THE ECOLOGY AND MANAGEMENT OF THE FISHES OF THE OKAVANGO DELTA, BOTSWANA, WITH PARTICULAR REFERENCE TO THE ROLE OF THE SEASONAL FLOODS

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by

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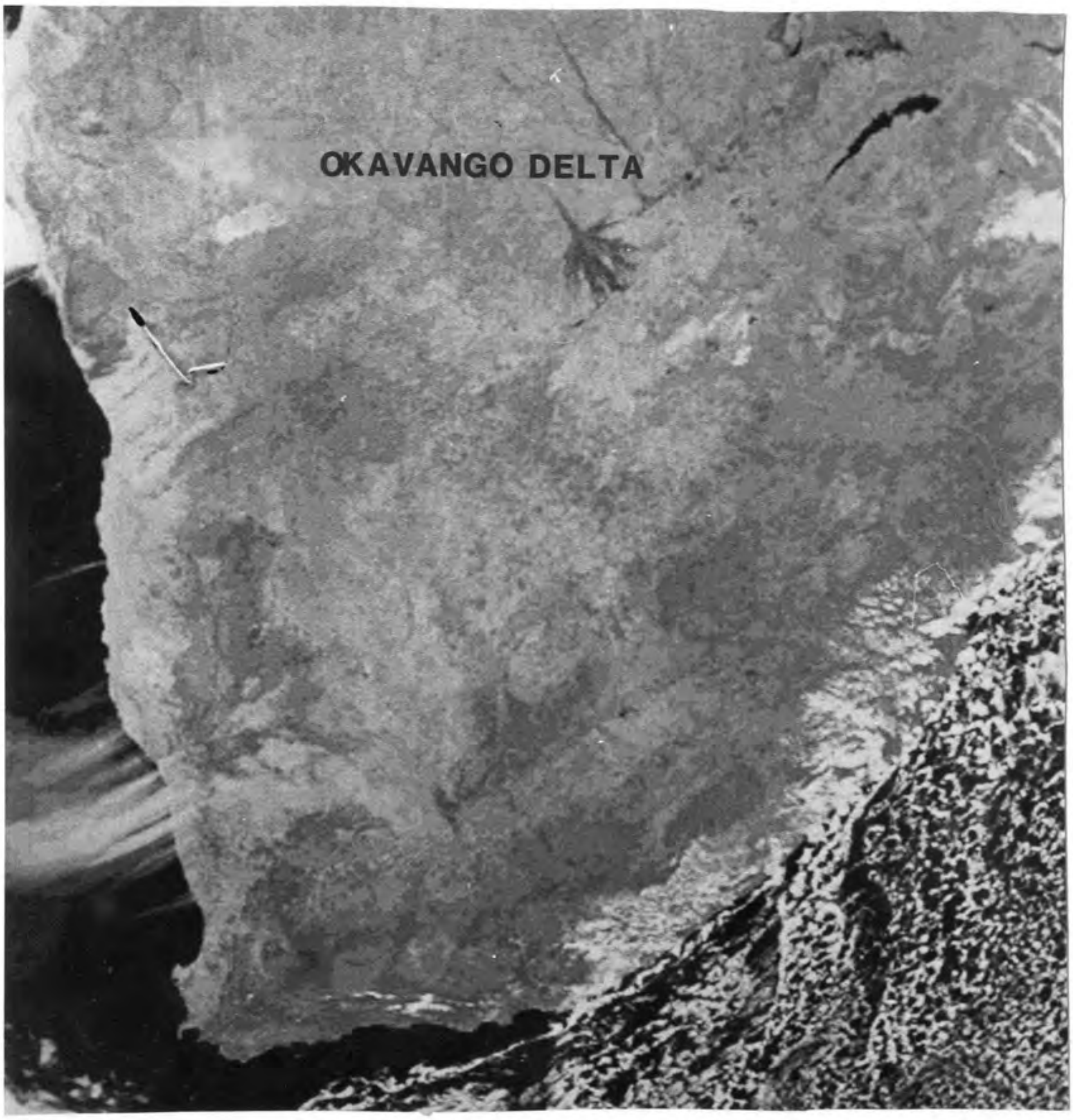
Dedicated to the memory of the late Professor Karl F. Lagler, University of Michigan, Ann Arbor, Michigan, USA.



"A town is saved not more by righteous men in it than by the woods and swamps that surround it."
Henry David Thoreau

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ABSTRACT

The Okavango is a vast inland delta system in northern Botswana which receives an annual flood from the highlands of southern Angola. There are distinct communities of fish in the Okavango which can be separated from each other by the physical characteristics of the different habitat types with which they co-evolved.

This thesis provides an account of the biology and ecology of selected fish species in the Okavango Delta. Their response to the annual flood regime, and the environmental factors which limit their distribution and abundance, are examined. The thesis emphasizes the importance of water fluctuations in determining the nature of the fish fauna and the reaction of the fishes in terms of community structure, movements, breeding, predator-prey interactions and feeding.

Four major ecotones were studied in the Okavango Delta. In the riverine floodplain and perennial swamp ecotones a higher species diversity was recorded than in the seasonal swamp and drainage rivers ecotones where diversity was lowest and comprised mainly of smaller fish species. A greater variety of habitat types was associated with the riverine floodplain and perennial swamp relative to the seasonal swamp and drainage rivers. The variety of habitat types between ecotones is associated with the degree of flood inundation in the respective ecotones.

During the course of this study, annual recruitment of fish into the drainage rivers was from refugia in the seasonal swamp whereas the greatest degree of lateral and longitudinal movement was in the riverine floodplain and perennial swamp. Movement was in response to both biological requirements, such as availability of food and spawning sites, and physical features of the environment, such as the changing water depth.

The total catch per unit effort (CPUE) of fish throughout the year was more constant in the riverine floodplain and perennial swamp than in the seasonal swamp and drainage rivers where CPUE fluctutated widely. An increase in CPUE during the duration of this study was apparent and related to the magnitude of the annual flood.

In contrast to most other African wetlands, the arrival of the annual flood in the Okavango Delta coincides largely with the dry winter months. This situation presented an opportunity to compare the influence of floods and water temperature on the reproductive biology of the selected fish species. The results show a definite pattern and indicate that both the flood cycle and increased water temperatures greatly influence the breeding cycles of the selected species.

The tilapia Oreochromis andersonii exhibited a considerable degree of phenotypic plasticity. Fish from the seasonally inundated areas showed a smaller mean size, egg size and larger number of eggs relative to fish in the perennially flooded areas. The size at sexual maturity was also smaller. These different reproductive characteristics exhibited by O. andersonii are dependent on the degree of water retention in the different habitats.

The fishes of the Okavango have adopted other reproductive strategies to survive the changing environmental conditions brought about by an annual flood cycle. These strategies include the construction of foam nests, as described for Hepsetus odoe, for guarding the young and to provide an oxygen-rich environment.

Two main non-piscivorous feeding pathways were identified in the Okavango. These are a detritus pathway based on dead plant and animal material, and an epiphyte pathway, based on algae and invertebrates that are attached to plant stems. Seasonal changes in diet in relation to the annual flood were recorded. The most dramatic change was demonstrated by the catfish Clarias gariepinus which congregates in mass aggregations in the northern regions of the Delta and hunt in packs. Pack-hunting by catfish is a regular response to the annual fluctuations in water level.

It is my conclusion that the main flow of biotic and abiotic stimuli within the Okavango Delta originates from the relatively hydrologically stable riverine floodplain and perennial swamp ecotones to the widely fluctuating seasonal swamp and drainage rivers ecotones. The relatively stable ecotones allow a diverse and biotically interdependent fish community to develop, whereas the widely fluctuating seasonal swamp and drainage rivers ecotones are characterized by a less diverse and interdependent fish community.

The degree of abiotic and biotic interdependence among fish in an ecotone is very important for the long term management of the Okavango Delta. Potential developers have to determine whether the effect of a given action by man is likely to result in a long term disturbance or merely in an elastic recoil to a more or less similar state. Recommendations are made on the conservation and management of Okavango fishes taking into account the ecological characteristics of the delta.

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CHAPTER 1

INTRODUCTION

Floodplain ecosystems, such as the Okavango Delta in northern Botswana (Fig. 1.1), are subject to regular cycles of flooding and draining. The timing, magnitude and duration of these floods are not constant from year to year and in the Okavango these parameters are determined largely by the periodicity and amount of annual rainfall within the highlands of southern Angola.

Floodplain fish populations are often characterized by a dependence on a natural, annual flood cycle for their survival (Lowe-McConnell, 1975; Welcomme, 1979). The floods periodically connect the water bodies on the floodplain to the river, and facilitate essential ecological functions, such as the movement and spawning of most fish species. By inundating low-lying regions, the flood waters also convert terrestrial plant and animal matter into food for fish and other aquatic organisms. This allochthonous food input is often utilized by the fish for the ripening of gonads before spawning, and for the growth of the fish fry (Lowe- McConnell, 1975; Welcomme, 1979). The inundation of shallow floodplains and adjacent terrestrial lands is also important for providing safe nursery sites for fish larvae and juveniles during their early stages of development (Bruton & Jackson, 1983). Within the Okavango Delta a similar pattern of annually fluctuating water levels which regulate the structure of the fish community is apparent, but the processes involved are not fully understood (Campbell et al., 1976).

The fishes of the Okavango Delta represent a valuable natural resource for the people of Botswana. Increased demand for fish has, however, resulted in an escalation in fishing effort over the last ten years. Through the efforts of the Botswana Fisheries Unit, an expanding commercial fishery now exists in the delta. Recreational fishing is also increasing as new "tourist" fishing camps are licensed and more people visit the delta to fish.

These exploitation pressures are further compounded by natural and artificial environmental perturbations. The extended period of drought and of low water levels since 1982 (broken in 1988) drastically changed the characteristics of the delta by decreasing the area of floodplain habitat.

Botswana's 2.2 million head of cattle form the basis for one of the main economies of the country. For many years nagana (sleeping sickness in cattle) kept the herds and people away from the Okavango Delta. Since the early 1970's campaigns to control the tsetse fly (Glossina morsitans),

