CENTRAL AMAZON FISH POPULATIONS: BIOMASS, PRODUCTION AND SOME DYNAMIC CHARACTERISTICS

by

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requirements for the Degree of
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The undersigned hereby certify that they have read and recommended to the Faculty of Graduate Studies for acceptance a thesis entitled " Central Amazone Fish Populations: Biomass, Production and some Dynamic Characteristics"

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ABSTRACT

A 2.5 year field study designed to estimate production of fish in the Amazon river provides a basis for understanding the fishery and certain features of floodplain ecology. Intensive sampling with a fine-mesh seine net throughout the hydrological cycle in a variety of floodplain habitats revealed the seasonal spawning sequences of many species, allowing identification of cohorts and estimates of early growth from the sequential samples. Using a block net and marked fish in the habitats sampled routinely, the efficiency of the seine net was estimated for various species groups and sizes. Thus seine catches could be converted to biomass density estimates. The overall estimate of fish and decapods was 160 gm^{-2} with 95% confidence limits of ±24. Growth of individual species appeared unaffected by the biomass of potentially competing species when the water was rising, and only two out of eleven species suggested density-dependent growth (at $p<.05$) during falling water. A strong seasonal variation in growth rate was observed.

A multispecies growth function which depends on weight, maximum weight of species, and hydrological season was derived from the growth rates of 14 common species. Fish plus decapod production averaged 280 $gm^{-2}yr^{-1}$, based on the biomass estimates and growth function. The estimated phytoplankton primary productivity of 290 $gCm^{-2}yr^{-1}$ is insufficient to sustain the fish productivity, and the importance of macrophytes was also evident from the gut contents of common species. The biomass distribution when plotted in logarithmic length intervals increased sharply with length. Non-conformity with the Sheldon spectrum for pelagic systems could be explained by many fish feeding on extremely small particles (fine detritus feeders) or very large particles (macrophyte herbivores). However, the prey to piscivore biomass ratio varied from 1.2 to 1.3, which was similar to Kerr's (1974) interpretation of the Sheldon spectrum.

Transfer efficiencies of 37% and 39% were estimated for two successive trophic levels, indicating a high predation efficiency and growth efficiency. The similarity in biomass ratios and predation efficiencies between the central Amazon and those estimated for pelagic systems is not paralleled by similar transfer efficiencies which are apparently much lower in pelagic systems. This implies higher gross growth efficiencies in Amazon fish which may be due to the higher prey/predator length ratio of .25. The system thus appears to be very efficient, yet only 2.7% of the total productivity is taken as yield by man in a more exploited part of the basin. It is concluded that the high predation efficiency leaves limited surplus production from lower trophic levels to support an expanded fishery, unless the latter can be managed in such a way as to exploit all piscivores, many of which have low market value at present.

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Firstly, I thank my wife who was not warned about this before we got married. The following list of my other collaborators who were instrumental in the success of this project is incomplete because it would be impossible to list them all. Heraldo Britski, Paul M. Brunelle, Paul J. Brunelle, Bernado Falcão, Alcides Guedes dos Santos, Paul Johns, Wolfgang Junk, Warick E. Kerr, Pedro Makiyama, Naercio Menezes, José C. Moreira, João Pena, Miguel Petrere Jr., Raimundo Sotero, Karl Sonnenburg, Richard Vari, Stanley H. Weitzmann.

Chapter 1: River-floodplain systems : why are they different?

1.1 Introduction

This thesis is based on a little studied system. The uncovering of new information is facile, and would be of only parochial interest if not seen in the context of river-floodplain systems in general.

This chapter discusses fundamental concepts that illustrate differences between true lakes, rivers and river-floodplain systems.

Traditionally, limnology has been concerned with true lakes which have limited water level fluctuations. Studies have been further restricted by emphasis on the pelagic subsystem, which has been relatively easy to sample and model. This bias has to some extent been compensated by Wetzel (1975), Straskraba (1963, 1964) and Pieczynska (1972, 1973) who have maintained that eulittoral or littoral production plays a significant part in organic input in most lakes. Junk(1980) presents a historical review of limnological theory and how it has led to a lack of understanding of floodplain ecology. The integrated nature of river-floodplain systems with reference to their fish populations is being recognized (Welcomme 1975, 1979; Kapetsky 1974; Holčick and Bastl 1976). The following discussion may also be biased by my experience in tropical river-floodplains (Central Amazon and R. Pilcomayo) and Lake Turkana (Kenya). It is a revised version of an earlier paper (Bayley 1980).

1.2 River Versus River-floodplain Systems

Rivers have for some time been neglected, partly because of an understandable desire by limnologists to study relatively closed systems. In addition, most studies have concentrated on temperate rivers which now have negligible floodplains due to artificial control of their hydrological regimes, such as the River Thames (Mann 1972). Notable exceptions are studies on the R. Illinois and its floodplain lakes (Richardson 1921) and the R. Danube floodplain (Holčick & Bastl 1976).

Generally acceptable divisions into lentic (lacustrine) and lotic (riverine) systems have been possible in temperate freshwaters. This is not so easy or advisable for river-floodplain systems. Many production processes, in particular those involving emergent macrophytes, take place in both subsystems. Many fish species regularly inhabit both subsystems during different parts of their life cycles.

There are also considerable abiotic interactions underlying production processes such as the hydrology and associated nutrient distribution. Their separation *a priori* into lentic and lotic components does not necessarily lead to a better understanding of the functional aspects of river-floodplain systems. Henceforth, the discussion deals with the river-floodplain system as a single dynamic entity.

1.3 Lakes Versus River-floodplain Systems

The closest limnological homologues which may assist in the understanding of river-floodplain production processes are the eulittoral and littoral zones in lakes. Wetzel (1975) has maintained that in most lakes, organic and nutrient input resulting from emergent macrophyte production usually exceeds that from other sources put together. Pieczyńska (1972) has demonstrated the importance of the eulittoral zones in Polish lakes, in particular those with emergent macrophytes. Richardson (1921) documents the highest invertebrate biomasses in the shallow, weedy areas of floodplain lakes. He noted that fish yield per unit area in the R. Illinois system was strongly correlated with regions of floodplain development (*op. cit.* pp.462-471). His results also showed that the differences in biomass of invertebrates between river and lake systems were not sufficient to explain the differences in the fish yields per unit area. He concluded that there was a higher productivity of invertebrates per unit biomass in the littoral zones of floodplain lakes.

The analogy between the eulittoral of lakes and the floodplain breaks down when one considers the effects of the extensive and prolonged flooding which often occurs in the latter. A relatively static lake shoreline involves the biocoenosis of dense macrophyte stands and invertebrates, but the access of fish can be restricted as Pieczynska (1973) and Straskraba (1965) have observed. By contrast, high densities of fish accompany the advancing shoreline of a floodplain (personal obs.) which is a zone where very large quantities of invertebrates have been reported (Junk 1973; Lim & Furtado 1975). In addition, the newly flooded zone has sufficient oxygen which is not always the case with the more static shoreline where the decomposing macrophytes are not left behind by the advancing water.

Prolonged flooding results in different biotopes such as forested areas. When these are inundated material from them contributes to the production of larger individuals of many fish species (Goulding 1980). 'Floating meadows' which consist of true floating plants or species which have severed their ground connection but still grow at the surface during high water form a habitat unique to floodplains (Junk 1970).

Further offshore, the seasonal changes of floodplain lakes distinguish them from true lakes. At low water wind mixing penetrates to the bottom, often increasing the turbidity as currents stir up the flocculent substrate. When the level rises, an almost permanent thermocline develops separating a well oxygenated epilimnion a few meters thick from a deoxygenated hypolimnion (Schmidt 1972). This occurs despite the annual influx of river water, which itself imposes an cycle of chemical and sedimentary changes unparalleled in true lakes.

The following section attempts to identify the mechanisms of production.

1.4 Functional Differences Between Lake and River-floodplain systems and effects on river-floodplain Productivity

1.4.1. Different subsets of mechanisms dominate each system.

In large and/or deep lakes, phytoplankton production may be more important than "littoral production", but in floodplains of similar size the latter is dominant in terms of primary production (Welcomme 1979; Bonetto et al 1969). This is probably due more to the high rate of turbid water input typical of large tropical rivers, which restricts phytoplankton production, than higher dissolved nutrients. Similarly, benthic algae production would be expected to be much less important in floodplains compared with either tropical lakes or temperate systems.

In the less turbid temperate rivers phytoplankton production is dominant (Mann 1972; Ertl 1976) even in the Danube system (Holčick, personal communication), which is one of the few large temperate floodplain rivers remaining.

Direct input of dissolved nutrients from rivers into river-floodplain systems is probably more important in "topping up" the system for long term benefits, than in controlling the year-to-year levels of production.

Localized decanting of solids does, however, cause high phytoplankton production (Schmidt 1973, Fisher 1979) in resticted zones where good light penetration and nutrient availability coincide.

Production of floating macrophytes deriving nutrients from the water column appears to be significant in river-floodplains e.g. Eichhornia and Pistia (see Junk, 1970). However, this production is minor compared with that of emergent macrophytes rooted in the substrate. It is possible that more nutrients are taken up from ground which has been recently flooded, either directly by solution or via macrophytes, than are contributed by the river. The benefits from either source will depend on the degree and duration of flooding.

Annually flooded terrestrial macrophytes also contribute significantly to organic input into the aquatic environment (in particular Gramineae), as well as providing food and shelter for young fishes (pers. observation).

One cannot presume that primary production of macrophytes and phytoplankton lead to an equal fish production, since phytoplankton is probably utilized more efficiently. However, the turnover rate of the macrophyte-detritus cycle in the river-floodplain is much faster than in the littoral zone of a lake, because the stranding (sometimes with 'burn-off', Visser & Imevbore 1969) and reflooding, allow aerobic breakdown and mineralization to be dominant (Junk 1976).

The abundant detrital aggregate typical of river-floodplains results in a dominance of detritivorous fishes, such as *Prochilodus* spp. in S. America and *Citharinus*, *Labeo* and *Sarotherodon* spp. in Africa.

Access to "allochthonous" sources of food in river-floodplains is less regular than in lakes or rivers, but is considerable when the flood invades pasture, scrub or forest. Whether these sources should be defined as allochthonous or not is debatable. Input of soluble organic compounds during this process may also be important.

When 'burn-off' or appropriate terrestrial herbivores are lacking, much of the decomposition occurs in the water, producing high BOD, thereby limiting the distribution of most fish species where complete deoxygenation occurs (Chapman *et al* 1971).

The above considerations suggest that different sets of production mechanisms are dominant in river-floodplain systems.

1.4.2. The dynamics of the mechanisms responsible for fish production in floodplain rivers have a quite different pattern from those in lakes or rivers.

The faster breakdown of macrophytes in river-floodplains has already been mentioned. Flood cycles (normally annual) in tropical river-floodplain systems also have a drastic effect on production processes (e.g. Lowe-McConnell 1964), which can exceed that due to seasonal temperature changes in temperate systems. The popular concept of high, year-round production in the tropics is misleading when applied to river-floodplain systems (Welcomme 1979). For example, the larger Cypriniformes and Siluriformes, which typically constitute most of the fish biomass (but see Kapetsky 1974), stop feeding during their migrations in the rivers, which can often take six months during the drawdown and low water seasons.

This 'physiological winter' can have more severe effects than winters in temperate systems, where production processes and feeding may continue well into the colder months, albeit at a slower rate. Even for non-migrating river-floodplain species their food sources are mostly from what is dry land during this period, with the probable exception of piscivores and parasites.

Arguments have been put forward (Wetzel 1975) that the emergent macrophyte-detritus cycle in the littoral zone adds stability to the lacustrine system. This is possible because of the physical stability of the biotope as well as the nature of the mechanisms involved. For example, the river-floodplain system contains a vast reservoir of organic matter and nutrients stored in the detrital aggregate and living macrophytes. To a certain extent this smooths out the effects of annual fluctuations in primary production, although the availability of detrital aggregate to the dominant, detritivorous fish species depends again on the degree of flooding. Short term stability in the flooded zone of the river-floodplain system is not possible because of the constant displacement of this zone, resulting in production mechanisms which are, most of the time, far from equilibrium levels. Within the year, the flooding season produces the aquatic equivalent of a 'rat race' in which plants and animals attempt to take advantage of a rapidly-expanding, food-rich environment. The situation is closer to that of a newly-flooded reservoir (e.g. L. Kainji: Lelek 1973) than to a lake or river, and the delay times involved may well lead to 'overshoot' of a long term equilibrium during some years. Thus, this annual expansion and contraction of the environment does not necessarily preclude density dependent processes from controlling fish growth (Dudley 1974). Conversely, any 'overshoot' may be damped by piscivores which are abundant in tropical floodplain systems (Lowe-McConnell 1964; 1969).

Long term stability in the river-floodplain is mostly dependent on the predictability of the flood regime. Annual maxima and minima, and rate of flooding can vary considerably in S. American (unpublished data) and African (Welcomme 1975) systems, affecting primary production and fish yields significantly. It is also probable that subtle changes in yearly water movements affect spawning success, changing fish species abundances (Lowe-McConnell 1964).

1.5 Conclusions And Suggested Approaches

It is clear that the production processes in river-floodplain systems are fully as complex as those in the littoral zones of lakes. Part of this apparent complexity arises from the dynamic nature and irregularity of the flooding itself. The higher faunal diversities of tropical river-floodplains add to their functional complexity, but may improve their stability (Lowe-McConnell 1969, 1975).

Under these conditions it seems premature to expect that modelling of a river-floodplain system on the basis of the mechanisms that have been studied separately would lead to much increased understanding of its productive potential.

I think one is limited to two approaches: (a) large scale comparative studies and (b) an intensive multispecies study of a 'typical' river-floodplain biotope.

The comparative approach, relying heavily on statistical methods, is a necessary first step. This can take the form of comparing the population properties of a single system from year to year, or comparing different systems with appropriate adjustment for geographical scale. Significant advances have been made within systems in which years of extensive flooding have been related to yield with a lag time of one or more years (Lagler et al 1971; Kapetsky 1974; Welcomme 1975; Holcick & Bastl 1976). The positive effects of flooding can be confounded by the higher mortalities during years with extended low water periods, and long time series will be necessary to resolve these. The second method of comparing between systems was developed by Welcomme (1976) in which he used alternative scaling factors of river basin area and main channel length, with a distinction between 'extensive' and 'normal' floodplains. Yield predictions within ±50% are possible using time series. Comparisons between systems allow appraisal of a new fishery (e.g. Bayley 1981). This method can be improved by more accurate and comprehensive aquatic resource evaluation, such as by remote sensing coupled with ground truth information (Welcomme 1979).

Comparative approaches have led to identification of driving forces such as degree of flooding, which in turn has formed the basis of a tentative model (Welcomme & Hagborg 1977) which is at least heuristic.

Although examples are given only from fishery studies, the comparative approach is equally valuable in limnological work, which should ideally be integrated with the former.

There are, however, limitations with comparative studies. One depends on the existence of contrasting situations to narrow the set of alternate mechanisms which may explain a statistical correlation. More than yield estimate information is required, but the number of systems which have comparable information such as fishing effort, species and size distributions are limited at present. Time series of data within systems are short.

The second approach, (b), involving a relatively intense study is the one undertaken in this thesis. It is not diametrically opposed to the comparative approach since many of the conclusions are based on comparisons between species or between habitats within the area of study. It is, however, a closer look at the productivity of the system, concentrating on fish and decapods between 15 and 1000mm long, with particular reference to juvenile fishes. The need for such studies has been pointed out by Welcomme (1979:169). There is no information on processes which link the various estimates of primary productivity with what emerges as yield to the fishery. We do not know what factors regulate the populations, with the exception of the occasional, spectacular fish kills due to large scale oxygen depletion.

The exploratory approach of this project demanded frequent, quantitative samples throughout the hydrological season and in different regions. The following chapter describes my view of the system (the Central Amazon floodplain) and how it influenced sampling strategy.

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Chapter 2: The Environment and Sampling Strategy

2.1 Geomorphology, Climate, Hydrology and Salient Features

This project was limited to the lower R. Solimões near its confluence with the R. Negro where its name changes to the R. Amazonas. Figure 2.1 outlines the area, and indicates the three sampling regions and the maximum area flooded by predominantly R. Solimões water. Near infra-red (band 7) LANDSAT images of this area are shown for low and high water levels in Plates 2.1 and 2.2 respectively.

The sediment-rich 'white' water of the R. Solimões-Amazonas has produced most of the floodplain soils. This has filled the 'drowned valleys' resulting from the last ice age, except where local, tributary catchments of practically zero sediment load such as the R. Negro exist.

Figure 2.1 Central Amazon showing 3 sampling regions.
Maximum area flooded shown hatched.

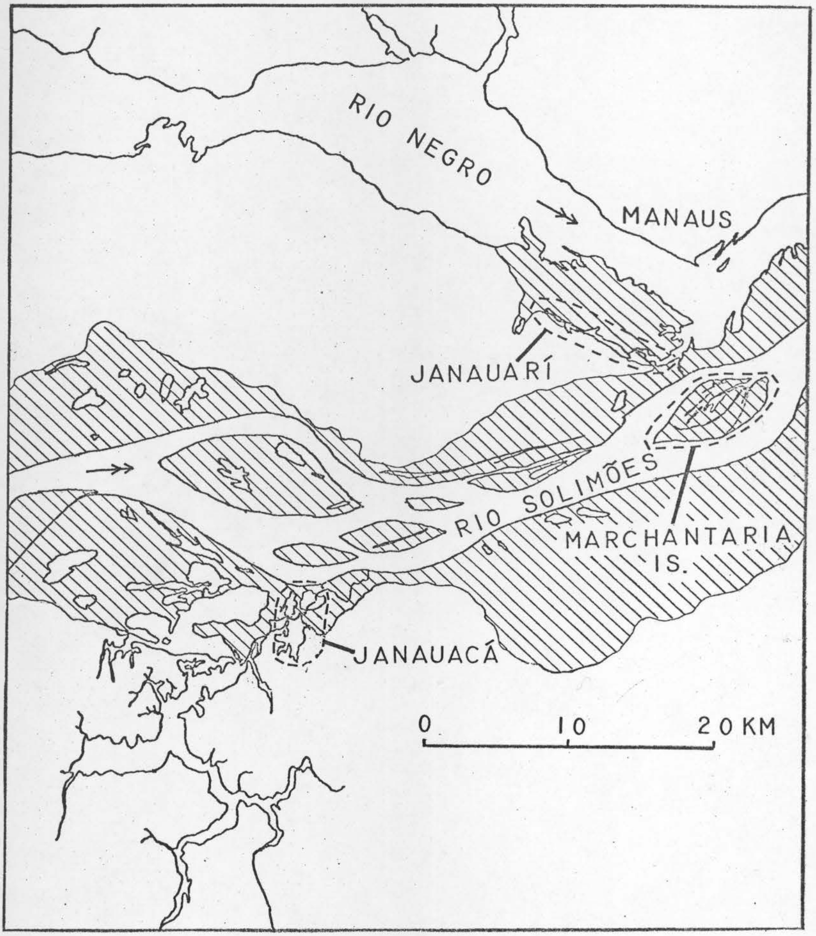

RIO NEGRO
MANAUS
JANAUARÍ
RIO SOLIMÕES
MARCHANTARIA IS.
JANAUACÁ
0
10
20 KM

Plate 2.1 LANDSAT image (near infra-red) at low water (Manaus gauge = 19.23 m.) [See Figure 2.1 for orientation]

Plate 2.2 LANDSAT image (near infra-red) at high water (Manaus gauge = 27.85 m.) [See Figure 2.1 for orientation]

0
20 KM

However, the lateral extent of the floodplain is mainly limited by the borders of a pedeplain of Tertiary sediments which is above the maximum flood level. Figure 2.2 shows a simplified section of the floodplain. This pedeplain occupies most of the basin, and its predominantly nutrient-poor, consolidated soils are referred to as *terra firme* to distinguish them from the relatively rich, *várzea* (=floodplain) soils of Quaternary or Recent age. The latter are seasonally flooded in most years.

Daily water level measurements, precipitation, insolation, air temperature and wind speed were available from Portobras and I.N.P.A. in Manaus. Annual precipitation averages close to 2m, but in 1977 and 1978 2.44 and 2.27m respectively were measured. It can rain during any month, but there is a distinct rainy season between January and April which does not coincide with the water level peak (Figure 2.3). In addition, during normal years there is a drier period from July to September, but 1977 was an exception. Local observations during sampling revealed that small amounts of precipitation can be very patchy.

Figure 2.2 Simplified cross section of a turbid river floodplain in the Amazon basin.

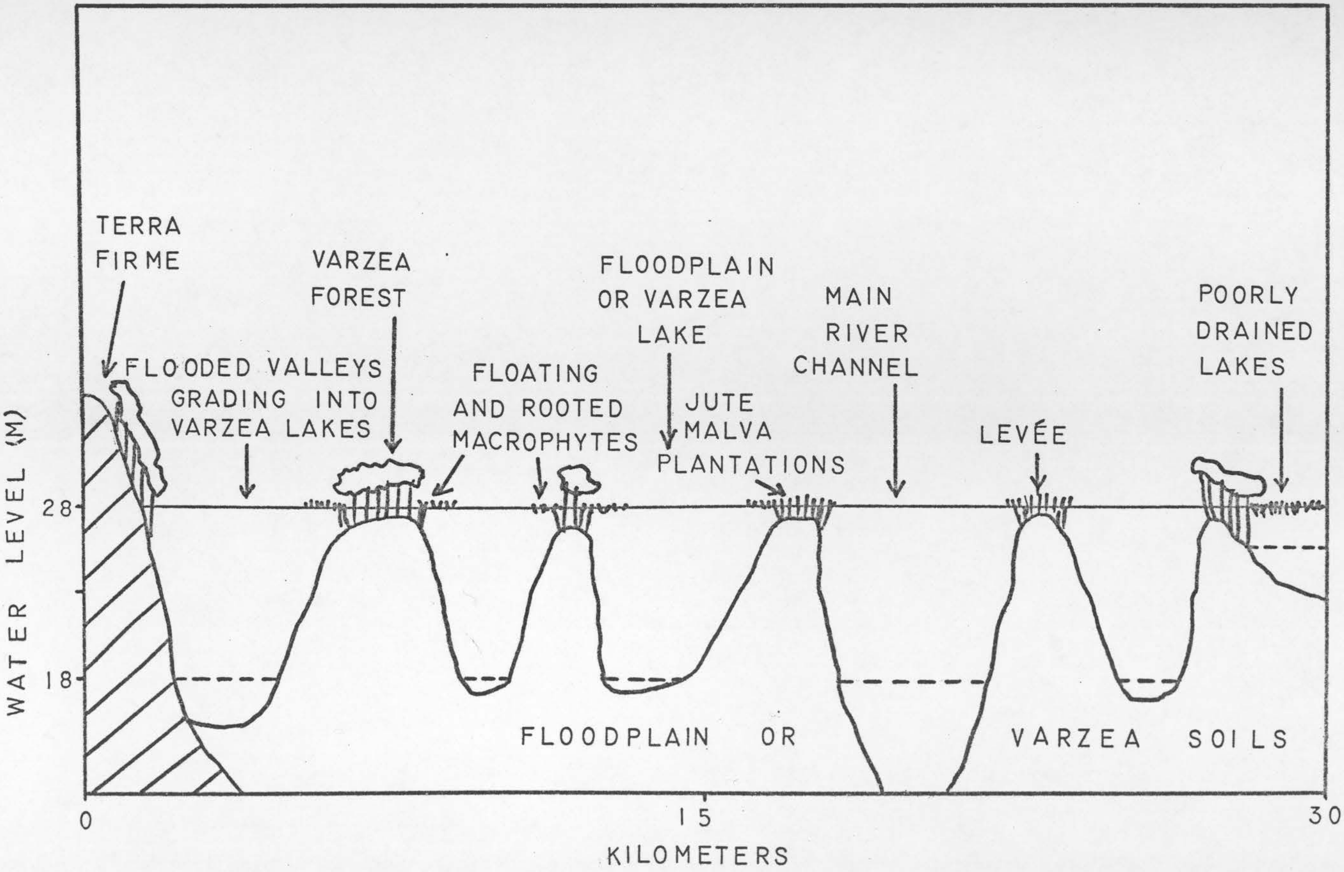
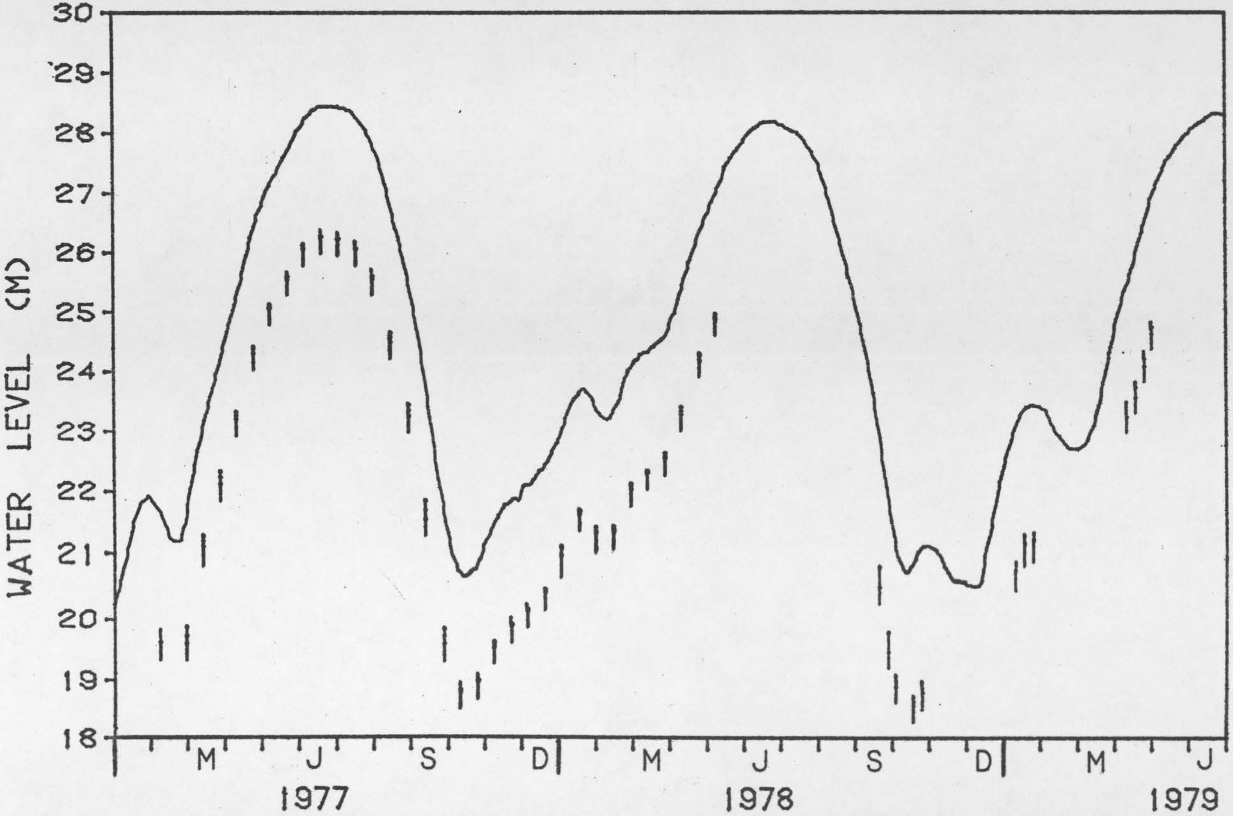

TERRA FIRME
VARZEA FOREST
FLOODPLAIN OR VARZEA LAKE
MAIN RIVER CHANNEL
POORLY DRAINED LAKES
FLOODED VALLEYS GRADING INTO VARZEA LAKES
FLOATING AND ROOTED MACROPHYTES
JUTE MALVA PLANTATIONS
LEVÉE
FLOODPLAIN OR VARZEA SOILS
WATER LEVEL (M)
28
18
0
15
30
KILOMETERS

Figure 2.3 Daily water levels (solid line) and times of sampling excursions (vertical lines) during the project.


WATER LEVEL (M)
30
29
28
27
26
25
24
23
22
21
20
19
18
M
J
S
D
M
J
S
D
M
J
1977
1978
1979

Wind is dominantly from the east. It is rarely strong except intermittently from July to September and during storms. Air temperatures and water temperatures are very constant, but small differences in the latter are sufficient to maintain stratification (Schmidt 1973a) due to the greater density change in the range 27 - 32°C

The annual flooding cycle averages close to 10m amplitude (70-year mean) as recorded at the Manaus gauge on the lower R. Negro. This movement almost entirely reflects changes in the R. Solimões which appears to back up the R. Negro as well as seasonally add water via various furus (=seasonal connecting channels) as far as 30km upstream on the R. Negro. The movement of the level at Manaus is very closely paralleled by that in L. do Castanho in the furthest sampling region of Janauacá (Figure 2.1) according to measurements by Schmidt (1973a). The daily levels during the sampling period are shown in Figure 2.3. In 1976 the second highest level since 1903, 29.61m, was recorded followed by a minimum of 18.05m which was low by recent standards.

For the ten years prior to 1977 the minimum averaged 19.38m (1.98 s.dev.) but this was 2m higher ($p<.001$) than the mean for 1903-1966. Comparing the same periods, maxima averaged 28.43m (.78 s.dev.) for the previous ten years, which was only slightly higher ($p<.05$)

than the mean of 27.57m (1.17 s.dev.) for the earlier period.

Despite these trends the single values for 1977 and 1978 were not outliers (at p=.05) with respect to any of these previous periods, but were much closer to the 1967-1976 means.

Standard deviations for the minima are about twice those for the maxima. Since greater flooding is associated with higher productivity whereas increased drawdown ought to be associated with higher mortality, the latter may be more variable from year to year.

The invading 'white' or turbid waters clear somewhat on sedimentation as the flow decelerates over the floodplain. They also mix with 'black' waters which predominate along the periphery of the floodplain in 'flooded valleys' cutting through the pedeplain. This mixing also clarifies the water somewhat.

'Black' waters in fact appear like strong tea due to dissolved humic and fulvic acids, having little organic sediment and no light-colored clay. They are characterized by extremely low electrolyte content (Sioli 1968) and one major source has been identified as podzol soils (Klinge 1967).

The R. Solimões-Amazonas upstream in Peru has a conductivity of >120 μmhos/cm Gibbs (1967) but further from the Andes the water is continually diluted by 'black' water, direct rainfall and smaller quantities of 'clear' (Sioli 1968) water which is more common downstream of the study area.

In the area of this study the R. Solimões itself had conductivities seasonally varying between 50 and 79 µmhos/cm which compares with the range reported by Schmidt (1972) of 45 to 84 also corrected to 20°C. Lowest values of both ranges occurred during high water in July/August.

However, inshore areas indicated much higher conductivities seasonally, while zones peripheral to the floodplain were found to have conductivities down to 11; practically as low as the R. Negro range of 6-10 µmhos/cm (see Figures 2.7 and 2.8).

Since conductivities are nearly proportional to the major nutrient concentrations, fish productivity would be expected to be indirectly affected by this edaphic variability as well as by the seasonal expansion of the environment.

The vegetation consists of forest, emergent or floating aquatic macrophytes, terrestrial grasses and shrubs. Jute and malva are cultivated extensively in the várzea. The forest is highly varied, some forming characteristic species associations which are regularly inundated by 'black' or 'white' dominated waters.

However, most of the forest in or near water in the Manaus area is in some stage of regrowth after being cleared.

The *várzea* or floodplain is dominated by levées, terraces, depression lakes, ox-bow lakes, swamps and connecting channels (*paranas* and *furus*). The significance of this area to fish production has been discussed in Chapter 1, and will be further elaborated on below.

In order to accurately depict the various habitats one would require a joint bathymetric-topographic survey with seasonal measurements of mobile features such as macrophytes. In the absence of such an expensive project, descriptions have been largely qualitative. Not even a hydrological budget has been attempted because of the lack of gauges, flow measurements and the complexities of the floodplain.

However, the RADAM survey quantified some habitats of interest on a large scale based on Side-looking Radar (SLAR) and ground truth measurements (RADAMBRASIL 1976).

A smaller scale description using LANDSAT images and multispectral data, 1:50,000 aerial photographs and ground truth confirmation has been initiated (unpublished data). A brief summary of this is presented in the following sections.

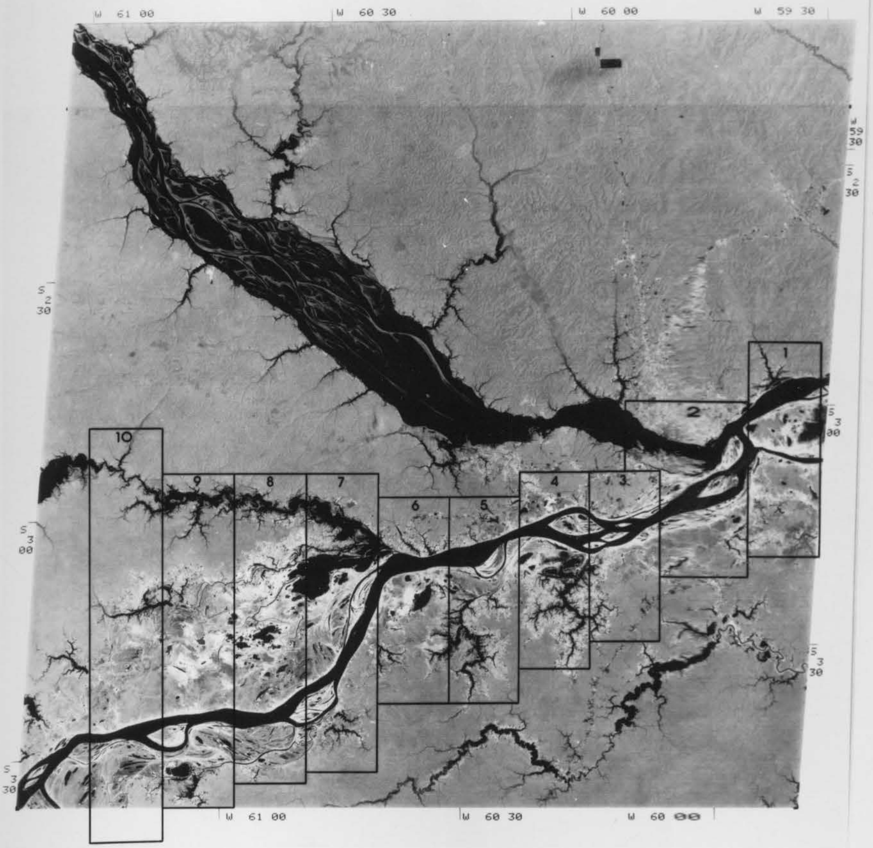
2.2 LANDSAT interpretations

A preliminary multispectral analysis involving a maximum likelihood classification of quadrats based on signatures from known features has been completed (Bayley & Moreira 1980) for the study area at high and low water. These quadrats are shown in Plate 2.3. Quadrat 2 has been expanded to include a flooded zone between L. Janauari and the R. Negro, which was associated with the Janauari sampling area (Figure 2.1).

Aquatic macrophytes were distinguished from damp grassland predominating near the peripheries of the flood waters near the maximum water level. 'White' or turbid waters were distinguished from 'black' waters and intermediate types including 'decanted white' and 'mixed' from the low water image. These distinctions were verified by further 'ground truth' checks of the classification.

Although the high water classification also distinguished these water types on the basis of 'training' in known, homogeneous areas, the classification was often incorrect in that deep decanted or mixed waters corresponded closest to the black water signature. This did not occur in the low water image.

Plate 2.3 LANDSAT image with numbered quadrats covering the floodplain of the R. Solimões-Amazonas which were used in multispectral analyses (section 2.2) at high and low water.


W 61 00
W 60 30
W 60 00
W 59 30
W 59 30
S 2 30
S 3 00
S 3 30
S 2 30
S 3 00
S 3 30
W 61 00
W 60 30
W 60 00
1
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10

Since in this area black waters do not expand appreciably during the flood period because they are backed up by the turbid Solimões water or mixed with it, the values for low water were applied to high water, the difference belonging to the mixed/decanted classification. In fact, there are seasonal differences on a smaller scale in some areas, including one of the sampling areas, Janauarí. There, waters from the R. Negro backed up by the R. Solimões-Amazonas temporarily displace mixed water at the extreme NW part of L. Janauarí (Figure 2.4).

Despite good training areas attempts to distinguish nonflooded and flooded forest biotopes were unsuccessful (Bayley & Moreira 1980). However, the multispectral analysis did succeed in classifying all other aquatic and terrestrial biotopes save a small percentage due to transmission defects and border effects. This combined with the ability to define the floodplain by interpreting the topography of low water, 1:500,000, band 7 LANDSAT images method (described in Bayley 1981) allowed me to determine the proportion of forest which is inundated at the highest water level. Interpretation of topography is also possible with SLAR images, but I have found the appropriate satellite images to be clearer and easier to identify with ground observations.

The estimates of major biotopes discussed are summarized by quadrat in Table 2.1. These data form the basis for extrapolating biomass and production estimates in Chapter 5 to compare them with the fishery yield. Further features in this table are discussed in the following section.

Table 2.1 Areas of aquatic habitats at high and low water based mostly on LANDSAT analyses (unpublished data). {See Plate 2.3 for locations of quadrats}.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
1	62	124	7	44	64	360	661	200	461	104	63	56	7	127	67	3.6
2	117	59	52	56	66	108	476	75	401	143	82	26	52	160	34	2.5
3	77	33	1	43	45	83	281	50	231	62	48	20	1	69	39	3.4
4	71	130	8	38	60	31	340	60	280	66	62	54	8	124	14	2.3
5	71	71	5	34	52	107	339	60	279	63	63	45	5	112	47	2.5
6	66	102	1	32	46	293	538	155	383	72	68	33	1	101	67	3.8
7	101	215	42	72	75	326	831	140	691	93	82	124	42	248	56	2.8
8	70	212	16	89	116	346	848	200	648	64	46	79	16	141	49	4.6
9	50	118	45	104	113	423	853	220	633	48	37	36	45	118	58	5.4
10	76	68	21	56	89	511	821	200	621	67	68	37	21	126	74	4.9

A: Quadrat number (see Plate 2.3).
B: 'White' water area*: at high water
C: Decanted or mixed water area: at high water
D: 'Black' water area (low water estimate used): at high water
E: Area of aquatic macrophytes: at high water
F: Area of wet or lightly-flooded grassland: at high water
G: Area of flooded forest: at high water
H: Maximum flooded area: at high water
I: Poorly-drained areas and wet grassland (part of E, F and G)
J: 'Active' floodplain area (H less I)
K: Area of river channel (R. Negro included in quadrats 1 and 2)
L: 'White' water area: at low water
M: Decanted or mixed water area: at low water
N: 'Black' water area: at low water
O: Total water area (inc. river channel): at low water
P: % of floodplain (H less low water area, O) still forested.
Q: Ratio of 'active' floodplain (J) to total low water area (O).

* all areas are in km^2

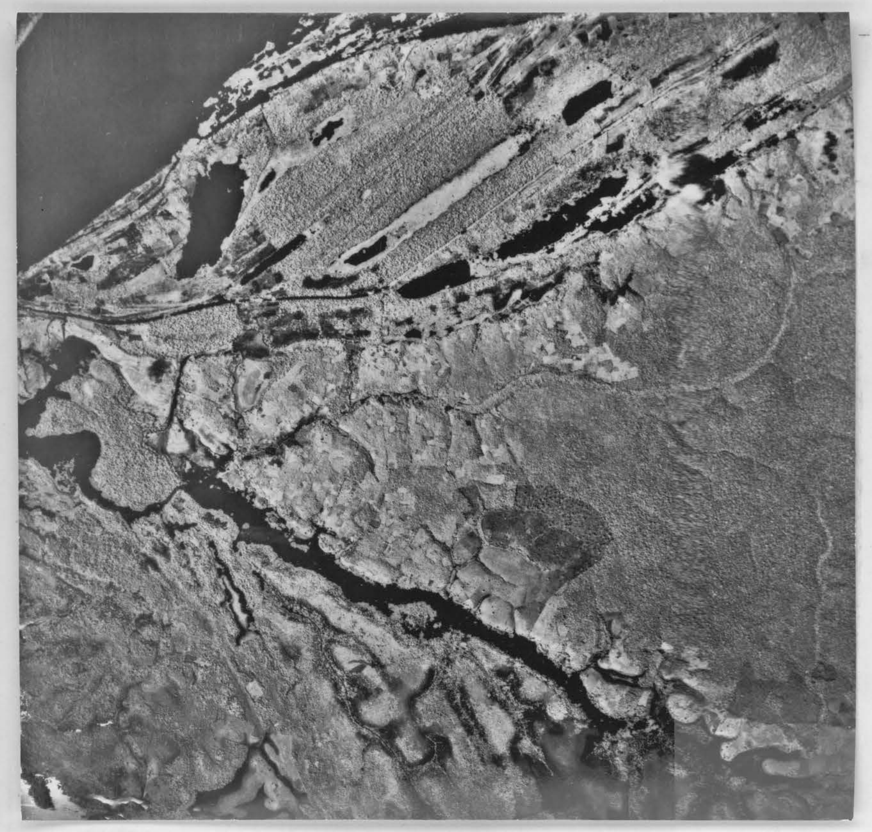
2.3 Floodplain biotopes and sampling considerations

Aerial, infra-red photographs were available for sampling regions Janauarí and Marchantaria which are shown in Plates 2.4 and 2.5 respectively. The sites sampled are indicated in Figures 2.4, 2.5 and 2.6.

The Janauacá sampling region shown in Figure 2.6 was based on enlarged LANDSAT images and ground truth observations since no aerial photography was available. Locally, the name Janauacá refers to the whole system draining via the paraná shown in Figure 2.6.

Even the small scale images presented here suggest a complex system. The complexity at biological scales is such that a brief summary is not possible. The following description is an oversimplification.

Plate 2.4 Aerial photograph (near infra-red) of the Janauarí region (see Figure 2.4 for sampling sites). [Taken by Servicos Aerofotogramétricos Cruzeiro Do Sul S.A.].



0 1 KM

Plate 2.5 Aerial photograph (near infra-red) of Marchantaria Island (see Figure 2.4 for sampling sites). [Taken by Servicos Aerofotogramétricos Cruzeiro Do Sul S.A.].

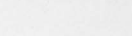
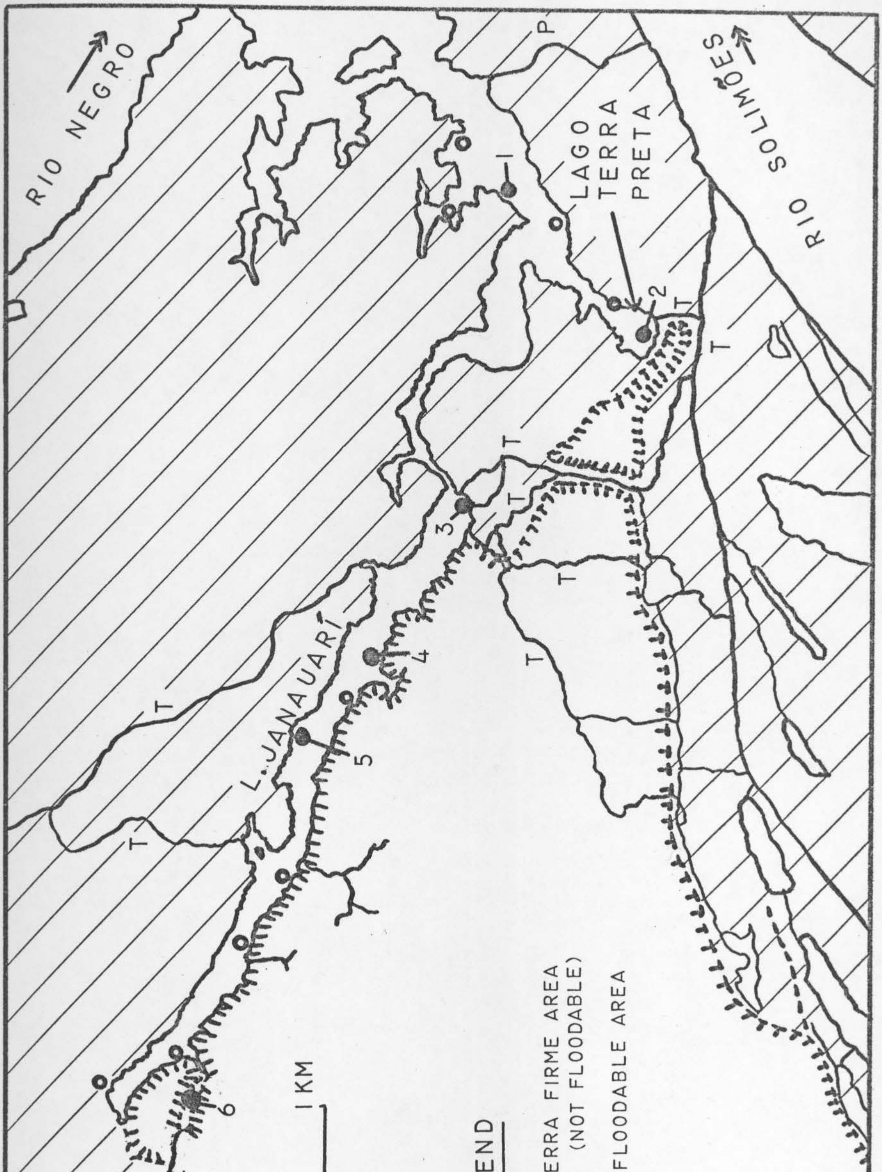

0
1 KM

Figure 2.4 The Janauarí sampling region. Regular sampling sites (solid circles) and occasional sites (open circles) shown. (Site 6 had to be moved to nearest occasional site in L. Janauarí at very low water)

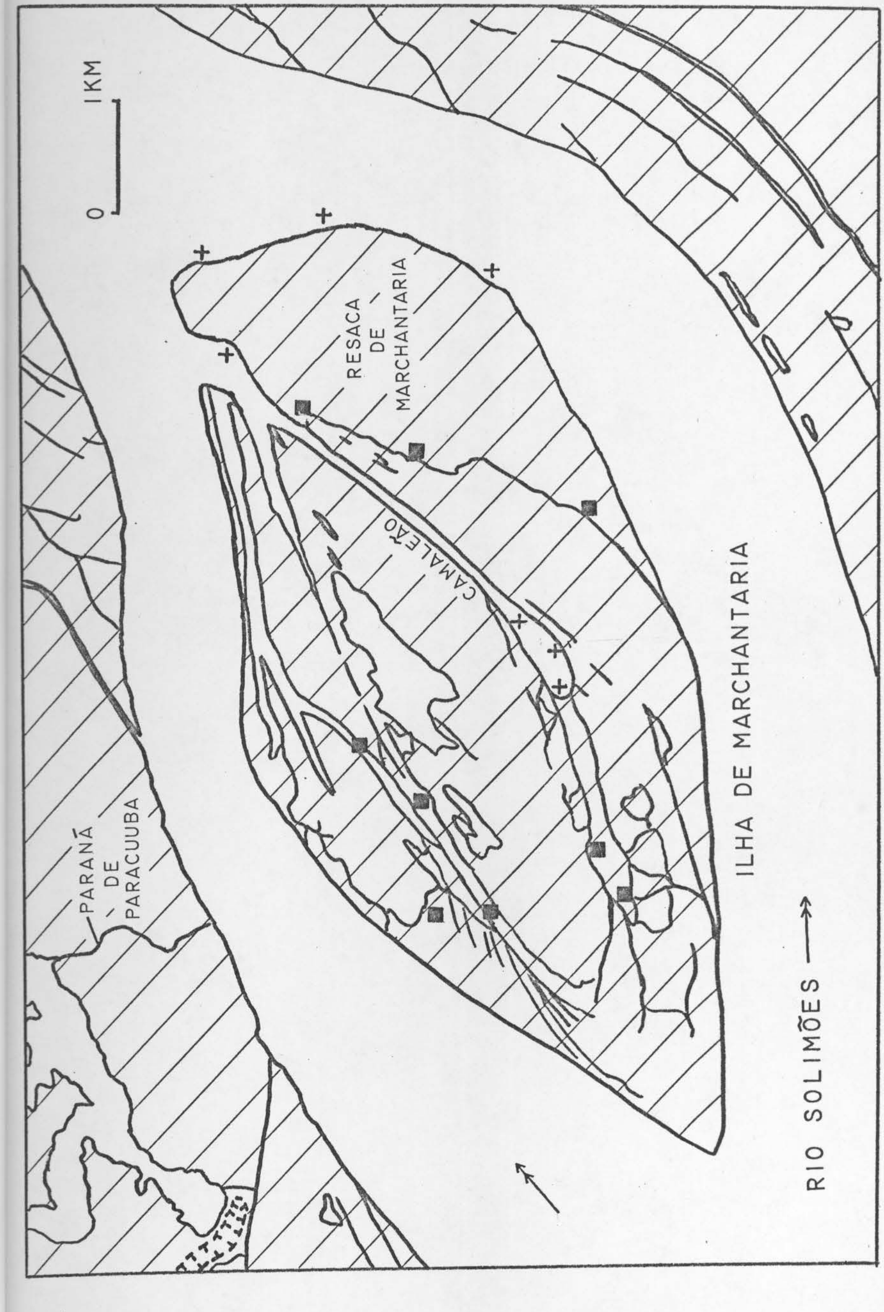
T = Temporary connecting channel.

