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Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities

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The feeding behaviour and diets of fishes in two tropical habitats, a marine reef and a freshwater pond, were studied comparatively in Brazil. Similarities were found in the tactics employed to obtain food, the social patterns during foraging, and the general diet, notwithstanding lower-level taxonomic differences between the food items. The feeding behaviours of about one-third of the fish fauna from each community were approximately equivalent. The feeding categories of these fishes are briefly described. The similarities in the feeding modes probably reflect structural and functional properties shared by the two communities. Additional behavioural similarities of fishes in both habitats are presented and the lack of some particular foraging modes in each community is noted. The picture emerged that different, unrelated fish assemblages have the ability to evolve towards a similar behavioural and structural organization in response to comparable situations and constraints. The value of underwater observations and naturalistic studies on tropical freshwater fish assemblages is indicated.

I. INTRODUCTION

Underwater studies of fishes in tropical marine communities have revealed an amazing diversity of behavioural adaptations to obtain food, including very specialized and complex interactions between species, such as joint hunting, following, cleaning, and mimicry (e.g., Hiatt & Strasburg, 1960; Hobson, 1974; Ehrlich, 1975; Fishelson, 1977; Losey, 1978; Ormond, 1980). On the other hand, although a comparable diversity and specialization of feeding habits may conceivably occur also in tropical freshwater communities (e.g., Géry, 1969; Roberts, 1972; Lowe-McConnell, 1975; Goulding, 1980), such knowledge to date is scarce and derived mainly from dietary studies (e.g., Knöppel, 1970; Saul, 1975; Goulding, 1980) and occasional above-surface watching. This applies to South American and Asian communities in general; some African and Central American cichlid assemblages have been studied underwater (e.g., Fryer & Iles, 1972; Barlow, 1974; McKaye, 1977; Kocher & McKaye, 1983).

During a study on the scale-eating habits of some neotropical fish species (Sazima, 1983) I had opportunity for underwater observations on the feeding behaviour of fishes in several communities, both marine and freshwater, and found a surprising match in the mode of obtaining food in many species. This paper describes and comments upon the similarities of feeding tactics between particular fish species belonging to a marine and a freshwater tropical community. Although several studies make comparisons between tropical reef fish assemblages (see reviews in Ehrlich, 1975; Goldman & Talbot, 1976; Sale, 1980), such an approach has been rare for marine and freshwater habitats (but see Barlow, 1974; Emery, 1978). One of the aims of this paper is to affirm the value of

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underwater observations and naturalistic studies of tropical freshwater fish assemblages, poorly known in relation to such assemblages in tropical reefs. The analyses derived from comparative studies between tropical marine and freshwater fish assemblages may prove fruitful and provocative (see Barlow, 1974).

II. STUDY SITES AND METHODS

Two habitats, a marine rocky reef and a freshwater pond, were selected for this comparison, based on their accessibility and similarities in size, water transparency and number of fish species present. The marine reef, situated near the Praia da Fortaleza, Ubatuba, São Paulo, south-eastern Brazil (*c.* 23°32′S, 45°09′W) consists of a very small inlet, about 50 m wide, surrounded by rocks and boulders ranging from a few cm to 2–3 m in diameter. Most of the area of the reef is subtidal with the depth of the water ranging from 0·1–1·5 m at low tide to 1·0–2·5 m at high tide. The bottom is mostly covered by sand and scattered patches of course gravel with occasional isolated slabs or boulders. The rocky substrate is sparsely to thickly colonized by algae, and some of the boulders are entirely covered by anthozoans. The freshwater pond, situated in the Pantanal region near Poconé, Mato Grosso, western Brazil (*c.* 16°30′S, 56°45′W) is interconnected with other ponds and marshes by slow-flowing creeks. The latter substantially reduce their flow during the dry season, eventually causing some ponds to dry up. The stretch studied is permanent, and its mean dimensions varied around 15 m in width by 40 m in length, with a maximum depth of about 1·7 m. The bottom consists of mud or sand, with scattered gravel patches. Aquatic vegetation is abundant, and in some places grows in dense mats or thickets (Sazima, 1983). Marsh plants border the perimeter of the pond.

The two habitats were studied intermittently from 1981 to 1983. Observations include both day and night sessions, although the nocturnal ones were reduced to a minimum in the Pantanal pond due to the real risk of attacks by caymans (territorial defence?). Feeding behaviour of the fishes in both communities was directly observed while snorkeling, as both studied habitats were shallow, and this simple procedure enables observations with the minimum of disturbance (Potts, 1973). In both areas, series of preliminary observations were made to allow the fishes to become used to the observer's presence and to make initial records of the fish fauna. Data to be recorded were first assessed in a series of preliminary dives and then, during actual observation sessions, behavioural events were recorded on a plastic slate or photographed. Special attention was paid to the modes employed by the fishes to obtain food, the sites habitually explored while foraging or waiting for prey, and the social patterns during foraging.

The food taken by the fishes was in most cases identified directly during underwater observations and checked by analysing gut contents of line-caught or netted specimens; literature data were verified for comparison (Randall, 1967; Knöppel, 1970; Saul, 1975). Diets were compared in terms of food types and the habits and distribution of food organisms in the habitat and not in terms of lower-level taxonomy. As some food type categories are absent from one or other habitat, a complete correspondence in dietary types is not to be expected, although it is possible to indicate general similarities in foraging tactics of the fishes.