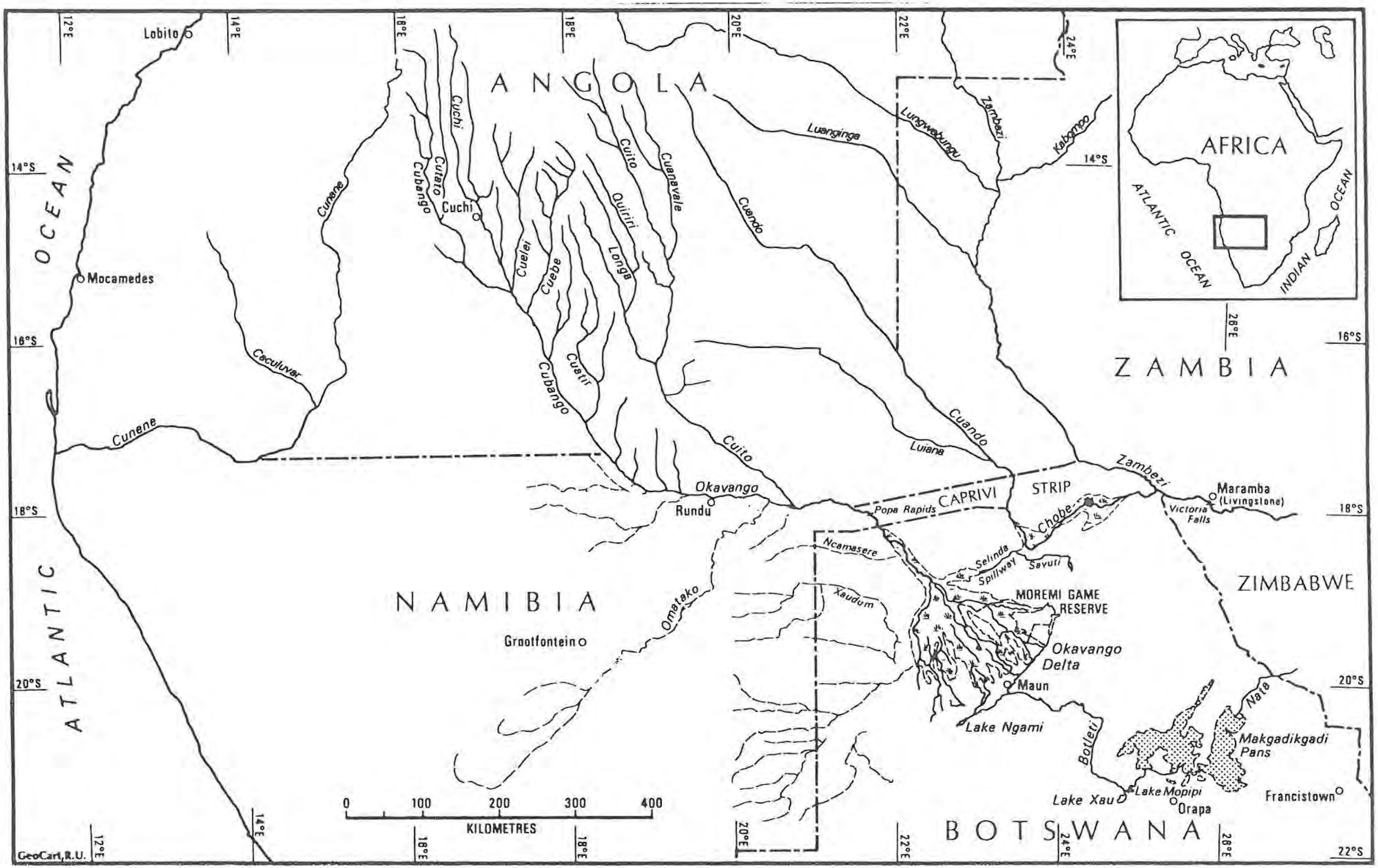


Figure 1.1. The Okavango Drainage system in Angola, Namibia and Botswana flanked in the west by the Cunene River and in the east by the Upper Zambezi system (from Skelton et al., 1985).

a vector of the disease, using insecticides have been successful in the delta (Davies & Bowles, 1976). However, because the tsetse fly readily recolonizes the Okavango from adjacent countries, particularly Namibia and Zambia, repeated applications of insecticides have been carried out in the delta (Merron & Bruton, 1989).

Throughout the course of this research project aerial spraying of insecticides occurred over large areas of the Okavango Delta. Although every effort has been made by the Botswana authorities to use ultra-low volumes of insecticides, repeated applications of insecticides have had an effect on certain non-target organisms, including fishes (Douthwaite et al., 1981; Matthiessen et al., 1982; Merron, 1986; Merron & Bruton, 1989, 1990a & b). In villages along the Okavango River in Namibia ground spraying of DDT for mosquito control also occurs, the magnitude of which is unknown. Petroleum pollution caused by military vehicles crossing the Okavango River prior to Namibia's (1990) independence has also been documented by Skelton & Merron (1987).

Botswana is a dry country; its average annual rainfall is 250 mm in the south and 650 mm in the north. The Okavango Delta contains over 95% of the country's surface water resources and therefore features strongly in industrial and agricultural development plans for Botswana. A water abstraction scheme at Rundu in Namibia (Fig. 1.1) and schemes to canalise and regulate the rivers in the southern areas of the Okavango near Maun (Fig. 1.1) are also being constructed and may affect the dynamics of the flood cycle.

It is apparent, therefore, that there are a variety of man-induced and natural stresses on the Okavango Delta. The potential of the delta to continue to supply vital natural resources, such as fish and water, to the people of Botswana may thus be detrimentally affected. It is therefore essential that adequate scientific information on the fish stocks should be obtained and that an understanding of the biology and ecology of the fishes and their responses to the annual flood regime should be reached.

During the recent drought in northern Botswana the area of Lake Ngami, a sump lake at the southern end of the Okavango system (Fig. 1.1), decreased from over 150 km^2 in 1979 to less than 1 km^2 in 1983 (Shaw, 1985). The fish community was reduced from 26 species, including benthic, pelagic, and littoral forms, to two scavengers, the catfishes, Clarias gariepinus and C. ngamensis (Bruton & Jackson, 1983). In late 1984 Lake Ngami once again received flood water and subsequently 12 fish species recolonized the lake (Merron & Bruton, 1988). This pattern demonstrates the resilience of both Lake Ngami and the recolonizing fish fauna to natural fluctuations in environmental conditions.

Floodplain ecosystems such as the Okavango are characterized by a fluctuating environment and have been described as generally unstable and fragile (Lowe- McConnell, 1975). It is my contention that the Okavango Delta is not unstable but that it is a changeable, regularly cycling ecosystem. The fish species inhabiting the Okavango can be classified as either having a very broad or narrow distribution that is influenced by the annual flood cycle. Stenotopic fish species exhibit resistant, density-dependent life history characteristics, whereas eurytopic species display resilient, density-independent life history characteristics. Similar life history characteristics in fish species described from other wetland systems (Welcomme, 1979; Furse et al., 1979; Kok, 1980; Benech et al., 1983) appear to support this classification.

The overall objective of this study was to establish the response of the fishes to the annual flood cycle and to identify the key factor or factors (e.g. timing, magnitude and duration) of the flood which determine the nature of the fish communities. The broad hypothesis is that the annual flood regime is important in maintaining the fish populations. The specific hypothesis is that the main factors determining the distribution and abundance of fish communities in the delta are the permanence (retention time) of water in particular habitats and whether or not the water is flowing. It is believed that these two factors determine other physical features such as the extent of aquatic macrophyte communities, substrate type and oxygen values, as shown for other wetland systems (Lowe-McConnell, 1975; Welcomme, 1979). Obviously these parameters will also affect food quantity and quality, spawning periodicity and other biological events in the delta.

This hypothesis is tested on a comparative basis by identifying the major habitat types such as perennially and seasonally inundated areas of the delta. Although both environs are subject to flooding, the enormous size of the delta (15,000 km^2 at high flood) causes the timing, magnitude and duration of flooding to vary, with the greatest fluctuations occurring in the southern (downstream) end of the system.

In addition, an interbasin comparative approach is made with the Pongolo floodplain, a riverine floodplain in Zululand, as this system was being studied simultaneously, although not to the same degree as the Okavango. This comparison provided an excellent opportunity to compare these two important floodplain ecosystems of southern Africa. Comparisons of Okavango fishes with the ichthyofaunae of other palustrine wetland ecosystems such as Lake Liambezi and the Kwando-Linyanti swamps (van der Waal, 1976; Merron, 1990), Kafue floodplain (Chapman et al., 1971; Lagler et al., 1971), Zambezi (Jackson, 1961a; Bell-Cross, 1974), Amazon (Goulding, 1980), Everglades (Kushlan, 1976, 1980) and Pongolo (Kok, 1980; Merron et al., 1989) were also made.

This research also offered an opportunity to test fundamental theories regarding community stability and alternative life-history styles. These theories were examined by using the permanence of the water in a particular locality as an indication of the stability ("predictability") or instability ("unpredictability") in the Okavango. The Okavango is predictable in the sense that it is driven by an annual flood cycle. What is irregular or unpredictable, however, is the water retention and flow rates which increases its effect on the fish fauna in a downstream direction.

CHAPTER 2

THE OKAVANGO DELTA ECOSYSTEM

The Okavango Delta is situated in northwestern Botswana (Fig. 1.1) and fluctuates in area from 15000 km^2 during the flood season to 6000 - 8000 km^2 during the dry season (Campbell, 1983). Geologically the Okavango is a young system (approximately 10000 years old) which, before major uplifting, formed a drainage channel into a great lake called Makgadikgadi (Campbell, 1983). Presently, the Okavango is the only large river of the world which forms an inland delta.

The Okavango River rises in a series of headwater streams on the southern slopes of the Angolan highlands (Fig. 1.1). These streams flow south and south-eastwards then gather to form a large mainstream (the Cubango), which turns eastwards shortly after reaching the Angola-Namibia border. A second major branch of the system (the Cuito) also rises in the Angolan highlands and joins the mainstream before it flows across and forms the western boundary of the Caprivi Strip (Fig. 1.1). The Okavango enters Botswana as a single broad river, approximately 150 m wide and 4 m deep, and meanders within a broad riverine floodplain (average width 15 km) bounded by fault lines running south-easterly from the Namibian border. It is only after the confines of the riverine floodplain (colloquially termed the riverine panhandle) that the Okavango branches out to form the anastomoses of the delta.

The flood waters arrive in the northern riverine floodplain in January and take approximately six months to traverse the delta reaching the drainage rivers in the south in June (Fig. 2.1). By the time the floodplains and rivers in the southern areas are full, the water level is low again in the northern regions. The timing, magnitude and duration of the flood is not constant from year to year. Due to the nonavailability of hydrological data for the Okavango Delta in Botswana, the daily discharge of water in the Okavango River at Rundu in Namibia from 1983 to 1986 is shown in Figure 2.2. It is apparent that between 1983-84, the highest discharge was recorded with a maximum in excess of 800 m^3s^{-1} and a minimum of 30 m^3s^{-1}. The 1984-85 flood cycle was the lowest recorded with a maximum daily discharge at the height of the flood of approximately 410 m^3s^{-1}. The 1985-86 flood cycle, although higher than the 1984-85 period, had a truncated duration when compared to former years.

One of the most important features to consider in this thesis is that the timing, magnitude and duration of the annual Okavango flood is different each year and that it has a cycle of high and low

