Fish assemblages across a complex, tropical freshwater/marine ecotone

Kirk O. Winemiller[1] & Mitchell A. Leslie
Department of Zoology & Texas Memorial Museum, The University of Texas, Austin, TX 78712, U.S.A.
[1] Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge,
TN 37831-6036, U.S.A.

Synopsis

Riverine fish assemblages in the temperate zone generally show strong longitudinal patterns of faunal turnover and increases in species richness with increasing stream order. We examined the composition and structure of tropical fish assemblages across a complex freshwater/marine ecotone in Tortuguero National Park on the Caribbean coast of Central America. Species turnover was high between four characteristic habitats that largely corresponded with a longitudinal gradient of stream order over distances of less than 30 km. Suites of common fish species characterized each habitat: creeks, rivers, lagoons, and the sea. In addition to the habitat endemics, several species spanned two habitat types, but only three species were collected in more than two habitats. Multivariate gradient analysis of fish assemblages reflected a gradient of habitats that to some extent corresponded to fluvial distances. Due to the unusual configuration of coastal lagoons lying parallel to the coast, the ordination gradient showed little correlation with linear distance to the coast. Environmental variables related to habitat size and salinity showed greatest correspondence with the fish assemblage ordination gradient. Invertebrate-feeding fishes were the predominant trophic group in 15 of 16 fish assemblages, and inland creek sites contained a greater proportion of herbivores and omnivores than other sites. The relative fraction of herbivorous and detritivorous fishes showed a monotonic decline along the longitudinal habitat gradient from inland to coast. Patterns of species composition and richness at Tortuguero Park appeared to agree well with earlier models of factors influencing temperate zone stream fishes. Headwaters have low aquatic primary productivity and contain small colonizing fish species subject to large fluctuations in local densities and intermittent competition. Lagoons contain both large and small species, the latter being restricted largely to shallow edge habitats by predation. Lagoons exhibit more lentic environmental conditions, experience relatively fewer periodic disturbances than headwaters, and their assemblages are inferred to be under relatively greater influence of biotic factors. Fish assemblages of rivers and caños (swampy side channels and braids) appear to be under less abiotic control than headwaters and influenced less by biotic factors than lagoons.

Introduction

Interest in the structure of natural fish communities is rooted in both ecological theory and fisheries management concerns, with a primary goal being improved understanding of the complex hierarchy of physical and biotic environmental factors impinging on the relative success of fish populations.

Species assemblages can be examined from several different perspectives, including spatiotemporal patterns of taxonomic composition, trophic ecology, and reproductive guilds. Investigations of riverine fish assemblages have resulted in general hypotheses of longitudinal zonation (Kuehne 1962, Sheldon 1968, Bishop 1973, Vannote et al. 1980, Schlosser 1987). Investigators working with fishes and aquatic invertebrates have identified strong gradients ranging between (1) low-diversity, headwater assemblages subject to periodic disturbance from high variation in water discharge levels (Fisher et al. 1982, Meffe & Minckley 1987), and (2) high-diversity assemblages in low-gradient, downstream reaches where biotic interactions appear to exert a relatively greater influence (Allan 1975, Schlosser 1987). Exceptions to this general pattern are usually associated with special geological or historical features, including rifting (Balon 1974, Balon & Stewart 1983) and desertification (Smith 1981). In estuaries, physicochemical gradients are again conspicuous and either directly or indirectly influence species assemblages. A number of parameters tend to be correlated with salinity and form gradients across the freshwater/marine interface, and these in turn influence species distributions and local abundances (Weinstein et al. 1980, Felley 1987, Rozas & Odum 1987, Odum 1988). Some species are directly limited by narrow physiological salinity tolerance, whereas other species having broad tolerances may be restricted from certain locations by physical or biotic factors that are correlated with salinity (e.g., nutrients, productivity, habitat structural heterogeneity).

Multivariate methods for ecological gradient analysis (Hill & Gauch 1980, Gauch 1982, Ter Braak 1986) have intensified interests in patterns of fish species association and distribution in relation to riverine gradients (e.g., Matthews & Robison 1988, Townsend & Peirson 1988, Ibarra & Stewart 1989). Most studies of fish assemblages have focused on patterns observed across large spatial scales corresponding to large watersheds or entire zoogeographic regions (Burton & Odum 1945, Saul 1975, Cashner & Brown 1977, Horwitz 1978, Graham & Hastings 1984, Matthews 1986, Ibarra & Stewart 1989). At small spatial scales, examination of species associations can be reduced to the question of between-habitat (beta) diversity, where strong longitudinal patterns of species association generally are replaced by a more complex spatial configuration associated with microhabitat heterogeneity (Gorman & Karr 1978, Angermeier & Karr 1983, Meffe & Sheldon 1988, Lyons & Schneider 1990).

This study investigates patterns of species association and longitudinal zonation of fishes in Tortuguero National Park, a region of 18 947 ha on Costa Rica's Caribbean coast. The park contains a mosaic of diverse terrestrial environments, ranging from speciose lowland tropical rainforest to palm swamps and beach communities consisting of a few colonizing species. Aquatic environments span a complex, feshwater/marine ecotone and include small headwater streams within distances of 0.3 to 13 km from the sea coast, swamps, rivers, estuaries, and ocean beach. One hundred-thirty fish species have been documented from fresh, brackish, and marine waters of Tortuguero National Park (Caldwell et al. 1959, Gilbert & Kelso 1971, Bussing 1987, Winemiller 1987). We employ multivariate methods of community gradient analysis and note levels of turnover in the fish fauna over small spatial scales that are comparable to patterns frequently observed across much larger watersheds. We then relate species distributions and assemblage affiliations to physical and biotic environmental factors.

Methods

Study region

Tortuguero National Park lies within the Caribbean coastal lowlands of Costa Rica's Limón province between 10° 20' and 10° 35' lat. N (Fig. 1). The region is among the wettest on earth, averaging about 5 m of rainfall per year with two main rainy seasons from July to August and November to January. Rainfall in excess of 7 m may occur during an exceptional year. Generally, no month receives less than 50 mm, and temperature shows little seasonal variation with an annual mean of 23–26° C
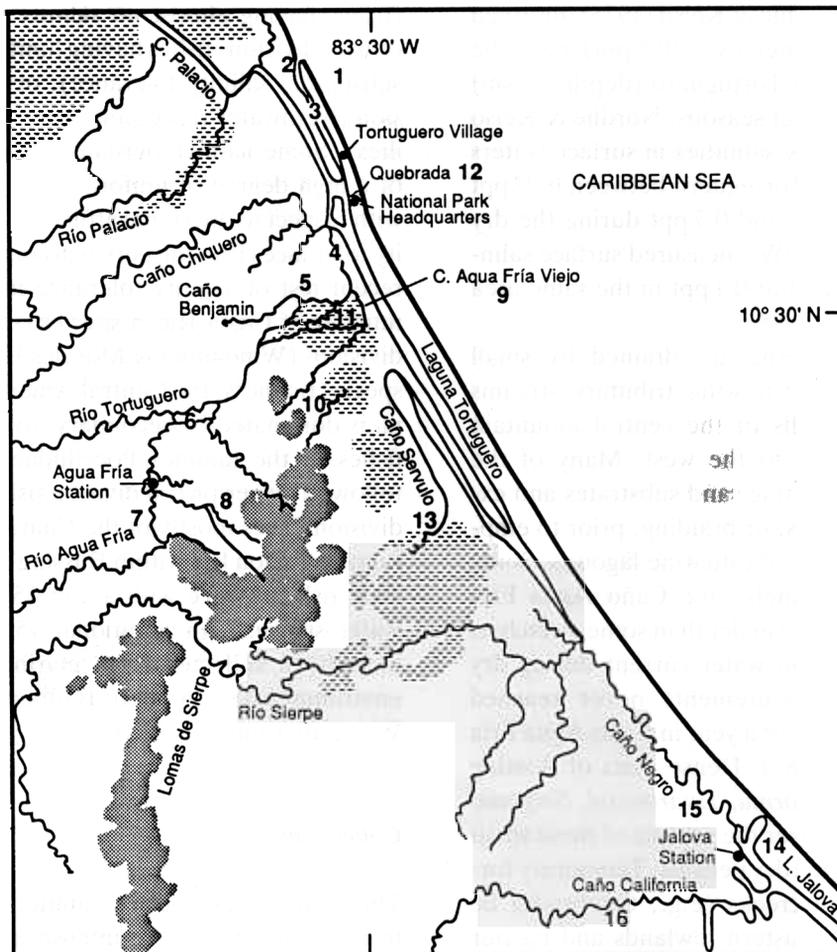
Fig. 1. Map of Tortuguero region. Locations of 16 study sites within the Río Tortuguero, Río Sierpe, and Caño California drainages are indicated by numbers. Dark shading represents Lomas de Sierpe, dashed regions represent low-lying, *Raphia* palm swamps.

(Hirth 1963). Most of the western area of the park is covered by pristine, lowland tropical rainforest, but at least four other vegetative zones have been recognized within the reserve: cativo swamp forest, low marsh woodland, herbaceous marshland, and halophytic coastal vegetation (Nuhn et al. 1967). Many of the low marsh woodlands are dominated by the palm *Raphia taedigera.*

Apart from the Lomas de Sierpe hills in the west (Fig. 1), most of the park is coastal plain lying only a few meters above sea level. Sediments of the plain are of alluvial origin, formed by a coalescence of river deltas. A distinctive network of narrow lagoons lies parallel to the coast (corresponding to Caño Palacio, Laguna Tortuguero, Caño Servulo,

Caño Negro, and Laguna Jalova in Fig. 1). The coastal lagoons are actually estuaries molded by the dynamic forces of river sedimentation and coastal currents. The Laguna Tortuguero averages approximately 7.5 m depth at midchannel between Tortuguero village (depth 13 m) and its mouth (Nordlie & Kelso 1975). Two openings to the sea lie at, or in close proximity to, the park boundary: a permanent northern outlet at the mouth of the Laguna Tortuguero, and the temporary Laguna Jalova outlet to the south. The outlet at the Laguna Jalova mouth only opens during periods of exceptional rainfall. For example, the mouth was open during the peak summer wet seasons in 1983 and 1986, but completely blocked by a sand ridge

throughout 1985. Nordlie & Kelso (1975) observed a tongue of saline water (8.7–10.5 ppt) near the bottom of the Laguna Tortuguero (depths > 5 m) during both dry and wet seasons. Nordlie & Kelso also reported high-tide salinities in surface waters of the upper Laguna Tortuguero between 0.07 ppt during the wet season and 0.7 ppt during the dry season. One of us (KOW) measured surface salinities less than or equal to 0.1 ppt in the same area throughout the year 1985.

