Mar. Freshwater Res., 1996, **47**, 563–73

Species Richness and Geographical Variation in Assemblage Structure of the Freshwater Fish Fauna of the Wet Tropics Region of Northern Queensland

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Abstract. A field survey of the freshwater piscifauna of the Wet Tropics region of northern Queensland was undertaken in August, September and October 1993. Sixty-six species of fishes, only two of which were exotic, were collected during the study, and reference to a further 12 species was found in the literature. The region contains two-thirds of the continent's fish genera and 40% of species. If the comparison is restricted to only those genera and species found in northern Australia, then the proportions increase to 80% and 55% respectively. Several species not previously recorded from Australia and one undescribed species from the family Percichthyidae, were collected. Ordination of the data set revealed a strong latitudinal gradient in assemblage structure, with the Bloomfield River and streams of the Cape Tribulation area and the Cardwell area containing the most distinctive faunas. The remaining seven drainages formed a homogenous group with little inter-basin separation, probably because they share similar hydrologies, water quality and contain a similar array of habitats. Discontinuities in river profile had a marked effect on assemblage structure.

Introduction

The Wet Tropics region of northern Queensland contains the largest continuous area of rainforests in Australia (Tracey 1982) and is recognized as being a centre of both diversity and endemism for plants (Tracey and Webb 1975), invertebrates (Bishop 1981; Kitching 1981; Main 1981) and most terrestrial vertebrate groups except lizards (Pianka and Schall 1981; Winter 1988). The region similarly contains a high number of aquatic invertebrate taxa (Pearson *et al.* 1986). There are comparatively few data concerning the distributional patterns and diversity of the region's piscifauna, although recent studies have examined fish assemblages in individual catchments within the Wet Tropics region. For example, Hortle and Pearson (1990) conducted a survey of the Annan River and its tributaries and related some variation in fish species distribution to environmental conditions and the effects of tin mining. Russell and Hales (1993) investigated the distribution of both estuarine and freshwater fish in the Johnstone River catchment as part of the Johnstone River Integrated Catchment Management Pilot Study. Pusey *et al.* (1995) reported that the piscifauna of the Mulgrave River was speciose considering the small size of the river. The high species diversity recorded in each of these rivers suggests that the entire region should also contain a rich fish fauna.

The aim of the present study was to document the biodiversity of the region's freshwater piscifauna, to define any between-river within-region differences in assemblage composition and to suggest those factors likely to be responsible for any observed patterns in assemblage structure within the constraint of the narrow 'temporal window' within which the study was undertaken (3 months). Throughout this report we refer to the Wet Tropics region in its broadest sense (Cooktown to Cardwell) and not just the area contained within the Wet Tropics World Heritage Area.

Methods

Site Location

Freshwater fish assemblages were sampled once during August–October 1993 at each of 92 sites within all the major drainage basins of the Wet Tropics regions with the exception of the Herbert and Johnstone rivers (Fig. 1). Site selection was constrained by accessibility, particularly in the Daintree River. Most of the sampling sites (65 of 92) were in streams or river reaches surrounded by riparian rainforest. Streams of the Cardwell area were surrounded by open dry sclerophyll woodland. Forty-nine of the sites were outside the boundaries of the Wet Tropics World Heritage Area and, of these, 40 were surrounded by freehold or leasehold land. Most of this freehold/leasehold land was still forested, however, with non-forested land being dominated by sugarcane and pasture production (13 and 8 sites respectively). Eleven lentic habitats were sampled during the survey and ranged from roadside impoundments of seepages, oxbow lakes and large swamps to floodplain lagoons. The remaining sites were located on streams and rivers. Most of the lotic sites (69 of 81) were on streams of Order 4 or more. None of the rivers studied here was greater than Order 7. In general, good coverage of the range of stream orders within the study area was achieved with the exception of first- and second-order tributary or headwater streams.

Most sites (97%) were of low conductivity (< 200 $\mu S\ cm^{-1}$) and acidic (84% of sites with a pH between 5·5 and 7·0), with water temperatures between 20° and 26°C (85%) and very high water clarity (Pusey and Kennard, unpublished data).

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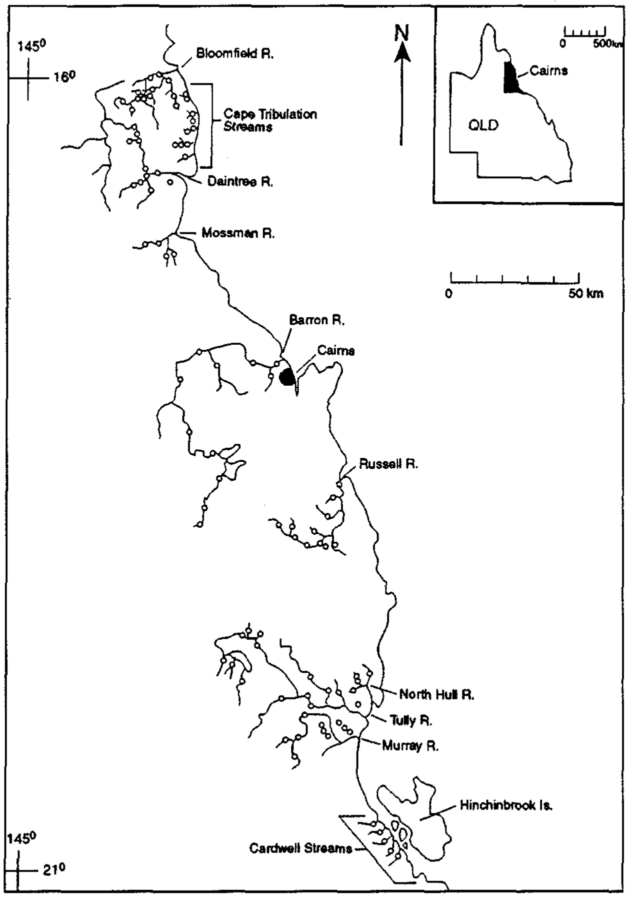

Fig. 1. Location of the 92 study sites within the 10 major and minor drainage basins of the Wet Tropics region included in the study. Major rivers not included in the study (the Mulgrave and the North and South Johnstone rivers) are not shown.