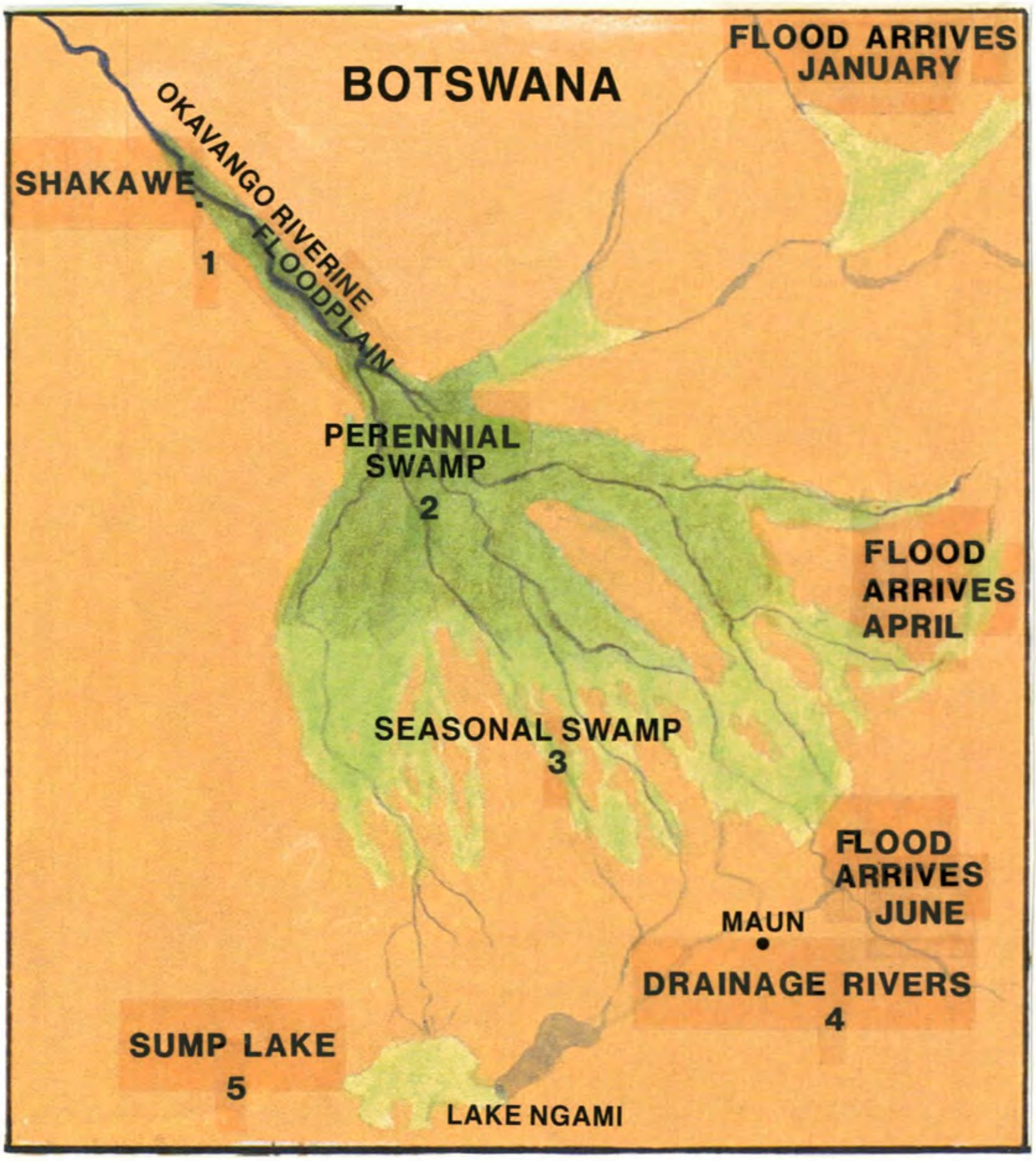


Figure 2.1. Map of the Okavango Delta, Botswana showing the approximate arrival of the annual flood waters and location of all ecotones. The following ecotones are shown: 1: Okavango riverine floodplain; 2: Perennial swamp; 3: Seasonal swamp; 4: Drainage rivers; 5: Sump lake.

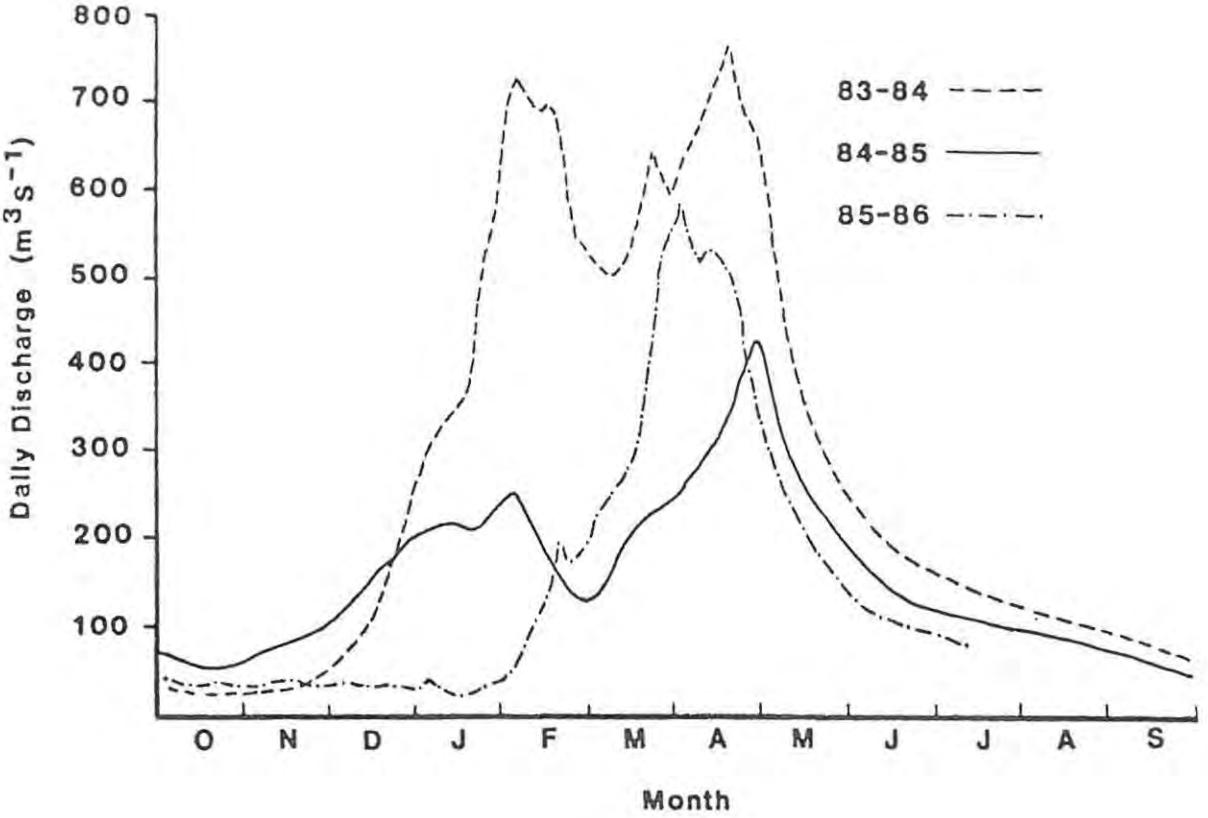


Figure 2.2. Daily discharge of the Okavango River at Rundu for the period October 1983 to July 1986. Discharge data provided by the Department of Water Affairs, Namibia.

water levels. However, the cycle does not return to the same point each year and fluctuates widely depending on the magnitude of the annual flood. Although there is a water level increase and a water level decrease each year, the starting point for the beginning of each annual cycle depends on the rainfall history in Angola and the nature of the drainage patterns in Botswana. It must be emphasized that the flow of water through the delta can be influenced by seismographic disturbance and channel blockages, which can alter the drainage patterns in a given year (Ernest, 1976). The Okavango is thus a dynamic system which varies in space and time and in major physico-chemical factors, such as water availability and quality, which can change each year among the different habitat types.

Globally, and in the context of its recent geological age, the Okavango Delta can be considered to be a stable ecosystem as it persists with time. Regionally, however, it is very changeable and unpredictable. In terms of its hydrology, the Okavango is more stable (predictable) in the northern regions and less stable (unpredictable) in the southern regions. The magnitude of difference in the area covered by water during different floods is in the order of 1 to 2 in the northern Delta and 1 to 10 in the southern seasonal areas (Wilson & Dincer, 1976). In addition, because the Okavango floods laterally, it therefore also operates along two dimensions.

DISTRIBUTION OF HABITATS

Five major ecological regions are recognized in the Okavango Delta (Fig. 2.1). These are the riverine floodplain, perennial swamp, seasonal swamp, drainage rivers and sump lakes. The sump lake region (e.g. Lake Ngami) was, however, virtually dry during the course of this study. The four ecological regions studied can be considered as ecotones (Holland, 1988) as they grade into, and are dependent on, one another.

The riverine floodplain and perennial swamp ecotones cover approximately two-thirds of the area of the delta. These areas have surface waters up to 3 m deep and are covered with a dense growth of papyrus (Cyperus papyrus), reeds (Phragmites australis), bulrushes (Typha latifolia subsp. capensis) and the fern (Cyclosorus interruptus). In the riverine floodplain the mainstream channel is approximately 150 m wide. The substrate is sandy. The water is clear with secchi disc readings ranging from 3 m at high water level to < 1 m at low water level. The mainstream channel flows at a steady velocity of approximately 1 m/sec at low water level and 4 m/sec at high water level. There are numerous tributaries and oxbow lagoons associated with the mainstream channel. These areas are lined with dense stands of aquatic macrophytes including Nymphaea capensis, Potamogeton thumbergi and Elodea densa. The adjacent sawgrass floodplains and isolated lagoons are flooded between February and June each year.

Upon entering the perennial swamp the mainstream channel splits into three distributary systems, the Thoage, Nqoga and Jao (Fig. 2.3). The Thoage is the western most distributary which, prior to 1960, served as a major drainage channel. However, due to seismographic shifting which resulted in a decreased flow rate, numerous blockages built up which have now choked this river below Nokaneng (Fig. 2.3). The Nqoga extends along the Moanachira and Kwai Rivers and during extremely high floods empties into the Mababe Salt Pan. Since 1960 the Jao has become the primary distributary of the central delta (Shaw, 1984) and after passing through Xo Lagoons is called the Boro River (Fig. 2.3). There is also a northeasterly extension of the upper perennial swamp north of the Moremi Game Reserve along the Selinda (Magwegqana) Spillway which empties into the Linyanti swamps at exceedingly high floods (Fig. 2.3).

The southern seasonal swamp covers about one-third of the area of the delta and is characterised mostly by shallow grass and sedge-covered floodplains. There are, however, certain perennial lagoons such as Nxaraga and Qorokwe (Fig. 2.3). The southern swamp is a seasonally inundated swamp which varies markedly in area, depending on the magnitude of the annual flood from Angola and the amount of local rainfall.

At the southeast end of the Okavango Delta, the main drainage channels, the Boro and the Santandadibe, re-unite along a fault line to form the southwestward-flowing Thamalakane River. The Thamalakane River abruptly changes course to the southeast at its bifurcation into the Nghabe and Boteti Rivers (Fig. 2.3). Lake Ngami, a sump lake in the southwestern corner of the delta, was once fed by the Thaoge River in the extreme west but is now more dependent on the Kunyere and Nghabe Rivers for its water supply (Shaw, 1985; Fig. 2.3). This feature also indicates the changeability of the system as the Boro was, before 1960, not an important drainage river of the delta (Shaw, 1984). Except for a relatively short period in 1982 and late 1984 to early 1985, Lake Ngami was dry during this study period. The Boteti River empties into Lakes Xau and Mopipi and, at high flood levels, into the extensive Makgadikgadi Salt Pans (Fig. 1.1).

ANNUAL FLOOD CYCLE AND LIMNOLOGICAL CHARACTERISTICS

The mean annual inflow into the delta from the headwaters in Angola is 11 x 10^9 m^3, with local rainfall contributing on the average about 5 x 10^9 m^3 (Ernest, 1976). The principal output (96%) is through evapotranspiration (15.4 x 10^9 m^3) with groundwater seepage claiming 0.3 x 10^9 m^3 (Ernest, 1976). The output through the Thamalakane River in the south, therefore, represents approximately 2% of the inflow into the swamps. It must be stressed, however, that these recordings were taken during periods of elevated flood regimes and probably do not represent the amount of water which entered Botswana during the period of this study. The Botswana Department of Water Affairs is actively taking various hydrological measurements to provide a longer time series of inflows into the delta. What is also not known is the frequency of the wet and dry cycles and significance of the one in ten year or one in twenty-five year flood cycle to the productivity of the delta.