P = Permanent connecting channel (during most years).

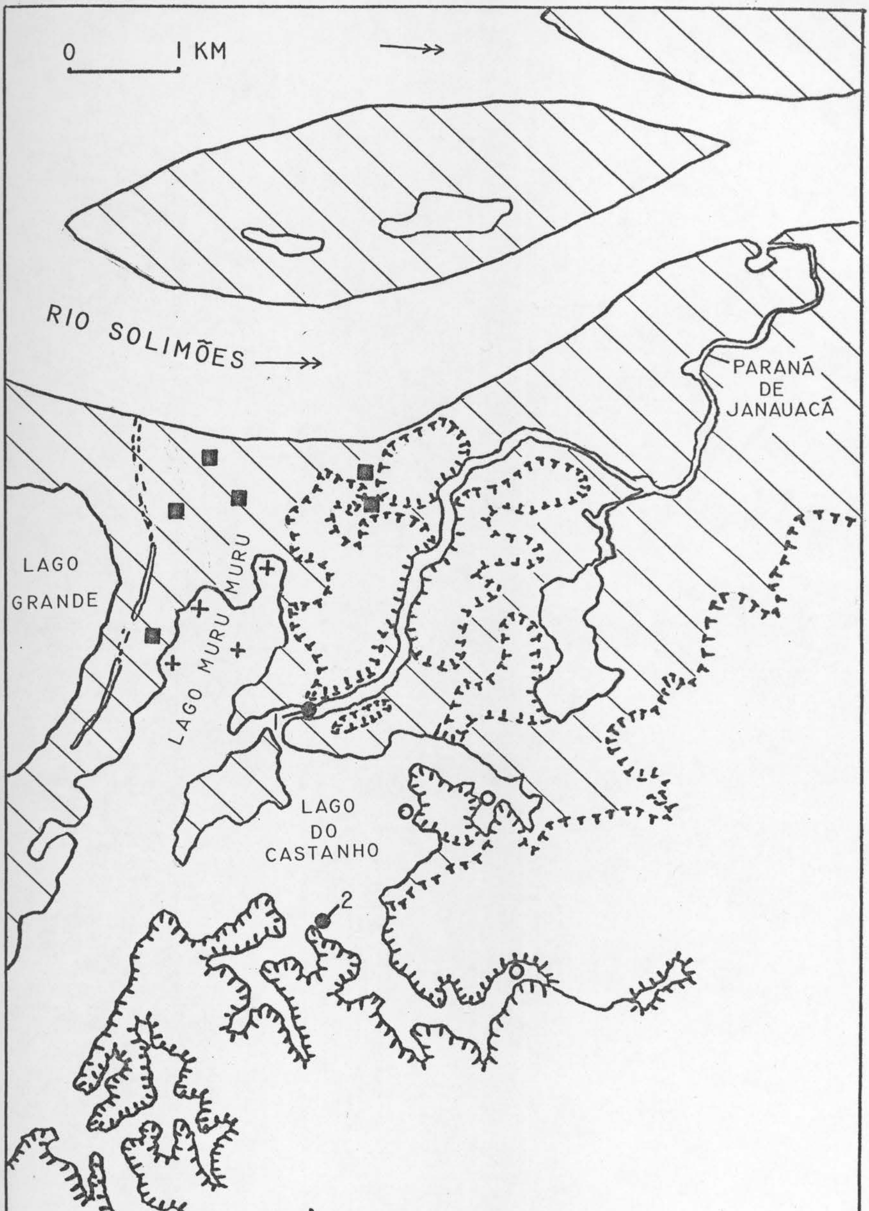
(see legend for other symbols).


RIO NEGRO
RIO SOLIMÕES
LAGO TERRA PRETA
L. JANAUARÍ
P
T
1
2
3
4
5
6
0
1 KM
LEGEND
TERRA FIRME AREA (NOT FLOODABLE)
FLOODABLE AREA

<u>Figure 2.5</u> The Marchantaria sampling region. Typical sampling locations are shown at low water (crosses) and high water (squares). The legend in Figure 2.4 applies.


0
1KM
PARANÃ DE PARACUUBA
RESACA DE MARCHANTARIA
CAMALEÃO
ILHA DE MARCHANTARIA
RIO SOLIMÕES →

<u>Figure 2.6</u> The Janauacá sampling region. Typical high water sampling areas are shown as squares and ones at low water as crosses. Regular sites with little geographic adjustment necessary for water level are shown as solid circles, and occasional sites as open circles. Legend in Figure 2.4 applies, but some small terra firme 'islands' are not shown.


0
1 KM
RIO SOLIMÕES
PARANÁ DE JANAUACÁ
LAGO GRANDE
MURU MURU
LAGO MURU MURU
LAGO DO CASTANHO
1
2

2.3.1 'Active' and poorly-drained areas.

There are well-drained soils, numerous levées and relatively well oxygenated waters predominating in parts of the floodplain closest to sediment-laden, 'white' water rivers, including all the islands in the R. Solimões-Amazonas shown in the Plates. I have termed this complex of habitats 'active' floodplain (Bayley 1981) to distinguish it from the poorly drained areas isolated from the full water fluctuations and exchanges. Estimates of the areas of 'active' and poorly-drained zones are shown in Table 2.1 under J and I respectively.

The latter consist of various types of swamps as well as marginal damp grassland zones, which are at most only flooded for short periods during some years. The swamps or wetlands have a varied local taxonomy, the terms *chavascão*, *pântano* and *buritizal* being often used. The latter refers to poorly drained depressions forested by *buriti* (*Mauritia flexuosa*) . The areas with more water such as *chavascão* are typically dominated by dense layers of slowly rotting vegetation (*matupá*) supporting an emergent flora. These variants have one or more of the following features:

1. Many areas are merely damp ground during most or all of the year.

2. Sufficiently inundated zones are often too far

from rivers to allow safe evacuation of fish when water recedes.

3. The poor drainage results in low turnover of nutrients and slow decomposition of thick vegetation resulting in lack of dissolved oxygen, H_2S presence and acid conditions.

Except for a minority of specialized animals which do not include commercial fish species, these areas are not important and should not be included in the area extrapolated from fish biomass and productivity estimates.

Their extent was estimated from their very flat topography and limited ground truth data, and are shown in Table 2.1. They could not be distinguished from 'active' floodplain using multispectral analysis because both contained water, some forest and aquatic macrophytes. Fortunately, in the area of study, poorly drained areas are not a large component of the total floodplain as opposed to other parts of Brazil and in Peru. Consequently, any inaccuracies in their determination would produce a minor bias in the overall estimates of fish productivity in this region.

2.3.2 Inshore biotopes.

The inshore biotopes within the 'active' floodplain which I had recognized on the basis of small fish distributions turned out to correspond closely to Junk's (1970) subdivision on the basis of aquatic macrophytes. A slightly modified version of his subdivision follows:

A. Current region of the R. Solimões-Amazonas.
  - a) strong currents.
  - b) deep water.
  - c) high inorganic sediment load.
  - d) homothermal layer of water.
  - e) pH close to 6.8, fairly high conductivity (see above).

B. Bank and sedimentation zones in the R. Solimões-Amazonas.
  - a) weak current.
  - b) shallow water; dry at low water level.
  - c) high inorganic sediment load.
  - d) homothermal layer.
  - e) pH close to 6.8, fairly high conductivity.

C. *Várzea* lakes with high fluctuations in water level (with continuous connection to the main river).

a) normally no current.

b) shallow water; low gradient in floodplain except where terra firme exists.

c) temperature stratification (see below).

d) variable pH and conductivity.

D. Vàrzea lakes with relatively small fluctuations in water level (connection with main river only during highest water levels).

a) no current.

b) water level remains relatively high during low water season, but some loss occurs through evaporation and seepage.

c) macrophyte communities differ as explained above.

d) other factors similar to C.

Biotope C was most intensively sampled during this project. B was sampled in parts of Marchantaria, but A and D were not sampled.

While these biotopes and the intervening levées are included in the 'active' floodplain, biotope D which is represented by relatively small lakes has some characteristics in common with the swamp areas described above. They contain many thick 'floating meadows' typified by Leersia hexandra stands which become so dense and deoxygenated that invertebrate abundance is drastically reduced (Junk 1970, 1973).

Macrophytes in biotope C are associated with the highest densities (>100,000 animals/m^2) of invertebrate fauna recorded in the region (Junk 1973, 1976). They are apparently supported by detritus and phytoplankton, much of the latter washed in from the open water. The production of the latter is 290 $gCm^{-2}yr^{-1}$ (calculated from Schmidt (1973b)) using the C-14 method in L. do Castanho which typifies open water associated with C. This is much higher than in permanently 'black' waters or turbid 'white' waters (Schmidt 1973b, 1976).

The only estimate of aquatic macrophyte production is a very approximate one made by Marlier (1967). Measurements were made of the recolonization of a cut area, producing an estimate of 6.2 $gCm^{-2}day^{-1}$ for the six month growing period, which is about 1050 $gCm^{-2}year^{-1}$ or about four times the phytoplankton productivity in similar decanted 'white' water.

Distribution of benthos parallels that of perizoon and zooplankton in macrophyte areas, but is much less abundant - due probably to O_2 deficiencies close to the bottom (Reiss 1976; Fittkau et al 1975).

Biotope A corresponds to the river area estimates (K in Table 2.1) except were the R. Negro was included. It also corresponds to the independent LANDSAT multispectral classification of 'white' water at low water

(L in Table 2.1) since at the time of that image wind was not stirring up the bottom of várzea lakes. The productivity of this biotope is so limited by light attenuation and other physical constraints that it can provide little food for small fish. However, in the study area the main channel forms a large proportion of the low water area (Table 2.1) and is occupied by small fish.

Biotopes B, C and D are included in the estimates for decanted/mixed water types (C or M in Table 2.1) and aquatic macrophytes (E) which are only significant above the low water level. Of these, biotopes D and B occupy a small proportion of the 'active' floodplain.

A, B and C comprise the 'open' system which has been continually interconnected by some route during most of the last ten years. Although there is a continuum of examples between biotopes C and D, the latter are typically isolated for more than half the year. Apart from their probable lower productivity they occupy a very small total area compared with interconnected bodies. Moreover the spawning of most commercial sized fishes occurs in the main river or in adjoining open areas before access to relatively closed areas is possible.

The macrophyte stands in B and D typically have lower faunal densities than in C although the peripheries of the floating meadows in B are similar (Junk 1973). Biotopes B, C and D were re-expressed in terms of macrophyte assemblages, with more emphasis on faunal densities by Junk (1973).

2.3.3 Other biotopes.

Although seasonally 'black' waters were sampled at the periphery of the floodplain in Janauarí and Janauacá, permanently 'black' water which is characterized by extremely low primary productivity (Schmidt 1976) was not sampled.

It was impossible to quantitatively sample in the flooded forest.

Offshore areas beyond the macrophyte beds were sampled at depths of about 2 to 4m.

2.3.4 Dissolved oxygen.

There are severe limitations to fish distribution in the 'active' floodplain which are more marked at higher water levels. These are due to a layer of permanantly deoxygenated water deeper than 3 to 6m in *várzea* lakes. Since virtually no parts of the floodplain excluding the main river are more than 2m deep at low water, this phenomenon is increasingly important relative to the area flooded at the higher water levels between April and

August/September. This was well documented for L. do Castanho in the Janauacá system (Figure 2.1) by Schmidt (1973a).

He also noted the ubiquitous association of H_2S with these layers, which would also exclude the air-breathing fish species.

It has been noted (Kramer et al 1978) that fish with accessory breathing organs are scarce in floodplain habitats, and the alternative for many species is 'aquatic surface respiration' (ASR) which assists survival during cool nights in sheltered habitats and occasionally during the day when overturn of the water column occurs during friagens or cold spells.

The measurements by Schmidt (1973a) were made in open water near the deepest part of L. do Castanho. Further inshore it has been noted that very low O_2 levels (<.5 mg/l) exist locally in lesser depths due to macrophtyes restricting circulation and their decaying products (Junk 1970).

2.4 Sampling strategy and description of sites

2.4.1 Introduction.

Since the primary purpose of this project was to estimate fish production more replicates were taken in areas where both the limnological evidence and that of fishermen working on the project was positive. Samples were also taken where possible in other areas such as those with very low conductivities and others bordering the main river.

The foregoing sections provide some evidence that most of the total fish production in the central Amazon floodplain is most likely to occur in the 'open', interconnected water bodies.

The sampling problems are considerable. But by concentrating on smaller fishes, including the first 1-2 years of the majority of commercial species, the problems are surmountable providing that extensive and frequent representative samples are taken. In addition a surprising number of large fish were caught, in particular piscivores.

The advantage of taking numerous samples using a gear of known efficiency (see Chapter 3) as opposed to a limited number of direct but possibly biased estimates of biomass in particular enclaves should be evident. Apart from the statistical advantages, a major problem with a population study in an open system is emigration and immigration. Extensive sampling going beyond the major nursery areas increases the number of species and size ranges whose subpopulations can be confidently delimited.

There are limitations which vary from species to species. This is inevitable in a very complex environment with marked seasonal changes and containing habitats which cannot be sampled quantitatively. Inshore sampling during high water was limited to a few areas which had been cleared previously for small scale agriculture - now constituting a major habitat in most of the Solimões-Amazonas floodplain and adjoining terra firme shores. Other areas containing woody vegetation which could not be removed by hand, including remaining floodplain forest, could not be sampled. Small fish are known to utilize these habitats (Goulding, personal comm.) which become significant from May to August. Some samples from sites adjoining areas of woody vegetation which have recently been drained during September produce large catches, suggesting that recent evacuation has occurred. On the other hand, many fish anticipate the reduction of a floodplain by migrating down paranàs to the main river such as in Janauacà (Figure 2.6).

To preselect spatially random samples in strata would have required the sampling information gained during this project plus expensive mapping mentioned in 2.1. An exception to this was the downstream shoreline of Marchantaria where random numbers before each excursion determined the distances along the shoreline for three sampling locations. Due to the water level movement which changed the habitat distributions markedly between two week sampling intervals, I doubt that these results were any more randomized than sampling at geographically similar locations. Distances between samples from a biotope within a region ranged from about 500m to 2km, a scale much larger than that of the habitats sampled with the exception of the offshore area. Periodically, replicates were taken at each regular sampling station and in the same habitat existing at the time, within 25 to 40m of the first sample. Their similarity was no greater than that between samples from similar habitats on a larger scale within the biotope.

The practical details of sampling are explained in Chapter 3 along with the calibration of the net under different modes of operation. Since the primary purposes of this project were to estimate biomass and production and only sampling during daytime hours could be quantified, night samples were not taken. Consequently, diurnal movements out of and into shoreline macrophytes known to exist were not studied. Occasionally calm, hot weather heated shallow water considerably, an occurrence associated with evacuation of the majority of fish from habitats close inshore. Except for a few such occasions which were noted, sampling in these conditions was avoided.

2.4.2 Frequency of sampling in three regions.

Three regions were selected (Figure 2.1) for a regular sampling program involving excursions every two weeks during a 15 month period beginning in February 1977, resulting in 600 samples with the 25m seine net. This was followed by 23 net calibration samples taken at Marchantaria between September 1978 and January 1979 and at Janauarí between April and May 1979. A further series of samples taken to collect fish for marking during the calibrations have yet to be analysed.

The three regions were chosen because a) they included a range of habitats typical of the Amazonian, turbid river floodplains, b) many habitats were replicated between regions which increase the possibilities for natural experiments. In the latter situation it may be assumed that populations of smaller fish do not migrate between regions during a limited period. Even with some larger fish, meristic differences have suggested discrete populations between the regions for <u>Semaprochilodus</u>

insignis (unpublished data) and _Hemiodus microlepis_ (P. Johns 1982).

The Marchantaria region is unique in that there is no influence of 'black' water and that no _terra firme_ shores exist. Similar habitats dominated by 'white' water or its decanted form exist in Janauacá and Janauarí, although the latter is dominated by sites with considerable 'black' water influence.

The Janauacá region was chosen partly because of the good limnological studies of Schmidt (1973a, 1973b) and others which had concentrated on L. do Castanho. Figure 2.3 shows the periodicity of the sampling with respect to the water level. In most parts of the floodplain sampling zones had to shift markedly due to the water level changes (e.g. Figure 2.5). Sites close to or on _terra firme_ could be sampled throughout the year by merely moving up or down the bank with the water level at Janauarí (Figure 2.4) and two sites in the Janauacá sampling region (Figure 2.6).

2.4.3 Descriptions of individual sites.

The following measurements and observations were made at each sample site:

1. Date and time of day.

2. Local name of site or appropriate directions.

3. Sampling method used (see Chapter 3).

4. Distance between the ends of the net (see Chapter 3).

5. Minimum and maximum depths enclosed by the net.

6. Photograph taken of site with net laid.

7. Approximate distance offshore of sample.

8. Shortest distance to R. Solimões as the fish swims (estimated later from position on map and from connections existing at the time).

9. Total vegetation/cover (an index represented by the number of man-minutes required to clear the vegetation and debris).

10. Percentage of water surface covered by emergent vegetation.

11. Dominant and subdominant vegetation species enclosed.

12. Dominant vegetation, if any, bordering open water samples.

13. Secchi disk reading (25cm diam. white disk); data from March 29,1977.

14. Color of water as observed on white disk background.

15. Conductivity of water, corrected to 20°C; data from June 21, 1977.

16. Bottom type (sandy, muddy or hard clay = _terra firme_).

17. Bottom hardness (three grades estimated).

18. Presence of thick, partially decayed vegetation (matupá) on the bottom.

19. Presence and quantity of tree trunks within encircled area.

20. Presence of water current.

21. Presence of fish doing ASR (aquatic surface respiration).

22. Presence of H_2S at water surface (nose test).

23. Recent occurrence of a shorter connection with the R. Solimões and the sample site.

24. Presence of large migration of fish down connecting channel.

25. Weather observations.

Water types were described by Wallace (1873), Sioli (1965, 1968) and recent limnologists on the basis of color and later by transparency and inorganic chemical characteristics. The subset studied during this project is portrayed in Figure 2.7. This figure does not illustrate two factors, one being the seasonal variability at a given site, the other being the 'shore effect' which often produces a higher conductivity, and a higher or lower transparency than near the center of the water body where limnological measurements are usually taken. Seasonal variability at Marchantaria and three sites in the other two regions is shown in Figure 2.8. The complex interplay between invading 'white' and 'black' waters, local concentration and leaching effects and rainfall result in different seasonal effects in different regions. The lack of 'black' water, the small influence of rainwater and local concentration effects account for the much higher values in Marchantaria. Among these, the highest values occurred in the Camaleão inlet (Figure 2.5) during falling water, when a distinct green color suggested a higher phytoplankton biomass (Figure 2.7).

It would have been very useful to measure dissolved oxygen but the spatial distribution is so complex and dynamic that a meaningful coverage of each sample site was not feasible. However, the presence of fish under respiratory stress (see 2.1) was observed on occasion, and confirmed by the presence of fleshy extensions on the lower lip (personal observation).

Figure 2.7 Conductivity versus Secchi disk measurements with visual estimates of water colour: 'black' water (squares); 'white' or turbid water (circles); 'white' decanted or black and white mixed (crosses); 'white'/green water (stars).

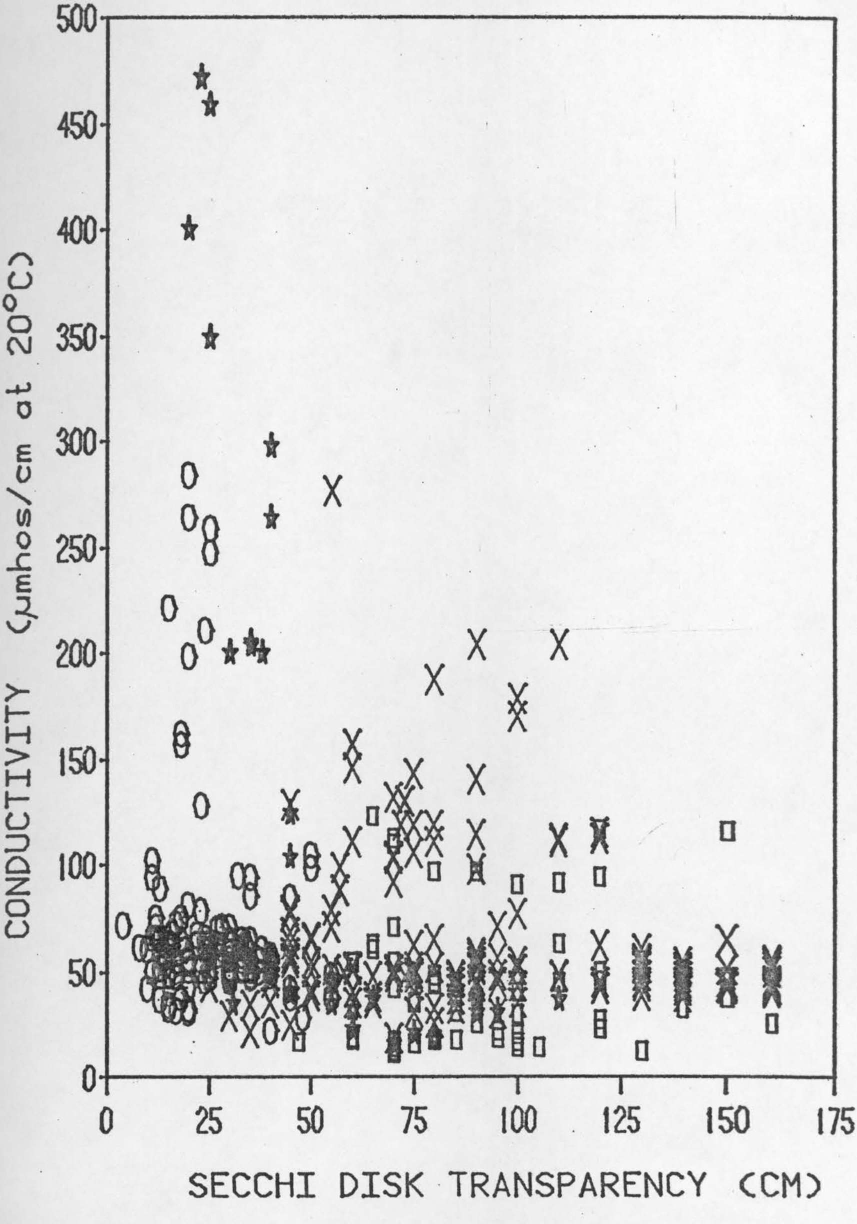

CONDUCTIVITY (µmhos/cm at 20°C)
0
50
100
150
200
250
300
350
400
450
500
0
25
50
75
100
125
150
175
SECCHI DISK TRANSPARENCY (CM)

Figure 2.8 Conductivity at 3 locations and 1 region by season.

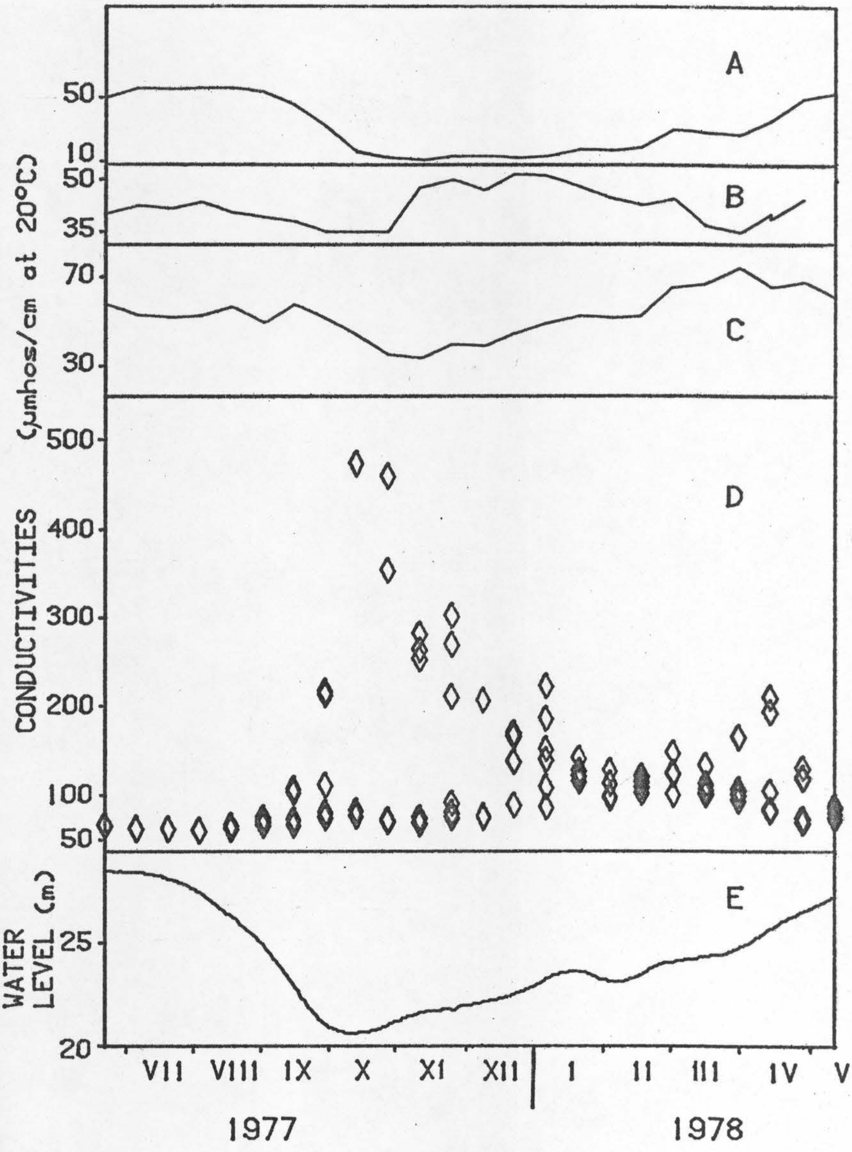
A = Canta Galos, Janauari (Site 6 or adjacent site on Figure 2.4)

B = São José, Janauacá (Site 2 on Figure 2.6)

C = L. Terra Preta, Janauari (Site 2 on Figure 2.4)

D = Marchantaria (all sites, see Figure 2.5)

E = Water level, Manaus gauge.


A
B
C
D
E
50
10
50
35
70
30
500
400
300
200
100
50
25
20
(µmhos/cm at 20°C)
CONDUCTIVITIES
WATER LEVEL (m)
VII
VIII
IX
X
XI
XII
I
II
III
IV
V
1977
1978

The average bottom gradient from shoreline to sample varied (Figure 2.9) the steeper gradients usually being associated with terra firme shores. Maximum depth ranged up to 4.3m.

Distance from the R. Solimões ranged from zero on the downstream shore of Marchantaria (the 'resaca' in Figure 2.5) to 13.5km near the extreme of L. Janauari. These distances were calculated by calibrating the speed of the canoe between points which could be identified on the aerial photographs or other images. This also confirmed the identification of sampling stations on the images. Distances of many of the same stations changed at particular water levels due to alternative connections being opened or closed. This variable is important for those fish species which spawn in or near the R. Solimões and disperse laterally with the advancing flood.

The two measures of 'vegetation' (9. and 10.) are poorly correlated (Figure 2.10). Even the most common truly submerged species, Utricularia was only occasionally dominant and only partially accounts for the poor relationship. Dead vegetation, recently flooded terrestrial vegetation and different proportions of rooted, emergent stages and truly floating vegetation partially account for this poor correlation.

Plant species were dominated by those of Graminaea, of which Paspalum repens was by far the most common species occurring within the sample sites. It was the dominant species in 18% and subdominant in 4% of all samples. It is the most dominant species in the *várzea* as a whole (Junk 1970).

In conclusion, I consider the sampling to be sufficiently intense and frequent to provide estimates of productivity and some ecological insight with respect to juveniles and adults of common species. Quantitative sampling in the forest or the log-infested rivers is not at present feasible, but qualitative data mentioned in Chapter 5 does provide some basis for extrapolation.

Operational details of the fishing process are more appropriately presented in the following chapter which explains how the efficiency of the standard seine was estimated.

<u>Figure 2.9</u> Minimum depth at sample site versus approximate distance offshore.

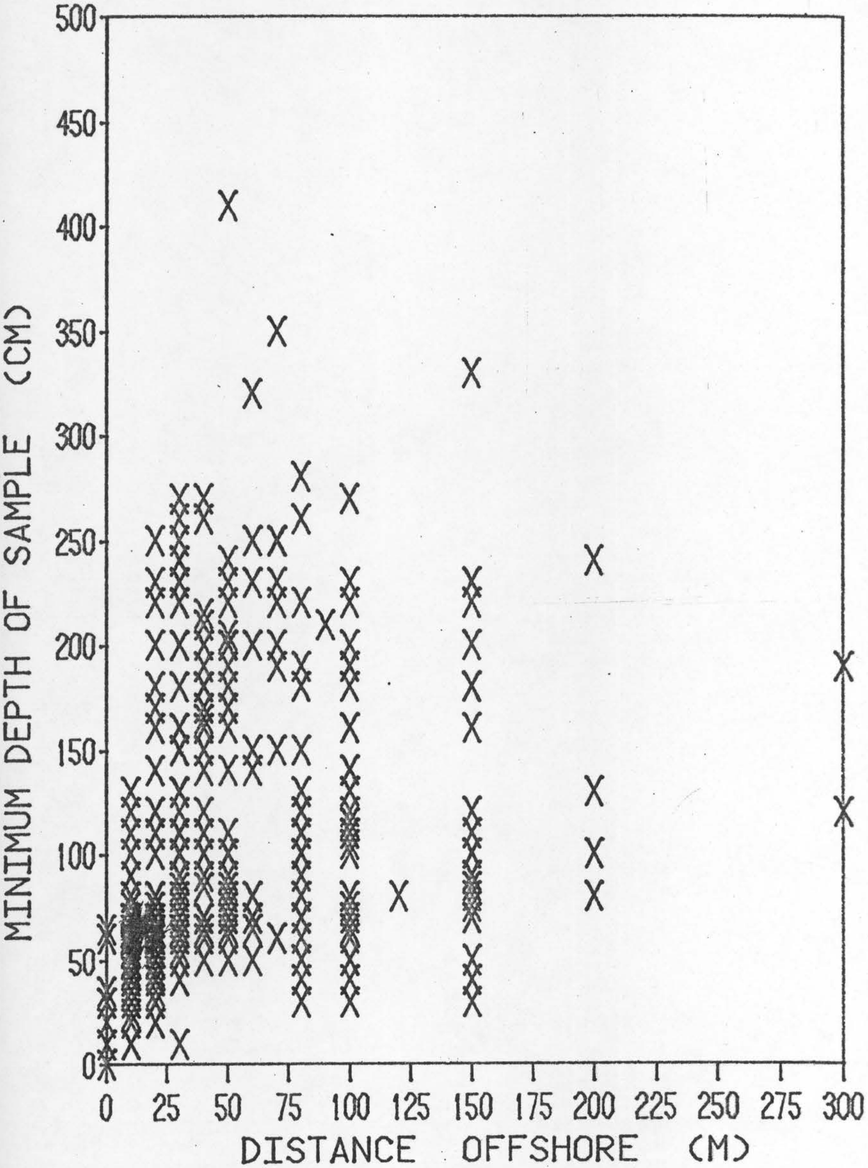
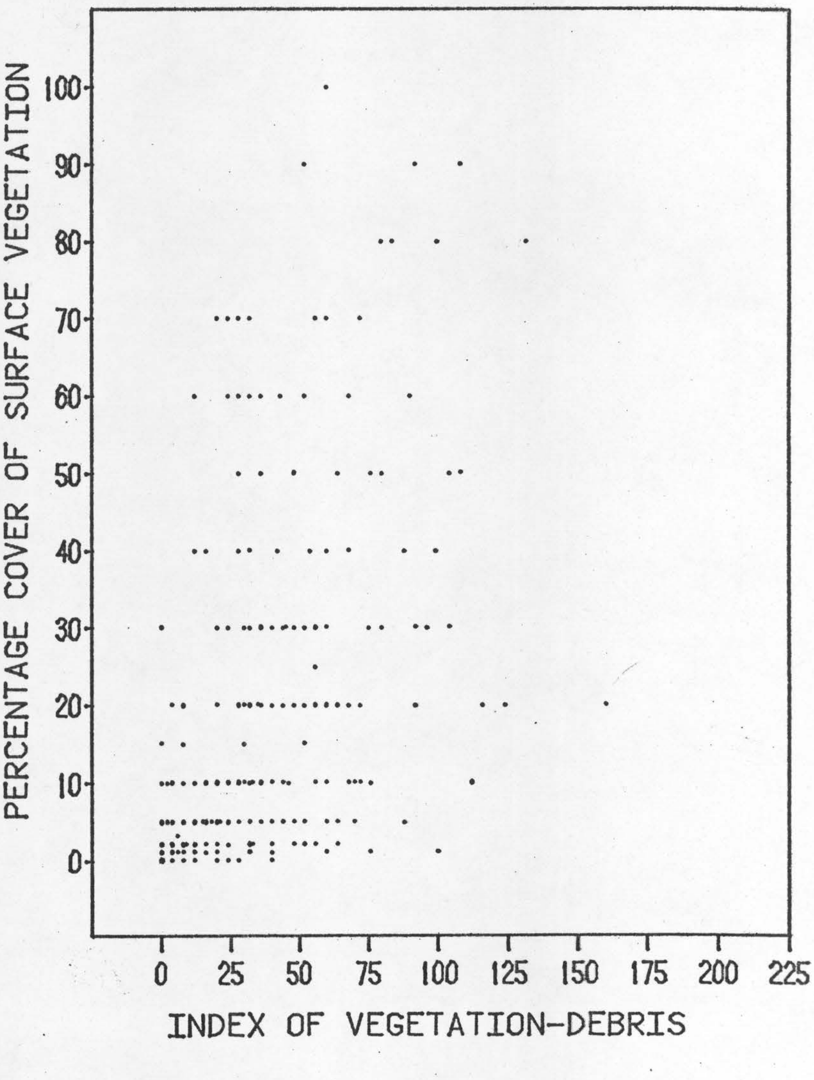

MINIMUM DEPTH OF SAMPLE (CM)
500
450
400
350
300
250
200
150
100
50
0
0
25
50
75
100
125
150
175
200
225
250
275
300
DISTANCE OFFSHORE (M)

Figure 2.10 Percentage cover of surface vegetation versus an index of vegetation-debris (or cover). The latter variable is the number of man-minutes taken to clear the area enclosed by the net.


PERCENTAGE COVER OF SURFACE VEGETATION
100
90
80
70
60
50
40
30
20
10
0
0
25
50
75
100
125
150
175
200
225
INDEX OF VEGETATION-DEBRIS

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Chapter 3: The efficiency of the seine net

3.1 Introduction

The purpose of this exercise was to calibrate the standard net in its various modes of use in order to estimate abundances and biomasses with confidence limits. Various methods exist for estimating biomass (e.g. Leslie & Davis 1939; deLury 1947; Seber & LeCren 1967) which conceivably could be used to estimate efficiency. But no existing methods were deemed appropriate for the following reasons.

Most methods, including those quoted, depend on repeated sampling of the same blocked area. The presumption of constant catchability is required, which also implies that individual fish have equal and constant probabilities of encounter by the gear throughout the operation. In addition, the ability of the block net or other enclosure to contain the isolated subpopulation needs to be known, but is often not estimated and is presumed to be 100 percent.

Interpretation of results from repeated hauls without control of emigration or immigration can be problematical (Williams 1965; Mathews 1971). A promising method described by Linfield (1981) using a seine net from a pontoon within a block net avoids the problem of repeated hauls, but concern was expressed about disturbance prior to setting the block net.

These problems were accounted for by Allen (1951). He determined abundance on the basis of computing the efficiency of the netting procedure by marking and recapturing at three month intervals. This method was facilitated by the relatively closed sections of the stream. In addition to controlling the boundaries, estimates were based on frequent and extensive samples.

Common habitats in the central Amazon floodplain and bordering flooded valleys often contain large quantities of vegetation and debris; factors which are correlated with higher fish densities. Repeated sampling is simply impossible without disturbing the habitat, and almost certainly the fish themselves. Even in a habitat without obvious structures unrealistic results can result, such as Lagler's team discovered when attempting to apply the Leslie method to a seine on an African river (Lagler *et al* 1971). They eventually used the first seine catch and related this to the block net catch, assuming the latter to be 100 percent efficient.

A serious problem is emigration from the area covered by the seine or block net while it is being layed. Chemofishing blocked off areas is a useful direct method, but emigration is suspected to bias the estimates (Kapetsky 1974). Also a single sample can require three days producing high variances due to limited replications and lack of extensive sampling.

The method described below attempts to solve these problems in an open system.

3.2 Theory

Briefly, the principle of the method is as follows. A block net is layed, marked fish are released inside, the standard net is fished inside once, and finally the block net is hauled. The different modes of fishing and the geometry are explained in 3.3. Marked and unmarked fish (and the decapod, *Machrobrachium*) are used in the analysis. The important features of the method are:

(a) The calibration of the standard net is made with respect to the quantity remaining within the block net after closure. Therefore, it is limited to a size range of fish within the maximum caught (850mm) and the minimum controlled by the 5mm mesh size (close to 12mm).

(b) The first role of the marked fish is to provide an estimate of catchability of the standard net based on the area it encloses, and the proportion of the marked fish vulnerable to capture on average. Therefore, a single estimate would be correct only if a large number of marked fish were evenly distributed within the block net.

(c) The second role of the marked fish concerns those remaining within the block net after the standard net has been fished. The proportion escaping when the block net is hauled provides an estimate of the number of unmarked fish lost, thereby an estimate of the number of unmarked fish originally vulnerable to capture by the standard net.

(d) The captures of unmarked fish in both nets, and the block net escapement estimated in (c), provide a second estimate of the catchability of the standard net, this time with respect to in situ, unmarked fish.

The variability of the estimates includes that due to spatial heterogeneity of the fish within the block net.

A few calibrations did not utilize marked fish to save time or when it was too hot to keep marked fish. An escapement function derived in 3.4 from the marked experiments as outlined in (c) was used for all calibrations as in (d).

There is an important distinction between two components of catchability:

(1) Evasion is defined as the change in numbers of fish in the area encircled by either net before it is closed. In individual samples 'negative evasion' or net influx is conceivable.

(2) Escapement is defined as the loss of fish after closure of either net. Its complement is referred to as "retention". This includes losses through the mesh and between the ends as well as under the leadline.

Some species are adept at jumping out on occasions, but during the calibrations only fifteen out of $4.2x10^4$ individuals jumped out of the standard net and one out of the block net. This was similar to that found during the standard net hauls. The numbers and approximate sizes of fish lost through jumping was based on a visual consensus between the three fishermen and myself positioned 6-8m away. Larger fish of four easily distinguished genera dominated those jumping out, and there was close agreement on the sizes of fish and numbers escaping. Therefore this loss by jumping was not included in this analysis, the estimates simply being added on after correcting the catch for efficiency. The results (3.5.3) indicated that this loss was negligible compared with those lost invisibly through evasion or escapement.

Consequently, (c) above only involves escapement, whereas (b) and (d) estimate total catchability less jumping, which is the product of the complements of (1) and (2)

Mathematically, the treatment is quite straightforward:

Let N, N_m be the numbers of unmarked and marked fish within the block net after enclosure respectively,

C_s, C_{ms} be the captures of the standard seine, unmarked and marked respectively,

C_b, C_{mb} be the captures of the block net, unmarked and marked respectively,

r be the proportion of marked or unmarked fish within the block net vulnerable to capture by the standard net,

q_1, q_{m1} be the catchabilities of the standard net with respect to unmarked and marked fish respectively; that is the proportions of those vulnerable which are actually caught,

q_2, q_{2m} be the proportions of unmarked and marked fish respectively which are caught in the block net relative to the quantities vulnerable after fishing the standard seine; that is the block net "retention" or the complement of "escapement".

All the above definitions and the following equations refer to species group-size groups and modes of standard net operation, as shown below in section 3.4. The following four equations summarize the relationships between the variables:

$$c_{ms} = rN_mq_{m1} \tag{1}$$

$$c_s = rNq_1 \tag{2}$$

$$c_{mb} = q_{m2}N_m(1-rq_{m1}) = q_{m2}(N_m-C_{ms}) \tag{3}$$

$$c_b = q_2N(1-rq_1) = q_2(N-C_s) \tag{4}$$

If A and a are the areas enclosed by the block and standard nets respectively, then $\hat{r} = a/A$ would be an unbiased estimator of r if the fish were distributed randomly or evenly inside the block net. If the block net was a random sample in a clumped distribution, and the presence of the net did not subsequently affect that distribution, the means of catchability estimates based on $\hat{r}$ would be unbiased. But the variance of the catchability would include a large component due to the clumped distribution of fish if it were on a small scale relative to that of the block net. This is discussed further in the light of results in 3.4.

An attempt was made to distribute the marked fish as evenly as possible to reduce the variance due to clumping.

In conclusion, equation (1) provides a direct estimate of catchability of the standard seine with respect to marked fish. A less direct method, but accounting for the net evasion behaviour of unhandled, unmarked fish involves an estimate of the retention, q_2, of the block net provided by q_{m2} using equation (3). Substituting in equation (4) provides an estimate of N, which in equation (2) provides a second estimate of the catchability.

It is considered unlikely that the relatively small number of fish which escape the standard seine during hauling which would again be subject to retention by the block net would significantly bias the estimates of retention of the whole group of fish concerned. Fish which have recent experience of evasion should not be affected because (1) that component of catchability with respect to the block net does not need to be known, and (2) all fish are disturbed before the block net retention comes into play.

3.3 Methods

3.3.1 Description of Nets.

The nets were designed by Alcides Guedes dos Santos, on the basis of 42 years fishing experience in the region, and P. T. Makiyama.

The standard seine or lampara net was used throughout the project, after tests indicated that it was capable of catching a considerable size range and diversity of fish. The mesh was dark blue, braided (knotless) nylon with a stretched mesh size of 5mm excluding the twine width of about 0.5mm.

The length when hung was 25m and consisted of 40m of netting which was tucked at intervals to form a series of bags. This design was superior to using a single, larger bag because operation was smoother (and quieter), subsequent sorting of fish from debris was more efficient and it allowed predators and dangerous species to be removed quickly. In addition, it is probable, as the fishermen claimed, that a series of bags reduces the tendency for fish to swim out before closure (i.e. "evasion" defined above).

The net was 6m deep, but tapered to 60cm at the ends which were supported by poles to facilitate hauling in shallow water. This depth permitted a considerable belly in the net, even when the maximum water depth was 3m, reducing the tendency of fish to jump while hauling.

The lead line consisted of 120g lead cylinders set at 35cm intervals. The floats were 10cm diam. by 4cm thick, and spaced at 30cm intervals.

The block net was also designed as a seine net, using the same mesh and depth, but with deeper ends to facilitate setting in deeper water. It was 50m long when hung and consisted of 85m of netting. Its lead weights were placed 50cm apart to reduce total weight, but the floats were placed 25cm apart to reduce escapement of smaller, surface-dwelling fish between them.

3.3.2 Operation of the standard seine net.

This description refers to the 600 samples taken prior to the efficiency tests, as well as the identical operations conducted within the block net.

In all modes of operation a heavy, wooden, eight-meter canoe was used. This enabled four men to stand on one side for hauling into the boat, aided its momentum in passing through vegetation and allowed quiet operation.

The head fisherman paddles at the prow, guiding the configuration of the net. After consultation with the author with respect to the desired habitat for sampling, he decides the precise location in advance so that snags in the path of the net can be avoided. Hauls rarely had to be abandoned due to being hung up on obstacles, although frequently trunks were deliberately enclosed and removed after the net was closed.

A second fisherman paddles aft, where the outboard motor was cocked free of the water.

A third stands between, paying out the net whilst keeping the lead line from sounding against the canoe.

These positions are shown in Plate 4.1 (Plates on pp. 120-121).

When approaching and encircling the site absolute silence is essential, even in the manner in which the paddles are operated.

There were three, distinct methods of using the same net:

Method A.

The net was fished as a lampara, or 'unpursed' seine. It was paid out from the canoe (Plate 4.1) which describes a circle, leaving 8 to 12m between the ends (the canoe was 8m long) when the whole net was laid. The leading rope was picked up and the net hauled. At this stage it is beneficial to make a noise stamping on the canoe boards to frighten fish into the belly of the net which may be trying to escape under the boat before the lead line surfaces. The hauling process, which in this method must be rapid to get the lead line in, results in the canoe moving over part of the sampling area, further reducing efficiency.

This method was used in deeper waters where the methods described below could not be employed, that is greater than 80cm but less than 4m. Efficiency was improved by hauling the net from the shallowest point. Material such as macrophytes were not cleared from within the net prior to hauling. In general this method was used in more open waters, or in areas where rooted plants were present but not sufficiently dense to impede hauling. Often mats of floating plants were enclosed, which were discarded when the float line was beside the boat.

Method B.

This is a standard beach seining operation. The net is laid as usual, and the canoe descibes a semicircle. When there is a very shallow shoreline zone, the ends of the net are left further offshore, but in less than 15cm of water. As the fishermen had predicted, fish were observed not to take advantage of this route. The maximum depth varied greatly, and sometimes sloped to 3.5m on _terra firme_ shores.

After laying, the lead line was immediately checked to make sure it was firmly on the bottom. The contents were then cleared, including any rooted vegetation, large detrital material and tree trunks. Fish did not jump out while the net was being cleared.

Hauling in was slow, with separate people pulling each lead and float line ends, working slowly towards the center until only the belly of the net remained in the shallows. Larger fish were removed, and for large catches, the net was transferred to the canoe keeping the belly and fish in the water. This keeps the majority of the fish alive whilst they are sorted from finer debris and put immediately in formalin. On many occasions when piscivores and abundant prey were present no indication was found of fish having been recently ingested due to crowding.

Method C.

The third method was used in shallow, offshore waters which are important nursery areas. A tighter circle is described by the canoe so that only 0-4m separate the ends of the net. Any gap is then closed, the lead line checked and contents cleared as in method B. Again, four people participate in the slow, hauling process, but this time they are close together. Those pulling the lead line with hands on the substrate squat in contact to provide as complete a human barrier as is anatomically possible (Plate 4.2). This requires courage as well as skill, since the catch can often be felt but not observed in the murky waters.

When the lead and float lines are gathered, they are immediately lifted into the canoe leaving the belly of the net and the fish in the water. Sorting and preservation then proceeds as in method B.

In order that those pulling the lead line can breath, this method can be used where the minimum depth is less than 80cm.

A variant of this method was used where hard, woody vegetation could hold up the lead line. A circle a little wider than the canoe is cleared, and the area is left for at least an hour. The net is then laid and fished as described, removing the hard vegetation inside the net after enclosure.

3.3.3 Fishing the block net.

In all cases the block net was laid and fished in a similar manner to method B or C. However, as the net was being drawn in occupants of a canoe lifted up the center part of the float line to prevent any fish jumping out.

During the earlier calibrations, rotenone was used in the expectation that the retention, q_2, would be increased. The unrefined 'timbó' was used, so tests with controls were conducted on various species in aquaria at various concentrations. Its efficiency was considerably improved if the powder was steeped in 96% ethanol for 12 hours. A concentration to make the most resistant species drowsy was aimed at, and the equivalent of 50ppm of 'timbó' was found to be generally effective within 30min. If the rotenone concentration in the powder was 4% as claimed, this would be equivalent to 2ppm of the alkaloid in water.

All species showed agitated, disoriented swimming to varying degrees. One <u>Cichlasoma</u> <u>festivum</u> of 6cm actually survived the ordeal, whereas other, often larger, species died.

