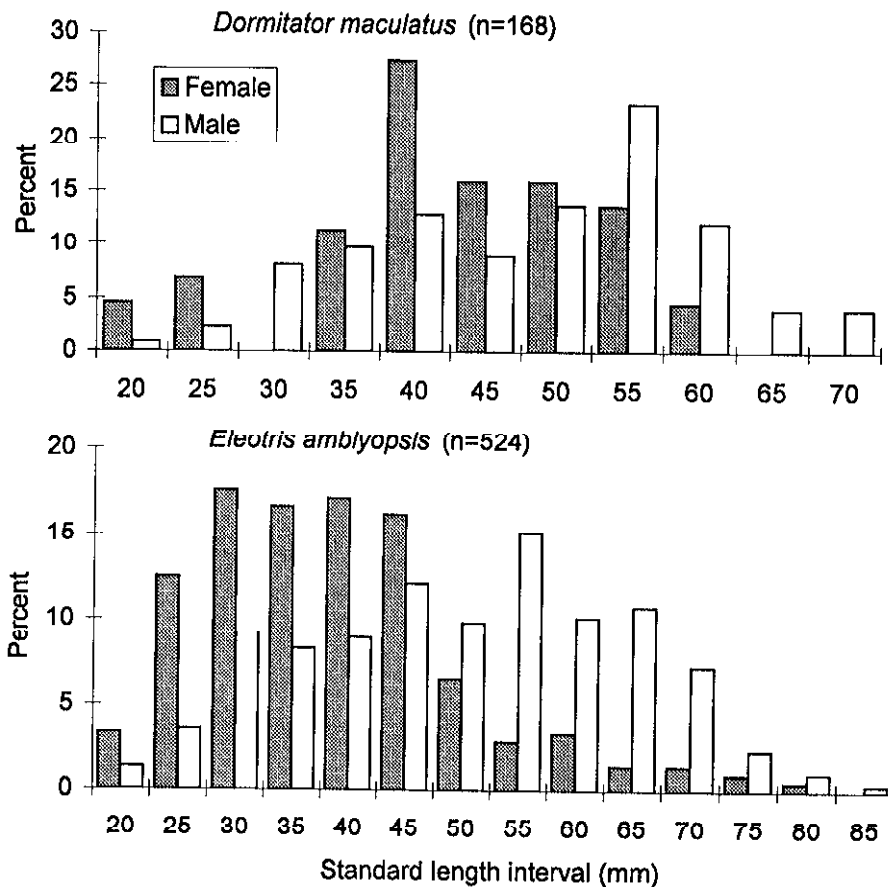


Figure 3. Length-frequency histograms of *Dormitator maculatus* and *Eleotris amblyopsis* segregated by sex based on combined Quebrada and Caño AFV samples.

morus dormitor had the greatest between-month variation in sample abundance at Caño AFV (coefficient of variation = 103.3) followed by *D. maculatus*

Table 1. Estimates of biomass per unit (mg m^{-2}) of eleotrid fishes in samples from channel and marginal vegetation at Caño Agua Fría Viejo during May (dry season) and December (wet season).

	channel		Marginal vegetation	
	May	Dec	May	Dec
<i>Dormitator maculatus</i>	0	0	<0.1	4.2
<i>Eleotris amblyopsis</i>	0.1	0.1	8.7	6.2
<i>Eleotris pisonis</i>	0	0	<0.1	2.3
<i>Gobiomorus dormitor</i>	<0.1	1.4	0	0
Total eleotrid biomass (g)	25.0	37.2	54.0	149.1
Total fish biomass (g)	203.0	125.8	75.0	192.45
Total area sampled (m^2)	182.7	174.0	6.24	11.7

tus (CV = 89.6), *E. pisonis* (CV = 86.1), and *E. amblyopsis* (CV = 38.8). *Eleotris amblyopsis* abundance declined markedly during June at Caño AFV. At Quebrada, *E. amblyopsis* was common (mean monthly abundance = 22.6) and the other three species were relatively uncommon (mean monthly abundance ranged from 2.2 to 6.7). A fifth eleotrid, *Guavina guavina*, was rare ($N = 4$) at Quebrada.