Sampling Methodology

Single-pass backpack electrofishing (Smith Root Model 12 POW), the principal collecting technique, was employed at each site for about 60 min along 200–400 m of stream following the procedure outlined in Pusey *et al.* (1993). Single-pass electrofishing is an effective technique for estimating species richness in a variety of habitat types (Pusey and Kennard, unpublished information) and is therefore well suited to studies devoted to determining patterns of diversity over large areas. However, it is less effective in deep water (> 1.5 m) and on fast-moving fishes that inhabit open water. In deep-water areas or areas that sustain populations of estuarine crocodiles, electrofishing was undertaken from an aluminium dinghy (four lotic and four lentic sites).

Supplementary sampling included seine-netting, gill-netting, underwater snorkelling and line-fishing. Seine-netting, usually five hauls of a 50-m or 10-m seine (10-mm stretched mesh), was employed at 26 sites. Gill-netting was infrequently used (two occasions). Each net was made up of three 10-m long, 3-m deep panels of 5, 7·5 and 10 cm stretched mesh and was set for 2 h immediately after sundown. Seine-netting revealed no additional species not already collected by electrofishing. Gill-netting and line-fishing each revealed one additional species not detected by electrofishing at that particular site. Underwater observations twice detected species additional to those detected by electrofishing at a particular site. Of all the species collected during this study, only one (*Nibea* sp. collected by line fishing) was not also collected by electrofishing.

Identification of Fish Species

Most fishes were identified to species level at the time of capture and released immediately. The remainder were anaesthetized (MS-222, Sandoz Pty Ltd), fixed (4% formaldehyde) and preserved in 70% alcohol and identified with the aid of published keys (Allen and Cross 1982; Allen 1989, 1991; Allen and Burgess 1993). Any fish not covered in the above keys or of still dubious identity was sent to the relevant taxonomic authority for identification.

Quantification of Habitat

Habitat structure at each site was quantified by estimating the proportional contribution of waterfalls, cascades, rapids, riffles, glides, runs, pools, backwaters and deep pools to the area sampled (see Pusey *et al.* 1995). Stream width, average water velocity and depth, maximum water velocity and depth and the proportional contribution of each substratum type [mud (particle size < 1 mm), sand (1–16 mm), fine gravel (17–32 mm), gravel (33–64 mm), cobbles (65–128 mm), boulders (129–512 mm) and bedrock] were estimated for each site. Cover elements (macrophytes, leaf litter, submerged vegetation, emergent vegetation, overhanging vegetation, filamentous algae, large woody debris (trunk diameter > 20 cm), small woody debri (trunk diameter < 20 cm), undercut banks and exposed root masses) were quantified by ranking on a scale of 0 to 4 corresponding to absent, uncommon, common, abundant and very abundant respectively. Riparian cover (the proportional amount of stream surface area directly covered by riparian vegetation) was estimated by eye. Catchment-related parameters (stream order, elevation, stream gradient, catchment area, distance from source, distance to river mouth and distance to confluence with first stream of a higher order) were estimated in the laboratory by reference to published maps of the area (1:50000 and 1:100000). The presence of barriers to upstream movement by fish was assessed by reference to plots of river profiles (elevation versus distance from source) (Pusey and Kennard, unpublished data).

Data Analysis—Species Richness and Catchment Area

The total species richness for each drainage basin was estimated from data collected by all sampling methods and regressed against catchment area (after log transformation). Individual streams of the Cape Tribulation and Cardwell areas were included in the regression as discrete entities.

Data Analysis—Ordination

Detrended correspondence analysis (DECORANA, Hill 1979) was used to examine spatial variation in composition of the piscifauna as determined by electrofishing only. Analyses were performed on the abundances of each species at each site. No transformations were used except that the downweighting procedure available within DECORANA was used to reduce the influence of rare species. Rare species are a persistent and frequent feature of natural communities, including fish communities (Sheldon 1987), and their inclusion in some analyses may obscure patterns of the distributions of species or the composition of assemblages (Gauch 1982). Eighteen species (all those represented by two specimens or fewer) received a weighting of less than 0·5. Exploratory analysis revealed that assemblages present at lentic sites and Site 61 (which contained only one, ordinarily rare, species, *Cairnsichthys rhombosomoides*) were substantially different from most remaining lotic sites and consequently obscured differences between the remaining sites. These outliers were therefore excluded from the analyses presented here (i.e. analyses were performed on the remaining 80 sites). In the second analysis presented here, all sites above barriers to fish movement (profile discontinuities) were excluded.

Data Analysis—Relationships between Fish Assemblages and Physical and Geographic Factors

Regression analyses were used to detect significant linear associations between ordination axes scores (axes 1, 2 and 3) and habitat and catchment related variables. To reduce the chance of Type I errors, a conservative significance level was used in multiple comparisons (i.e. $P = 0.05$ divided by the number of variables considered).

Results

Fish Species Richness and Abundance

In total, 7325 fish from 66 species were collected (Table 1). Only two species were exotic: *Oreochromis mossambica* (Tilapia) and *Poecilia reticulata* (Guppy). The former was restricted to one site within a single drainage basin (Freshwater Creek, Barron River) and the latter was recorded from three sites in two drainage basins (Mossman River and Murray River). The most speciose families recorded from the Wet Tropics region were the Gobiidae and the Eleotridae, each represented by 12 species. Chandidae was the next most speciose, with six species. Thus, almost 50% of the fish biodiversity recorded during this survey was contained within only three families.

