Environmental Biology of Fishes **54**: 389–404, 1999.

Fishes of floodplain habitats of the Fly River system, Papua New Guinea, and changes associated with El Niño droughts and algal blooms

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Received 30 September 1997 Accepted 11 May 1998

Key words: oxbow lakes, fish catches, biomonitoring, species richness, Strickland River

Synopsis

Biological monitoring of the Fly River system in Papua New Guinea has shown that floodplain habitats (oxbow lakes, blocked valley lakes and seasonally inundated grassed floodplain) support diverse and abundant populations of freshwater fishes. Since monitoring first commenced in the early 1980's, a total of 66 fish species representing 33 families has been sampled, with gillnets and rotenone, from a range of sites located on the floodplains of the Fly and Strickland rivers. The fish fauna was dominated by catfishes in the families Ariidae (11 species) and Plotosidae (7 species), with aquatic invertivores being the dominant feeding group. Herring species (*Nematalosa* spp.) were often very abundant in the oxbow lakes, forming 66% of the total catch in all the floodplain habitats. The fish communities in the oxbow lakes and blocked valley lakes were distinctly different, with several of the smaller fish species being more abundant in the blocked valley lakes, while the oxbow lakes supported more of the larger predatory species. Catches in the oxbow lakes were also generally higher and more diverse than the blocked valley lakes or grassed floodplain sites. Since the commencement of monitoring, catches from the floodplain sites have varied considerably, both spatially and temporally. Reduced catches seen at some sites are probably associated with natural climatic factors, particularly 'El Niño'-induced droughts and algal blooms. Introduced species and increased commercial and artisanal fishing may also be affecting stocks of native fish. Fish populations were shown to recover only slowly in lakes affected by severe drought conditions, with extensive mats of floating grasses hindering fish recolonisation. Fish stocks in a lake affected by an algal bloom recovered more quickly than stocks in lakes affected by drought.

Introduction

The Fly River is one of the largest rivers in Australasia (mean annual discharge $\sim$ 6 000 m^3 sec^{-1}), with a catchment area of 76 000 km^2, and flows for over 1200 km from its source in the central-west cordillera to its mouth in the Gulf of Papua. The Ok Tedi and Strickland rivers are the two major tributaries of the Fly, with the latter contributing approximately 60% of the entire flow. Much of the catchment of the Fly River, particularly in the upper reaches, consists of dense primary tropical rainforest, while in the middle and lower reaches open savannah forest, swamp forest and seasonally inundated grasslands predominate. The area is sparsely populated, with an average human density of one to two persons per square kilometre.

Although the upper catchment extends to altitudes of up to 3500 m, the majority of the drainage basin is low-lying and flat, to the extent that the port of Kiunga, which is 800 river km from the coast, is only 22 m above sea-level. The combination of the flat land and high rainfall has resulted in a large seasonally inundated floodplain, with extensive shallow lake systems, occupying an area of 45 000 km^2, making it the largest wetland system in the country. Lake Murray (surface area 65 000 ha), situated on the floodplain of the Strickland River, is the largest lake in the country and also one of the largest in Australasia. The wetlands of the Fly River are high ly productive systems and play an important role in the ecology of the river system. The wetland fauna includes a diverse and productive fish community, which provides an important food source for villages along the river. The fish populations in the various floodplain habitats have been regularly monitored to provide an overall indicator of the 'health' and productivity of the floodplain ecosystem in relation to the possible effects of waste discharges from the Ok Tedi copper mine, located in the headwaters of the system (see Figure 1).

The freshwater fish fauna of the Fly River is the most diverse in the Australasian region, with 128 recorded species, (Roberts 1978, Coates 1993). Seventeen species are known only from the Fly basin and thirty or more are known only from the Fly and one or more of the large rivers in central-southern New Guinea (Roberts 1978). The fishes of the Fly River are characterised by the large size of some species, the abundance of endemic species and the dominance by groups that are poorly represented in other parts of the world, particularly the ariid and plotosid catfishes. In most other ways the composition of the freshwater fish fauna is largely determined by its position in the Australasian zoogeographical zone (Coates op.cit., Roberts op.cit.).

This paper describes the fishes of floodplain habitats of the Fly River system investigated during biological monitoring over the period 1983–1996 and their response to recent droughts and algal blooms. Normally, the Fly catchment is subject to very high rainfall conditions, with over 10 m of rain annually in the upper reaches, falling to 3–4 m in the middle and lower reaches. However, recently there has been a number of severe El Niño-induced droughts (in 1982, 1986, 1992 and most recently 1997) which have caused the river flow to decline substantially for long periods of time and many of the floodplain waterbodies to largely dry out. The utilisation of floodplain habitats by the fishes of the Fly River system has been described previously (Smith & Bakowa 1994), but the response of fish populations to the effects of recent El Niño droughts and algal blooms has not yet been documented.

Methods

Study sites

The studies which are reported here are concerned mostly with the river section known as the middle Fly, which extends between D'Albertis Junction, where the Ok Tedi meets the Fly, and Everill Junction, where the Strickland River meets the Fly (Figure 1). There are four major habitat types in the floodplain of the middle Fly: *blocked valley lakes* (total area 245 km^2), created where the Fly River acts as a hydraulic dam to flood broad, shallow valleys; *oxbow lakes* (122 km^2) from cut-off meander bends of the river; *grassed floodplain*, and *forested floodplain* (2473 km^2 combined) (Smith & Bakowa 1994). Currently, the monitoring programme includes six sites, two blocked valley lakes [Bosset Lagoon (sites BOS10 and BOS11) and Lake Daviumbu (DAV01)], three oxbow lakes [Sembe Oxbow (OXB03), Lake Pangua (OXB05), and an unnamed oxbow (OXB06)], and one seasonally inundated grassed floodplain site (FLD15). In addition, there are two sites on the Strickland River, one unnamed oxbow lake located in the middle reaches (OXB08) and one grassed floodplain site (SFL01), located near the junction with the Fly River (see Figure 1). The majority of these waterbodies are of small to moderate size ($\sim$ 0.5–20 ha).

The two blocked valley lakes, Bosset Lagoon and Lake Daviumbu, are shallow lakes (mean depth 4–6 m), and dry out in drought years. In contrast, oxbow lakes, e.g. OXB06, OXB03, OXB05, OXB08, are deeper (mean depth 10–20 m) and rarely dry out, acting as refuges for fishes during droughts. Both lake types are connected to the main Fly River