At Caño AFV, *D. maculatus* and the two *Eleotris* species were almost always captured from the dense beds of floating aquatic macrophytes that lined the stream margins and sometimes completely covered the channel. The two *Eleotris*, and to a lesser extent *D. maculatus*, also were occasionally captured from submerged stalks of immature water hyacinth, *Eichhornia crassipes*. Juvenile *G. dormitor* were rarely captured in aquatic vegetation, although individuals of all sizes were sometimes cap-

tured near or underneath patches of floating plants. Eleotrid biomass per unit area varied by habitat at Caño AFV during the dry (May) and wet season (Dec) (Table 1). In these samples, *G. dormitor* was only taken in channel areas and its biomass density was greater during December. The other three eleotrids were taken almost exclusively from marginal vegetation, with *D. maculatus* and *E. pisonis* biomass densities being greater during December. The numeric abundance of *D. maculatus* was actually lower during December than May (Figure 2), but this apparent discrepancy with the biomass estimates is explained by the fact that average size was greater during December (mean SL = 53.2) than May (mean SL = 38.5).

All four eleotrids revealed a broad range of size classes during all periods at both streams. *Dormitor maculatus* ranged from 15.0–89.6 mm SL at Quebrada and from 17.8–70.0 mm at Caño AFV. *Eleotris amblyopsis* ranged from 18.4–86.0 mm at Quebrada and from 16.5–86.2 mm at Caño AFV. *Eleotris pisonis* ranged from 34.9–121.5 mm at Quebrada and from 19.4–125.5 mm at Caño AFV. *Gobiomorus dormitor* ranged from 17.3–235.0 mm at Quebrada and from 18.7–250.0 mm at Caño AFV. Female *D. maculatus* and *E. amblyopsis* were smaller than males (*D. maculatus* $t = 2.88$, $df = 166$, $p < 0.005$; *E. amblyopsis* $t = 10.19$, $df = 522$, $p < 0.0001$) and comprised 26% and 42% of the aggregate sample for each species respectively (Figure 3). Sizes of the two sexes overlapped broadly, and no evidence of sequential hermaphroditism was found during examination of gonads under a dissecting microscope (e.g., presence of ovarian and testicular tissues of varying stages of development or degeneration in the same gonad) or via histological examination of gonads from a subsample of 40–60 mm SL *E. amblyopsis* (Cole K.S. personal communication). Mean sizes of sexes were not significantly different for *E. pisonis* ($t = 0.44$, $df = 112$, $p = 0.33$) or *G. dormitor* ($t = 0.11$, $df = 41$, $p = 0.45$). Females comprised 66% of the total *E. pisonis* sample. Our field sampling methods did not efficiently collect eleotrids smaller than 30 mm SL, but nonetheless did collect juvenile eleotrids (20–30 mm) at both sites consistently throughout the study period.

Both male and female *D. maculatus* tended to

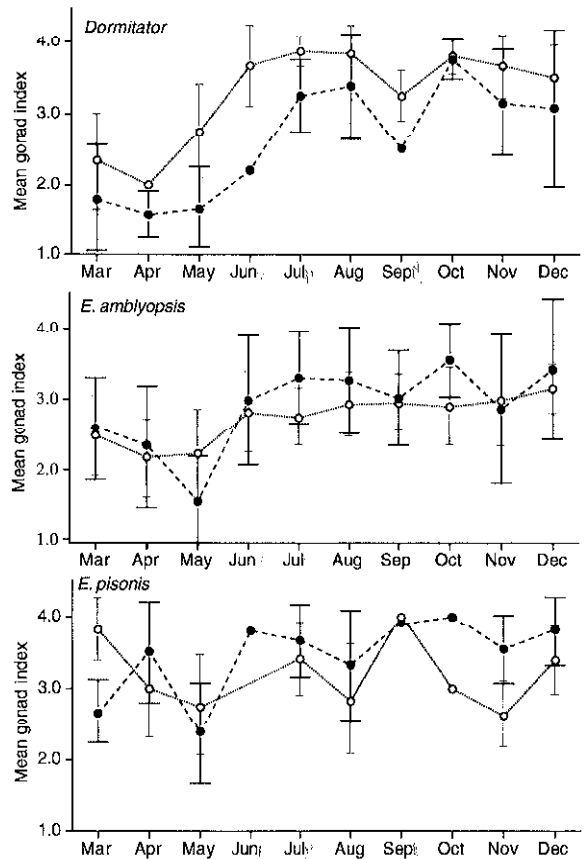


Figure 4. Index of gonadal maturation for male (filled circles) and female (open circles) eleotrid fishes over a 10 month interval at Tortuguero based on combined Quebrada and Caño AFV samples.