Visual censuses combined with angling, netting, and small-scale poisoning were used to sample the fish faunas of both communities (poisoning was done on the reef only). This somewhat crude sampling probably overlooked some species but allowed overall comparisons between the two fish assemblages. Voucher specimens of several fish species are deposited in the fish collections of the following institutions: Departamento de Zoologia, Universidade Estadual de Campinas, Campinas (ZUEC); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP); Naturhistoriska riksmuseet, Stockholm (NRM); Museum of Natural History, Smithsonian Institution, Washington (USNM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

III. RESULTS

In the marine, rocky reef, 64 species representing 35 families and 10 orders were recorded. In the freshwater pond, 61 species of 16 families and 5 orders were recorded. An initial analysis of these fish species' foraging tactics and diets revealed many striking parallels between fishes of the two communities (Table I, Fig. 1). In order to avoid cases of similarities explainable in terms of phylogenetic proximity, the 12 examples considered here in greater detail exclude closely related species such as the belonid needlefishes *Strongylura timucu* (Walbaum, 1792) (marine) and *Potamorrhaphis eigenmanni* Ribeiro, 1915 (freshwater).

FEEDING CATEGORIES

Foraging tactics and general diet of the fishes considered are as follows (in each comparison the marine species is presented first); unless otherwise stated, main feeding activity period is diurnal.

(a) *Surface pickers* swim inquisitively near the surface, picking up small floating organisms and organic debris. *Xenomelaniris brasiliensis* (Quoy & Gaimard, 1824) feeds mainly on algae, crustaceans and debris; *Moenkhausia intermedia* Eigenmann, 1908 picks up insects, seeds, and algae. This latter fish may sometimes show crepuscular feeding. Both species occasionally join schools of other surface-living fishes [in some ponds *Bryconops melanurus* (Bloch 1794) replaces *M. intermedia* in the ' surface picker ' role].

(b) *Roving predators* patrol while swimming near the surface or at mid-water, lunging mainly at small fishes. *Caranx latus* Agassiz, 1831 preys on fishes and swimming crustaceans and seems to forage mainly at twilight; *Acestrorhynchus altus* Menezes, 1969 is almost exclusively a piscivore, foraging all day round. Both species occasionally swim with other open-water fishes.

(c) *Stalking predators* are bottom-dwellers that lurk near plants or other cover and stealthily approach prey, striking from close quartes. *Mycteroperca rubra* (Bloch, 1793) eats mainly benthic crustaceans and small fishes; *Crenicichla lepidota* (Heckel, 1840) preys on insects and small fishes. Changes of colouration may occur during stalking [Fig. 2(a),(b)]. Both species may occasionally join substrate grubbers for brief periods, where they prey on the disturbed bottom animals and on small fishes attracted by the grubbers' feeding activity. Larger *M. rubra* may feed at night.

(d) *Mud-eaters* swim near the bottom when feeding, and scoop up and ingest portions of substrate containing their food [Fig. 2(c),(d)]. Ingested sand and mud passes through the alimentary tract. *Mugil curema* Valenciennes, 1836 consumes mainly diatoms and, to a lesser degree, plant detritus; *Curimata spilura* Guenther, 1864 ingests diatoms and desmids besides grazing on epiphytic filamentous algae. Both species have robust shovel-shaped lower jaws with thick lips, a thick-walled, gizzard-like stomach and a very long intestine.

(e) *Mutilators* approach larger fishes stealthily or with the use of cover, and on occasion swim together with similar-sized prey. Attack is launched at close proximity, and the prey lose some scales in every successful bite or strike. *Oligoplites saurus* (Bloch & Schneider, 1801) eats fish scales, small fishes and swimming crustaceans (this species discards the scale-eating habit as it grows); *Catoprion mento* (Cuvier, 1819) subsists almost entirely on fish scales, but when young it

TABLE I. Similarities of feeding behaviour in 12 pairs of fish species in a marine (Ubatuba) and a freshwater (Pantanal) community. Numbers in brackets, after family names, indicate approximate size ranges of observed individuals, as total length in mm