The collections were numerically dominated by relatively few species. For example, *Melanotaenia splendida splendida, Pseudomugil signifer, Hypseleotris compressa* and *Anguilla reinhardtii* collectively represent 65% of the total number of fish collected. The six next most abundant fish contribute only a further 18% of the total. Clearly, the fauna contains many numerically uncommon species. The numerically abundant species had widespread distributions within Queensland and were also widely distributed within the study area. The four species listed above occurred in 61 ± 4 (s.e.) of the 92 sites and the 10 most common species occurred, on average, in 40 ± 6 sites. Three species (*P. signifer, H. compressa* and *A. reinhardtii*) occurred in all 10 drainage basins, whereas *M. s. splendida* was absent from streams of the Cape Tribulation area.

A significant positive relationship between catchment area (log transformed) and species richness was detected and best described by the following relationship: species richness = 9·26(area) − 1·17, $r = 0{\cdot}95$, $n = 20$, $P < 0{\cdot}001$. (Fig. 2).

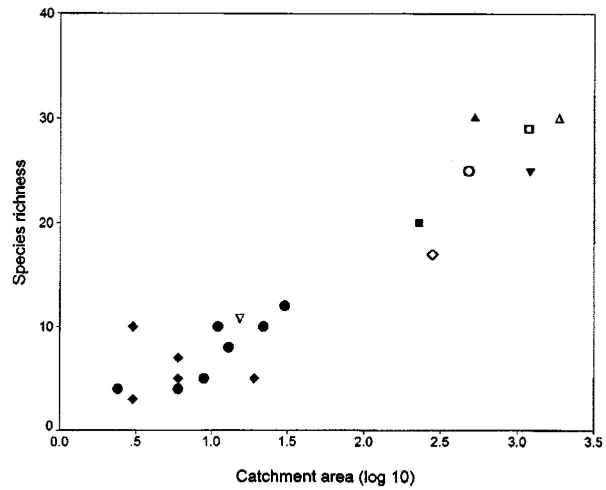

Fig. 2. The relationship between catchment area (km^2, log transformed) and fish species richness. Drainage basins are distinguished by the following symbols: ○, Bloomfield River; ●, Cape Tribulation area; □, Daintree River; ■, Mossman River; △, Barron River; ▲, Russell River; ▽, North Hull River; ▼, Tully River; ◇, Murray River; ◆, Cardwell area.

Fish Assemblage Structure

Discontinuities in stream profile had a strong effect on the presence and abundance of many species. In the ordination of fish species abundances from the 80 lotic sites (total eigenvalue 1.568, of which Axes 1, 2 and 3 explained 38%, 29% and 18% of the total variation respectively), sites upstream of profile discontinuities were clearly separated from the remaining sites, being arrayed to the far right on Axis 1 (Fig. 3). The relatively depauperate streams of the Cardwell area also clustered with this group. This group of sites was dominated by *M. s. splendida* and *Mogurnda adspersa*, both of which were arrayed to the right in the equivalent species ordination space (Fig. 3). Sites upstream of barriers also contained *A. reinhardtii*, but this species was common and widely distributed within and between rivers of the Wet Tropics region. Axis 1 scores were positively correlated with distance from the river mouth and elevation, and were negatively correlated with average and maximum water velocity and the proportional contribution of cobble and gravel (Table 2). Sites above barriers tended to be high in the catchment and distant from the coast. Surprisingly, they tended to be dominated by pools with little current and a bedrock substratum. The Bloomfield River and streams of the Cape Tribulation area were faunistically different from most other rivers (Fig. 3). Differences between the remaining rivers (gauged by the degree of separation in ordination space) were not well defined, suggesting a relatively homogeneous distribution of fish species. Streams of Cape Tribulation and the lower Bloomfield River, which were close to the coast, had higher current velocities and a cobble–gravel substrate. Fishes characteristic of these sites were often estuarine forms (Fig. 3, Table 1).

Little separation of river drainages was evident on Axis 2, except that the Cape Tribulation streams and the Bloomfield River sites segregated from other drainages on this axis also. Sites located low on Axis 2 tended to have a higher average flow and more of the substratum characterized by cobbles (Table 2). Sites located higher on Axis 2 had lower gradients, slower water velocities, finer substrata and a greater abundance of macrophytes. A significant north–south cline in assemblage structure was suggested by the correlations between Axis 2 scores and latitude (Table 2). The correlation with longitude arises because the coastline does not have a north–south orientation (Fig. 1). The gudgeons, *Eleotris fusca*, *E. melanosoma* and

Table 1. Fish species recorded from the Wet Tropics region, their habitat preference[A], distribution[B], frequency of incidence (sites and basins)[C] and abundance