The Lomas de Sierpe are drained by small streams that join east-flowing tributary streams that drain the foothills of the central mountain range lying 50–60 km to the west. Many of the park's rivers have shifting sand substrates and exhibit multiple channels, or braiding, prior to emptying into the network of estuarine lagoons. Some of the old river channels, like Caño Agua Fría Viejo, are in excess of 3 m depth in some stretches, and exhibit little or no water current during dry periods. Salinity measurements never reached 0.1 ppt over the course of a year in Caño Agua Fría Viejo (Winemiller 1987). Dense mats of floating aquatic plants (*Eichhornia, Hydrocotyl, Salvinia, Azolla*) sometimes cover the surface of these small caños during extended dry periods. Temporary forest pools and small creeks (e.g., Quebrada) lie scattered about the eastern lowlands and barrier islands that form partitions between sea and lagoons. These small creeks have negligible gradients and drain directly into the lower reaches of rivers and lagoons. Salinity measurements from the upper reaches of Quebrada and nearby forest pools never exceeded 0.1 ppt during 1985.

The Central American freshwater fish fauna is comprised of three basic groups: (1) a major component of South American-derived freshwater species, (2) a very minor component of North American-derived species, and (3) marine-derived peripheral species (Myers 1966, Miller 1966, Bussing 1976). The last group corresponds to species belonging to predominantly marine or brackish water families that are physiologically and ecologically adapted to live either all, or a portion, of their lives in freshwater environments (Myers 1938, 1966). Myers (1938) classified Central American species from freshwater families as either primary division

(fishes having almost no salinity tolerance), secondary division (fishes having limited or sometimes substantial salinity tolerance), or peripheral division (freshwater representatives from marine families). Some ichthyologists question the existence of a high degree of uniformity within higher taxa with respect to divisional affiliations based on salinity tolerance (Bussing personal communication). A recent test of salinity tolerance involving a small number of Costa Rican species confirmed Myer's divisions (Winemiller & Morales 1990). In terms of species richness, the Central American ichthyofauna is dominated by secondary division freshwater fishes of the families Poeciliidae and Cichlidae, followed by peripheral division fishes, and primary division fishes mostly of the Characidae. The Tortuguero region lies within Bussing's (1976) Río San Juan fish province with about 55 reported freshwater species. An additional 75 marine species have been collected from marine and estuarine environments of the park (Gilbert & Kelso 1971, Winemiller unpublished).

Collections

This study uses species' numerical abundances from 16 sites that were intensively sampled from June–August 1983, February–December 1985, and August 1986. We combined our species numerical abundances with primary data reported by Gilbert & Kelso (1971) from earlier collections at many of the same sites. Because our collections were more frequent and intense at southern and inland locations and earlier collections were more frequent at northern estuarine and ocean/beach sites, the two data sets complemented one another in providing a data set portraying regional species distributions and relative abundances across a broad range of aquatic habitats. Fishes were collected using seines (6.2 × 1.9 m, 4.7 mm mesh; 2.5 × 1.9 m, 3.2 mm mesh), dipnets (3.2 mm mesh), castnets (1.9 m diam., 1 cm mesh), gillnets (25 m, 5 cm mesh; 25 m, 10 cm mesh), and hook and line. In addition, Gilbert & Kelso (1971) used rotenone at several of the inland stream sites. At a given site, all aquatic habitats were sampled intensively with the primary

goal being attainment of a sample with all species in relative proportions approximating those of the local assemblage. A given sampling effort lasted from approximately 0.5 to 5 days, and the effort was continued until an hour or more of collecting produced no additional species for the sample (further details given in Winemiller 1987, 1990). Obviously, some sites were more efficiently and frequently sampled than others, however by summing many individual samples into annual site totals and conversion of species' numerical counts into fractional abundances, our estimates of species' relative abundances and spatial distributions should have minimized most strong systematic biases. Two modifications were made on entries in the Gilbert & Kelso (1971) data set. Gilbert & Kelso's sample of 2689 *Pomadasys crocro* larvae from the Laguna Tortuguero on August 15, 1963 represented an unusual collection from a single massive aggregation of migrating fish larvae. Because this large number would have greatly affected the entire distribution of species' numerical relative abundances for Laguna Tortuguero, it was entered as one individual for the present analysis. This adjustment yielded a total of 95 individuals for the site, which we feel more accurately represented the annual relative abundance of the species within the assemblage context. Also, three species were listed by Gilbert & Kelso as 'many' in the central Laguna Tortuguero (*Eleotris* spp., *Gobionellus fasciatus*) because they were the predominant fish components of the tismiche (huge migrating aggregations of postlarval shrimp and larval fishes). We entered each of these as 250 individuals.

At each sample site during the 1983–1986 collections, stream width and depth were measured to the nearest 1 cm with a tape (at 3–4 points in a lateral transect). Water current velocity was estimated by timing the passage of a film canister filled half-way with water over a measured distance in midchannel. Dissolved oxygen was estimated by Winkler titration, salinity was measured by meter or calculated from density measurements, pH was measured with reagent grade pH paper, and water color was estimated with the Hazen scale (each performed 2–6 × per sample date). Qualitative shoreline characteristics, substrate, aquatic macro-

phyte composition and relative coverage were recorded at each site. Habitat measurements were generally made between 1200 and 1400 h on the day the sampling effort was initiated. Complete records of sample sites and dates are on file at the Texas Natural History Collection of the Texas Memorial Museum. Sample sites used in the analysis are as follows: (1) ocean/beach environment adjacent to the park and Tortuguero village, (2) the mouth/outlet of the Laguna Tortuguero, (3) Laguna Tortuguero between its outlet and national park headquarters, (4) Río Tortuguero between Caño Benjamin and its confluence with the Laguna Tortuguero, (5) Caño Benjamin, a sluggish, blackwater western tributary of the Río Tortuguero, (6) side channel of the Río Agua Fría (station 31 in Gilbert & Kelso, 1971), (7) Río Agua Fría, a stretch within 1 km of Agua Fría park station, (8) small west-slope streams draining the Lomas de Sierpe and entering the Río Agua Fría in the vicinity of Agua Fría park station, (9) Caño Agua Fría Viejo, an old swampy channel (braid) of the Río Tortuguero, (10) east-slope streams draining the Lomas de Sierpe and entering old channels of the Río Tortuguero northeast of the Lomas, (11) forest pool, isolated during the dry season and approximately 100 m from Caño Agua Fría Viejo, (12) Quebrada, a small stream draining the barrier island and lying on the park's northern boundary approximately 20 m north of the national park headquarters, (13) Caño Servulo, a deep, sluggish blackwater slough entering the Laguna Tortuguero in the central eastern park, (14) Laguna Jalova, a temporary inlet at the park's southeastern border, (15) Caño Negro, a narrow, winding channel connecting the Laguna Tortuguero and Laguna Jalova, (16) Caño California, a river forming part of the park's southern boundary and flowing into the Laguna Jalova (Fig. 1).

Data analysis

Fishes were identified following Lopez-Sanchez (1968), Gilbert & Kelso (1971), Villa (1982), Rivas (1986), and Bussing (1987). Specimens were deposited in the Florida State Museum, Gainesville (Gil-

bert & Kelso 1971), the Natural History Museum of the University of Costa Rica, San Jose, and the Texas Memorial Museum, Austin. Species' numerical abundance data were combined for sites that were sampled repeatedly, and sample totals were converted to species' relative abundances. Differences in relative abundances between wet and dry seasons were recorded for Quebrada, Caño Agua Fría Viejo, Laguna Tortuguero, Laguna Tortuguero mouth, Caño Negro, and forest pool. Species diversity at each site was calculated as the index of Shannon & Weaver (1963):

$$H' = -\sum N_i/N \log_{10} N_i/N$$

The Shannon index is a function of two components, species richness (i.e., length of the frequency distribution of species' relative abundances) and evenness (i.e., degree to which a distribution is platykurtic), and here we contrast H' with species richness as a simple comparative index of relative evenness (Tramer 1969, Hurlbert 1971). Turnover of species between adjacent sites along longitudinal gradients was examined by calculating the percentage of species shared between adjacent sites from downstream to upstream, and by plotting the percentage of original species remaining from a given site while moving through sequential samples along the upstream gradient.

Detrended correspondence analysis (DCA) served as an ordination method for identifying assemblage gradients based on species' relative abundances (Hill 1979, Hill & Gauch 1980, Gauch 1982). We used the rare-species downweighting option on raw relative abundances and 26 segments for detrending site scores on the gradient axes. We also performed DCA without downweighting and with detrending by polynomials rather than segments using CANOCO (Ter Braak 1986, 1988). Since very little variation was observed among tests using the same data set, especially on the first gradient axis, we report only the results from DCA with downweighting and detrending by segments. Correlations between fluvial distance (i.e., river distance between site and sea outlet) and the first DCA axis provided one indirect estimate of gradient analysis (Ter Braak 1986). Fluvial distances

as well as linear distances to the coast were measured to the nearest 0.1 km on a 1 : 50 000 map (Servicio de Parques Nacionales, Ministerio de Agricultura y Ganaderia, San José, Costa Rica). In addition to DCA, a direct gradient analysis was performed with detrended canonical correspondence analysis (DCCA), a multivariate technique that ordinates sites using information from both species abundances and a set of environmental variables (Ter Braak 1986, 1988). In addition to fluvial distance, we placed the following environmental variables into discrete categories: average channel width, average depth, water current, water color (clear versus tannin-stained), salinity (calculated from density), and substrate. Categories were based on the measurements or estimates that were repeated over time at each site, with the exception of the lomas creeks which were sampled only during June 1985. Recorded temperature, dissolved oxygen, and pH values did not show large between-site or temporal variation and thus were excluded from further consideration.

Euclidean distances based on site scores on the first two DCA axes were used as estimates of similarity in clustering by a hierarchical linkage algorithm (Wilkinson 1989). A jackknifing method was used to estimate the consistency of nodes and terminal units of the dendrogram (Ibarra & Stewart 1989). Consistency of nodes and site arrangements in the dendrogram were estimated by comparisons with a series of dendrograms in which one of the 16 sites was removed sequentially from the data set. The trophic status of each species was categorized as either piscivore, invertebrate-feeder, omnivore, or herbivore (the latter includes varying degrees of detritivory) based on stomach contents data gathered by Winemiller (1987, 1990, unpublished, Winemiller & Pianka 1990).

Results

Species richness of Tortuguero Park fish assemblages varied from a low of 6 in the forest pool to a high of 80 in the Laguna Tortuguero. High faunal turnovers (i.e., the inverse of species retention), ranging from about 60% to more than 90% re-

Fig. 2. Species turnover (expressed as percentages of species shared between adjacent sites moving upstream) in the Río Tortuguero drainage (top), Caño Servulo drainage (middle), and Caño California drainage (bottom).