A comparison of the escapement using and not using rotenone is presented in 3.4.

3.3.4 Geometry of the nets.

Normally, the standard net was fished concentrically within the block net. However, when the bottom was sloping considerably such as in type B samples, one expects a stratification of at least some species and sizes with depth. Each depth included in the block net needs to be sampled proportionately by the standard net. Figure 3.1 (Figures on pp 122-136) shows the geometry and Plate 3.3 shows calibration 617 as an example of this using method B. The bouy at the mid point of each net was painted differently to assist in correct setting.

Given the standard, semicircular configuration of a type B haul by the standard net, the block net configuration is derived as follows:

let f(x) be the configuration of the block net

R be the radius of the standard net

K be the proportion of a strip X metres from shore which is fished by the standard net (= Z/W in Figure 3.1).

$$\text{therefore } K = (R^2 - X^2)^{.5} / f(x)$$

$$\text{rearranging: } \frac{(f(x))^2}{R^2} .K^2 + \frac{X^2}{R^2} = 1$$

This is the equation of an ellipse, whose minor axis, R, is known and whose major axis, R/K can be estimated iteratively using an approximate formula for the circumference, U:

where $U = \pi\{1.5(R + R/K) - (R2_{K})1/2\}$

= twice the length of the block net = 100m

Thus given R, the positions on the bank for the ends of the two nets could be calculated. These were marked prior to fishing as a guide to the fishermen (Plate 3.3). A similar calculation for a type C haul on a sloping bottom also produced an ellipse of half the circumference. This was used in calibrations 619 and 620.

3.3.5 Marked fish

Considerable thought was given to the capture, marking, holding and release of marked fish. The marking needed to be effective for three hours at the most. The fish obviously had to be in a good but undomesticated condition to be comparable with the in situ, unmarked fish. This ruled out the use of MS222 with its after effects lasting 24 hours or more.

The galvano-narcotic trough

A direct current of appropriate voltage can hold a fish headed towards the anode in a state of galvano-narcosis (Blancheteau et al 1961; Lamarque 1963). The body muscles are relaxed, but respiration is stimulated a little. There is no after effect. Even the most vigorous species which managed to jerk forward a few centimeters calmed down in a few seconds. A DC voltage which is too high or too low can induce movement towards the anode, whereas a fish pointed towards the cathode under high voltage can suffer tetany (Lamarque 1963). Eight motorcycle batteries in series, producing 48 volts gave excellent results for a wide variety of taxa.

Part of the galvano-narcotic trough (Gosset 1974; Lamarque, personal comm.) is shown in operation in Plate 3.4. At this voltage fish which drifted to point towards the cathode were unaffected. The water level was adjusted so that the fish lay on one side, facilitating photography for subsequent identification and measurement using the one centimeter grid sealed in the bottom (Plate 3.4). A small correction to these measurements was found by calibration. The anode and cathode consisted of sheet metal which occupied the full width of the trough. The latter could be moved toward the anode to increase the voltage gradient, which was necessary for fish less than about 5cm. At 48 volts fish which drifted round so that their head pointed toward the cathode showed no change in condition, and were equally fit when the power was disconnected. The trough worked well with conductivities down to 50µmhos/cm(20°C). A minimum quantity of salt was added to bring the conductivity up to that level when necessary. Fish could be fin-clipped without handling, and could be cupped from the net to the trough, and subsequently to the holding bins without them ever being removed from the water, or injuring themselves through fright within the water. Small specimens could be clipped by merely placing a finger underneath to steady them in the water. The voltage appeared to have little effect on prawns, but it was possible to clip small portions of the tails of specimens over 4cm total length.

Many delicate species of fish, which especially from the low conductivity, 'black' waters often showed instability (symptoms of osmotic imbalance) and often death if the net was lifted clear of the water, could be processed by this method. The only taxa which did not survive were the Engraulidae and Clupeidae, which suffered from the original netting process even though they were never removed from the water.

It is unfortunate that this simple method is not more widely used in other fish handling situations.

Marking

A rapid method for marking large quantities of fish for a short duration experiment was called for, and a form of fin clipping was adopted. Each marked fish had to be identified and measured, and marked only to distinguish it from unmarked specimens. Clipping of paired or median fins other than the caudal was laborious and very difficult for small fish. Therefore, an oblique cut removing a small area of the upper part of the caudal fin was made (Plate 3.4). The cut is distinct in place and form from those produced by piranhas, numerous examples of which had been observed in previous samples.

With practice it was possible using the trough to clip fish down to 20mm long with good survival.

Experiments with dyes

Previously, it was thought that fin clipping of small fish would not be possible. In a review of dyes as markers Deacon (1961) noted success with Bismark Brown Y after testing 22 dyes. Deacon had used 50ppm at 85°F and 200ppm at 65°F for 3 hours on a selection of N. American cyprinids and a siluriform. I conducted experiments with controls using this dye (kindly provided by T. Bullock) using 25, 50 and 100ppm baths for up to six hours. The temperature was 24°C. Specimens of *Prochilodus nigricans*, *Semaprochilodus insignis*, *Chalceus eurythurus*, *Cichlasoma festivum* and *Triportheus* ranging from 4 to 12cm long were tested. All *Chalceus eurythurus* died within the first hour in the two higher concentrations. All specimens died or were ailing except for the controls by the time the experiment was terminated at 6 hours. Unfortunately, the specimens which survived the lower concentration did not exhibit the dye either when fresh or preserved in formalin. It was even difficult to detect the dye after 3h in the 50ppm bath.

The discrepancy between these results and those of Deacon (1961) may be due to the different water supply or the shelf age (unknown) of the dye rather than the species involved. Mathews (1970) tested 31 dyes including Bismarck Brown and also reported mortalities. However, mortality increased with density, problems with handling were mentioned, and no controls were used. There was no point in further experiments with smaller fish. It was fortunately discovered later that fin clipping of small fish using the galvano-narcotic trough was possible and convenient.

3.3.6 Summary of calibration routine.

1. After an area of activity was chosen, including the site of the calibration, fish were captured for marking with the standard net. Methods A and either B or C were employed to obtain a good selection of the species and sizes dominant in the habitat. Samples were taken in areas with little detritus to avoid respiratory stress to the fish when the habitat was disturbed.

3. Fish from each catch were kept in the water in a portion of the net over the side of the boat, whilst samples were

transferred to the galvano-narcotic trough which was switched on beforehand. Smooth-sided plastic containers of a range of sizes were used. Large fish did not struggle if a container only slightly larger was used.

3. When a sufficient quantity of large or small fish were under galvano-narcosis, the water level was lowered so that all but the small, thin fish were on one side (Plate 3.4). Fin clipping was followed by photography using two cameras. If any fish were overlapping, they were rearranged and extra shots taken.

4. Fish were then removed from the trough using a transparent container for the smaller specimens. Each subsample was checked for fin clips, and the approximate size and species was noted for each individual to cross-check with the photographs later. The subsamples were distributed among holding buckets, separating large specimens from small, but splitting similar species groups-size groups among various buckets to spread their subsequent distribution. Although offshore water was used in the trough and holding buckets, floodplain waters can be notoriously high in B.O.D., and a minimum amount of oxygen was diffused into the buckets and trough to maintain a normal respiration rate. Fish (and <u>Macrobrachium</u>) were thus maintained under vigilance for a maximum of 2 hours and a minimum of 30min before release. A small proportion of

individuals whose swimming habits were in any way abnormal were removed and preserved to be subtracted from the total marked.

5. The 50m block net was laid and the lead line checked from the outside. When the habitat included patches of emergent macrophytes, the site enclosed by the block net was selected so that a similar density would be subsequently sampled by the standard net. If there was a breeze, the configuration of the block net was maintained by inserting a number of PVC pipes upwind.

6. The marked fish were released using the holding buckets pushed out and inverted by long poles tied to them. This enabled introduction to be quiet, and at no time boats or personnel entered the area of the block net. Distribution was made as evenly as possible within the block net. Fish in the holding buckets were lively, and one *Semaprochilodus* jumped out when a bucket was carelessly uncovered. Other fish jumped out within the block net before the buckets were inverted, since their covers had then been removed. Introduction took 5 to 10 minutes, and was completed 10 to 15min after the block net had been set. How long to leave the fish before sampling was a subject of much thought and discussion with fishermen. To fish immediately would have given the marked fish too little time to settle down and disperse. Waiting too long may have resulted in fish

congregating near the block net. A consensus resulted in a 10 minute wait after the last released fish.

7. The standard 8-meter wooden canoe with three fishermen was then paddled over the block net, and the standard seine was laid and fished using one of the three techniques outlined above. Fish which were not measured fresh were preserved together since subsequent sorting of marked fish was easier. This operation was the first time that canoes or personnel entered the blocked off area. The subsequent disturbances, including the clearance of any macrophytes and debris within the standard net, and later within the remainder of the blocked area do not affect the remaining task of the calibration which involves the assumption of no differential escapement between marked and unmarked fish.

8. In some calibrations, bottles of 'timbó' steeped in ethanol were manually spread within the block net to the 50ppm concentration described previously. Surfacing fish were then hand netted and preserved before hauling. In all calibrations, the block net was hauled as method B for the standard net, or firstly dragged to the shore when necessary. As it was being beached, two personnel in a canoe held up the float line near its center to prevent jumping being a successful form of escape.

9. All fresh and preserved piscivores were examined for

marked fish. One marked Cichlasoma festivum found in the stomach of a Cichla ocellaris had to be discounted.

10. Fish were measured using a board to the extremity of the median caudal fin rays ('fork' length for many species) except for the following genera which have extended median rays. Triportheus and Raphiodon were measured to the end of the shortest caudal ray between the median extension and the upper lobe. Standard length, but still using the measuring board, was used for Plagioscion and Pachypops. Since high precision was not required, the length of Macrobrachium specimens was taken from the tip of the rostrum to the extremity of the tail for convenience. For preserved fish a special measuring board which took into account a mean of 1% shrinkage (unpublished data) was used so that equivalent fresh lengths were used throughout. Fresh fish were weighed in the field using calibrated spring balances of appropriate sizes. Other fresh fish were measured within two hours at the laboratory using a Mettler balance, which was also used for preserved fish.

The care taken when handling fish may seem exaggerated. While it may be true that many species of fish suffer no effects when removed from the water with a net, this is not true for many Amazon species.

In these habitats it should be apparent that it is impossible to randomly select the sites. There is usually no advance indication of how many fish will be caught. However, surface swimming fish can sometimes be observed, and grasses moving often indicated that detritivores such as Prochilodus nigricans were feeding. Therefore it was imperative that the head fisherman understood that site selection should only be governed by considerations of a snag-free path and appropriate depth. The statistical analysis implicitly assumes that there is no bias in the sampling of the habitat concerned.

3.3.7 Habitats and taxa sampled.

Calibrations were made at Marchantaria Is. and the São José inlet of L. Janaurari, which are in two of the three regions sampled during the project. The samples were taken during September, October 1978 and January 1979 at Marchantaria, and in April and May 1979 at Janauari. Habitats were chosen to represent all those regularly sampled previously using the standard net. Thus, the sample sites were representative of the ranges of values of factors which possibly influenced catchability, such as Secchi disk, depth, vegetation and cover in general. Table 3.1 lists these values for 22 of the 23 calibrations attempted (Tables on pp 137-157). Number 611 was abandoned because of the block net snagging.

Table 3.2 (p.138) summarizes the quantities and size ranges of 'fish' (inc. prawns) marked and unmarked. The range for all the previous 600 samples taken with the standard net was 9 to 995mm.

Marchantaria Is. is within the R. Solimões-Amazonas and completely influenced by its turbid or 'white' waters. Thus the fauna are dominated by Characoidei and Siluriformes.

Conversely, the São José part of L. Janaurari is at the extremity of turbid water influence, and mixing with black waters from the Rio Negro and local catchment results in relatively clear water. This area is dominated by Cichlidae, although both areas show considerable overlap even down to the species level in some cases.

Initially, 26 species groups were constructed for exploratory analysis with respect to their catchability and retention in the block net. They are summarized down to genus in Table 3.3 (p.139). This subjective grouping took into account their morphology and pertinent behavioural characteristics, much of the latter being information gained from fishermen. Therefore these and subsequent groups are not necessarily monophyletic.

The following section describes the analysis resulting from 22 calibrations.

3.4 Analysis and results

The results, their cross validations and confidence limits are presented in 3.5. A detailed description of the analytical process follows.

3.4.1 Rationale of the analytical approach.

This data base was to some extent dependent on natural circumstances; complete experimental control was not possible. Consequently it was necessary to look for interactions between factors and other non-linear effects between determining variables and the responses q_{m1}, q_{m2} and q_1.

Since individuals are either caught or not, binomial statistics were considered. However, the binomial variance underestimates the real variance because it is necessary to deal with heterogeneous populations.

There were insufficient samples for a partial correlation analysis, but exploratory analyses of variance can provide evidence of effects which could otherwise lie undetected if the only criterion was the best fit in a multiple regression. However, since the conditions for multi-way anovas are difficult to test and are probably not satisfied they are only used as guides as to how to split up the data and identify predictors which would be most reliable in regression anaylsis. The effect of chopping up continuous variables into classes for anovas also reduces the sensitivity of the F tests, and so it is not uncommon to find apparently insignificant effects become significant when the number of factors is reduced.

The choice of how many individuals should be used for each estimate is also crucial. Small numbers increase the degrees of freedom between classes but introduce a large component of within class variability and a discontinuity error. Large numbers may mask effects by reducing the number of estimates per cell.

Length intervals of fish were chosen in order to provide a sufficient number of samples per cell.

Non-orthogonal anova designs were unavoidable, resulting in non-additive effects.

The order of listing of the species groups in Table 3.3 (p.139) is from surface to bottom inhabitants, although many are found in various depths. Common species were separately identified in order to allow comparisons between similar groups, such as group 14 with 13, rather than because they were considered *a priori* to be distinct in their escapement or evasion responses.

For multivariate analyses the species groups in Table 3.3 were too numerous for the computer capacity available, and in any case some show strong association with small subsets of the calibrations. Grouping species according to formal clustering techniques was considered, but not undertaken because many lower taxa occur in only a few samples and an automated technique based on the response only would almost certainly group some taxa due to their chance vulnerabilities in particular samples. Therefore *a priori* decisions on groups which were broadly represented among the samples were followed by exploratory analyses of the responses and factors in a search for consistent differences between the groups. For example, since *Cichlasoma festivum* spends much of its time at the surface it was initially included in group A (Table 3.4, p.140). However its responses were closer to those of group C to which most of the Cichlidae belong, and therefore was changed to that group.

This preliminary analysis resulted in the designation of six groups which are shown in Table 3.4 along with characteristics which may be instrumental in determining their catchability and/or escapement.

These groups were further analysed for each response. When interactions were indicated, decisions were made whether to further coalesce groups or treat them separately, the criterion being to minimize variance within groups.

Since the same species groups do not necessarily behave the same with respect to the retention by block net and catchability of the standard net the following sections treat each exploratory process in turn.

It was not possible to simultaneously examine sample effects with those of species group and fish length. Initially environmental factors defining subsets of samples were analysed for retention and catchability with species and length effects. Residuals were then tested with sample effects as explained in 3.4.5.

The term 'sample' refers to each of the 22 calibration samples. Statistical samples within 'samples' defined by length interval and species group are qualified accordingly. 'Fish' includes decapods.

It is impractical to list all the raw data files created, but they are available on request.

3.4.2 Retention by the block net

Retention, q_{m2}, or the complement of escapement, as defined in 3.2, is calculated using equation (3). Thus, it is based on marked fish which had not previously been captured by the standard net. Factors which could conceivably affect q_{m2} are species, size, depth, bottom hardness and whether rotenone was used. Since (1) vegetation had been cleared, (2) the fish were already disturbed at this stage, and (3) all come into contact with the net at some time, factors associated with swimming speed, perception of and reaction to danger before contact are considered to be secondary to those affecting their ability to squeeze under the net. This rules out secchi disk and vegetation/cover as possible factors.

A preliminary five-way analysis of variance for the six species groups and including the factors mentioned is shown in Table 3.5 (p.141), with the fish divided into four length groups. The limited number of cases (averaging 9.4 individuals for each case or q_{m2} estimate) distributed unevenly among the cells and the division of continuous variables into classes tends to decrease the probability of detecting differences (Type II error). But it does indicate that length is an important factor. Since no interactions or other effects were indicated, the relationship between retention and length only was examined. This simplification allowed results to be pooled in eight length groups, which are plotted in Figure 3.2 (p.123). Most variance, but still only 24%, was explained by a hyperbolic function. This was derived by linear regression of q_{m2} versus 1/length, weighting each point according to the number of individuals used. This gave a reasonable intercept of 10mm when q_{m2} is zero (see Figure 3.2). The residuals were symmetrically distributed around zero and its variance showed no trend with length.

The results of the first anova (Table 3.5) were then checked by calculating residuals of retention by subtracting the expected value predicted by the hyperbolic function and comparing them with the other effects as shown in Table 3.6 (p.142). Insufficient computing capacity prevented a covariance analysis using the inverse of length.

Rotenone is apparently important, but an interaction with species groups is suggested. These effects were not evident in the previous anova. This interaction is real because rotenone could not be used in Janaurari where species of group D were more abundant and those of C less than in Marchantaria.

Consequently, further analyses were made of retention with and without rotenone, with the six species groups and four length groups. These are shown in Table 3.7 (p.143). With rotenone no species effect was indicated. In contrast, the significance of species group without rotenone is clear from the second anova in Table 3.7.

In order to test for possible differences among species groups the effect of length was removed as described above, using separate regressions with and without rotenone. In neither case did the residuals produce homogeneity of variances among the species groups, but the residuals of the log transformed retention (see Table 3.8, p.144) did. The one-way tests with and without rotenone in Table 3.8 confirm the results shown in Table 3.7. The Student-Newman-Keuls test indicates two homogeneous groups. The first omits species groups B and C and the second group E. Also, group E shows the lowest retention which is not surprising since it consists of bottom living or eel-like fish (Table 3.4). The other excluded groups, B and C, showed the highest retention. These consist of predominantly mid-water, schooling species. Therefore the following three species groups were used for estimating retention when rotenone was not used.

I comprising former groups B and C,

II comprising groups A, D, and F,

III comprising group E only. Data were pooled across the samples, arranged in contiguous length groups with similar numbers of fish per group (see Table 3.9, p.145) and plotted in Figure 3.3 (p.124). Various functions were tried, and again the hyperbolic explained most variance and produced reasonable intercepts (see Figure 3.3 and Table 3.10, p.146). Predicted versus measured retention is shown in Figure 3.4 (p.125) for the four cases.

These functions were used in the derivation of catchabilities of unmarked fish as described in section 3.4.4.

3.4.3 Selection due to mesh size

The mesh size of the block net was the same as that of the standard net (3.3.3). A smaller mesh size for the former would have resulted in excessive drag and debris.

Large catches of small fish were accumulated by standard net sampling during two and a half years. Sampling with finer mesh hand nets and a slurp gun at some of the sites revealed that smaller fish are common inshore.

Length frequency data for morphologically distinct taxa are shown in Figure 3.5 (p.126) from the pooled standard net samples. Considering that the forms included deep-bodied Serrasalmidae, narrow-bodied Hemiodontidae and Anostomidae, and Siluriformes with pectoral and dorsal spines, the differences between the apparent selection ogives is not very marked.

If studies of small fishes on the scale of millimeters were intended, these differences would be important. For the purposes of this study, assuming a mean length of 13mm for zero catchability for all species was sufficiently accurate.

This was used in the catchability function derived in the following section.

3.4.4 Catchability of the standard net

Since both q_1 and q_{ml} are estimates of catchability, they are treated concurrently in this section. Initially the six species groups in Table 3.4 were used.

Data within each species group and sample were classified in four logarithmic length intervals. Calculated values based on less than four individuals were not included in the anovas.

It was impossible to explore all the factors in Table 3.1 simultaneously because of the excessive computer demand. Therefore sufficient cross-sections of the data consisting of overlapping subsets of factors were explored so that two and three-way interactions could be identified and main effects interpreted. Those which are not discussed here were of low significance ($p>.1$).

Since sites had been chosen so as to include a range of conditions for each method (3.3.1) and included similar fish size ranges (Table 3.2) tentative anovas with method, length and species group were made (see Tables 3.11 and 3.12, pp.147-148).

The method used is important, as is shown for both catchability estimates. The deviations indicate that method A (hauling into canoe) gives much lower values in both cases, which is not surprising considering the opportunities for escapement using this method (3.3.1). Although the deviations in both tables were higher for method C (offshore seining) than B (beach seining), subsequent tests indicated that this difference was insignificant. Furthermore, since there were no interactions between methods B and C and other factors, these methods were no longer distinguished, but were treated separately from method A data.

The adjusted residuals (deviations) by length class (Tables 3.11 and 3.12) suggested a curved relationship but the length effect in Table 3.11 was not significant. A curve is suggested in Figure 3.6 (p.127) from results pooled over samples within eight length groups. The results for marked fish using method A (Figure 3.6D) were based on only two samples (Table 3.1) and residuals were not analysed for these data.

A lognormal distribution function (two-parameter gamma function) fitted these curves best. The points were weighted according to the number of individuals. The curves shown are the result of least squares fits of the weighted data after linearizing the variables to produce the parabola:

$$\log(q+1) = a\log(L-12) - b(\log(L-12))^2 \;......(5)$$

where q is the catchability of marked or unmarked fish as a percentage,

L is the mean length in mm of the group of individuals per estimate

a,b are the parabolic constants.

The intercept of 13mm (3.4.3) for zero catchability has been incorporated.

These provisional fits were used to remove the non-linear length effect so that the residuals could be related to other factors.

Other parallels between marked and unmarked fish can be seen. The grand means of catchability are similar, but more qualified comparisons are made below. Also the lowest and second lowest deviations in species group were E and D respectively for both marked and unmarked fish. However, a possible interaction between species group and length is indicated for marked fish (Table 3.12). This may be due to empty cells, since only 88 estimates were spread among the 72 cells of the anova. But due to this apparent interaction as well as others involving species group with secchi disk and vegetation, ways were explored to find subsets of species groups for separate analyses.

This was accomplished by studying the residuals after the general length effect as depicted in Figure 3.6 had been removed. But effects due to different samples may interact with species groups, due to environmental or unobserved factors affecting subsets of samples.

Anovas for unmarked and marked estimates for methods B and C combined are shown in Table 3.13 (p.149). A strong interaction between species group and sample was evident from unmarked estimates. The data from marked fish showed significant unexplained variance.

In addition, Table 3.13 shows an anova for method A with unmarked fish. Some heterogeneity between species groups is suggested.

Because of the interaction with unmarked fish (1st anova, Table 3.13), different subsets from the six species groups were similarly treated until they neither interacted with sample nor showed significant differences between groups within each subset. As before the residuals were analysed after taking account of the length effect.

This resulted in three groups:

(a) comprising groups A, B, C, and F (defined in Table 3.4, p.140),

(b) comprising group D only,

(c) comprising group E only.

Method A data also showed significant effects of this species grouping with the same ranking (Table 3.16, p.152). This is in accordance with the ranking of the species group deviations as shown at the bottom of Tables 3.11 and 3.12 (pp. 147-148). The parallels between the different fishing methods suggests that these groups are not statistical artefacts. For example, one would expect bottom-living fish to have lower catchabilities than surface or midwater species. This is discussed further in 3.6.

3.4.5 Environmental effects on catchability

Some of the new species groups indicated that between sample variance was still high. However, the deviations of samples were not consistent among the species groups. Table 3.14 (p.150) shows anovas for the largest species group, (a). Both confirm the lack of species group differences and interactions, but with unmarked fish there was significant heterogeneity between samples. The extent to which this was due to environmental attributes of samples

(Table 3.1) was investigated. Although the ranges of environmental values were representative of those encountered during the project, not all combinations could be tested. The residual catchabilities in the following analyses were based on the fit of equation (5) applied to each species group separately, thereby accounting for length as a continuous variable.

There were positive correlations between secchi, vegetation and depth for methods B and C combined. However, subsets of the 17 samples could be chosen in which two of these three variables are relatively constant and are uncorrelated with the third. The third variable was then examined in relation to the catchability residuals for each of the three species groups. The results are shown in Table 3.15 (p.151) for unmarked fish for methods B and C.

Only one correlation is apparently significant at p=.03, but the significance level is for individual tests, not multiple ones. One would have expected negative correlations with secchi, but the higher transparencies are apparently insufficient to increase evasion of the net.

Similar tests with marked fish using methods B and C did not reveal significant effects.

Therefore, I was unsuccessful in reducing the unexplained variance for methods B and C after length and species had been taken into account.

Environmental variables for method A samples are intercorrelated (Table 3.1). However, I would not expect the same species groups to show a response to water transparency or cover any more than that indicated in Table 3.15. But due to the process of lifting the lead line which is peculiar to method A, depth may be important. The anova and deviations shown in Table 3.16 (p.152) indicate that the effect of depth was probably insignificant and secondary to the species effect.

3.5 Results

3.5.1 Predictive functions and cross-validation for catchability estimates

The lognormal distribution function (equation (5) in 3.4.4) was used in regressions of data classified by species group and sampling method. The 174 catchability estimates used were means of unmarked fish within eight length groups from each sample, and comprised on average 240 individuals/estimate. They were weighted according to the number of fish but those with less than eight individuals were excluded. The results, shown in Table 3.17 (p.153), are very similar to those resulting from a coarser classification into four length groups.

Despite the effort to distribute the marked fish evenly inside the block net, the results were much more variable than those for unmarked fish. This was also true when alternative models were used and when unforced regressions were compared. This was surprising also since marked fish are direct estimates whereas unmarked estimates are subject to variability in the block net retention estimates, q_{m2}. No correlation was found between deviations of unmarked catchability, q_1, and q_{m2} when data were pooled within samples. This suggests that q_1 was not biased by using the general retention functions (Table 3.10).

Pseudo-values of catchability using the jackknife method (Mosteller and Tukey 1977) are plotted in Figures 3.7A-3.7F (pp.128-130). The results were numerically indistinguishable at 1% precision from the values predicted by the parameters based on the estimates given in Table 3.17. Species group (c) (bottom inhabitants) averaged only 2% efficiency using method A (hauling into the boat), and this rough estimate was used independently of length for this combination. The confidence limits for given lengths shown in Figure 3.7 for the other combinations were not estimated from the pseudo values resulting from the jackknife method. They were based on simple cross-validation residuals (Mosteller & Tukey 1977) as described in the following section.

Cross validation for unmarked fish catchabilities was carried out at various levels, predicting the value concerned based on least squares estimates based on all other samples using equation (5).

The first level involved the 174 observations used to derive the results in Table 3.17. The residuals are shown in Figure 3.8A (p.131). The confidence limits in Figure 3.7 were based on these residuals. No individual species groups indicated a significant under- or overestimation. Most of the variability is ascribed to the unequal vulnerability of groups within samples due to non-even distributions within the block net.

The second level involved the above results pooled across species groups within four length groups for each sample. Here, 'pool' means that predicted and measured catchabilities are weighted according to the numbers of individuals used before calculating the mean. Thus the variability is between samples for each length group for all species combined, and is illustrated in Figure 3.8B (p.131).

The third level involved the data pooled for each sample. The 22 labelled results are shown in Figure 3.9 (p.132). Since deviations of samples could not be explained in the foregoing analysis and no particular circumstances could be invoked to explain the most deviant samples, there was no basis for their rejection.

All these cross validations point to the necessity of combining a number of samples to obtain a reasonable accuracy. This is the policy adopted for the analyses in

Chapters 4 and 5.

3.5.2 Confidence limits

Confidence limits were based on the residuals, being the difference between the value calculated from data within each sample and that predicted using the coefficients in Table 3.17. The residuals for the first level are shown in Figure 3.10A (p.133) versus length. There was no trend with length, but there was a significant positive skewness as would be expected from the model.

However, log transformation produced significant negative skewness while the square root transformation gave results which did not indicate non-normality (see Figure 3.10B, p.133) using skewness and kurtosis criteria. Subsets of these results corresponding to combinations of species group and sampling method gave similar results.

This brought the original model to question. Regressions using the square root of catchability instead of the logarithm as the independent variable in equation (5) were compared. But the amount of variance explained was always inferior, and the original model was retained.

The weighted square root residuals were used to estimate the 95% confidence limits for means of ten samples which are shown in Figure 3.7(A-D).

The second level in which species groups are combined is useful for confidence limit estimates of overall biomass. The data could have been reanalysed in terms of weight, but these estimates are sufficiently accurate if the length intervals used are not too large. The residuals are shown in Figure 3.11A (p.134) which again showed a significant positive skewness. Similarly the square root transformation rather than the logarithmic produced a distribution not significantly departing from a normal one (Figure 3.11B).

To estimate abundance (biomass) and confidence limits from the efficiency data requires that one multiplies the inverse of the latter by the catch. Using the central limit theorem the number of samples required to obtain a given accuracy at a given significance for various abundance or biomass estimates is given by:

$$n = \frac{t^2 V}{100q(1-(1/(1+LU))^{.5})^2} \quad \ldots\ldots\ldots\ldots\ldots(6)$$

where

V = weighted variance of the residuals, being the difference between the square root of the predicted and observed catchabilities weighted by the number of individuals used in each determination;

q = catchability ($=q_1$) of the standard net as a fraction, weighted as in V;

LU = upper confidence interval as a fraction of the mean value of abundance (or biomass) estimated.

It is presumed that the central limit theorem holds for means of n samples, t being 1.96 for 95% confidence.

Table 3.18 (p.154) shows the results for the two sampling method classifications by species group and length group for LU = .2 or 20% at 95% confidence. At this interval, the lower interval is 15.4% less than the estimated abundance. These estimates serve as an approximate guide as to how many samples with the standard net would be required for a given accuracy on the local scale of the block net. Accuracy and precision on a larger scale are discussed in 3.6.3.

The greatest source of uncertainty is the estimate of variance, V, which is derived from varying numbers of estimates which are based on varying numbers of individuals. Both these quantities are given in Table 3.18.

These results may only slightly underestimate sampling required for individual species if they are dominant for the subsets analysed, providing that the latter are selected from independent criteria. They would obviously underestimate subdominants, unless the unusual circumstance of a less clumped distribution prevails.

Table 3.19 (p.155) is from the second level of data pooling, where species groups are combined within length groups and samples. Total biomass depends on the weight distribution: obviously greater weight is needed for heavier rather than longer fish. Examples in which the predicted catchability and variance for each size group are weighted according to a typical weight distribution are shown for methods B, C and A in Table 3.19.

The estimates in Tables 3.18 and 3.19 depend on the spatial scale of the block net. They reflect the distribution of fish within the enclosure as well as the variability of response of individuals or schools to capture. Data on variability on the scale covered by the project is presented in 3.6.3.

3.5.3 Bias with large fish and total biomass estimation.

There is a computational problem when using the parameters of equation (5) (Table 3.17) for larger fish with some combinations of species group and method. Zero catchability is predicted at certain lengths when calculating q_1 from the term $\log(100q_1+1)$. For species group (a) this occurs at 325mm and for group (b) at only 95mm using method A. Predictions from methods B or C for groups (a), (b) and (c) are 675mm, 3100mm and 995mm respectively. But larger fish of groups (a) and (b) are frequently caught using method A, and even from group (a) using the other methods. This is reflected in the positive bias of the cross-validation residuals of larger fish shown in Figure 3.11.

If appropriate software had been available, a maximum likelihood fit may have produced better results.

Here, I have adopted a minimum catchability level for larger fish based on residuals to account for this bias. Distributions of biomass by length are compared for the different fishing methods assuming a minimum catchability of 2% (Figures 3.12 and 3.13, p.135) and of 4% (Figures 3.14 and 3.15, p.136) using the standard net data excluding the calibration samples. Also the original mean weights caught are shown to illustrate the decreasing efficiency with fish length. The proportion of fish jumping out (see 3.2) has also been plotted in Figure 3.12 but is so small that it is barely visible.

There is very little effect of minimum catchability for methods B and C, but for method A the total biomass predicted is 23% less when 4% is presumed instead of 2%. The increase of biomass offshore by both length groups between 120 and 480mm assuming 2% (comparing Figure 3.12 with 3.13) is much more in accordance with gillnet data than the ambiguous trend shown in Figures 3.14 and 3.15. I have adopted a value of 2%, but the sensitivity of estimates for larger fish to the uncertainty inherent in this assessment should be apparent.

In Chapter 5 the biological significance of the biomass distribution is studied.

3.6 Discussion

3.6.1 Marked versus unmarked estimates

The comparisons of pooled data in Figure 3.6 suggest that catchability of marked fish peaks at a larger size than for unmarked fish. Also within the range 100 - 200mm the average catchabilities of marked fish are significantly higher. This could be a result of the caudal fin clipping adversely affecting the ability of larger fish to evade the net. Alternatively, the reason might be due to the larger marked fish being kept in relatively smaller bins. One cannot compare the comfort of a 250mm fish in a 400mm diameter bin with that of a 50mm fish in a bin 200mm wide.

However, with respect to the retention of marked fish in the block net, the values for fish killed or stupefied by rotenone were not universally higher than for live fish (Figure 3.3). Also the unmarked catchability estimates were not biased by deviations in block net retention in individual samples (3.5.1).

The lower variability of the catchability estimates for unmarked fish reflected their larger size range, species diversity, total number of individuals and number of calibration samples involved.

3.6.2 Biases

The catchability averaged only 2% for species group (c) when using method A. This would not have been apparent from the catches, since many specimens of this group were caught by this method during the project. Notwithstanding this, many species of this group will have escaped from individual samples, and separate analyses of this species group from method A samples were not undertaken.

Species group (c) using methods B or C showed higher variability in the catchability than the other groups. The low block net retention (Figure 3.3C) implies that the retention of the standard net may be as responsible for the variability as the evasion component.

Species group (b) using methods B and C (Figure 3.7A and 3.7C) indicates higher catchability with larger fish. Since this group is dominated by Cichlidae whose adults are territorial, this result is not surprising.

Larger fish are difficult to estimate accurately using method A (3.4.7), and the net is clearly not optimal when used in this manner even though individuals up to 995mm long have been caught. Considering the dimensions and mesh size of the net, it was a surprise to me (not the fishermen) that so many large fish of various species were caught. Inshore day and night gillnet catches using large meshes in Janauacá did not reveal many species and sizes which were not at some time caught by the standard net. However, one common species, Osteoglossum bicirrhosum, is very poorly represented. It waits for prey at the surface and is unusually sensitive to an approaching canoe.

3.6.3 Comparisons with other gear and general applicability of the method

Preliminary, non-stratified results from the non-calibration samples usiog the standard net are compared with some results from active gear in the literature in Table 3.20 (pp.156-157). Method A was used in 40% of the routine samples. As in Table 3.19, numbers of samples required for a given precision is used which is proportional to the square of the coefficient of variation. The published data are all estimates of precision, so the results from this study are presented in two forms:

The actual catch data are used in (1) (Table 3.20) and therefore estimates precision, whereas in (2) the estimated biomasses for each sample using the efficiency estimates derived above are used. The latter can be regarded as an estimate of accuracy if there is no significant bias in my estimates for large fish. The numerous samples required is often quietly forgotten in fisheries studies; a tendency which may be enhanced by the fact that all the references in Table 3.20 are from the 'grey' literature. However, these results are unstratified and appropriate stratification can reduce the variance considerably (Hennemuth 1976).

As Bagenal (1979) suggested, the largest source of variability on a smaller scale is probably due to the shoaling of fish. This could be generalized to include any behaviour producing a contagious distribution during the time interval of the sampling process.

The precision estimates underestimate the biomass variability as indicated from this study by (1) and (2) in Table 3.20. The difference is not much larger than the small scale variability shown in Table 3.19 from the calibrations, which includes the variability associated with individual fish or schools avoiding the net. Thus the small scale variance using this method is much smaller than the between-sample variance which is on a scale appropriate for population studies. From the sampling efficiency point of view it is much better to use a calibrated gear more frequently than attempt a limited number of more accurate biomass estimates.

From Bagenal's (1979) account of bottom and surface seining in three Finnish lakes, one of which had a known population, I would agree with his conclusion that those seines and the other methods used cannot be used for accurate stock assessment without destroying most of the population. At first sight it seems surprising that the daytime hauls using a shorter net as presented here should be more precise than those from the Finnish lakes (Table 3.20) using much longer nets to catch smaller fish.

One difference is that the maximum height of both nets used in Finland is 5.75m, yet they were mostly fished in maximum depths of 8 to 12m. The full water depth was always covered in methods B and C, producing higher efficiency and lower variance. In method A the 6m deep net was fished up to maximum depths of 4m but the lead line had to be lifted into the boat, lowering the catchability through the retention component.

Another factor may be the water transparency. Working in the same area, Muntz (1982) estimated that vision by fish would be impossible below 2.3m in the R. Solimões (Secchi = .1 to .3 m) and below 9m in the clearest waters he could find (Secchi = 4m). The maximium Secchi disk reading was only 1.5m in the calibration areas and was less than 1.70m for routine samples. P. Tuunainen (pers. comm.) estimated that fish can probably see the seine about two meters away in the Finnish lakes included in Bagenal's study. Anyone who has attempted to seine inshore in a clear lake or stream can often witness the evasion of fish before the net even enters the water.

The applicability of this method will also depend on other circumstances such as how good and consistent the fishermen are. A longer net with larger mesh would catch larger fish more efficiently, but its calibration with an even larger enclosure would require much more investment.

3.7 References

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Plate 3.1 Setting the seine net at Marchantaria Is.

Plate 3.2 Hauling the standard seine by method C
(calibration no. 606 at Marchantaria)

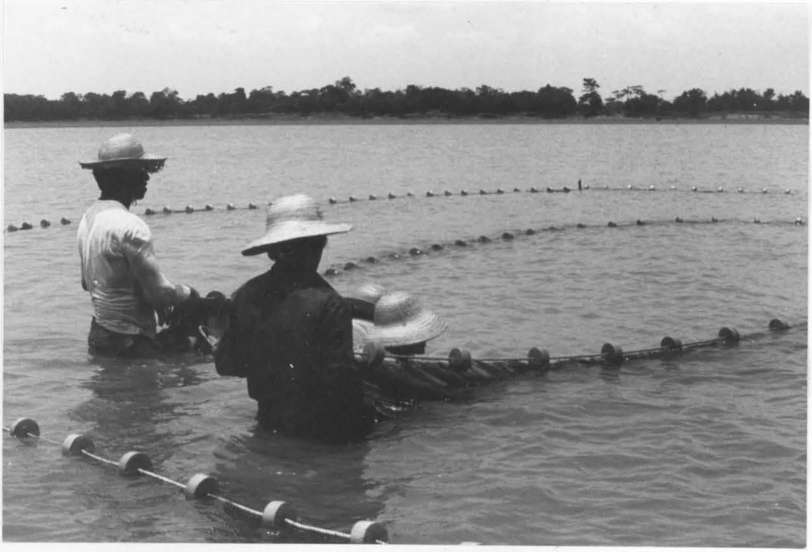


Plate 3.3 Block and standard net configuration for method B (calibration no. 617 at Janaurari)

Plate 3.4 Fish under voltage in the galvano-narcotic trough (a subsample of marked fish for calibration no. 608)

<u>Figure 3.1</u> Geometry of nets for method B calibrations (see text for symbol definitions)

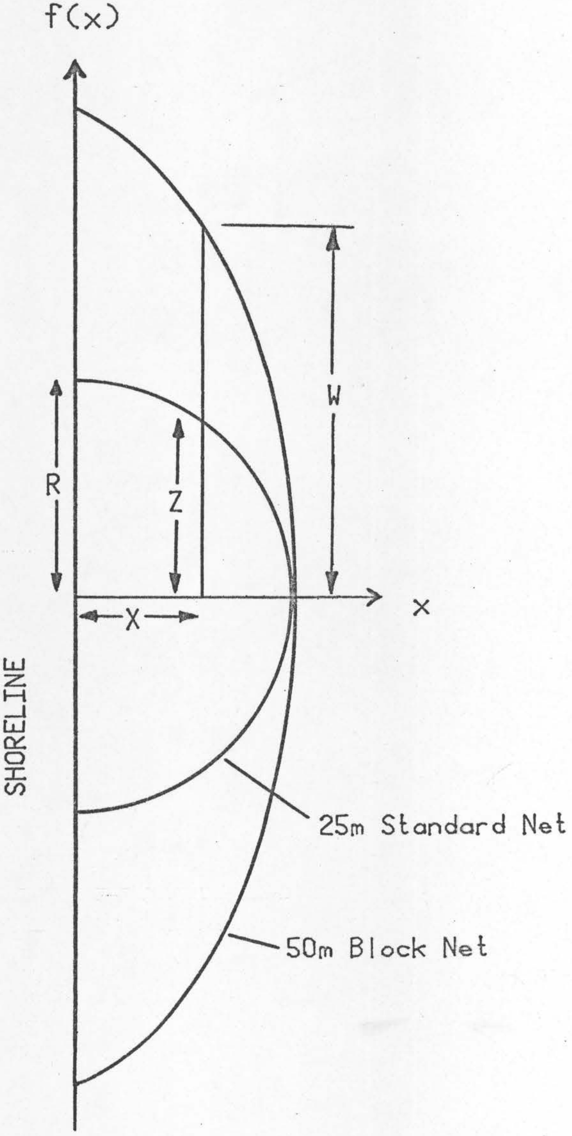
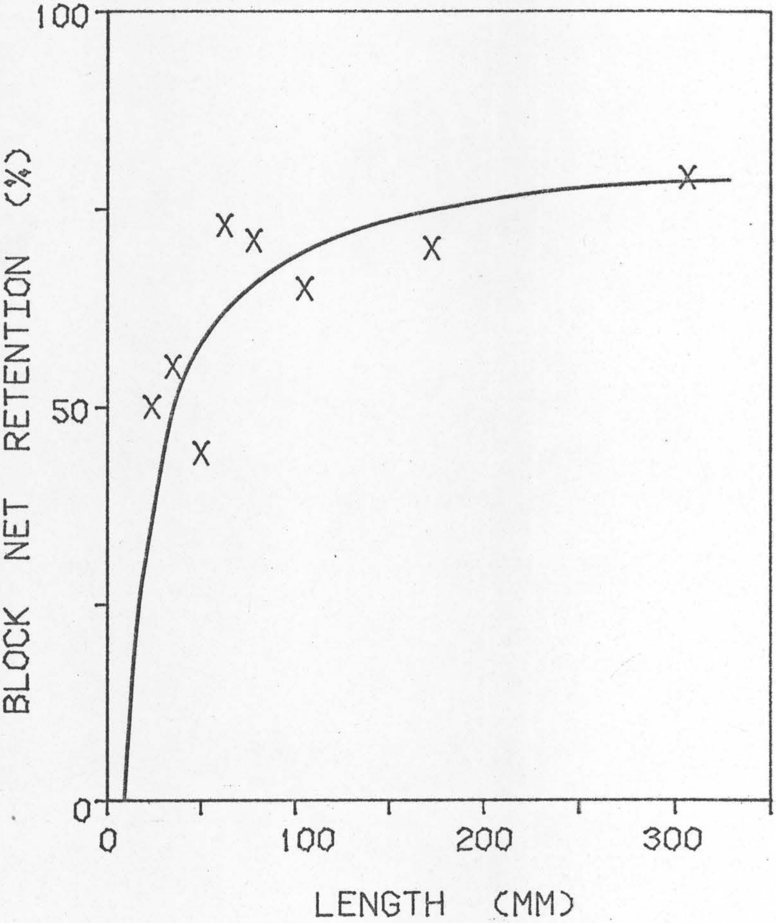

f(x)
W
R
Z
X
x
SHORELINE
25m Standard Net
50m Block Net

Figure 3.2 Retention, q_{m2}, of marked fish by block net versus mean length of fish from data pooled within 8 length intervals.


100
50
0
0
100
200
300
BLOCK NET RETENTION (%)
LENGTH (MM)

<u>Figure 3.3</u> Retention, q_{m2}, of marked fish by block net versus length; A: Species group I without rotenone,

B: Species group II without rotenone,

C: Species group III without rotenone,

D: All species groups, with rotenone.

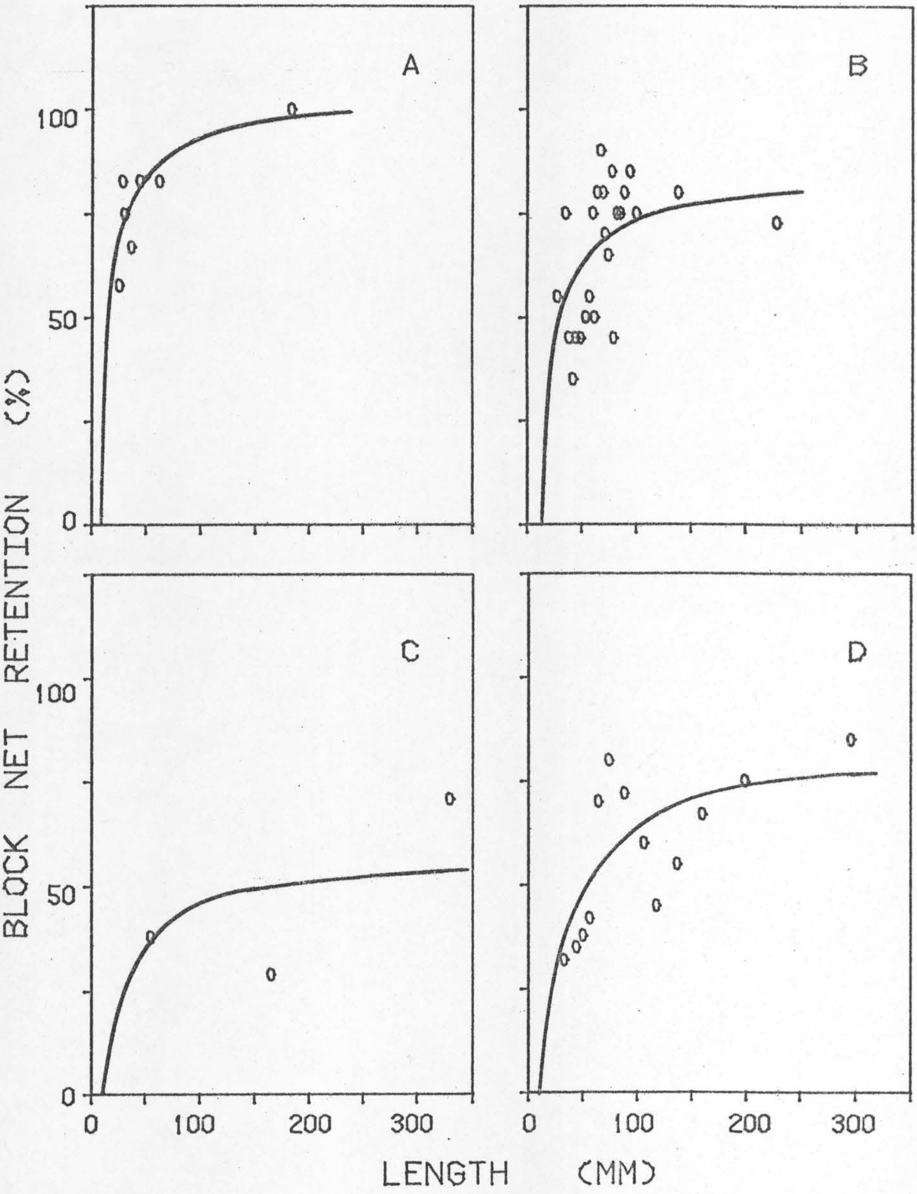

A
B
C
D
100
50
0
100
50
0
0
100
200
300
0
100
200
300
BLOCK NET RETENTION (%)
LENGTH (MM)

Figure 3.4 Predicted versus measured retention, q_{m2}, by block net;

A: Species group I without rotenone,

B: Species group II without rotenone,

C: Species group III without rotenone,

D: All species groups, with rotenone.