have less developed gonads during the relatively dry months of March through May (Figure 4). Fish from the September sample (prior to the October dry period) also showed a slight decline in the average gonad maturation state by both sexes. *Eleotris amblyopsis* showed male and female patterns of gonad maturation that were similar to but less pronounced than those of *D. maculatus*. Male *E. pisonis* tended to have less developed testes during March and May than the other months, and the condition of female gonads declined during the period March through May and again during September–October. None of the males from the June samples were large individuals, and we presume that during this period most adult males (and many females also) had migrated out of these streams toward the estuary. Sample sizes for adult *G. dormitor* were too

small to plot monthly averages for the gonad index. The maximum oocyte diameters recorded for preserved eleotrid females with gonads in state 3.5 or 4.0 were as follows: *D. maculatus* 0.25 mm, *F. amblyopsis* 0.25–0.30 mm, *E. pisonis* 0.25–0.30 mm, and *G. dormitor* 0.35 mm.

Feeding interrelationships

Dormitator maculatus consumed mostly coarse vegetative detritus and relatively minor amounts of filamentous algae and diatoms (Table 2). Protozoa, rotifers, microcrustacea, and other small invertebrates collectively comprised a very minor fraction (< 4%) of the diet by volume. In contrast, both *Eleotris* species, *G. dormitor*, and *G. guavina* were carnivorous. *Eleotris amblyopsis* consumed mostly decapod crustacea (shrimp), eleotrids, and poeciliid fishes. The diet of *E. pisonis* was strongly dominated by shrimp, followed by eleotrid and poeciliid fishes (mostly *Phallichthys amates*) then molluscs. *Gobiomorus dormitor* also fed heavily on shrimp, followed by cichlids and other fishes. The small

sample size for *Guavina* gut contents revealed only an eleotrid and a poeciliid fish.

Intraguild predation was present among the two *Eleotris* species and *G. dormitor*. At least 5.3% of *G. dormitor*'s diet at Caño AFV and 24.5% of its diet at Quebrada was comprised of *E. amblyopsis*. By volume, *E. pisonis*'s diet consisted of at least 9.6% *E. amblyopsis* at Caño AFV. The diet of *E. amblyopsis* consisted of 24.5% conspecifics at Caño AFV, but no cannibalism was noted from samples from Quebrada.

Ontogenetic diet shifts occurred in all four of the common eleotrids, but the size classes at which these shifts occurred differed (Figure 5). *Dormitator maculatus* shifted from a diet dominated by microinvertebrates to one dominated by detritus at about 25 mm. *Eleotris amblyopsis* shifted from macroinvertebrate feeding (mostly aquatic insects and shrimp of the genus *Macrobrachium*) to piscivory at about 70 mm. In contrast, *E. pisonis* of all sizes consumed mostly shrimp, although sample sizes for some size intervals were relatively small, and a shift toward piscivory seemed to occur at about 90 mm. Similarly, small *G. dormitor* fed mostly on

Table 2. Diet composition of eleotrid fishes based on volumetric percentages for the entire 10-month sampling period at Tortuguero.

	<i>D. maculatus</i>	<i>F. amblyopsis</i>	<i>E. pisonis</i>	<i>G. dormitor</i>	<i>G. guavina</i>
Algae	9.75	< 0.01			
Detritus/substrate	86.07	0.97	0.02	0.06	
Vegetation	0.31	0.01	0.01		
Protozoa/rotifers	2.59	0.05			
Microcrustacea	0.63	0.59	0.24	9.74	
Decapod crustacea		36.74	79.22	51.12	
Colcoptera (aquatic)	0.01	0.70			
Diptera (aquatic)	0.25	1.67	0.03	0.93	
Ephemeroptera (aq.)	0.05	0.35	0.01	6.25	
Hemiptera (aquatic)		0.40			
Odonata (aquatic)	< 0.01	0.98	0.26	0.16	
Other aquatic insects	0.05	2.46	0.60	2.24	
Terrestrial arthropods	0.03	0.27	0.26	2.02	
Molluscs		1.46	3.14	0.40	
Worms	0.24	0.35		0.01	
Characids		5.24			
Cichlids		1.71	0.66	10.12	
Eleotrids		30.49	6.61	1.21	50.00
Poeciliids		11.05	6.77	0.20	50.00
Unidentified fishes		4.49	2.08	15.51	
Sample N	222	625	156	187	4