Foraging tactics and type of food	Ubatuba reef	Pantanal pond
(a) Surface pickers feeding on various items	*Xenomelaniris brasiliensis*$^{2(3)}$* Atherinidae (60–110)	*Moenkhausia intermedia*$^{2(3)}$ Characidae (50–60)
(b) Roving predators of small fishes	*Caranx latus*^{2} Carangidae (120–150)	*Acestrorhynchus altus*^{2} Characidae (110–170)
(c) Stalking predators of fishes and bottom animals	*Mycteroperca rubra*^{1} Serranidae (90–170)	*Crenicichla lepidota*^{1} Cichlidae (80–140)
(d) Mud-eaters (soft substrate feeders on minute organisms)	*Mugil curema*$^{2(3)}$ Mugilidae (110–170)	*Curimata spilura*$^{2(3)}$ Curimatidae (60–80)
(e) Mutilators feeding on larger fishes' scales	*Oligoplites saurus*^{1} Carangidae (45–80)	*Catoprion mento*^{1} Characidae (60–90)
(f) Diggers of localized excavations, feeding on bottom animals	*Eucinostomus argenteus*$^{1(2)}$ Gerreidae (55–90)	*Satanoperca pappaterra*$^{1(2)}$ Cichlidae (80–110)
(g) Grubbers excavating while moving, feeding on bottom animals	*Pseudupeneus maculatus*^{2} Mullidae (90–120)	*Corydoras polystictus*$^{3(2)}$ Callichthyidae (30–35)
(h) Followers of substrate grubbers, feeding on bottom animals	*Diplodus argenteus*$^{2(1)}$ Sparidae (60–90)	*Astyanax bimaculatus*$^{2(1)}$ Characidae (45–80)
(i) Sit-and-wait predators of bottom animals	*Labrisomus nuchipinnis*^{1} Labrisomidae (60–110)	*Jobertina lateralis*^{1} Characidae (25–30)
(j) Browsers biting off small pieces of plants	*Kyphosus sectatrix*^{2} Kyphosidae (80–130)	*Metynnis maculatus*^{2} Characidae (60–70)
(k) Nibblers feeding on various items	*Stephanolepis hispidus*^{1} Balistidae (40–120)	*Leporinus lacustris*^{1} Anostomidae (80–110)
(l) Crepuscular to nocturnal predators of bottom animals	*Haemulon steindachneri*^{2} Haemulidae (60–100)	*Pimelodella gracilis*$^{2(3)}$ Pimelodidae (60–90)

*Numbers refer to social patterns habitually observed during foraging; 1, solitary; 2, small group of up to 5–6 individuals; 3, school of up to 20–30 individuals; brackets indicate less common alternatives.

also ingests insects. Both species have very specialized teeth directed outwards from the mouth, and pick up loose scales in the water column and on the bottom.

(f) *Diggers* of localized excavations are bottom-dwellers that plunge the protrusible mouth into the soft substrate, filling it with sediment, withdraw and then sort out food items inside the mouth. The bulk of the mouthful is expelled through the opercular openings and/or mouth, producing a cloud of fine sediment (' substrate sifting '). This feeding method is repeated and leaves a series of pits and mounds on the bottom. *Eucinostomus argenteus* Baird & Girard, 1854 preys mainly on crustaceans, polychaetes, and molluscs; *Satanoperca pappaterra* (Heckel, 1840) feeds on insect larvae, crustaceans, plant debris and loose scales.

(g) *Grubbers*, which excavate while moving, are bottom-dwelling fishes that swim close to the substrate, probing with the snout and working the barbels through the sediment. During feeding, ingested material may be expelled in bursts through the opercular openings (' substrate sifting '). *Pseudupeneus maculatus* (Bloch, 1793) is very active and consumes mainly crustaceans and polychaetes; *Corydoras*