Fig. 3. Plots of the first two DCA axes based on species relative abundances for all 16 sites (a), and 15 sites with the isolated forest pools excluded (b). Lines connect adjacent sites within the Río Tortuguero drainage (stemming from site 1) and Caño California drainage (stemming from site 14).

placement of species from the previous downstream station, were observed in 9 out of 14 transitions in the Río Tortuguero/Laguna Tortuguero drainage and two of three transitions tested in the Laguna Jalova drainage (Fig. 2, Appendix 1). Some of these distinct faunal transitions occurred over distances as small as a few meters, as between the Laguna Tortuguero and the small barrier island creek, Quebrada (20% species retention). Five of the 21 species recorded from Quebrada (*Gymnotus, Rhamdia, Rivulus, Synbranchus, Cichlasoma alfari*) were never collected from the adjacent lagoon.

The first DCA axis described a longitudinal gradient running from low-order tributary streams containing relatively few species (low scores) to more speciose downstream sites and finally the ocean (Fig. 3, eigenvalue = 0.844). The second DCA axis (eigenvalue = 0.328) was much more difficult to interpret, but appeared to order tributary stream sites along an east (high scores) to west (low scores) gradient when all sites were included in the analysis (Fig. 3a). When the isolated forest pool (site 11) was eliminated from the analysis, the ordination of the remaining sites on the first DCA axis was virtually unchanged (Fig. 3b), and ordination of sites on DCA axis 2 yielded no general pattern of interpretation (Caño Servulo, Negro, and Laguna Jalova with high scores versus Caño California and a side channel of the Río Agua Fría with low scores).

The longitudinal pattern of zonation implied from the first DCA axis can be seen clearly in the spatial pattern of distribution of the most common
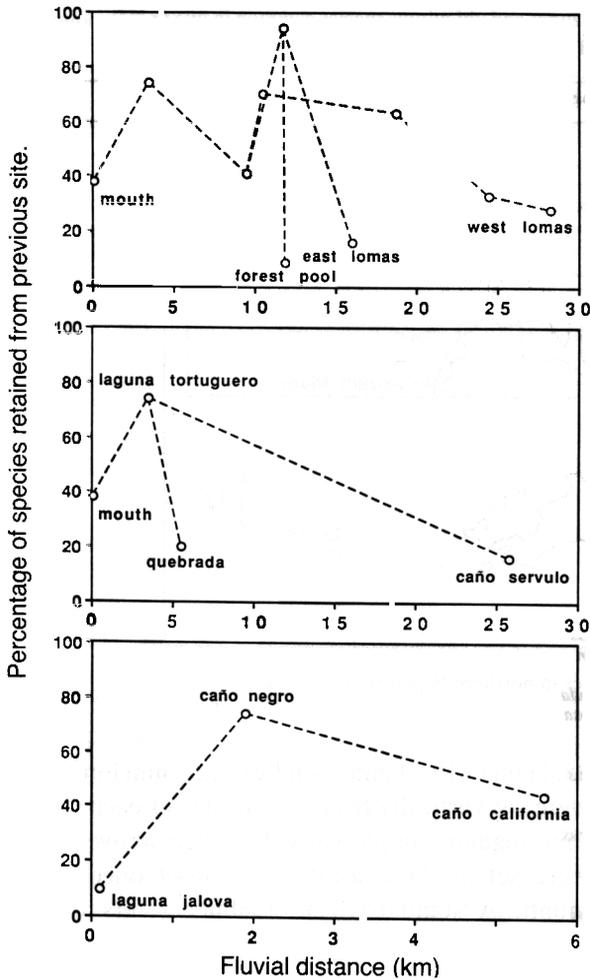
Fig. 2. Species turnover (expressed as percentages of species shared between adjacent sites moving upstream) in the Río Tortuguero drainage (top), Caño Servulo drainage (middle), and Caño California drainage (bottom).
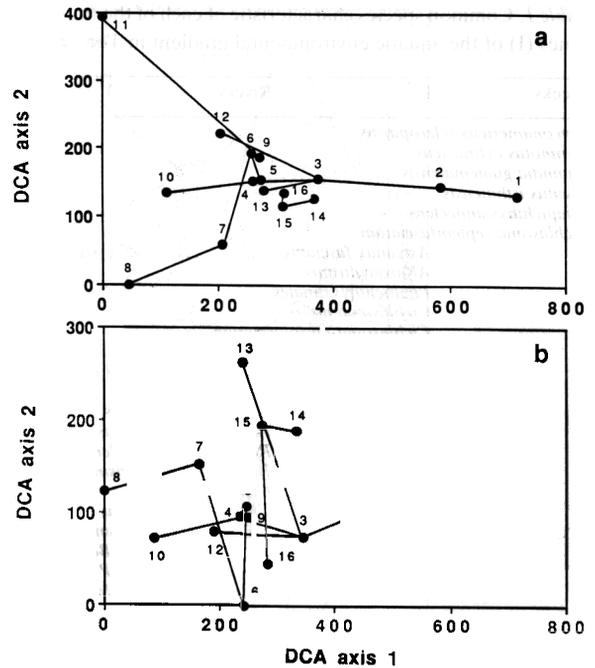

Fig. 3. Plots of the first two DCA axes based on species relative abundances for all 16 sites (a), and 15 sites with the isolated forest pools excluded (b). Lines connect adjacent sites within the Río Tortuguero drainage (stemming from site 1) and Caño California drainage (stemming from site 14).

placement of species from the previous downstream station, were observed in 9 out of 14 transitions in the Río Tortuguero/Laguna Tortuguero drainage and two of three transitions tested in the Laguna Jalova drainage (Fig. 2, Appendix 1). Some of these distinct faunal transitions occurred over distances as small as a few meters, as between the Laguna Tortuguero and the small barrier island creek, Quebrada (20% species retention). Five of the 21 species recorded from Quebrada (*Gymnotus, Rhamdia, Rivulus, Synbranchus, Cichlasoma alfari*) were never collected from the adjacent lagoon.

The first DCA axis described a longitudinal gradient running from low-order tributary streams containing relatively few species (low scores) to more speciose downstream sites and finally the ocean (Fig. 3, eigenvalue = 0.844). The second DCA axis (eigenvalue = 0.328) was much more difficult to interpret, but appeared to order tributary stream sites along an east (high scores) to west (low scores) gradient when all sites were included in the analysis (Fig. 3a). When the isolated forest pool (site 11) was eliminated from the analysis, the ordination of the remaining sites on the first DCA axis was virtually unchanged (Fig. 3b), and ordination of sites on DCA axis 2 yielded no general pattern of interpretation (Caño Servulo, Negro, and Laguna Jalova with high scores versus Caño California and a side channel of the Río Agua Fría with low scores).

The longitudinal pattern of zonation implied from the first DCA axis can be seen clearly in the spatial pattern of distribution of the most common
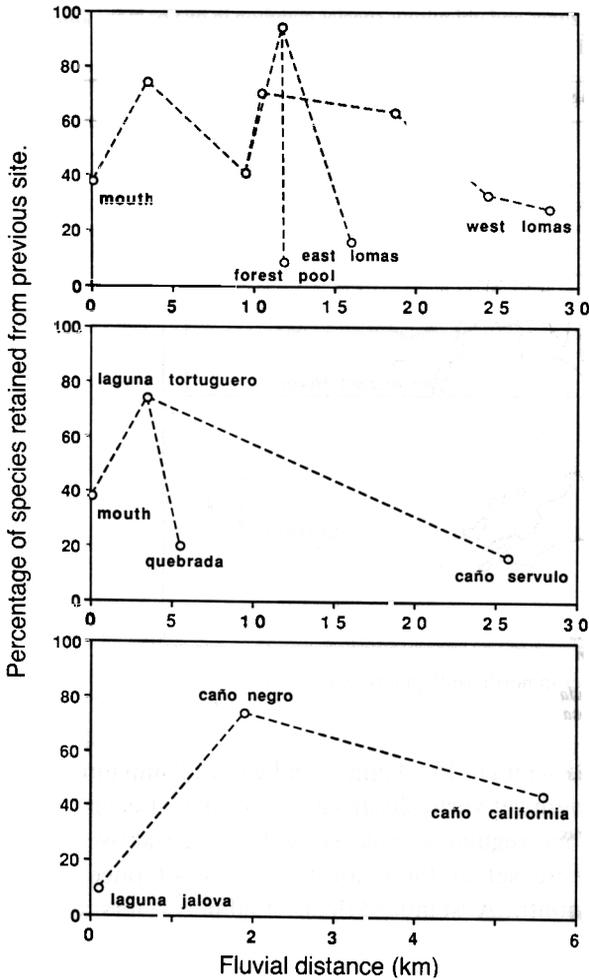
Table 1. Common species characteristic of each of the four major faunal zones and ubiquitous species common in two or more adjacent zones (I) of the aquatic environmental gradient in Tortuguero National Park.

Creeks	Rivers	Lagoons	Ocean
Bryconamericus scleroparius			
Gymnotus cylindricus			
Rhamdia guatemalensis			
Rivulus isthmensis			
Priapichthys annectens			
Cichlasoma septemfasciatum			
Astyanax fasciatus.......	*Astyanax fasciatus*		
Alfaro cultratus			
Phallichthys amates			
Cichlasoma alfari			
Cichlasoma nigrofasciatum			
Gobiomorus dormitor	*Gobiomorus dormitor*		
Eleotris amblyopsis	*Eleotris amblyopsis*		
Eleotris pisonis			
	Atractosteus tropicus		
	Brycon guatemalensis		
	Roeboides guatemalensis		
	Brachyrhaphis parismina		
	Cichlasoma dovii		
	Cichlasoma nicaraguense		
	Cichlasoma rostratum		
		Belonesox belizanus	
		Poecilia gilli	
		Melaniris milleri	
		Strongylura timucu	
		Cichlasoma centrarchus	
		Cichlasoma citrinellum	
		Cichlasoma loisellei	
		Cichlasoma maculicauda	
		Herotilapia multispinosa	
		Pomadasys crocro	
		Lutjanus jocu	
		Centropomus pectinatus	
		Oostethus lineatus	
		Achirus lineatus	
		Citharichthys spilopterus	
		Trinectes paulistanus	
		Dormitator maculatus	
		Evorthodus lyricus	
		Gobionellus boleosoma	
		Gobionellus fasciatus	
		Gobiosoma spes	
		Anchoa lamprotaenia	
		Anchoviella elongata	
		Myrophis punctatus	
		Hyporhamphus roberti	
		Centropomus parallelus	
		Diapterus plumieri	
		Diapterus rhombeus	
		Eucinostomus melanopterus	
		Bairdella ronchus	
		Micropogonias furnieri	
		Microdesmus carri	
		Bathygobius soporator	
		Sphoeroides testudineus	
			Megalops atlanticus
			Mugil curema
			Caranx hippos
			Caranx latus
			Oligoplites palometa
			Centropomus undecimalis
			Harengula jaguana
			Odontognathus compressus
			Opisthonema oglinum
			Pellona harroweri
			Coleotropis blackburni
			Polydactylus virginicus
			Conodon nobilis
			Pomadasys corvinaeformis
			Larimus breviceps
			Ophioscion panamensis
			Stellifer colonensis

