

Fish ecology and management of the Sepik-Ramu, New Guinea, a large contemporary tropical river basin

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Synopsis

The ichthyofauna of the Sepik-Ramu basin is composed of diadromous species and the freshwater derivatives of marine families. Fish species diversity, ichthyomass and fish catches are low even by Australasian standards. Three major factors have produced the depauperate ichthyofauna and restricted fishery within the basin: First, the zoogeographic origins of the ichthyofauna. Australasian freshwater fishes, being mainly derived from marine families, generally exhibit ecological characteristics that have evolved for life in estuaries, not rivers. This has led to peculiarities in river fish ecology and explains the probable low fish production from rivers in this region in general. Several important riverine trophic resources are not exploited by the Australasian freshwater ichthyofauna. The modes of reproduction amongst the Australasian freshwater ichthyofauna have limited the colonisation and exploitation of floodplain habitats. Second, Sepik-Ramu lowland habitats, especially floodplains, are very young. This has resulted in low fish species diversity in lowlands, whilst diversity at higher altitudes is equable, in comparison to river systems in southern New Guinea/ northern Australia. Third, the Sepik-Ramu lacks an estuary in sharp contrast to river systems in southern New Guinea or northern Australia. Most of the 18 families of Australasian fishes missing from the Sepik-Ramu are probably absent because of this factor alone. In particular, the Sepik-Ramu has not been colonised by any family of fishes having pelagic eggs, resulting in the loss from the fauna of the few Australasian fish taxa with high reproductive rates. Consequently, the general problems with river fish ecology in Australasia are exacerbated within the Sepik-Ramu by the particular development and morphology of the basin. Fish species diversity in the Sepik-Ramu is low, even in comparison with those taxa representative of marine families resident in rivers in nearby zoogeographic regions (S.E. Asia) whose ichthyofaunas are otherwise dominated by freshwater dispersant groups. The Sepik-Ramu ichthyofauna is considered noteworthy for what is absent, not what is present. Ichthyomass and fish production can be increased by fish species introductions whilst, in theory, biodiversity of the native fish fauna can be maintained. The directions in which ecological evaluations of proposed introductions might proceed in practice for the Sepik-Ramu are discussed but are constrained by the lack of knowledge on species interactions from other areas.

Introduction

The freshwater fish fauna of the Australasian conti-

nent (including Australia, New Zealand, New Guinea and associated islands east of 'Wallace's Line') is dominated by diadromous species and freshwater

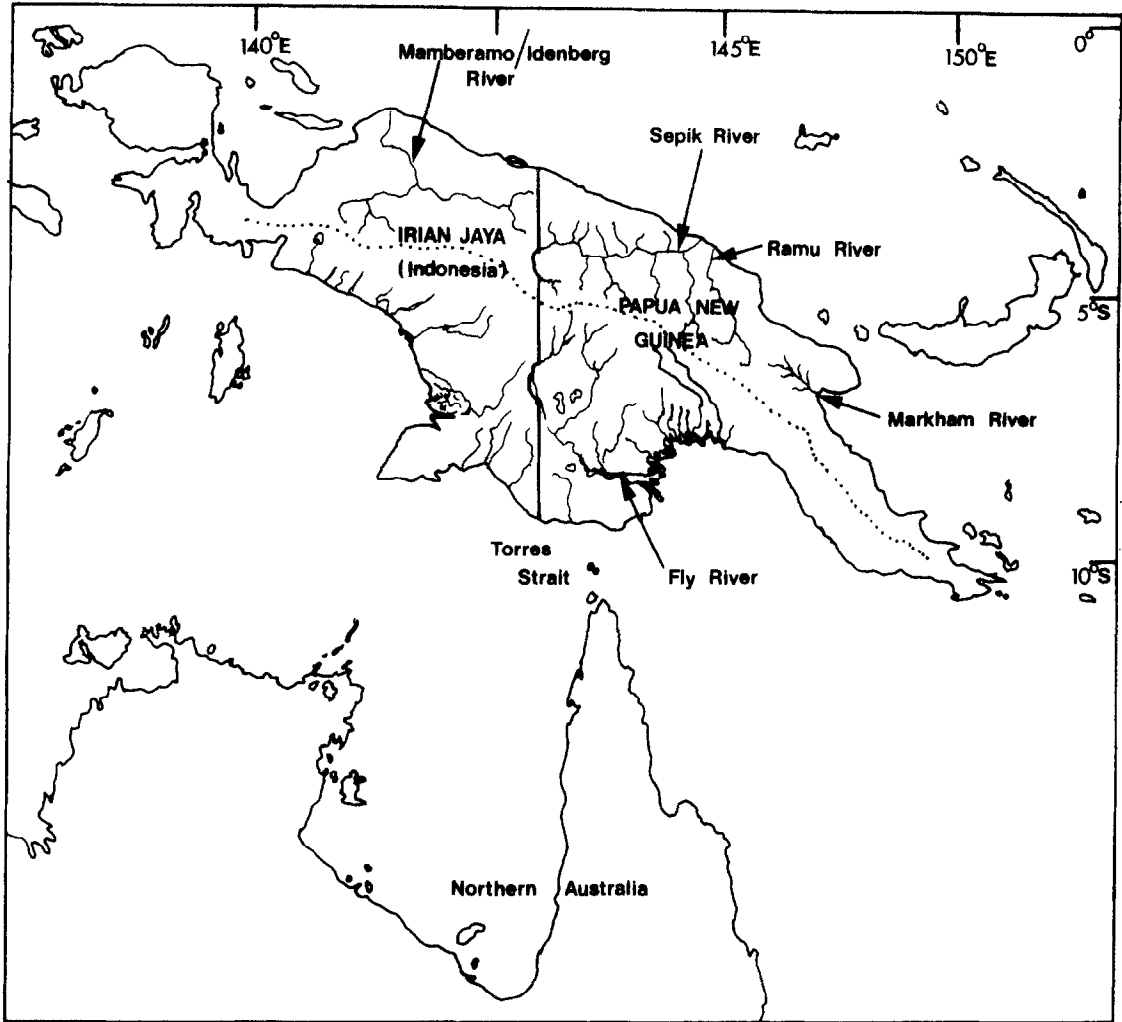


Fig. 1. Map of New Guinea and northern Australia. The eastern half of the island of New Guinea forms the mainland of the independent country of Papua New Guinea, the western half is Irian Jaya (a province of Indonesia). The stippled line running longitudinally across the island is the approximate position of the central dividing range of mountains (central cordillera) dividing the island into northern and southern biogeographic zones (see also Fig. 2).

representatives of marine families (Roberts 1978, McDowall 1981, Allen & Coates 1990). Here, major inland fisheries that provide essential food occur mainly in New Guinea (Coates 1987a), the world's largest and highest tropical island (Fig. 1). Most people in New Guinea live inland, leading subsistence lifestyles, and severe protein shortages exist (Coates 1987a) so that freshwater fisheries development is particularly important. One of the largest basins on the island is that drained by the Sepik and Ramu Rivers where natural constraints to fisheries development are the low fish species diversity and

poor fish catches, especially by comparison to regions outside Australasia (Coates 1985, Van Zwieten 1990) and even within the region. The zoogeographic location, and recent geological history, of the Sepik-Ramu basin are known to be the major causes of this situation (Coates 1985, Allen & Coates 1990, Van Zwieten 1990). However, this has not been properly explained and the present paper is intended to expand on the reasons why the Sepik-Ramu ichthyofauna has its present composition and why this constrains fish production and, hence, inland fisheries development. To achieve this aim,

explanations of the geological origins of the region and its freshwater ichthyofauna are presented. This is followed by an analysis of the implications of these considerations in zoogeographic and then in fish ecology and management terms.

Fish introductions have been proposed (Coates 1987a), and are being implemented (Coates 1993a), as a management strategy to improve the fishery in the Sepik-Ramu basin. Decisions on whether introductions should actually occur in the Sepik-Ramu were influenced greatly by social considerations beyond the scope of this paper. Methodologies for addressing this question included the first full implementation of an international code of practice for the introduction of aquatic organisms (Coates 1993a). The broader issue of placing fish introductions within the proper framework of the sustainable use of resources is also discussed by Coates (1993b). A second objective of this paper is to publish the ecological reasoning on which this management strategy is based. Hopefully, this may reduce the latitude for ecological errors arising from introductions. Put simply, before making an introduction, it is prudent to have a satisfactory explanation of why the organism (or its ecological equivalent) is not already present in the ecosystem in question. This process is of considerable help in predicting the need for, and impact of, an introduction (Coates 1993a).

Origins and relationships of the Australasian freshwater ichthyofauna: general ecological implications

The Australia/New Guinea region has been geographically isolated since the continent moved away from Antarctica (McDowall 1981). The origins of the Australian continent, its derivations from Gondwanaland, and its passage through a variety of climatic zones, especially recent glaciation, have had a profound influence on the characteristics and development of its freshwater ichthyofauna. The resultant impoverished freshwater fish fauna comprises derivatives of marine species with a few ancient primary division freshwater fishes, such as the lungfish *Neoceratodus* sp. and the osteoglos-

sid *Scleropages* sp. In addition, a characteristic of the region is the high proportion of diadromous fish species (Myers 1949, Roberts 1978, Allen & Coates 1990). The ichthyofaunas of two major New Guinea river systems are depicted in Appendix 1.

The Fly system (Fig. 1) has 128 recorded native species and the Sepik-Ramu has 70 (Appendix 1). On the basis of species-area data for African or South American river systems (Welcomme 1985), the Fly should contain about 60 or 84 species, respectively, and the Sepik-Ramu about 82 or 117 species. On this basis, species richness in New Guinea systems is not particularly unusual. However, Appendix 1 lists a large proportion of diadromous fishes including 'vagrant' marine species briefly entering the lower sections of the rivers; over 47% of species qualify in this category in the Sepik-Ramu. Therefore, such comparisons are not strictly valid. In addition, recent studies have shown that Welcomme's data may be based on under-estimates of species richness for certain systems. For example, a single tributary of the Amazon River contains an estimated 750 species (Goulding et al. 1988). The Kapuas system, in Kalimantan Barat (Borneo), Indonesia, contains 290 species (Roberts 1989), none being diadromous, yet is no larger than the Sepik-Ramu. Nevertheless, comparisons of systems based on total species counts alone do not satisfactorily explain reduced fish catches in the Sepik-Ramu. The general ecological attributes of the ichthyofauna, due to its origin, are much more relevant.

Of the 28 families of fish occurring in Australasian freshwaters listed by McDowall (1981), only 4 are endemic to this region. Since the freshwater fish fauna is mainly derived from marine groups, families are, of course, generally widespread throughout the Indo-Pacific region. More importantly, Australasian freshwater fish families are commonly represented in freshwaters in other regions. For example, the Mekong system also contains 28 families of marine origin (Mekong Committee 1976), the majority of which occur in freshwater in Australasia. The Australia-New Guinea freshwater fish fauna is often considered 'unique' (e.g. Merrick & Schmida 1984, Allen 1991). Whilst there is much endemicity of freshwater genera and species, this equally applies to other zoogeographic regions. I

conclude that what is really 'unique' about the ichthyofauna is what is absent, i.e. freshwater dispersant (primary and secondary) groups, not what is present, a point that I amplify later.