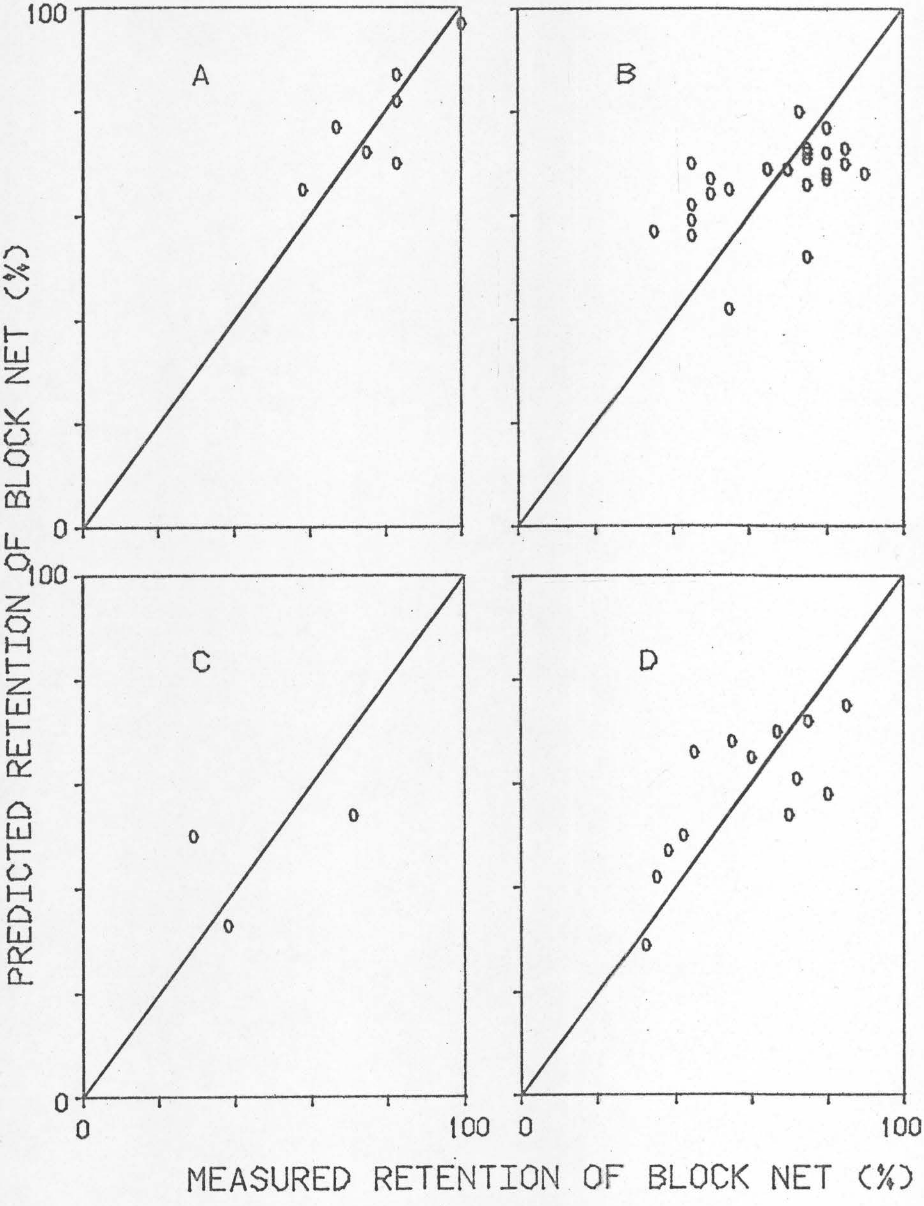

A
B
C
D
100
0
100
0
0
100
0
100
PREDICTED RETENTION OF BLOCK NET (%)
MEASURED RETENTION OF BLOCK NET (%)

Figure 3.5 Frequency distributions of smaller fish from taxa of extreme morphology.

(data pooled from standard net samples, ordinate = no. of individuals, abscissa = length in mm).

Upper graph: slim-bodied fish (Hemiodontidae and Anostomidae).

Center graph: catfish with pectoral and dorsal spines (Siluriformes, not including Trichomycteridae).

Lower graph: deep-bodied fish (Serrasalmidae).

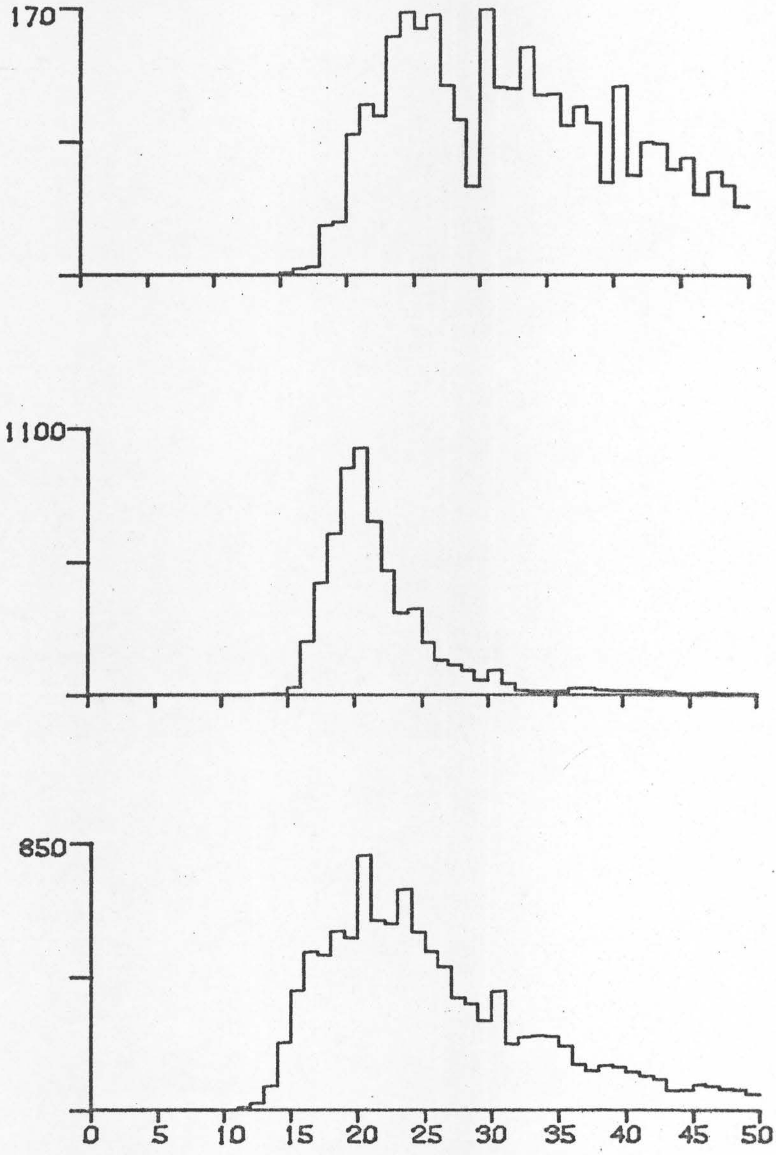

170
1100
850
0
5
10
15
20
25
30
35
40
45
50

Figure 3.6 Standard net catchability versus fish length pooled within 8 length intervals;

A: Unmarked fish data for methods B and C, (q_l)

B: Unmarked fish data for method A, (q_l)

C: Marked fish data for methods B and C, (q_{ml})

D: Marked fish data for method A, (q_{ml})

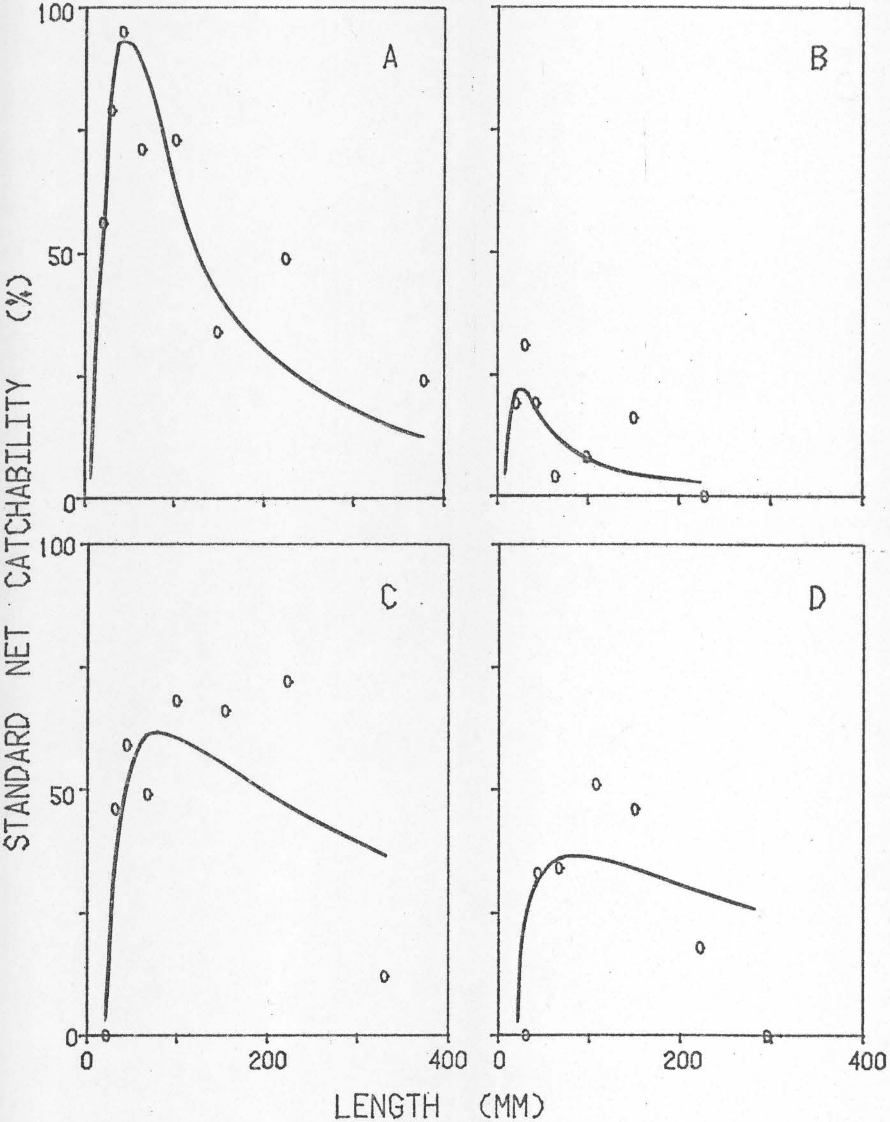

100
50
0
A
B
C
D
STANDARD NET CATCHABILITY (%)
0
200
400
LENGTH (MM)

Figure 3.7, A & B Jackknifed pseudo-values of standard net catchability, q_1, and 95% confidence intervals for means of 10 samples;

A: Species group (a) using methods B or C,

B: Species group (a) using method A.

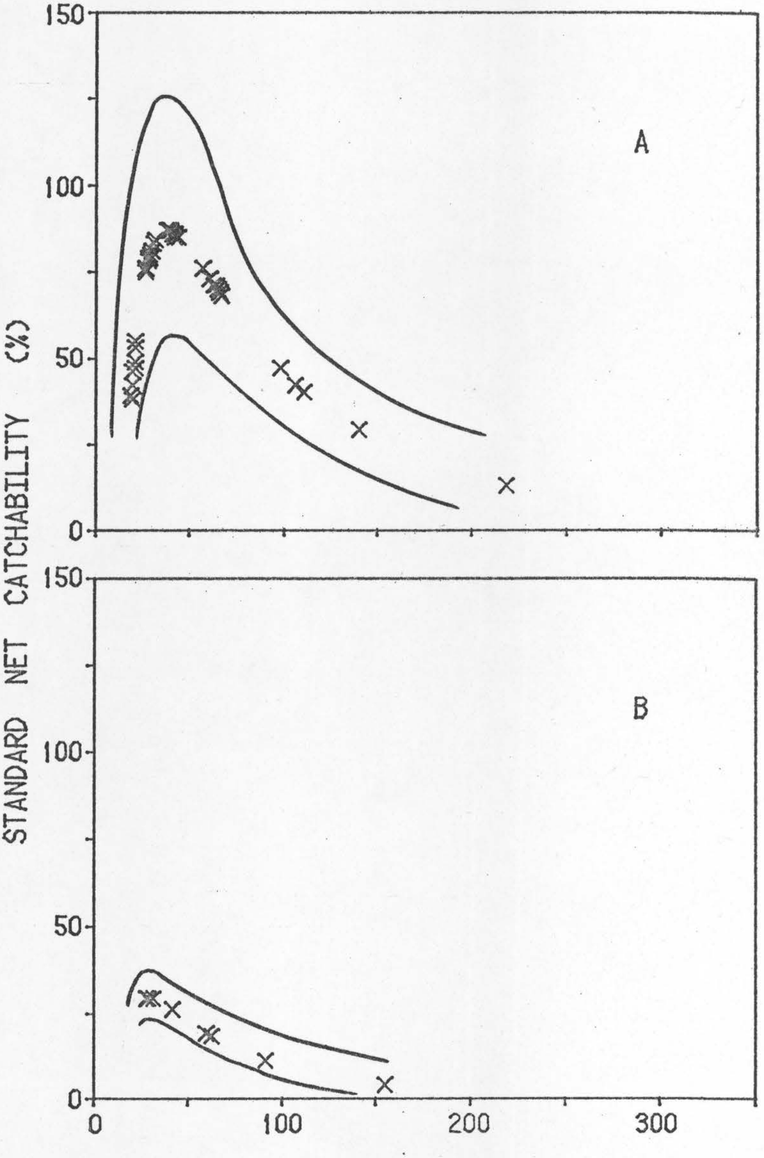

150
100
50
0
A
150
100
50
0
B
0
100
200
300
STANDARD NET CATCHABILITY (%)
LENGTH (MM)

Figure 3.7, C & D Jackknifed pseudo-values of standard net catchability, q_1, and 95% confidence intervals for means of 10 samples;

C: Species group (b) using methods B or C,

D: Species group (b) using method A.

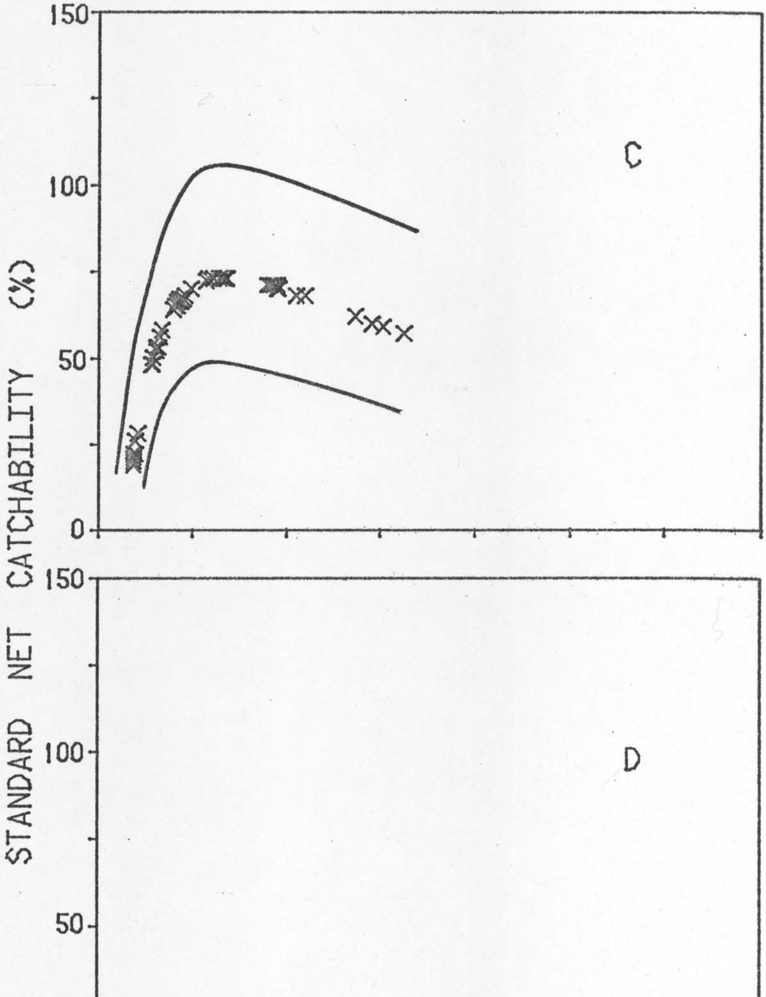

150
100
50
0
C
150
100
50
0
D
0
100
200
300
STANDARD NET CATCHABILITY (%)
LENGTH (MM)

Figure 3.7, E & F Jackknifed pseudo-values of standard net catchability, q_1, and 95% confidence intervals for means of 10 samples;

E: Species group (c) using methods B or C,

F: Species group (c) using method A.

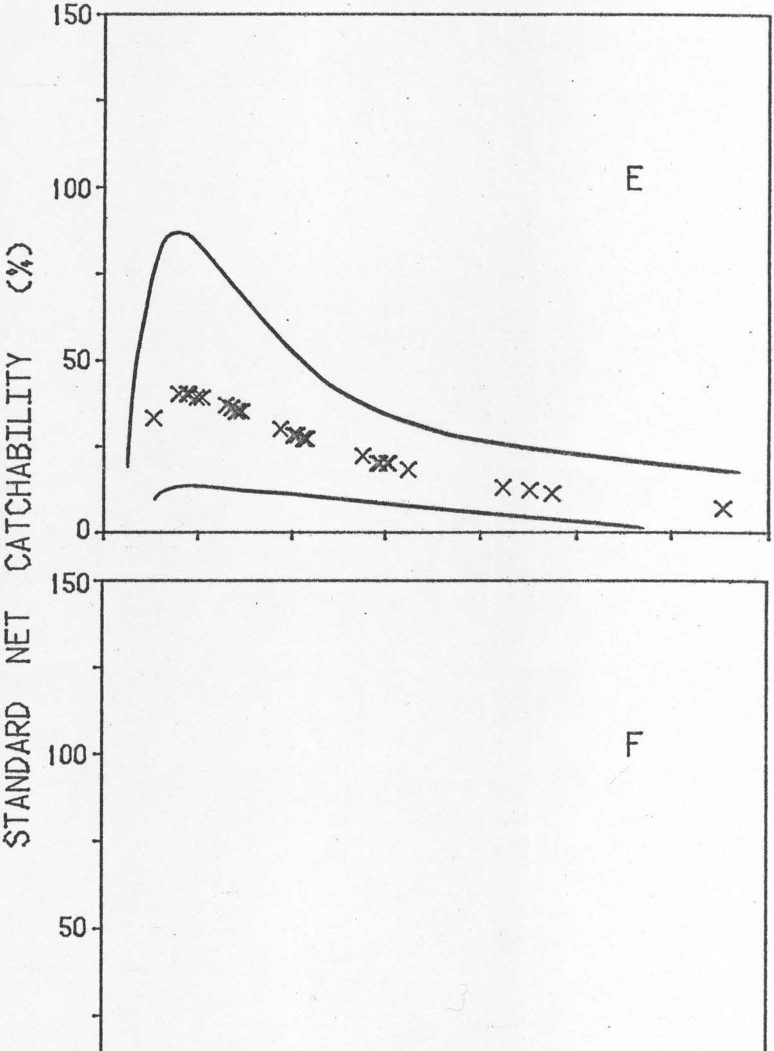

150
100
50
0
E
150
100
50
0
F
0
100
200
300
STANDARD NET CATCHABILITY (%)
LENGTH (MM)

Figure 3.8 Predicted versus observed catchability, q_1, for unmarked fish;

A: From species group-length group combinations in each sample,

B: From length groups pooled across species in each sample.

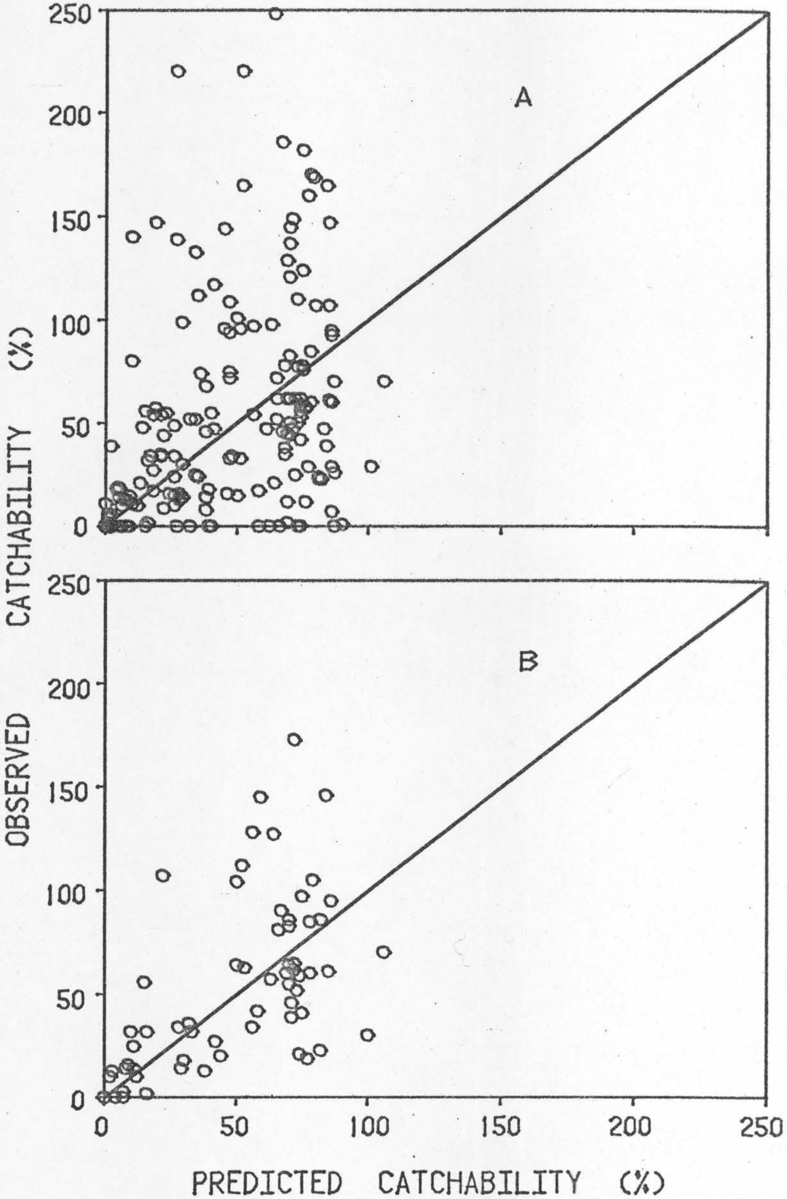

A
B
OBSERVED CATCHABILITY (%)
PREDICTED CATCHABILITY (%)
0
50
100
150
200
250
0
50
100
150
200
250
0
50
100
150
200
250

Figure 3.9 Predicted versus observed catchability, q_1, for unmarked fish using data pooled within each sample.

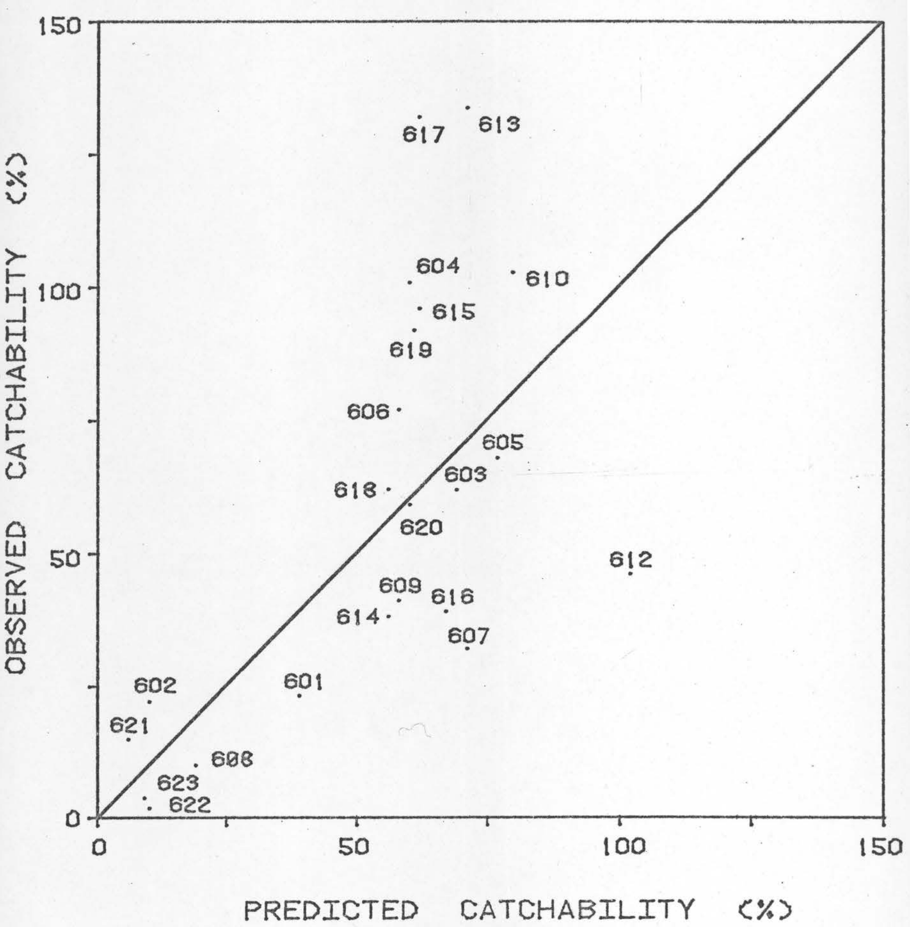

150
100
50
0
0
50
100
150
OBSERVED CATCHABILITY (%)
PREDICTED CATCHABILITY (%)
617
613
604
610
615
619
606
605
603
618
620
612
609
616
614
607
602
601
621
608
623
622

Figure 3.10 Residuals versus fish length from species group-length group combinations in each sample,

A: Untransformed residuals (measured - predicted catchability)

B: Transformed residuals (difference between square roots of measured and predicted catchability)

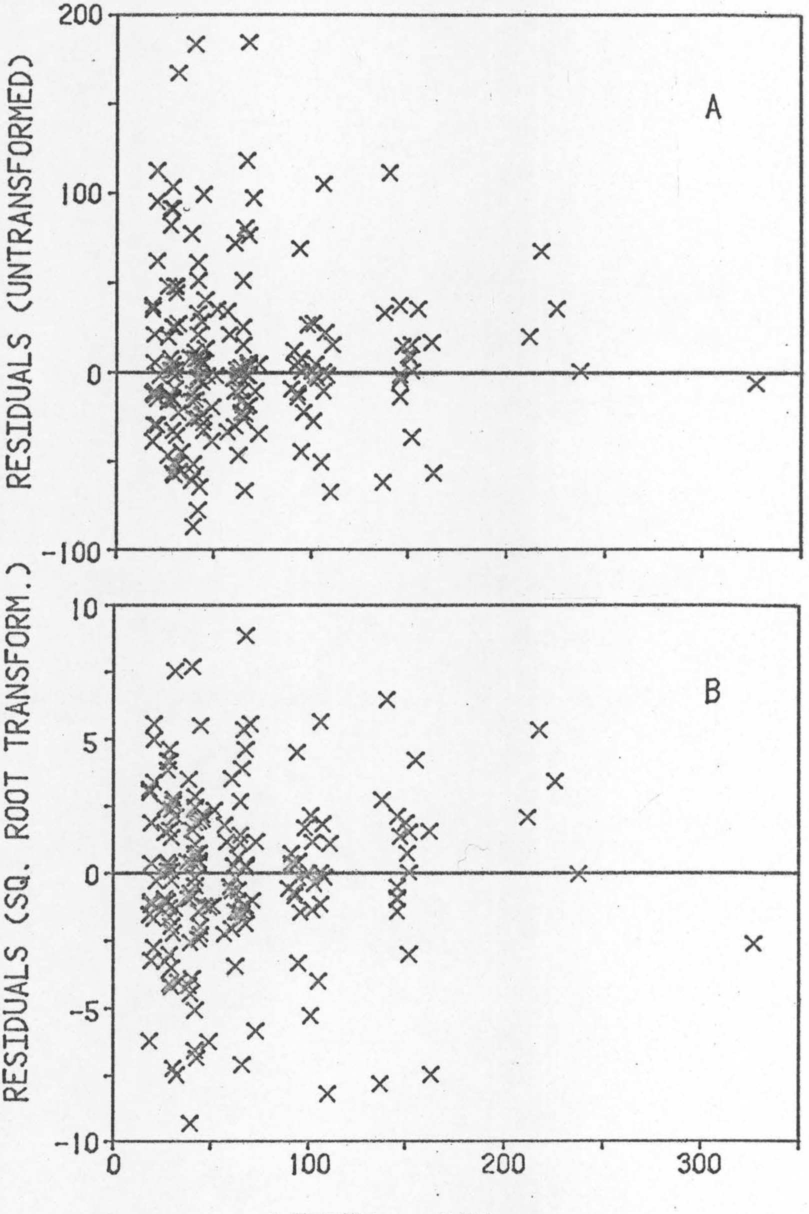

RESIDUALS (UNTRANSFORMED)
200
100
0
-100
A
RESIDUALS (SQ. ROOT TRANSFORM.)
10
5
0
-5
-10
B
0
100
200
300
LENGTH (MM)

Figure 3.11 Residuals versus fish length from length groups pooled across species in each sample,

A: Untransformed residuals (measured - predicted catchability)

B: Transformed residuals (difference between square roots of measured and predicted catchability)

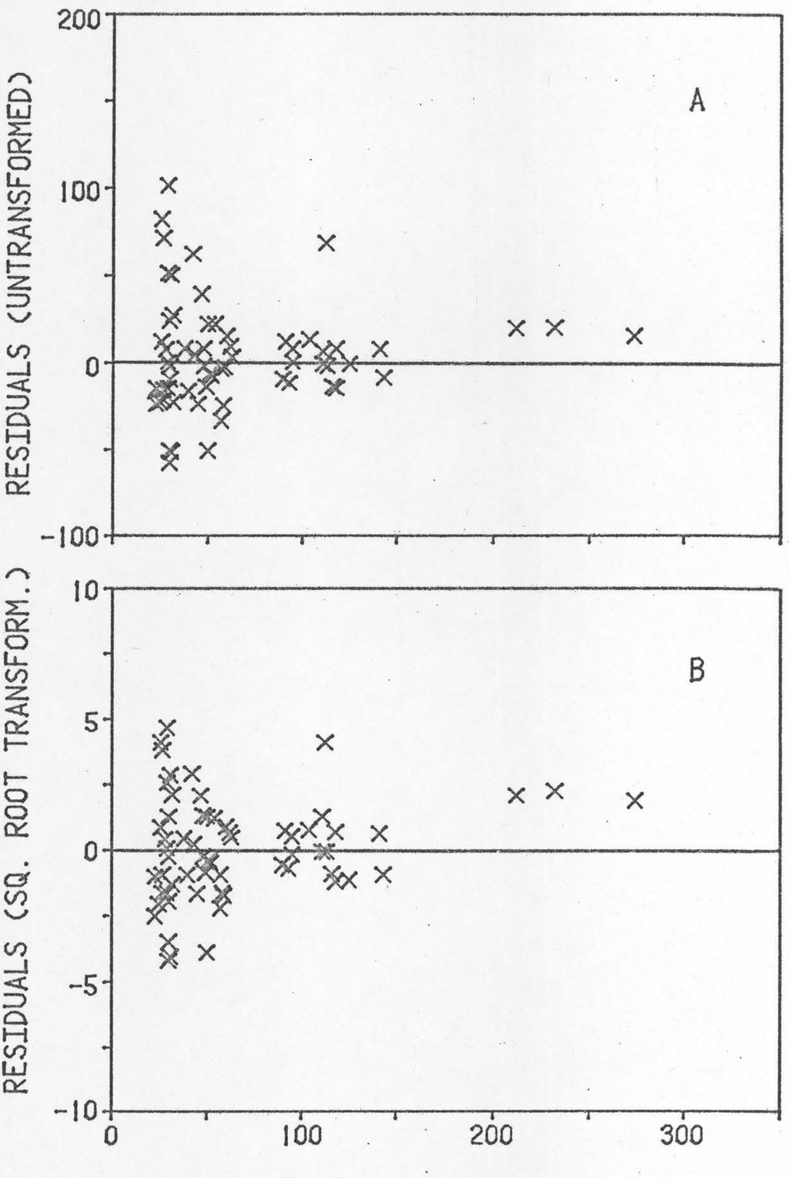
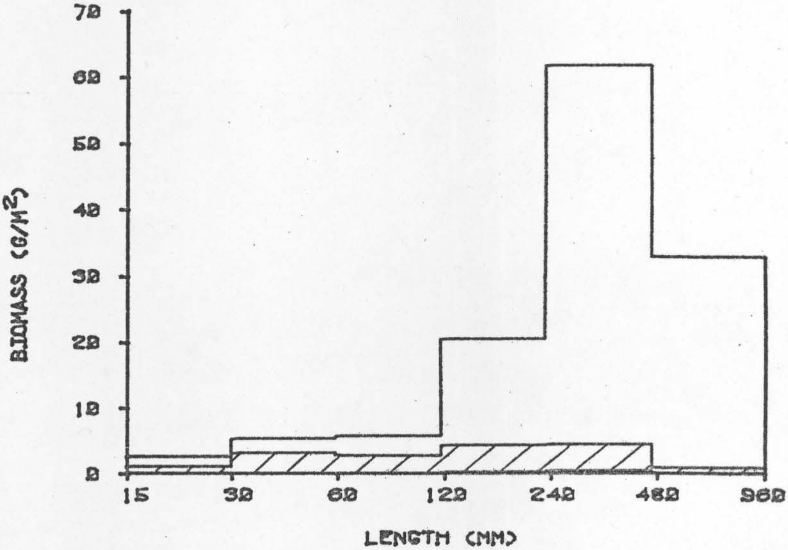

200
100
0
-100
RESIDUALS (UNTRANSFORMED)
A
10
5
0
-5
-10
RESIDUALS (SQ. ROOT TRANSFORM.)
B
0
100
200
300
LENGTH (MM)

Figure 3.12 Estimated total biomass by length for standard net samples using methods B and C, and assuming 2% minimum efficiency. (hatched area indicates actual catch per unit area; solid area represents the proportion of 'catch' which jumped out: this can barely be distinguished from the abscissa line)

Figure 3.13 Estimated total biomass by length for standard net samples using method A, and assuming 2% minimum efficiency. (hatched area indicates actual catch per unit area)


70
60
50
40
30
20
10
0
BIOMASS (G/M^2)
15
30
60
120
240
480
960
LENGTH (MM)

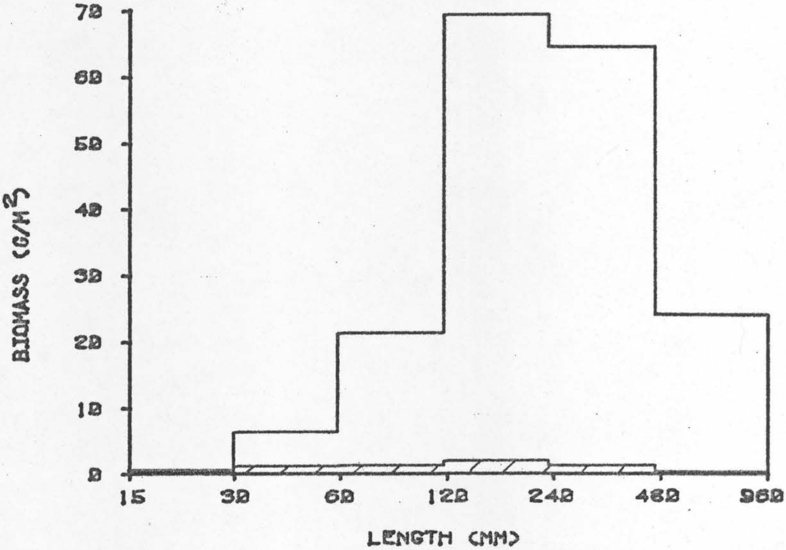
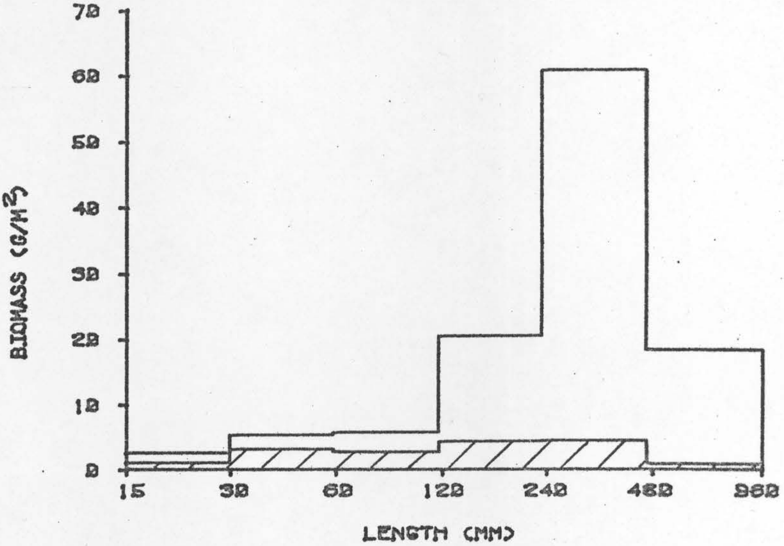

70
60
50
40
30
20
10
0
BIOMASS (G/M^2)
15
30
60
120
240
480
960
LENGTH (MM)

Figure 3.14 Estimated total biomass by length for standard net samples using methods B and C, and assuming 4% minimum efficiency. (hatched area indicates actual catch per unit area)

Figure 3.15 Estimated total biomass by length for standard net samples using method A, and assuming 4% minimum efficiency (except for group (c) for which 2% was used throughout).

(hatched area indicates actual catch per unit area)


70
60
50
40
30
20
10
0
BIOMASS (G/M^2)
15
30
60
120
240
480
960
LENGTH (MM)

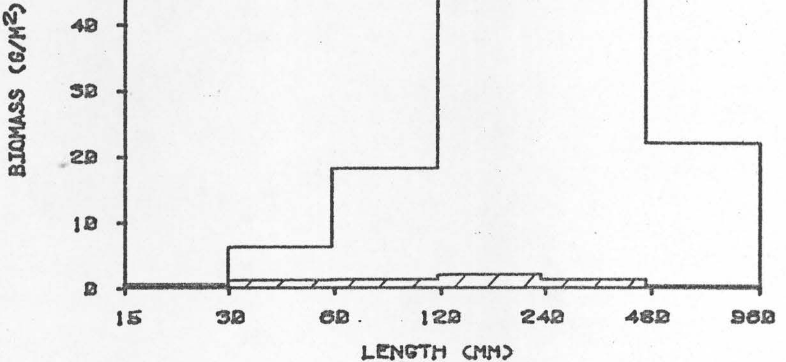

70
60
50
40
30
20
10
0
BIOMASS (G/M^2)
15
30
60
120
240
480
960
LENGTH (MM)

Table 3.1 Habitat and Operational Features of the Calibrations

A	B	C	D	E	F	G	H	I	J
A	602	yes	.38	13	60	60	0	2	yes
A	608	yes	.38	20	80	160	0	2	yes
A	621	no	.47	140	70	150	4	3	no
A	622	no	.49	140	80	280	8	3	no
A	623	no	.40	140	60	230	8	3	no
B	607	yes	.30	20	0	90	0	2	yes
B	615	no	.45	100	0	140	8	3	yes
B	616	no	.45	120	0	160	36	3	yes
B	617	no	.45	150	0	135	44	3	yes
B	618	no	.45	140	0	130	32	3	yes
C	601	yes	.36	13	65	70	4	2	yes
C	603	yes	.29	15	50	60	0	1	yes
C	604	yes	.44	20	65	90	0	1	yes
C	605	yes	.38	20	85	95	0	1	yes
C	606	yes	.38	17	70	100	0	1	yes
C	609	no	.29	100	80	80	12	3	yes
C	610	no	.29	60	80	80	64	3	no
C	612	yes	.29	70	75	80	80	3	yes
C	613	no	.26	50	70	75	60	3	yes
C	619	no	.45	100	30	150	28	3	yes
C	620	no	.46	140	30	130	8	3	no

Legend

A: Method by which standard net was fished (see 3.3.2).
B: Sample number in chronological orderμ those 613 or less were made at Marchantaria Is., the remainder at Lago Janauari.
C: If rotenone was used when fishing the block net.
D: Fraction 'r' of area enclosed by the block net which was encircled by the standard net.
E: Secchi disk reading in cm.
F: Minimum depth in cm.
G: Maximum depth in cm.
H: Index of total quantity of macrophytes and debris within standard net, measured as the number of man-minutes required to clear it. (referred to as 'vegetation' or 'cover' in text).
I: Bottom hardness assessed subjectively from 1=soft to 3=hard.
J: If marked fish were used in the calibration.

Table 3.2 Summary Statistics of Fish Released and Caught.

A	B	C	D	E	F	G	H	I	J	K
A	602	1152	216	16	225	74	12	39	28	270
A	608	167	11	18	55	52	6	25	36	295
A	621	325	41	18	200	-	-	-	-	-
A	622	108	2	16	445	-	-	-	-	-
A	623	102	3	19	145	-	-	-	-	-
B	607	1895	246	13	195	40	7	27	43	325
B	614	318	79	15	330	104	11	57	20	345
B	615	556	305	13	215	45	7	24	51	390
B	616	224	59	14	155	94	12	46	27	355
B	617	1403	977	14	345	82	26	39	35	290
B	618	2107	851	13	645	47	15	24	25	320
C	601	305	41	20	345	91	20	35	26	385
C	603	716	258	12	255	98	24	40	35	340
C	604	13499	9695	13	490	144	63	47	29	310
C	605	5880	4040	10	425	69	11	42	34	345
C	606	521	217	14	485	71	26	25	35	230
C	609	523	117	14	410	52	3	34	24	245
C	610	1166	542	14	110	-	-	-	-	-
C	612	5104	1648	14	485	39	3	11	26	150
C	613	4682	2362	15	510	106	21	50	20	78
C	619	826	450	15	795	168	27	112	34	120
C	620	304	108	16	165	-	-	-	-	-
	ALL	41883	22268	10	795	1376	294	677	20	390

Legend

A: Method by which standard net was fished (see 3.3.2).

B: Sample number in chronological orderμ those 613 or less were made at Marchantaria Is., the remainder at Lago Janaurari.

C: Total number of unmarked fish (inc. prawns) caught.

D: Number of unmarked fish caught in standard net.

E: Min. length of unmarked fish ('fork' length in mm).

F: Max. length of unmarked fish ('fork' length down to nearest 5mm).

G: Total number of fish (inc. prawns) marked.

H: Number of marked fish caught in standard net.

I: Number of marked fish caught in block net.

J: Min. length of marked fish ('fork' length in mm).

K: Max. length of marked fish ('fork' length down to nearest 5mm).

Table 3.3 Initial Species Groups Considered

Species group	Taxa included in group
1	Clupeidae, *Osteoglossum*, Cynodontidae, *Agionates*, *Chalceus*
2	*Potamorrhaphis*, *Boulengerella*, *Raphiodon*
3	*Triportheus*
4	*Cichlasoma festivum*
5	Engraulidae
6	Hemiodontidae
7	Anostomidae
8	Characidae not included elsewhere
9	Pyrrhulinini, Gobioidae, *Colomesus*, Hypophthalmidae*
10	*Cichla*, Sciaenidae, *Arapaima*
11	*Roeboides*
12	Serrasalmidae
13	Cichlidae not included elsewhere
14	*Acarichthys heckeli*
15	*Geophagus*
16	Prochilodontidae
17	Curimatidae
18	Erythrinidae
19	Callichthidae
20	Doradidae
21	*Pimelodus*
22	Pimelodidae not included elsewhere
23	*Pseudoplatystoma*, *Sorubim*, *Sorubimichthys*, Ageneiosidae
24	Loricariidae, *Potamotrygon*, Bunocephalidae, Soleidae
25	Gymnotiformes, *Crenicichla*, *Batrachops* *Synbranchus*,
26	*Macrobrachium*

* not encountered in calibrations.

Table 3.4 Six Species Groups used in Exploratory Analyses

Species group	Composition of species groups from Table 3.3	Description
A	1 to 3	surface inhabitantsμ slim-bodied, schooling and fast swimming
B	12	deep-bodiedμ schooling, generally mid-water
C	5 to 9,11	generalized shape, schooling fish occupying many depths
D	4,10,13,14,15,26	slower swimming or territorial
E	18 to 25	bottom living or eel-like fish
F	16,17	fast swimming, Prochilodontidae and Curimatidae

Table 3.5 Anova of q_{m2} with all factors

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	1.46	12	.12	2.52	.01
species group(spg)	.24	5	.05	1.01	.42
length	1.09	3	.37	7.58	.001
rotenone	.12	1	.12	2.52	.12
bottom hardness	.04	2	.02	.42	.66
depth	.04	1	.04	.86	.36
2-way interactions*	2.18	41	.05	1.11	.36
3-way interactions*	.35	6	.06	1.20	.32
explained	3.99	59	.07	1.40	.11
residual	2.55	53	.05		

113 estimates of q_{m2} were analysed

* minimum significance of a single interaction was .14

Table 3.6 Anova of $q_{m2}\%$ residuals from Figure 3.2 with remaining factors

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	5039	9	560	1.16	.33
species group(spg)	1712	5	342	.71	.62
rotenone	1699	1	1699	3.52	.06
bottom hardness	614	2	307	.64	.53
depth	37	1	37	.08	.78
2-way interactions	17378	20	869	1.80	.04
spg x rotenone	6138	5	1228	2.54	.04
spg x bottom	6182	8	773	1.60	.14
spg x depth	2224	5	445	0.92	.47
rotenone x depth	132	1	132	0.27	.60
bottom x depth	43	1	43	0.09	.77
3-way interactions*	2654	8	332	0.69	.70
explained	25070	37	678	1.40	.11
residual	36244	75	483		

113 estimates of q_{m2} residuals were analysed

* minimum significance of a single interaction was .44

Table 3.7 Anovas of q_{m2} with and without rotenone versus species group and length

With Rotenone

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	1.01	8	.13	2.16	.06
species group(spg)	.29	5	.06	1.00	.43
length	.54	3	.18	3.09	.04
spg x length	.32	11	.03	0.49	.90
explained	1.33	19	.07	1.19	.32
residual	2.05	35	.06		

55 estimates of q_{m2} were analysed

Without Rotenone

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	1.16	8	.15	2.75	.002
species group(spg)	.72	5	.14	2.73	.007
length	.57	3	.19	4.92	.005
spg x length	.23	6	.04	1.02	.43
explained	1.39	14	.10	2.58	.009
residual	1.65	43	.04		

58 estimates of q_{m2} were analysed

Table 3.8 Anova of transformed q_{m2} residuals versus species group with an *a posteriori* test.

Transformed q_{m2} = Ln(q_{m2}/(predicted q_{m2}))

With Rotenone

Homogeneity of Variance test (Bartlett-Box): F=.61, p=.70

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
between groups	0.63	5	.13	0.91	.49
within groups	5.69	41	.14		

Without Rotenone

Homogeneity of Variance test (Bartlett-Box): F=.91, p=.47

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
between groups	2.48	5	.50	5.01	.0008
within groups	5.06	51	.10		

Student-Newman-Keuls test at p=.05 (without rotenone)

1st Homogeneous subset:

Species Group:	E	D	A	F
Mean Value	-.522	-.071	-.040	.056

2nd Homogeneous subset:

Species Group:	D	A	F	C	B
Mean Value	-.071	-.040	-.056	.446	.518

Table 3.9 Pooled Data for Block Net Retention, q_{m2}%

Rotenone used?	Species group*	Mean length	No. of fish	Measured q_{m2}%	Predicted q_{m2}%	Residual
no	I	25	12	58	65	-7
no	I	28	12	83	70	14
no	I	30	12	75	72	3
no	I	36	12	67	77	-10
no	I	44	12	83	82	2
no	I	62	12	83	87	-4
no	I	183	11	100	97	3
no	II	28	20	55	42	13
no	II	35	20	75	52	23
no	II	39	20	45	56	-11
no	II	42	20	35	57	-22
no	II	45	20	45	59	-14
no	II	49	20	45	62	-17
no	II	54	20	50	64	-14
no	II	57	20	55	65	-10
no	II	60	20	75	66	9
no	II	62	20	50	67	-17
no	II	64	20	80	67	13
no	II	67	20	90	68	22
no	II	69	20	80	68	12
no	II	71	20	70	69	1
no	II	74	20	65	69	-4
no	II	77	20	85	70	15
no	II	79	20	45	70	-25
no	II	82	20	75	71	4
no	II	85	20	75	72	3
no	II	89	20	80	72	8
no	II	94	20	85	73	12
no	II	100	20	75	73	2
no	II	139	20	80	77	3
no	II	228	11	73	80	-7
no	III	55	8	38	33	4
no	III	165	7	29	50	-21
no	III	329	7	71	54	17
yes	ALL	33	40	32	29	3
yes	ALL	44	40	35	42	-7
yes	ALL	50	40	38	47	-9
yes	ALL	56	40	42	50	-8
yes	ALL	64	40	70	54	16
yes	ALL	74	40	80	58	22
yes	ALL	88	40	72	61	11
yes	ALL	106	40	60	65	-5
yes	ALL	118	40	45	66	-21
yes	ALL	137	40	55	68	-13
yes	ALL	160	40	67	70	-2
yes	ALL	199	40	75	72	3
yes	ALL	295	26	85	75	10 *

Species group I = B+C, II = A+D+F, III = E (see Table 3.4)

Table 3.10 Parameters Used in Hyperbolic Functions Derived from Least Squares Fits for Block Net Retention, q_{m2}.