fish species (Table 1). A large number of species were characteristic of only one type of aquatic habitat in the region. For example the characid, *Bryconamericus scleroparius*, and the poeciliid, *Priapichthys annectens*, were only found in the small streams of the Lomas de Sierpe, and the killifish, *Rivulus isthmensis*, was only taken in flooded forests, isolated forest pools, and the upper reaches of Quebrada (also forested). Similarly, the characid, *Brycon guatemalensis*, and the poeciliid, *Brachyrhaphis parismina*, were common in rivers but exceedingly rare or absent from feeder creeks and lagoons. A large number of species were found only in the marine environment (Table 1, Appendix 1), whereas another group of essentially marine species were almost always encountered in the essentially freshwater (with brackish layer beneath) lagoons (e.g., *Eucinostomus melanopterus, Sphoeroides testudineus*). Another large group is comprised of species that were common in two different habitats, but generally not more than two. Examples include *Alfaro cultratus* inhabiting creek-pools and river-edge habitats, and the pike livebearer, *Belonesox belizanus*, common along shorelines of both rivers and lagoons. Only three of the 130 species collected from the region could be considered common components of the fish assemblages of more than two general habitat types. The primary division fish, *Astyanx fasciatus* was abundant in nearly all aquatic environments of the park, with the exclusion of lagoon outlets and the marine environment. The sleepers, *Eleotris amblyopsis* and *Gobiomorus dormitor* were taken in small tributary streams, rivers, caños, and lagoon littoral zones. *Eleotris amblyopsis*, was thought to be the first or second most important larval fish component of the tismiche (huge aggregations of postlarval palaemonid shrimp and larval fishes) entering the Tortuguero lagoon (Gilbert & Kelso 1971, Winemiller unpublished).

Clustering based on similarities of scores on the first two DCA axes produced large separations between fish assemblages of the ocean, Laguna Tortuguero outlet, and the other 14 sites (Fig. 4). Within the freshwater/estuarine cluster, four subgroups are identified at distance of 63 DCA units: (1) sites running along a gradient between Laguna
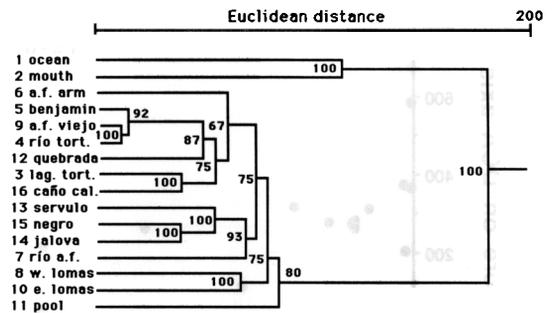
Fig. 4. Dendrogram based on average clustering algorithm showing site groupings based on DCA 1 and 2 scores. Horizontal axis is the average Euclidean distance between samples and nodes. Numbers by nodes indicate percent consistencies based on the jacknifing technique. Seven basic clusters were indentified: a single isolated forest pool, an inland stream group, two inland river sites, two heterogeneous groupings comprised of downstream river sites, and a coastal group.

Tortuguero and the lower Río Agua Fría (including Quebrada) plus Caño California, (2) Caño Servulo, Caño Negro, Laguna Jalova, and the Río Agua Fría, (3) the two Lomas creeks, and (4) the forest pool. The Río Agua Fría assemblage's affiliation with southern coastal systems arises from similar loadings on DCA axis 2 (Fig. 3). Although substantial differences between the two assemblages were apparent, Río Agua Fría and Caño Negro shared several species in similar relative proportions (e.g., *Brycon guatemalensis, Roeboides guatemalensis, Cichlasoma dovii, C. rostratum*).

Site scores on the first DCA axis showed weak negative correlations with linear and fluvial distances from the coast (Fig. 5). Species diversity was not significantly correlated with DCA axis 1, and species richness showed a weak positive correlation. Species richness showed a general decline with increasing distance from the sea within the Río Tortuguero/Laguna Tortuguero drainage (Fig. 6). Laguna Tortuguero contained the greatest number of species (N = 80), followed by the swampy side-channel, Caño Agua Fría Viejo (N = 58) located approximately 8 km upstream. Species diversity (H') showed no consistent trend and relatively little variation (range = 0.68–0.89) over the course of the flow between the lomas headwaters and the ocean. Species richness and diversity were uncorre-
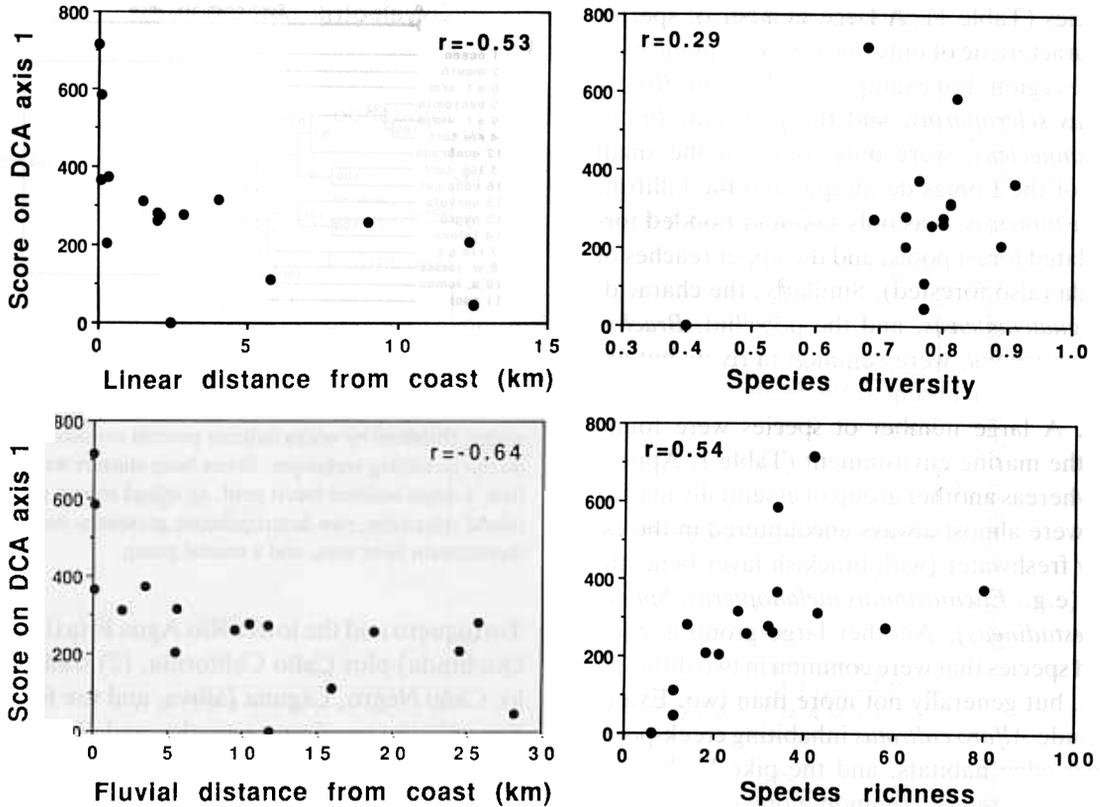
Fig. 5. Plots and correlations of site scores on the first DCA axis with site distance from coast, fluvial distance, species diversity, and species richness.

lated within the Río Tortuguero drainage (r = 0.09).

Plots of percent species remaining at successive upstream sites starting from three initial downstream sites in the Río Tortuguero drainage (ocean, mouth, lagoon) show a rapid initial turnover of species within the first 10 km (Fig. 7). Beyond 10 km, the rate of species deletions and replacements falls off sharply until all of the original ocean and lagoon outlet species are replaced in the creeks on the western slope of the lomas. Only one lagoon species, *Gobiomorus dormitor,* was found both in the lagoon and small creeks on the western slope of the lomas.

Environmental characteristics of the 16 sample sites varied widely, often over very short distances between adjacent habitats (Table 2). Substrates were generally sandy with vegetative litter and silt collecting in forest pools and deep, sluggish caños

(e.g., Caño Servulo). In general, clear headwaters gradually gave rise to increased levels of staining from leached organic compounds in the downstream direction. Fast water currents ($>0.35\,\text{ms}^{-1}$) were only observed on the ocean coast and in rivers during periods of high rainfall. The transition between freshwater and saline water is apparently rather abrupt near the surface of the water column (i.e., lagoon salinity measurements never exceeded 1.0 ppt over 10 months in 1985) whereas most mixing probably occurs near lagoon mouths. Bottom salinities in coastal lagoons exhibit a much more complex pattern of variation. Salinities at bottom depths ranged between 8.7 and 10.5 ppt during both wet and dry seasons over a distance of 5 km in the lower Laguna Tortuguero (Nordlie & Kelso 1975). During the dry season, lagoon bottom salinities ranged from 8.7 to 10.3 between low and high tides.
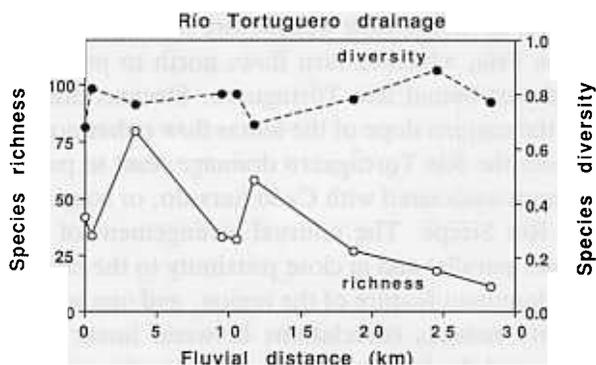
Fig. 6. Relationship between species richness and diversity plotted by fluvial distance in the Río Tortuguero drainage (longitudinal course from mouth to western lomas streams).

Fig. 7. Percentages of fish species from the initial assemblage remaining in comparisons of successive longitudinal samples moving upstream from the ocean/beach (a), Laguna Tortuguero mouth (b), and Laguna Tortuguero (c).

Canonical correspondence analysis (DCCA) resulted in the same ordination of sites along the first gradient axis (eigenvalue = 0.782) with coastal sites having low scores and headwaters having high scores. A Monte Carlo test of statistical significance employing 99 null randomizations (Ter Braak 1988) resulted in p < 0.025 for the first axis with an overall trace at p < 0.05. Of the 7 physical variables listed in Table 2 (water type = salinity, clarity), channel width (− 185), depth (134), and salinity (144) had high loadings on the first gradient axis (fluvial distance − 63, current − 79, clarity − 62, substrate 79). The second axis (eigenvalue = 0.323) was also influenced primarily by channel width (− 91) and depth (83) plus substrate (109). Loadings of the other four environmental variables on axis 2 ranged between − 77 (clarity) and 2 (fluvial distance).

