The University of Hull

The Biology and Ecology of *Oreochromis mossambicus* (Peters, 1852) (Pisces: Cichlidae) in the Sepik River, Papua New Guinea - with reference to the management of the fishery

being a Dissertation submitted in partial fulfilment
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by

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ABSTRACT

The introduced species *Oreochromis mossambicus* was studied to determine biological and ecological factors which may underly the rapid initial distribution of the species from its introduction in the 1950's to the relatively low catch rates experienced in recent years. Actual yield, determined from catch statistics for all species, was significantly lower than theoretical yield, based on formulae developed from other similar river systems. The importance of *O. mossambicus* to the fishery was indicated by the proportional contribution of this species to the catch (approximately 50%). Fluctuations in catch may be related to changes in water levels with a significant decrease in *O. mossambicus* catch as the water levels rose and this species moved onto the floodplain areas. Analysis of stomach contents revealed a predominance of diatom species, algae and flocculent detritus. There were some differences in diatom species consumed between sites and season although the general food quality was thought to be good based on monthly condition factors. Reproductive traits were similar to those found in other areas. Females incubated the fertilised eggs orally and behavioural differences were noted from changes in sex ratios and mean size caught each month. Condition of females was significantly lower during the dry season post spawning which could relate to the behavioural trait of mouthbrooding when females do not feed. Mean fecundity was low (475 per 100g body weight) and there was evidence of bimodal peaks in spawning activity which corresponded to rising and falling water levels. Growth throughout the year was not significantly affected by the potential changes in food availability created by the degree of floodplain inundation and an increase in allochthonous food sources. Scale rings were found to be formed bi-annually and may correspond to increased feeding prior to spawning. CPUE varied between sites but was low overall and von Bertalanffy growth parameters indicated that males reached a larger maximum size than females over the same time period (L_∞ = 35 and 26.56 respectively). Total mortality was relatively high ($Z = 0.56$/yr) but figures may relate to local conditions only since many habitats and environmental conditions would be represented in a river of the size of the Sepik. The potential impact of proposed introductions of fish to the river are discussed with regard to management issues.

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Chapter 1 INTRODUCTION

1.1 Papua New Guinea-geological history

Papua New Guinea and its islands are situated to the north of Australia (Figure1.1) and has been described by Gressit (1982) as being a country of extremes. It is the largest tropical island where most kinds of environment can be found, from glacial mountains to tropical rainforests. Much of the way of life in some areas has not changed substantially since the stone-age. The main island is divided into two countries, Papua New Guinea to the east and Irian Jaya, a province of Indonesia, to the west. Prior to World War ll the country was known as Papua and New Guinea, the two areas being administered by Australian Trust and Germany respectively. After 1945 the whole country (now Papua New Guinea) was then governed by Australia until independence in 1975.

The island is divided geographically by a central mountain range which runs from west to east and separates the river systems lying to the north and south. The actual landmass of New Guinea and the smaller islands lie between two major plates, the stable continental plate of Australia to the south and the deeper Pacific basin to the north (Figure 1.2). The collision and subsequent northward movement of the former and the westward movement of the latter plate has created uplifted sections in the centre of the island thus forming the Central Highlands. This mountain range formed the beginnings of Papua New Guinea's landmass as early as the lower Miocene period. However it was in the late upper Pliocene period that the present day formation emerged. This later stage is represented by the Torricelli-Bewani mountain ranges. There is evidence for continuing uplift in these areas since raised coral platforms of varying age from Pleistocene to Present are evident. Plate interaction is still in evidence in areas where most of the volcanic activity occurs.

These mountain ranges effectively create two different zoogeographic zones corresponding to the northern and southern regions of New Guinea. Freshwater fish fauna in the two regions

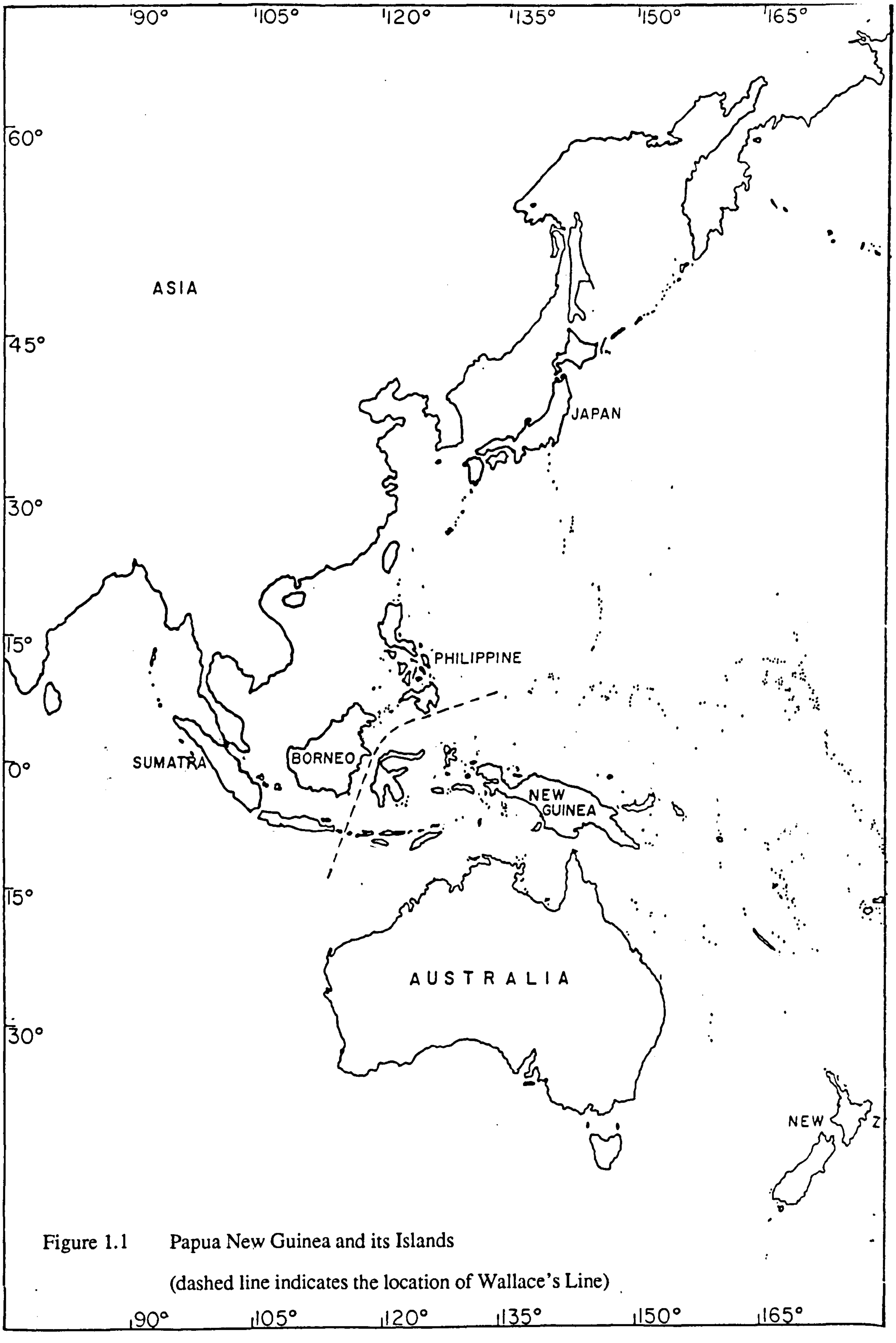


Figure 1.1 Papua New Guinea and its Islands

(dashed line indicates the location of Wallace's Line)

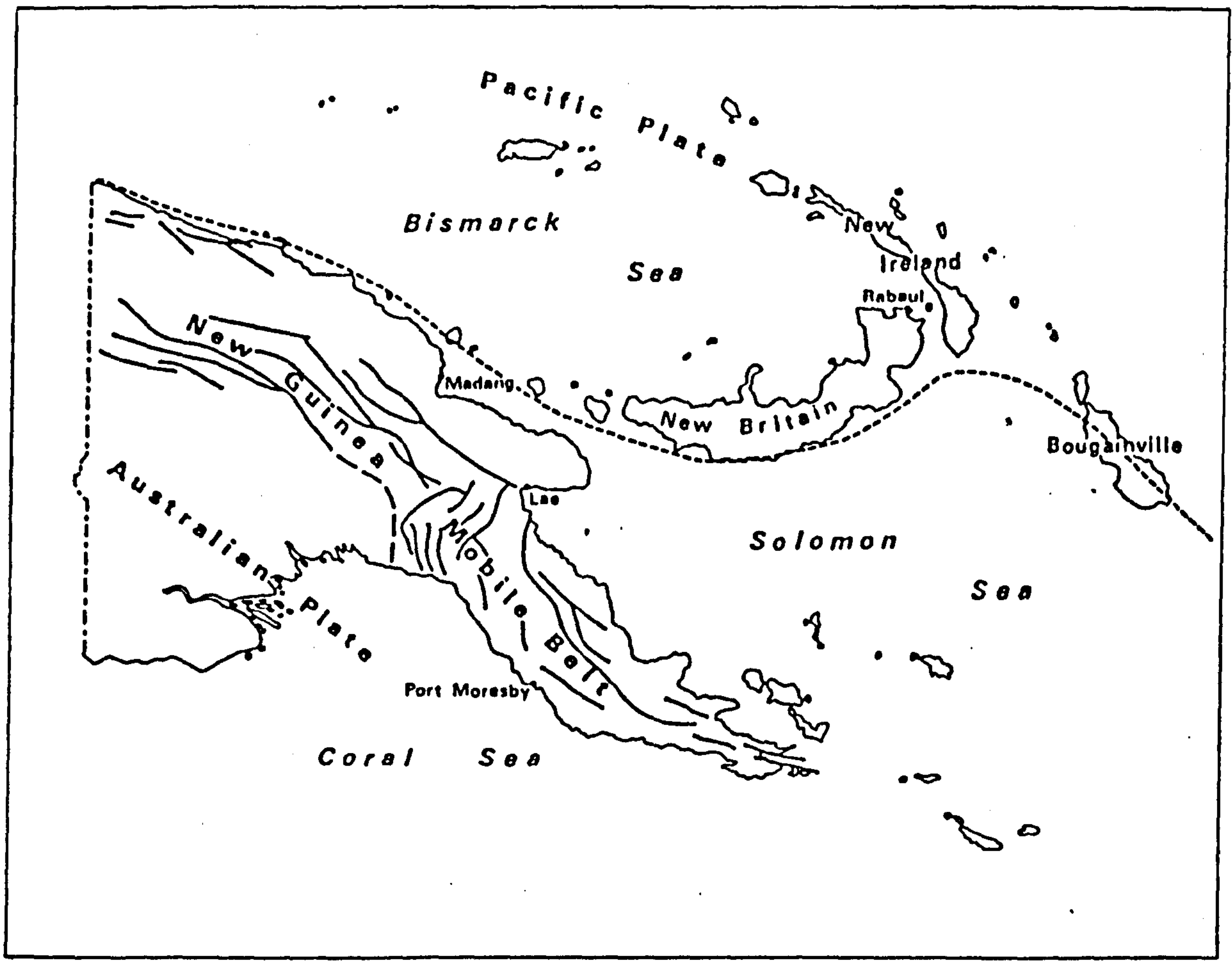


Figure 1.2 The main fault lines and crustal elements of Papua New Guinea (from Löffler 1977)

are distinct, the southern species show a resemblance to the fauna of northern Australia whereas those in the north show a high degree of endemism (Allen and Coates 1989).

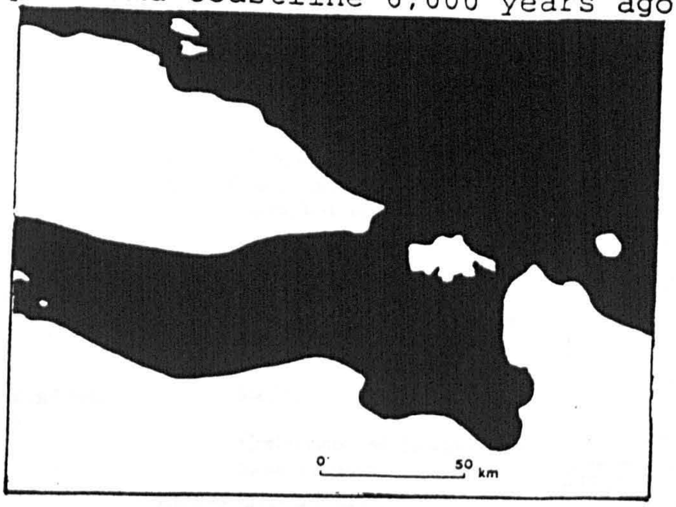
Papua New Guinea has substantial freshwater resources compared with the rest of the Australasian countries and has three of the largest rivers in the region. These include the Fly (southern PNG), the Sepik (Northern PNG) and the Mamberambo/Idenberg (northern Irian Jaya). In Papua New Guinea the river fisheries are an important source of food and income since approximately 60% of the population live inland and have little or no access to the coast (Frielink, 1983). Fisheries development has been an important consideration in a country where it is estimated that 50% of children in the 0-5 year age group are malnourished. One of the largest and best known rivers, the Sepik, supports an important subsistence fishery. With a high population density more attention is now being paid to the rational and sustainable development of fish stocks as an important source of protein.

1.2 Formation of the Sepik Basin.

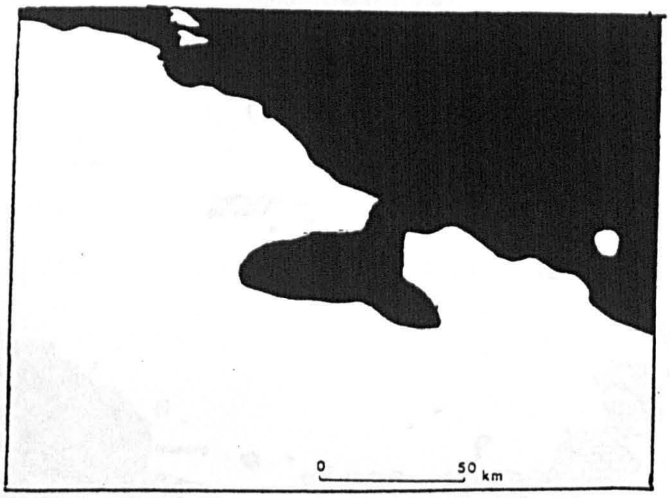
One of the major structural regions is the Sepik-Markham depression in which the Sepik and Ramu River catchment areas are contained. It has been estimated that this has been an area of subsidence since the Tertiary period. This basin was possibly formed by the process of downwarping caused by compressional forces between the Continental and Pacific plates as the island was formed. The Sepik floodplains are known to now occupy an area which was once an inland sea bordered by the Torricelli/Bewani mountains to the north and the Central Dividing Range to the south (Figure 1.3). The development of the Sepik floodplain as a result of rapid alluvial deposition is thought to be fairly recent and is associated with the recent rise in sea-level (Loffler 1977). The present day geological formation is shown in figure 1.4.

Archaeological evidence from floodplain sites 70 to 600 km inland suggests that these areas were marine/coastal habitats from between 5000 and 20,000 years ago (Swadling *et al.* 1988). The development of the floodplain is therefore considered to be very recent in the

The Sepik-Ramu coastline 6,000 years ago:



The Sepik-Ramu coastline 2,000 years ago:



The Sepik-Ramu coastline today:

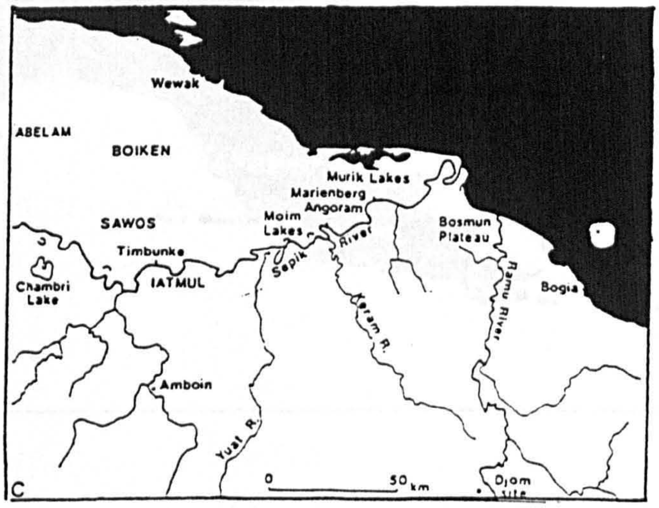


Figure 1.3 Formation of the Sepik floodplain (from Swadling 1988)

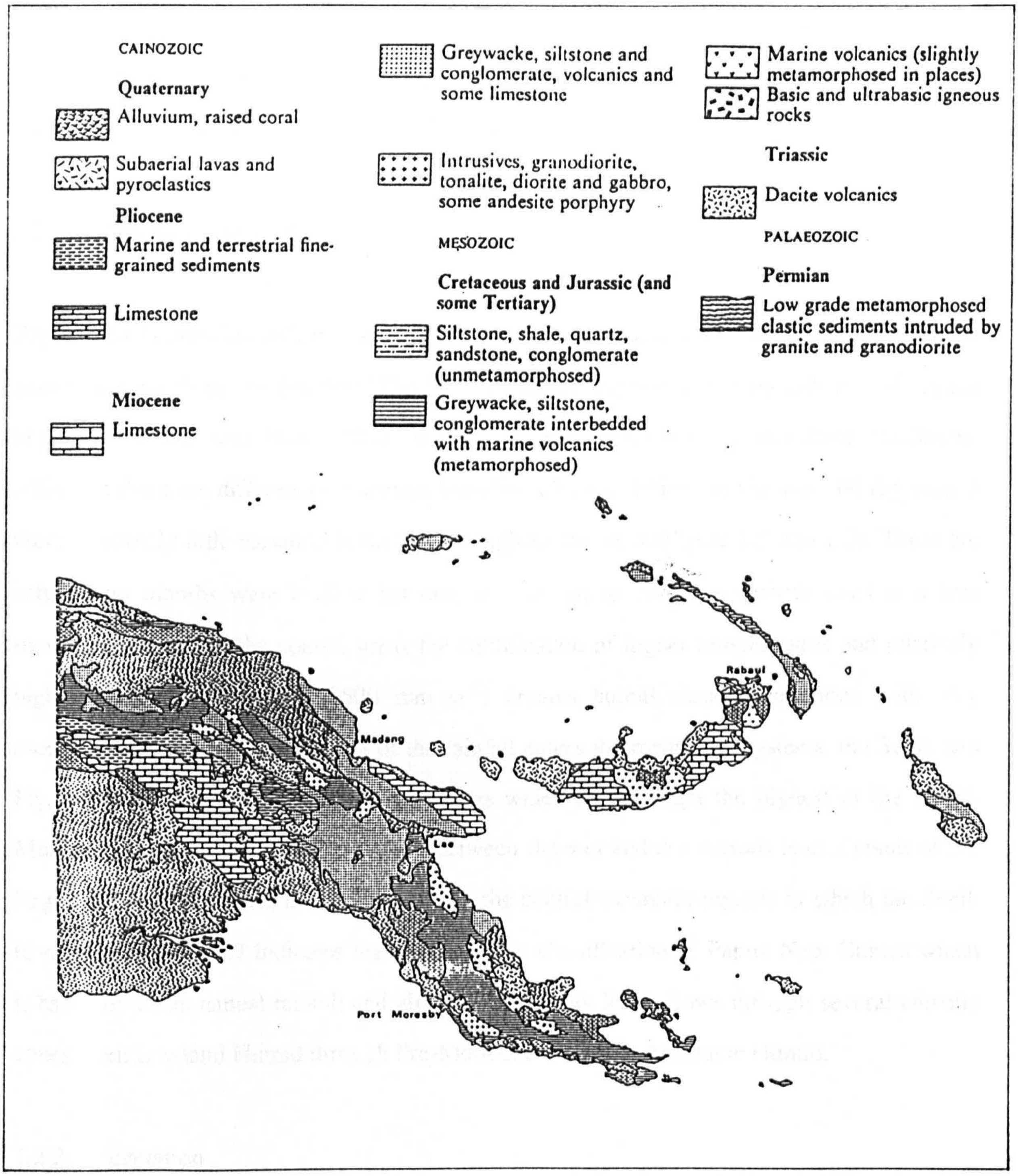


Figure 1.4 Geological Formation of Papua New Guinea (from Löffler 1977)

geological timescale. This can be compared to the geological history and evolution of fishes in some of the African lakes, for example, Lake Victoria is described as one of the younger lakes (Lowe-McConnell 1975) but is in fact 750,000 years old.

1.2.1 Climatic Conditions

Papua New Guinea has a diverse climate although the annual temperature regime is relatively stable over much of the country (23-32^{0}C). However temperatures may fall to 11^{0}C in the highland regions, and above 4000 m there is often settled snow and frost conditions. Although there are differences in annual humidity which is defined as the wet and dry season there is actually little variation in rainfall throughout the year (Figure 1.5 and 1.6). There are actually no months were it does not rain, in contrast to conditions which exist in a true monsoon climate. In the coastal areas the combination of higher temperatures and relatively high rainfall (between 2500-3500 mm yr^{-1}) creates humid cloudy conditions with only moderate evaporation. Thus much of the rainfall enters the main river systems, the Sepik and Fly, which consequently have discharge rates which are amongst the highest in the world. Much of the variation in river discharge between the wet and dry periods is as a result of the larger seasonal difference in rainfall found in the central mountain regions in which the Sepik River rises. Figure 1.7 indicates the main climatic classification of Papua New Guinea which is based on mean annual rainfall and altitude. The Sepik River flows through several climatic zones from Lowland Humid through Pre-Montaine Humid to Montaine Humid.

1.2.2. Vegetation

Primary forest still covers large areas of the country (Figure 1.8). At the present time over 20,000 different plant species are known to exist which is as a result of the large range of altitudinal and climatic conditions. The Sepik and Ramu rivers both flow through a variety of vegetation types from source to the sea as shown below:

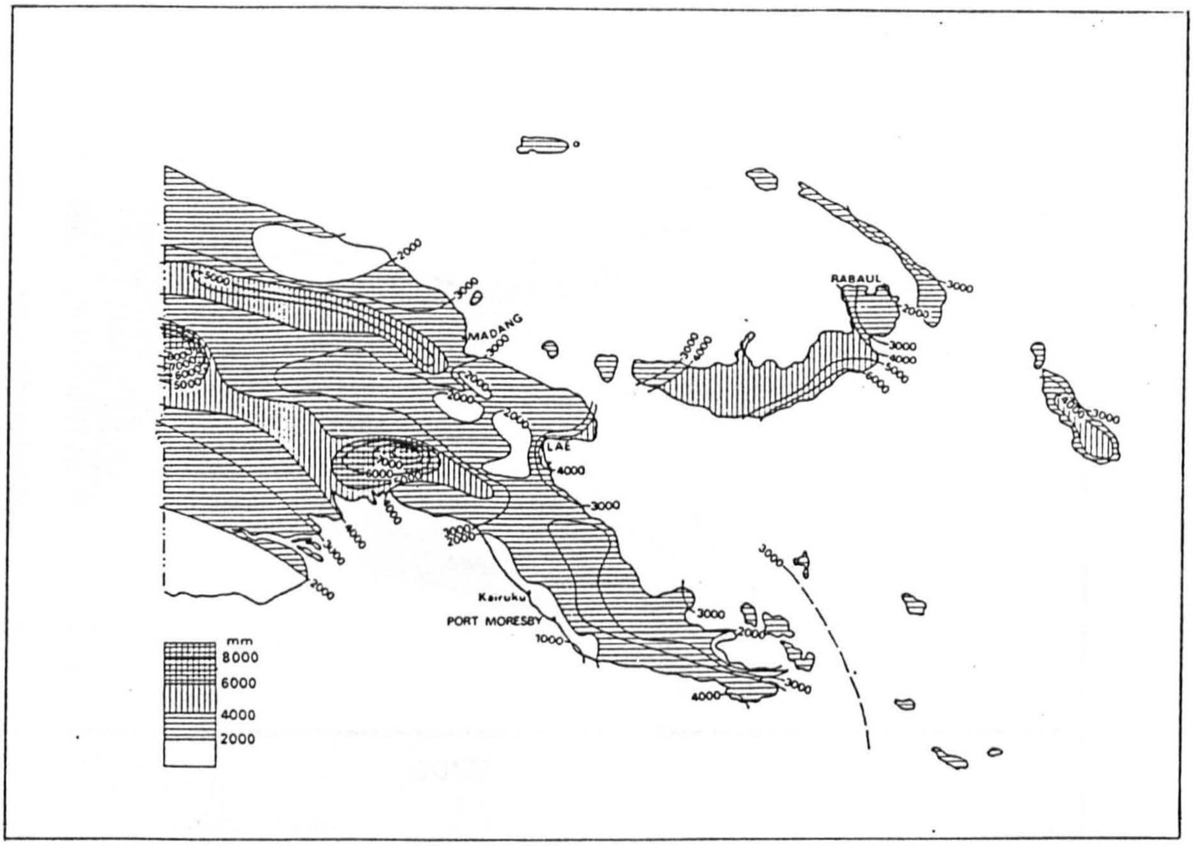


Figure 1.5 Mean annual rainfall over PNG (from McAlpine *et al.* 1983)

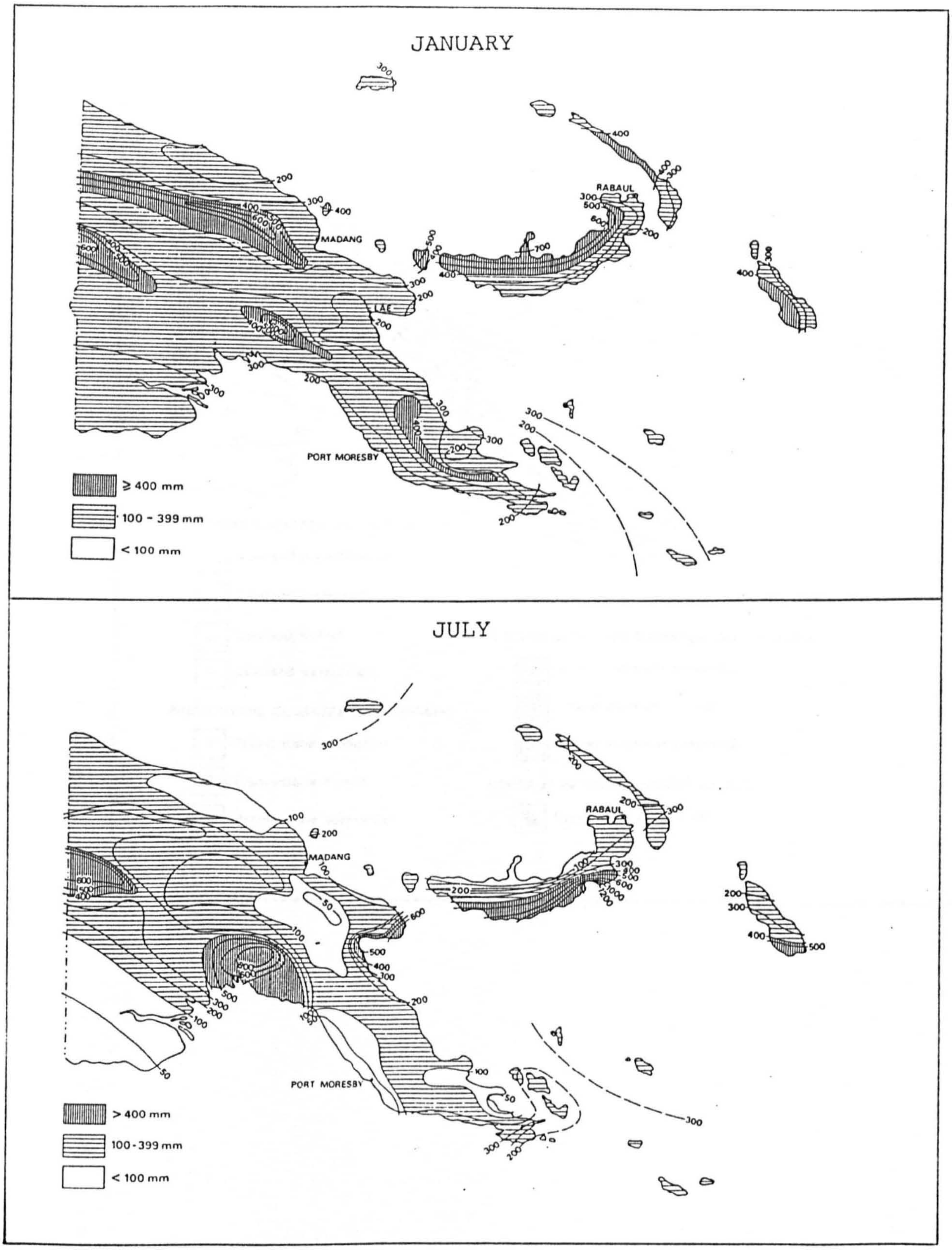


Figure 1.6 Seasonal rainfall patterns over PNG (from McAlpine *et al* 1983)

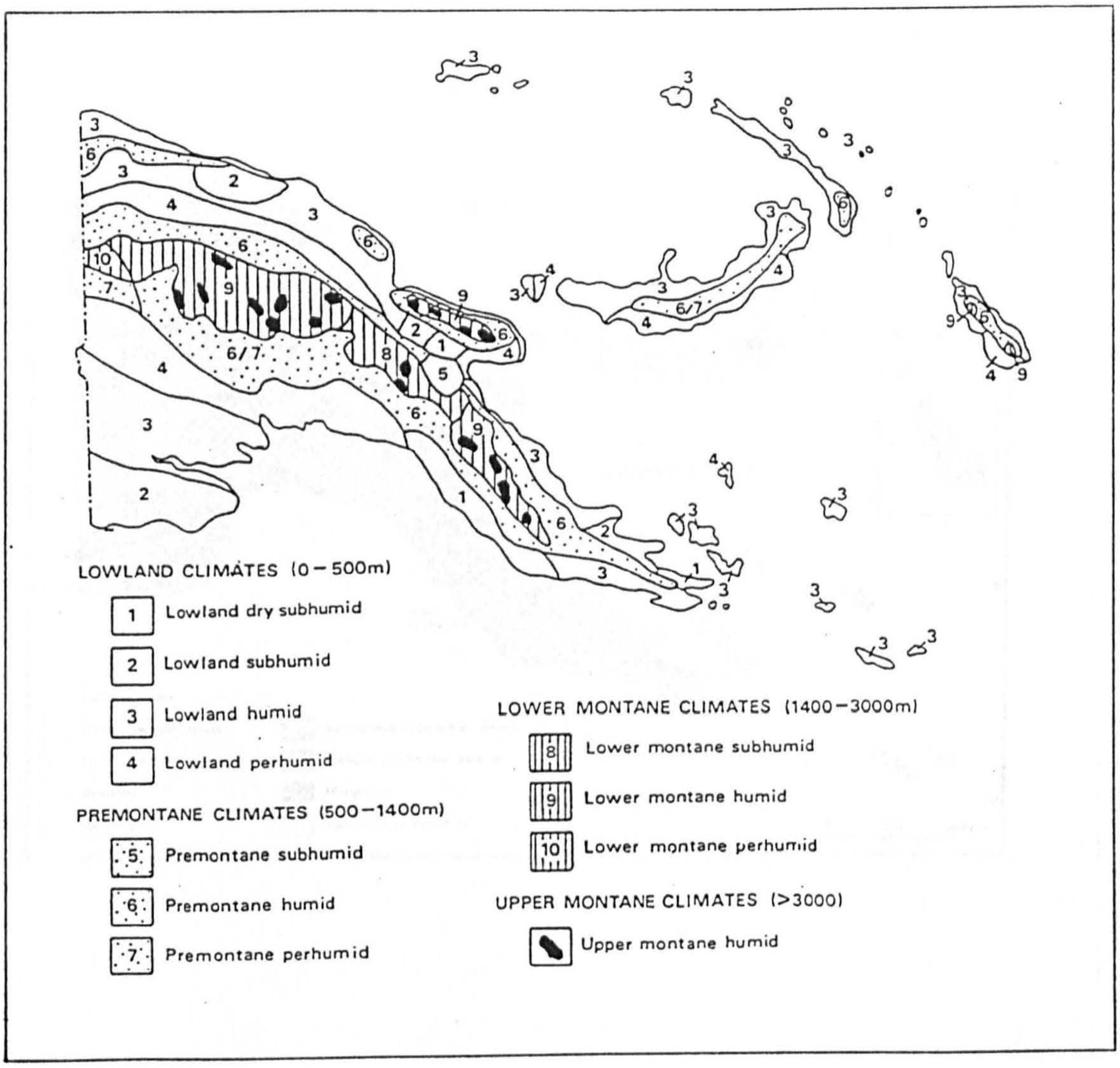


Figure 1.7 Climatic classification in terms of altitude and mean annual rainfall (from McAlpine *et al* 1983)

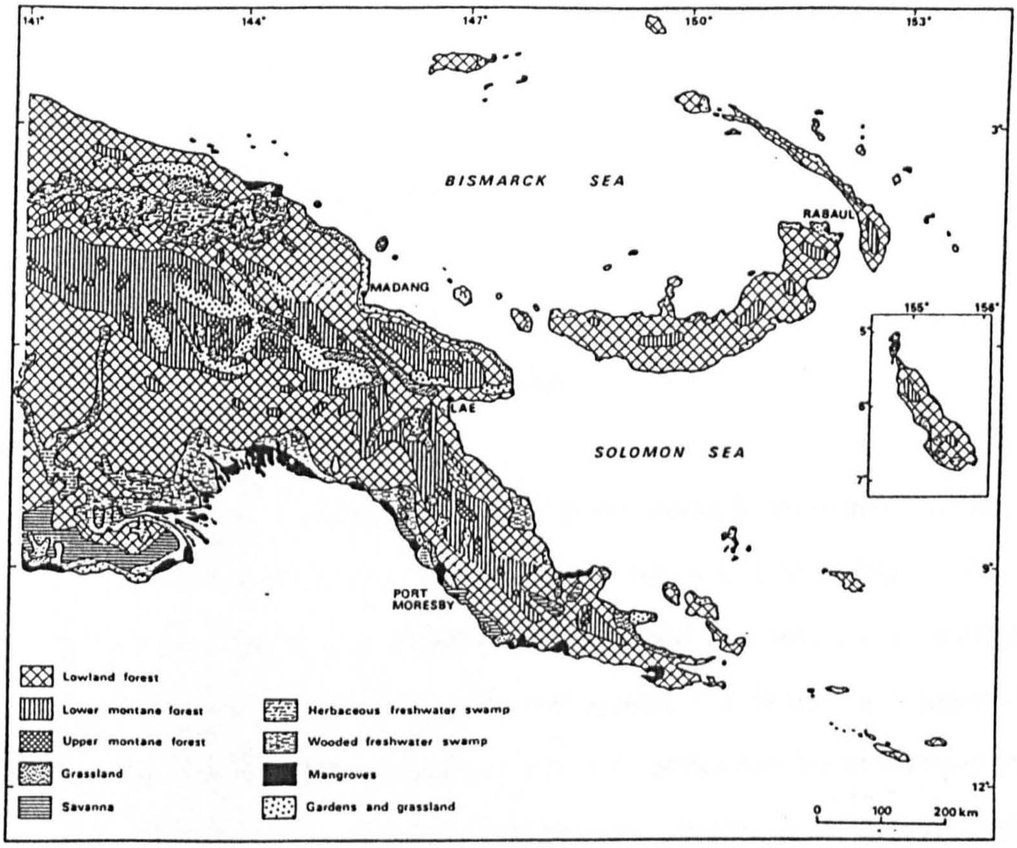


Figure 1.8 Major vegetation types (from Paijmans 1982)

Source	Upper montaine forest
	Lower montaine forest
	Lower forest and grassland
	Gardens and grassland
	Wooded and herbaceous freshwater swamp
Sea	Mangroves

1.3 The Sepik River System and faunal evolution

The Sepik River system is amongst the largest in the world. In comparison to the 50 largest rivers in the world ranked by mean discharge the Sepik would be ranked number 21 (Table 1.1). However the Sepik is often missing from published data which is an indication of the lack of historical research carried out on the river system. The Sepik is also reported to be the largest faunal province in terms of physical size and species number in northern Papua New Guinea. The Sepik River is part of the intermontaine trough which extends approximately 1100 km from the Huon Gulf in PNG to Geelvink Bay in Irian Jaya and contains the river valleys of the Ramu, Markham, Sepik and Mamberamo (in Irian Jaya) (Figure 1.9). The area drained by the Sepik is substantial (78,000 km^2) (Löffler, 1977) and the river has a floodplain of up to 70 km wide with an area of 7600 km^2. Much of the floodplain is shallow swamp land with areas of sago palm and grassland. The discharge varies throughout the year, from 4363 m^3 s^{-1} in the dry season to 10,963 m^3 s^{-1} during the wet season which continues from November to April/May (Mitchell *et al.*, 1980).

The geology of the highlands catchment area of the Sepik is characterised by greywake, siltstone and conglomerate interbedded with marine volcanics and limestone whereas the lower floodplain area is based on lavas overlaid with recent alluvial sediments (Coates *et al* 1983). The influence of the bedrock over which a river flows on its flora and fauna is well documented (Whitton 1975, Welcomme 1983, 1985). The floodplain of the lower

River	Continent	Country	mean discharge $100m^3sec^{-1}$	drainage area $1000km^2$	length km	rank by length
Amazon	S. America	Brazil	212.5	5711	6437	2
Congo/Zaire	Africa	Zaire	39.7	3968	4700	8
Yangtze	Asia	China	21.8	1920	5980	4
Brahmaputra	Asia	Bangladesh	19.8	924	2900	31
Ganges	Asia	India	18.7	1047	2506	48
Yenisei	Asia	USSR	17.4	2560	5540	5
Mississippi/Missouri	N. America	U.S.A.	17.3	3184	6020	3
Orinoco	S. America	Venezuela	17.0	870	2151	60
Lena	Asia	USSR	15.5	23.96	4400	10
Parana	S. America	Argentina	14.9	2278	3998	18
St. Lawrence	N. America	Canada	14.1	1274	4000	16
Irrawaddy	Asia	Burma	13.5	424	2100	63
Ob	Asia	USSR	12.5	2455	5410	6
Mekong	Asia	Thailand	11.0	793	4000	16
Amur	Asia	USSR	11.0	1822	4444	9
Tocantins	S. America	Brazil	10.2	896	2700	38
Mackenzie	N. America	Canada	7.9	1784	4241	13
Magdelana	S. America	Columbia	7.5	238	1600	—
Columbia	N. America	Canada	7.3	660	1954	76
Zambezi	Africa	Mozambique	7.1	1280	3500	14
Danube	Europe	Romania	6.2	806	2850	34
Niger	Africa	Nigeria	6.1	1100	4200	14
Indus	Asia	Pakistan	5.6	916	2900	31
Yukon	N. America	Canada	5.1	921	2654	44
Pechora	Europe	USSR	4.1	322	1809	88
Uraguay	S. America	Uraguay	3.9	230	1612	—
Kolyma	Asia	USSR	3.8	637	2513	47
Sankal	Asia	China	3.6	117	1957	74
Godavari	Asia	India	3.6	294	1440	
Dvina	Europe	USSR	3.5	355	726	
Hwang-Ho	Asia	China	3.3	665	4845	7
Frazer	N. America	Canada	3.2	235	1360	
Nile	Africa	Egypt	2.8	2944	6650	1
Sao Francisco	S. America	Brazil	2.8	665	2900	31
Neva	Europe	USSR	2.6	279	—	
Pyasina	Asia	USSR	2.5	189	1056	
Nelson	N. America	Canada	2.3	1059	2570	43
Rhine	Europe	Netherlands	2.2	143	1312	
Krishna	Asia	India	2.0	304	1120	
Indigirka	Asia	USSR	1.8	355	1725	95
Dnepr	Europe	USSR	1.7	496	2200	58
Rhone	Europe	France	1.7	94	816	
Mobile/Tombigbee	N. America	U.S.A.	1.6	107	598	
Salween	Asia	Burma	1.5	276	2400	52
Tigris/Euphrates	Asia	Iraq	1.4	535	1900	81
Po	Europe	Italy	1.4	69	648	
Vistula	Europe	Poland	1.1	194	1084	
Susquehanna	N. America	U.S.A.	1.1	71	710	
Yana	Asia	USSR	1.0	243	1067	
Senegal	Africa	Senegal	0.9	338	1633	100
Sepik	Australasia	Papua New Guinea	7.0	78	1700	95

(after Welcomme 1985)

Table 1.1. The 50 largest rivers of the world, ranked by mean annual discharge at the mouth, compared to the River Sepik.

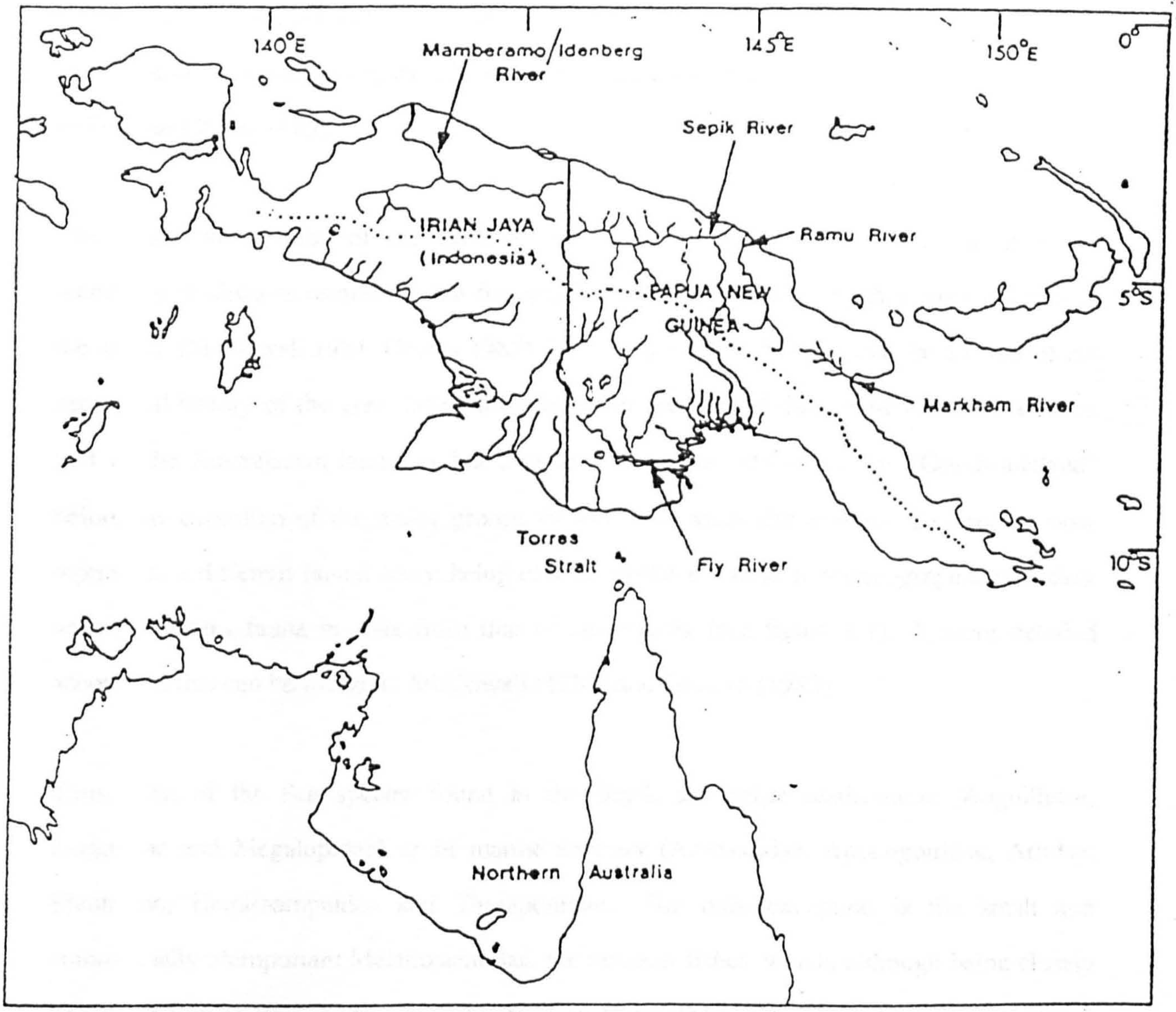


Figure 1.9 Major river systems in Papua New Guinea (after Coates 1983)

section is extensive with numerous oxbow lakes (roundwaters) and shallow depression lakes. This area is the main fish production area despite forming only 10% of the total catchment (Figure 1.10). Although the larger river valleys of the Sepik and Mamberamo are separated they have a common geological history and a similarity of fish fauna in their river waters (Allen and Coates 1989).

The faunal composition of the fresh waters of New Guinea is devoid of primary and secondary freshwater ostariophysian fish species commonly found in other river systems in the world (McDowall 1981, Coates 1985). This fairly unique situation may be a result of the geological history of the area during the process of continental drift. New Guinea was once part of the Australasian landmass but separated from the area known as "Gondwanaland" before the evolution of the major groups of true freshwater fish species. This region now represents a different faunal zone: being east of 'Wallace's Line' a zoogeographic boundary which separates fauna in Asia from that of Australasia (see figure 1.1). A more detailed account of this can be found in McDowall (1981) and Gressitt (1982).

Thus most of the fish species found in the Sepik are either diadromous (Anguillidae, Lutjanidae and Megalopidae) or of marine ancestry (Ambassidae, Aponogonidae, Ariidae, Eleotridae, Hemirhamphidae and Theraponidae). The only exception is the small and commercially unimportant Melanotaeniidae, the rainbow fishes, which, although being closely related to marine groups are generally found in freshwaters. This creates an unusual faunal composition in comparison to many other riverine habitats throughout the world. In addition none of the families of fish in the Sepik freshwaters are represented in major proportions in the freshwater ichthyofauna outside of Australasia (Coates 1989).

In the Sepik over 58 species from 35 genera and 23 families have been described (Table 1.2) (Allen and Coates 1989). This can be compared to many more species found in similar river systems in Africa. Figure 1.11 indicates the number of species found in rivers of varying basin area. The relationship between basin size and species number has been described for various rivers by Welcomme (1983) and is discussed in relation to species diversity in the Sepik River in Chapter Three.

Several genera are absent in the Sepik when compared to the ichthyofauna found in the Fly River in southern Papua New Guinea (Roberts, 1978). Iredale and Whitely (1935) described the differences in Australian fish fauna in flowing waters as being associated with different environments; for example, climate, land barriers and river drainage systems. Coates (1986) used the terminology to describe the fauna of the northern (Sepik) area, which is separated by a central caudillera, as being 'Gaimardian' and those of the southern (Fly) region as 'Leichartian' since they resemble the fauna in northern Australia.

The main native species of potential commercial value are few in number and none actually support commercial inland fisheries outside Australasia. These include, the ariid catfishes, the eleotrid gudgeons *Oxyeleotris herwerdeni* (Weber), and *Ophieleotris aporos* (Bleeker), and Tarpon *Megalops cyprinoides* (Broussonet).

Other potential commercial species include the common carp *Cyprinus carpio* L., and tilapia *Oreochromis mossambicus* (Peters). Both of these species have been introduced into the river as a result of escapees from fish ponds and are well established. *O. mossambicus* was introduced into the country in 1954 for culture purposes and into ponds in the East Sepik in 1964 and now form between 30% and 50% of the weight in gill net catches and are the basis of the only commercial fishery on the Sepik (Redding 1989). Another species *Gambusia affinis* which is now well established, was introduced to control mosquitoes which proliferate throughout the river basin.

In the lower order hill streams the species have a slightly different species distribution with eleotrids, theraponids, plotosids and rainbowfishes dominating the catch and ariid catfishes, tarpon and tilapia being less important (van Zweiten 1989).

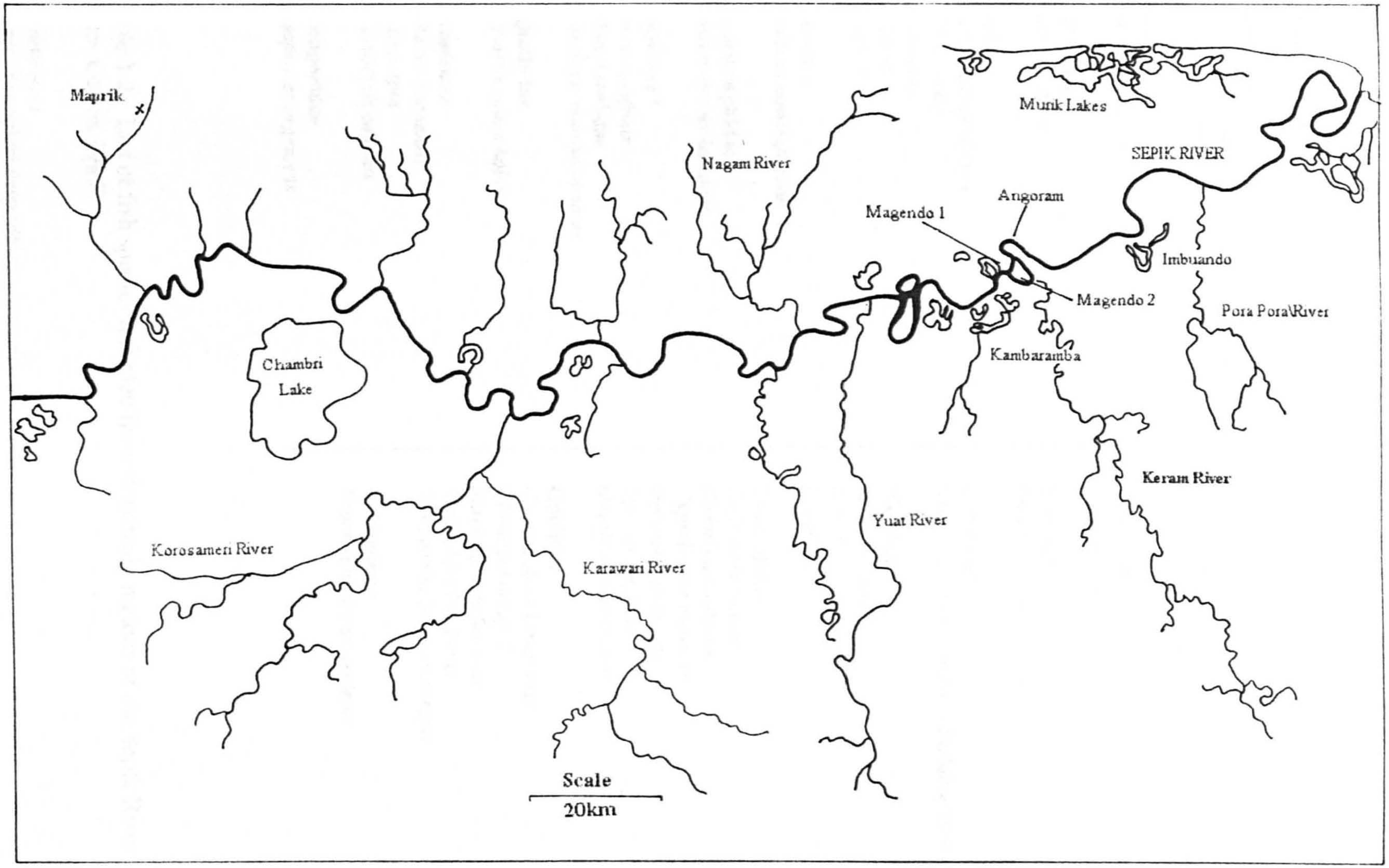


Figure 1.10 The Lower Regions of the Sepik Basin

Pristidae
Pristis microdon

Megalopidea
Megalops cyprinoides

Anguillidae
Anguilla marmorata
A. bicolor pacifica

Chanidae
Chanos chanos

Cyprinidae*
Cyprinus carpio

Ariidae
Arius (Brustiarius) nox
A. (B.) solidus
A. velutinus
A. utarus
A. coatesi

Plotosidae
Tandanus novaeguineae

Hemirhamphidae
Zenarchopterus kampeni

Poeciliidae*
Gambusia affinis
Melanotaeniidae
Glossolepis multisquamatus

Sygnathidae
Microphis spinachoides

Ambassidae
Ambassis buruensis
A. interrupta
Parambassis confinis

Theraponidae
Mesopristes argenteus

Kuhlidae
Khulia rupestris
K. marginata

Apogonidae
Glossamia gjellerupi [1]

Carangidae
Caranx sexfasciatus

Lutjanidae
Lutjanus goldiei

Sciaenidae
Pseudosciaena soldado

Cichlidae*
Oreochromis mossambicus Redding 1989

Mugilidae
Liza macrolepis
L. melinoptera
L. tade

Eleotrididae
Butis amboinensis
Eleotris aquadulcis
Hypseleotris guntheri
Ophieleotris aporos
Op. porocephala
Oxyeleotris heterodon

Gobiidae
Glossogobius koragensis
Glossogobius sp. 2
Mugilogobius fusculus
Redigobius bikolanus
Stenogobius laterisquamatus

Gobiodidae
Brachyamblyopus urolepis

Table 1.2 . List of fish species recorded from floodplain regions of the Sepik River (after Coates 1989)

* introduced
[1] enters floodplain from tributary streams

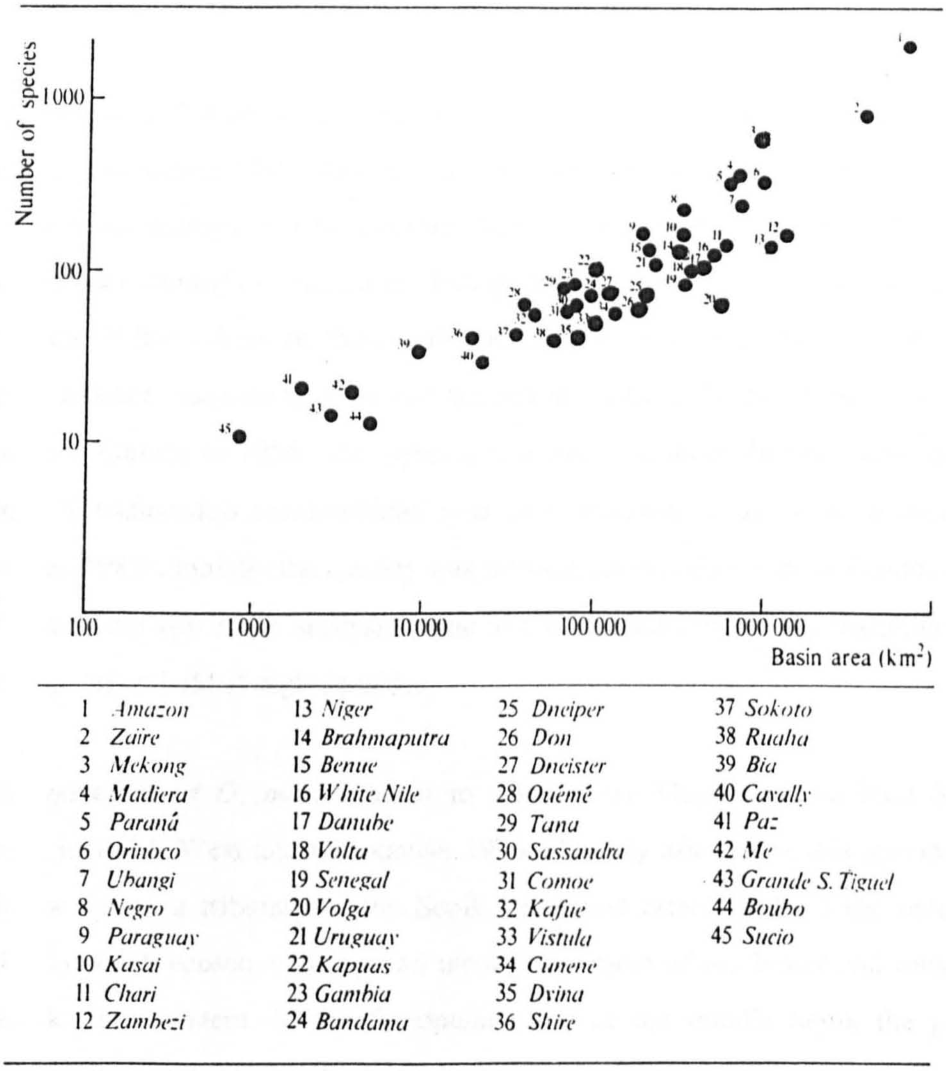


Figure 1.11 Number of species of fish present in different river systems plotted according to their basin area (from Welcomme 1985)

1.4 General history of tilapia production in the Sepik

The introduction of tilapias has been extensive throughout the tropical and sub-tropical world (Philippart and Ruwet 1982). Outside of Africa the first probable accidental introduction was that of *O. mossambicus* into Java before 1939. Since then this species has been introduced to many tropical countries, including Papua New Guinea, and more recently, Australia (Arthington 1986). Many of these introductions were to stock ponds from which the fish escaped. *Tilapia mossambica,* as this species was originally classified, was introduced into Papua New Guinea in 1954. This species is a maternal mouthbrooder and having first been renamed *Sarotherodon mossambicus* it is now referred to as *Oreochromis mossambicus* (Trewavas 1983). Initially the species was introduced into Papua New Guinea specifically for pond culture but was never successful due to the problems with early maturation and stunting of the population held at high densities.

The introduction of *O. mossambicus* to ponds near Maprik in the East Sepik Province occurred in 1964 (West and Glucksman 1976). Shortly afterwards this species was found in the Screw River, a tributary of the Sepik River and established a large naturally breeding population which subsequently spread throughout most of the lower and middle sections of the Sepik River system. In the floodplain areas of the middle Sepik the population was sufficiently abundant by the 1970's to support a small salted-fillet industry. The industry was based entirely on this species and fishermen throughout the area supplied the processing plant with fish caught in 4 and 5 inch stretched mesh gill nets.

The industry never reached its projected output and by the mid 1980's production of salted fillets had decreased significantly.

1.5 The Artisanal Fishery and the 'Solpis' salted fillet industry

Of the 3-4 million people who live in Papua New Guinea almost 87% live inland (Coates 1982). The East and West Sepik Provinces have the largest rural population outside of the highlands and are considered to be amongst the poorer provinces. The total population is estimated to be in the region of 350,000 but this figure is continually changing since this region also has the highest rate of emigration in the country (Skeldon 1977).