Each year the water level in the northern area of the delta recedes from the floodplains, between June and August, leaving behind numerous isolated floodplain lagoons. Depending on the rainfall patterns in the Okavango catchment, the annual floodwaters from Angola begin to arrive at Shakawe in January and reach Maun, at the southernmost part of the delta, in June (see Fig. 2.1). This slow pattern of inundation is due to the extremely low gradient (1:36000) which causes the water to spread out to form the Okavango Delta. The slow flood cycle causes water to reach the

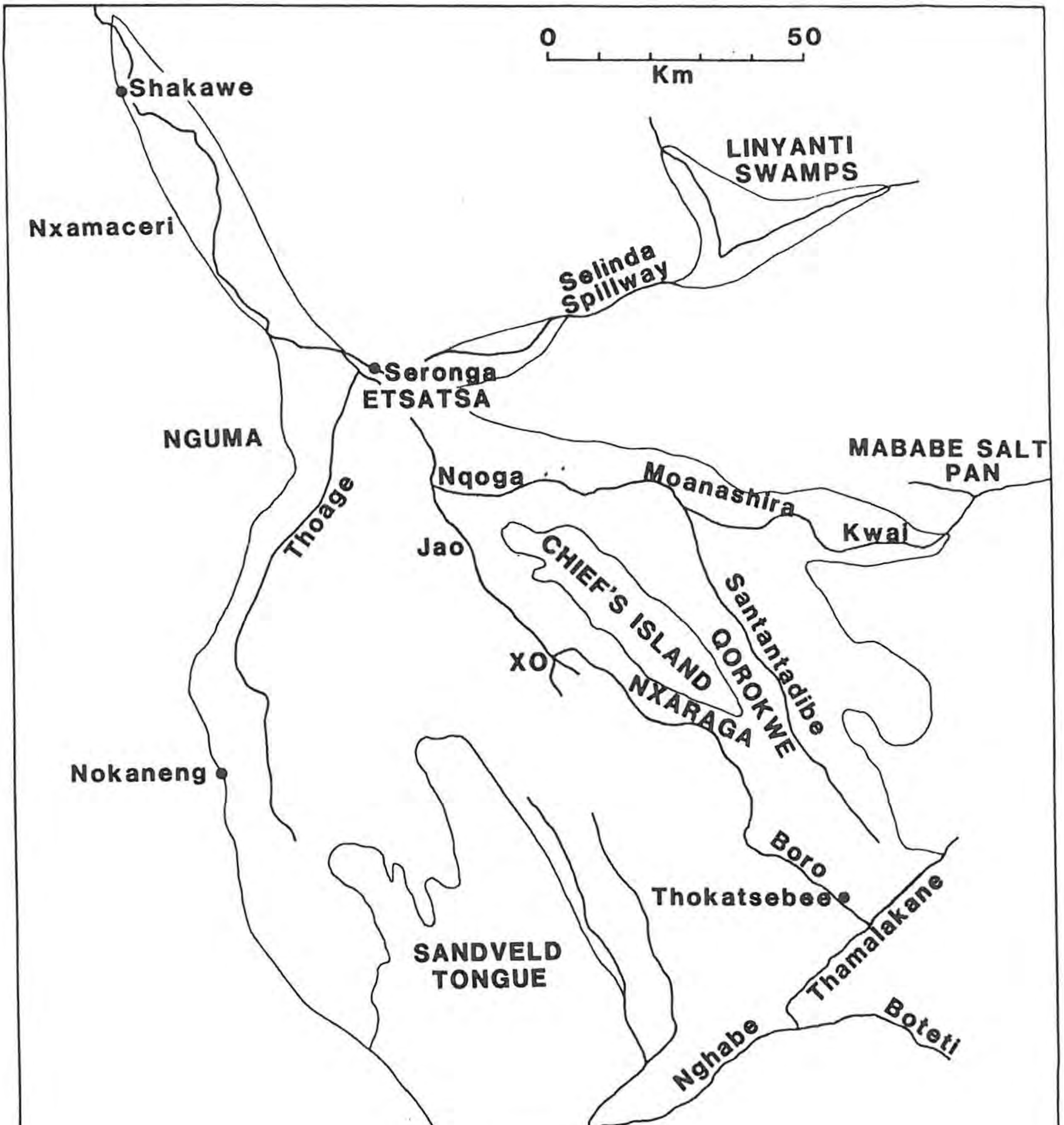


Figure 2.3. Map of the Okavango Delta in Botswana showing the location of all major river systems and place names used throughout this thesis.

southern parts of the swamp during the coldest months when water temperatures are lowest (average June temperature 16°C).

Wetlands such as the Okavango Delta are typically dynamic ecosystems which have high biological productivity. The Okavango system is, however, low in available nutrients when compared to other tropical wetlands and has a water conductivity in the region of 8 uS cm-1 (Thompson, 1976; Hart, 1986; Allanson et al., 1990). The relatively low conductivity may partly be due to the source of the waters (e.g. rainfall in southern Angola) which drains off relatively infertile soils. Upon entering Botswana the watershed does not contribute significantly to the nutrient input from run-off as the topography is flat Kalahari sand with a high moisture deficit and a high seepage rate. The nutrient input into the Okavango largely comes from decomposing aquatic macrophytes and dung deposited by the large numbers of game in the numerous central floodplains or cattle along the fringes of the delta.

The limnology of this system has, however, not yet been fully studied and a paucity of quantitative information exists. During the course of this research project I encouraged limnologists from Rhodes University to provide meaningful information and many have assisted on an "ad hoc" basis. Unfortunately it was beyond the scope of this study to perform an in-depth limnological survey, although readings for various physico-chemical parameters were taken when possible.

Water temperatures have been recorded in the range of 9- 38°C depending on season and site (Reavell et al., 1973; Merron & Bruton, 1984a, 1988). Measurements of pH indicate slightly acidic water in the northern reaches with values between 5.8 and 6.7; whereas in the southern reaches slightly alkaline water is apparent with values between 7.1 and 8.2 (Douthwaite et al., 1981; Merron & Bruton, 1984a & b). The alkaline water in the southern end of the system can be attributed to the large amounts of bicarbonate and carbonate salts that are inundated each year with the flood (pers. observation). Secchi disc transparency during the flood peak is high, often reaching the bottom of most waterbodies (i.e. 2 - 3 m). During the receding and low water level an increase in the amount of organic and inorganic matter moving into the mainstream channel results in a relatively low water transparency with a secchi disc reading of < 1 m.

Oxygen values are low in certain areas, especially in the mainstream channels, during the receding and low water phase when surface oxygen saturation ranged from 39.7 to 65.3% and water temperatures ranged from 26.9 to 28.5°C (Maar, 1965; Merron & Bruton, 1988). The receding flood waters are low in oxygen as a result of the abundant decomposing vegetation on the floodplain. The preliminary evidence suggests that a "wave" of reduced oxygen moves southeastwards in the mainstream channel as the water level recedes. There is also a wide diurnal fluctuation in oxygen levels probably due to the deficit caused by photosynthesis during the day. Oxygen values in slow-flowing parts of the delta can fall below 10% saturation (Merron & Bruton, 1988). Because the physical features of the Okavanga Delta play an important role in determining the composition of fish communities, obvious physical factors such as the depth and flow rates of the water, as well as substrate and macrophyte cover, were recorded at each sampling site and used in the multivariate community analysis.

BRIEF REVIEW OF PREVIOUS FISH RESEARCH

Despite the diversity of and great interest in the fish fauna in other parts of Africa, the Okavango fauna is poorly known. The early history of ichthyological work in the delta is reviewed by Jubb & Gaigher (1971) and Skelton et al. (1985). The latter authors provide an up-to-date checklist of the fishes of the Okavango drainage in Angola, Namibia and Botswana and a review of recent ichthyological research there. It should be emphasized that the major proportion of prior research work on fishes in the Okavango consisted of taxonomic studies and distributional surveys. A total of 83 species have been recorded from the Okavango River and Delta. However, only alpha taxonomic studies have been performed and several phylogenetic problems still remain to be resolved (Skelton et al., 1985).

There are few ecological and biological studies on Okavango fishes. Maar (1965) conducted an early fisheries study for the Oxford Committee for Famine Relief (OXFAM). Brief accounts on the fish and the fishery have also appeared in the Proceedings of the Symposium on the Okavango Delta (Fox, 1976; Gilmore, 1976). Gilmore (1979a & b) examined the food preferences and trophic relationships of certain fish species, particularly with regard to the effects of insecticide spraying. Douthwaite et al. (1981) examined the mortality of fish to insecticides and Bruton (1979, 1980) outlined the results of two multi-disciplinary expeditions from Rhodes University to the Okavango Delta and Lake Ngami. Skelton et al. (1983) outline the results of an expedition to Lake Ngami in December 1982 and Merron et al. (1983) provide a preliminary account of the fish communities in the riverine floodplain at Nxamaceri (see Fig. 2.3) in February 1983.

A quantitative fisheries research programme was launched by the J.L.B. Smith Institute of Ichthyology in November 1983 at the request of the Botswana Fisheries Unit to gather biological data on commercially important fish species. This information was required by the Fisheries Unit to serve as a foundation for recommending ways to increase the local harvest of fish while conserving the long term integrity of this important resource. A partial report on the results of this research programme is given by Merron & Bruton (1988). Recommendations on fisheries management based on species composition, relative abundance and mass contributions in different mesh-size gillnets have already been implemented by the Fisheries Unit and are explained in greater detail in Chapter 8. This thesis is an attempt to synthesize this information so as to provide a detailed interpretation of selected fish species and their responses to the annual flood cycle.

CHAPTER 3

SAMPLING SITES, METHODS AND GENERAL TECHNIQUES

The present study was conducted over the period November 1983 to December 1986. From November 1983 until April 1985 the research was based from the J.L.B. Smith Institute of Ichthyology, 2200 km south of the Okavango. A fully functional research station was set up in April 1985 at the DeBeers (Debswana) Maun Base Camp, 14 km upstream from Maun on the south bank of the Thamalakane River at Matlapaneng (Fig. 2.3).

It should be emphasized that there were considerable constraints in working in an undeveloped country and numerous hazards and logistical problems working in the Okavango Delta. At many of the camp sites lions, leopards, elephants and venomous snakes were a constant threat. On one occasion a staff member, Mr. V. Yose, was confined to a truck for two-days as a pride of eight lions kept a vigil by him. Fortunately the lions lost interest. An indication of one of the campsites used during quarterly surveys is shown in Figure 3.1. Within the numerous waterbodies and channels hippopotami, crocodiles and elephants often disrupted the equipment. On a few occasions hippopotami tipped the boat over, sending staff frantically swimming to shore. In addition, the rough terrain necessitated off-road four wheel driving at times taking two days to reach a sampling site 300 km away! The research vehicle used during 1984 and 1985 the majority of this study is shown in Figure 3.2. Notwithstanding these constraints, the data presented in this thesis does, however, represent the first attempt at obtaining a standardized set of quantitative information for the fishes of the Okavango Delta in relation to the annual flood regime.

Because of the logistical difficulty with accessibility in the mosaic of islands, floodplains, lagoons and river systems in the Okavango Delta, a quarterly sampling programme was followed as accurately as possible. Since the physical and biological features of the delta are extremely variable, the effective sampling of the system required the use of a wide selection of fishing gear, the characteristics and uses of which are detailed below.

Figure 3.1. One of the many campsites used throughout the course of this study. This particular campsite was located approximately 10 km southeast of Nxaraga Lagoon, June 1984. Mr Xavier von Berra, a field assistant during the June-July 1984 survey is present.

Figure 3.2. The forward control 4x4 land rover used during 1984 and 1985 in the Okavango Delta.

SAMPLING SITES

The sampling sites chosen to study the abundance, biology and ecology of selected commercially and ecologically important species were located in all the major ecotones of the delta. Within the riverine floodplain, sampling was conducted between the mainstream channel at Seronga and Dungu floodplain lagoon (Fig. 3..3). Habitat types within this ecotone consist of a mainstream channel, oxbow lagoons, backwater channels, seasonal floodplains, and floodplain-connected lagoons such as Dungu. Figures 3.4 and 3.5 provide a visual impression of the prominent habitat types within this ecotone.

Within the perennial swamp sampling was conducted in the northeastern corner of Moremi Game Reserve from Xakanixa Lagoon southwards to Maxegana Pools (Fig. 3.3). Habitat types within this ecotone were similar to those in the riverine floodplain and consisted of perennially flowing river channels (Moanachira and Kwai), perennial lagoons (Xakanixa) and floodplain lagoons (Maxegana Pools). Although the water level in the perennial swamp does not fluctuate as dramatically as in the seasonal swamp, the surrounding floodplain does become inundated seasonally. Flood waters, on average, reach Xakanixa Lagoon in June each year. Figures 3.6 and 3.7 provide a visual impression of the prominent habitat types within this ecotone.