Species	Habitat	Distribution	New record[D]	Incidence Sites	Incidence Basins	Number collected
Gobiidae (Gobies)						
Glossogobius celebius (Valenciennes)	F	W.Pac		31	7	148
G. giurus (Hamilton)	F	Indo W.Pac		2	1	5
G. biocellatus (Valenciennes)	F/E	PNG, NT		2	1	4
G. bicirrhosis (Weber)	F/E	PNG, NT		1	1	1
Glossogobius sp. B.	F	FNQ		1	1	30
Redigobius bikolanus (Herre)	F/E	Trop-Pac		16	6	53
R. chrysosoma (Bleeker)	F/E	Trop-Pac		1	1	1
Awaous crassilabrus (Günther)	F	FNQ, ?W.Pac		17	7	33
Sicyopterus sp. (cf. *macrostetholepis*)	F	?Indonesia, PNG	*	1	1	3
Schismatogobius sp.	F	FNQ		5	3	30
Mugilogobius (cf. *stigmaticus*)	F/E	NT, ?		1	1	8
M. notospilus DeVis	F/E	NT, ?		1	1	1
Eleotridae (Gudgeons)						
Eleotris fusca (Bloch & Schneider)	F/E	E.Afr, W.Pac		13	7	44
E. melanosoma Bleeker	F/E	E.Afr, Pac		4	4	15
Oxyeleotris gyrinoides (Bleeker)	F	SEA, PNG, N.Aust 17		6		54
O. lineolatus (Steindachner)	F	PNG, N.Aust		1	1	1
Oxyeleotris sp. (cf. *aruensis*)	F	FNQ	*	4	2	12
O. fimbriata (Weber)	F	PNG, CYP, FNQ		–[E]	–	
O. aruensis (Weber)	F	PNG, CYP		–	–	
O. nullipora Roberts	F	PNG, CYP		–	–	
Butis butis (Hamilton)	F/E	PNG, N.Aust		1	1	1
Ophiocara porocephala (Valenciennes)	F/E	E.Afr, W.Pac		1	1	1
Ophieleotris aporos (Bleeker)	F	E.Afr, Melan, N.Aust		23	8	103
Hypseleotris compressa (Krefft)	F	PNG, N.Aust		59	9	789
Hypseleotris sp. A.	F	MDB, S.E.Qld		3	2	31
Mogurnda adspersa (Castelnau)	F	MDB, NSW, Qld		29	7	278
M. mogurnda (Richardson)	F	PNG, N.Aust, CYP, FNQ		1	1	3
Chandidae (Glass perchlets)						
Ambassis agrammus Günther	F	PNG, NT, CYP		18	5	213
A. interruptus Bleeker	F/E	SEA, PNG, N.Aust		6	4	101
A. mulleri Klunzinger	F	N.WA, NT, CYP, LEB		1	1	2
A. miops Günther	F	Indo-Pac, PNG, FNQ		6	4	14
A. agassizii Steindachner	F	SA, VIC, NSW, MDB, Qld		1	1	4
Denariusa bandata Whitley	F	PNG, NT, FNQ		1	1	11
Terapontidae						
Hephaestus fuliginosus (Macleay)	F	PNG, N.Aust		24	5	259
Leiopotherapon unicolor (Günther)	F	N. Aust		6	1	18
Mesopristes argenteus (Cuvier)	F/E	W.Pac, PNG, CYP		1	1	1
Amniataba percoides Günther	F	N.Aust		–	–	
Hephaestus sp. (Tully Grunter)	F	FNQ		–	–	
Melanotaeniidae (Rainbowfishes)						
Melanotaenia splendida splendida (Peters)	F	East Qld		62	9	2090
M. maccullochi Ogilby	F	PNG, CYP, FNQ		2	1	7
M. trifasciata (Rendahl)	F	PNG, CYP		–	–	
Cairnsichthys rhombosomoides (Nichols & Raven)	F	FNQ		3	2	84
Plotosidae (catfishes)						
Neosilurus ater (Perugia)	F	PNG, N.Aust		11	4	58
N. hyrtlii Steindachner	F	N.Aust.		1	1	1
Porochilus rendahli (Whitley)	F	NT, CYP		8	2	13
Tandanus tandanus Mitchell	F	MDB, E.Aust		33	7	194
Anguillidae (Eels)						
Anguilla reinhardtii Steindachner	F	PNG, E.Aust		72	10	450
A. obscura Günther	F	S.Pac, PNG, Qld		9	3	18
A. megastoma Kaup	F	W.Pac, PNG	*	1	1	1
Synbranchidae (Swamp eels)						
Monopterus albus Zuiew	F	Asia, SEA, Qld		3	2	3
Ophisternon bengalense McClelland	F/E	Asia, SEA, PNG	*	2	1	2

Table 1. *continued*

Species	Habitat	Distribution	New record[D]	Incidence Sites	Basins	Number collected
O. gutterale (Richardson)	F	PNG, NT, CYP		–	–	
Pseudomugilidae (Blue eyes)						
Pseudomugil signifer Kner	F	E.Aust		52	10	1464
P. gertrudae Weber	F	PNG, N.Aust		4	3	7
Apogonidae (Cardinalfishes)						
Glossamia aprion (Richardson)	F	PNG, N.Aust		25	5	89
Apogon hyalosoma Bleeker	F/E	E.Afr, PNG, N.Aust		1	1	3
Kuhliidae (Flagtails or Jungle Perches)						
Kuhlia rupestris (Lacépède)	F	Indo-Pac		34	9	154
K. marginata (Cuvier)	F	SEA, PNG	*	1	1	1
Atherinidae (Hardyheads)						
Craterocephalus stercusmuscarum (Günther)	F	NT, CYP, E.Aust		21	4	190
Percichthyidae (Perches)						
Unnamed species	F	Bloomfield River	*	2	1	13
Scorpaenidae (Scorpionfish)						
Notesthes robusta (Günther)	F	E. Aust		23	6	62
Centropomidae (Giant Perches)						
Lates calcarifer (Bloch)	F/E	Asia, SEA, PNG, N.Aust		8	3	21
Lutjanidae (Snappers)						
Lutjanus argentimaculatus (Forskål)	F/E	Indo-Pac		11	7	16
Toxotidae (Archerfishes)						
Toxotes chatareus (Hamilton)	F/E	India, SEA, PNG, N.Aust		2	1	5
Clupeidae (Herrings)						
Nematalosa erebi (Günther)	F	MDB, N. Aust		4	3	6
Gerriidae (Silver Biddies)						
Gerres filamentosus (Cuvier)	F/E	Indo-W.Pac, Aust		6	5	6
Scatophagidae (Scats)						
Scatophagus argus (Linnaeus)	F/E	India, SEA, PNG, N.Aust		1	1	1
Hemiramphidae (Halfbeaks)						
Arramphus sclerolepis (Günther)	F/E	PNG, N.Aust		1	1	1
Tetradontidae (Toadfishes)						
Marilyna meraukensis (de Beaufort)	E	PNG, N.Aust		1	1	1
Sciaenidae (Croakers)						
Nibea sp.	E	SEA, PNG, N.Aust		1	1	1
Mugilidae (Mullet)						
Mugil cephalus Linnaeus	E/F	Worldwide		1	1	1
Soleidae (Soles)						
Brachirus selheimi (Macleay)	F	NT, CYP, FNQ		–	–	
Ariidae						
Arius graeffei Kner & Steindachner	F/E	PNG, N.Aust		–	–	
Belonidae (Long Tom)						
Strongylura kreffti Günther	F/E	PNG, N.Aust		–	–	
Megalopidae (Tarpon)						
Megalops cyprinoides (Broussonet)	F/E	Indo W Pac, N.Aust		–	–	
Monodactylidae (Moonfishes)						
Monodactylus argenteus (Linnaeus)	F/E	Indo W Pac		–	–	
Cichlidae (Cichlids)						
Oreochromis mossambicus (Peters)	F/E	exotic		1	1	1
Poeciliidae (Topminnows)						
Poecilia reticulata Peters	F	exotic		2	1	15

