

Comparison of Deep-River and Adjacent Sandy-Beach Fish Assemblages in the Napo River Basin, Eastern Ecuador

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We sampled fishes with a small trawl in the deep midchannel and with beach seines on nearby sandy beaches at five sites along two parallel headwater tributaries of the upper Amazon in Eastern Ecuador. We quantified ecological distance between fish assemblages of deep-river and beach habitats and compared assemblage composition, species richness, and diversity. Results of detrended correspondence analyses (DCA) and two-way indicator species analyses (TWINSpan) clearly revealed the presence of a striking faunal change (i.e., about 92% dissimilarity) between beach-zone and off-shore fishes. The boundary between these assemblages occurred at about 2 m depth. Beach samples collected as far apart as 325 km were more similar to each other than to trawl samples taken only 10s of meters away. The beach-zone fish assemblage was strongly dominated by small characins, whereas the deep-river habitat was dominated by catfishes and weakly electric gymnotiforms. Apparent adaptations to deep-water habitats included small size, flattened or elongated body, ventral mouths, reduced eyes, and sensory specializations for life in what may be a nearly light-less environment (e.g., chemo- and electroreceptors). Visually oriented fishes and those dependent on algal or detrital foods were mostly absent from the deep-river samples. We caught many more species along the beaches, but after correcting for higher numbers of individuals collected in beach habitats, species richness was not noticeably different between the two habitats. Species diversity also averaged slightly higher for beach samples, but the difference was not significant. We infer that the deep-river habitat was undersampled and that further effort in the deep river would reveal the presence of many more species.

Muestreamos peces con una malla de rastra en el canal profundo del río y con redes playeras en las playas vecinas, en cinco sitios a lo largo de dos tributarios paralelos del Alto Amazonas en el Este del Ecuador. Quantificamos la distancia ecológica entre ensamblajes de peces de las profundidades del río y de los habitats de playa, y comparamos la composición de esos ensamblajes, la riqueza de especies y la diversidad. Los resultados de ‘detrended correspondence analyses (DCA)’ y ‘two-way indicator species analyses (TWINSpan)’ claramente revelaron la presencia de una marcado cambio faunístico (i.e., cerca de 92% disimilarity) entre la zona de playa y los peces del centro del río. La barrera entre estos ensamblajes ocurrió a cerca de 2 m de profundidad. Muestras de playa colectadas a distancias de hasta de 325 km fueron más similares de unas a otras que a muestras de rastra tomadas a solo unas decenas de metros de distancia. El ensamblaje de peces de playa fue markadamente dominado por carácidos, mientras que el hábitat de aguas profundas fue dominado por bagres y gimnotiformes débilmente eléctricos. Adaptaciones aparentes para los habitats de aguas profundas incluyeron tamaño pequeño, cuerpo aplastado o alargado, bocas ventrales, ojos reducidos, y especializaciones sensoriales para vivir en lo que problemamente es un ambiente casi completamente oscuro (e.g., quimo- y electroreceptores). Peces visualmete orientados y aquellos que dependen de alga o detritus como alimento estuvieron en su mayoría ausentes en las muestras de aguas profundas. Colectamos más especies a lo largo de las playas, pero después de corregir por el número alto de individuos, la riqueza específica no fue notoriamente diferente entre estos dos habitats. El promedio de la diversidad específica también fue un poco más alto en las muestras de playa, pero la diferencia no fue significativa. Inferimos que el hábitat de aguas profundas no fue muestreado suficientement y que esfuerzos futuros en aguas profundas podrían revelar la presencia de muchas más especies.

FISH assemblages living in deep, midchannel habitats of large tropical rivers are poorly known. In the present context, such habitats are

defined as waters about 3 m or more in depth. In Africa, Poll (1959) trawled over sandy-bottom areas in Malebo Pool of the lower Zaire River

and discovered a fish assemblage dominated by bagrid catfishes and weakly electric mormyrids. Roberts and Stewart (1976) explored the lower Zaire River rapids at low water and found a highly specialized fauna including five species of blind fishes apparently adapted to live in interstices or to burrow in the sediment. Samples from the Zaire rapids mostly were taken among rocks at depths less than 2 m, but those sites were open to much deeper water and covered by several more meters of water for all but a few weeks each year. In South America, sampling with trawls in deep channels of the lower Orinoco River revealed a diverse fish assemblage dominated by catfishes and weakly electric gymnotoid fishes (López-Rojas et al., 1984; Lundberg et al., 1987, 1991). Most recently, J. Lundberg and Brazilian colleagues have been exploring the deeper channels of the middle and lower Amazon basin, with trawl samples taken at depths up to 50 m. Those trawl collections have yielded some 240 species, also dominated by catfishes and gymnotoids, and have included blind fishes (Lundberg and Rapp Py-Daniel, 1994; Friel and Lundberg, 1996; Lundberg et al., 1996; Cox Fernandes, 1999). A common feature of all these studies on deep-river fishes is that they report an unexpectedly diverse fauna with many rare or new taxa (e.g., Lundberg et al., 1996). Many of these fishes have unusual morphological and physiological adaptations such as reduction or loss of eyes and apparent compensatory hypertrophy of other sensory structures (e.g., Stewart, 1985a; Lundberg and Rapp Py-Daniel, 1994).

Management of Amazonian fishes for sustainable harvest and conservation of biodiversity requires knowledge of species distributions and how they converge to form communities. The Napo River basin is within an area of exceptionally high diversity and endemism for many groups of plants and animals (Prance, 1982). Thus, it should be a priority area for conservation of Neotropical biodiversity. The Napo basin also occupies a central position along the N-S axis of the Andes, making it a suitable model for community patterns and ecosystem processes all along the Upper Amazon from Colombia to Bolivia. More than 500 species of fish have been reported from just the Ecuadorian portion of that basin (Stewart et al., 1987; Ibarra and Stewart, 1989; Galacatos et al., 1996), and our recent field studies have increased that number to about 575 (Galacatos 2001; unpubl. data). This high regional species richness of fishes may be explained, in part, by marked habitat specialization of many of the taxa. For example, fish assemblages associated with sandy beaches in