The rain pool habitat type was found throughout the delta, although they occurred with the greatest frequency in the northern areas of the delta. Throughout this study rain pools were mainly sampled along the extreme margins of the Kwai and Moanashira floodplains, in the perennial swamp ecotone (see Fig. 2.3). These rain pools were only connected to the surrounding floodplains during the relatively high flood levels of 1984 and 1986 and were primarily maintained by local rainfall and underground seepage. Many of the rain pool sampling sites were sometimes reduced to a mud pool or had dried completely. Figure 3.8 provides a visual impression of this habitat type.

In the southern seasonal swamp, Nxaraga Lagoon and the Boro River at the southeast end of Chief's Island were surveyed as well as the surrounding floodplain and floodplain lagoons (Fig. 3.1). Figure 3.9 provides a visual impression of the seasonal swamp habitat type.

Within the drainage river ecotone the Thamalakane River at Matlapaneng (Fig. 3.1) was surveyed. As previously mentioned the drainage rivers experience a widely fluctuating flood regime. Figures 3.10 and 3.11 provide an indication of the drainage river habitat type at both high and low water level. In addition, the Boteti River at Chanoga Lagoon was surveyed (Fig. 3.1). Chanoga Lagoon was one of a few perennial waterbodies along the Boteti River during the drought (i.e. 1982-88). Much of the river below Chanoga Lagoon was reduced to a series of mud pools, especially in 1983

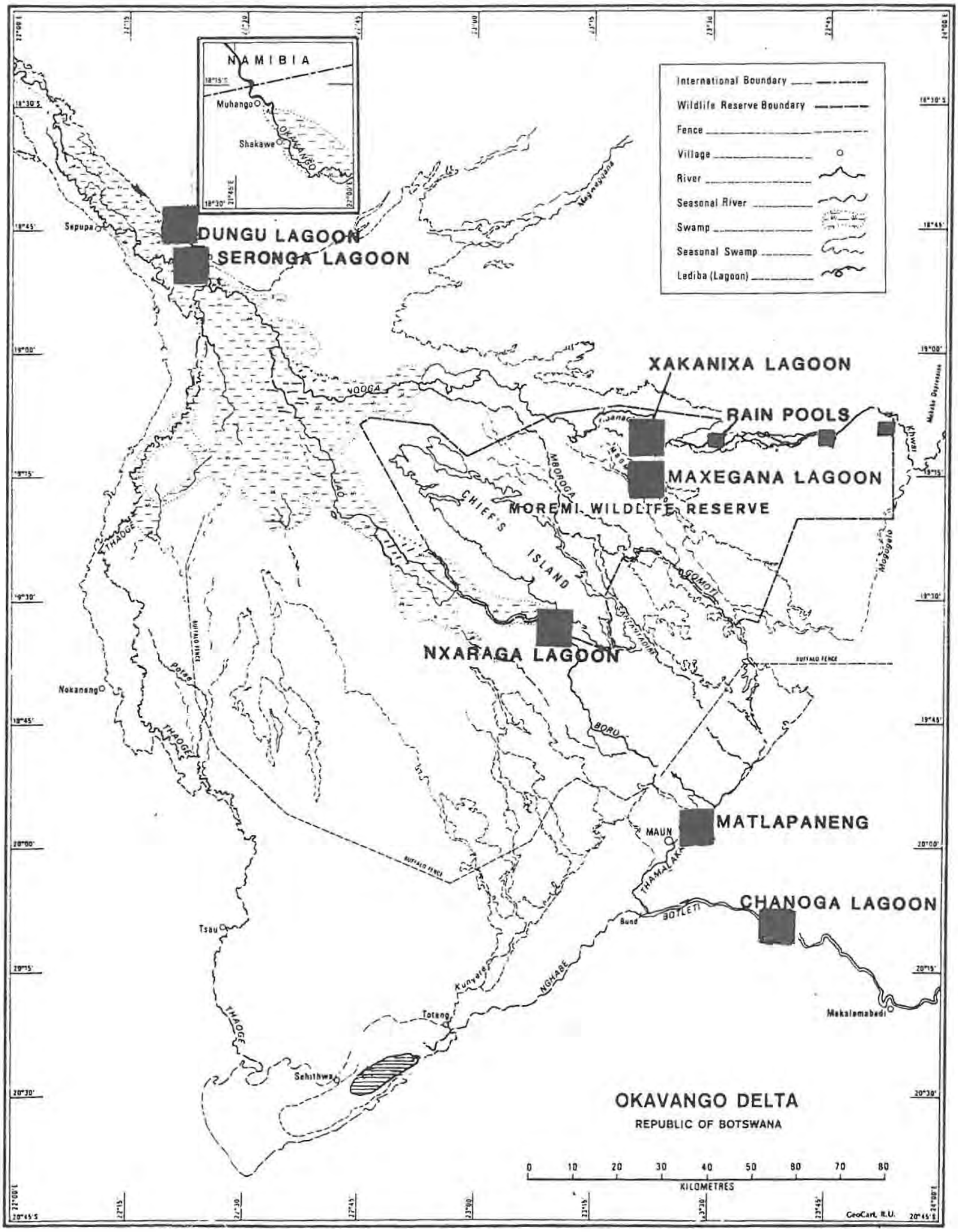


Figure 3.3. Map of the Okavango system in Botswana showing the location of all major sampling sites used throughout this study.

and 1985. Figure 3.12 provides a visual impression of Chanoga Lagoon. Figure 3.13 provides an indication of the effects of the drought on the Boteti River and to the cattle which often became stranded in the mud and perished. The sump lake habitat type (i.e. Lake Ngami) was dry during most of the study period. However, Bruton & Jackson (1983) and Merron & Bruton (1988) provide information on fish population changes within this ecotone. All the above sampling sites were chosen because they represent different habitat types and were accessible throughout the year.

Table 3.1 provides the sampling codes and select physical parameters for the eight sampling sites. These physical parameters include a qualitative indication of water retention, depth, flow, substrate type and amount of emergent, submerged and floating aquatic vegetation. These physical parameters are used in this thesis to classify the sampling sites and assist in determining the factors which limit the distribution and abundance of the fish communities.

In addition to these sites which were surveyed on a quarterly basis from November 1983 to December 1986, "ad hoc" collections where made throughout the rivers and floodplains of the Okavango system during the course of this project. Of particular interest were three ichthyological surveys of the fish communities along the Okavango River in Namibia between 1984 and 1986 (Skelton & Merron, 1984, 1985, 1987). In the riverine floodplain additional surveys were conducted at Nxamaceri and Etsatsa (see Fig. 2.3) and in the perennial swamp Gadikwe, Jao, Nguma and Xo Lagoons were also periodically surveyed (see Fig. 2.3).

In the seasonal swamp collections of fish were also made around the village of Thokatsebee (see Fig. 2.3) as this area represented the transitional zone between the southern seasonal swamp and the drainage rivers. In the drainage rivers collections were made in the Kunyere River near Lake Ngami (see Fig. 2.3) in December 1982 and 1984.

Figure 3.4. Typical habitat type of the riverine floodplain mainstream channel, Okavango Delta, October 1986.

Figure 3.5. Typical habitat type of a riverine floodplain-connected lagoon, Dungu, Okavango Delta, October 1986. Professor Tom Hecht on the extreme right supervising the seine netting while Dr. Humphry Greenwood, with red hat, pulls in one end.

Figure 3.6. Typical habitat type of the perennial swamp at Xakanixa Lagoon, Okavango Delta, January 1986.

Figure 3.7. Typical habitat type of the perennial swamp floodplain-connected lagoons, Okavango Delta, August 1985. Hippopotami can be seen in the middle distance.

Figure 3.8. Typical habitat type of rain pools, Kwai floodplain, Okavango Delta, June 1984. This photo was taken during high water level.

Figure 3.9. Typical habitat type in the seasonal swamp at Nxaraga Lagoon, Okavango Delta, November 1985.

Figure 3.10. Typical habitat type of the Thamalakane River at Matlapeneng, Okavango Delta, April 1985. This photo was taken during the low flood level.

Figure 3.11. The Thamalakane River at Matlapaneng, Okavango Delta, September 1984. This photo was taken during the high water level.

Figure 3.12. Typical habitat type of Chanoga Lagoon, Boteti River, Okavango Delta, November 1984.

Figure 3.13. The Boteti River below Chanoga Lagoon during the drought in June 1985. Note the extreme desiccation of the river and effect on cattle, which often became stranded in the mud.

Table 3.1. The survey codes and select physical parameters for the eight sampling sites used in the Okavango Delta, Botswana, during the course of this study.

Sampling site	Sampling code	*Ecotone	Water retention	Mean depth	Flow	Substrate	Emergent vegetation	Submerged vegetation	Floating vegetation
Chanoga Lagoon	1	dr	moderate	1.0 m	0.2 m/sec	muddy	common	abundant	common
Thamalakane river	2	dr	low	1.0 m	0.5 m/sec	mud-sand	rare	limited	common
Nxaraga Lagoon	3	ss	high	1.5 m	1.0 m/sec	mud-sand	common	abundant	abundant
Xakanixa Lagoon	4	ps	high	2.0 m	2.5 m/sec	sand	abundant	common	common
Maxegana Pools	5	ps	high	1.5 m	0.5 m/sec	muddy	abundant	muddy	abundant
Rain Pools	6	ps	low	0.3 m	0.0 m/sec	sand-mud	none	rare	rare
Mainstream channel	7	rf	high	2.5 m	2-7 m/sec	sand	abundant	common	common
Floodplain lagoons	8	rf	high	1.5 m	0.5 m/sec	sand-mud	common	abundant	abundant

*dr= drainage rivers; ss= seasonal swamp; ps= perennial swamp; rf= riverine floodplain

SAMPLING METHODS

Gillnets

From November 1983 until December 1986 gillnets were set on a quarterly basis in all sites except the riverine floodplain. Although qualitative sampling began in the riverine floodplain in February 1983 (Merron et al., 1983) and continued in November 1984 (Merron et al., 1985), quarterly gillnet sampling only began in April 1985. This was mainly due to logistical and financial constraints.

A wide variety of gillnets was used to sample the fish populations during each quarterly survey. A monofilament gillnet fleet consisting of stretch-mesh sizes 24, 40, 50, and 110 mm and a multifilament fleet consisting of stretch- mesh sizes 60, 75, 96, 110 and 143 mm were used in all sampling periods. Gillnets were set on at least two consecutive nights in each sampling site. All nets were 25 m long, 2.0 m deep and hung by the half.

The annual overnight frequency distribution, by sampling site, for an experimental gillnet fleet (24 - 143 mm) set in the Okavango Delta, between November 1983 and December 1986 is presented in Table 3.2. The use of different gillnet mesh sizes made it possible to determine the species and size of fish caught in each mesh size and the relation of mesh size to the number and weight of fish caught per net. In addition to collecting fish in experimental gillnets, considerable time and effort was put into monitoring and recording the activities and catches of commercial, recreational and artisanal fishermen.

The gillnets were checked everyday for holes caused by crocodiles and hippopotami. Nets which had minor holes were assigned a percentage torn value and the abundance of all fish species was based on the percentage of effective net used the previous night. Many of the small holes in the multifilament nets were then repaired. Monofilament gillnets lasted about three months before they were greater than 25% torn, after which they were removed from the float.

Seine nets and rotenone ichthyocide

Seine nets and rotenone ichthyocide were also extensively used in all sampling sites throughout the study period. Table 3.3 shows the annual frequency distribution for the total number of seine net and rotenone collections in the different sampling sites within the various ecotones.