The population centres are distributed in clusters along the banks of the Sepik River and in the more upland areas around Maprik - Yangoru and the western coastal fringe (Figure 1.12). Approximately 90% of the population of the Sepik/Ramu catchment areas live in the more upland regions and not on the floodplain (Coates and Mys, 1989).

The human population in and around the Sepik floodplain is estimated to be at 80,000 and is the poorest in the province. The 1986 National Nutrition Survey (NNS) indicated that the rates of malnutrition of children under 5 years old in the Maprik District (Wosera) were the highest in the country (Heywood *et al.* 1986). There is a land shortage in the Wosera area to the extent that many of the families have been resettled on land purchased in West New Britain and Gavien (East Sepik). Many of the settlements along the river rely on sago, fish, a few vegetable crops and coconuts for food (Curtain 1978). Soil fertility is poor and crop yields are low. Consequently the nutritional status of the population is poor as are the financial returns for the cash crops such as coffee, peanuts, tobacco, cocoa and some vegetables.

The main diet in the Wosera is yam and sago with very little protein intake since fresh meat and fish are said to be in short supply. One source of protein is imported tinned fish but, because of the poverty levels in the Wosera, a family will only consume one 350 g can, per household of 6, per week. This is compared to the national average consumption of 735 g or 2.1 cans, per 6 person family, per week. Heywood *et al.* (1986) proposed that the cause of the severe malnutrition in this particular area could not be attributed to a lack in the quantity of food since there seemed to be an apparent adequate production of food through subsistence farming despite the poor yields. The diet is, however, unbalanced and the nutritional quality may be the cause of the malnutrition symptoms seen in children under 5 years of age in this area. Protein malnutrition is also apparent in children under 5 years old in the highland areas where the small streams do not support a large fish biomass and the distribution of fresh fish from the river areas is hindered by poor transport facilities.

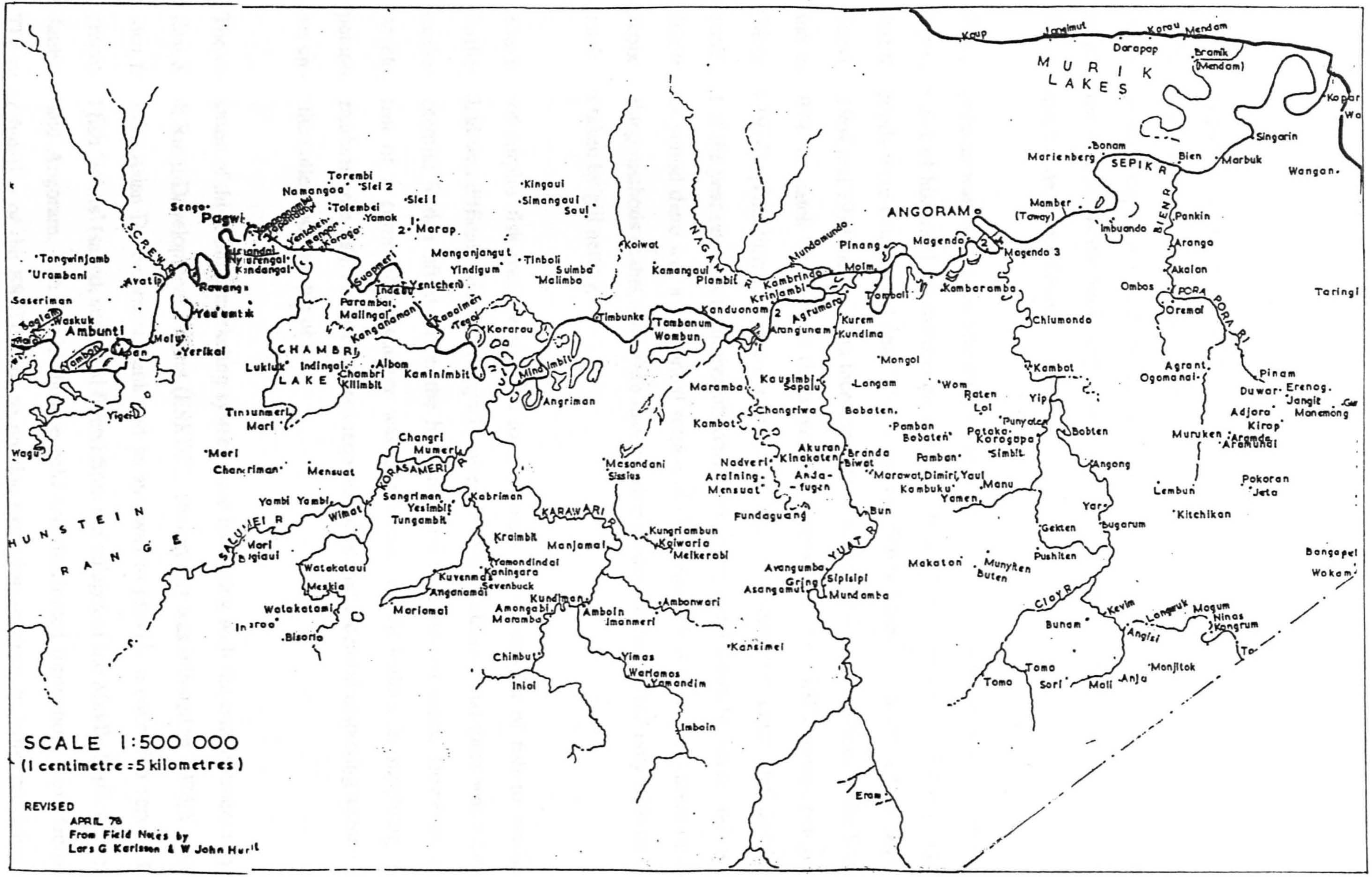


Figure 1.12 : Population centres of the Sepik Basin

It the latter part of the 1970's efforts were made to enhance the socio-economic status of the Sepik area through the exploitation of fish species found in the river. The initial effort was towards establishing commercial production of fish and to provide resettlement areas for many of the poorer Middle Sepik population. The historical background to this commercial fishing project is described below.

O. mossambicus was introduced into Papua New Guinea initially for pond culture. Although there is a lack of historical information on where the first introduction occurred it is thought that the ponds were constructed near Maprik and the Screw River, a tributary of the Sepik. Between 1964 and 1974 there was an increase in the numbers of *O. mossambicus* in the Sepik and by 1974 the catch by artisanal fisherman was estimated to be 10,891 tonnes per year (Munnull 1974). (This figure may be overestimated since the study was conducted during a small part of the year on a small number of fishermen). The general trend, however, indicated that by this period there was a substantial surplus of *O. mossambicus* from most areas of the Sepik. Fishing methods at this time were mainly using spears and hooks and only 18% of the catch was taken by gill netting.

The sale of surplus fish was through the local markets since transport of fish to markets further afield was difficult. Market surveys between 1978-80 indicated that there was a large market potential further afield i.e. in the highlands and other inland areas. However, the development of a commercial industry was constrained by difficulties in supplying the potential markets with fish. Further surveys recommended that a central marketing agency be set up for the collection and sale of fish.

The realisation of this central marketing system came into being with the establishment of the East Sepik Rural Development Project (ESRDP). The project was initiated in 1974/5 with a loan from the Asian Development Bank and its aim was to provide a collection service for processed fish 'solpis' (salted, sun-dried fillets) from the villages of the Middle Sepik between Ambunti and Angoram. Fish would then be sold and distributed throughout New Guinea. The other function of the ESRDP was to provide extension services, training, provision of equipment and supplies (such as gillnets), to organise the market and to distribute the salted fish. One great change seen in the Sepik during this period was the sudden increase in the numbers of 4-5 inch (10.16 mm stretched mesh, 50 mesh deep x 100 m length) gill nets used.

A total of 208 villages were to be serviced by the project although in reality only 50% of these villages were consistently involved in the initial stages. In another study it was noted that in 1979 there were only 16 villages out of 84 producing "solpis" whereas in 1977 and 1978 the figures were 35 and 63 respectively (Curtain and May 1981) (Table 1.3). The numbers of fishermen involved from each village also decreased in later years. At this time it was thought that the potential production from the floodplain could be as high as 30-40,000 tonnes per annum and the subsistence catch around 8000 tonnes/yr (Glucksman 1978).

By 1981 81% of the salted fish production was from 4 main villages on the upper Keram (Rodwell 1982). At this time 10.3 tonnes of salted fillet were produced which was lower than the predicted 350 tonnes for the fifth year of the project (Glucksman 1978).

The projected levels of production were never reached (Table 1.4). The maximum amount produced in one year was 40.3 tonnes in 1979, a shortfall of 84 tonnes. By 1988 the production of salted fillets had fallen to 2 tonnes. In addition the financial problems which emerged later were exacerbated by the fact that the infrastructure initially set up was based on a much higher anticipated production. The possible reasons for this decline in production are discussed below.

The comparison of project revenue and project costs is given in Table 1.5. This is an indication that even if prices for salted fillets and nets were increased by 10% and 21% respectively the revenue would still not cover the costs of the project. The only possible way to recover costs and potentially develop a little profit would have been to increase the production of salted fillets. This in itself would have been difficult, firstly because of lack of interest and loss of contact with many of the villages and secondly, there may not have been the stocks present to support a greater fishing effort.

The availability of tinned fish provided an alternative to salted and fresh fish. The price in 1989 for a fresh tilapia caught in a 4 inch net was approximately 40 toea (34 pence). If the

Months in production	Number of villages per year				
	1977	1978	1979	1980	1981
0	68	35	56	57	69
1-3	22	47	29	25	25
4-6	8	5	4	5	4
7-9	2	7	3	13	3
>9	3	9	11	3	3

(after Rodwell 1982)

Table 1.3 Number of villages producing salted fish and months involved in production

Year	**Projected (Tonnes)**	**Actual (tonnes)**	**Shortfall (tonnes)**	**Percentage production**
1977	20.7	14.5	6.2	70
1978	60.8	22.3	38.5	36.7
1979	125.2	40.3	84.9	32.2
1980	214.6	20.9	194.7	9.7
1981	357.7	10.3	347.4	2.9

(after Rodwell 1982)

Table 1.4 Solpis production 1977-1981 (Actual and Projected tonnes)

Year	Total revenue	Total costs	Total cost minus Development costs	%Total costs covered	%Total minus development costs covered
1980	40346	223926	60976	18	66.1
1981	29557	145150	80951	20.4	36.5

(after Rodwell 1982)

Table 1.5 Projected costs and revenues for the Solpis industry (1980-1981) (Figures are in Kina. 1 kina = £0.80) mean weight for a fish was 350 g, then the price per kilogram of fresh fish was K1.14 (K= kina). In comparison, a 350 g (15 oz) tin of fish was approximately 75 toea (1 Kina = 100 toea) which is equivalent to K1.65 per kilogram. A fresh fish requires gutting, de-boning and de-heading and a tin of fish may be a cheaper and convenient alternative. There is still a large market, however, for fresh fish because of its superior palatability. In the larger towns away from the river prices may vary considerably depending on the availability of fish. If the catch was to increase considerably and more fish were sold in the main markets, then the prices for fresh tilapia might become far more competitive and general consumption would increase.

Many reasons were given for the decline in the salted fish industry, the most likely being that the production of the salted fish was labour intensive and that the prices paid for the fish often only covered the salt required for the processing. Villagers could get a better price in the local market for less effort. During this period, fillets of salted fish were bought from the villagers for K1.00 per kilogram. If the conversion ratio between salted and fresh fish is assumed to be 7.4-1 (Rodwell 1982) then the actual equivalent price for a kilogram of fresh fish is 13.5 toea as opposed to the market price, at that time, of 40 toea. The number of fishermen and villages involved consequently tended to lose interest in processing fish.

The emergence in the late 1970's of the aquatic weed *Salvinia molesta* may not have affected the actual amount of fish in the river but it did hinder access to, and movement of, the nets. Curtain (1978) estimated that the weed reduced the activity of the fishermen by 30%. A later biological control programme using a species of beetle (*Cyrtobagous* sp) to reduce the amount of *Salvinia molesta* in the river had little effect on the decline of the industry. Unfortunately no regular records were kept and no experimental fishing was carried out to provide evidence that the reason for the decline in production was a result of reduced fishing activities or a reduction in fish resulting from the presence of *Salvinia molesta*.

1.6 Objectives of this study

Previous reports of the Sepik River fauna and fisheries indicated that although there seemed to be a good potential for beginning a small commercial fishery on the river based on the introduced fish *O. mossambicus* this potential was never realised. In addition with protein malnutrition being prevalent amoungst young children in the population centres in and around the Sepik basin there was a need for an improvement in protein rich food supplies. There are few alternative protein sources to be found in the area thus the investigation focussed on the fish fauna of the river.

The management of a large floodplain river such as the Sepik for the purposes of food production poses many problems, environmental, social and economic. With little prior knowledge or documented studies having been carried out before this present work there was little baseline data with which to attempt to develop any form of strategy. To propose the exploitation of such a vast and complex system would be unsound without a full investigation into the biology and ecology of the fauna (both native and introduced) and its commercial and nutritive value. There are many examples of detrimental exploitation of stocks as a consequence of lack of understanding or lack of data on the biology and interactions between existing and introduced species and the environment (Pitcher and Hart 1995). There are drawbacks to such studies, as they are often time consuming, require the commitment of capital over a long period of time and short term results are not always possible.

This study was carried out as part of a wider fisheries survey of the fish fauna of the Sepik River which is ongoing and under the auspices of the FAO Stock Enhancement Programme. This report, while looking at some aspects of the relationship between all species in the fishery, focused to a great extent on one introduced species (*Oreochromis mossambicus*) which formed the basis on which the only commercial fishery was started, and the data collected were used for a more comprehensive analysis of the biology and ecology of this species. The biology of the other important species found in the river are described in another study by Coates (1986). The majority of data was collected from November 1981 to February 1983. Sampling was carried out by the author with members of the fisheries team an all *O. mossambicus* were separated from the other species for further analysis by the author alone.

The main objectives of the study were:

- To describe the biotic and abiotic environment of the lower river system in relation to the seasonal changes in water levels (Chapter 2)

- To compare potential with actual artisanal yield of the important 'commercial species' with rivers of similar size and to determine the importance of the introduced *Oreochromis mossambicus* to the overall catch. This also involves a determination of 'potential 'species diversity in comparison to the number of species caught in the river. An assessment of the influence of seasonal changes on the behaviour of the fish species and subsequent catch rates is an important aspect in determining the potential of the river for a commercial fishery (Chapter 3)

- To describe the biology of *Oreochromis mossambicus* through an assessment of feeding and reproductive biology (Chapters 4 and 5)

- To assess the population dynamics of the population of *O. mossambicus* in the lower Sepik (Chapter 6)

- To discuss the potential problems associated with enhancing the Sepik stocks through the introduction of new species (Chapter 7).

- To discuss the reasons for the initial success of *O.mossambicus* and the later decline in catch and the reasons for commercial catches falling below predicted levels. To discuss potential management issues arising from the study (Chapter 7).

Chapter 2 HYDROLOGY AND LIMNOLOGY OF THE LOWER SEPIK RIVER

2.1 Introduction

The hydrology, and nutrient dynamics of riverine systems have a direct influence on the distribution and abundance of living organisms (Kapetsky 1974). The rate of flow is considered as being an important parameter since it affects other factors such as oxygen and temperature which act directly on the fish population and other aquatic organisms (Welcomme 1983, 1985; Walling and Webb 1994). In a review by Welcomme (1985) on the fisheries of the worlds largest rivers the Sepik river was only briefly mentioned yet it has a discharge rate and drainage area comparable to some of the largest rivers in the world (see Table 1.2- Chapter 1). For example, in comparison with the Magdalena River in Colombia, the Sepik has a similar mean discharge rate yet its basin area is one third of the size. The Sepik could generally be described as being unstable, as characterised by rapid changes in deposition patterns and the presence of floodplain features such as the formation of ox-bow lakes.

The general characteristics of the Sepik places the main area of study for this project in the potamon reaches (Welcomme 1985) (Figure 2.1) where there are distinct channels and floodplain areas with both lentic and lotic waters present. Prior to this study there was very little information on the hydrology of the Sepik except for some river level recordings taken at Angoram by the Bureau of Water Resources.

2.2 Methods

This part of the study has re-analysed, for statistical purposes, data collected for an internal report to the Department of Fisheries by the author with other researchers. Full details of the work can be found in Coates, Redding and Osborne (1983). Sample sites are indicated in figure 2.2. These corresponded with sites from which fish were collected and all sites are described in detail in Chapter 3. Water samples were also collected from the river channel close to the village of Angoram where water depth was approximately 16 m. Data was collected during the study period of January to December 1982.

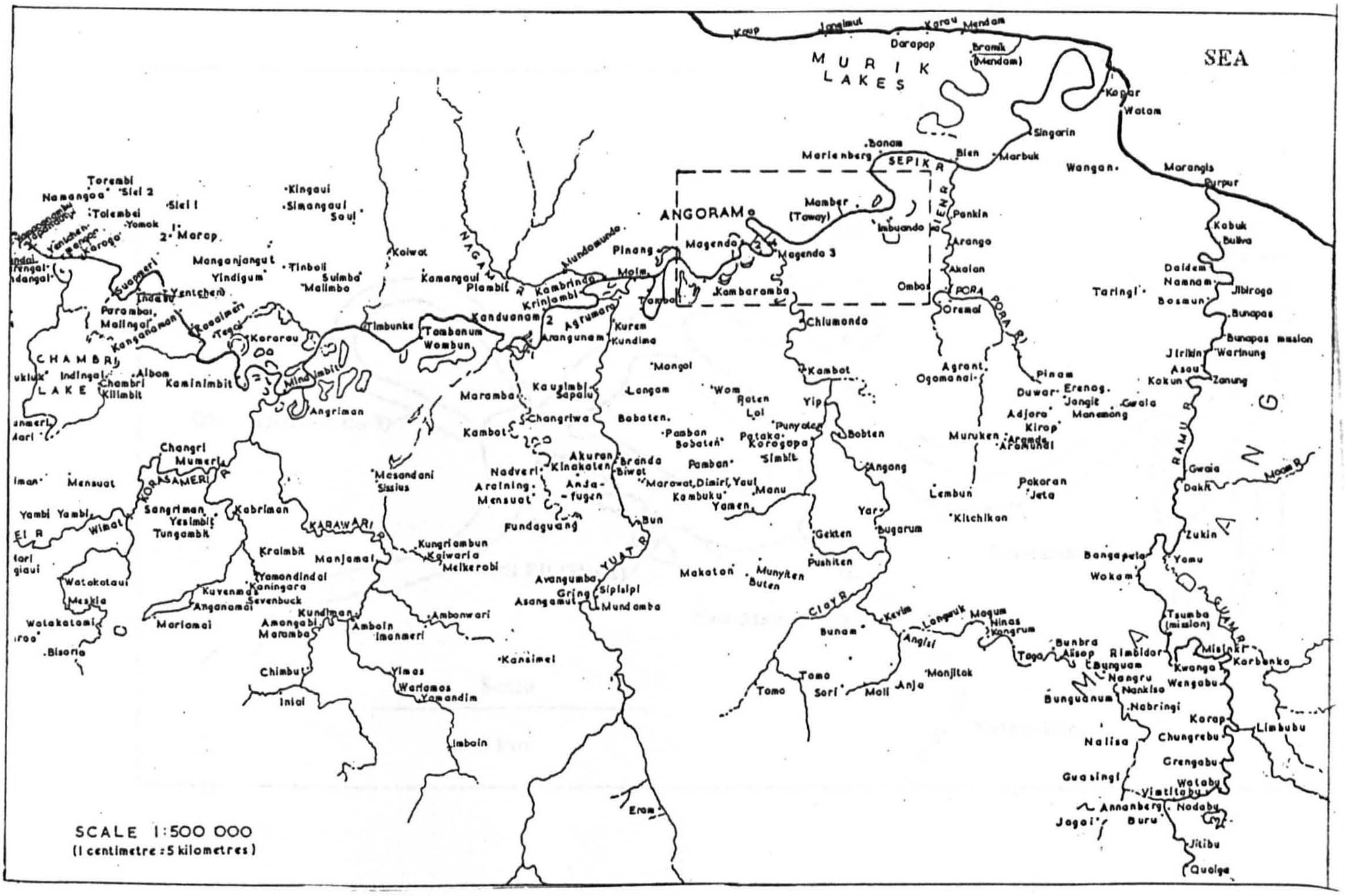


Figure 2.1 The potamon reaches of the Sepik River with associated ox-bow lakes (Roundwaters) (Boxed area indicates main area of study)

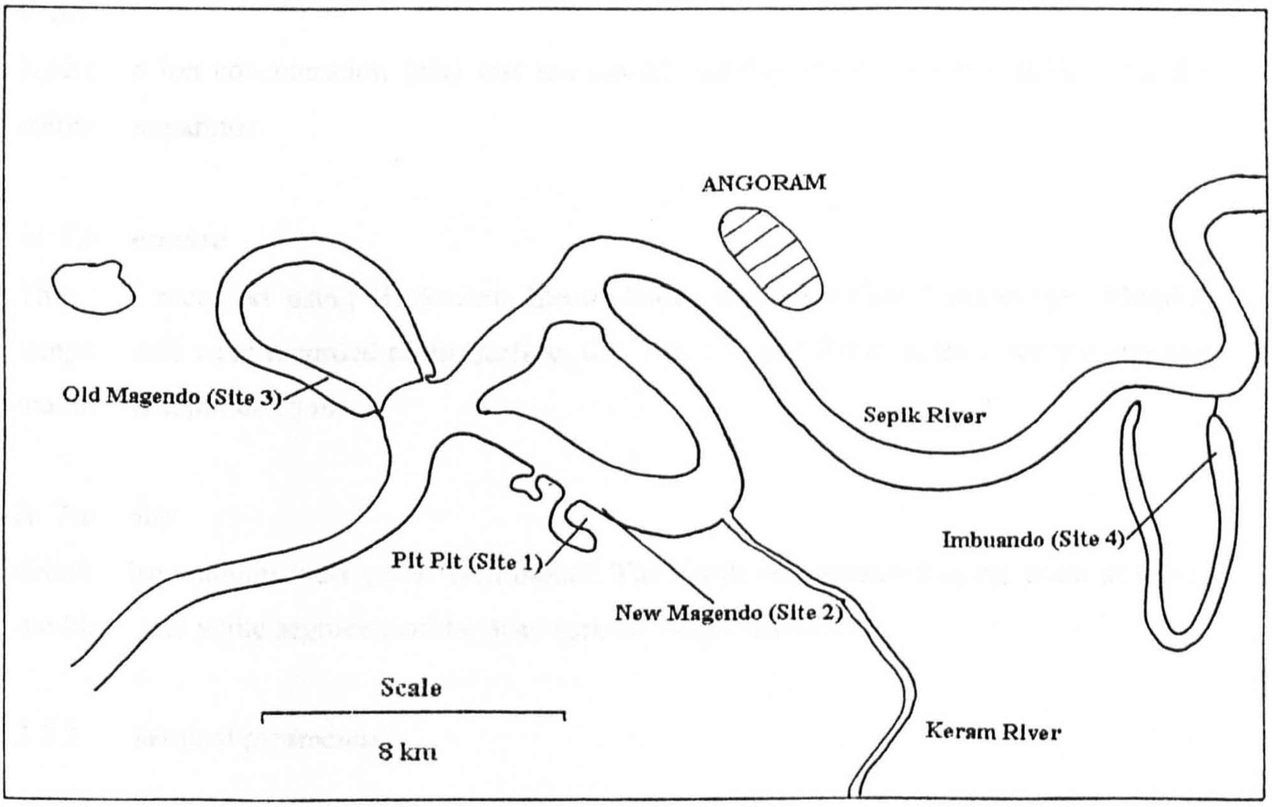


Figure 2.2 Hydrological sample sites (the same areas as for the gill net study)

2.2.1 Physical parameters

i River height

River height was recorded manually, the automatic recorder having broken some years prior to this study. Height rather than depth was taken since the former determined the extent of lateral flow across the floodplain and the area inundated. Recordings were made each day at 0800 and the mean level was recorded for every 10 day period.

ii pH

Hydrogen ion concentration (pH) was monitored monthly using universal indicator and a colour comparator.

iii Temperature

This was recorded using Beckmann Electrodeless Induction Coil Salinometer. Monthly temperatures were recorded at the surface, 0.5, 1.0, 1.5, and 2.0 m at then every meter to a maximum depth of 15 m.

iv Turbidity

Secchi disc readings were taken each month. The depth was recorded as the point at which the black and white segments of the disc were no longer discernible.

2.2.2 Chemical parameters

i Chlorophyll a

Water samples from the first meter depths (composite) for pigment analysis were collected in 1 litre flasks and filtered. Algal pigments were extracted and stored at 4 deg.C before the optical density of *a* pigments were found using spectrophotometry and concentrations calculated (in mg m^{-3}). Methods are detailed in Golterman (1971).

ii Soluble nutrients

Water samples for nutrient analysis were filtered and analysed for soluble reactive phosphorous (SRP) and ammonium nitrogen (NH_4-N), using molybdenum blue, and phenol hypochlorite methods respectively (Stainton *et al.* 1977). Nitrate-nitrogen (NO_3-N) was determined using methods described by Strickland and Parsons (1972).

2.2.3 Data Analysis

Significant seasonal changes in concentrations of chlorophyll *a* and nutrients were determined (non-paired t-Test) for the present study to assess the possible influence of river hydrology on productivity.

2.3 Results and Discussion

2.3.1 Physical parameters

i Flow Regime

The river level heights of the Sepik had been recorded for several years before the present project began (1982-1983)(Figure 2.3 and Table 2.1). This indicated that there were years prior to this study when flood levels were higher than others. Lower peaks seem to be in 1969, 1970 and 1971 followed by a much greater peak flood in 1972/3 and 1982/3. This corresponds with conditions found in other rivers (Welcomme 1985). Depth would be influenced by channel width and the changing structure of mud banks and although tidal influences were apparent they were not thought to have any significant impact on the monthly average. Variability in the flood maximum heights could be attributed to longer term patterns in the global climate (Winstanley 1975, Bryson 1974) and by human impact (Burt 1994). Although there is little evidence of direct human impact on the rivers' regime the potential indirect impact of the traditional practice of slash and burn agriculture and increasing deforestation should be considered as a potential influence. The local inhabitants indicated that these peaks and troughs occurred every 7-10 years although this cannot be substantiated without more historical data. However the grouping of peaks into high and low periods will have substantial effects on not only fish communities but also the dynamics of floodplain ecology (Welcomme 1983). River heights during the period of study are shown in figure 2.4. The regime indicates a definite flood season which begins in November/December and reaches a peak in March/April although there are fluctuations. By May the water had fallen rapidly to a low level and this continued for six months with a water level minimum around August/October.

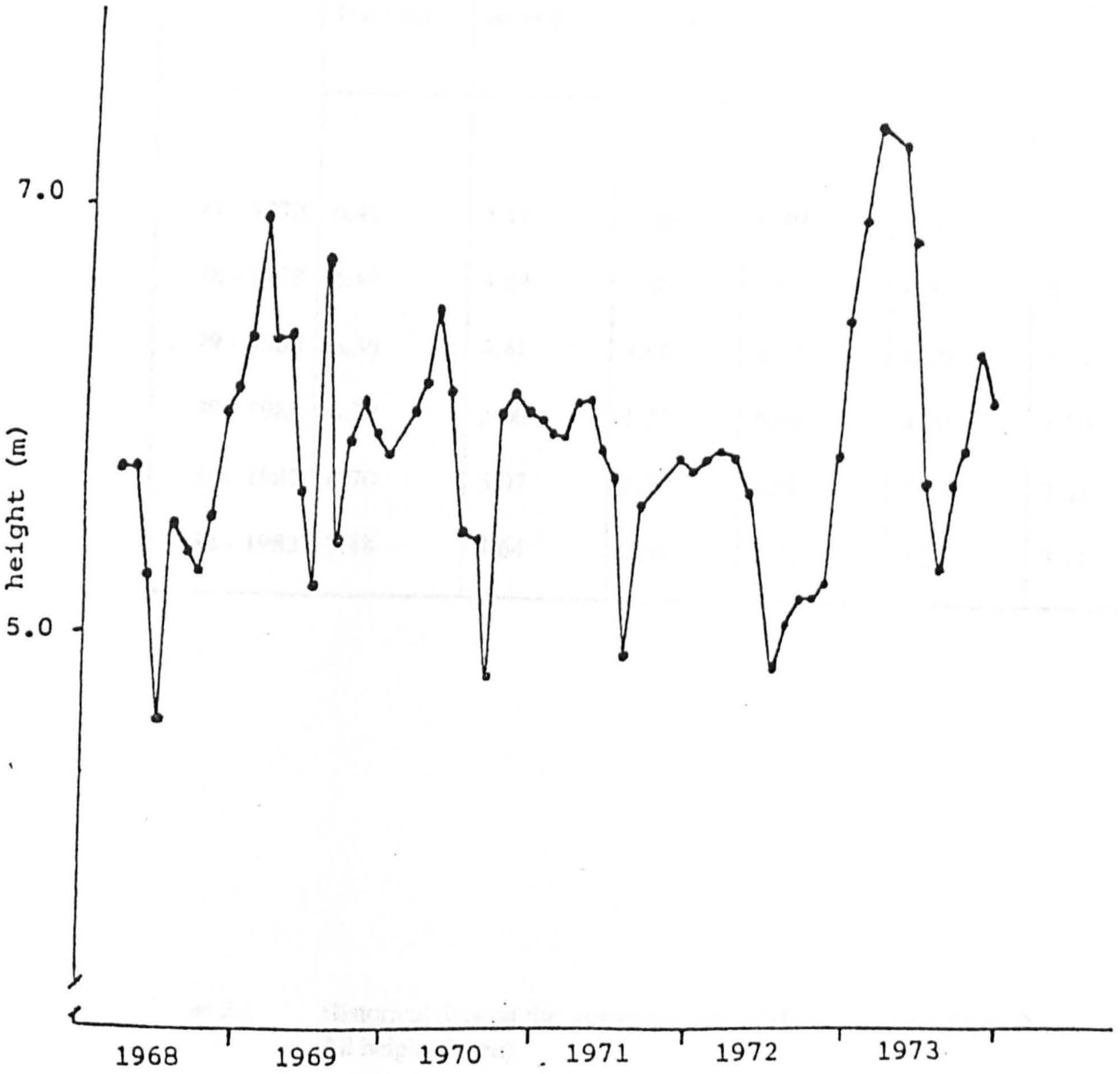


Figure 2.3 River levels 1968-1973

Season	maximum mean monthly level (a)	minimum mean monthly level (b)	mean height change (a - b)	maximum height recorded (c)	minumum height recorded (d)	max. total height change (c - d)
1977 - 1978	6.42	5.17	1.25	6.49	4.69	1.8
1978 - 1979	6.49	4.64	1.85	6.61	4.5	2.11
1979 - 1980	6.36	4.41	1.95	6.43	4.26	2.17
1980 - 1981	6.22	5.00	1.22	6.40	4.70	1.70
1981 - 1982	6.70	5.07	1.63	6.89	4.27	2.62
1982 - 1983	7.18	4.64	2.54	7.32	4.21	3.11

Table 2.1 Historical data on the seasonal cycle of flooding of the Sepik River. All heights in (m)

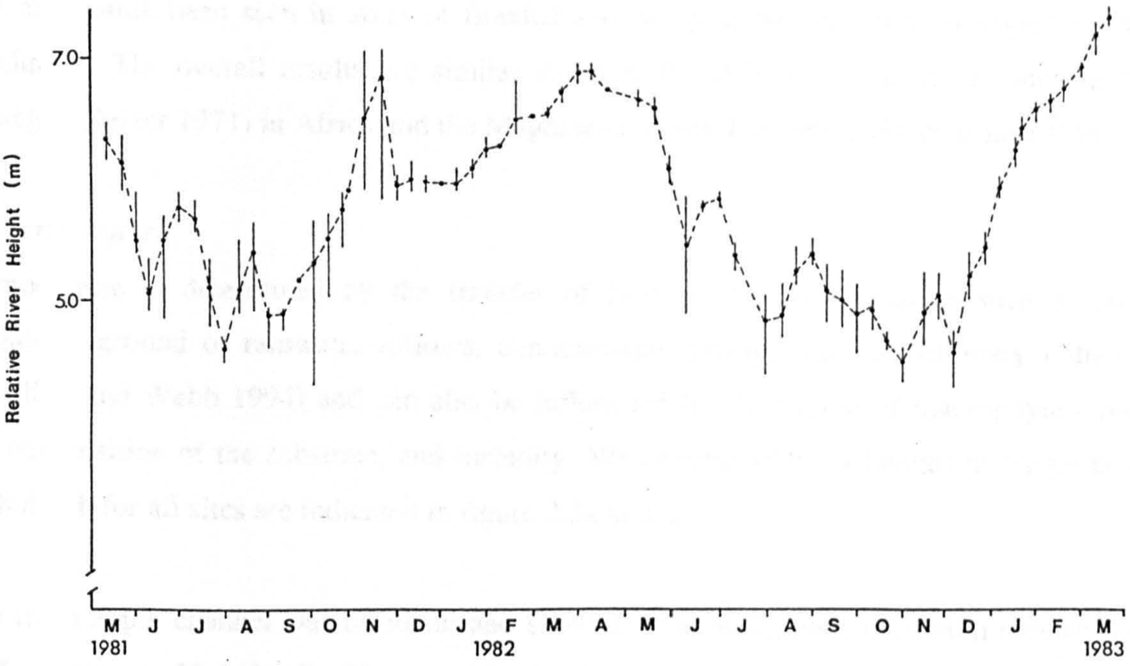


Figure 2.4 Mean river levels during the study period

The crest of the flood was seen at different times in the river channel depending on the location, although the regular sample sites had peaks at approximately the same time. Welcomme (1985) describes the rate of travel of flood crests in the main river channel to be approximately 17 km/day in the Niger, Senegal and Chari Rivers. In the Sepik sample sites were either in permanent ox-bow lakes or in lakes formed on higher land which was inundated only during the flood season. These were not influenced by the effects of crests in the main river channel.

ii Hydrogen Ion Concentration (pH)

Hydrogen ion concentration taken at various locations is shown in table 2.2 and most samples are neutral to slightly acidic, the lowest value being pH 6.2 for Pit Pit in March. This could be associated with respiration and photosynthesis of the phytoplankton during the day since this site was a shallow area with good light penetration to the bottom. Gradients in pH have often been seen in areas of flooded and decaying vegetation with higher surface readings. The overall results are similar to those found in savannah rivers such as the Senegal (Reizer 1971) in Africa and the Magdalena in South America (Ducharme 1975).

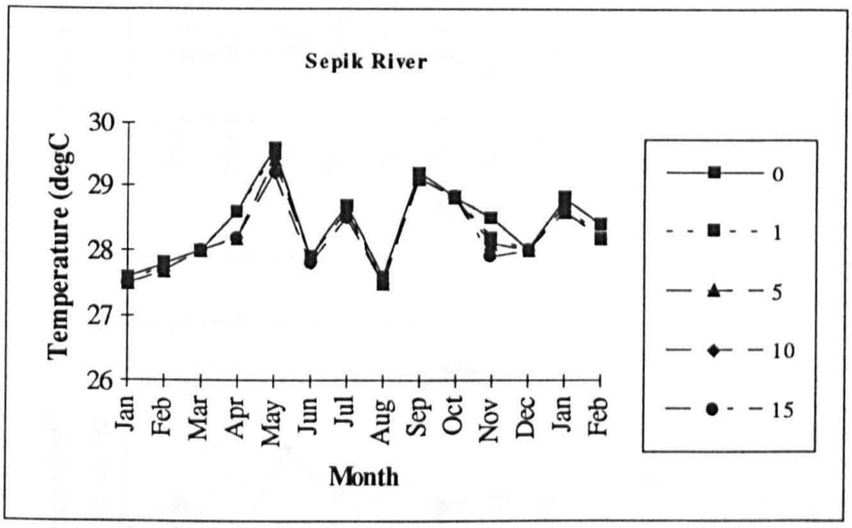
iii Temperature

Temperature is determined by the transfer of heat energy from sources such as solar radiation, ground or rainwater inflows, condensation, precipitation and forestry radiation (Walling and Webb 1994) and can also be influenced by the degree of macrophyte cover, the composition of the substrate, and turbidity (Welcomme 1979). Changes in temperature with depth for all sites are indicated in figure 2.5a and b.

The main Sepik channel was turbulent and showed no stratification (minimum temperature 27.5 maximum 29.6 degC). The combined effects of high temperatures and suspended sediment loads will have a direct effect on the distribution and potentially the evolution of aquatic organisms in the river (Crisp 1988). Very few fishermen were seen fishing in the main river channel during the study and there is little evidence that the river channel is a productive source of fish (see Chapter 3). The deeper more static roundwaters (ox-bow lakes) showed a degree of stratification throughout the year with a large decrease in temperature in the first meter.

Location	**Month**	**pH**
Sepik River, Pagwi	October	7.4
Chambri Lake	October	6.9
Angisi	May	6.5
Panban	June	7.0
Tambali	August	7.0
Avatip	November	7.0
Imbuando (regular site 4)	March	6.9
Magendo 1 (regular site 3)	March	7.0
Magendo 2 (regular site 2)	March	7.0
Pitpit (regular site 1)	March	6.2
Sepik River	March	7.2

Table 2.2. Recordings of pH during the study (see also Coates *et al.*1983) (site details in Chapter 3)



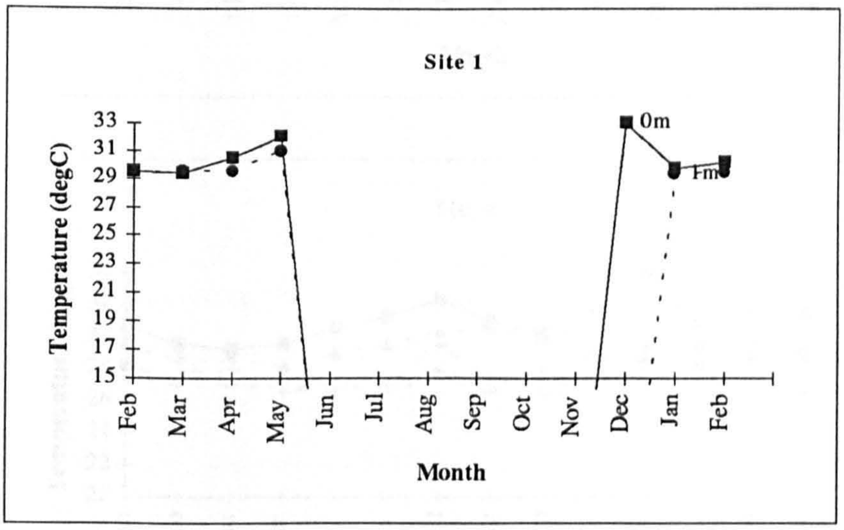


Figure 2.5a Changes in temperature with depth (River and Site 1)

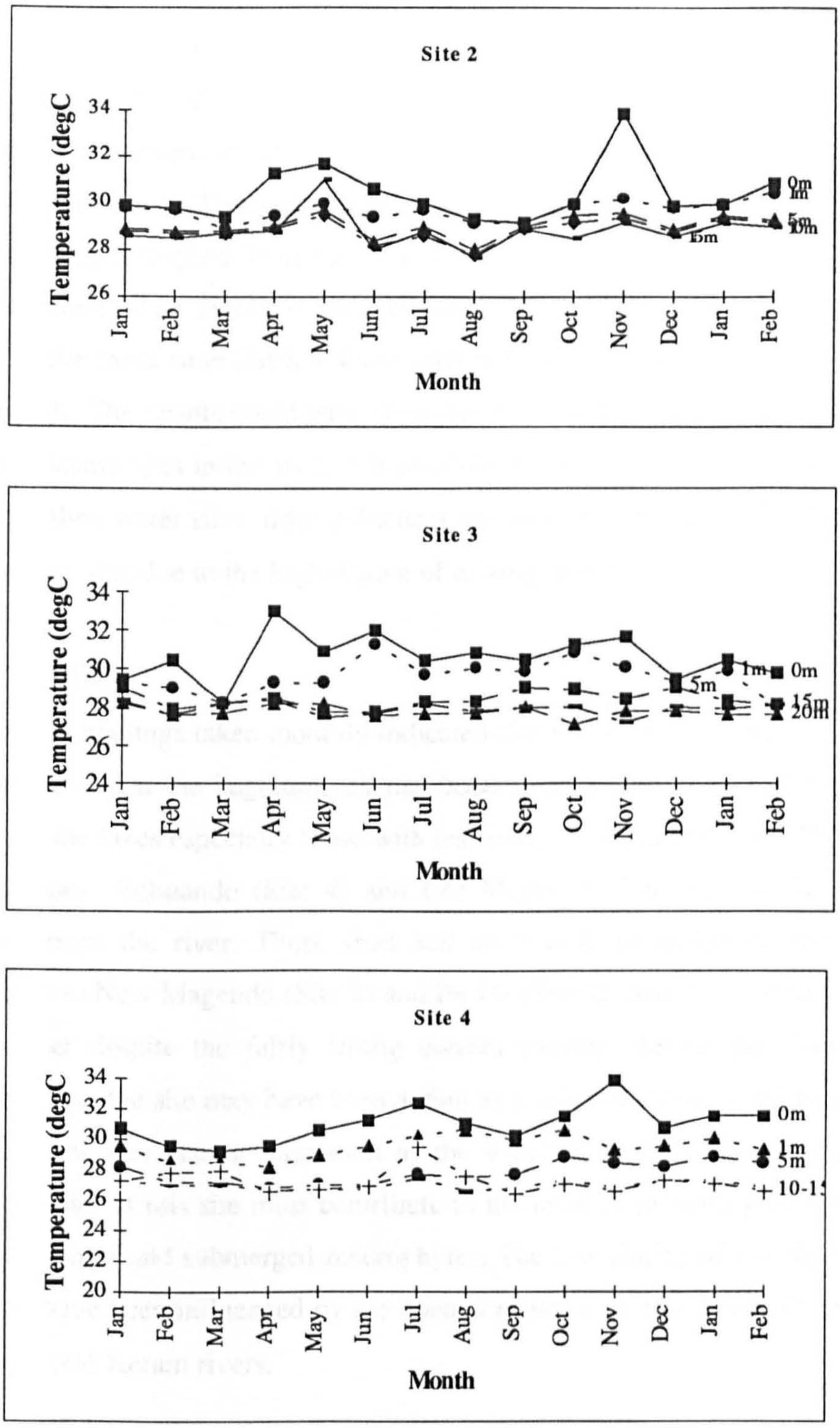


Figure 2.5b Changes in temperature with depth (Sites 2-4)

The oldest formed ox-bow lake, Imbuando, (Site 4) had a greater degree of stratification which reflects its isolation from the main river channel and its depth. The waters in this lake always appeared black and still. The shallow ephemeral site, Pit Pit (Site 1) had generally elevated temperatures in January, May and August and fish catches were poor during these periods (Chapter 3). Temperature inversions occurred with depth in New Magendo (Site 2) and Old Magendo (Site 3) in June and for several months in Imbuando (Site 4). Although readings were taken several times the results remained the same. Instrument readings in the Sepik at the same time did not show such results which suggested that the equipment was not at fault. The results could have been due to local geothermal activity as there are several active volcanic sites in the area. It is possible that the inversions were due to the influx of a plug of saline water since tidal influences are present in this area. Sepik recordings may not have shown this due to the high degree of mixing in the water.

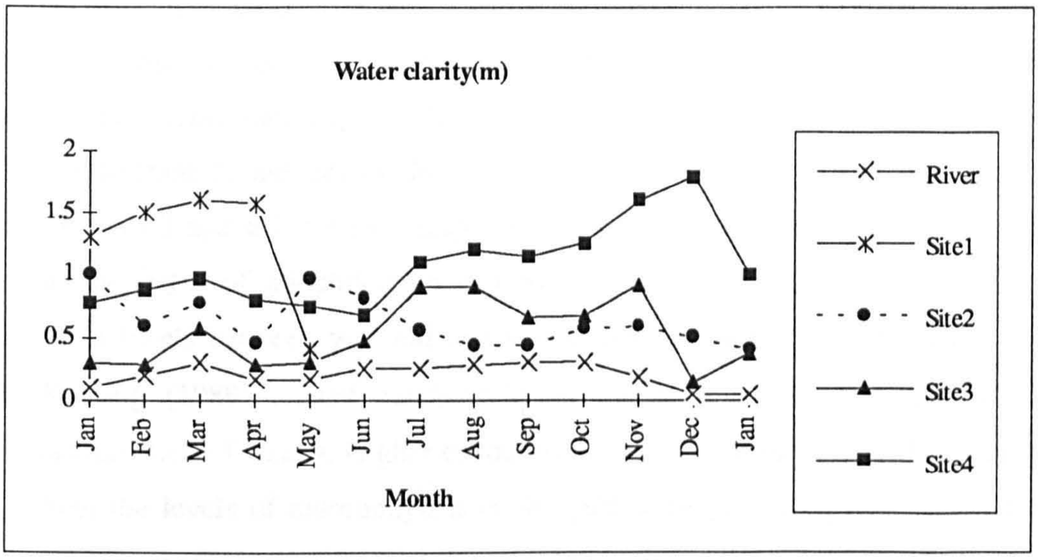
iv Water clarity

Secchi disc readings taken monthly indicated that the main river channel remained turbid all year especially at the beginning of the flood (Figure 2.6). This turbidity influences water clarity in the lakes especially those with less isolation from the river. This is reflected in the results from Imbuando (Site 4) and Old Magendo (Site 3), two lakes which are more isolated from the river. These sites had an overall increased clarity in the dry season compared to New Magendo (Site 2) and Pit Pit (Site 1). Site 1, the floodplain site, remained fairly clear despite the fairly strong current running during the flood. The amount of vegetation on the site may have been acting as a sediment trap. A reduction in clarity in this site in April was due to stagnation as the water level fell. The general high clarity and shallow water at this site must contribute to the level of primary production by benthic and epiphytic algae and submerged macrophytes. The low clarity of the New Magendo (Site 2) site may have been influenced by the open connection of this newly formed ox-bow to both the Sepik and Keram rivers.

2.3.2 Chemical Parameters

i Chlorophyll a (Figure 2.6)

The low levels of chlorophyll *a* found in the Sepik reflects the low nutrient status of the river which may be influenced by the high turbidity of the water which limits light penetration.



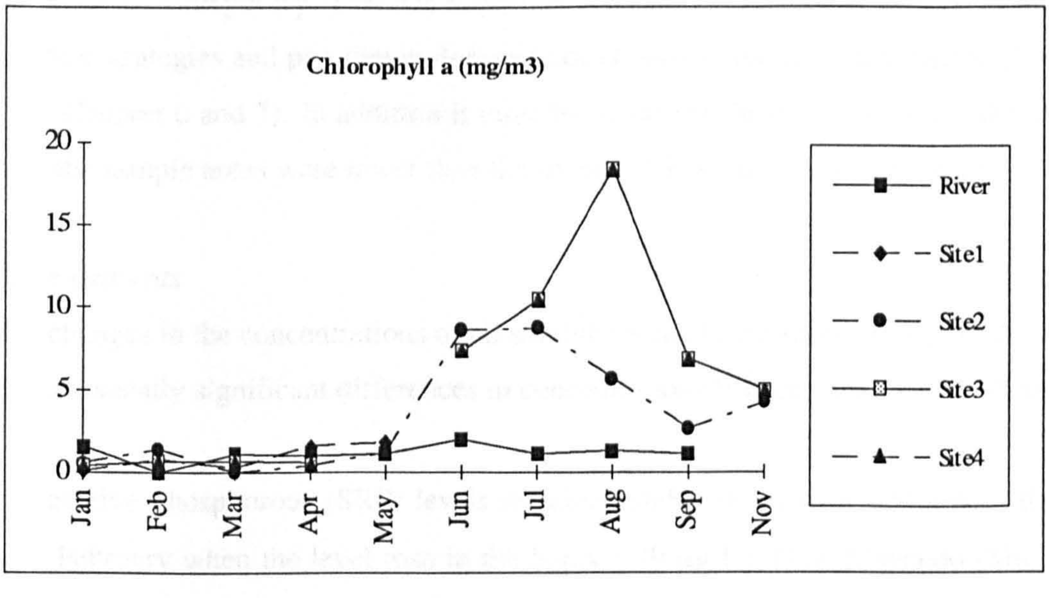


Figure 2.6 Monthly water clarity and Chlorophyll ä levels

There was no significant difference in measurements between wet and dry season for this site or for site 1. The low levels found in Site 1 (Pit Pit) may be not be a true representation of the level of primary production which would be expected from a shallow site with a high level of vegetation. The readings may have been affected by the strong currents seen running through this site during sampling. At the more lentic sites such as Old Magendo (Site 3) and New Magendo (Site 2) and Imbuando (Site 4) chlorophyll *a* levels rose significantly after May to 18.4, 10.0 and 8.7 mg m ^{3} respectively, which corresponded to the falling water levels and the input of allochthonous nutrients from the floodplain. The difference in chlorophyll *a* levels between wet and dry season was statistically significant (t Test $p = <0.05$). Kolding (1989) related conductivity to the relative flushing rate of water in Fergusons Gulf, Lake Turkana. Higher conductivity indicated a higher residence time of the water. When the levels of chlorophyll *a* in the gulf were plotted against conductivity the high regression coefficients indicated a relationship between high algal productivity and stagnation. This author also noted an apparent relationship between high primary production and the survival of tilapia fry. This has important consequences and may also be influencing reproductive strategies and population dynamics of *O. mossambicus* in the Sepik (discussed further in Chapter 6 and 7). In addition it must be noted that in Fergusons Gulf the average depths in the sample areas were lower than the ox-bow lakes studied in this report.

ii Soluble nutrients

Monthly changes in the concentrations of all soluble nutrients are shown in figure 2.7. There were no statistically significant differences in concentrations between seasons for all sites.

Soluble reactive phosphorous (SRP) levels remained stable in all sites throughout the year except in February when the level rose in the Sepik (49 µg l^{-1}), New Magendo (Site 2 ; 36 µg l^{-1}) Old Magendo (Site 3 ; 43µg l^{-1}) and Imbuando (Site 4 ; 24µg l^{-1}), and to a lesser degree in Pit Pit (Site 1 ; 18µg l^{-1}). In the larger tropical rivers the chemical components such as phosphorous are derived from rain and the rock over which the river flows (Welcomme 1985, Whitton 1975). When flow increases at the start of the flood nutrient levels may be higher, as seen in February at all the sites. Earlier studies by Mitchell *et al* (1980) described levels between 1.2 - 18.7 µg l^{-1} which are substantially lower than those found in this study. However during the period of the previous study there was substantially more water surface covered by the water weed *Salvinia molesta*. Although the biomass

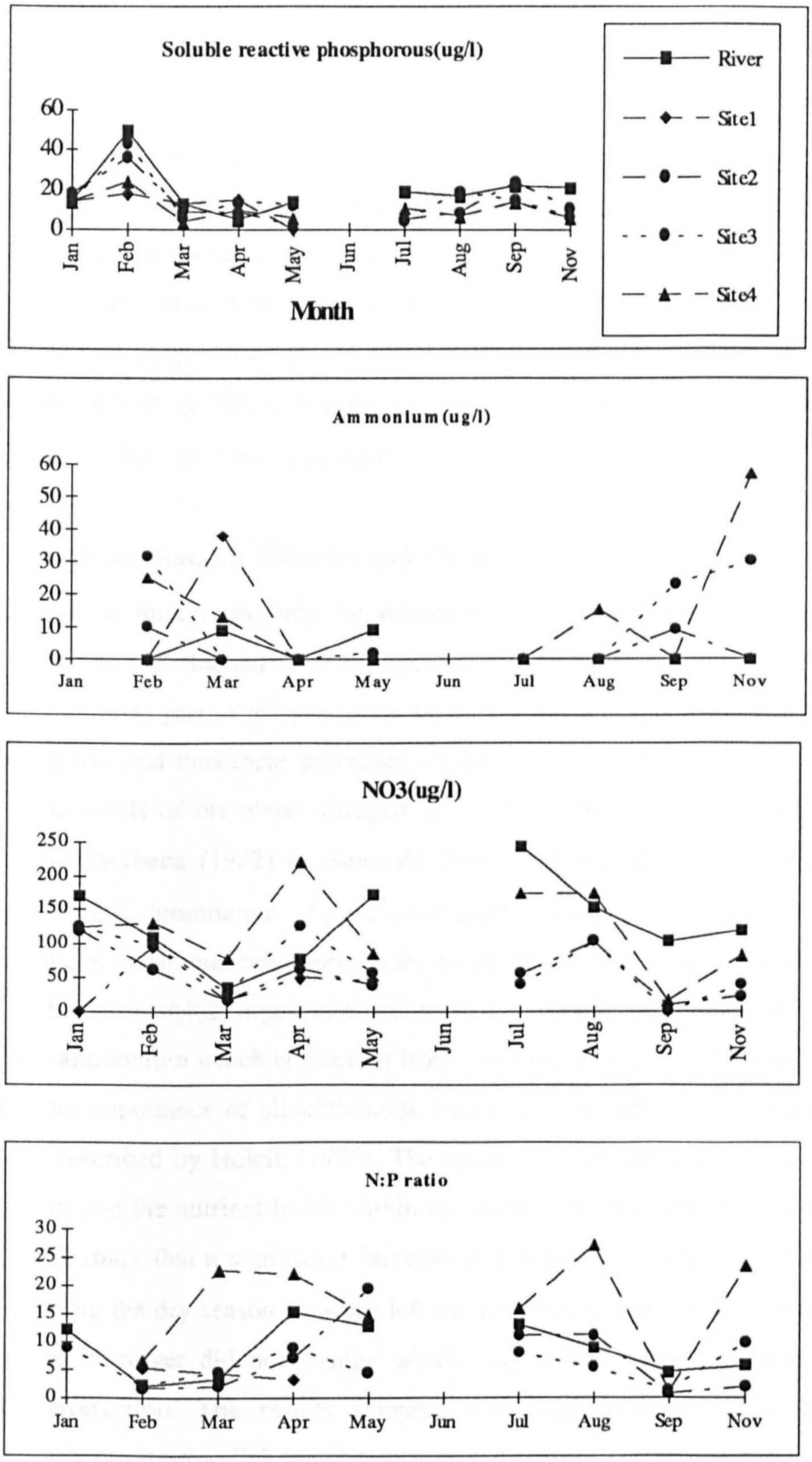


Figure 2.7 Monthly concentrations of nutrients per site.

of this plant was not measured it may have influenced the level of SRP through uptake.

In most areas Ammonium-Nitrogen (NH_4-N) was undetectable except in February in New Magendo (Site 2) and Old Magendo (Site 3) and Imbuando (Site 4) with levels of 10, 32 and 25 $\mu g\ l^{-1}$ respectively showing the same trend as in SRP levels. This could be related to the increased flow and turbidity at this time. Again the results are higher in contrast to those found by Mitchell *et al* (1980) in August 1978 and this may also have been influenced by the presence of large areas of *S. molesta* cover in the river basin during this period. Phytoplankton take up NH_4-N in preference to NO_3-N (Gaudet 1973) which may explain the difference in values for these parameters.

Levels of nitrate-nitrogen (NO_3-N) and nitrite-nitrogen (NO_2-N) in the Sepik fluctuated from month to month and may be related to the lower biomass of phytoplankton and macrophytes in the channel. The nitrogen cycle in a river is more complex than that of phosphorous since part of the processes which involve nitrogen also involve exchange with the atmosphere and thus these processes are not enclosed within the water body (Newbold 1992). The levels of dissolved nitrogen in rivers which can be classed as unpolluted are detailed by Meybeck (1982) in Newbold 1992) as being; dissolved nitrogen 260 $\mu g\ l^{-1}$, nitrate 100 $\mu g\ l^{-1}$, ammonium 15 $\mu g\ l^{-1}$, and nitrite 1 $\mu g\ l^{-1}$. This compares favourably with concentrations of all nutrients found in the Sepik River. The biomass of primary producers, algae and heterotrophic organisms are related to levels of nutrient in the water body especially ammonium which is released from consumers back into the water body (Newbold 1992). The importance of allochthonous inputs in determining the productivity of a river system is described by Holcik (1996). The degree of inundation will influence the level of these inputs and the nutrient levels within the system and the subsequent production. It was seen in this study that a significant increase in chlorophyll *a* occurred in the oxbow lakes studied during the dry season as water left the floodplain. The levels of primary production in the river however did not change which may relate to the flow and turbidity levels limiting production. The results suggests that food availability for herbivorous and consequently piscivorous fish may be greater in the ox bow lakes which may be indicated by the greater catch in these areas in comparison to those in the main river channel (Chapter 3).

Chapter 3 SPECIES COMPOSITION, CATCH PER UNIT EFFORT AND FISHING METHODS

3.1 Introduction

Fisheries yields from floodplain rivers of Africa, Asia and South America have been estimated from various morphological and edaphic parameters and have formed the basis to the development of management strategies (Welcomme, 1976, 1979; Bayley, 1981). The fish faunas of all these three continents are long established and diverse and show a definite ecological convergence (Lowe-McConnell, 1975). This evidence justifies the direct comparison between Amazonian and African rivers. However there is a general poverty in the diversity of freshwater fish species in northern New Guinea compared to rivers in Africa and South America and species diversity estimates based on calculations used for African rivers may not relate to the situation in the Sepik (Coates 1985).

Freshwater bodies including both lacustrine and river systems are important contributors to world fish catch with 14.6 million tonnes produced from these sources in 1991 (FAO 1991). Potential yield from major river systems change with the influence of natural events or the impact of human activity (Muncy 1978). Flood regimes in floodplain rivers are known to affect catch statistics for species which utilise the floodplain (Welcomme 1985, Gerking 1967) and the difficulties of sampling large rivers are described by Norris *et al* 1992).