When data were broken down by season, several common species in Laguna Tortuguero showed substantial seasonal shifts in their relative abundances (Table 3). Melaniris milleri, Eucinostomus melanopterus, and Eleotris amblyopsis had the greatest relative abundances during the wet season. Wet season increases in the numbers of E. amblyopsis in the Laguna Tortuguero were due largely to downstream rafting in floating mats of aquatic vegetation torn free from swampy upstream locations by fast water. M. milleri had higher levels of reproduction during the wet season at Tortuguero (Winemiller unpublished). Marine species Centropomus pectinatus and Bairdiella ron-

chus were more abundant in Laguna Tortuguero during the dry season.

Relative percentages of species assigned to four trophic categories (herbivore/detritivore, omnivore, invertebrate feeder, piscivore) exhibited intersite variation (Fig. 8). Contingency table analysis for frequencies of species in four trophic categories in 16 sites was nonsignificant ($\chi^2 = 39.3$, 45 df, p = 0.71). Invertebrate feeders were the most species rich group at 15 of the 16 sites. The omnivorous cichlid, Cichlasoma nigrofasciatum, was a numerically-dominant species at Caño Servulo, a blackwater site with low fish density and species richness (N = 14). When fish assemblages were grouped by basic habitat (4 creeks, 5 rivers, 5 lagoons, 1 ocean), significant associations emerged for both the number of individuals collected and number of species collected within the various trophic categories (Table 4). Mean relative percentages of individuals in different trophic categories was significantly associated with habitat ($\chi^2 = 81.5$, 9 df, p < 0.0001). Sampling in a downstream progression, herbivorous fishes dropped out of assemblages, from a high of 30% in creeks to a low of 5% in the sea. Omnivores were not a dominant group in any habitat and were entirely absent from the sea. Much of the decline in these two groups was associated with a reciprocal increase in invertebrate-feeding fishes in lagoon and ocean environments. Mean relative percentages of species in different trophic categories showed the

same trends as individual percentages ($\chi^2 = 43.3$, 9 df, p < 0.0001). The absolute number of different species revealed no consistent pattern between trophic categories and habitats ($\chi^2 = 16.46$, 9 df, p = 0.058).

Discussion

Fish assemblages of the Tortuguero region exhibit a strong pattern of longitudinal zonation over a fluvial distance of only 28 km between creeks draining the Lomas de Sierpe and the sea. This longitudinal zonation is similar to patterns observed in temperate zone coastal faunas (Felley 1987, Rozas & Odum 1987, Odum 1988) and is accompanied by a series of species replacements and deletions in successive downstream locations. Yet, the site clusterings that combined two drainages indicated that fluvial zonation does not always have a high correspondence with spatial coordinates. The complex mosaic of waterways within Tortuguero Park resulted in poor correlation between zonation of fish assemblages and minimum linear distance to the sea coast. Streams on the western slope of the

Lomas de Sierpe flow west before joining the Río Agua Fría, which in turn flows north to join the northeast-bound Río Tortuguero. Streams draining the eastern slope of the lomas flow either north to join the Río Tortuguero drainage, east to palm swamps associated with Caño Servulo, or south to the Río Sierpe. The unusual arrangement of lagoons, parallel and in close proximity to the coast, is a dominant feature of the region, and one which greatly reduces correlations between linear distance and fluvial distance. In addition, the coastal lagoons receive effluent waters from numerous independent tributaries that vary greatly in size and environmental conditions. For example, the Laguna Tortuguero/Laguna Jalova network has six major western tributaries plus an unknown number of small forest creeks entering from the west and from the barrier island to the east. Due to the high and fairly evenly distributed annual rainfall, the small creeks, even those under tidal influence, are essentially freshwater environments throughout the year.

At least six of the common species from creek assemblages appeared to be largely restricted to creek environments (Table 1). Quebrada is sep-

Table 2. Some physical features of the principal sample sites during the wet season. Water current was classified as slow (S, 0–0.10 m s^{-1}), moderate (M, 0.10–0.35 m s^{-1}), or fast (F, > 0.35 m s^{-1}). Water type was classified as clear (C) or tanin-stained (T) and saline (S, salinity 10–35 ppt), brackish (B, 1–10 ppt), or fresh (F, < 1 ppt). Substrate type was classified as fine silt/mud (M), sand (S), or vegetative litter (L).

Site	Fluvial distance (m)	Ave. width (m)	Ave. depth (m)	Current	Water type	Substrate type
Ocean	0	–	–	F	C, S	S
Mouth Laguna Tortuguero	0.1	110	6.0	F	B, S/B	S
Laguna Tortuguero	3.5	300	10.0	M/S	B, B/F	S/L
Río Tortuguero	9.5	40	2.0	F/M	B, F	S/L
Caño Benjamin	10.5	4.0	1.0	M/S	B, F	S/L/M
Río Agua Fría Arm	18.7	20	1.5	M	T/C, F	S/L
Río Agua Fría	24.5	7.0	1.1	F/M	C, F	S/L
West Lomas Creeks	28.2	1.7	0.3	S/N	C, F	S/L
Caño Agua Fría Viejo	11.7	26.3	1.5	M	T, F	S/L
East Lomas Creeks	16.0	1.5	0.5	M/S	C, F	S
Forest Pool	11.8	6.0	0.4	N	C, F	L/M
Quebrada	5.5	2.5	0.4	S	C, F	S/L/M
Caño Servulo	25.7	50	10.0	S	T, F	L/M
Laguna Jalova	0.1	100	6.0	S	T, B	S
Caño Negro	1.9	50	2.0	S	T, B/F	S/L
Caño California	5.6	60	2.0	M	T, B/F	S/L

arated from the coast by only 200–300 m (linear distance), but its faunal composition was a blend of species characteristic of inland creeks and small, edge-dwelling lagoon and river species. *Hyphessobrycon, Gymnotus, Rhamdia,* and *Rivulus* exhibited large gaps in regional distribution between lomas streams and Quebrada. The Río Tortuguero and lagoon environments apparently inhibit invasion by these and other inland species for reasons that are currently unknown. Salinity alone does not restrict freshwater fishes from invading the lagoons, because the upper water column layer is generally <1 ppt and is essentially freshwater (<0.1 ppt) during the 7–8 wettest months. Opportunities for dispersal from inland to coastal creeks would abound during wet seasons in the form of drifting rafts of *Hydrocotyl* and other floating aquatic macrophytes.

Inland penetration and establishment of many marine fish species is clearly a consequence of limitations in physiological mechanisms for dealing with a hypotonic environment. Sixty-two percent of fishes comprising the ocean assemblage were never found beyond the mouth of the lagoon, and 86% were never encountered further inland than the coastal lagoons. Several essentially marine species with obvious capabilities for adjusting to the freshwater environment were extremely rare in freshwaters upstream from lagoons and dropped out altogether in the smaller rivers and streams (e.g., *Centropomus* spp., *Eucinostomus* spp., *Caranx* spp., *Mugil curema*). Similarly, most if not all of the species from freshwater families cannot tolerate salinities at levels encountered at the lagoon mouth and sea coast. Yet, a number of freshwater species were firmly established components of the upper and middle reaches of coastal lagoons throughout the year. The characid, *Astyanax fasciatus,* was a dominant species at a large number of sites, including coastal lagoons. *A. fasciatus* is a generalized omnivore (Winemiller 1982, 1987, 1990) with a very wide geographic distribution. As the species is currently defined, *A. fasciatus* ranges throughout much of the neotropics from northern Argentina to central Mexico (Miller 1966). Whereas *A. fasciatus* was the most numerically abundant species within the region (comprising approximately 10% of the total regional fish sample), two peripheral freshwater species from marine-affiliated families, *Eleotris amblyopsis* and *Gobiomorus dormitor,* showed the widest distributions along the longitudinal stream gradient. *Gobiomorus* and several marine species (*Carcharinus leucas, Pristis perotteti, Tarpon atlanticus*) have established stocks as far inland as Lake Nicaragua (Villa 1982, Bussing 1987).

Table 3. Fish species showing seasonal shifts in relative abundance in Laguna Tortuguero in the region of the national park headquarters during 1985.

Species	Wet months		Dry months	
	No. sampled	Relative abundance	No. sampled	Relative abundance
Melaniris milleri	84	(0.122)	34	(0.044)
Centropomus pectinatus	81	(0.118)	330	(0.429)
Eucinostomus melanopterus	41	(0.059)	9	(0.012)
Bairdella ronchus	9	(0.013)	146	(0.190)
Eleotris amblyopsis	76	(0.110)	4	(0.005)
Primary division species	2	(0.04)		(0.02)
Primary div. individuals	13	(0.02)	17	(0.02)
Secondary div. species	10	(0.20)	9	(0.20)
Secondary div. individuals	75	(0.11)	42	(0.06)
Peripheral & marine species	37	(0.76)	36	(0.78)
Peripheral & marine indiv.	589	(0.87)	710	(0.92)
Total species	49		46	
Total individuals	679		769	
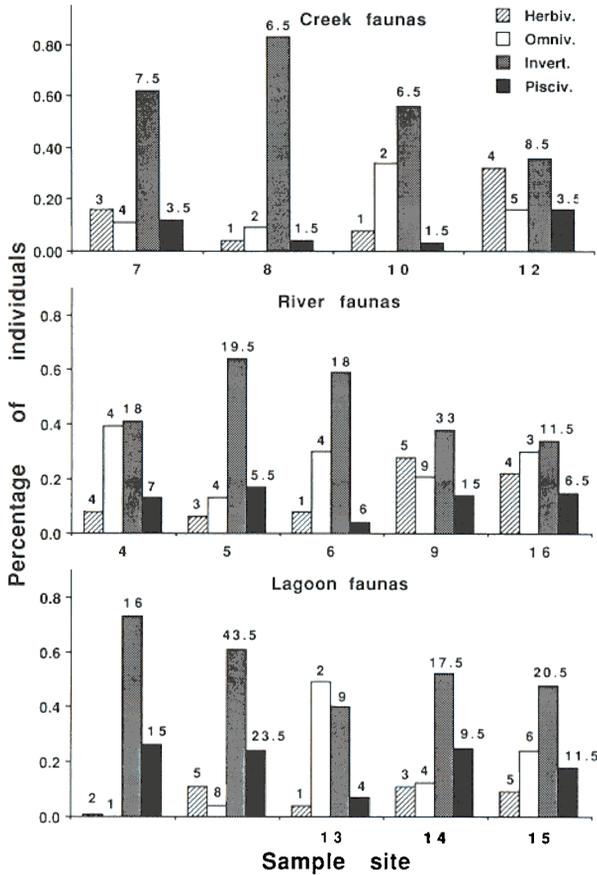
Fig. 8. Distributions of percentages of total individuals collected from four trophic categories in 14 Tortuguero Park fish assemblages. Numbers above bars are total number of species collected in each category at each site (fractional values resulted from species exhibiting major ontogenetic feeding shifts that received half assignment to two different trophic categories).