Data from Table 3.10 fitted to:

$$q_{m2} = B/L + A$$

q_{m2} is block net retention (as fraction),
L is length of fish in mm,
A is assymptotic value of retention,
B is rate of increase of retention with the reciprocal of length,
also, L_o is the length in mm when retention is zero where $L_o = -B/A$

Rotenone used?	Species group*	R^2	A	S.error of A	B	S.error of B	Sig. of Fit	L_o
no	I	.81	1.02	.084	-9.10	2.95	.027	9
no	II	.52	.85	.073	-11.57	4.10	.010	14
no	III	.49	.58	.26	-11.4	20.1	.67	20
yes	ALL	.73	.81	.072	-16.8	4.72	.004	21

* Species group I = B+C, II = A+D+F, III = E (see Table 3.4)

Table 3.11 Anova of catchability estimates of unmarked fish (q_1) with sampling method, length and species groupµ including adjusted deviations.

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	8.29	10	.83	2.00	.002
method	5.49	2	2.74	9.94	.001
length	.70	3	.23	.85	.47
species group(spg)	2.02	5	.40	1.47	.21
2-way interactions	7.15	28	.26	.93	.58
method x length	.40	6	.07	.24	.96
method x spg	3.84	10	.38	1.39	.19
length x spg	3.04	12	.25	.92	.53
3-way interaction	1.67	12	.14	.51	.91
explained	17.11	50	.34	1.24	.17
residual	35.60	129	.28		

180 estimates of q_1 were analysed (grand mean = .548)

Deviations for each classification, adjusted for other factors

Factor	Category	No. of estimates	Adjusted deviation
method	A	32	-.37
method	B	50	.02
method	C	98	.11
length	up to 35mm	52	-.10
length	36 to 80mm	72	.06
length	81 to 189mm	45	.02
length	190mm +	11	.03
spg	A	13	.04
spg	B	17	-.02
spg	C	40	.16
spg	D	48	-.06
spg	E	32	-.17
spg	F	30	.06

Table 3.12 Anova of catchability estimates of marked fish (q_{m1}) with sampling method, length and species groupμ including adjusted deviations.

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	5.53	10	.55	3.00	.005
method	1.35	2	.67	3.65	.03
length	2.25	3	.75	4.06	.012
species group(spg)	1.97	5	.39	3.13	.08
2-way interactions	6.21	24	.26	1.40	.16
method x length	.27	5	.05	.29	.91
method x spg	.62	8	.08	.42	.91
length x spg	4.53	11	.41	2.23	.03
3-way interaction	.29	4	.07	.39	.82
explained	12.03	38	.32	1.71	.04
residual	9.05	49	.18		

88 estimates of q_{m1} were analysed (grand mean = .554)

Deviations for each classification, adjusted for other factors

Factor	Category	No. of estimates	Adjusted deviation
method	A	13	-.25
method	B	21	-.08
method	C	54	.09
length	up to 35mm	11	-.38
length	36 to 80mm	35	.01
length	81 to 189mm	32	.16
length	190mm +	10	-.12
spg	A	8	.27
spg	B	5	.13
spg	C	21	.06
spg	D	27	-.17
spg	E	12	-.20
spg	F	15	.20

Table 3.13 Anovas of catchability residuals versus species group and sample for methods B and C combined, and for method A with unmarked fish only.

Methods B and C: unmarked fish

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	8.35	21	.40	1.91	.02
species group(spg)	.87	5	.17	.84	.53
sample	7.69	16	.48	2.31	.008
spg x sample	22.60	50	.47	2.27	.001
explained	31.95	71	.45	2.16	.001
residual	15.82	76	.21	2.16	.001

148 estimates of q_1 were analysed

Methods B and C: marked fish

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	6.66	19	.35	2.01	.04
species group(spg)	1.87	5	.37	2.14	.09
sample	4.55	14	.32	1.86	.08
spg x sample	5.80	25	.23	1.33	.23
explained	12.47	44	.28	1.62	.08
residual	5.24	30	.17		

75 estimates of q_{m1} were analysed

Method A: unmarked fish

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	1.31	9	.15	2.26	.08
species group(spg)	.95	5	.19	2.94	.05
sample	.30	4	.08	1.16	.36
spg x sample	.19	6	.03	.50	.80
explained	1.50	15	.10	1.56	.19
residual	1.03	16	.06		

32 estimates of q_1 were analysed

Table 3.14 Anovas of catchability residuals versus species group and sample for methods A and B combined, for group (a) (species groups A, B, C and F) only.

Unmarked fish

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	10.81	19	.57	2.21	.02
species group(spg)	.25	3	.08	.32	.81
sample	10.52	16	.66	2.55	.009
spg x sample	10.69	28	.38	1.48	.13
explained	21.50	47	.46	1.77	.035
residual	9.79	38	.26		

148 estimates of q_1 were analysed

Marked Fish

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	3.11	14	.22	.65	.78
species group(spg)	.90	3	.30	.88	.48
sample	2.55	11	.23	.68	.74
spg x sample	2.76	13	.21	.62	.80
explained	5.87	27	.22	.64	.85
residual	10.31	40	.26		

41 estimates of q_{m1} were analysed

Table 3.15 Correlations of Catchability Residuals with Environmental Variables for unmarked fish using methods B and C.

Species group	Secchi range	Depth (max.) range	Cover range	No. of samples	No. of q_1 estimates	Corr. coeff. (r)	Sig. of r (p)
(a)	13-140*	70-140	0- 8	8	36	-.09	.31
(b)	13-140*	70-140	0- 8	8	36	+.02	.46
(c)	13- 20*	70-100	0- 4	6	22	+.41	.03
(a)	50-100*	75- 80	12-80	4	13	-.18	.28
(c)	50- 70*	75- 80	60-80	2	3	-.54	.32
(a)	13- 20	60-100*	0- 4	6	30	+.13	.26
(b)	13- 20	60-100*	0- 4	6	24	+.16	.22
(c)	13- 20	60-100*	0- 4	6	26	+.08	.43
(a)	100-150	130-160	8-44*	6	22	+.11	.32
(b)	100-150	130-160	8-44*	6	34	+.09	.30
(c)	100-150	130-150	28-44*	3	6	-.38	.23

* variable used in correlation with catchability, q_1

Table 3.16 Anova of residuals of catchability estimates of unmarked fish for method A, by species group and maximum depthμ including adjusted deviations.

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig. of F
main effects	.59	4	.15	4.64	.004
species group(spg)	.36	2	.18	5.63	.007
depth	.20	2	.10	3.08	.058
depth x spg	.03	3	.01	.36	.78
explained	.63	7	.09	2.81	.019
residual	1.18	37	.032		

45 estimates of q_1 residuals were analysed (grand mean = .015)

Deviations for each classification, adjusted for other factors

Factor	Category	No. of estimates	Adjusted deviation
depth	up to 100cm	13	+.017
depth	100 to 200cm	21	+.054
depth	over 200cm	11	-.123
spg	(a)	14	.124
spg	(b)	21	-.029
spg	(c)	10	-.113

Table 3.17 Parameters derived for catchability predictions from unmarked fish by sampling method and species group

Data from file with 8 length groups and 3 species groups by sample is fitted by least squares after weighting estimates to:

$$\mathrm{Log}(100q_1 + 1) = (a(\mathrm{Log}(L-12)) - b(\mathrm{Log}(L-12)^2))$$

where

q_1 is standard net catchability estimate from unmarked fish
L is length of fish in mm,
a,b are parabolic constants*

Method	Species group	a	b	Multiple R2	S.error of regression
B + C	(a)	2.76	.425	.976	.693
B + C	(b)	2.14	.266	.968	.756
B + C	(c)	2.15	.312	.912	1.047
A	(a)	2.37	.412	.973	.540
A	(b)	2.57	.579	.845	.846
A	(c)	0.35	.023	.623	.806

* all fitted parameters were significant at $p<.01$ except 'b' for sp. group (c), method A.

Table 3.18 Samples required for 20% accuracy in abundance estimates by species group, length group and sampling method. (Based on variability at the scale of the block net area, see Table 3.20 for large scale estimates)

Species group	Length group*	Predicted catchability,q*	Variance ofaResiduals,V*	No. of estimates for q,V	Mean No. of individuals per estimate	No. of samples n*
methods B and C:						
(a)	1,2	76	6.6	24	560	44
(a)	3,4	85	6.3	23	273	37
(a)	5,6	42	2.2	4	49	27
(a)	7,8	-	-	1	-	-
(b)	1,2	44	4.9	18	119	57
(b)	3,4	69	5.2	22	280	38
(b)	5,6	67	6.4	16	18	48
(c)	1,2	-	-	1	-	-
(c)	3,4	37	17.6	13	35	242
(c)	5,6	23	2.3	13	34	51
(c)	7,8	11	5.1	4	15	237
method A:						
(a)	1,2	29	0.8	3	73	14
(a)	3,4	25	0.4	5	121	7
(a)	5,6	9	3.1	2	17	172
(b)	1,2	12	0.6	4	55	25
(b)	3,4	4.3	2.3	9	37	265
(b)	5,6	.01	.02	4	15	425
(c)	3,4	1.7	.6	4	48	182
(c)	5,6	2.0	2.1	4	20	524

* length groups: 1,2 = 13 to 35mm
3,4 = 36 to 81mm
5,6 = 82 to 189mm
7,8 = 190 to 480mm

q is the weighted mean of estimates based on parameters in Table 3.15.

V is the weighted variance of the differences between the square roots of the estimates and measured values of catchability, q_1.

q and V are weighted by the number of individuals per estimate.

n is an estimate of the number of samples required such that the estimated abundance or biomass be within +20% and -15,4% of the predicted value with 95% confidence.

Table 3.19 Samples required for 20% accuracy in abundance estimates by length group and sampling methodμ and for total biomass assuming typical weight distributions of the catch. (Based on variability at the scale of the block net area, see Table 3.20 for large scale estimates)

Length group*	Weight% of catch	Predicted catchability, q*	Variance of Residuals, V*	No. of estimates for q,V	Mean No. of individuals per estimate	No. of samples n*
methods B and C:						
1,2	7	72	5.9	17	919	42
3,4	37	76	2.4	16	810	16
5,6	32	41	3.5	13	78	42
7,8	25	15	1.1	6	19	37
weighted mean:		50	2.7			27
=method A:						
1,2	2.5	21	1.9	5	92	46
3,4	42	15	.43	5	229	14
5,6	55	2.8	.25	4	50	45
weighted mean:		8.3	.37			22

* definitions as for Table 3.18

Table 3.20 Estimates of precision of active gear compared with precision and accuracy estimates from this study (all unstratified samples).

Values expressed as number of samples required, n, to estimate the mean within ±20% with 95% confidence, where

$n = (tCV/.2)^2$
$t = 1.96$
CV = coefficient of variation (S.D./mean)

Gear (day or night samples)	Ground rope length(m)	Area of	Species	Length range (cm)	No. of samples (n)	Source
bottom trawl	50	Georges Bank	Haddock	-	338	Grosslein (1971)
''	''	''	Yellow-tail flounder	-	253	''
bottom trawl	50	ICNAF areas 4,5,6	Various ground-fish	-	96	Hennemuth (1976)
''	''	''	Herring or mackerel	-	216	''
bottom trawl (daytime)	30m	Three Finnish lakes	All	10-22	384	Bagenal (1979)
mid-water trawl(night)	21m	''	All	12-19	85	''
bottom seine(day)	158m	''	''	>10	225	''
surface seine(night)	152m	''	''	6-20	80	''
shore seine(day)	50m	Lake Turkana	*Labeo horie*	3-60	175	Bayley (1978)
seine: methods B + C (1)	25	Central Amazon	All	1.5-96	105	This study
seine: methods B + C (2)	''	''	''	''	169	''

continued....

Table 3.20 continued

seine: method A (1)	''	'' ''	''	1.5-99	136	''
seine: method A (2)	''	''	''	''	197	''

(1) = estimates of precision (as in all preceding data) based on actual catches per unit area from standard net samples.

(2) = estimates of accuracy based on biomass per unit area predicted by net efficiency for each standard net sample.

Chapter 4: Growth

4.1 Introduction

Although growth is only one variable controlling the dynamics of a population, it has been selected for study for the following reasons:

(a) Instantaneous growth (G) estimated over short periods is a good estimate of the turnover rate or P/B ratio (Greze,1968, Waters,1969, Mathews,1970), thus providing one method for estimating production using the gear efficiency parameters (Chapter 3) to estimate biomass.

(b) Evidence of intra- or interspecific competition can be investigated by testing for density dependent growth;

(c) Growth may be dependent on hydrological season (Chapter 1).

It was also remarked in Chapter 1 that many floodplain species have regular spawning seasons. The present study has confirmed this for a number of species on the basis of modal progressions of young fish. This has led to a model for predicting growth in other species and hence estimates of overall production. This has been compared to primary production and the fishery yield, and has also provided some insight into predator-prey interactions (Chapter 5).

During this project 5×10^5 fish and 6×10^4 prawns (Macrobrachium spp.) weighing 1040 kg were caught, of which 9.4×10^4 individuals were measured and 1.6×10^4 were weighed. So far over 230 taxa have been separated, including all the commercial species.

The following section briefly describes the processing of this information.

4.2 Methods

4.2.1 Taxonomy and preservation.

The major problem in Amazon fish taxonomy is the scattered literature of varying quality and the resulting crop of synonyms. Even with the intensity of sampling during this project, few new species have so far been discovered. Separation and identification of young specimens has been possible because of the continuous size series obtained. Larval fish were not caught, but would probably have been much more difficult to distinguish.

Large specimens which could be identified (the majority could be identified to species) were measured and weighed in the field. These comprised 7% of all the individuals caught. The others were preserved in 5% formaldehyde, larger specimens and medium to large detritivores were injected or perforated to speed access by the preservative. After one to three weeks the samples were transfered to 70% ethanol, the latter being renewed every two or three years.

A large part of the collection which has already been separated into species and measured has been deposited at the Museu de Zoologia, Universidade de São Paulo where identification and cataloguing is being carried out. A similar process is being carried out on other samples deposited at the Smithsonian Institution. The taxa which I have separated and which are discussed in this thesis have been confirmed by specialists in both institutions, even though in some cases an unequivocal specific name has not been given because of pending revision of the literature and type specimens. Appendix A contains a list of taxa which have been separated so far. Some taxa have been divided into genera or species for the larger specimens only. Species which are still in higher taxa are either small (e.g. the Tetragonopterinae) or very uncommon (e.g. many Siluriformes species), with the exception of the piranha group within the Serrasalmidae. This group is common and contains species up to 42cm long (Serrasalmus rhombeus, personal observation). Conversely, some higher taxa with small species have been separated down to the specific level, such as the Engraulidae, Curimatidae and Pyrrhulinini.

4.2.2 Length and weight measurements.

Obviously it was not possible to identify, measure and weigh small fish in the field. Since they change length and weight due to preservation, a long term experiment was set up in 1977 to calibrate the changes in length and weight of 77 specimens covering a range of taxa and lengths. This experiment is still in progress, but is briefly described here.

Samples were transported live to the laboratory where they were killed and immediately weighed and measured before preserving in 5% formaldehyde. Measurements were continued periodically, the time intervals between recordings increasing geometrically. Groups were transfered to 70% ethanol at different times.

The results for length changes were quite uniform. Within a few days of their fixation in formalin the length reduced by a mean of 1.0% and remained stable for the following four years. This relative reduction was independent of the size or taxon. Consequently, measuring boards were constructed with a scale reduced by 1.0% for use with preserved fish.

Weight changes were found to be dependent on both size and time spent in both formalin and ethanol, but were independent of taxa. Weights increased in formalin, approaching an asymptote. When transferred to ethanol their weight decreased according to a negative exponential, the rate being higher for smaller fish. After one year a 600g fish would lose 3% and a .2g fish 16% in weight. An empirical equation was derived to cover the time period of routine weight measurements.

Routine measurements of both fresh and preserved fish were made down to the nearest millimeter for fish less than 100mm long and down to the nearest 5 millimeter multiple for larger fish. Lengths and weights were measured as described in Chapter 3. Random subsamples for measuring were taken from large, unimodal distributions of limited length range, that is from large cohorts of young fish. Otherwise all fish were measured.

Smaller random subsamples were taken for weighing smaller fish, but most of the larger fish were weighed whether they were fresh or preserved. All routinely weighed individuals were measured down to the nearest millimeter (in the calibration, smaller fish were measured to the nearest .5mm).

The random subsamples were made by arranging the fish in a special tray containing numbered channels which facilitated the rapid allocation of numbers to individual fish (or equal sized groups for small fish) and prevented weight loss by keeping them immersed in water. Individuals or individual groups were selected using pseudo-random numbers generated from a calculator program seeded with a random number.

All fish in groups of 50 or less were measured when the groups were of single species. Subsampling in groups over 50 was proportionately smaller. Subsamples of 50 were taken from groups numbering 50 to 99, 75 from those between 100 and 200, and 100 individuals were taken from larger groups.

Since this density of subsampling was carried out on groups of limited length range the additional variance is negligible compared with that due to the sampling itself.

Overall, 17% of the fish measured were also weighed. The proportion was highest for larger fish, and lowest for large subsamples of smaller fish.

Log(weight) versus log(length) plots indicated no changes in allometry, and there were no differences between the fresh weights estimated from preserved weights and direct fresh measurements for comparable length ranges. Allometric parameters were derived from the log-transformed data using the GM regression (Ricker, 1973) although the predictive regression would have given very similar results because the correlation coefficients were close to 1 (e.g. see Table 4.1, p 207). Plots and derived parameters not shown in Table 4.1 are available on request.

4.3 Interpretation of length frequency distributions

Abundant species representing various higher taxa, different food preferences and maximum sizes were chosen for generation of length frequencies corresponding to each sampling excursion and region.

In treating each region separately I have assumed that mixing of populations does not occur during the appropriate life stages of each species. There is evidence for the existence of distinct populations of 0+ group Semaprochilodus insignis (unpublished data) despite the fact that older groups partake in long migrations. Random samples of 32 and 41 specimens from Marchantaria and Janauacá respectively had lateral line scale counts which were significantly different ($X2$ test, $p<.005$). Transverse scale counts also indicated a similar difference in this well-defined species. Another common characin, Hemiodus microlepis, was found to have significantly different scale counts between samples from the two closest regions, Marchantaria and Janauarí (Johns 1982). However, the assumption of non-mixing would not be invalidated if there were evidence of a common genetic stock with some species.

When there is no independent evidence for distinguishing cohorts, their separation within regions involves some subjective assessment no matter how sophisticated the technique may be. I have preferred to be subjective at the level of linking cohorts from the estimated length distributions rather than attempt to choose among many arbitrary options for restructuring the data such as in Pauly & David (1980).

The actual frequencies were estimated by correcting for net efficiency (Chapter 3) to avoid distortion where efficiency changes rapidly with length.

Of the 24 species examined, the distributions of 14 indicated clear modal progressions while the other 10 (5 Cichlidae and 5 Characoidei) were rejected due to extended and apparently continuous spawning periods during part of the year. The species used in this analysis are listed in Table 4.1 along with biometric data.

With most species, cohorts were distant from their neighbours due to the existence of a single cohort per year. An example of this is Triportheus albus shown in Figure 4.1 (see pp. 189-206 for Figures). Some species obviously had more than one cohort per year, but were selected for analysis when cohorts could be traced between successive spawning periods. An example of this is Curimata latior shown in Figure 4.2.

Samples of only 4 individual fish showed clear modal progressions except for Engraulidae sp.A_1 when the subset of distributions comprising 20 individuals or more was used.

The mean fresh weight calculated for each cohort within each distribution was plotted against time for each species (Figures 4.3 through 4.16). Since weight is on a logarithmic scale it can be observed that the instantaneous growth rate, G, represented by the slope, decreases with increasing age as would be expected.

4.4 Growth model and species effects

The aims of (a) obtaining production estimates across species and (b) examining density-dependence influenced the choice of a growth model. The data portrayed in Figures 4.3 through 4.16 could have been tackled by a battery of models. The one explaining the most variance could well be different for different species and each could consist of many parameters difficult to interpret. Conversely a simple model whose residuals can be tested with biologically realistic variables might provide insight into factors affecting growth.

The allometric relationship proposed by Parker & Larkin (1959)

$$dw/dt = kW^{x}$$

provides good empirical fits (e.g. Ware, 1978 and references therein) and can be related to energetic models (Paloheimo & Dickie, 1965, Ware, 1978). Using the discrete form, $\Delta W/\Delta T=kW^{x}$, of the model the data within cohorts in Figures 4.3 through 4.16 can be used to explore the applicability of the model.

The figures indicate temporary loss of mean weight within some cohorts. It is conceivable that weight may be lost even with small fish, but the weights were calculated from lengths since the variation in condition factor was small. The possibility of loss of length with juvenile fish is discounted, and the losses were ascribed to sampling variance. Consequently the data have been smoothed by taking the weighted mean of the first point representing a decrease in weight and the preceding point. This is equivalent to pooling the respective length distributions. With some cohorts, this process had to be repeated until all weight changes were positive. This method of smoothing keeps the loss of degrees of freedom to a minimum but produces estimates which are based on independent data. The latter would not be the case if a moving average were applied.

A total of 301 estimates of growth increments over the 14 species were obtained. These are shown in Appendix B along with mean weight and abiotic data.

Firstly the species were analysed separately. The log transform of the Parker & Larkin model indicated a significant effect of weight except for the Plagioscion spp whose data were very limited in range. Figure 4.17 shows the regression and ranges for each species. The ranges show considerable overlap in weight. Table 4.2 shows the data for each of the twelve species which gave significant regressions.

The slopes averaged .673 (±.07 s.e.), but this does not account for the different errors of separate species regressions. A better estimate of the mean regression is obtained by pooling the sums of squares of deviations from each species regression (the 'common' regression of Snedecor & Cochran 1967:434). This resulted in the the following equation:

$$\Delta W/\Delta T = .184W^{.657} \quad \ldots\ldots\ldots\ldots \quad (1)$$

in units of g/week. This mean regression is shown in Figure 4.18 along with data for individual weight increments by species. The mean slope is less than the range of .71 to .76 for juvenile N. Atlantic species and a pacific salmon quoted in Ware (1978) and Fenchel's (1974) estimate of .725.

The slope determines the rate of change of growth rate with weight. A slope less than one ensures that the specific growth rate decreases with increasing size, but does not reach an asymptote as for example in the von Bertalanffy model.

Although much of the scatter must be due to sampling errors there are some obvious growth rate differences between species when one compares Figures 4.3 through 4.17. Species which eventually attain a larger size (Table 4.1) grow faster during the first year. Although the slopes for separate species were uncorrelated with maximum size, the deviations of growth from the mean slope were (at p=.00006). Despite the variability, Figure 4.17 indicates generally higher elevations for larger species such as Colossoma and Brycon, and the lowest for the smallest species (Engraulidae sp.A_1). The growth rate at any mean weight is a function of both the slope and the elevation. However, a species with a higher elevation for the same slope indicates a faster growth rate at any size. Faster growth rates for larger species at all ages is indicated by data from Africa and the Paraná system quoted in Welcomme (1979:139)

This effect is incorporated into a general growth function (4.7). The following two sections analyse the residuals from both the separate species regressions and the mean regression with respect to density of potential competitors and hydrological factors.

4.5 Feeding, competition and density-dependence in growth

Competition for a limited food supply should be reflected in a growth rate which is inversely related to the density of all competing species, providing that the food concentration is constant. Dudley (1974) found a significant (at $p<.1$) density-dependent growth in one adult age-group of Tilapia macrochir, one of three species he studied. Kapetsky (1974) failed to find density dependent growth for any combinations of species and year class in the Kafue floodplain, but found significant effects of hydrological factors.

Obviously competition between species is dependent on the degree of overlap of food types eaten, a factor which is impossible to quantify using the published data for Amazon floodplains. However, the studies which have been completed along with personal observations of species in this collection do provide a basis on which to assess which taxa could potentially compete with each of the 14 species studied for growth. A brief description of feeding and the taxa I have grouped follows.

Studies have been conducted mainly on smaller rivers and streams (Knöppel 1970; Saul 1975; Soares 1979) or on larger fish in flooded forests (Goulding 1980). However, Marlier (1967,1968) and in part Knöppel (1970) and Saul (1975) present some data on fish from floodplain habitats.

Good reviews are to be found in Welcomme (1979) and Lowe-McConnel (1975). Recently, detailed seasonal studies of adult and subadult commercial species in floodplain habitats near Manaus have been completed (Santos 1979; Almeida 1980; Paixão 1980; Carvalho,F.M. 1979; Carvalho,M.L. 1981; Barthem 1981). These studies have strongly influenced my grouping of juvenile fishes, although they did not include the very small juveniles. Older fish of many species exhibit increasing specialization. For example Santos (1979) found that the herbivorous Schizodon fasciatus contained significant amounts of animal remains when less than 100mm long.

For 0+ group fishes these studies suggest that within three major groups there exists considerable overlap in food preferences. These groups are described below with reference to the 14 species of this study.

Detritivores.

The most distinct group comprises the mud and fine-detritus feeders, referred to here as detritivores and often elsewhere as iliophagous species. Welcomme (1979:130) distinguishes between mud and detritus feeders but it is not clear how large the decomposing plant material has to be to qualify as the latter. However, this is a valid point since many species under my omnivcrous classification consume coarser detrital vegetable matter along with other items.

The three Prochilodontidae species and most if not all of the Curimatidae qualify for the detritivore group from a very small size. Diatoms are also found in species of this group (Saul 1975). Personal observations of *Semaprochilodus taeniatus*, *S. insignis*, *Curimata latior*, *C. kneri* and *C.* cf. *semiornata* down to 18mm long revealed full stomachs of fine detritus and a small proportion of mineral grains. In addition to these fish species, *Macrobrachium* spp. are also regarded as detritivores, since plant debris has been observed in stomach contents by Marlier (1967). The detritivores comprised 40% of the 1977 fisheries yield of 9900t (Bayley 1981) between Manaus and the R. Purus mouth.

A major difference between this group and the two following is the almost constant small particle size of the food which is independent of the size of the consumer.

Piscivores.

I have included in this group fish which also prey on *Macrobrachium* spp. The most dominant members are *Cichla ocellaris* (Cichlidae) and *Hoplias malabaricus* (Erythrinidae). *Raphiodon vulpinis* and *Acestrorhynchus* spp. are also common members of this group. These species begin feeding on fish when only 4cm long (personal observation). Less frequent members are *Crenicichla* spp., *Batrachops* spp., the larger *Pellona* spp., *Potamorrhaphis* guianensis, Synbranchus marmoratus, Arapaima gigas, Pseudoplatystoma spp., Sorubim lima, Sorubimichthys planiceps, Hemisorubim platyrhynchos, Phractocephalus hemiliopterus, Hydrolycus, Plagioscion squamosissimus and P. montei. Growth estimates of the last two species of this list were made but were limited to very young stages. I have excluded piranhas from this group because of the abundant evidence indicating a variety of foods such as fruits from trees (Goulding 1980) and vegetation as well as fish remains (personal observations).

Piscivores as defined here were only about 4% of the 1977 fisheries yield but were 35% of the biomass estimated here.

Omnivores.

Despite the more generalized feeding of the 0+ fish, this is a heterogeneous group.

Although terrestrial and aquatic sources as well as vegetable and animal sources are indicated by the stomach contents of most species one is obliged to eliminate some taxa when considering each of the remaining species comprising the growth study:

Engraulidae sp.A_1, the most common species of this family, feeds on zooplankton (Cladocera and Copepoda, personal observations of 5 specimens 30 to 62mm long). It probably also feeds on phytoplankton as Marlier(1967) reports for the engraulid *Anchoviella brevirostris*. Common groups which are potentially competing are Clupeidae, Engraulidae, *Anodus* spp. (including *Eigenmannina*), *Triportheus* spp, *Brycon* spp, *Chalceus eurythurus* and Tetragonopterinae spp.

The young of three species of *Triportheus* studied here and *Brycon melanopterum* are predominantly surface omnivores. Another species, *Triportheus culter*, is a zooplankton feeder (Almeida 1980) which was not common in my samples. *Triportheus albus*, which Almeida did not study, feeds on terrestrial insects (inc. ants), small seeds and Cladocera (personal observations of 7 specimens 24 to 130mm long). I have included all groups except Siluriformes (but not including Hypophthalmidae), *Geophagus*, 'detritivores' and 'piscivores' as potential competitors with the 3 *Triportheus* spp. and *Brycon melanopterum* of this study.

Acarichthys heckeli (Cichlidae) and *Colossoma macropomum* are considered to be capable of competing with all the 'omnivores', notwithstanding the fact that larger juveniles of *Colossoma macropomum* contain a large proportion of zooplankters (Carvalho,M.L. 1981).

In conclusion, I have taken a very broad view of groups within which competition is conceivable. With the exception of the detritivores, I regard size as being at least as important as species. For each growth estimate, there is a length range which encompasses the distributions used for the estimate. This was found to be close to ±50% of the mean length of the pooled distribution. The mean biomass density of potential competitors was calculated for fish within this length range, and from samples taken during the time interval and region corresponding to each growth estimate. Samples were not included which were outside the geographic range of the particular species, or outside the depth range occupied by the species at the size range concerned.

Biomass density estimates of potential competitors were estimated for each of the 301 growth increment estimates made as described above. The mean number of samples corresponding to each biomass estimate was 19 ±1 s.e. Competitor biomass estimates ranged from 2 to 83 g/m2.

Results.

Tests were conducted using residuals from the separate species regressions (Figure 4.17, Table 4.2) and from the mean regression (equation 1). These residuals are the deviations of the log-transformed growth rates from the appropriate log-log regressions. They were examined in relation to the competitor biomass densities or their logarithmic transforms. Correlations between residuals and competitor biomass were attempted under the following conditions:

I. Using the regressions for separate species.

(a) All data by species.

(b) During rising water by species.

(c) During falling water by species.

(d) All species under the above conditions, but using residuals from separate regressions.

II. Using the mean regression for all species.

The full data set.

At high water (>24m).

At lower water levels (<24m).

During the period of rising water level.

During the period of reducing water level.

The results of I(a), (b) and (c) are shown in Table 4.3. Sign tests of correlations were not significant. However, two out of eleven species indicated density-dependent growth at $p<.05$ during falling water, and one of these indicated a reverse effect during rising water. Test I(d) did not indicate significance under condition (a), (b) or (c).

In tests under II, there were no significant negative correlations at $p<.1$. Positive correlations (at $p<.02$) were found when the water level was rising and when the level was less than 24m.

There is a distinction between density-dependent growth and food limited growth. The latter will only be reflected as a density-dependent phenomenon if the food concentration is fairly constant. This is clearly not the case during different seasons as explained in Chapter 2 and references therein. The period of reduced food supply during falling water would be expected to limit growth, as the two apparently significant correlations in Table 4.2 suggest. These aspects are discussed in the following section where growth is compared with hydrological variables.

4.6 Growth and hydrological season

The first two chapters attempt to describe the littoral zone during the rising and falling water levels. This is briefly summarized with respect to my observations of fish in this zone.

Young of the year accompanied by piscivores follow the water's edge as the level rises, exploiting 'allochthonous' food sources in the newly inundated areas (see also Chapman et al 1971). At the same time, nutrients are released from the ground and contribute to the rapid aquatic macrophyte growth which keeps up with the advancing water. Associated with these macrophytes are the largest concentrations of invertebrates reported from the biotope and a rich source of detritus which also derives from the terrestrial vegetation and phytoplankton. As the rate of increase slows or stops at high water level, oxygen drops as the vegetation decays, as also reported by Dudley(1974) and Chapman et al (1971). Also, the processes of increasing food production and availability would be expected to be slowed. When the water level drops, which on average occurs in about half the time it takes to rise, vegetation is stranded and the associated rich food supply is lost. There is emigration from the forested and deforested floodplain, but rising concentrations of fish in the littoral zone are somewhat mitigated by emigration of some larger species to the channels and rivers.

A two-way analysis of covariance of $\mathrm{Ln}(\Delta W/\Delta T)$ between periods of rising and falling water and between three classes of maximum weight (<300g, 300-2000g, >2000g) with Ln(mean weight) as the covariate indicated a highly significant seasonal difference ($p<.001$). Growth was on average 60% faster during the rising period when adjusted for the covariate and maximum weight. Maximum weight was also a significant main effect ($p=.003$) with larger species showing more positive deviations. There were no significant interactions at $p<.1$ between maximum weight and season or between either of these and the covariate.

It is conceivable that the seasonal growth effects indicated may be due to growth patterns of individual species not determined by maximum size. Consequently the data for individual species were analysed separately using the Parker & Larkin model, except for the very limited data for Plagioscion. The residuals from 9 out of 12 species were positively correlated with the rate of rise of water level, of which three were significant at $p<.05$ and another at $p<.01$. When these residuals were combined the correlation with rate of water level increase was significant at $p=.001$, but when the rising and falling water periods were separated the former was highly significant ($p=.0002$) whereas during the latter period no significant effect was found ($p=.13$).

The residuals from the mean regression were tested with rate of water increase during the rising and falling periods separately. Within the falling period, no correlation between the residuals was found. Conversely during rising water the residuals were significantly correlated with rate of change of level:

Conditions	r	n	p
a. all year	+.17	301	.005
b. during rising water	+.27	237	.00001
c. during falling water	-.20	64	.055

Similar results but at lower probabilities were obtained using absolute water level and the standardized product between this and the rate of level increase.

The foregoing correlations and tests at least indicate that there is a variation in growth which depends on the hydrological season, as Kapetsky (1974) and Dudley (1974) have shown for larger fish in an African floodplain.

Is the rate of rise the most appropriate variable? In 1977 and 1978 there were contrasting rates of flooding (see Figure 2.3). This rate in 1977 was 2.5 times that in 1978 within the same water levels of 21m and 27m. An analysis of covariance of $Ln(\Delta W/\Delta T)$ between years with Ln(W) and Ln(maximum weight) as covariates indicated a highly significant difference ($F=14$, $p=.001$) within these water levels. The untransformed growth rate adjusted for covariates was 65% greater in 1977. This could not be explained by a change in density: the mean biomass during the 1977 period was 120g/m2 compared with 116g/m2 in 1978.

Also there is evidence in the form of mean fullness of fish stomachs from the Janauacá region. Santos (1979:54) divided the hydrological season into high, falling, low and rising periods. The mean stomach fullness of juveniles of all three species investigated was highest during the rising water period. His results for adults were less consistent, however. The results of Paixão(1980) for <u>Mylossoma duriventris</u> suggest a similar seasonal relationship for juveniles and adults, but there was some feeding during all months of the year.

In conclusion, the circumstantial evidence supports the statistical indication that growth is enhanced when the rate of flooding increases. Conversely, a lower growth rate is indicated during falling water, but is not influenced by the rate of fall. There was some indication of density-dependent growth for two species during this period. These results suggest a density-dependent process with respect to a seasonally varying food density. The implications of this result and the findings of section 4.5 are discussed in Chapter 5.

4.7 A general growth function

There is no consistent evidence of density-dependent effects on growth. This concurs with the findings of Kapetsky (1974) and most of Dudley's (1974) results. There have been no similar studies in tropical floodplains other than these. The only indication of density dependent growth in this study was for two species during the falling water period only, during which growth is in any case depressed. Also this season lasts for only 3 - 4 months during the year, and effects of any general density dependent effects on total production would be small.

However, seasonal growth variability should be accounted for. The rate of rise of water level is the best available predictor in lieu of more direct but elusive variables. I have introduced this variable with a dummy variable so that no effect of negative level changes are introduced (see 4.6).

It was noted in 4.4 that larger species tended to grow faster. To determine whether the effects of maximum weight and rate of water level increase were independent, a two-way analysis of covariance of Ln($\Delta W/\Delta T$) was examined during rising water only with Ln(mean weight) as the covariate. There were no interactions at $p<.1$ between the main effects of maximum weight (3 classes as in 4.6) and rate of level increase (2 classes: >.26 and <.26 m/week), nor between these and the covariate. Similar results were obtained in an analysis of variance of the deviations from the log-transformed equation (1) using the same classifications.

Correlations of various transformations of maximum weight with the deviations from the log-transformed mean regression suggested that the inverse of log(max. weight) was the best function, explaining 6% of the variance ($p=.00001$). This resulted in a function which concorded with growth rates of larger fish as discussed below.

The rate of water level rise was best correlated with the deviations from the log-transformed equation (1) as a simple linear function. These two effects were combined in a joint regression with the deviations from the mean regression to produce the following relation:

$$\Delta W/\Delta T = aW^{x} e^{c+dRD} \quad .... (2)$$

where $a = .234$ g/week $(+.030, -.026$ s.e.)

$x = 0.657$ $(\pm.037$ s.e.)

$c = -2.95(\pm.65$ s.e.)/Ln(max. weight in g)

$d = 1.26$ $(\pm.25$ s.e.)

W = mean fresh weight corresponding to the growth rate $\Delta W/\Delta T$, in g.

R = rate of change in the water level (m/week).

D = dummy variable, being 1 during rising water and 0 otherwise.

All the constants were significant at $p<.001$. The effect on seasonal growth of the last term can be marked. For the maximum recorded rise of .82m/week the predicted growth rate is about three times higher for a given size and species than for falling water.

This function is derived from 14 abundant species from a variety of taxa and trophic groups. There are few data available to test this relationship with larger fish. A market sample of 3000 <u>Colossoma</u> <u>macropomum</u> caught with non-selective gear during a two month period indicated an annual growth increase of 1.5 - 2 kg between ages 2 and 5 (M. Petrere & P.B.Bayley, unpublished data). Equation (2) integrated under average hydrological conditions indicated a mean increase of 1.8 kg for these ages and a similar sized species. Preliminary daily growth ring analysis of Plagioscion squamosissimus otoliths (H. Worthmann, pers. comm.) indicated weights of about 110g, 395g and 720g at ages 1,2 and 3 respectively. Equation (2) indicated corresponding weights of 45g, 300g and 950g for a species of similar maximum size. Equation (2) predicted growth rates within the range of those quoted in Welcomme (1979:139) for R. Niger species. This equation is not intended to predict the growth of individual species but to estimate the productivity of large groups of species as described in Chapter 5. When more growth data become available, the constancy of the slope, x, and the incorporation of alternative scaling factors for species should be investigated. This may provide a more accurate relationship to explore the production processes in more detail than in the following chapter.

4.8 References

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Figure 4.1 Length distributions by region and time for *Triportheus albus*.

Data were corrected for net efficiency.

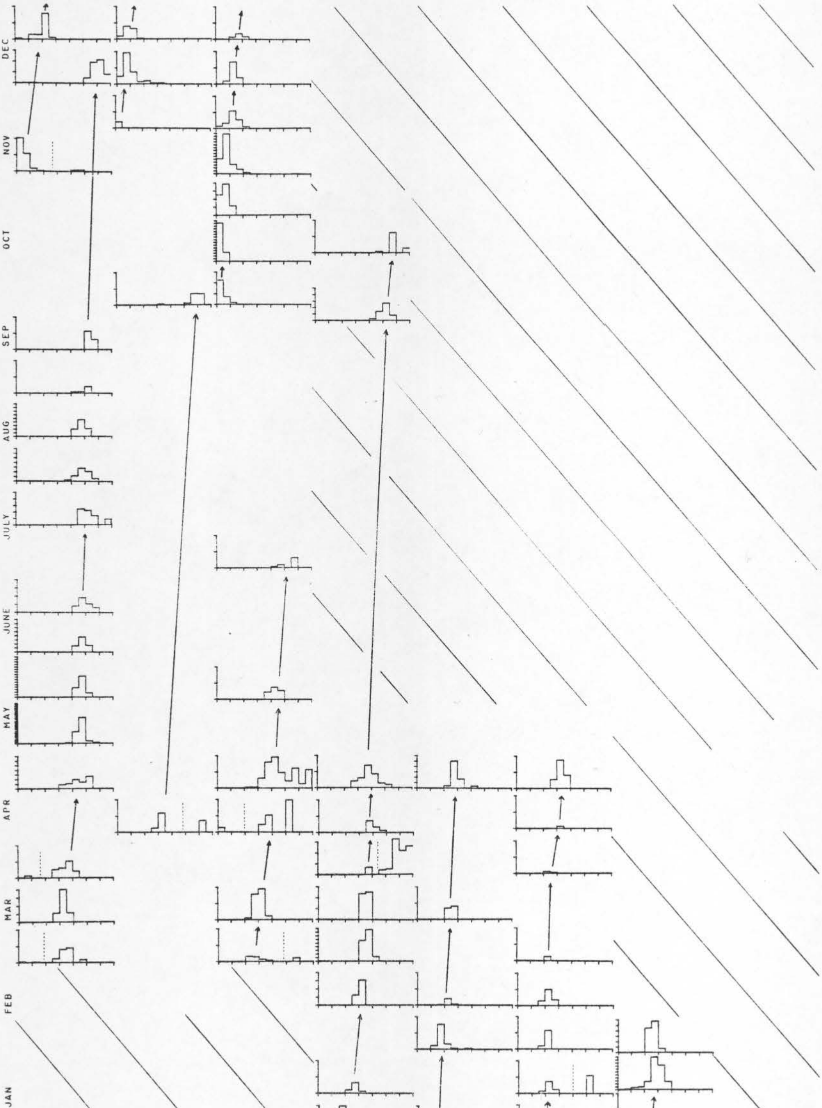
Frequencies are marked on the ordinate: 1 space= 25 individuals.

Lengths are in mm (fork length).

Hatched areas indicate no sampling took place.

Vertical dotted lines indicate where the distribution was divided.

Arrows indicate interpretation of cohort progression.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135
REGION: 1
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2
3
1
3
YEAR:
1977
1978
1979

Figure 4.2 Length distributions by region and time for *Curimata latior*.

Data were corrected for net efficiency.

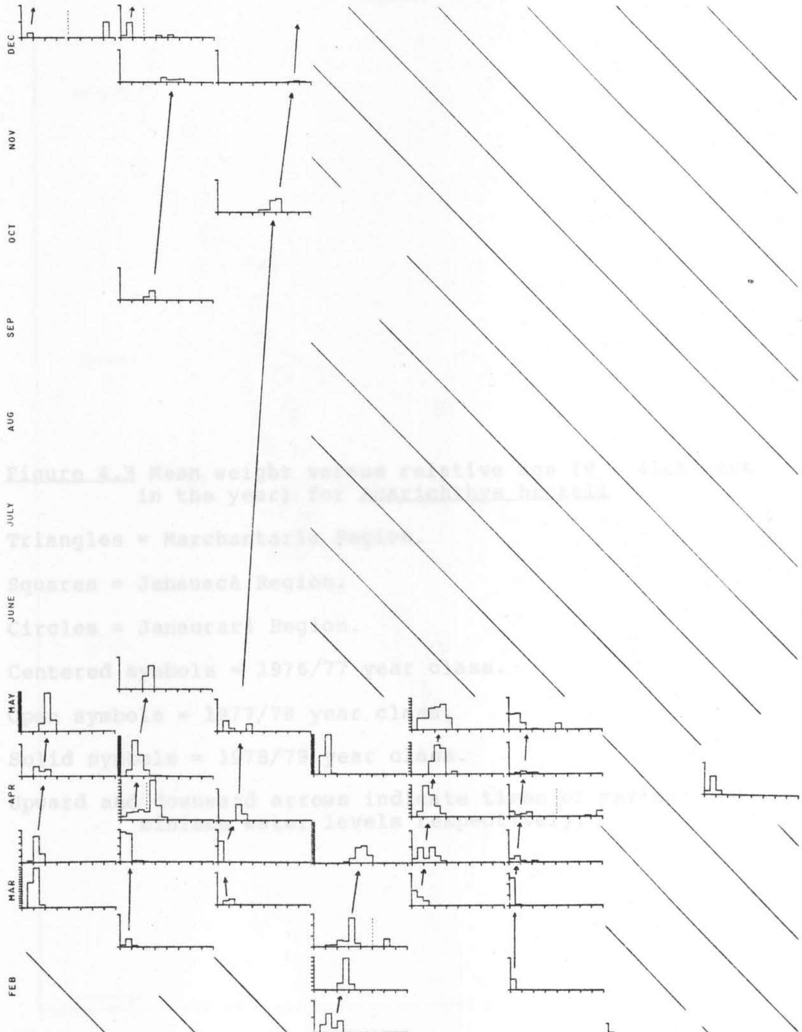
Frequencies are marked on the ordinate: 1 space= 25 individuals.

Lengths are in mm (fork length).

Hatched areas indicate no sampling took place.

Vertical dotted lines indicate where the distribution was divided.

Arrows indicate interpretation of cohort progression.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REGION: 1
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YEAR:
1977
1978
1979

Figure 4.3 Mean weight versus relative age (0 = 41st week in the year) for *Acarichthys heckeli*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

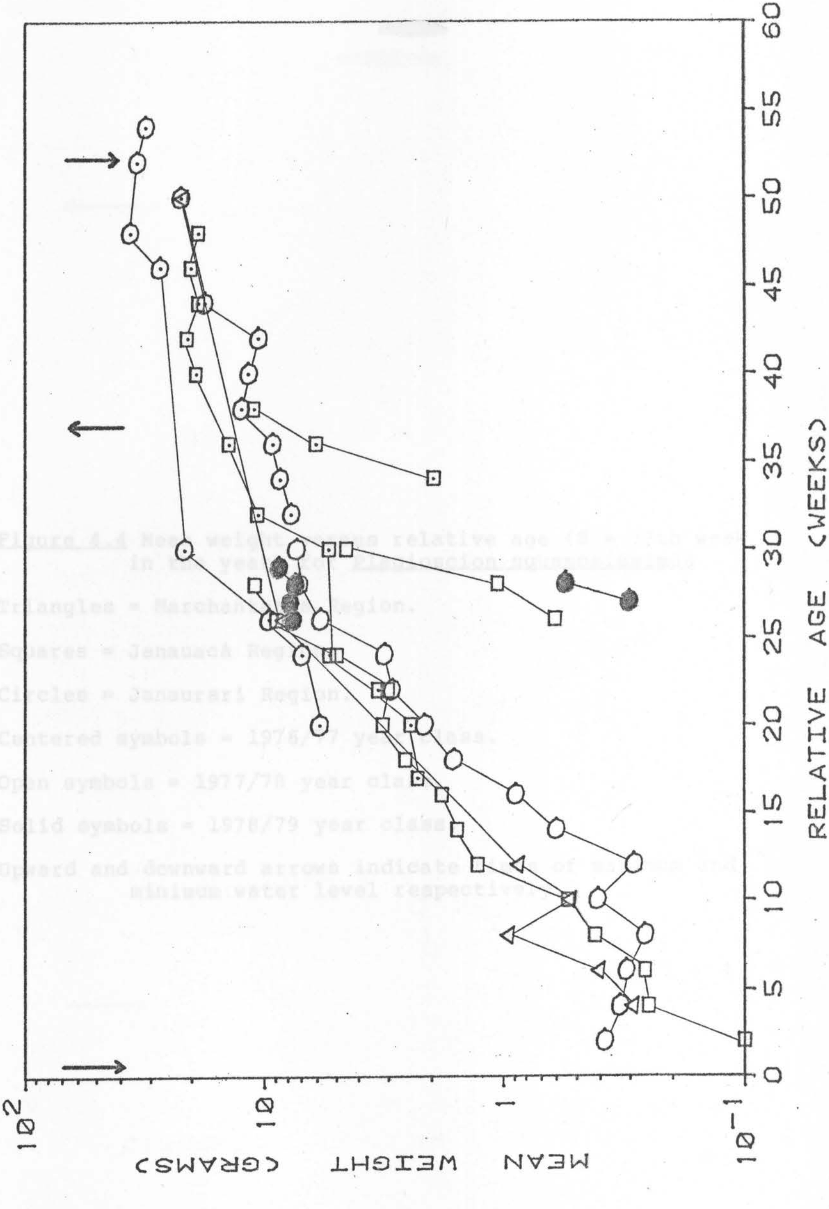


Figure 4.4 Mean weight versus relative age (0 = 15th week in the year) for *Plagioscion squamosissimus*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janauari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water level respectively.