The exploitation of a resource such as a riverine fish population requires a prediction on the total yield of the system as well as a determination of the proportion available for removal without threatening the sustainability of the fishery (Bayley and Li 1992). One important area which requires clarification before yield estimates and management decisions can be made, in a river with a distinct flood cycle, is the effects of changes in water level on fish production. This can be achieved by the analysis of changes in the catch over a period which covers the hydrological cycle. The amount of lateral coverage of a floodplain will affect the level of input into the system from allochthonous and autochthonous sources and will indirectly affect production in the higher trophic levels (Holcik 1996)

Historical research suggests that there may be a strong relationship between biological production and hydrological regime (Kolding 1989, Welcomme 1985, Kapetsky 1974). There is evidence that in rivers and lakes in Africa variations in catch are related to the annual flood cycle. Kolding (1989) showed a significant relationship between the water level in Lake Turkana and the catch per boat. It is also suggested that some species may have a greater effect on the catch rates than others, especially those that utilise the floodplain as the river rises. This chapter considers the contribution of all species to the catch in the different sample areas and aims to establish the relationship between catch composition and catch per unit effort with fluctuating river levels

3.2 Methods

River levels

Recordings of river levels were taken every day throughout the period of study from a fixed marker in the river at Angoram. The relative height and lateral spread of the river was noted from these readings. Historical data on river levels were also collected to ensure that during the period of study the range of heights fell within normal variability.

In this section catch rates for all species are analysed with reference to river levels to determine whether there is a relationship between river levels and yield of native species and that of *O. mossambicus.*

Catch data were obtained using four regular sampling sites (see below) which were close to Angoram (Figure 3.1). In addition, to determine whether species composition varied significantly throughout the length of the river system, additional samples were collected from several other sites using identical fishing methods. The following section describes the sample sites, fishing methods, biological data collection and field procedures. Analytical methods and statistical manipulation of the data are described fully in the relevant chapters.

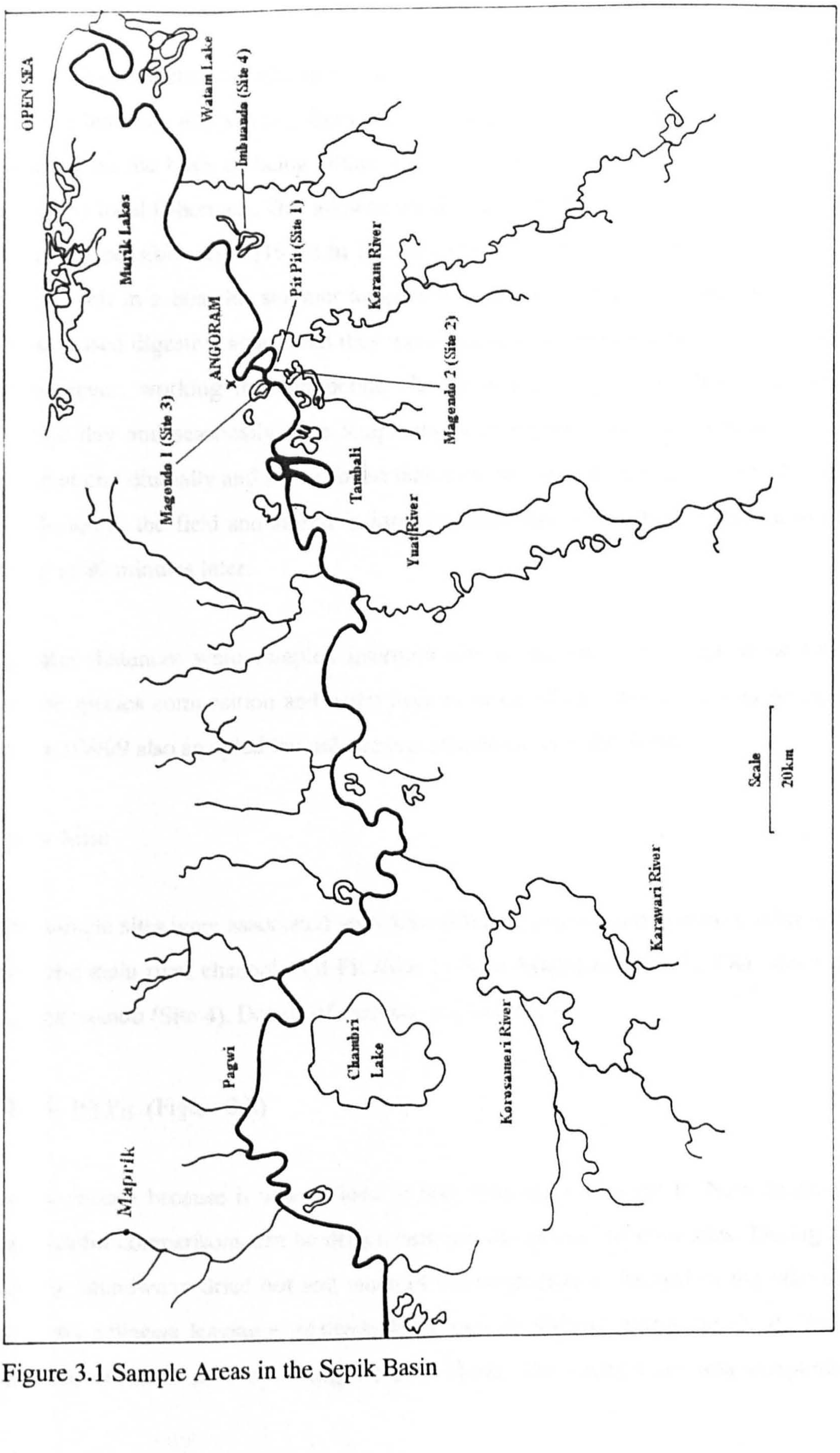


Figure 3.1 Sample Areas in the Sepik Basin

3.2.1 Sample Sites

The size of the river system and distances involved precluded regular sampling of sites at a greater distance than one day's travel from the laboratory. Four regular sample sites were therefore chosen on the basis of being within a day's travel from the laboratory and which were also used by local fishermen. This allowed for dissection and analysis of the fish samples in the fastest time possible. Ball (1948) in Ricker 1971) noted that the stomach contents of fish caught and left in a boat in summer temperatures for more than 30 minutes were so affected by increased digestive action that they were rendered useless for analysis. The author cited was, however, working in a temperate climate where temperature differences vary throughout the day and seasonally. The temperatures in Papua New Guinea remain fairly constant all year and diurnally and it was found that there was no difference between stomach contents collected in the field and stored in formalin immediately and those removed in the laboratory up to 80 minutes later.

Sites at greater distances were sampled intermittently as indicated below to allow for a comparison of species composition and catch over as much of the river system as possible. Later work in 1988/9 also sampled the hill streams associated with the Sepik.

3.2.2 Regular Sites

The regular sample sites were associated with four different roundwaters (ox-bow lakes with access from the main river channel): Pit Pit (Site 1) New Magendo (Site 2), Old Magendo (Site 3) and Imbuando (Site 4). Details of each site is given below.

Site 1 Pit Pit (Figure 3.2)

This site was chosen because it was an area of true floodplain adjacent to New Magendo (Site 2) and useful comparisons can be drawn between the catches of both sites. During the dry season the roundwater dried out and much of the vegetation in the bed of the lake was burnt off by the villagers leaving a relatively clear area for fishing during the flood. Water depth varied by as much as 2 m during the peak flood. The roundwater was surrounded

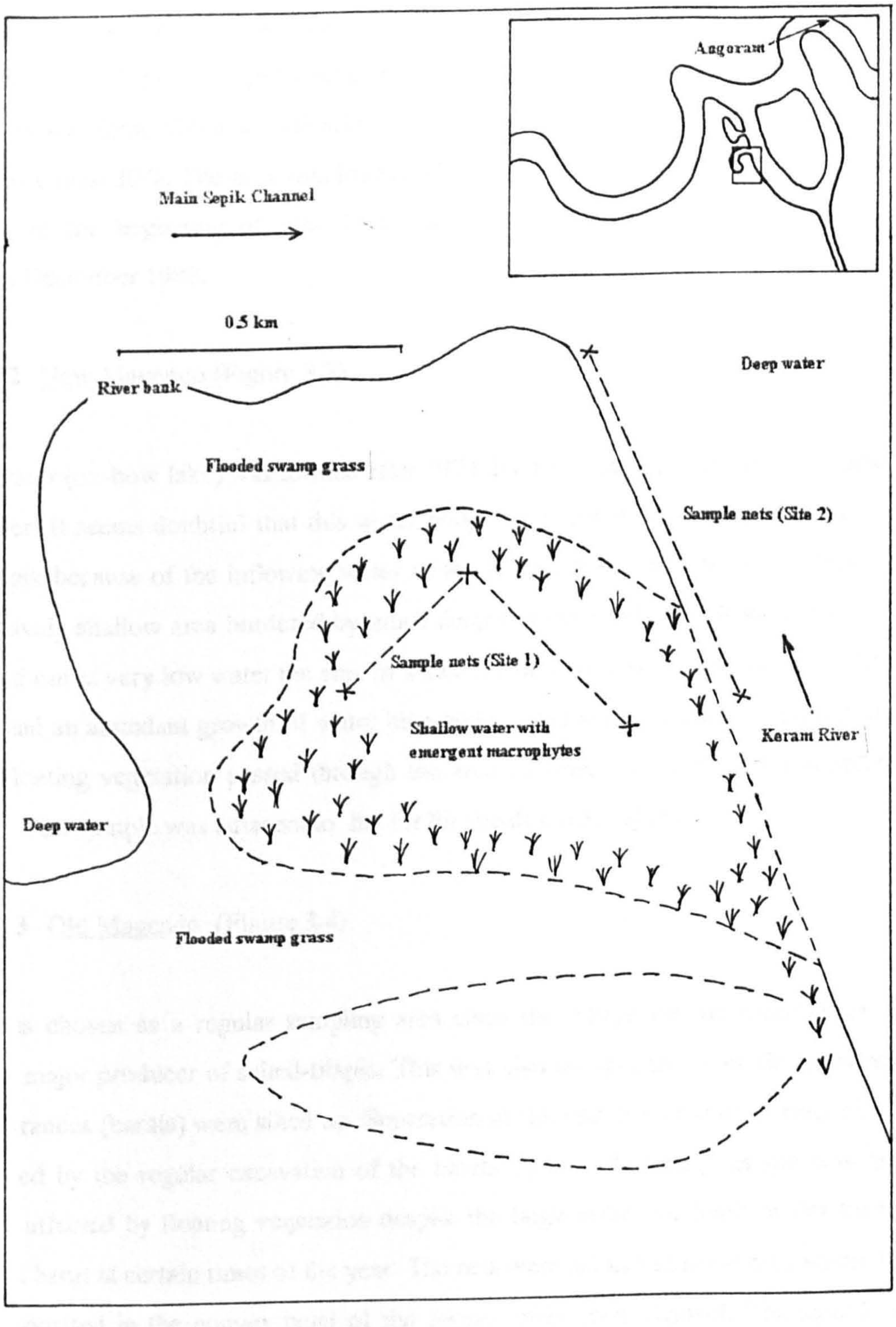


Figure 3.2 Sketch of Site 1 (Pit Pit). (Box indicates the site in relation to the river course and arrows indicate direction of flow)

by dense growths of swamp grasses, mainly *Saccharum robusta* and other species of aquatic vegetation such as *Cyperus cephaloides, Ludwigia adscendens, Ipomea aquatica* and *Ceratophyllum* sp. Some Salvinia (*Salvinia molesta)* was present in the area but the cover was never more than 20%. The area was inundated in mid-December 1981 and dry again six months later at the beginning of June 1982, this was followed by a further period of inundation in December 1982.

Site 2 New Magendo (Figure 3.3)

This roundwater (ox-bow lake) was formed after 1974 due to a major change in the course of the main river. It seems doubtful that this water body will become completely isolated from the main Sepik because of the inflowing water of the Keram River into the area. Nets were set in a relatively shallow area bordered by much deeper water as shown. Although some of the area dried out at very low water the area in which the nets were set remain covered. Much of the area had an abundant growth of water lilies and submerged vegetation. Although large amount of floating vegetation passed through the area all results were obtained in areas of open water. This sample was adjacent to the Pit Pit site described above.

Site 3 Old Magendo (Figure 3.4)

This site was chosen as a regular sampling area since the village on the roundwater was previously a major producer of salted-tilapia. This was also thought to be an old roundwater and both entrances (barats) were silted up. Separation of the lake from the main river channel was prevented by the regular excavation of the barats by the villagers. This site was never significantly affected by floating vegetation despite the large inflow of Sepik water through the upstream barat at certain times of the year. The nets were set in a shallow area where mud had been deposited in the convex bend of the former main river channel. The sample site never dried out completely and depths of water varied between 1-2 m in the dry season and 2.5-3.5m in the wet season. The area had copious growths of water lilies and submerged vegetation (especially *Ceratophyllum* sp.).

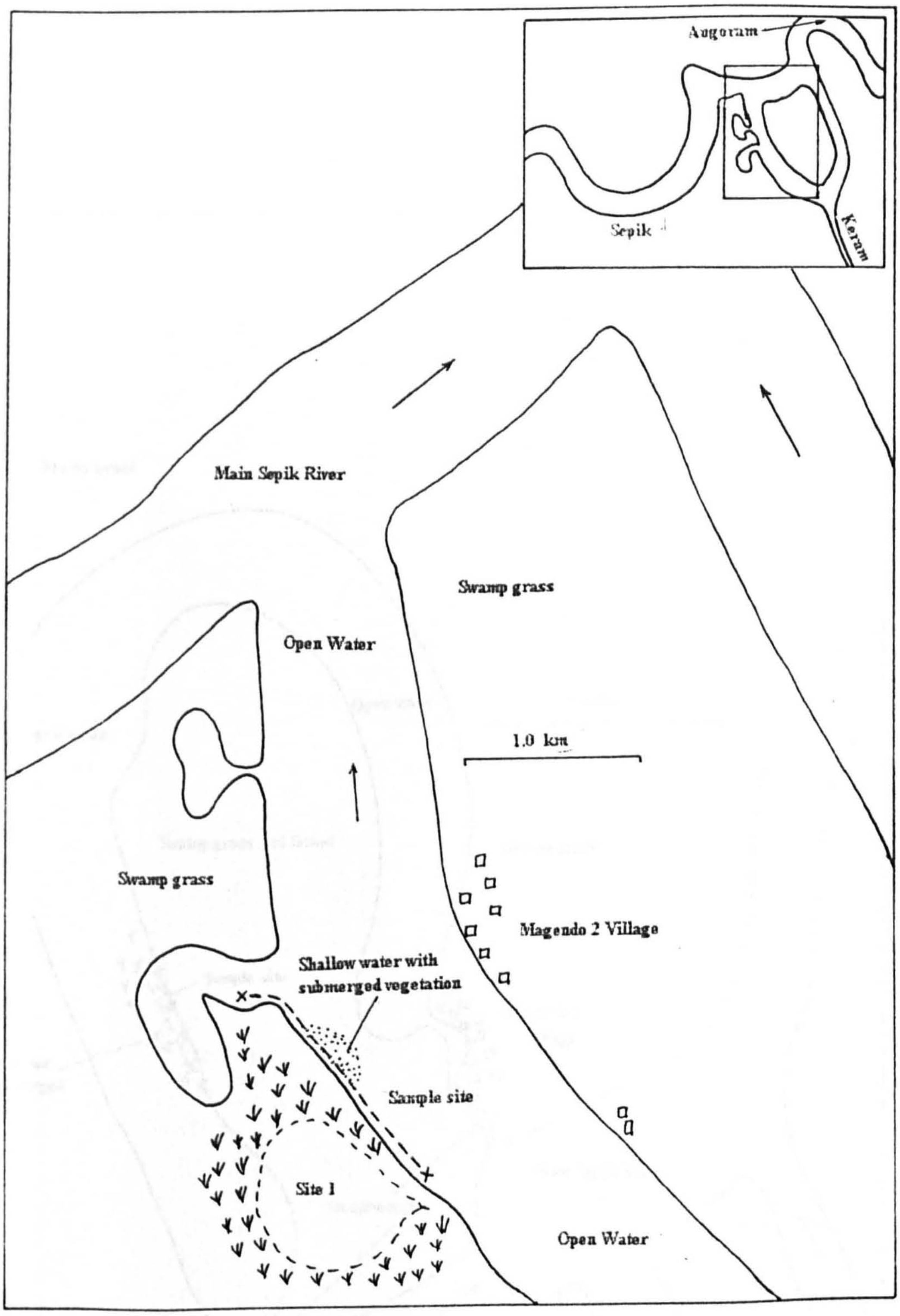


Figure 3.3 Sketch of Site 2 (New Magendo) (Box indicates relation to the river course and arrow indicates direction of flow)

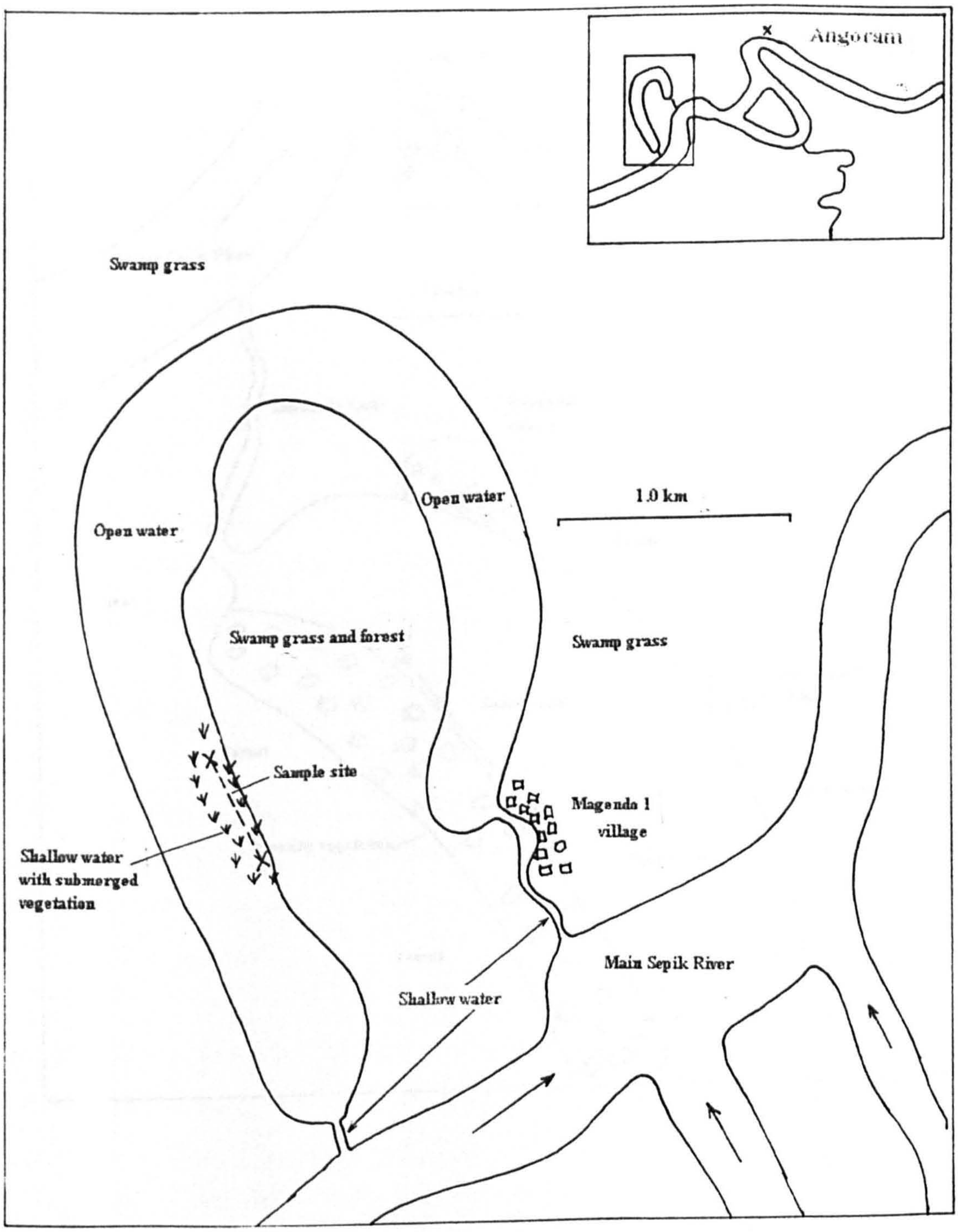


Figure 3.4 Sketch of Site 3 (Old Magendo) (Box indicates site in relation to the river course and arrow indicates the direction of flow)

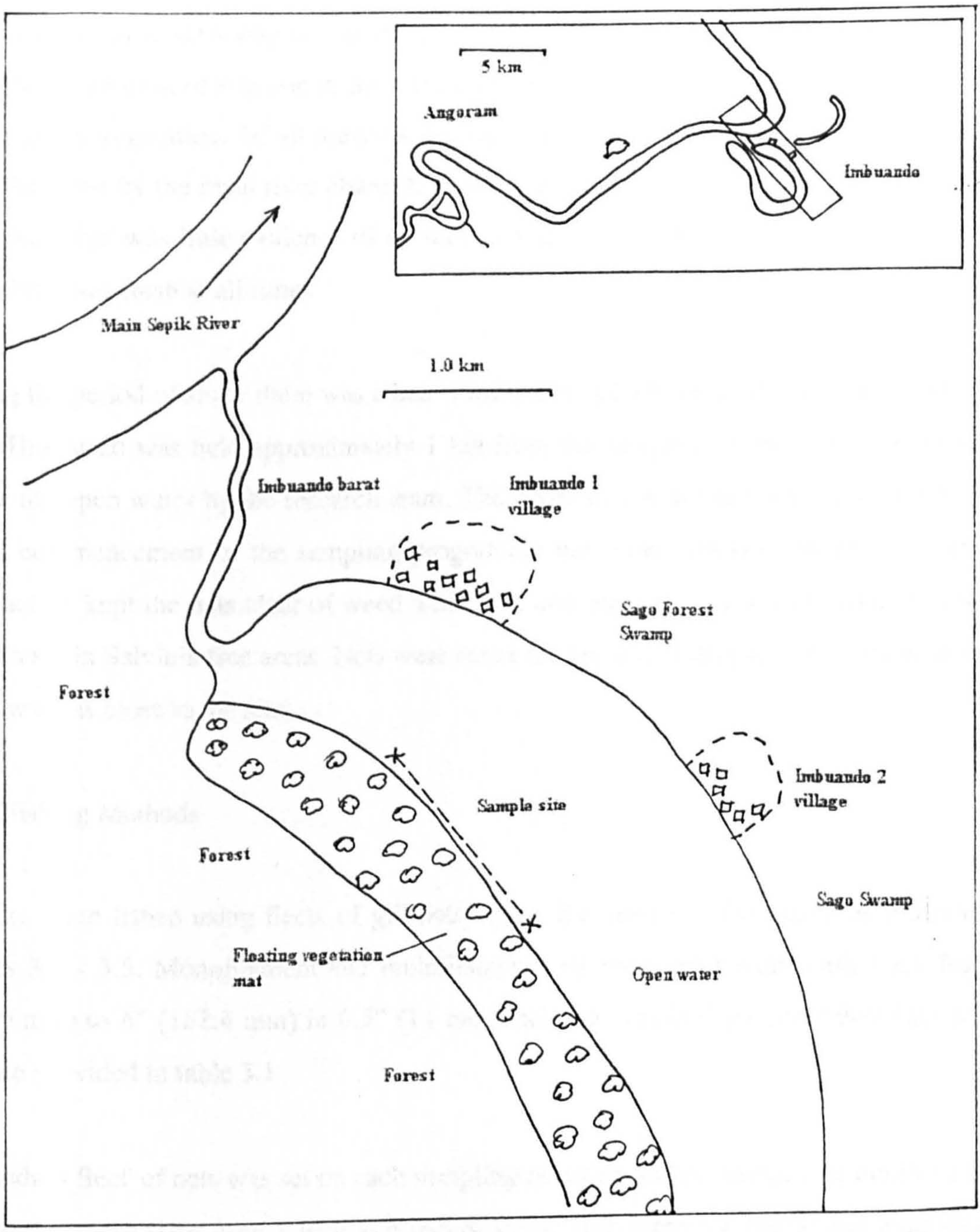


Figure 3.5 Sketch of Site 4 (Imbuando). (Box indicates site in relation to the river course and arrow indicates the direction of flow)

Site 4 Imbuando (Figure 3.5)

This roundwater is relatively old as indicated by its degree of isolation from the main river channel, the amount of siltation in the barats (canoe/passages, entrances) and the thick cover of secondary vegetation. Of all the sites this one was the closest to the sea being just 55 km from the coast by the main river channel. There was a marked tidal influence observed in the barat but there was little evidence of an influx of salt water into the area sampled since the water here was fresh at all times.

During the period of study there was a heavy infestation of *Salvinia molesta* over most of this lake. This weed was held approximately 1 km from the sample area by a boom constructed across the open water by the research team. The boom was in position for three months prior to the commencement of the sampling programme but broke towards the end. Fortunately wind action kept the nets clear of weed whilst the nets were set. All results from this site are for nets set in Salvinia free areas. Nets were set at the surface in deep-water as there were no shallow areas close to the site.

3.2.3 Fishing Methods

All sites were fished using fleets of gill-nets set by the author in the positions indicated on figures 3.2 - 3.5. Monofilament and multifilament nets were used with mesh sizes from 1" (25.40 mm) to 6" (152.4 mm) in 0.5" (14 mm) intervals. Dimensions and other data for the nets are provided in table 3.1

A 'standard fleet' of nets was set on each sampling occasion and consisted of a number of nets of different mesh sizes from 1 inch to 6 inches at half inch intervals. Mono and multifilament nets were used. Initially two multifilament 6" nets were used but as these never caught any fish they were discontinued. All nets were set to hang vertically from the surface. In Site 4 (Imbuando) nets were always set in deep water but in both Sites 2 and 3 (New and Old Magendo respectively) nets were set in variable depths of water according to the season. During the dry season the lead line would often touch the lake substrate. The nets set in Site 1 (Pit Pit) would invariably extend from the surface to the bottom substrate. A clear space of at

Net	Mesh size inches, (mm) (diagonal, knot to knot)	Length (m)	Number of meshes deep	Depth when hung (m)	Area (m2)	colour	Nsf
multi-filament							
1	1.0, (25.4)	25	200	2.5	62.5	pink	2
2	2.0 (50.8)	25	100	2.5	62.5	green	2
3	3.0, (76.2)	25	50	1.87	46.8	red	2
4	4.0, (101.6)	25	50	2.5	62.5	green	2
5	5.0, (127.0)	25	50	1.56	39.0	pink	2
6	6.0, (152.4)	25	25	1.87	46.8	red	0
mono-filament							
1	1.0, (25.4)	21	100	2.0	42.0	blue	2
1.5	1.5, (38.1)	43	50	1.5	64.5	blue	1
2	2.0, (50.8)	43	50	2.0	86.0	blue	1
2.5	2.5, (63.5)	44	50	2.5	110.5	blue	1
3	3.0, (76.2)	43	50	3.0	129.0	blue	1
3.5	3.5, (88.9)	45	50	4.0	180.0	blue	1
4	4.0, (101.6)	43	50	4.5	193.5	blue	1
5	5.0, (127.0)	45	50	5.5	247.5	blue	1
6	6.0, (152.4)	44	25	3.5	154.0	blue	1

Table 3.1 Gill net dimensions. (Also indicated is the number of nets of each type used in a 'Standard Fleet' (Nsf). All monofilament nets were transparent pale blue).

least 2 m was always kept between adjacent nets to allow fish to swim along nets and around the ends. This avoided 'funnelling' fish along the nets until they became caught in a net of the appropriate mesh size.

Nets were always set for a standard period of time (the 'standard set time'). Setting commenced at 1500 hr and nets were lifted and cleared starting at 0800hr the next day. Nets were lifted in the same sequence in which they were set and catch data presented in the results always apply to this time period.

Nets were set during the first quarter of the lunar cycle and not on a monthly calendar. It has been shown that for some marine, and cichlid species growth and reproductive periodicity may be synchronised by external factors such as lunar cycles (Taylor 1984, Farbridge and Leatherhead 1987, Schwank 1987, Robertson *et al.* 1988, Wootton 1990, Nakai *et al.* 1990).

In the preceding months before the true sampling programme began experimental net fleets were continually interfered with and fish often disappeared. Therefore during the regular sampling period nets were guarded using a boat anchored nearby.

3.3 Data Collection and Analysis

All fish caught during the regular sampling programme were taken to the laboratory in Angoram. All *O. mossambicus* were separated from the other species in the catch and processed separately. Biological data collected from *O. mossambicus* included:

Length (Total and Standard)
Weight (Whole and Gutted)
Otolith width and weight
Sex
Gonad Weight and State
Stomach Fullness
Fat Content
Scale diameter and ring counts

3.3.1 Gill net selectivity

Gill nets are known to be selective for a narrow size range and larger fish of the same age will often escape capture. In this study 30 nets of a range of sizes were set. These included two monofilament nets for each mesh size ranging from 1 inch to 6 inches in 0.5 inch gradations and two of each multifilament mesh sizes from 1 inch to 6 inches. To pinpoint possible bias in fishing effort on fish size, selectivity curves from length frequency data were constructed for each net.

3.3.2 Catch Per Unit Effort (CPUE)

Catch varies considerably during the day and night and, therefore, data has not been converted to catch per net per unit time as it was felt that these figure would be misleading. Catch data are presented per unit area (g m^{-2}) of net used to indicate catch per unit of effort, effort in this case being the 'standard set time'. This also enables catch for different mesh sizes to be compared. Rates of catch for *O. mossambicus* were processed separately from the other main species caught. This enabled a comparison of catch and an assessment of the possible influence of the flood regime on both introduced and native species of fish.

3.3.3 Relationship between river levels and CPUE

Statistical analysis (two-way ANOVA) was undertaken on CPUE and river levels to determine the influence of season and changing water levels on *O. mossambicus* in comparison to all other species combined. This would enable a comparison of behavioural responses of both introduced and native species to physical and environmental changes during the year. For this analysis river levels were categorised as, Rising, Peak and Falling.

3.3.4 Bottom set gill nets

Fishing trials with bottom set nets in each of the regular sample sites were also carried out for comparative purposes. Depths varied according to the flood cycle but were generally between 16 and 19 m deep as described below. Monofilament nets identical to those described in table 3.1 were used with a heavily weighted bottom line. These nets were set by the usual method and left for the standard time as previously described. Nets in Site 4 (Imbuando) were set in the same place as the regular surface settings but those in Sites 2 and 3 (New and Old Magendo) were set directly opposite the regular sites. Depths set were 19 m in Site 2, 16m in Site 3 and 17m in Site 4. Six days of fishing were undertaken in Site 2 and 4 and five days in Site 3.

Since the results indicate that *O. mossambicus* were not caught in bottom set nets. The only significant catches were of large fork-tailed catfish (Ariidae) or large *Megalops cyprinoides*. Thus in the main data analysis the results from bottom set nets were not used since the surface gill nets were considered to be set in the main area inhabited by the fish population and a true representation of potential yield from the system.

3.3.5 Additional sample sites

To determine species composition of the fish population of the Sepik comparative gillnet samples were obtained from other locations between the regular sample periods. All nets were set on the surface for the standard set time unless indicated. Species caught in the nets were identified and used in composition tables.

Sites which were sampled occasionally are shown in figure 3.6 and included;

i Angoram

Nets were set in May and June towards the end of high water levels and in August when water levels were low. Nets were set on the inner bend of the main river channel opposite Angoram town.

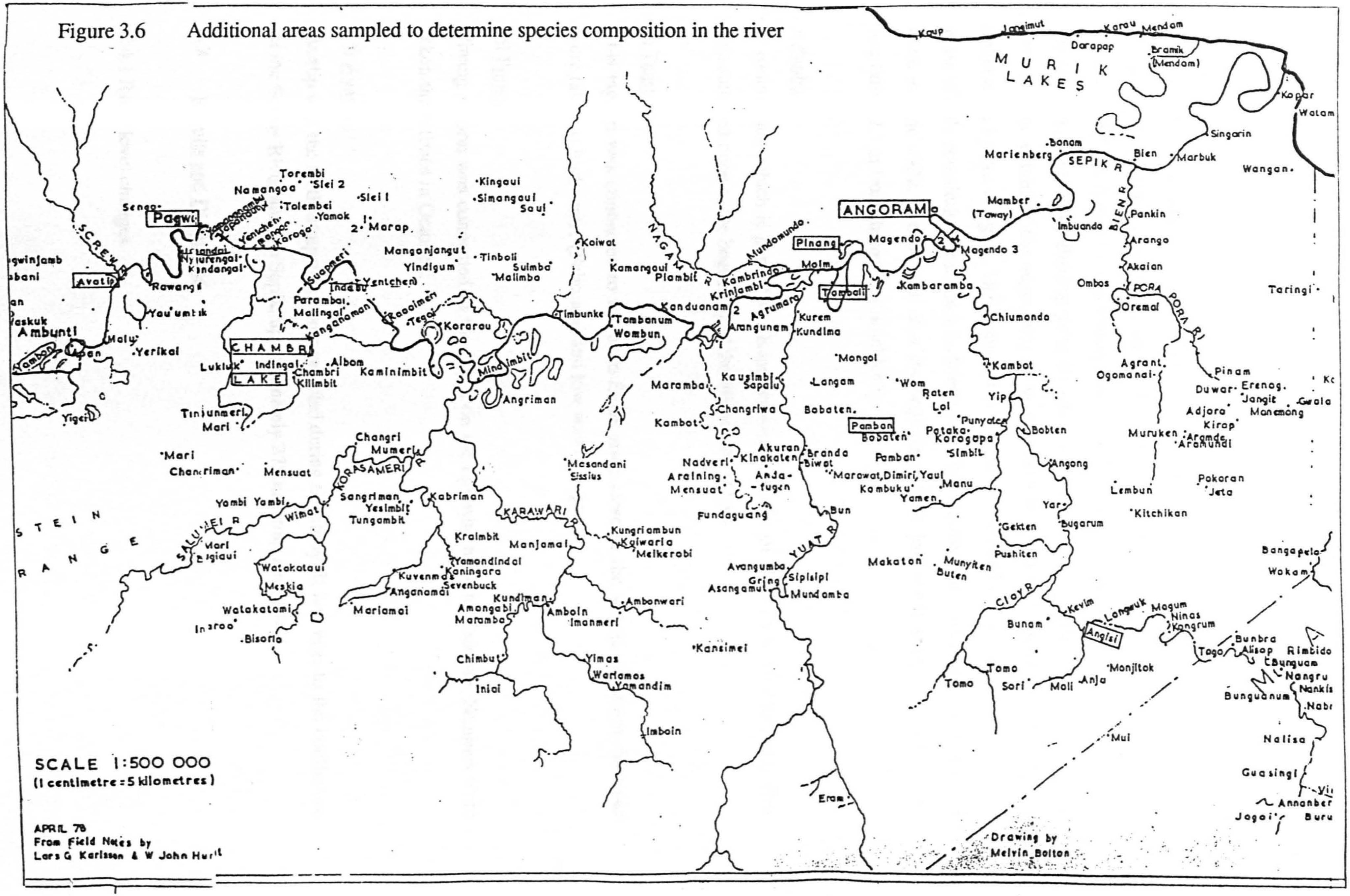
ii Pagwi

Nets were set in May (high water) and October, towards the end of the dry season). Nets were set in the main river channel opposite Pagwi village on the inner bend of the river.

iii Chambri Lake

This is a large shallow depression lake, of over 200 km^2 including the floodplain at high water, and is connected to the main river channels by numerous barats. There is a large area of floodplain associated with the lake during the wet season. The area of the lake varies seasonally as does the amount of floating vegetation, which consists of large grass islands and *Salvinia molesta*. At the time of sampling the water level was very low and thus a complete survey of the lake was not possible. The samples collected came from an area near the main barat leaving the lake.

Figure 3.6 Additional areas sampled to determine species composition in the river



iv Angisi

This lagoon was an extensive area of shallow water and swamp close to the Keram River and was not formed from a main river channel. The village was the main producer of salted tilapia fillets in 1982 and it was for this reason that a sample was taken here. Approximately 90% of the area was covered by floating grass islands and other natural vegetation. Salvinia was not present. The extent of the vegetation cover is usually related to the amount of burning off undertaken by the villagers. This event did not occur in 1981 and at the time of sampling the grass islands constituted a serious interference with boat movement. This lagoon was sampled once in June 1982, two months after the beginning of the low water season when the river had fallen 2.5 m from the normal flood level.

v Panban

A roundwater which is part of the Kambaramba network of lakes close to Angoram. This was sampled once at the beginning of the dry season (July).

vi Tambali

This lagoon was connected to the main Sepik river close to the village of Moim. Samples were taken at high water (February) and low water (August).

vii Pinang

Pinang lagoon was connected to the Sepik on the opposite bank to Tambali. Samples were taken three times in October.

viii Avatip

Avatip was the furthest upstream site sampled during the study. It was near to the confluence of the Screw River and the Sepik, approximately 275 km from Angoram.

3.4 Results and Discussion

3.4.1 River level changes

The river level regime reflects approximately six months wet/flood season from November/December to April/May inclusively and a six month dry season from June to October/November inclusively. River heights during the period of study are shown in figure 3.7. The regime indicates that the flood level reaches a peak in March/April. By May the water was falling rapidly and this continued for six months with a water level minimum between August and November. The regular sample sites had peaks at approximately the same time although Site 1 was higher land inundated only during the flood season.

River level changes are neither smooth nor regular and the average total flooded area during the wet season has been estimated at 7600 km^2. The river level heights of the Sepik had been recorded for several years before the present project began and are discussed in chapter 2. This indicated that there were years when flood levels were higher than others with greater peak flood in 1972/3 and another increase in maximum level in 1982/3. This corresponds with conditions found in other rivers (Welcomme 1985). Winstanley (1975) Bryson (1974) and Burt (1994) concluded that this variability in the flood maximum heights could be attributed to longer term patterns in the global climate. This has been discussed previously in chapter 2 but the influence of the flood regime on the dynamics of the aquatic flora and fauna may have important implications with respect to predictions of yield and future management.

The proportion of the floodplain which remains inundated during this period varies with the fluctuations in river level. During the flood the main river channel which is, in places 16 m deep, is full and flows rapidly. Discharge rates increase from approximately 4363 $m^3 s^{-1}$ the dry season to 10,963 $m^3 s^{-1}$ during the flood. The width of the river in the lower reaches around Angoram during the rainy season was over 1 km and large masses of vegetation were often seen floating downstream, occasionally inhabited by people on their way to market or on one occasion by a small aircraft which had crash landed upstream. During the whole period of sampling very few fish and no *O. mossambicus* were caught in the main river channel.

3.4.2 Gill net selectivity

Figure 3.8 details the distribution of sizes caught in each gillnet. This indicates there was an overlap in all sizes caught and it was concluded that the fleet of nets used were not selecting

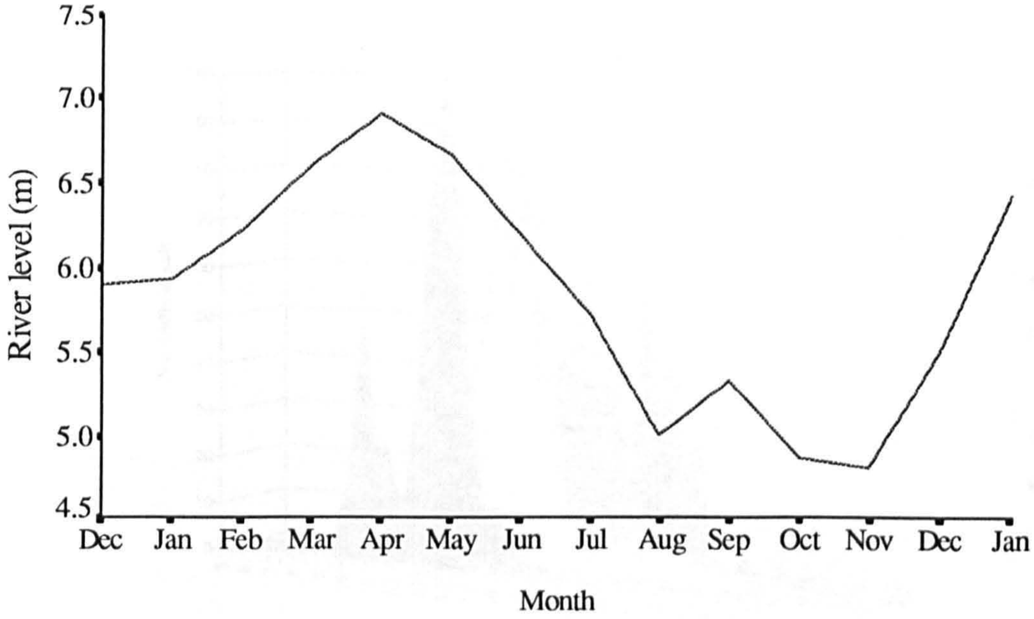


Figure 3.7 Annual mean river levels (m)

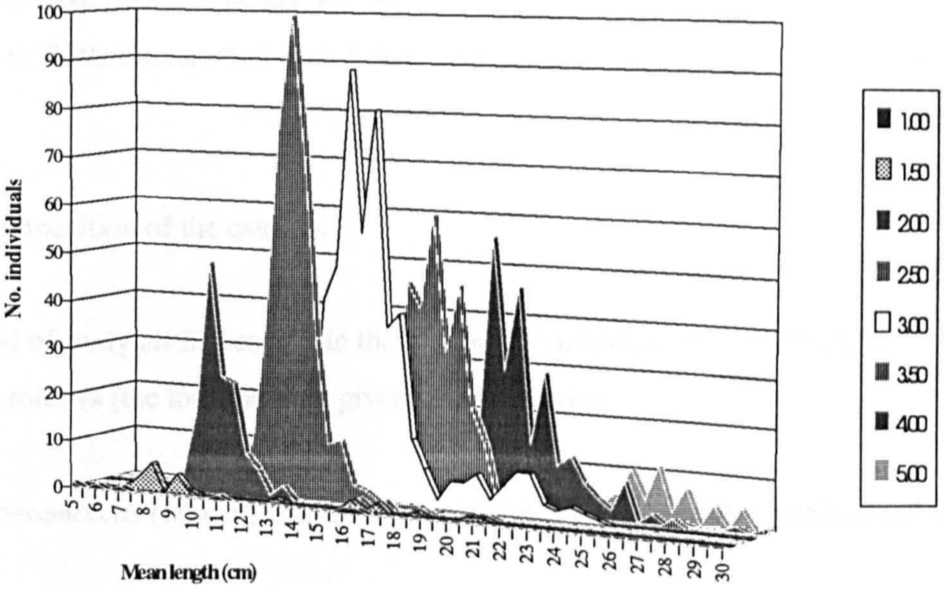


Figure 3.8 Selectivity of gill nets used in the study (legend values are in inches)

an unrepresentative sample of the fish population. The largest 6 inch gillnet failed to catch *O. mossambicus* indicating that this method was sampling the largest fish present. Fish which were too small to be caught in the smallest 1 inch net were designated as 'juvenile stock' and were only found in dense vegetation.

It is possible that traditional 'experimental gill-nets' used by the Department of Fisheries in the past and consisting of various mesh sizes sewn together in a matrix gave results that were biased as fish may have been 'funnelled' towards the margins and escaped. The setting of nets of various sizes in fleets interspersed with a gap between individual nets my have overcome this problem.

3.4.3 Species composition of the catches.

During the period of study all fish caught in the nets in the sample areas were grouped into six major species as follows (the local name is given in parenthesis):

Oreochromis mossambicus (Macau) Omnivorous introduced species with a maximum size of (400 mm TL)

Oxyeleotris spp. (Bigmaus) Often termed 'Gudgeon' or 'Loters' with a larger bodysize (up to 500 mm TL) Generally predators of small fish and prawns)

Ophieleotris aporos (Mangen or Grillepis). Often known as the snake headed gudgeon. A smaller fish (maximum size 250 mm TL) with bright skin colouration and generally omnivorous.

Megalops cyprinoides (Bunpis or Bigeye). Called the ox-eye herring or tarpon, a larger fish (maximum size 750 mm TL) which migrates from the estuarine waters.

Ariidae spp. (Mausgras or Nilpis) The fork tailed catfishes with dorsal and pelvic spines. Although the taxonomy of these fish is poorly understood eight different species of these estuarine fish were identified. For the purposes of this study these were all grouped together as Ariidae spp.

All other species. These were grouped together since their individual contribution to the overall catch was small. They include:

Glossolepis multisquamatus (Melanotaenidae)
Parambassis confinis confinis (Chandidae)
Anguilla bicolor pacifica (Anguillidae)
Paroxyurichthys laterisquamatus (Gobiidae)
Glossogobius giurus (Gobiidae)
Zenarchopterus sepikensis (Hemiramphidae)
Neosiluris novaeguinae niger (Plotosidae)
Neosiluris brevidorsalis (Plotosidae)
Caranx sexfasciatus (Carangidae)
Lutjanus argentimaculatus (Lutjanidae)

The species composition of the catch varied between location and season during the sampling period but generally the number of fish species recorded decreased after 100 km from the sea (Figure 3.9). *O. mossambicus* accounted for 30.2% of the overall weight of fish caught although the contribution between sites varied greatly. Table 3.2 indicates that in the older, deeper sites with little vegetation cover at the edges, Site 4 (Imbuando) and Site 3 (Old Magendo), the percentage of *O. mossambicus* in the catch was low at 2.19% and 19.37% respectively while in the other sites, Site 2 (New Magendo) and the adjacent Site 1 (Pit Pit) the proportion of *O. mossambicus* in the catch was far greater, 42.57% and 46.07% respectively. These results indicate the preference by *O. mossambicus* for the shallow floodplain areas where potential nesting sites and juvenile shelter are readily available. In the catch of Site 4 *Ophieliotris aporos* and the Ariidae predominated overall and in Site 3 the major percentage of the catch was *Arius* spp.

In terms of the commercial catch *O. mossambicus* accounted for almost 50%. During the same time period it was observed that approximately 65% of the weight of fish

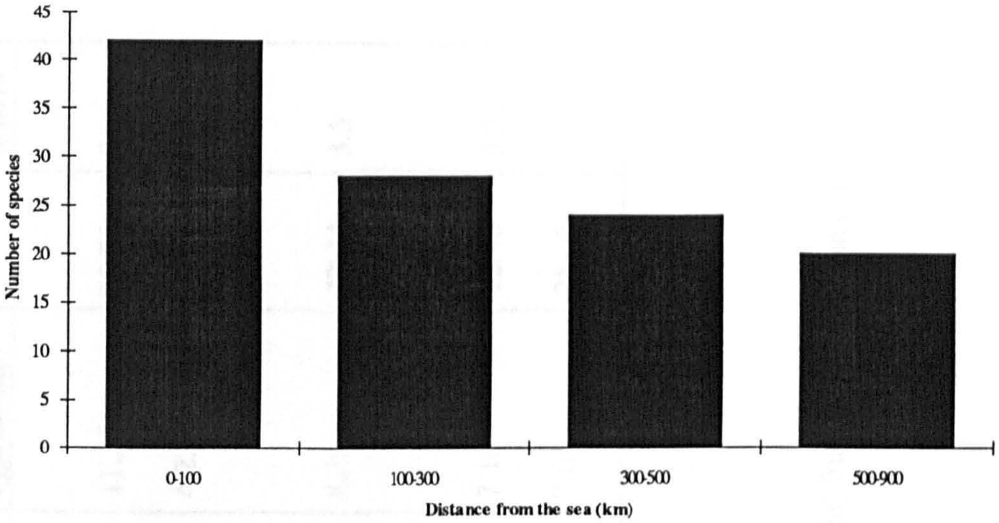


Figure 3.9 Numbers of fish species recorded in the Sepik River against distance from the sea

Location	**site**	***Oreochromis mossambicus***	***Oxyeleotris* spp.**	***Ophieliotris aporos***	***Megalops cyprinoides***	**Ariidae**	**all others**
Site 4 (Imbuando)	4	2.19	12.66	42.77	11.25	30.92	0.21
Site 3 (Old Magendo)	3	19.37	16.58	5.71	4.22	32.72	21.41
Site 2 (New Magendo)	2	42.57	13.27	10.04	8.28	22.34	3.5
Site 1 (Pitpit)	1	46.07	10.43	16.37	7.16	16.43	3.51
all sample sites		30.2	13.29	16.66	7.61	25.07	7.17

Table 3.2 The percentage composition of gill net catches (by weight) from all of the regular sampling sites. This table is based on the data in Coates (1983)

passing through the local market was *O. mossambicus.* This demonstrated the importance of the species not only in the subsistence fishery but also in terms of the commercial catch.

3.4.5 Catch per unit effort (CPUE) during the sampling period

Monthly CPUE (g m^{-2}) varied between sites and during the sample period and results for each site for *O. mossambicus* and all other species are presented separately (Figure 3.10). Changes in the mean length group of *O. mossambicus* caught per month is displayed in figure 3.11.

Site 1

In Site 1 (Pit Pit) the total catch for all species including *O. mossambicus* showed an increase from 0 g m^{-2} to approximately 250 g m^{-2} in February and March as the river level rose (from fig 3.10). However at the maximum water level in April there was a decline in catch of *O. mossambicus* as this species dispersed over the shallow floodplain surrounding the site. In comparison, although catch of other species decreased in April, there was a peak again in May which was due to a sudden increase in catch of *Megalops* spp. *Ariidae* and *Ophieliotris* spp. These species are migratory and piscivorous and may have entered the area as there was an increase in smaller fish. Figure 3.11 shows that the mean standard length of *O. mossambicus* falls at the same period as the water level rises and covers the floodplain and there is a concomitant increase in primary production as allochthonous nutrients enter the water system. Kolding (1989) suggested that there is a positive relationship between an increase in primary production and juvenile tilapia production. Although the mean standard length of *O. mossambicus* caught during April was not small (between 15 and 16.0 cm), at this time the juveniles were probably taking shelter in the shallow areas around the periphery of the site. As the water receded in May the catch of all species declined as water drained from the area.

Site 2

The relationship between river level and CPUE is different in Site 2 (New Magendo). Here CPUE for all species together and for *O. mossambicus* catch show a similar trend and indicated that *O. mossambicus* was the main species caught (figure 3.10). CPUE

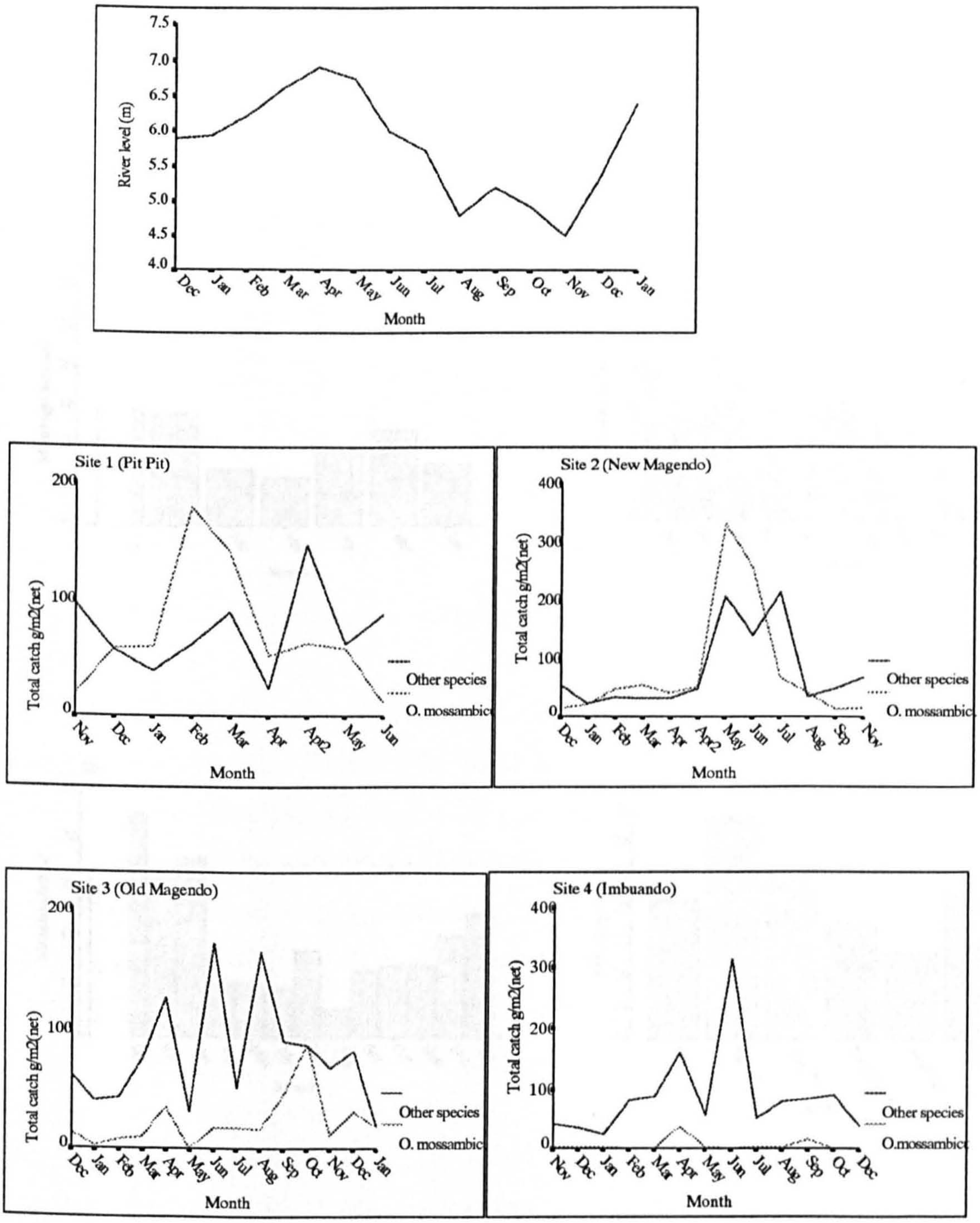


Figure 3.10 Mean monthly catch for *O. mossambicus* and other species in relation to river levels (Apr2 (site 2) relates to the two measurements in April due to lunar periodicity)

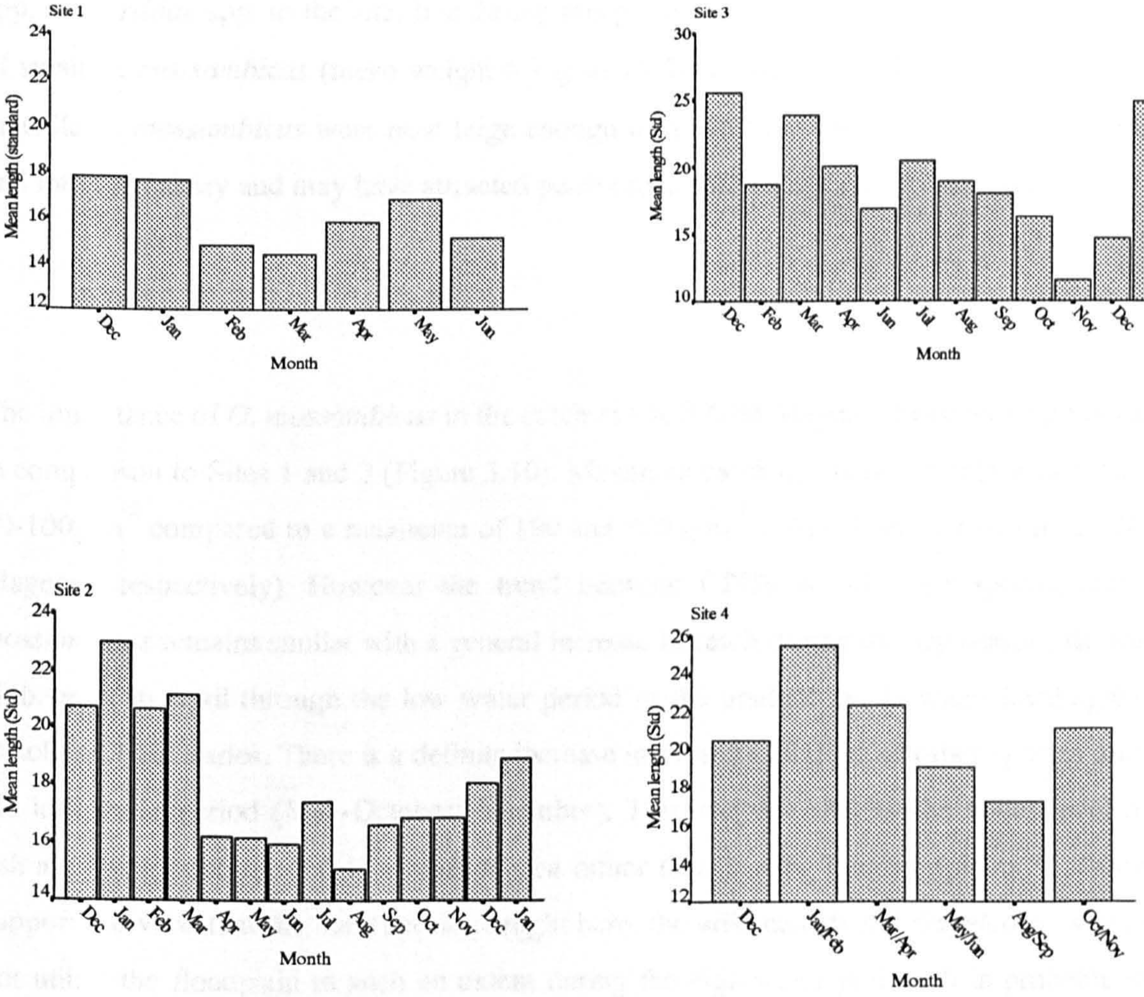


Figure 3.11 Mean length of *O. mossambicus* at each site per month

for all species increased as the river level began to fall in May. The increase in CPUE for *O. mossambicus* corresponds to a fall in CPUE for the same species at Site 1 (Pit Pit) which suggests that fish may have moved from Site 1 to Site 2 (New Magendo) which is connected by water at this time. In addition, at the end of May there is a sudden influx of *Oxyeleotris* spp. and *Ariidae* spp. to the site. It is during this period also that there is an increase in catch of small *O. mossambicus* (mean weight 6.7 g sd ±4.3) (figure 3.11) which suggests that the juvenile *O. mossambicus* were now large enough to move from the shelter of the floodplain and into the fishery and may have attracted piscivorous species of fish into the area.