the Napo basin and elsewhere are dominated by small characins (i.e., less than about 100 mm SL; Ibarra and Stewart, 1989; Jepsen, 1997), and lagoon assemblages are dominated by curimatids, cichlids, and small characins (Galacatos et al., 1996; Silvano et al., 2000). The small characins in lagoons, however, are nearly all different species from those along the sandy beaches of white-water rivers (Galacatos et al., 1996). In marked contrast to those habitats, fishes sampled with trawls in deeper, midriver channels yielded many distinctive catfishes (e.g., Isbrücker and Nijssen, 1986; Stewart, 1985a,b, 1986) and gymnotoids (e.g., Mago-Leccia et al., 1985; Lundberg and Mago-Leccia, 1986) that appear to be components of a highly specialized assemblage similar to that reported from the lower Orinoco and middle to lower Amazon basins. Objectives of this paper are (1) to quantify ecological distance between fish assemblages of deep-river and adjacent sandy-beach habitats in the Napo basin; and (2) to compare assemblage composition, species richness and diversity between those two habitats.

MATERIALS AND METHODS

Sampling.—All samples were collected in the dry periods of September to November 1981, and September to December 1983. The beach samples analyzed here were composites of several seine hauls at a site near or adjacent to a deep-water site and were part of a broader study of beach-zone fishes (Ibarra and Stewart, 1989). We also have included data from the beach at Cuyabeno because that was the most comprehensive beach collection from the middle reaches of the Aguarico River. We collected samples from the offshore waters near the beaches in depths ranging from 1.5 to about 8 m using a 4-m otter trawl with 3-mm mesh in the wings and body. The cod end of the trawl had a liner of nylon fly screen (1.5-mm mesh). The trawl typically was pulled with a 12–15 m long, flat-bottomed, metal riverboat using a rigging similar to that reported by López-Rojas et al. (1984). All tows were pulled in an upstream direction because strong currents and abundant snags made it dangerous to tow downstream. A long rope with float was attached to the cod end of the trawl to retrieve it from downstream when it caught on the abundant woody snags. Depth along each tow was monitored continuously with a portable echosounder.

Collection sites (Fig. 1) and associated habitat data are as follows: (1) Coca—Napo River, about 10.7 km upstream from the bridge at Puerto Francisco de Orellana (Coca), 0°32.6'S,

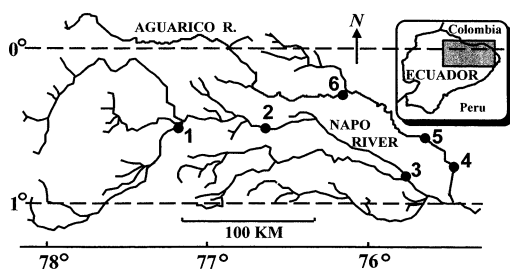


Fig. 1. Location of sampling sites in the Napo River basin of Eastern Ecuador for paired trawl and beach seine samples. Cuyabeno site (6) was sampled only with beach seine.

77°2.9'W, at 1.5–3 m depth; 21 September 1981; (2) Añangu—Napo River near Añangu, in the middle of the river, 4 tows at 0°31.6'S, 76°24.0'W and 2 tows at 0°0.8'S, 76°24.0'W, at 3–7 m depth; 12 October 1981; (3) Tiputini—Tiputini River at confluence with Napo River, 0°48.9'S, 75°32.5'W, at 3–7 m depth; 28 October 1981; (4) Lagartococha—Aguarico River 1–2 km upstream from confluence with Lagartococha River, 0°38'S, 75°18'W, at 1.5–6 m depth; 2 November 1983; (5) Zancudo—Aguarico River about 6 km downstream from Zancudo Military Camp, 0°33'S, 75° 27'W, at 2–7 m depth; 27 October 1983; and (6) Cuyabeno—Aguarico River near Cuyabeno Military Camp and confluence with Cuyabeno River, 0°15.5'S, 75°53.5'W, beach seine only; 21–24 October 1983.

We preserved specimens in 10–12% formalin and later transferred them to 75% ethanol. Collections are deposited in the Field Museum of Natural History, Chicago, Illinois, and Museo de la Escuela Politécnica Nacional, Quito. We sorted specimens to the species level and identified as many taxa as possible. However, many taxa in these collections are undescribed or belong to genera lacking a recent revision so they are designated with a generic name and letter (e.g., *Loricaria* sp. A).

Analyses of community patterns.—Methods for community analyses are those detailed in Ibarra and Stewart (1989) and Galacatos et al. (1996). A sites-by-species abundance matrix was analyzed using the multivariate techniques of ordination (detrended correspondence analysis, DCA) and hierarchical classification (two-way indicator species analysis, TWINSpan; Gauch, 1982). We standardized abundances by a $\log_{10}(n + 1)$ transformation and applied a down-weighting algorithm as recommended by Hill and Gauch (1980). We used PC-ORD software (Multivariate analysis of ecological data, vers. 2.03, McCune and Mefford, MjM Software, Glen

neden Beach, OR, 1995, unpubl.) for DCA and TWINSpan. The importance of rare species was deemphasized by removing species represented at only one location. Calculation of between-sample similarities in the ordination follows Gauch (1973). A jackknifing procedure involving the sequential deletion of one site at a time from the TWINSpan was used to test the consistency of the classification (Ibarra and Stewart, 1989). The percentage persistence of clusters present at each node of the original dendrogram gives an indication of the classification robustness.

Estimation of diversity patterns.—For each site and habitat, we evaluated species richness and diversity (Ibarra and Stewart, 1989). Species richness comparisons were done with normalized data using rarefaction to the smallest sample (Simberloff, 1972; using software of Krebs, 1989), because sampling efforts were not standardized. We estimated diversity with the reciprocal of Simpson's index (Krebs, 1989). Pairwise comparisons of differences in richness and diversity between the two habitats were made with rank sum tests (i.e., Mann-Whitney *U*-test, exact permutation test of Manly, 1991; implemented with Statistix for windows, vers. 2.2, Analytical Software, LaJolla, CA, 2000, unpubl.).