Figure 4.4 Mean weight versus relative age (0 = 37th week in the year) for *Plagioscion squamosissimus*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water level respectively.

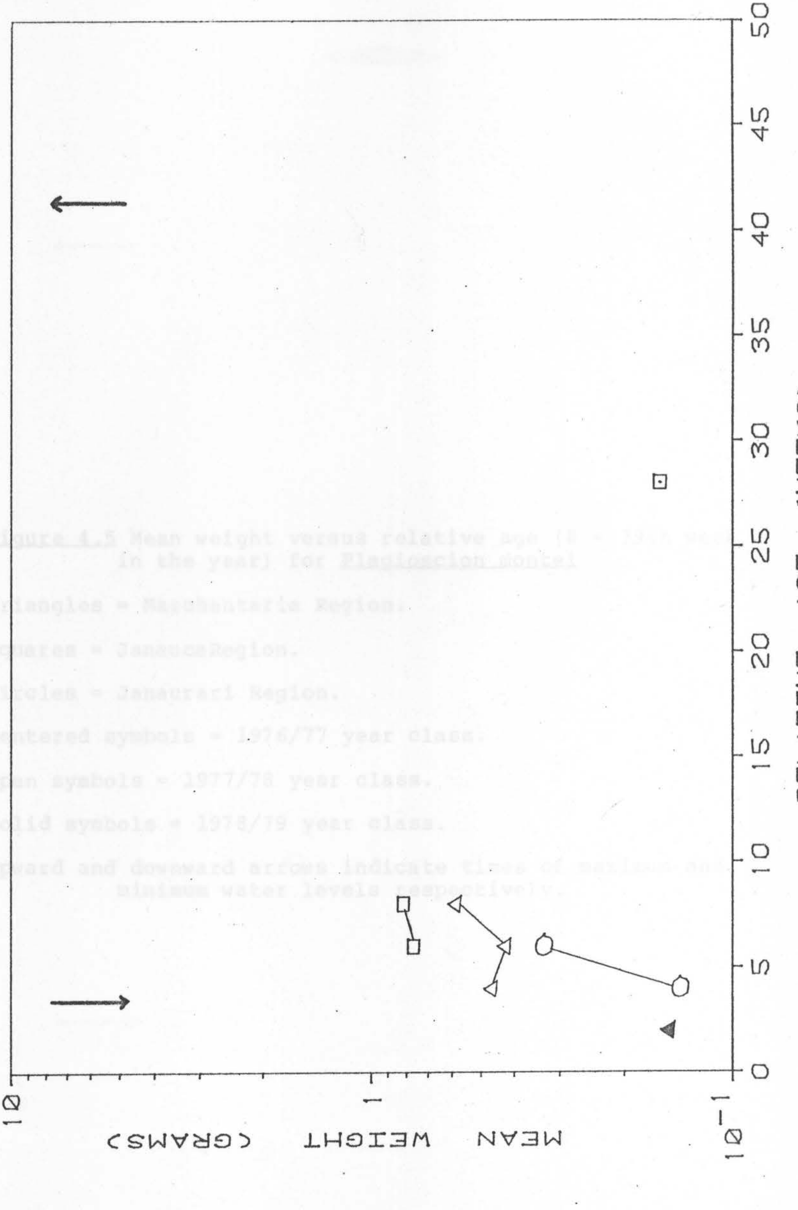


Figure 4.5 Mean weight versus relative age (0 = [illegible] week in the year) for *Plagioscion montei*

Triangles = Marchantaria Region.

Squares = JanaucaRegion.

Circles = Janauacá Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

Figure 4.5 Mean weight versus relative age (0 = 39th week in the year) for *Plagioscion montei*

Triangles = Marchantaria Region.

Squares = JanaucaRegion.

Circles = Janaurari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

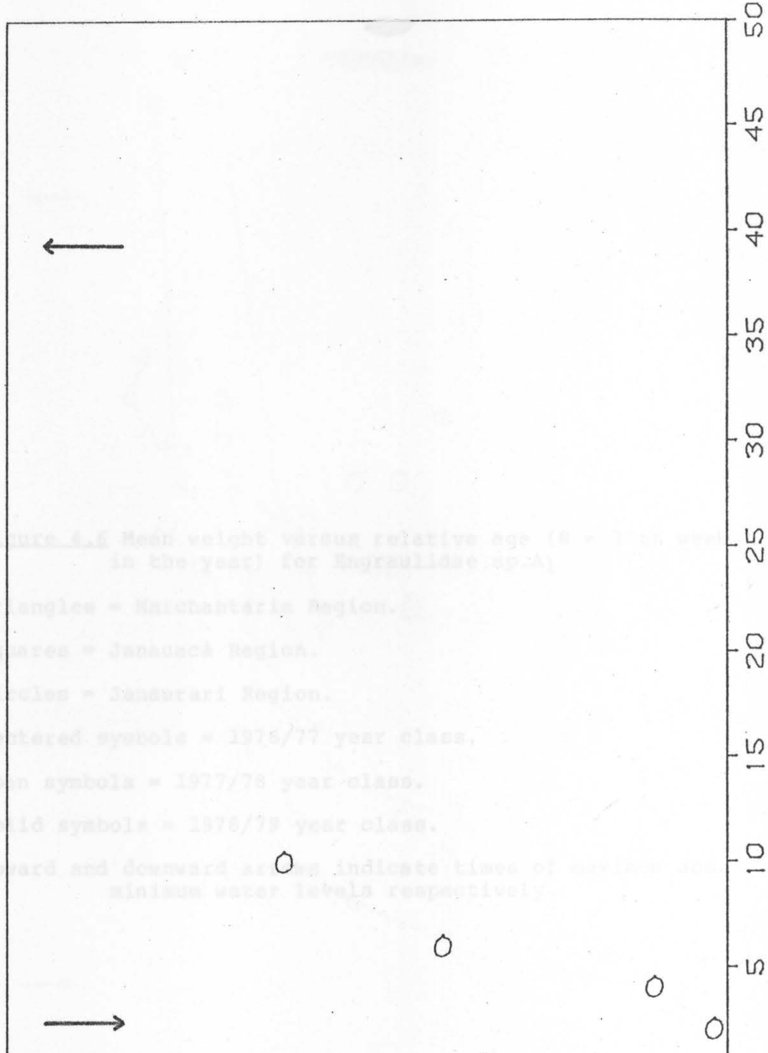

RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50
MEAN WEIGHT (GRAMS)
10^{-1}
1
10

Figure 4.6 Mean weight versus relative age (0 = 37th week in the year) for Engraulidae sp.A_1

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

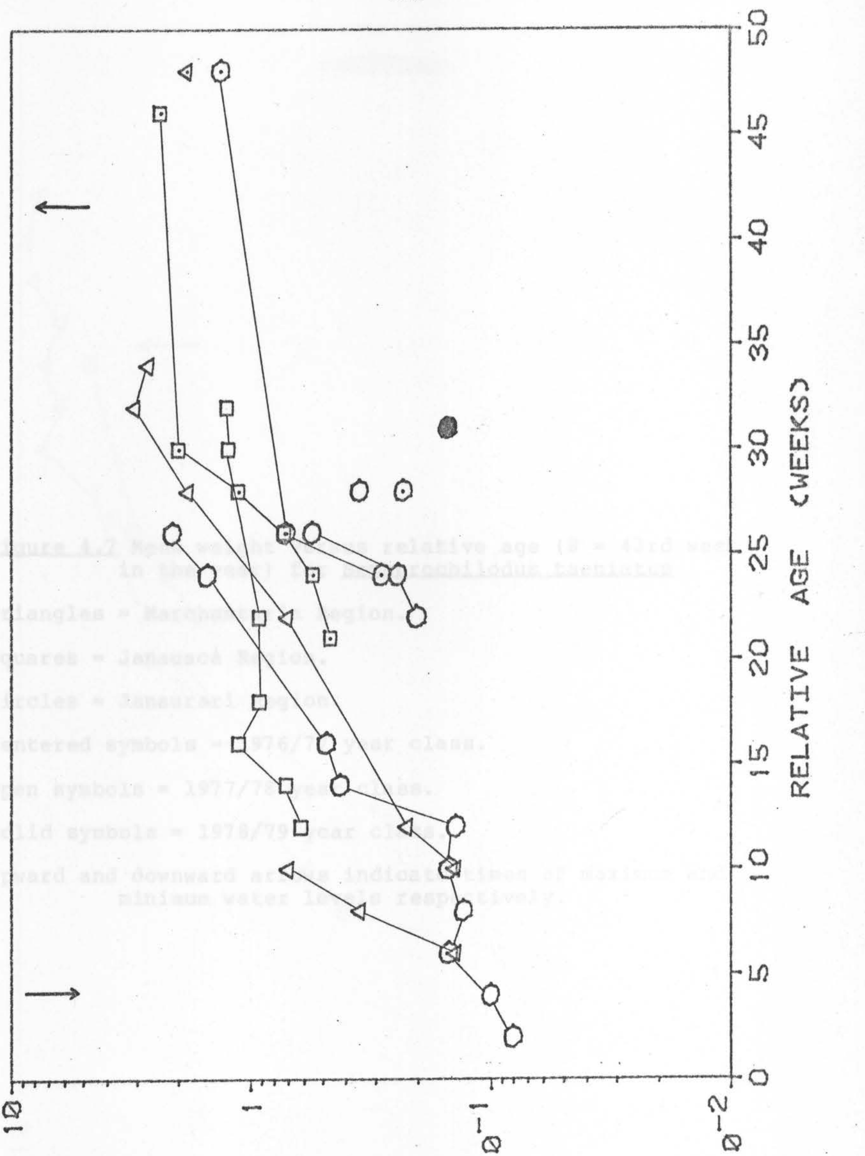


Figure 4.7 Mean weight versus relative age (0 = 43rd week in the year) for Semaprochilodus taeniatus

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janauari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

Figure 4.7 Mean weight versus relative age (0 = 43rd week in the year) for *Semaprochilodus taeniatus*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

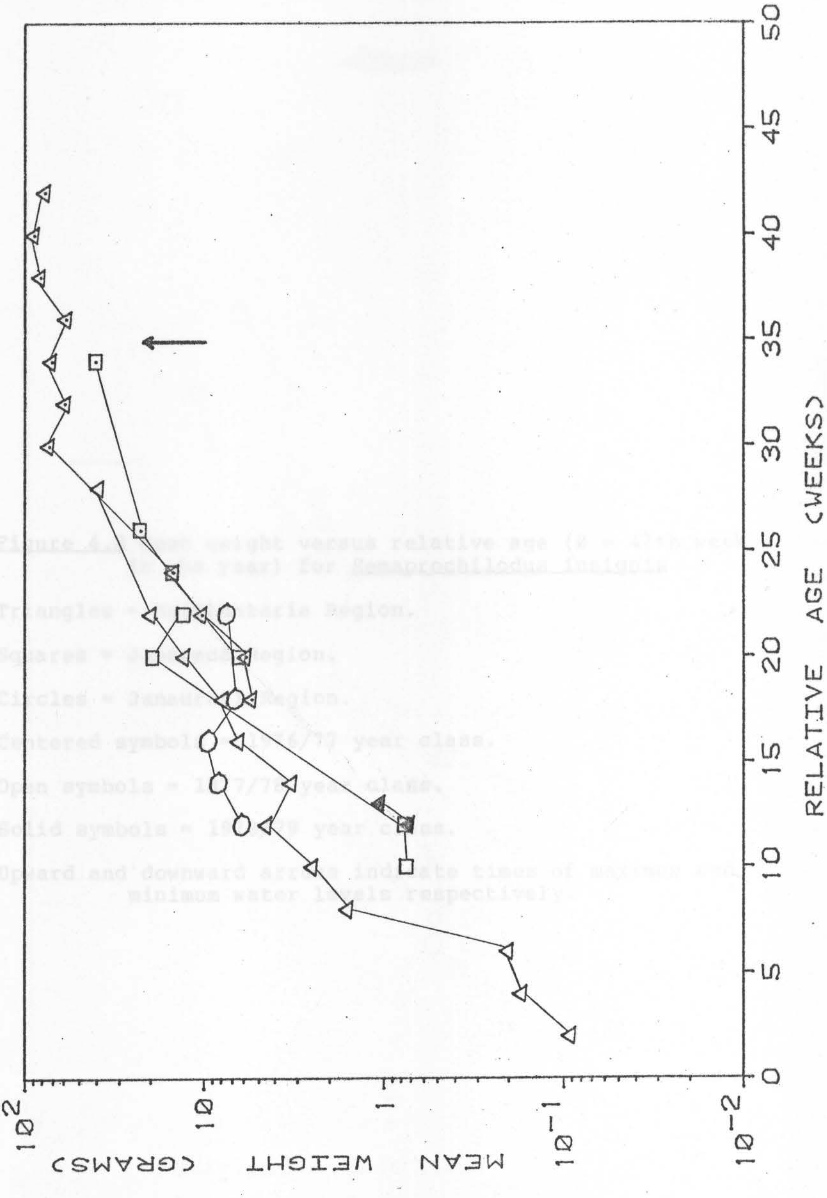

MEAN WEIGHT (GRAMS)
10^2
10
1
10^-1
10^-2
RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50

Figure 4.8 Mean weight versus relative age (0 = 47th week in the year) for *Semaprochilodus insignis*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

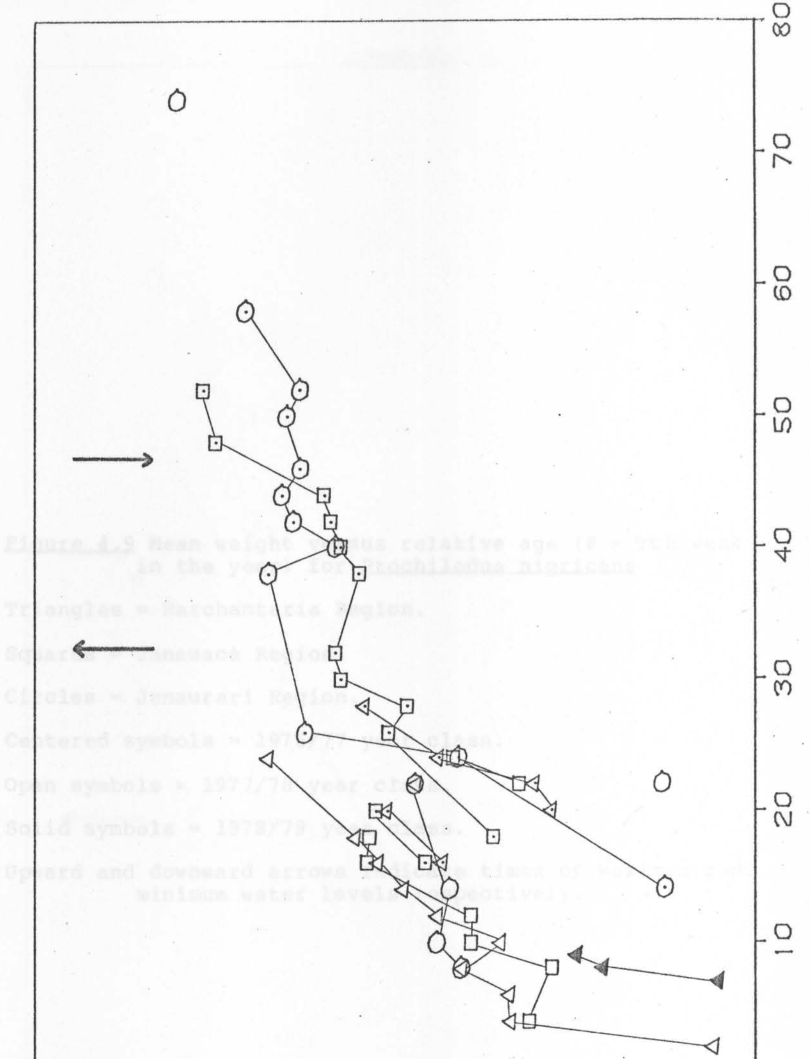


Figure 4.9 Mean weight versus relative age (0 = 9th week in the year) for Prochilodus nigricans

Triangles = Marchantaria Region.

Squares = Janauaca Region.

Circles = Janauari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

Figure 4.9 Mean weight versus relative age (0 = 9th week in the year) for *Prochilodus nigricans*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

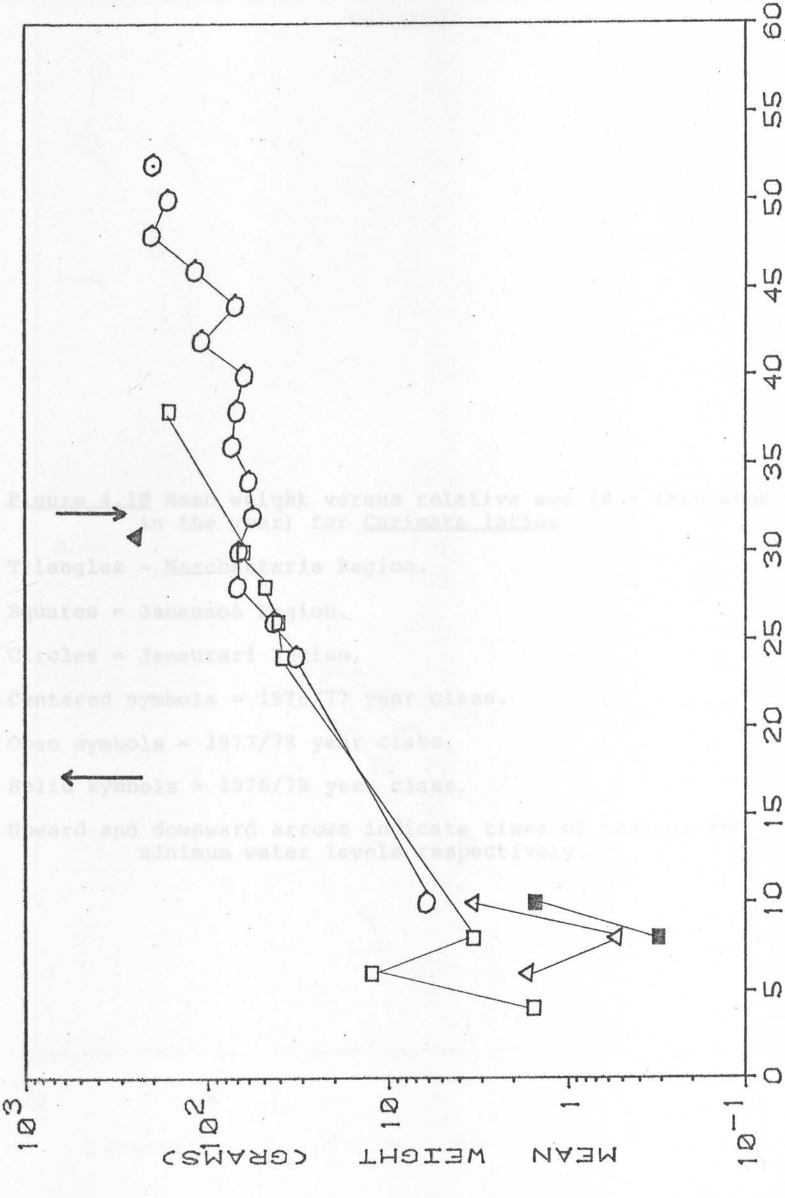
Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.


MEAN WEIGHT (GRAMS)
10^3
10^2
10
1
10^-1
RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50
55
60

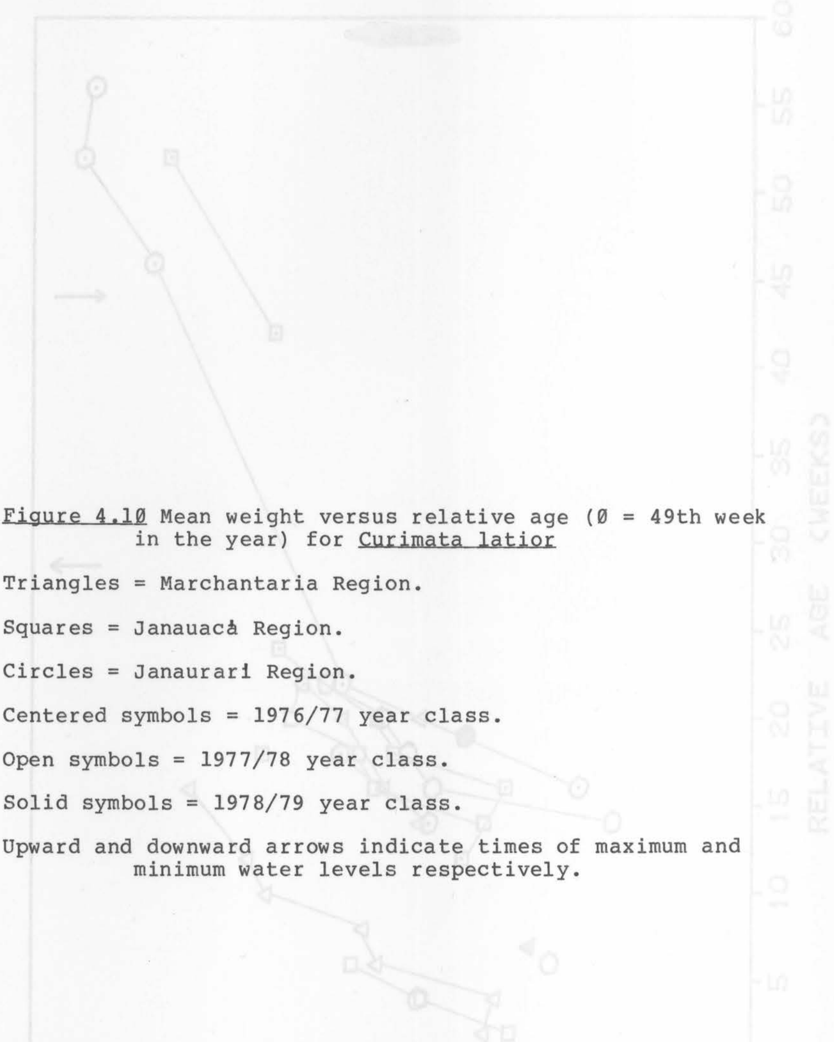


Figure 4.10 Mean weight versus relative age (0 = 49th week in the year) for *Curimata latior*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

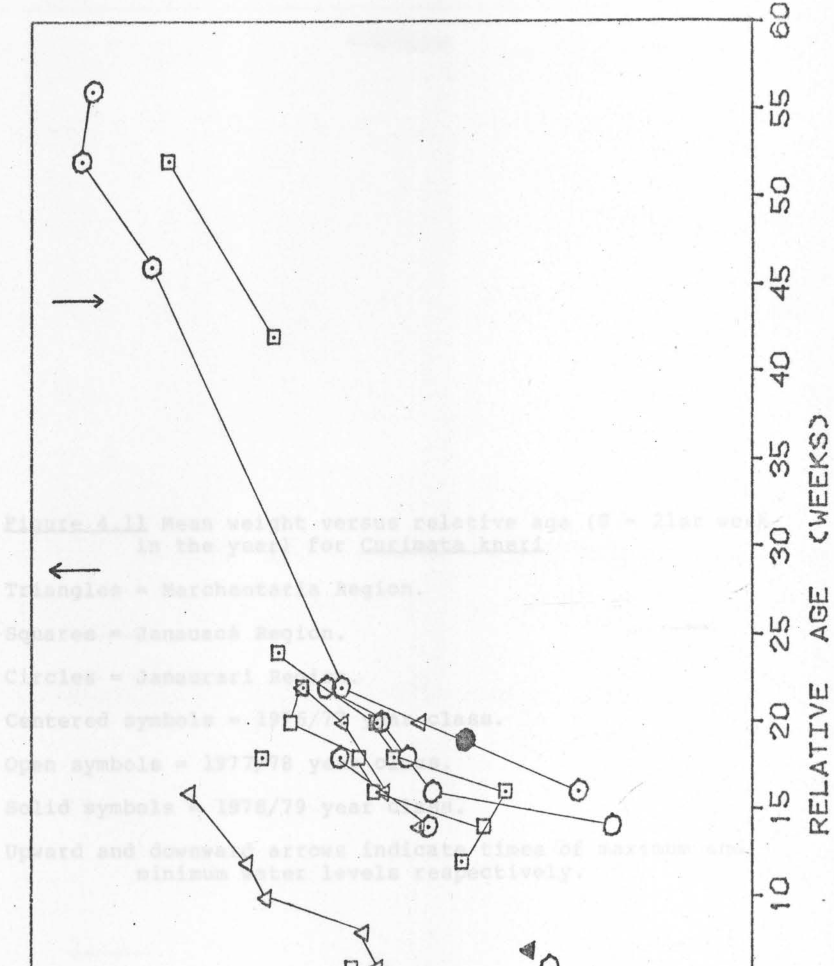
Circles = Janaurari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.


MEAN WEIGHT (GRAMS)
10²
10
1
10⁻¹
10⁻²
RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50
55
60

<u>Figure 4.11</u> Mean weight versus relative age (0 = 21st week in the year) for *Curimata kneri*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

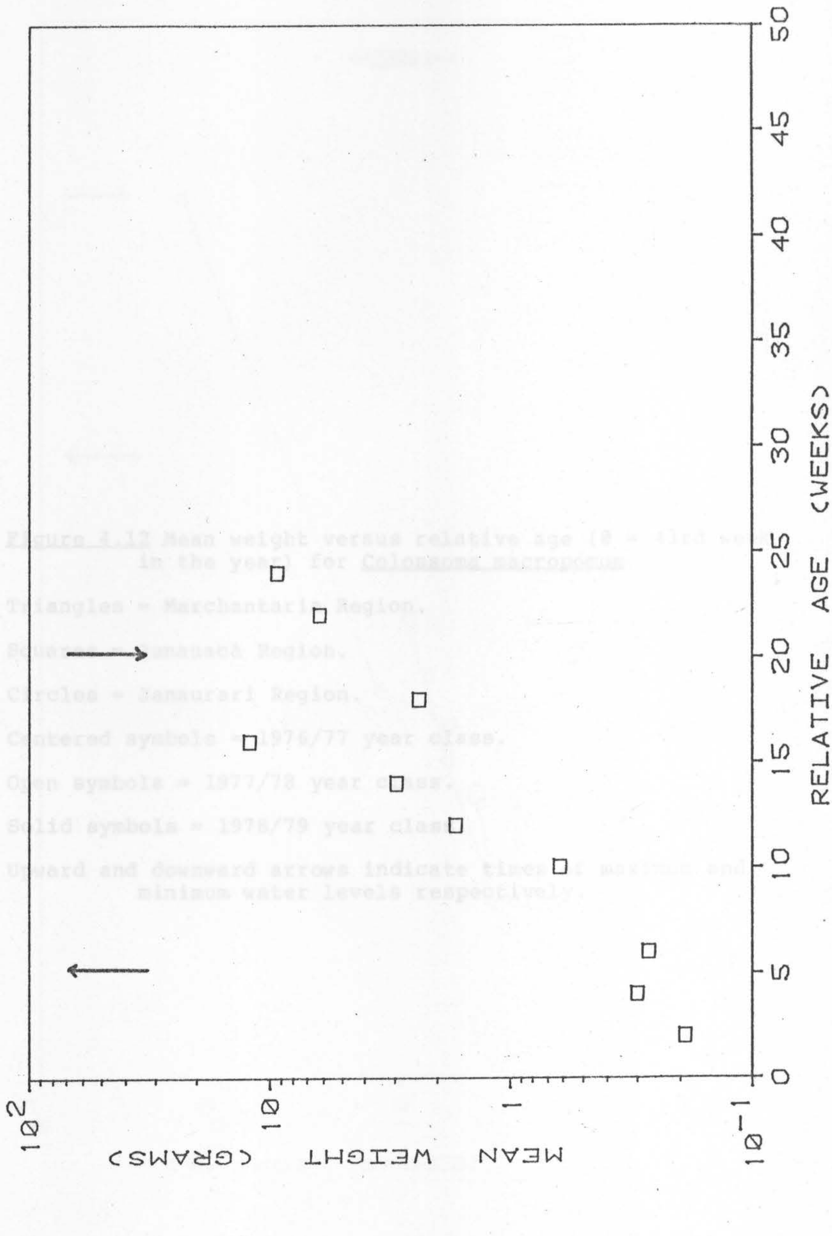

MEAN WEIGHT (GRAMS)
10²
10
1
10⁻¹
RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50

Figure 4.12 Mean weight versus relative age (0 = 43rd week in the year) for *Colossoma macropomum*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janauarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

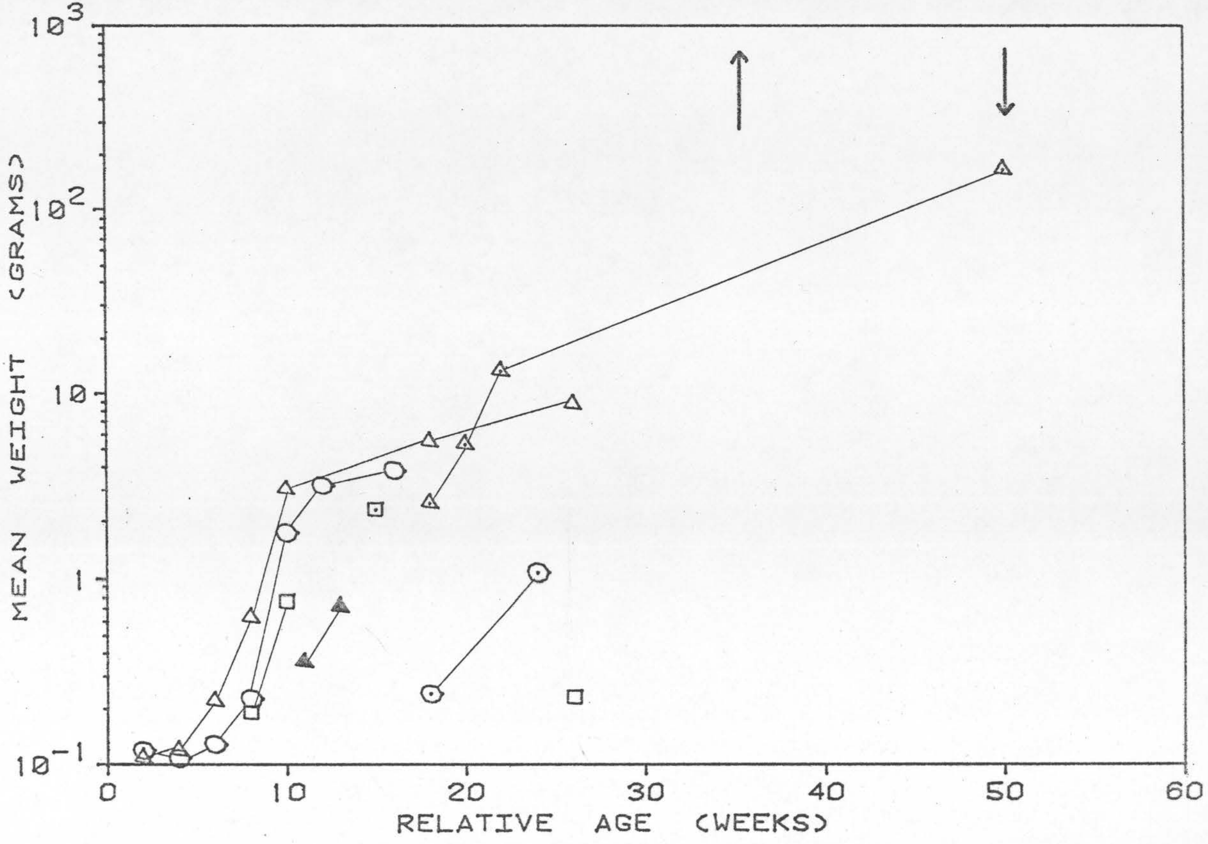

10^3
10^2
10
1
10^{-1}
MEAN WEIGHT (GRAMS)
0
10
20
30
40
50
60
RELATIVE AGE (WEEKS)

Figure 4.13 Mean weight versus relative age (0 = 37th week in the year) for *Triportheus albus*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

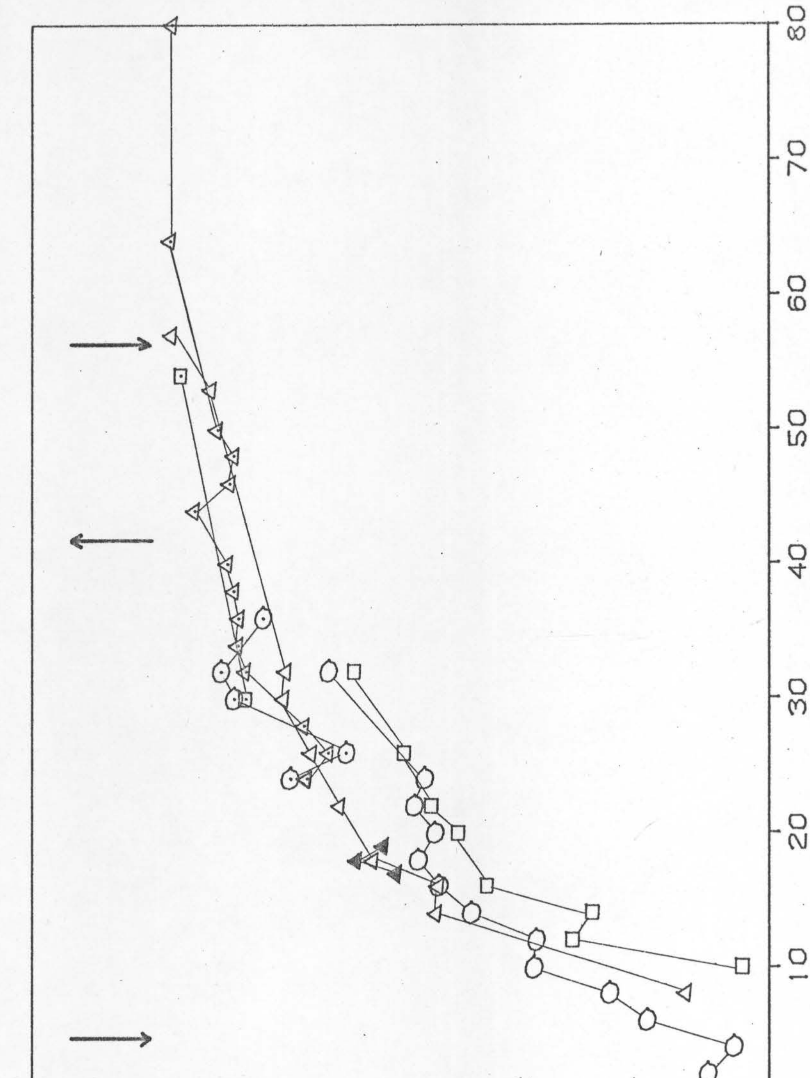

MEAN WEIGHT (GRAMS)
10^2
10
1
10^-1
RELATIVE AGE (WEEKS)
0
10
20
30
40
50
60
70
80

Figure 4.14 Mean weight versus relative age (0 = 47th week in the year) for *Triportheus angulatus*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

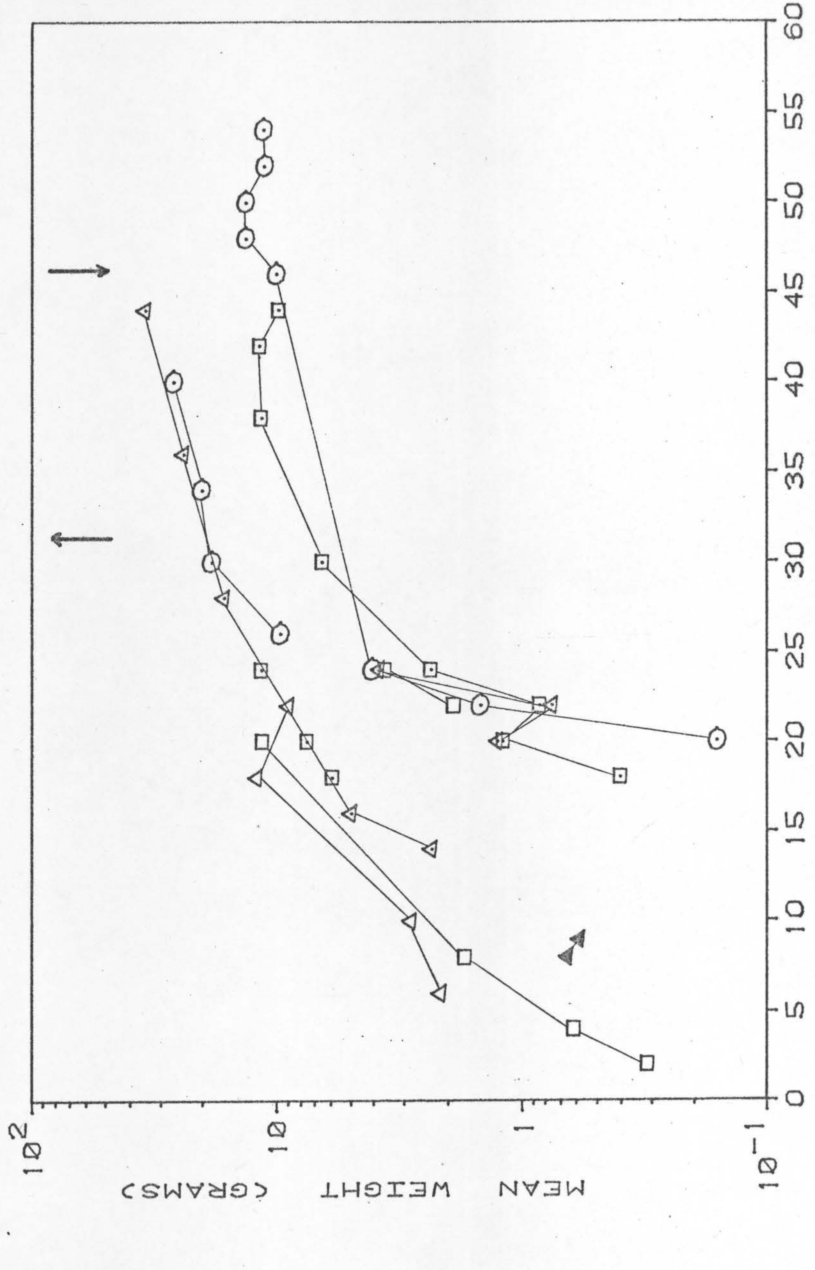

MEAN WEIGHT (GRAMS)
10^2
10
1
10^{-1}
RELATIVE AGE (WEEKS)
0
5
10
15
20
25
30
35
40
45
50
55
60

Figure 4.15 Mean weight versus relative age (0 = 43rd week in the year) for Triportheus elongatus

Triangles = Marchantaria Region.

Squares = Janauacá Region.

Circles = Janaurari Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.

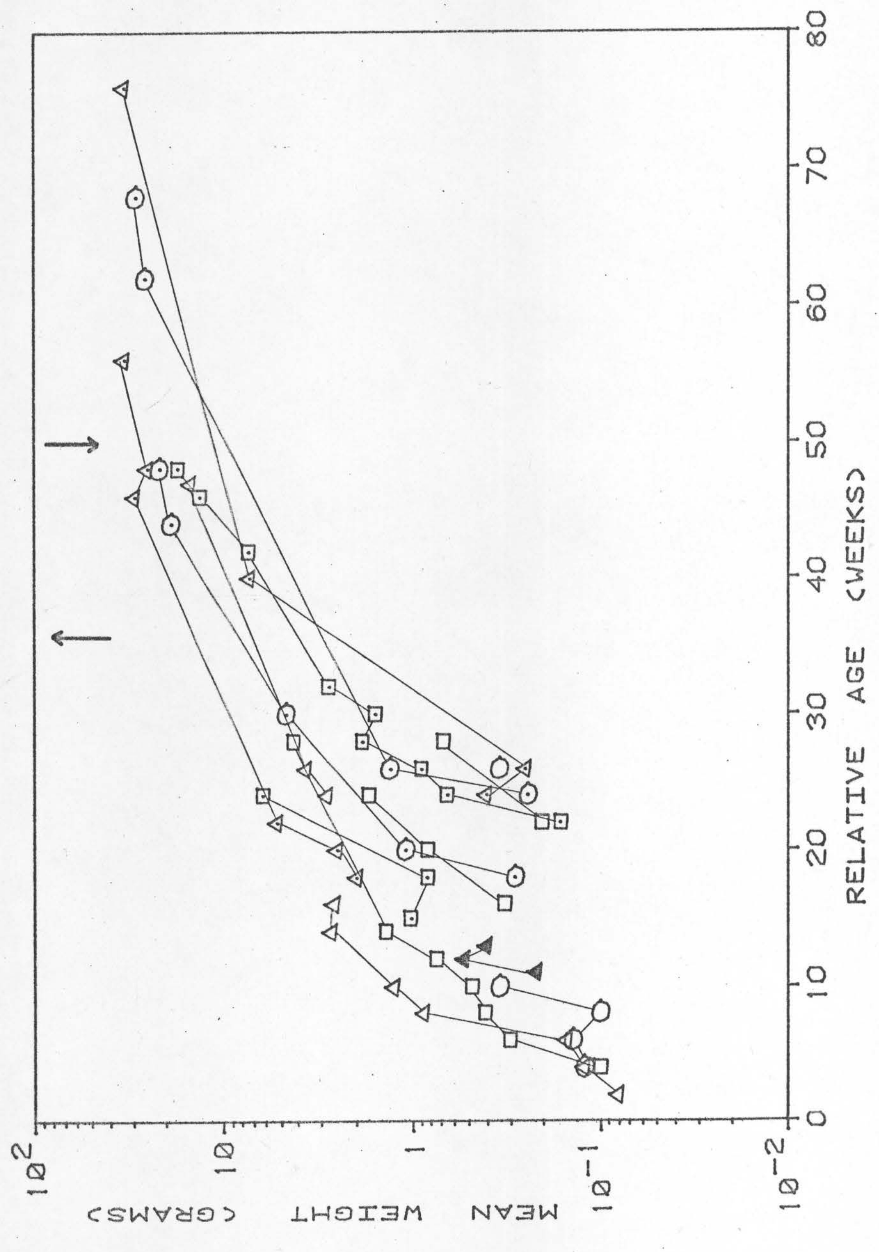

MEAN WEIGHT (GRAMS)
10^2
10
1
10^-1
10^-2
RELATIVE AGE (WEEKS)
0
10
20
30
40
50
60
70
80

Figure 4.16 Mean weight versus relative age (0 = 43rd week in the year) for *Brycon melanopterum*

Triangles = Marchantaria Region.

Squares = Janauacá Region.

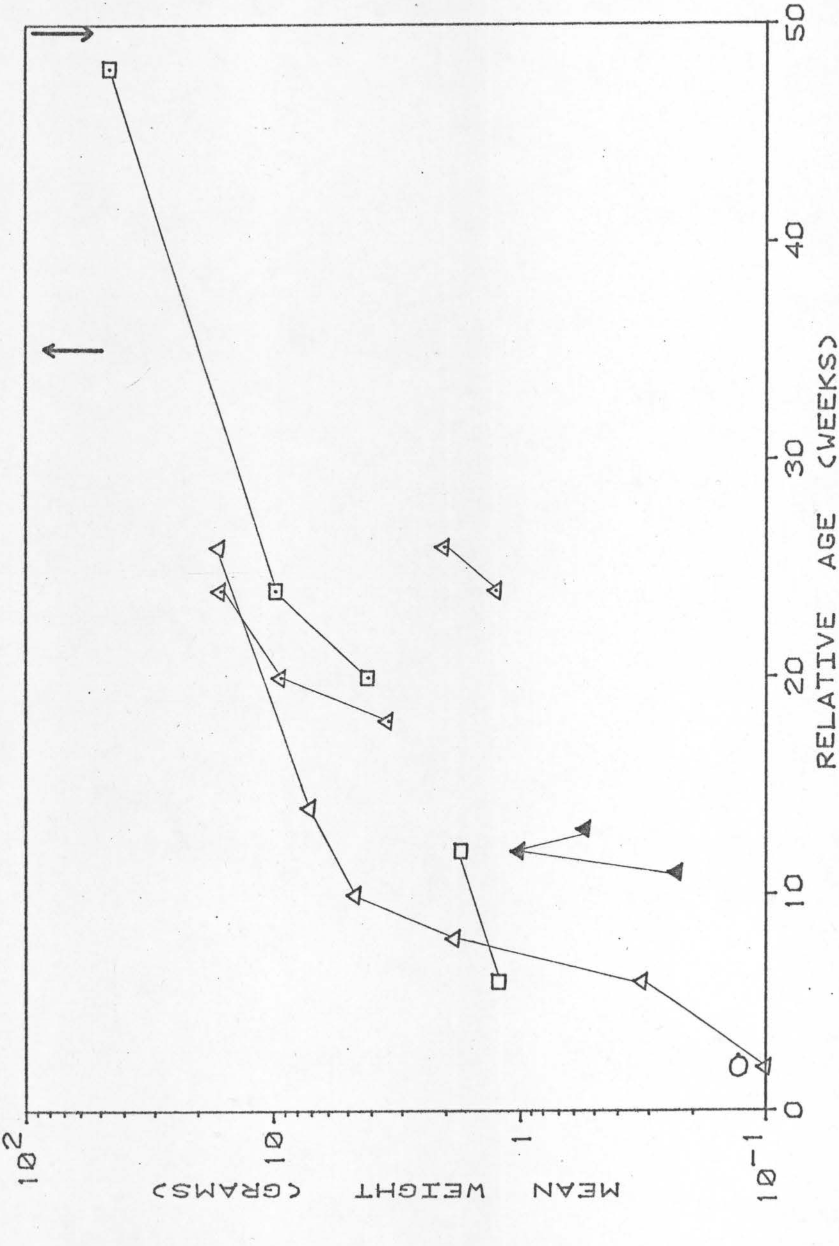
Circles = Janaurarí Region.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels respectively.


10^2
10
1
10^-1
MEAN WEIGHT (GRAMS)
0
10
20
30
40
50
RELATIVE AGE (WEEKS)

<u>Figure 4.17</u> Growth rate versus weight with regressions for separate species.

The regressions labelled as follows

Cross (x) = *Acarichthys heckeli*

Cross (+) = Engraulidae sp.A_1

Centered circle = *Semaprochilodus taeniatus*

Centered diamond = *Semaprochilodus insignis*

Centered square = *Prochilodus nigricans*

Centered triangle = *Curimata latior*

Centered star = *Curimata kneri*

Square = *Colossoma macropomum*

Diamond = *Triportheus albus*

Circle = *Triportheus angulatus*

Triangle = *Triportheus elongatus*

Star = *Brycon melanopterum*

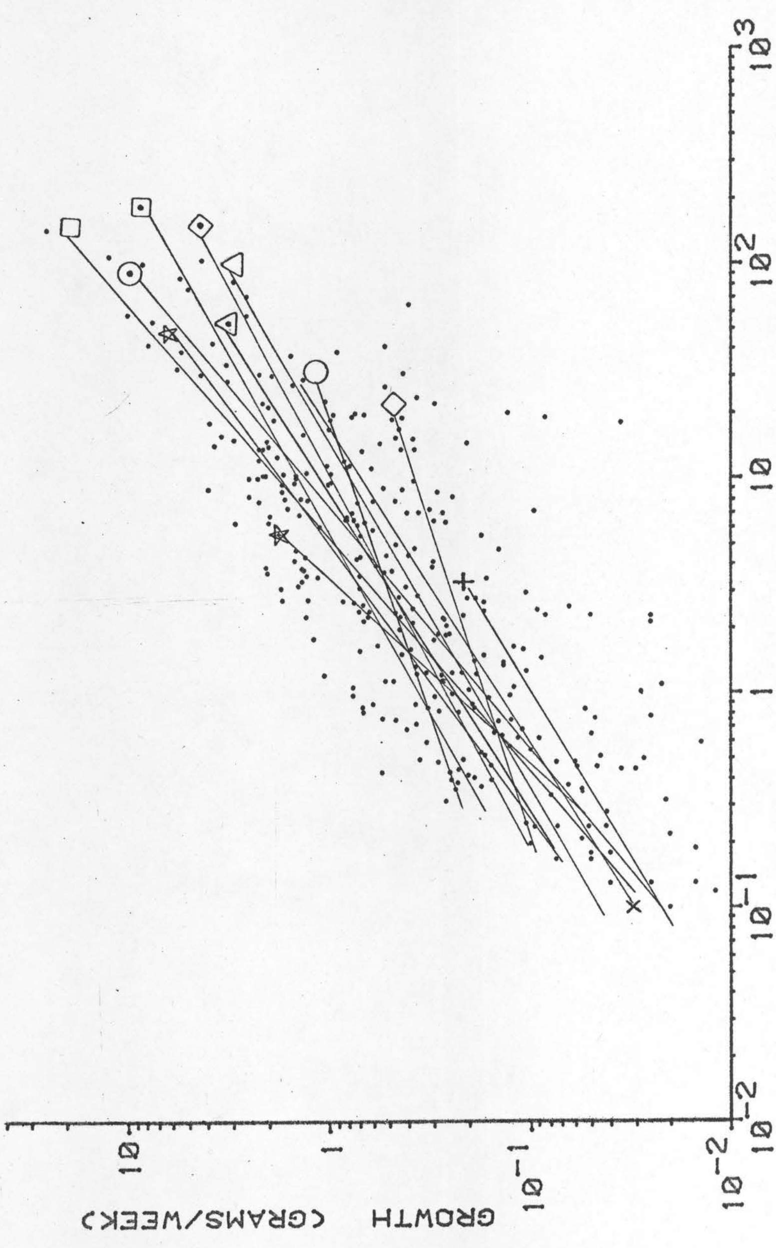

GROWTH (GRAMS/WEEK)
10
1
10^{-1}
10^{-2}
10^{-2}
10^{-1}
1
10
10^{2}
10^{3}
MEAN WEIGHT (GRAMS)

Figure 4.18 Growth rate versus weight with mean regression from separate species regressions.

