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PAPUA NEW GUINEA

Report on the biology and ecology of the introduced tilapia *Oreochromis mossambicus* (Peters) (Pisces:Cichlidae) in the Sepik River, Papua New Guinea, and the social and economic impact of its introduction.

A report prepared for project PNG/85/001
Sepik River Fish Stock Enhancement Project

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1. INTRODUCTION

1.1 Papua New Guinea-geological history

The actual landmass of New Guinea and the smaller islands lie between the two major plates, the stable continental plate of Australia to the south and the deeper Pacific basin to the north (Coates 1989). 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. These mountain ranges effectively create two different zoogeographic zones in the northern and southern regions of New Guinea. Freshwater fish fauna in the two regions are distinct, the southern species shown a resemblance to the fauna of northern Australian whereas those in the north show a high degree of endemism (Allen and Coates 1989).

1.2 The Sepik River System and faunal evolution

The Sepik River system is amongst the largest in the world and is 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). The area drained by the Sepik is substantial (78,000 km^2) 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 October to April/May.

The catchment area is characterised by greywake, siltstone and conglomerate interbedded to marine volcanics and limestone whereas the lower floodplain area is characterised by lavas overlaid with alluvial sediments (Coates, Osborne and Redding 1983). The floodplain of the lower section is the main fish production area although they form only 10% of the total catchment area.

Although the larger river valleys, those 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 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 drifted/split from the area known as "Gondwanaland" before the evolution of the major groups of true freshwater fish species.

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, Melanotaeniidae and Theraponidae). 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).

1.2.1 Formation of the Sepik Basin.

This basin was possibly formed by the process of downwarping caused by compressional forces between the Continental and Pacific plates between which 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 (Coates 1989). 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.

Archaeological evidence from floodplain sites 70 to 600km 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 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.

1.2.2. Yield of the Sepik Floodplain

There is thus a general poverty in terms of freshwater fish species in northern New Guinea compared to rivers in Africa and South America. In the Sepik 58 species from 35 genera and 23 families have been described (Allen and Coates 1989). This can be compared to many more species in similar river systems in Africa.

Coates (1985) estimated that the floodplain fishery yields between 3000 and 5000 t/yr of which 50% of the catch would be the introduced species Oreochromis mossambicus. The total yield from the river is far lower than catches expected in African rivers (10%). Since the natural fauna of the river represent only half of the catch then the actual difference between the potential of the Sepik and an African river is smaller (5%) (Coates 1985).

2. HISTORY OF TILAPIA IN THE SEPIK

The introduction of tilapias has been fairly 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) (Figure 1). Many of these introductions were to stock ponds from which the fish inevitably escaped. Tilapia mossambica was introduced into Papua New Guinea in 1954 and has since been renamed Sarotherodon mossambicus. This species is a maternal mouthbrooder and is now referred to as Oreochromis mossambicus (Trewawas 1983). Initially the species was introduced into Papua New Guinea specifically for pond culture but was never successful due to the problems with overbreeding and stunting of the population.

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 began to establish 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 became particularly abundant and was in sufficient numbers 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 fish from gill netting (4-5 inch stretched mesh).

Despite the initial enthusiasm the industry never reached its projected levels and has since decreased production to minimal levels. Section 3 describes the history and decline of the industry in terms of its socio-economic impact, the problems which evolved and the possible reasons for its decline.

3. THE SEPIK ARTISANAL FISHERIES AND "SOLPIS" 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 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 outmigration in the country (Skeldon 1977). The population centres are mainly clustered along the banks of the Sepik River and in the more upland areas around Maprik - Yangoru and the western coastal fringe. Recent estimates have indicated that 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 population centred on and around the Sepik floodplain is estimated at 80,000 and is the poorest in the province. The recent 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 genuine 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). Much of this land is now used for rubber plantations and vegetable crops. Many of the settlements along the river rely on sago, fishing, minimal vegetable crops and coconuts for food (Curtain 1978). Soil fertility is poor and consequently crop yields are low thus the nutritional status 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. A popular protein source is imported tinned fish but, because of the poverty levels in the Wosera, a family will only consume one 15 ounce can, per household of 6, per week. This is compared to the national average consumption of 2.1 (15oz) 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 5yrs old.

There are also problems with protein malnutrition mainly 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.

It was not until the latter part of the 1970's that efforts were made to enhance the socio-economic status of the

Sepik area by exploiting one of the few resources, that of fish. The initial effort was towards establishing some form of 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.

As mentioned earlier Oreochromis 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. The events that followed the escape of these fish into the main river system became the basis for the first attempt at producing commercial quantities of fish in the Sepik basin.

Between 1964 and 1974 there seemed to be a meteoric increase in the population of O. mossambicus to the extent that 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, it assumed that the catch rate for the fisherman studied was constant throughout the year and that all able bodied persons fished and captured the same amount as the sample 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 proved to be difficult. Various 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 setting up 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 (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 number of 4-5 inch (10.16mm stretched mesh, 50 mesh deep x 100m length) gill-nets being 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). 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). The same author estimated that each 100m net was regularly catching 28 kg of O. mossambicus. If we assume that these nets were approximately 2.0m in depth then the catch would be equivalent of $140g/m^2$ in 4 inch mesh nets.

In the later study, 1981-2, this amount was never reached and the maximum catch rate recorded was $93.49\ g/m^2$ from a 3 inch gill net. The mean catch rates for all sized nets were much lower. It is possible that these early estimates were rather optimistic and did not take into account the fact that catch rates for O. mossambicus vary throughout the year and that area and year class recruitment each year is dependant, to some extent, on the area of floodplain inundated during the wet season in previous years.

By 1981 81% of the salted fish production was from 4 main villages on the upper Keram. According to Rodwell (1982) these villages were using all their resources for fishing thus the amount of salted fillets produced could not be increased even if the price for fillets was raised. The salted fish production in 1981 was 10.3 tonnes, a somewhat lower figure than the 350 tonnes envisaged by Glucksman (1978) for the fifth year of the project.

At no time were the projected levels of production ever reached (Table 2). The maximum amount produced in one year was 40.3 tonnes in 1979, a shortfall of 84 tonnes and the amount produced since this time has decreased rapidly. 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 is discussed below.

The comparison of project revenue and project costs is given in Table 3. 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 be to increase the production of salted fillets. This in itself would be difficult, firstly because of lack of interest and loss of contact with many of the villages and secondly, there may not be the stocks present to support a greater fishing effort.

The influx of tinned fish has already provided a popular economic alternative to salted and fresh fish. The present price for a fresh tilapia caught in a 4 inch net is approximately 40 toea (34 pence). If the mean weight for a fish is 350g, then the price per kilogram of fresh fish is K1.14. In comparison, a 15 ounce tin of fish is approximately 75 toea which is equivalent to K1.65 per kilogram. If we consider that a fresh fish needs to be gutted, deboned and headed, then a tin of fish is probably a more economic 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 were to increase considerably and more fish were sold in the main markets then the prices for fresh tilapia may 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 per kilogram as opposed to the market price, at that time, of 40 toea per kilogram. The number of fishermen and villages involved subsequently tended to lose interest in processing fish.

Another factor which is quoted as having an effect on the salted fish programme was the emergence of the aquatic weed Salvinia molesta. Although the weed may not have affected the actual amount of fish in the river it did hinder access to, and movement of, the nets. Curtain (1978) estimated that the weed reduced the activity of the fishermen by 30%. It is also interesting to note that after the initial success of the biological control programme for Salvinia, despite the reduction in the amount of the weed present, the production of salted fish continued to decline. 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.

There are several possible reasons for the industry failing to produce the amount predicted some of which have been mentioned above. Other factors which could have influenced the decline are as follows;

a. The basis of predictions

The initial estimates of the potential production from the Sepik were high and may have been based on the a good catch in 1975 which may have been related to the largescale flooding which occurred in 1973 (Coates et al. 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. 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). In the Sepik O. mossambicus was possibly the only species affected by the higher water levels since most of the other species do not utilise the floodplain to any great extent thus the increase in abundance was readily apparent in this species.

Thus with a relatively good recruitment of juveniles coinciding with the increase in the use of more efficient fishing methods (gill-nets), the catch rates would have seemed to be substantially higher during this period. Previous estimates may have been made during this period of increased fishing effort and relatively good catches. These earlier estimates were also made in only a couple of areas where catch rates are traditionally higher and thus may not have been representative of the whole area. In the later study of 1981-2 the four areas studied showed significant differences in catch rates. The areas adjacent to the floodplain with relatively shallow water had far greater catch rates compared with the deeper ox-bow lakes.

b. Fishing effort

In 1981, when the latest economic review was carried out the greatest amount of revenue for the project was from the sale of gillnets (56% of income). 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 (Table

4). 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 an 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 waters of the Sepik were being overfished through the sudden influx of standard 4 inch stretched mesh gillnets and that the maximum sustainable yield (MSY) was rapidly reached and exceeded during the first few years (1973-78).

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.

c. Intrinsic population controls

An alternative possibility is that the meteoric increase in the population of O.mossambicus on the floodplain could have brought into effect density dependent factors which controlled the actual total population. If there was then a sudden, intense and very selective fishing effort which concentrated on the breeding sized fish then the population would not have had the time to respond in the normal way and increase the recruitment rate.

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.

The other factor, in the case of the Sepik, is that there were no other fish which were important or fished as heavily during this period. Thus the whole effort was concentrated on the one species. If this is the case then the fishing effort may have exceeded the MSY and the population is now declining. 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.

However, the above points are only suggestions, before any concrete answers can be obtained an appraisal of the population of O. mossambicus in terms of the biology, ecology and population dynamics had to be undertaken. This was the objective of the study which began in 1981.

4. THE BIOLOGY OF OREOCHROMIS MOSSAMBICUS IN THE SEPIK RIVER

The history of the introduction of O. mossambicus into the Sepik River has been discussed elsewhere in this report. This section deals with the biological and ecological conclusions drawn from an extended period of study from 1981 to the present.

The study on the populations of O. mossambicus in the Sepik was centred on the main areas of fish production in the middle section of the river. The four main areas fished every lunar month are described in detail by Coates (1986) and briefly included:

a. a deep fairly isolated ox-bow lake which was connected to the river by a small channel only (Imbuando),

b. a long established ox-bow lake with a shallow sample site and abundant growth of the water lily Nelumbo nucifera. The village on this site was once the major salt-fish producer for the area (Magendo 1),

c. a more recently formed ox-bow lake which opened directly into the main river channel and was adjacent to the floodplain site described below (Magendo 2), and

d. an area of floodplain adjacent to Magendo 2, which was only inundated during the wet season from December to May. At other times the vegetation was burnt down by the villagers to create a clear area (Pit Pit).

The other occasional sampling sites are described by Coates (1986). The monthly gill net fleets were set in all areas described. Nets of 25 - 45 metres in length and stretched mesh sizes of one to six inches at half inch intervals were used. In addition market surveys were regularly carried out in order to assess the relative importance of tilapia in the fishery.

4.1 Species composition of the catches.

O. mossambicus accounted for 30.2% of the overall weight of fish caught. The species composition of the various mesh sizes of gillnets is shown in Table 5. In terms of the useful (commercial) catch O.mossambicus accounted for almost 50% of the catch. In the market the same species also accounted for 65% of the weight of fish passing through the market. This demonstrated the importance of the species not only in the subsistence fishery but also it terms of the commercial catch.

The catch rates showed a marked seasonality both in the market and the study areas (Figures 2 and 3) and varied between the areas fished. Shallower sites (Magendo 2 and Pit Pit) adjacent to the floodplain tended to yield more fish than the deeper roundwaters (Imbuando and Magendo 1) although the fish from the latter sites were larger, on average (Table 6).

O. mossambicus were 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 metres 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 12m although in this study smaller fish were never caught in the bottom set gillnets.

Before discussing the actual catch rates obtained during this period of study the theoretical yield possible in the Sepik is estimated. The formulae used are based on those formulated from work on African river fisheries (Welcomme 1979).

4.2 Theoretical yield estimates

The Sepik river is fairly unique in that it does not conform to theoretical yield formulae that have been successfully used on African rivers. In many African, South American and Asian rivers the yield can be related to morphological and edaphic parameters (Welcomme 1979, 1985). One reason for this discrepancy lies in the geological history of the region which lies east of "Wallace's 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 here and the species diversity is low in comparison (61 species throughout the whole basin).

It is both possible and necessary for management purposes to make an approximate yield estimate based on several methods. Theoretical yields based on the relationship between catch (C) and basin area (A) (km^2) have been proposed by Welcomme (1985). If the formula $C = 0.44A^{0.90}$ is used for the Sepik floodplain ($A = 78,000km^2$) then the theoretical catch would be approximately 11,500 tonnes per year. This formula however is based on rivers whose flooded area exceeds 2% of the basin area. The Sepik floodplain covers approximately 10% of the flooded area, thus this yield estimate would be considered low. If the Sepik was a normally exploited floodplain, the yield would be expected to be in the region of 40-60 $kg/hm^2/yr$ or 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 Welcomme's (1979) formula;

$$C = 3.87\ (0.91^N)$$

where;

C = catch
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). It is now estimated that there are 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.

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 of 44,000 tonnes quoted by Coates (1985), based on comparisons with African rivers.

Coates (1985) based his catch data on figures obtained from the commercial salted fish project and used the area producing most fish, the villages supplying the majority of fish and the fishermen who had the greatest fishing effort throughout the year. The results were far short of catch rates for even the average catch by African fishermen (0.44t as opposed to 3.87t for the average catch in Africa). The difference may be in the effort used but based on the findings of the study, to achieve such results would entail an unrealistic increase in fishing effort.

4.3. Actual catch rates during 1981-83

The catch rates were related to the level of water in the river and hence on the floodplain with greater catches during the periods of low or falling water levels when most of the fish were concentrated in the deeper waters (Figure 2 and 3).

Catch rates in the basin were generally low in comparison to the yield obtained in African rivers. The greatest catch was from Magendo 2 with a total weight of 197.12 kg of tilapia caught over the whole period. From all of the four sites studied a total of 364.73 kg 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 (107.966kg). 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 107.966/185 = 0.583 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 0.583 x 200 = 116.6 kg/yr. If one fisherman were to set 8 nets for 200 days per year then the total catch would only be 932 kg/yr (0.932 tonnes).

To achieve a yearly catch comparable to the average yearly landings of fishermen in Africa (3.87 tonnes for all species- see Coates 1985) the fishing effort would have to increase to an unrealistic level. To equal the average yearly African catch, a Sepik fisherman would have to increase the fishing effort and set approximately 33 nets for a period of 200 days per year. Since the distribution of O. mossambicus in the Sepik is not uniform, this effort would have to be further increased in the less productive areas. This represents an unrealistic increase in fishing effort in order to equal the amount of fish caught in other river systems.

Even if all fishermen were supplied with 33 nets there may not be the stocks to support this effort. There is little potential, therefore, for a viable commercial fishery in the Sepik based solely on tilapia.