RESULTS

Faunal composition.—A total of 5078 specimens were collected, 297 with the trawl and 4781 with seines. Trawl samples yielded a total of 41 species; from these, 20 were caught only in deep waters, 21 were also found in the beach samples, 13 were collected only at one site, and six were represented by a single fish (Appendix 1). The beach samples adjacent to the deep-water collection sites yielded 112 species, 90 were only present in beach samples, 45 of those were present at only one locality, and 26 were represented by a single specimen.

In the samples taken at depths greater than 2 m, the dominant forms were the siluriforms with 66% of species and 64% of individuals, followed by gymnotiforms with 21% of species and 34% of individuals; characiforms and pleuronectiforms each had 6% of species and 1% of individuals. In contrast, the most numerous fish in the beach samples were the characiforms with 47% of species and 81% of individuals. Siluriforms were 44% of species and 15% of individuals; the remaining 4% of individuals were of the families Engraulidae, Rhamphichthyidae, Sternopygidae, Belonidae, Aplocheilidae, Scia-

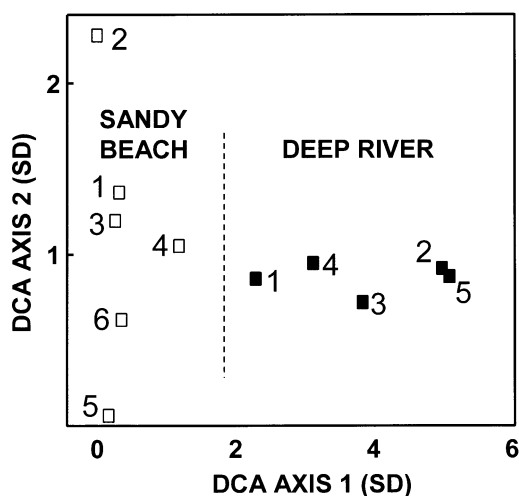


Fig. 2. DCA ordination of 11 samples of fishes collected by trawling in midriver and by seining on adjacent sandy beaches in the Napo and Aguarico River basins. This ordination was based on a matrix of 74 species, excluding those present in only one sample because the latter were uninformative about between-site relationships (Appendix 1). Axis scales are in units of average standard deviations of faunal turnover (Hill and Gauch, 1980). Site numbers correspond to those in Figure 1.

nidae, Cichlidae, Achiridae, and Tetraodontidae.

We observed marked contrasts in the composition of collections from deep water and those from beaches. One difference was the low number of individuals collected with the trawl. Some of that difference could be the result of a lower efficiency of the trawl, but it was also apparent (from trawls taken closer to shore, e.g., site 1 near Coca) that fish densities were lower in deep water. The main difference, however, was the taxonomic composition of the samples (Appendix 1). The indicator species of deep water habitats were the siluriforms—*Xiliphius melanopterus*, pimelodid sp. a, *Megalonema platycephalus* and *Apistoloricaria condei*. The dominant sandy beach species were small characins less than about 100 mm SL (Ibarra and Stewart, 1989). *Knodus victorae septentrionale*, *K. cf. beta*, and *Moenkhausia copei* were present in all sites; the former species comprised 36% of individuals caught with the seine.

Community patterns.—In the DCA analysis of 11 sites (Fig. 2), beach samples are tightly grouped within 1.2 SD at the left end of the axis. All beach samples except Lagartococha were more than 92% similar among themselves. Lagartococha had 67% similarity to its nearest neigh-

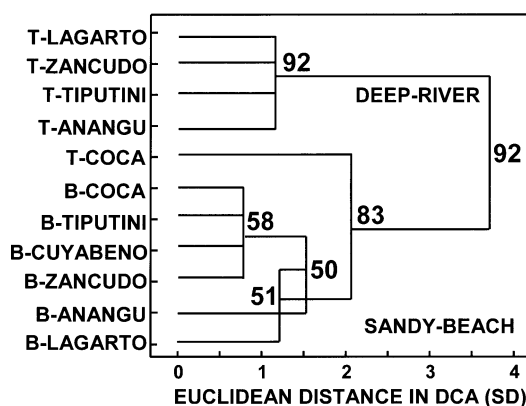


Fig. 3. TWINSpan dendrogram of the same 11 samples ordinated in Figure 2. The horizontal axis is the average Euclidean distance in the DCA sample ordination (Gauch and Whittaker, 1981). The percentages indicate persistence of a cluster after jackknifing.

bor. These samples were similar to each other even though they were collected in sites separated by at least 30 km and as much as 325 km by river. Next along this gradient is the Coca trawl sample. Most specimens of that sample were collected in water less than 2 m deep, and the sample was dominated by species characteristic of sandy beaches. The positions of trawl samples at the right side of the graph demonstrate that they were more similar among themselves, regardless of the geographic location of the site, than they are to their adjacent beach samples. The wider distribution of deep-water samples along 2.7 SD indicates that the trawl cluster is less uniform than that for the beach. The higher variability in the composition of the trawl tows is probably the result of small sample sizes. The length of the second axis was only 1.4 SD. That axis does not seem to be associated with environmental gradients but apparently reflects the effects of sample size on estimated species composition, because the smallest beach samples are at the extremes of the axis.

The classification of samples with TWINSpan produced two clusters that are about 90% different (Fig. 3); a Euclidean distance of 4.0 would represent 100% change (Gauch, 1982). The jackknifing analysis revealed 92% consistency of the primary dichotomy. The first cluster includes the beach samples plus the shallow Coca trawl. The second cluster groups the trawl samples except for that from Coca. The base level of differences between sites within each cluster is about 1.0 SD ($\pm$ approximately 0.3), which represents about a 50% change in composition. The lowest within-cluster distances were among the beach sites (Fig. 3).

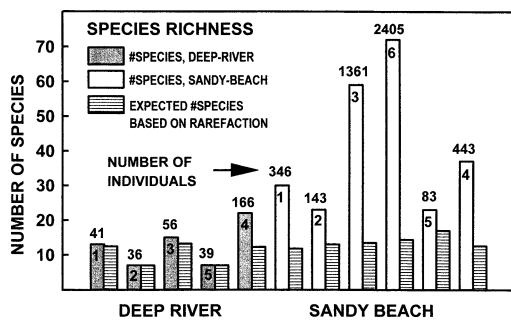


Fig. 4. Comparison of species richness between deep-river (grey bars) and sandy-beach (white bars) habitats in the Napo and Aguarico River basins. Richness was expressed as total number of species collected at a site; expected number of species (striped bars) was based on rarefaction standardization to the smallest sample size ($n = 36$ individuals). Site numbers on the bars correspond to those in Figure 1.