[A]E, estuarine; F, freshwater.
[B]Defined by information in Allen (1991), Allen (1989), Allen and Burgess (1990), Allen and Cross (1982), Wager (1993), Pusey *et al.* (1995), Herbert *et al.* (1995), H. Larson (personal communication). FNQ, far northern Queensland; CYP, Cape York Peninsula; NWA, northern Western Australia; MDB, Murray Darling Basin; LEB, Lake Eyre Basin; PNG, Papua New Guinea; Melan., Melanesia; E.Afr., eastern Africa including Madagasgar; SEA, South East Asia; Trop Pac, tropical Pacific; W.Pac, west Pacific; Indo-W.Pac, Indo west Pacific. Commonly used abbreviations of Australian mainland states are used.
[C]Frequency of incidence refers to the number of sites or drainage basins in which a particular species was recorded.
[D]An asterisk denotes that no published reference to a species' presence in Australian inland waters could be found.
[E]Denotes that reference to a species presence in the Wet Tropics region occurred in the literature listed above but that it was not recorded in the present study.

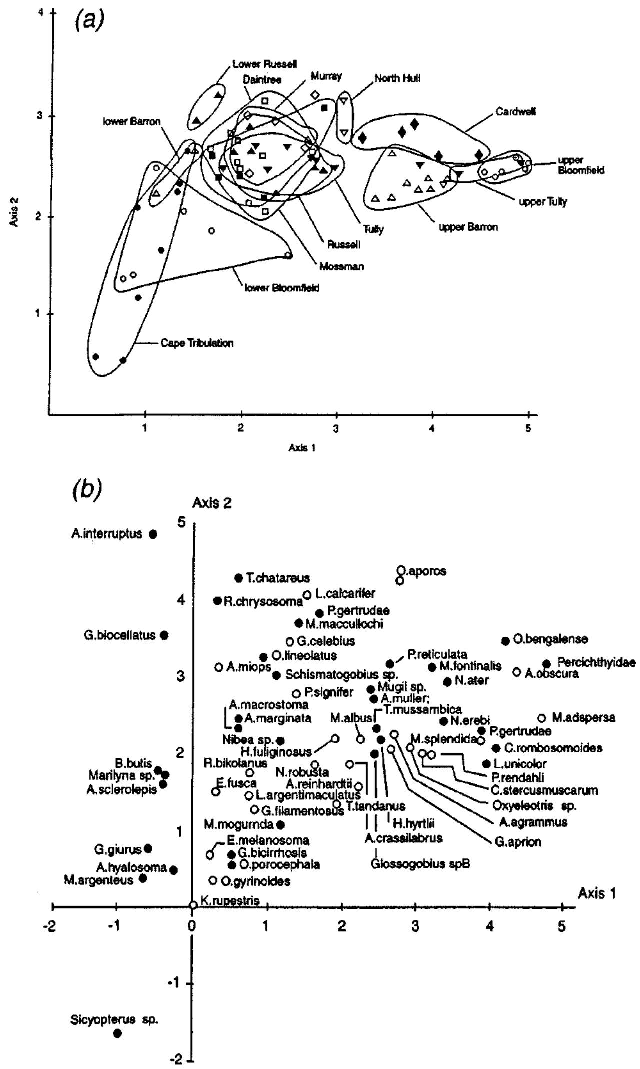

Fig. 3. The distribution of study sites in ordination space as defined by DECORANA Axes 1 and 2 of an ordination of weighted species abundance data from only lotic sites. *(a)* Drainage basins are distinguished by the same symbols as in Fig. 2. *(b)* The distribution of species within the equivalent ordination space. Species for which the weighting factor was above 0.5 are shown by ○.

Oxyeleotris gyrinoides, were distributed low on Axis 2 in the equivalent ordination space (Fig. 3). Other estuarine species such as *Monodactylus argenteus*, *Apogon hyalosoma* and *Glossogobius bicirrhosis* were also located low on this axis, as was *Kuhlia rupestris* (which breeds in estuarine habitats). These species were more common in the Bloomfield River and the Cape Tribulation sites.

Although significant associations between habitat-related variables and Axes 1, 2 and 3 scores were detected, none were particularly strong (>0.52). This suggests that habitat structure played only a minor role in influencing presence and abundance of fish species; however, this may have resulted from the inclusion in the analysis of sites located above barriers. The following analysis excluded all those sites identified in Fig. 3 as being in the upper Bloomfield, upper Barron or upper Tully rivers.

Table 2. Correlation coefficients (significant at $P < 0{\cdot}001$) for associations between DECORANA axes scores and habitat descriptors
The results presented are for the two analyses described in the text

Parameter	Axis 1	Axis 2	Axis 3
All lotic sites			
Distance from mouth	0·36		–0·48
Distance from higher order			–0·33
Elevation	0·51		
Gradient		–0·42	
Longitude		0·34	
Latitude		0·40	–0·38
% Pool	0·41		
Average flow	–0·41	–0·36	
Maximum flow	–0·39		
% Gravel	–0·41		
% Cobble	–0·42	–0·52	
% Bedrock	0·42		
Macrophytes		0·38	
% Rapids			–0·35
Undercut banks			–0·46
Only those sites downstream of profile discontinuities			
Latitude	–0·76		
Longitude	–0·67		
Average flow	0·39		
Maximum flow	0·45		
% Gravel	0·40		
Gradient		–0·44	
% Rapid			0·39
% Pool			–0·43
% Mud			–0·54
Undercut banks			0·56

A strong latitudinal (and longitudinal) gradient was present on Axis 1 of the resulting ordination (without barriers) (Table 2, Fig. 4). The Bloomfield River and Cape Tribulation streams were arrayed to the right on Axis 1 and the Cardwell streams were arrayed to the left (reverse of distribution shown in Fig. 3). This axis accounted for 43% of the variation (total eigenvalue 1·280). Sites located to the right on this axis tended to have higher water velocities and a substratum dominated by gravel (Table 2). Stream gradient was negatively correlated with Axis 2 scores, with the higher-gradient streams of the Cape Tribulation area and of the Bloomfield River being located low on this axis (Table 2). Correlations with Axis 3 scores reflected a gradient in habitat type from slowly flowing, muddy habitats to faster-flowing habitats typical of rapids. The Russell and Tully rivers were distributed high on Axis 3, suggesting that the fauna present at those sites tended to be more characteristic of environments of higher water velocities and stream gradient (Table 2).