The introduction of another species of fish could provide a greater yield with little increase in effort and would thus be beneficial to both subsistence and commercial fishermen.

4.4 Market surveys

Market surveys at the time revealed that there was an increase in numbers of fish being sold in April, May and August and September. The fish originated from several areas including Magendo and a larger ox-bow lake areas called

Kamabaramba.

More recently (1989) a brief market study (in Angoram) revealed that the mean fish size being sold in the market appeared to be smaller than that of 5 years ago and that the majority of fish were being caught in one major area only (i.e Kambaramba - an area not studied during the 1981-83 survey). Gillnet sizes now used are between 2.5 and 3.5 inches whereas in 1978 it was reported that the usual size was around 4.0 inches (Glucksman 1978). During the period of study the maximum biomass of O.mossambicus was caught in 4.0 inch mesh, although the greatest numbers were caught in the 3.0 and 3.5 inch mesh nets. Although there seemed to be a surplus reaching the market in Angoram there would still be insufficient fish to supply all the areas in need.

4.5 Population movements

The general conclusions from the catch data and the market surveys were that during the flood season O. mossambicus moves onto the floodplain and becomes less accessible. In the Sepik basin it is O. mossambicus which utilises the floodplain to a far greater extent than any of the native species. Figure 3 illustrates that this species shows a movement from the floodplain (Pit Pit) to areas of more permanent water such as the ox-bow lakes (Magendo 2) at the beginning of the dry season.

Observations on the GSI, gonad states, breeding and feeding behaviour show that the shallow water areas are important breeding and feeding habitats for this species. Similar findings have been reported for O. mossambicus in South Africa (Bruton and Boltt 1975) for T. lidole in Malawi (Lowe 1953) and for T. macrochir in Lake Mweru (Carey 1965).

Although there is evidence of a movement of fish from the floodplain site to the more deeper water it is not in the form of a mass population movement. There are important differences between the behaviour of the males, females and juvenile fish. The males built nests in the shallow littoral areas but not on the floodplain itself. The main nesting site found in this area was in a depth of water averaging 0.8-1.0m on a fine, silty mud substrate. Nests were constructed in areas which were unlikely to dry out during the fluctuations in river level during the wet season. Females moved into the nesting areas during the breeding seasons for spawning then retreated to the nursery areas, further into the floodplain, to brood the young. Nursery areas tended to be inaccessible, thus juvenile stages could not be monitored at regular times during the year.

The variation in the catch rates on the floodplain site (Pit Pit) could be related to its proximity to one of the main nesting sites of the area. During March there was a significant fall in the catch rate of both males and females. This could be due to either adult fish moving onto the nesting sites outside the area or the influx of juveniles or a combination of both. The floodplain site dried out in May/June as the water level receded. There appeared to be a general migration of fish into the adjacent Magendo 2 site at the same time. There was also an increase in the catch rates at the same site during February / March / April which could represent the influx of "ready to breed" adults onto the nesting areas.

It appears that the juveniles remain hidden in the inaccessible areas of the floodplain until they reach a mean size of 125mm. In Lake Kariba juvenile O. mossambicus are reported to enter the fishery at a similar size and are thought to be in the third year of life (Krupka 1974). In Sri Lanka juveniles are reported to enter the fishery at a length of 180-210mm and were considered to be two to three years old (De Silva and Fernando 1980). Thus, there is a delay between the peak breeding period and the emergence of recruits, although the entry of the recruits to the fishery seems to occur at the same time of peak breeding. In Magendo 2 there was an increased catch in the smaller meshed nets (1, 1.5 and 2 inch mesh) in the latter part of May and in June and July the mean length at this time also decreased (Figure 4).

In the floodplain site (Pit Pit) the mean fish length fell in February and March (Figure 5). This suggests that the smaller fish are moving from the floodplain site to the deeper water. The mean length in the Pit Pit site in March was below 150mm and in April the mean length of fish in Magendo was just above 150mm which may be a result of the movement of younger fish from one site to the other.

It has been suggested that juveniles remain in the shallow vegetated areas of the floodplain to avoid heavy predation in the more open water areas. In the Sepik, however, there are few natural predators of O.mossambicus (except Man), which was a significant factor in its initial success on the floodplain. It is likely that the dietary requirements of the juvenile fish are a major factor in determining the habitat preferences at this size.

4.6 Food and feeding

4.6.1. Feeding structures

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.

Recent studies on the functional significance of the microbranchiospines found on the second, third and fourth gill arches were inconclusive. It is thought that they play an incidental role only in filter feeding and protection of the gill filaments (Beveridge et al. 1988). Much of the mechanical breakdown of the food occurs in the pharyngeal cavity. 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, Caulton 1976).

4.6.2 Food

The floodplain is an important feeding area, since during inundation the submerged and emergent macrophytes provide a source of epiphytic diatoms and algae as well as vegetable matter. O. mossambicus was found to be feeding on a variety of autochthonous material in the form of epiphytic and benthic algae, diatom species including Synedra sp. and Nitzschia sp., pieces of macrophyte (which may have been incidental to the ingestion of the epiphytic algae) and detritus. In the shallow areas the diet also included benthic diatom species whereas in the deeper ox-bow lake sites the main food items included epiphytic diatom species, algae and detritus. The more shallow water 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 was an important part of the diet.

The substrate in the deeper areas 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. With the abundance of food in other areas these regions would be avoided as a food source.

Juvenile stages were found to be feeding on diatoms and invertebrates, primarily insect larvae such as Cladocera. Green et al. (1978) found that juvenile (8-18mm) O. mossambicus in Java were feeding on zooplankton, as well as cyclopoid copepods, rotifers and ostracods. A similar finding was reported by Le Roux (1956) where juvenile (5-7.5cm) O.mossambicus in freshwater ponds were feeding mainly on Entomostraca.

Both juveniles and adults are reported to be opportunistic feeders (Schuster 1956, Neil 1966, Man and Hodgkiss 1977). Preliminary analysis of stomach contents in the Sepik fish indicate that there may be differences in the quality of food consumed in different areas.

4.6.3 Feeding and Stomach Fullness

Stomach fullness can be related to the condition factor and was significantly higher for fish on the floodplain compared with those in the adjacent round waters (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 in this area when it is covered in water (Figure 6). The mean stomach fullness tended to decrease as the water began to recede in March-May on the floodplain site (Pit Pit) (Figure 6). The pressure for food would be greater at this time since it appears 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 for specific months as there would be an expected delay between fullness and the increase in condition. Compared to Oreochromis mossambicus populations found in Lake Sibaya, South Africa (Bruton and Boltt 1975), the general condition of the fish was good.

4.7 Condition Factors and Gonadosomatic Index (GSI)

The condition factor (K) gives an idea of the general condition of the fish and can be related to breeding and feeding activities. Brooding females do not feed during the period of egg incubation. Therefore we would expect that the condition factor for females would be related to the breeding cycles. In Magendo 2 the K values appeared to be higher during the flood season when food is abundant on the floodplain (Figures 7 and 8) but the results were not conclusive for either sex. Differences in stomach fullness between high and low water periods were statistically significant for the females only (t-test, $p<0.05$). The males fed continuously throughout the year. The fluctuations in K values for the females tended to follow the fluctuations in the gonado-somatic index (GSI) (Figures 9 and 10).

When the GSI was high, indicating increased breeding activity, the K values were generally lower. The GSI and K values for females in Magendo 2 (see Figure 9) were compared over the same time period. The results suggest the K values were low when the GSI values peaked i.e. in December 1981, March 1982, May 1982 and January 1983. However, prior to these periods there was an increase in K values. This indicates that females were in good condition prior to breeding to enable survival during the period of non-feeding whilst brooding eggs.

The general fall in condition during May 1982 could have been due to two factors. Firstly the decrease in the water levels and the reduction in food availability and secondly, the influx of juveniles feeding on the same food source. Prior to entering the fishable population juveniles are reported to feed, almost exclusively, on invertebrates.

4.8 Reproduction

The breeding pattern of many of the tilapia species is related to the form of parental care exhibited (Wittenberger and Tilson 1980). O. mossambicus are polygamous mouthbrooders which originated in the eastern coasts, lakes and rivers of East Africa as far south as the Bushmans River near Port Elizabeth (Bruton and Boltt 1975, Philippart and Ruwet 1982).

4.8.1 Minimum breeding sizes

The minimum size at maturity for females was between 141-160mm whereas for males this was 161-180mm. The size at which the majority of females and males were in stage 5 was 181-200mm and 201-220mm respectively (Figures 11 and 12). There is usually a distinct sexual dimorphism, with the males of the same age being larger. O. mossambicus will reproduce prolifically given abundant food and space and has the tendency to overpopulate. This leads to overcrowding, reduced growth rates and small sexually mature fish.

In Lake Sibaya, South Africa the minimum size for sexually mature females is 68mm and males 104mm (Bruton and Boltt 1975). This is a reflection on the low mortality and high recruitment in a population where the nutritional quality of food is inadequate. Studies in pond situations on the other hand have found that excessive feeding rates resulted in reduced growth rates of O. mossambicus (Java strain) (Shell 1978). Thus stunted populations could occur in environments that are either food-rich or food-poor and where mortality rates are low.

In the Sepik, although natural predation is low, there does not seem to be evidence of stunting or overcrowding. Fish in the local markets are being sold at smaller sizes but this may be a reflection on the smaller meshed gill-nets now being used.

4.8.2 Breeding seasons

Breeding occurs throughout the year with distinct peaks 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). Fish movements, condition, feeding and breeding do not have a distinct pattern. Rather, they show trends which are irregular in nature. This may be due to the rather erratic nature of the changes in water level in the Sepik River. There is no precise distinction between wet and dry seasons as found in a monsoon climate; at both high and low waters there are always fluctuations occurring.

Figures 11 and 12 show the numbers of fish in the various stages of maturity. Generally stages 4 and 5 are ripe and running ripe respectively and stage 6 is spent. The calculation of the gonadosomatic indices for both males and females indicated that there were several peaks throughout the year for both sexes. The distinct peaks for females in Magendo 2 occurred every two or three months with the maximum peaks being in December 1982 and January 1983. The majority of females with a GSI over 1.0 were found in May, this is probably due to the migration of the females from the floodplain to the nesting sites at this time. Generally, females showed continuous breeding patterns with GSI falling in the interim periods. The results suggest that the main breeding periods were in December/January 1982, March 1982, May 1982 and again in December/January 1983.

GSI levels showed much smaller peaks in August and November which is the period of low water and presumably when less food is available. Figure 13 indicates the percentage of females at each stage of maturity throughout the year and can be correlated to the GSI and periods of breeding activity. The results supported the view that breeding occurs throughout the year since during the study fish were found in ripe and running ripe stages (Figure 13).

4.8.3 Nesting sites

Nesting appears 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 <u>Scirpus littoralis</u> and <u>Potamogeton pectinatus.</u> The floodplain itself is not a common nesting area because of the great abundance of vegetation and the periodic drying out of large areas during minor fluctuations of the high water levels.

A more recent aerial survey showed that nesting sites were more abundant than originally thought but may still be a constraint to production. In addition, the river is constantly changing course and either permanently exposing potential sites and creating others in different areas. In the last five years the river has changed course significantly and the original nesting area studied in 1981/2 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 returns to the same area to spawn each year the changing river pattern would upset the breeding cycle. This would need to be studied in more detail before any conclusions could be drawn.

Nests found in these areas were not uniform in size as found by De Silva and Sirisena (1988) in Sri Lankan reservoirs. In the Sepik, nests were found at a depth of 0.8-1.5m at mean peak flood and were, on average, 1.0m in diameter. Smaller nests were found 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). The nesting sites were only seen from the boat when the water level decreased and exposed the area. It was difficult to assess to what depth the nests extended. It would be logical to conclude that males build nests close to the main floodplain in areas which would not dry out until after spawning.

4.8.4 Fecundity and the breeding cycle

Fecundity measured per 100g of female body weight was low (520) compared to species of fish which do not exhibit any form of parental care.

It has been found that in the reproduction of one strain of O. mossambicus (Philippine red tilapia) there is a correlation between the weight of females and the number of larvae produced. Older females (3-5yrs) of over 500gms produced between 1200-3000 eggs whereas the younger females (4-24 months and 40-200g) gave an average of 300-500 eggs per spawn. However, the spawning frequency of the older fish tended to decrease in number from once every 3 weeks to every 4-6 weeks (Galman et al. 1988).

Ovaries taken from the Sepik tilapia were found to contain both primary and secondary ova. This is thought to be related to the number of spawnings throughout the year. Aravindan and Padmanbhan (1972) found various stages of oocytes and oogonia in the germinal endothelium which they considered to be material for successive spawnings.

Bruton and Boltt (1975) found that the 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 mouth after approximately 10-14 days (Vaas and Hofstede 1952, Russock and Schein 1977). For 20-22 days the fry will remain in, or in the vicinity of, the female's mouth before entering the floodplain vegetation (approximately 9mm SL) where they remain until large enough to enter the fishable population (approximately 125mm).

De Silva and Fernando (1980) reported that juvenile O. mossambicus enter the fishery at a total length of 180mm 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 125mm. In the Sepik the age at first capture has not yet been determined but it is thought that during the dry season the juveniles less than 125mm are actually in the deeper waters but smallest mesh nets are unable to capture them. Hand netting in the littoral areas during the period of draw-down did yield a small number of juveniles less than 125mm. Brooding females were seldom caught since there is a tendency for the females to eject fry or eggs from the mouth when caught. A few times fry were founded in the mouth of the female and these individuals ranged in sizes between 7-11mm.

4.8.5 Sex-Ratios

There was a generally greater proportion of males in the catches both on the floodplain and in the adjacent round waters (Figure 14). This supports the idea that the females move into more protected areas whilst brooding. It was not possible to sample the nursery areas regularly but fry caught in these areas were found to be over 30mm. In addition, the site at Magendo 2 was a major nesting site where males tended to be in increased numbers throughout the year. Bruton and Boltt (1975) found that at certain times of the year brooding females were found in large shoals in the shallower waters. This was thought to be an adaptation to predator pressure. This phenomenon was not seen in the Sepik in the areas studied but this may be due to the lack of predators.

4.9 Summary

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 areas, whether introduced (Reidel 1965, Hodgkiss and Man 1977, 1978, Man and Hodgkiss 1977, 1977a, De Silva and Chandrasoma 1980) or naturally occurring (Bruton and Boltt 1975, Bowen 1979, Bruton 1979). In other environments where there has been a vacant ecological "niche", this species has been able to establish and form a stable population, thus augmenting local fishery resources (Man and Hodgkiss 1977, 1977a, Hodgkiss and Man 1977,1978).

From these results the possible reasons for the success of the species in the Sepik Basin can be postulated and the potential constraints that may be operating to prevent the increase in the stocks can be implied. From this, it is also possible to suggest the areas of vulnerability of O. mossambicus to further introductions of exotic species.