Colonisation of Australasian freshwaters by species of marine fishes must have required transition through brackishwater, especially estuaries. It is, therefore, important to consider that Australasian freshwater fishes probably developed from brackishwater species rather than 'marine' species. The inadequate study of Indo-Pacific brackishwater fish assemblages is unfortunate because their ecology will have had a major influence on that of the freshwater fish assemblage (because most species developed from it). However, I make some generalised observations here. Characteristics of estuarine environments include highly variable conditions of salinity, temperature, turbidity and oxygen concentration, both temporally and spatially. In response to these conditions, the majority of fish breeding in estuaries either produce large numbers of small pelagic or demersal eggs or improve survival by producing a smaller number of larger eggs accompanied by various degrees of parental care (Dando 1984). This may partly explain why parental care, accompanied by low fecundities, is particularly common amongst the Australasian freshwater ichthyofauna. The major trophic opportunities available for fish probably greatly differ between marine, estuarine and freshwater environments. Submerged and emergent aquatic macrophytes, allochthonous materials (e.g. leaves, fruits, seeds, insects, etc. from terrestrial sources) and detritus are likely less important sources of food in the sea and estuaries than they are in tropical freshwaters. This likely explains why fish species feeding on fresh aquatic macrophytes are absent from the Australasian freshwater fish assemblage, while those feeding predominantly on allochthonous inputs are rare (possibly limited to hemiramphids, Coates & Van Zwieten 1992) as are detritivores (with the exception of mullets). By comparison, Goulding et al. (1988) list over 70, 100 and 60 fish species, respectively, feeding predominantly, many exclusively, on these resources in an Amazon tributary. The Australasian freshwater fish fauna is dominated by omnivorous taxa with a high incidence of feeding pre-

dominantly on aquatic invertebrates. For example, Roberts (1978) considers the fish fauna 'unspecialised' and the adaptations seen probably evolved in marine/estuarine environments, not rivers or freshwater lakes. Later references to the Sepik-Ramu illustrate the importance of these factors in fish ecology terms.

The relationships of the New Guinea freshwater ichthyofauna

Northern Australia was connected to New Guinea by a land bridge until recent rises in sea level separated the two regions (Löffler 1977). As a consequence, their freshwater ichthyofaunas are similar at the familial and generic level and a number of entirely freshwater species are common to both southern New Guinea and northern Australia (Roberts 1978, Allen & Coates 1990). The development of the central range of mountains running longitudinally across New Guinea (Fig. 1) has resulted in the northern section of the island being considered a separate zoogeographic province within the region (Allen & Coates 1990). Although most northern New Guinea freshwater fish families and genera are shared with southern New Guinea (and hence northern Australia), there is much endemism at the species level (Allen & Coates 1990). However, total familial, generic and species richness are lower in northern than southern New Guinea (Appendix 1). The Sepik-Ramu basin is approximately 1.4 times the area of the Fly basin but the number of fish species is only about 55% by comparison. This discrepancy was explained by geological differences (Coates 1987a) and especially by northern New Guinea being younger (Coates 1985, Allen & Coates 1990). However, I now consider such explanations over-simplified and misleading and I rectify this later in this paper.

Geological history of northern New Guinea and the Sepik-Ramu basin

The New Guinea area lies in the zone of interaction between the northward moving Australian conti-

mental plate and the westward moving deep Pacific Ocean Basin plate (Löffler 1977). Since the Cretaceous, the interaction has produced upthrusting along the centre of the island forming the 'central cordillera', the New Guinea highlands (Fig. 1, 2). Hence, northern and southern New Guinea have a common origin, but their freshwaters have been separated for some time as witnessed by their classification as different zoogeographic provinces.

It was not until the upper Pliocene that the framework of the existing landscape became visible. At this time there was a shift northwards in the zone of interaction between the two plates. As a result, the mountain range along the present northern coast appeared (the Torricelli-Bewani mountains, Fig. 2) which still experiences uplifting at a spectacular rate in geological terms (Löffler 1977). At this time the Sepik-Markham depression (also known as the central intermontane trough) was formed and extends from Geelvink Bay in Irian Jaya to the Huon Gulf in Papua New Guinea. This delimits Sepik-Ramu lowlands. There is, therefore, a close similarity between freshwater fishes in the western (principally the Mamberamo/Idenburg River, Irian Jaya) and eastern (Sepik-Ramu) sections of northern New Guinea (Allen & Coates 1990). Draining into this depression in the present Sepik-Ramu basin are rivers arising from the central cordillera and the Torricelli-Bewani and Finisterre Ranges.

During the above development the intermontane trough was originally marine. Present Sepik-Ramu lowlands were previously part of an inland sea, up to 200 m deep, referred to as the 'Sepik-Ramu Sea' (Fig. 2). Due to intense erosion and deposition of alluvium within this basin, rapid uplifting of the northern coast and recent rises in sea level, the entire Sepik-Ramu Sea started to become freshwater as little as 6000 years ago (Swadling et al. 1988).

The lower reaches of the Sepik and Ramu rivers are now inter-connected by numerous channels that pass through an area of low-lying alluvium. The freshwater ichthyofaunas of the Sepik and Ramu basins are very similar, although there is a modest degree of species endemism in both regions (Allen 1991). Consequently, recent discussion of the Sepik River basin, its ichthyofauna and fishery, has in-

cluded the Ramu River basin, adopting the general term Sepik-Ramu.

Recent sea-level changes will have also affected the lowland environments of the Fly (and other southern New Guinea systems) and Australian rivers. However, in such regions, there were probably gradual changes in the extent of lowland freshwater habitats. In the Sepik-Ramu basin certain types of extensive lowland freshwater habitats, especially floodplain, swamps and associated lakes, would have suddenly appeared. Alternatively, such habitats were obliterated and re-appeared, depending upon the precise timing of geological events and the changes in sea-level considered. Löffler (1977) considers that changes in sea-level probably had drastic effects on the Sepik compared with the Fly.

In view of the above factors, the following conclusions are relevant to the origins and speciation of the Sepik-Ramu ichthyofauna: (i) The present extensive Sepik-Ramu lowland freshwater habitats (Fig. 2) are very young and much younger than those of the Fly system, or those in northern Australia. (ii) All rivers draining into the Sepik-Ramu Sea arose from steep mountains and would have had negligible floodplains, therefore, the extensive floodplains presently existing are extremely young (< 6000 yr). (iii) Amongst higher altitudes within the Sepik-Ramu basin, freshwaters of the three major mountain areas have been relatively isolated and their relative age increases in the order Torricelli-Bewani Range/Finisterre Range/central cordillera; and (iv) The Sepik and Ramu rivers, in common with other major northern New Guinea systems, discharge into deep water and have no deltas. Estuarine zones inland are negligible. As water discharges into the sea, brackishwater zones form offshore at the surface of very deep oceanic water. Mangrove habitats along the north coast of New Guinea are also limited, partly due to the absence of extensive estuaries but also due to rapid coastal uplifting. In contrast, rivers in southern New Guinea and northern Australia, draining into regions of shallow continental plate, generally have well-developed deltas, mangrove systems and extensive estuarine environments (e.g. Petr 1983).

In relation to all of the above, I present the fol-

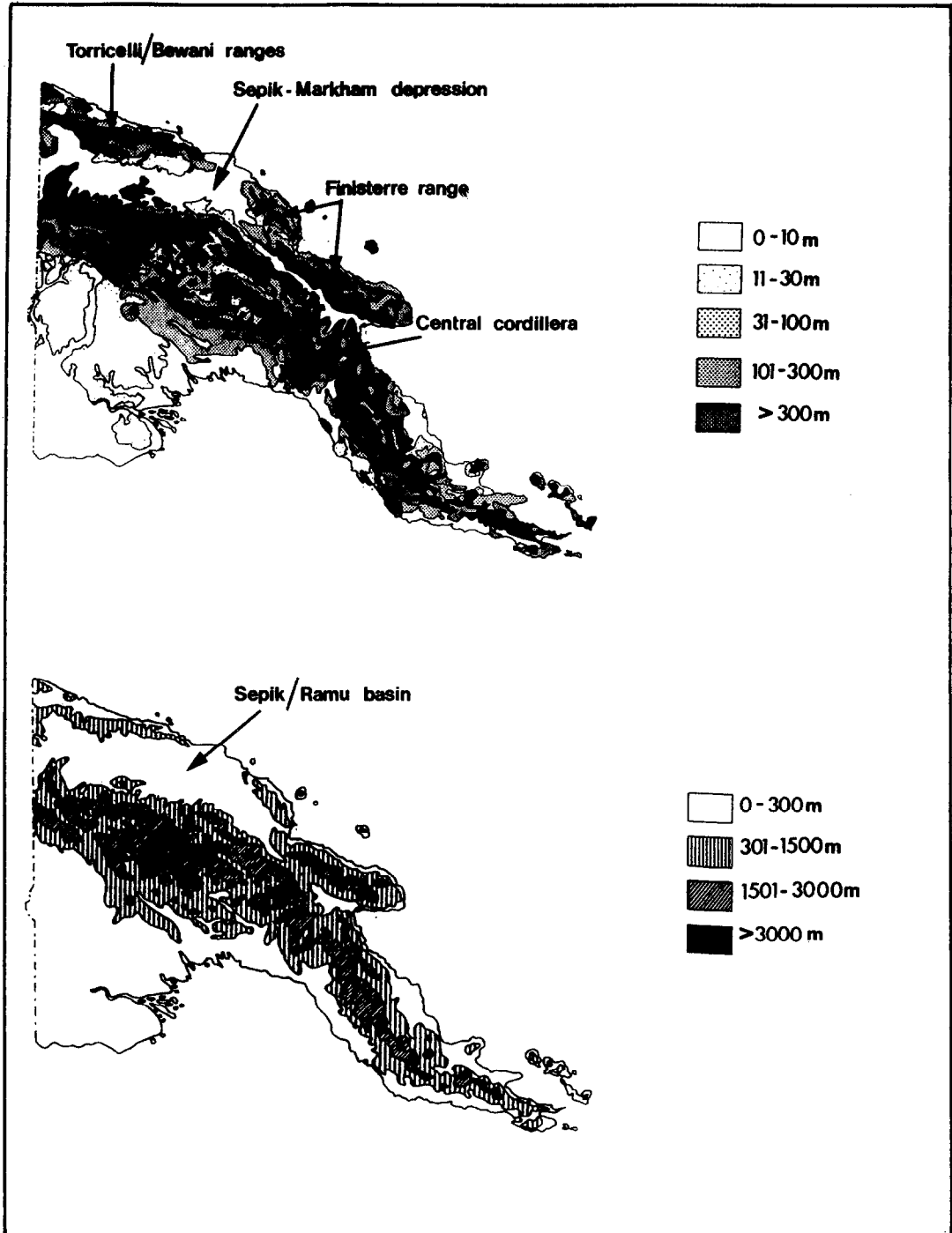


Fig. 2. Local relief classes (upper figure) and altitudinal zones (lower figure) of Papua New Guinea (after Löffler 1977). The Sepik-Markham depression delimits the lowlands of the Sepik-Ramu basin. Lowlands within this depression (less than about 10 m, upper figure) are existing Sepik-Ramu floodplain regions. These lowlands were previously marine, the Sepik-Ramu Sea, up until very recent times (Löffler 1977, Swadling et al. 1988). Note that when such lowlands were marine, rivers draining into them arose from steep mountains in the Torricelli-Bewani and Finisterre Ranges and the central cordillera. The two ranges were previously islands surrounded by sea. Locations of major rivers are shown in Figure 1, which also provides a scale.

lowing hypotheses and test them against existing knowledge of freshwater fish in New Guinea:

Origins, speciation and adaptations of the Sepik-Ramu ichthyofauna

Hypothesis 1: The characteristics of the Sepik-Ramu estuary will limit colonisation of the basin by fishes dependent upon estuaries for their life-cycles

The most striking feature of the northern New Guinea freshwater ichthyofauna is the absence there of at least 18 families that occur in drainages in either southern New Guinea and/or northern Australia (Appendix 1). Most of the missing families are primarily marine, often with widespread distributions surrounding northern New Guinea (McDowall 1981), and often occur in coastal waters of northern New Guinea itself (Collette 1983). Only the Osteoglossidae, Iriatherinidae and Pseudomugilidae consist either entirely or predominantly of freshwater representatives. Hence, only these might be excluded from northern New Guinea by the requirement for dispersal through freshwater.