Site 3

The importance of *O. mossambicus* in the catch at site 3 (Old Magendo) declines significantly in comparison to Sites 1 and 2 (Figure 3.10). Maximum catch in any one month was between 80-100g m^{-2} compared to a maximum of 190 and 350 g m^{-2} at Site 1 and 2 (Pit Pit and New Magendo respectively). However the trend between CPUE of all other species and *O. mossambicus* remains similar with a general increase in catch during the dry season. Between high water in April through the low water period to the gradual rise in water level again in October CPUE varies. There is a definite increase in overall CPUE of all other species during the low water period (May-October/November). This suggests that as the water level falls fish are being concentrated in a smaller area rather than leaving the floodplain. This would support the view that the main species caught here, the ariid catfish and *Oxyeleotris* spp., do not utilise the floodplain to such an extent during the high water period. It is probable that this site is a less favoured feeding and breeding area especially for *O. mossambicus* since shallow areas suitable for nesting sites and juvenile protection were not much in evidence.

Site 4

A similar situation existed in Site 4 (Imbuando) where the CPUE corresponded to a decrease in water level (Figure 3.10). There was a small peak during high water (March/April) when there was an increase in catch of ariid catfish, *Oxyeleotris* spp. and *O. mossambicus*. This peak in the catch of *O. mossambicus* corresponded to an increase in mean length which indicated that larger fish were predominant in the catch (small numbers but with a high average weight) (Figure 3.11). The overall weight of *O. mossambicus* was smaller at this site in comparison to Site 1, 2 and 3 and this may have been influenced by the physical and chemical characteristics of the site which is a deep water site with little surrounding shallow areas suitable for feeding and breeding.

3.4.6 River level and CPUE

A comparison of the general monthly CPUE (*O. mossambicus* and all other species were considered independently) and the variation in river level indicated that there may be a relationship between catch and water level (Figures 3.10). In the permanent ox-bow lakes (Sites 2, 3, and 4) greater catches were achieved during the periods of low or falling water levels when most of the fish were concentrated in a smaller volume of water. The figures indicate that the relationship between river levels and *O. mossambicus* catch and catch of all other species varies between sites. Catches of *O. mossambicus* tended to fall rapidly as the water level rose and at peak flood the catch of this species was significantly reduced. This trend was not observed as clearly in the other species.

Two way Analysis of Variance (ANOVA) indicated that although there was a significant result in the relationship between catch of *O. mossambicus* and river levels and month ($p < 0.05$) this was not the case with the other all species. (Table 3.3). This suggests that the introduced species *O. mossambicus* is moving onto the floodplain as the river rises and is then 'lost' from the fishery. The success of this species and its subsequent contribution to the commercial catch may have been, in part, due to its ability to exploit an under-utilised niche with little competition from native species. Coates (1986) described the biology of most of the native species of fish in the Sepik and found that most (including those of commercial value) were not associated with the floodplain to any great extent.

3.4.7 Total Yield

i *All species*

Although the total yield (CPUE) per site showed a marked seasonality there was also a difference between the overall catch at each site sampled (Table 3.4). The shallower sites

Catch other species	**F**	**P**
Main Effects	1.507	0.195 ns
Month	1.173	0.361 ns
Category*	0.812	0.457 ns

Catch *O.mossambicus*	**F**	**P**
Main effects	3.333	<0.01
Month	3.230	<0.01
Category*	14.23	<0.001

* - Rising, Peak and Falling water level categories.

Table 3.3 Results of two-way ANOVA on the relationship between river level categories, month and catch

			Site 1		Site 2		Site 3		Site 4	
net (inches)	**area m^2**	**n**	**g m^{-2}**	**total/net**	**g m^{-2}**	**total/net**	**g m^{-2}**	**total/nets**	**g m^{-2}**	**total/nets**
Mono-filament										
1	42	2	8.71	732	8.56	719	99.35	8345	6.09	512
1.5	64.5	1	70.27	4533	43.08	2779	94.33	6084	174.61	11262
2	86.0	1	101.16	8700	128.63	11034	50.58	4350	238.03	20471
2.5	110.0	1	293.46	32281	150.07	16508	80.88	8897	69.16	7608
3	129	1	147.41	19016	177.18	22856	100.85	1910	87.36	11269
3.5	180.0	1	85.92	15466	180.09	32416	152.66	27479	73.31	13196
4	193.5	1	83.43	16144	126.51	24480	111.55	21585	61.1	18823
5	247.5	1	9.12	2257	116.31	28787	69.94	14558	76.96	19048
6	154.0	1	11.49	1770	12.46	1919	58.82	9058	0	0
Multi-filament										
1	62.5	2	53.25	66.56	54.34	6792	172.92	21615	27.82	3478
2	62.5	2	132.19	16524	194.92	24365	99.6	12450	162.11	20264
3	46.8	2	162.94	15251	387.25	18123	86.88	8132	87.23	8165
4	62.5	2	127.17	15896	271.28	33910	140.04	17505	114.92	14365
5	39.0	2	121.07	9443	55.32	4315	97.68	7619	39.91	3113
Total yield/site (all nets) g m^{-2}				164669 (6 months)		229003		169587		144574

Table 3.4 Total yield (g m^{-2}) by area and net (all species)

(Sites 1 and 2) adjacent to the floodplain tended to yield more fish (164.7 kg m^{-2} for a 6 month period only and 229 kg $m^{-2} yr^{-1}$ respectively) than the deeper ox-bow lakes represented by Sites 3 and 4 (Old Magendo and Imbuando) (169.5 kg m^{-2} and 144.6 kg m^{-2} respectively). During this study however a fleet of various sized nets was used continually. A Sepik fisherman would generally use only a standard 4 inch net. The overall catches from the 4 inch nets set each time during the experimental fishing indicates that the one monofilament and two multifilament nets were set at all four sites a total of 144 times in a year (once every 2.5 days) and the yield was approximately 0.155 tonnes (Table 3.4)

ii *O. mossambicus*

The greatest catch was from Site 2 with a total weight of 97.12 kg of tilapia caught over the whole period (extrapolated from tables 3.2 and 3.4). From all of the four sites studied a total of 215 kg of *O. mossambicus* were landed during the whole period of study (14 months).

During the study the 4 inch mesh gillnets caught the greatest biomass of *O. mossambicus* (72 kg) (54% of catch for monofilament nets and 34% of catch for multifilament nets). A total of 185 x 4 inch gillnets were set over a period of 14 months. Thus the average biomass per gillnet/day would be 72/185 = 0.38 kg. If each net is set for an average of 200 days per year the total potential catch per year from one net would be 0.383 x 200 = 77 kg/yr. If one fisherman were to set 8 nets for 200 days per year then the total catch would only be 616 kg/yr (0.616 tonnes). This in comparison to an average catch from an African fisherman of 3.87 t per year based on Welcommes' (1979) formulae (see section 3.3.6 below). Low catches are not therefore due to lack of effort there are other mechanisms which may have had an influence on the unusually low yield from such a large river.

O. mossambicus was restricted to the surface waters since bottom set gillnets failed to catch any fish. Bruton and Boltt (1975) found that adult *O. mossambicus* were seldom found below 12 meters and other authors have also reported that the profundal zone is beyond the normal range of adult tilapias (Gee 1968, Fryer and Iles 1972, Caulton and Hill 1973). The same authors found that juveniles were capable of tolerating depths below 12 m although in this study smaller fish were never caught in the bottom set gillnets.

3.4.8 Theoretical yield of the Sepik

The theoretical yield possible in the Sepik has been estimated previously by Coates (1985) using formulae developed from work on African river fisheries by Welcomme (1979).

It is both possible and necessary for management purposes to make a yield estimate and there are several methods of doing so. Theoretical yields based on the relationship between catch in tons (C) and the drainage basin area (A) (km^2) have been proposed by Welcomme (1985) using the formula $C = 0.44A^{0.90}$. If the basin area for the Sepik is substituted ($A = 78{,}000$ km^2) then the theoretical catch would be approximately 11,500 tonnes per year (see also Coates 1985). This formula however is based on rivers whose basin area exceeds 2% of the basin area whereas the Sepik floodplain covers approximately 10% of the flooded area, thus this yield estimate would be considered low. If the Sepik floodplain was fully exploited as a fishery the yield would be expected to be in the region 30-40,000 tonnes per year.

Coates (1985) estimated that there are 11,500 potential fishermen in the floodplain areas of the Sepik. Theoretically these fishermen could catch 44,000 tonnes of fish per year based on the formula relating catch (tons) and number of fishermen (per km^2) (Welcomme 1985);

$$C = 3.87\,(0.91^{N})$$

where;

C = catch (tons)
N = number of fishermen per km^2

The numbers of fishermen on the floodplain have increased by an estimated 25% since 1980 (the figure of 11,500 was extrapolated from the 1980 population survey). In 1989 there were an estimated 80,000 people inhabiting the floodplain of which approximately 16.8% can be considered to be potentially commercial fishermen (Frielink 1983). This means that there are now 13,440 potential commercial fishermen on the floodplain with a theoretical catch of 3.80

tonnes per fisherman per year or 50,000 tonnes from the whole area. This is in comparison to 44,000 tons similarly calculated by Coates (1985).

In terms of the subsistence fishermen almost all the population from the age of about 5 years will fish using both traditional methods (hook and line, spears and traps) as well as the more recent gill-nets. The catch is then expected to be much greater than the figure quoted above.

From data collected for the commercial salted fish project it has been estimated that the floodplain fishery yields between 3000 and 5000 t/yr of which 50% of the catch is the introduced species *Oreochromis mossambicus* (Coates 1985). These estimates were small in comparison to the potential catch based on the formulae above. Therefore an increase in fishing effort would be needed to equal the amount of fish caught in other river systems. This is based on the assumption that the fishery is under-exploited at present.

3.5 General Discussion

Species diversity

The relationship between species diversity and river basin size as described by Welcomme (1983) is:

$$N = FA^b$$

where:

N = Number of species
A = Basin Area in km^2

Thus with an increase in basin area there is an relative increase in species number. Using regression analysis on data from 47 large rivers (See figure 1.11 Chapter 1) from five different regions Welcomme (1985) showed that the model:

$$N = 0.297A^{0.477}$$

could be used to describe the general relationship between river basin and species number. There were however variations on the model between the five regions and latitudinally, with species number increasing towards the tropics. Using the general model described above and substituting the river basin area for the Sepik River (78,000 km^2) then 120 native species can be expected to be found in the Sepik. This is far more than has actually been found which poses the question as to why the fauna is so poorly represented. Part of the answer may lie in the geological history of the country and the river basins as described in Chapter 1. The Sepik River is a relatively young in geological terms and thus has had less time for the diversity of species found in many of the much older African and Asian systems to evolve.

Although the total number of species found in the Sepik is less than expected, the pattern of numbers of species caught compared to distance from the sea is similar to the findings of Gorman and Karr (1978). These authors found that with increasing stream order the diversity of habitat increased and therefore the numbers of species present also increased. In the Sepik the number of species found in the catch decreases with distance from the sea with the majority of species found within 100 km of the river mouth.

One reason for the discrepancy in species diversity lies in the geological history of the region which lies east of "Wallaces' line" and therefore represents a different faunal zone (McDowall 1981, Coates 1985). Very few of the fish species commonly found in other regions are found in the Sepik and species diversity is low.

Yield

The results suggest that there may not be the potential for a viable commercial fishery in the Sepik to be based solely on *O. mossambicus.* The Sepik river is fairly unique in that it does not conform to theoretical yield formulae that have been successfully used on other rivers. In many African, South American and Asian rivers the yield can be related to morphological and edaphic parameters (Welcomme 1979, 1985). The yield formulae developed for these rivers may not be suitable for the conditions operating in the Sepik.

These findings have important implications when considering the management of the river for commercial exploitation. Despite the increase in catch since the introduction of *O. mossambicus* in 1964 the overall catch rates in the Sepik basin were generally low in comparison to the yield obtained in similar rivers (Welcomme 1985). Very often in these circumstances increased fishing effort may improve the catch rates. However as has been shown in this study the flood regime has a different influence on each species.

Increasing the effort at certain times of the year may place increasing pressure on some of the native species which remain in the deeper waters, some of which have a low fecundity, for example, some of the ariid catfishes (Coates 1986). This family contributes substantially to the native catch and would probably be the first to become over-fished. Welcomme (1979) described the effect of fishing pressure on a multispecies fishery. As exploitation continues there is a change in species composition from larger fish with a slower reproductive rate to smaller species which grow faster and reproduce more rapidly. In the Sepik this progression of species would be detrimental to the fishery since there are few small species with high reproductive rates to support such effort (Coates 1987).

With the estimated human population increase in the Sepik-Ramu basin from 3 million in 1980 to an estimated 6.5 million by the year 2015 (Coates 1993) and the immediate need for improved protein sources there is now a need for the development of sustainable food supplies from the freshwater fisheries sector.

One proposed method of improving fish stocks is by the introduction of other species of fish into the basin. Introductions into Papua New Guinea and the Sepik is not new. Since 1948 an estimated 29 species have been introduced for various purposes (West and Glucksman 1976). The rationale and code of practice for new introductions of various species into the Sepik are discussed elsewhere (Coates 1993). However it has been proposed that species being used for introduction are initially held in a culture system before transferral to the river.

The use of culture facilities in the management of river stocks has several advantages, some of which include acting as a quarantine procedure for fish obtained from overseas and for the purpose of producing sufficient numbers of fish within the country for restocking thus limiting the reliance on overseas sources of fish. The decision to enhance the stocks in the Sepik have been based on many years of research and consideration by many experts and government bodies. In other parts of the world such detailed evaluation has not been carried out prior to introducing a new species. Fish which have been introduced for 'aquaculture' purposes with all its numerous definitions (New and Crispoldi-Hotta 1992) have contributed 36.2% of species introductions world-wide (Welcomme 1988). Exotic introductions can be either beneficial or detrimental environmentally, socially and economically. It could be argued that the introduction and subsequent escape of tilapia reared in ponds in the Sepik have been of some benefit. This is not a case for allowing unlimited introductions without a detailed biological and socio-economic assessment of the situation.

Chapter 4 FOOD AND FEEDING RELATIONSHIPS

4.1 Introduction

In many species of fish there is evidence of ontogenetic and seasonal dietary changes (Windell 1971, Bogdanova 1970, Hartman and Brandt 1995). Ecomorphological differences often result in different patterns of food resource utilisation (Wootton 1990). For example small fish with smaller mouth parts and restricted gape consuming smaller items or portions of food. The energy requirements for smaller fish tend to be greater than larger fish which consume larger items of prey and invest less energy in finding food (Moss 1980). Thus food resource availability and quality will influence growth in juvenile fish and potentially the future recruitment levels.

Juvenile fish of a herbivorous or detritivorous species have been found to feed on zooplankton exclusively which may be related to the greater energy requirements of smaller fish and the higher protein and digestibility of such prey (Moriarty 1973, Moss 1980). There may also be differences between male and female diets during the spawning season (Hamerlynk and Catrijsse 1994). Dietary changes may also occur in areas where there are seasonal environmental changes (Welcomme 1985).

Food availability in a floodplain river will change as the water rises and inundates the surrounding plain. (Welcomme 1985). Species of fish which exploit the floodplain as feeding areas may have significant changes in their diet between wet and dry seasons and potential changes in the degree of interspecific competition for food. Such qualitative changes may have concomitant changes in food quality (Bowen 1979) and associated influences on breeding success.

Resource separation in terms of diet, changes in dietary breadth and overlap may also occur intra-specifically based on fish size, sex, season (temporal) or location (spatial). Analysis of the diet over a period of time will provide information on the variation in feeding behaviour between males and females and with changes in size, and season.

4.1.1 General feeding ecology of *Oreochromis mossambicus*

The dietary preferences of *O. mossambicus* has been described by various authors as opportunistic (Bogdanova 1970, De Silva *et al* 1984), detritivorous and omnivorous (Munro 1967, Moriarty 1973, Man and Hodgkiss 1977a, Whitfield and Blaber 1978, Bowen 1980, 1982, Trewavas 1983, Getachew 1993). General indications of dietary preference can often be related to feeding structures in the mouth and some cichlid species have very specialised mouthparts (Fryer and Iles 1972).

The feeding apparatus in *O.mossambicus* is relatively simple with small jaw teeth (uncuspid, bicuspid and tricuspid) which are arranged in one to four rows (Bowen 1976). Although the structures within the buccal cavity are not considered to be specialised for feeding there is considerable variation in the pharyngeal apparatus in different species of tilapia (Fryer and Iles 1972, Wootton 1990).

Recent studies on the functional significance of the microbranchiospines found on the second third and fourth gill arches in *O. mossambicus* were inconclusive. It is thought that they play an incidental role only in filter feeding and protection of the gill filaments (Drenner *et al.* 1984, Beveridge *et al.* 1988). The method of ingesting algal species is thought to be through a filter feeding mechanism. Much of the mechanical breakdown of the food occurs in the pharyngeal cavity prior to entering the stomach which is a small sac followed by a long coiled intestine, the ontogeny of which is described in Zihler (1982).

Most digestion and assimilation takes place in posterior part of the stomach and the intestine. Gastric fluids have been found to have a pH in the range of 2.0-2.2 but this can drop to 1.5 in actively digesting tilapias (Moriarty 1973, Bowen 1976, 1981, Caulton 1976). The low pH in the digestive juices is thought to have an important role in the breakdown of inorganic matter and the availability of detrital non-protein amino acids used for growth. Stomach and rectal content analysis has shown that cytoplasm within the diatom shells can be attacked by digestive enzymes entering through the pores or raphe, whereas other food items such as some algal or desmid species are left intact and have been cultured from rectal samples (Vaas and Hofstede 1952, Fish 1955, Man and Hodgkiss 1977a, Getachew 1993). In higher temperatures diatom shell walls have been found to contain less silica and are consequently fragile and the cytoplasm easily assimilated (Werner 1978).

Previous studies on the diet and feeding intensity of wild populations of *O. mossambicus* have found similar results. Mathes (1966), Moriarty and Moriarty (1973) and Man and Hodgkiss (1977a) found that feeding intensity varies seasonally and diurnally with most food being consumed during the daylight hours. Changes in feeding intensity varied between males and females during the breeding season. Females will not feed while brooding eggs or young in the mouth (Welcomme 1965, Hodgkiss and Man (1977). In floodplain areas increased feeding intensity and growth has been associated with the high water period (Lowe-McConnell 1979). Juveniles under 7 cm total length may also feed on small invertebrates as well as diatoms (Mathes 1966, Redding 1989). Bowen (1978) found this species to be feeding exclusively on benthic detrital aggregate rich in diatoms in Lake Sibaya, South Africa. Since diatoms tend to be limited by the depth of the euphotic zone the distribution of grazing *O. mossambicus* was limited to shallower areas. The importance of diatoms in the diet of *Oreochromis* species has also been noted by other authors (Fish 1955 Mathes 1966, Welcomme 1966, Man and Hodgkiss 1977a, Bogdanova 1970, Redding 1989, Getachew 1993).

One of the objectives of this study is to describe the way in which *O. mossambicus* utilises its environment and comment on the possible reasons for its successful colonisation of areas in the Sepik since its introduction and any potential interspecific and intraspecific competition for resources that might subsequently affect yield. A comprehensive knowledge of interspecific and intraspecific interactions is essential prior to the development of sustainable river management strategies.

In order to do this the niche occupied by *O. mossambicus* must be described. One important dimension of the niche, once described by Hutchinson (1957, 1965) as an "n-dimensional hyperspace", is food. This chapter therefore aims to assesses dietary preferences, feeding strategies, resource utilisation, environmental influences and intraspecific competition within and between the sites studied over a specific time period.

4.2 Materials and Methods

Sub-samples of fish from monthly gillnetting were used for this analysis from three environmentally different sites. These were:

i Site 1 (Pit Pit) - a floodplain site inundated seasonally,

ii Site 2 (New Magendo) - a relatively shallow site close to the floodplain site, with sandy substrata in some areas.

iii Site 3 (Old Magendo) - an older deeper roundwater with surrounding floating vegetation.

All sites have been fully described in Chapter 3.

4.2.1 Stomach content analysis

All fish were transported immediately to the laboratory where stomach and hind gut were removed. Stomach and hind gut fullness were given a subjective score of between 0 for empty and 10 for full to allow for comparisons of feeding behaviour between season and sites. Stomachs and hind guts were stored separately in 10% buffered formalin prior to analysis.

The following methodology was developed by the author (see section 4.2.2).

Stomachs were later removed from the storage fluid and placed in distilled water for 24 hours. The contents were agitated to remove the surrounding tissue. A sample from each stomach was placed on five slides and examined under x40 power. An eyepiece graticule containing an engraved cross was fitted and each slide was examined under five fields of view. The prey item with the edge nearest the crosspiece and the prey item with the central point nearest the crosspiece was noted. Two observations were carried out to determine whether or not the size of the prey item would skew the results. A larger item such as a piece of macrophyte may have the edge nearest the crosspiece but a smaller diatom may have the central point closer to the crosspiece. Each sample was therefore examined 25 times for items with the edge nearest the crosspiece and likewise for those with the central point closer. For each fish the number of different prey items found in each stomach using the above method was recorded.

An initial study compared the results of analysing the contents of ten different stomach under both high (x40) and low power (x10). It was felt that using a higher power the observer did not get a general picture of the types of item found on the slide. Differences between results using high and low power were tested statistically (Chi-Squared test) and found not to differ significantly. The rest of the samples were then observed under a lower power(x10).

4.2.2 Rationale for the methodology developed

Feeding habits can be influenced by habitat preferences, season, temperature, fish size, daily feeding periodicity's, competitor species and many other factors (Windell 1971, Lowe-McConnell 1987, 1996). In addition, the quantity and quality of food is directly related to yield in a fish population.

Much of the literature on stomach content analysis (Hynes 1950, Windell 1971, Davis and Warren 1971, Hyslop 1980, Wootton 1990) describe methods of assessing stomach contents both quantitatively and qualitatively. However many of the methods only provide a very general picture of the relative importance of various categories and often are suitable only for items which are of a larger size, can be recognised and weighed easily and are still intact.

The application of each method of analysing stomach contents with respect to assessing the diet of *O. mossambicus* was considered in detail and it was concluded that most were not suitable for the purposes of this study. The reasons for rejecting various analytical methods are stated below.

Any analysis involving volumetric or weight assessments of food such as the Index of preponderance (Natarajan and Jhingran 1961), the later Simple Resultant Index and the Weighted Resultant Index (Mohan and Sankaran 1988) and those described by Hynes (1950), Hyslop (1980), Windell (1971), Rosecchi and Nouaze (1987), Martinez-Palacios and Ross (1988), are not suitable since a large proportion of the stomach contents of *O. mossambicus* consist of microscopic diatom species, algae and unidentifiable detritus. Many of the methods and parameters commonly used in stomach content analysis, such as those described above, often have the same criteria, as follows:

All prey items in the stomach or sample thereof are identified counted and/or weighed (gravimetric or volumetric) and results calculated as:

- the percentage of occurrence or frequency of occurrence (F) (percentage/proportion of all stomachs containing the prey item)
- the percentage of total number or proportional abundance of prey (P)(the percentage that each prey item contributes to total number of prey items in all stomachs.
- percentage of total volume (the percentage that each prey item contributes to the total volume of prey items in all stomachs)
- the average of volume percentages

The data collected were then used in calculations of dietary breadth overlap, diversity and other indices as described below. There are a few associated problems with reliance on calculations based on such methods of stomach content analysis. The percentage occurrence and percentage of total number will characterise a diet but do not take into account smaller prey items which may take up a small volume. Thus using these measurements in assessing overlap may be misleading especially if calorific value is important (Wallace 1981). Percentage volume is a valuable measure with respect to calorific importance but cannot be reliably measured in species of fish which consume microscopic prey items.

An initial survey of the stomach contents of *O. mossambicus* from the Sepik River indicated that many of the items were microscopic (benthic and epiphytic diatoms) or broken up to such an extent that volumetric or numeric methods were not applicable. Thus in order to describe the diet, intra-specific dietary overlap and seasonal dietary changes without introducing the type of bias associated with the traditional methods of collecting data (percentage occurrence and percentage of total numbers) it was necessary to develop a different method of stomach content analysis as described above.

4.3 Data Analysis

4.3.1 Between sites

i *General Dietary Composition*

An initial survey was carried out using several stomachs collected at random from the three main areas surveyed, namely Pit Pit (Site 1) and New Magendo (Site 2) and Old Magendo (Site 3). Fish caught in nets ranging from 2.5 to 5 inches stretched mesh were used. All diatom species found in these stomachs were identified by Dr Haworth from the Freshwater Biological Association, UK.

ii Spatial differences in dietary composition.

Over the period of time in which samples were caught and analysed all prey species were identified and coded. Differences in number of prey species taken at each site were noted and can be used to described the differences in diversity and food preferences at each site. It was not possible to assess the electivity of fishes at each site.

iii Dietary niche breadth and overlap

Difference in food utilisation and degree of specialisation could occur in different habitats found in the Sepik River. Quantitative measurements of degree of specialisation were measured using Levins measure of niche breadth (B) (Krebs 1989) where:

$$B = 1/\sum p_j^2$$

B = Levins measure of niche breadth

p_j^2 = Proportion of individuals using prey species j.

This figure was standardised to express the measure on a scale of 0 - 1 where:

$$B_A = \quad \sum(X_{ij} - Y_{jk}) / \sum(X_{ij} + Y_{ik})$$

B_A = Levins Standardised measure of niche breadth

The degree to which the diet changes in relation to the spatial environment (site) environmental change (season) or biological characteristics such as fish size, sex or sexual status is an indication of the level of intraspecific interaction or competition. The Bray Curtis Measure of Dissimilarity sorts and groups the similarity coefficient of individual fish and then produces clusters in the form of a dendrogram. Similarity is measured on a scale of 0 (groups are identical) to 1 (groups are dissimilar). Clusters indicate similarity of samples and can used as an indication of niche overlap. All data from all sites were analysed using this method.

TWINSPAN (Two Way Indicator Species Analysis) classification analysis (Hill 1979) was used on data from all sites together to assess if there were any significant distinctions in dietary classification between populations of fish at all three sites.

iv Feeding strategies

In many indices used to describe the diet (e.g diversity, niche overlap) the importance of dominant or rare individual prey items and the general homogeneity of the diet is often taken into account subjectively (Costello 1990). The feeding strategy of a population i.e. specialist vs. generalist can be determined graphically by plotting mean individual feeding diversity (ID) against population diversity (PD) (Tokeshi 1991). For this purpose the Shannon function as an index of diversity was used, where:

$$ID = \sum_{j=1}^{n} \left(-\sum_{i=1} P_{ij} \log_e P_{ij}\right)/N$$

and

$$PD = -\sum_{i=1}^{n} P_i \log_e P_i$$

N = total number of samples (fish)

P_{ij} = proportion of prey i in jth predator

P_i = proportion of prey i in the whole predator population

Specialist feeders are represented by a low ID and PD and a generalist with a homogenous diet by a high ID and PD (Figure 4.1). ID and PD for each site was plotted to determined whether feeding strategies were similar in different areas.

4.3.2 Site Specific Analysis

Data from each site were analysed separately in order to assess the possible differences in the diet and feeding strategies under various environmental conditions pertinent to each site.

i Ontogenetic Changes and Feeding Strategies

TWINSPAN classification was used on data from each site to indicate groups of fish with similar indicator prey items in the stomach/diet. All options within the programme were set for default and groups were separated at the fourth division. To determine whether seasonal or biological parameters were significantly different between the groups indicated by TWINSPAN, data on size, weight, sex, season and sexual status of fish in each group were analysed. For this purpose two way ANOVA and Tukeys HSD test was used to determine significant differences in size and weight. Any significant separation of groups based on sex, and sexual status was determined by Chi-Squared analysis. Since TWINSPAN classification does not give an indication of the dominant food items in each group, further analysis

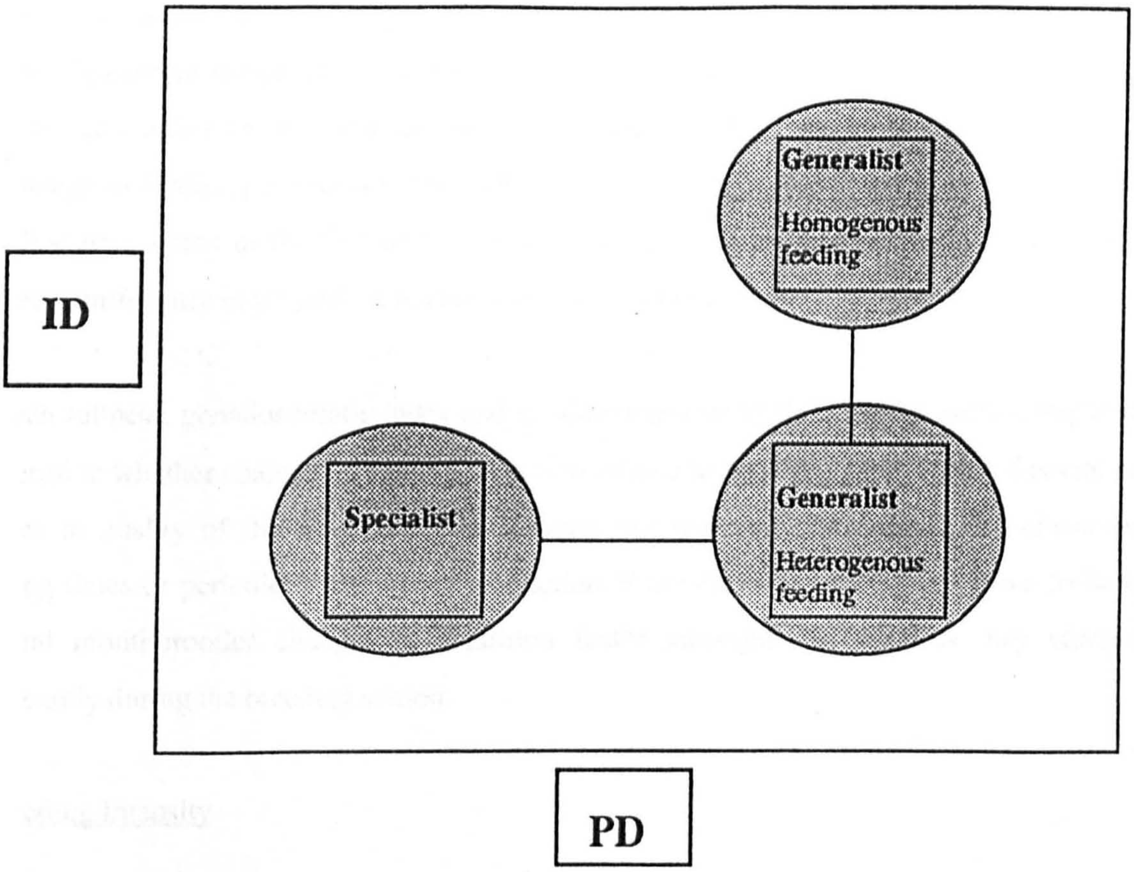


Figure 4.1 Feeding Strategies after Tokeshi (1991)

was carried out. Dominant food items for each TWINSPAN group generated were presented graphically.

ii *Seasonal Changes*

Significant seasonal (wet and dry seasons) changes in overall dietary composition were assessed (Spearman rank correlation coefficient was used on all stomach content data). This would indicate either a movement into the floodplain as different food items became available or a change in feeding preferences. Mann-Whitney non-paired, ranked test was then used on individual prey items in the diet to determine which prey species in the stomach contents changes significantly in proportion between the wet and dry season.

Stomach fullness, gonadosomatic index and condition factors in ripe females were compared to determine whether changes in feeding were also related to breeding periods and if potential changes in quality of the food available between the wet and dry season may constrain breeding times or periodicity and hence production. Since *O. mossambicus* is known to be a maternal mouthbrooder changes in condition factor amongst ripe females may change significantly during the breeding season.

4.3 Feeding Intensity

Stomach fullness was taken as an indication of feeding intensity over the sampling period for all fish of all sizes. Changes in feeding intensity may be related to seasonal changes in food availability and spawning behaviour and these changes may affect condition. The relationship between these parameters are described for Sites 1 and 2.

4.4 Results and Discussion

4.4.1 All sites

i Dietary Composition.

The initial survey of all prey items found in the random sample indicated that *O. mossambicus* was feeding on a variety of autochthonous material in the form of epiphytic, littoral, planktonic and benthic algae and diatom species. In addition to this pieces of macrophyte (which may have been incidental to the ingestion of the epiphytic algae), seeds, sand and detritus were also present in many stomachs. During the initial survey over 75 different species of diatom were identified from stomachs from fish from different areas. Some prey species were more frequently found than others (Table 4.1).

ii Spatial differences in dietary composition

In the three sites surveyed over a 12 month period a total of 52 different prey items were identified from stomach content analysis. These were recorded and coded for later analysis (Table 4.2) Although diatom species formed the most abundant item, various algal types , macrophytes and unidentifiable detrital matter were also important. Flocculent detritus was identified as possibly mucus which may have entered the gut along with food particles. There were some similarities in items present in stomachs from all sites. These included mainly items such as detritus, algae, sand and macrophytes. However some prey items were specific to each site. For example the diatom species genus *Hantzchia* was found only in stomachs from Pit Pit (Site 1) (Table 4.3). This may be due to the different environmental conditions such as water depth, substrate and vegetation type which affect food availability and degree of inundation of the surrounding plain during the wet season. Site 1 (Pit Pit) was a shallow ephemeral lagoon with a substrate of inundated macrophytes and epiphytic species such as *Eunotia sp* and *Cymbella.* Also, a greater number of stomachs at this site contained filamentous algal species.

New Magendo (Site 2) had a sandy/silty substrate and was covered all year with water to a maximum depth of 6 meters. Stomach contents from this site revealed greater proportions of sand and silt and diatom species such as *Synedra sp.* and *Melosira sp* which are often associated with epiphytic and planktonic habitats in richer waters (Haworth pers comm.) (Table 4.3). Old Magendo (Site 3) was a deeper lagoon with surrounding vegetation but little in the way of shallow areas. Prey items such as the epiphytic and sometimes epilithic *Synedra* sp., larger algal species and seed pods were more prevalent (Table 4.3).

Some species tended to be generally more prevalent than others. For example *Navicula bacillum* was present in most stomachs in Site 2 throughout the period but not so prevalent in

Table 4.1

Diatom taxa and Areas sampled	**1 Site1**	**2 Site1**	**3 Site1**	**4 Site2**	**5 Site 2**	**6 Site 2**
Achnanthes exigua var. heterovalvata	f	+				
Achnanthes sp. (small)	+					
Anomoeoneis exilis var. lanceolata Mayer					+	
Anomoeoneis serians var. brachysira (Brebisson) Cleve	f	f	+			+
Caloneis silicula var. gibberula (Kutzing) Grunow					+	
Cyclotella meneghiniana Kutzing	r	r			+	
Cyclotella pseudostelligera Hustedt						+
Cyclotella cf. stelligeroides Hustedt					+	
Cymbella turgida Gregory		+				
Cymbella ventricosa Agardh	+	+	+	+		
Cymbella sp.						
Eunotia didyma Grunow		f	f			
Eunotia didyma var. claviculata Hustedt	f	f	f			
Eunotia lunaris (Ehrenberg)Grunow	+	+			+	
Eunotia pectinalis (Dillwyn) Rabenhorst			+			
Eunotia pectinalis var. undulata Ralfs	f	+	+			
Eunotia cf. rhomboidea Hustedt	+					+
Eunotia veneris (Kutzing) Muller				+		
Fragilaria pinnata var. lancettula (Schumann) Hustedt						f
Fragilaria cf. virescens Ralfs						+
Frustulia rhomboides (Ehrenberg) de Toni			+		+	
Gomphonema acuminatum var. coronata (Ehrenberg) W Smith		+				
Gomphonema gracile Ehrenberg			+		+	
Gomphonema lanceolatum (Agardh) Ehrenberg						+
Gomphonema parvulum Kutzing	f	+	+		+	
Gomphonema wulasiense Foged					+	+
Gomphonema sp.						
Gyrosignma acumiantum (Kutzing) Rabenhorst					+	f
Hantzschia amphioxys (Ehrenberg) Grunow					+	
Melosira granulata (Ehrenberg) Ralfs			+	v	+	+
Melosira granulata var. angustissima Muller		+			+	
Navicula cf. arvensis Hustedt	f	f			+	+
Navicula bacillum Ehrenberg	+	+			+	
Navicula bacillum fo. lanceolata (Ostrur) Hustadt					+	
Navicula cari var. angusta Grunow			+		+	
Navicula cf. cincta (Ehrenberg)					+	

Ralfs						
Navicula cocconeiformis Gregory						+
Navicula confervacea (Kutzing) Grunow	f	f	+	+		
Navicula cuspidata Kutzing					+	
Navicula disjuncta Hustedt					+	+
Navicula exigua (Gregory) Muller				f	+	+
Navicula pupula Kutzing	+	f	+	+		
Navicula pupula cf. var. elliptica Hustedt					+	
Navicula pupula fo. rectangularis (Gregory) Hustedt	+	f	+		+	
Navicula radiosa Kutzing		+	+		+	
Navicula cf. seminuloides Hustedt	+	+	+			
Neidium sp.						
Nitzschia cf. acicularis (Kutzing) W. Smith		f			+	
Nitzschia cf. bacata Hustedt		+	+			
Nitzschia dissipata (Kutzing) Grunow						+
Nitzschia palea (Kutzing) W. Smith	+					
Nitzschia scalaris (Ehrenberg) W Smith				f	+	+
Nitzschia tryblionella var. victoriae Grunow						+
Nitzschia spp.	+	+	+		+	+
Pinnularia acrosphaeria Brebisson			+			
Pinnularia acrosphaeria fo. *undulata* Cleve	+	+	+			
Pinnularia braunii var. amphicephala (Mayer) Hustedt	+	f	+			
Pinnularia cf. divergens W. Smith						+
Pinnularia gibba var. sancta Grunow		+	+			
Pinnularia microstauron (Ehrenberg) Cleve					+	
Pinnularia stomatophoroides Mayer					+	
Rhopalodia gibberula var. van heurckii Muller					+	
Pinnularia viridis (Nitzsch) Ehrenberg		+	+			
Pinnularia sp.						
Stauroneis cf. anceps var. hyalina Brun & Paragallo				+		
Stauroneis phoenicenteron (Nitzsch) Ehrenberg		+			+	
Stenopterobia intermedia (Lewis) Van Heurck		+				
Surirella cf. fimbricata Hustedt						f
Surirella cf. tenera Gregory						f
Synedra rumpens var. fragilarioides Grunow					f	f
Synedra ulna (Nitzsch) Ehrenberg		y			+	
Tabellaria flocculosa (Roth Kutzing (short)					+	
Tetracyclus lacustris Ralfs					r	
Tropidoneis lepidoptera var.					+	f

javanica Hustedt						
Neidium sp				+		
Nitzschia amphibia					f	
Melosira sp.			+			

f = frequent ie. obvious in the sample
+ = present
r = rare, only seen once
y = unsure of identification

Table 4.1 Diatom taxa identified from stomach contents of six *O. mossambicus* from different sites (in association with E. Howarth FBA)

Code	Name	Species
1	Achna	Achnanthes sp.
2	Anomo	Anomoeoneis sp.
3	Calon	Caloneis sp.
4	Cyclo	Cyclotella sp.
5	Cymbe	Cymbella sp.
6	Eunot	Eunotia sp.
7	Fragi	Fragilaria sp.
8	Frust	Frustulia sp.
9	G.lan	Gomphonema laceolatum
10	Gyros	Gyrosigma sp.
11	Hantz	Hantzchia sp.
12	Melos	Melosira sp.
13	N.bac	Navicula bacillum
14	N.pup	Navicula pupula
15	N.hal	Navicula halophila
16	Nav4	Navicula sp. 4
17	Nav5	Navicula sp. 5
18	Nav6	Navicula sp. 6
19	Nav7	Navicula sp. 7
20	Neid	Neidium sp.
21	Ni.S	Nitzchia scolaris
22	Nit2	Nitzchia sp. 2
23	P.gi	Pinnularia gibba
24	Pin2	Pinnularia sp. 2
25	Pin3	Pinnularia sp. 3
26	Rhop	Rhodaphalodia sp.
27	St.p	Stauroneis phenicentron
28	Sto2	Stauroneis sp. 2
29	Sten	Stenopterobia sp.
30	Si.t	Sirurella tenera
31	Sir2	Sirurella sp. 2
32	Syn1	Synedra sp. 1
33	Syn2	Synedra sp. 2
34	Tabe	Tabellaria sp.
35	Tetr	Tetracyclus sp.
36	Trop	Tropodoneis sp.
37	Anab	Anabaena sp.
38	Spyr	Spyrogyra
39	AlgF	Filamentous algae
40	AlgM	Medium Algae
41	AlgL	Large Algae
42	Floc	Flocculent detritus (mucus)
43	Macr	Macrophyte piece
44	Seed	Seeds
45	Sand	Sand/Silt
46	Sili	Silica particles (crystals)
47	Spic	Spicules
48	Inve	Invertebrate pieces
49	Anom	Unidentified item
50	Spik	Green spikelets
51	Rock	Rock pieces
52	Ach2	Achnanthes sp. 2

Table 4.2 Species list and code names used in TWINSPAN analysis

	Pit Pit	Site 1		New Magendo Site 2			Old Magendo Site 3		
Species	%Stom with item	Mean % Occurence		%Stom with item	Mean % Occurence		%Stom. with item	Mean % Occurence	
Achn	61.22	8.53		5.81	4.11		9.09	5.86	
Anom	46.94	5.48		6.98	4.12		3.64	4.79	
Calo	-	-		-	-		-	-	
Cycl	12.24	4.70		-	-		-	-	
Cymb	14.29	4.94		1.16	2.86		7.27	7.10	
Euno	34.69	8.95		5.81	4.85		20.00	4.83	
Frag	2.04	4.00		5.81	8.88		-	-	
Frus	-	-		-	-		-	-	
Glan	2.04	4.00		6.98	6.71		-	-	
Gyro	-	-		18.60	5.26		50.91	35.55	
Hant	32.65	12.54		-	-		-	-	
Melo	2.04	16.00		48.84	16.34		5.45	5.70	
Nbac	42.86	5.08		60.47	18.81		3.64	5.63	
Npup	16.33	4.43		2.33	3.13		38.18	11.45	
Nhal	8.16	4.95		2.33	4.29		18.18	6.71	
Nav4	77.55	22.74		5.81	4.16		1.82	2.94	
Nav5	-	-		30.23	7.20		5.45	3.20	
Nav6	-	-		11.63	4.47		-	-	
Nav7	-	-		10.47	4.41		-	-	
Ni.S	-	-		20.93	7.36		5.45	7.19	
Nit2	-	-		1.16	5.00		5.45	3.40	
P.gi	-	-		5.81	4.48		1.82	2.94	
Pin2	-	-		12.79	10.29		0.00		
Pin3	-	-		29.07	7.43		27.27	6.21	
Rhop	-	-		-	-		-	-	
St.p	-	-		26.74	5.83		5.45	3.54	
Sto2	-	-		18.60	6.33		-	-	
Sten	38.78	6.01		-	-		-	-	
Si.t	-	-		12.79	6.71		18.18	5.69	
Sir2	36.73	4.56		2.33	5.84		1.82	4.76	
Syn1	-	-		11.63	6.23		65.45	16.52	
Syn2	-	-		63.95	19.09		67.27	13.40	
Anab	40.82	7.49		13.95	13.79		18.18	8.47	
Spyr	12.24	7.45		-	-		-	-	
AlgF	28.57	5.85		4.65	8.14		20.00	11.97	
AlgM	85.71	20.19		1.16	2.56		12.73	18.42	
AlgL	30.61	15.10		73.26	16.82		65.45	17.66	
Floc	97.96	14.81		91.86	20.37		94.55	15.76	
Macr	93.88	16.92		46.51	7.63		58.18	13.65	
Seed	-	-		6.98	5.78		21.82	5.44	
Sand	-	-		63.95	20.56		5.45	3.61	
Sili	-	-		11.63	7.22		1.82	12.50	
Spic	2.04	12.00		11.63	7.49		9.09	7.22	
Inve	2.04	4.00		1.16	8.33		-	-	
Anon	-	-		-	-		3.64	12.84	
Spik	-	-		-	-		10.91	27.30	
Rock	-	-		-	-		1.82	8.33	
Ach2	-	-		-	-		25.45	13.23	
Total No. Species		24.00			37.00			34.00	

Table 4.3 Percentage occurrence of all prey items in fish from different sites

stomachs from other sites. Naviculoid diatom species are often associated with sandy sediments or aquatic macrophytes.

iii Dietary Niche Breadth and Overlap

Levins index of niche breadth indicated that the three sites were similar with an average standardised niche breadth of 0.26 ± 0.07 (Table 4.4). Removal of flocculent detritus from the calculations had little effect on the overall results. Diversity in terms of number of different prey items found in the stomachs was greatest in Site 2 (New Magendo) and least in Site 1 (Pit Pit). The latter figure is possibly a reflection of the ephemeral nature of the site which is only inundated during the wet season. Consequently the development of prey items would be limited to those which rapidly colonise submerged vegetation. Stomach contents from fish captured at this site indicated that a greater proportion of algal species and macrophytes were ingested.(Table 4.3). The greater diversity of prey species found in stomachs from Site 2 (New Magendo) may be related to the shallow nature of this ox-bow which had both vegetation and sandy substrate within the euphotic zone. This provided a large area for the development of diatomaceous detrital aggregate, a preferred food of *O. mossambicus* (Bowen 1982).

Bray Curtis cluster analysis can be used as a measure of overlap. The results indicate that there is little or no overlap in the diet of *O. mossambicus* between the sites (Figure 4.2). Cluster analysis revealed distinct groups at the 0.50 level. Individual fish found in each group were found to be from the same site which indicates that fish from different sites form distinct populations in terms of feeding areas and should be analysed separately.

TWINSPAN classification analysis on all sites and samples identified four major groups at the third classification division and seven at the fourth division (Figure 4.3). It is clear from the results that the majority of individual samples in each group came from the same site. Thus it was concluded that dietary composition at each of the three sites was distinct. This supports the findings using Bray Curtis analysis.

		Pit Pit		**New Magendo**		**Old Magendo**
Levins Niche Breadth		13.56		16.01		14.68
Standardised Breadth		0.24		0.29		0.27
Without detritus						
	Levins	13.06		16.17		14.97
	Standrd	0.24		0.31		0.27
Prey Diversity		24		37		34

Table 4.4 Levins Niche Breadth and Prey Diversity

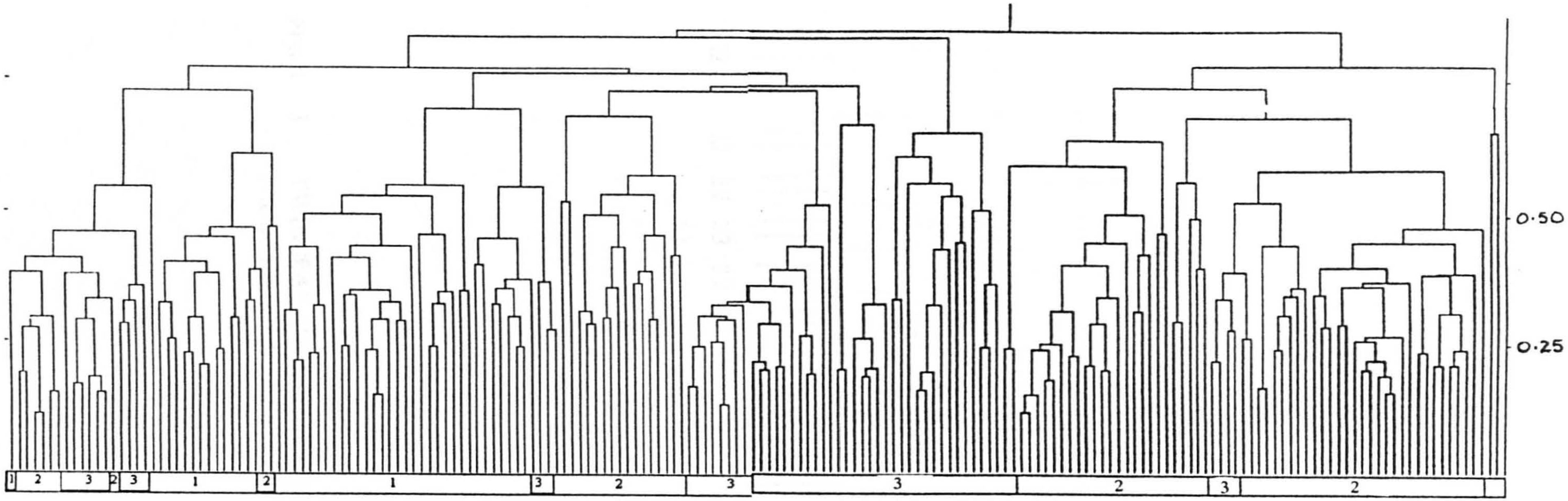


Figure 4.2 Cluster analysis based on the classification of prey species in stomachs from all fish from all sites (numbers in boxes indicate sites)

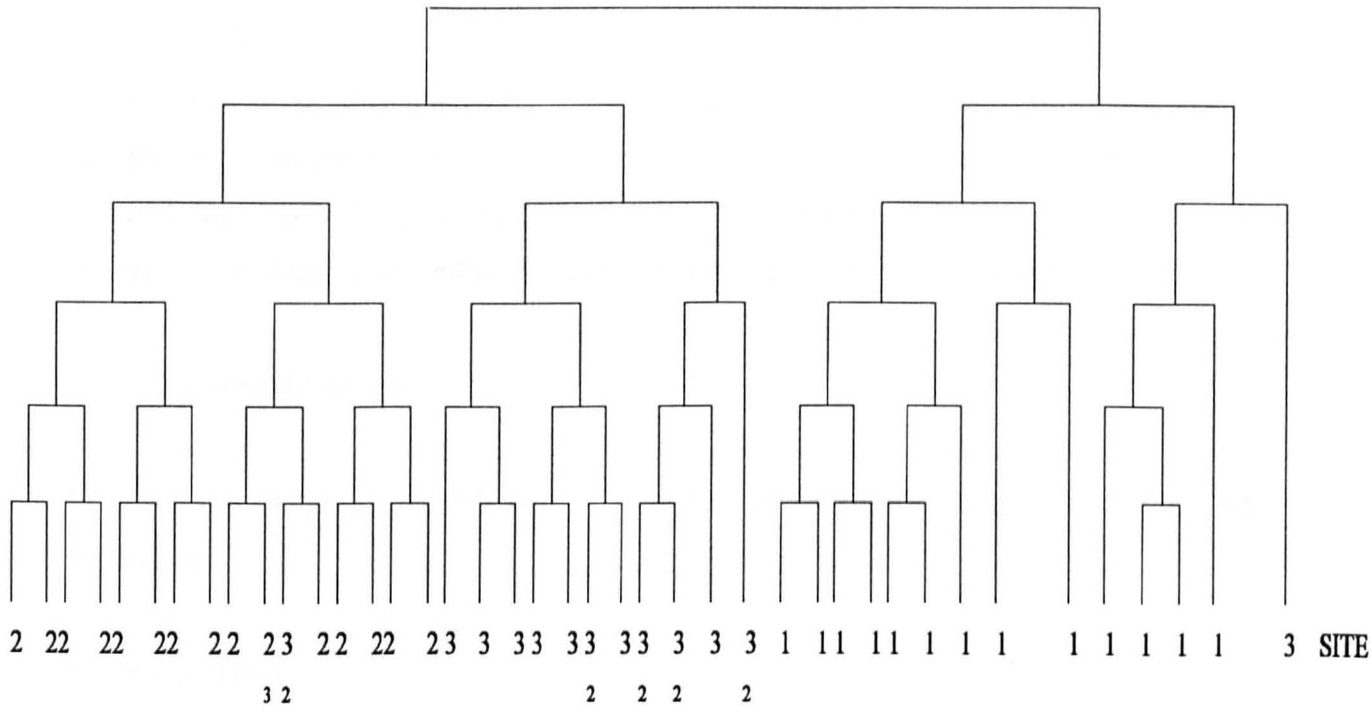


Figure 4.3 TWINSPAN classification for all sites. Numbers denote sites 1 = Site 1 (Pit Pit) 2 = Site 2(New Magendo)3 = Site 3(Old Magendo)

iv Feeding Strategies

Results of this analysis indicated that the species at all sites could be classified as generalist homogenous feeders (Figure 4.4). All sites were similar although fish from Site 1 (Pit Pit) had the smallest population diversity of prey, but the greatest individual diversity which suggests that foraging covered most habitats within the site or that the prey species are evenly dispersed. The greater population diversity found in Site 2 (New Magendo) may reflect the variety of habitats found within the site *i.e.* vegetation, sand/silt substrate and greater levels or organic detritus accumulating on the sediment. Since Site 1 (Pit Pit) is an ephemeral shallow site the accumulation of detrital aggregate with mature organic decomposition would be minimal. Site 3 (Old Magendo) is a deeper water site and few fish were caught below the euphotic zone. Thus food availability would be restricted to the surrounding vegetation.

4.4.2. Site Specific Analysis

Each site was analysed separately and results of all analyses carried out are presented on a site by site basis.

i *Site 1 (Pit Pit)*

This site was inundated with water only during the wet season (Oct/Nov-Apr/May) and could be described as a true floodplain site. Any classification analysis would therefore group individuals based on factors other than seasonal differences. Group differences in this site would possibly reveal relationships between diet and biological factors such as size, sex, and sexual status. TWINSPAN classification indicated that samples could be placed into five distinct groups based on indicator prey items (Figure 4.5). Groups were distinct at the 4th level of classification. The first division which separated groups 1, 2 and 3 from 4 and 5 was based on the diatoms *Achnanthes* sp. and *Navicula baccilum* with macrophyte pieces and algal species (M)(group 1,2,3) as opposed to diatoms *Eunotia* sp. *Navicula* sp.4 and *Hantzchia* sp. (Group 4,5). Group 1 could be separated from 2 and 3 due to the presence of *Stenopterobia* sp and *Navicula baccilum.* Group and 2 and 3 were separated at the fourth division with the presence of algal spF in group 3. Group 4 and 5 were separated at the

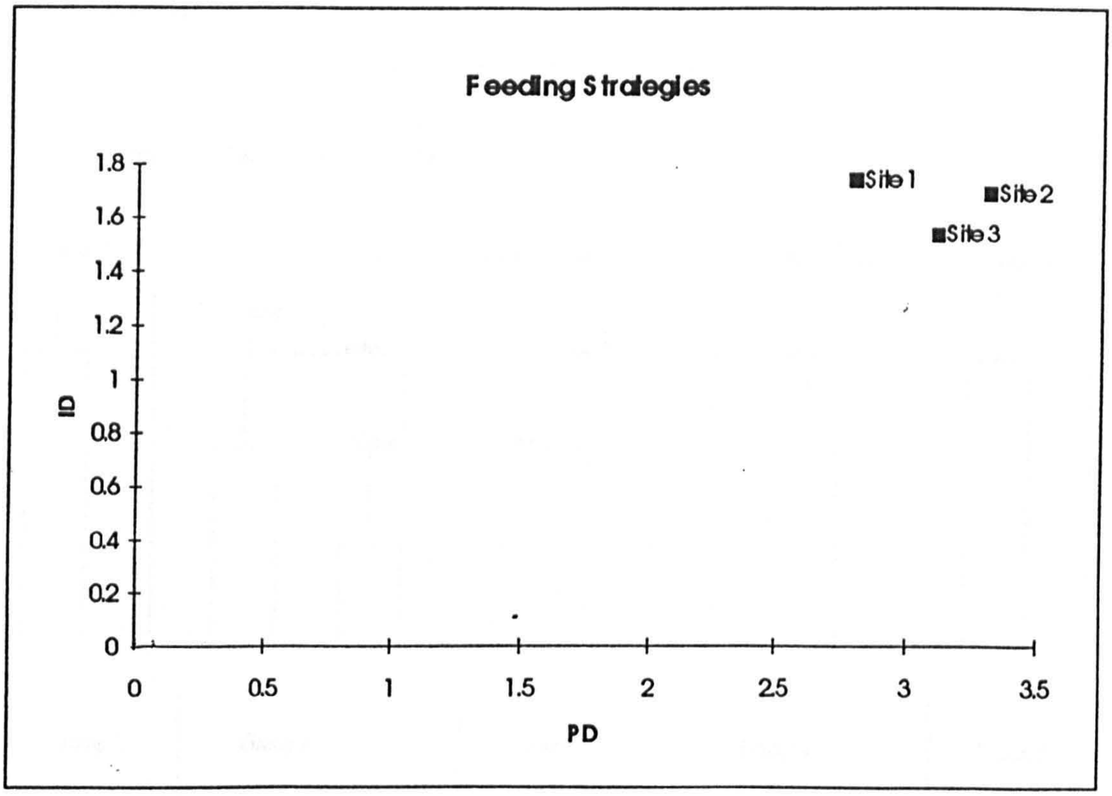


Figure 4.4 Feeding Strategies determined for each site using the formula developed by Tokeshi 1991 (see pages 91 and 92)(ID = individual diversity PD = population diversity)

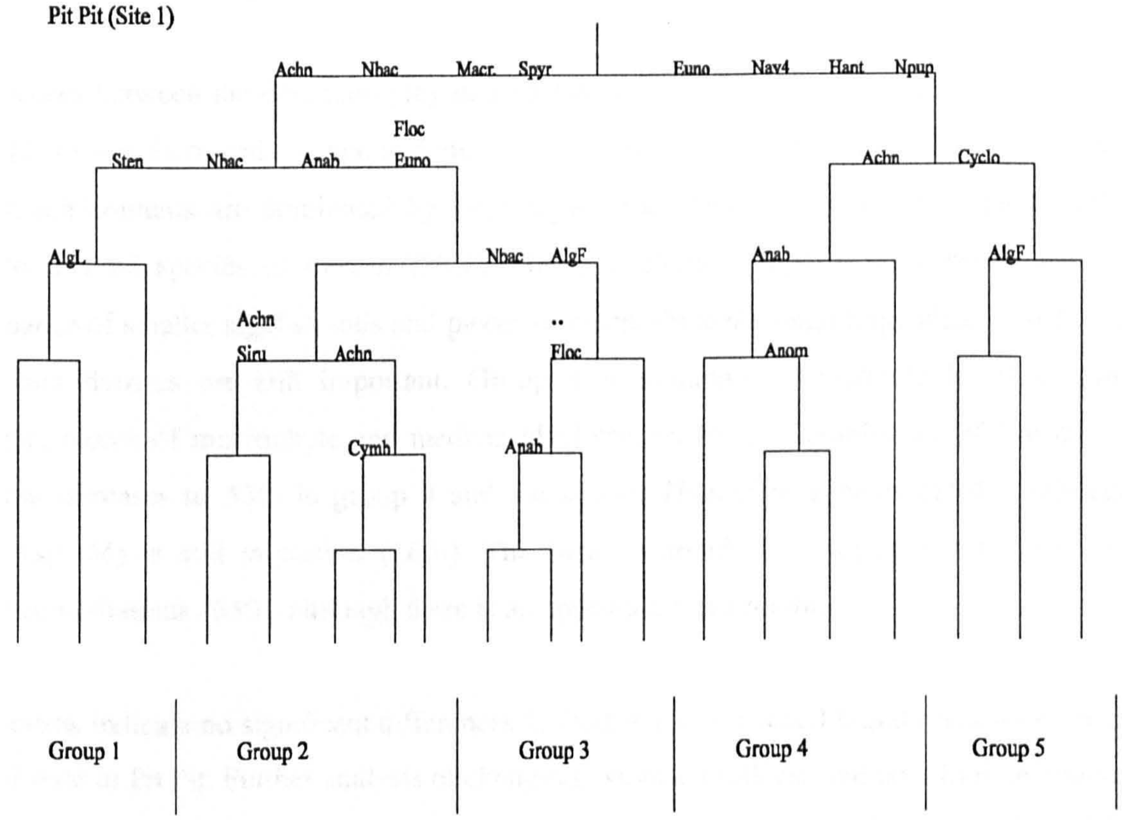


Figure 4.5 Site 1 (Pit Pit) TWINSPAN analysis of stomach contents. (Groups refer to most dominant species detailed in figure 4.6)

second division by the presence of *Cyclotella* sp in group 5 and *Achnanthes* sp in group 4.