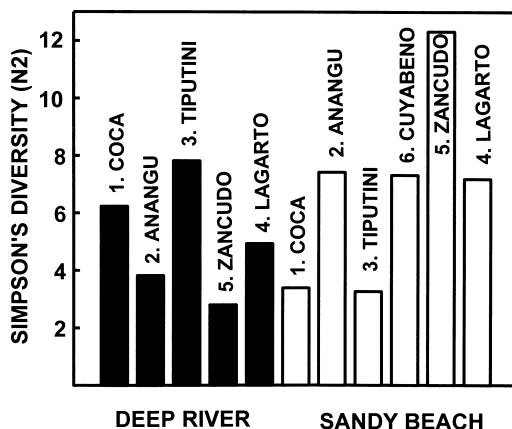


Fig. 5. Comparison of Simpson's diversity indices between deep-river (black bars) and sandy-beach (white bars) habitats in the Napo River basin. Site numbers correspond to those in Figure 1.

Species richness and diversity.—The raw data for species richness indicated significantly higher values for the beach samples (Fig. 4; Mann-Whitney U -test, exact permutation test, $P = 0.002$). After rarefaction, species richness values for sandy-beach assemblages and neighboring deep-water assemblages were similar (Mann-Whitney U -test, $P = 0.087$). These results provide a clear example of the effects of sample size, expressed as number of individuals, on estimates of species richness. Simpson's diversity averaged slightly higher near beaches than in deep waters (Fig. 5), but that difference was not statistically significant (Mann-Whitney U -test, $p = 0.31$). At a given site on the white-water mainstream, the specialized deep-river fishes comprised about 17–25% of the total species richness (i.e., of beach and deep-channel fishes combined).

Morphological patterns.—As noted above, the majority of the deep-river fishes were weakly electric fishes and catfishes. Thus, it is clear that the deep-river assemblage is characterized by fishes that can find their prey using electro- or chemoreceptors and that fishes dependent upon vision for feeding or social interactions are largely absent. Some of the catfishes have numerous or elaborately branched barbels, and most of them have small eyes or, at least, eyes without a free orbital rim. Many of the deep-river fishes that we caught had small, strongly flattened or elongate body forms, suggesting adaptations to life in the boundary layer at the bottom or perhaps to burrowing into the substrate. Relatively little is known about energy sources for the deep-river fishes of the Napo, but most of the fishes

collected there have small, conical teeth and many of them have subterminal to ventral mouths. These features suggest a dependence on benthic or allochthonous micro- and macro-invertebrates, but the gymnotiid genus *Rhabdolichops*, at least, feeds on pelagic zooplankton (Lundberg et al., 1987).

Most of the characins that were collected in trawls were taken near beaches in water less than about 2 m (i.e., upstream from Coca and one of the tows near Lagartococha). Catfishes with relatively larger eyes and free orbital rims (e.g., *Pimelodella* spp.) were taken primarily in those same shallow trawl samples and, like the characins, were typical of the beach assemblage. Notably absent from the deep-river were fishes known to depend on periphyton or detritus, for example *Prochilodus*, various curimatids, and genera of the loricariid subfamily Hypostominae.

DISCUSSION

Community structure.—Community analysis reveals one distinct fish assemblage associated with the shallow waters adjacent to sandy beaches and a second, benthic assemblage associated with waters deeper than 2 m. The sandy-beach community is practically unchanged along the 325 km of river studied as indicated by the high similarity among the beach samples (Figs. 2–3). Our deep-water samples, in contrast, are not as homogeneous a group as shown by the separation of trawl samples along the first DCA axis. That heterogeneity is at least in part a result of the small sample sizes, perhaps combined with patchy distributions. High variability among

trawl tows is an indication of the extremely high diversity of tropical deep waters (Lundberg et al., 1996). Our comparison of species richness after rarefaction suggests that the number of species in the deep-water habitat could be comparable to that of the beach samples for a given number of individuals. In other words, further exploration of deep-river channels of the Napo basin would probably more than double the species richness for that habitat. Larger samples at each site should reveal a more uniform assemblage among areas. Extensive sampling in lagoon and small-stream habitats of the Napo basin over the past 20 years (e.g., Galacatos et al., 1996; and unpubl. data) gives us added confidence that what we consider deep-river fishes are largely restricted to that habitat.

The deep-water assemblage described in this paper was sampled in the dry season. It is possible that some upstream migrants are added to this assemblage when many species migrate upstream to spawn (e.g., Winemiller and Jepsen, 1998). Also, the larvae of some migratory catfishes and characoids may use the deep channels to move from spawning sites in the upper Amazon to nursery sites farther downstream in Perú and Brazil (e.g., Barthem et al., 1991; Barthem and Goulding, 1997; Araujo-Lima and Oliveira, 1998). Recent sampling for pelagic larval fishes in the mainstream of the Napo River in Ecuador revealed the presence of abundant catfishes and characins drifting downstream at rates of over $100 \text{ km} \cdot \text{d}^{-1}$ (unpubl. data).

Our perspective of the deep-river and sandy-beach assemblages is strongly influenced by abundances of small-sized fishes that cannot out-swim our trawls and seines. Supplemental sampling with hook and line and gillnets has revealed the presence of various species of large-sized catfishes (i.e., $> 50 \text{ cm SL}$), especially pimelodids like *Brachyplatystoma* spp. and *Goslinea*. Our observations indicate that many of those big fishes avoid shallow water, so their inclusion in our analyses would reinforce our basic conclusions about community patterns. The larger Neotropical rivers also may have an offshore pelagic assemblage, but to date, that dimension remains largely unstudied (except for studies on larvae).