Zonation of Tortuguero fish assemblages corresponded to four basic habitats: creeks, rivers, lagoons, and the sea. Even though creek habitats exhibit an irregular spatial arrangement within the region's mosaic of winding, low-gradient water courses, fairly distinctive fish assemblages can be mapped over a general longitudinal pattern of fluvial habitat zonation that in large part corresponded to the first axis from DCA. Lomas creeks contained three species that were encountered in no other region of the park. Apparently, the Lomas de Sierpe constitute the eastern-most limit of suitable habitat for *Bryconamericus scleroparius, Priapichthys annectens*, and *Brachyrhaphis holdridgei*, spe-

cies encountered in greater abundances in drainages to the west of Tortuguero Park (Bussing 1987, Winemiller unpublished). Similarly, *Cichlasoma nicaraguense, C. septemfasciatum,* and *C. tuba* were much more abundant in forested regions to the west of the park. Several related taxa have very similar ecologies and seemed to replace one another in different habitats. As stream size increases, *Alfaro cultratus* replaces *Priapichthys annectens* as the dominant insectivorous poeciliid. In some of the smallest forest streams, *Priapichthys* may be joined by a second insectivorous poeciliid, *Brachyrhaphis holdrigei*. In rivers and caños, *Alfaro* inhabits quieter and shallower waters than another surface-dwelling insectivore, *Brachyrhaphis parismina*. The algae-grazing poeciliid *Phallichthys amates* was more abundant in smaller streams, and the larger *Poecilia gilli* was more prevalent in lagoons. The two species coexisted in large numbers in intermediate environments such as river backwaters and caños. *Cichlasoma tuba* is a large detritivorous/algivorous cichlid of clearwater rivers, such as the Río Agua Fría, Río Sierpe, upper Caño California, and higher gradient rivers lying to the west. *Cichlasoma tuba* is entirely replaced by the deeper-bodied *C. maculicauda* in the lower reaches of rivers, caños, and coastal lagoons.

These observations lead us to the general question of whether regional patterns of species turnover reflect fishes' physiological responses to their physicochemical environment, or response to the biological forces of predation and competition? For example, Matthews (1987) found good correspondence between the responsiveness of North American cyprinids to harsh conditions in laboratory tests and their distributions in the wild. Three out of seven physical environmental variables that we included in DCCA had high loadings on the first ordination axis. Among these, the physiological effects of salinity level are obviously of major importance in structuring fish assemblages across the lower reaches of the freshwater/marine ecotone (i.e., from deep waters of lagoons to the ocean). Salinity was probably not a major factor influencing fish assemblages further inland. The other two dominant variables in DCCA, stream width and depth, are components of habitat size. Of course

many variables, both measured and unmeasured, might be expected to covary to some extent with habitat size within a fluvial gradient. Yet, the most species rich assemblages were not necessarily associated with the largest habitats. Laguna Tortuguero yielded a richer ichthyofauna (80 species) than the ocean/beach (42 species). Some of this difference could have been associated with lower efficiency in sampling the deeper and more turbulent waters of the coast. Caño Agua Fría Viejo had the second highest number of species (N = 58) but only ranked eighth in size of habitat (Table 2). Species richness in this swampy channel is probably influenced by a habitat edge effect (i.e., 'mass effect' of Shmida & Wilson 1985) that fosters elements associated with both river and lagoon environments. In effect, caños and backwaters represent an additional kind of ecotone involving a transition between (1) small clearwater rivers dominated by freshwater division fishes and (2) the predominantly lentic environment of lagoons containing many marine faunal elements. Several fish species common in either rivers or lagoons, but not both (Table 1), coexisted in Caño Agua Fría Viejo. In addition, caño and lagoon habitats contained the greatest structural heterogeneity in the form of diverse aquatic vegetation, submerged trees and limbs, coarse detritus, and leaf packs. Species diversity of fishes and other vertebrates is often positively correlated with habitat structural heterogeneity (Gorman & Karr 1978).

Compared with physicochemical parameters, the relative influence of biotic interactions on the structure of Tortuguero fish assemblages is somewhat more difficult to infer. However, additional ecological information concerning two of the assemblages indicates that biotic interactions probably assume a greater relative role in structuring more species rich assemblages. Winemiller (1991) performed an ecomorphological analysis of the core species from the Quebrada and Caño Agua Fría fish assemblages, plus eight other freshwater fish assemblages from three continents. The total range of estimated morphological space was greater in the more species-rich Agua Fría Viejo assemblage compared with Quebrada fishes, and the average distance between species was not significantly smaller in more diverse systems. These patterns suggest greater levels of ecological specialization in the Agua Fría Viejo assemblage in association with either an expanded resource base, species packing, or a combination of both. In addition,

Table 4. Mean percentages of individual fishes and species in four trophic categories collected from four creek sites, five river sites, five lagoon sites, and ocean beach sites in the Tortuguero region.

	Mean percentages by number of individuals collected				
	Herbivores	Omnivores	Invert.-feeders	Piscivores	Total no. indiv.
Creeks	30%	15%	39%	16%	2,545
Rivers	26%	22%	39%	13%	12,151
Lagoons	10%	7%	60%	23%	5,485
Ocean	5%	0%	85%	10%	733
Total no. indiv.	4,549	3,405	9,684	3,376	20,914

	Mean percentages by number of species collected				
	Herbivores	Omnivores	Invert.-feeders	Piscivores	Total no. spp.
Creeks	14%	21%	51%	14%	37
Rivers	10%	13%	55%	22%	66
Lagoons	9%	9%	51%	31%	94
Ocean	2%	0%	60%	38%	42
Total no. spp.	7	11	74.5	37.5	130

Winemiller & Pianka (1990) employed a null model to statistically examine two forms of trophic organization in the Quebrada and Caño Agua Fría Viejo assemblages. Both assemblages showed significant community-wide resource segregation during both wet and dry seasons. Significant guild structure was observed among Caño Agua Fría Viejo fishes during both seasons and among Quebrada fishes during the wet season. Non-random guild structure and resource segregation, in particular, strongly imply a major effect of biotic interactions on community structure (Lawlor 1980, Winemiller & Pianka 1990).

Relative proportions of both individuals and species in the four trophic categories reflected a major longitudinal gradient in the utilization of benthic detrital and periphyton resources. Percentages of herbivore-detritivores declined montonically along a headwater to ocean gradient. In contrast to stream herbivores, which generally are dominated by insects plus a significant number of algae-scraping fish species in the neotropics (Power 1984, Winemiller 1990), phytoplanktivorous microcrustacea assume dominance in the role of primary consumer in lentic freshwater and marine environments. Fruits and seeds are additional resources available to freshwater herbivores and omnivores that are essentially unavailable in the sea. The sharp decline in the number of individual herbivorous and omnivorous fishes at sea was associated with a large increase in the relative fraction of invertebrate feeders, mostly in the form of zooplanktivores. While the relative proportion of piscivores was actually smaller in the sea than freshwater habitats, the fraction of species that were piscivorous was greater. Marine piscivores were for the most part large species (e.g., *Tarpon, Thunnus, Sphyraena*), and the disparity between numerical and specific proportions could be attributed to sampling error associated with the high mobility and patchy distributions of these species in the nearshore marine environment. Even so, data for trophic categories clearly reflect major differences in the resource base in different Tortuguero habitats. Most primary consumption is by zooplankton in the nearshore marine environment, and the great importance of this resource for fishes can be seen in the dominance of the marine assemblage by invertebrate-feeders.

Patterns observed in the Tortuguero fish fauna and their relations to characteristics of the region's aquatic environments generally agree with recent conceptual models of factors influencing longitudinal stream succession reviewed recently by Vannote et al. (1980), Fisher (1983), Schlosser (1982, 1987), and Odum (1988). The few fish species inhabiting small feeder streams and forest pools were, for the most part, small species capable of rapid colonization of periodically disturbed habitats. Viviparity and rapid maturation make poeciliids particularly efficient colonizers. The cyprinodontid killifish, *Rivulus isthmensis,* may be the most effective colonizing species at Tortuguero. *Rivulus* exhibited continuous reproduction, small clutches, and very rapid maturation, traits associated with a high intrinsic rate of population growth and colonizing ability in fishes (Winemiller 1989). These disturbances occur in the form of seasonal dessication of ephemeral, forest pool habitats, and short-lived but turbulent flash floods in the higher gradient streams of the lomas. Generalist insectivores and herbivores/detritivores predominate in these small creek assemblages. The rainforest canopy is generally quite dense, blocking much of the sunlight. As a consequence, a very large fraction of the total energy consumed by fishes and aquatic invertebrates is of terrestrial origin in these small forest streams. Ants and other terrestrial insects were a principal fish food resource in forest streams and pools. Although competition among fishes for limited space and food resources is probably important in these small oligotrophic systems, it is probably intermittent due to periodic disturbances followed by episodes of recolonization.

Downstream, aquatic environments become larger and relatively more stable in terms of the disruptive effects of increased discharge rates during the rainy season. A large portion of the aquatic vegetation mats in caños are swept out during the periods of highest rainfall. Dense rafts of aquatic plants, some as large as $50\,m^2$, were commonly observed floating down the estuary toward the sea during summer wet seasons. These rafts transport invertebrates and fishes, especially eleotrids, from

inland locations to the estuary. Although floods certainly alter the structural features and primary production base of rivers and caños (Winemiller 1990), their effects on these inland fish communities are probably small compared with headwaters. In these low-gradient regions, flood waters tend to be much more evenly distributed over both time and space than floods of higher gradient streams. Many of the smaller species of rivers and caños moved into the flooded forest during the wet season. A number of these fishes exhibited a seasonal burst of reproduction, leaving hundreds of offspring in the flooded forest where predators were encountered at extremely low densities (e.g., *Astyanax*, *Rhamdia*, *Poecilia*, *Cichlasoma nigrofasciatum*, *Herotilapia multispinosa*). To some extent, seasonal reproduction by fishes influenced assemblage composition in lagoons as well. Large aggregations of croakers, *Micropogonias furnieri*, with ripe gonads were caught from the Laguna Tortuguero by villagers during the late November of 1985. A dense aggregation of juvenile croakers, *Pomadasys crocro*, was encountered in Laguna Tortuguero in June 1963 (Gilbert & Kelso 1971). As noted previously, at least some of the seasonal shifts in relative species' abundances in Table 3 were due to reproductive behavior. Several predatory marine species appeared to enter freshwaters primarily for reproduction. KOW collected tarpon, *Tarpon atlanticus*, and snook, *Centropomus undecimalis*, with ripe gonads at the mouth of the Laguna Tortuguero during irregular intervals throughout the year. These species feed while in the estuary and undoubtedly influence community structure. In addition, the periodic arrival of the tismiche (huge aggregations of postlarval shrimp and larval fishes originating from the sea) into coastal lagoons must have a major effect on community trophic interactions.