Table 3.2. The annual overnight frequency distribution of effort, by sampling site (=code), for an experimental gillnet fleet (24 - 143 mm) set in the Okavango Delta, between November 1983 and December 1986.

Date	Sampling code*							
	1	2	3	4	5	6	7	8
1983	2	2	3	2	2	0	0	0
1984	16	15	16	16	14	14	0	0
1985	16	17	16	16	18	16	18	17
1986	16	16	16	16	16	15	17	19
Total	50	50	51	50	50	45**	35	36

*sampling codes as given in Table 3.1.

**gillnet catches are lowest in rain pools as these habitats were sometimes dry.

A 12 mm stretched-mesh seine net was used which had a mounted length of 10 m, a 1.5 m purse and a 2.5 m effective haul depth. The seine net was used in both exposed and moderately vegetated littoral areas. The procedure entailed one person in the water paying the net out from shore perpendicular to shore. The net was then pulled parallel to shore in a half circle covering an approximate 100 m^2 sampling area (see Fig. 3.5).

The rotenone ichthyocide used contained 6.8% active ingredient. This ichthyocide is miscible with water after pre-treatment with 50% iso-propanol. Rotenone sampling proved to be very effective in areas where gillnets or seine nets could not be used, such as in heavily vegetated floodplains or in the dense papyrus mats.

At selected sites concentrations of rotenone at 5 - 7 ppm, depending on water temperature, were used and the solution slowly stirred into the collecting area. These collections covered an area of approximately 100 m^2. These areas were blocked off with enclosure nets where possible. The treated site was worked for 2 - 4 h during which the bulk of the fishes were collected. The site was then left, although it was revisited over a 48 h period when possible.

Table 3.3. The annual diurnal frequency distribution for the total number of seine net and rotenone collections in different sampling sites (=codes) within the various ecotones of the Okavango Delta, between November 1983 and December 1986.

Year	Sampling code*							
	1	2	3	4	5	6	7	8
1983	4	8	10	8	6	4	0	0
1984	18	19	17	19	15	18	0	0
1985	17	15	15	16	23	12	24	20
1986	21	16	20	18	16	12	21	27
Total	60	60	62	61	60	46	45	47

*sampling codes as given in Table 3.1.

Electrofishing

In November 1983 and March 1984 an electrofisher was tried in an effort to collect fish. Unfortunately due to the low conductivity of the Okavango waters this method proved to be of little value and was discontinued.

Fish tagging

In an attempt to help substantiate the movements of the selected species for study, a tagging programme was undertaken from March 1984 to November 1985. Fish were captured mainly with rod and line or using gillnets and marked by inserting a Floy FD-67 spaghetti tag under the dorsal fin. Out of a total of 1219 marked fish, only 2 (0.2%) were recaptured by November 1985. This poor return rate is a result of the dispersed nature of the fish species and size of the Okavango Delta which mitigated against a high recapture rate. Therefore, no reliable results were being obtained for the amount of effort put into this method and tagging ceased in November 1985.

GENERAL TECHNIQUES

Measurement

Fish captured in gillnets were measured for standard length (SL), to the nearest millimetre, and weighed in the field to the nearest gramme on a 3.0 kg digital balance. Standard length was found to be more consistently measurable as the caudal fins of many fish were either bitten by crabs and smaller fish or damaged while in the nets. Heavier fishes were weighed to the nearest 10 g on a 10 kg capacity Pesola spring balance. Where stomach and gonad samples were required for laboratory analysis, the abdominal cavity was slit open and the entire viscera removed, labelled and preserved in 10% buffered formalin fixative.

Preservation and curation

All fishes caught in seine nets or with rotenone were fixed in 10% formalin solution and brought back to the J.L.B. Smith Institute of Ichthyology or research station in Maun. These fishes were identified, sorted, and weighed no later than one-month after capture. The fish were then preserved in 50% iso-propanol. All the specimens are housed in the collection of the J.L.B. Smith Institute of Ichthyology (OK 83-1 to OK 86-113).

Statistical analysis

All the relevant biological and ecological information was stored on an IBM-PC computer. Summations of relative abundance and mass compositions, catch per unit effort, gonad maturation indices and fecundity relationships were performed using the LOTUS-123 statistical programme.

Two-way indicator species analysis (TWINSPAN; Gauch, 1982) was used to determine a community classification for the different sampling sites and to help explain the factors limiting the distribution and abundance of fish. TWIN-SPAN constructs an ordering of the data sets and classifies the samples using dichotomies. The aim of the TWIN-SPAN arrangement is to identify the most important features of the data set and to group together species with similar ecological preferences.

The entire data set was entered on the Rhodes University mainframe computer together with data on pertinent physical properties of each sampling site such as the depth of water, whether or not the site was perennially or seasonally flooded, flow rates, substrate type and amount of floating, emergent and submergent aquatic vegetation (see Table 3.1). The data set was then used to obtain an ordered dendrogram that expresses each species synecological relationships.

Ordination of the data sets was carried out using CANOCO, a computer programme which performs Partial Detrended Canonical Correspondence Analysis and is an extension of the Cornell University Ecology Programme DECORANA (Ter Braak, 1987). This programme was used to derive clusters that quantify the degree of similarity or dissimilarity in fish collections made in the different sampling sites.

Selection of species

The species chosen for detailed study throughout this thesis include the sharptooth catfish Clarias gariepinus, silver catfish Schilbe mystus (now synonomized with Eutropius depressirostris; De Vos, 1984), tigerfish Hydrocynus vittatus, African pike, Hepsetus odoe and threespot tilapia Oreochromis andersonii (Table 3.4). These five species were selected for study because of their ecological importance in the food chain and their importance in the commercial, artisanal and recreational fisheries. Additional information on the biology and ecology of each of these species is presented in Table 3.4.

Table 3.4. The five selected species chosen for detailed study in the Okavango Delta, between November 1983 and December 1986 and relevant taxonomic and biological information.

Species	mean standard length	trophic group	reproductive guild
Clarias gariepinus	474 mm	omnivore/predator	non-guarder
Schilbe mystus	195 mm	insectivore/predator	non-guarder
Hydrocynus vittatus	326 mm	piscivore	non-guarder
Hepsetus odoe	254 mm	piscivore	guarder
Oreochromis andersonii	227 mm	detritivore	bearer

Clarias gariepinus (Burchell, 1822). Sharptooth catfish.

Distribution and abundance: The sharptooth catfish (Fig. 3.14a) is found in every habitat type in the Okavango Delta including the fast-flowing stretches of the main river channels, tributaries, oxbow and floodplain lagoons and rain pools (Chapter 4). The length-frequency histogram for fishes collected in gillnets (24 - 143 mm) between November 1983 and December 1986 indicates that the mean standard length is 474 mm in a range from 210 to 920 mm SL (Fig. 3.14b). C. gariepinus is one of the most important species caught in the commercial and artisanal fisheries.

Biology: C. gariepinus can survive long periods in thick viscous mud in drying up lagoons and floodplains by breathing atmospheric oxygen. The ability of the catfish Clarias gariepinus to survive almost total habitat desiccation has been reviewed by Bruton (1979), and further instances of their ability to survive in fluid mud have been observed on the Pongolo floodplain (Merron et al., 1987). At the posterior end of the head are two sponge-like supra-branchial organs that allow for oxygen transfer in or out of the water. Spawning takes place between July and March in different parts of the Delta (Chapter 6). Females are highly fecund with up to 236000 eggs recorded from a 770 mm fish (Chapter 6). The eggs are broadcast among aquatic vegetation in slow-flowing river channels and shallow floodplains. C. gariepinus is an omnivorous predator with a diet consisting mainly of fish, aquatic and terrestrial insects, plant material, seeds, fruit and shrimps (Chapter 7).

Schilbe mystus (Linnaeus, 1758). Silver catfish.

Distribution and abundance: The silver catfish (Fig. 3.15a) is found throughout the Okavango Delta in large numbers in the open water areas of slow-flowing rivers and lagoons (Chapter 4). The length-frequency histogram for fishes collected in gillnets (24 - 143 mm) between November 1983 and and December 1986 indicates that the mean standard length is 195 mm in a range from 90 to 260mm (Fig.3.15b). This species is important in the commercial and artisanal fisheries.

Biology: Gonad examination indicates that the silver catfish has a relatively high fecundity (e.g. 13500 eggs for a 221 mm fish; Chapter 6) and spawns between July and March in different parts of the Delta (Chapter 6). S. mystus is an insectivore predator which mainly feed on adult aquatic and terrestrial insects and fish (Chapter 7).

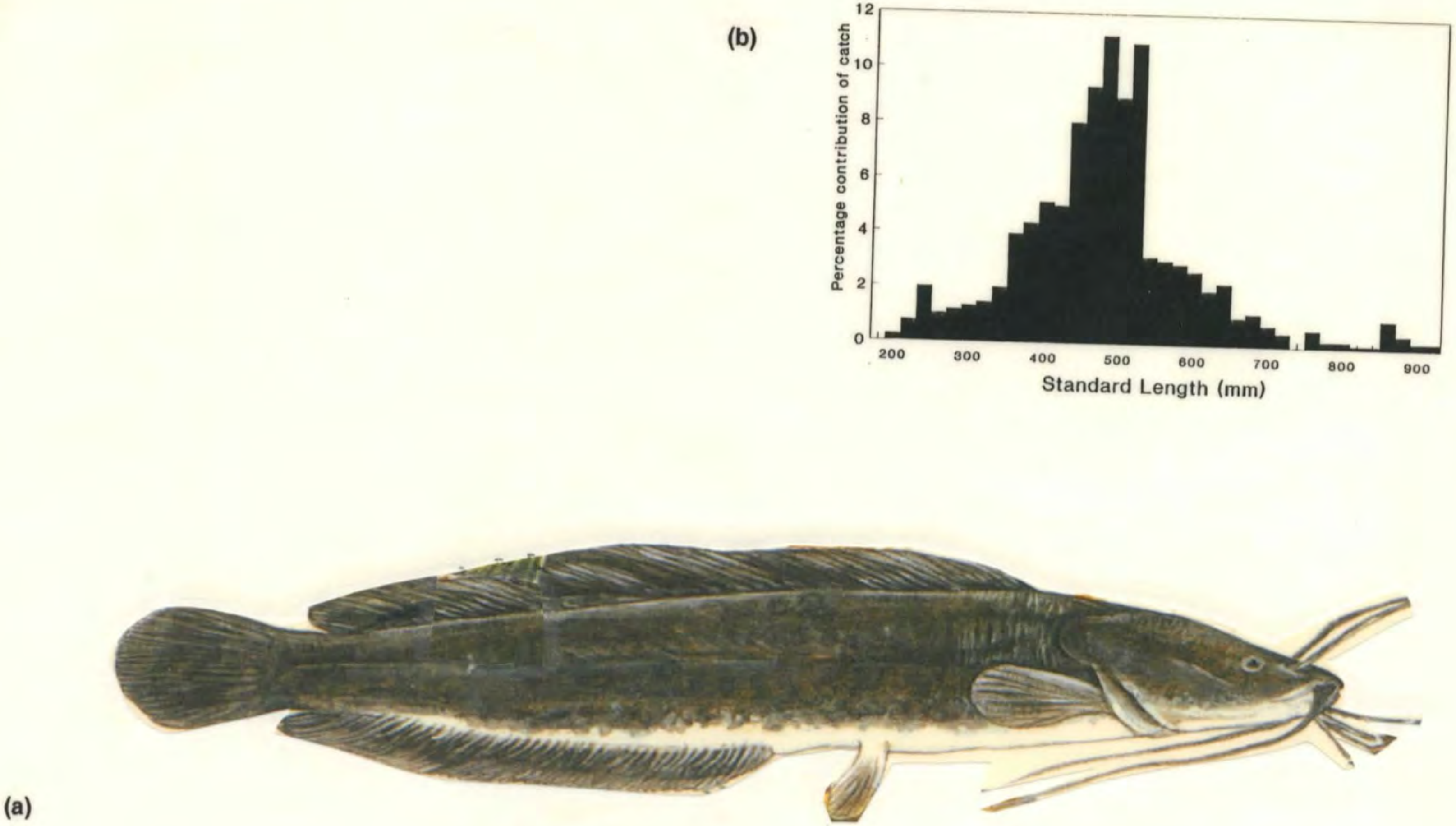


Figure 3.14. An illustration of a sharptooth catfish (C. gariepinus) from the Okavango Delta, May 1986 (a), and respective length-frequency histogram (b) for fish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 (n = 759).