Species richness along a river gradient generally increases downstream because of the addition of deeper habitats (Sheldon, 1968; Schlooser, 1987; Rahel and Hubert 1991). In lower reaches of large rivers like the Amazon, floodplains, flooded forests, and sharp pH gradients add further complexity (Ibarra and Stewart, 1989; Sedell et al., 1989; Saint-Paul et al., 2000). In smaller rivers of French Guiana, fish

species richness increased with increasing habitat complexity regardless of stream size at a site (Mérigoux et al., 1998). Increased water depth results in greater habitat diversity in a large white-water river like the Napo because a nearly light-less habitat is added when turbidity and depths are sufficient. The same applies to lakes throughout the world that are deep enough to stratify, but in the case of deep lakes, both light and temperature contribute to vertical segregation of fish assemblages. In the Ecuadorian Napo River basin, habitat partitioning at 2–3 m depth in sandy river channels notably increases alpha diversity of sites below 250 m altitude. Some species of the deep-river assemblage may occur upriver from the 250 m altitudinal contour, but abundant rocks and logs makes sampling them extremely difficult. López-Rojas et al. (1986) suggested that vertical habitat partitioning occurs in the main channels in the lower Orinoco River; however, precise depths for transitions and supporting analyses were not presented. An analysis of 40 species of electric fishes taken in trawls at depths of 2–40 m in the Brazilian Amazon revealed the presence of two assemblages (Cox Fernandes 1999). Whitewater habitats were dominated by apteronotids, whereas lower reaches of black and clearwater tributaries were dominated by sternopygids. Cox Fernandes (1999) also noted that the sternopygids tended to prefer shallower water than the apteronotids. In the reaches of the Napo and Aguarico Rivers that we sampled, we did not find any sites deeper than 10 m during the dry season. Even though we attribute community changes to changes in water depth, depth may be simply a correlate of the key variables structuring river communities. Light penetration and velocity of the current may be the ultimate factors influencing the evolution of morphologically similar assemblages adapted to the deep waters and the rocky rapids of large rivers (e.g., Roberts and Stewart, 1976).

Habitat partitioning of fishes (e.g., Gorman and Karr, 1978; Watson and Balon, 1984) is evident when comparing paired samples from beach and adjacent deep water. All beach samples were noticeably different from trawl samples. At Anangu and Zancudo, that dissimilarity was 98%. The dissimilarity for the Coca and Lagartococha pairs was lower, 67% and 66%, respectively. In the latter two sites, at least one trawl was pulled at depths as shallow as 1.5 m. Moreover, near Lagartococha, the beach samples were taken after a rain event that resulted in high water levels. Deep-water dwellers may move near shore to avoid increased water velocities during floods (e.g., *Apistoloricaria* and *Me-*

galonema in the Lagartococha beach sample, Appendix 1). Many of the smaller taxa in the deep channel appear to be adapted to living in the boundary layer or to burrowing in the surficial sediments so, once displaced up into the water column, they may not be able to swim against the strong currents. On one occasion, we observed a 4-m rise in water level during a 24-h period; water level can fall almost as fast after the flood crest passes. Thus, the boundary between beach and offshore assemblages could move laterally, depending on slope of the bottom and flow conditions of the river.

Morphological adaptations.—Adaptations to deep-water habitats include small size, flattened or elongated body, ventral mouths, and reduced eyes (Roberts and Stewart, 1976; Lundberg and Rapp Py-Daniel, 1994). Independent evolution of these traits is taxonomically widespread and appears in fishes living in deep-river channels and in rocky rapids of large rivers. We have measured surface currents in the midchannel that exceed $1 \text{ m} \times \text{s}^{-1}$, but the small and flattened fishes may be using a boundary-layer microhabitat near the bottom where currents would be considerably less. Because light is extremely faint or absent in the deep-river channels (pers. obs. by DJS while diving), there is a strong tendency for reduction of eyes. As with cave fishes, the absence of light would lead to a relaxation of selection pressures favoring large eyes and associated skin pigmentation (Lundberg and Rapp Py-Daniel, 1994). Ryder and Pesendorfer (1989) also suggested that eyes of fishes in turbid rivers might be reduced as a protection against suspended particles. Fishes that burrow into the substrate could be subjected to additional selection pressures for reduced eyes resulting from abrasion effects similar to those affecting burrowing terrestrial vertebrates. Reduction of eyes is often compensated by enhancement of other sensory organs that probably replace vision for finding food. For example, *Xiliphius* spp., *Ernstichthys intonsus*, and *Apistoloriaria condei* have numerous ventral barbels (Stewart, 1985a; Isbrücker and Nijssen, 1986). *Bathycetopsis oliveirai* has enlarged olfactory organs, and some catfishes may have electrosensory capabilities (Lundberg and Rapp Py-Daniel, 1994). The African mormyrids and Neotropical gymnotiforms have electric organs and surprisingly convergent morphologies for feeding on invertebrates (Winemiller and Adite, 1997). Some fishes also might use tactile receptors or the acoustico-lateralis system (e.g., achirids). Catfishes and weakly electric fishes are typically nocturnal; thus, in many cases, they may have

been pre-adapted to living at depth with little or no light.

Conservation and management.—The extent to which the deep-river fish community of the Napo differs from similar assemblages farther downstream in Perú, Brazil or elsewhere is unknown. At least some of the species collected in our trawl samples have been collected several hundred kilometers downstream and even in deep channels of the Orinoco River basin. If the Napo assemblage is an upriver extension of a broadly distributed deep-river assemblage, then local disturbances will not lead to species extinctions. It is possible that some of the deep-river fishes are restricted to the Napo basin, but it will be many years before we completely know the Napo basin fish fauna and full distribution patterns of component species. Nonetheless, it is not too early to consider conservation measures.

Our conclusion that the deep-river channels of the Napo River basin harbor a specialized fish assemblage that is distinct from other fish communities in Ecuador has important implications. Several areas in the Ecuadorian Napo have been set aside as National Parks or faunal reserves, at least in part, to protect and conserve biodiversity. The deep-river channels generally have been used as boundaries to those protected areas so the deep-river communities may not be specifically included. This situation closely parallels that for the lowland whitewater assemblage of sandy-beach fishes (Ibarra and Stewart, 1989). Generally, the large whitewater rivers like the Napo and Aguarico extend well upstream from the protected areas so the deep-river habitats are vulnerable to human disturbances upstream. Such disturbances may include siltation related to deforestation, dam construction, nutrient loading, oil spills, or discharge of toxic chemicals (e.g., Smith, 1985; Kimerling et al., 1993; Allan and Flecker, 1993). Pesticides used in intensive agricultural systems like that for oil palm might also be a problem. If migratory fishes of commercial importance spawn in these river channels, then habitat degradation might adversely affect future harvests in Ecuador, Perú and Brazil (Barthem and Goulding 1997). If many of the fishes are burrowing into the substrate or otherwise in intimate contact with the sediment, then their conservation depends, in part, on maintaining the substrate in its natural state. For these reasons, the Napo and other Amazonian headwater systems need to be managed as watersheds with careful attention to downstream effects of development activities.