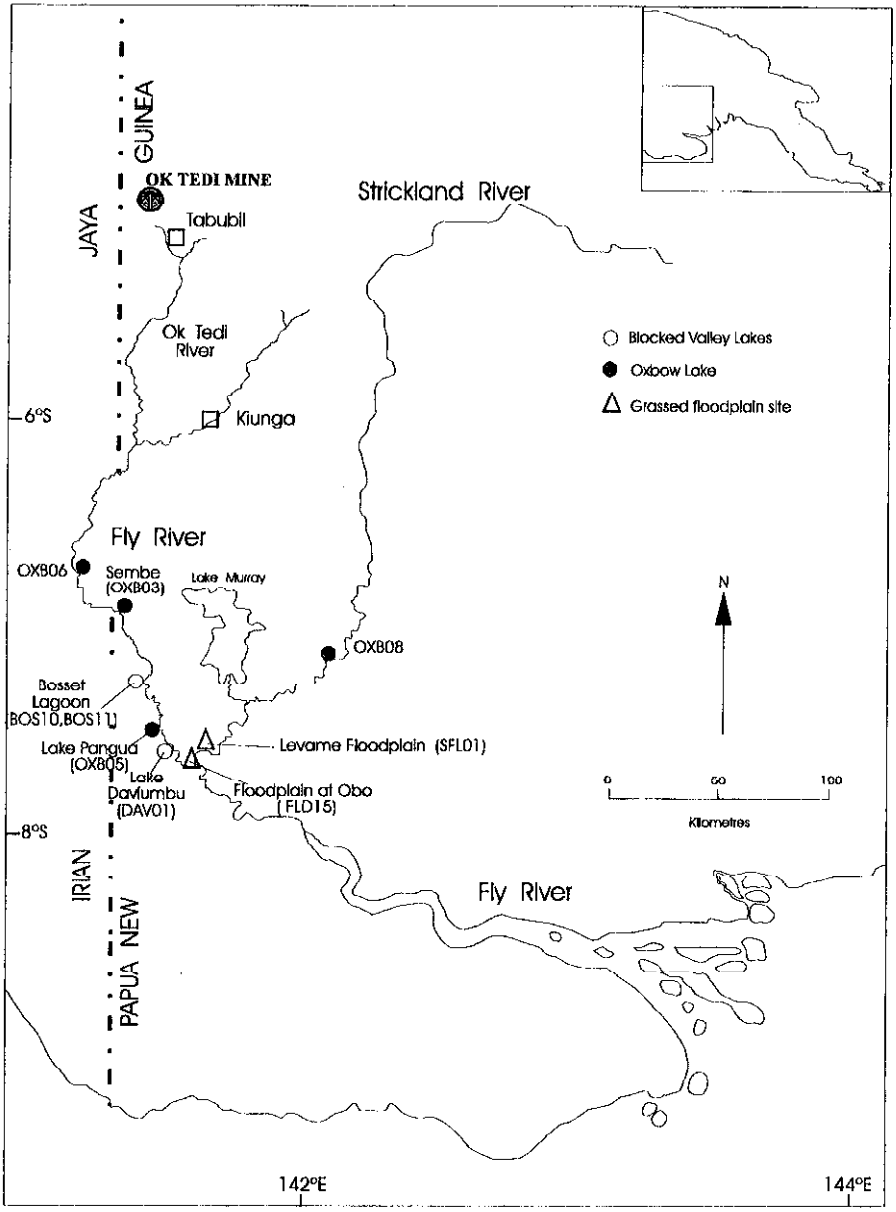

Figure 1. Location of floodplain sampling sites in the Fly River system.

by 'tie-channels', with the velocity and direction of water flow in the tie-channels depending on water levels and flow in the main river channel and floodplain. Water levels on the floodplain are largely determined by the extent of wet season flooding (November–February) and changes in river level in the dry season (March–October). The floodplain is subject to seasonal rainfall, with a monsoonally-influenced wet season. During this time, water tends to flow from local catchments onto the floodplain and so into the river. However, in the headwaters there is no marked seasonality in rainfall, and prolonged rainfall in the upper catchment during the floodplain dry season can result in a large rise in river level, with water flowing onto the floodplain and into the lakes through tie-channels. Conversely, a large drop in river level due to low rainfall in the headwaters may cause rapid draining of the lakes on the floodplain, which has been known to cause large fish-kills in the main river due to the sudden influx of deoxygenated water (OTML)[1].

Floodplain vegetation in the middle Fly includes fringing swamp forest (notably *Melaleuca, Barringtonia* spp.), but is dominated by herbaceous swamp vegetation, including *Ludwigia* spp., *Polygunum* spp. and the reed *Phragmites karka*. Large areas of the lakes can be covered in floating mats of aquatics, notably the aquatic fern, *Azola pinata*, grasses and the lilies, *Nymphaea* spp. and *Nelumbo nucifera*. This is particularly evident following 'El Niño'-influenced droughts, when re-flooded blocked valley lakes can be completely grass covered (Busse 1991). Two of the oxbow lakes (OXB08 and OXB06) are surrounded by seasonally flooded swamp forest, and two (OXB05 and OXB03) are surrounded by herbaceous swamp. The two floodplain sites (FLD15 and SFL01) are both shallow (mean depth 2 m), densely vegetated areas, situated close to the main river.

Mean monthly water quality parameters measured at selected floodplain sites during the year 1996–1997 are summarised in Table 1. Flow hydrographs for the Fly River at Kiunga during the years 1984–1997 are shown in Figure 2. The very low river flows during the latter half of 1997 were attributable to severe El Niño-induced drought conditions experienced in the catchment during which the floodplain lakes, with the exception of the deeper oxbow lakes, largely dried out. Less severe El Niño droughts also occurred in 1982, 1986 and 1992–1993, with many floodplain lakes in the middle Fly River also drying out.

In addition to freshwater fishes, the wetland fauna also includes crocodiles, both estuarine, *Crocodylus porosus*, and New Guinea freshwater, *C. novaeguineae*, and turtles, *Carettochelys insculpta* and *Chelodina* sp., which are relatively common. Large numbers of waterbirds also occur on the floodplain (Halse et al. 1995). The introduced Rusa deer, *Cer-*

[1] OTML. 1994. Report on a fish kill in the Fly River – October 1994. Report ENV 94–15 by Environment Department, Ok Tedi Mining Limited. 39 pp.

Table 1. Summary of mean monthly (standard deviation in parentheses) water quality parameters at selected floodplain sampling sites in the Fly River, 1996–1997.

	Sampling site				
	OXB03	OXB05	BOS10	DAV01	FLD15
Temp (° C)	29.1 (1.4)	33.1 (11.8)	28.9 (2.1)	29.2 (1.9)	27.7 (1.4)
pH	7.51 (0.40)	7.42 (0.38)	7.33 (0.49)	7.36 (0.32)	7.29 (0.33)
Conductivity (μs cm^{-1})	144 (30)	107 (38)	94 (48)	94 (38)	150 (45)
Alkalinity (mg l^{-1})	82 (19)	53 (24)	53 (16)	53 (16)	70 (17)
DO (mg l^{-1})	4.7 (1.6)	6.0 (1.6)	6.7 (1.8)	6.6 (1.9)	5.9 (3.3)
DOC (mg l^{-1})	2.4 (0.9)	4.4 (1.1)	5.1 (2.0)	5.4 (1.3)	3.8 (1.6)
dCu (μg l^{-1})	8.2 (6.6)	8.1 (3.8)	7.2 (4.0)	7.9 (4.1)	13.8 (9.8)
dZn (μg l^{-1})	1.1 (0.8)	1.6 (1.3)	1.4 (0.7)	1.3 (0.7)	2.0 (1.8)
dMn (μg l^{-1})	1.2 (2.0)	1.2 (2.1)	0.9 (0.4)	2.8 (4.5)	5.1 (10.2)
dFe (μg l^{-1})	59 (58)	197 (196)	393 (348)	378 (333)	228 (306)