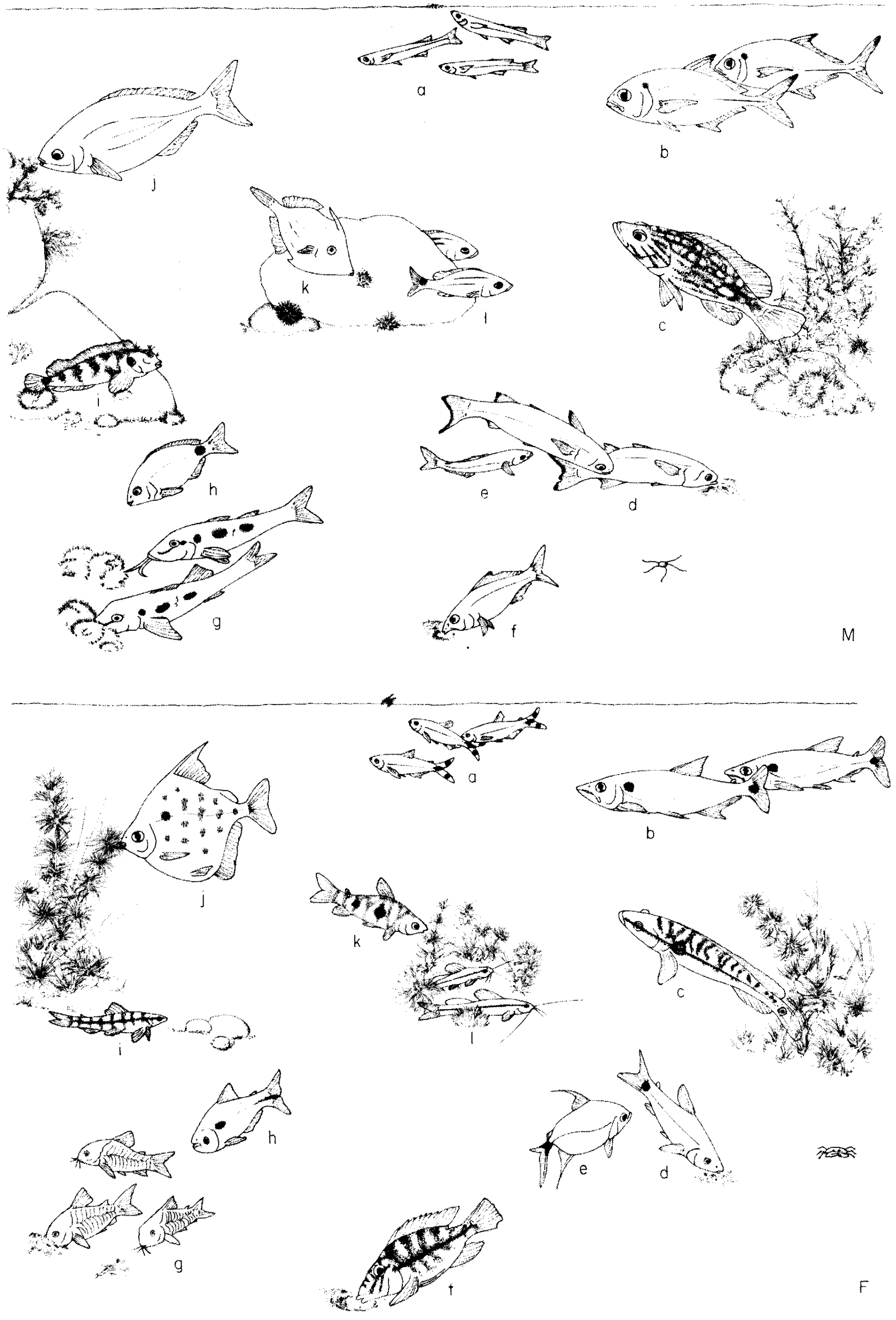
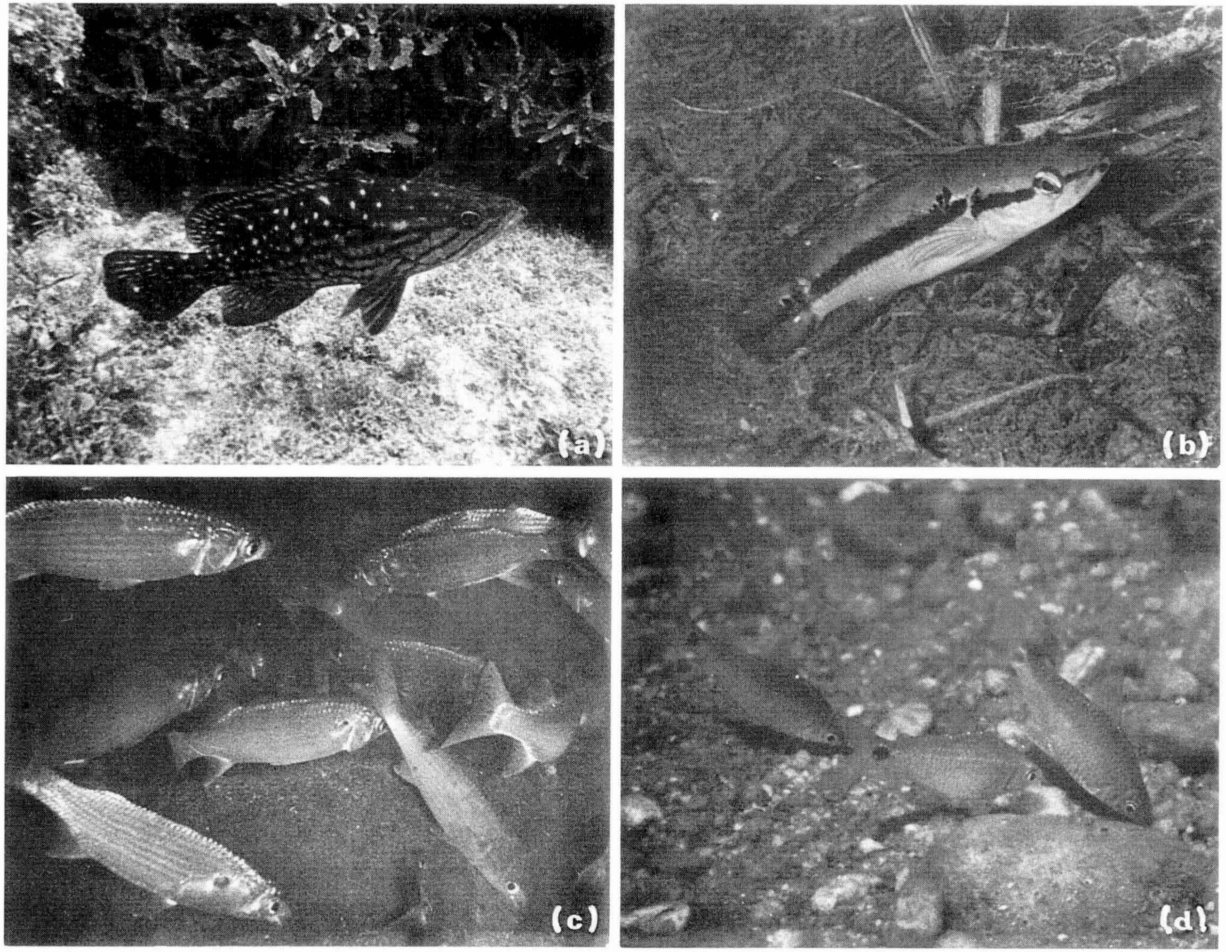


FIG. 1. Similarities of feeding behaviour in 12 pairs of fish species in a marine (M) and a freshwater (F) tropical community. Letters correspond to foraging tactics and fish names in Table I. Not all fishes drawn to scale; see Table I for actual sizes.