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LITERATURE CITED

- ALLAN, J. D., AND A. FLECKER. 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. *BioScience* 43:32–43.
- ARAUJO-LIMA, C. A. R. M., AND E. C. OLIVEIRA. 1998. Transport of larval fish in the Amazon. *J. Fish Biol.* 53(Suppl. A):297–306.
- BARTHEM, R. B., AND M. GOULDING. 1997. The catfish connection: Amazon conservation at the ecosystem level. Columbia Univ. Press, New York.
- , M. RIBEIRO, AND M. PETRERE, JR. 1991. Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon Basin. *Biol. Conserv.* 55:339–345.
- COX FERNANDES, C. 1999. Detrended canonical correspondence analysis (DCCA) of electric fish assemblages in the Amazon, p. 21–39. *In: Biology of tropical fishes*. A. L. Val and V. M. F. Almeida-Val (eds.). INPA, Manaus, Brazil.
- FRIEL, J. P., AND J. G. LUNDBERG. 1996. *Micromyzon akamai*, Gen. et Sp. Nov., a small and eyeless banjo catfish (Siluriformes: Aspredinidae) from the river channels of the Lower Amazon Basin. *Copeia* 1996: 641–648.
- GALACATOS, K. 2001. Community ecology of fishes and aquatic insects in rainforests of the Ecuadorian Amazon. Unpubl. Ph.D. diss., State Univ. of New York Coll. Environ. Sci. For., Syracuse.
- , D. J. STEWART AND M. IBARRA. 1996. Fish community patterns of lagoons and associated tributaries in the Ecuadorian Amazon. *Copeia* 1996:875–894.
- GAUCH, H. G. 1973. The relationship between sample similarity and ecological distance. *Ecology* 54:829–836.
- . 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, New York.
- , AND R. H. WHITTAKER. 1981. Hierarchical classification of community data. *J. Ecol.* 69:537–557.
- GORMAN, O. T., AND J. R. KARR. 1978. Habitat structure and stream fish communities. *Ecology* 59:507–515.
- HILL, M. O., AND H. G. GAUCH. 1980. Detrended Correspondence Analysis, an improved ordination technique. *Vegetatio* 42:47–58.
- IBARRA, M., AND D. J. STEWART. 1989. Longitudinal zonation of sandy beach fishes in the Napo River Basin, eastern Ecuador. *Copeia* 1989:364–381.
- ISBRÜCKER, I. J. H., AND H. NIJSSEN. 1986. *Apistoloricaria condei*, nouveau genre et nouvelle espèce de Poisson-Chat curiassé, tribu Loricariini Bonaparte, 1831, du Bassin du Rio Napo, Haute Amazonie, Equateur (Pisces, Siluriformes, Loricariidae). *Rev. fr. Aquariol. Herpetol.* 12:103–108.
- JEPSEN, D. B. 1997. Fish species diversity in sand bank habitats of a neotropical river. *Environ. Biol. Fish.* 49:449–460.
- KIMERLING, J., CON FEDERACIÓN DE COMUNAS UNIÓN DE NATIVOS DE LA AMAZONÍA ECUATORIANA, F.C.U.N.A.E. 1993. *Crudo Amazonica*. Abya Yala (Publisher), Quito, Ecuador.
- KREBS, C. J. 1989. *Ecological methodology*. Harper Collins Publishers, New York.
- LÓPEZ-ROJAS, H., J. G. LUNDBERG, AND E. MARSH. 1984. Design and operation of a small trawling apparatus for use with dugout canoes. *N. Am. J. Fish. Manag.* 4:331–334.
- LUNDBERG, J. G., AND F. MAGO-LECCIA. 1986. A review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a genus of South American freshwater fishes, with descriptions of four new species. *Proc. Acad. Nat. Sci. Phila.* 138:53–85.
- , AND L. RAPP PY-DANIEL. 1994. *Bathycetopsis oliveirai*, Gen. et Sp. Nov., a blind and depigmented catfish (Siluriformes: Cetopsidae) from the Brazilian Amazon. *Copeia* 1994:381–390.
- , W. M. LEWIS JR., J. F. SAUNDERS III, AND F. MAGO-LECCIA. 1987. Evidence for a major food web component in the main channel of the Orinoco River based on specialized electric fishes. *Science* 237:81–83.
- , F. MAGO-LECCIA, AND P. NASS. 1991. *Exalodontus aguanai*, a new genus and species of Pimelodidae (Teleostei, Siluriformes) from deep river channels of South America and delimitation of the subfamily Pimelodinae. *Proc. Biol. Soc. Wash.* 104:840–869.
- , C. COX FERNANDES, J. S. ALBERT, AND M. GARCIA. 1996. *Magosternarchus*, a new genus with two new species of electric fishes (Gymnotiformes: Apterontidae) from the Amazon River Basin, South America. *Copeia* 1996:657–670.
- MAGO-LECCIA, F., J. G. LUNDBERG, AND J. N. BASKIN. 1985. Systematics of the South American freshwater fish genus *Adontosternarchus* (Gymnotiformes, Apterontidae). *Contrib. Sci. Nat. Hist. Mus. Los Angeles Co.* 358:1–19.
- MANLY, B. F. J. 1991. *Randomization and Monte Carlo methods in biology*. Chapman and Hall, London, UK.
- MÉRIGOUX, S., D. PONTON, AND B. DE MÉRONA. 1998.

- Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environ. Biol. Fish.* 51:25–39.
- POLL, M. 1959. Resultats scientifiques des missions zoologiques au Stanley Pool subsidiees par le Cemubac (Universite Libre de Bruxelles) et le Musée Royal du Congo (1957–1958). III. Recherches sur la fauna ichthyologique de la région du Stanley Pool. *Ann. Mus. Roy. Congo Belge, Tervuren (Belgique), Sci. Zool., Ser. 8*, 71:75–174.
- PRANCE, G. T. (ED.). 1982. Biological diversification in the tropics. Columbia Univ. Press, New York.
- RAHEL, F. J., AND W. A. HUBERT. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. *Trans. Am. Fish. Soc.* 120:319–332.
- ROBERTS, T. R., AND D. J. STEWART. 1976. An ecological and systematic survey of fishes in the rapids of the Lower Zaïre or Congo River. *Bull. Mus. Comp. Zool.* 147:239–317.
- RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In*: D. P. Dodge (ed.). *Proceedings of the international large river symposium*. Department of Fisheries and Oceans, Ottawa, ON, Canada.
- SAINT-PAUL, U., J. ZUANON, M. A. VILLACORTA CORREA, M. GARCÍA, N. NOEMI FABRÉ, U. BERGER, AND W. J. JUNK. 2000. Fish communities in central Amazonian white- and blackwater floodplains. *Environ. Biol. Fish.* 57:235–250.
- SCHLOSSER, I. J. 1987. A conceptual framework for fish communities in small warmwater streams, p. 17–24. *In*: W. J. Matthews and D. C. Heins (eds.). *Community and evolutionary ecology of North American stream fishes*. Univ. of Oklahoma Press, Norman.
- SEDELL, J. R., J. E. RICHEY, AND F. J. SWANSON. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? p. 110–127. *In*: D. P. Dodge (ed.). *Proceedings of the international large river symposium*. Department of Fisheries and Oceans, Ottawa, ON, Canada.
- SHELDON, A. L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193–198.
- SILVANO, R. A. M., B. D. DO AMARAL, AND O. T. OYAKAWA. 2000. Spatial and temporal patterns of diversity and distribution of the Upper Juruá River fish community (Brazilian Amazon). *Environ. Biol. Fish.* 57:25–35.
- SIMBERLOFF, D. S. 1972. Properties of the rarefaction diversity measurement. *Am. Nat.* 106:414–418.
- SMITH, N. J. H. 1985. The impact of cultural and ecological change on Amazonian fisheries. *Biol. Conserv.* 32:355–373.
- STEWART, D. J. 1985a. A review of the South American catfish tribe Hoplomyzontini (Pisces, Aspredinidae) with descriptions of new species from Ecuador. *Feldiana, New Ser.* 25:1–19.
- . 1985b. A new species of *Cetopsorhamdia* (Pisces: Pimelodidae) from the Rio Napo Basin of Eastern Ecuador. *Copeia* 1985:339–344.
- . 1986. A new pimelodid catfish from the deep-river channel of the Rio Napo, eastern Ecuador (Pisces: Pimelodidae). *Proc. Acad. Nat. Sci. Phila.* 138:46–52.
- , R. E. BARRIGA-SALAZAR, AND M. IBARRA. 1987. Ictiofauna de la cuenca del río Napo, Ecuador oriental: lista anotada de especies. *Politécnica, Ser. Biol.* 1:9–63.
- WATSON, D. J., AND E. K. BALON. 1984. Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *J. Fish Biol.* 25:371–384.
- WINEMILLER, K. O., AND A. ADITE. 1997. Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environ. Biol. Fish.* 49:175–186.
- , AND D. B. JEPSEN. 1998. Effects of seasonality and fish movement on tropical river fish food webs. *J. Fish Biol.* 53 (Suppl. A):267–296.
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APPENDIX 1. NUMBER OF INDIVIDUALS OF EACH SPECIES COLLECTED AT SIX SITES ALONG THE NAPO AND AGUARICO RIVERS OF EASTERN ECUADOR. For five of the sites, samples were taken by seine on the beach and by trawl in adjacent midchannel habitats. Site names correspond to those in Figure 1; abbreviations are LA = Lagartococha, AN = Añangu, ZA = Zancudo, CU = Cuyabeno, TI = Tiputini, and CO = Coca. Arrangement of samples and species is that obtained from a TWINSpan of 74 species (Fig. 3). An additional 59 species that occurred in only one sample were omitted from the analysis because they were uninformative about relationships among samples. Thirteen of this latter group were collected only in the deep river as follows: Co-t: *Nannoptopoma spectabilis* (1); An-t: *Horiomyzon retropinnatus* (1); *Emistichthys intonsus* (1); *Paracanthopoma* cf. *parva* (1); TI-t: *Pinelodus* cf. *altissimus* (2); pimelodid sp. B (11); *Adontosternarchus clarkae* (1); *Apterionotus macrostoma* (1); *Apterionotus apurensis* (1); *Apionichthys* sp. A (1); Za-t: *Malacoglanis gelatinosus* (2); La-t: *Rhabdolichops caviceps* (13); *Rhabdolichops eastwardi* (2). Other such taxa for the beach samples are given in Ibarra and Stewart (1989).