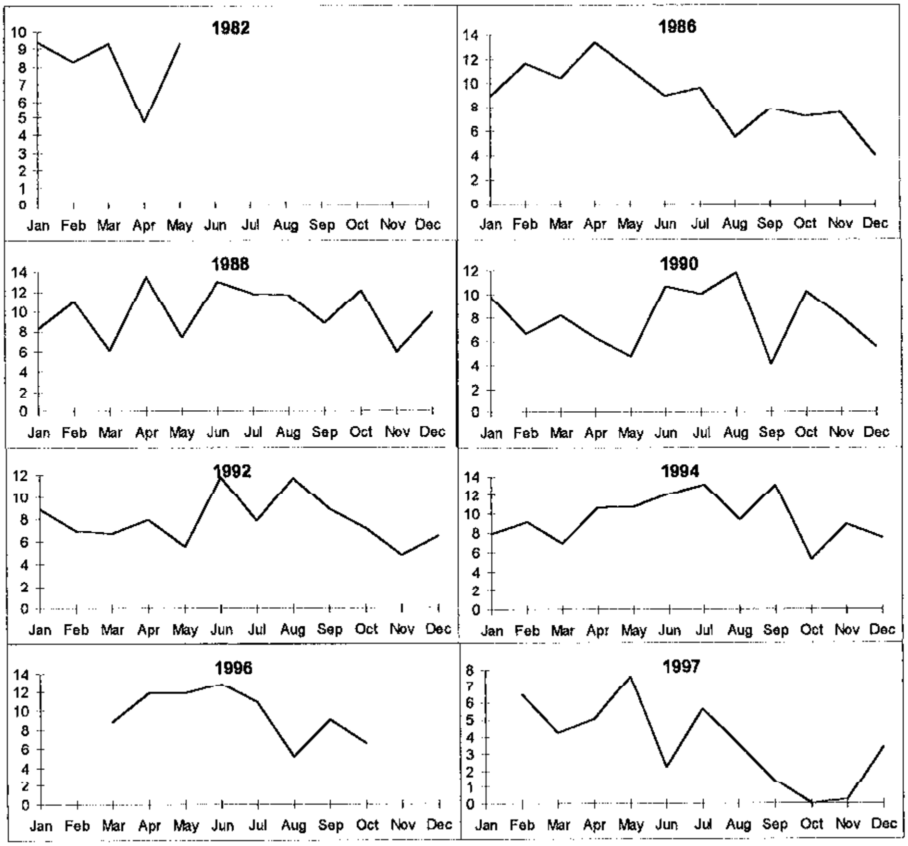

Figure 2. Mean monthly river levels (m) for the Fly River At Kiunga, 1982–1997.

vus timorensis, also occur in large numbers on the middle Fly floodplain (Busse 1991).

Sampling procedures

Fish populations were sampled through gillnetting and by the use of a fish toxicant (rotenone), using standardised procedures. Sampling was generally carried out at each site during the year on a quarterly basis.

Gillnetting

A standard set of 13 gillnets ranging in stretched mesh size from 25 mm to 175 mm, was utilised at each site. The nets were tied perpendicular to the bank in a series, each net separated from the next by a large enough disance to allow fish movements between the nets (usually 50 m). The order in which nets were set was from larger nets at each end of the series to smaller nets in the middle. The nets were set for 24 hours and checked at dawn, dusk and the end of the sampling period.

Rotenone

Rotenone was used at each site as a qualitative sampling method only as the water depth and dense vegetation precluded the containment of a known area. In each sample, 500 g of powdered rotenone was mixed with water and a small quality of detergent. The mixture was then applied to a small bay ($\sim$ 0.1 ha) and affected fish collected for one hour after application by means of dip-nets used from a small boat.

Sample processing

At each gillnet check, fishes were removed from the nets, identified to species, measured in length to the nearest 1 mm (standard or total length, depending on body shape) and weighed to the nearest 1 gram up to 6 kg and then to the nearest 100 g. All fishes were then given away to local villagers. When large numbers of a single species were caught in a net, a random subsample of approximately 100 specimens was measured individually, and the remainder counted and their total weight determined.

Rotenone samples contained small specimens which were difficult to identify in the field. These specimens were preserved and returned to the laboratory for processing, where they were identified, weighed to the nearest 0.1 g and fork length measured to the nearest 1 mm.

Feeding groups

Fish species were assigned to six feeding guilds (aquatic insectivores, terrestrial invertivores, predators, herbivores, detritivores, planktivores) according to information provided in Smith & Hortle (1991). Species which had one or two main food types were included in each of the appropriate feeding categories.

Statistical analysis

Differences in fish biomass at each site between years were tested by one-way analysis of variance using quaterly fish catch data as replicates within each year. Tukey's standardised range tests were applied to identify between year differences where there were significant main effects. Spearman rank correlations were used to follow monotonic changes in fish biomass over time at each site. The strength and direction of the relationship was indicated by the significance level and the correlation coefficient (r).

Similarity in the structure of fish communities in the six water bodies on the middle Fly floodplain were assessed using the agglomerative clustering technique *U*nweighted *P*airgroup Arith*m*etic *A*veraging (UPGMA) in the Pattern Analysis Package (Belbin)[2]. Combined gillnet and rotenone catches from each site, collected between June 1993 and September 1996 were utilised, taking the mean abundance of each species across all sampling occasions (n = 12). This was the longest period over which all sites were sampled (e.g. OXB06 was first sampled on 3 June 1993), giving a balanced sampling effort across sites. Averaging across multiple samples was used to buffer the effect of data collected during any suboptimal sampling occasions (e.g. El Niño droughts or algal blooms). Analysis was based on the Bray-Curtis dissimilarity coefficient, and species which occurred at only one site were omitted to avoid 'rare' species having a disproportionate effect on the analysis.

[2] Belbin, L. 1995. PATN, Pattern Analysis Package. Division of Wildlife & Ecology, CSIRO, Canberra.

Results

Fish catch composition

A total of 66 fish species representing 33 families has been captured from sites on the floodplain of the Fly River system since sampling first commenced in 1983 (Appendix). This compares with 84 species representing 32 families recorded from sites in the main channel of the Fly River, from the headwaters to the estuary, over the same time period (Swales et al. 1999). In terms of species richness, the fish fauna was dominated by catfish in the families Ariidae (11 species) and Plotosidae (7 species). The number of fish species recorded at individual floodplain sites ranged from a minimum of 29 (BOS11) to a maximum of 46 (BOS10). The number of species recorded from oxbow lakes varied from 32 (OXB06) to 44 (OXB05), while at grassed floodplain sites the maximum number of species (44) was recorded at SFL01. The relative proportions of the

Table 2. Total catches of the ten numerically dominant fish species sampled in Fly River floodplain sites.

Species	Total number sampled	Proportion of total catch
Nematalosa spp.	62565	65.91%
Arius berneyi	7041	7.42%
Ambassis agrammus	4717	4.97%
Neosilurus ater	4564	4.81%
Craterocephalus randi	4106	4.33%
Megalops cyprinoides	2592	2.73%
Arius leptaspis	2487	2.62%
Strongylura kreffti	2343	2.47%
Melanotaenia splendida rubrostriata	2306	2.43%
Anabas testudineus (exotic species)	2211	2.33%

ten most numerically dominant species captured from all the floodplain sites combined are shown in Table 2. Fly and Strickland River herrings (*Nematalosa flyensis* and *N. papuensis*) were by far the dominant species numerically in both sampling areas, forming over 65% of catches.