(a)
(b)
(c)
(d)

polystictus Regan, 1912 is less mobile and feeds on insect larvae, crustaceans, and microalgae. When feeding, both species of grubbers stir up loose sediment, and this may attract other fish species. *Corydoras* may feed at night.

(h) *Followers* of substrate grubbers are opportunistic species attracted by the feeding activities of other fishes, especially those which disturb the substrate. Following is a part-time habit and, depending on the species, may be frequent or occasional. Followers feed on small bottom animals disturbed or dug out mainly by grubbers. *Diplodus argenteus* (Valenciennes, 1830) feeds on crustaceans, molluscs and polychaetes as well as seaweeds; *Astyanax bimaculatus* (Linnaeus, 1758) ingests insects, crustaceans, plant debris and algae. Both fishes often join schools of other fish species of similar size and swimming behaviour.

(i) *Sit-and-wait predators* are sedentary fishes that ambush prey by staying motionless and dashing at it from close quarters. They periodically change position or waiting place by moving short distances. *Labrisomus nuchipinnis* (Quoy & Gaimard, 1824) preys on crustaceans, molluscs, and polychaetes; *Jobertina lateralis* (Boulenger, 1895) eats insect larvae and crustaceans. The colour pattern of both species may adjust to the surrounding substrate. *Malacoctenus delalandii* Valenciennes, 1836 may well substitute *L. nuchipinnis* over some patches of the reef.

(j) *Browsers* are mid-water fishes that bite off pieces of plants that project above the substrate; both larger plants and epiphytic algae are browsed. *Kyphosus sectatrix* (Linnaeus, 1758) feeds on algae; *Metynnis maculatus* (Kner, 1860) feeds on macrophytes and algae. Both species have specialized, shearing teeth, and may join schools of other plant-eating fish species.

(k) *Nibblers* are opportunistic species that search the substrate to bite at larger items or pick up small items, either animals or plants; they occasionally engage in fin-biting or scale-eating of other fishes, and even scavenge. *Stephanolepis hispidus* (Linnaeus, 1758) feeds on various invertebrates and algae, nips at fins and scales of other fishes, and ingests carrion rarely; *Leporinus lacustris* Campos, 1945 eats insect larvae, crustaceans and molluscs, occasionally feeding on carrion or nipping at fins and scales of other fishes. Both species have but a few sharp projecting incisor-like teeth suited to removing small pieces of food.

(l) *Crepuscular to nocturnal predators* include generalized bottom-dwelling carnivores that search the substrate for small prey. There is occasional diurnal feeding activity near the resting sites. *Haemulon steindachneri* (Jordan & Gilbert, 1882) feeds on a variety of benthic invertebrates; *Pimelodella gracilis* (Valenciennes, 1840) preys on insect larvae and crustaceans, and occasionally scavenges.

Additional examples of feeding behaviour similarities between the Ubatuba reef and the Pantanal pond include the following: the scoopers and substrate pickers *Trachinotus falcatus* (Linnaeus, 1758) (Carangidae) and '*Aequidens*' *vittatus* (Heckel, 1840) (Cichlidae), both of which feed on bottom animals

FIG. 2. Two pairs of fish species showing convergence in appearance, posture, and foraging behaviour. (a) *Mycteroperca rubra*, a stalking predator from the marine reef, and (b) *Crenicichla lepidota*, its counterpart from the freshwater pond; both these fishes change their colour pattern during hunting. (c) *Mugil curema*, a marine microphage or mud-eater, and (d) *Curimata spilura*, its freshwater equivalent; both latter species forage in groups.

and forage in small groups; the solitary, eel-like nocturnal searching predators of fishes and bottom animals, *Gymnothorax ocellatus* Agassiz, 1831 (Muraenidae) and *Gymnotus carapo* Linnaeus, 1758 (Gymnotidae); the nibblers feeding on epiphytic or epilithic algae and sessile animals, *Pomacanthus paru* (Bloch, 1787) (Pomacanthidae) and *Mesonauta festivus* (Heckel, 1840) (Cichlidae). Further examples may be added to some foraging categories, such as *Hyporhamphus unifasciatus* (Ranzani, 1842) (Exocoetidae) and *Triportheus angulatus* (Spix, 1829) (Characidae) among the surface pickers, and *Sphoeroides greeleyi* Gilbert, 1900 (Tetraodontidae) and *Hyphessobrycon callistus* (Boulenger, 1900) (Characidae) among the occasional followers of substrate grubbers.