Species name	Beach seine samples						Trawl samples				Tot. N	
	LA-B	AN-B	ZA-B	CU-B	TI-B	CO-B	CO-T	AN-T	TI-T	ZA-T		LA-T
<i>Apariodon pongense</i>	—	—	—	4	—	2	—	—	—	—	—	6
<i>Prochilodus nigricans</i>	—	—	—	1	2	2	—	—	—	—	—	5
<i>Steindachnerina planiventris</i>	—	—	—	2	2	—	—	—	—	—	—	4
<i>Thoracocharax stellatus</i>	—	—	—	15	—	1	—	—	—	—	—	16
<i>Aphyocharax</i> sp. A	—	—	—	9	2	14	—	—	—	—	—	25
<i>Creagrutus geophyrus</i>	—	—	—	82	3	10	—	—	—	—	—	95
<i>Hemibrycon jabonero</i>	—	—	—	6	2	—	—	—	—	—	—	8
<i>Odontostilbe</i> sp. B	—	—	5	381	—	—	—	—	—	—	—	386
<i>Prionobrama filigera</i>	—	—	3	15	10	—	—	—	—	—	—	28
<i>Cheirocerus eques</i>	—	—	—	2	1	—	—	—	—	—	—	3
<i>Pinelodella</i> sp. B	—	—	—	16	65	3	—	—	—	—	—	84
<i>Pinelodella</i> sp. E	—	—	5	14	43	—	—	—	—	—	—	62
<i>Hypostomus</i> sp. B	—	—	1	3	—	—	—	—	—	—	—	4
<i>Limatulichthys punctatus</i>	—	—	—	1	13	—	—	—	—	—	—	14
<i>Pachyrurus</i> sp.	—	—	—	—	2	1	—	—	—	—	—	3
<i>Hypoclinemus mentalis</i>	—	—	—	1	3	—	—	—	—	—	—	4
<i>Steindachnerina dobula</i>	—	2	—	20	22	—	—	—	—	—	—	44
<i>Characidium steindachneri</i>	—	1	—	15	1	1	—	—	—	—	—	18
<i>Ctenobrycon hauxwellianus</i>	—	1	—	—	11	—	—	—	—	—	—	12
<i>Holostes</i> sp.	—	38	4	179	10	9	—	—	—	—	—	240
<i>Odontostilbe</i> sp. A	—	13	1	250	—	2	—	—	—	—	—	266
<i>Hemiodus unimaculatus</i>	—	1	—	—	—	1	—	—	—	—	—	2
<i>Moenkhausia megalops</i>	—	3	—	2	19	—	—	—	—	—	—	24
<i>Vandellia</i> sp. B	—	1	—	—	8	1	—	—	—	—	—	9
<i>Pseudotrylosurus angusticeps</i>	—	3	—	—	—	—	—	—	—	—	—	4
<i>Chelichthys asellus</i>	—	15	—	1	4	2	—	—	—	—	—	22
<i>Knodus v. septentrionalis</i>	61	4	10	708	739	81	—	—	—	—	—	1703
<i>Moenkhausia copei</i>	28	19	3	72	39	6	—	—	—	—	—	167

APPENDIX 1. CONTINUED.

SPECIES NAME	BEACH SEINE SAMPLES					TRAWL SAMPLES					Tot. N	
	LA-B	AN-B	ZA-B	CU-B	TI-B	CO-B	CO-T	AN-T	TI-T	ZA-T		LA-T
<i>Tetragonopterus argenteus</i>	2	—	3	1	13	2	—	—	—	—	—	21
<i>Henonemus punctatus</i>	3	1	1	11	19	3	—	—	—	—	—	38
<i>Vandellia</i> sp. A	1	—	1	3	—	1	—	—	—	—	—	6
<i>Hypostomus emarginatus</i>	1	1	—	30	12	1	—	—	—	—	—	45
<i>Aphanotoxus unicolor</i>	2	—	—	5	53	—	—	—	—	—	—	60
<i>Surisoma</i> cf. <i>nigrostrum</i>	1	—	1	10	6	—	—	—	—	—	—	18
<i>Acestrocephalus boellkei</i>	2	5	—	38	5	4	—	—	—	—	2	56
<i>Engraulisoma taeniatum</i>	5	—	—	—	14	14	—	—	—	—	—	33
<i>Knodus</i> cf. <i>bela</i>	49	21	3	112	24	4	—	—	—	—	—	213
<i>Paragoniates alburnus</i>	3	1	3	19	14	—	—	—	—	—	—	40
<i>Farlowella nattereri</i>	1	—	2	4	—	—	—	—	—	—	—	8
<i>Imparfinis stictionotus</i>	1	5	—	—	—	—	—	—	—	—	—	6
<i>Pimelodus</i> cf. <i>rigidus</i>	1	2	—	1	2	—	—	—	—	—	—	6
<i>Moenkhausia</i> cf. <i>intermedia</i>	10	1	1	2	—	—	—	—	—	—	—	14
<i>Nemadoras trimaculatus</i>	3	—	—	—	1	—	—	—	—	—	—	4
<i>Pseudostegophilus nemurus</i>	8	—	—	1	6	—	—	—	—	—	—	15
<i>Nannoptopoma sternopychum</i>	1	—	—	—	1	—	—	—	—	—	—	2
<i>Greagrutus</i> sp. C	79	—	9	100	69	3	4	—	—	—	—	264
<i>Pimelodella</i> sp. C	4	—	13	4	—	—	2	—	—	—	—	23
<i>Astyanax fasciatus</i>	—	2	—	3	—	—	1	—	—	—	—	6
<i>Greagrutus</i> cf. <i>muelleri</i>	—	—	—	—	—	3	10	—	—	—	—	13
<i>Pimelodus pictus</i>	5	—	—	1	1	—	11	—	—	—	—	18
<i>Loricaria similima</i>	—	—	—	1	—	—	1	—	—	—	—	2
<i>Greagrutus</i> sp. D	15	2	—	—	—	18	—	—	—	—	2	37
<i>Pimelodella</i> sp. D	17	—	—	6	4	29	3	—	—	—	4	63
<i>Acanthopoma bondi</i>	2	—	—	36	1	2	—	—	—	—	1	42
<i>Loricaria</i> sp. A	—	1	—	—	6	—	—	—	—	—	2	9
<i>Eigenmannia</i> cf. <i>macrops</i>	2	—	—	20	6	—	—	—	2	—	62	92
<i>Nemadoras</i> sp. B	9	—	—	—	—	—	—	—	—	—	3	12
<i>Pimelodella</i> sp. H	115	—	—	—	45	—	—	—	—	—	36	196
<i>Gymnorhamphichthys hypostomus</i>	1	—	—	2	—	—	—	—	—	—	2	5
<i>Cetopsorhamdia phantasia</i>	—	—	—	—	—	—	—	—	—	3	2	5
<i>Megalonema</i> cf. <i>xanthum</i>	—	—	—	2	—	—	—	—	—	—	2	4
<i>pimelodid</i> sp. A	—	—	—	1	—	—	—	15	4	21	7	48
<i>Xitiphius melanopterus</i>	—	—	—	—	—	—	—	6	1	9	2	18
<i>Pseudohemiodon</i> sp. B	—	—	—	—	—	—	—	—	3	1	1	5