5. REASONS FOR THE SUCCESS OF O. MOSSAMBICUS IN THE SEPIK

5.1 Niche exploitation

Much of the work carried out in the Sepik basin has been in establishing the niche occupied by the fish species already present and in identifying possible vacant niches within the system. The concept of the "niche" has often been described as a characteristic of the environment rather than a quality of the species within the ecosystem. All too often the assumed niche requirements (the fundamental niche) of an introduced species, based on its natural habitat, has proved to be different to the "realised" niche adopted in a new environment. The niche occupied by one species is seldom distinct since interactions between species will occur and these interactions are fundamentally variable. Svardson (1976) proposed that there is a hierarchical nature to the standing crops in lakes and that the removal or alteration of the more dominant species tends to have drastic results on the rest of the population.

The productivity of any body of water is dependent on the level of energy entering the system through primary production and allochthonous sources. 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 simply resulted in a change in the composition of the catch rather than an increased yield.

In many Southeast Asian lakes and reservoirs the introduction of O. mossambicus has been correlated with an increased yield in the water body. 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 niches which can be readily occupied by better adapted lacustrine species 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. O. mossambicus was therefore able to successfully utilise this niche and in a very short time the population biomass was sufficient to support an artisanal and commercial fishery.

For the purpose of this report interactions of the native fauna with O. mossambicus would only occur if there was an overlap in niche requirements. The species which could be interacting 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 inundation (Coates 1989). All three species have distinct food preferences, G. multisquamatus being primarily a carnivorous species which consumes a wide variety of small invertebrates, Op. aporos is primarily insectivorous and Ox. heterodon feeds on Op. aporos. In contrast O. mossambicus feeds on detritus, epiphytic and benthic diatoms and algal species (Table 7). None of these species are known to be predators of O. mossambicus and other piscivorous species tended to be restricted to the main river channel.

Piscivorous species are not found on the floodplain except Ox. heterodon which only preys on Op. aporos and no major piscivores occur in the main river channel. Therefore, there are no abundant predators of O. mossambicus.

A full review of the biology and ecology of the other species in the Sepik River can be found in Allen and Coates

(1989). None of the other Sepik species, except for those mentioned above, utilise the floodplain to any significant extent.

5.2 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 the movement of brooding females to the sheltered areas would naturally avoid a high mortality due to predation and other factors. In the Sepik, juvenile predation is considered to be very low which would theoretically lead to good recruitment if recruitment were solely related to predator levels.

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 181-200mm for females and 201-220mm for males. This can be compared to findings in Sri Lankan reservoirs where the mean size at maturity for females is 160-210mm (De Silva 1986). This implies that the population in the Sepik is not stunted. The mean length at maturity L_m has been found to vary between populations (Lowe McConnell 1982, De Silva 1986) and could be correlated to the body condition of the fish, and the size of the water body (De Silva 1986).

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). If this is the case then the area of the Sepik in which O. mossambicus could inhabit is huge. However, evidence from this study indicated that this species is found in relatively shallower areas since catch rates for the deeper ox-bow lakes and the main Sepik River were minimal. Catch rates were highest for areas adjacent to the floodplain indicating 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 water body may be much smaller than originally realised.

5.3 Breeding seasons

O. mossambicus was found to be breeding continuously throughout the year in the Sepik with two or three periods of peak reproduction. These corresponded to the higher water periods when food is plentiful and the 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 low. This would lead to reduced breeding activity and subsequent periods of lower recruitment. This would influence the catch rates throughout the year in addition to the influence of the water levels on fishable stocks.

Few of the indigenous species of fish utilise the floodplain for breeding purposes thus O.mossambicus has, in effect, the whole floodplain to itself. It is the only species to utilise the shallow areas for nest building and is the only nest builder anywhere in the river at lower altitudes.

5.4 Mortality

5.4.1 Predation

Other authors have suggested the reasons for the success of O.mossambicus in other areas is 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 large biomass of O. mossambicus in Sri Lankan reservoirs. However, in the Sepik there are few potential predators. Most of the ariid catfish do not utilise the floodplain and in fact show a positive avoidance of this habitat. Only A.nox exploits the floodplain to a very small degree. 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 are limited to the eleotrid Oxeleotris heterodon, which has been found to selectively consume Ophieleotris aporos and not O. mossambicus.

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 to a significant degree, therefore there may be other factors operating which are regulating the recruitment patterns and the biomass of the population.

5.4.2 Fishing pressure

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 species which are captured. These fish are usually the older, slower growing fish with a slower reproductive rate, although in the case of O. mossambicus these fish had generally higher fecundity within the Sepik.

The 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. During the period of the 1981/3 study catch rates in the floodplain areas were highest in the 3.5-4.0 inch gillnets. The gillnets of 3.0-3.5 inch mesh are now catching the largest numbers of fish (although larger meshes are still used). These observations may point to a situation where the species is showing signs of being overfished although the evidence is inconclusive.

The idea that the population is showing signs of stunting is ruled out since the minimum breeding size correlates well with other populations where stunting is not occurring. If fishing pressure is low and recruitment high and the population is not showing signs of stunting, although the mean sizes caught are slightly smaller, there are two opposing hypotheses that could be put forward. Firstly, the population is still at a period of exponential growth and the MSY is far from being reached or, alternatively, there are other factors restricting the recruitment e.g. a lack of nesting sites. The fishing pressure may be sufficient to have overstepped the MSY and the yield would then be decreasing, as would the size of fish most abundant.

It is very difficult to suggest which factors are operating in the Sepik since the major areas of production are patchy and tend to change with time as the river continuously changes course. It may be the case that in certain areas where the stocks are low there could be overfishing whereas in other areas where the fish is abundant there is little evidence of depletion of the stocks. To pinpoint the areas where stocks are either high or low would be a considerable and lengthy task given the size of the river and the floodplain.

5.5 Competition for food and space.

Very few of the other species of fish actually enter the floodplain areas for any reason. Most ariids are restricted to lakes and river channels so one of the major factors in the success of O. mossambicus in the fishery lies in its ability to exploit the floodplain without competition. The more recent appearance of the common carp in the system does not pose a threat to the tilapia since this species has a different habitat preference.

O. mossambicus is probably the major species in the river which uses the floodplain extensively. Only three of the native species are found in any numbers here. These are Oxyeleotris heterodon, Ophieleotris aporos and Glossolepis multisquamatus. None of these species are predators of tilapia and none have the same food preferences (Table 7). The main food source for adult O. mossambicus is epiphytic and benthic algae, detritus and mulm (periphytic aggregate). 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 are unspecialised in their feeding habits (Allen and Coates 1989).

The majority of the native species consume invertebrates (terrestrial and aquatic) of one form or another (Table 7). The only other species which exhibit similar food preferences to O. mossambicus is Zenarchopterus kampeni but this species does not utilise the floodplain to any extent. Food for the adult O. mossambicus during the flood season is therefore abundant. This species is also known to be able to change its food preference depending on availability. It can also digest blue-green algae commonly found in planktonic vegetation, zooplankton, phytoplankton and detrital material (Maitipe and DeSilva 1985, DeSilva 1985).

In this study the stomach contents did appear to vary between the different areas sampled. The background levels and composition of epiphytic and detrital algae are as yet unrecorded but may be a rich source of food and the basis of the initial success of both adult O.mossambicus and the other introduced exotic, Cyprinus carpio. It is recommended that further studies on the nutritive value of the food source, both epiphytic and detrital, be undertaken.

Juvenile O. mossambicus exhibited a preference for invertebrates as a food source as well as diatom species for the first few months of life. Once they enter the fishable population the food preferences change to an adult diet.

It is not clear whether juvenile O. mossambicus are in competition with other species of fish for invertebrate food sources. The other species of fish which occupies the floodplain in any numbers is Ophieleotris aporos the diet of which is mainly invertebrates. If competition occurs and if the standing stock of invertebrate fauna is found to be low, then this would be a considerable constraint to increasing the recruitment rates. The initial success may have occurred as juveniles began exploiting a food source of which there was a certain surplus; once the surplus is consumed there is little possibility of support for a larger population of juveniles. This is all speculation at present.

6. TILAPIA IN LOWER ORDER STREAMS

Although previous studies were restricted to the main floodplain areas of the Sepik, later studies on the biology of O. mossambicus in the lower order hill streams indicate the plasticity of this species with respect to adaptations to the environment.

The later work concentrated on fish populations in the tributaries of the Sepik/Ramu systems at various altitudes (see Van Zwieten 1989). Although much of the data still requires analysis, several comparisons can be made between the stocks of O. mossambicus on the floodplain and those found at different altitudes.

In general fish stocks are low in the tributaries and there is an absence of fish above 800-1000 metres, the exception being two species of eel, Anguilla bicolor and A. marmorata. O. mossambicus is not found above altitudes of 300m and at elevations above 100m this species does not reach sizes greater than 120mm. This can be compared to the maximum size of O. mossambicus on the floodplain of 380mm. The altitude preferences may be a reflection on factors such as the vegetation, temperature, and stream gradients.

In rivers and streams with gradients above 0.1m/m O. mossambicus were not caught. This species was found mainly at gradients between 0-0.05m/m which indicates its preference for slower flowing waters with fairly stable substrates. This type of environment is suitable for the growth of food material such as macrophytes and associated epiphytic algae as well as benthic algae and detritus. The presence of suitable substrates for nesting sites will also affect the distribution of this species. Streams without soft substrates would not be suitable unless there were areas of slower flowing water within the system.

There are strong indications that stunting occurs in O. mossambicus populations with increases in altitude. Evidence to support this is shown in the smaller size at maturity seen with altitude (Table 13). The presence of fish in all stages of maturity indicates that these are resident populations and are not individuals migrating from the floodplain. The smallest female found in stage 5 (running ripe gonads) had a total weight of 13g and a length of 67mm. This size of fish would be considered a juvenile in the floodplain and fish of this size were never found with ripe gonads in the Sepik. Whether the smaller size also represents a younger age at maturity will be decided at a future date when otolith and scale readings can be carried out.

Table 14 indicates that the maximum size decreases with altitude and the maximum size of fish at 240m is almost half that of fish at 40m. The difference in maximum weight between 240 m and 40m is even more distinct (124.6 g at 40m and 14.5g at 240m). With altitude there are indications that the actual range in size of fish decreases. At 40 m there was a 60% increase in size from minimum to maximum whereas at 240m this difference fell to 33%. This may indicate a situation where at higher altitudes the larger fish have been removed from the population. This fact was supported by villagers who had noticed that over the last few years the size of fish they were catching had decreased notably.

At both altitudes the minimum size of fish caught decreased (90mm at 40m and 53mm at 240m). These results indicate that fry are not being caught in the streams in either situation. Fry will probably be hidden in the floodplain vegetation at the lower altitudes whereas at higher altitudes the general lack of vegetation will favour still pools as habitats for the fry. Samples were not taken from these pools but in areas where there were pools there were smaller fish present. Although at the higher altitudes the maximum and minimum size of fish caught decreased this may not represent a difference in age if stunting is occurring. Alternatively, fish may leave the juvenile habitats at a younger age at higher altitudes if there is a lack of suitable food, thus, fish may either change from a juvenile to adult diet at a younger age or a younger size. The answer to this question will become apparent after a more comprehensive study of otoliths, scales and stomach contents.

There is also evidence that both biomass and numbers of O. mossambicus also decrease with altitudes above 120m (Van Zwieten 1989). Thus, fish at higher altitudes are not only in smaller numbers but are also too small to be of much nutritional or commercial value.

The danger is then, that at the higher altitudes fish stocks will be more susceptible to over fishing given that there is a considerable fishing pressure on a few main species, of which O. mossambicus is one, and that there are few alternative protein sources.

Stunting in a population may be an adaptation to several environmental factors, overcrowding and/or poor nutritional value of the food or competition for a food source. In the higher order rivers and streams most of the indigenous species are generalised feeders with a large part of the diet being composed of invertebrates. None of these species feed on detritus, filamentous or benthic algae. A preliminary analysis of the stomach contents of O. mossambicus indicated that adults and juveniles were consuming a proportion of different food items in different areas although filamentous and benthic algae and diatoms were found in most stomachs.

Juveniles were found to be consuming a range of food items. Fish smaller than 50mm had stomachs and hind guts containing invertebrates. In one area Cladocera formed almost 90% of the stomach contents whereas a similar sized fish in another sample site had large amounts of algal filaments and invertebrates in the form of chironomids rather than Cladocera. Some of the larger adults also consumed invertebrates (usually chironomids) but these fish were in rivers above the floodplain which had little vegetation and algal biomass. The ability of O. mossambicus to inhabit lower order streams with little vegetation may be due to an increased consumption of invertebrates rather than algae in adults. This could relate to the findings of Dudgeon (1989) that a greater biomass of invertebrates occurs at higher altitudes.

In the floodplain itself there were no invertebrates in the stomachs analysed, although these samples do not represent a very large proportion of the samples collected. A more detailed analysis will be undertaken in the future.

There is, therefore, little evidence of competition for food between the indigenous species and adult tilapia. Juveniles in which the main food item is Cladocera would have little competition from the indigenous species since there are no examples of the latter consuming Cladocera (Van Zwieten 1989a). However there may be competition between O.mossambicus and other species which consume other species of invertebrate such as chironomids and insects.

In terms of the effects of O. mossambicus on the indigenous species in the river this is difficult to assess and would require an extended period of study of all the sample sites throughout the year. There seems to be little effects on the composition of the native species.

The importance of O.mossambicus in the subsistence fishery in hill streams has been described by Mys and Van Zwieten (1989). In areas where O. mossambicus was found to be an important part of the diet the biomass in the rivers sampled was very low. This could be a result of overfishing since in the lower order streams only a few species are consumed. These include O. mossambicus, Ophieleotris aporos and Glossamia gjellerupi. There is, therefore, a fairly intense fishing pressure on these species in areas where the human diet is distinctly lacking sufficient protein. It is, therefore, a priority to consider these areas important for restocking since there are few alternative sources of protein and insufficient infrastructure at present to allow for the transport of surplus fish from the floodplain.

7. AREAS OF POTENTIAL VULNERABILITY OF SEPIK O. MOSSAMBICUS IN RELATION TO FURTHER SPECIES INTRODUCTIONS

7.1 Effects of introductions of other tilapias in general

In the search for a species of fish that will not only provide an acceptable source of protein but one which will also complement the existing stocks within a water body there are several fundamental questions to be asked. The choice of species must be based on biological, social and financial considerations. In aquaculture, fast growing, deep bodied species with a good food conversion ratio and a high market price are preferred. In a riverine fishery an abundance of market sized fish with little fishing effort is the main criteria for a successful operation. In monoculture practices the interactions with other species are often not considered since the object is to hold the fish in separate enclosures. However, there are many examples of escapees having detrimental effects on the natural population. Similarly the introduction of species into a natural systems is not without a history of mistakes.