The gross differences in estuarine environments between northern and southern New Guinea/northern Australia are arguably responsible for the major differences in their ichthyofaunas. An examination of the known or presumed life-histories of most of the families is highly supportive of the hypothesis.

Of the 15 missing Sepik-Ramu families (excluding the Osteoglossidae, Iriatherinidae, Pseudomugilidae) at least eight have pelagic eggs: Moringuidae, Muraenidae, Lobotidae, Sparidae (Breder & Rosen 1966), Engraulidae (Breder & Rosen 1966, Merrick & Schmida 1984), Toxotidae, Soleidae and Cynoglossidae (Merrick & Schmida 1984). Most of these lay eggs in shallow mangrove or other estuarine regions. Any species producing pelagic eggs in brackish water at the mouth of the Sepik-Ramu would have considerable problems maintaining its populations. For example, pelagic eggs laid immediately seaward of the river mouth (upstream is fully freshwater) would drift into open sea with a depth of at least 500 m within about 30 minutes (data from Australian Hydrographic Service chart Aus 388).

From here they would quickly enter oceanic water and drift away from the area at between 3.5 and 6.0 km h⁻¹. None of the Sepik-Ramu fishes breeding in freshwater produce pelagic eggs. This is undoubtedly the major factor contributing to severely reduced familial diversity in the Sepik-Ramu.

Some southern New Guinea species with pelagic eggs can breed entirely in freshwater; for example in the upper Fly (*Clupeoides venulosus*) or in lakes (*Nematalosa* sp.). Fly (or southern New Guinea and northern Australia) estuarine environments probably facilitated the colonisation of freshwaters, and the speciation within them, of fish taxa with pelagic eggs. In the Sepik-Ramu, such taxa have not been able to make that initial entry.

Taxa having pelagic eggs in the Sepik-Ramu, but not breeding there, are usually restricted to 'vagrant' widely ranging Indo-Pacific marine species entering the lower river; for example, *Escualosa thoracata* (Clupeidae), *Chanos chanos* (Chanidae), *Caranx sexfasciatus* (Carangidae) and *Nibea soldado* (Sciaenidae). Significantly, both the clupeids and sciaenids are not only far more abundant within the Fly but have also developed freshwater representatives endemic to that system, or to the southern New Guinea region (Appendix 1). Similarly, mullets (Mugilidae) and scats (Scatophagidae) are more abundant within the Fly (Coates et al. 1989); mullets tend to be pelagic spawners in shallow estuaries (Breder & Rosen 1966). *Lutjanus goldiei* (Lutjanidae) presumably lays pelagic eggs (Breder & Rosen 1966) but its spawning grounds are not known. The species is not common in either system. The tarpon, *Megalops cyprinoides* (Megalopidae), is more common in both systems but is a widely ranging species, juveniles of which enter rivers from marine populations (Coates 1987b).

The barramundi, *Lates calcarifer*, is abundant within the Fly and its range extends from Australia through to south-east Asia (Grey 1987). Significantly, it is absent from northern New Guinea. Since the species spawns in estuaries, probably having pelagic eggs, and juveniles spend at least the first year of life in shallow, predominantly mangrove, brackishwater areas (Moore 1982) its absence from the Sepik-Ramu is hardly surprising; an observation endorsed by Moore (1980).

There is insufficient information on the life-histories of the Atherinidae and Tetraodontidae to explain their absence from the Sepik-Ramu. The remaining three missing Sepik-Ramu families (Dasyatidae, Belonidae and Kurtidae) have life-histories, in theory, enabling entry. However, the lecithotrichlyviviparous Dasyatidae are known only from photographs of a single, presumably freshwater, stingray taken from the upper Fly (Compagno & Roberts 1982). Belonids have large adhesive eggs generally laid amongst the roots of mangroves (Breder & Rosen 1966, Collette et al. 1984, Merrick & Schmida 1984); the relative absence of mangroves might explain their absence from the Sepik-Ramu. The Kurtidae exhibit paternal mouthbrooding in freshwater but their known distribution excludes the Pacific (Merrick & Schmida 1984); i.e. they are absent from coastal waters of northern New Guinea.

Hypothesis 2: Recent geological history of the Sepik-Ramu basin will have limited speciation in fish taxa in lowlands more than at the higher altitudes

The majority of the disparity between the numbers of fish species in the Sepik-Ramu and Fly River basins is accounted for by (a) the absence of certain families from the Sepik-Ramu (discussed above); this factor alone accounts for 35 of the 58 or so missing Sepik-Ramu species, and (b) greater speciation in genera common to both systems, or additional genera in common families, within lowland habitats in the Fly. There is little doubt that the data available support the hypothesis in this respect. Amongst taxa inhabiting lowland freshwaters in both systems, those with diadromous habits tend to be conspecific (Appendix 1), as expected, since such fish can move between systems. The important comparison is between those families, and their genera, that contain permanent inhabitants of lowland freshwaters. These families are generally much more speciose, and usually contain more genera, in the Fly (Table 1).

The only family inhabiting lowland waters and possibly showing greater diversity in the Sepik-Ramu is the Syngnathidae (Appendix 1, Table 1). This family more likely entered northern New Guinea from south-east Asia where freshwater syn-

gnathids are more common (Mekong Committee 1976, Roberts 1989) and zoogeographic factors other than those relevant here may explain their occurrence in the Sepik-Ramu. The Fly River probably has a diadromous pipefish species not yet recorded entering its lower reaches (Allen & Coates 1990). Certain genera in Table 1 could be lacking from the Sepik-Ramu for reasons other than the geological history of the region (for example, differences in water conditions). However, even considering only genera common to both systems, they are still usually more speciose in the lowlands of the Fly River; for example, *Arius* (Fly 9 spp. versus Sepik-Ramu 5 spp.), *Neosilurus* (3 vs. 1), *Glossamia* (4 vs. 1), *Glossogobius* (6 vs. 2) and *Oxyeleotris* (5 vs. 1). The genus *Eleotris* is the only exception (Appendix 1). Further support for the hypothesis comes from a comparison of diadromous families/genera common to both systems. Many of the taxa with only diadromous representatives in the Sepik-Ramu have totally freshwater representatives at low altitudes in the Fly River. These include the Clupeidae, Gobioidae, Sciaenidae, Periophthalmidae, *Ambassis* spp. and *Hypseleotris* sp. Conversely, *Eleotris* is the only genus common to both systems that has an endemic species in the Sepik-Ramu but only diadromous species in the Fly River. Furthermore, the examples of apparent serial or linear replacement of fish species by more or less closely related forms

Table 1. Number of genera and species of families of fishes common to both Fly and Sepik-Ramu low altitude freshwaters (i.e. RC, LRC, MRC, URC, F or L in Appendix 1). Those species that are known to be diadromous are excluded.

| Family | Fly basin | | Sepik-Ramu basin | |
|-----------------|-----------|---------|------------------|---------|
| | Genera | Species | Genera | Species |
| Ariidae | 4 | 13 | 1 | 5 |
| Plotosidae | 4 | 7 | 1 | 1 |
| Hemiramphidae | 1 | 1 | 1 | 1 |
| Melanotaeniidae | 1 | 1 | 1 | 1 |
| Syngnathidae | 0 | 0 | 1 | 1 |
| Ambassidae | 3 | 4 | 1 | 1 |
| Terapontidae | 3 | 4 | 0 | 0 |
| Gobiidae | 3 | 9 | 2 | 3 |
| Eleotrididae | 4 | 9 | 3 | 3 |
| Total | 23 | 48 | 11 | 16 |

between 'upstream' and 'downstream' sections in lowland regions of the Fly River provided by Roberts (1978) do not occur in the Sepik-Ramu (Appendix 1). This observation also illustrates the low speciation and adaptive radiation within Sepik-Ramu lowland habitats compared with those in the Fly River.

Evidence of increased speciation at the higher altitudes compared with the low altitudes in the Sepik-Ramu is more difficult to obtain. Species diversity decreases drastically with altitude in the Sepik-Ramu (Van Zwieten 1990), but this also occurs in the Fly (Roberts 1978) and appears to be a general feature of river basins (Lowe-McConnell 1975). In order to examine fish speciation at higher altitudes in the Sepik-Ramu one must compare diversity in families that occur in both lowlands and the higher altitudes (> 200 m above sea-level). It is prudent to exclude species known to migrate between the two regions, and species whose distributions overlap only at the lower altitudes. Considerable evidence for greater fish speciation at higher altitudes in the Sepik-Ramu comes especially from the Plotosidae (one species in Sepik-Ramu lowlands versus an additional three at higher altitudes), Melanotaeniidae (1 or 2 vs. 7 or 6, in two additional genera), Gobiidae (2 *Glossogobius* sp. vs. 3) and Eleotrididae (3 spp. in 3 genera vs. 4 sp. in 2 genera) (Appendix 1). Most significantly, the only truly freshwater grunter (Terapontidae) in the Sepik-Ramu occurs only in non-floodplain regions. Conversely, none of the freshwater taxa resident in Sepik-Ramu tributary streams at higher altitudes are more speciose in lowlands.

Plotosids, eleotridids, gobiids and terapontids have also speciated in Fly tributary environments (Appendix 1). Importantly, in the Fly River these taxa have also speciated extensively (by Australasian standards) in lowlands, which is not the case with the Sepik-Ramu. The melanotaeniids are essentially diverse inhabitants of tributary streams in both the Fly and Sepik-Ramu rivers. A comparison of total fish species diversity at higher altitudes (above floodplains) reveals that about 23 species predominantly occupy this environment in the Fly and a similar number do so in the Sepik-Ramu rivers. However, the Iriatherinidae, Atherinidae and

Pseudomugilidae are absent from the Sepik-Ramu, and account for 7 of such species in the Fly. Consequently, diversity at higher altitudes in the Sepik-Ramu is presumably at least equable to, if not greater than, that in the Fly River. This contrasts with the situation in lowlands.

Fish ecology considerations

The low catch and biomass arising from native fish species in the Sepik-Ramu is the most important practical factor requiring explanation. Tropical river basins normally support relatively productive floodplain fisheries characterised by large increases in secondary production associated with the flooding cycle (Welcomme 1985). I conclude that the history of the Sepik-Ramu has resulted in an ichthyofauna ill-adapted to exploit floodplains, explaining the poor catches achieved there (Coates 1985). The basin was colonised by taxa derived from estuaries, but life on river floodplains generally requires quite different specialisations.