IV. DISCUSSION

COMPARISONS BETWEEN THE COMMUNITIES

Although marine and freshwater habitats can be regarded as supporting very different communities with floristically and faunistically distinct assemblages, they may share a number of structural and functional features. Both the Ubatuba marine reef and the Pantanal freshwater pond have shallow sunlit waters, soft bottoms, and abundant aquatic vegetation. Cover in the reef is supplied mainly by the boulders and algae whereas in the pond it is provided by submerged plants and irregularities on the bank, such as crannies and holes. A rich invertebrate fauna (arthropods, molluscs) is present in both habitats, although more diversified in the reef, which harbours groups not found in fresh water. Thus, in the two studied communities there apparently are certain common ecological conditions and pressures for the evolution of analogous traits in the behaviour of their largely unrelated fish assemblages; shared selection pressures often result in similar behaviour (cf. Alcock, 1979; Morse, 1980). For example, invertebrates hidden in a soft substrate would exert similar pressures on the fishes exploiting them in each habitat, eventually resulting in their being exploited by a semi-stationary digger with protrusible mouth and a moving grubber with sensitive barbels, in both the marine reef and the freshwater pond. On the other hand, when some of these invertebrates emerge at night, they are preyed on by opportunistic, nocturnal bottom-dwelling carnivores. The soft bottom rich in micro-organisms would favour exploitation by shovel-jawed, scooping mud-eaters, and the rich, diversified vegetation can be cropped by several kinds of browsers and grazers. Small prey fish and invertebrates may be hunted using several distinct techniques, favouring either speed, furtiveness, or immobility. Several of these foraging techniques and many others are described and discussed, for marine fishes, in the impressive works of Hiatt & Strasburg (1960) and Hobson (1968, 1974).

Among the examples here described, the similiarity in feeding behaviour in some instances is very close, whereas it is superficial in others. In the mud-eaters *M. curema* and *C. spilura* the correspondence extends beyond behavioural aspects, their appearance [Fig. 2 (c),(d)] and alimentary apparatus being also very similar; these two species seem to have almost the same feeding role in their communities. The stalkers *M. rubra* and *C. lepidota* [Fig. 2(a),(b)], the diggers *E. argenteus* and *S. pappaterra*, and the grubbers *P. maculatus* and *C. polystictus*, among others, can also be regarded as closely equivalent in their feeding behaviour, their sensory and motor modes of obtaining food appearing to be very similar. At the other extreme, the crepuscular predators *H. steindachneri* and *P. gracilis* have little in common other than their activity periods, grouping habits, and generalized carnivorous diets. Notwithstanding their differences, each of these two species possibly exerts similar pressures on their prey, diurnally resting or nocturnally active invertebrates, and the feeding role of both fishes is certainly closer if regarded from this more restricted, basically functional point of view (Alcock, 1979).

Feeding behaviour similarities were observed in about 30% of the total fish fauna sampled in each community here studied. In both communities the species richness was roughly equivalent, but the marine reef was taxonomically more diverse at higher levels than the freshwater pond: there were 1·9 genera per family in the reef and 3·9 in the pond. Table I shows that in the pond two families alone, Characidae and Cichlidae, had half the foraging modes displayed by six families in the reef. Characiforms and cichlids, together with siluriforms, are dominant freshwater fish groups in South America (Lowe-McConnell, 1975; Fink & Fink, 1979).

ADDITIONAL COMPARISONS BETWEEN THE FISH ASSEMBLAGES

Comparing the fish community structures in various marine and freshwater habitats, Emery (1978) suggested that richness in a given community is related to a number of factors, with no isolated predominant factor, and stressed the relevance of an organic matrix (sessile invertebrates and plants) to explain the structural complexity and richness of a given community. Ehrlich (1975) discussed several characteristics of coral reef fishes, such as schooling, colouration, mimicry, attack strategies, and cleaning behaviour, as relevant to the reef community structure, and Fishelson (1977) suggested that the ability to use various types of food, the social patterns of locating and utilizing food, and the specialization for micro-habitat use promote the high diversity of fish forms on the coral reef environment. Thus, the ways in which the fishes behave should be regarded as an essential part of the community structure itself. Following this reasoning, further comparisons may be made between the Ubatuba marine reef and the Pantanal freshwater pond, to point out additional similarities. For example, Ehrlich (1975) noted that limitations of space in marine reefs are increased by intra- and interspecific territoriality. In the Ubatuba reef, territorial behaviour associated with feeding areas was observed mainly for the pomacentrids *Stegastes* cf. *fuscus* (Cuvier, 1830) and *S. variabilis* (Castelnau, 1855), and the serranids *Mycteroperca rubra* and *Epinephelus guaza* (Linnaeus, 1758). In the Pantanal pond, intraspecific territorial behaviour during feeding activities was observed for the characiforms *Catoprion mento* and *Curimata spilura*, and territoriality was also observed in the cichlids *Crenicichla lepidota* and *'Aequidens' vittatus*. Interspecific foraging groups, a common feature in marine reefs (Hiatt & Strasburg, 1960; Hobson, 1974; Ehrlich, 1975; Fishelson, 1977), and commonly observed in the Ubatuba reef, were also found in the Pantanal pond, where they may be composed of mud-eating curimatids only, *C. spilura* and *C. nitens* Holmberg, 1891, by similar-looking cichlids *Satanoperca pappaterra* and *' A.' vittatus,* or by mixed associations of moving grubbers, their followers, and some opportunistic stalking predators such as *Crenicichla lepidota.*

Readiness to converge on the feeding movements of other species, especially on new sources of food, was pointed out for reef fishes by Fishelson (1977), and was noted for several small species of carnivores and omnivores in the Ubatuba reef. This tendency was observed also in the Pantanal pond, where the small opportunistic characids *Astyanax bimaculatus* and *Moenkhausia intermedia* were often the first to find and use new food. Their activity around the food attracted larger characiforms, such as the omnivore *Leporinus lacustris*, the predatory and scavenging piranha, *Serrasalmus spilopleura* Kner, 1860, and as the scale-eater *Catoprion mento,* the latter two feeding mainly on fins and scales of the aggregated fishes. The piscivores *Acestrorhynchus altus* and *Crenicichla lepidota* were also attracted to these groupings and fed on smaller fishes. I do not consider here the influence that piscivorous fishes exert on the feeding patterns of potential prey fish—an important behavioural constraint in both communities.