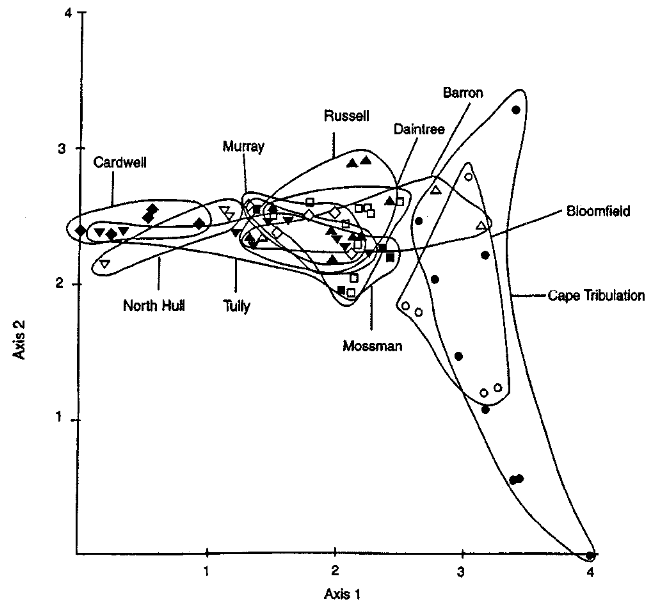

Fig. 4. The distribution of study sites in ordination space as defined by DECORANA Axes 1and 2 of an ordination of weighted species abundance data from which all sites located above major discontinuities in river profile were omitted. Drainage basins are distinguished by the same symbols as in Fig. 2.

The strong latitudinal gradient evident in this second ordination arises principally because of the distinctive faunas present in the Cape Tribulation area and the Bloomfield River and the distinctive but depauperate fauna present in streams of the Cardwell area. The remaining rivers, the Murray, Tully, Russell, lower Barron, Mossman and Daintree Rivers, form a relatively homogeneous group. Streams of the Cape Tribulation area and Bloomfield River catchment displayed more within-group variation in assemblage structure than was observed elsewhere (Fig. 3). This, and the absence of Melanotaeniidae in the Cape Tribulation streams, were the most notable features of this group.

Discussion

Species Richness

The Australian inland piscifauna is characterized by the high proportional representation by estuarine fishes and the general ability of Australian fishes to tolerate elevated salinities (Allen 1989; Bishop and Forbes 1991). In some respects, this obscures the distinction between freshwater and estuarine fishes and this is well reflected by the results of the present survey. Twenty-one of the 64 native species were classified as freshwater/estuarine species and undoubtably some debate over the validity of some of the listings could occur. We do not view this as problematic; instead, we view the results of the present study as indicating the number of species that make use of the freshwater environments of the Wet Tropics region. With this in mind, some comparisons can be made between the fish diversity of the Wet Tropics region and Australia as a whole.

Allen (1989) lists the Australian fauna as being composed of 35 families (one of which, the Nannopercidae, has been subsumed within the Percichthyidae [Johnson 1984]). Twenty-two families were recorded during this study (excluding the marine families Sciaenidae and Tetradontidae); therefore, the Wet Tropics region contains about two-thirds of the freshwater fish families occurring in Australia. If the additional species listed in Table 1 are used in this comparison, the total number of families increases to 25 with the addition of the Megalopidae, the Ariidae and the Soleidae, and the proportional contribution increases to 71%. Eight of the eleven families not represented in the Wet Tropics region are families limited to the southern half of the continent; the three northern families are the Ceratodidae (lungfishes), the Osteoglossidae (saratoga) and the Kurtidae (nursery fish), all of which contain few species (one, two and one species respectively) and, with the exception of the osteoglossid *Scleropages jardinii*, are of limited distribution. Therefore, the Wet Tropics region contains nearly all (90%) of the freshwater fish families of northern Australia (i.e. north of the Tropic of Capricorn).

Forty-two genera were recorded during the study and a further six genera are known to occur in the Wet Tropics region (Table 1); this is two-thirds of the Australian total. If the comparison is limited to genera within those families typical of northern Australia, the proportion increases to 80%. The region also contains 41% of the freshwater fish species of Australia and 55% of the species within families typical of northern Australia. This is an exceptionally high diversity considering that the area surveyed is contained within a narrow (<100 km) coastal strip passing through only 4° of latitude. It must also be borne in mind that the Herbert River was not surveyed during this study, that these estimates of species diversity are the result of a 'one-off' survey and that the survey focussed most strongly on shallow streams; these estimates of total fish species richness are almost certainly an underestimate.