Cross (x) = *Acarichthys heckeli*

Arrow up = *Plagioscion squamosissimus*

Arrow down = *Plagioscion montei*

Cross (+) = Engraulidae sp.A_1

Centered circle = *Semaprochilodus taeniatus*

Centered diamond = *Semaprochilodus insignis*

Centered square = *Prochilodus nigricans*

Centered triangle = *Curimata latior*

Centered star = *Curimata kneri*

Square = *Colossoma macropomum*

Diamond = *Triportheus albus*

Circle = *Triportheus angulatus*

Triangle = *Triportheus elongatus*

Star = *Brycon melanopterum*

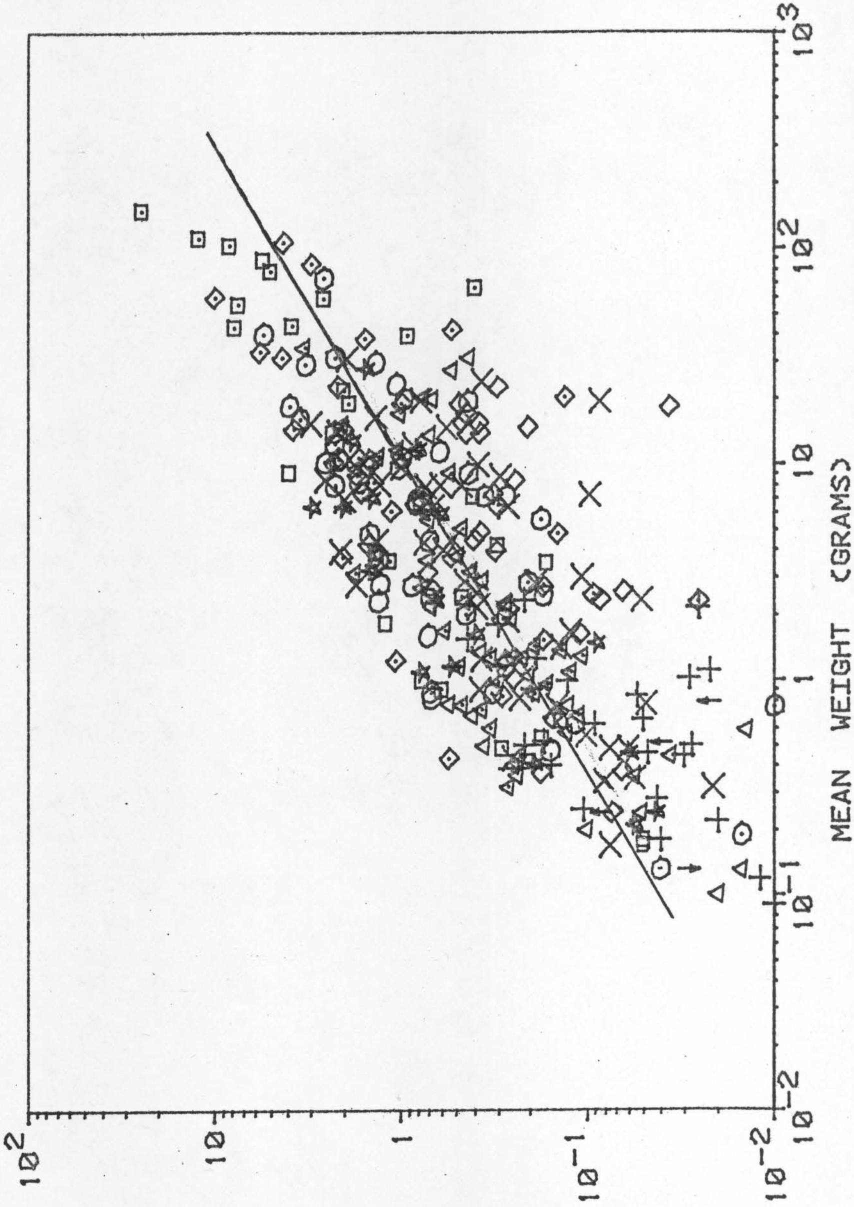

GROWTH (GRAMS/WEEK)
10^2
10
1
10^-1
10^-2
MEAN WEIGHT (GRAMS)
10^-2
10^-1
1
10
10^2
10^3

Table 4.1 Biometric and relative abundance data for 14 species used in growth analysis (including parameter in weight-length relation $w = aL^b$, w in (g), L in mm, using GM regression of Ricker (1973) of the log transformed variables).

Max. Wt.^{a} (g)	a	b ±std. error	r^2	S.error of log regression	% of Family biomass	% of total biomass	% of species yield in fishery^b
Acarichthys heckeli							
145	1.466E-5	3.055±.006	.996	.059	17	2.1	-
Plagioscion squamosissimus							
1300	2.177E-5	2.986±.026	.996	.062	53	.3	.6
Plagioscion montei							
500	2.177E-5	2.986±.026	.996	.062	47	.2	
Engraulidae sp.A_1							
9.7	1.711E-6	3.439±.031	.978	.063	60	.1	-
Semaprochilodus taeniatus							
540	2.296E-5	2.976±.018	.990	.084	19	1.6	5.1
Semaprochilodus insignis							
810	2.596E-5	2.976±.015	.989	.073	20	1.6	
Prochilodus nigricans							
2300	1.768E-5	3.028±.014	.994	.046	61	5.0	25.4
Curimata latior							
385	7.146E-6	3.160±.018	.992	.070	21	.7	.5
Curimata kneri							
325	1.001E-5	3.169±.015	.998	.048	6	.2	

continued...

Colossoma macropomum							
27000	2.064E-5	3.053±.016	.995	.068	9	.9	2.3
Triportheus albus							
430	1.808E-5	2.900±.013	.992	.062	8	.8	
Triportheus angulatus							
460	1.162E-5	3.026±.009	.995	.049	14	1.4	1.3
Triportheus elongatus							
165	1.319E-5	2.927±.016	.992	.066	24	2.4	
Brycon melanopterum							
5200	1.134E-5	3.117±.029	.990	.073	6	.6	.1
						---	----
Totals:						18	35

a. Maximum weights were taken from gillnet or market data (unpublished) when they exceeded the maxima from the seine samples.

b. These percentages assume none of the species occur in the non-commercial part of the yield. *Curimata latior*, *Curimata kneri* and the *Triportheus* species may be underestimated.

Table 4.2 Regression statistics of allometric growth equation (log(growth) versus log(weight)) shown in Figure 4.17.

Slope±s.e.	Weight range (g)	Log$_e$(intercept)	No.points
Acarichthys heckeli			
.702±.101	.10 - 36.2	-1.95	50
Engraulidae sp.A_1			
.671±.215	.08 - 3.03	-2.35	24
Semaprochilodus taeniatus			
.914±.125	.09 - 77.0	-1.87	22
Semaprochilodus insignis			
.559±.152	.16 - 98.6	-1.22	31
Prochilodus nigricans			
.582±.166	.31 - 243.6	-0.96	15
Curimata latior			
.635±.105	.06 - 52.6	-1.28	25
Curimata kneri			
1.244±.172	.19 - 12.1	-1.43	5
Colossoma macropomum			
.947±.159	.11 - 165.4	-1.66	17
Triportheus albus			
.362±.112	.13 - 27.4	-1.77	33
Triportheus angulatus			
.354±.115	.16 - 34.6	-1.01	24
Triportheus elongatus			
.605±.081	.08 - 103.8	-1.71	37
Brycon melanopterum			
.677±.162	.10 - 45.5	-1.29	12

Table 4.3 Density-dependent growth tests by species (Residuals of log-transformed allometric growth function for each species correlated with log(biomass of competitors during appropriate time period)). Sign of correlation shown with significance in parentheses.

	All data	Rising water period	Falling water period
Acarichthys heckeli	- (.22)	- (.20)	+ (.36)
Engraulidae sp.A_1	+ (.30)	+ (.41)	- (2 pts. only)
Semaprochilodus taeniatus	- (.25)	- (.35)	- (2 pts. only)
Semaprochilodus insignis	+ (.37)	+ (.28)	- (.34)
Prochilodus nigricans	+ (.38)	- (.31)	+ (.14)
Curimata latior	+ (.26)	+ (.26)	+ (.43)
Curimata kneri	+ (.07)	no data	+ (.12)
Colossoma macropomum	+ (.23)	+ (.11)	+ (2 pts. only)
Triportheus albus	- (.50)	+ (.02)*	- (.03)*
Triportheus angulatus	- (.27)	+ (.48)	+ (.20)
Triportheus elongatus	- (.18)	+ (.42)	- (.02)*
Brycon melanopterum	+ (.15)	+ (.13)	no data

Chapter 5: Biomass, Production and the Fishery

5.1 Introduction

A general review of the central and upper Amazon fishery has been attempted based on comparative yield data (Bayley 1981). The major points resulting from that analysis were as follows:

(1) The limitations of a management strategy for optimizing total yield are economic, cultural and technological more than biological.

(2) The main biological consequence of increasing the total yield, say to the levels typical of Africa, would diversify the yield but depress the larger, more valuable species.

(3) The limitations of a strategy of optimizing the yield of a few large species are biological and economic. Large species apparently have a high vulnerability to

capture, in particular with respect to gillnets. This coupled with the enormous cost of effective management may offset the benefits of (3). At best, a few expensive fish would supply an exclusive market, while other people will be deprived in an region where 74% of animal protein consumption is from fish.

This chapter attempts to explore some biological ramifications of the preceding analysis in a more quantified ecological framework so that the fishery potential and response to perturbations might be better understood. It draws on results from the previous three chapters to provide estimates of biomass and production and explore some of the concepts discussed in Chapter 1. Biomass and productivity are compared with with primary productivity in 5.3, with biomass spectra in 5.4, and with the fishery in 5.6. An analysis of the piscivore-prey relationship is presented in 5.5.

5.2 Methods

5.2.1 Biomass and production computation.

Biomass and production estimates from the sample catches corrected for net efficiency were made for the period March 1, 1977 to May 12, 1978 when regular sampling at two week intervals was maintained in all three regions. Samples replicated between years were averaged for the annual estimates. Nineteen samples were not included in these estimates for one of the following reasons:

1. If fish were concentrated at the surface exhibiting respiratory stress, resulting in an obvious overestimate of typical biomass density.

2. If a snag was encountered by the net, which may have affected fishing efficiency.

3. If warmer water was encountered inshore which induces most fish to move to cooler areas of less than about 33°C.

4. On one occasion an extraordinary quantity of fish were observed migrating down the Paraná de Janauacá (Figure 2.6) during falling water, an event which was not ignored by a large concentration of piscivorous birds.

The decision not to include these samples in this analysis was made at the time of sampling, the samples being retained for other purposes.

Production was estimated for each species and length range as follows:

$$\text{Production} = \sum_{i=1}^{26} \sum_{j=1}^{j=j_{max}} \frac{2}{W_{i,j}} \left(\frac{\Delta W}{\Delta t}\right)_{i,j} B_{i,j}$$

where i = fortnight number during year

j = length group counter (by 1mm interval for fish less than 100mm long, otherwise by 5mm)

$W_{i,j}$ = predicted individual weight based on mean length for ith fortnight and jth length group.

$(\Delta W/\Delta t)_{i,j}$ = growth rate predicted by equation (2), p.183 based on $W_{i,j}$, season and species.

$B_{i,j}$ = mean biomass density estimated for ith fortnight and jth length group after correcting each sample for catchability.

The energy equivalent of biomass and production was expressed in grams wet weight because of its approximate equivalence to Kcalories (Winberg 1956) and the equivalence of grams per square meter (gm^{-2}) and tons per square kilometer ($t(km)^{-2}$). Those who prefer Joules are welcome to multiply the results by 4.19.

5.2.2 The area of study and the 'productive area'.

The area chosen is that enclosed by the R. Solimões and its floodplain between the confluence of the R. Negro near Manaus upriver to a point just below the mouth of the R. Purus, (quadrats 2 through 10 in Plate 2.3), which comprises a 190km stretch of the R. Solimões. Evidence has been presented (Chapter 2) that the areas covered by these samples are among the most productive in the system, so that extrapolation to the whole inundated area would overestimate productivity. Sizes of aquatic biotopes for high and low water were presented in Table 2.1 (p 33). The maximum and minimum areas covered by water are 5330 and 1200 km^2 respectively, of which the main river channel area is 680 km^2.

The samples in this study did not include all the productive habitats. There is indirect evidence from these samples and from Goulding (1980 and pers. comm.) that many if not all of the species common in this collection are found in the flooded forest, feed there, and contribute to the diets of numerous piscivores. The hiatus of samples during the high water months of April to September shown in Figures 4.1 and 4.2 are typical of many species. Conversely, the main channel is not very productive, except for dolphins and piscivorous catfish which consume large commercial species (Goulding 1981, and pers. comm.). Although many commercial fish spawn in or near the main river, their progeny quickly reach the postlarval stage when they are abundant in inshore areas. Many species use the main river as a 'freeway' for longitudinal migrations, without feeding in the channel itself. The evidence for low productivity in 'black' waters is also strong.

The 'productive area' is smaller than the 'active floodplain' because black and very turbid waters must be excluded because of their much lower productivity (Chapter

2). Much of the area occupied by aquatic macrophytes in well drained areas is very productive.

Consequently, the 'productive area' used for extrapolating the biomass and productivity estimates includes areas of mixed or decanted water, aquatic macrophytes and flooded forest. This is notwithstanding the fact that a proportion of macrophytes occurs in poorly drained areas, which are not extensive in the study area (Table 2.1). Most of the flooded forest there is influenced to some extent by the richer R. Solimões water. Ground truth measurements indicated that the LANDSAT classification of turbid and mixed/decanted waters was defined at a Sechhi disk value of about 30cm, so the slow flowing parts of the R. Solimões itself are also included.

My definition of 'productive area' does include biases which cannot be estimated. Some of the primary production outside the area benefits fish to some extent. Conversely, seasonal and local effects which deoxygenate zones within the area affect the distribution and productivity of fish negatively.

I have estimated areas at high and fairly low water, but the form of the relationship between flooded area and level is not known. For the purposes of the ensuing estimates I have assumed a linear relationship. This would not be realistic for levels of below 19m because much of the water is confined to channels. During this study, the level did not fall below 20.5m.

The 'productive area' was estimated to vary between 700 km^2 at low water and and 2100 km^2 at high water for the period March 1,1977 to May 12, 1978. Measurement errors are unlikely to be more than ±10%, and their influence on results is discussed below.

5.2.3 Fishery yield.

Estimates of the fishery yield of this area during 1977, including the subsistence fishery are available (Bayley 1981), as is the breakdown of major species in the commercial yield (Petrere Jr., unpublished data). A breakdown of the subsistence yield, which is 35% of the total for this area (Bayley 1981), is not possible, but the subsistence fishery does not contain significant quantities of the species of commercial value.

5.3 Primary productivity and fish production

In Chapter 1 I speculated about the relative roles of phytoplankton and higher plants in river-floodplain systems. The limnological information in the Amazon reviewed in Chapter 2 failed to clarify the situation because of the lack of reliable estimates of macrophyte production and the relative efficiencies of the processes leading to fish production.

It is well known that the nutritive value of most phytoplankton species is higher than vascular plants per unit carbon or energy content. Also the careful C14 measurements of Schmidt (1973) producing a seasonally weighted mean of 290 $gCm^{-2}yr^{-1}$ for L. do Castanho in Janauacá suggests a dominant role for the phytoplankton. Fisher (1979) obtained similar results for the rising water period in the same water body and also reported high zooplankton densities of 13 - 15 gm^{-3}. He suggested that phytoplankton is a major source of organic material in areas influenced by white water, and is sufficient to provide a trophic base for the fishery. He also acknowledged that vascular plants do contribute via a detrital-heterotrophic pathway.

The productivity of aquatic macrophytes from Marlier's (1967) work (Chapter 2) is approximately 1050 $gCm^{-2}yr^{-1}$. There are also unknown quantities of synthesized carbon from the flooded forest and true terrestrial vegetation.

The hypothesis that the estimated phytoplankton production can support the fish productivity can be tested. The most efficient route for most of the phytoplankton is via one intermediate zooplankton step. Direct grazing of phytoplankton (e.g. by some Engraulids) is minimal. For a very conservative estimate I confine the comparison to fish between 15 and 60 mm long. The annual mean productivity of this group is estimated at 45 $gm^{-2}yr^{-1}$ which is approximately equivalent to 4.5 $gCm^{-2}yr^{-1}$ or 1.6% of the phytoplankton primary production. The latter could support this group if two links with 13% transfer efficiencies were assumed.

However, larger Engraulidae, Hypophthalmidae, Anodus spp. and Colossoma macropomum and many other species which feed to some extent on zooplankton have not been included. Also the detritivores undoubtedly consume phytoplankton and their detrital products which settle out of the water column. Carvalho (1979) reports many phytoplankton species in the guts of Potamorrhina pristigaster. Fish less than 15mm long are not included, yet the high quality nutrition of plankton is probably vital during early life history.

The total fish production of 280 $gm^{-2}yr^{-1}$, of which a high proportion is from piscivores (5.5), is 10% of phytoplankton primary production.

Evidence is now accumulating in support of a high dependency of fish diets on macrophytes or large detrital matter derived therefrom (Santos 1979; Almeida 1980; Paixão 1980; Goulding 1980). In addition these authors also document fruits from trees, grass seeds, filamentous algae and a variety of terrestrial insects in guts of abundant genera. The detritivores undoubtedly obtain a large amount of energy from the macrophyte detritus and associated heterotrophic microorganisms. The relative importance of aquatic macrophytes and so-called allochthonous material in fish production is unknown.

In conclusion I suggest the following as hypotheses. (1) Phytoplankton plays a minor role in the trophic base for fish production, but may be important for larval and post-larval stages. (2) In terms of energy and carbon, zooplankton production is not entirely dependent on phytoplankton and assimilates significant quantities of detritus and/or associated microflora.

5.4 The biomass distribution

The overall mean annual biomass is 160 gm^{-2} ±24 (95% confidence intervals from estimates of accuracy in Chapter 3) based on all fish and prawns between 15 and 960mm. This compares with the 125 gm^{-2} calculated from the data of Mathews(1971) from the eutrophicated R. Thames, which is high by temperate standards. Balon (1974) estimated 386 gm^{-2} for the fish inhabited area of L. Kariba and Lagler _et al_ (1971) estimated 34 gm^{-2} at high water and 43 gm^{-2} at low water based on a limited number of chemofishing samples in the Kafue floodplain. High water (>25m) and low water (<22m) means from this study were 220 gm^{-2} and 110 gm^{-2} respectively.

The biomass size distribution shown in Figure 5.1 (see pp.243-246 for Figures) is on a body-length octave scale, the four divisions being equivalent to eighteen of Sheldon _et al_'s (1972) size classes based on equivalent spherical diameter. It is not as flat as particle size theory for the oceanic pelagic zone (Sheldon et al 1972; 1977) would suggest. This is hardly surprising for two reasons.

Firstly Schwinghamer et al (1983) produce strong evidence that the relatively flat offshore pelagic spectrum becomes peaked at predictable sizes inshore in both marine and freshwater systems. These peaks are complemented by others from the benthic system which are related to effects of physical substrate. They hypothesized that this reflected strong pelagic-benthic coupling inshore. Although true benthic communities are limited in the Amazon due to low dissolved O_2 (Chapter 2), the rich communities associated with macrophytes may well show a distribution which reflects the physical structure of the habitat in a parallel manner. This may in turn affect the biomass distribution of fish and decapods, whose peak happens to be at a size only slightly larger than third peak in the distribution of benthic animals discussed by Schwinghammer et al (1982).

Secondly, the biomass distribution was not expected to conform to the deep-sea pelagic model because of the significant proportion of detritivores (Figure 5.1) whose food particle size remains very small as the fish grows. There is also the complication of the significant amount of macrophyte herbivory among the fish (Goulding 1980; Santos

1979; Paixão 1980; Almeida 1980).

In conclusion, these complications are sufficient to prevent a simple interpretation of the biomass distribution for all the species combined. But when the 'terrestrial' type components are allowed for, predator/prey biomass ratios do have relevence to the trophic model outlined in Kerr (1974) and Sheldon et al (1977). This view is developed in the following section.

5.5 Piscivore-prey relations

One of the most striking features of these results is the large quantity of piscivores (Figures 5.3 and 5.5). They contribute 35% of the total biomass and 25% of the production in the study area. Goulding (1980, 1981) reported similarly large quantities from other habitats, and the gillnet results of Barthem (1981) from five regions during all hydrological seasons averaged 35% by weight of piscivores. Two of his five regions are within the study area (Janauacá and Manaquiri, in quadrats 4 and 5 respectively in Plate 2.3), and piscivores from these averaged 43% from a total of 193 kg of fish caught from September 1978 to April 1979. The results from my study appear to be typical of a wider range of habitats sampled with different gear.

The estimates provide an opportunity to explore the energetics of the piscivore-prey interaction in the light of recent models. Amazonian piscivores take relatively large individual prey compared with predators in offshore pelagic systems (e.g.Sheldon *et al* 1977). Goulding (1980:182) examined 470 stomachs from five common species of piscivores from the forest and open water areas in the Rio Machado in the upper R. Madeira, of which 176 contained prey. He could not detect any seasonal variation in stomach fullness. Prey lengths were variable, and ranged from 5 to 61% of piscivore length. The common *Raphiodon vulpinis* had prey ranging in length from 30 to 50% of the predator. Barthem (1981) found similar results from his regions of study.

Goulding (1980) did not find significant correlations of predator and prey length within species, but the length ranges of piscivores were limited. Personal observations of stomachs from *Cichla ocellaris*, *Hoplias malabaricus* and *Raphiodon vulpinis* of only 42 - 65mm revealed prey 23 - 43% of their length. As a first approximation, I assume a mean relative prey length of 25% for the piscivores in this study area. The consequences of errors in this estimate are discussed below.

Personal observations from this collection indicate that a wide range of species, including the spiny fin-rayed Cichlidae, are taken as prey. Goulding (1980) noted that the catfish families Pimelodidae and Loricariidae were found in guts of Plagioscion squamosissimus and Raphiodon vulpinis. While it is conceivable that catfish have a low electivity, they form a negligible part of the biomass in the first four length groups. Cannibalism has been observed in Hoplias malabaricus (personal observation) but not so far in the other major predator, Cichla ocellaris. The proportion of the young of the latter in the total biomass is negligible,and its inclusion or exclusion does not affect the results.

Therefore, I have included all species of appropriate length as prey. Table 5.2 shows the breakdown by length group of biomass and productivity of piscivores and prey. The prey-predator length ratio of .25 means that on average group n feeds on group n-2. In view of the range of sizes consumed, I have combined pairs of groups, so that groups 3 and 4 feed on 1 and 2 for example.

Two estimates of predator/prey production ratios (transfer efficiencies) were obtained for different size ranges:

predator sizes	prey sizes	production ratio
60 - 240	15 - 60	37%
240 - 960	60 - 240	39%

The ratio is the product of gross growth efficiency (Ivlev's K_1 (1945); Sheldon et al's G_e (1977)) and the predation efficiency (Sheldon et al's C_e, op cit):

Predator production/prey production = k_1C_e

To what extent is the production ratio estimate influenced by the prey/predator size ratio which is in the region of .25? Extreme values of .12 and .5 for the latter would result in production ratio estimates of 64% and 28% respectively. The first estimate is almost certainly too high. Errors of 10% in the estimates of 'productive area' (5.2.2) only affect the estimates of production ratio by about 3%, because the proportion of piscivores does not vary sufficiently between high and low water levels.

An alternative approach to predation efficiency would be to define 'rate of predation', F, as the proportion of prey biomass ingested by predators as Dickie (1976) has suggested. 'Predation efficiency' is therefore the 'rate of predation' normalized through division by the P/B ratio, and is a dimensionless variable unaffected by different turnover rates.

Either approach can be used to assess the ecological efficiency of Slobodkin as developed in Dickie (1976), providing that predation efficiencies (or rates) and growth efficiencies are known for two adjacent trophic levels. Assuming a constant gross growth efficiency, the predation rates, F, for the two levels defined above are estimated to be 2.5 yr^{-1} (lower) and 1.1 yr^{-1} (higher). The ratio of these is about half the 4:1 value predicted by Dickie (1976) on the basis of an ecological efficiency of 20% and a prey/predator biomass ratio of 1.25. These data suggest an ecological efficiency of the order of 30 to 40% for piscivore-prey interactions. A more accurate estimate requires estimates of growth efficiencies for the prey and predators concerned.

Whichever measure of efficiency is used, the data suggest that this system is very efficient for energy transfers between 'particle sizes' within the length range of 15 to 960 mm, which happens to consist mainly of fish and a few decapods.

Kerr (1974) developed a model for pelagic systems dominated by predator-prey interactions based on energetic considerations:

$$\text{prey/predator biomass} = q^{b}/p(\alpha W^{\gamma+b-1}/k+1)\ldots(3)$$

where α, γ are the constants for the allometric equation relating total metabolism to weight.

q = prey weight/predator weight.

b = weight exponent of doubling time relation (= $1-x$), where x is the exponent of the Parker & Larkin equation derived independently by Kerr.

p = proportion of prey production which is either unutilized or nonassimilated.

k = growth rate constant, identical to that of Parker & Larkin (1959).

W = mean weight of predators

Kerr's p is the proportion of ingested food assimilated (Paloheimo & Dickie's p (1965)) multiplied by the predation efficiency (Sheldon et al's (1977) C_e).

If one assumes that the exponents of the growth equation (x=1-b) and of the metabolism equation (γ) are equal as Kerr did, the relation is functionally identical to that derived later by Sheldon et al 1977. Assuming p = .7, q = $.05^3$ and a gross growth efficiency of 20% Kerr estimated a prey/predator biomass ratio of about 1.2, assuming that 80% of the ingested food is assimilated. Thus the predation efficiency, C_e, would be .7/.8 = 90%.

These approximate but realistic estimates by Kerr for a pelagic system are interesting, because my results show biomass ratios of 1.3 and 1.2 for the smaller and larger length ranges respectively. Yet the prey/predator length ratio was estimated to be about .25 compared with Kerr's .05 for pelagic systems. The larger ratio in this study is associated with higher growth efficiency. For a maximum predation efficiency of 100%, the extreme production ratio estimates of 28 - 64% represent minimum gross growth efficiencies corresponding to mean prey/predator size ratios ranging from .5 to .12. High efficiencies when fish is used as a ration have been noted by Paloheimo & Dickie (1966). Brett & Groves (1979) reviewed energy budgets for carnivorous fish feeding on invertebrates or prepared foods, estimating a mean efficiency of 29%. Baldwin (1956) found similar values for trout fed on live fish. Niimi & Beamish (1973) reported values reaching 40% for largemouth bass fed on dead fish. Bjørnson (pers. comm.) estimated 50% from experimental studies of cod hunting fish in tanks. The maximum possible efficiency is close to 60% estimated on biochemical grounds.

Although there are numerous assumptions in these calculations, the results when compared to a pelagic system provide empirical evidence which support the theoretical arguments of Kerr (1971) that predator growth efficiency decreases when prey become relatively smaller. Developing this analysis further, as proposed in Kerr (1982) will depend on the acquisition of data on metabolism or ration size.

There are a number of factors which may bias the foregoing estimates, the most critical of which are:

(1) Equilibrium.

'Short term' disequilibrium during a hydrological cycle (Chapter 1) almost certainly occurs, hence my integration of the results over an average year. The question here is whether there is year to year disequilibrium between the biomasses of prey and predator. There are fluctuations of individual species, as noted by Lowe-McConnell (1964), but the prey and predator groups considered here consist of numerous species with a variety of life strategies for coping with variations in the hydrological regime. While the process of including large length ranges will smooth over differences in year class strength, there is no evidence that events affecting large groups of species of different ages will not cause fluctuations.

The causes of such fluctuations are probably related to hydrological variations. It was commented in Chapter 2 that the water movements during the period of study were not significantly different from the average regime during this century. However, as noted in 4.6 the water level rose 2.5 times faster in 1977 than during the succeeding cycle. Also 1976 was a very high flood year yet the water level subsequently plunged to 18.0m.

Figures 5.7 and 5.8 compare the biomasses of the two years during rising water between the levels of 21 and 27m. The predator/prey production ratios, calculated as previously for the two groups, are:

predator sizes	prey sizes	1977	1978
60 - 240	15 - 60	22%	25%
240 - 960	60 - 240	27%	60%

Despite large differences in total production due to the growth phenomenon (4.6), and the hydrological fluctuations since 1976, the smaller length group estimates are fairly constant. The biomass ratios for the smaller group were 2.1 in both years, reflecting a seasonal increase in prey due to increased spawning. This is associated with the generally lower transfer efficiencies compared with the annual value of 38%, and could be due to lower predation efficiencies during a period of higher prey densities. The biomass ratios for the larger group were apparently less stable, being 1.8 in 1977 and 0.9 in 1978. The instability suggested for the larger fish is difficult to confirm because of the higher sampling variance as noted in (b) below.

(2) Errors in estimation.

(a) I have only considered fish specialized in piscivory. There are omnivores including fish in their diets. Also there are significant piscivorous bird populations and the fish bat, <u>Noctilo</u> (Goulding 1980: 183). Larger fish are increasingly vulnerable to caimans, the occasional shark, and abundant dolphins and large piscivorous catfish in the main rivers (Goulding, pers. comm.).

(b)The largest two size groups have a high variance and the estimates could be biased due to the very low catchability (Chapter 3).

(c) The growth function derived in Chapter 4 needs to be refined when more data from larger fish are available.

(d) The growth rates were estimated from length distributions. If predation was size selective enough to cause differential mortalities between faster and slower growers in a cohort, the growth and hence production estimates would be biased. I find this difficult to conceive in an environment with a large size range of predators consuming a large size range of prey. For the production ratios to be biased, the cohorts of 'prey' and 'predator' would have to be affected differentially by their appropriate predators.

In conclusion, since gross growth efficiency is likely to lie between 30 and 50%, the mean piscivore/prey production ratio of 38% indicates a high predation efficiency of 75 - 100%. Because of bias 2(a), the mean value is probably near the top of this range.

5.6 Productivity and the Fishery

The mean annual productivity of 280 $gm^{-2}yr^{-1}$ is within the range of other productive systems. Only 1% of this 'fish' productivity is from decapods. Mathews (1971) and Mann _et al_ (1972) estimated 200 $gm^{-2}yr^{-1}$ for R. Thames fish productivity which is high by temperate standards because of the enriched environment. The 347 $gm^{-2}yr^{-1}$ estimated by Balon(1974) for the fish inhabited area of L. Kariba is somewhat higher than these results, yet the P/B ratio was only about 1, which is less than the overall value shown in Table 5.1, p 247.

Mean annual production per unit area by size class is shown for all species and detritivores only in Figure 5.2. Figures 5.3 and 5.4 show the total biomass and production estimates for the study area. The similarity between these figures and the previous two suggests that the latter distributions are not overly distorted due to seasonal differences. Table 5.1 summarizes the production, biomass and P/B ratio data by logarithmic size class and mean individual weight.

The estimated fish productivity for the study area, which takes into account seasonal variation in growth rate and water area, totals 366,000 $t(yr)^{-1}$ of which the annual fishery yield of 9900t is a mere 2.7%. I have assumed that immigration of fish into the study area equals emigration. The fishery is dominated by fish over 25cm long. The productivity of fish exceeding this length is estimated at 134,000 $t(yr)^{-1}$ of which the fishery yield comprises only 7.4%. This low value is partly due to the underutilization of the available fish resources due to lack of market for many species (Bayley 1981).

There is other evidence that the resource as a whole is not being heavily exploited. Moderately exploited floodplain fisheries in Africa and Asia typically yield 4 to 6 $t(km)^{-2}yr^{-1}$ of <u>maximum</u> flooded area (Welcomme 1979:221), compared to the 1.9 $t(km)^{-2}yr^{-1}$ of this area which is itself higher than for the basin as a whole. Using the 'productive area' and adjusting for seasonal variation the latter yield would be about 7.7 $t(km)^{-2}yr^{-1}$. Established temperate marine fisheries in the 1960's ranged from 2.9 to 3.3 $t/km^2/yr$ (Dickie 1972).

An intensive study in five areas by Barthem (1981) using a fleet of gillets ranging from 4 to 12cm stretched mesh fishing a total of 493 hours produced an average catch rate of 64kg/100m of net/day which he compared with the range of 6.2 to 24 reported by Welcomme (1979:185) for a variety of floodplain fisheries in Africa, Asia and Colombia.

The three major species comprising 31% of the yield are the detritivores <u>Prochilodus</u> <u>nigricans</u>, <u>Semaprochilodus</u> <u>taeniatus</u> and <u>S.</u> <u>insignis</u>, which were also included in the growth analysis presented here. Their combined yield of 3040t was mostly of 1+ and 2+ fish, and the total production was estimated at 46,000t/year, of which about 6,600t was from the exploited age groups. The latter is an underestimate because there are seasonal migrations of these age groups beyond the sampling area. Therefore the proportion of productivity of recruited fish of these species taken by the fishery, 46%, is an overestimate.

In spite of the evidence that the fishery as a whole is not exploited to its potential, there is good evidence that the large species Arapaima gigas and Colossoma macropomum have declined markedly due to fishing effort. In this area of study which is relatively more exploited these species only totalled 2.3% of the 1977 yield. Yet they used to dominate the yield in this area as they still do to a diminishing extent in the Amazon as a whole (Petrere 1979; Bayley 1981; Hanek 1982). Further comments on the fishery are in the following section.

5.7 Discussion

Many separate items have been discussed in the preceding sections. With our very limited knowledge of floodplain systems, the greatest value of these results will accrue when quantitative information is available from other systems. However, the preceding analyses at least suggest hypotheses which may be testable by further studies.

There was a seasonal growth variation but no consistent indication of density dependence. As shown in Chapter 4 no density dependent growth was indicated by any of twelve species studied; nor was there a significant sign test of the correlations. Conversely, during falling water two of eleven species did indicate the phenomenon at $p<.05$ but again the sign test was not significant.

It appears that growth is somewhat food limited during the period of environmental contraction, whereas during rising water no competition was indicated. As explained in 4.6 and Chapter 2 food in general is much more abundant during the rising water period than during the draw-down season. The concept of 'short term disequilibrium' was introduced in Chapter 1. During rising water the constantly changing environment and food supply could prevent competition from developing to the point where growth rate is affected. This effect would be enhanced by predation which has a high efficiency even during this period (5.5). I believe the analogy of a 'rat race' alluded to in Chapter 1 to be appropriate for this hydrological season.

Although predation is even higher during the falling water period, the severe food limitation was apparently sufficient to be reflected in density dependent growth in a minority of species studied (4.5). There is probably a close interplay between predation and competition during this period. The selection pressures resulting from a need to grow fast when the environment is expanding to reach a size relatively safe from predation, and to mature early (at 1+ or 2+ years) may well be dominant, as Lowe-McConnell (1969) has suggested. This in turn may have caused the piscivores to respond by adapting to the capture of larger prey as observed. This study has not eliminated the possibility that competition exists between piscivores.

Implications of these results for human exploitation could be far-reaching. Although further developments in the fishery are limited by economic and technological factors, there are biological limits to the species composition in the catch if these constraints were to be mitigated in the future.

The high predation efficiencies indicated for piscivores, and the short food chains indicated by the fine detritus - fish and macrophyte - fish links suggest that this floodplain system is very efficient once the plant material has been assimilated. This is noteworthy considering the seasonal inundation cycles and irregular fish kills due to deoxygenation. However, the former is fairly predictable in the central Amazon and the fish kills appear significant but probably account for a small proportion of total mortality considering the abundance of piscivores.

The high efficiency does not mean that the fishery ought to be very productive. Tight coupling between trophic levels suggests that much of the surplus production is consumed by predators, a scenario considered by May _et al_ (1979) and Pauly (1979). They suggested that one level may exploit another near its 'maximum sustainable yield' (MSY) which would profoundly affect the joint yield to a top predator such as man. However, Beddington & May (1977) argued that harvesting a population at its MSY in a randomly fluctuating environment would result in a collapse of the fishery. Therefore to accept both arguments one needs to presume that natural populations of predators adjust their exploitation to suit random fluctuations in prey populations much more effectively than man. This could be achieved more easily if they exploit various populations whose total variability is much less than components which are subject to the vicissitudes of year class strength. I find this easier to conceive in a tropical environment of high species diversity than in the temperate systems considered by May _et al_ (1979). The diversity of prey exploited by predators mentioned in Chapter 4 is high, and reflects the diversity of food types available much more than the morphological specializations of their consumers suggest. It is speculated that greater overall stability does exist in tropical aquatic systems, but this is due to the greater opportunity of natural predators to exploit a large number of populations rather than being more specialized (cf Pauly 1979). Overall stability is stressed because individual populations can fluctuate considerably. Conversely, a specialized exploitation strategy, including one by humans, could decrease stability.

The catholic tastes of natural populations are not reflected by the fishermen exploiting them in the Amazon and S. America in general. Conversely, the higher yields obtained in African floodplains are associated with greater species diversity in the catch. I hypothesize that this is due to the strong predatory interactions between species which permit a higher yield if the composition of this yield were diverse and flexible. The alternative would be that the yield is increased simply by exploiting more species, which implies that interactions are minor and populations can be managed independently.

The dominant role of piscivores shown by Barthem's (1980) study and this one were not reflected in the Central Amazon fishery yields. Proportions of piscivores were 4.7% in the Manaus market (Petrere 1978) and 12% from the R. Amazon near Itacoatiara (Smith 1981). Apart from three valued genera, piscivores have low market value. The strategy of increasing total yield could founder if the presently low-valued piscivorous species such as the ubiquitous Hoplias malabaricus and Raphiodon vulpinis do not receive at least a proportionate share of the increased fishing intensity. These comments apply to the central region. In areas near the periphery of the basin specialized fisheries for piscivorous catfish exist in the upper R.&Madeira (Goulding 1981), Bolivian tributaries (personal obs.) and Colombia (Scully, pers. comm.).

However, in no area has exploitation been observed in which all the large piscivores are caught in proportion to their abundances. Since actual or potential competition between piscivores cannot be ruled out, none of the present fishery regimes can be guaranteed to release the considerable productive capacity of lower trophic levels for long term exploitation.

5.8 References

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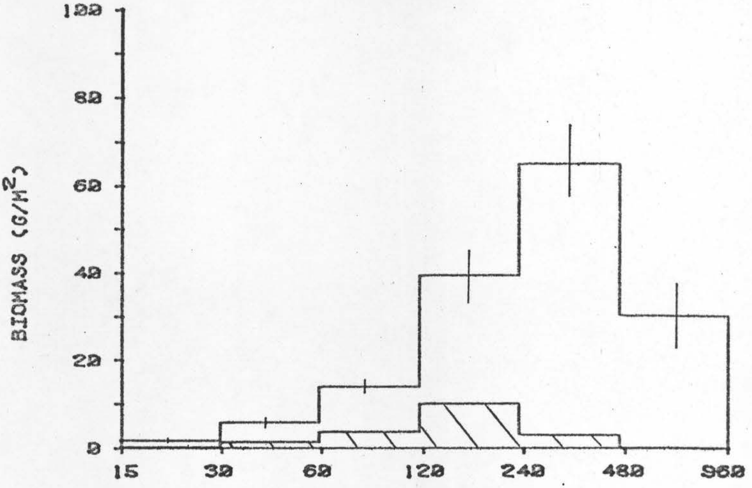
Figure 5.1 Mean biomass density by length group, all species (hatched area is for detritivores only, vertical lines are standard errors indicating seasonal variability after pooling the data in 26 fortnightly periods)

All figures in this chapter are based on samples corrected for catchability and do not include fishery catch data.

Figure 5.2 Total production by length group (hatched area is for detritivores only, vertical lines are standard errors indicating seasonal variability after pooling the data in 26 fortnightly periods)


BIOMASS (G/M^2)
100
80
60
40
20
0
15
30
60
120
240
480
960

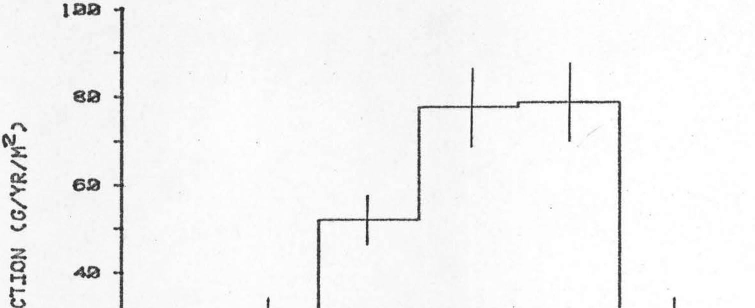
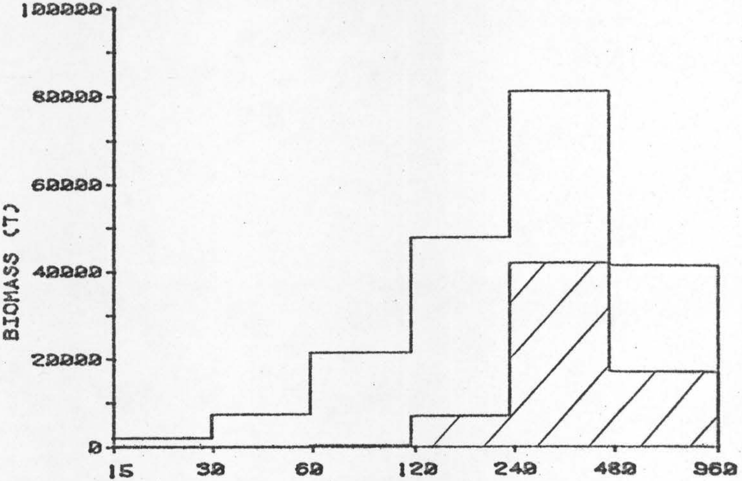

PRODUCTION (G/YR/M^2)
100
80
60
40
20
0
15
30
60
120
240
480
960
LENGTH (MM)

Figure 5.3 Biomass in the study area by length group, all species (hatched area is for piscivores only; data are weighted seasonally according to the estimated 'productive area' at each of 26 intervals per year)

Figure 5.4 Production in the study area by length group, all species (hatched area is for piscivores only; data are weighted seasonally according to the estimated 'productive area' at each of 26 intervals per year)


100000
80000
60000
40000
20000
0
BIOMASS (T)
15
30
60
120
240
480
960

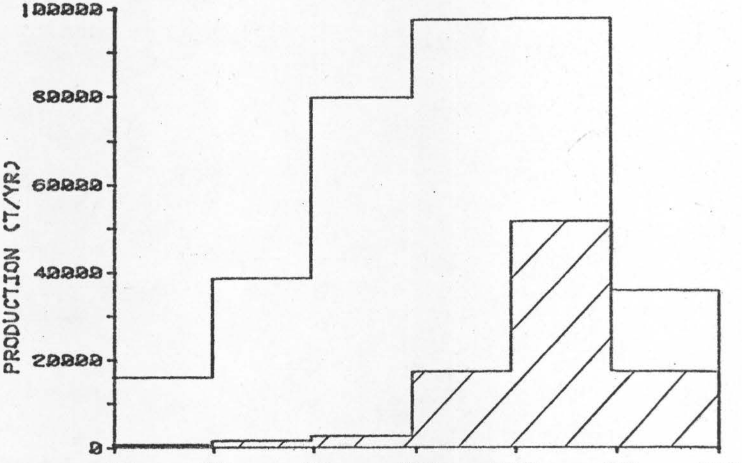
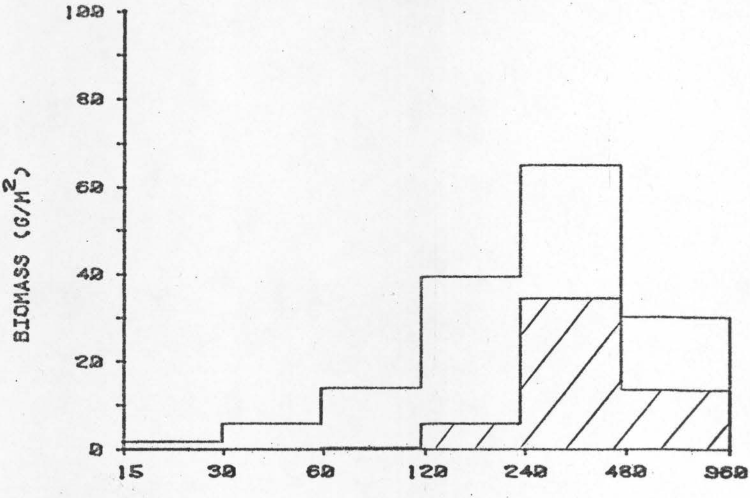

100000
80000
60000
40000
20000
0
PRODUCTION (T/YR)
15
30
60
120
240
480
960
LENGTH (MM)

Figure 5.5 Mean biomass density by length group, all species (hatched area is for piscivores only)

Figure 5.6 Total production by length group (hatched area is for piscivores only)


BIOMASS (G/M^2)
100
80
60
40
20
0
15
30
60
120
240
480
960

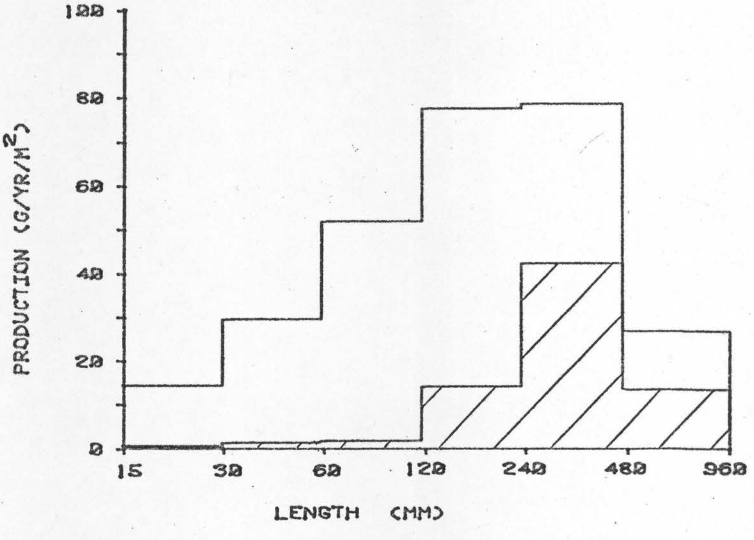
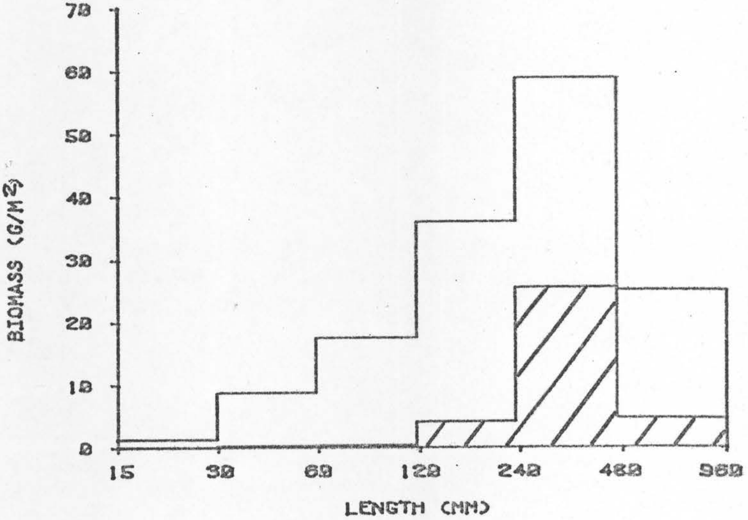

PRODUCTION (G/YR/M^2)
100
80
60
40
20
0
15
30
60
120
240
480
960
LENGTH (MM)

Figure 5.7 Total biomass versus piscivore biomass (hatched area) for rising water between the 21 and 27m levels;i.e. during March to May 1977.