In the last 40 years 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 up 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. Other introductions have created adverse effects on the native fishery. For example, 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 been vastly modified by 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 within Africa, including; stocking lakes where no tilapia occur, eg. T. zillii and S. spilurus niger into Lake Naivasha (Philippart and Ruwet 1982); introductions to fill an ecological niche eg. T. zillii into lake Victoria; the introduction into artificial water bodies to enable the establishment of a new fishery; fish culture in rice fields, especially in Asia; involuntary introductions as found in the Sepik river e.g O. mossambicus. Some introductions have resulted in small catastrophes.

O. mossambicus has now been introduced into Java, USA, Malaysia, Sri Lanka, Papua New Guinea, Philippines, Thailand, Bangladesh, Hong Kong, Taiwan, North Vietnam, China, Australia and Japan (see Philippart and Ruwet 1982 for details). Other examples of 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 classified 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 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 the introduction and culture is legally banned because of the fear of 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 supposedly "noxious" species (Arthington 1986). It is still not known, however, whether this species does actually have a detrimental effect on the environment in Australia.

Despite the potential negative aspects of introducing these fish, either for aquaculture purposes or for fisheries enhancement, throughout the world there is a general consensus that the tilapias could become the most important warmwater fish if basic questions such as, which is most suitable species to stock in different areas, can be answered (Pullin 1981). The choice is wide since there are 29 species of the genus Tilapia, the substrate spawners, and many more in the mouthbrooding genera of Oreochromis, Sarotherodon and Danakilia (Trewawas 1982).

The main species which have been selected as being important for aquaculture purposes are shown in Table 8. Table 9 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 countries 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.

Although these species have remarkable attributes the annual world production of tilapias remains small with less than 200,000 tonnes in 1977 and an estimated 233,000 tonnes produced in 1986 according to figures published by FAO in 1988. This figure represents less than 2% of the worlds total inland water production of fish.

7.2 Potential hybridisation and use of hybrids

The use of hybrids in aquaculture is becoming increasingly popular in terms of enhanced growth, colouration and the production of a monosex population. 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 1966). 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 for 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 misnamed species. Trewawas (1982) and Philippart and Ruwet (1982) cite cases where T. rendalli, T. guineesis, T. tholloni, and T. zilli have all be quoted as being T. melanopleura. It would be advisable, therefore, before any consideration of species for restocking are considered, to determine the "pedigree" of the species. In the past confusion over O. aureus and O. niloticus has led to the use of hybrids rather than a pure strain in research (McBay 1961).

Although there has been no hybridisation of Sarotherodon and Oreochromis species for commercial use and the likelihood of such species producing viable offspring in natural environments is negligible, 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 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 yields in manured ponds (10t/ha/yr) without supplementary feeding (Hopkins and Cruz 1982). However this performance fell dramatically within two years and growth rates fell to 40% 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). When the growth rates of the F3 inbred generation were studied it was found that the rate was lower. This is possibly due to a loss of heterozygosity and to genetic combination of negative traits (Gavlan et al. 1988). Other authors 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 that have the red gene (Gavlan et al 1988).

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.

In the Sepik it could be argued that the natural population has already been disturbed by 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 could lead to a breakdown of local species differences and will make the job of a selective fish breeder difficult (Payne and Collison 1983).

The transfer of O. niloticus to Asia is described in Pullin and Capili (1988). The conclusions drawn from Asia is that the genetic diversity of cultured O. niloticus is low and is a poor base from which to start selective breeding programmes. In addition the presence of O. mossambicus in many of Asia's waters will have led to introgressive hybridisation with O. niloticus (Macaranas et al 1986). An example of the result of hybridisation between O. mossambicus and O. niloticus is the Taiwan strain which has a characteristic red colouration. The colouration is controlled by a single gene where normally pigmented and white fish are homozygous and red fish heterozygous (McGinty 1983).

Because of previous indiscriminate introductions of tilapia, both pure and hybrid, strains, there is a danger of losing sight of the 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. 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 is thus NOT recommended for introduction into the Sepik.

8. ALTERNATIVES SPECIES OF TILAPIA THOUGHT SUITABLE FOR INTRODUCTION

Although O.mossambicus has successfully exploited the floodplain areas the stocks are, at present, fairly low compared to yields in African rivers (Coates 1985). The subsistence fishery is reliant to a great extent upon one species O. mossambicus. There are enough fish to support a limited number of villages which are located on the floodplain. However the evidence of protein malnutrition in the areas away from the river (e.g. Wosera) has prompted the idea that if another species were to be introduced the increased yield would provide sufficient surplus to enable these inland areas to increase the consumption of fish. This is rather an idealised situation since the outcome will depend on the infrastructure available to distribute the fish, the knowledge that the fishing effort will not decrease as more fish are caught per net, and that more fish will be consumed if it is made available.

Bearing the above points in mind it is possible to suggest alternative tilapias which could be considered for introduction. Based on the assessment of available niches in the Sepik basin and to avoid any possible incidence of hybridisation, it is suggested that the species to be considered should be in the first instance a macrophyte feeder.

To avoid the danger of possible hybridisation with O. mossambicus, for reasons described above, one alternative is to consider a species from the genus Tilapia. This genus contains the monogamous species of the tilapias, the behaviour of which, is characterised by the 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.

Tilapia species which are macrophagous e.g. T. rendalli, T. zillii, T. sparmanni and T. tholloni. These species feed on filamentous algae, aquatic macrophytes and terrestrial vegetation, e.g. leaves and plants (Philippart and Ruwet 1982). Some species are opportunistic especially in waters of poor aquatic vegetation e.g. T. zillii in Lake Kinneret in Israel is known to also feed on blue green algae (Spataru 1978), as well as species of Coleoptera and chironomid pupae. While breeding, this species feeds on benthic prey. Although some of the Tilapia species are macrophyte feeders, all are substrate spawners, thus in terms of feeding they would occupy a different niche to O. mossambicus but may compete during spawning for nesting sites.

The experiences with culturing species such as T. zillii and T. rendalli have been mixed. In Latin America both species were found to have a slow growth rate and excessive breeding, whereas, in Africa, Caulton (1979) considered T. rendalli to have a good potential and Gosse (1963) believed this species is superior to T. zillii. Comparative growth rates for Oreochromis and T. rendalli are shown in Table 10.

In terms of the qualities as food fish, T. rendalli has a larger maximum body size than either O. mossambicus or T. zillii. Maximum body size for the three species are 450mm, 260mm, 390mm, respectively. 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.

9. POTENTIAL PROBLEMS WITH THE INTRODUCTION OF T. RENDALLI OR T. ZILLII.

9.1 Water level fluctuations

The magnitude and occurrence of fluctuations in the water levels in both riverine and lacustrine environments will affect the species which are substrate spawners i.e. most of the Tilapia species. The depths at which most nests are found vary, but are usually above the 2m level. In Sri Lanka nests of O. mossambicus are commonly found between 0.5 -0.8m depth and rarely below 2 metres (De Silva and Chandrasoma 1980). In the Sepik, nests were found between 0.5 and 1.0 metres. 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 0.5-2m. Abnormal fluctuations in water levels could be catastrophic for species which are associated with the nests throughout the breeding period (e.g. tilapias).

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. 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 total loss of nests, food resources and subsequent production.

Mouthbrooding species of Sarotherodon and Oreochromis are more adaptable to such conditions since the alevins can be moved to deeper waters by the parents. Ruwet (1962) noted that water level fluctuations in Lake Mwandingusha, Zaire affected T. rendalli far more than S. macrochir. 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 a result of a decrease in the water level of only 1.2% which 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.

9.2 Competition for nesting sites

Suitable nesting sites were seldom seen in the Sepik during the period of study. This factor could influence the production levels of O. mossambicus.

Since most of the tilapias require shallow water and suitable nesting or territorial areas for breeding, the competition for sites would intensify if further introductions of tilapia were attempted. The more aggressive the species the greater its success in competing for sites. For example, T. zillii is renown for its aggression to such an extent that it is of little interest to Taiwanese aquaculturists (Chen 1976). This species competes with T. rendalli in ponds in Zaire and in Lake Victoria it has supplanted S. variabilis (Gosse 1963).

9.3 Specialised requirements for nesting sites.

O.mossambicus, O. niloticus and T. zillii require specific substrates and vegetation for breeding (Ita 1978). In Lake Kainji, for example, there is a distinct predominance of S. galilaeus over both O. niloticus and T. zillii for the above reason.

Both T. zillii and T. rendalli are known to breed throughout the year, especially during the rainy season, in suitable temperatures (over 20°C) (Bardach et al 1972, De Silva and Chandrasoma 1981). Both species build nests in shallow water associated with a sandy bottom and 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 one nest of 1m diameter. In tilapias the period to hatching and first feeding is shorter than in the Oreochromis sp. and the fecundity greater (in T. rendalli 760-6160 eggs are produced by fish of 18.8-25.8 cm). The possibility of competition for nesting sites has already been mentioned.

The substratum has an important influence on the numbers of nests constructed. In areas in the reservoirs of Sri Lanka (Pakrama Samudra) where there is a predominance of steep slopes 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 tended to be 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.

Nest sites in the Sepik were only discovered as the water receded because the turbidity of the water is high throughout the year. This factor itself may also be a constraint to production levels since the number of nests in an area may 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 Sirisena (1988). The aforementioned 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 (>50cm) 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).

9.4 Feeding and food relationships

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 but in addition to macrophytes and detritus it may also consume aquatic and terrestrial insects. In this respect T. rendalli has to be viewed with caution since most of the other species in the basin also consume aquatic and terrestrial invertebrates. The juvenile stages of both T. rendalli and T. zillii feed on invertebrates and algae and thus may compete with juvenile O. mossambicus.

T. rendalli is known to be a voracious feeder; a 200g fish will consume 3.3g dry mass equivalent of Panicum repens per day and a 100g fish was found to consume 2.2g 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°C) the energy required for catabolic processes also increases, thus at increased temperatures food intake also increases.

T. zillii, on the other hand, has the reputation of being an aggressive species and will compete successfully for nesting sites. This species also has a slower growth rate and is little appreciated by fish culturists. Both species also require shallow water and a similar substrate to O. mossambicus for spawning and nesting, which may create competition if such sites were limited in the Sepik.

The introduction of both these species of Tilapia is not without a few setbacks (see Table 11 and Table 12) and thus the possibility of introducing either species should be carefully considered. The main negative effects 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 upset the ecology of the waters through either overpopulation, destruction of vegetation or through disturbing the ecology. It is reported that in Madagascar T. rendalli was accidentally introduced and proceeded to wipe out 3000 hectares of Ceratophyllum and Nymphaea in three years and, as a result, one valuable species of indigenous fish Paretropus petiti was almost wiped out (Lamarque et al. 1975).

Unfortunately, there is insufficient background information on these previous occurrences to determine whether a detrimental effect of introducing a species of Tilapia into the Sepik is possible. 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 areas where the detrimental effects of T. rendalli introductions are known to have occurred.

The possibility of upsetting the ecology of a region should be considered carefully. Both of the above species are capable of destroying areas of vegetation (T. zillii has often been used as a weed control agent). In addition to consuming vegetation there will also be an effect on the food sources of O. mossambicus since this species feeds to a large extent on epiphytic algae (i.e found on vegetation consumed by 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 and as mentioned previously this may remove the main source of food for some of the 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. The Sepik is a large and very varied ecosystem and may easily to absorb such introductions without any detrimental effects to the environment.

10. CONCLUSIONS

The initial establishment and success of O. mossambicus in the Sepik river can be attributed mainly to its ability to occupy and exploit a vacant niche, 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 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 and basically 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 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 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 definitely NOT be considered due to the potential hybridisation with O. mossambicus and subsequent problems that may arise as explained in this report.

b. If a macrophyte feeder is considered 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 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 to be 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 or not 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 tendency to overpopulate and stunt if not regulated. If the fishing pressure is low, or the control on the population size, there is a potential that the population may become stunted.

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Table 11 Results of introductions of T.rendalli outside Africa (from Lowe-McConnell 1982)

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 occasionally has a serious effect on the 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, probably due to competition from local species (Welcomme 1979)
Brazil	reared intensively in the northeast and the central-south of the country and established in natural waters, notably Lake Pinheiro in Brazilia and in numerous hydro-electric reservoirs in Sao Paulo State; but many reports of overpopulation and distruction of the vegetation (Nomura 1976, 1977)
Colombia	cultivated in ponds and established in naturalwaters in the Valle del Cauca between 1000m and 1400m; but the transfer into other regions is forbidden until more is known of the effects on the ecosystems and the native species (Norena 1977)
Peru	cultivated in ponds and established in certain lakes (FAO 1977)
Bolivia, Paraguay	only cultivated in ponds (FAO 1977)
Mexico	cultivated in ponds up to an altitude of 1500m in the center and south of the country (FAO 1977)

Table 12 Results of introductions of *T. zillii* outside Africa

AREA	RESULTS
Madagascar	established in numerous ponds lakes and rivers (Lamarque et al 1975)
Malacca, Fiji	introduced and established (?)
Taiwan	little appreciated by fish culturists because of its aggressiveness (Chen 1976)
U.S.A	introduced into Hawaii (?); established in natural waters in Florida; reared commercially in geothermal waters in Idaho (Ray 1978; TVA 1978); experiments of biological control of vegetation in California but progressively abandoned because of mortalities and slow feeding activities due to low temperatures (Hauser 1977, Platt and Hauser 1978)
Europe (UK)	introduced accidentally and considered acclimatised in a canal receiving thermal effluent from an electricity station (Wheeler and Maitland 1973)

(from Lowe-McConnell 1982)

Table 13 Females in gonad stage 4 (ripe). Various parameters related to different altitudes

Alt (m)	Max size (TW) mm (g)	Min size (TW) mm (g)	MTW (g)	MSL (mm)	K	GSI
40	195(239)	107(48)	89	131	3.61	4.55
80	116(58)	86(28)	44	104	3.64	2.90
160	110(49)	75(18)	34	98	3.45	3.21
200	119(63)	73(15)	30	90	3.72	4.23
240	70(14)	55(7)	12	65	4.32	4.37

N = 195

Key:

MTW - Mean total weight (g)
MSL - Mean standard length (mm)
K - Condition factor
GSI - Gonadosomatic index

Table 14. Mean maximum and minimum size (standard length and total weight) of all females found at different altitudes

ALT	MINSL	MAXSL	SDL	MINTW	MAXTW	SDW
40	89.75	144.5	15.7	33.27	124.6	111.2
80	77.75	136.25	17.0	18.6	97.1	21.7
160	59.75	137.00	15.6	9.6	105.0	19.9
200	60.20	107.00	14.0	9.0	48.0	11.8
240	52.25	70.00	8.6	6.5	14.5	3.9

Key:

MINSL - Mean minimum standard length (mm) for all females
MAXSL - Mean maximum standard length (mm) for all females
SDL - Mean standard deviation for length
MINTW - Mean minimum total weight (g) for all females
MAXTW - Mean maximum total weight (g) for all females
SDW - Mean standard deviation for weight.