Over one-third (29/76) of the species known to occur in fresh waters of the Wet Tropics region also occur throughout south-east Asia or parts of the Pacific basin and are not limited to the Sahulian land mass. This is in considerable contrast to observations for the Australian piscifauna as a whole (Merrick and Schmida 1984; Allen 1989). Of these widespread species, 21 were characterized by an estuarine/freshwater habit or the need to spawn in estuarine or marine waters. Obviously, these species have colonized continental fresh waters via a marine route and probably continue to do so. Over 80% of the total number of fishes collected was accounted for by the ten most commmon species and, of these species, only *Glossogobius celebius* is not endemic to Australia or New Guinea. The remainder are widespread throughout northern or eastern Australia. Only four species are confined to the Wet Tropics region: the Cairns rainbowfish *C. rhombosomoides*, the Mulgrave River goby *Glossogobius* sp. B, the scaleless goby *Schismatogobius* sp., and the undescribed species in Percichthyidae. This latter species and *Glossogobius* sp. B have the most restricted distributions within the Wet Tropics region, both being confined to a single drainage basin. Both *Mugilogobius* cf. *stigmaticus* and *Sicyopterus* cf. *macrostetholepis* may also be confined to the Wet Tropics region if they are determined to be new species.

Eighty-eight fish species were recorded from Cape York Peninsula by the CYPLUS surveys of 1992–93 (Herbert *et al.* 1995). Fifty-two species present in Cape York were also recorded from the Wet Tropics Region during the present study or in prior research (e.g. additional species listed in Table 1). Thus, the Wet Tropics region and Cape York Peninsula collectively contain about 80% and 55% of the species diversity of northern Australia and the entire Australian continent respectively.

Pusey *et al.* (1995), in a comparison of the species richness of the Mulgrave River with the Burdekin River, Black-Alice River, three rivers of eastern Cape York Peninsula and the Jardine River, showed that the fish fauna of the Mulgrave River was richer than that of these larger rivers, and they suggested that this may be a result of a greater diversity of habitats and a greater constancy of flow in the Mulgrave River. Flow constancy provided a more predictable and constant availability of particular habitat types and therefore provided the circumstances allowing the evolution of more restricted habitat requirements and consequently greater species packing (Pusey *et al.* 1995). In addition, most of the rivers of northern Australia tend to be long, low-gradient systems with a dominant substrate of fine particles and hence of less habitat complexity. The Mulgrave River does not have a more diverse fish fauna than other rivers of the Wet Tropics region, after allowance is made for differences in catchment area (Pusey *et al.* 1995). Most large rivers of the Wet Tropics have flow regimes similar to that of the Mulgrave River (Pusey, unpublished data) because their general close proximity ensures that all are influenced by the same weather patterns, and the generally common relationships of their catchments to the Great Dividing Range ensure that any orographic influences are similar throughout the region. Moreover, most rivers of the region share a similar array of habitats (with the exception of the presence of floodplain lagoons) (Pusey and Kennard, unpublished data). These two factors, a reliable flow tending towards constancy and a diverse and reliably available array of lotic habitats are, we believe, the major reasons for the exceptionally high diversity occurring in the Wet Tropics. In addition, the area contains elements of the fauna typical of areas both to the north and the south.

Geographic Variation within the Wet Tropics Region

Ordination was useful for delineating geographical variation in fish distribution and abundance. The most noticeable feature within the Wet Tropics is that profile discontinuities have a major impact on the distribution of fish. The effects of barriers to fish movement have been reported for other tropical rivers (Berra *et al.* 1975; Balon and Stewart 1983; Moyle and Senanayake 1984; Bishop and Forbes 1991; Pusey *et al.* 1995). As gradient increases, fewer fish are able to penetrate upstream unless they have specific mechanisms for overcoming obstacles such as long sections of rapids, cascades or waterfalls. Within the Wet Tropics region, the species most capable of colonizing such areas are *M. splendida*, *A. reinhardtii* and *M. adspersa*. The Barron River, above the Barron Falls, contained these species and *Hephaestus fuliginosus*, *Craterocephalus stercusmuscarum*, *Glossamia aprion*, *Leiopotherapon unicolor* and *Porochilus rendahli*. It is known that some of these species were translocated into the Barron River but it is also possible that some species may have been present prior to stocking programmes.

Drainage capture is a common occurrence in rivers of eastern Australia (Ollier 1982; Fried and Smith 1992; Haworth and Ollier 1992) and it is probable that the Barron River originally flowed into the Gulf of Carpentaria prior to reversal during the early Tertiary (Coventry *et al.* 1980). The presence of *L. unicolor*, *C. stercusmuscarum*, *H. fuliginosus* and *P. rendahli*, all of which occur in westward-flowing streams of the Gulf region, may therefore be a result of such long-term landscape evolution. The presence of the undescribed percichthyid above the Bloomfield Falls is anomolous, not only because this family is generally limited to southern Australia (Johnson 1984), but also because it was sympatric with species known for their ability to negotiate barriers. It would be instructive to know the timing and origin of the Bloomfield Falls or whether there has been river capture within this drainage also.

Ordination revealed a strong north–south gradient in assemblage structure, but since significant associations between assemblage structure and habitat structure and site location (distance to the sea) were also detected and given that the headwaters of southern rivers were more accessible, this may be partly artefactual. Nevertheless, substantial differences were observed among the assemblages of the lower Bloomfield River, streams of the Cape Tribulation area and, to a lesser extent, some of the sites located on the Daintree river and those elsewhere. Estuarine and marine vagrant species were common (e.g. *A. hyalosoma*, *Lutjanus argentimaculatus*) in these sites. This was almost certainly due to the proximity of the coast, because similar species were recorded from the most-downstream sites on the Barron and Russell rivers. These drainage systems were characterized by high proportional representation of *E. melanosoma*, *E. fusca* and particularly *O. gyrinoides*; these species are not abundant in more-southerly drainages but arre common in rivers of Cape York (Herbert *et al.* 1995), and the northern drainages of the Wet Tropics region may represent an area of overlap in faunas that does not persist strongly further south.