Gillnet catches

A total of 55 species (83% of the total number recorded in the Fly River system) has been sampled by gillnetting from the Fly River floodplain sites, compared to 43 species (81% of the total) in the Strickland River floodplain sites (Table 3). The total number of species recorded using gillnets was similar between different habitat types. However, in oxbow lakes, catches in the deeper waters, where gillnets were set, tended to be dominated by shoaling species such as herrings, *Nematalosa* spp., which were often extremely abundant, and larger species such as barramundi, *Lates calcarifer*, saratoga, *Scleropages jardinii*, and catfishes, *Arius berneyi* and *A. leptaspis*. Due to their close proximity to the main river channel, catches at the grassed floodplain sites tended to be much more affected by river level than the other floodplain habitats. The sites sampled were open water areas and so strictly speaking were not true seasonally-inundated grassed floodplain sites, which are difficult to sample due to the dense cover of tall aquatic grasses and reeds (> 2 m) and are more akin to true wetland habitats.

Rotenone catches

In both the Fly and Strickland River floodplain sites the number of species sampled using rotenone was around 25% fewer than obtained by gillnetting (Table 3), although up to 11 species were captured by rotenone alone. The most abundant species sampled were small species (average individual biomass ranged from 0.4 g to 6.7 g) such as *Nematalosa* spp., *Ambassis agrammus, Anabas testudineus* and *Melanotaenia splendida rubrostriata*. In addition, catches also included small and larger juveniles of larger species such as *Arius leptaspis, Arius berneyi, Neosilurus ater, Strongylura krefftii, Oxyeleotris herwerdenii, Scleropages jardinii* and *Parambassis gulliveri*, indicating that the sampling sites were breeding or nursery areas, but also that large individuals tend to sense the toxicant and move away from the area before being affected.

Feeding groups

Aquatic invertebrate feeders (invertivores) were the predominant feeding group in each habitat type, particularly oxbow lakes, followed by terrestrial invertivores and predators. Herbivores, detritivores and planktivores were not well represented (Figure 3).

Temporal changes in fish catches

Fish catches showed considerable temporal and spatial variation. Temporal plots of mean fish biomass and species richness at each site since the commencement of sampling are shown in Figure 4. Catches were much more consistent at the oxbow lake sites than at the blocked valley lakes and grassed floodplain sites, where marked inter-annual variations were often apparent.

Estimates of mean fish biomass recorded at each site since the start of monitoring (Figure 5), show that overall catches have generally been higher at the oxbow lake sites (mean biomass range 214–

Table 3. Number of fish species sampled in Fly River and Strickland floodplain sites using rotenone and gillnets.

	Total number of species recorded by all methods	Total number of species sampled using rotenone	Number of species sampled only by rotenone	Total number of species sampled by gillnets
Fly River	66	41 (62.1%)	11 (16.7%)	55 (83.3%)
Strickland River	53	30 (56.6%)	10 (18.9%)	43 (81.1%)

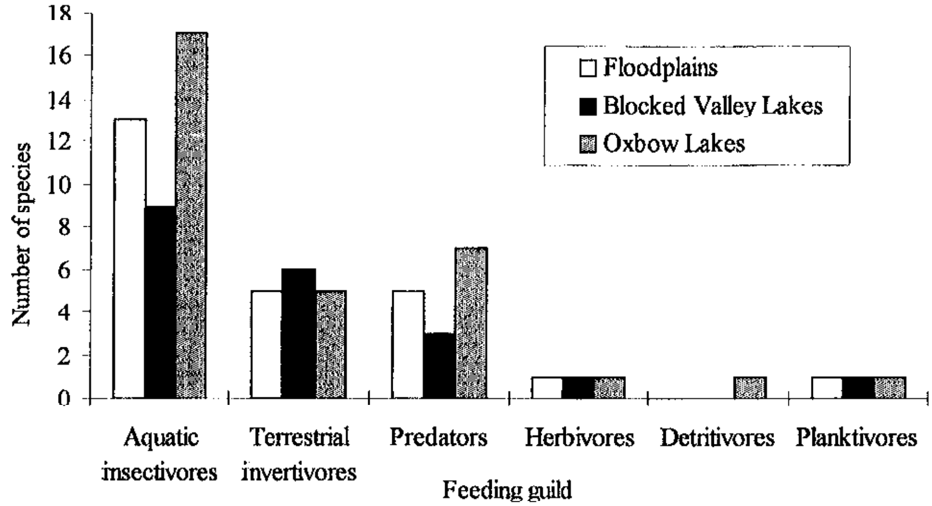

Figure 3. Number of fish species in each feeding guild recorded from each type of floodplain site for the period October 1995 – September 1996.

280 kg) than at the blocked valley lakes (54–144 kg) and floodplain sites (47–104 kg). However, total species richness estimates were more similar across sites, although mean fish species numbers at the oxbow lakes were generally higher than at either the blocked valley lakes or grassed floodplain sites.

ANOVA detected significant inter-annual differences in fish catch at OXB03, BOS10, OXB05 and DAV01 (Table 4). In most cases, catches in 1994

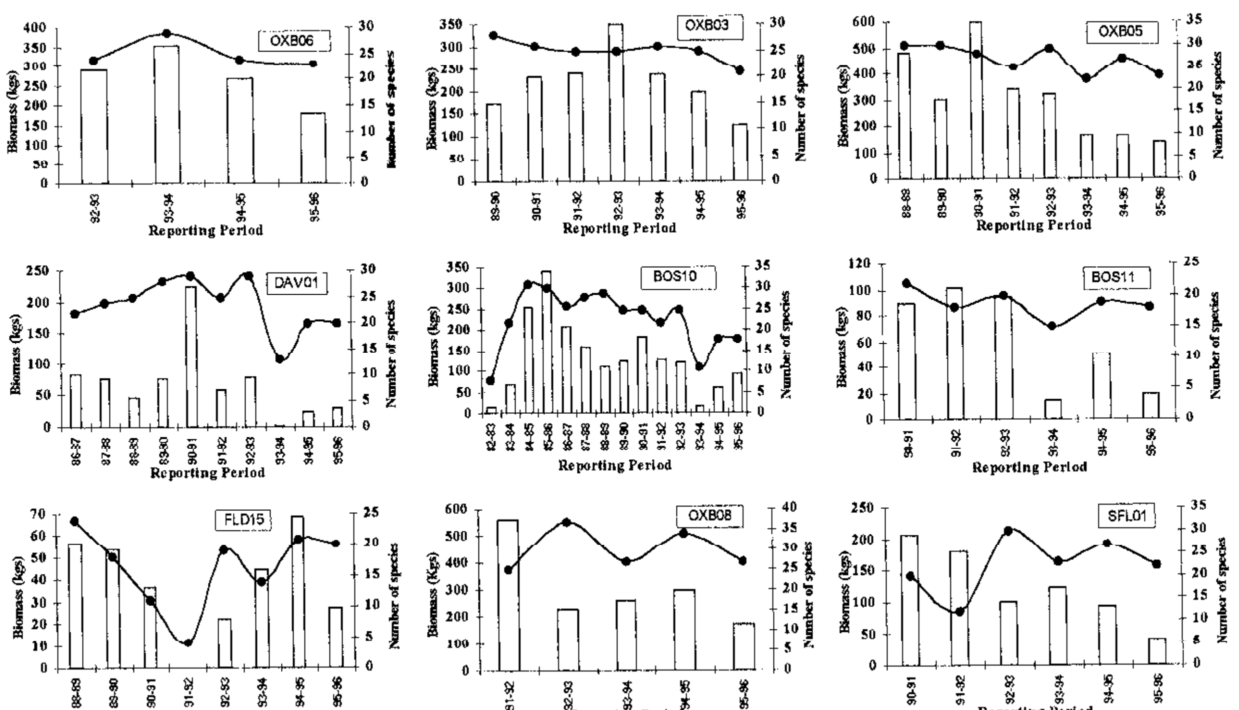

Figure 4. Mean fish catch biomass (bars) and richness (solid line) estimates at each floodplain site since the commencement of sampling.