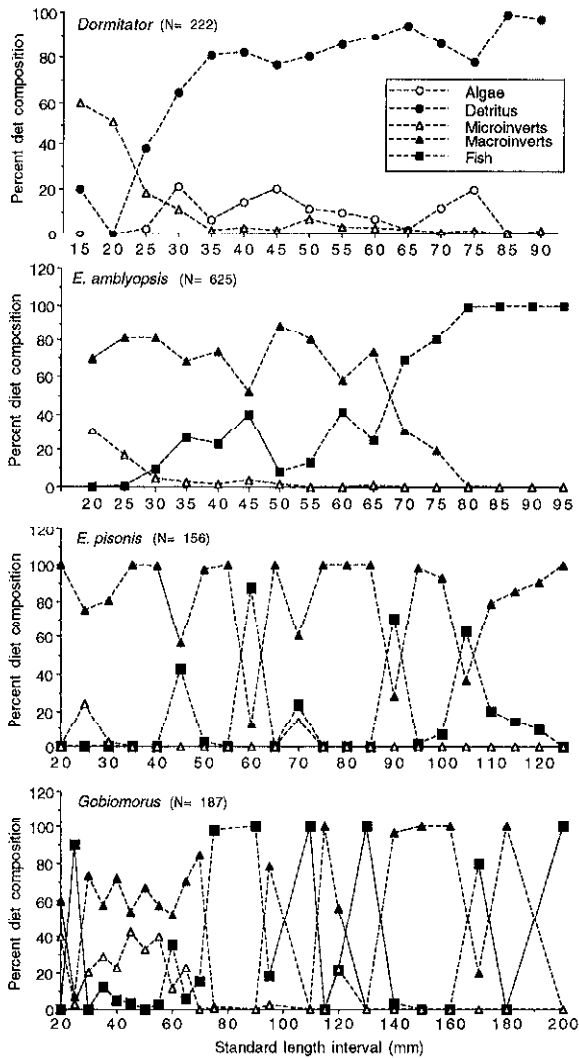


Figure 5. Proportions of algae, macrophytes, microinvertebrates, macroinvertebrates, and fishes in the diets of electroid fishes in relation to standard length.

shrimp and the species shifted to feeding on a combination of fishes and shrimp at sizes greater than 70 mm.

During both wet and dry seasons at Quebrada, the dietary niche breadth of *E. amblyopsis* was about two to three times larger than those of the other electroid species (Table 3), however the former was the only truly abundant electroid in this stream. At Caño AFV where four electroids were common, *E. amblyopsis* and *G. dormitor* had the largest diet breadths during the dry season. *Gobiomorus*'s diet breadth declined markedly during the

wet season at Caño AFV. *Dormitor* had lower diet breadth during the dry season at both sites. Seasonal shifts in diet breadth were relatively minor (< 1.0 diet breadth unit) for *Eleotris* species.

Diet overlap between the detritivore, *Dormitor*, and the three carnivorous electroids was expectedly low during both wet and dry periods (Table 3). In all four interspecific seasonal comparisons among carnivores, pairwise diet overlap was lower during the wet season (mean seasonal difference = 0.54), the period when potential prey are dispersed at lower per-unit-area densities within flooded marginal terrain.

Interspecific differences in relative mouth gape and gut length were consistent with results from dietary analysis (Figure 6). *Dormitor maculatus*, the detritivore, has a much longer gut and smaller mouth gape than the three carnivorous electroids. *Gobiomorus dormitor* has a larger mouth gape than the two *Eleotris* species, which is consistent with its consumption of larger prey. Cichlid fishes, including juveniles of the piscivore *Cichlasoma doyii*, comprised at least 10% of the *G. dormitor* diet (15.5% of fish material from stomachs was unidentified). In addition, mouth gape probably is associated with differences in foraging behavior. All three electroids are largely sit-and-wait predators that lurch to engulf or grasp their prey. *Eleotris* species inhabit dense vegetation mats and leaf litter packs and attack prey that pass within close proximity. In contrast, *G. dormitor* generally rest on the substrate and attack prey from greater distances in more open habitats.