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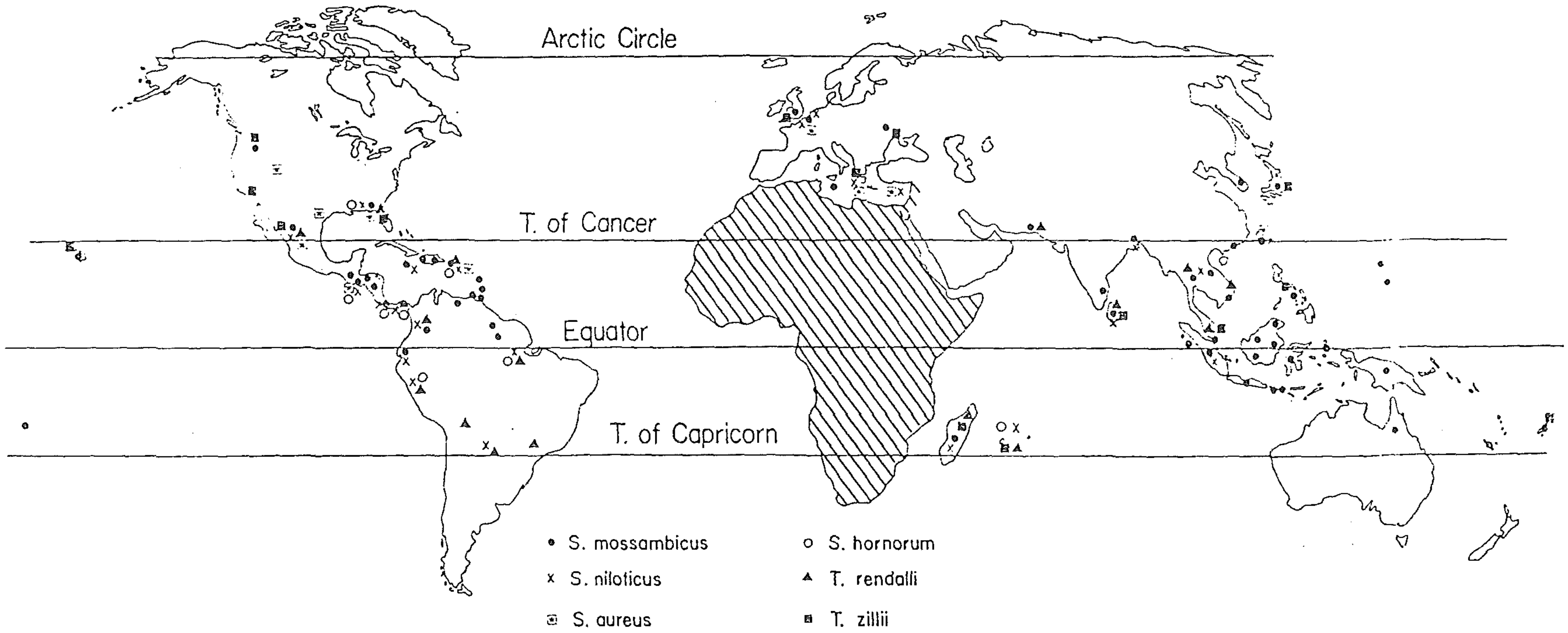


Figure 1. Introductions of tilapias outside of Africa (six main species)