River and lagoon assemblages contained more species of much greater average size and showing greater levels of ecological and morphological specializations compared with headwater faunas. Small fishes within these ecosystems are restricted primarily to shallow littoral zone habitats, presumably in response to predation on a proximate and perhaps even a coevolutionary time scale. Excep-

tions to this general spatial segregation by small fishes are seen in schooling midwater planktivores (i.e., *Melaniris*, *Anchoa*, *Anchoviella*) and cryptic and burrowing benthic fishes (e.g., *Citharichthys*, *Microdesmus*). The lotic/lentic ecotone embodied in the caños seems to harbor high numbers of species from adjacent creek and river habitats by providing excellent structural refugia for small fishes, and stable deepwater habitat for large species such as gar, *Atractosteus tropicus*, and tarpon snook, *Centropomus pectinatus*. A blend of Schlosser's (1987) conceptual framework for the role of predation, competition, and physical disturbance in temperate zone stream fishes and Odum's (1988) generalizations about abiotic factors influencing coastal marsh communities appears to explain many of the patterns produced by tropical fish assemblages across the complex freshwater/marine ecotone at Tortuguero.

Acknowledgements

References cited

Allan, J.D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040–1053.

Angermeier, P.L. & J.R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Env. Biol. Fish. 9: 117–135.

Balon, E.K. 1974. Fishes from the edge of Victoria Falls: demise of a physical barrier for downstream invasions. Copeia 1974: 643–660.

Balon, E.K. & D.J. Stewart. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa-Zaire system), reflections on river zonation, and description of another new species. Env. Biol. Fish. 9: 225–252.

Bishop, J.E. 1973. Limnology of a small Malayan river Sungai Gombak. Monographiae Biologicae 22, Dr W. Junk Publishers, The Hague, 485 pp.

Burton, J.W. & E.P. Odum. 1945. The distribution of stream fishes in the vicinity of mountain Lake, Virginia. Ecology 26: 182–194.

Bussing, W.A. 1976. Geographic distribution of the San Juan ichthyofauna of Central America with remarks on its origin and ecology. pp. 157–175. In: T.B. Thorson (ed.) Investigations of the Ichthyofauna of Nicaraguan lakes, University of Nebraska, Lincoln.

Bussing, W.A. 1987. Peces de las Aguas Continentales de Costa Rica (Freshwater fishes of Costa Rica). Editorial de la Universidad de Costa Rica, San José. 271 pp. (in Spanish).

Caldwell, D.K., L.H. Ogren & L. Giovannoli. 1959. Systematic and ecological notes on some fishes collected in the vicinity of Tortuguero, Caribbean coast of Costa Rica. Rev. Biol. Trop. 7: 7–33.

Cashner, R.C. & J.D. Brown. 1977. Longitudinal distribution of fishes of the Buffalo River in northwestern Arkansas. Tulane Studies in Zool. Bot. 19: 37–46.

Felley, J.D. 1987. Nekton assemblages of three tributaries to the Calcasieu estuary, Louisiana. Estuaries 10: 321–329.

Fisher, S.G. 1983. Succession in streams. pp. 7–27. In: J.R. Barnes & G.W. Marshall (ed.) Stream Ecology, Application and Testing of General Ecological Theory, Plenum Press, New York.

Fisher, S.G., L.J. Gray, N.B. Grimm & D.E. Bush. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecol. Monogr. 52: 93–110.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298 pp.

Gilbert, C.R. & D.P. Kelso. 1971. Fishes of the Tortuguero area, Caribbean Costa Rica. Bull. Florida State Mus., Biol. Sci. 16: 1–54.

Gorman, O.T. & J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

Graham, J.H. & R.W. Hastings. 1984. Distributional patterns of sunfishes on the New Jersey coastal plain. Env. Biol. Fish. 10: 137–148.

Hill, M.O. 1979. DECORANA: A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell, University, Ithaca. 52 pp.

Hill, M.O. & H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

Hirth, H.F. 1963. The ecology of two lizards on a tropical beach. Ecol. Monogr. 33: 83–112.

Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecol. Monog. 48: 307–321.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577–586.

Ibarra, M. & D.J. Stewart. 1989. Longitudinal zonation of sandy beach fishes in the Napo River basin, eastern Ecuador. Copeia 1989: 364–381.

Kuehne, R.A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. Ecology 43: 608–614.

Lawlor, L.R. 1980. Structure and stability in natural and randomly constructed competitive communities. Amer. Nat. 116: 394–408.

López Sánchez, M.I. 1968. Clave para los peces de las aguas continentales de Costa Rica (Key for the freshwater fishes of Costa Rica). Fac. Cienc. Letras, Universidad de Costa Rica, San José. 31 pp. (in Spanish).

Lyons, J.L. & D.W. Schneider. 1990. Factors influencing fish distribution and diversity in a small coastal river in southwestern Costa Rica. Hydrobiologia 203: 1–14.

Matthews, W.J. 1986. Fish faunal 'breaks' and stream order in the eastern and central United States. Env. Biol. Fish. 17: 81–92.

Matthews, W.J. 1987. Physiological tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. pp. 111–120. In: W.J. Matthews & D.C. Heins (ed.) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Matthews, W.J. & H.W. Robison. 1988. The distribution of fishes in Arkansas: a multivariate analysis. Copeia 1988: 358–374.

Meffe, G.K. & W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. Amer. Midl. Nat. 117: 177–191.

Meffe, G.K. & A.L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. Amer. Midl. Nat. 120: 225–240.

Miller, R.R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966: 773–802.

Myers, G.S. 1938. Freshwater fishes and West Indian zoogeography. Ann. Rept. Smithsonian Inst. 1937: 339–364.

Myers, G.S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia 1966: 766–773.

Nordlie, F.G. 1981. Feeding and reproductive biology of eleotrid fishes in a tropical estuary. J. Fish. Biol. 18: 97–110.

Nordlie, F.G. & D.P. Kelso. 1975. Trophic relationships in a tropical estuary. Rev. Biol. Trop. 23: 77–99.

Nuhn, H., R. Pérez, et al. 1967. Estudio geografico regional de la zona Atlántica norte de Costa Rica (Regional geographic study of the north Atlantic zone of Costa Rica). Instituto de Tierras y Colonización, San José. 360 pp. (in Spanish).

Odum, W.E. 1988. Comparative ecology of tidal freshwater and salt marshes. Ann. Rev. Ecol. Syst. 19: 147–176.

Power, M.E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. J. Anim. Ecol. 53: 357–374.

Rivas, L.R. 1986. Systematic review of the perciform fishes of the genus *Centropomus*. Copeia 1986: 579–611.

Rozas, L.P. & W.E. Odum. 1987. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. Estuaries 10: 36–43.

Saul, W.G. 1975. An ecological study of fishes at a site in Upper Amazonian Ecuador. Proc. Acad. Nat. Sci. Philadelphia 127: 93–134.

Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Monogr. 52: 395–414.

Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. pp. 17–24. *In:* W.J. Matthews & D.C. Heins (ed.) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Shannon, C.E. & W. Weaver. 1963. The mathematical theory of communication. Univ. of Illinois Press, Urbana. 117 pp.

Sheldon, A.L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49: 193–198.

Shmida, A. & M.V. Wilson. 1985. Biological determinants of species diversity. J. Biogeogr. 12: 1–20.

Smith, G.R. 1981. Effects of habitat size on species richness and adult body sizes of desert fishes. pp. 125–171. *In:* R.J. Naiman & D.L. Soltz (ed.) Fishes in North American Deserts, John Wiley & Sons, New York.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

Ter Braak, C.J.F. 1988. CANOCO – a FORTRAN program for canonical community ordination by correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Report LWA-88-02, Agricultural Mathematics Group, Wageningen. 95 pp.

Townsend, C.R. & G. Peirson. 1988. Fish community structure in lowland drainage channels. J. Fish. Biol. 32: 283–295.

Tramer, E.J. 1969. Bird species diversity: components of Shannon's formula. Ecology 50: 927–929.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell & C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Villa, J. 1982. Peces Nicaraguenses de Agua Dulce (Nicaraguan freshwater fishes). Banco de America, Managua/ 253 pp. (in Spanish).

Weinstein, M.P., S.L. Weiss & M.F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape fear River Estuary, North Carolina. USA. Mar. Biol. 58: 227–243.

Wilkinson, L. 1989. Systat: the system for statistics. Systat, Inc., Evanston. 638 pp.

Winemiller, K.O. 1982. An introduction to the freshwater fish communities of Corcovado National Park, Costa Rica. Brenesia 21: 47–66.

Winemiller, K.O. 1987. Tests of ecomorphological and community level convergence among neotropical fish assemblages. Ph.D. Dissertation, University of Texas, Austin. 370 pp.

Winemiller, K.O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia 81: 225–241.

Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. 60: 331–367.

Winemiller, K.O. 1991. Ecomorphological diversification in lowland feshwater fish assemblages from five biotic regions. Ecology (in press).

Winemiller, K.O. & N.E. Morales. 1990. Comunidades de peces del Parque Nacional Corcovado luego del cese de las actividades mineras (Fish communities of Corcovado National Park following the cessation of mining activities). Brenesia 31: 75–91. (in Spanish).

Winemiller, K.O. & E.R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Monogr. 60: 27–55.

Appendix 1.

Sample sizes and trophic classifications for fishes collected from 16 sites in Tortuguero National Park, Costa Rica. Abundance data are pooled samples from Gilbert & Kelso (1971) and Winemiller (1987 and unpublished). Sample sites are as follows: 1 – Ocean or beach, 2 – Mouth of Laguna Tortuguero, 3 – Laguna Tortuguero, 4 – Río Tortuguero, 5 – Caño Benjamin, 6 – Arm of Río Agua Fría, 7 – Río Agua Fría, 8 – Creeks on west slope of Lomas, 9 – Caño Agua Fría Viejo, 10 – Creeks on east slope of Lomas, 11 – Forest pool near Caño Agua Fría Viejo, 12 – Quebrada, 13 – Caño Servulo, 14 – Laguna Jalova, 15 – Caño Negro, 16 – Caño California and tributaries. Trophic categories are: H – herbivore, I – invertebrate feeder, P – piscivore, O – omnivore.