Figure 5.8 Total biomass versus piscivore biomass (hatched area) for rising water between the 21 and 27m levels;i.e. during November 1977 to May 1977).


70
60
50
40
30
20
10
0
BIOMASS (G/M2)
15
30
60
120
240
480
960
LENGTH (MM)

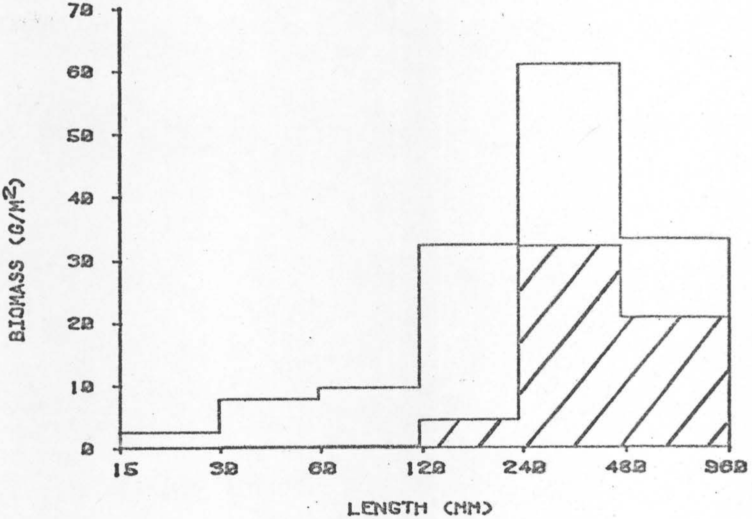

70
60
50
40
30
20
10
0
BIOMASS (G/M2)
15
30
60
120
240
480
960
LENGTH (MM)

Table 5.1 Mean production, biomass and annual P/B ratios by size group

Group no:	1	2	3	4	5	6	
Length range (mm)	15-29	30-59	60-119	120-239	240-479	480-960	Totals
Production ($g/m^2/yr$)	15	30	52	78	79	27	280
Biomass (g/m^2)	1.8	6.1	14	39	65	30	157
P/B(/yr)	8.0	4.9	3.7	2.0	1.2	0.9	1.8
Mean weight (g)	.16	1.0	9.0	80	340	940	-

Table 5.2 Total annual production (in 1000's of tons) for all species and piscivores for the study area.

Group no:	1	2	3	4	5	6	
Length range (mm)	15-29	30-59	60-119	120-239	240-479	480-960	Totals
All species	16.1	38.7	80	98	98	36	366
Piscivores only	.7	1.9	2.7	17.7	52	17	92

Appendix A: list of taxa separated as of September, 1982.
(reptiles, amphibians and crabs omitted)

Ostariophysi
Characoidei
Characidae
Triportheus albus
Triportheus angulatus
Triportheus elongatus
Triportheus culter
Chalceus eurythurus
Brycon melanopterum
Brycon sp.B
Brycon sp.C
Roestes sp.
Acestrorhynchus spp.
Agionates anchovia
Roeboides prognathus
Roeboides myersi
Roeboides spp.
Characidium sp.
Iguanodectes spp.
Bryconamericus spp.
Tetragonopterinae spp.

Gastrocephalidae
Thorocharax stellatus

Cynodontidae
Raphiodon vulpinis
Hydrolycus sp.A
Hydrolycus sp.B

Erythrinidae
Hoplias malabaricus
Erythrinus erythrinus

Ctenolucidae
Boulengerella sp.

Serrasalmidae
Pygocentrus nattereri
Serrasalmus rhombeus
Serrasalmus elongatus
Serrasalmus cf. *elongatus*
Serrasalmus sp.A
Serrasalmus sp.B
Serrasalmus sp.C
Serrasalmus sp.D
Serrasalmus β *Pygocentrus* spp.

Mylossoma duriventris
Mylossoma aureum
Mylossoma sp.T
Metynnis spp.(*M.luna* β *maculatus*)
Myloplus cf.*rhomboidalis*
Colossoma macropomum
Colossoma brachypomum

Anostomidae
Schizodon fasciatus
Leporinus friderici
Leporinus trifasciatus
Leporinus cylindriformes
Leporinus cf*amazonicus*
Leporinus fasciatus
Leporinus agassizi
Rhytiodus microlepis
Rhytiodus argenteofuscus
Laemolyta varia
Laemolita taeniata
Abramites sp.

Hemiodontidae
Anodus (Eigenmannina) melagopon
Anodus steatops
Anodus elongatus
Anodus sp.X
Hemiodus unimaculatus
Hemiodus (Hemiodopsis) microlepis
Hemiodus (Hemiodopsis) immaculatus
Hemiodus (Hemiodopsis) semitaeniatus
Argonectes sp.

Curimatidae
Curimata latior
Curimata altamazonica
Curimata kneri
Curimata sp.E
Curimata cf. *semiornata*
Curimata ciliata
Curimata leuciscus
Curimata vittata
Curimata sp.J
Curimata sp.K
Curimata spilura
Curimata rutiloides
Curimata sp.Q
Curimata cf. *metae*
Curimata sp.V
Curimata sp.T
Potamorrhina pristigaster

Curimatella dorsalis
Curimatella alburnus
Curimatopsis macrolepis

Prochilodontidae
Semaprochilodus taeniatus
Semaprochilodus insignis
Semaprochilodus sp.A
Prochilodus nigricans

Chilodontidae

Lebiasinidae
Pyrrhulina australis
Copella nigrofasciata
Lebiasinidae sp.C

Nannostomidae
Nannostomus unifasciatus
Nannostomus digrammus
Nannostomus eques
Nannostomus sp.D

Siluriformes
Pimelodidae
Pimelodus spp.
Pimelodella sp.A
Pimelodella sp.B
Pimelodella sp.C
Pimelodella sp.D
Pimelodella spp.
Pseudoplatystoma tigrinum
Pseudoplatystoma fasciatum
Sorubim lima
Sorubimichthys planiceps
Hemisorubim platyrhynchos
Pimelodina sp.A
Pimelodina sp.B
Rhamdia sp.A (jandia)
Rhamdia sp.B
Rhamdia sp.C
Phractocephalus hemiliopterus
Callophysus macropterus
Pinirampus pirinampu

Auchenipteridae
Pseudoauchenipterus sp.
Trachycorystes sp.
Centromochlus sp.
Auchenipterus sp.

Ageneiosidae
- *Ageneiosus* sp.

Hypophthalmidae
- *Hypophthalmus edentatus*
- *Hypophthalmus* sp.A
- *Hypophthalmus* spp.

Doradidae
- *Oxydoras niger*
- *Megalodoras*
- *Anadoras* spp.
- *Acanthodoras* sp.
- *Agamyxis* sp.
- *Hemidoras* sp.A
- *Hemidoras* sp.B
- *Hemidoras* sp.C
- *Hemidoras* sp.D
- *Hemidoras* sp.E
- *Hemidoras* sp.F
- *Hemidoras* sp.G
- *Hemidoras* spp.
- *Hassar* sp.A

Bunocephalidae
- *Bunocephalus* sp.

Loricariidae
- *Hemiancistrus* sp.
- *Plecostomus* sp.A (acari de praia)
- *Plecostomus* sp.B (acari amarelo)
- *Plecostomus* spp.
- *Pterygoplichthys* spp.
- *Hypoptopoma* sp.
- *Loricariichthys* spp.
- *Loricaria* spp.
- *Pseudoloricaria* sp.
- *Farlowella* sp.
- *Rineloricaria* sp.
- *Hemiodontichthys* sp.
- *Ancistrus* sp.
- *Otocinclus* sp.
- *Oxyropsis* sp.
- *Neoplecostomus* sp.(acari pedra)

Callichthidae
- *Hoplosternum littorale*
- *Hoplosternum* sp.A
- *Corydoras* sp.A
- *Corydoras* spp.

- Trichomycteridae
  - *Ochmacanthus* sp.
  - *Stegophilus* sp.
  - *Vandellia* sp.
  - *Apomatoceros* sp. skip2
- Gymnotiformes
  - Sternopygidae
    - *Eigenmannia virescens*
    - *Eigenmannia humboldti*
    - *Eigenmannia* sp.A
    - *Eigenmannia* spp.
    - *Distocyclus* sp.
    - *Sternopygus* cf. *macrurus*

  - Rhamphichthyidae
    - *Rhamphichthys*
    - *Gymnorhamphichthys*

  - Hypopomidae
    - *Hypopomus* spp.
    - Hypopomidae (sp.A)

  - Apteronotidae
    - *Adontosternarchus*
    - *Apteronotus* sp.
    - *Sternarchella* sp.
    - Apteronotinae sp.A
    - *Orthosternarchus* sp.

  - Electrophoridae
    - *Electrophorus electricus*

- Perciformes
  - Cichlidae
    - *Cichlasoma severum*
    - *Cichlasoma festivum*
    - *Cichlasoma temporale*
    - *Cichlasoma bimaculatum*
    - *Cichlasoma coryphaenoides*
    - *Cichlasoma psittacum*
    - *Astronotus ocellatus*
    - *Acarichthys heckeli*
    - *Chaetobranchus semifasciatus*
    - *Chaetobranchus flavescens*
    - *Chaetobranchopsis orbicularis*
    - *Acaronia nassa*
    - *Biotodoma cupido*
    - *Biotoecus opercularis*
    - *Pterophyllum scalare*
    - *Geophagus surinamensis*

Geophagus acuticeps
Geophagus jurupari
Geophagus daemon
Uaru amphiacanthoides
Cichla ocellaris
Cichla temensis
Aequidens duopunctata
Aequidens tetramerus
Aequidens cf. *curviceps*
Apistogramma spp
Crenicichla spp.
Batrachops spp.

Sciaenidae
Plagioscion squamosissimuss
Plagioscion montei
Pachypops grunniens

Cyprinidontiformes
Cyprinidontidae
Fluviphylax pygmaus
Rivulus sp.

Osteoglossiformes
Osteoglossidae
Arapaima gigas
Osteoglossum bicirrhosum skip2 Dipnoi
Lepidosiren paradoxa

Synbranchiformes
Synbranchidae
Synbranchus marmoratus

Clupeiformes
Clupeidae
Pellona castelnaeana
Pellona flavipinnis
Pristogaster cayana
small Clupeids, mostly *Pellona* spp

Engraulidae
Engraulidae sp.A_1
Engraulidae sp.A_2
Engraulidae sp.B
Engraulidae sp.C
Engraulidae sp.D

Tetraodontiformes
    Tetraodontidae
        Colomesus psittacus

Pleuronectiformes
    Soleidae
        Achirus spp.
        Achiropsis spp.

Gobioidae spp.

Beloniformes
    Belonidae
        Potamorrhaphis guianensis

Rajiformes
        Potamotrygon sp.A
        Potamotrygon sp.B

Decapoda
        Macrobrachium spp.

Appendix B: Data used in growth estimates from 14 species

Table B.1 *Acarichthys heckeli* data for growth analysis. (12012 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	4	.29	49	6	77	1
1	6	.40	303	6	77	1
1	8	.94	141	6	77	1
1	10	.52	179	6	77	1
1	12	.85	27	7	77	1
1	26	8.13	6	7	77	1
1	50	21.50	9	2	77	1
2	17	2.27	37	11	76	1
2	20	2.42	93	3	76	1
2	22	3.32	172	5	76	1
2	24	5.29	49	4	76	1
2	30	5.29	6	9	76	1
2	32	10.53	17	6	76	1
2	34	16.92	5	5	76	1
2	36	13.89	41	6	76	1
2	40	19.24	20	6	76	1
2	42	20.82	19	6	76	1
2	44	18.81	22	7	76	1
2	46	20.17	32	6	76	1
2	48	18.70	19	4	76	1
2	34	1.93	9	5	76	2
2	36	6.01	22	6	76	2
2	38	10.96	13	6	76	2
2	2	.10	68	7	77	1
2	4	.25	232	5	77	1
2	6	.26	312	5	77	1
2	8	.42	616	6	77	1
2	10	.54	978	8	77	1
2	12	1.28	229	5	77	1
2	14	1.55	137	7	77	1
2	16	1.79	182	7	77	1
2	18	2.56	142	7	77	1
2	20	3.17	55	6	77	1
2	22	3.02	47	6	77	1
2	24	4.91	26	6	77	1
2	26	8.83	41	6	77	1
2	28	10.76	21	6	77	1
2	26	.60	20	6	77	2
2	28	1.05	6	6	77	2

2	30	4.46	6	8	77	2
3	20	5.83	6	5	76	1
3	24	6.88	33	5	76	1
3	26	9.41	14	7	76	1
3	30	21.38	27	5	76	1
3	46	27.11	96	5	76	1
3	48	36.19	32	5	76	1
3	52	33.73	12	6	76	1
3	54	31.11	10	6	76	1
3	32	7.57	15	5	76	2
3	34	8.50	68	6	76	2
3	36	9.07	27	5	76	2
3	38	12.30	26	6	76	2
3	40	11.46	36	5	76	2
3	42	10.34	97	5	76	2
3	44	17.54	128	5	76	2
3	50	22.11	30	5	76	2
3	2	.38	29	6	77	1
3	4	.33	285	6	77	1
3	6	.31	551	6	77	1
3	8	.26	1597	6	77	1
3	10	.41	897	6	77	1
3	12	.29	551	7	77	1
3	14	.60	412	7	77	1
3	16	.89	494	7	77	1
3	18	1.62	327	6	77	1
3	20	2.14	134	8	77	1
3	22	2.90	218	7	77	1
3	24	3.11	305	6	77	1
3	26	5.74	60	7	77	1
3	28	7.05	24	8	77	1
3	30	7.24	46	7	77	1
3	26	7.52	128	1	78	1
3	27	7.71	193	2	78	1
3	28	7.36	273	2	78	1
3	29	8.59	387	5	78	1
3	27	.30	17	2	78	2
3	28	.55	24	2	78	2

Table B.2 *Plagioscion squamosissimus* data for growth analysis. (195 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	4	.46	17	6	77	1
1	6	.42	13	6	77	1
1	8	.58	4	6	77	1
1	2	.15	32	2	78	1

2	28	.16	7	4	76	1
2	6	.76	37	7	77	1
2	8	.81	11	5	77	1
3	4	.14	67	6	77	1
3	6	.33	7	6	77	1

Table B.3 *Plagioscion montei* data for growth analysis.
(200 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
3	2	.11	130	6	77	0
3	4	.16	44	6	77	0
3	6	.62	21	6	77	0
3	10	1.70	5	6	77	0

Table B.4 Engraulidae sp.A01 data for growth analysis.
(8991 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	48	1.83	22	8	76	2
1	6	.14	119	6	77	1
1	8	.35	41	6	77	1
1	10	.69	78	6	77	1
1	10	.14	82	6	77	2
1	12	.22	42	6	77	2
1	22	.69	18	7	77	2
1	28	1.81	94	6	77	2
1	32	3.03	26	7	77	2
1	34	2.66	20	7	77	2
2	21	.46	679	11	76	1
2	24	.54	765	3	76	1
2	26	.72	211	5	76	1
2	28	1.11	156	4	76	1
2	30	1.98	140	5	76	1
2	46	2.38	38	6	76	1
2	12	.61	18	6	77	1
2	14	.71	13	8	77	1
2	16	1.11	629	5	77	1
2	18	.91	195	7	77	1
2	22	.91	832	7	77	1
2	30	1.23	1234	6	77	1
2	32	1.24	155	6	77	1
3	24	.28	273	5	76	1

3	26	.71	56	7	76	1
3	48	1.32	145	5	76	1
3	28	.23	285	5	76	2
3	2	.08	20	5	77	1
3	4	.10	62	6	77	1
3	6	.15	1242	6	77	1
3	8	.13	783	6	77	1
3	10	.15	61	6	77	1
3	12	.14	167	6	77	1
3	14	.42	20	6	77	1
3	16	.48	32	7	77	1
3	24	1.50	34	8	77	1
3	26	2.10	11	7	77	1
3	22	.20	31	6	77	2
3	24	.24	22	8	77	2
3	26	.55	80	7	77	2
3	28	.35	32	6	77	2
3	31	.15	28	2	78	2

Table B.5 *Semaprochilodus taeniatus* data for growth analysis. (9033 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	18	5.40	20	7	76	1
1	20	5.75	86	6	76	1
1	22	10.19	9	5	76	1
1	24	14.66	42	5	76	1
1	30	73.74	14	7	76	1
1	32	59.33	6	7	76	1
1	34	70.90	6	7	76	1
1	36	58.58	19	6	76	1
1	38	81.98	23	6	76	1
1	40	88.43	9	6	76	1
1	42	77.04	17	8	76	1
1	2	.09	63	6	77	1
1	4	.17	37	6	77	1
1	6	.20	357	6	77	1
1	8	1.56	67	6	77	1
1	10	2.44	186	7	77	1
1	12	4.46	5	7	77	1
1	14	3.20	175	6	77	1
1	16	6.26	114	7	77	1
1	18	7.79	48	6	77	1
1	20	12.75	56	7	77	1
1	22	19.61	31	6	77	1
1	28	38.61	31	7	77	1
1	12	.71	557	2	78	1

1	13	1.03	734	2	78	1
2	20	6.34	20	5	76	1
2	24	14.88	31	5	76	1
2	26	22.64	11	6	76	1
2	34	40.28	16	6	76	1
2	10	.74	10	5	77	1
2	12	.76	93	7	77	1
2	20	19.37	6	6	77	1
2	22	13.07	8	6	77	1
3	12	6.10	49	7	77	1
3	14	8.24	10	7	77	1
3	16	9.42	28	6	77	1
3	18	6.66	29	8	77	1
3	22	7.36	10	6	77	1

Table B.6 *Semaprochilodus insignis* data for growth analysis. (11334 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	16	5.48	9	6	76	1
1	20	11.01	118	5	76	1
1	20	1.36	530	5	76	2
1	22	1.70	513	7	76	2
1	24	5.73	34	8	76	2
1	28	14.78	8	7	76	2
1	2	.17	068	6	77	1
1	4	2.28	135	6	77	1
1	6	2.33	230	7	77	1
1	8	4.29	29	7	77	1
1	10	2.61	576	6	77	1
1	12	5.79	27	7	77	1
1	14	8.98	6	6	77	1
1	16	12.31	25	7	77	1
1	18	16.32	20	6	77	1
1	24	50.11	13	7	77	1
1	22	7.64	213	7	77	2
1	7	.16	79	1	78	1
1	8	.70	192	2	78	1
1	9	.98	394	2	78	1
2	16	6.86	18	5	76	1
2	20	12.74	162	5	76	1
2	18	2.85	21	4	76	2
2	26	10.80	6	6	76	2
2	28	8.46	9	5	76	2
2	30	19.88	65	6	76	2
2	32	21.15	32	6	76	2
2	38	15.65	59	7	76	2

2	40	19.98	16	6	76	2
2	42	22.63	69	4	76	2
2	44	24.62	72	5	76	2
2	48	98.60	13	7	76	2
2	52	15.61	7	5	76	2
2	4	1.80	19	8	77	1
2	8	1.34	133	7	77	1
2	10	3.82	6	7	77	1
2	12	3.84	7	7	77	1
2	16	14.21	9	6	77	1
2	18	13.72	11	6	77	1
2	22	2.05	13	6	77	2
2	24	4.77	54	8	77	2
3	14	.32	7	5	76	2
3	24	4.49	27	5	76	2
3	26	31.54	10	5	76	2
3	38	50.60	17	5	76	2
3	40	21.37	79	5	76	2
3	42	36.43	19	5	76	2
3	44	41.99	33	5	76	2
3	46	33.04	9	6	76	2
3	50	39.90	12	6	76	2
3	52	33.48	8	6	76	2
3	58	67.36	6	7	76	2
3	8	4.37	16	7	77	1
3	10	5.91	6	7	77	1
3	14	4.99	33	8	77	1
3	22	7.70	10	8	77	1
3	74	63.07	6	2	77	1
3	22	.33	16	8	77	2

Table B.7 *Prochilodus nigricans* data for growth analysis. (1234 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	6	1.65	52	5	77	1
1	8	.53	7	7	77	1
1	10	3.29	4	8	77	1
1	31	243.55	10	1	78	1
2	4	1.54	6	4	77	1
2	6	12.25	5	5	77	1
2	8	3.30	15	6	77	1
2	24	38.51	6	7	77	1
2	26	40.31	6	6	77	1
2	28	47.89	18	4	77	1
2	30	62.79	53	5	77	1
2	38	160.35	8	5	77	1

2	8	.31	19	6	78	1
2	10	1.50	4	8	78	1
3	52	196.11	4	5	76	1
3	10	6.09	403	5	77	1
3	24	32.18	13	5	77	1
3	26	43.09	102	5	77	1
3	28	68.87	74	5	77	1
3	30	67.14	155	5	77	1
3	32	56.01	49	6	77	1
3	34	59.51	18	6	77	1
3	36	72.80	38	6	77	1
3	38	68.42	25	6	77	1
3	40	61.98	52	6	77	1
3	42	107.16	36	6	77	1
3	44	68.97	28	7	77	1
3	46	116.16	8	7	77	1
3	48	200.17	10	7	77	1
3	50	161.29	6	6	77	1

Table B.8 *Curimata latior* data for growth analysis. (5337 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	14	.68	198	6	76	2
1	16	1.06	37	5	76	2
1	20	1.81	4	7	76	2
1	22	3.07	283	8	76	2
1	2	.30	6	6	77	1
1	4	.26	18	7	77	1
1	6	1.18	260	7	77	1
1	8	1.39	18	6	77	1
1	10	4.86	45	7	77	1
1	12	6.25	17	6	77	1
1	16	13.07	74	6	77	1
1	20	.67	1922	7	77	2
1	7	.17	50	2	78	1
2	18	5.24	77	5	76	1
2	12	.40	7	3	76	2
2	16	.23	125	4	76	2
2	18	.96	76	5	76	2
2	20	1.20	671	6	76	2
2	24	4.22	5	6	76	2
2	42	4.47	7	5	76	3
2	52	17.43	5	6	76	3
2	2	.22	10	8	77	1
2	4	.67	65	5	77	1
2	6	1.63	7	7	77	1

2	14	.30	16	6	77	2
2	16	1.23	60	6	77	2
2	18	1.50	377	6	77	2
2	20	3.63	105	6	77	2
2	22	3.05	626	8	77	2
3	14	.61	7	7	76	1
3	18	1.91	4	7	76	1
3	16	.09	7	5	76	2
3	22	1.86	6	5	76	2
3	46	21.25	10	6	76	2
3	52	52.63	4	6	76	2
3	56	45.36	6	7	76	2
3	4	.70	5	7	77	1
3	6	.13	20	7	77	1
3	14	.06	16	7	77	2
3	16	.58	7	6	77	2
3	18	.80	8	7	77	2
3	20	1.12	5	8	77	2
3	22	2.26	44	7	77	2
3	19	.38	17	2	78	2

Table B.9 *Curimata kneri* data for growth analysis.
(857 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
2	2	.19	166	5	77	1
2	4	.30	104	6	77	1
2	6	.27	26	6	77	1
2	10	.62	10	6	77	1
2	12	1.68	11	7	77	1
2	14	2.95	158	6	77	1
2	16	12.05	260	4	77	1
2	18	2.37	70	5	77	1
2	22	6.09	15	7	77	1
2	24	9.24	37	5	77	1

Table B.10 *Colossoma macropomum* data for growth analysis.
(846 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	18	2.52	32	7	76	1
1	20	5.24	25	6	76	1
1	22	13.17	35	5	76	1

1	50	165.40	11	6	76	1
1	2	.11	16	6	77	1
1	4	.12	69	6	77	1
1	6	.22	178	6	77	1
1	8	.63	47	6	77	1
1	10	3.01	8	7	77	1
1	18	5.42	13	6	77	1
1	26	8.71	14	7	77	1
1	11	.36	4	1	78	1
1	13	.71	106	2	78	1
2	15	2.32	9	11	76	1
2	8	.19	17	8	77	1
2	10	.76	5	5	77	1
2	26	.23	12	6	77	2
3	18	.24	66	5	76	1
3	24	1.06	12	7	76	1
3	2	.12	13	6	77	1
3	4	.11	5	6	77	1
3	6	.13	9	6	77	1
3	8	.23	5	6	77	1
3	10	1.75	17	7	77	1
3	12	3.16	22	7	77	1
3	16	3.81	6	6	77	1

Table B.11 *Triportheus albus* data for growth analysis. (2537 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	24	7.60	30	7	76	0
1	26	6.23	38	6	76	0
1	28	7.75	8	5	76	0
1	32	13.49	19	7	76	0
1	34	14.50	72	8	76	0
1	36	14.32	30	7	76	0
1	38	15.15	15	7	76	0
1	40	16.08	9	7	76	0
1	44	21.85	12	6	76	0
1	46	15.69	16	6	76	0
1	48	15.15	19	8	76	0
1	50	17.72	6	6	76	0
1	64	27.36	8	6	76	0
1	80	26.76	15	6	76	0
1	8	.22	51	6	77	0
1	14	2.27	35	6	77	0
1	16	2.21	80	7	77	0
1	18	4.05	14	7	77	0
1	22	5.54	33	7	77	0

1	24	7.73	57	6	77	0
1	26	7.21	20	7	77	0
1	30	9.44	15	7	77	0
1	32	9.20	49	7	77	0
1	53	18.65	33	2	77	0
1	57	27.20	5	3	77	0
1	17	3.29	10	1	78	0
1	18	4.78	125	2	78	0
1	19	3.70	192	2	78	0
2	30	13.53	6	5	76	0
2	54	25.01	13	5	76	0
2	10	.13	5	5	77	0
2	12	.63	70	6	77	0
2	14	.53	35	8	77	0
2	16	1.41	41	5	77	0
2	20	1.84	45	7	77	0
2	22	2.36	10	7	77	0
2	26	3.04	7	6	77	0
2	32	4.88	29	6	77	0
3	24	8.85	16	5	76	0
3	26	5.23	59	7	76	0
3	30	15.00	7	7	76	0
3	32	16.95	65	6	76	0
3	36	11.39	13	5	76	0
3	2	.18	42	5	77	0
3	4	.14	222	6	77	0
3	6	.32	136	6	77	0
3	8	.45	458	6	77	0
3	10	.91	46	6	77	0
3	12	.88	42	6	77	0
3	14	1.63	13	6	77	0
3	16	2.20	16	7	77	0
3	18	2.68	21	7	77	0
3	20	2.28	26	7	77	0
3	22	2.76	31	6	77	0
3	24	2.51	5	8	77	0
3	32	6.23	42	8	77	0

Table B.12 *Triportheus angulatus* data for growth analysis. (6953 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	14	2.31	479	7	76	1
1	16	4.91	241	6	76	1
1	28	16.47	23	7	76	1
1	36	23.96	30	6	76	1
1	44	34.63	20	5	76	1

1	20	1.25	57	5	76	2
1	22	.75	273	7	76	2
1	24	3.80	31	8	76	2
1	6	2.12	11	7	77	1
1	10	2.80	6	6	77	1
1	18	12.02	12	6	77	1
1	22	8.85	13	7	77	1
1	8	.65	170	2	78	1
1	9	.58	40	2	78	1
2	18	5.92	127	4	76	1
2	20	7.54	539	5	76	1
2	24	11.55	15	9	76	1
2	18	.40	464	4	76	2
2	20	1.19	35	5	76	2
2	22	.84	828	6	76	2
2	24	2.33	41	9	76	2
2	30	6.51	80	6	76	2
2	38	11.55	30	7	76	2
2	42	11.68	245	4	76	2
2	44	9.73	21	5	76	2
2	2	.31	24	6	77	1
2	4	.62	71	8	77	1
2	8	1.71	186	7	77	1
2	20	11.44	33	6	77	1
2	22	1.88	72	6	77	2
2	24	3.59	183	8	77	2
3	26	9.69	55	5	76	1
3	30	18.58	36	5	76	1
3	34	20.29	19	5	76	1
3	40	26.49	29	5	76	1
3	20	.16	366	7	76	2
3	22	1.49	27	6	76	2
3	24	4.05	1834	5	76	2
3	46	10.01	30	6	76	2
3	48	13.38	16	6	76	2
3	50	13.40	98	6	76	2
3	52	11.15	20	6	76	2
3	54	11.25	23	6	76	2

Table B.13 *Triportheus elongatus* data for growth analysis. (1799 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
3	118	103.75	25	7	75	2
1	18	1.97	19	7	76	1
1	20	2.50	6	6	76	1
1	22	5.18	4	5	76	1

1	46	29.56	55	6	76	1
1	48	25.14	5	5	76	1
1	56	33.33	4	6	76	1
1	24	.40	51	5	76	2
1	26	.25	213	7	76	2
1	40	7.25	5	6	76	2
1	76	33.59	12	7	76	2
1	2	.08	19	6	77	1
1	4	.12	8	6	77	1
1	6	.15	4	6	77	1
1	8	.86	142	6	77	1
1	10	1.26	87	7	77	1
1	14	2.64	9	6	77	1
1	16	2.58	18	7	77	1
1	24	2.79	4	7	77	3
1	26	3.62	34	7	77	3
1	47	14.86	9	2	77	3
1	11	.22	79	1	78	1
1	12	.53	246	2	78	1
1	13	.40	65	2	78	1
2	15	1.02	6	11	76	1
2	18	.83	6	3	76	1
2	24	6.23	4	5	76	1
2	22	.16	13	4	76	2
2	24	.65	21	5	76	2
2	26	.90	30	6	76	2
2	28	1.85	28	9	76	2
2	30	1.57	8	6	76	2
2	32	2.76	5	5	76	2
2	42	7.37	7	7	76	2
2	46	13.14	9	4	76	2
2	48	17.18	33	5	76	2
2	4	.10	15	5	77	1
2	6	.30	51	6	77	1
2	8	.41	18	8	77	1
2	10	.48	13	5	77	1
2	12	.74	11	7	77	1
2	14	1.37	7	7	77	1
2	28	.68	188	8	77	1
2	22	.20	4	6	77	2
2	28	4.22	5	8	77	2
2	16	.32	7	7	77	3
2	20	.83	6	6	77	3
2	24	1.70	10	6	77	3
3	24	.24	34	7	76	2
3	26	1.32	8	6	76	2
3	62	25.89	13	7	76	2
3	68	29.02	6	6	76	2
3	18	.28	10	5	76	3
3	20	1.09	4	7	76	3
3	30	4.69	19	5	76	3

3	44	18.84	13	5	76	3
3	48	21.49	23	5	76	3
3	4	.12	5	6	77	1
3	6	.14	17	6	77	1
3	8	.10	4	6	77	1
3	10	.34	4	7	77	1
3	26	.34	11	8	77	2

Table B.14 *Brycon melanopterum* data for growth analysis. (1463 individuals caught).

Region (year)	Age (Weeks)	Mean Weight (g)	No.of Fish	No.of Samples	Year Class	Cohort No.
1	18	3.44	31	7	76	2
1	20	9.29	64	6	76	2
1	24	16.40	5	5	76	2
1	24	1.24	8	5	76	3
1	26	2.02	4	7	76	3
1	2	.10	31	6	77	1
1	6	.32	111	6	77	1
1	8	1.84	19	6	77	1
1	10	4.67	44	7	77	1
1	14	7.08	20	6	77	1
1	26	16.53	5	7	77	1
1	11	.23	243	1	78	2
1	12	1.00	82	2	78	2
1	13	.54	745	2	78	2
2	20	4.19	6	5	76	2
2	24	9.83	6	5	76	2
2	48	45.48	7	5	76	2
2	6	1.21	5	6	77	1
2	12	1.74	14	7	77	1
3	2	.13	13	6	77	1

Table B.15 Growth estimates derived from data in Table B.1 and water level changes for *Acarichthys heckeli*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	8.29	.055	.35	.19	77	1
1	9.36	.100	.55	.14	77	1
1	3.21	.048	.78	.23	77	1
1	6.02	.520	4.49	.17	77	1

1	1.95	.557	14.81	-.16	77	1
2	1.10	.050	2.34	-.01	76	1
2	8.15	.450	2.87	.82	76	1
2	8.81	.730	4.30	.51	76	1
2	4.71	.718	7.91	.44	76	1
2	3.57	.840	12.21	.18	76	1
2	4.19	1.338	16.56	-.05	76	1
2	.22	.083	19.46	-.46	76	1
2	26.72	2.040	3.97	.10	76	2
2	15.16	2.475	8.48	-.01	76	2
2	22.28	.075	.17	.32	77	1
2	1.02	.005	.26	.18	77	1
2	12.23	.080	.34	.12	77	1
2	6.50	.060	.48	.17	77	1
2	21.14	.370	.91	.30	77	1
2	4.96	.135	1.41	.31	77	1
2	3.73	.120	1.67	-.17	77	1
2	9.20	.385	2.17	.02	77	1
2	3.42	.186	2.83	.29	77	1
2	7.58	.584	4.00	.13	77	1
2	14.83	1.960	6.87	.40	77	1
2	5.12	.965	9.80	.48	77	1
2	14.18	.225	.82	.48	77	2
2	32.18	1.705	2.76	.34	77	2
3	2.14	.262	6.36	.64	76	1
3	8.07	1.265	8.14	.53	76	1
3	10.10	2.992	15.40	.47	76	1
3	.76	.358	24.25	-.12	76	1
3	3.19	1.897	30.91	-.73	76	1
3	3.00	.465	8.03	.25	76	2
3	1.68	.285	8.79	.10	76	2
3	1.95	.376	9.99	-.10	76	2
3	7.81	2.139	14.23	-.43	76	2
3	1.99	.762	19.83	-.85	76	2
3	3.42	.021	.32	.19	77	1
3	8.12	.075	.48	.31	77	1
3	10.12	.145	.75	-.19	77	1
3	15.12	.365	1.25	.05	77	1
3	7.19	.260	1.88	.36	77	1
3	7.84	.380	2.52	.12	77	1
3	1.81	.105	3.01	.14	77	1
3	15.45	1.315	4.43	.42	77	1
3	5.32	.655	6.40	.47	77	1
3	.69	.095	7.15	.35	77	1
3	3.87	.600	8.05	.53	78	1
3	30.58	.250	.43	.52	78	2

Table B.16 Growth estimates derived from data in Table B.2 and water level changes for *Plagioscion squamosissimus*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	4.60	.045	.51	.22	77	1
2	1.65	.025	.79	.32	77	1
3	21.02	.095	.24	.11	77	1

Table B.17 Growth estimates derived from data in Table B.3 and water level changes for *Plagioscion montei*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
3	9.63	.025	.13	.11	77	1
3	30.66	.230	.39	.32	177	1
3	12.10	.270	1.16	.14	177	1

Table B.18 Growth estimates derived from data in Table B.4 and water level changes for Engraulidae sp.A 1

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	22.28	.105	.25	.31	77	1
1	17.00	.170	.52	.19	77	1
1	11.55	.040	.18	.13	77	2
1	5.37	.047	.46	.12	77	2
1	7.76	.187	1.25	.21	77	2
1	4.80	.216	2.34	.42	77	2
2	2.77	.027	.50	-.01	76	1
2	7.42	.090	.63	.82	76	1
2	11.08	.195	.91	.52	76	1
2	14.64	.435	1.55	.56	76	1
2	.59	.025	2.18	.15	76	1
2	3.93	.050	.66	.17	77	1
2	3.23	.053	.85	.15	77	1
2	1.03	.022	1.11	.21	77	1
3	22.58	.215	.50	.73	76	1
3	1.42	.028	1.02	.15	76	1
3	5.77	.010	.09	-.41	77	1

3	5.25	.012	.12	.17	77	1
3	7.76	.042	.28	.18	77	1
3	3.46	.030	.45	.31	77	1
3	6.69	.127	.99	.13	77	1
3	8.66	.300	1.80	.12	77	1
3	4.72	.020	.22	.36	77	2
3	20.40	.155	.40	.12	77	2

Table B.19 Growth estimates derived from data in Table B.5 and water level changes for *Semaprochilodus taeniatus*

Region	Specific Growth Rate,G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	1.63	.175	5.58	.72	76	1
1	14.48	2.220	7.97	.56	76	1
1	9.35	2.235	12.43	.52	76	1
1	7.06	5.417	39.85	.32	76	1
1	1.79	2.525	73.24	-.08	76	1
1	16.00	.040	.13	.19	77	1
1	4.21	.015	.19	.13	77	1
1	40.18	.680	.88	.15	77	1
1	11.44	.440	2.00	.26	77	1
1	3.75	.205	2.84	.11	77	1
1	15.74	1.438	4.75	-.03	77	1
1	5.66	.765	7.03	.37	77	1
1	12.55	2.480	10.27	.14	77	1
1	11.02	3.430	16.18	.12	77	1
1	5.65	3.167	29.11	.41	77	1
1	19.12	.320	.87	.06	78	1
2	10.46	2.135	10.61	.54	76	1
2	10.75	3.880	18.76	.57	76	1
2	3.64	2.205	31.46	.25	76	1
2	.69	.010	.75	.31	77	1
2	10.37	1.649	8.26	.09	77	1
3	2.59	.351	7.03	.02	77	1

Table B.20 Growth estimates derived from data in Table B.6 and water level changes for *Semaprochilodus insignis*

Region	Specific Growth Rate,G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	8.71	1.382	8.25	.54	76	1
1	5.77	.170	1.53	.58	76	2

1	28.20	2.015	3.72	.39	76	2
1	11.47	2.262	10.25	.26	76	2
1	44.78	1.055	1.23	.15	77	1
1	.56	.025	2.31	.26	77	1
1	1.91	.092	2.51	.11	77	1
1	18.10	1.476	4.24	-.03	77	1
1	11.23	1.595	7.39	.37	77	1
1	8.13	1.665	10.65	.14	77	1
1	7.28	2.005	14.32	.12	77	1
1	8.81	5.632	33.21	.41	77	1
1	65.30	.540	.43	.37	78	1
1	17.33	.280	.84	.06	78	1
2	7.80	1.470	9.80	.54	76	1
2	6.04	.712	6.13	.42	76	2
2	13.29	3.743	14.64	.14	76	2
2	.32	.128	20.54	-.38	76	2
2	8.61	9.924	59.89	-.47	76	2
2	2.06	4.253	107.11	.25	76	2
2	13.42	.675	2.61	-.05	77	1
2	9.86	1.685	8.88	.19	77	1
2	20.73	1.360	3.41	.34	77	2
3	9.38	1.093	6.06	.53	76	2
3	2.63	.970	19.17	-.12	76	2
3	7.09	4.296	31.49	-.87	76	2
3	2.06	1.517	38.25	-.93	76	2
3	.63	.517	42.16	.08	76	2
3	1.54	.141	4.75	.06	77	1
3	2.42	.299	6.41	.28	77	1
3	1.82	2.988	85.38	-.00	77	1

Table B.21 Growth estimates derived from data in Table B.7 and water level changes for *Prochilodus nigricans*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	10.07	.466	2.41	.47	77	1
2	16.78	1.143	3.54	.57	77	1
2	4.71	1.998	22.02	.03	77	1
2	1.18	.900	39.41	-.63	77	1
2	4.46	3.790	44.10	-.87	77	1
2	7.00	7.450	55.34	-1.03	77	1
2	5.68	12.195	111.57	.03	77	1
2	34.18	.595	.91	.34	78	1
3	5.06	1.864	19.13	-.05	77	1
3	9.38	7.768	43.06	-.73	77	1
3	2.23	2.532	59.00	-.83	77	1
3	.31	.392	65.51	.08	77	1

3	3.30	4.998	78.70	.19	77	1
3	4.17	8.294	103.30	.31	77	1
3	8.54	24.796	150.88	-.13	77	1

Table B.22 Growth estimates derived from data in Table B.8 and water level changes for *Curimata latior*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	11.35	.190	.87	.56	76	2
1	6.79	.188	1.44	.55	76	2
1	13.42	.630	2.44	.39	76	2
1	26.10	.364	.73	.32	77	1
1	4.24	.105	1.29	-.13	77	1
1	28.87	1.735	3.13	-.03	77	1
1	6.50	.695	5.56	.37	77	1
1	9.17	1.705	9.66	.13	77	1
2	28.36	.327	.60	.57	76	2
2	5.77	.120	1.08	.57	76	2
2	14.48	.755	2.71	.32	76	2
2	6.15	1.296	10.95	.05	76	3
2	26.29	.225	.45	.30	77	1
2	21.70	.480	1.15	.31	77	1
2	31.60	.465	.77	.14	77	2
2	5.14	.135	1.37	.40	77	2
2	9.89	.441	2.31	.42	77	2
3	13.41	.325	1.26	.54	76	1
3	15.73	.295	.98	.49	76	2
3	3.63	.808	11.56	-.27	76	2
3	4.81	3.217	34.76	.21	76	2
3	42.25	.260	.32	.14	77	2
3	8.29	.110	.69	.42	77	2
3	8.66	.160	.96	.47	77	2
3	17.53	.570	1.69	.35	77	2

Table B.23 Growth estimates derived from data in Table B.9 and water level changes for *Curimata kneri*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
2	9.02	.042	.24	.08	77	1
2	6.73	.059	.46	-.13	77	1
2	23.96	.530	1.15	-.52	77	1

2	14.26	.635	2.31	-.63	77	1
2	16.40	2.006	6.36	-.72	77	1

Table B.24 Growth estimates derived from data in Table B.10 and water level changes for *Colossoma macropomum*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	18.22	1.360	3.88	.72	76	1
1	22.39	3.965	9.20	.56	76	1
1	3.16	5.437	89.28	-.12	76	1
1	2.26	.005	.12	.19	77	1
1	15.29	.050	.17	.13	77	1
1	25.08	.205	.42	.15	77	1
1	34.00	1.190	1.82	.26	77	1
1	3.71	.301	4.22	.14	77	1
1	3.02	.411	7.06	.28	77	1
1	17.00	.175	.54	.21	78	1
2	31.20	.285	.48	.30	77	1
3	10.93	.137	.65	.60	76	1
3	1.22	.003	.13	.14	77	1
3	14.44	.050	.18	.18	77	1
3	39.91	.760	.99	.31	77	1
3	14.93	.705	2.45	.30	77	1
3	2.42	.163	3.48	-.07	77	1

Table B.25 Growth estimates derived from data in Table B.11 and water level changes for *Triportheus albus*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	2.26	.317	7.29	.60	76	1
1	7.02	1.435	10.62	.55	76	1
1	1.37	.369	13.97	.36	76	1
1	.72	.206	14.80	.26	76	1
1	1.54	.465	15.62	.11	76	1
1	1.33	.441	17.21	-.09	76	1
1	.09	.035	18.46	-.36	76	1
1	.67	.294	22.67	-.03	76	1
1	11.53	.272	1.23	.18	77	1
1	11.59	.700	3.14	.32	77	1
1	4.04	.372	4.80	-.08	77	1
1	6.49	.820	6.56	.32	77	1

1	1.47	.239	8.43	.28	77	1
1	1.62	.437	13.95	-.16	77	1
1	4.84	2.138	22.93	-.54	77	1
1	7.35	.525	3.71	.26	78	1
2	1.29	.478	19.27	-.15	76	1
2	24.80	.174	.37	.13	77	1
2	12.70	.245	1.00	.25	77	1
2	3.44	.108	1.63	.07	77	1
2	6.43	.260	2.10	.02	77	1
2	3.27	.170	2.70	.24	77	1
2	4.02	.307	3.96	.34	77	1
3	10.13	2.045	10.50	.56	76	1
3	1.26	.378	15.51	.50	76	1
3	16.35	.074	.24	.03	77	1
3	8.77	.065	.38	.32	77	1
3	11.55	.150	.67	.14	77	1
3	10.00	.243	1.27	.17	77	1
3	7.73	.285	1.92	.31	77	1
3	1.87	.084	2.33	.13	77	1
3	1.28	.064	2.59	.00	77	1
3	4.67	.402	4.48	.33	77	1

<u>Table B.26</u> Growth estimates derived from data in Table B.12 and water level changes for <u>Triportheus angulatus</u>

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	18.72	1.300	3.61	.72	76	1
1	4.68	.963	10.69	.43	76	1
1	2.40	.936	20.22	-.06	76	1
1	2.36	1.334	29.30	-.75	76	1
1	28.84	1.287	2.32	.43	76	2
1	3.59	.170	2.46	.11	77	1
1	5.91	.750	6.59	.21	77	1
2	6.25	.810	6.73	.56	76	1
2	5.46	1.002	9.55	.47	76	1
2	9.60	.115	.63	.57	76	2
2	23.04	.705	1.59	.38	76	2
2	8.19	.697	4.42	.21	76	2
2	2.47	.429	9.02	-.39	76	2
2	17.33	.155	.47	.17	77	1
2	12.16	.272	1.16	.31	77	1
2	6.41	.811	6.57	.15	77	1
2	16.25	.855	2.73	.34	77	2
3	8.17	2.222	14.14	.17	76	1
3	1.14	.427	19.44	-.06	76	1
3	2.29	1.033	23.39	-.48	76	1

3	41.91	.665	.83	.56	76	2
3	24.02	1.280	2.77	.37	76	2
3	2.00	.271	7.03	-.30	76	2
3	2.76	.607	11.41	.20	76	2

Table B.27 Growth estimates derived from data in Table B.13 and water level changes for *Triportheus elongatus*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	6.16	.265	2.23	.72	76	1
1	18.14	1.340	3.84	.56	76	1
1	3.00	.992	17.19	-.02	76	1
1	.70	.422	31.26	-.19	76	1
1	6.68	.484	3.77	.11	76	2
1	1.86	.732	20.42	-.07	76	2
1	10.40	.020	.10	.19	77	1
1	5.77	.015	.13	.13	77	1
1	36.55	.355	.50	.15	77	1
1	9.81	.200	1.06	.26	77	1
1	6.81	.253	1.93	.07	77	1
1	6.73	.415	3.21	.49	77	3
1	3.01	.535	9.24	-.17	77	3
1	33.70	.233	.36	.32	78	1
2	10.26	.707	3.58	.51	76	1
2	31.45	.245	.40	.56	76	2
2	8.38	.125	.77	.57	76	2
2	14.33	.371	1.34	.36	76	2
2	6.15	.269	2.28	.25	76	2
2	4.73	.461	5.06	-.16	76	2
2	7.31	1.442	10.25	-.75	76	2
2	6.92	2.020	15.16	-1.03	76	2
2	26.00	.100	.20	.12	77	1
2	8.05	.055	.36	.17	77	1
2	4.09	.035	.45	.30	77	1
2	1.20	.014	.59	.22	77	1
2	15.76	.670	2.21	.41	77	2
2	11.53	.127	.57	.24	77	3
2	8.94	.218	1.27	.27	77	3
3	36.00	.540	.78	.56	76	2
3	2.60	.682	13.61	-.10	76	2
3	.98	.522	27.46	.05	76	2
3	30.74	.405	.69	.73	76	3
3	6.47	.360	2.89	.45	76	3
3	4.46	1.011	11.77	-.17	76	3
3	1.70	.662	20.17	-.96	76	3
3	11.33	.051	.24	.24	77	1

Table B.28 Growth estimates derived from data in Table B.14 and water level changes for *Brycon melanopterum*

Region	Specific Growth Rate, G (/year)	Weight Increment (g/week)	Mean Weight (g)	Water Level Change (m/week)	Year Class	Cohort No.
1	23.89	2.925	6.37	.72	76	2
1	7.19	1.777	12.85	.54	76	2
1	12.44	.390	1.63	.58	76	3
1	13.61	.055	.21	.16	77	1
1	36.59	.760	1.08	.15	77	1
1	22.60	1.415	3.25	.26	77	1
1	5.33	.603	5.88	.11	77	1
1	3.46	.787	11.81	.24	77	1
1	24.03	.189	.41	.22	78	2
2	10.45	1.410	7.01	.54	76	2
2	2.79	1.485	27.65	-.15	76	2
2	3.11	.088	1.48	.26	77	1