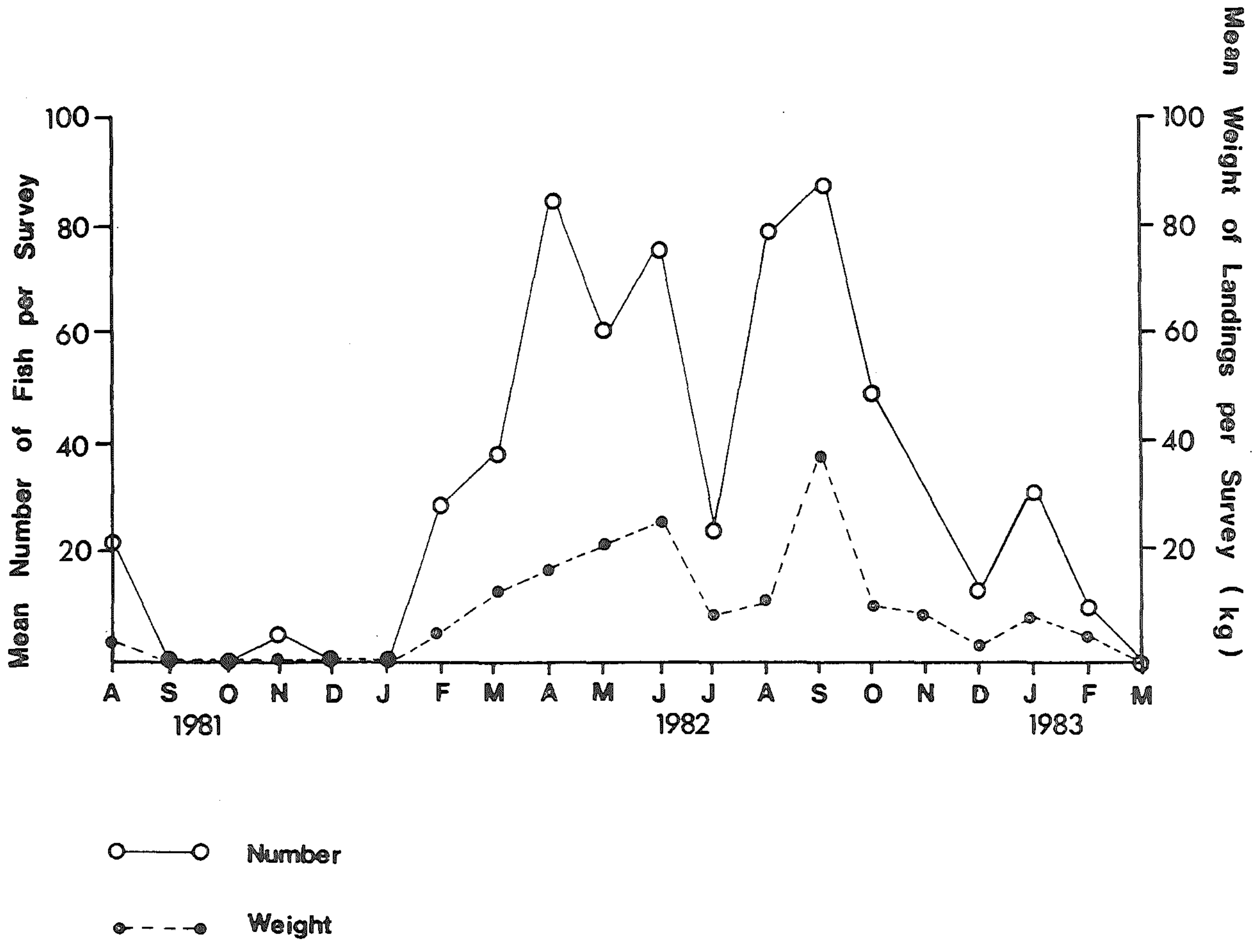


Figure 2. Recordings of <u>Oreochromis</u> brought to Angoram for sale

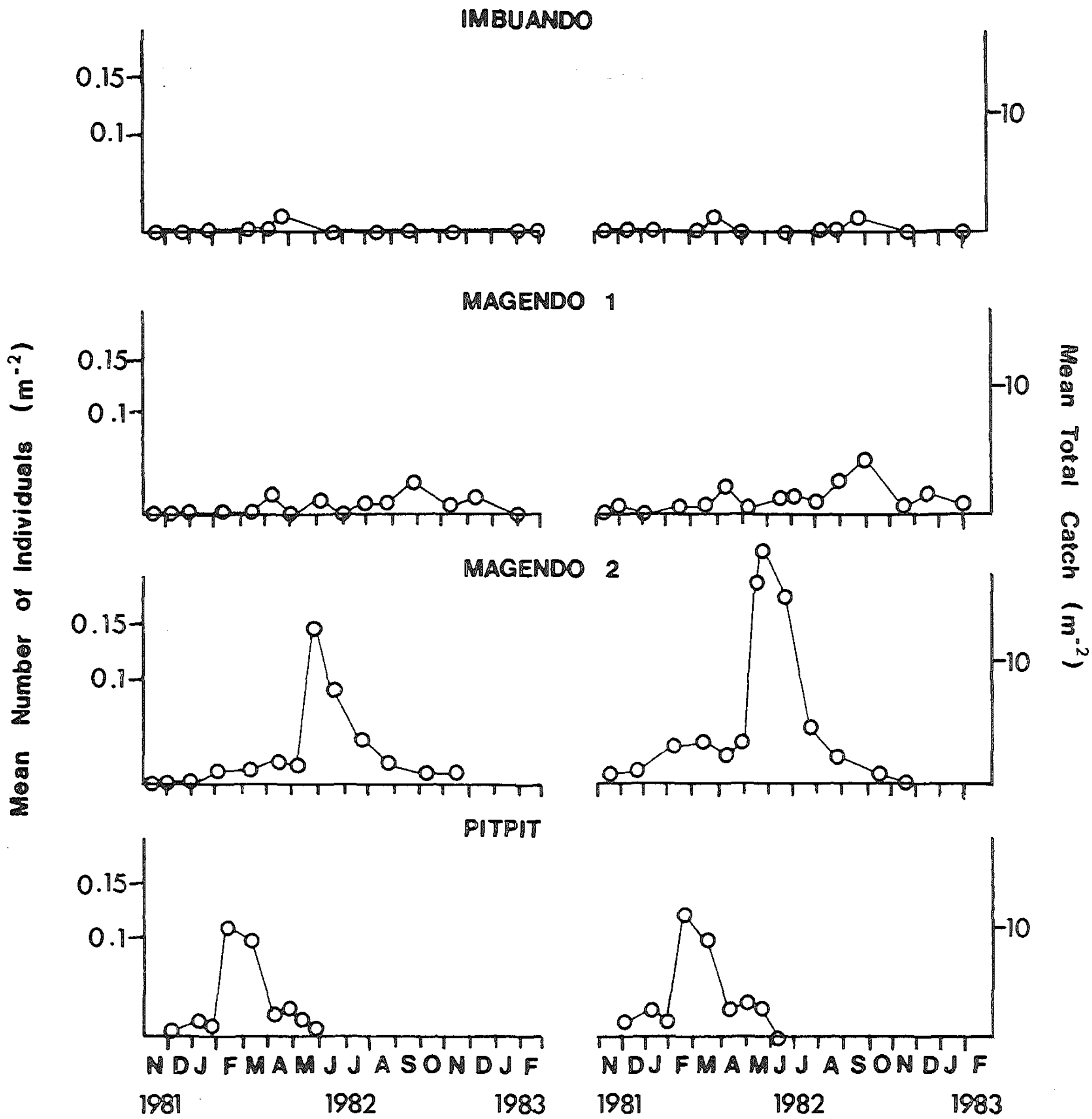


Figure 3. Gillnet catch for each of the four regular sample sites

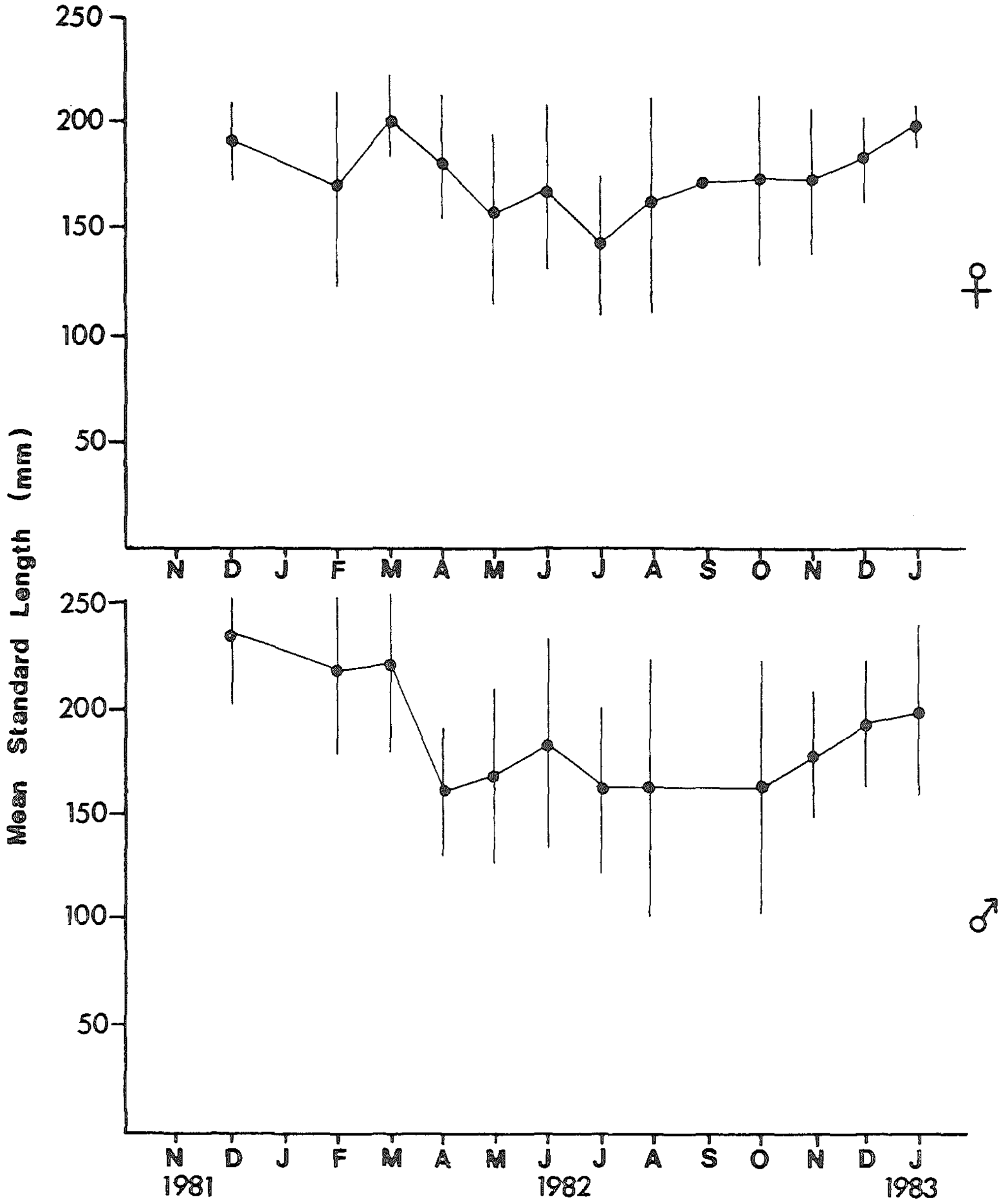


Figure 4. Magendo 2. Mean fish length over the sampling period

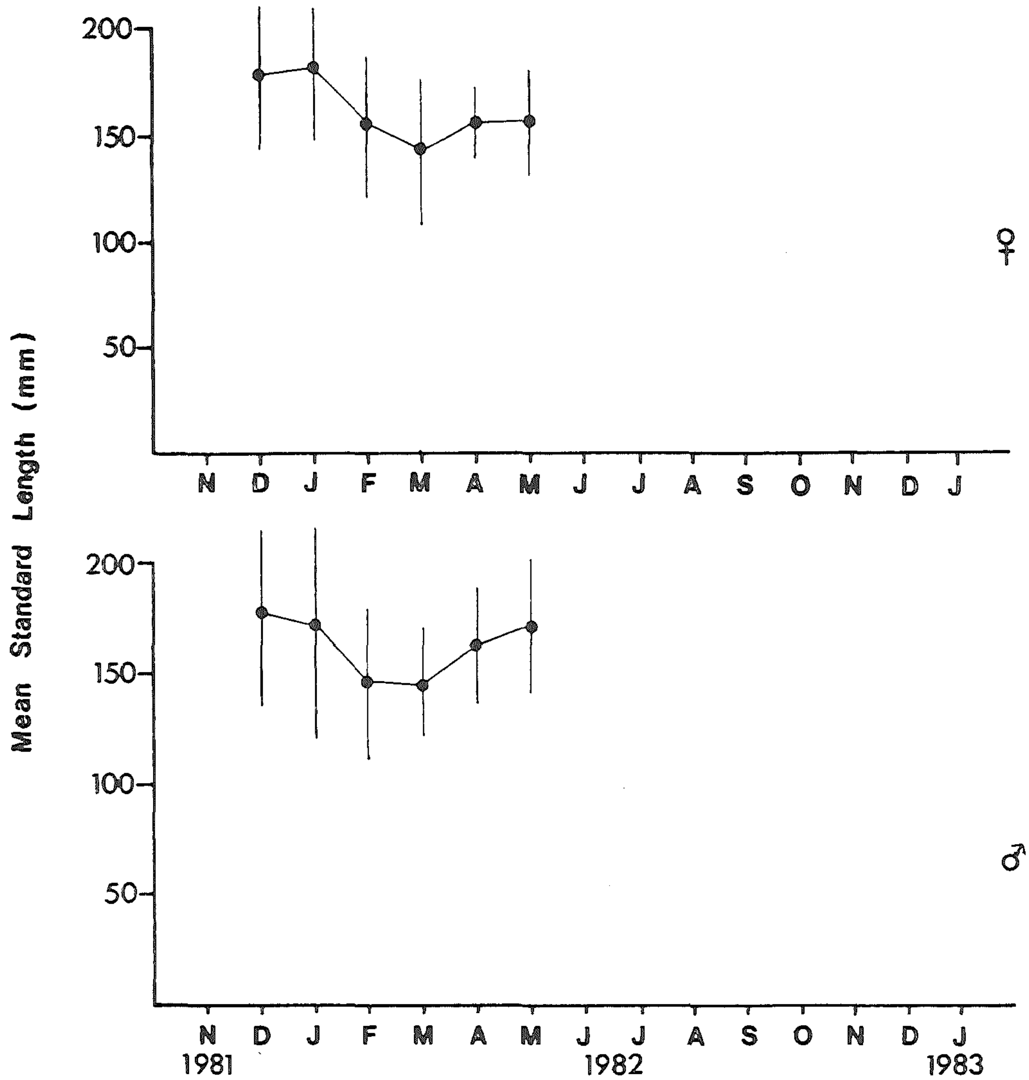


Figure 5. Pit Pit. Mean fish length over the sampling period

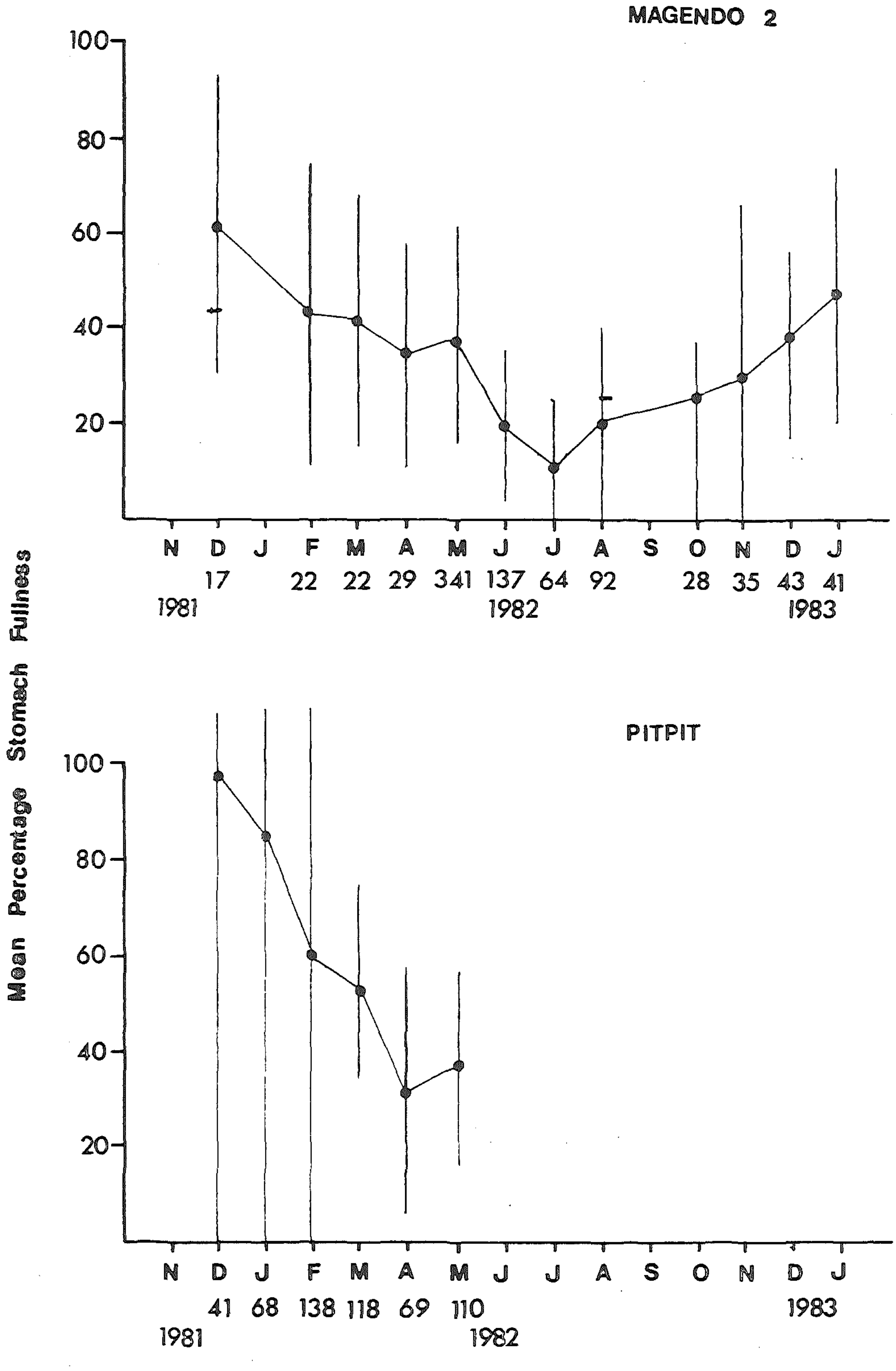


Figure 6. Mean stomach fullness over the sampling period

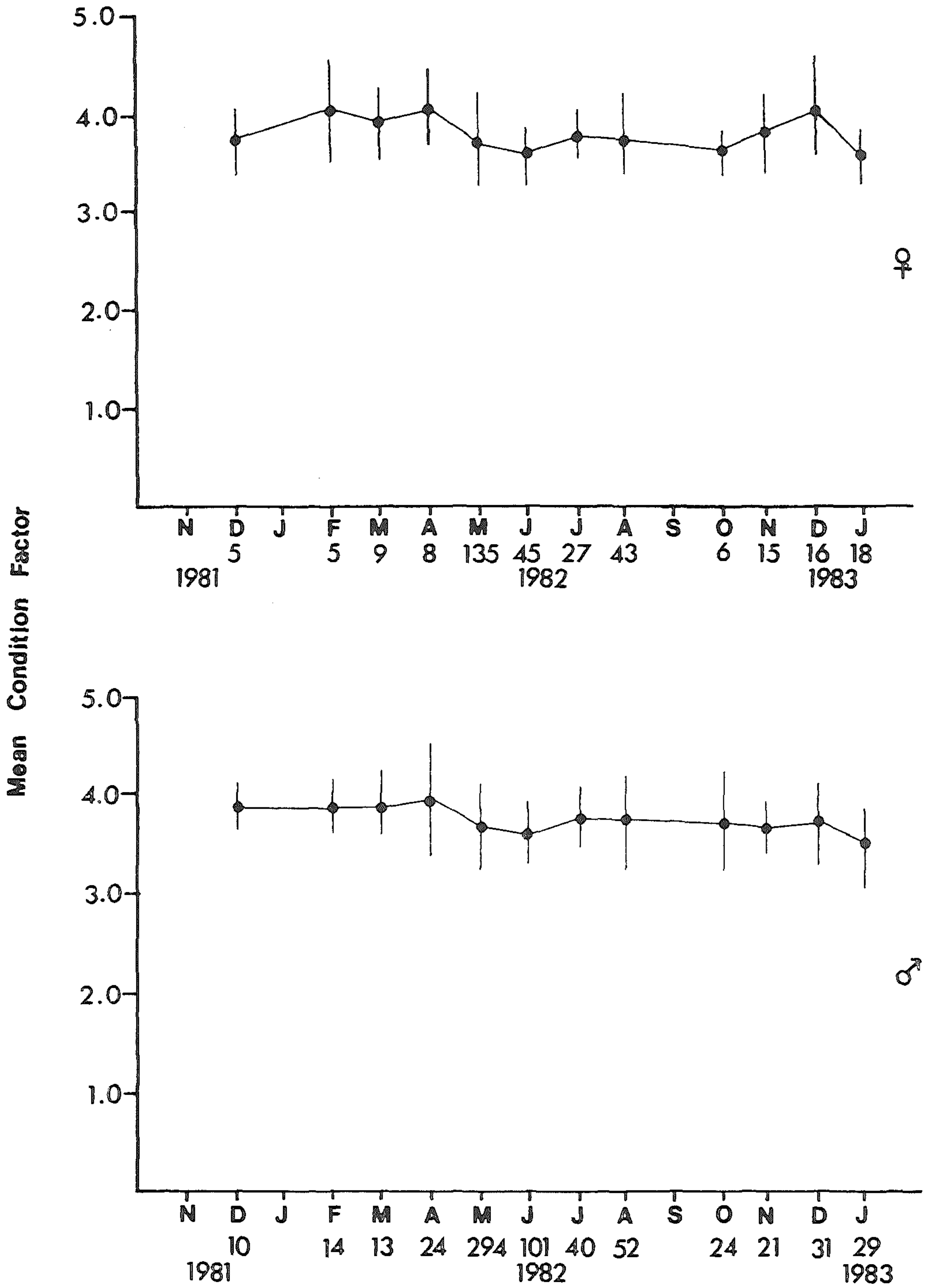