Tismiche observations

During 1985, the senior author observed the initiation of two 'tismiches' along the east bank of the Laguna Tortuguero at the Tortuguero village (17 August, 1 November). *Eleotris* was the dominant fish in the August tismiche, and very few fish larvae were observed in the November tismiche. Other fish species present in the August tismiches included *Pomadasys crocro*, *Oostethus lineatus*, and *Gobionellus fasciatus*. In each case, the tismiche began as dense aggregations of continuously moving (in a

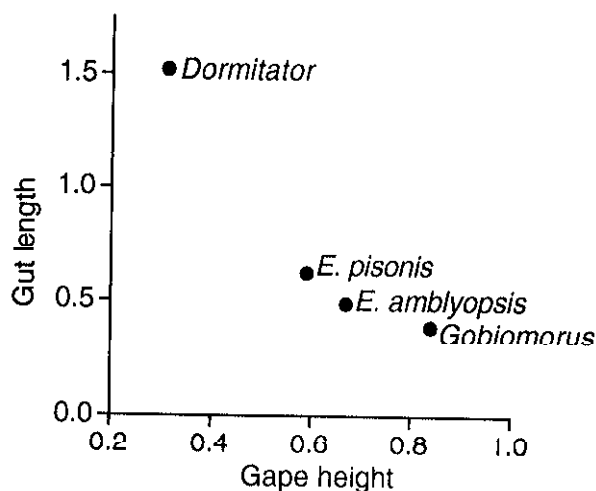


Figure 6. Comparisons of mean relative gape height (mouth gape/head height measured in a vertical line through pupil) and mean relative gut length (total gut length/SL) for Tortuguero eleotrids (values are means based on 10 adult conspecifics).

direction away from the estuary mouth) organisms that persisted for 4–21 days. By the third or fourth day, the stream of organisms was smaller and comprised of scattered aggregations of migrants.

Discussion

The patterns of relative abundance and microhabitat association among eleotrid fishes of freshwater streams at Tortuguero were similar to those described by Nordlie (1970, 1972) for the estuary (La-

guna Tortuguero). By a considerable margin, *E. amblyopsis* was the most abundant eleotrid within both streams and the estuary. Almost all of the *D. maculatus* captured from the estuary by Nordlie were small juveniles, whereas a wide range of sizes were collected in freshwater streams. Nordlie captured an additional rare benthic eleotrid from the estuary, *Leptophilypnus fluviatilis*, which was not found in our stream systems. An additional rare eleotrid captured from leaf litter in Quebrada, *Guavina guavina* (4 individuals 26.4–144.2 mm), has not been captured from the estuary. *Dormitator maculatus* and the two *Eleotris* species were most commonly captured from the root masses of dense beds of floating aquatic macrophytes in both Caño AFV and the estuary. The small forest stream, Quebrada, had almost no aquatic macrophytes, and in this system these species commonly were associated with leaf litter packs. In all three systems, *G. dormitor* was associated with more open habitats, although usually it was observed or captured near woody debris, submerged macrophytes, or from beneath floating macrophytes.

Diets of eleotrids inhabiting streams were similar to those reported by Nordlie (1979, 1981) for estuarine eleotrids. In freshwater streams, *D. maculatus* was essentially detritivorous with some individuals also consuming minor fractions of microinvertebrates. Nordlie characterized *D. maculatus* as an omnivore (plant material and aquatic invertebrates), but he did not distinguish between recently

Table 3. Diet breadths and species pairwise diet overlaps of eleotrid fishes by season for Quebrada and Caño Agua Fria Viejo. Wet season overlaps appear above the diagonal in each matrix, and dry season overlaps appear below the diagonal.

	B _{wet} :B _{dry}	Overlap			
		<i>D. maculatus</i>	<i>E. amblyopsis</i>	<i>E. pisonis</i>	<i>G. dormitor</i>
Quebrada					
<i>Dormitator maculatus</i>	3.46/2.42	×	0.01	0.03	0
<i>Eleotris amblyopsis</i>	8.46/7.68	0.06	×	0.14	0.20
<i>Eleotris pisonis</i>	/3.03			×	0.56
<i>Gobiomorus dormitor</i>	4.98/2.02	< 0.01	0.38		×
Caño Agua Fria Viejo					
<i>Dormitator maculatus</i>	2.72/2.32	×	< 0.01	< 0.01	< 0.01
<i>Eleotris amblyopsis</i>	3.89/4.40	< 0.01	×	0.38	0.34
<i>Eleotris pisonis</i>	1.78/1.36	< 0.01	0.91	×	0.38
<i>Gobiomorus dormitor</i>	1.50/5.25	< 0.01	0.88	0.98	×