Few Sepik-Ramu fishes exhibit morphological characteristics considered to be adaptations to river floodplain conditions. The same is probably true of the whole Australasian freshwater fish fauna. Respiratory modifications allowing air-breathing in areas of low oxygen concentrations, tolerance of high temperatures and desiccation, and modified body forms are features of fishes inhabiting floodplains in other regions (Welcomme 1985). The life-histories and trophic habits of fishes inhabiting the Sepik-Ramu are, however, probably more pertinent.

Reproductive styles

The difference in reproductive adaptations required in estuaries and on river floodplains is probably a major reason for limited exploitation of Sepik-Ramu floodplains. Life on floodplains is unpredictable, and especially so for fishes, due to their periodic drying out. As adaptations to these uncertainties, floodplain-dwelling species tend to have high fecundities, rapid growth and early matu-

riety, and are consequently characterised by high reproductive rates (Welcomme 1985). By contrast, large eggs and low fecundities are the norms for Sepik-Ramu fish species breeding in freshwater (Table 2).

Low fecundity is a major reason why most Sepik-Ramu fish species either avoid, or do not preferentially inhabit, floodplains (Coates 1988, 1991, Coates & Van Zwieten 1992). The strongest evidence supporting this conclusion comes from the three species that do preferentially inhabit Sepik-Ramu floodplains, *Oxyeleotris heterodon*, *Ophieleotris aporos* (Coates 1992) and *Glossolepis multisquamatus* (Coates 1990a). These are the only Sepik-Ramu fishes breeding in freshwater that have a relatively high fecundity (Table 2). The reproductive rates of *G. multisquamatus*, and especially *Op. aporos*, also

increase due to a relatively small size at maturity (Coates 1990a, 1992). Reduced egg size in *G. multisquamatus* results in a much higher fecundity than occurs in stream dwelling rainbowfish species (Coates 1990a). High fecundities in these three species is possibly a pre-adaptation to floodplain conditions. The latter species also probably entered contemporary floodplains from an antecedent freshwater lacustrine stock since the genus is otherwise restricted to lakes in northern New Guinea (Allen & Cross 1982).

The majority of freshwater fish families in Australasia likely have limited reproductive adaptations to floodplain conditions. With the Sepik-Ramu fish assemblage, this trend is significantly amplified due to the absence of species with pelagic breeding habits. Hence, the Sepik-Ramu ichthyo-

Table 2. Reproductive styles (after Balon 1990) and fecundities of families and species of fishes breeding, or thought to breed, in freshwater in the Sepik-Ramu.

| Family species | Reproductive style | Egg diameter (mm) | Fecundity | | References |
|----------------------------|-------------------------------|-------------------|--|------------------------|-------------------------------------|
| | | | eggs individual ⁻¹ | eggs kg ⁻¹ | |
| Pristidae | bearers, internal livebearers | – | < 10 | – | Breder & Rosen (1966) |
| Carcharinidae | bearers, internal livebearers | – | < 10 | – | Breder & Rosen (1966) |
| Ariidae | bearers, mouth brooders | 11.2–13.1 | 5–173 | 25–40 | Coates (1988) |
| Plotosidae | guarders, nesters | | | | Merrick & Schmida (1984) |
| <i>N. novaeguineae</i> | | 2.0 | 500–1500 | 2500 | Coates unpublished |
| Hemiramphidae | non-guarders, plant spawners | | | | Collette et al. (1984) |
| <i>Zenarchopterus</i> spp. | | | | | |
| <i>Z. kampeni</i> | | 3.5 | 100–200 | 5000 | Coates & Van Zwieten (1992) |
| Melanotaeniidae | non-guarders, plant spawners | 2.0 | | | Allen & Cross (1982) |
| <i>G. multisquamatus</i> | | 0.69 | 200–700 | 33 × 10 ³ | Coates (1990a) |
| Syngnathidae | bearers, pouch brooders | – | < 20 | – | Dawson (1984) |
| Terapontidae | non-guarders, plant spawners | – | – | – | Breder & Rosen (1966) |
| <i>H. transmontanus</i> | | relatively large | relatively low | – | Van Zwieten, personal communication |
| Apogonidae | bearers, mouth brooders | | | | Breder & Rosen (1966) |
| <i>G. gjellerupi</i> | | 3.3 | 88–800 | – | Van Zwieten personal communication |
| Gobiidae | guarders, tenders | | | | Breder & Rosen (1966) |
| all Sepik-Ramu spp. | | relatively large | relatively low | – | Coates & Van Zwieten unpublished |
| Eleotrididae | guarders, nesters | | | | Breder & Rosen (1966) |
| <i>Op. aporos</i> | | 0.3 | 5 × 10 ⁵ –15 × 10 ⁵ | 13.0 × 10 ⁶ | Coates (1992b) |
| <i>Ox. heterodon</i> | | 0.46 | 15 × 10 ⁵ –35 × 10 ⁵ | 0.16 × 10 ⁶ | Coates (1992b) |
| <i>Mogurnda</i> spp. | | relatively large | relatively low | – | Van Zwieten personal communication |

fauna is devoid of most of the limited number of Australasian freshwater fish taxa with relatively high fecundities. All of the diadromous Sepik-Ramu fishes either avoid or do not preferentially inhabit floodplains. Most are pelagic spawners with high fecundities. However, these are generally limited to brief incursions into the lower river from essentially marine populations for reasons already outlined.

Increased egg sizes in freshwater representatives of marine families occur in a number of cases: Ambassidae (Coates 1990b), Hemiramphidae (Coates & Van Zwieten 1992), Apogonidae (Coates & Allen unpublished). The apparent tendency of fish taxa to produce larger eggs when colonising freshwater from marine environments would further contribute to potentially reproductive rates amongst the Australasian freshwater ichthyofauna. Unfortunately, lack of data on marine counterpart taxa hinders further analysis.

The introduced tilapia, *Oreochromis mossambicus* (Cichlidae) and common carp, *Cyprinus carpio* (Cyprinidae), both exploit Sepik-Ramu floodplains (Coates 1985, Ulaiwi 1990). Although a mouth brooding species, the tilapia has a high reproductive rate by Sepik-Ramu standards due to its small eggs (in comparison with Sepik-Ramu species exhibiting parental care) and young age at maturity. Common carp are highly fecund by Sepik-Ramu standards. Tilapia account for about half of the fish catch from lowlands (Coates 1985) and common carp, a more recent introduction, are also becoming abundant (Ulaiwi 1990). The significance of these two species in present fish catches illustrates the limited utilisation of Sepik-Ramu floodplain by native fish taxa and the importance of appropriate life-histories for their exploitation.

Trophic adaptations

In common with the rest of Australasia, the ichthyofauna of the Sepik-Ramu exhibits a remarkable lack of feeding specialisations compared to those found in tropical river basins outside this region. Only a limited number of species have even modest dietary specialisations and most feed on aquatic in-

vertebrates (Table 3). All comparisons made where data exist confirm that the trophic habits of Sepik-Ramu fishes differ little from their marine/estuarine counterparts (references in Table 3). A number of major riverine food resources have remained under-exploited by the ichthyofauna of the Sepik-Ramu and I conclude that this is a significant factor further contributing to the low fish productivity within the basin.

Although insectivores and omnivores are common in most river basins, there are major under-exploited food resources for fish in Sepik-Ramu, for example, algae (including phytoplankton), macrophytes, detritus (in its various forms), and allochthonous food sources (including fruits, seeds, berries, leaves and invertebrates, especially from flooded forest). These potential food resources are, or are likely to be, in at least adequate, and more usually abundant, supply within the Sepik-Ramu (Dudgeon 1990, Coates 1993a, Bowen unpublished). Piscivores are also conspicuously absent but the forage fish resource may be limiting except for *Op. aporos* which is eaten almost exclusively by *Ox. heterodon* (Table 3). Molluscivores are also absent but it is not known if this is a major potential trophic opportunity.

The lack of detritivores has probably had the greatest influence on fish production and biomass in the Sepik-Ramu. Bowen (1983) regards detritivory as a highly specialised feeding habit due to the morphological and behavioural adaptations required for its efficient exploitation. Detritivores contribute significantly to fish biomass within most tropical rivers outside Australasia. For example, a single detritivorous species accounts for 60% of the total ichthyomass of the Rio Parana, S. America (Bowen 1983). Truly detritivorous native species are absent from the Sepik-Ramu and are not recorded anywhere in Australasian freshwaters (except possibly mullets). The biomass produced by the introduced tilapia in the Sepik-Ramu illustrates the importance of detritus. Allochthonous inputs are another major food resource for fishes within tropical rivers, certainly in terms of specialisations for their exploitation, but probably also in terms of fish production (e.g. Goulding 1980, Goulding et al. 1988). Only *Zenarchopterus kampeni* exploits this

trophic opportunity within the Sepik-Ramu but this small species has a limited distribution, low biomass and a very low reproductive rate (Coates & Van Zwieten 1992).

Fishery management considerations

Hypothesis 3: (i) It is possible to increase potential fish catches of the Sepik-Ramu basin, and (ii) maintain the diversity of the native ichthyofauna, by introducing appropriate fish species

Potential for increased fish catches in the Sepik-Ramu through fish introductions is self-evident. Two inadvertently introduced fish species, tilapia, *O. mossambicus*, and carp, *C. carpio*, already have possibly shown this. Regrettably, neither of these fish

Table 3. Trophic habits of adults of the major elements of the Sepik-Ramu ichthyofauna. Key: Feeding position – B = bottom, MW = mid-water, S = surface; food types – AI = aquatic insects and their larvae, ITS = insects from terrestrial sources, AVM = allochthonous vegetable matter, C = crabs, CP = caridinid prawns, MP = *Macrobrachium* spp. prawns, S = scales, WF = whole fish.

| Family species | Feeding position | | | Food types | | | | | | | References | | | |
|-----------------------|------------------|----|---|------------|-----|-----|-----|-----------|----|----|------------|------|----|---|
| | B | MW | S | AI | | ITS | AVM | Crustacea | | | | Fish | | |
| | | | | lg. | sm. | | | C | CP | MP | | S | WF | |
| Megalopidae | | | | | | | | | | | | | | |
| <i>M. cyprinoides</i> | - | + | + | + | - | + | - | - | + | - | - | - | - | Coates (1987b) |
| Anguillidae | + | + | + | + | + | - | - | - | - | - | - | - | - | Allen & Coates (1990) |
| Ariidae | | | | | | | | | | | | | | |
| <i>A. utarus</i> | + | + | - | + | - | - | - | - | + | + | + | - | - | Coates (1991) |
| <i>A. solidus</i> | + | + | - | + | - | - | - | - | + | + | + | - | - | Coates (1991) |
| <i>A. coatesi</i> | + | + | - | + | - | - | - | - | + | - | - | - | - | Coates (1991) |
| <i>A. nox</i> | - | + | - | + | + | - | - | - | - | - | - | - | - | Coates (1991) |
| <i>A. velutinus</i> | + | + | + | + | - | + | - | - | - | - | - | - | - | Coates (1991) |
| Plotosidae | + | + | - | + | + | - | - | - | - | - | - | - | - | Allen & Coates (1990); Van Zwieten personal communication |
| Hemiramphidae | | | | | | | | | | | | | | |
| <i>Z. kampeni</i> | - | - | + | - | + | + | + | - | - | - | - | - | - | Coates & Van Zwieten (1992) |
| Melanotaeniidae | - | + | + | - | + | + | - | - | - | - | - | - | - | Coates (1990a); Van Zwieten personal communication |
| Apogonidae | | | | | | | | | | | | | | |
| <i>G. gjellerupi</i> | + | + | - | + | - | - | - | + | + | - | - | + | - | Van Zwieten personal communication |
| Ambassidae | | | | | | | | | | | | | | |
| <i>A. interrupta</i> | - | + | - | - | + | - | - | - | - | - | - | - | - | Coates (1990b) |
| Gobiidae | + | - | - | + | + | - | - | - | - | - | - | - | - | Allen & Coates (1990); Van Zwieten personal communication |
| Eleotrididae | | | | | | | | | | | | | | |
| <i>Ox. heterodon</i> | - | + | - | - | - | - | - | - | - | + | - | + | - | Coates (1992b) |
| <i>Op. aporos</i> | + | + | - | + | - | - | - | - | + | - | - | - | - | Coates (1992b) |
| <i>E. aquadulcis</i> | + | + | - | + | - | - | - | - | + | - | - | - | - | Allen & Coates (1990) |
| other spp. | + | + | - | + | + | - | - | - | - | - | - | - | - | Van Zwieten personal communication |

¹ fish eaten are exclusively *Op. aporos*.

were subject to pre-introduction study and their impact cannot be quantified. The available evidence clearly indicates an increase in fish crops by both species (Coates 1985, Ulaiwi 1990). The potential increase in fish production through further stocking is significant since Coates (1985) estimated catches from floodplain regions, 50% of which is already tilapia, to be only about 10% of those anticipated.