Figure 7. Magendo 2. Mean condition factor (K) over the sampling period

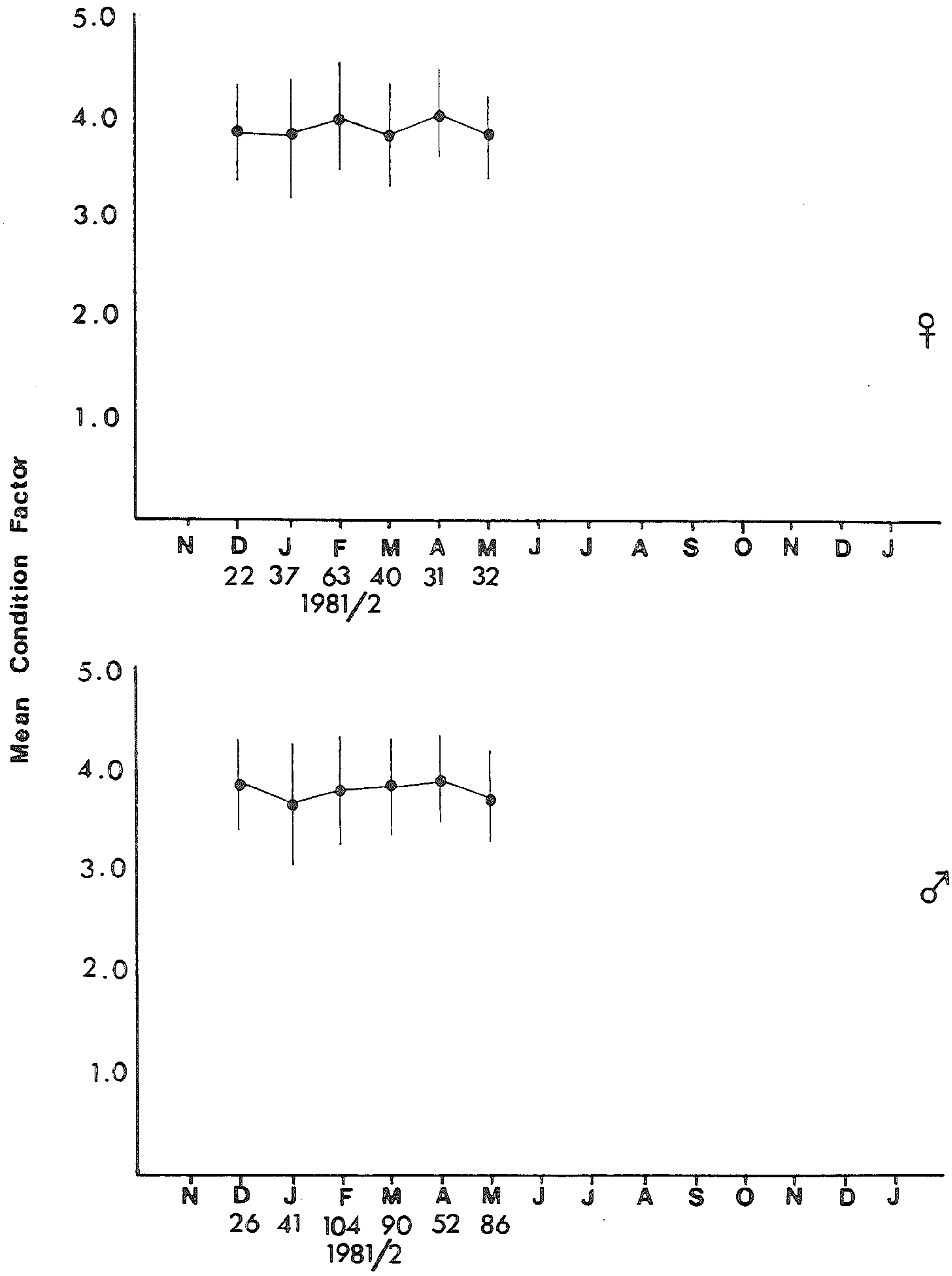


Figure 8. Pit Pit. Mean condition factor (K) over the sampling period

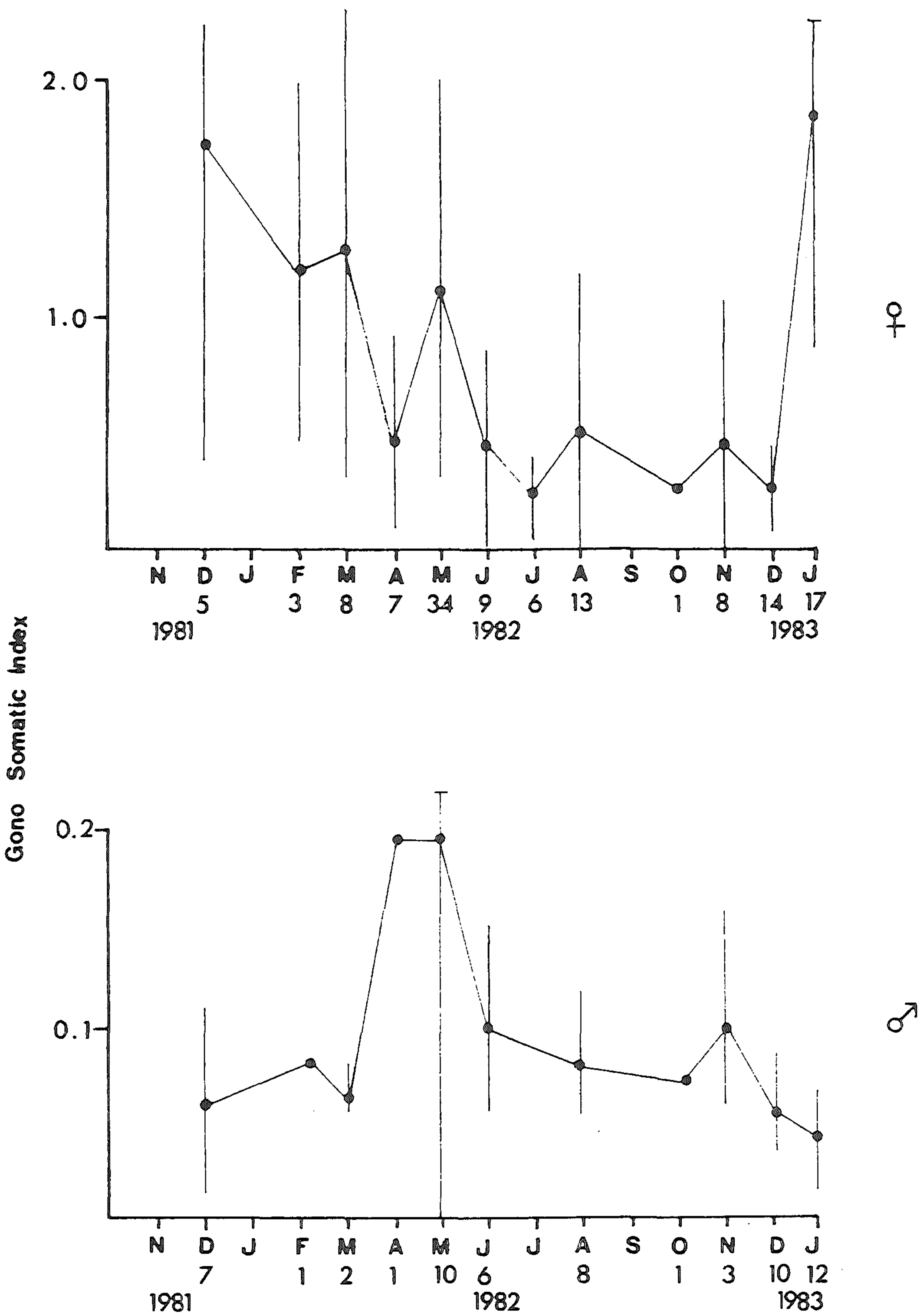


Figure 9. Magendo 2. Mean gonadosomatic index over the sampling period (for fish above the minimum breeding size)

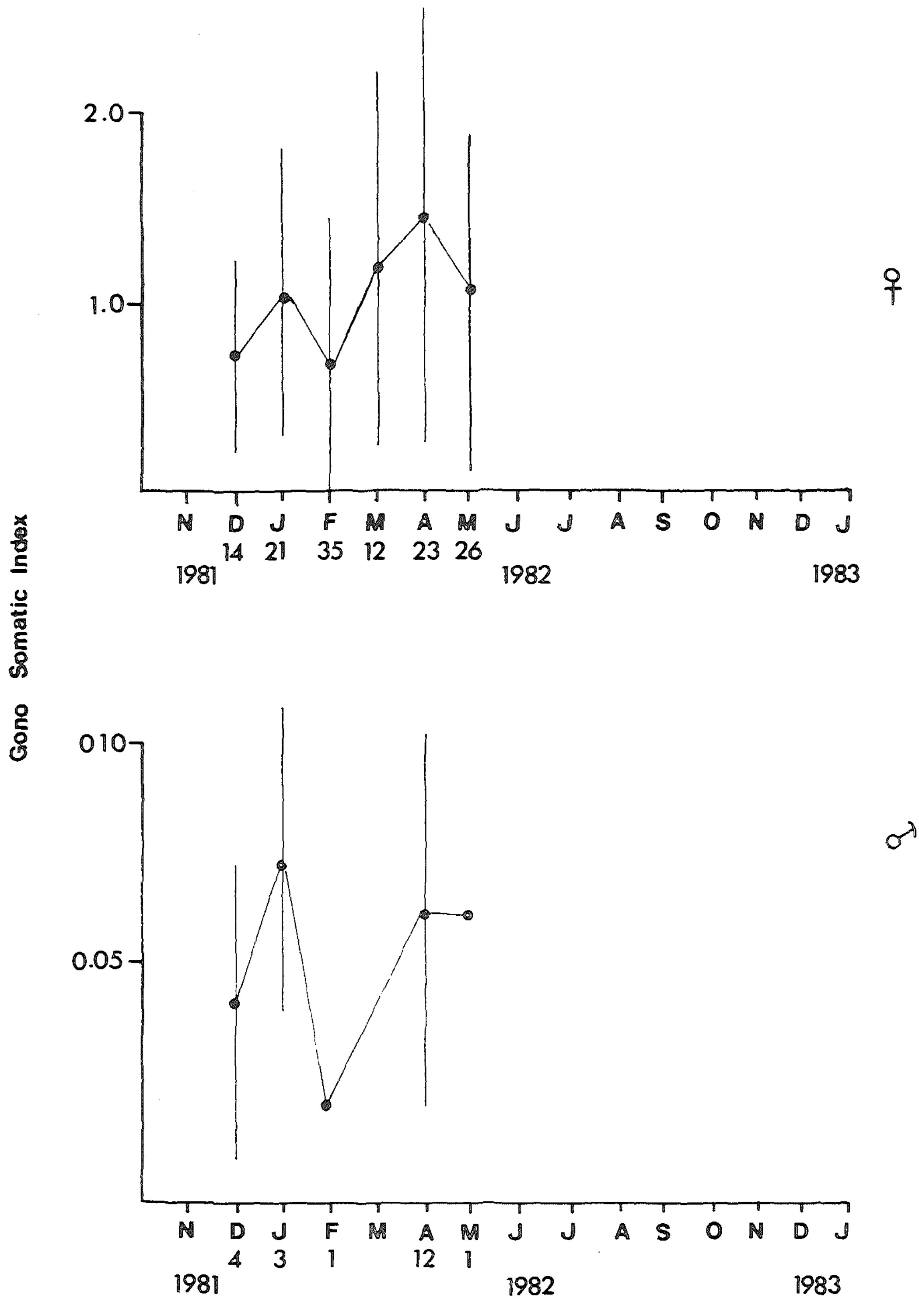
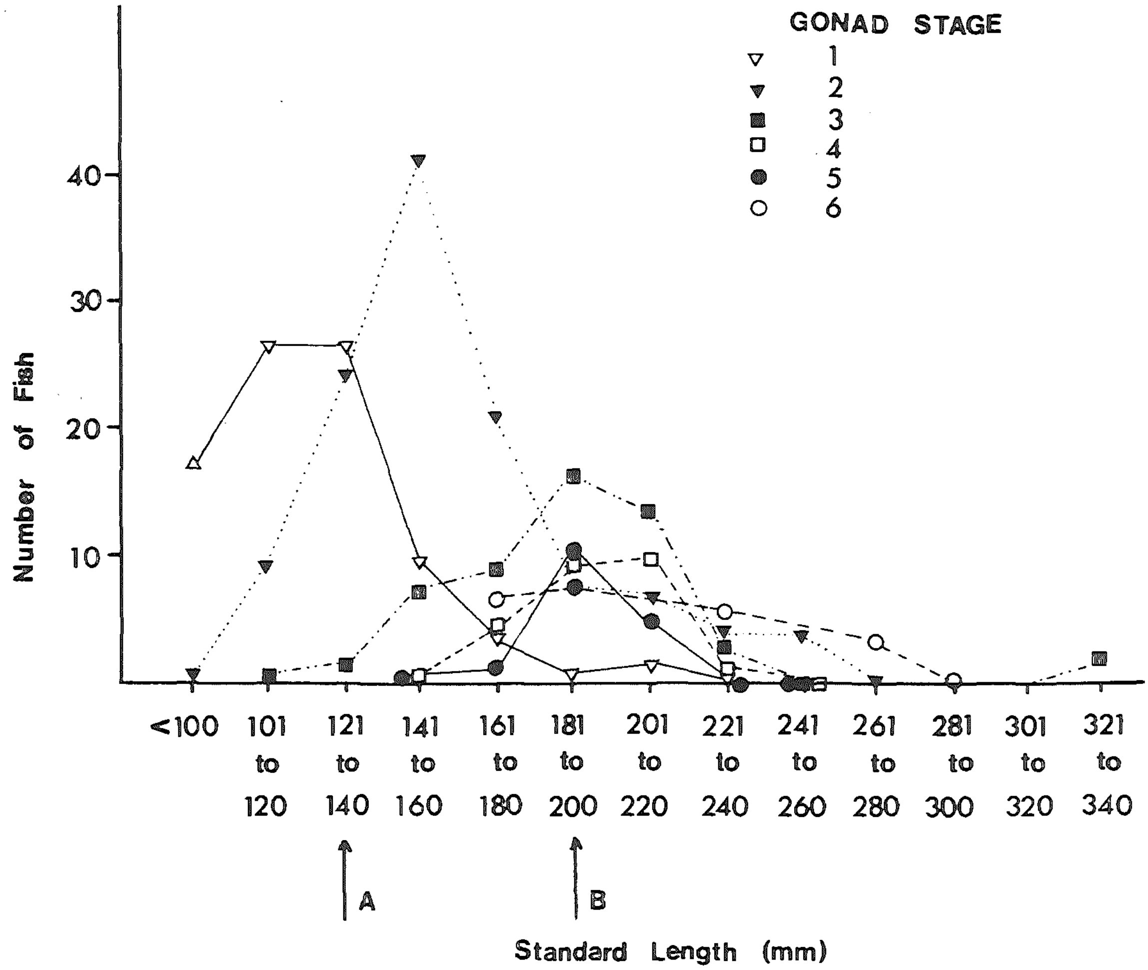
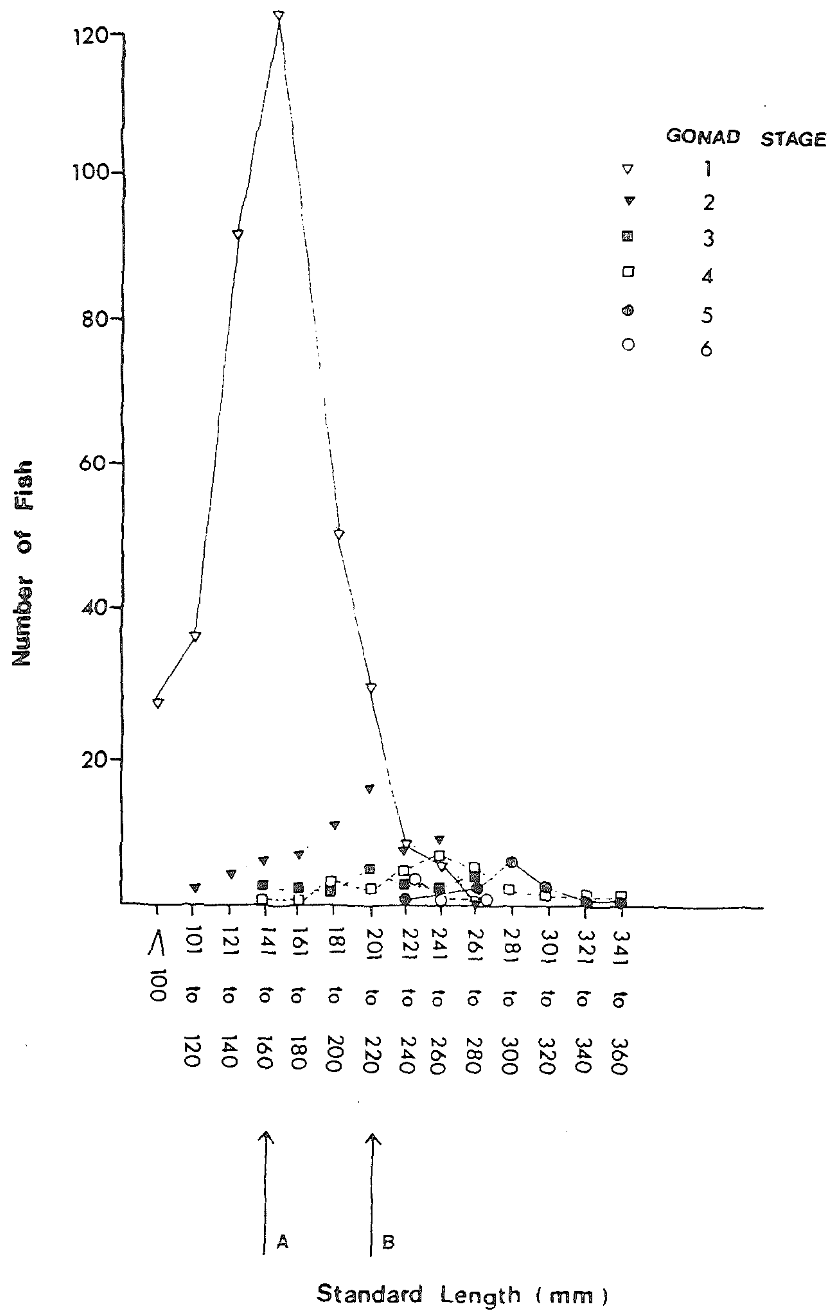


Figure 10. Pit Pit. Mean gonadosomatic index over the sampling period (for fish above the minimum breeding size).