MISSING EXAMPLES, AND REMARKS

Some outstanding behavioural features of the fishes of marine reefs were missing in the Pantanal pond fishes and vice-versa. For example, cleaning behaviour, a prominent characteristic among tropical marine reef fishes (Ehrlich, 1975; Losey, 1978) was demonstrated by young pomacentrid *Abudefduf saxatilis* (Linnaeus, 1758) and young sparid *Diplodus argenteus* in the Ubatuba reef but was not observed in the Pantanal pond (nevertheless, small characids, mainly *M. intermedia* and *A. bimaculatus*, frequently nipped at my neck and legs, pulling hairs and picking out particles adhering to the skin). Schooling planktivores, found everywhere in marine reefs and represented by the clupeid *Harengula clupeola* (Cuvier, 1829) in the Ubatuba reef, were notably absent in the Pantanal pond. On the other hand, group-living, mutilating predators and scavengers such as the piranhas *Serrasalmus spilopleura* and *S. nattereri* (Kner, 1860), a very important component of the Pantanal communities, have no obvious counterparts in the marine reef. The above-mentioned behavioural modes may be lacking in one or the other community because of the absence of a fish able to perform a particular behaviour, because the role is already occupied by an organism other than a fish, or simply because a particular community does not permit such a role. This latter conjecture seems to apply to the case of parrotfishes (Scaridae) that graze on algae and corals and are important in converting parts of the reef into soft sediments (Hiatt & Strasburg, 1960; Randall, 1965; 1968; Ehrlich, 1975; Fishelson, 1977). Clearly, with the absence of coral there is no place for such a foraging mode in freshwater communities. Armoured catfishes (Loricariidae) were the most important algal grazers in the Pantanal pond. The apparent absence in tropical freshwater communities of complex symbiotic and commensal relationships between fishes and invertebrates, characteristic of tropical marine communities, has been commented upon elsewhere (Roberts, 1972).

Mimicry occurs among several marine reef fishes (Ehrlich, 1975; Russell *et al.*, 1976; Ormond, 1980). I was unable to detect any obvious case of mimicry among the fishes in the freshwater pond community. However, some similarities in appearance may not be entirely fortuitous, e.g., the cichlid pair *Satanoperca pappaterra* and '*Aequidens*' *vittatus* which often school together, and the minute, armoured, callichthyid catfish *Corydoras hastatus* Eigenmann & Eigenmann, 1888 that closely resembles and schools with several small characid species. Also included here may be the curimatid *Curimata nitens* which bears some resemblance to the spiny and venomous catfish *Pimelodella gracilis* (these two species are bottom-dwelling fishes whose groups often mix together). However, mimicry among tropical freshwater fishes has been reported (Trewavas, 1947; Lowe-McConnell, 1975; Sazima, 1977; Brichard, 1978) and may eventually be found in the rich and complex Pantanal ponds.

In an underwater study of the twilight activities of fishes in a temperate lake, Helfman (1981) found a pattern of behavioural events surprisingly similar to those described for marine reef fishes (Collette & Talbot, 1972; Hobson, 1972; Domm & Domm, 1973). The present study showed similarities of feeding behaviour patterns between fishes in a marine and a freshwater tropical habitat. This correspondence probably reflects structural and functional ecological properties shared by the two communities and the ability of different, mostly unrelated fish assemblages to evolve towards similar behavioural and structural organization when faced with similar situations and constraints. I expect that additional similarities will be found for several other aspects of fish behaviour and ecology in marine and freshwater habitats once more complete data become available, especially on tropical communities rich in species and with complex interspecific interactions (Roberts, 1972; Ehrlich, 1975; Lowe-McConnell, 1975; Robinson, 1978; Gladfelter *et al.*, 1980; Goulding, 1980; Sale, 1980).

In several tropical countries many freshwater habitats are currently under serious threat due to man-made alterations (Balon, 1978; Goulding, 1980; Lelek, 1983). Hopefully, the present study on underwater natural history will stimulate further interest and research on tropical freshwater, as well as marine, fish assemblages.

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References

Alcock, J. (1979). *Animal Behavior: an Evolutionary Approach*, 2nd edn. Sunderland: Sinauer Associates.

Balon, E. K. (1978). Kariba: the dubious benefits of large dams. *Ambio* **7,** 40–48.

Barlow, G. W. (1974). Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Am. Zool.* **14,** 9–34.

Brichard, P. (1978). *Fishes of Lake Tanganyika.* Neptune City: TFH Publications.

Collette, B. B. & Talbot, F. H. (1972). Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. In *Results of the Tektite Program: Ecology of Coral Reef Fishes.* (B. B. Collette & S. A. Earle, eds), pp. 98–124. *Los Angeles County Nat. Hist. Mus. Sci. Bull.* **14.**

Domm, S. B. & Domm, A. J. (1973). The sequence of appearance at dawn and disappearance at dusk of some coral reef fishes. *Pacific Sci.* **27,** 128–135.