More fish introductions into the Sepik-Ramu will occur, either intentionally (Coates 1993a) or otherwise.

Despite the prominent contribution of tilapia to lowland ichthyomass, all native fish species known to occur in the Sepik-Ramu before its entry are still present thirty years later (Allen & Coates 1990). While the Sepik-Ramu ichthyofauna may yet stabilise in response to this exotic fish species, the example provides no evidence that native fish species extinctions are an inevitable result of introductions.

When considering the impact of exotic fish introductions on native fish species, an empirical question arises: Is the Sepik-Ramu ichthyofauna considered novel because of what it contains (suggesting that fish introductions may be more likely to cause extinctions of native fish species) or considered novel because of what it is missing (suggesting that there may be 'room' for more species)? An important related issue is whether the composition of the native ichthyofauna is due to the absence of taxa that are freshwater dispersants. One means of exploring this question is to consider what happens to the diversity of Australasian freshwater fish taxa in regions naturally dominated by freshwater dispersant groups (i.e. can they survive within diverse riverine ichthyofauna?).

The Kapuas River basin (Indonesia) is well suited for comparison, being suitably close, just to the west of Wallace's line, and reasonably well studied (Roberts 1989). Its ichthyofauna includes at least 290 species, distributed in 120 genera, representing about 40 families. Both freshwater dispersant and marine families occur and none of the species are diadromous. Compared with the Sepik-Ramu, the increase in both generic and species diversity within the Kapuas due to the presence there of freshwater dispersants is clear (Table 4). The Cyprinidae, for

example, account for almost half of the fish species diversity of the Kapuas (Roberts 1989).

Comparison of diversity amongst families common to the Fly and Kapuas illustrates that scope exists to increase the number of fish species in New Guinea freshwaters (Table 4). Most of such families

Table 4. Comparisons of the ichthyofauna of the Kapuas River basin (based on Roberts 1989) with that of the Fly and Sepik-Ramu basins in New Guinea, excluding diadromous species (from Appendix 1). X = family is absent; ? = there is uncertainty about whether certain Fly species are diadromous.

| | Number of genera/species | | |
|---|--------------------------|----------------|------------|
| | Kapuas | Fly | Sepik-Ramu |
| Freshwater representatives of marine families | | | |
| Dasyatidae | 1/1 | 1/1 | X |
| Clupeidae | 2/2 | 2/4 | X |
| Engraulidae | 2/2 | 1/2 (?) | X |
| Sundasalangidae (salmoniformes) | 1/2 | X | X |
| Ariidae | 2/3 | 4/13 | 1/5 |
| Belonidae | 1/1 | 1/2 | X |
| Hemiramphidae | 2/4 | 1/1 | 1/1 |
| Syngnathidae | 1/4 | X | 1/1 |
| Chanidae (= Ambassidae) | 3/5 | 3/4 (5?) | 1/1 |
| Datnioididae | 1/2 | X | X |
| Toxotidae | 1/1 | 1/1 (?) | X |
| Eleotrididae | 2/4 | 4/9 | 4/7 |
| Gobiidae | 6/9 | 3/8 | 2/6 |
| Soleidae | 1/3 | 2/2 | X |
| Cynoglossidae | 1/2 | 1/1 | X |
| Tetraodontidae | 2/6 | X | X |
| Plotosidae | X | 4/7 | 1/4 |
| Melanotaeniidae | X | 1/6 | 3/8 |
| Atherinidae | X | 1/2 | X |
| Iriatherinidae | X | 1/1 | X |
| Pseudomugilidae | X | 2/4 | X |
| Terapontidae | X | 3/5 | 1/1 |
| Sciaenidae | X | 1/1 | X |
| Periophthalmidae | X | 1/2 | X |
| Kurtidae | X | 1/1 | X |
| Total families/genera/species | 16/29/51 | 21/39/77 (78?) | 9/15/35 |
| Freshwater dispersant families: | | | |
| Osteoglossidae | 1/1 | 1/1 | X |
| Others | 90/238 | X | x |
| Total families/genera/species | 23/91/239 | 1/1/1/ | X |

are equivalently speciose between the two systems. The Ariidae, Eleotrididae, Clupeidae and Belontiidae have more species in the Fly River. However, several families are either marginally (Hemiramphidae, Soleidae, Cynoglossidae, Gobiidae) or notably (Tetraodontidae) more diverse in the Kapuas. Comparisons of the Sepik-Ramu and Kapuas are biased, in favour of my argument, because the Sepik-Ramu has a low fish species diversity compared with that of the Fly River for reasons already outlined. With the exception of ariids and eleotridids, families common to the Sepik-Ramu and Kapuas are more speciose in the latter system. For example, the existence of one freshwater pipefish species in the Sepik-Ramu and four species in the Kapuas is a remarkable denunciation of any theory that the presence of a diverse freshwater dispersant fish fauna necessarily reduces diversity of, or eliminates, freshwater fish taxa of marine origin.

A number of families of fishes in New Guinea freshwaters are absent from the Kapuas (Table 4). Of these the Melanotaeniidae, Iriatherinidae and Pseudomugilidae are restricted to Australasia. These may be less relevant to the comparison at hand. Their absence from the Kapuas could be due to zoogeographic phenomena other than the existence there of other freshwater groups. The absence of the latter two families from the Sepik-Ramu supports this conclusion; similarly for the Atherinidae. Plotosids are absent from the Kapuas. Both generic and species diversity of the ariids are significantly lower in the Kapuas by comparison with New Guinea. However, the two genera and three species of ariids in the Kapuas occur in the presence of 39 species of freshwater dispersant catfishes in 16 genera and 7 families. These include the Bagridae, Clariidae, Schilbeidae and Pangassidae (all large, aggressive, higher order river channel dwellers, as are the ariids, Coates 1991). Clearly, such catfishes have not displaced ariids from the Kapuas. The Kurtidae are absent from the Kapuas but also from the Sepik-Ramu. Freshwater representatives of the Sciaenidae, Periophthalmidae and the Terapontidae are absent from the Kapuas. Conversely, the Salmoniformes (Sundasalangidae) and Datnioididae have freshwater representatives in the Kapuas but not in New Guinea.

Although uncertainty exists with a number of taxa, one cannot conclude that the differences in fish families (representing marine taxa) resident in Kapuas and New Guinea freshwaters are generally due to the presence of diverse freshwater dispersant groups within the Kapuas. Even stronger support for this conclusion comes from a comparison of the Sepik-Ramu and Kapuas ichthyofaunas. On the contrary, total species richness (amongst taxa representative of marine families) is higher in the Kapuas. Fish species diversity, even based solely on groups representative of marine families, is clearly well below that which a river system of size of the Sepik-Ramu can support. This supports the hypothesis in that, theoretically, introductions can increase species richness in the Sepik-Ramu without lowering richness of native fish species.

A practical aspect of this paper is to help discriminate the kinds of fishes that may be suitable for introduction into the Sepik-Ramu without reducing the diversity of native fish species; if not with certainty, at least by reducing the latitude for error. Since the Sepik-Ramu, and freshwater Australasian, fish faunas are generally unspecialised, it is reasonable to assume that the introduction of fish species specialised in appropriate ways might have the least likelihood of affecting the native fauna while still increasing fish production. The majority of Sepik-Ramu fish species feed on aquatic insects and prawns, and species with such feeding habits may be inappropriate for introduction. Extreme caution should be taken over the introduction of piscivorous species into the Sepik-Ramu. There are indications that Sepik-Ramu fishes are poorly adapted to cope with high mortality rates, due mainly to low fecundities (e.g. Coates 1991). The fact that the only major piscivore in the Sepik-Ramu (*Ox. heterodon*) feeds exclusively on the only species with a high reproductive rate (*Op. aporos*) supports this conclusion (Coates 1992). Food resources apparently underexploited by the existing fishes are sensible areas to investigate further. In particular, those species feeding on detritus, macrophytes, algae and allochthonous inputs of vegetable matter hold the greatest promise for safer introduction. The situation is complicated by the relative absence of fishes at altitudes above about 800 m.a.s.l.

(Van Zwieten 1990), where aquatic insects may be both more diverse and more abundant than in lowlands (Dudgeon personal communication).

Unfortunately, the assumption that introductions from within the region might be preferable to those from further afield, since such taxa may be better 'co-adapted' (Li & Moyle 1981), creates two distinct problems for the Sepik-Ramu. First, many taxa could probably not be transferred successfully because of the differing ecological characteristics of the Sepik-Ramu (no estuarine breeding grounds). Second, no fish species within the region utilises the important under-exploited food resources in the Sepik-Ramu. Consequently, Australasia holds little promise of suitable species. There are, however, a number of interesting exceptions. For example, certain pelagic spawning taxa in the Fly River (clupeids and engraulids) have evolved populations breeding in freshwater. The transfer of such species to the Sepik-Ramu may be successful. In effect, this compensates for the inability of such taxa to colonise the Sepik-Ramu by natural means. Unfortunately, a number of such species are piscivorous in the Fly River and the others are insectivorous (Roberts 1978), contradicting previous conclusions concerning the minimisation of competition within the Sepik-Ramu. In addition, none are particularly useful species for commercial fishery purposes. In almost every case, potential transfers within Australasia cause similar theoretical problems. Compromises between the preference for within region transfers and the ecological logic that species from further afield may fulfil requirements more appropriately inevitably result.