(A - smallest category with gonads in stage 3)
(B - smallest category with gonads in stage 4,5,6 mature)

Figure 11 Females. Number of fish with gonads in each stage of maturity.



(A - smallest fish with gonads in stage 3 - ripening)
(B - smallest fish where most are mature - stage 4,5,6)

Figure 12. Males. Number of fish with gonads in each stage of maturity.

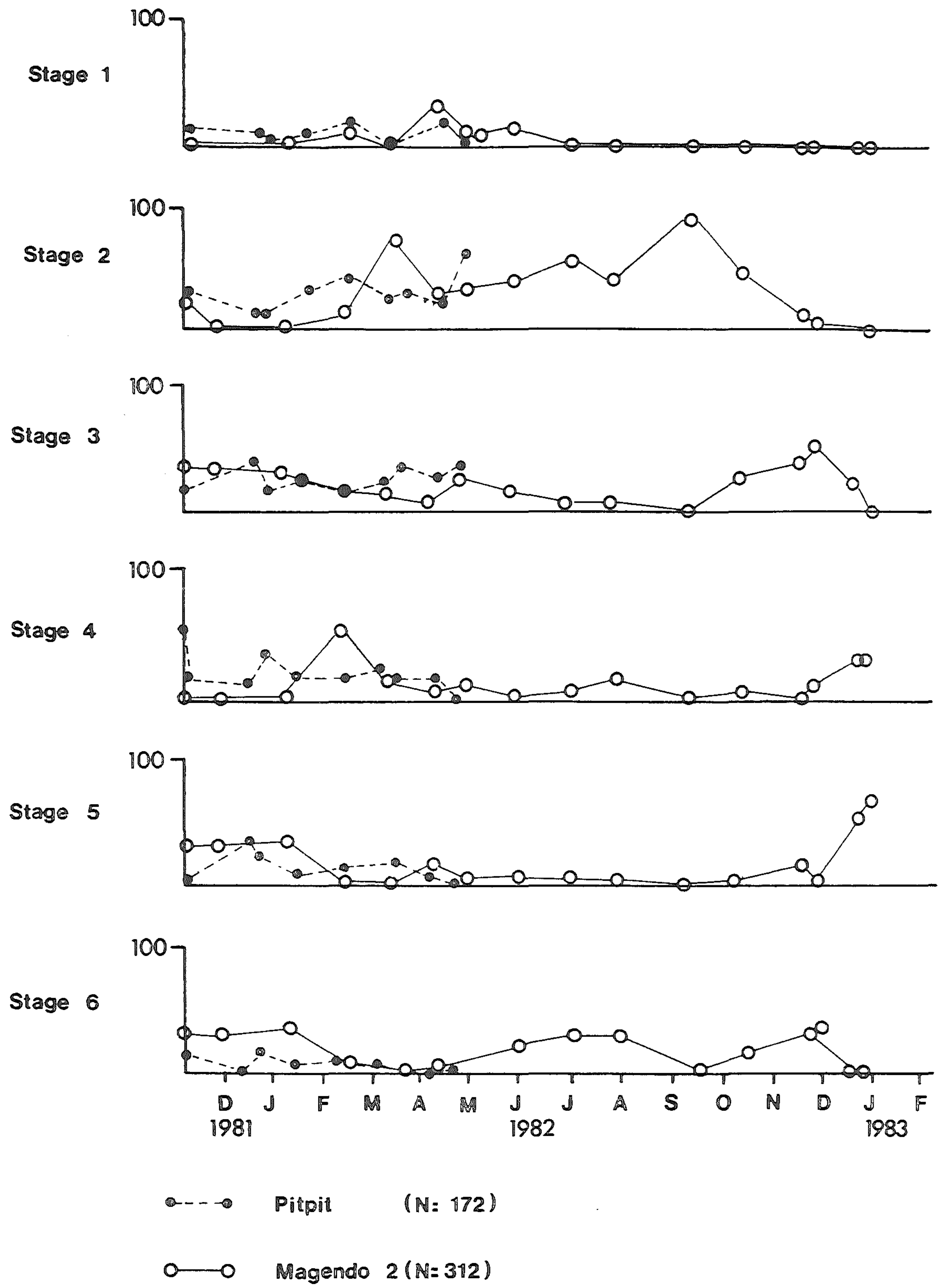


Figure 13 Percentage of females with ovaries in each of the six maturity stages.

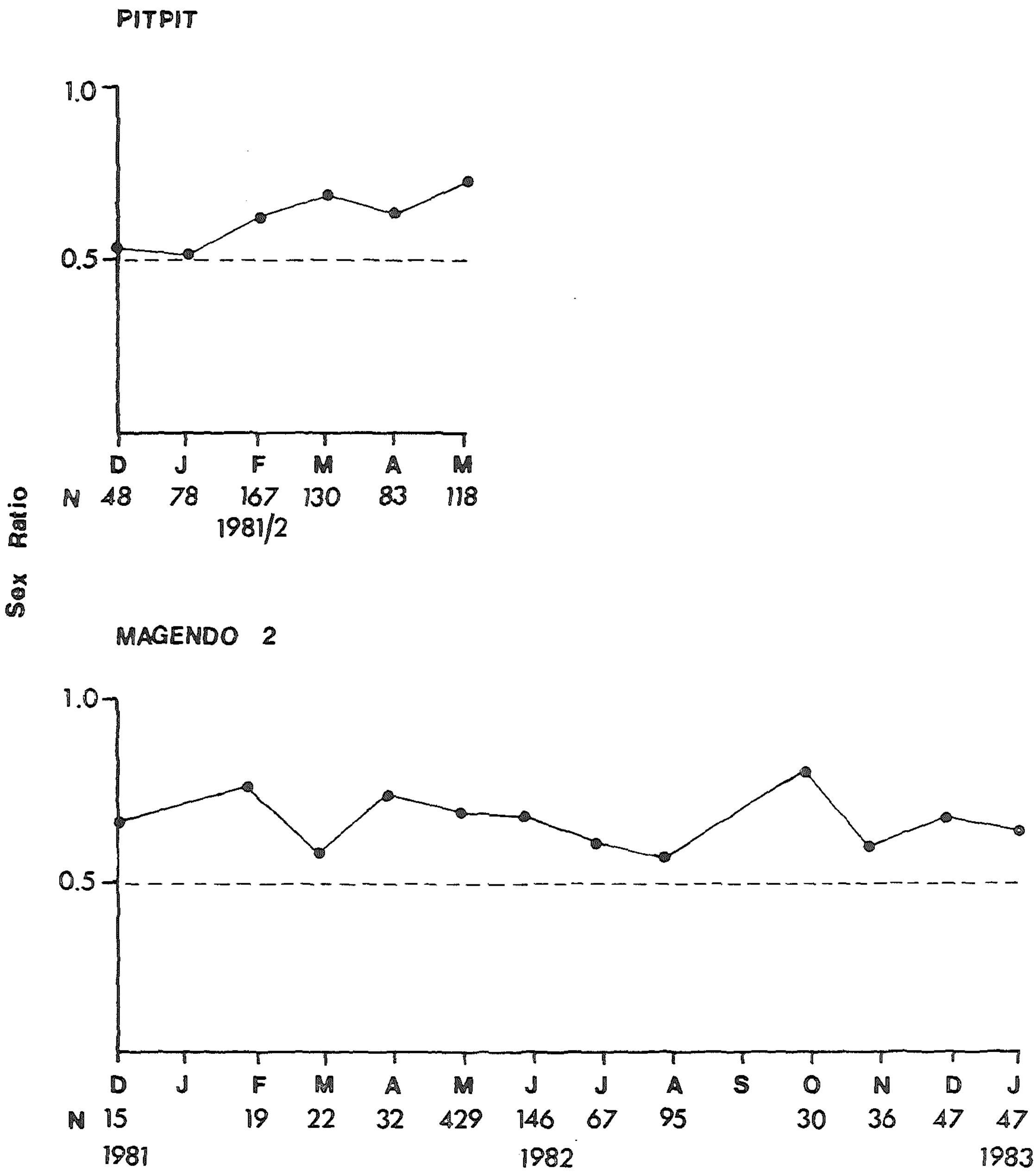


Figure 14 Sex ratio at Pit Pit and Magendo sites over the sampling period.

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Table 1. Number of villages producing salted fish and months involved in production

Months in production	No. 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

(from Rodwell 1982)

Table 2 Solpis production 1977 to 1981 (Actual and projected levels)

Year	Projected (tonnes)	Actual (tonnes)	Shortfall (tonnes)	Percentage production
1977	20.7	14.5	6.2	70.0
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

(from Rodwell 1982)

Table 3. Project costs and revenues for 1980/81
(after Rodwell 1982)

Year	TR	TC	TC - DC	%TC Covered	%TC-DC Covered
1980	40346	223926	60976	18	66.1
1981	29557	145150	80951	20.4	36.5

(from Rodwell 1982)

Key:

TR - Total revenue

TC - Total cost

DC - Development cost

Table 4. Revenue for the ESRDP project 1980/1 from Angoram, Pagwi and Ambunti centres.

	SALTED FISH		OTHER SALES		
Year	Amount sold (kgs)	Revenue (Kina)	Net	Salt	Other
1980	19,712	23,778	9630	2732	4205
1981	7406	9954	14,320	2090	3191

Total Revenue (Kina)

1980	40,346
1981	29,566

(after Rodwell 1982)

Table 5 The percentage composition of gill net catches (by weight) from all the regular sample sites. This table is based on the data supplied in Coates (1986)

Area	O.moss	Oxy.spp	Op.ap	M.cypr	Ariidae	Others
Imb.	02.19	12.66	42.77	11.25	30.92	0.21
Mag1	19.37	16.58	05.72	04.22	32.72	21.41
Mag2	42.57	13.27	10.04	08.28	22.34	03.50
Pit.	46.07	10.43	16.37	07.16	16.43	03.54
All	30.20	13.29	16.66	07.61	25.07	07.17

Key for species:

O.moss - Oreochromis mossambicus

Oxy.spp - Oxyeleotris spp.

Op.ap. - Opieleotris aporos

M.cypr - Megalops cyprinoides

Ariidae - Ariidae

Table 6 Catch data for each sized net

Area A - Pit Pit

Net size (ins)	Total Wt. (g)	Mean Wt. (g)	Mean Length (cm)
1.0	-	-	-
1.5	51	17	7.5
2.0	1808	33	7.1
2.5	13596	66	10.8
3.0	29688	148	15.2
3.5	20849	204	17.2
4.0	32148	321	20.8
5.0	3455	576	24.0
6.0	-	-	-
Total	101577	150	14.3
Area B - New Magendo			
1.0	538	77	11.1
1.5	295	21	8.7
2.0	4753	44	9.7
2.5	13744	73	13.1
3.0	47041	160	16.2
3.5	41630	210	18.2
4.0	54234	341	21.1
5.0	32969	622	26.1
6.0	1981	959	30.0
Total	197122	193	16.5
Area C - Old Magendo			
1.0	9	4	6.5
2.0	1289	48	10.7
2.5	2972	71	12.4
3.0	12387	165	15.5
3.5	5703	285	18.6
4.0	18029	328	20.0
5.0	8591	661	23.7
6.0	4575	1144	29.9
Total	53555	225	16.3
Area D - Imbuando			
2.0	45	45	10.0
2.5	150	75	13.0
3.0	1830	366	20.9
3.5	1468	245	18.8
4.0	4940	329	21.2
5.0	4045	674	26.6
Total	12478	357	20.9

Table 7 Feeding Preferences - Sepik species of fish

Species	DIET				
	Inverts. Prawns Ins. 1 Anne. Mo.	Fish	Macro.	Algae	Det.
Megalops cyprinoides	*	*[1]			
Anguilla bicolor pac.				*	*
C.carpio	*				
Arius nox	*				*
A. solidus	*	*		*	*
A. velutinus	*				
A.utarus	*				
A.coatesi	*	*			*
Plotosidae	*				
Zenarchopterus kampeni	*			*[f]	
Gambusia affinis	*				
Chilatherina sp.	*			*[f]	
Glossolepis multisquam.	*				
Ambassidae	*	*			
Theraponidae	*	*[2]			
Apogonidae	*	*?			
Carangidae	*	*?			
Lutjanidae (cont)	*?	*?			

Species	Inverts. Prawns Ins. 1 Anne. Mo.	Fish	Macro.	Algae	Det.
O.mossambicus				*[d]	*
Mugilidae				*[d]	*
Eleotrididae	*	*[3]		*[f]	
Glossogobius	*				*

Key:

Ins.1 - Insect larvae, aquatic and terrestrial, nymphs etc
Anne. - annelids,
Mo. - molluscs

*[1] - species consumed include Ophieleotris aporos, Oxyeleotris heterodon, Ambassis interrupta and occasionally O. mossambicus

*[2] - small eleotrids consumed

*[3] - Eleotris aquadulcis, feeding on juvenile O.heterodon and adult O.heterodon feeding on Ophieleotris aporos

*[f] - Filamentous algae consumed

*[d] - Diatoms (epiphytic and benthic), algae

*[?] - fishes possibly consumed (reported)

Table 8 Main species of tilapia which are important in aquaculture (after Schoenen 1982)

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

Table 9 Tolerance of *O. mossambicus* to temperature, salinity, dissolved oxygen concentration, pH, turbidity and depth.

Environmental Factor	Level	Effect	Reference
Temp. (°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)	0-120	Tolerated after acclimation	Whitfield and Blaber (1979)
	0-49	Breeding poss.	Hora and Pillay (1962) Popper and Lichatowich (1975)
Dissolved O_2 (mg/l)	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)

(from Arthington 1987)

Table 10 Growth rates and monthly production of *Oreochromis* species and *Tilapia rendalli* in extensive, semi-intensive and intensive cage culture (after Coche 1982)

SPECIES	EXTENSIVE		SEMI-INTENSIVE		INTENSIVE	
	Growth	Prod^n	Growth	Prod^n	Growth	Prod^n
O.aureus						
A.	0.78	12.7	-	-	0.5-1.4	7.8-20.6
B.	0.72	14.1	-	-	1.1-1.7	16.0-24.4
O.niloticus						
C.	0.60	3.5	0.80	2.3	0.9-2.0	5.8-10.0
T.rendalli						
A.	-	-	0.34	2.0	-	-
B.	-	-	0.5-1.3	2.7-3.9	-	-

Key:

Growth measured in grams/day (g/d)

Production measured in kg/m^3/month

A. - Stocked at 10-15g

B. - Stocked at 20-30g

C. - Stocked at 25g