There were no significant differences in weight between groups (two-way ANOVA with Tukeys HSD). Further analysis (Chi-squared) revealed no significant difference between groups based on sex or gonad state.

Differences between the dominant prey items found in fish in each group are shown in figure 4.6. There was an overall change in dominant food items found from groups 1 to 5. In group 1 stomach contents are dominated by large algae, flocculent detritus (approximately 27%) and Naviculoid species of diatom (18%). Group 2 changes slightly with the increase in dominance of smaller algal strands and pieces of macrophyte although large algal strands and flocculent detritus are still important. Group 4 is dominated completely by Naviculoid diatoms, pieces of macrophyte and medium algal species M. The dominance of Naviculoid diatoms increases to 53% in group 4 and the species *Hantzchia* appears (15%), although algae (sp. M) is still important (16%). The final group (5) is completely dominated by Naviculoid diatoms (63%) although there is an appearance of *Eunotia*.

The results indicate no significant differences in food items consumed based on size or sex or sexual state in Pit Pit. Further analysis of changes in stomach fullness and condition in relation to GSI in ripe females at this site indicates that during the breeding periods, as indicated by peak GSI values in January and April, mean stomach fullness decreases (Figure 4.7) which supports the view that brooding females do not feed. However , during this period there is also little change in condition which suggests the quality of food available is sufficient to enable the females to build up fat stores and maintain condition whilst brooding larval fish.

ii *Site 2 (New Magendo)*

TWINSPAN analysis on prey items identified 6 main groups at the fourth division (Figure 4.8). Groups 1, 2 and 3 can be characterised by the presence of *Stauroneis* sp. Algal; sps L *Anabaena, Stauroneis sp2,* Sand and *Melosira.* These are further divided at the second division with group 1 containing *Navicula* sps 5. Group 2 and 3 are separated at division three with Macrophytes as the indicator species for group 2. Groups 4 and 5 can be

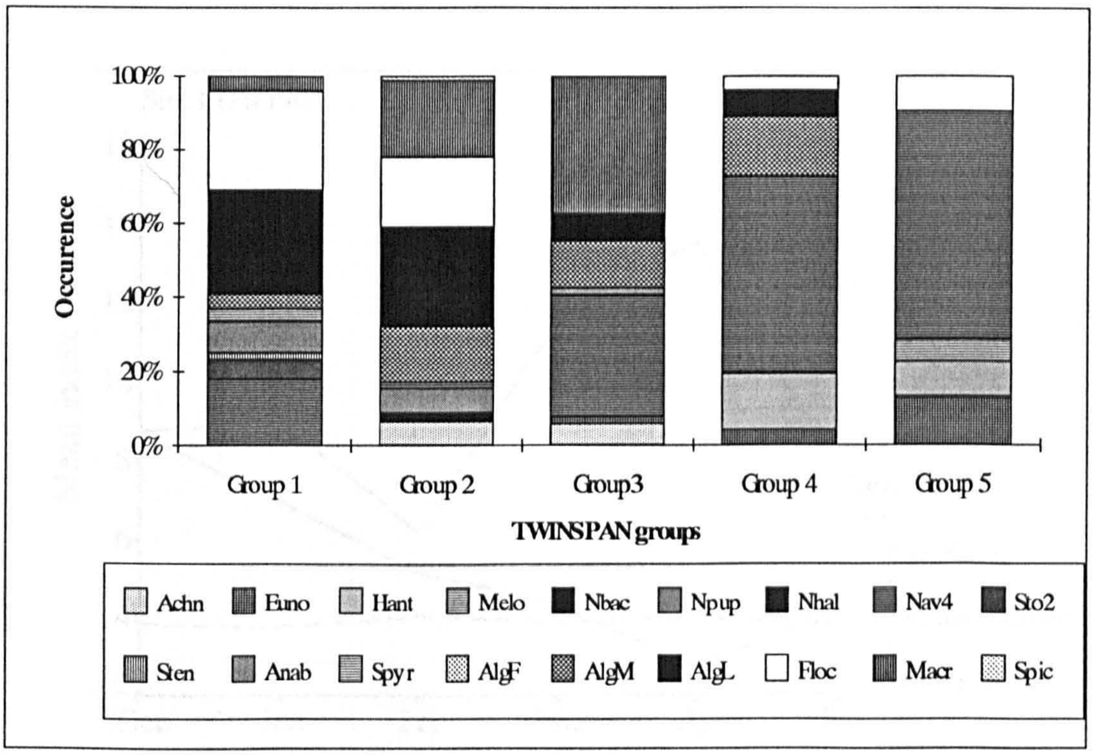


Figure 4.6 Site 1. Occurrence of dominant food items (TWINSPAN derived). (codes refer to page 97)

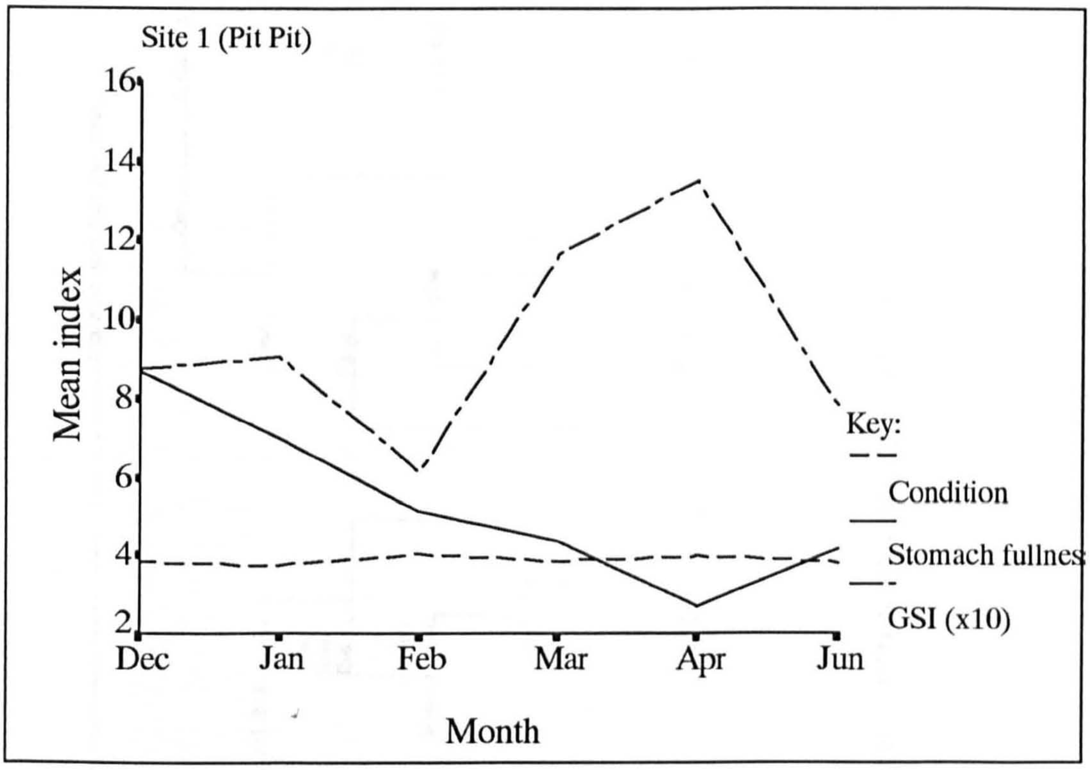


Figure 4.7 Site 1 - Relationship between GSI, stomach fullness and condition in ripe females

New Magendo

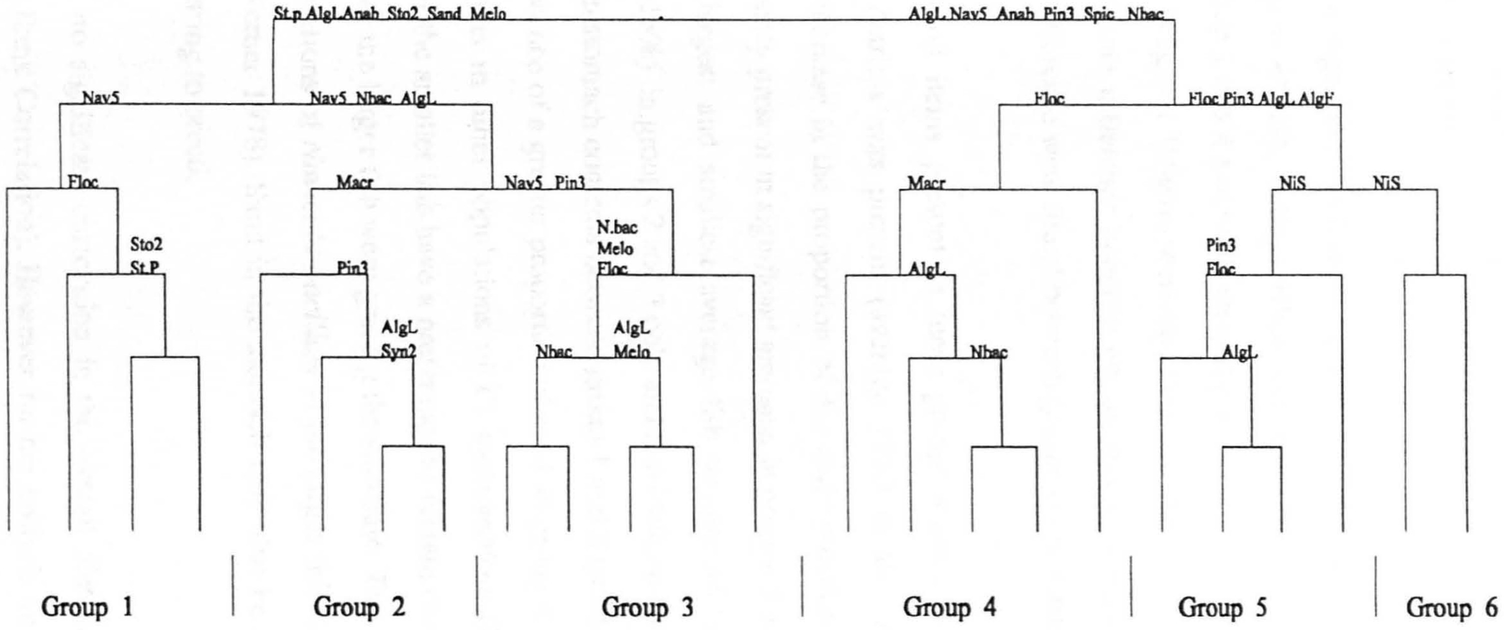


Figure 4.8 Site 2. TWINSPAN analysis of stomach contents. (Groups refer to most dominant species indicated in figure 4.9)

separated at the third division by the presence of *Pinnularia* sp3, large algae and filamentous algal species in group 5. Group 5 and 6 are distinct by the presence of indicator species *Nitschia* spS in group 5.

There was a significant difference between TWINSPAN groups based on weight of fish (ANOVA $p = <0.05$). Tukeys HSD test indicated significant differences in fish weight between group 1 and 4 and between group 2 and 4. The average weight of groups 1, 2 and 4 are 103.6g, 113g and 359g respectively. Pearsons chi squared analysis revealed that there was also a significant difference between groups based on season ($p = < 0.005$). However no significant difference were found between groups on the basis of gonad state or sex.

Dominant food items present in these groups were presented graphically (Figure 4.9). Flocculent detritus was present (average 17%) in all but group 5 where there was a substantial increase in the proportion of *Navicula bacillum* (41%) and sand (31%). Large algae were only present in significant amounts in groups 1 and 4 which were also the groups with the largest and smallest average fish weight. *Melosira* was present in substantial amounts (>15%) in groups 2 and 3 only and *Navicula baccilum* in all but group 3. The main difference in stomach contents between group 1 and 2 (smaller fish) and group 4 (larger fish) was the presence of a greater proportion of sand in group 4. Larger fish are known to feed at greater depths in other populations of *O. mossambicus* (Bowen 1982) and these results suggest that the smaller fish have a preference to remain closer to the marginal vegetation to feed whereas the larger fish were grazing the substrate. This may also explain the presence of larger proportions of *Navicula bacillum* in the larger fish since this species is thought to be epipelic (Werner 1978). Sand in the stomach may also be an indication of nest building in males preparing to breed.

There was no significant correlation in the overall diet between the wet and dry season (Spearman Rank Correlation). However further analysis on individual prey items revealed a significant difference in proportions of 6 prey items between the wet and dry seasons. (Table 4.5 Mann-Whitney test). These were diatoms *Melosira* sp. *Stauroneis phenecentron*, and *Synedra* sp and filamentous algae species. There was also a significant difference between the proportions of macrophyte pieces and sand particles.

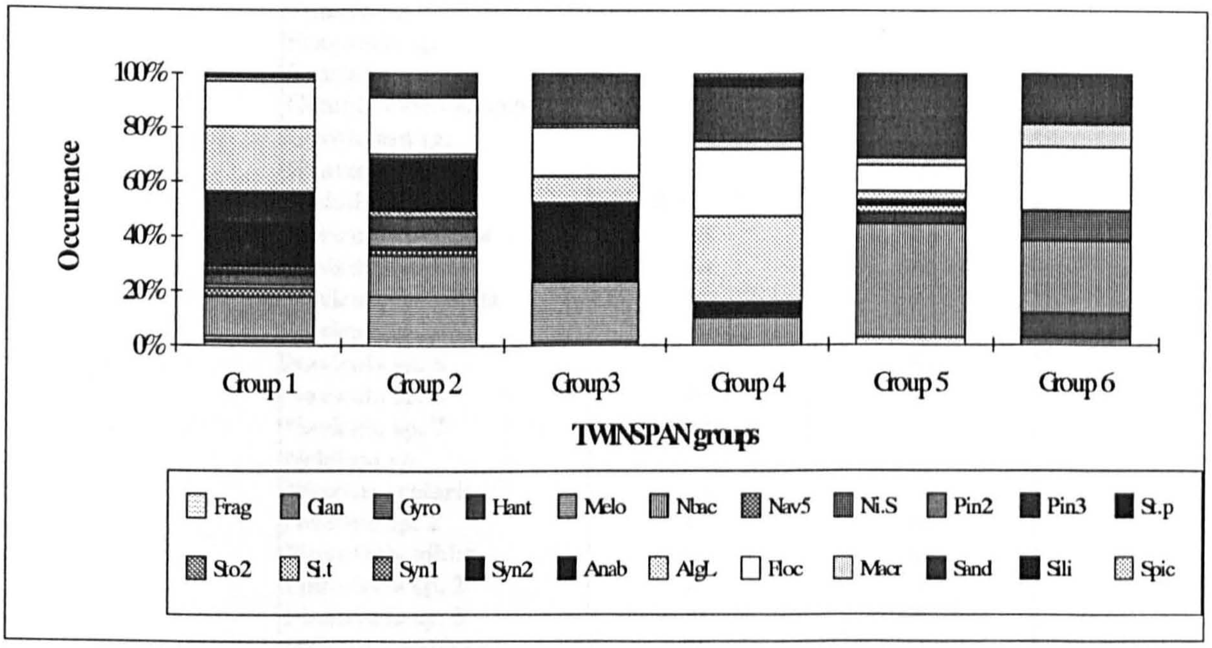


Figure 4.9 Site 2. Occurrence of dominant food items in stomachs (TWINSPAN derived) (Codes in the key refer to page 97)

	New Magendo	**Old Magendo**
Prey Items	2-tailed P	2-tailed P
Achnanthes sp.	ns	ns
Anomoeoneis sp.	ns	ns
Caloneis sp.	/	/
Cyclotella sp.	ns	/
Cymbella sp.	ns	ns
Eunotia sp.	ns	ns
Fragilaria sp.	/	/
Frustulia sp.	ns	/
Gomphonema lanceo.	ns	/
Gyrosigma sp.	ns	<0.001 ***
Hantzchia sp.	/	/
Melosira sp.	<0.05 **	ns
Navicula bacillum	ns	ns
Navicula pupula	ns	ns
Navicula halophila	ns	ns
Navicula sp. 4	ns	ns
Navicula sp. 5	ns	ns
Navicula sp. 6	ns	/
Navicula sp. 7	ns	/
Neidium sp.	/	/
Nitzchia scolaris	ns	ns
Nitzchia sp. 2	ns	ns
Pinnularia gibba	ns	ns
Pinnularia sp. 2	ns	/
Pinnularia sp. 3	ns	<0.05 **
Rhodaphalodia sp.	/	/
Stauroneis phenicentron	<0.05 **	ns
Stauroneis sp. 2	ns	/
Stenopterobia sp.	/	/
Sirurella tenera	ns	<0.01 **
Sirurella sp. 2	ns	ns
Synedra sp. 1	ns	<0.005 ***
Synedra sp. 2	<0.001 ***	ns
Tabellaria sp.	/	/
Tetracyclus sp.	/	/
Tropodoneis sp.	/	/
Anabaena sp.	ns	ns
Spyrogyra	/	/
Filamentous algae	<0.001 ***	<0.05 **
Medium Algae	ns	ns
Large Algae	ns	<0.001 ***
Flocculent detritus	ns	ns
Macrophyte piece	<0.05 **	ns
Seeds	ns	ns
Sand/Silt	<0.05 **	ns
Silica particle	ns	ns
Spicules	ns	ns
Invertebrate pieces	ns	/
Unidentified item	/	ns
Green spikelets	/	ns
Rock pieces	/	ns
Achnanthes sp. 2	/	<0.05 **

Table 4.5 Analysis of seasonal changes in prey items consumed (Mann-Whitney non-paired test)

Figure 4.10 shows the relationship between condition, GSI and stomach fullness (feeding intensity) in ripe females over the whole sampling period. Feeding intensity is greatest during the high water levels (November - April) and just prior to the peak in GSI. Condition remained relatively stable except for a period between December and January when breeding occurs.

iii *Site 3 (Old Magendo)*

TWINSPAN classification identified six groups of individuals at the fourth division (Figure 4.11). Groups 1,2 and 3 were separated from groups 5 and 6 on the basis of indicator prey items *Pinnularia* sp3, *Sirurella tenera*, and *Navicula pupula*. Indicator species separating groups 1, 2, 3 and 4 were *Navicula bacillum*, large algal species, *Eunotia* sp. and *Navicula bacillum* respectively. Groups 5 and 6 were separated by the presence of medium algal species and seeds respectively. There was no significant difference between groups based on weight (one-way ANOVA with Tukeys HSD test), sex or gonad states (Pearsons Chi-squared) but significant differences were found on the basis of season (Pearsons Chi-squared $p = <0.001$). Individuals placed in group 5 and 6 were caught predominantly in the wet season.

Percentage occurrence of the major food items in each group shows a greater proportion of large algae present in groups 5 and 6 (and macrophytes in group 6) when compared to groups 1 - 4 (Figure 4.12). This may be related to rising water levels, inundation of fresh vegetation and algal production. Fish in groups 2, 3 and 4 had a greater proportion of *Gyrosigma* in the stomach whereas fish in group 1 had a greater level of *Synedra* sp2 and *N. pupula*. There was a significant correlation between diets in the wet and dry season (Spearman correlation coefficient $p = <0.001$) which suggests that although some individual prey items may change in proportion between the wet and dry season dietary composition does not change significantly, which suggests that there is little seasonal change in food availability.

Changes in the proportions of individual prey items in the diets between wet and dry season showed a significant difference in six species of prey consumed (Table 4.5). These included the diatom species *Gyrosigma* sp., *Pinnularia* sp., *Sirurella tenera*, *Achnanthes* sp. and *Synedra* sp. as well as filamentous and large algal species. In contrast to the shallower New

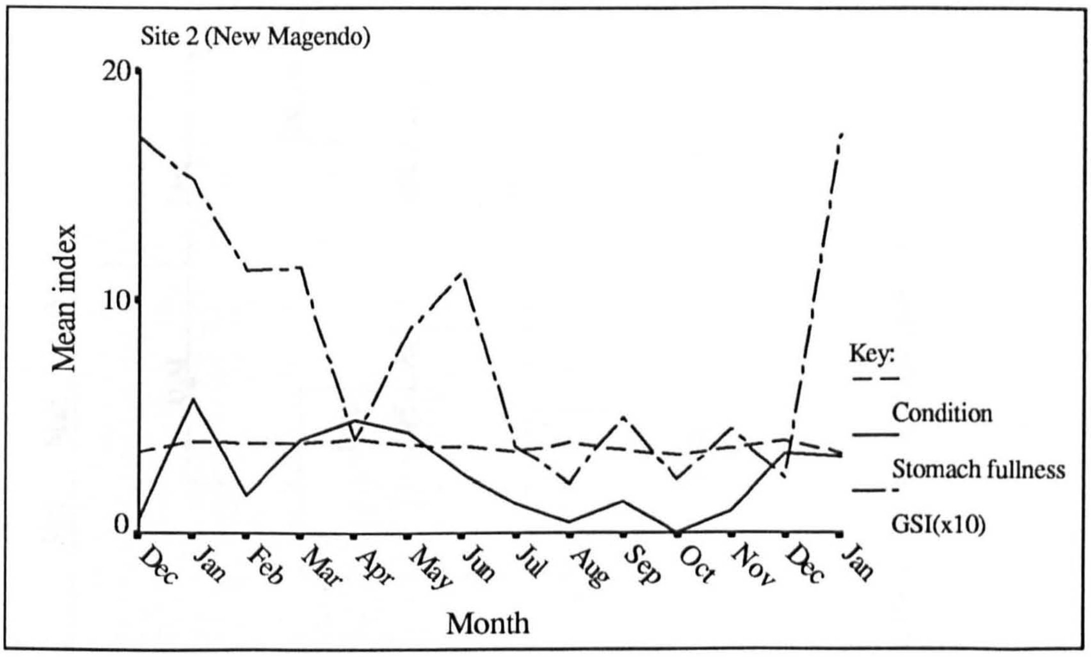


Figure 4.10 Site 2 - Relationship between GSI, Condition and Stomach fullness in ripe females

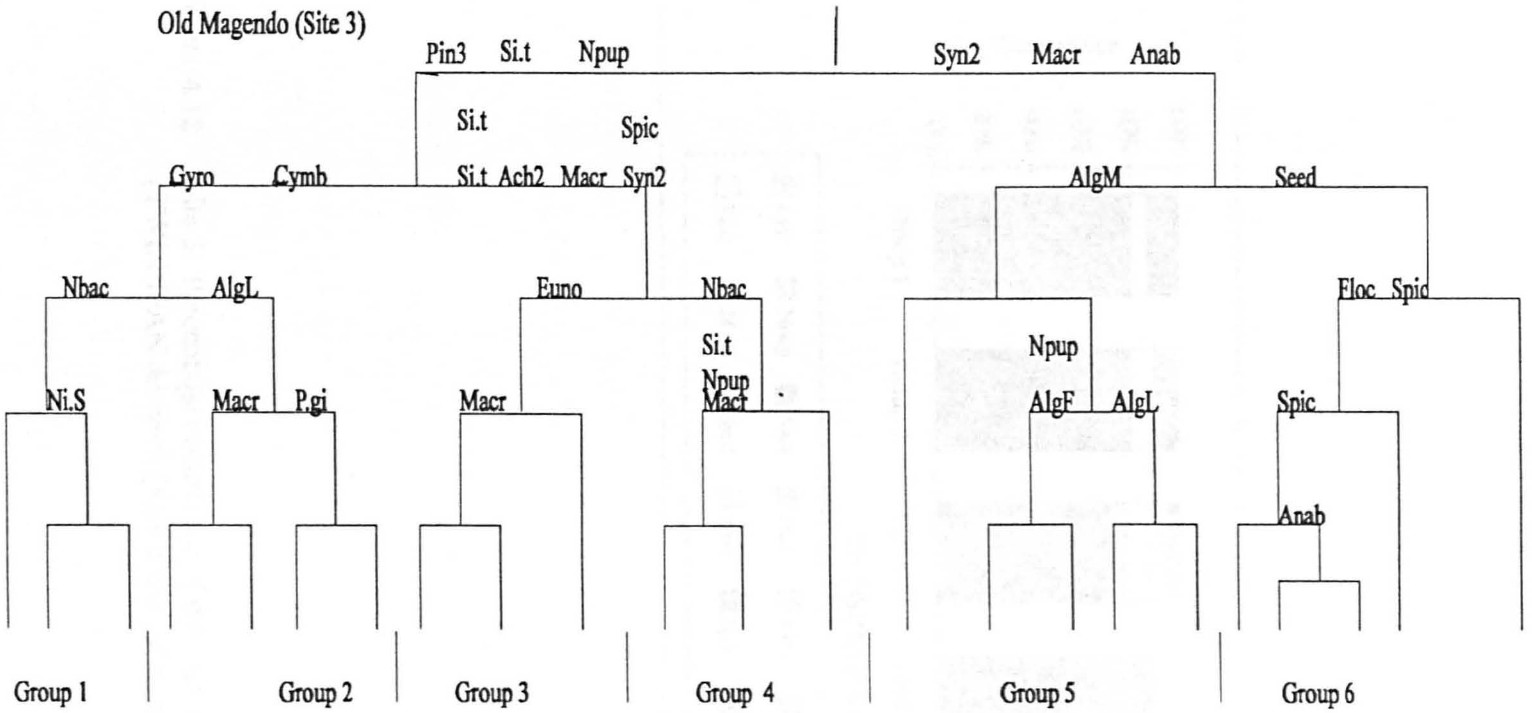


Figure 4.11 Site 3. TWINSPAN analysis of stomach contents. (Groups refer to dominant items indicated in figure 4.12)

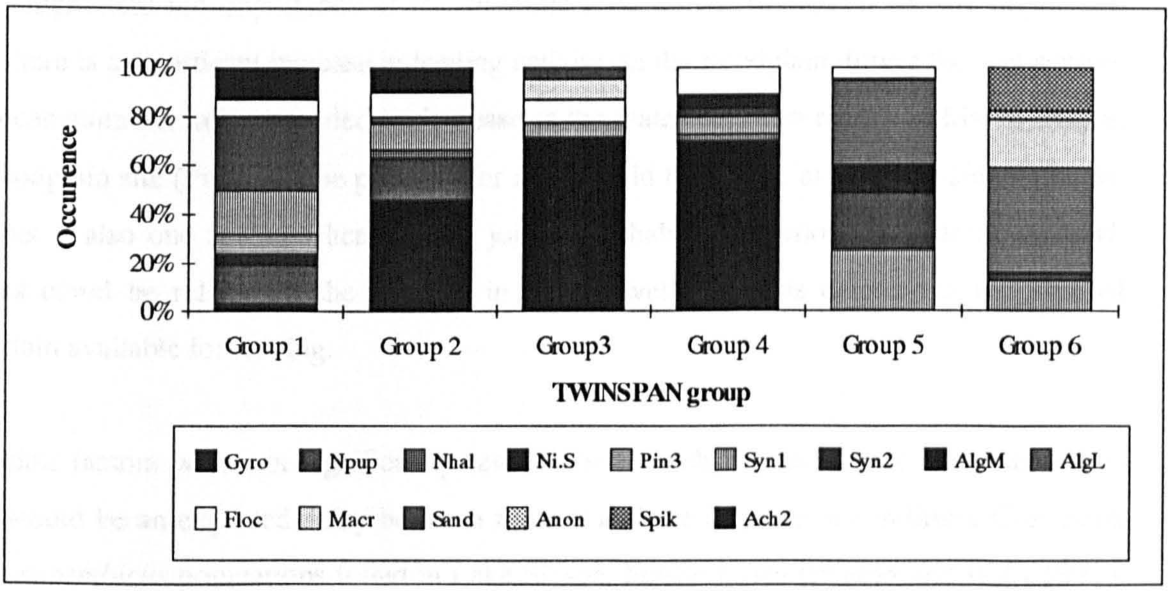


Figure 4.12 Site 3. Percentage occurrence of dominant food items in stomachs (TWINSPAN derived) (Key codes refer to those on page 97)

Magendo site there was no significant difference in the proportion of macrophyte pieces and sand consumed.

4.4.3 Feeding Intensity

Stomach fullness can be related to the condition factor and was significantly higher overall for fish on the floodplain i.e. site 1(Pit Pit) compared with those in the deeper roundwaters i.e. sites 2 and 3 (New Magendo and Old Magendo) (t-test, $p<0.05$) during the same period. This again emphasises the importance of the available food on the floodplain for the population since there is a significant increase in feeding activity on the floodplain during the wet season. The mean stomach fullness tended to decrease as the water began to recede in March-May at the floodplain site (Pit Pit). The pressure for food would be greater at this time since it seems that this is also one period when recruits join the fishable population. In general, stomach fullness could be related to the changes in water level since this determines the area of floodplain available for feeding.

Condition factors were not significantly related to stomach fullness in the same month as there would be an expected delay between fullness and the increase in condition. Compared to *O.mossambicus* populations found in Lake Sibaya, South Africa (Bruton and Boltt 1975), the general condition of the fish in the Sepik was good and thus food quality could not be considered as a limiting factor to growth.

4.5 General Discussion

The introduction of *O. mossambicus* into the Sepik River system without prior knowledge of the ecology of the existing fish assemblage could have had significant consequences in terms of interspecific competition. There is historical evidence from catch data that this species rapidly extended its spatial distribution and successfully occupied the floodplain and ox-bow lake areas (roundwaters). In this chapter the feeding ecology of *O. mossambicus* is described to determine the reasons for its rapid distribution throughout the Sepik Basin.

The analysis of dietary composition and feeding strategies indicated that fish from all sites were generalist feeders which is similar to findings in other studies on the qualitative aspects of the diet of *O. mossambicus* (Bowen 1982, Getachew 1987). The results also emphasise the importance of diatoms and detrital aggregate in the diet. There was little overlap in the diet of fish from different sites (Bray Curtis/TWINSPAN) and little difference in niche breadth although fish from the floodplain site 1 (Pit Pit) consumed fewer species of prey than elsewhere. This is related to the relatively short period of time in which the site has water and the subsequent paucity of species which are established. However on a site specific basis there were differences in prey items consumed during the wet and dry seasons. This emphasised the importance of the floodplain as a feeding area since during inundation the submerged and emergent macrophytes provide a fresh source of epiphytic diatoms and algae as well as higher plants.

In the shallow area (Site 2, New Magendo) the diet also included benthic diatom species and sand whereas in the deeper ox-bow lake site (Site 3, Old Magendo) the main food items included epiphytic diatom species, algae and detritus. These shallow areas would allow access to benthic detrital aggregate, reported to be a preferred food of *O. mossambicus* and one suitable for better growth. Bowen (1976) proposed that periphytal detrital aggregate with its associated bacterial component provided a good source of non-protein amino acids and was an important part of the diet.

Fish from all sites showed a considerable amount of 'flocculent detritus' in the gut. This was identified as mucus which was thought to have entered the gut with entrapped food particles and supports the idea that an important part of the feeding mechanism is an interaction between negatively charged mucus and the surface chemistry of food particles (Northcott and Beveridge 1988).

During the study the substrate in the deeper site (Site 3, Old Magendo) was found to be almost anoxic with an abundance of decaying vegetation. The lack of oxygen and the possible presence of hydrogen sulphide in the bottom sediments would create unfavourable conditions for *O. mossambicus* and would be avoided as a food source. Fewer fish were caught here during the period of study (Chapter 3)

Species Type	**Invertebrates Insects, Annelid, Molluscs**	**Fish** **$^?$ - reported**	**Macrophytes**	**Algae** **^{d} - diatoms** **^{f} - filament.**	**Detritus**
Megalops cyprinoides	y	y			
Anguilla bicolor				y	y
C. carpio	y				
Arius nox	y				y
A. solidus	y	y		y	y
A.velutinus	y				
A. utarus	y				
A. coatesii	y	y			y
Plotosidae sp.	y				
Zenarchopterus kampeni	y			y^f	
Gambusia affinis	y				
Chilatherina sp.	y			y^f	
Glossolepis multisquamatus	y				
Ambassidae	y	y			
Theraponidae	y	y			
Carangidae	y	$y^?$			
Lutjanidae	$y^?$	$y^?$			
O. mossambicus				y^{df}	y
Mugilidae				y^d	y
Eleotridae	y	y			
Glossogobius	y				y

Table 4.6 Main feeding preferences of Sepik River fish species

Although there were differences in food items ingested between sites the results do support the view that this species owes its widespread distribution to its degree of plasticity in feeding habits. However there may be a case for describing this species a specialist detritivore rather than a generalist for the following reasons. Although there were over 52 items identified in stomachs from the three sites these were mainly diatoms, algae and detritus but also sand and macrophytes which may have been ingested incidentally along with benthic and epiphytic diatoms respectively. If all diatom species were classed as one prey item the diversity of prey items consumed would be considerably reduced. This species was feeding on the food resources of a vast floodplain with little or no competition for food or spatial territory. Potential alternative food items could be found in great numbers on the plain *e.g.* benthic invertebrates (Dudgeon 1982) yet not one stomach contained anything but the items described above. Thus *O. mossambicus* could be considered as consuming a fairly narrow range of food items. Although *O. mossambicus* is generally considered to be opportunistic and thus able to colonise new habitats successfully (Getachew 1987, Bluhdorn *et al.* 1990, Dempster *et al.* 1995) the initial success seen in the Sepik may have been partly due to complete lack of competition for food and nesting sites and the ability to breed rapidly. An analysis of food preferences of the other species of fish in the river is shown in table 4.6. Potential competitors for food resources include *Zenarchopterus kampeni* and a couple of the ariid catfish species although none of these species inhabit the floodplain during the wet season.

The initial rapid distribution of *O. mossambicus* in the Sepik could be related to its ability to utilise a food source few other species in the river had exploited. There is evidence that feeding intensity increases as the water level rises and that the main breeding periods are during the wet season. The generally good condition of the females throughout the breeding season may relate to the quality of food available during this time.

However it is also important to remember that the initial predictions of catch for this species were never realised and in more recent years there have been newly introduced species utilising the floodplain such as carp *Cyprinus carpio* (Redding 1989). The reasons for the limited yield may lie in other factors other than either the quality of the diet or potential recent competition for food from carp.

Chapter 5 REPRODUCTION

5.1 Introduction

In the analysis of reproductive traits in fish, terms such as 'strategies' and 'tactics' have been used in the context of the wide range of adaptations (strategies) shown in many species to the surrounding environment which may be adverse and subject to wide variations or cyclical change (Wootton 1984, Paine 1990). Adaptive strategies which are present in many species are as a result of selection for those traits best suited to the environment and the success is the best use of those traits (Wootton 1984). Successful reproductive strategies for any natural (endemic) fish population are reflected in the recruitment patterns and the population structure. In the case of fish species which have been introduced into an environment outside of their natural range the ability to exploit available resources will depend on the plasticity or range of variation of reproductive strategies and tactics available to that species.

It is well documented that cichlids have very diverse reproductive traits (Fryer and Iles 1972, Lowe-McConnell 1979, McKaye 1984) which are closely linked to the evolution of often complex cichlid community organisation. The breeding pattern of many of the tilapia species is related to the form of parental care exhibited (Wittenberger and Tilson 1980). Parental care in fishes varies from simple guarding of fertilised eggs to mouthbrooding is thought to be related to predation pressure (Fryer and Iles 1973, McKaye 1984, Wittenberger and Tilson 1980). Very often it is the male of the species which provides the care and biparental or maternal care is less common (Smith and Wootton 1995b). It is generally thought that the development of parental care patterns have evolved from no care through paternal, biparental to maternal protection (Keenleyside 1980).

Oreochromis mossambicus are polygamous, maternal mouthbrooders which originated in the eastern coasts, lakes and rivers of East Africa as far south as the Bushmans (Boesmans) River near Port Elizabeth (Bruton and Boltt 1975, Philippart and Ruwet 1982, Trewavas 1983). This species shows a preference for standing waters or slow flowing rivers although saline conditions are also tolerated (Tinley 1964, Whitfield and Blaber 1979) and breeding has been carried out successfully in such conditions (Canargartnam 1968).

In this species body colouration changes during growth and maturation and there is distinct sexual dimorphism shown in adult fish with males of the same age tending to be larger. Juvenile fish (>60 mm) have been found with darker vertical bands on a pale grey-olive background. Adult fish have been reported with differing colouration from grey to olive with and without bands but with distinct breeding colours in males only (Trewavas 1983). Actively breeding males become almost black with a hint of blue on the body with red margins to the dorsal and caudal fins. (Vaas and Hofstede 1952, Neil 1966).

The general pattern of breeding activity and behaviour in *O. mossambicus* and other cichlids is well documented (Baerends and Baerends van Roon 1950, Vaas and Hofstede 1952, Lowe-McConnell 1959, Reidel 1965, Bruton and Boltt 1975, Silverman 1978, Schwank 1987, Trewavas 1983), and can be summarised as follows. Males establish nesting sites or arenas in shallow areas with usually sandy substrata prior to spawning, nests are shallow pits varying in diameter from 11-110 cm (De Silva and Siresena 1988). Once territories are established and females courted, eggs are released, fertilised and taken into the females buccal cavity. Females then move into shallower marginal vegetation and incubate the eggs until the larvae/juveniles are ready to leave the protection of the mother after approximately 22 days. Social behavioural patterns are important in stimulating the breeding patterns. Females are found in groups during the breeding season which is thought to stimulate synchronous spawning. Experimental isolation of females had the effect of affecting ovarian development and consequently delaying spawning (Silverman 1978, Schwank 1987) Multiple synchronous spawning in *O. mossambicus* has been seen in previous studies (Jubb 1967) and males are sometimes, but very rarely, found with eggs or larvae in the mouth (Bruton and Boltt 1975, Arthington and Milton 1986). Once the juvenile fish have reached approximately 10 mm the females leave the brooding areas and the young remain in shoals and take refuge in the marginal vegetation areas until ready to enter deeper waters and the fishery (Lowe-McConnell 1956).

As mentioned in previous sections *O. mossambicus* was introduced into the Sepik River in the 1950's. Its widespread distribution and entry into the fishery since that time is an indication of its ability to adapt to the environment and the successful utilisation of available resources. Although the specific reproductive biology of *O. mossambicus* in natural and man-made water bodies has been studied elsewhere (Bruton and Allanson 1974, Bruton and Boltt 1975, Hodgkiss and Man 1978, De Silva and Chandrasoma 1980, Arthington and Milton 1986), there are no studies relating to the introduced population in the Sepik. Although the studies mentioned have shown similar traits, the development of either precocial or altricial breeding strategies have varied depending on outside pressure such as commercial fishing (Noakes and Balon 1982, Arthington and Milton 1986). This chapter attempts to describe the general reproductive biology, strategies and tactics of *O. mossambicus* in the Sepik River. Since the productivity of a population is a function of the fertility of the species (Welcomme 1967) a comprehensive assessment of the reproductive biology of this species will provide an insight into the underlying reasons for its initial success outside its natural range and may also provide some answers to its later perceived decline in catch rates. Without such knowledge future exploitation of a potential commercial species would be neither rational or sound.

5.2 Methods and Materials

Ripe gonads were removed from female fish, weighed and stored in formalin (10% buffered) to harden the oocytes prior to examination. All male gonads in stages 3 or above were weighed in a fresh state.

Other parameters were recorded as described in chapter three.

A sample of ovaries collected were washed through a series of sieves of mesh sizes 140µ, 250µ, 600µ, 1000µ, 1320µ, and 2000µ to determine the variation in diameter, assess the proportional development of primary (perinucleolar) secondary (vitellogenic with yolk vesicle) and mature (hydrated) oocytes within the gonad and to relate these factors to the potential number of spawning periods.

Absolute fecundity was measured by counting the total number of mature oocytes in both ovaries stored in formalin, since paired ovaries were often of different sizes, and one ovary contained more ripe oocytes. As mature oocytes are oval the mean transverse diameter of 20-

30 oocytes was measured using a compound microscope with a calibrated eyepiece graticule. The weight (•0.0001g) of this sample was recorded to determine the individual oocyte weight. Shrinkage is complete for oocytes stored in formalin for a period in excess of three months therefore the data on the diameter and individual weight were used in determining differences in reproductive biology between sites.

5.2.1 Gonad States

Gonad states were recorded on a scale of 1 to 6 modified from Hodgkiss and Man (1978) as follows:

Gonad State	Male	Female
1 Immature	Small threadlike testes transparent, colourless, close to abdominal wall	Small ovaries clear to grey or opaque, close to abdominal wall
2 Maturing	Testes wider, opaque becoming firmer	Ovaries more opaque, larger, eggs small and visible, gonads occupy almost half the ventral cavity
3 Developed	Testes yellow-white firm but no milt with pressure	Ovaries yellow/white eggs larger and clearly visible, gonads fill two thirds the ventral cavity
4 Ripe	Testes white/silvery firm, fills half dorsal cavity	Ovaries fill most of the ventral cavity, eggs pale yellow, large (up to 2mm diam)
5 Running ripe	Milt runs under pressure	Eggs fully mature and run with abdominal pressure
6 Spent	Testes pink to reddish with blood capillaries, less firm	Ovaries flaccid, pink to red with blood capillaries and residual eggs still present

5.3 Data assessment

i Fecundity/Size relationships

The relationship between fecundity and three other independent variables *i.e.* standard length, total weight and gonad weight was calculated separately for the population at each site by regression analysis (least squares method). Analyses were carried out on data from sites 1 and 2 only, since there was insufficient numbers of ripe females caught at the other sites. For each site predictive equations for fecundity were calculated and analysis of co-variance (ANCOVA) was used to determine significant location differences in the relationship of fecundity to standard length, total weight and gonad weight.

ii Spawning periods

The percentage of females found in each of the six gonad states was used as an indication of breeding periods during the year at each site. In addition, the gonadosomatic index (GSI) was calculated as a further indication of spawning periods when gonad size was greatest in relation to body weight.

The Gonadosomatic Index (GSI) was calculated by the formula:

100 (weight of gonad/ total body weight-gonad weight)

(Wootton 1990)

iii Seasonal changes in GSI/Condition

Data on GSI were assessed to determine whether spawning periods were continuous throughout the year or if there were peak periods of activity. The relationship between spawning activity and water level changes was also explored. In addition it is well documented that maternal mouthbrooders do not feed whilst brooding the young (Trewavas

1983) thus the relationship between condition and breeding period in females as compared to males may change over the annual cycle.

Condition factor (K) was calculated using the formula:

$$K = \frac{\text{weight (g)} \times 10^5}{(\text{standard length mm})^3}$$

after Daget (1957). Total fish weight was used, not gutted weight.

Students T-test was used to determine the possible influence of environmental changes (wet and dry seasons) on reproduction and condition in both males and females. Only samples in which variance was found to be homogenous according to Levines test were analysed by this method (Sokal and Rohlf 1981). Those samples which violated the assumptions of the normal t-test were analysed using the non-parametric Mann-Whitney non-paired test. Only data collected from sites 2, 3 and 4 were used since site 1 was only covered in water during the wet season.

iv Minimum breeding sizes

Minimum breeding sizes for males and females were calculated separately using the number of individuals in each of gonad states 3 and 4 (maturing and ripe) using size increments of 0.5 cm. This also enabled the mean breeding size of males and females to be determined and provided evidence on whether early maturation at a small body size was occurring under certain conditions. In addition the presence of sexual dimorphism and spatial differences in reproductive strategies could be deduced.

v Sex ratios

Changes in the proportion of males and females by month and size were calculated separately for each site. Temporal changes in proportions of either sex may be an indication of behavioural differences in males and female according to either environmental (site), temporal (month, season) or physiological (size) conditions. Significant changes in proportions of males and females over the sampling period was analysed using the binomial test (Sokal and Rohlf 1981).

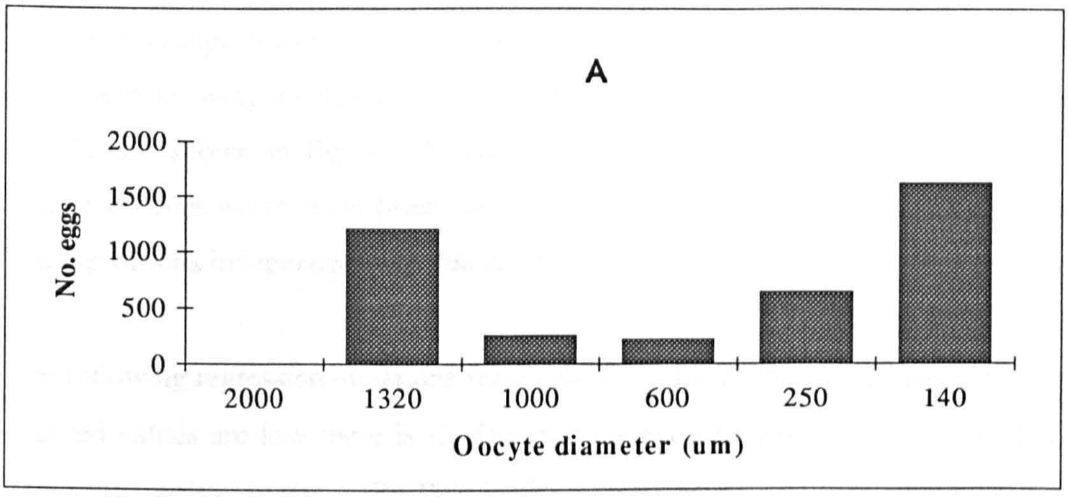
vi Nesting sites

A shallow muddy area in the vicinity of site 2 (New Magendo) where *O.mossambicus* were found to have been constructing nests was examined. The diameter of each nest and the distance to its nearest neighbour was measured along transects from the vegetation edge to the main water channel. Nests at distances of 0m, 25m 35m 150m and 250m were measured to determine the changes in nest diameter and nest spacing with depth. Significant differences in diameter and spacing of nests with distance form the vegetation were analysed using analysis of variance (ANOVA).

5.4 Results

i Fecundity/Egg diameter and frequency

There is evidence of bi-modal peaks in oocyte diameters in the gonad of ripe females (stage 4) but not in those maturing (stage 3). Figure 5.1 indicates the progression of development from one peak of small (0.140 mm) perinucleoler oocytes in the maturing (stage 3) gonads to two peaks in ripe gonads. Analysis of the numbers and diameters of oocytes in ovaries in state 4 (ripe/breeding) revealed the two peaks represented oocytes with a mean diameter of 1.32 mm and 0.14 mm respectively. The number of mature oocytes varied according to body size but the average number for a fish with a total length of 24 cm (the mean fish size at stage 4) was 1200. The second peak of perinucleolar oocytes in ripe females were found to be greater in number with a mean of 1300. This can be compared to over 7000 primary oocytes found in the maturing gonads.



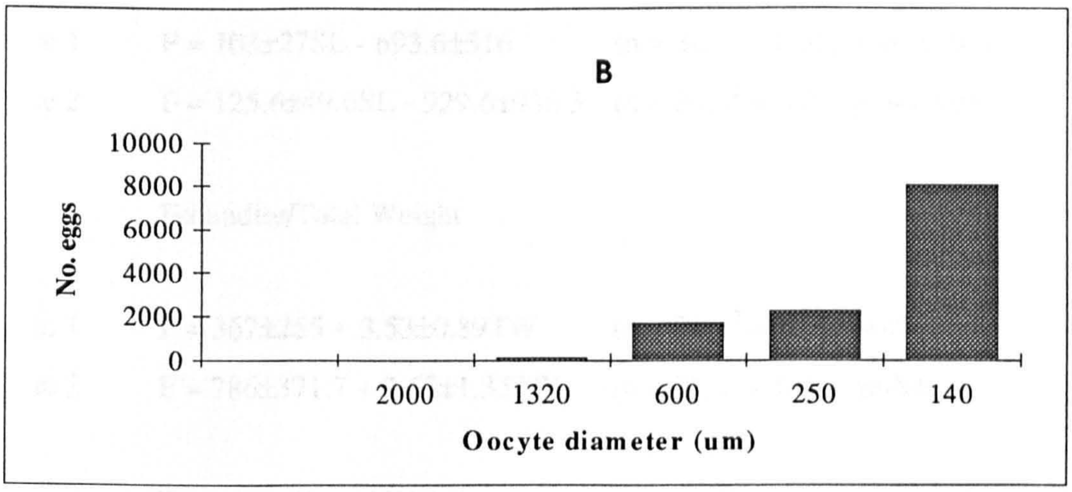


Figure 5.1 A = frequency distribution of oocytes in ripe gonads
B = frequency distribution of oocytes in maturing gonads

ii Fecundity/ Size relationships

The relationships between absolute fecundity (number of ripe eggs) and standard length (cm), somatic weight (g), and gonad weight (g) were plotted separately for Sites 1 and 2. Results are shown in figure 5.2a and b and indicate a wide scatter of points about the regression lines which were fitted by least squares. The linear relationship between fecundity and the various independent variable can be described by the equation ($F = a+bX$).

The following regression equations were calculated for each site and parameter. Although r-squared values are low there is significant correlation between fecundity and length, weight and gonad weight in site 1 (Pit Pit); in site 2 (New Magendo) only length and gonad weight were significantly related to fecundity.

Fecundity/Standard length

Site 1 $F = 103 \pm 27SL - 693.6 \pm 516$ ($n = 36, r^2 = 0.30, p =<0.001$)
Site 2 $F = 125.6 \pm 49.6SL - 929.6 \pm 956.3$ ($n = 26, r^2 = 0.21, p =<0.05$)

Fecundity/Total Weight

Site 1 $F = 367 \pm 255 + 3.53 \pm 0.89TW$ ($n = 38, r^2 = 0.30, p=<0.001$)
Site 2 $F = 786 \pm 371.7 + 2.63 \pm 1.35TW$ ($n = 25, r^2 = 0.14$, p=NS)

Fecundity/Gonad Weight

Site 1 $F = 783 \pm 166 + 118.3 \pm 31GW$ ($n = 37, r^2 = 0.27, p=<0.001$)
Site 2 $F = 775.9 \pm 210 + 131 \pm 36GW$ ($n = 24, r^2 = 0.35, p=<0.01$)

where:

F = Absolute fecundity as determined by total number of hydrated oocytes in ripe gonads.
SL=Standard length (cm)
GW = Gonad weight (g)

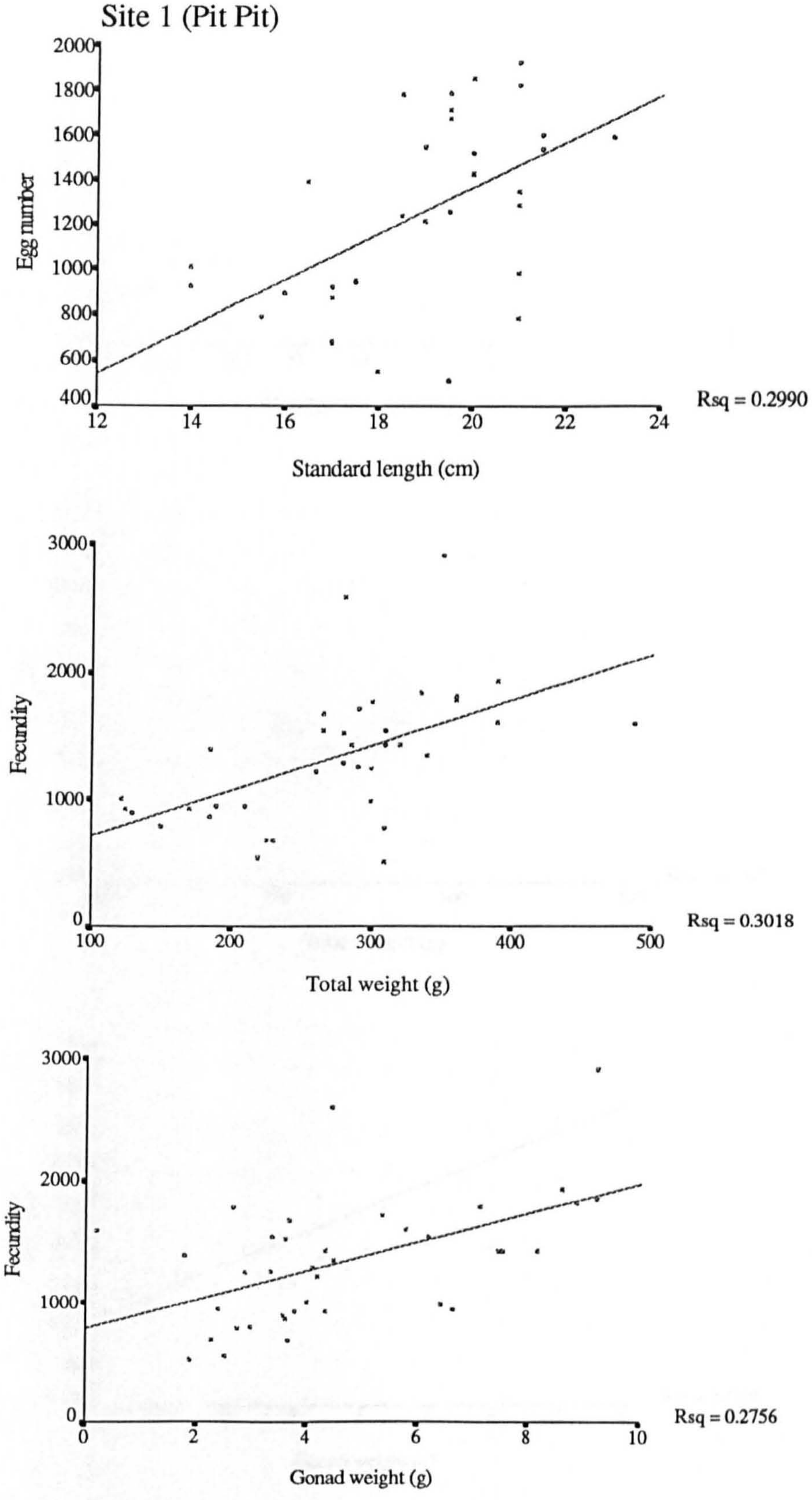


Figure 5.2a Site 1 - Relationship between fecundity and size, weight and gonad weight

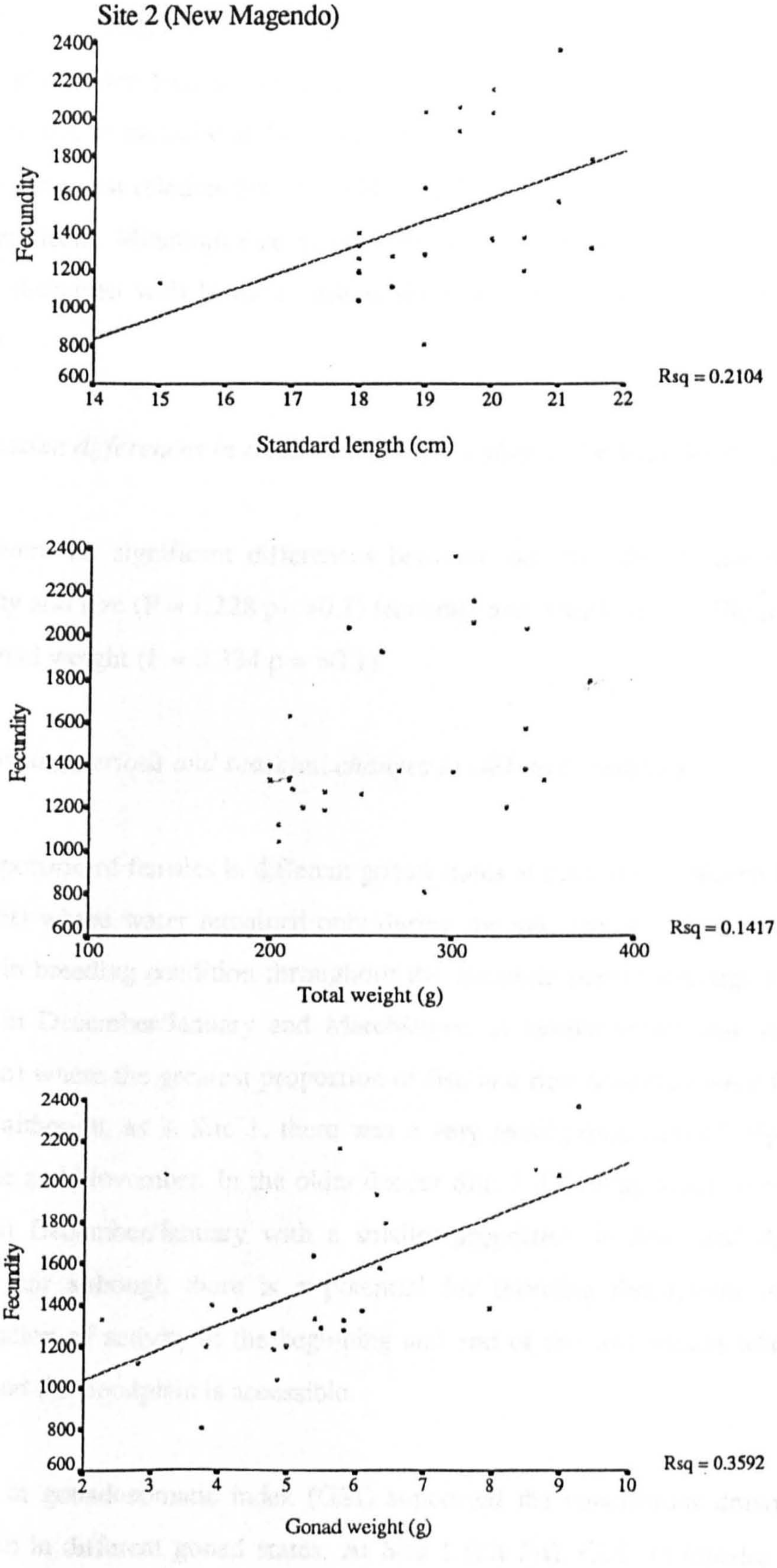


Figure 5.2b Site 2 - Relationship between fecundity and size, weight and gonad weight

Fecundity increased linearly with size and weight and gonad weight at both sites. There was a strong relationship between fecundity and length, weight and gonad size at site 1 but with a minimum size at maturity of 14.7 cm in females. At site 2 however, the relationship changed and the strongest relationship was with length, followed by gonad weight with weight being non significant. Minimum size at maturity was slightly greater at 15.5 cm. The predictive models displayed with lower r^2 values show greater variability and although valid are less reliable.

iii Location differences in relationship of fecundity to the three independent variables

There were no significant differences between the two sites in the relationship between fecundity and size (F = 1.228 p= >0.1) fecundity and weight (F = 2.786 p = 0.1) or fecundity and gonad weight (F = 0.334 p = >0.1).

iv Spawning periods and seasonal changes in GSI and condition

The proportion of females in different gonad states at each site is shown in figure 5.3. In site 1 (Pit Pit) where water remained only during the wet season it was clear that there were females in breeding condition throughout the sampling period although there was a peak of activity in December/January and March/April. A similar result was seen in site 2 (New Magendo) where the greatest proportion of fish in a ripe condition were found in March and January although, as in Site 1, there was a very small proportion of ripe females found in May/June and November. In the older deeper Site 3 (Old Magendo) most ripe females were caught in December/January with a smaller proportion in June and August. The results indicate that although there is a potential for breeding throughout the year there is a concentration of activity at the beginning and end of the wet season when water levels are highest and the floodplain is accessible.