General discussion

Considering the ecology of Australasian freshwater fishes from the point of view of their origins requires a much more holistic approach than is currently evident within the region. The result can be rewarding and has led to improved interpretation of the ecology of the Sepik-Ramu ichthyofauna. It also points to the need for more studies on the ecology of Indo-Pacific brackish water ichthyofaunas from which the Australasian freshwater fish assem-

blage mainly arose. The approach shows that three main factors influence the fish ecology of the Sepik-Ramu: (1) the ichthyofauna being Australasian in origin; (2) the very recent development of extensive Sepik-Ramu lowland habitats; and, (3) the limited extent of the estuarine environment. The latter two factors account for the depauperate Sepik-Ramu fish assemblage compared with those of southern New Guinea and northern Australian systems and exacerbates the general peculiarities of the Australasian freshwater fish fauna. As a result, fish catches are low in the Sepik-Ramu both by comparisons within the New Guinea (Hortle 1989) or worldwide (Coates 1985). The much higher catches recorded from the Fly River (Hortle 1989), for example, are mainly due to the presence there of the barramundi and pelagic spawning freshwater herrings (*Nematalosa* spp.); both noted to be absent from the Sepik-Ramu because of its limited estuary. Low fish catches, by world standards, are probably a general feature of tropical Australasian river systems where the unspecialised ichthyofauna exhibits limited exploitation of the trophic resources available. Observations from the Sepik-Ramu also suggest that diadromous fishes and those with low fecundities do not exploit floodplains. The preponderance of such species in Australasia probably further constrains fish production from its freshwaters. However, by contrast to New Guinea, Australian river systems do not supply essential protein for the majority of the population and this may explain the lack of attention to their fish ecology and production. That Australian freshwaters can be productive for fish is illustrated by the success of introduced exotic fish species there (e.g. Fletcher et al. 1985), as in the Sepik-Ramu.

Allen (1991) recorded 11 species in the Sepik-Ramu, but only 8 in the Fly River, above 600 metres above sea-level, supporting the view that diversity of the existing higher altitude fishes in the Sepik-Ramu is equable to or greater than that in the Fly. However, problems with the fish ecology of the Sepik-Ramu also occur in these lower-order, tributary, streams. The reduction of fish species diversity with altitude results in negligible fish stocks above about 800 metres above sea-level (Van Zwieten 1990), whereas the basin extends beyond 4500 m.

Considerable attention to these regions within the Sepik-Ramu is required because of the large number of people who would benefit from improved fisheries resources there. This drastic decline in fish stocks with altitude may be particularly evident in Australasian river systems. The region is conspicuously devoid of fish species adapted to cooler rhithronic sections of tropical rivers.

Limited scope exists for significantly improving Sepik-Ramu catches based on native fish species alone. Excluding lowlands, the majority of the catchment has a negligible stock of fish. In lowlands, most species are unlikely to be able to cope with increased mortality arising from increased fishing pressure due to their low reproductive rates (Coates 1987a, 1988, 1991) or the peculiarities of their predator-prey relationships (Coates 1992). The fishery is probably not even sustainable at present levels of exploitation per capita given the current population growth rate of about 2.3% per annum. Given this scenario, Coates (1993b) placed further fish introductions into the Sepik-Ramu within the framework of sustainable development, including attention to the maintenance of biodiversity. This is best achieved through rational evaluations, of which this paper forms part, and adherence to a code of practice regarding fish introductions (Coates 1993a). This represents a considerable shift in approach from the capricious introductions that have occurred in most countries, including the 20 species of freshwater fishes brought to Papua New Guinea under previous administrations (West & Glucksman 1976).

Predicting accurately the outcomes of species transfer may be difficult, if not impossible, to achieve. There is a particular lack of knowledge of potential interactions between alien fish and other, non-fish, biota that are also relevant to biodiversity issues. I do, however, regard the Sepik-Ramu ichthyofauna as distinctive because of what is absent, not what is present, as witnessed by comparisons with the ichthyofaunas of other regions. The hypothesis that the introduction of fish can both increase fish production and have minimal impacts of

the native ichthyofauna is not meaningless in practice. The native ichthyofauna is safeguarded better in this fashion because it indicates a logical direction in which to proceed and one on which to base necessary management decisions and further research.

Regardless of considerable attention to the effects of alien freshwater fishes on ecosystems, there has been little utilitarian outcome. A notable exception is the development of codes of practice regarding fish species transfers (Turner 1988), although they are largely ignored (e.g. Courtenay & Robins 1989). Such codes promote a more rational approach to decision making but the appraisal of the ecological basis of fish transfers remains an area of considerable speculation (Coates 1993a). Much of the debate is negative in its approach and less than helpful in a Sepik-Ramu situation. Here, most of the under-privileged people strive to exploit a fishery resource that is clearly inadequate, and in places non-existent. Emphasis should shift towards practical assistance, via improving the understanding of the interactions of alien and native biota and, hence, assisting with pre-introduction appraisals. I hope that this paper is at least a step in the right direction in this respect.

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Appendix continued.

| | Distribution | | | Habit | Habitat | | | | | | | | | | |
|---|--------------|------------|---------|-------|---------|----|-----|-----|-----|---|---|------|------|------|--|
| | Fly | Sepik-Ramu | Other | | LRO | RC | LRC | MRC | URC | L | F | TSLA | TSMA | TSHA | |
| <i>Stolephorus indicus</i> (van Hasselt) | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Stolephorus bataviensis</i> Hardenberg | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Thryssa scratchleyi</i> (Ramsay & Ogilby) | + | - | SNG | D | - | - | - | + | + | - | - | - | - | - | |
| <i>Thryssa rastroso</i> Roberts | + | - | EFR | | - | - | - | - | + | - | - | - | - | - | |
| <i>Thryssa brevicauda</i> Roberts | + | - | EFR? | D? | + | - | - | - | - | - | - | - | - | - | |
| <i>Thryssa spinidens</i> (Jordan & Seale) | ? | - | | | | | | | | | | | | | |
| <i>Thryssa hamiltoni</i> Gray | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| Osteoglossidae | | XX | | | | | | | | | | | | | |
| <i>Scleropages jardini</i> (Saville-Kent) | + | - | SNG | | - | - | - | + | - | + | - | - | - | - | |
| Ariidae | | | | | | | | | | | | | | | |
| <i>Arius leptaspis</i> (Bleeker) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius latirostris</i> Macleay | + | - | SNG | | - | - | - | - | + | - | - | + | + | + | |
| <i>Arius carinatus</i> Weber | + | - | SNG | | - | - | + | + | - | - | - | - | - | - | |
| <i>Arius augustus</i> Roberts | + | - | EFR | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius berneyi</i> (Whitley) | + | - | SNG | | - | - | - | + | + | - | - | - | - | - | |
| <i>Arius stirlingi</i> Ogilby | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius graeffei</i> Kner & Steindachner | + | - | SNG | D | - | - | - | + | - | - | - | - | - | - | |
| <i>A. (Hemipimelodus)</i> <i>crassilabris</i> ¹ | + | - | SNG | | - | - | - | + | + | - | - | - | - | - | |
| <i>Arius (H.) macrorhynchus</i> Weber | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius (H.) taylori</i> Roberts | + | - | EFR | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius solidus</i> Herre | - | + | NNG | | - | + | - | - | - | + | - | - | - | - | |
| <i>Arius velutinus</i> (Weber) | - | + | NNG | | - | + | - | - | - | - | + | + | - | - | |
| <i>Arius utarus</i> Kailola | - | + | NNG | | - | + | - | - | - | + | - | - | - | - | |
| <i>Arius coatesi</i> Kailola | - | + | NNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Arius nox</i> Herre | - | + | NNG | | - | + | - | - | - | + | - | - | - | - | |
| <i>Cinetodus froggati</i> (Ramsay & Ogilby) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Nedystoma dayi</i> (Ramsay & Ogilby) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Cochlefelis spatula</i> (Ramsay & Ogilby) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Cochlefelis danielsi</i> (Regan) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| Plotosidae | | | | | | | | | | | | | | | |
| <i>Porochilus obbesi</i> Weber | + | - | SNG | | - | - | + | + | - | + | - | - | - | - | |
| <i>Porochilus meraukensis</i> (Weber) | + | - | SNG | | - | - | + | + | - | - | - | - | - | - | |
| <i>Neosilurus brevidorsalis</i> (Gunther) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Neosilurus ater</i> (Perugia) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Neosilurus equinnus</i> (Weber) | + | - | SNG | | - | - | - | - | + | - | + | + | + | + | |
| <i>Neosilurus gjellerupi coatesi</i> Allen | - | + | ESR | | - | - | - | - | - | - | - | + | - | - | |
| <i>Neosilurus gjellerupi</i> <i>gjellerupi</i> (Weber) | - | + | NNG,SNG | | - | - | - | - | - | - | + | + | + | + | |
| <i>Neosilurus idenburgi</i> Nichols | - | + | NNG | | - | - | - | - | - | - | - | + | - | - | |
| <i>Neosilurus novaeguineae</i> (Weber) | - | + | NNG | | - | + | - | - | - | - | + | - | - | - | |
| <i>Neosilurus</i> sp. (Allen 1991) | - | + | ESR | | - | - | - | - | - | - | + | - | - | - | |
| <i>Plotosus papuensis</i> Weber | + | - | SNG | | - | - | - | + | + | - | - | - | - | - | |
| <i>Plotosus canius</i> (Hamilton-Buchanan) | + | - | SNG | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Oloplotosus luteus</i> Gomon & Roberts | + | - | EFR | | - | - | - | - | - | - | - | - | + | + | |

¹ Ramsay & Ogilby.

Appendix continued.