Another feature of the assemblages of the lower Bloomfield and the streams of Cape Tribulation was the near and complete absence, respectively, of the rainbowfish *M. splendida*. This species occurs in nearly every type of aquatic habitat in every drainage of north-eastern Queensland (Allen 1989). It is not particularly common in high-velocity environments of the Mulgrave and South Johnstone rivers (Pusey *et al.* 1995) and its absence from streams of the Cape Tribulation area may be due to an aversion to this common type of habitat. However, it is equally likely that the absence is related to difficulty in colonization, given the short nature of these streams and the absence of any appreciable floodplains over which fish could move during periods of high flow. Finally, these drainages showed greater between-stream within-drainage variation in assemblage structure than was observed for other drainages. This variability is even more marked when it is compared with the intra-basin variability in other drainages, which included habitats as different as headwater streams, lowland tributaries and lowland main-channel habitats. In keeping with our suggestion that these coastal streams are more accessible to colonization by marine vagrants, we suggest that the high variability is also a function of random colonization processes that lead to greater randomness in assemblage structure.

The short coastal streams of the Cardwell area do not show this same variability despite being of equivalent size and apparent accessibility. Cardwell receives less total rain (2190 mm per annum) and less dry-season rain (13% of the total) than do areas to the north (Tracey 1982); hence, the Cardwell streams may have a more seasonal flow regime than more northern streams. Since the catchments of these streams are small, stream flow is more likely to be 'flashy' and less likely to have a significant baseflow component. The dominance of dry sclerophyll vegetation within these catchments suggests a more seasonal and episodic rainfall pattern than that found further north in the rainforest. Although colonization of the Cardwell streams may be dynamic and tending towards randomness, the harsher dry-season conditions that prevail because of reduced flow may limit the persistence of many species and thus lead to less variability in assemblage composition. It would be instructive to sample these same streams during the wet season to test this hypothesis.

If the drainages on the extreme limits of the Wet Tropics region are not considered, there is little suggestion of a latitudinal gradient in assemblage structure (at least on the first two axes of the ordinations). The Tully, Murray and Russell rivers tended to be only slightly different from the Mossman and Daintree rivers because of the increased abundance of *H. fuliginosus* in the former group. However, as mentioned above, the southern rivers were more accessible by road and consequently more lower-order streams were sampled, and this may be partly responsible for the differences suggested by ordination. These data suggest that within the major drainages of the Wet Tropics region, the factors that structure the distribution and abundance of fishes are common to all drainages. These appear to be related most strongly to aspects of water velocity, gradient, substratum and bank structure, and they reflect the transition within rivers from slowly flowing lowland sections with a sand-and-mud substratum through to middle reaches with higher gradient, faster flows, gravel and cobble substrata and undercut banks and finally to high-gradient swift streams with cobble and rock substrata. A similar pattern was observed in the Mulgrave River (Pusey *et al.* 1995).

The low among-basin differences in assemblage structure may also have some historical basis. During the Pleistocene period, at the time of the ice maxima, the coastline of north-eastern Australia extended eastward to the present 100–130 m submarine contour (Coventry *et al.* 1980). At this time, it is probable that many of the currently distinct rivers of the region coalesced to form fewer, larger rivers as occurred in north-western Western Australia and the Gulf of Carpentaria (see Keenan 1995). Additionally, a more extensive floodplain system that facilitated greater between-basin connection during periods of high flow, such as now occurs between the Tully and Murray rivers, would have existed. These conditions, less than 15000 years BP, would have been conducive to between-basin transfer of fishes and hence to a decrease in faunistic heterogeneity throughout the Wet Tropics region. Historical variation in sea levels may have influenced the present distribution of freshwater fishes (Koehn and O'Connor 1990) and of one crustacean genus (Horwitz 1988) in southern Australia and *Lates calcarifer* in northern Australia (Keenan 1995). It is therefore not surprising that those species limited in distribution to a single drainage basin (*Glossogobius* sp. B and the unnamed species in Percichthyidae) are both restricted to upstream habitats. Moreover, massive freshwater flood plumes, occurring about every 25 years, are capable of extending significant distances along the coastline of north-eastern Australia (Keenan 1995) and may facilitate the dispersal of freshwater species between separate river basins. Keenan (1995) postulated that this was the most likely explanation for the low genetic differentiation between geographically isolated populations of barramundi of north-eastern Australia. A general tolerance to elevated salinity evident in the Australian piscifauna would also increase the likelihood of this occurrence. Unlike other faunal groups, the fish fauna of the Wet Tropics region, although speciose, does not show a high degree of endemism (five species), suggesting that dispersal within and outside the boundaries of the Wet Tropics may occur frequently. The historical perspective suggested here may therefore contain a component of very recent history. It would be instructive to know the extent of genetic differentiation between populations occurring in different rivers of the Wet Tropics region as has been studied for some species of birds and reptiles (Moritz *et al.* 1993; Joseph and Moritz 1994) in order to gain some indication of the extent of present or geologically recent population mixing.

In summary, this study has found that the Wet Tropics region contains a high diversity of freshwater fishes that included one undescribed species and several species not previously recorded from Australian inland waters. A latitudinal gradient in fish assemblage structure reflected a greater representation by eleotrid and oxyeleotrid gudgeons in the north and a greater abundance of *H. fuliginosus* and *M. splendida* in the south. Streams of the Cape Tribulation area and the lower Bloomfield River were particularly distinct and variable. Strong distinction among the faunas of the remaining drainages was not evident, probably because the rivers share similar paleohistory, hydrological regimes, water quality and diversity and availability of habitat types.

Acknowledgments

We are indebted to the many private landholders who allowed us access to rivers running through or bordering their properties. Dr G. Allen (Western Australian Museum), Ms H. Larson (Museum and Art Galleries of the Northern Territory), Dr C. Keenan (QDPI, Fisheries) and Mr R. Mackay (Queensland Museum) identified many specimens. The comments of two anonymous referees greatly improved the manuscript. We express our gratitude to Professor Andrew Sheldon, University of Montana, for his assistance during the first half of the project and for suggesting that random colonization processes in short coastal streams may lead to increased variability in assemblage composition. This research was conducted under QDPI permit No. 4994, State Forests permit No. 553 and Queensland National Parks and Wildlife Service permit No. 1742. Funding was provided by the Wet Tropics Management Agency and we are grateful for the opportunity to undertake this research.

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Manuscript received 29 May 1995; revised and accepted 23 November 1995