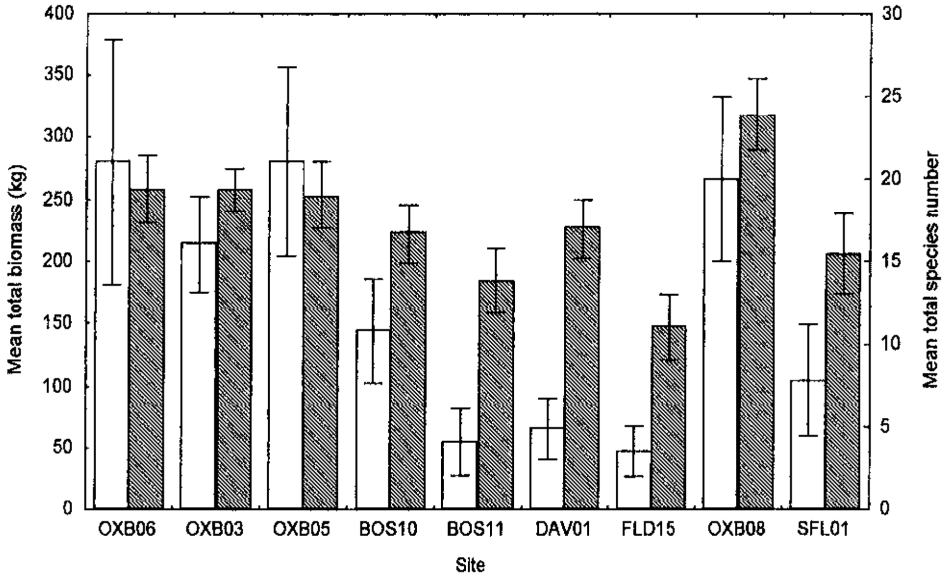

Figure 5. Mean fish biomass (open bars) and species diversity (shaded bars) estimates (± 95% confidence limits) recorded at each floodplain site since the commencement of biological monitoring.

were lower than in previous years and catches in following years were either higher or not significantly different from those in 1994. Spearman rank correlations showed significant negative correlations of fish catch with time at sites OXB06, BOS11, OXB05, DAV01 and SFL01 (Table 5).

Table 4. Summary of ANOVAs on between-year differences in fish biomass from floodplain sites (year differences are arranged in descending order, ns = not significant).

Site	df	F-value	p	Tukey's Multiple range test													
OXB06	3,8	1.28	ns														
OXB03	7,22	4.57	0.0065	93	91	94	92	95	90	89	96						
BOS10	13,30	3.23	0.0039	86	91	87	85	93	84	96	90	88	89	92	95	94	83
BOS11	5,9	1.28	ns														
OXB05	7,17	4.16	0.0077	91	90	92	93	89	95	96	94						
DAV01	9,19	5.30	0.0011	90	91	92	88	96	89	93	87	95	94				
FLD15	6,10	0.51	ns														
SFL01	5,7	2.14	ns														
OXB08	4,9	1.24	ns														

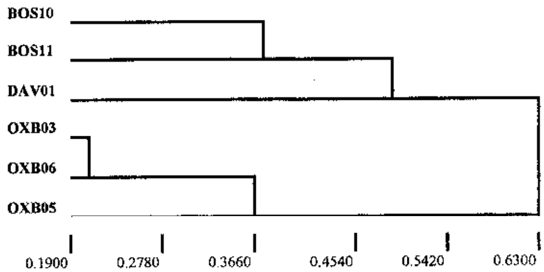

Figure 6. Classification of oxbow lake and blocked valley lake sites according to fish community composition and abundance.

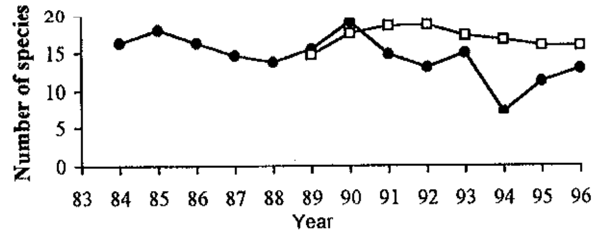

Figure 7. Annual number of fish species recorded in blocked valley lakes (●) and oxbow lakes (□) since the commencement of biological monitoring.

Comparison of fish communities in oxbow and blocked valley lakes

UPGMA classification demonstrated a clear separation of blocked valley lakes from oxbow lakes (Figure 6). Within the blocked valley lakes, replicate sites within Bosset Lagoon (BOS10 & BOS11) were more similar in community structure than to Lake Daviumbu (DAV01). OXB03 and OXB06 were the most similar oxbow lakes. This result corresponds with field observations, which suggest that fish communities in blocked valley lakes are distinct from those in oxbow lakes. The main difference between the two lake types appears to be that several of the smaller fish species, such as *Iriatherina werneri, Ambassis agrammus* and *Melanotaenia* sp., were more abundant in the shallower, well vegetated blocked valley lakes, while the deeper oxbow lakes supported more of the larger predatory species e.g. *Lates calcarifer* and *Scleropages jardinii.* In 1995–1996, eleven species recorded from the oxbow lakes (*Cinetodus froggati, Nedystoma dayi, Lates calcarifer, Parambassis gulliveri, Clarias batrachus, Ophieleotris aporos, Thryssa rastrosa, Thryssa scratchleyi, Kurtus gulliveri, Lutjanus goldei, Pristis microdon*) were not recorded from the blocked valley lakes, while only one species (*Iriatherina werneri*) present in the blocked valley lakes was not recorded from the oxbow lakes.

The mean number of species of fishes recorded in oxbow lakes and blocked valley lakes since the commencement of monitoring are shown in Figure 7. Fish richness in the oxbow lakes has remained relatively constant over the perod of monitoring, whereas there has been much more variation in the blocked valley lakes, with a marked decline in 1993–1994 coinciding with the El Niño drought conditions, with very low river flows and the drying out of many of the floodplain lake habitats.

Table 5. Summary of Spearman rank correlations of fish biomass versus time for data collected to 30 September 1996. Correlation coefficients and direction (+ = increase; – = decrease) are presented with level of significance (ns = not significant; * $p < 0.05$).