| | Distribution | | | Habit | Habitat | | | | | | | | | |
|---|--------------|------------|---------|-------|---------|----|-----|-----|-----|---|---|------|------|------|
| | Fly | Sepik-Ramu | Other | | LRO | RC | LRC | MRC | URC | L | F | TSLA | TSMA | TSHA |
| Belontiidae | | XX | | | | | | | | | | | | |
| <i>Strongylura stongylura</i> (van Hasselt) | + | - | SNG | | + | - | - | - | - | - | - | - | - | - |
| <i>Strongylura krefftii</i> (Gunther) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - |
| Hemiramphidae | | | | | | | | | | | | | | |
| <i>Arrhamphus sclerolepis</i> Günther | + | - | SNG | D | + | - | - | - | - | - | - | - | - | - |
| <i>Zenarchopterus dispar</i> (Valenciennes) | + | - | SNG,NNG | D | + | - | - | - | - | - | - | - | - | - |
| <i>Zenarchopterus novaeguineae</i> (Weber) | + | - | SNG | | - | - | - | - | + | - | - | - | - | - |
| <i>Zenarchopterus kampeni</i> (Weber) | - | + | NNG | | - | + | - | - | - | - | + | - | - | - |
| Melanotaeniidae | | | | | | | | | | | | | | |
| <i>Melanotaenia oktediensis</i> Allen & Cross | + | - | EFR | | - | - | - | - | - | - | - | + | + | - |
| <i>Melanotaenia sexlineata</i> (Munro) | + | - | EFR | | - | - | - | - | - | - | - | + | - | - |
| <i>Melanotaenia splendida</i> <i>rubrostriata</i> ¹ | + | - | SNG | | - | - | - | - | - | - | + | - | - | - |
| <i>Melanotaenia iris</i> Allen | + | - | EFR | | - | - | - | - | - | - | - | - | - | + |
| <i>Melanotaenia maccullochi</i> Ogilby | + | - | SNG | | - | - | - | - | - | - | + | - | - | - |
| <i>Melanotaenia goldiei</i> Macleay | + | - | SNG | | - | - | - | - | - | - | + | - | - | - |
| <i>Melanotaenia affinis</i> Weber | - | + | NNG | | - | - | - | - | - | - | + | + | + | - |
| <i>Chilatherina campsi</i> (Whitley) | - | + | NNG,SNG | | - | - | - | - | - | - | + | + | + | - |
| <i>Chilatherina fasciata</i> (Weber) | - | + | NNG | | - | - | - | - | - | - | + | + | + | - |
| <i>Chilatherina crassispinosa</i> (Weber) | - | + | NNG | | - | - | - | - | - | - | + | + | + | - |
| <i>Chilatherina bulolo</i> (Whitley) | - | + | ESR | | - | - | - | - | - | - | + | + | + | - |
| <i>Glossolepis maculosus</i> Allen | - | + | ESR | | - | - | - | - | - | - | + | + | + | - |
| <i>Glossolepis ramuensis</i> Allen | - | + | ESR | | - | - | - | - | - | - | + | + | + | - |
| <i>G. multiguamatus</i> (Weber & de Beaufort) | - | + | NNG | | - | + | - | - | - | + | + | - | - | - |
| Atherinidae | | XX | | | | | | | | | | | | |
| <i>Craterocephalus randi</i> Nichols | + | - | SNG | | - | - | - | - | - | - | + | - | - | - |
| <i>Craterocephalus nouhuysi</i> (Weber) | + | - | SNG | | - | - | - | - | - | - | - | + | + | - |
| Iriatherinidae | | XX | | | | | | | | | | | | |
| <i>Iriatherina werneri</i> Meinken | + | - | SNG | | - | - | - | + | - | - | + | - | - | - |
| Pseudomugilidae | | XX | | | | | | | | | | | | |
| <i>Pseudomugil gertrudae</i> Weber | + | - | SNG | | - | - | - | - | - | + | - | + | - | - |
| <i>Pseudomugil inconspicuus</i> Roberts | + | - | SNG | D | + | - | - | - | - | - | - | - | - | - |
| <i>Pseudomugil novaeguineae</i> Weber | + | - | SNG | | - | - | - | - | - | - | + | - | - | - |
| <i>Pseudomugil paskai</i> Allen & Ivanstovff | + | - | EFR | | - | - | - | - | - | - | + | - | - | - |
| <i>Kiunga ballochi</i> Allen | + | - | EFR | | - | - | - | - | - | - | + | - | - | - |
| Syngnathidae | | | | | | | | | | | | | | |
| <i>Microphis spinachoides</i> (Duncker) | - | + | ESR | | - | - | + | + | - | - | - | - | - | - |
| <i>Microphis brachyurus</i> (Bleeker) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |

¹ Ramsay & Ogilby.

Appendix continued.

| | Distribution | | | Habit | Habitat | | | | | | | | | |
|--|--------------|------------|---------|-------|---------|----|-----|-----|-----|---|---|------|------|------|
| | Fly | Sepik-Ramu | Other | | LRO | RC | LRC | MRC | URC | L | F | TSLA | TSMA | TSHA |
| Toxotidae | | XX | | | | | | | | | | | | |
| <i>Toxotes chatareus</i> (Hamilton-Buchanan) | + | - | W | D | - | + | - | - | - | - | - | - | - | - |
| <i>Toxotes lorentzi</i> Weber | + | - | SNG | | - | - | + | + | - | - | - | - | - | - |
| Scatophagidea | | | | | | | | | | | | | | |
| <i>Scatophagus argus</i> (Linnaeus) | + | + | W | D | + | - | - | - | - | - | - | - | - | - |
| Leiognathidae | | | | | | | | | | | | | | |
| <i>Leiognathus eguulus</i> (Forskål) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |
| Mugilidae | | | | | | | | | | | | | | |
| <i>Crenimugil hetrocheilus</i> (Bleeker) | + | - | W | D | - | + | - | - | - | - | - | - | - | - |
| <i>Liza diadema</i> (Gilchrist & Thompson) | + | - | W | D | - | + | - | - | - | - | - | - | - | - |
| <i>Liza oligolepis</i> (Bleeker) | + | - | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Liza macrolepis</i> (Smith) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Liza melinoptera</i> (Valenciennes) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Liza tade</i> (Forskål) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Liza alata</i> (Steindachner) | * | + | W | D | + | - | - | - | - | - | - | - | - | - |
| Blennidae | | XX | | | | | | | | | | | | |
| <i>Omobranchus</i> sp. (Roberts 1978) | + | - | W? | D? | + | - | - | - | - | - | - | - | - | - |
| Gobiidae | | | | | | | | | | | | | | |
| <i>Glossogobius giurus</i> (Hamilton-Buchanan) | + | + | W | D? | - | + | - | - | - | - | - | - | - | - |
| <i>Glossogobius celebius</i> (Valenciennes) | + | - | W | | - | - | + | - | - | - | - | - | - | - |
| <i>Glossogobius concavifrons</i> ¹ | + | - | SNG | | - | - | - | - | + | - | - | + | + | - |
| <i>Glossogobius</i> sp. 1 (Allen 1991) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - |
| <i>Glossogobius</i> sp. 2 (Allen 1991) | + | - | EFR | | - | - | - | - | + | - | - | - | - | - |
| <i>Glossogobius</i> sp. 7 (Allen 1991) | + | - | EFR | | - | - | - | - | + | - | - | + | + | + |
| <i>Glossogobius</i> sp. 11 (Allen 1991) | + | - | EFR | | - | - | - | - | + | - | - | + | - | - |
| <i>Glossogobius</i> sp. 14 (Allen 1991) | - | + | ESR | | - | - | - | - | - | - | - | - | - | + |
| <i>Glossogobius bulmeri</i> Whitley | - | + | NNG | | - | - | - | - | - | - | - | + | + | + |
| <i>Glossogobius koragensis</i> Herre | - | + | ESR | | - | + | - | - | - | + | - | - | - | - |
| <i>Glossogobius coatesi</i> Hoese & Allen | - | + | ESR | | - | + | - | - | - | - | - | + | - | - |
| <i>Glossogobius torrentis</i> Hoese & Allen | - | + | ESR | | - | - | - | - | - | - | - | - | - | + |
| <i>Gobiopterus semivestitus</i> (Munro) | ? | - | | | - | - | + | - | - | - | - | - | - | - |
| <i>Gobiopterus</i> sp. (Roberts 1978) | + | - | EFR | | - | - | + | + | - | - | - | - | - | - |
| <i>Oxyurichthys jaarmani</i> Weber | + | - | SNG?,W? | D? | + | - | - | - | - | - | - | - | - | - |
| <i>Stenogobius laterisguamatus</i> (Weber) | - | + | NNG | | - | + | - | - | - | - | - | - | - | - |
| <i>St. genivittatus</i> (Cuvier & Valenciennes) | + | - | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Stenogobius</i> sp. 3 (Allen 1991) | + | - | SNG | | - | - | + | - | - | - | - | - | - | - |

¹ Ramsay & Ogilby.

Appendix continued.

| | Distribution | | | Habit | Habitat | | | | | | | | | | |
|---|--------------|------------|---------|-------|---------|----|-----|-----|-----|---|---|------|------|------|--|
| | Fly | Sepik-Ramu | Other | | LRO | RC | LRC | MRC | URC | L | F | TSLA | TSMA | TSHA | |
| <i>Mugilogobius fuscus</i> (Nichols) ² | *? | + | ? | | + | - | - | - | - | - | - | - | - | - | |
| <i>Redigobius bikolanus</i> (Herre) | * | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Redigobius romeri</i> Weber | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| Eleotrididae | | | | | | | | | | | | | | | |
| <i>Bostrychus strigogenys</i> Nichols | + | - | EFR | | - | - | - | - | + | - | - | + | - | - | |
| <i>Oxyeleotris herwerdenii</i> (Weber) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Oxyeleotris aruensis</i> (Weber) | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |
| <i>Oxyeleotris paucipora</i> Roberts | + | - | EFR | | - | - | - | - | + | - | - | - | - | - | |
| <i>Oxyeleotris nullipora</i> Roberts | + | - | EFR | | - | - | + | + | - | + | - | - | - | - | |
| <i>Oxyeleotris fimbriata</i> (Weber) ³ | + | + | SNG,NNG | | - | + | - | - | - | + | - | + | + | - | |
| <i>Oxyeleotris heterodon</i> (Weber) | - | + | NNG | | - | + | - | - | - | + | + | - | - | - | |
| <i>Oxyeleotris gyronoides</i> (Bleeker) | * | + | W | | - | - | - | - | - | - | - | - | + | - | |
| <i>Butis butis</i> (Hamilton-Buchanan) | + | - | SNG | D? | - | + | - | - | - | - | - | - | - | - | |
| <i>Butis ambionensis</i> (Bleeker) | * | + | W | D | - | + | - | - | - | - | - | - | - | - | |
| <i>Eleotris fusca</i> (Bloch & Schneider) | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Eleotris aquadulcis</i> Allen & Coates | - | + | ESR | | - | - | - | - | - | + | - | - | - | - | |
| <i>Eleotris melanosoma</i> Bleeker | * | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Mogurnda mogurnda</i> (Richardson) | + | - | SNG | | - | - | + | - | - | - | - | - | - | - | |
| <i>Mogurnda cingulata</i> Allen & Hoese | + | - | EFR | | - | - | - | - | + | - | - | + | + | + | |
| <i>Mogurnda aurofodinae</i> Whitley | - | + | NNG | | - | - | - | - | - | - | - | + | + | + | |
| <i>Mogurnda nesolepis</i> (Weber) | - | + | NNG | | - | - | - | - | - | - | - | + | + | - | |
| <i>Ophiocara porocephala</i> (Valenciennes) | + | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Ophieleotris aporos</i> (Bleeker) | * | + | W | | - | + | - | - | - | + | + | + | - | - | |
| <i>Prionobutis microps</i> (Weber) | ? | - | | | + | - | - | - | - | - | - | - | - | - | |
| <i>Hypseleotris guntheri</i> (Bleeker) | - | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Hypseleotris compressa</i> (Krefft) | + | - | SNG | | - | - | + | - | - | - | - | - | - | - | |
| Periophthalmidae | | | | | | | | | | | | | | | |
| <i>Periophthalmus novaeguineensis</i> Eggert | + | - | SNG | | + | - | - | - | - | - | - | - | - | - | |
| <i>Periophthalmus weberi</i> Eggert | + | - | SNG | | + | - | - | - | - | - | - | - | - | - | |
| <i>Zappa confluentus</i> (Roberts) | + | + | SNG,NNG | D | + | - | - | - | - | - | - | - | - | - | |
| Gobioidae | | | | | | | | | | | | | | | |
| <i>Brachyamblyopus urolepis</i> (Bleeker) | + | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Taenioides anguillaris</i> (Linnaeus) | * | + | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Taenioides cirratus</i> (Blyth) | + | - | W | D | + | - | - | - | - | - | - | - | - | - | |
| <i>Taenioides</i> sp. (Allen 1991) | + | - | EFR | | - | - | + | - | - | - | - | - | - | - | |
| Kurtidae | | | | | | | | | | | | | | | |
| <i>Kurtus gulliveri</i> Castelnau | + | - | SNG | | - | + | - | - | - | - | - | - | - | - | |

² distribution and habitats with New Guinea unknown.³ SNG & NNG populations possibly different taxa, Allen & Coates 1990.