living versus dead and decaying plant tissue as we did, and his analysis was based on frequency of occurrence rather than volumetric proportions. In addition, Nordlie's (1981) diet sample for estuarine *D. maculatus* was small ($n = 21$) and dominated by juveniles. Our analysis of ontogenetic niche shifts showed that juvenile *D. maculatus* consume greater proportions of invertebrates. Small fishes and shrimp were the major prey of *G. dormitor* and *Eleotris* species in both streams and the estuary. Nordlie's (1981) diet samples for estuarine *E. pisonis* and *G. dormitor* were very small ($N = 3$ and 5 , respectively), but nonetheless indicated the importance of these two food resource categories. Contrary to our results, Nordlie (1979, 1981) did not report intraguild predation or cannibalism, however, large sample sizes are required to reveal the incidence of cannibalism. Coates (1992) described a major predator-prey interaction between two eleotrid species from river floodplains in Papua New Guinea. On a seasonal basis, between 50–90% of the diet volume of *Oxyeleotris heterodon* consisted of *Ophieleotris aporos*. In Tortuguero streams, predation on eleotrids by other eleotrids was much less prevalent (seasonal volumetric proportions ranged between 5–24%). The abundant *E. amblyopsis* was the primary eleotrid species consumed by other eleotrids.

Without exception, pairwise diet similarity among the three common carnivorous eleotrids was lower during the wet season, and this could represent a classic case of niche compression in response to food resource limitation and interspecific competition. During the wet period, small fishes and other aquatic organisms that are potential prey for these eleotrids dispersed within the flooded forest floor of the stream floodplains. Even though absolute local population abundances of major prey, such as shrimp and pociliid fishes, may be unchanged or even increase in response to reproduction, the per-unit-area densities are greatly reduced during these extended periods of flooding (Winemiller 1993). For stream piscivores in particular, the expanded aquatic habitats of the wet season should represent the period of relative resource scarcity. Because these species' size-frequency distributions did not change appreciably over time at either

stream (i.e., the smallest and largest size classes were present in virtually all monthly samples), ontogenetic diet shifts probably had little effect on seasonal differences in species diet similarity. The seasonal variation in rainfall at Tortuguero is actually relatively low compared to some of the tropical savanna regions of continents (Winemiller 1989, 1990).

All four of the common eleotrids from Tortuguero streams had some individuals with ripe or ripening gonads during each of the 10 months of field study. This is consistent with an inference of year-round reproduction by at least some population segments, as evidenced also by the presence of juveniles (15–30 mm) in nearly every monthly sample of each species. However, two observations suggest that periods of peak reproduction may occur during a given year.

First, the time-series plots of gonad condition (Figure 4) showed a decline in average gonad maturation state during the period just prior to and/or during the major dry season of April–May and during September just prior to the minor dry season. If indeed fewer adults of these stream populations are ripe during these periods, it may be because there is a reduction in reproductive activity that occurs locally, or it may result from emigration of ripe individuals that spawn in another location such as the estuary. Because small juveniles are present year-round at both locations, it seems unlikely that reproduction/juvenile recruitment declines over a continuous 3-month period. Todd (1975) observed that *Dormitator latifrons* in Panama spawn in curyhaline estuarine habitats with low current velocity. He described how the early larvae of this species appear to be behaviorally adapted to seek areas of better habitat quality within these highly heterogeneous and variable systems. We hypothesize that stream-dwelling eleotrids at Tortuguero move some distance downstream, perhaps into marginal habitats of the estuary, during the dry seasons in order to increase the probability that their eggs, embryos, and larvae occupy the lower estuary or coastal marine habitat just beyond the estuary.

The second observation is the eleotrid component of the 'tismiche', the massive immigration of juvenile shrimp and fishes into the Laguna Tortu-

guero. Our 1985 observations agree closely with those described by Gilbert & Kelso (1971) involving tismiche occurrences in the lower Laguna Tortuguero that began on or near 3 September 1958, 21 August 1963, 4 May 1964, and 19 July 1964. During 1996, the junior author observed tismiches along the east and west banks of Laguna Tortuguero just north of the village beginning on 12 July, 9 August, and 16 September. Hence, it appears that tismiches tend to be concentrated during the mid to latter portion of the summer wet season from mid July to early September, and more sporadically and to a lesser extent with fewer fish larvae and juveniles involved during the remainder of the year (e.g., May, September, November). Nordlie & Kelso (1975) reported a mid-September 1970 tismiche that lacked fish.

The pulse nature of the tismiche indicates that the intensity of reproduction by *Eleotris* must have a component of within-year seasonal variation. The tismiche also indicates that *Eleotris* eggs, which are presumed to be demersal, and early larvae are somehow placed within or transported into the lower estuary or coastal marine habitats. Because they are important members of coastal fish communities that respond to habitat heterogeneity at several different spatial scales, eleotrid fishes deserve to be the focus of additional research aimed at revealing the adaptive nature of life history styles and migration.

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