Changes in gonadosomatic index (GSI) supported the conclusions drawn from changes in proportion in different gonad states. At Site 1 (Pit Pit), GSI in females rose to above 0.8 during three distinct periods; early December, early January and mid April (Figure 5.4). The same pattern was present for males, except for early December. In New Magendo (Site 2)

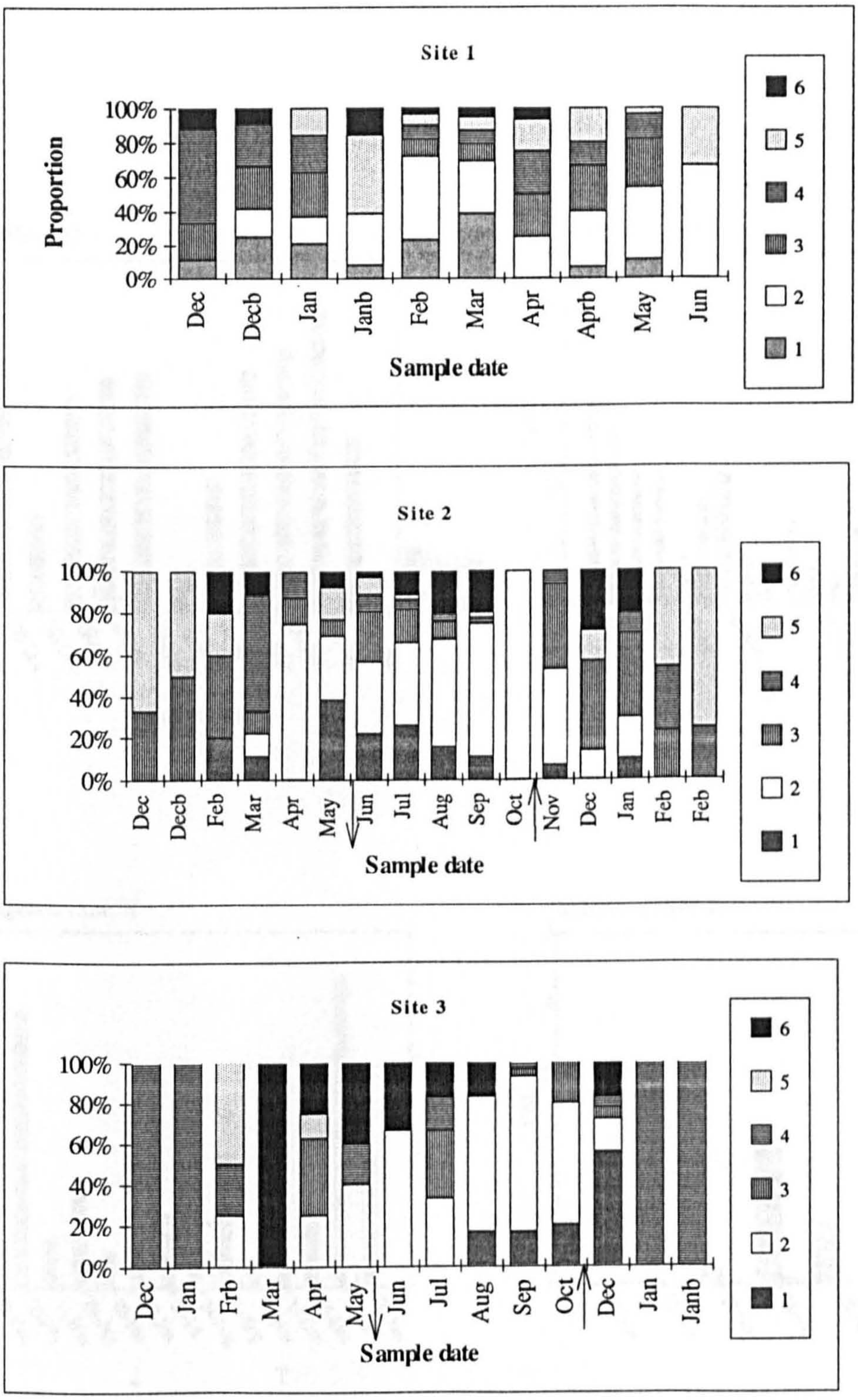
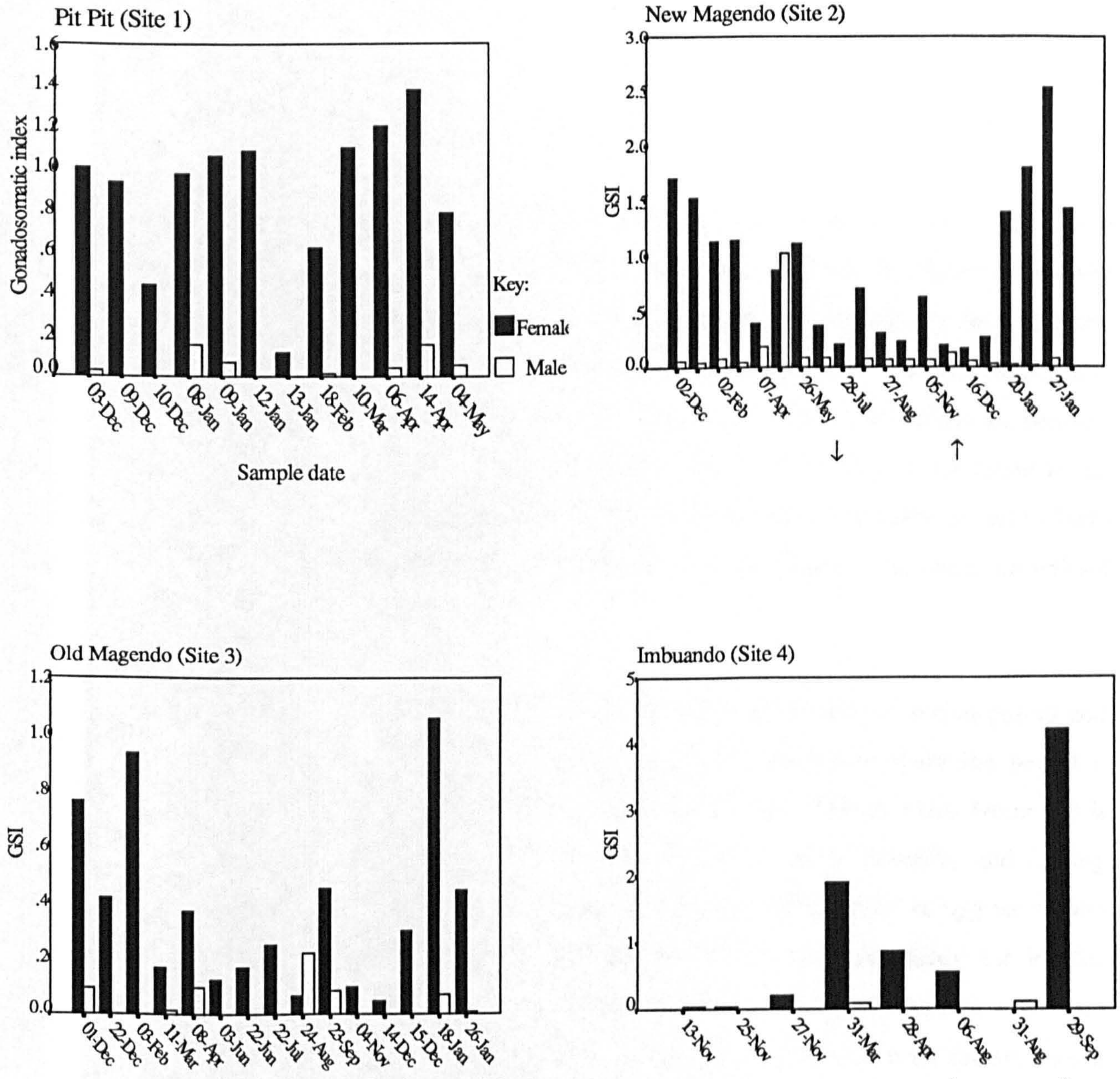


Figure 5.3 Females. Proportions of fish in various gonad states per month (arrow denotes falling and rising water periods and numbers relate to gonad state)



(↑ = rising water (wetseason))
(↓ = falling water (dry season))

Figure 5.4 Mean Gonadosomatic index - all sites which was adjacent and connected during high water to Site 1 (Pit Pit) GSI in females increased above 1.0 during December of the first year and late January of the following year. There was a small peak in early May. Male GSI at the same site showed one distinct peak in early May just before the onset of the dry period. The majority of fish at this site were caught at the onset of the dry season when the waters were receding (May-July). Spawning activity at this site during the wet season (November to May) was significantly greater for both male and female fish (Man-Whitney test $p = <0.05$ and $p = <0.001$ respectively (Table 5.1).

In the deeper oxbow lake Old Magendo (site 3) there was a rise in GSI above 1.0 in December in the first year and late January in the second year. This may be related to the later onset of the wet season in the second year as shown in the river level maxima for each year. There is also a small peak in GSI in August/September which may be related to a small rise in water level for a short period during this period. There was no significant difference between spawning activity (GSI levels) and season at this site although this may be attributed to the low numbers of fish which were caught with gonads which were noticeably present (Table 5.1). Since very few fish were found in site 4 (Imbuando) significance tests were not utilised on data from this site.

A further indication of the cessation of feeding in females during the incubation period and adding support to the idea that an increase in GSI is an indication of spawning period is shown in the variation of mean condition for females at each site. The condition factor (K) is indicative of the general condition of the fish and can be related to breeding and feeding activities. Brooding females are thought to cease feeding during the period of egg incubation and larval protection. Therefore it would be expected that the condition factor for females would be related to the breeding cycles and season but this would not be the case with male fish. Temporal changes in condition factor (KF) for females and males for each site are shown in figure 5.5. In Site 1 (Pit Pit) condition in females decreased in December, January and May just after peak GSI although the general condition remain high through the period of inundation. Male condition showed a smaller fall in mid-January and May following the peak in breeding activity although the decrease was not as marked as in females.

Significant differences between wet and dry season in both males and females at all sites is shown in Table 5.1. In New Magendo (Site 2) condition in females was significantly lower

(Mann-Whitney Test)

Site		K		GSI
	Female	Male	Female	Male
2	<0.05	ns	<0.001	<0.05
(n)	(325)	(625)	(125)	(62)
3	<0.05	<0.05	ns	ns
(n)	(90)	(131)	(40)	(12)
4	ns	ns	ns	ns
(n)	(10)	(24)	(9)	(9)

Table 5.1 Seasonal changes (wet and dry season) in GSI and Condition (figures in parenthesis relate to numbers of fish)

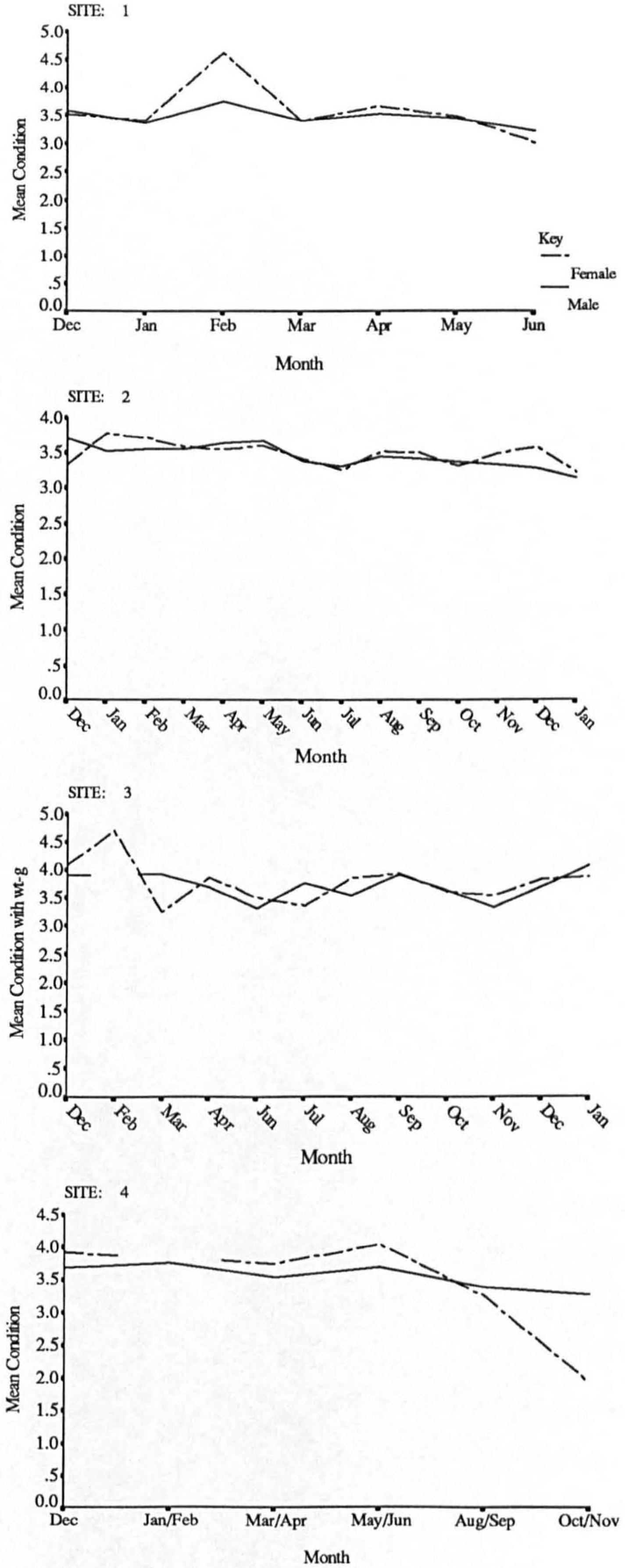


Figure 5.5 Mean monthly condition for males and females

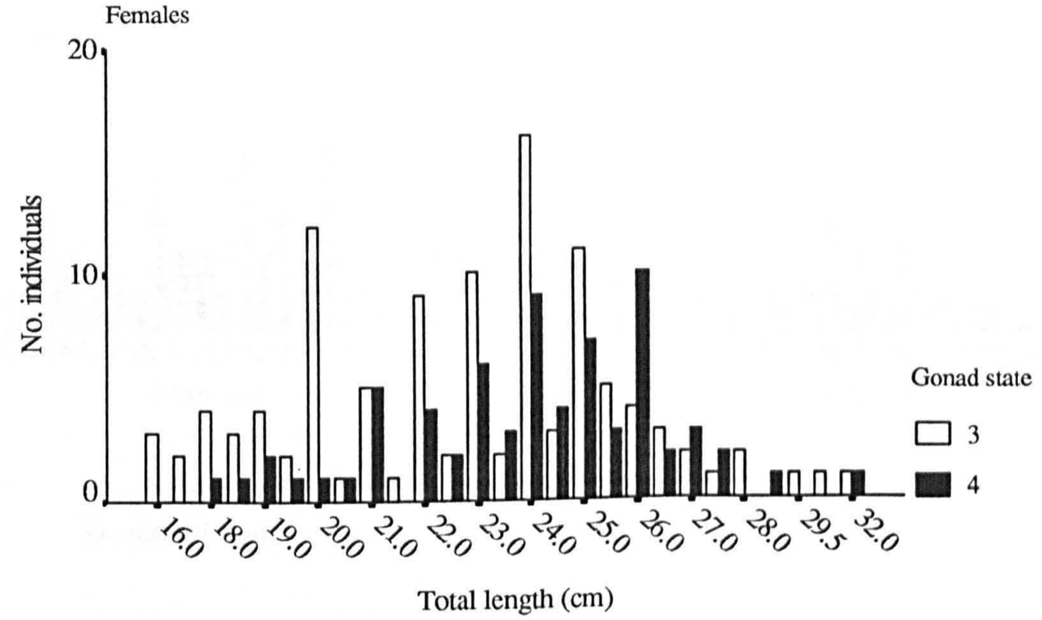
during the dry season (Man Whitney 2 tailed test $p = <0.05$), and specifically in late May and late January after peak GSI levels. Similar results were found at site 3 (Old Magendo) where there was a significant decrease in the condition of females during the dry season (Man Whitney test $p = <0.05$) and the lowest mean condition in March, June and January following a peak in GSI. Condition in male fish was significantly lower in the dry season at Site 3 only. This indicates that females were in good condition prior to breeding enabling survival during the period of non-feeding whilst brooding eggs. The general decrease in condition during May 1982 could have been due to two factors. Firstly the fall in the water levels and the reduction in food availability and secondly the influx of older juveniles feeding on the same food source. Prior to entering the fishable population juveniles may be feeding exclusively on invertebrates.

v Minimum breeding sizes, mean length at maturity

For all sites the minimum mean size of females caught in maturing (stage 3) and ripe (stage 4) breeding condition was 15-16 cm and 18 cm total length respectively. In mature males these sizes increased to 17.5-18.5 (stage 3) and 19.5-20 cm (stage 4) (Figure 5.6). The same values for Sites 1 and 2 varied slightly although the maximum sized mature fish in Site 2 (New Magendo) were larger (Figure 5.7 and Figure 5.8)

iv Sex Ratios

At all sites (especially Sites 1 and 2) there were more males caught than females (binomial test Site 1 $p < 0.001$ Site 2 $p < 0.001$ Site 3 $p < 0.05$ Site 4 $p < 0.05$). Analysis of numbers of each sex caught according to size revealed that a greater proportion of large males (29-38 cm total length) were caught at all sites (Figure 5.9) Differences in numbers of males and female in the smaller size ranges varied with site. In Site 1 (Pit Pit) and 2 (New Magendo) there were greater numbers of males in the size ranges 13-23.5 and 14-28.5 respectively and similar proportion in the lower sizes, whereas in site 3 (Old Magendo) there were a larger proportion of males between 7-17.5 cm. However there were a greater proportion of females of 24-25 cm caught at all sites which corresponds to the mean female breeding size.



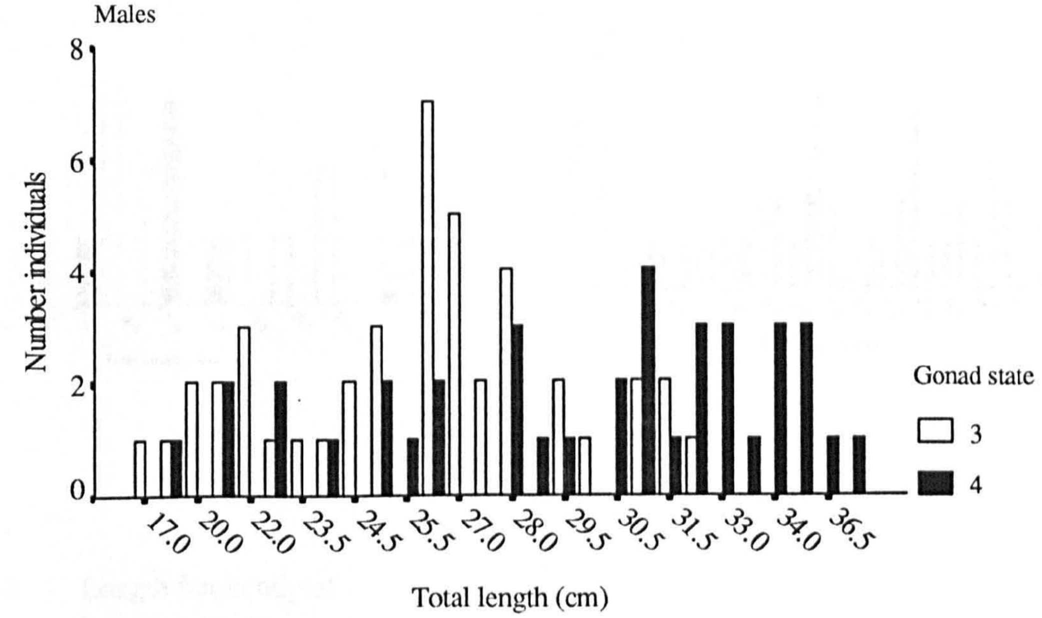


Figure 5.6 Length frequency of fish in breeding condition for all sites (male and female)

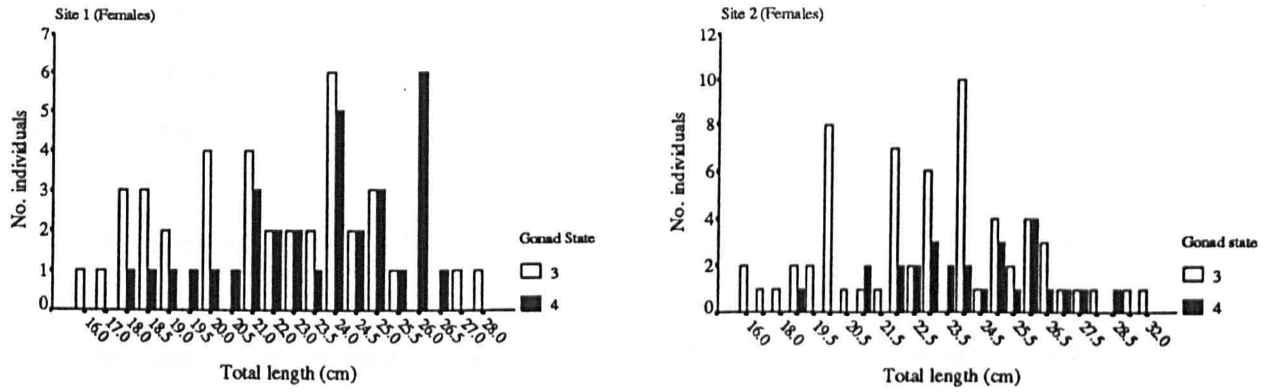


Figure 5.7 Length frequency of breeding females

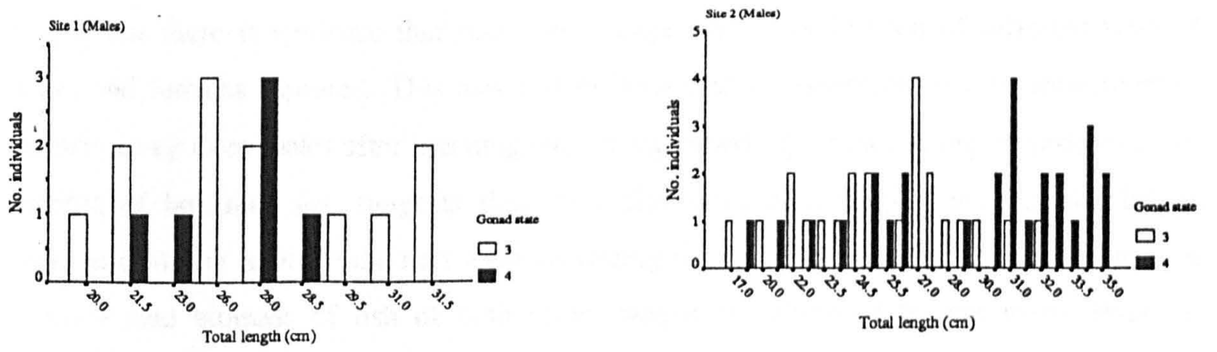


Figure 5.8 Length frequency of breeding males

Figure 5.10 displays the total numbers of males and females caught at each site during the sample period. Although the variations in total number of both male and females caught between the wet and dry season are similar at each site the data analysis indicates that more males were caught in every sample and not just at specific times of the year. Generally there were more fish of both sexes caught around the breeding period of January to April at Site 1, whereas at Site 2 and 3 an increase in numbers occurred as the water levels were falling and when both sexes were more prone to capture due to the decrease in floodplain area.

In the two sites which were adjacent and connected (Sites 1 and 2) there is evidence of an influx of both males and females from Site 1 to Site 2 as the water levels fall, but not from the other sites due to the distances involved. Figure 5.11 indicates the changes in mean size of males and females over the sampling period and shows that larger fish are caught during the breeding period at Sites 1 to 3. As water levels fall the mean size of fish caught decreases which suggests that the older fish move into deeper water during the dry season leaving the smaller fish and juveniles, which have reached the minimum capture size, to occupy the shallower marginal areas where the fleet of gill nets were set.

This suggests that there is little seasonal influence on the proportion of males to females caught but there is evidence that there are changes in the proportion of different sizes of males and females captured. This may reflect behavioural differences such as movement of females away from males after breeding and during brooding period. A higher proportion of females of breeding size suggests that these fish were congregating near to the littoral vegetation which is where the nets were set during the breeding periods. The change in total numbers and biomass of fish of both sexes caught is influenced by the water levels as indicated above.

vi Nest Areas

Figure 5.11 indicates the changes of nest diameter and distance to the nearest neighbour with distance from the marginal vegetation. A significant increase in both parameters occurred with distance (ANOVA $p= <0.05$). The change in mean of nest sizes with depth are illustrated in figure 5.12. Close to the marginal vegetation there was a range of sizes from 70-105 cm

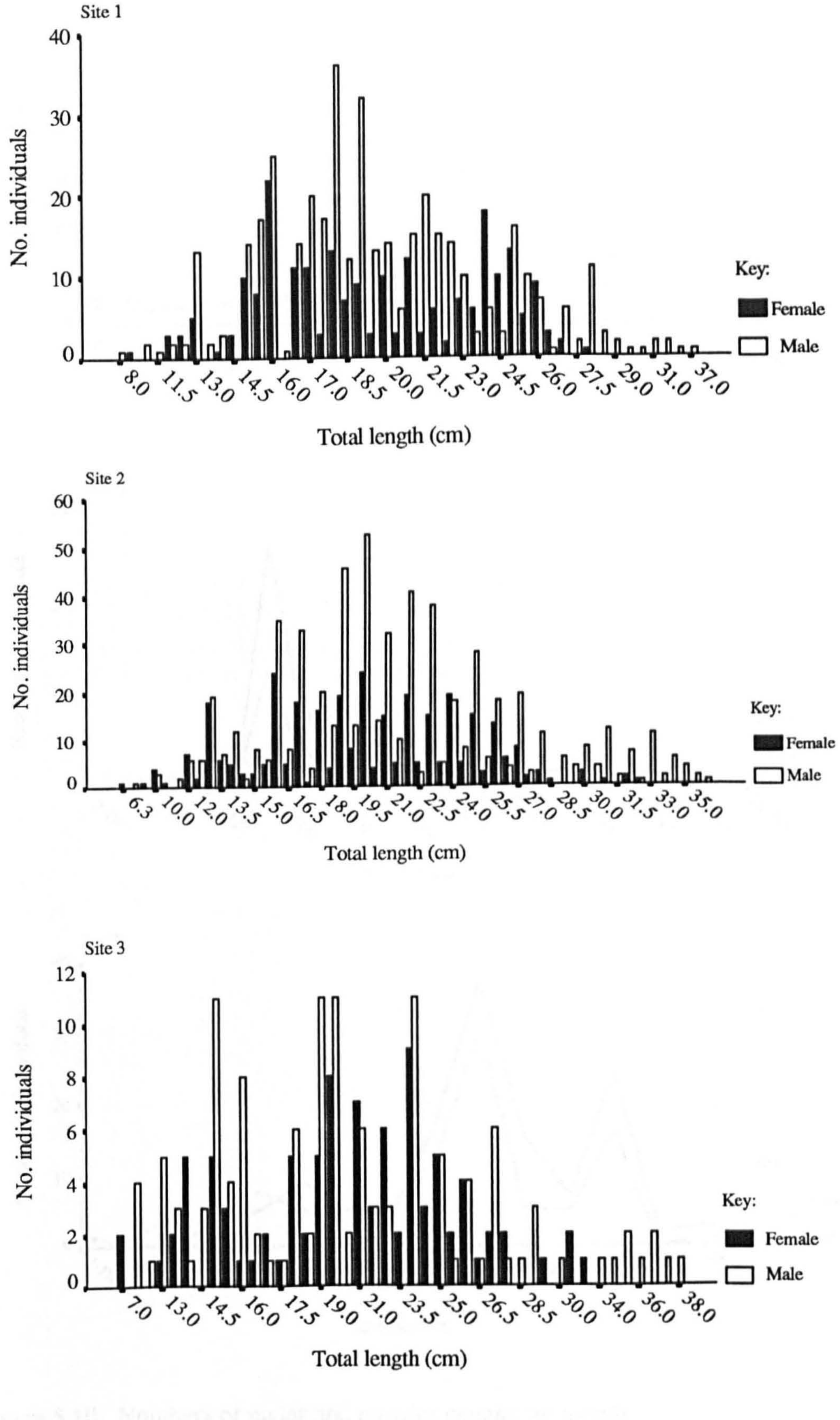


Figure 5.9 Ratio of males and females in different length classes for sites 1-3

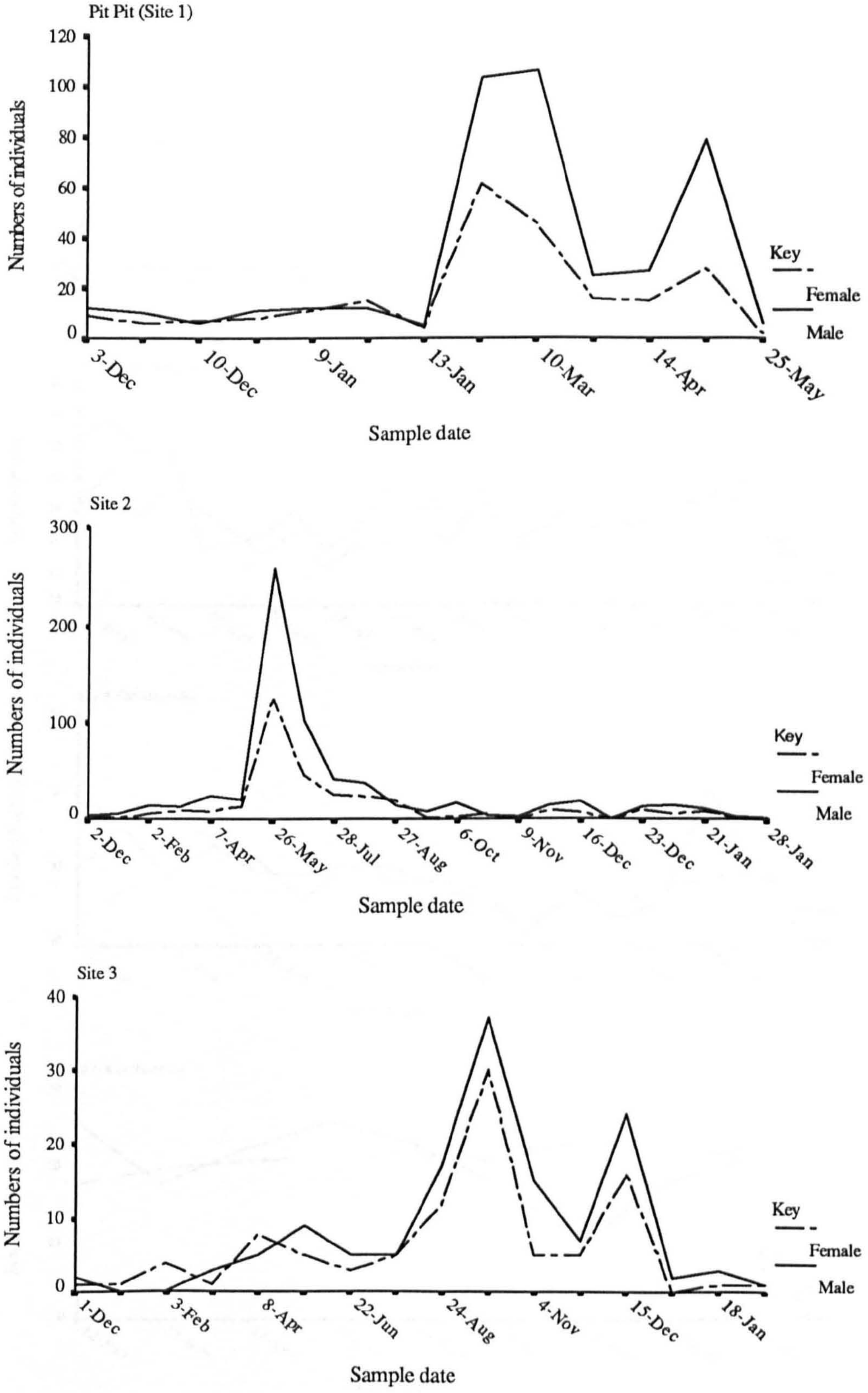


Figure 5.10 Numbers of males and females caught per month

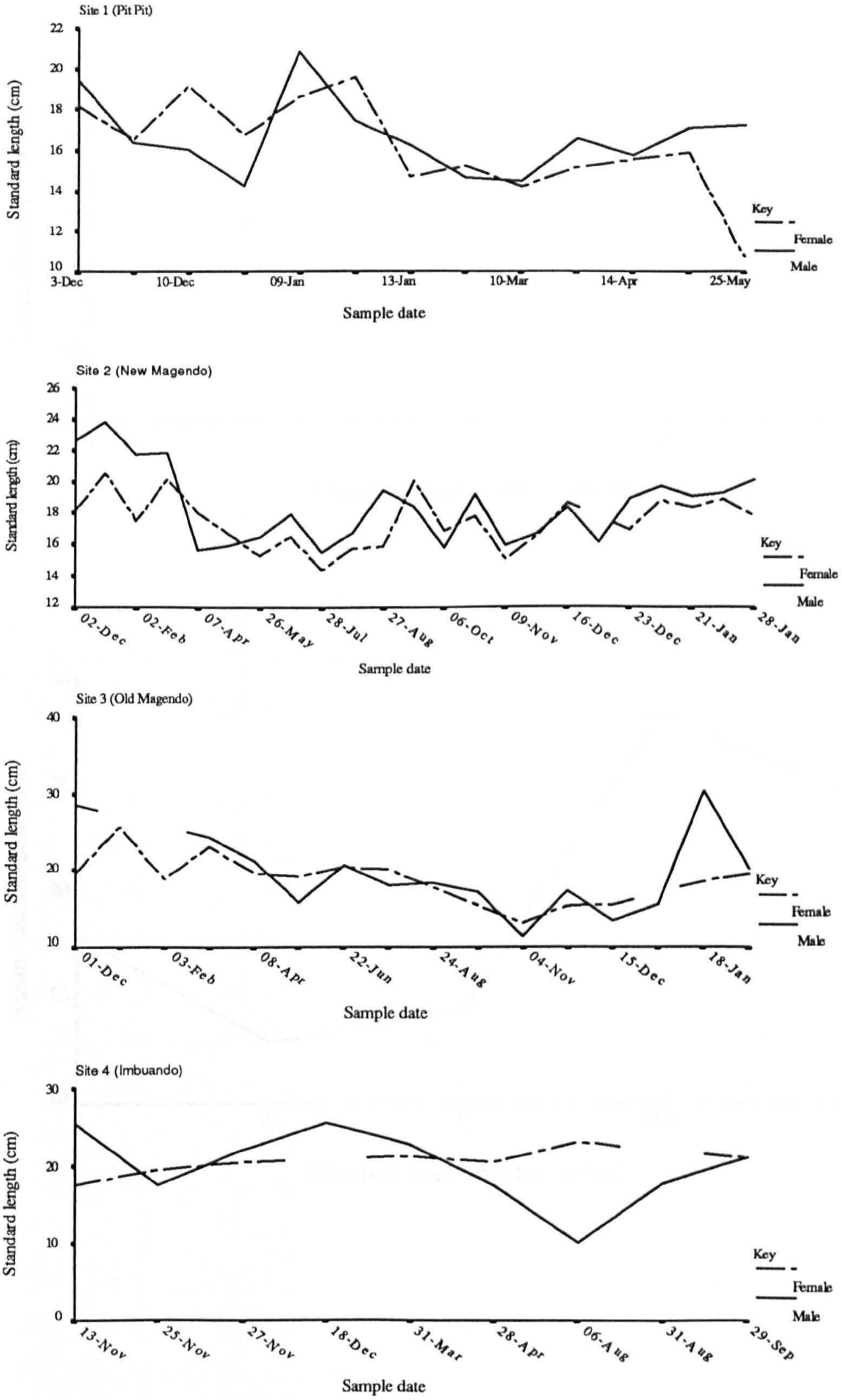
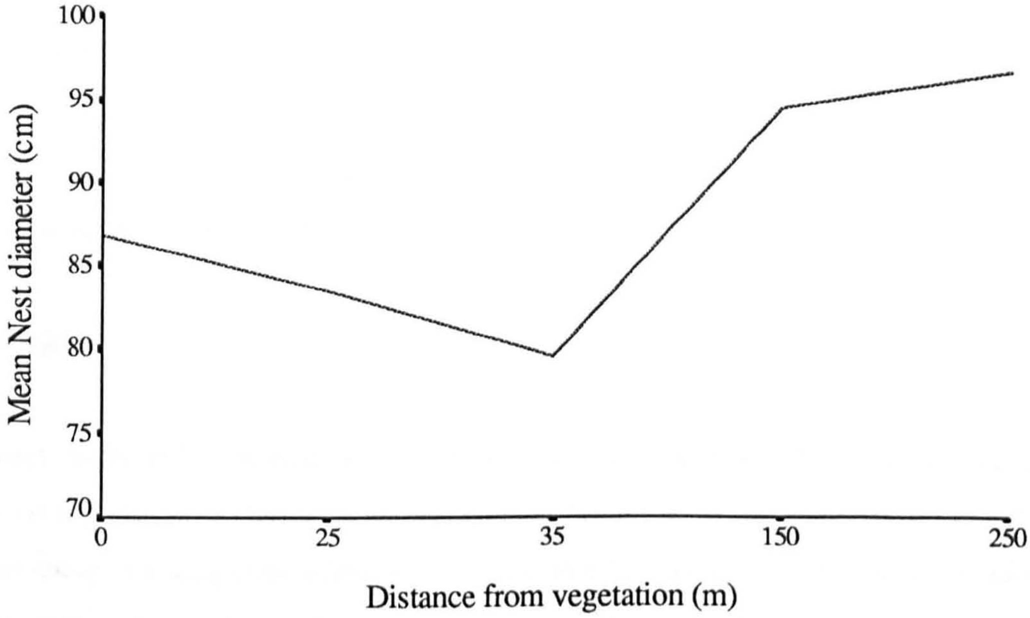


Figure 5.11 Mean length of male and females caught per month



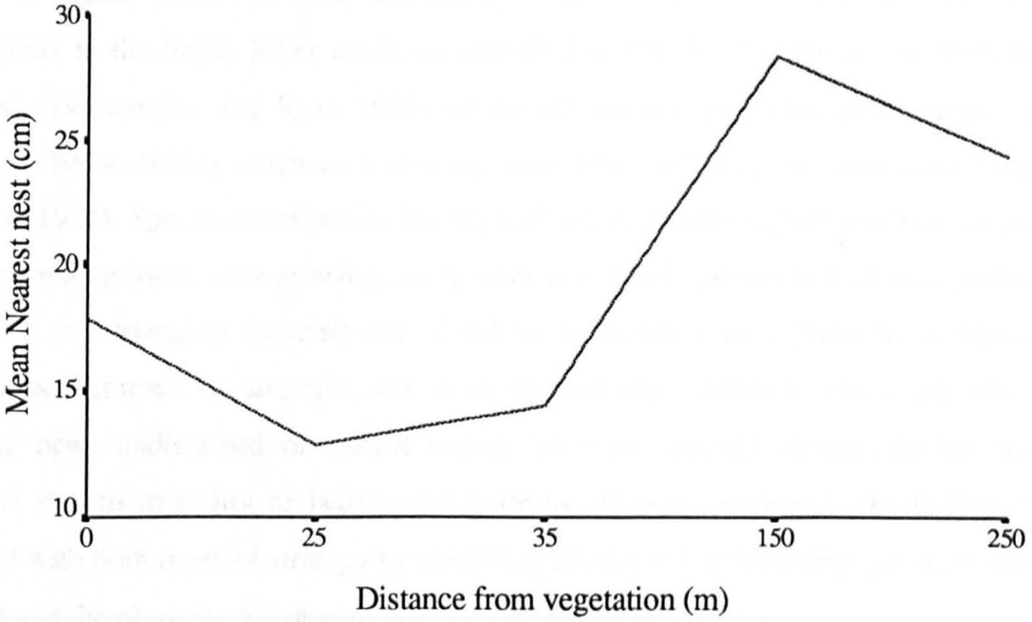


Figure 5.12 Changes in nest diameter and distance from nearest nest with distance from marginal vegetation

with a mean diameter of 86.8 cm. The distance to the nearest nest remained relatively unchanged at 12-17 cm. The change in diameter did not increase significantly until the nests were further than 35 metres from the margins. However the range in diameter increased beyond 35 meters as indicated by the changes in standard deviation. From a distance of 150 metres the mean nest diameter increased to approximately 96 cm.

5.5 Discussion

The present study indicates that environmental conditions in the Sepik have a substantial influence on the spawning strategies and general life history traits displayed by the introduced *O. mossambicus*. In temperate climates environmental factors such as temperature and day length are important stimulants of gonad development (Bye 1984, Potter *et al.* 1994) whereas in tropical areas both temperature and seasonal changes are minimal. Thus the environmental parameters influencing gonad development will relate to site specific variables, such as changes in water levels or food availability. The life history traits exhibited by *O. mossambicus* in the Sepik River could be classified within those described as 'equilibrium strategies' (Winemiller and Rose 1992) or the atricial and precocial styles described by Noakes and Balon (1982) which are sometimes associated with the r- K-continuum described by Pianka (1970). Species described as having evolved K-strategies (precocial) of adaptation are generally long lived, slow growing, iteroparous with few large ova and a low reproductive effort. The 'r' strategists (atricial) are found to be adapted to environments which are classified as disturbed or stressful and often display characteristics which are suited to colonising new 'undisturbed or vacant niches' or those already vacated by the natural population due to mortality or behavioural patterns. Thus *O. mossambicus* displays traits associated with both types of strategy by exhibiting relatively low fecundity, yet with multiple spawning and the plasticity to colonise new habitats relatively rapidly.

The results found during the survey suggest that the general habits of *O. mossambicus* in the Sepik are similar to those of populations in other tropical areas, whether introduced (Reidel 1965, Hodgkiss and Man 1977, 1978, Man and Hodgkiss 1977a, 1977b, De Silva and Chandrasoma 1980) or naturally occurring (Bruton and Boltt 1975, Bowen 1979, Bruton 1979). Breeding occurs throughout the year with distinct peaks in spawning activity during the wet season. This breeding pattern is similar to the patterns noted in other areas (Lowe-McConnell 1975, Welcomme 1970, De Silva and Chandrasoma 1980, Arthington and Milton 1986, McKaye 1984) (table 5.2). Fish movements, condition, and breeding do have a distinct pattern which reflect the cyclical nature of the flood regime in the Sepik. However there is not a precise distinction between wet and dry seasons as in a monsoon climate; during both high and low water periods there are perturbations in the water levels.

The spawning pattern demonstrated by changes in GSI and proportion of fish in various reproductive states can be classed as bimodal with two seasonal peaks. The initial period of spawning takes place just after the start of the rainy season as water levels are rising and again just prior to the commencement of falling water levels. The gonadosomatic index showed much smaller peaks in August and November which is the period of low water and presumably when less food is available. Evidence for two peak spawning periods is supported by the presence of a bimodal and synchronous development of oocytes in maturing and ripe females. The evolution of synchronous multiple spawning patterns (heterochronous spawning) with determinate development of oocytes (McEvoy and McEvoy 1992) conveys the advantages of increased fecundity in a species where the absolute fecundity (batch size) is relatively small compared to species of fish which do not exhibit any form of parental care.

Oreochromis mossambicus has a mean fecundity per 100 g of female body weight of 475 mature hydrated oocytes compared to species such as cyprinids with 10,000. *O. mossambicus* also breed at a relatively small size and the size of the body cavity will act as a constraint to fecundity (Paine 1990). Having the ability to spawn several times removes the constraint of body size to some extent as does the evidence that the gonads may occupy a larger proportion of body weight in smaller fish. However, there is a balance to achieve between producing the maximum numbers of ova per batch as well as providing space for developing pre-vitellogenic oocytes. This is achieved in *O. mossambicus* by the production of both larger oocytes which hydrate just prior to spawning and microscopic primary oocytes in the gonad. To achieve maximum fecundity the primary oocytes must develop rapidly to be ready for the next spawning period. Oocyte size is large by comparison with highly fecund species, which is consistent with a general tendency for oocyte size to increase in relation to the increase in parental care (Safe harbour Hypothesis-Shine 1978). The consequent loss of fecundity is then

Life History trait	**Sepik River Papua New Guinea**	**Tingalpa Reservoir Australia**	**North Pine Dam Australia**	**Plover Cove Hong Kong**	**Pakrama Samudra Sri Lanka**	**Lake Sibaya South Africa**
Author		1	1	2	3	4
Minimum breeding size - females (TL)(mm)	**160**	180	174	162	150	68
Maximum breeding size females (mm TL)	**320**	267	240	250	319	220
Min/Max females	**0.50**	0.67	0.73	0.65	0.47	0.31
Minimum breeding size males (mm TL)	**200**	152	191	178	200	104
Max breeding size - males (mm TL)	**370**	297	260	250	340	290
Min/Max. - males	**0.54**	0.51	0.73	0.71	0.59	0.36
Age at maturity (months)	12-18	12-15	12-15	12	-	12-24
Fecundity (per 100g) female	**475**	438	490	626	552	-
Mean oocyte diameter mature females (mm)	**1.1-2.0**	1.7-2.6	-	2.0	1.2-3.6	-
Life Span (Years)	≈4-5	4	3	4	-	7-8

(adapted from Arthington and Milton 1986)

Authors

1 - Arthington and Milton (1986)
2 - Hodgkiss and Man (1977-78)
3 - DeSilva and Chandrasoma (1980)
4 - Bruton and Allanson (1974) Bruton and Boltt (1975)

Table 5.2 Life history traits of *O. mossambicus* from the Sepik, Australia, Sri Lanka, Hong Kong and South Africa offset by increased survival rate of the young. The costs of the evolution of parental care are discussed elsewhere (Keenleyside 1991, Stearns 1992, Smith and Wootton 1995a,b,). The maternal nutritional status, which can be related to condition is an important factor in influencing the rates of atresia (Kjesbu *et al* 1991), and the amount of investment in reproduction which could affect the growth and survival patterns of larval fish in the first growing season (Sparholt 1985, Smith and Wootton 1995a). Spawning after the rise in water levels will allow female fish in the Sepik to feed on the increased food available on the floodplain in order to build up fat reserves which will maintain nutritional status throughout the first spawning period and during mouthbrooding. The break between peak spawning times in the Sepik which is also at a time when the water levels and food availability are still high. will allow for greater investment per offspring.

The timing of spawning periods in many fish species has evolved to enable the greatest chance of survival for the offspring (Cushing 1990). There is a good correlation between spatial and temporal peaks in the availability of food and there is also evidence that the time of reproduction is influenced by the period in which the optimum environment is present for fish at the end of the first growth period (Munro *et al.* 1990). This has been further developed as the match-mismatch theory of Cushing (1990).

In the Sepik *O. mossambicus* begin the breeding cycle at the beginning of the rains which ensures a plentiful supply of food for the newly emerged fry after approximately 2 weeks. However from evidence of GSI and oocyte development the second spawning period occurs as the water level is falling and the variety of food available is not as diverse. This may be a strategy not related so much to food availability but more to increasing the production of offspring over the year since the number of young produced per female per spawning period is relatively low. Food quality and quantity for the emerging larval fish, although important, may not be controlling the periods of spawning . Other environmental or physical parameters may be limiting spawning success. If nesting sites, for example, were at a premium then to gain the greatest utilisation of such sites the strategy would be to use them more than once whilst water levels were sufficiently high to create the optimum water depth over the sandy substratum. Since water levels are only high during five to six months and time is required for fish to recondition between spawning periods then the maximum number of breeding periods in the correct environmental conditions is approximately two. This can be calculated from data on brooding and reconditioning periods documented from other studies and is supported by the findings of this study.

Bruton and Boltt (1975) found that the total incubation period for *O. mossambicus* was 36 days (22 days for incubation and 14 days between broods). Eggs are usually incubated for 3 to 5 days before hatching and the fry are released from the buccal cavity after approximately 10-14 days (Vaas and Hofstede 1952, Russock and Schein 1977, Trewavas 1983). For 20-22 days the fry will remain in or near the vicinity of the females mouth before entering the floodplain vegetation at a mean size of 9 mm SL. At this time there is still sufficient water on the floodplain to create a refuge in the marginal vegetation as well as a food supply for the fry. The fry will remain in or around the shallower areas until old enough to enter the fishery. (Fishery being the age of first capture in smallest gillnet). Therefore fish breeding during December to January will be able to spawn again in March to April. This is the approximate period between spawning times seen in the Sepik although there is a longer period than 36 days between broods.

De Silva and Fernando (1980) reported that juvenile *O. mossambicus* enter the fishery at a total length of 180 mm correlating to the third year of life, and Krupka (1974) estimated that a sub-species of *O. mossambicus* in Lake Kariba entered the fishery in the third year of life at a minimum size of 125 mm. In the Sepik the age at first capture is discussed in the following chapters but it is thought that during the dry season the juveniles less than 100 mm are actually in the deeper waters but are simply too small to be caught in the smallest mesh nets. Hand netting in the littoral areas during the period of draw-down did yield a small number of juveniles less than 100 mm SL. Brooding females were seldom caught since there is a tendency for the females to eject fry or eggs from the mouth when caught. The only times fry were found in the mouth of the female, they ranged in size between 7-11 mm. Evidence that the smaller fish (>10 cm) remain in the marginal and sometimes shallower areas and may only move out into slightly deeper water to feed is shown in mean sizes of fish caught in marginally set gillnets as the water levels fall. This supports findings made by Bowen and Allanson (1982) in Lake Sibaya where juveniles (2.5-10.0 cm Total Length) remained in littoral protected habitats unless feeding, when there was a movement into deeper waters.

In this study the minimum size at maturity for females was 150 -160 mm whereas for males this was 180 - 200 mm. This corresponds to fish aged 1+ to 2 years (Chapter 6). There is therefore a distinct sexual dimorphism with the males of the same age being larger than the females, which is consistent with other studies (Hodgkiss and Man 1978). In Lake Sibaya, South Africa the minimum size at sexual maturity in females is 68 mm and in males 104 mm (Bruton and Allanson 1975). This may be an adaptive response to a situation where the nutritional quality of food is inadequate (Bowen 1981). Studies in ponds have found that excessive feeding rates resulted in reduced growth rates of *O. mossambicus* (Java strain) (Shell 1978).

Stunted populations as a result of prolific breeding can occur in environments that are either food-rich or food-poor where mortality rates are low or high but generally unstable. This type of adaptive evolution of reproductive strategies is in response to either a harsh or unstable environment (Payne and Collinson 1983) and can be generally related to species with a tendency towards the 'r' strategist. In comparison to fish in Lake Sibaya *O. mossambicus* in the Sepik has a larger minimum and maximum breeding size in both males and females and there was no evidence of the development of either stunting or prolific breeding.

In the Sepik reproductive success for *O. mossambicus* will relate to the provision of suitable nest sites. Without such areas there will be a considerable limitation on the levels of recruitment to the fishery. In the Sepik nesting tends to be in specific areas where the water is shallow and the substrate is of fine mud. These sites are usually in areas of more permanent water and close to littoral vegetation. Bruton and Boltt (1975) found that 95% of nests in Lake Sibaya, South Africa were in association with plants, especially *Scirpus littoralis* and *Potamogeton pectinatus*. The floodplain itself is not a common nesting area because of the abundance of vegetation and periodic drying out during minor fluctuations of the high water levels.

Nest sites were only found in shallow areas where slower flows had deposited fine mud and silt onto the substrata. During the study only two such sites were found in the lower Sepik. Nests found in these areas were not uniform in size in contrast to the findings of De Silva and

Sirisena (1988) in Sri Lankan reservoirs. In the Sepik nests were found in water of 0.8-1.5 m depth at mean peak flood and were on average 1.0 m in diameter. Smaller nests were found closer to the marginal vegetation and on the periphery of the area suggesting that the larger, more dominant males were holding the more favourable sites since male size has been positively correlated to nest size (De Silva and Sirisena 1988). As the water depth increased the distance between nests increased, which may be related to increased territory size with the larger males. The nesting sites were assessed from a boat when the area was exposed as the water level decreased. It is not known to what depth the nests extended but a logical conclusion is that males built nests that would not dry out until after spawning and that were close to the main floodplain.

A more recent aerial survey (Welcomme pers. comm.) indicated that nesting sites were more abundant than originally thought but may still be a constraint to the reproductive levels. In addition the river is constantly changing course and either permanently exposing potential sites and creating others in different areas. Since this study the river has changed course significantly and the original nesting area studied no longer exists. Consequently there may be years when sites are abundant and other times when there is serious competition for sites. If *O. mossambicus* habitually return to the same area to spawn each year the changing river pattern would upset the breeding cycle. This would have to be studied in more detail before any conclusions could be drawn.

Chapter 6 PRODUCTION, GROWTH AND POPULATION DYNAMICS

6.1 Introduction

An assessment of growth, age structure and mortality in a fish population is an important aspect in the determination of present life histories, stock composition, longevity, age at recruitment to the fishery and in the prediction of present and future production. Rational and sustainable exploitation of fish resources cannot occur without a sound knowledge of the population dynamics of the species.

The analysis of length frequency distributions (the Petersen Method) is a general method of assessing the age structure of a population providing there is a distinct size range of fish of the same age (De Bont 1967, Ricker 1971). This method cannot be utilised in determining age and growth of individual fish but gives a general assessment of the growth and strength of individual year classes. Hard structures such as scales, otoliths, vertebrae and operculi, which are thought to grow in proportion to somatic growth are also used in determining age and growth of individual fish (Pannella 1971, Grant 1992, Secor *et al* 1995). The most frequently used method of determining age is by counting the marks or checks which have been formed in hard structures in relation to a change in the growth of the fish (see e.g. Weatherley 1972, Bagenal 1974, Weatherley and Gill 1987, Summerfelt and Hall 1987, Paul 1992). There are several assumptions associated with the use of growth checks for assessing age and growth data. These include the knowledge that the growth checks are made at the same time each year and are made in response to the same stimuli, that there are optimal conditions for growth and that growth of the hard structure is in proportion to somatic growth.

There is still, however, discussion over the validity of the various methodologies used especially as it is now thought that the relationship between hard structures such as otoliths and body growth may not be a simple one (Wright *et al.,* 1990, Zivkov 1996). Underestimates of the true age, particularly in older fish, has been a common error when using annual rings on scales and otoliths to determine age (Beamish and McFarlane 1987, Casselman 1987, 1990). Some species have been found not to form scale annuli each year (O'Gorman *et al* 1987) or daily growth increments in larval fish otoliths (Geffen 1982, Geffen and Nash 1995). Thus ageing fish using one method only risks underestimating the true age structure of the population. Previous studies which have attempted to verify age using annual scale rings have found that scale readings have shown fish to be younger than the age determined from the number of otolith bands present and has been found to be especially prevalent in ageing larger, older fish (O'Gorman *et al* 1987). This discrepancy varies with the degree of exploitation of the stock, with heavily fished stocks showing less discrepancy since larger older fish are less likely to be present. Age underestimation may have serious consequences for stock assessment and management programmes and may lead to over exploitation (Summerfelt 1987).