Appendix continued.

| | Distribution | | | Habit | Habitat | | | | | | | | | |
|--|--------------|------------|-------|-------|---------|----|-----|-----|-----|---|---|------|------|------|
| | Fly | Sepik-Ramu | Other | | LRO | RC | LRC | MRC | URC | L | F | TSLA | TSMA | TSHA |
| Soleidae | | XX | | | | | | | | | | | | |
| <i>Aseraggodes klunzingeri</i> (Weber) | + | - | SNG | D? | - | - | + | - | - | - | - | - | - | - |
| <i>Synaptura villosus</i> Weber | + | - | SNG | | - | + | - | - | - | - | - | - | - | - |
| Cynoglossidae | | XX | | | | | | | | | | | | |
| <i>Cynoglossus heterolepis</i> Weber | + | - | SNG | D? | - | + | - | - | - | - | - | - | - | - |
| Tetraodontidae | | XX | | | | | | | | | | | | |
| <i>Marilyna meraukensis</i> (de Beaufort) | + | - | SNG | D? | + | - | - | - | - | - | - | - | - | - |
| <i>Tetraodon erythroaenia</i> Bleeker | + | - | W | D | + | - | - | - | - | - | - | - | - | - |
| <i>Sphoeroides pleurostictus</i> (Gunther) | + | - | W | D | + | - | - | - | - | - | - | - | - | - |

References cited

- Allen, G.R. 1991. Freshwater fishes of New Guinea. Christensen Research Institute, Publication 9, Madang. 268 pp.
- Allen, G.R. & D. Coates. 1990. An ichthyological survey of the Sepik River system, Papua New Guinea. Records of the Western Australian Museum Suppl. 34: 31–116.
- Allen, G.R. & N.J. Cross. 1982. Rainbowfishes of Australia and New Guinea. T.F.H. Publications, Neptune City. 141 pp.
- Balon, E.K. 1990. Epigenesis of an epigeneticist: the development of some alternative concepts of the early ontogeny and evolution of fishes. Guelph Ichthyol. Rev. 1: 1–48.
- Bowen, S.H. 1983. Detritivory in neotropical fish communities. Env. Biol. Fish. 9: 137–144.
- Breder, C.M. Jr. & D.E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City. 941 pp.
- Coates, D. 1985. Fish yield estimates for the Sepik River, Papua New Guinea, a large floodplain system east of 'Wallace's Line'. J. Fish Biol. 27: 431–443.
- Coates, D. 1987a. Consideration of fish introductions into the Sepik River, Papua New Guinea. Aqua. Fish. Manag. 18: 231–241.
- Coates, D. 1987b. Observations on the biology of tarpon, *Megalops cyprinoides* (Broussonet) (Pisces: Megalopidae), in the Sepik River, northern Papua New Guinea. Aust. J. Mar. Freshw. Res. 38: 529–535.
- Coates, D. 1988. Length-dependent changes in egg size and fecundity in females, and brooded embryo size in males, of fork-tailed catfishes (Pisces: Ariidae) from the Sepik River, Papua New Guinea, with some implications for stock assessment. J. Fish Biol. 33: 455–464.
- Coates, D. 1990a. Biology of the rainbowfish, *Glossolepis multisquamatus* (Melanotaeniidae) from the Sepik River floodplains, Papua New Guinea. Env. Biol. Fish. 29: 119–126.
- Coates, D. 1990b. Biology of the perchlet *Ambassis interrupta* Bleeker (Pisces: Ambassidae) in the Sepik River, Papua New Guinea. Aust. J. Mar. Freshw. Res. 41: 267–274.
- Coates, D. 1991. Biology of fork-tailed catfishes from the Sepik River, Papua New Guinea. Env. Biol. Fish. 31: 55–74.
- Coates, D. 1992. Biology of *Oxyeleotris heterodon* and its major prey, *Ophieleotris aporos*, two floodplains sleepers (Pisces: Eleotrididae) of the Sepik River fishery, northern Papua New Guinea. Env. Biol. Fish. 34: 51–64.
- Coates, D. 1993a. Implementation of the EIFAC/ICES code of practice: experiences with the evaluation of international fish transfers into the Sepik River basin, Papua New Guinea. Proceedings of the World Fisheries Congress, Athens, May 1992 (in press).
- Coates, D. 1993b. Environmental management implications of aquatic species introductions: a case study of fish introductions into the Sepik-Ramu Basin, Papua, New Guinea. Asian Journal of Environmental Management 1: 39–49.
- Coates, D., M.J. Nunn & K.R. Uwate. 1989. Epizootic ulcerative disease of freshwater fish in Papua New Guinea. Science in New Guinea 15: 1–11.
- Coates, D. & P.A.M. Van Zwieten. 1992. Biology of the freshwater halfbeak *Zenarchopterus kampeni* (Teleostei: Hemiramphidae) from the Sepik and Ramu River basin, northern Papua New Guinea. Ichthyol. Explor. Freshwaters 3: 25–36.
- Collette, B.B. 1983. Mangrove fishes of New Guinea. pp. 91–102. In: H.J. Teas (ed.) Tasks for Vegetation Science, 8, Dr W. Junk Publishers, The Hague.
- Collette, B.B., G.E. McGowen, N.V. Parin & S. Mito. 1984. Beloniformes: development and relationships. pp. 335–354. In: H.G. Moser et al. (ed.) Ontogeny and Systematics of Fishes, Amer. Soc. Ich. Herp. Spec. Pub. No. 1, Lawrence.
- Compagno, L.J.V. & T.R. Roberts. 1982. Freshwater dasyatid stingrays of Southeast Asia and New Guinea, with description of a new species. Env. Biol. Fish. 7: 321–339.
- Courtenay, W.R. Jr. & C.R. Robins. 1989. Fish introductions:

- good management, mismanagement or no management? *Rev. Aquat. Sci.* 1: 159–172.
- Dando, P.R. 1984. Reproduction in estuarine fish. pp. 155–170. *In*: G. Potts & R.J. Wootton (ed.) *Fish Reproduction: Strategy and Tactics*, Academic Press, London.
- Dawson, C.E. 1984. Revision of the genus *Microphis* Kaup (Pisces : Syngnathidae). *Bull. Mar. Sci.* 35: 117–181.
- Dudgeon, D. 1990. Benthic community structure and the effect of rotenone piscicide on invertebrate drift and standing stocks in two Papua New Guinea streams. *Arch. Hydrobiol.* 119: 35–53.
- Fletcher, A.R., A.K. Morison & D.J. Hume. 1985. Effects of carp, *Cyprinus carpio* L., on communities of aquatic vegetation and turbidity of waterbodies in the lower Goulburn River basin. *Aust. J. Mar. Freshw. Res.* 36: 311–327.
- Goulding, M. 1980. *The fishes and the forest: explorations in Amazonian natural history*. University of California Press, Berkeley. 208 pp.
- Goulding, M., M.L. Carvalho & E.G. Ferreira. 1988. Rio Negro: rich life in poor water. SPB Academic Publishing, The Hague. 200 pp.
- Grey, D.L. 1987. An overview of *Lates calcarifer* in Australia and Asia. pp. 15–21. *In*: J.W. Copland & D.L. Grey (ed.) *Management of Wild and Cultured Sea Bass/Barramundi (Lates calcarifer)*, Australian Center for International Agricultural Research Proceedings 20, Canberra.
- Hortle, K.G. 1987. First records of freshwater eels from the Fly River system, Papua New Guinea. *Fishes of Sahul*. S.R. Frankland Publishers, Moorabin 5: 202–204.
- Hortle, K.G. 1989. The potential for introduction of Fly River fishes to the Sepik. pp. 162–166. *In*: D.A. Pollard (ed.) *Introduced and Translocated Fishes and Their Ecological Effects*, Department of Primary Industries and Energy, Bureau of Rural Resources, Proc. 8, Canberra.
- Li, H.W. & P.B. Moyle. 1981. Ecological analysis of species introductions into aquatic systems. *Trans. Amer. Fish. Soc.* 110: 772–782.
- Löffler, E. 1977. *Geomorphology of Papua New Guinea*. CSIRO and Australian National University Press, Canberra. 195 pp.
- Lowe-McConnell, R.H. 1975. *Fish communities in tropical freshwaters*. Longman, London. 337 pp.
- McDowall, R.M. 1981. The relationships of Australian freshwater fishes. pp. 1253–1273. *In*: A. Keast (ed.) *Ecological Biogeography of Australia*, Dr. W. Junk Publishers, The Hague.
- Mekong Committee. 1976. *Fisheries and integrated Mekong River basin development, terminal report of the Mekong basinwise fishery studies*. University of Michigan, Ann Arbor. 367 pp.
- Merrick, J.R. & G.E. Schmida. 1984. *Australian freshwater fishes: biology and management*. Griffin Press, Netley. 409 pp.
- Moore, R. 1980. Migration and reproduction in the percoid fish *Lates calcarifer* (Bloch). Ph.D. Thesis, University of London, London. 215 pp.
- Moore, R. 1982. Spawning and early life history of barramundi, *Lates calcarifer* (Bloch), in Papua New Guinea. *Aust. J. Mar. Freshw. Res.* 33: 647–661.
- Munro, I.S.R. 1967. *The fishes of New Guinea*. Department of Agriculture, Stock and Fisheries, Port Moresby. 651 pp.
- Myers, G.S. 1949. Salt tolerance of freshwater fish groups in relation to zoogeographical problems. *Bijdragen tot de dierkunde* 28: 315–322.
- Petr, T. (ed.) 1983. *The Purari – tropical environment of a high rainfall river basin*. Monographiae Biologicae 51, Dr W. Junk Publishers, The Hague. 624 pp.
- Roberts, T.R. 1978. An ichthyological survey of the Fly River in Papua New Guinea with descriptions of new species. *Smithson. Cont. Zool.* 281. 72 pp.
- Roberts, T.R. 1989. *The freshwater fishes of Western Borneo (Kalimantan Barat, Indonesia)*. *Mem. Calif. Acad. Sci.* 14. 210 pp.
- Swadling, P., B. Hauser-Schaublin, P. Gorecki & F. Tiesler. 1988. *The Sepik-Ramu*. National Museum, Papua New Guinea, Port Moresby. 76 pp.
- Turner, G.E. 1988. Codes of practice and manual of procedures for consideration of introductions and transfers of marine and freshwater organisms. EIFAC/CECPI Occ. Pap. 23. 44 pp.
- Ulaiwi, W.K. 1990. The occurrence and spread of common carp, *Cyprinus carpio* L., in the Sepik River system, Papua New Guinea. pp. 765–768. *In*: R. Hirano & I. Hanyu (ed.) *Proceedings of the Second Asian Fisheries Forum*, Tokyo.
- Van Zwieten, P.A.M. 1990. Preliminary analysis of biomass, density and distribution of fish in tributaries and hillstreams of the Sepik-Ramu River system (Papua New Guinea). pp. 829–834. *In*: R. Hirano & I. Hanyu (ed.) *Proceedings of the Second Asian Fisheries Forum*, Tokyo.
- Welcomme, R.L. 1985. *River fisheries*. FAO Fish. Tech. Pap. 262. 330 pp.
- West, G.J. & J. Glucksman. 1976. Introduction and distribution of exotic fishes in Papua New Guinea. *Papua New Guinea Agriculture Journal* 27: 19–48.