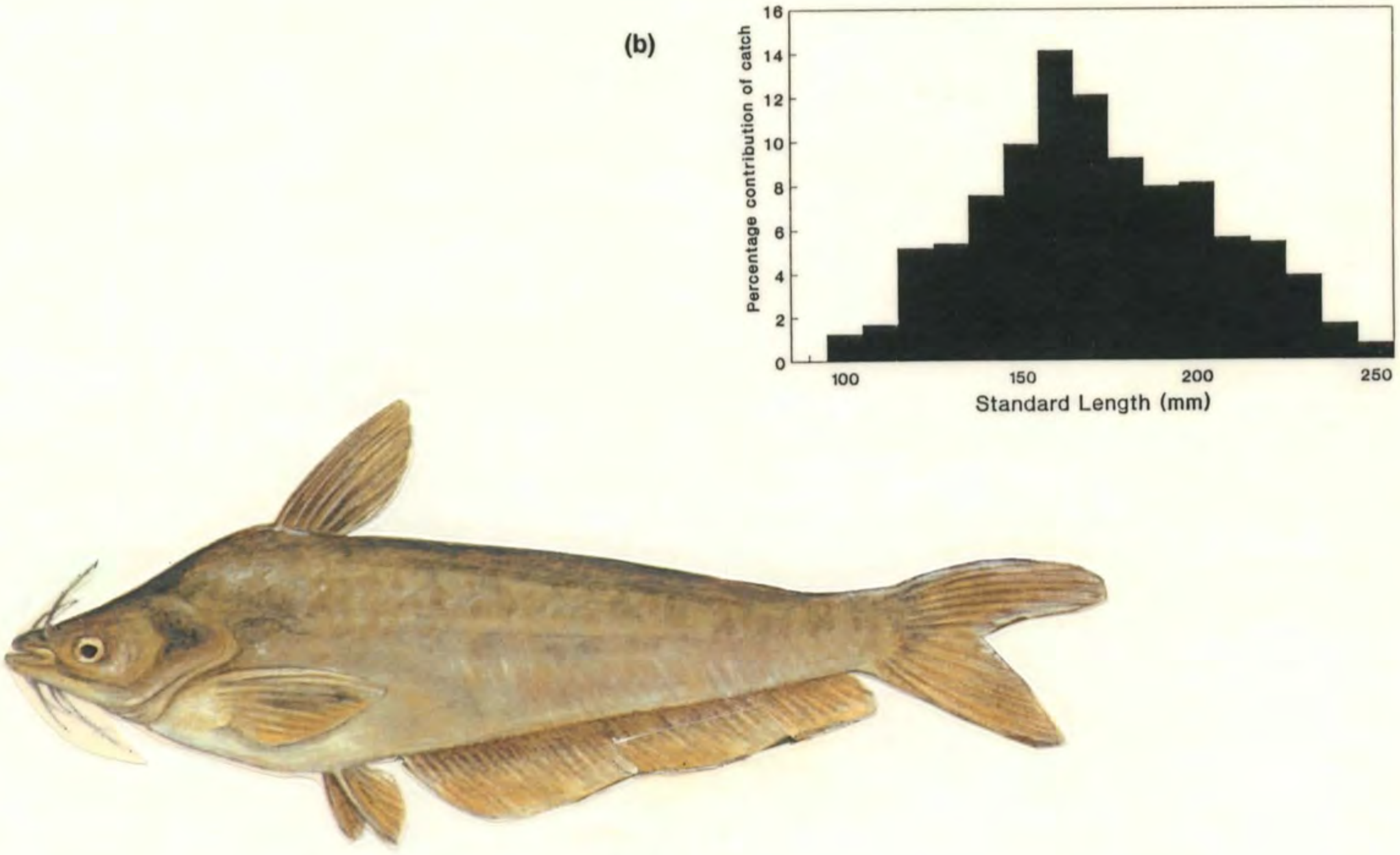


Figure 3.15. An illustration of a silver catfish (S. mystus) from the Okavango Delta, April 1985 (a), and respective length- frequency histogram (b) for fish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 (n = 1429).

Hydrocynus vittatus (Cuvier, 1819). Tigerfish.

Distribution and abundance: The tigerfish (Fig. 3.16a) is an open water species found mainly in the perennial waters of the Okavango (Chapter 4). The main ecological factors limiting their distribution in the Okavango appear to be water permanency, depth and flow. The length-frequency histogram for tigerfish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 indicates that the mean standard length is 326 mm in a range from 210 to 620 mm SL (Fig. 3.16b). Tigerfish are not a commercially exploited species, although they are an important component of the recreational and artisanal fisheries.

Biology: Tigerfish spawn in early summer in the papyrus fringe of the mainstream channel and oxbow lagoons (Chapter 6). Females are highly fecund, spawning over 200000 eggs at a time and attain a larger size than males (Chapter 6). The tigerfish is an extremely active and voracious predator with a diet consisting largely of fish (Chapter 7).

Hepsetus odoe (Bloch, 1794). African pike.

Distribution and abundance: The African pike (Fig. 3.17a) prefers the slower-flowing reaches of the seasonal swamp and drainage rivers from which tigerfish were absent (Chapter 4). These two predatory species do not normally co-exist in the same habitat. The length-frequency histogram for pike collected in gillnets (24 - 143 mm) between November 1983 and December 1986 indicates that the mean standard length is 254 mm in a range from 110 to 390 mm SL (Fig. 3.17b). Pike are not a commercially important species although they are important in the artisanal and recreational fisheries.

Biology: Pike spawn between October and March in different parts of the Delta (Chapter 6). This species has one of the most interesting breeding behaviours of fish in the Delta. The fertilized eggs are deposited in a foam nest which is guarded by the parents (Chapter 6). These nests are found along the fringe of the river channels and oxbow lagoons as well as in the floodplains. Foam nests appear to be a predator avoidance mechanism as well as an adaptation to fluctuating water levels. Fecundity is relatively low with a mean number of 2627 eggs. Gonad examination reveals eggs of varying sizes which suggests that this species is a multiple spawner.

The pike is an ambush predator, unlike the tigerfish which is a fast-swimming, marauding predator. The stomach contents of pike indicate an almost exclusive piscivorous diet with a wide range of fish species such as topminnows, barbs and juvenile cichlids consumed (Chapter 7).

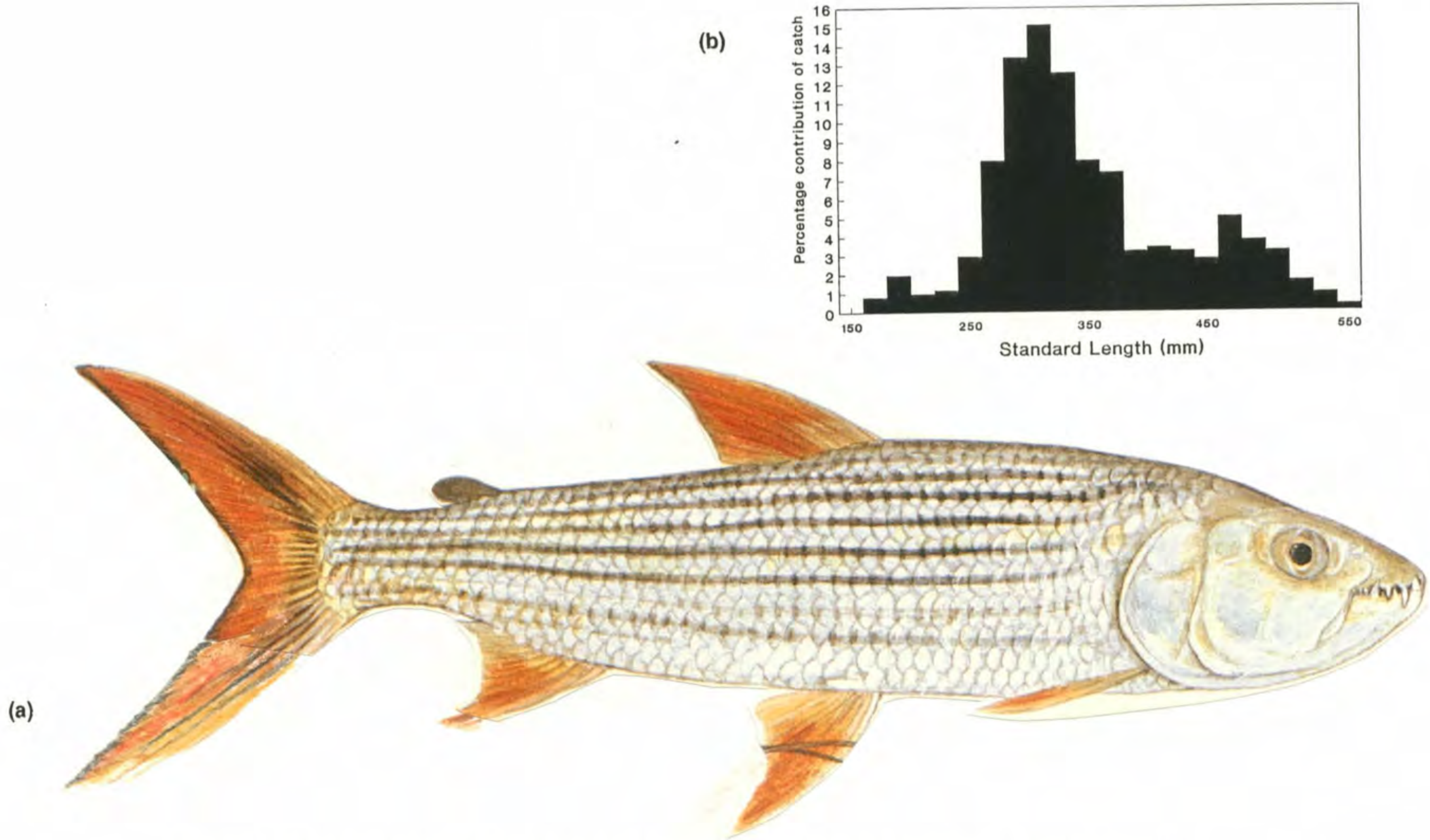


Figure 3.16. An illustration of a tigerfish (H. vittatus) from the Okavango Delta, October 1986 (a), and respective length- frequency histogram for fish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 (n = 1113).