Site	Sample size (n)	Significance	Correlation coefficient
OXB06	12	*	– 0.685
OXB03	23	ns	– 0.127
BOS10	44	ns	– 0.231
BOS11	15	*	– 0.514
OXB05	25	*	– 0.583
DAV01	29	*	– 0.416
FLD15	17	ns	– 0.311
SFL01	13	*	– 0.637
OXB08	14	ns	– 0.433

Recovery of fish populations in blocked valley and oxbow lakes following drought and algal bloom

Fish catches (biomass and species richness) in Bosset Lagoon (sites BOS10, BOS11), Lake Pangua (OXB05) and Lake Daviumbu (DAV01) declined dramatically following the severe El Niño drought of late 1993/early 1994, in which some lakes (Bosset Lagoon and Lake Daviumbu) dried out completely. Since then, catches at most of these sites have gradually increased, although levels are still generally less then before the drought (Figure 8). Following the refilling of Bosset Lagoon during 1994, fish numbers and biomass both increased. High catches recorded in the first quarter of 1994 coincided with

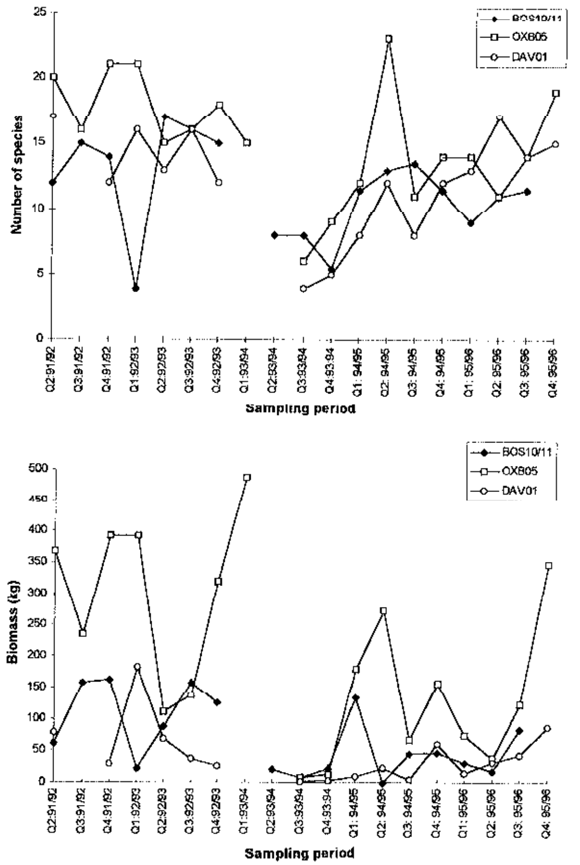

Figure 8. Fish biomass and species number recorded at Bosset Lagoon (sites BOS10, BOS11), Lake Daviumbu (DAV01), and Lake Pangua (OXB05) in each annual quarter (Q1–Q4) since 1990.

very low river levels and it seems that this may have been associated with fish being concentrated in a smaller lake area and being more vulnerable to capture. Fish numbers and biomass initially declined with increasing river levels as the lake area increased, but catches then increased as the lake was gradually recolonised.

The Lake Pangua (OXB05) fish community was severely depleted in April 1994 following an algal bloom of green, single celled filamentous algae (*Staurastrum* sp.) and subsequent low oxygen levels in the lake. The algal bloom occurred shortly after 'El Niño' conditions had resulted in both Bosset Lagoon and Lake Daviumbu drying out, so the subsequent recovery in fish stocks may have been influenced by both events. It is likely that fishes moved out of the lake onto the floodplain to avoid unfavourable conditions during the algal bloom and then moved back into the lake as conditions improved. Similar patterns were seen in fish biomass and diversity, with a rapid increase in fish catches and a steady increase in fish species richness following the cessation of the algal bloom (Figure 8).

Discussion

Biological monitoring has shown that sites on the floodplain of the Fly River support diverse and abundant communities of freshwater fishes. The combined use of gillnets and rotenone enabled a range of habitats to be sampled effectively. Gillnets sampled deeper waters and at all sites captured a wide range of fish species, while rotenone was generally effective in sampling the shallower areas, which tended to be important nursery habitats for juveniles and provided refuge areas for smaller fish species. In the Fly River, 20 fish species have been recorded from riverine sites which have not been recorded from floodplain sites (Swales et al. 1998), while only five species have been recorded from the floodplain which have not been recorded from the riverine sites.

The large catches of *Nematalosa* herrings, and their dominance in the fish community, was a notable feature of oxbow lake sites. These pelagic, shoaling fish provide an important food source for barramundi, *Lates calcarifer*, which in turn supports important commercial and artisanal fisheries in the Fly River system (Opnai & Tenakanai)[3]. In contrast, the Sepik River in northern New Guinea, which is comparable in size to the Fly, lacks both barramundi, because of its limited estuary, and also *Nematalosa* herrings (Coates 1993). In total, at least 18 families that occur in drainages in either southern New Guinea or northern Australia are not present in the Sepik. Additionally, only three native species and two introduced species preferentially inhabit floodplain areas of the Sepik River. It has

[3] Opnai, J & C.D. Tenakanai. 1986. A review of barramundi fisheries in Papua New Guinea. pp. 50–55. In: Management of Wild and Cultured Sea Bass/Barramundi (*Lates calcarifer*). Proceedings of An International Workshop Held at Darwin, N.T., Australia, 24–30 September 1986.

been hypothesised that the absence of fishes from the floodplain is associated with the mode of reproduction of Sepik River fishes, with most species showing low fecundities (Coates op. cit.). In contrast, many species inhabiting Fly River floodplain habitats, such as *Nematalosa* spp., have high fecundities (Allen 1991, Roberts 1978). In addition, the composition of the fish fauna is also influenced by zoogeographic factors, with the Fly River fauna being more closely related to that in northern Australia than the Sepik River fish fauna (Coates op. cit.).

The results described here support Smith & Bakowa (1994) who reported differences in the composition of the fish communities between habitats on the Fly River floodplain. The differences which were found in the fish communities of oxbow lakes and blocked valley lakes appear to reflect the physical habitat differences between the two habitat types. However, as reported by Smith & Bakowa (op. cit.), most fish species occur in more than one habitat type, although there are significant inter-habitat differences between the communities. The differences between the habitat types may also reflect the tendency for the shallower blocked valley lakes to dry out in times of severe drought, when the more permanent waters of oxbow lakes provide a valuable refuge for fishes. However, as seen in Lake Pangua, fish populations in the Fly River system have the ability to quickly recolonise lakes which have dried out due to drought or have been affected by algal blooms.

The higher catches recorded in the oxbow lakes compared to the other habitats sampled suggest that these areas are the most productive habitats on the floodplain. However, it should be noted that true floodplain habitat (i.e. seasonally inundated floodplain set back from the river and covered by tall, dense grasses and reeds) was not sampled in this study due to the logistic difficulties of sampling these areas. Smith & Bakowa (1994) suggested that when the large areas of seasonally inundated grassed floodplain in the middle Fly (10–20 times greater in area than blocked valley and oxbow lakes, respectively) are inundated they appear to support a greater stock of fishes than the oxbow and blocked valley lakes.

The high productivity and diversity of fish stocks in the oxbow lakes may be due to their permanence, compared to the more ephemeral waters of the grassed floodplain habitats and blocked valley lakes. Consequently, fish stocks are able to utilise the oxbows as refuges from severe conditions on the floodplain and the permanence of the habitat seems to allow the fish community to increase in number and to diversify over time. The annual cycles of droughts and floods play an important role in the ecology of fish in tropical river systems (Lowe-McConnell 1987, Welcomme 1979, 1985) and fishes in tropical floodplain habitats respond to changes in their abiotic and biotic environments, many of which are predictable on a seasonal or annual basis but unpredictable in the short-term (Winemiller 1996).