Daily growth rings in otoliths have been used to determine age of fish (Pannella 1971), although there are still inherent problems with this method especially in the determination of true daily rings and the time period in which rings begin formation (Campana and Neilson 1985). Otoliths are composed of calcium carbonate crystals which are deposited in layers and continue to grow over the lifetime of the fish. As the fish grows rapidly calcium is deposited to form opaque layers in which daily growth rings appear widely spaced. During period of slower growth less calcium is present and the hyaline (protein) or translucent zone is apparent (Fagade 1974). Little of the calcium however is from a dietary source, the main origin is from the surrounding water via the gills (Fenton and Short 1992). This is reflected in studies which have indicated that otolith growth continues when fish are starved or have a poor quality diet (Tzeng and Yu 1992, Bradford and Geen 1992).

Otolith growth may not follow all body growth fluctuations and may be influenced to a greater extent by temperature which affects metabolic rate and oxygen consumption, and internal circadian rhythms (Mosegaard *et al.* 1988, Wright 1991) and photoperiod (Campana and Neilson 1985, Tzeng and Yu 1992). Other studies have shown that daily and sub-daily rings may occur each day from the day of hatch (Wright and Huntingford 1993) or may not form at all (Neilson and Geen 1982). The use of incremental width in otoliths may therefore be an unreliable ageing method unless verification by an alternative assessment method is used.

The use of annual scale markings in determining the age and growth of fish is well documented (Bagenal 1974, Summerfelt and Hall 1987). Teleost scales are commonly either cycloid or ctenoid and are classified on the basis of the structure of the surface (Simkiss 1974). Ctenoid scales have rows of small projections or ctenii in the posterior field. Scales are composed of two layers, the superficial or hyalodentine calcified or mineralised layer with a lamellar sheet below (Simkiss 1974). Growth occurs at the edge of the hyalodentine layer, thus scales increase in radius but not in depth. Each deposit is in the form of a calcified ring which form the circuli used in the determination of growth. During faster periods of growth the circuli are widely spaced and as growth slows, due to various influences, the circuli become tightly packed (Barber and Walker 1988). At this point a scale ring or growth check can be seen. These can be easily determined in some fish and are produced in temperate species in response to changing seasonal temperature and associated changes in endogenous rhythms and food supply. Growth of the scales is associated with calcium metabolism in the fish and a reversal of the process of calcium deposition has been seen in trout (the Crichton Effect) (Crichton 1935 **in** Simkiss 1974) and may be associated with periods of calcium deficiency (Garrod and Newell 1958). A linear association between scale radius and growth has been found in some species which enables the reconstruction of growth patterns over time although these calculations must be verified or validated using other methods such as the analysis of length frequency patterns or tank experiments (Wootton 1990)

Studies on the age and growth of tropical fish have been limited since there are numerous known influences on the growth of fish in tropical environments. These habitats lack the distinct seasonal changes in environmental parameters such as temperature and photoperiod, which are found in temperate regions (Pannella 1971, Brothers 1981, 1983, Dong Chun Lou 1992). Annual growth changes could be influenced by a variety of factors other than temperature. Many tropical floodplain rivers undergo seasonal flood cycles which inundate large areas of land (Welcomme 1985, Bayley 1988, Junk *et al.,* 1989, Lowe-McConnell 1987). Lateral water movements which form the floodplain will have an effect on abiotic conditions and the functioning of biological systems. These effects are seen in the movement of fish populations, changes in catch rates and spawning behaviour (Bayley and Li 1992). During the period of inundation food availability changes as the flood covers large areas of vegetation with associated changes in allochthonous and autochthonous production input.

Therefore growth patterns in tropical fish species may be influenced by a variety of factors associated with the cyclical pattern of flooding in such systems.

The age structure and growth of cohorts in a population can be determined by the analysis of length frequency data by eye or through the use of computerised packages such as Electronic Length Frequency Analysis (ELEFAN) (MacDonald and Pitcher 1979, Pauly and Morgan 1987). Growth models can then be constructed as an aid to predicting growth for management purposes. Such models have the basic premise that growth at a specified time is a function of the fish size at the same time. Various growth models which describe the general form of the growth curve have been developed using the specific growth rate (g) as a function of weight (W). These include the Gompertz, Logistic and Richards Models where g is a linear function of W, $\log_e W$ and W^n respectively (Moreau 1987, Wootton 1990). The most commonly used model of fish growth is the von Bertalanffy Growth Function (VBGF) which establishes mean weight or length at time (age) assuming growth is constant without variation due to spawning or environmental change. Using data on numbers of fish at age (catch curves) so derived, the mortality rate (Z) can also be determined (Paul 1992).

6.2 Methods

As there may be errors associated with the use of only scale or otolith readings (see section 6.1) this study used two indirect methods of data assessment to determine age and growth. These included scale readings, and the analysis of length frequency data. This allowed verification of the methods used, but validation was not possible in the conditions present at the time, although it was attempted. All specimens of *O. mossambicus* caught in each net were measured for total and standard length and weighed to two decimal places (see Chapter 3). A sample of 5-15 fish from each size of net was used in scale determinations of age. Six adjacent scales from each fish were removed from above the lateral line and starting in line with the beginning of the dorsal fin, these key scales were used for all age determinations. Scales were initially stored in a solution of 1% ethyl alcohol and glycerol. Prior to examination scales were removed dried and placed between two microscope slides.

Scales were viewed with transmitted light under a stereo microscope which was connected to a video recorder and a computer. Total scale radius (distance from the focus to the nearest point on the anterior margin) and distance of the focus to each scale mark was measured along the same axis using an image analysis system (NIH Imager). Scale marks were identified by a change in the distance between bands or a gap in the banding pattern. A proportion of scales (10%) were read independently by two other experienced research staff at Port Erin Marine Sciences Laboratory (Dr A Geffen, Mr D Hornby) to ensure an accurate reading was being taken. Instruction on the techniques involved in image enhancement with computer analysis and scale reading were given by Dr A Geffen.

6.2.1 Data Analysis

i Length Weight Relationships

The relationship between length and weight is an indication of changes in body proportions (and growth rate) in relation to environmental changes and maturity. The length weight relationship in fish from different sites was established using log/log regression analysis (least squares). Spatial (site) influences on the relationship between length and weight was determined by analysis of co-variance (ANCOVA) (Sokal and Rohlf 1981). Significant differences between slope and/or elevation of lines of regression would suggest that an average or 'standard relationship' (Ricker 1971) could not be made for fish from all sites. If spatial differences were found to be significant, age and growth studies would need to be site specific. This analysis was therefore carried out prior to the commencement of any ageing or growth studies.

ii Scale radius: length relationship

The relationship between scale radius and length (standard and total) was determined through regression analysis (least squares method). To use scales in the accurate determination of age and growth there is an underlying assumption that there is a linear or proportional relationship between somatic growth and the increase in the distance from the focus to the edge of the scale. Once such a relationship is established changes in growth of the fish with time will be reflected in changes in scale size.

iii Length at age

For the purposes of data analysis, the number of rings were used to denote a length at age (L(age)) group from L1 (one ring) to L8 (eight rings). The terminology describes the change in length with time. As rings may have been formed annually or biannually or with greater periodicity this time period may not be one year. Mean length of fish in each group (L1-L8) was calculated for all fish in the sample. To compare the accuracy of evaluating number of rings per scale back calculations of lengths at which rings were formed were determined using a modified version of the direct proportionality formula (Fraser-Lee model) (Ricker 1971):

$$l_n - a = S_n/S(l - a)$$

where:

l_n = length of fish when ring (n) was formed

l = length of the fish at the time of capture

S_n = distance from focus to ring (n)

S = total scale radius

To test the hypothesis that there was no difference in the determination of length at age (L[age]) determined by ring counts and length at age determined by back calculation (L[calc]) a t-test was used (unpaired) on data from each length group (L1-L8) (Sokal and Rohlf 1981).

iv Marginal Scale Increment Analysis (MSI)

Marginal scale increment (MSI) was calculated as the amount of scale growth (from the last ring to the margin) in relation to the distance between the last two scale rings. The formula developed by the author as part of this study was as follows:

$$MSI = (SR - R_{n+1})/ (R_n - R_{n+1}/100)$$

where:

MSI	=	Marginal scale increment (%)
SR -	=	Total scale radius
R_n	=	penultimate scale ring
R_{n+1}	=	last scale ring formed

Calculations of mean MSI per month for all fish aged were determined to assess the periods during which low and high mean incremental growth occurred. Further calculations of mean MSI per month for each of age groups (L1, L2, L3 and L4-L8) were used to determine whether scale growth rates changed during the lifetime of a fish from juvenile to maturity and old age.

One way ANOVA (with Tukeys LSD post hoc) was used to test the hypothesis that there were no seasonal influences on MSI. As the change from one season to another may not be distinct Students t-Test was used to determine whether there were significant changes in MSI between times during which peak flood (March) and low water level (July) conditions existed.

v Length Frequency Distribution Analysis (LFDA) and Growth Models using Electronic Length Frequency Analysis (ELEFAN)

Monthly length frequency distributions were plotted for all fish combined, and for males and females separately for each month for the most productive sites determined from catch data (Chapter 3) over a period of one year. Length frequencies were converted to age frequencies using estimated growth curves derived through a computer based Length Frequency Distribution Analysis (LFDA) (version 3.10) (MRAG 1992). Months were coded as proportions of one year *e.g.* the first month (December) was coded 1/12 = 0.0833, the second month 2/12 = 0.1667 and so on up to the following January coded as 13/12 = 1.08. The analysis allowed for the determination of parameters of the von Bertalanffy growth formula (VBGF) where:

$$L(t) = L_\infty(1\text{-}\exp(-K(t-t_0)))$$

L_t = predicted length at age t

K = the growth constant

L_∞ = asymptotic length (or the mean length of fish in a stock if they were to grow to infinity (Pauly 1987)

t_0 = time or age at which the fish would have had a length of zero

Total mortality (Z) was estimated from the age frequency distribution data using the method described by Beverton and Holt (1957) as follows:

$$Z = K((L_\infty - L)/(L - L_c)))$$

The estimation of Z follows the assumption that mortality does not change with time, that there is constant recruitment and that growth is well defined by the von Bertalanffy growth curve.

The use of the LFDA assumes that the fish sampled are a representative portion of the whole population. Gill net selectivity of the range of nets used in the study was discussed in Chapter 3 and the sample was taken as being representative.

vi Changes in Abundance

The level of agreement between growth determined by scale reading methods and LFDA (length at age, number of fish caught per age and growth rates) was used to determine whether calculations of abundance based on the sample of fish used in scale analysis could be related to abundance of all fish caught during the study. The aim was to assess the changes in age class strength (proportion of fish per age caught) between the initial months of sampling during the flood period (December to April) and the end of the sampling period also during the flood period (September to January) This could then provide an indication of mortality at age (both natural and fishing) between the beginning and end of the study. Changes in abundance for each size group over time could be used to indicate the influence of recruitment patterns on catch rates with constant fishing pressure over time and would provide a general view of the level of exploitation of the population.

vii Seasonal and Biological influences on growth.

The hypothesis that variations in monthly marginal scale increment (MSI), gonadosomatic index (GSI), and condition factor (KF) are independent for both males and females was tested using Pearsons Correlation Coefficient. The possible influence of the wet and dry season on GSI, KF and MSI for males and females separately was tested using analysis of variance ANOVA (one way).

6.3 Results

6.3.1 Data Analysis

i Length Weight relationships

Figure 6.1 indicates the relationship between length and weight (log transformed) for each site. The following formulae indicate the relationships derived through regression analysis between length and weight at each of the four sites sampled.

Site 1 $W = \text{antilog } 1.92L^{3.155}$ $(n = 675, r^2 = 0.96, p = <0.001)$
Site 2 $W = \text{antilog } 1.85L^{3.11}$ $(n = 1022, r^2 = 0.98, p = <0.001)$
Site 3 $W = \text{antilog } 1.94L^{3.18}$ $(n = 237, r^2 = 0.97, p = <0.001)$
Site 4 $W = \text{antilog } 1.83L^{3.10}$ $(n = 35, r^2 = 0.64, p = 0.01)$

Fish at all sites indicate a relationship with a weight to length exponent just above 3.00 which suggests growth is allometric at all sites. The smaller regression coefficient at site 4 is indicative of the smaller numbers of fish caught at this site.

Analysis of covariance (ANCOVA) indicated that there was no significant difference in length weight relationships between sites. Thus for age and growth studies data were combined from the two most productive and adjacent sites (Sites 1 and 2, see Chapter 3).

ii Scale radius: length relationships

Regression analysis (least squares) indicated a linear but not directly proportional (i.e. 1:1) relationship between scale radius and length (figure 6.2). Regression equations for total length (TL) and standard length (SL) were extrapolated as being:

$SL = 0.82 \pm 0.017\ SR + 1.58 \pm 0.35$ $(r^2 = 0.94\ p =< 0.001)$
$TL = 0.95 \pm 0.021\ SR + 2.477 \pm 0.422$ $(r^2 = 0.95\ p = <0.001)$

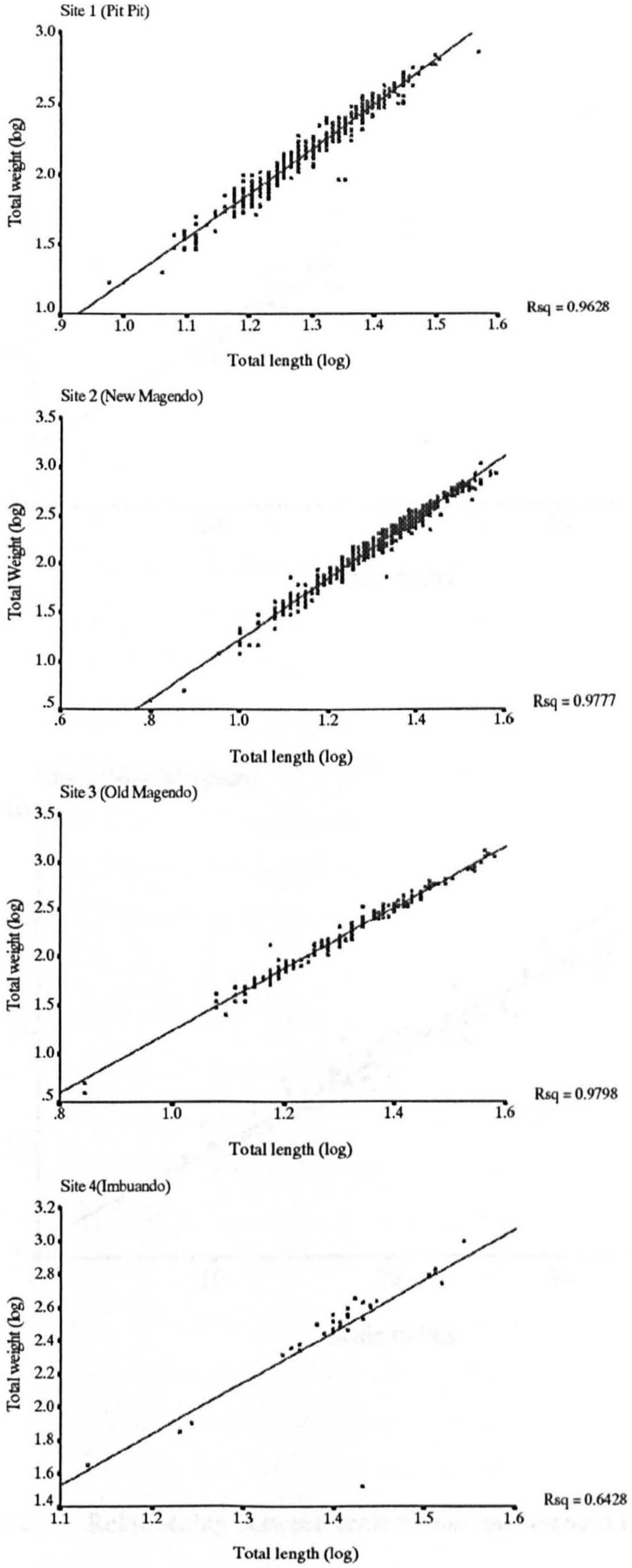
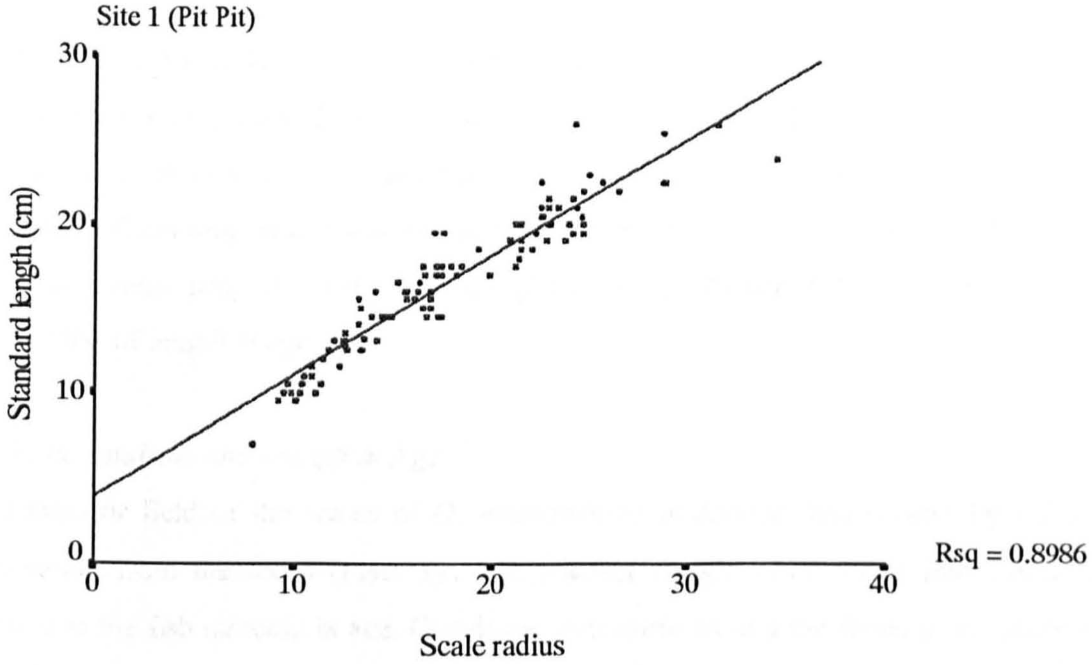


Figure 6.1 Site specific length weight relationships.



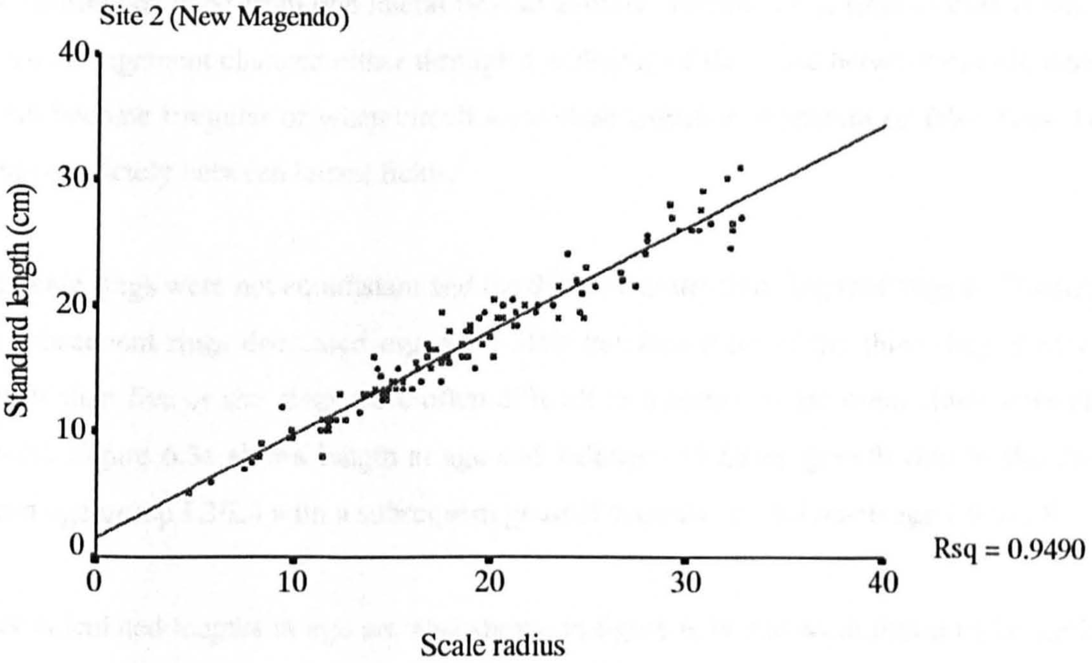


Figure 6.2 Relationship between scale radius and standard length

There was a statistically highly significant correlation between scale radius and length which is indicative of a proportional growth relationship between somatic growth and scale growth. The results of this analysis indicated that the intercept on the length axis was a positive value. Thus the relationship was linear but not directly proportional (i.e. not 1:1). Therefore the modified direct proportionality formula (Fraser-Lea) (Ricker 1971) was used for back calculation of length at age.

iii Scale Analysis and Length at Age

The anterior field of the scales of *O. mossambicus* is divided into sectors by radial lines originating from the focus (Plate 1).. The anterior margin often forms into ridges which deepen as the fish increase in age. Circuli are concentric around the focus in the anterior and lateral fields only. The posterior portion contains ctenii.

Rings were formed in a variety of ways but were only regarded as true rings if they extended in a continuous band from one lateral field to another. Formation of rings occurred when the circuli arrangement changed either through a widening of the space between circuli, when the circuli become irregular or when circuli were close together. Apparent or false rings did not form completely between lateral fields.

The scale rings were not equidistant and the distance to the first ring was largest. Distances to the subsequent rings decreased especially after the formation of the third ring. Scales with greater than five or six rings were often difficult to measure as the outer rings were closely spaced. Figure 6.3a shows length at age and indicates an faster growth rate to the third or fourth age group L3/L4 with a subsequent gradual decrease as fish reach age L6 to L8.

Back calculated lengths at age are also shown in figure 6.3a and were found to be similar to length at age. There was no significant difference between the two lines (unpaired t-Test for each length group). The back calculated length at age (L[calc]) for L1 may be more representative of the growth rate at this age, as the first ring was usually difficult to determine and may have led to an underestimation of the rate of growth of the younger fish.

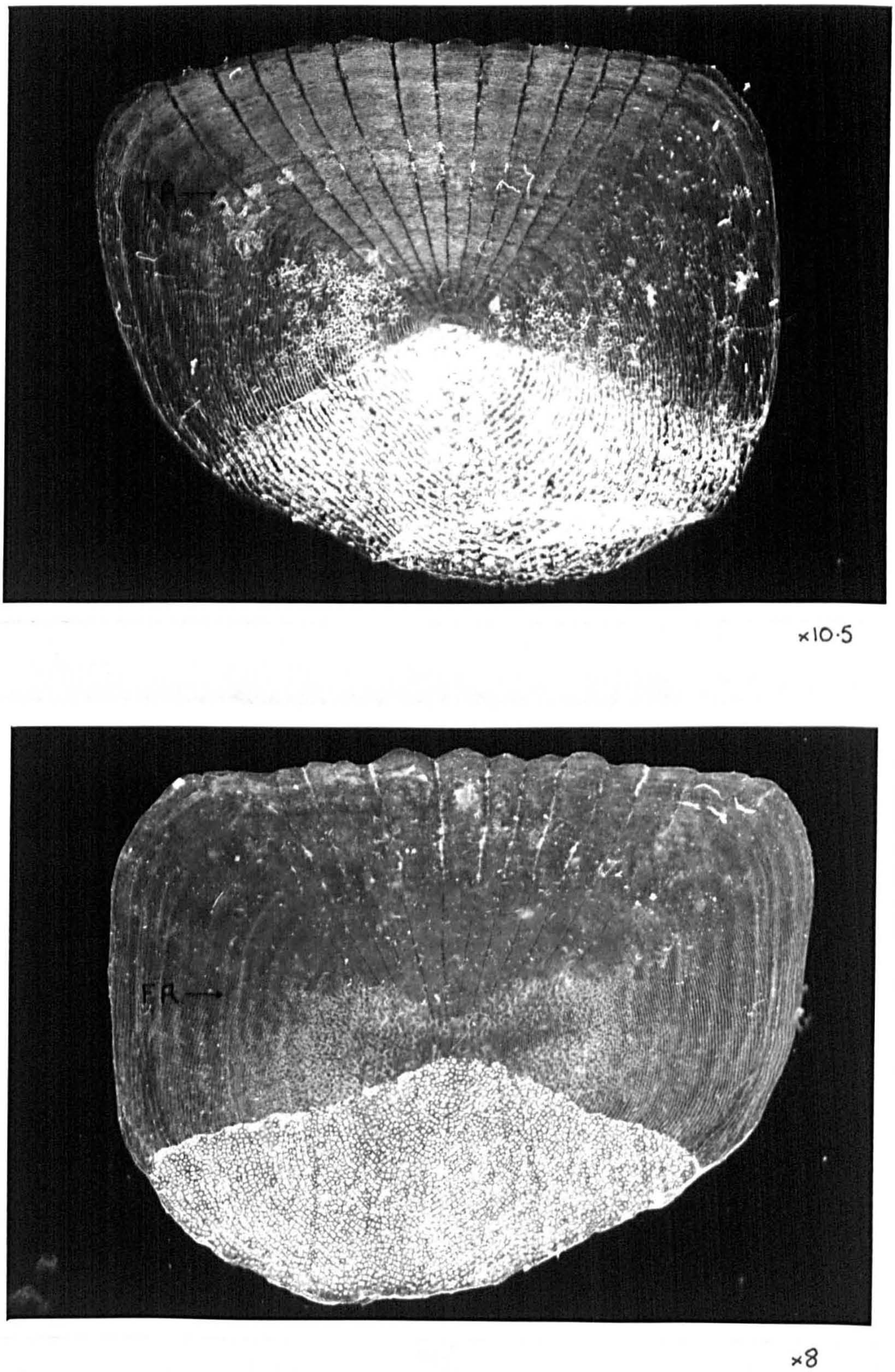


Plate 1 Scales of adult *Oreochromis mossambicus.* (TR = True ring, FR = false ring)

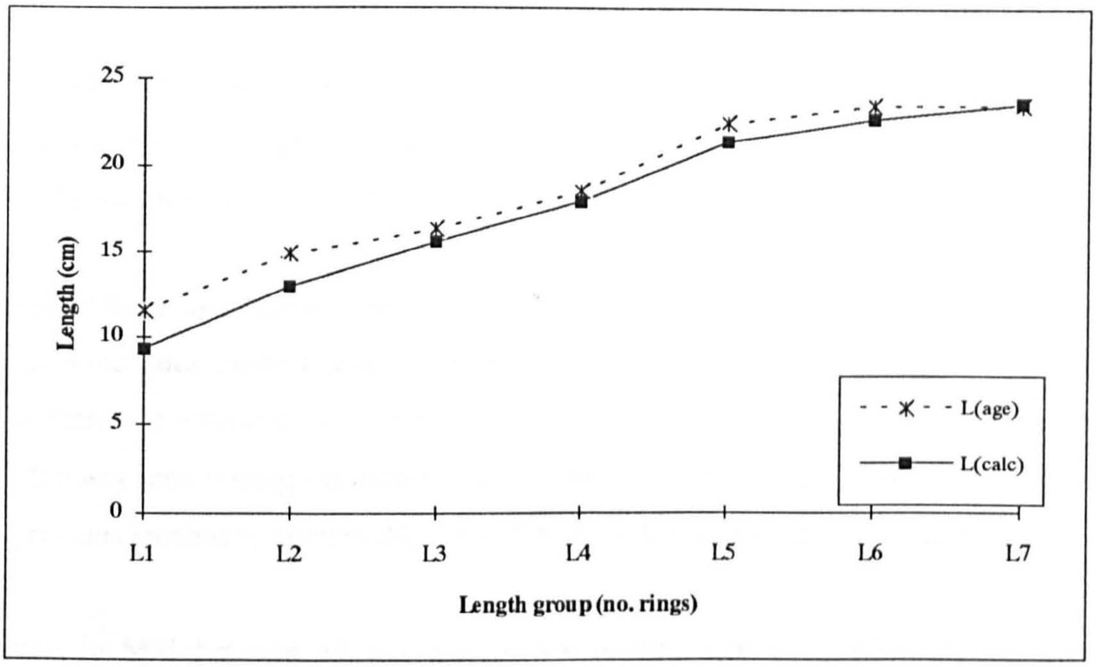


Figure 6.3a Comparison of length of fish per number of rings(L(age) with back calculated length of fish (L(calc))

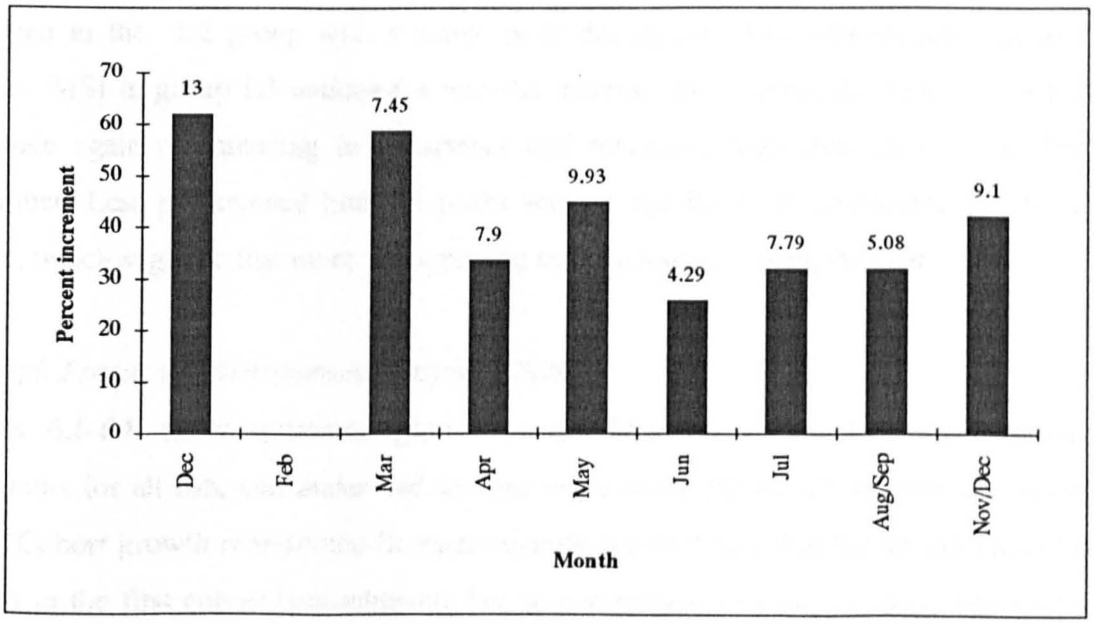


Figure 6.3b Monthly Marginal Scale Increment (MSI) (Numbers indicate mean standard error)

Length distribution for age groups are shown in figure 6.4. Length variation for each age group is relatively large which may be due large variations in the growth rate among individuals. However the general pattern is of faster growth between ages L0 and L4/L5 followed by a slowing of the growth rate towards the asymptotic length.

iv Marginal Scale Increments (MSI)

Figure 6.3b indicates a reduction in the percentage increment for all fish during the dry season (June to October) followed by an increase as the water levels rose in November/December. During the wet season marginal increments were found to be approximately 60% of the size of the previous increment whereas this figure fell to 25-30% during the dry season.

Difference in MSI between all wet and all dry months was not statistically significant. However there was a significant difference in MSI during peak flood period (March) and low water period (July) (t - Test $t = 2.169$ $P = <0.05$). This may be related to the gradual changes in water level between each season.

Percentage increment analysis per age revealed that fish in the age groups L1 displayed a single peak in MSI as the water rose in October to December (Figure 6.5). A similar result was seen in the L2 group with a single peak during the December/January period. In contrast MSI in group L3 indicated a bimodal increase once during the March/May period and once again commencing in September and remaining high throughout October to December. Less pronounced bimodal peaks seen in age R4 to 8 correspond to the flood season, which suggests that more than one ring may be formed during the year.

v Length Frequency Distribution Analysis (LFDA)

Figures 6.6-6.8 show estimated growth curves fitted to polymodal length frequency histograms for all fish, and males and females respectively (ELEFAN analysis coefficient = 0.41). Cohort growth represented by each separate line indicates that for all fish (figure 6.6) growth in the first cohort was relatively fast in comparison to older cohorts. The first two curves may represent one cohort and indicated that growth in the first year was between 6 - 15/16 cm, in the second year cohort growth was from 16 - 23 cm and then from 23 - 28 cm. Growth for males alone showed a similar pattern (figure 6.7) with a maximum size of

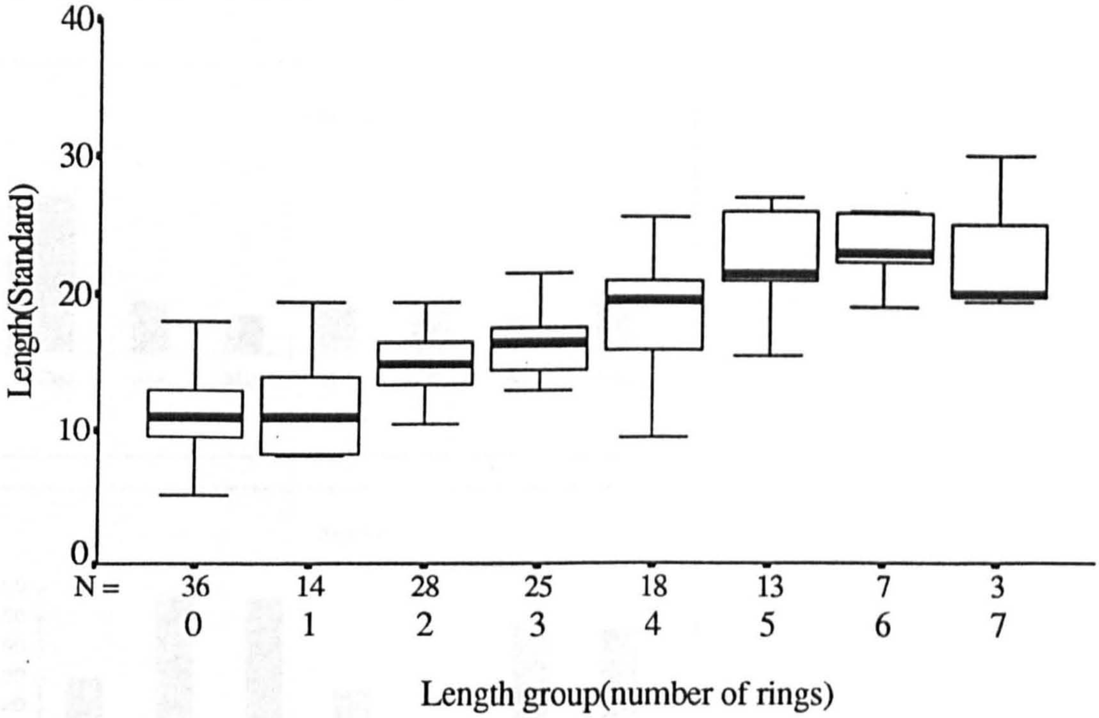


Figure 6.4 Length distribution (box-plot) for fish with various numbers of scale rings.

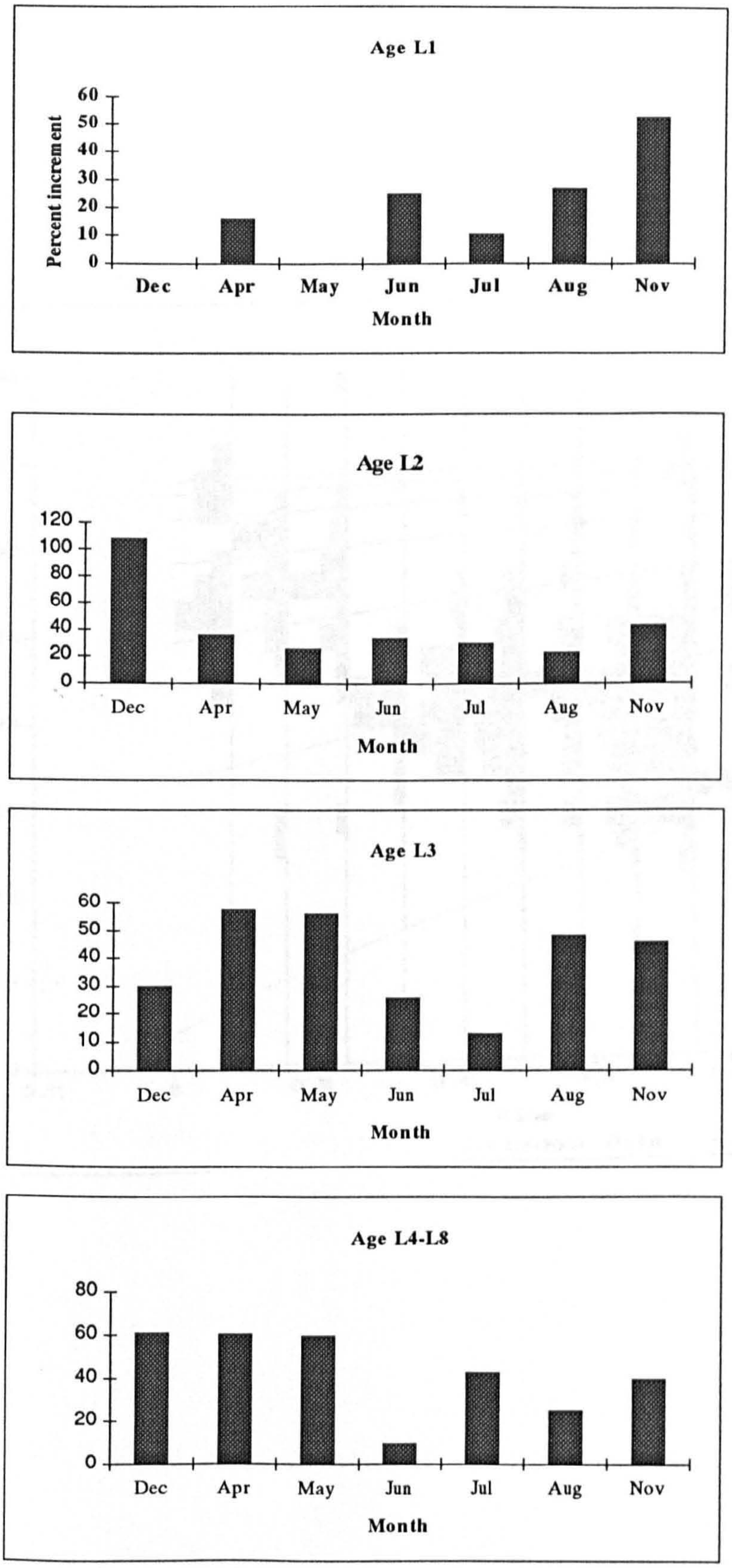


Figure 6.5 Marginal scale increments for each age group

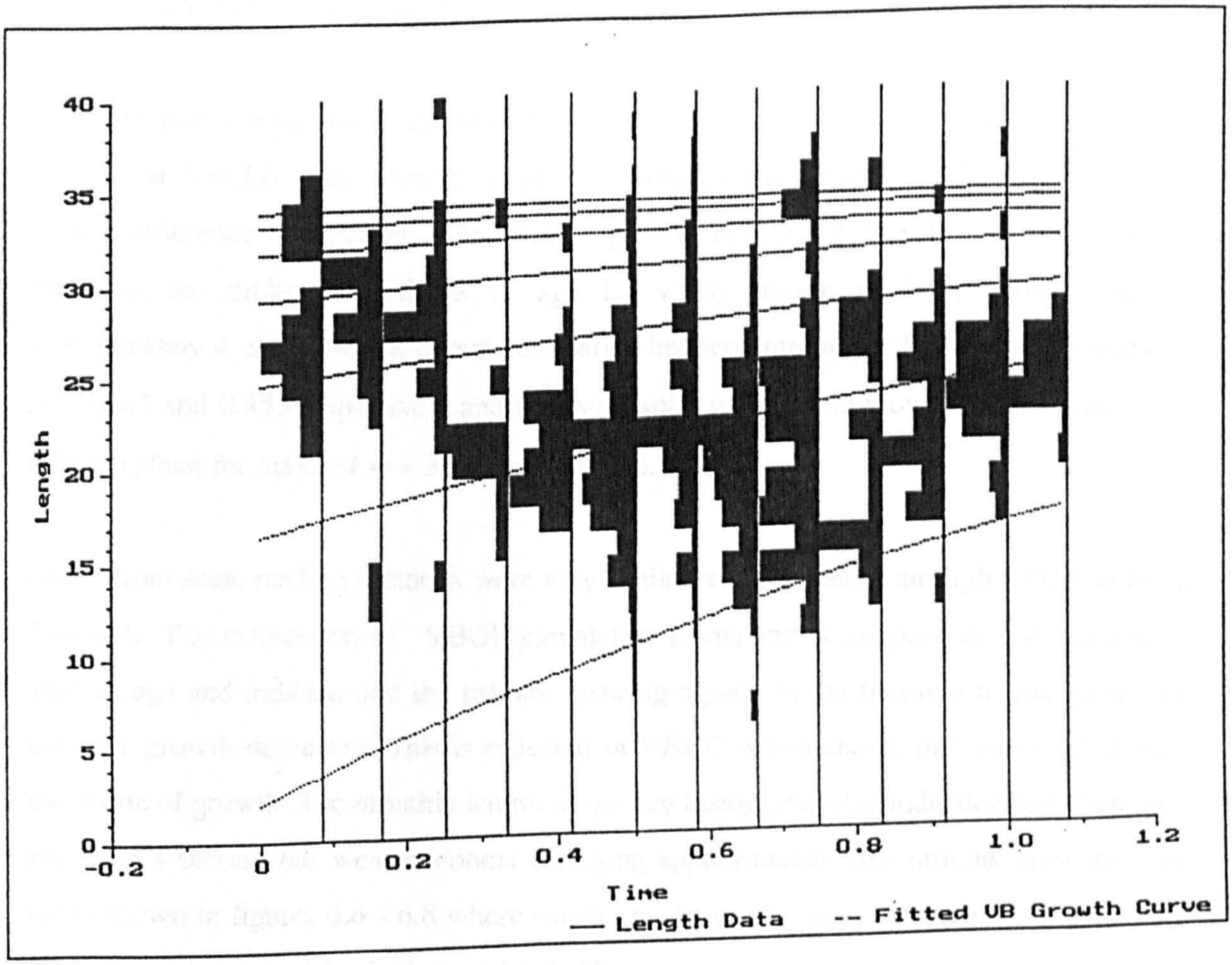


Figure 6.6 All *O. mossambicus*. Length frequency distribution analysis with fitted growth curves (ELEFAN)

approximately 35 cm, whereas growth in females was slightly slower with a maximum size of 25-27 cm (figure 6.8). Table 6.1 compares the mean length increase for each year class for each sex with the overall mean length at age found through scale analysis and back calculation. Although both sexes are combined in the determination of length at age figures there is a general agreement between both methods and the results suggest that two scale rings are formed yearly with the third ring, L3, representing the initiation of spawning.

Growth in year 1 is similar to growth found between L0 and L2/3, year 2 relates to L3/4 to L6 and year 3 to L6 - L8. During the period of study cohort/year 2 or L3 - L5 showed the greatest difference between male and female growth rate (8 cm and 4.5 cm respectively). Thereafter the difference reduces to age L8 when growth of both sexes is similar (approximately 4 cm). Growth parameters varied between males and females with values for K of 0.683 and 0.453 respectively and the asymptotic weight being lower for females ($L\infty$ = 26.56 cm) than for males ($L\infty$ = 35.0 cm) (Table 6.2).

Results from scale reading methods were very similar to those found through LFDA in terms of growth. The calculation of VBGF parameters L(inf) and K support the calculations of length at age and indicate that the fish are growing rapidly in the first one to two years and thereafter growth decreases. This is reflected in VBGC which shows that older fish have a slower rate of growth The monthly length frequency histograms also indicated that there may have been a second but weaker cohort emerging approximately five months after the first. This is shown in figures 6.6 - 6.8 where smaller peaks can be seen between the main cohort growth curves commencing in August (dotted lines).

vi Mortality

Total mortality values (Z) were higher for males than female at 0.74/yr and 0.25/yr respectively (Table 6.2). The overall rate for both sexes combined was 0.56/yr.

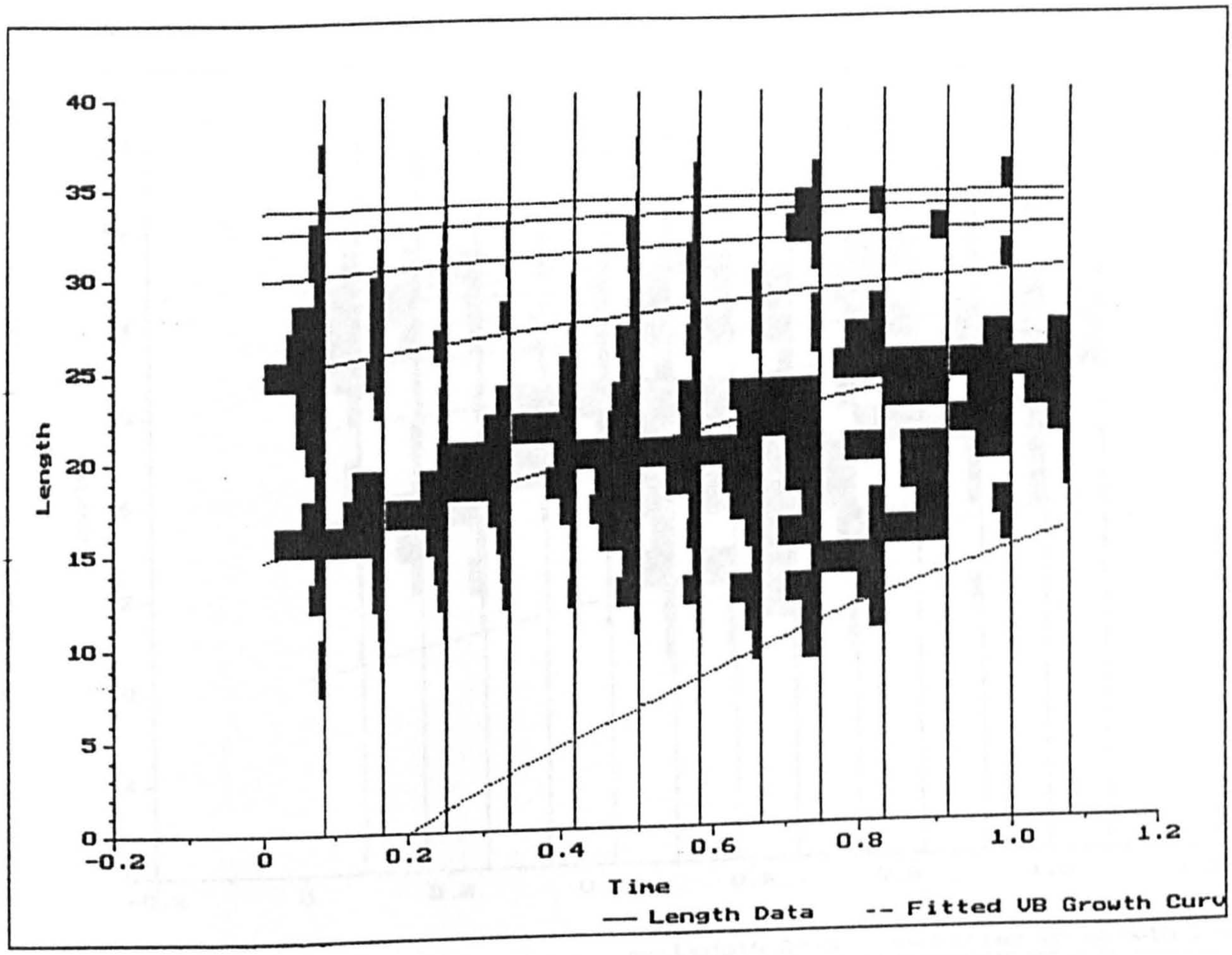


Figure 6.7 Male *O. mossambicus*. Length frequency distribution analysis with fitted growth curves (ELEFAN)

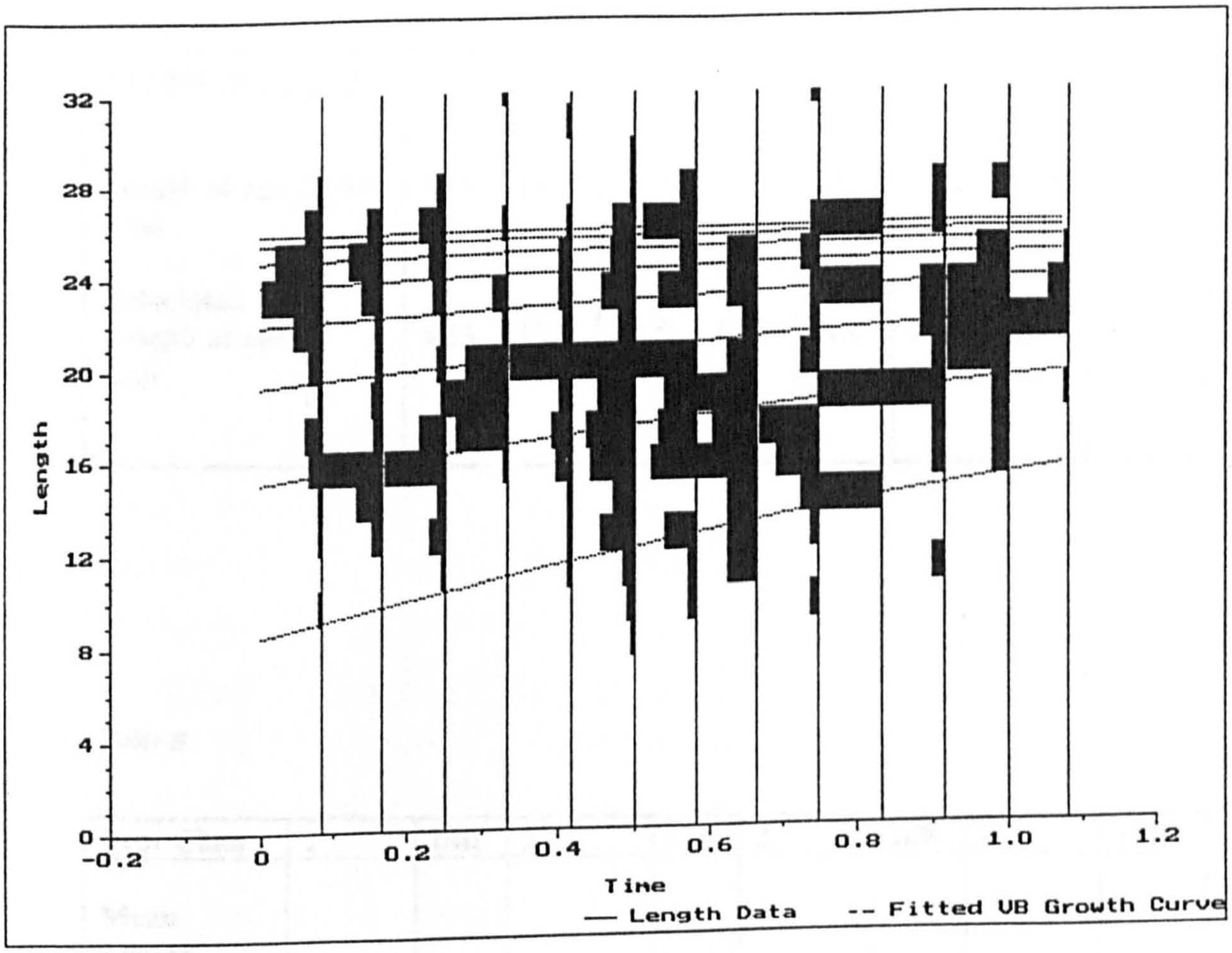


Figure 6.8 Female *O. mossambicus*. Length frequency distribution analysis with fitted growth curves (ELEFAN)

Table A

Age groups	L0	L1	L2	L3	L4	L5	L6	L7	L8
Length at age (cm)	10.9	11.5	14.9	16.3	18.5	22.4	23.4	23.4	28
Calculated Length at age (cm)	-	9.33	13.1	15.6	17.9	21.4	22.7	23.5	27.3

Table B

Year Class	1	Diff	2	Diff	3	Diff	4	Diff
Mean Length								
All fish	**6-16**	10	**16-24**	8	**24-28**	4	**28-32**	4
Male	**7-15**	8	**15-23**	8	**24-29**	5	**29-33**	4
Female	**7-14.5**	7.5	**14.5-19**	4.5	**19-22**	3	**22-25**	3

Table 6.1 Comparison of growth rates found through scale analysis(Table A) with those derived from length frequency analysis (Table B)

Growth and Mortality parameters	Growth constant K	Asymptotic length L_∞(cm)	Total mortality
Male	0.683	35	0.75
Female	0.453	26.56	0.25
Both sexes	0.580	34.3	0.56

Table 6.2 von Bertalanffy growth parameters and Beverton Holt total mortality estimates derived through ELEFAN

vii Changes in Abundance

Changes in year class strength (abundance), as determined from the sub-sample, were distinct between the beginning and end of the sampling period. The two periods analysed were both during the wet period to avoid the effects of overlap in environmental changes (Figure 6.9). In the initial period a greater proportion of older fish (ages L3 and L5) were caught but by the end of the yearly sampling period the age of capture had decreased with a greater number of individuals present in age L2 to L3. The high level of L0 fish present at the initial period may be an anomaly related to scale reading error.

Total number of fish caught in each length group at the beginning and end of the study for all *O. mossambicus* caught, are shown in figure 6.10. In the initial period two length groups predominate in the catch *i.e.* 14 cm and 20 cm. These sizes related to age classes L2/3 and L5 respectively. This compares well with the results from the sub-sample. However during the final period the fish with a mean length of 19-20 cm predominated. This corresponded to age group L4/5. The results overall indicate that abundance fell for all length and age groups during the study with a greater decrease in fish of size 14 - 16 cm. This mean length corresponds to the range of size caught in the 2.5 inch gill net (Table 6.3).

viii Seasonal and Biological Influences on Growth

As the river levels decreased there was an apparent decrease in MSI for both males and females (figure 6.11). Condition factor for both sexes remained stable during the period whereas GSI in females indicated a peak in activity during December /January with a smaller rise in April/May. Spawning activities in males was similar with a peak in December/January and April/May. There was also evidence of activity in June although this figure was calculated from very small numbers of males and may be not be a true reflection of activity. There was no significant correlation (Pearsons correlation) for either male or female fish between for MSI, GSI and condition factors. However there was a significant difference in MSI between seasons for all fish (ANOVA $p = <0.05$) and between GSI and season for females (ANOVA $p = <0.001$). There was no significant changes in GSI and KF for males between seasons.