Ehrlich, P. R. (1975). The population biology of coral reef fishes. *Ann. Rev. Ecol. Systemat.* **6,** 211–247.

Emery, A. R. (1978). The basis of fish community structure: marine and freshwater comparisons. *Environm. Biol. Fishes* **1,** 33–47.

Fink, W. L. & Fink, S. V. (1979). Central Amazonia and its fishes. *Comp. Biochem. Physiol.* **62A,** 13–29.

Fishelson, L. (1977). Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Elat (= Gulf of 'Aqaba), Red Sea. *Israel J. Zool.* **26,** 114–134.

Fryer, G. & Iles, T. D. (1972). *The Cichlid Fishes of the Great Lakes of Africa, their Biology and Evolution.* Neptune City: TFH Publications.

Géry, J. (1969). The freshwater fishes of South America. *Biogeography and Ecology in South America.* Vol. 2 (E. J. Fittkau, J. Iles, H. Klinge, G. H. Schwabe & H. Sioli, eds), pp. 828–848. The Hague: Dr. W. Junk Publishers.

Gladfelter, W. B., Ogden, J. C. & Gladfelter, E. H. (1980). Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology* **61,** 1156–1168.

Goldman, B. & Talbot, F. H. (1976). Aspects of the ecology of reef fishes. In *Biology and Geology of Coral Reefs,* Vol. 3, *Biology 2* (O. A. Jones & R. Endean, eds), pp. 125–154. New York: Academic Press.

Goulding, M. (1980). *The Fishes and the Forest: Explorations in Amazonian Natural History.* Berkeley: University of California Press.

Helfman, G. S. (1981). Twilight activities and temporal structure in a freshwater fish community. *Can. J. Fish. Aquat. Sci.* **38,** 1405–1420.

Hiatt, R. W. & Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* **30,** 65–127.

Hobson, E. S. (1968). Predatory behavior of some shore fishes in the Gulf of California. *U.S. Fish Wildl. Serv. Res. Rep.* **73,** 1–92.

Hobson, E. S. (1972). Activity of Hawaiian reef fishes during evening and morning transitions between daylight and darkness. *Fish. Bull.* **70,** 715–740.

Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.* **72,** 915–1031.

Knöppel, H. A. (1970). Food on central Amazonian fishes. Contribution to the nutrient-ecology of Amazonian rain-forest streams. *Amazoniana* **2,** 257–352.

Kocher, T. D. & McKaye, K. R. (1983). Defense of heterospecific cichlids by *Cyrtocara moorii* in Lake Malawi, Africa. *Copeia* **1983,** 544–547.

Lelek, A. (1983). Ökologische Aspekte der Stauung eines Flusses auf Borneo. *Natur und Museum* **113,** 321–332.

Losey, Jr. G. S. (1978). The symbiotic behavior of fishes. In *The Behavior of Fish and Other Aquatic Animals* (D. I. Mostofsky, ed.), pp. 1–31. New York: Academic Press.

Lowe-McConnell, R. H. (1975). *Fish Communities in Tropical Freshwaters.* London: Longman.

McKaye, K. R. (1977). Competition for breeding sites between the cichlid fishes of Lake Jiloá, Nicaragua. *Ecol.* **58,** 291–302.

Morse, D. H. (1980). *Behavioral Mechanisms in Ecology.* Cambridge: Harvard University Press.

Ormond, R. F. G. (1980). Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. *J. Zool., Lond.* **191,** 247–262.

Potts, G. W. (1973). The ethology of *Labroides dimidiatus* (Cuv. & Val.) (Labridae, Pisces) on Aldabra. *Animal Behav.* **21,** 250–291.

Randall, J. E. (1965). Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* **46,** 255–260.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Stud. Tropical Oceanogr.* **5,** 665–847.

Randall, J. E. (1968). *Caribbean Reef Fishes.* Neptune City: TFH Publications.

Roberts, T. R. (1972). Ecology of fishes in the Amazon and Congo basins. *Bull. Mus. Comp. Zool.* **143,** 117–147.

Robinson, M. H. (1978). Is tropical biology real? *Tropical Ecol.* **19,** 30–50.

Russell, B. C., Allen, G. R. & Lubbock, H. R. (1976). New cases of mimicry in marine fishes. *J. Zool., Lond.* **180,** 407–423.

Sale, P. F. (1980). The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.* **18,** 367–421.

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

Sazima, I. (1977). Possible case of aggressive mimicry in a neotropical scale-eating fish. *Nature, Lond.* **270,** 510–512.

Sazima, I. (1983). Scale-eating in characoids and other fishes. *Environm. Biol. Fishes* **9,** 87–101.

Trewavas, E. (1947). An example of ' mimicry ' in fishes. *Nature, Lond.* **160,** 120.

NOTE ADDED IN PROOF—A small group of five individuals of the cichlid *Chaetobranchopsis australis* Eigenmann & Ward, 1907 was observed feeding on planktonic organisms, in another deeper (2–3 m) and larger pond in another site of the Pantanal, in April 1986. This would add a ' schooling ' planktivore to the Pantanal freshwater communities as well, although not strictly comparable to the clupeid *Harengula clupeola* in the Ubatuba marine reef (mainly because of the school size of the latter species: 30–200 individuals, or even more).