The available evidence suggests that the declines in fish catches which were recorded at some sites may be attributable to natural climatic factors, associated particularly with the effects of drought and algal blooms. Both Lake Daviumbu and Bossett Lagoon dried out completely during the El Niño induced drought of 1993–1994. Once refilled, these lakes were connected directly to the main river, via tie-channels, and also the surrounding floodplain, and it was expected that recolonisation by fishes would be rapid. However, recolonisation was slower than expected, possibly due to the dense cover of floating grasses which developed on both lakes, which were largely grass-free before the onset of the drought. As the lakes refilled, grass species (*Echinochloa praestans* and *Leersia hexandra*) detached from the lake bed and formed dense floating mats, extending approximately 0.5 m below and 1 m above the water surface. These mats covered an estimated 95% of the surface area of the lakes and persisted for at least 18 months following refilling. A similar phenomenon was seen in Bosset Lagoon in 1983 (Busse 1991; cf. reduced fish biomass at site BOS10 in 1983, see Figure 4) and 1986 (K. Hortle personal communication). It is likely that environmental conditions beneath the floating mats (low levels of light, low dissolved oxygen and no food) would have been generally unsuitable for the survival of fishes and other aquatic life. While the floating grass mats persisted at these sites, gillnetting was restricted to the few remaining areas of open water, which may have been unrepresentative of the lakes as a whole (i.e. the few fishes in the lakes concentrated in the open water areas, leading to overestimates of population sizes). However, fish catches slowly increased once the grass mats started to disperse. Similar conditions were observed in other blocked valley lakes on the Fly River floodplain, where sampling was not carried out. The deeper oxbow lakes did not develop these floating grass mats since, due to their waters, the lakes never dried out.

The algal bloom recorded in Lake Pangua was also observed in other waterbodies on the Fly River floodplain around the same time (A.W. Storey personal observation), although these sites were not sampled for fishes. The limnological characteristics of these floodplain waterbodies have been little studied, although it is known that deeper lakes may thermally stratify (Chambers 1988). Consequently, the algal blooms recorded may have been due to nutrients being released from hypolimnetic water as a result of water mixing, although this has not been verified. Alternatively, the blooms may have been stimulated by the release of nutrients associated with annual burning of floodplain vegetation by local villagers, which was particularly severe during the El Niño drought. When fish catches in Lake Pangua declined considerably during the algal bloom periodic sampling in adjacent inundated grassed floodplain recorded high fish biomass, diversity and abundance, suggesting that fish had moved out of the lake and on to the floodplain. Also, in times of drought and low water conditions, water on the floodplain can become oxygen depleted as the large quantities of organic matter decay. Local villagers stated that small-scale fishkills are regularly observed on the floodplain. A sudden drop in river level at this time has been known to result in large fishkills in the main river channel when deoxygenated waters drain off the floodplain into the Fly River (OTML[1]).

Although the discharge of mine wastes from the Ok Tedi copper mine has marked effects on the main channel environment of the Ok Tedi and Fly rivers (Lee et al.,[4] Swales et al. 1998), the effects on the floodplain of the middle Fly are in comparison much reduced. The quantities of sediment deposited on the floodplain, because of the limiting hydraulic characteristics of flow transfer between the river channel and floodplain waterbodies, are estimated to be less than 3% of the total sediment load of the river (Higgens 1990). Furthermore, water quality conditions in the floodplain waterbodies are much better than in the main river channel, with very low concentrations of suspended sediment ($< 20\ \mu g\ l^{-1}$) and lower copper levels. A recent study showed that there was little difference in the generic composition or diversity of unicellular algae between mine-impacted lakes in the Fly River system and control sites in the Strickland River, and that most of the mine-derived copper in the system is bound to dissolved organic carbon and is largely not bioavailable (Stauber 1995, Stauber & Apte[5]).

The two exotic fish species, the climbing perch, *Anabas testudineus,* and the walking catfish, *Clarias batrachus*, have also recently become widespread and abundant in the Fly River catchment (Storey et al.[6]). The climbing perch, in particular, shows dietary overlap with several native species and can also cause mortality in some piscivorous species, through spines on the operculum and fins lodging in the pharyngeal cavity of the predator (Storey et al.[6]). High numbers of dead catfish with climbing perch lodged in their throats are a frequent occurrence in the river and floodplain habitats of the middle Fly (Swales personal observation). The walking catfish is a more recent introduction and possible interactions with native species have yet to be investigated.

The Fly River system also supports limited commercial (mainly for barramundi) and artisanal fisheries, which have increased in size over recent years as villagers have become more affluent through the community benefits associated with the mine, through which they have acquired more gillnets and

[4] Lee, M.C., K. Voigt, L. Murray & M. Lane. Environmental benefits and issues, engineering studies and risk analysis of mitigation options to reduce mine-derived effects on the Ok Tedi/Fly River system. Unpublished Report.

[5] Stauber, J.L. & S.C. Apte. 1996. Bioavailability of copper to algae in the Fly River system, Papue New Guinea. CSIRO Investigation Report CET/IR 464R. 78 pp.

[6] Storey, A.W., I.D. Roderick, R.E.W. Smith & A.Y. Maie. 1998. Spread of the introduced Climbing Perch (*Anabas testudineus* Bloch, Anabantidae: Perciformes) in the Fly River system, Papua New Guinea, with comments on possible ecological effects. Unpublished manuscript.

boats. These fisheries may be affecting the size of fish stocks in the river and floodplain habitats, although the extent of the fisheries and their impacts on fish stocks is currently largely unknown.

In conclusion, fish populations in most floodplain habitats of the Fly River system were generally abundant and diverse, although they showed considerable temporal and spatial variability. Variations in catches at several sites are known to be associated with changes in water level and quality due to natural climatic factors, particularly 'El Niño' droughts and algal blooms. At the time of writing (January 1998) Papua New Guinea is once again in the grip of a severe El Niño-induced drought and the Fly River floodplain has largely dried out, with the exception of the deeper oxbow lakes. It is likely that such major climatic events play an important role in the ecology of tropical river and floodplain ecosystems. Consequently, global climate changes associated with phenomena such as 'greenhouse warming', which have the potential for altering the frequency or severity of droughts, may have a wide-ranging repercussions for tropical river fisheries and aquatic ecology.

Acknowledgements

The authors would like to thank the staff of the Biology Section of the Environment Department of Ok Tedi Mining Limited. Without their efforts this study would not have been possible. Particular thanks due to David Balloch, Kent Hortle and Ross Smith, who developed the bases of the biological monitoring programme, and the numerous biologists and technical staff involved in field sampling. We would also like to thank Don Carroll and Basil Bulkua of the Hydrology Section, Environment Department, who kindly supplied river flow hydrographs. Thanks to Monica Rau and Marshall Lee for reviewing drafts of the manuscript. The continued support of Ok Tedi Mining Limited is also gratefully acknowledged.

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Appendix. Fish species recorded from the floodplain sampling sites since the commencement of sampling [G = sampled using gillnets; R = sampled using Rotenone; classification according to Roberts (1978), Allen (1991), Munro (1967), Coates (1993)].