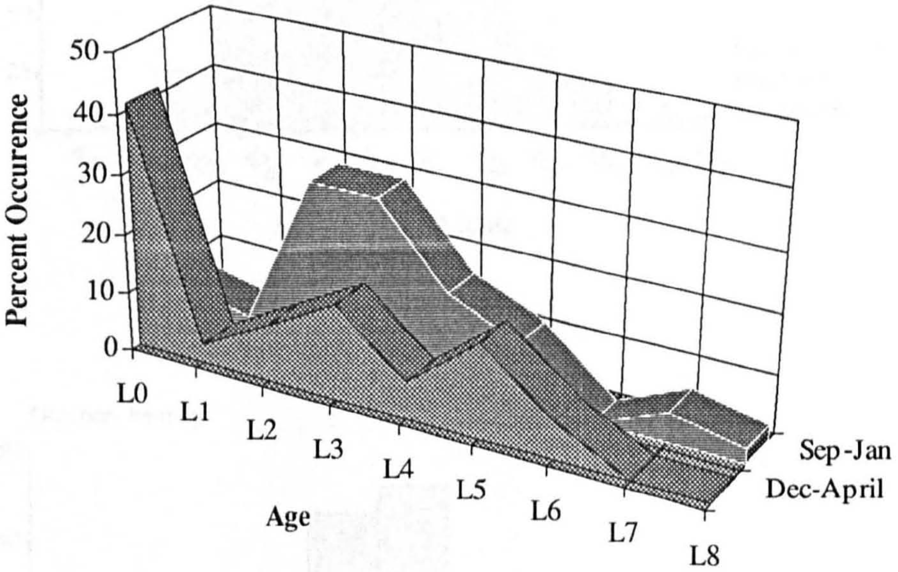


Figure 6.9 Changes in proportions of different age groups from the beginning (Dec - April) and the from the end (Sep - Jan) of the sample period (using the sub-sample)

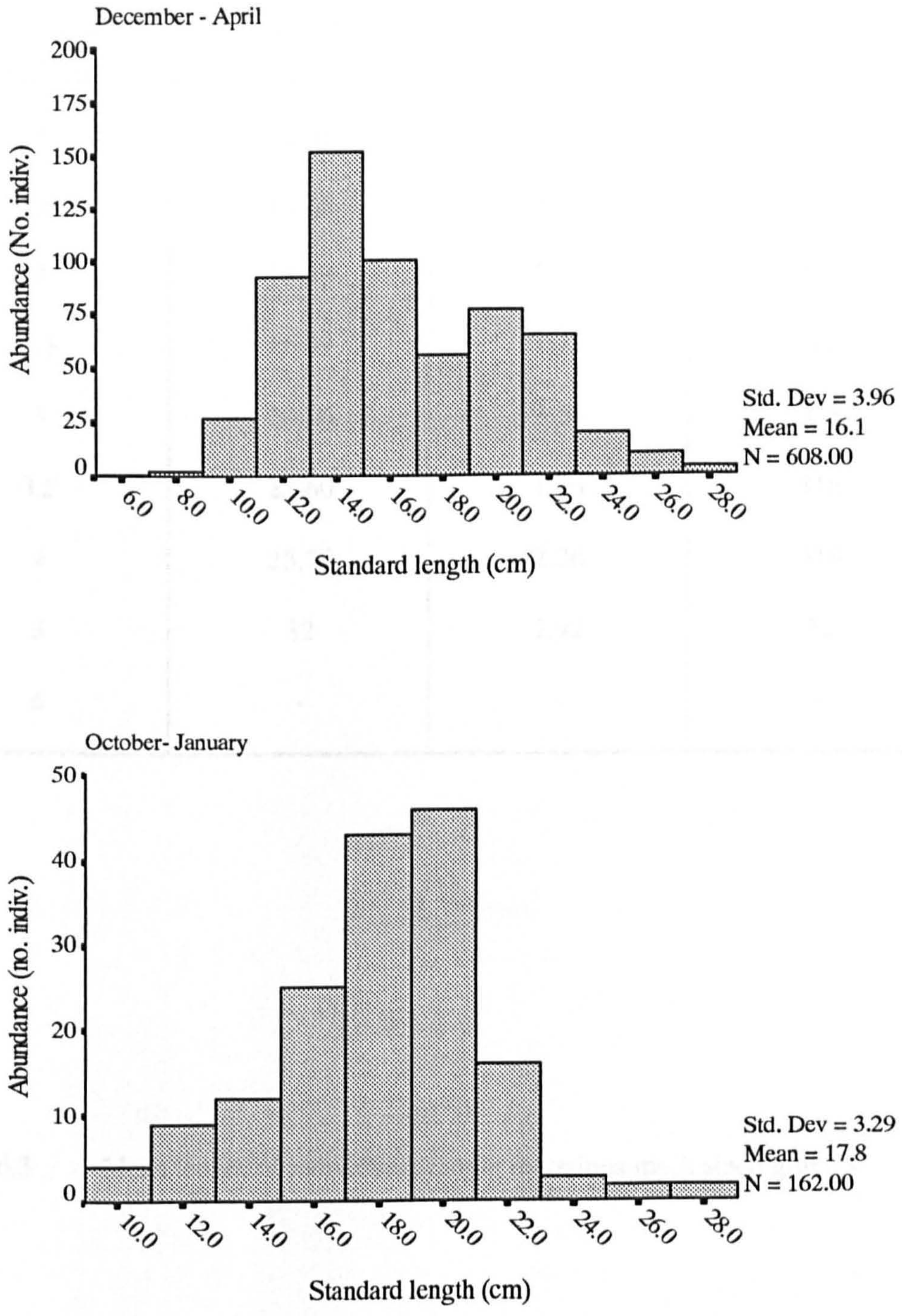


Figure 6.10 Changes in abundance per length group between the beginning and end of the sampling period

Mesh Size (inches)	**Mean length (cm)**	**Standard deviation**	**Number of individuals**
1	12.31	6.1	9
1.5	19.68	1.54	16
2	13.73	2.13	171
2.5	16.39	1.12	400
3	20.26	2.54	558
3.5	22.60	1.76	316
4	25.76	2.26	318
5	32	1.92	72
6	-	-	-

Table 6.3 Mean length of individuals caught in various mesh sized gillnets

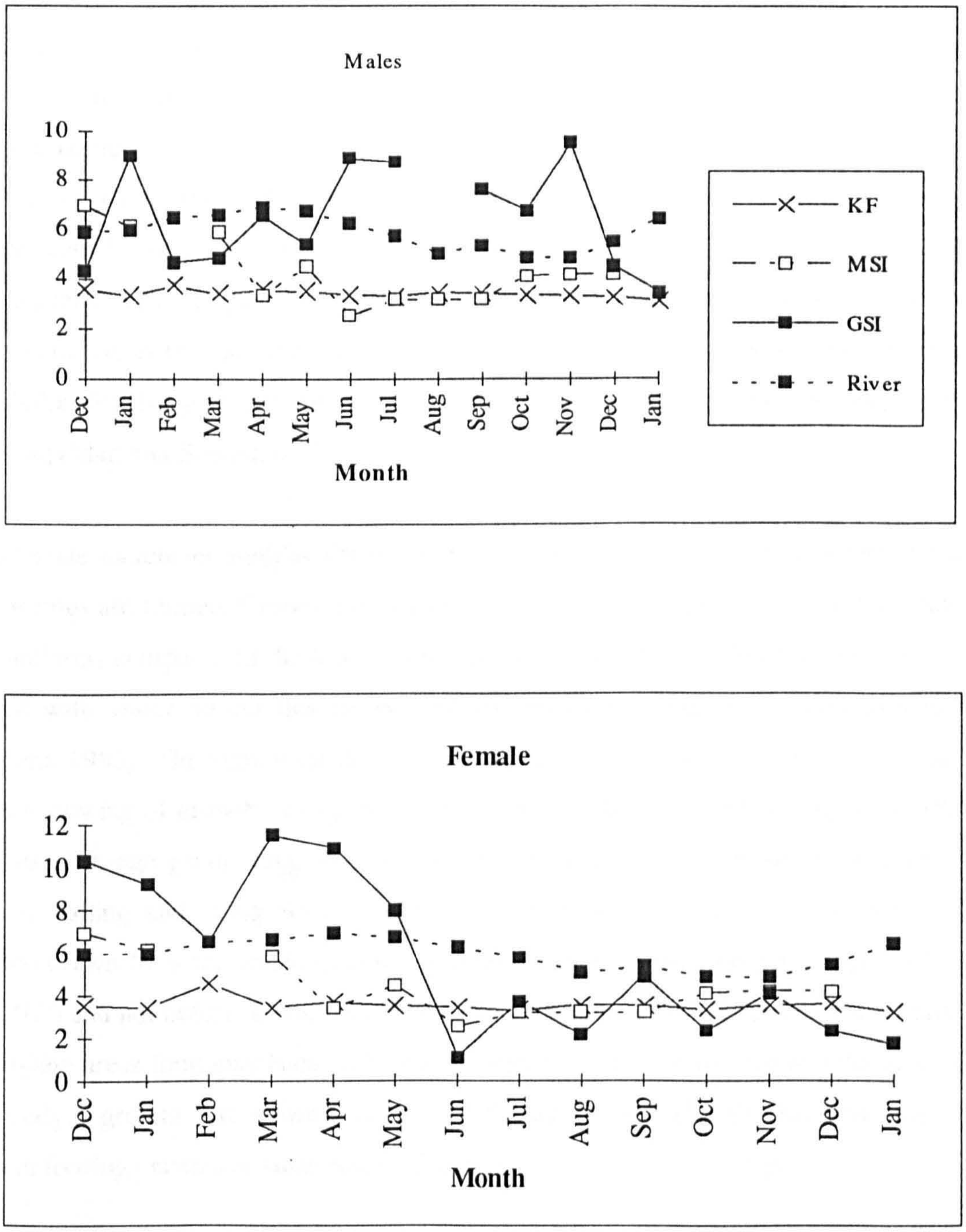


Figure 6.11 Changes in gonadosomatic index (GSI) Marginal Scale Increment (MSI) Condition Factor (KF) with river level fluctuations. (GSI values x 10(females) x 100(males), (MSI values /10)

6.4 Discussion

The significant linear correlation between scale radius and length (total) through regression analysis for all fish gives confidence in using scale marks to back calculate length at age and compare to actual length at age. The close correlation between these two methods indicated that scale reading fulfilled the initial assumptions made *i.e.* that growth rings relate in some way to the age of the fish and that an increase in number of rings correlates with increased body size and this is a constant ratio. The determination of length at age by both methods indicate a greater rate of growth during growth periods L1 to L3 with a subsequent slowing of the growth rate as the fish reached period L4. The looser correlation between each method of calculation for the youngest fish is a reflection of the difficulties in determining the first growth ring (Man and Steinmetz 1985).

Marginal scale increment analysis (MSI) could be related to the periods in which growth checks or rings are formed. Growth in scale increment was significantly greater at the peak of flood conditions compared to the lowest water period. This may be related to the large area inundated with water during this period and the associated increase in food availability (Welcomme 1985). The significant decrease in increment formation during the dry season suggests a slowing of growth during this period. The analysis of monthly changes in MSI in relation to each age group suggested that growth rings could be formed twice a year in relation to falling and rising water levels, or potentially, in relation to spawning. The conclusion drawn from the results is that a spawning ring is formed when the fish reach age group 3 (L3) and not before. Lowe-McConnell (1987) indicates that as the water level falls in the floodplain areas food may become limiting as fish are concentrated in a smaller area, and consequently, growth rate slows. Hecht (1980) and Dudley (1974) also conclude that changes in feeding patterns or spawning may influence the formation of rings.

Growth curves as determined through length frequency distribution analysis (LFDA) (ELEFAN) on the whole population showed very similar growth patterns to those obtained through scale analysis. This gives confidence in that the results determined from a sub-sample of the fish caught are representative of the total sample caught. The analysis also indicated that the greatest difference in male and female growth rate occurs when the fish are in the second year of growth. This also corresponds to the period when fish mature, commence breeding and females cease feeding whilst brooding young. These results may also be indicative of the age and size at which fish have the greatest breeding potential. A managed fishery should therefore avoid the capture of fish with the greatest potential for successful breeding as this would inevitably affect recruitment.

Length frequency distribution analysis (LFDA) also supports the findings of marginal increment analysis which suggested that scale rings are formed twice a year with a spawning ring formed at L3 when fish reach maturity at approximately 15-16 cm. This relates well to minimum breeding sizes found in the analysis of the proportion of fish in different length groups with mature gonads (Chapter -5, Figure 5.6). Growth formula parameters L and K compare well to those found in other studies (Moreau *et al.* 1986, De Silva *et al.* 1988, Iles 1971) (Table 6.4) and suggest a fast growing fish which reaches maturity within its first or second year. Males grew faster especially during the second year of growth when most fish reach maturity. This period would correspond to the period in which females would begin brooding young and would cease feeding for a period of time. This may have had an effect on the growth rate in females, which lagged behind that of males except during the initial year prior to maturity. Sexual dimorphism has been shown in other populations of *O. mossambicus* (see Table 6.4) but the degree of difference may well reflect the life history patterns of species with different environmental influences on reproduction and feeding.

The close agreement between mean length at age calculated from scale analysis and growth rates derived from length frequency analysis and the von Bertalanffy growth equation suggests that the methodology used gives a true reflection of the population dynamics and growth of *O. mossambicus.* Marginal scale increment analysis in comparison to LFDA suggests that the third ring formed (L3) in the scale may be a spawning ring and growth checks are produced twice a year. On this basis the yearly growth rate would relate to two scale marks each year although the results are somewhat skewed by the varying growth rates between males and female and the cessation of feeding in breeding females. The combined analyses also suggest that the peak spawning lengths for females and males are 16 cm and 18 cm respectively which has implications for managing a fishery in terms of setting gillnet mesh sizes for sustainable yield.

Asymptotic length L_∞	**Growth constant K (cm)**	**Sex**	**Author**
Range 26.7-39.3	0.32-0.7	both	DeSilva *et al* 1988
31.1	0.50	“	“
21.6	0.36	male	Bruton and Allanson 1974
21.7	0.24	female	
24.5-38.7	0.196-0.684	both	Hecht 1980
31.2	0.644	both	Koura and el Bolock 1958
37.6	0.362	male	Man and Hodgkiss (1977c)
31.3	0.395	female	
35	**0.683**	**male**	**This study**
26.56	**0.453**	**female**	

Table 6.4 Comparison of von Bertalanffy growth parameters for *O. mossambicus*

The general pattern which emerged from the LFDA analysis was that as the river rises and the main period of spawning occurs during November/December the 1st cohort grows rapidly as food is plentiful and enters the fishable population just as another peak in breeding activity occurs during April/May. There was evidence from the length frequency histograms that a second but smaller strength cohort was present. As river levels fall during April to June the floodplain is supporting an influx of juveniles from both spawning periods. As more fish are concentrated in a smaller area resources in terms of food and space become limited. Therefore there may be both environmental and biological influences on the growth and age structure.

Production in a tropical river system may be influenced by environmental changes (Holcik 1996) and may vary in respect to biomass with changes in allochthonous input (Fernando and Holcik 1982). The quantity of such inputs may be related to the flood regime as seen in the Sepik and will affect food availability. Significant changes in gonadosomatic index with season was seen in females which suggest that peak periods of spawning may be related to food availability for the larval fish. The importance of food availability for growth was indicated by the significant increase in marginal scale increments during the wet season.

Mortality rates suggest the population is being moderately fished or subject to high natural mortality (R. Nash pers. comm). Previous studies on the other species of fish in the river suggest that there are few natural predators of *O. mossambicus.* Therefore during this period of study fishing pressure may have been high enough to deplete the local population to such a degree that natural recruitment could not sustain continuous fishing effort in the local area.

Mortality was higher for males than females ($Z= 0.74$ and 0.25 respectively) which may relate to differences in behaviour especially during the breeding periods. Females will enter the marginal vegetation whilst brooding the larvae and are less likely to be caught. The changes in male to female ratios at different times of the year may reflect this behaviour. The influx of smaller 'sneak' males into the breeding areas may have altered the ratio considerably at certain times of the year (see Chapter 5). Thus an increase in fishing pressure (i.e. increase in the number of traditional 3.5 inch nets) may have a direct or indirect effect on recruitment through the alteration of sex ratios, with subsequent changes in breeding success and recruitment patterns.

The analysis of abundance could be related to changes in mortality at age from the beginning of the fishing period to the end. There was an indication that the abundance of all length (at age) groups were reduced especially in fish with lengths between 14-16 cm. This corresponds to the mean length of maturity and should be considered in management decisions concerning the regulation of gill net mesh sizes.

The changes in abundance of different length groups seen during the sample period may be an indication that the population is unable to recover after this level of fishing pressure. This may be as a result of lack of recruitment to the fishery. This may be related to other potentially limiting factors seen in the area studied such as lack of nesting areas (see chapter 5). In this situation the only migrants into the area to create recovery may be larger 'vagrant' males and females rather than juveniles. Therefore, if the fishing increases to same level used during the study or higher, the population may not be able to recover and catch will decrease towards the end of the sampling period. Since the sample area during this study was small in relation to the size of the Sepik and its floodplain area these findings may relate only to the local population of fish. However, since most fishing areas in the Sepik are traditional sites, an increase in pressure in these areas may create a situation where the local population of fish may not have sufficient recruitment to sustain the fishery. In the present study 30 nets were used in four areas every month which may have caused the relatively moderate to high mortality estimations. The traditional practice is to set far fewer nets (up to five) which may be the correct level of pressure to allow sustainable exploitation. As the prediction for the potential yield (see chapter 3) of the Sepik is far greater than the actual yield then there may be a limiting influence on the recruitment pattern.

Increasing the fishing pressure in an effort to increase the yield in order to overcome protein malnutrition may not be sustainable in the local area. This study was carried out in the lower Sepik and the conclusions may not be reflected throughout the system. However overcoming the problems of low catch rates requires careful management considerations especially in relation to proposals to introduce other species into the system.

Chapter 7 GENERAL DISCUSSION

This discussion is presented in two parts. The first section discusses the findings of the present study on the biology and ecology of the introduced species *O. mossambicus* and the possible reasons for its initial 'success' in the Sepik River, PNG. The term 'success' is used to describe the ability of a population with a high growth potential to provide a sustainable harvest (Garrod and Horwood 1984). The failure of the only commercial fishery in the Sepik is discussed in relation to the findings of the present study. The second part of the discussion reviews the potential positive and negative impact of further proposed introductions of tilapia species on the *O. mossambicus* population already present in the Sepik River.

7.1 The biology and ecology of *O. mossambicus* in the Sepik River in relation to its initial success.

The geological history of the Sepik basin in comparison to rivers of similar sizes in Africa and Asia is relatively recent. Geological evidence suggests that the basin was a marine habitat between 5000 and 20,000 years ago (Swadling *et al* 1988) which can be compared to one of the younger African lakes, Lake Victoria which is estimated as being 750,000 years old (Lowe-McConnell 1975). As a consequence, the endemic fauna may not have evolved a rich diversity of species which may make predictions of the potential yield, based on models of similarly sized rivers difficult. Prior to the introduction of other fish species the large number of habitats present in the river may not have been exploited. There are several potential reasons for the initial increase in distribution and abundance of *O. mossambicus* in the Sepik River since its introduction in the 1950's and the later perceived decline of catch rates. These areas are discussed in the light of the results of this study.

7.1.1 Habitat exploitation

Much of the present work carried out in the Sepik basin has been in establishing the niche of *O. mossambicus* and identifying possible competition with other species, native or introduced, within the system. The concept of the "niche" has often been described as the 'role' of the organism in the environment (Odum 1993). The assumed niche requirements (the fundamental niche) of an introduced species are often based on its role in its natural habitat and may not take into account the "realised" niche adopted in a new environment. Introductions may have either beneficial or detrimental effects on the ecosystem as the niche occupied by one species is seldom distinct and interactions between species due to overlap will occur. These interactions are fundamentally variable and as there is a hierarchical nature to the standing crops in lakes, the removal or alteration in the abundance of the more dominant species tends to have large scale effects on the remainder of the population (Svardson (1976).

The productivity of a body of water is dependent on the level of energy entering the system through primary production and allochthonous sources. River systems are dependent to a larger extent than are lakes on allochthonous sources of nutrients for production (Holcik 1996). The introduction of a consumer into a stable ecosystem may have several effects. If the introduced species occupies a previously unexploited niche then the competition for resources such as food and breeding sites will be minimal and the fishery yield may be enhanced. In many cases the effect of introductions has resulted in a change in species composition, an initial increase in yield followed by a decline *e.g* Lake Victoria (O'Riordan 1996).

In many Southeast Asian lakes and reservoirs the introduction of *O. mossambicus* has been correlated with an increased yield in the water body (Fernando and Holcik 1982). In geologically young lakes and reservoirs this effect is more marked since many of the native fish inhabiting these waters are of riverine origin and not totally adapted to this change in environmental conditions. According to Fernando and Holcik (1982), in more recently formed lakes which are inhabited by riverine species of fish there are greater numbers of "free" ecological habitats which can be readily occupied by species better adapted to lacustrine environments such as the cichlid *O. mossambicus*. This latter point is the reason for the success of tilapias and their role in enhancing the fishery yield in many areas.

A similar situation may have existed in the Sepik floodplain prior to the introduction of *O. mossambicus*. All of the native Sepik species are of marine ancestry and thus not totally adapted to the environmental conditions existing on the floodplain (see Chapter 1). *O. mossambicus* was therefore able to successfully utilise this habitat and in a very short time the population biomass was sufficient to support an artisanal and commercial fishery. In other areas the decline in a fishery has led to the introduction of exotic species and consequent changes in species diversity e.g. in Lake Victoria the introduction of tilapias and the predator *Lates niloticus* (Lowe-McConnell 1996).

7.1.2 Competition for food and space.

Interactions of the native fauna with *O. mossambicus* would only occur if there was an overlap in niche requirements. In the Sepik species which could be in competition for resources are those which also utilise the floodplain, are predators or have similar feeding or breeding preferences. In the Sepik *O. mossambicus, Glossolepis multisquamatus, Oxyeleotris heterodon* and *Ophieleotris aporos* are the main species which show any utilisation of the floodplain during periods of innundation (Allen and Coates 1989). All three species have distinct food preferences, *G. multisquamatus* being primarily a carnivorous species which consumes a wide variety of small invertebrates, *O. aporos* is primarily insectivorous and *O. heterodon* feeds on *O. aporos*.

The main food source for adult *O. mossambicus* is epiphytic and benthic algae, detritus and mulm (periphytic aggregate)(Chapter 4). Although the diet of tilapias may seem in the first instance to be fairly unselective there is evidence that detritus feeding is highly specialised (Bowen 1982). In Lake Valencia, Venezuela, *O. mossambicus* was found to be selectively feeding on periphytic detrital aggregate attached to macrophytes and the protein content of the food resource was directly proportional to the slope of the littoral zone. Adult fish feed selectively in areas where detrital amino acids were abundant and produced maximum growth (Bowen 1981). In contrast, the native species of the Sepik were found to have different food requirements.

The majority of the native species consume invertebrates (terrestrial and aquatic) (Table 4.6 chapter 4) and the only other species which exhibit similar food preferences to *O. mossambicus* is *Zenarchopterus kampeni* although this species does not utilise the floodplain to any extent (Allen and Coates 1989). The plasticity of *O. mossambicus* is reflected in its ability to change its food preference depending on availablity and the ability to digest blue- green algae commonly found in planktonic vegetation as well as zooplankton, phytoplankton and detrital material (Maitipe and De Silva 1985, De Silva 1985). Stomach contents analysis in the present study revealed that the diet did vary between locations in terms of species of diatom and proportions of algal biomass. This can be related to the differences in hydrobiological and environmental differences between sites.

The background levels and composition of epiphytic and detrital algae are as yet unrecorded but may be a rich source of food and a basis to the initial success of both adult *O.mossambicus* and the later introduced exotic species *Cyprinus carpio.* Food quality was found to be suitable, as condition factors were good throughout the year in comparison to populations with a known poor quality diet (Bowen 1982). It is recommended that further studies on the nutritive value of the food source, both epiphytic and detrital, be undertaken. Stomach content analysis was not possible for juvenile *O. mossambicus,* however the small numbers found exhibited a preference for invertebrates as a food source as well as diatom species for the first few months of life (Redding 1989). The evidence suggests that once they enter the fishable population the food preferences change.

It was not possible to determine whether juvenile *O. mossambicus* were in competition with other species of fish for invertebrate food sources. The other species of fish which occupies the floodplain in any numbers, *Ophieleotris aporos,* includes mainly invertebrates in its diet. If competition occurs and if the standing stock of invertebrate fauna is found to be low, then this may have the effect of limiting recruitment of *O. mossambicus* to the fishery.

7.1.3 Reproductive strategies

Although the relative fecundity of *O. mossambicus* is low and is related to body weight and length (fish of 20 cm total length having between 700-1000 viable eggs in each spawning), the parental care exhibited through mouthbrooding and movement of brooding females to the sheltered areas would naturally avoid a high mortality due to predation and other factors. The presence of a bimodal peak in spawning activity is similar to patterns found in other areas subject to wet and dry seasons (De Silva and Chandrasoma 1980) and conveys an advantage of increased relative fecundity (McEvoy and McEvoy 1992).

The minimum size at maturity will affect the fecundity of the population since the greater the size the more fecund the individual. In the Sepik the *mean* size at maturity was between 181-200 mm for females and 201-220 mm for males. This can be compared to findings in Sri Lankan reservoirs where the mean size at maturity for females is 160-210 mm (De Silva and Chandrasoma 1980) and other areas (see table 5.2 Chapter 5). This implies that the population in the Sepik is not stunted although a later study of *O. mossambicus* in tributaries of the Sepik suggests that size at maturity decreases with increasing altitude (Van Zweiten 1989, Redding 1989). The mean length at maturity L_m has been found to vary between populations (Lowe McConnell 1982, De Silva *et al.* 1988) and could be correlated to the body condition of the fish, and the size of the water body (De Silva *et al.*1988). The size of the water body is also thought to have an influence on the maturation size and final size of the fish (Chen and Prowse 1964, Pauly 1984). This may be related to density dependent factors which restrict body size when a population is subject to spatial limitations. Space is not limited in the Sepik floodplan and thus there is the potential for larger breeding fish to be present in the population.

O. mossambicus was commonly found in relatively shallow areas (*i.e* the catch was higher in nets set in shallower areas adjacent to the floodplain in comparison to the minimal catch in the deeper ox- bow lakes and the main Sepik River). This indicates the importance of the floodplain for breeding, recruitment and feeding. It is not clear how far *O. mossambicus* move onto the floodplain during periods of high water but nesting sites are located in areas which will escape drying as the water recedes. Thus the actual area of inhabited floodplain may be much smaller than originally realised and may have an effect on predictions for potential yield.

O. mossambicus was found to be breeding continuously throughout the year in the Sepik with two periods of peak reproduction during the higher water periods when food is plentiful and sheltered areas in the floodplain are close to the nesting sites. During the drier periods nesting sites would be at a premium and food supplies decreased, thus leading to reduced breeding activity and periods of lower recruitment. This would influence the catch rates throughout the year in addition to the influence of the water levels on the movement of *O. mossambicus* from the fishing areas and onto the floodplain. Few of the indigenous species of fish utilise the floodplain for breeding purposes and *O.mossambicus* is the only species to utilise the shallow areas for nest building and is the only nest building species in the river at lower altitudes.

7.1.4 Natural mortality

Previous studies have suggested the reasons for the success of *O.mossambicus* in other areas to be due to several factors. Fernando and Indrasena (1969) suggest that the paucity of lacustrine species in the indigenous fauna, and a substantial level of predation on the juveniles are two factors contributing to the high biomass of *O. mossambicus* in Sri Lankan reservoirs. However, in the Sepik there are few potential natural predators. Potential predators are the arriid catfishes but this species is thought not to utilise the floodplain and only *Arius nox* exploits the floodplain to a very small degree (Coates 1986). This behaviour is not significant in terms of the survival of *O. mossambicus* since this is the smallest catfish. Piscivorous species which enter the floodplain i.e. the eleotrid *Oxyeleotris heterodon* has been found to selectively consume *Ophieleotris aporos* and not *O. mossambicus.* (Allen and Coates 1989)

The lack of predators in the Sepik could result in a greater density of individuals and the potential for intrinsic density dependent factors such as stunting to become apparent. This does not occur which suggests that there may be other factors operating which are regulating the recruitment patterns and the biomass of the population.

7.1.5 Population dymamics, total mortality and fishing pressure

In other environments where there has been a vacant ecological "niche", *O. mossambicus* has been able to establish and form a stable population to augment local fishery resources (Man and Hodgkiss 1977a, 1977b, Hodgkiss and Man 1977,1978). In 1976 Glucksman (1978) estimated that each 4 inch gillnet of 100 metres in length and 2 metres depth was regularly catching 28 kg of *O. mossambicus* or the equivalent of 140 g m^{-2}. In this study, this amount was never reached and the maximum catch rate recorded was 72.49 g m^{-2} from a smaller meshed gill net (3 inches). The mean catch rates for all other sized nets were much lower and it is possible that early estimates did not consider the effect of seasonal variations and population movements on the potential yield of *O. mossambicus.*

Traditional fishing pressure does not seem to be very high but there have been few studies on the numbers of fishermen and gillnets operating in the Sepik. Initially, as populations are first exploited, it is the larger individuals which are taken. These fish are usually the older slower growing fishes with a reduced rate of reproduction, although in the Sepik larger fish still had a generally high fecundity (Chapter 5).

The fairly sudden influx of 4 inch gillnets around 1974 in the basin would have effectively reduced this portion of the population to such an extent that the smaller sized fish formed the basis of the breeding population. This study revealed that catch in the floodplain areas were highest in the 3.5-4.0 inch gillnets. The gillnet size most frequently used in traditional fishing has now reduced to 3.0-3.5 inch mesh (although larger meshes are still used) in order to catch sufficient numbers of fish.

An analysis of changes in abundance of fish caught during the period of research suggested that with constant fishing pressure utilising 30 nets set each month there was evidence of over fishing and lack of recruitment which may be related to lack of nesting sites (Chapter 5 and Chapter 6). The analysis of length frequency distributions and estimations of von Bertallanffy growth parameters suggest that growth is comparable to stocks elsewhere (Chapter 6 - Table 6.2) although cohort size is small. The catch per unit effort varied between different sites which suggests that distribution of *O. mossambicus* throughout the Sepik may be patchy and the conclusion drawn from this study may relate to the local population. However since a large human population in this area rely on subsistence fishing the conclusions drawn are pertinent in relation to the developement of management strategies.

7.1.6 The decline of the commercial 'solpis' industry

The introduction of *O. mossambicus* may have had a significant influence on social and economic status of the human population and was the basis of the salted fish industry. In the light of this present study there are several possible reasons for the industry failing to produce the amount predicted. An analysis of the historical basis of yield predictions for the Sepik revealed that the initial estimates of the potential production from the Sepik were high and may have been based on the documented high catches of *O. mossambicus* in 1975. These are thought to be related to the largescale flooding which occurred in 1973 which may have providing greater potential food availability and increased recruitment (Coates 1983). Welcomme (1979) suggests that the degree of inundation of a floodplain affects the production of fish species utilising the flooded areas for breeding and feeding. This present study supports the view that the flood regime influences the breeding and feeding behaviour of *O. mossambicus*. De Silva (1985) also noted that there is a relationship between water level fluctuations and the abundance of *O mossambicus* in Sri Lankan reservoirs. After an abnormally large fluctuation in water levels there is often a successful year class recruitment seen approximately 3 years later (Dudley 1979, De Silva 1985). The present study has indicated that *O. mossambicus* was possibly the only species influenced by the higher water levels since most of the other species do not utilise the floodplain to any great extent (Coates 1986). This may have had an effect on the initial increase in abundance in the 1970's.

Increased recruitment of juveniles may have coincided with the increase in the use of more efficient fishing methods (gill-nets) during the late 1970's to early 1980's. As a result the catch rates would have seemed to be substantially higher during this period. Earlier predictions of stock biomass were also made in restricted areas where catch rates were traditionally higher and thus may not have been representative of the whole area. In this study the four areas studied showed significant differences in catch rates. The areas adjacent to the floodplain (Site 1 and 2) with relatively shallow water had far greater catch rates compared with the deeper ox-bow lakes (Site 3 and 4). This leads to the conclusion that the distribution of *O. mossambicus* may be patchy and estimates of abundance prior to the present study may not have taken this into account.

In 1981, when an economic review was carried out on the 'Solpis' industry the greatest amount of revenue for the project was from the sale of gillnets (56% of income) (Rodwell 1982). The actual sale of salted fish fillets provided 34% of the revenue in the same year and 11% was from the sales of sundry items such as knives. The number of nets sold in 1980 was 233 and this figure rose by 54% to 358 in 1981 (Rodwell 1982). This substantial increase in gillnets in the Sepik would suggest that there was an accompanying increase in the fishing effort. However, since the production of salted fish still declined, either the fish caught were sold elsewhere as fresh fish, or the population consumed more fish in the village, or despite increased effort the catch rates still declined. The latter point could be an indication that the stocks of fish in the Sepik were under pressure from the sudden influx of standard 4 inch stretched mesh gillnets and that the population may have been was significantly reduced during the first few years (1973-78) and either was not able to recover under such fishing pressure or there were limiting influences preventing a response to fishing effort. The present study also indicated that abundance is low in most of the areas sampled despite using a relatively high fishing pressure in comparison to the traditional level.

Usually, in an unexploited population the increase in fishing effort will initially result in an increased catch as the population responds with greater recruitment (Gulland 1977). After this initial increase, if the effort continues to rise, there comes a point where the MSY is reached and where the fishing effort only removes the same quantity of fish that will be replaced by yearly recruitment. Greater fishing effort will then decrease the stocks to a point where recovery is impossible. At this point the fishery becomes unsustainable. Although in river fisheries it is not usual to determine MSY in the same manner as for marine stocks, the response of the population to fishing mortality remains the same. Therefore the decline in catch rates may be related to the size and number of gill nets introduced into the area. A sudden, intense and very selective fishing effort which concentrated on the breeding sized fish may have the effect of limiting recruitment. This may have occurred in the Sepik with the introduction large numbers of 4 inch gillnets.

Alternatively, the population may have responded by increasing the recruitment but only for a very short period which was not sustained since the gillnetting pressure continued increasing. This could account for the increased catches in 1979 which were very short lived. Thus the population of *O. mossambicus* in the Sepik could have been demonstrating an expected response to continuously increasing fishing effort but over a much shorter space of time compared to fisheries found in African lakes and marine fisheries.

Fishing effort in the 1970's was also concentrated on *O. mossambicus* and may have exceeded the sustainable catch rates and the population was unable to recover. The solution would be to reduce the fishing effort or introduce another species which will then buffer the exploitation of *O. mossambicus* and allow the recovery of stocks. This has been proposed, and the following section reviews the potential impact of introducing further species of tilapia on the *O. mossambicus* population assessed studied during the present study.

7.2 The impact of further introductions of tilapia species on the *O. mossambicus* populations in the Sepik River

7.2.1.Review of the introduction of species

The choice of species for introduction must fulfill several conditions, including the provision of an acceptable source of protein and the ability to complement the existing stocks within a water body. The choice of species must be based on biological, social and financial considerations. In a riverine fishery the main criteria is in the production of abundant market sized fish without overexploitation of the stock through overfishing or detrimental impact to the species already present.

Since the 1950's fish introductions for various purposes have involved approximately 237 fish species and 140 different countries (Welcomme 1988). Initially, many introductions were unplanned and poorly researched. As a result there were a large number of failures, despite an increased awareness of the importance of preliminary scientific research after the second world war (EIFAC 1984). For example, prior to 1957, of the 51 species of fish transplanted into 1398 lakes in the USSR only 12% became established and of all introductions up to 1978 only 3% gave any commercial benefit (Krzywosz *et al.* 1980). Other introductions have created adverse effects on the native fishery, such as the introduction of the grass carp *Ctenopharyngodon idella* into both natural and manmade lakes in the USSR created an unforseen change in the composition of higher plants and phytoplankton with the result that the fish catch declined dramatically (Krzywosz *et al.* 1980). The main reasons for these failures were considered to be the lack of biological research and justification for the introductions, a lack of planning and implementation of the projects and the lack of project analysis and evaluation (EIFAC 1984). In Africa the original distribution of tilapias has changed considerable due to the deliberate or unplanned introduction of various species outside their natural habitats. Many are recorded by Philippart and Ruwet (1982), a summary of which follows;

Various reasons are given for the introductions of various species of tilapia within Africa. These include;

- the stocking of lakes where no tilapia species occur e.g. *T. zillii* and *S. spilurus niger* into Lake Naivasha (Philippart and Ruwet 1982)

- introduction to fill an ecological niche and support declining fish catches eg. *T. zillii* into Lake Victoria (Lowe-McConnell 1996)

- the introduction into artificial water bodies to enable the establishment of a new fishery

- fish culture in rice fields, especially in Asia,

- involuntary introductions of *O. mossambicus* as found in the Sepik River

O. mossambicus has now been introduced into many countries including Java, USA, Malaysia, Sri Lanka, Papua New Guinea, Philippines, Thailand, Bangladesh, Hong Kong, Taiwan, North Vietnam, China, Australia and Japan (Philippart and Ruwet 1982, Lowe-McConnell 1982). The impact of introductions on the indigenous species have been reported from various other countries. In the USA *O. mossambicus* is known to have displaced the population of the Californian Killifish in the San Gabriel River (Knaggs 1977) and in Hawaiian streams it has been indicated as having a great potential impact on the natural fish communities (Maciolek 1984).

Reports from the Philippines suggest that the introduction of *O. mossambicus* has led to the destruction of some milkfish (*Chanos chanos)* populations in ponds used for culture (Philippart and Ruwet 1982). In Australia *O. mossambicus* has been classified as a noxious species and legislation now exists to ban further introductions and culture due to the predicted competition for food and habitat with species important in the sport fishery.

Populations of *O. mossambicus* in Australia have spread into a wide area of inland and brackish water habitats in Queensland and substantial resources have been used in an attempt to eradicate this species (Arthington 1986).

Despite the potential negative impacts of introducing tilapia species for aquaculture purposes or for fisheries enhancement, there is a general concensus that the tilapias could become the most important warmwater fish in this regard if the problems of stocking the most suitable species are overcome (Pullin 1981). There are 29 species of the genus *Tilapia,* the substratum spawners, and many more in the mouthbrooding genera of *Oreochromis, Sarotherodon* and *Danakilia* (Trewavas 1983).

The main species which are important for aquaculture purposes are shown in Table 7.1. Table 7.2 gives an indication of the physiological tolerance of *O. mossambicus* to a wide range of environmental conditions. Many of the tilapias show a preference for food at the base of the food chain (algae, macrophytes and detritus) and hence a capacity to establish populations in many areas outside their natural range. Thus the species are not only suitable for pond culture but could also form a major part of many fisheries operations.

Despite the plasticity and tolerance limits shown by these species the world production of cultured tilapias remains small in comparison to cyprinid culture. The estimated production in 1994 from 75 countries culturing tilapia was 590,000 tonnes (Urch 1996) and represents a relatively small proportion of the worlds total inland water production of fish (Wolfarth and Hulata 1983).

7.2.2 Potential hybridisation with existing stocks and the use of hybrids

Hybrids species of fish are becoming extensively utilised in aquaculture production due to the selection for fish with advantageous traits such as enhanced growth, colouration and the production of a monosex populations. In the past the production of hybrids between *Oreochromis* species has been undertaken mainly to increase fish yields at low cost and to provide more acceptable fish for the consumer. There is little difficulty in producing viable hybrids from different *Oreochromis* species (Wohlfarth and Hulata 1983) since the maternal mouthbrooding behaviour of these species is very similar (Peters 1963, Fishelson 1988).

SPECIES
Oreochromis (Nyasalapia) macrochir (Boulenger, 1912)
Oreochromis (Oreochromis) aureus (Steindacher, 1964)
Oreochromis (O.) hornorum (Trewavas, 1966)
Oreochromis (O.) mossambicus (Peters, 1852)
Oreochromis (O.) niloticus (Linnaeus, 1757)
Sarotherodon galileus (Hasselquist, 1957)
Tilapia rendalli (Boulenger, 1896)
Tilapia zillii (Gervais, 1848)

Table 7.1 Main species of tilapia used in aquaculture (after Schoenen, 1982)

Environmental factor	**Level**	**Effect**	**Reference**
Temp. (^{0}C)	8-10	Death	Chimits (1957)
	15.6	Feeding ceased	Philippart and Ruwet (1982)
	20-24	Breeding activity begins	Bruton and Boltt (1975)
Salinity (mg l^{-1})	0.120	Tolerated after acclimation	Whitfield and Blaber (1979)
	0-49	Breeding possible	Hora and Pillay (1962) Popper and Lichatowich (1975)
Dissolved oxygen (mg l^{-1})	0.1	Tolerated	Maruyama (1958)
pH	4-11	Tolerated	Swingle (1961)
	7-8	Recommended for culture	Philippart and Ruwet (1982)
Turbidity	High	Tolerated	Philippart and Ruwet (1982)
Depth (m)	<12	Adult range	Bruton and Boltt (1975)
	>12	Juvenile range	Bruton and Boltt (1975)

(after Arthington 1986)

Table 7.2 Tolerance of *O. mossambicus* to various environmental parameters

Hybrids of *O. niloticus* x *O. aureus* are cultured from Africa to S.E. Asia and various other species have been successfully hybridised to provide culturists with increased yields and all male populations.

However, there has been a considerable confusion in the literature over the rates of growth, fecundity and other attributes relating to various hybrid species. This has been due in part to the lack of knowledge of the origin of the stocks used and the occasional mistaken identification or misnaming of species. Trewavas (1983) and Philippart and Ruwet (1982) cite cases where *T. rendalli, T. guineensis, T. tholloni,* and *T. zillii* have all been identified as being *T. melanopleura* and past confusion over *O. aureus* and *O. niloticus* has led to the use of hybrids in research programmes rather than a pure strain (McBay 1961). The genetic identification of the species is necessary prior to any considerations for restocking in the Sepik.

There has been no documented hybridisation of *Sarotherodon* and *Oreochromis* species for commercial use and the likelyhood of such species producing viable offspring in natural environments is neglegible although experiments have shown that it is possible to produce hybrids under controlled conditions (Fishelson 1988). In situations such as a natural river system there is a strong possibility that the introduction of two *Oreochromis* species would result in the production of hybrids and the loss of a pure strain of one or more species of *Oreochromis*. In the Philippines a strain of *O. niloticus* (FAC strain) was initially found to give good yield in manured ponds (10 t/ha/yr) without supplementary feeding (Hopkins and Cruz 1982). However this performance fell dramatically within two years and growth rates fell to 40% of those of the local stock. The cause was thought to be the contamination of the strain with wild *O. mossambicus* and the possibility that the original strain was actually a hybrid between *O. aureus* and *O. niloticus*.

Similarly growth of the Philippine tilapia was similar to that of the Taiwanese red tilapia (a cross between *O. mossambicus* and *O.niloticus*). The colouration is controlled by a single gene where normally pigmented and white fish are homozygous and red fish heterozygous (McGinty 1983). When the growth rates of the F3 inbred generation were studied it was found that they were lower. This was possibly due to a loss of heterozygosity and to genetic combination of negative traits (Galman *et al.* 1988). Other authors have found that with the segregation of the red gene in hybrid tilapias to produce homozygous populations there was a corresponding negative influence on growth rates. This may have implications for the introduction of species into the Sepik which are likely to breed with *O. mossambicus* and have the red gene.

The transfer of tilapia species, strains and hybrids will continue to be considered acceptable where improved strains will enhance the established aquaculture practices especially for rural populations (Pullin and Capili 1988). However when the transfer or introduction of a new species could upset an established population then the importance of conservation of genetic resources should be carefully considered. Pullin and Capili (1988) suggest that all undisturbed riverine and lacustrine populations throughout Africa should be excluded from such introductions.

The natural population of fish in the Sepik has already been disturbed through the introduction of species such as *O. mossambicus*, *Cyprinus carpio* and *Gambusia affinis.* However, the further introduction of a species that is likely to breed with the existing tilapia stocks would not only upset the genetic makeup of the population but it would risk losing a genetic resource in the form of pure strains of *O. mossambicus.* In Lake Manzala, for example, the widespread transfer of stocks which have had uncertain origins and genetic background can lead to a breakdown of local species differences and will make the job of a selective fish breeder difficult (Payne and Collison 1983).

Studies on the impacts of the transfer of *O. niloticus* to Asia have concluded that the genetic diversity of cultured *O. niloticus* is low and is a poor base from which to start selective breeding programmes (Pullin and Capili 1988). The presence of *O. mossambicus* in many Asian waters is thought to have caused introgressive hybridisation with *O. niloticus* (Macaranas *et al* 1986). Previous indiscriminate introductions of tilapia, both pure and hybrid strains, has led to a loss of pure genetic strains. In the Sepik electrophoretic studies have already been undertaken on *O: mossambicus* and it has been found that this stock is a pure population of this species (Pullin pers comm). It is also known that the population has very low genetic variability and originated from the small "gene pool" introduced into Asia in the

1950's (Pullin, pers. comm.). To introduce a species which would potentially breed with the existing stocks would not enhance the fishery in the long run for the reasons described above. It would also create the loss of one of the remaining pure breeding populations in the world. The genus *Oreochromis* would not be a suitable choice for introduction into the Sepik.

7.2.3. Potential alternative species

Although *O. mossambicus* has successfully exploited the floodplain areas the stocks are, at present, fairly low in comparison to yields in similarly sized African rivers (Coates 1985). The subsistence fishery relies mostly on one species, *O. mossambicus*. Although the results of the study suggests that there was sufficient biomass to support a limited number of villages located on the floodplain there was still the evidence of protein malnutrition in the areas away from the river (e.g. Wosera) which has prompted the focus on introductions by the government of PNG. The aim is to increased the yield and provide sufficient surplus to enable these inland areas to increase the consumption of fish. This is based on the assumptions that the infrastructure will be available for distribution of fish, that the fishing effort will not decrease as more fish are caught per net, and that with a greater abundance of fish more will be consumed.

Alternative species which could be considered for introduction are based on the findings of the present study. To avoid negative impact in terms of competitive elimination for food and space and the avoidance of hybridisation, it is suggested that the species to be considered should be in the first instance a macrophyte feeder.

In order to avoid the danger of possible hybridisation with *O. mossambicus*, for reasons described above, one alternative would be to consider the introduction of a species from the genus *Tilapia*. This genus is characterised by monogamous species of the tilapias the behaviour of which is includes a long courtship period, a large number of small eggs, shared parental care of the nest, and territorial displays only when breeding. These species tend to show aggressive, rather than defensive behaviour.

Species of tilapia which are macrophagous e.g. *T. rendalli, T. zillii, T. sparmanni* and *T. tholloni,* feed on filamentous algae, aquatic macrophytes and terrestrial vegetation, e.g. leaves, plants (Philippart and Ruwet 1982, Trewavas 1983). Some species have been found to be opportunistic feeders especially where there is a lack of aquatic vegetation. In Lake Kinneret in Israel *T. zillii* is known to feed on blue green algae, *Coleoptera* sp. and chironomid pupae, and while breeding, on benthic prey (Spataru 1978). Although some of the *Tilapia* species are macrophyte feeders, all are substratum spawners, thus in terms of feeding they would not compete with *O. mossambicus* but may occupy the same spawning areas.

Both species of *T. zillii* and *T. rendalli* have been found to have a slow growth rate and excessive breeding under culture conditions, whereas, in Africa, Caulton (1979) considered *T. rendalli* to have a good potential and Gosse (1963) believed this species is superior to *T. zillii.*

T. rendalli has a larger maximum body size than either *O. mossambicus* or *T. zillii.* which would be an advantage in increasing the weight of fish caught per unit effort. Maximum body size for the three species are 450 mm (*T. rendalli*), 260 mm (*O. mossambicus*), 390 mm (*T. zillii*). Longevity for all species range from 5-10 years with 5 years being the average life span. Of the Tilapia species *T. zillii* and *T. rendalli* appear to have the greatest potential for introduction into the Sepik/Ramu river systems.

7.2.4 Abiotic and biotic influences of the Sepik environment on T. rendalli or T. zillii

i Water level fluctuations

The magnitude and occurrence of fluctuations in the water levels in both riverine and lacustrine environments may affect species which are substratum spawners such as *Tilapia* sp.. The depths at which most nests were found in the Sepik varied between 0.5-0.8 m, but were consistently above 2 m. In Sri Lanka nests of *O. mossambicus* are commonly found between 0.5 -0.8 m depth and rarely below 2 m (De Silva and Chandrasoma 1980, De Silva and Siresena 1988). A depth limitation for nest construction may be set by turbidity levels and light penetration, since courtship displays and protection of the young are visual activities. During the breeding period(s) the young and adults of these species are associated with the nesting sites, which are often located in shallow water close to the shore. Bruton and Boltt (1975) found that nearly all nests of *O. mossambicus* were to be found associated with the littoral vegetation and 75% were at depths between 0.5-2 m. Abnormal fluctuations in water levels could have serious consequences for *Tilapia* species which remain with the nests until the young are able to defend themselves (Trewavas 1983).

In the Sepik, the fluctuations in water level are fairly uniform and predictable but there have been years when the water levels were abnormally high or low (see Chapter 2). Evidence of these fluctuations can be seen in areas of the Sepik where former villages (now deserted) have been built on stilts which are 10- 20 feet above the present water level. This may also have been due in part to the uplifting which has occurred in the area. The consequences of abnormal water levels for an introduced *Tilapia* species would be in the form of loss of nesting areas, food resources and a subsequent decrease in recruitment.

Mouthbrooding species of *Sarotherodon* and *Oreochromis* are more adaptable to such conditions since the fry can be moved to deeper waters by the parents. Ruwet (1962) noted that water level fluctuations in Lake Mwandingusha, Zaire, affected *T. rendalli* to a greater extent than *S. machrochir*. Coche (1974) reported the widespread destruction of nests of *Tilapia* and *Haplochromis* species in Lake Kariba during a large seasonal fluctuation which occurred during the active nesting season. This was due to a decrease in the water level of 1.2% which subsequently exposed over 10% of the total area previously under water. The timing of the water level changes in addition to the amplitude will have significant results on production levels within a water body. The introduction of *T. rendalli* and/or *T. zillii* into an environment such as the Sepik River would subject these species to potential abnormal fluctuations in water level and subsequent loss of production if the period of reproduction coincided with the period of abnormally high or low water.

ii Competition for nesting sites

Suitable nesting sites were seldom seen in the Sepik during the period of study. This factor is thought to influence the production levels of *O. mossambicus*. Since most of the *Tilapia* species require shallow water and suitable nesting or territorial areas for breeding, the competition for sites may intensify if further introductions of *Tilapia* were attempted. The more aggressive the species the greater its success in competing for sites. *T. zillii* is renown for its aggression to such an extent that it less suitable for culture systems (Chen 1976). This species is reported to have competed with *T. rendalli* in ponds in Zaire, and in Lake Victoria has also out competed *S. variabilis* (Gosse 1963).

O. mossambicus, O. niloticus and *T. zillii* require specific substrates and vegetation for breeding (Ita 1978). *T. zillii* and *T. rendalli* are known to breed throughout the year, especially during the rainy season, in temperatures over 20^{deg}C (Bardach *et al* 1972, De Silva and Chandrasoma 1981). Both species build nests in shallow water associated with a sandy substrata and marginal vegetation. *T. zillii* is thought to have more specialised requirements in terms of substrate and vegetation. *T. rendalli* will produce a series of smaller holes in which to deposit eggs whereas *T. zillii* builds a single nest 1 metre in diameter. In tilapias the period to hatching and first feeding is shorter than that of *Oreochromis sp.* and the fecundity greater *(in T. rendalli* 760-6160 eggs are produced by fish of 18.8-25.8 cm). There would therefore be potential competition for nesting sites in the Sepik.

The characteristics of the substratum has an important influence on the numbers of nests constructed. In areas where there is a predominance of steep slopes in the reservoirs of Sri Lanka (Pakrama Samudra) nests are seldom found (De Silva 1985). In the Sepik very few nesting sites were found in the areas studied but were found in clusters or arenas as described by Fryer and Iles (1972) and Lowe-McConnell (1956) for *T. variabilis.* These areas were shallow (< 1.0m) with a muddy substrate close to the littoral vegetation, a pattern also found by other authors (Welcomme 1970, Lowe-McConnell 1975). The presence of the vegetation would provide cover for the mouthbrooding females and alevins prior to their entry into the fishery.

In the present study nest sites in the Sepik were only discovered as the water receded, since the turbidity of the water precluded direct monitoring throughout the year (Chapter 5). Lack of nesting areas may be a constraint to production levels since the number of nests in an area is thought to be related to the population size (Ruwet 1962). Nests of all sizes were found in one area contrary to the findings of De Silva and Siresena (1988). These authors found that nest density ranged between 0.47 and 6.31 per m^2 and were from 11 - 110 cm in diameter. Small (10 - 50cm) and large nests (>50 cm) were found at different sites. In the nest area studied in the Sepik, smaller shallower nests were found on the periphery of the area and in smaller numbers. This may be due to the displacement of the less dominant and/or smaller individuals with lower fecundity (De Silva 1985).

iii Potential competition for food resources

Both *T. zillii* and *T. rendalli* are macrophyte feeders although they are both known to consume "aufwuchs" i.e. attached periphyton, bacteria algae and detritus. In many tropical waters where the competition for food is intense *T. zillii* is a strict macrophyte feeder. However, in other areas with less competition for other food sources this species will consume plankton and benthos (Lowe-McConnell 1982). In Lake Kinneret in Israel *T. zillii* can also assimilate blue green algae. *T. rendalli* consumes *Ceratophyllum demersum* in preference to other plants but will also feed on *Panicum repens* and aquatic grasses if available. *T. rendalli* prefers waters with dense growths of aquatic plants. In addition to consuming macrophytes and detritus it may also injest aquatic and terrestrial insects which may compete with other species in the river (see Chapter 4). The juvenile stages of both *T. rendalli* and *T. zillii* feed on invertebrates and algae and may compete for food with juvenile *O. mossambicus*.

T. rendalli is known to be a voracious feeder and a 200 g fish is reported to be able to consume 3.3 g dry mass equivalent of *Panicum repens* per day and a 100 g fish can injest up to 2.2 g of food per day (Caulton 1977). This is compared to an algal feeder such as *O. niloticus* which consumes just over 2.0g/day at a weight of 200g. Because the assimilation efficiency (AE) (amount assimilated/amount ingested x 100) of macrophyte feeders is fairly low (approx. 50), large volumes of plant material are required to obtain sufficient nutrients for growth. Although the assimilation efficiency increases with temperature (increase of 18.6% efficiency from 18-34^{deg}C) the energy required for catabolic processes also increases, thus at increased temperatures food intake also increases.

Area	Result
Madagascar	established in numerous lakes and rivers but has seriously perturbed the ecology of Lake Kinkony (Lamarque *et al.*, 1975)
Mauritius	introduced for fish culture in 1956, it escaped into rivers and reservoirs where it was described as having a serious negative effect on indigenous flora and fauna (George 1976)
Sri Lanka	well established in natural waters where a vacant ecological niche existed (Welcomme 1979)
Thailand	at first well established in natural waters, then progressively regressing and disappearing, possibly due to competition from local species (Welcomme 1979)
Brazil	reared intensively in the northeast and central southern areas, established in natural waters notably Lake Pinheiro in Brazilia and in numerous hydro-electric reservoirs in Sao Paulo State: many reports of overpopulation and destruction of vegetation (Nomura 1976, 1977)
Colombia	cultivated in ponds and established in natural waters in the Valle del Cauca (1000m - 1400m) transfer to other regions prohibited until the effect on the ecosystem was known (Nomura 1977)
Peru	cultivated in ponds and established in certain lakes (FAO 1977)
Bolivia, Paraguay	cultivated in ponds (FAO 1977)
Mexico	cultivated in ponds to 1500 m, central and southern regions (FAO 1977)

Table 7.3 Impact of introductions of *T. rendalli* outside Africa (after Philippart and Ruwet 1982)

T. zillii is an aggressive species which competes successfuly for nesting sites but also has a slower growth rate and is not utilised by fish culturists. Both species also require shallow water and a similar substrata to *O. mossambicus* for spawning and nesting which may create competition if such sites were limited in the Sepik.

The consequences of introductions of both *T. rendalli* and *T. zillii* are described in Table 7.3). The main negative impact on the environment caused by *T. rendalli* has been due to its voracious feeding habits. In Mauritius (George 1976), Brazil (Nomura 1976, 1977), and Madagascar (Lamarque *et al.* 1975) *T. rendalli* is reported to have had an effect on the ecology of the waters through either overpopulation, destruction of vegetation or through disturbing the dynamics of biotic environment. It is reported that in Madagascar *T. rendalli* was accidentally introduced and subsequently destroyed 3000 hectares of *Ceratophyllum* and *Nymphaea* in a period of three years and as a result one valuable species of indigenous fish *Paretropus petiti* was almost wiped out (Lamarque *et al.* 1975).

There is insufficient background information on these previous occurrences to determine whether a detrimental effect in the Sepik would occur with the introduction of a species of *Tilapia*. It is not known to what extent the environmental conditions at these previous locations resemble those in the Sepik. The Sepik is likely to be a much larger ecosystem, with more variable habitats and ecological conditions than in the previous instances where the detrimental effects of *T. rendalli* introductions are known to have occurred.

The potential impact of introduced tilapia species on the biotic environment in the Sepik should be considered carefully. Both *T. zillii* and *T. rendalli* are capable of destroying large areas of vegetation (*T. zillii* has often been used as a weed control agent). In addition to consuming vegetation there may also be a direct effect on the food resources of *O. mossambicus* since this species feeds to a large extent on epiphytic algae which may be associated with the food source of *T. rendalli* and *T. zillii*.

In addition, there will also be an effect on the primary productivity of the system if macrophytes and associated algae are significantly removed. If this happens the effect on the rest of the food chain may be considerable. The potential loss of aquatic and terrestrial insect habitats may result in the removal of the main source of food for other species of fish in the basin. However, it must be realised that these are potential and not probable results of introducing another exotic species into the basin, since the Sepik is a large and very varied ecosystem and may easily to absorb such introductions without any detrimental effects to the environment.

7.3 Summary and Recommendations

The initial establishment and success of *O. mossambicus* in the Sepik river can be attributed mainly to its ability to occupy and exploit a habitat not utilised by other species, that of the floodplain. There is little or no competition for food resources and there are no major predators which have any impact on the mortality rates. It is unlikely that *O. mossambicus* has had a major impact on any of the other species in the river since the majority of indigenous species in the river are not adapted to floodplain conditions. However due to the lack of data on the ecology of the river system prior to the introduction of *O. mossambicus* it is difficult to state categorically that this is the true historical situation.

In terms of stocking the floodplain, there are socio- economic considerations which must be taken into account. These are outlined in this report and elsewhere by the Sepik River Stock Enhancement Project (FAO) and relate to whether or not it is necessary to stock in this area at present in view of the socio-economic constraints on the development of the fishery. Decisions on these factors rest with other bodies.

The evidence obtained in the present study on the biology and ecology of *O. mossambicus* in the Sepik, suggests that the stocks are not as plentiful as was previously estimated. In 1978 it was estimated that the potential yield from the floodplain could be as high as 40,000 tonnes with an estimated catch of 8000 tonnes from the subsistence fishery (Glucksman 1978). The results from the present study indicated that the actual subsistence catch is substantially lower. In addition, to even equal the average African catch the fishing effort would have to be increased by 30 times, which is both unrealistic and not feasible.

The previous attempts to develop a commercially based fishery were not successful. There is evidence that during this period there was a possibility that stocks could have been over-exploited and/or more likely, that the stocks may have been limiting the development of the industry. The yields of *O. mossambicus* that were thought possible were never realised at any stage during the project.

If the decision to introduce another species of tilapia to enhance the *O. mossambicus* stocks of the floodplain areas is positive then there are certain recommendations and points that should be raised. These include:

a. Other species of *Oreochromis* should not be considered due to the potential hybridisation with *O. mossambicus* and subsequent problems that may arise (see section 7.2).

b. If a macrophyte feeding species were thought desirable then either *T. rendalli or T. zillii* might be appropriate. Each of these species have different attributes which can be appraised accordingly by the project.

c. It should be noted that both *T. rendalli* and *T. zilli* have the potential to create ecological disturbances if introduced into the Sepik River. The likelihood of this occurring should be considered carefully by the project advisors and other experts in an appraisal of the introduction of either of these species. Severe detrimental effects are unlikely since the Sepik has a wide range of habitats and is probably able to absorb an introduced species. However, the potential for ecological disturbances cannot be ruled out since both *T. zillii* and *T. rendalli* are both voracious macrophyte feeders. If substantial amounts of macrophytes are systematically removed then there may be a subsequent effect on the rest of the food chain through the removal of epiphytic algae (food for *O. mossambicus*), habitats for invertebrates (food for the endemic species of fish) and an ultimate reduction in primary productivity.

d. There are also major socio-economic decisions which must be made in the near future on whether commercial fish production is to be developed in the Sepik basin. At present there are sufficient stocks to support a subsistence fishery only. Any further development towards a commercial production either in the short term or in the future will have to consider at this time the possibility of introducing an exotic species into the river system.

e. If stock enhancement is carried out using a species of tilapia then there should be an awareness that with such species there is a tendancy to overpopulate and stunt if not regulated. If the fishing pressure is low and the stock present in greater quantity or there are few intrinsic control mechanisms there is the potential that the population may become stunted.

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