Species / Sites	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Cod
Family Carcharhinidae																	
Carcharhinus leucas	1	3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Carcharhinus limbatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Family Dasyatidae																	
Dasyatis sabina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Himantura schmardae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Lepisosteidae																	
Atractosteus tropicus	0	0	0	1	0	0	0	0	11	0	0	0	0	0	0	0	P
Family Elopidae																	
Elops saurus	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Megalops atlantica	5	4	8	0	0	0	0	0	0	0	0	0	0	2	2	0	P
Family Chirocentridae																	
Chirocentrodon bleekerianus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Clupeidae																	
Anchoa lamprotaenia	2	0	19	0	0	0	0	0	0	0	0	0	0	0	12	0	I
Anchoviella elongata	5	0	360	0	43	0	0	0	2	0	0	0	0	0	0	0	I
Ctengraulis edentulus	0	5	0	0	0	0	0	0	0	0	0	0	0	2	0	0	I
Harengula jaguana (= pensacolae)	19	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Odontognathus compressus	67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Opisthonema oglinum	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Pellona harroweri	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Sardinella anchovia	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Synbranchidae																	
Synbranchus marmoratus	0	0	0	0	0	1	0	0	7	0	0	2	0	0	0	0	I
Family Anguillidae																	
Anguilla rostrata	0	0	1	0	0	0	0	0	11	0	0	0	0	0	0	0	I
Family Ophichthidae																	
Myrophis punctatus	0	0	178	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Characidae																	
Astyanax fasciatus	0	0	3	84	19	39	4	1	1783	30	15	173	0	0	43	34	O
Astyanax nasutus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	O
Bramocharax bransfordi	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	P
Brycon guatemalensis	0	0	1	35	9	12	2	0	123	0	0	0	0	1	12	32	O
Bryconamericus scleroparius	0	0	0	0	0	0	0	3	0	9	0	0	0	0	0	0	O
Carlana eigenmannia	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	O
Hyphessobrycon tortuguerae	0	0	7	2	0	0	0	0	2	0	0	4	0	0	0	4	O
Roeboides guatemalensis	0	0	0	15	5	0	3	0	123	0	0	0	0	0	40	0	I
Family Ariidae																	
Arius melanopus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Bagre filamentosus	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Pimelodidae																	
Rhamdia guatemalensis	0	0	0	0	3	1	0	1	1	2	0	189	1	0	1	0	I/P
Family Gymnotidae																	
Gymnotus cylindricus	0	0	0	1	0	3	2	1	0	0	0	19	0	0	0	0	I
Family Poeciliidae																	
Alfaro cultratus	0	0	3	27	17	33	0	5	0	0	29	243	2	0	0	0	I
Belonesox belizanus	0	0	8	3	4	2	0	0	221	0	0	17	2	0	7	4	P
Brachyrhaphis holdridgei	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	I
Brachyrhaphis parismina	0	0	0	6	0	5	12	0	60	0	0	0	0	0	0	2	I
Phallichthys amates	0	1	7	8	10	14	5	2	1329	9	15	434	0	0	0	0	H
Poecilia gilli	0	0	179	1	2	0	6	0	1213	0	0	257	0	7	35	10	H
Poecilia mexicana	0	0	4	0	0	0	0	0	0	0	0	0	0	0	6	0	H

Appendix 1. (Continued).

Species / Sites	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Code
Priapichthys annectens	0	0	0	0	0	0	0	20	0	23	0	0	0	0	0	0	
Family Cyprinodontidae																	
Rivulus isthmensis	0	0	0	0	0	0	0	0	0	0	270	80	0	0	0	0	
Family Belonidae																	
Strongylura marina	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	
Strongylura timucu	4	0	44	1	0	0	0	0	7	0	0	0	0	1	0	12	
Family Exocoetidae																	
Hyporhamphus roberti hildebrandi	5	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Bothidae																	
Citharichthys spilopterus	0	0	79	6	2	6	0	0	22	0	0	0	0	2	1	0	
Citharichthys uhleri	0	2	6	0	0	13	0	0	0	0	0	0	0	0	0	0	
Family Soleidae																	
Achirus lineatus	0	0	44	0	0	0	0	0	100	0	0	0	0	0	1	0	
Trinectes paulistanus	0	0	11	0	0	2	0	0	117	0	0	0	0	0	0	n	
Family Cynoglossidae																	
Symphurus plagiusa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Syngnathidae																	
Oostethus lineatus	0	20	21	7	1	0	0	0	379	0	0	53	1	4	1	0	
Pseudophallus mindii	0	0	4		0	0	0	0	7	0	0	0	0	0	0	0	
Family Atherinidae																	
Coleotropis blackburni	129	37	_	0	0	0	0	0	0	0	0	0	0	0	0	0	
Melaniris chagresi	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	
Melaniris milleri	0	0	272	0	8	0	0	0	467	0	0	0	0	14	35	40	
Family Mugilidae																	
Agonostomus monticola	0	0	2	2	5	0	0	2	3	0	0	0	0	0	0	10	
Mugil curema	34	1	9	0	0	0	0	0	1	0	0	0	0	0	1	10	H
Family Polynemidae																	
Polydactylus virginicus	190	14	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Sphyraenidae																	
Sphyraena guachancho	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Family Scombridae																	
Scomberomorus cavalla	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Scomberomorus maculatus	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Thunnus sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Family Carangidae																	
Caranx hippos	_	3	31	0	0	0	0	0	0	0	0	0	0	0	2	0	P
Caranx latus	0	1	26	0	0	0	0	0	0	0	0	0	0	1	6	1	P
Chloroscombrus chrysurus	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Oligoplites palometa	32	3	27	1	0	0	0	0	0	0	0	0	0	1	0	0	P
Selene setapinnis	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Trachinotus carolinus	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Trachinotus goodei	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Family Centropomidae																	
Centropomus ensiferus	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2	0	P
Centropomus parallelus	0	0	16	0	1	1	0	0	6	0	0	0	0	0	36	0	P
Centropomus pectinatus	0	0	369	0	0	0	0	0	18	0	0	0	1	9	31	0	P
Centropomus undecimalis	0	20	15	0	0	0	0	0	4	0	0	0	0	0	0	0	P
Family Serranidae																	
Epinephelus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Family Lutjanidae																	
Lutjanus griseus	0	2	9	0	0	0	0	0	1	0	0	0	0	0	0	_	P
Lutjanus jocu	0	1	49	0	0	0	0	0	48	0	0	0	0	5	7	7	P/I
Lutjanus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	P/I
Family Pomadasyidae																	
Conodon nobilis	15	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Pomadasys corvinaeformis	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Pomadasys crocro	51	4	95	3	1	2	1	0	122	0	0	0	0	0	4	1	I
Family Sparidae																	
Archosargus probatocephalus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	O
Family Gerreidae																	
Diapterus olisthostomus	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	
Diapterus plumieri	0	0	17	0	0	0	0	0	2	0	0	0	0	1	5	1	
Diapterus rhombeus	0	0	55	0	0	0	0	0	4	0	0	0	0	3	6	1	
Eucinostomus argenteus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	
Eucinostomus melanopterus	15	0	157	2	1	4	2	0	3	0	0	0	0	2	6	2	

Appendix 1. (Continued).

Species Sites		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Code
Family Sciaenidae																	
Bairdiella ronchus	0	0	191	0	3	0	0	0	0	0	0	0	0	1	1	0	
Bairdiella sanctaeluciae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	_
Cynoscion jamaicensis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Larimus breviceps	276	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	I
Menticirrhus americanus	0		1	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Menticirrhus littoralis	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Micropogonias furnieri	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ophioscion costaricensis	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ophioscion panamensis	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Stellifer colonensis	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Umbrina broussoneti	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Cichlidae																	
Cichlasoma alfari	0	0	0	2	_	5	0	3	34	1	0	22	0	0	1	0	_
Cichlasoma centrarchus	0	0	26	2	4	0	0	0	345	0	0	0	3	3	76	5	I
Cichlasoma citrinellum	0	0	164	0	7	1	0	0	84	0	0	0	4	10	59	1	I
Cichlasoma dovii	0	0	1	13	18	0	7	0	159	0	0	0	0	1	9	8	P
Cichlasoma loisellei	0	0	944	0	0	70	0	39	52	18	7	8	11	0	0	79	I
Cichlasoma maculicauda	0	0	284	18	6	0	0	0	451	0	0	9	3	1	11	26	H
Cichlasoma managuense	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	P
Cichlasoma nicaraguense	0	0	0	2	0	1	8	0	0	0	0	0	0	0	0	0	I
Cichlasoma nigrofasciatum	0	_	4	22	8	4	1	0	132	0	1	86	32	3	18	0	O
Cichlasoma rostratum	0	0	0	5	3	1	4	0	11	0	0	0	4	0	4	0	
Cichlasoma septemfasciatum	0	0	0	3	0	0	7	9	7	7	0	0	0	0	1	1	_
Cichlasoma tuba	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	H
Herotilapia multispinosa	0	0	2	0	0	0	1	0	4	0	0	16	0	0	62	0	O
Family Eleotridae																	
Dormitator maculatus	0	0	36	0	0	0	0	0	251	0	0	9	2	2	2	1	O
Eleotris amblyopsis	0	9	375	22	38	4	0	0	1689	1	3	526	3	2	5	6	P/I
Eleotris pisonis	0	9	253	22		1	1	0	278	2	0	90	0	1	0	2	P/I
Gobiomorus dormitor	0	0	56	7	4	2	1		168	0	0	25	1	3	6	0	P
Guavina guavina	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Leptophilypnus fluviatilis	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Gobiidae																	
Awaous tajasica	0	7	0	0	0	0	0	0	6	1	0	0	0		0	0	_
Bathygobius soporator	0	0	19	0		0	0	0	0	0	0	0	0	_	0	0	I
Evorthodus lyricus	0	0	12	1	0	0	0	0	84	0	0	57	0	2	2	0	H
Gobionellus boleosoma	0	0	17	0	0	15	0	0	0	0	0	0	0		0	0	I
Gobionellus fasciatus	0	10	328	8	4	42	0	0	142	0	0	0	2		5	0	
Gobionellus pseudofasciatus	0	0	13	0	_	2	0	0	2	0	0	0	0	_	0	0	
Gobiosoma spes	0	0	226	0	0	3	0	0	9	0	0	0	0	0	0	0	
Family Echeneidae																	
Echeneis naucrates	0	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Family Dactyloscopidae																	
Dactylagnus peratikos	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P
Family Microdesmidae																	
Microdesmus carri	0	34	3	0	0	0	0	0	0	0	0	0	0	0	0	0	
Family Batrachoididae																	
Batrachoides gilberti	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Batrachoides surinamensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Porichthys pauciradiatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Porichthys plectrodon	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	P/I
Family Tetraodontidae																	
Sphoeroides testudineus	0	0	139	0		0	0	0		0	0	0	0	4	5	0	O
Family Uranoscopidae																	
Astroscopus y-graecum	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	