Family	Species	Site								
		BOS10	BOS11	DAV01	OXB03	OXB05	OXB06	FLD15	OXB08	SFL01
Anabantidae	*Anabas testudineus* (Bloch) (climbing perch)	G, R	G	G	G, R	G, R	G, R	G, R	G, R	G, R
Apogonidae	*Glossamia aprion* (Richardson) (mouth almighty)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G
	Glossamia narindica (Roberts) (slender mouth almighty)			R						
	Glossamia trifasciata (Weber) (three-barred mouth almighty	R	R	G, R	R	R	R		R	R
Ariidae	*Arius augustus* (Roberts) (short barbelled catfish)	G				G			G	G
	Arius berneyi (Whitley) (berney's catfish)	G, R	G, R	G	G, R	G, R	G, R	G	G, R	G
	Arius carinatus (Weber) (comb-spined catfish)								G	G
	Arius crassilabris (Ramsay & Ogilby) (thick-lipped catfish)								G	G
	Arius latirostris (Macleay) broad-snouted catfish)									G
	Arius leptaspis(Bleeker) (triangular shield catfish)	G, R	G	G	G, R	G	G	G, R	G, R	G
	Arius macrorhynchus (Weber) (sharp-nosed catfish)									G
	Cinetodus froggatti (Ramsay & Ogilby) (froggatt's catfish)	G		G		G			G	
	Cochlefelis danielsi (Regan) (Daniel's catfish)					G			G	G
	Cochlefelis spatula (Ramsay & Ogilby) (duckbilled catfish)	G				G				G
	Nedystoma dayi (Ramsay & Ogilby) ((Day's catfish)				G				G	G
Atherinidae	*Craterocephalus randi* (Nichols) (kubuna hardyhead)	R	R	R	G, R	R	R	R	R	R
Belonidae	*Strongylura kreffti* (Gunther) (freshwater longtom)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	R
Centropomidae	*Lates calcarifer* (Bloch) (barramundi)	G	G	G	G	G	G	G	G	G
Chandidae	*Ambassis* spp. (Gunther) (glass perchlets)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	R
	Denarusia bandata (Whitley) (pennyfish)	G, R	R	G, R	R	R		R	R	R
	Parambassis gulliveri (Castelnau) (giant glass perchlet)	G	G	G	G, R	G		G	G, R	G, R
Clariidae	*Clarias batrachus* (Linneaus) (walking catfish)	G	G		G	G		G		G
Clupeidae	*Clupeoides papuensis* (Ramsay & Ogilby) (toothed river herring)	R			R	R	R	R	R	R
	Nematalosa spp. (Munro) (herrings)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R
Datnioididae	*Datnioides quadrifasciatus* (Sevastinov) (four-banded tigerfish)	G		G	G	G	G		G	
Eleotrididae	*Ophieleotris aporos* (Bleeker) (snakehead gudgeon)			G				G, R		G, R
	Oxyeleotris fimbriata (Weber) (fimbriate gudgeon)	G, R	G	G	G, R	G, R	G	G	G, R	G
	Oxyeleotris herwerdenii (Weber) ((blackbanded guavina)	G, R	G, R	G, R	G	G, R	G	G	G, R	G, R
	Oxyeleotris lineolatus (Steindachner) (sleepy cod)	G, R	G	G, R	G	G	G	G, R	G	G
	Oxyeleotris nullipora (Roberts) (poreless gudgeon)			R						
Mugilidae	*Liza alata* (Steindachner) (basket mullet)	G		G	G	G	G	G	G	G
Osteoglossidae	*Scleropages jardinii* (Saville-Kent) (saratoga)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G	G
Plotosidae	*Neosilurus ater* (Perugia) (narrow-fronted Tandan)	G, R	G, R	G, R	G, R	G, R	G	G, R	G, R	G

Appendix. Continued.

Family	Species	Site								
		BOS10	BOS11	DAV01	OXB03	OXB05	OXB06	FLD15	OXB08	SEL01
	Neosilurus brevidorsalis (Gunther) (short-finned tandan)	G			G					
	Neosilurus species C			G						
	Oloplotosus luteus (Gomon & Roberts) (pale yellow tandan)			G	G					
	Plotosus papuensis (Weber) (papuan tandan)	G		G			G		G	
	Porochilus spp. (*obbesi* and *meraukensis*) (Weber) (tandans)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R
Pristidae	*Pristis microdon* (Latham) (sawfish)	G		R				G	G	G
Pseudomugilidae	*Pseudomugil gertrudae* (Weber) (spotted blue-eye)	R								
Sciaenidae	*Nibea* sp. (Allen 1991) (sharpnose jewfish)					G			G	G
Scatophagidae	*Scatophagus argus* (Linneaus) (spotted scat)					G				
Soleidae	*Aseraggodes klunzingeri* (Weber) (tailed sole)	R								
Sparidae	*Acanthopagrus berda* (Forskål) (pikey bream)			G		G			G	
Terapontidae	*Amniataba affinis* (Mees & Kaiola) (tiger grunter)	G, R	G, R	G, R	G, R	G, R	G, R	R	G, R	R
	Hephaestus roemeri (Weber) (tiger grunter)	G, R	G, R	G, R	G, R	G, R	G, R	R	G, R	R
	Hephaestus roemeri (Weber) (Röemer's grunter)			R						
	Pingalla lorentzi (Weber) (Lorentz's grunter)	G	G	G		G	G	G		
	Varia lacustris (Mees & Kaiola) (lake grunter)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	R
	Mogurnda spp. (*cingulata* and *mogurnda*) (Richardson) (banded and trout mogurnda)	R		R	R	R		R		R
Engraulididae	*Thryssa rastrosa* (Roberts) (fly river thryssa)	R	G	G	G	R	G	G, R	G, R	G, R
	Thryssa scratchleyi (Ramsay & Ogilby) (freshwater anchovy)	G, R	G	G	G	G	G		G	G, R
Gobiidae	*Glossogobius giurus* (Hamilton-Buchanan) (flathead goby)	R						R		
	Glossogobius spp. (Allen 1991) (goby)			R			R			R
	Stenogobius lachneri (Watson)					G				G
Hemiramphidae	*Zenarchopterus novaeguinae* (Weber) (Fly River garfish)	R		R	R	G	R			
Kurtidae	*Kurtus gulliveri* (Castelnau) (nurseryfish)	G			G		G		G	
Lutjanidae	*Lutjanus* spp. (*goldei* and *argentimaculatus*) (Forskål & Macleay) (Papuan black bass and mangrove jack)	G		G	G	G	G		G	G
Megalopidae	*Megalops cyprinoides* (Broussonet) (oxeye herring)	G	G	G	G	G	G	G	G	G
Melanotaenidae	*Iriatherina werneri* (Meinken) (threadfin rainbowfish)	R	R	R		R		R		R
	Melanotaenia maccullochi (Ogilby) (Maculloch's rainbowfish)	R			G	R		R		
	Melanotaenia sexlineata (Munro) (Fly River rainbowfish)				R					
	Melanotaenia splendida (Ramsay & Ogilby) (red-striped rainbowfish)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R
Toxotidae	*Toxotes chatareus* (Hamilton-Buchanan) (seven-spot archerfish)	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R	G, R
	Toxotes lorentzi (Weber) (Lorentz's archerfish)	G, R	G	G, R	G	G, R		R		
Total number of species		46	29	45	39	44	32	34	40	44
Number of species sampled using gillnets		35	25	35	33	36	27	25	36	33
Number of species sampled using rotenone		31	17	25	24	24	17	24	21	21