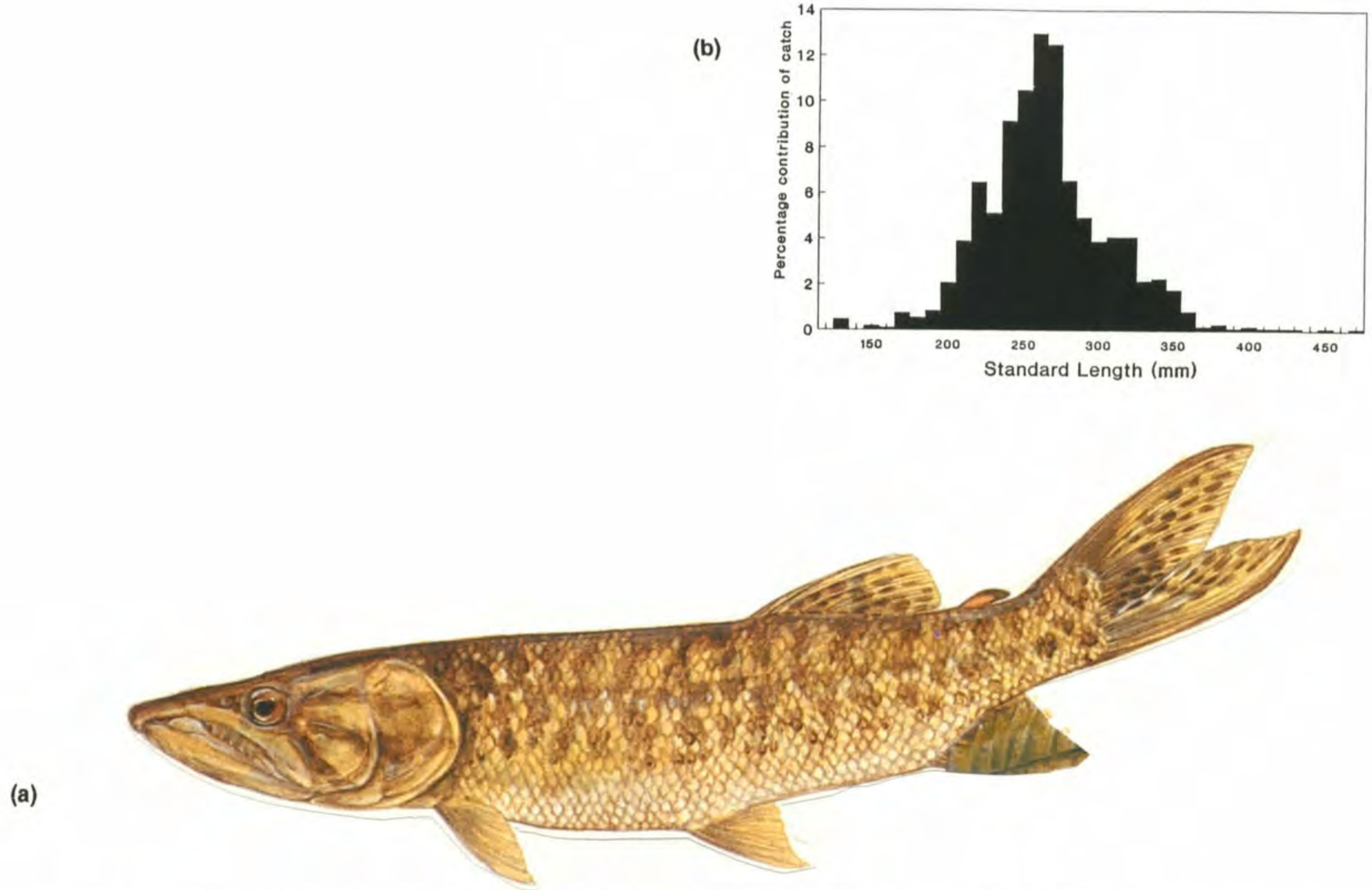


Figure 3.17. An illustration of an African pike (<u>H. odoe</u>) from the Okavango Delta, February 1986 (a), and respective length- frequency histogram (b) for fish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 (n = 1048).

Oreochromis andersonii (Castelnau, 1861). Threespot tilapia.

Distribution and abundance: The threespot tilapia (Fig. 3.18a) is one of the most common and ubiquitous small-mouthed cichlids found in the Okavango Delta (Chapter 4). O. andersonii is tolerant of fluctuating environmental conditions, and is one of the last species to survive desiccating conditions. O. andersonii is also one of the first species to colonize recently inundated water bodies. The length-frequency histogram for fishes collected in gillnets (24 - 143 mm) between November 1983 and December 1986 indicates that the mean standard length is 227 mm in a range from 50 to 395 mmSL (Fig. 3.18b). This cichlid species is one of the most common fishes in the commercial and artisanal catch and is highly valued in the recreational fishery.

Biology: O. andersonii is a mouth-brooder and multiple spawner with a low fecundity (e.g. 1223 eggs for a 210 mm fish; Chapter 6). Spawning behaviour involves the male setting up territories in arenas or "leks" and preparing nests in which mating occurs with a succession of receptive females. The male attracts a female which then lays her eggs in the nest for the male to fertilize. The female then picks up the eggs in her mouth where they are incubated for about one month after which the juveniles move away into very shallow margins of the floodplains. This species feeds mainly on detritus, digesting the bacteria and diatoms and passing the mud through the intestine (Chapter 7).

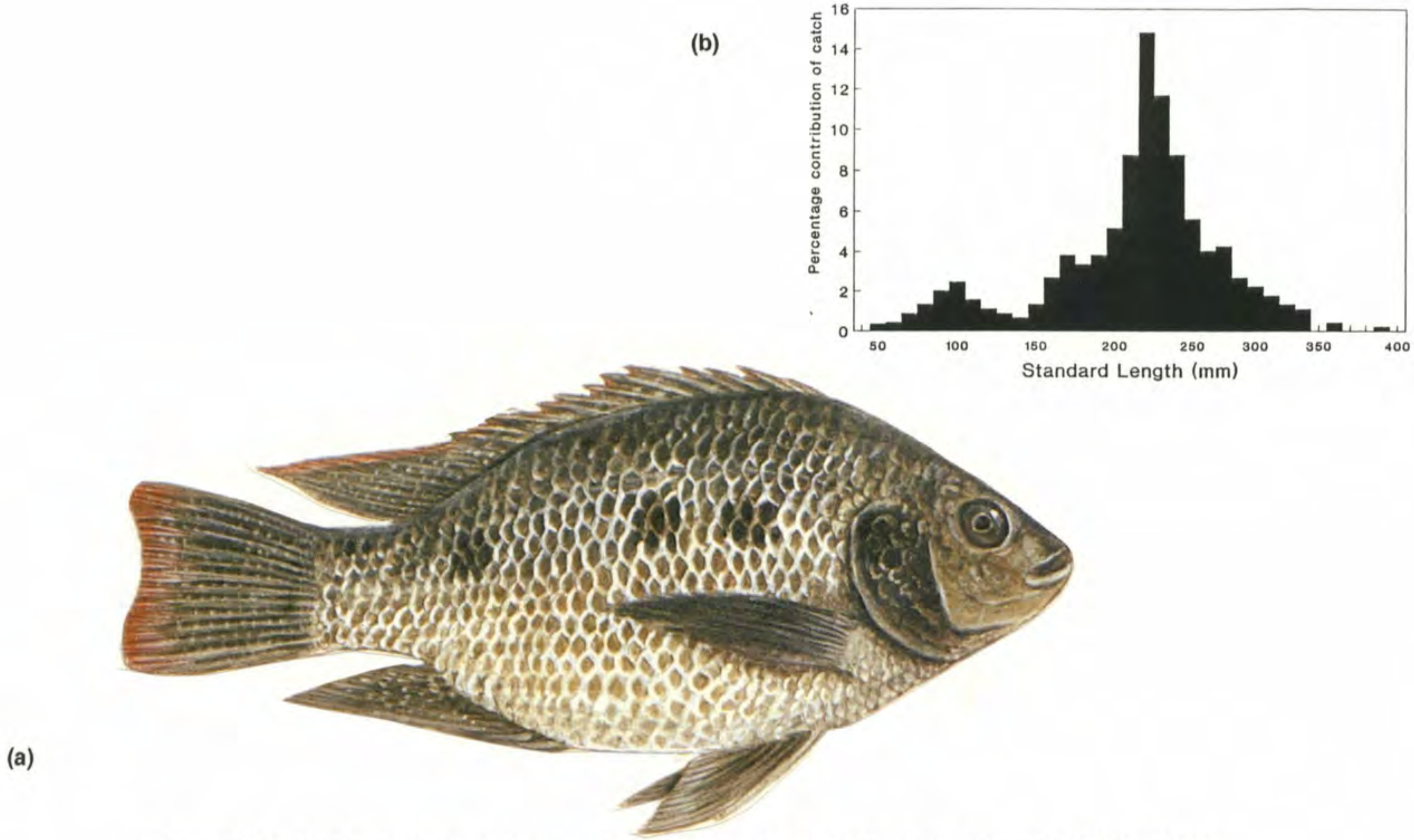


Figure 3.18. An illustration of a threespot tilapia (O. andersonii) from the Okavango Delta, June 1984 (a), and respective length- frequency histogram (b) for fish collected in gillnets (24 - 143 mm) between November 1983 and December 1986 (n = 586).

CHAPTER 4

POPULATION DEMOGRAPHY AND FAUNAL ASSOCIATIONS OF SELECTED SAMPLING SITES

INTRODUCTION

This chapter provides a quantitative account of the species diversity, relative abundance and mass compositions of fishes collected in the different sampling sites studied in the Okavango. This information provides an understanding of the faunal associations and the factors which determine the distribution and abundance of species.

MATERIALS AND METHODS

To ascertain the population demography and faunal associations of fishes in the delta, particularly the five selected species, the percentage numeric and mass contributions were summed from all gillnet catches, and seine and rotenone collections for each respective sampling site as described in Chapter 3. A total of 367 overnight gillnet settings were carried out between November 1983 and December 1986 (Table 3.2). A total of 441 seine net and rotenone collections were also carried out between November 1983 and December 1986 (Table 3.3). The results presented below are a summation of all the sampling methods for each individual species and site. All collections within a given sampling site between November 1983 and December 1986 were grouped together for this analysis.

It is apparent from Table 3.2 and 3.3 that, although quantitative quarterly sampling only began in the riverine floodplain in April 1985, a relatively uniform distribution of effort using standardized methods throughout the Okavango Delta was achieved. It is therefore reasonable to assume that the catches of the selected species in each sampling site are related to the proportional contribution made by that species to the faunal composition of that particular sampling site. It should, however, be stated that the habitat characteristics of a particular sampling site determined to a large extent the effectiveness of the different sampling methods. For example, seine nets were often more effective than gillnets in the rain pool environs and rotenone sampling was more effective in the slower moving drainage rivers than in the faster flowing mainstream channel. Although the sampling efficiency was not standardized as much as would be desired, it was unavoidable as each sampling site had characteristics unique to it.

These data were used to construct pie diagrams of species composition and relative abundance, based on numbers and mass, for each sampling site. This was necessary to provide a holistic interpretation of the fauna and to circumvent the biases associated with reporting on only one of these variables. It should be noted that within the genus Synodontis only 4 species (e.g. S. leopardinus, S. nigromaculatus, S. macrostigma and S. woosnami) were recognized in the present analysis, although Skelton and White (1990) recognize two additional species (i.e. S. macrostoma and S. vanderwaali).

The results are presented firstly as an overall assessment of the entire Okavango fauna, and secondly as a broad description of the distribution and abundance of species, and therefore the communities in different sampling sites. These data were then further analysed using multivariate analytical techniques (e.g. TWIN-SPAN community classification & CANOCO similarity analysis) to determine the respective ordination and degree of similarity in fish communities between the sampling sites. Various physical features of the different sampling sites are considered in this analysis including the permanence (retention time) of water, flow rates, depth, substrate type, and extent of floating, emergent and submergent aquatic macrophyte communities as given in Table 3.1.

As the pie diagrams only allow 12 slices, one group of fishes represented in the pie charts labelled "Others" requires further mention. The group "Others" represents species which contributed on average less than 1% each to the total number or mass of fish at each site. All numeric and mass figures within the pie diagrams are reported to one decimal place. It should also be noted that the 17 species of the family Cichlidae contributed considerably to the numeric and mass compositions of the communities relative to other families of fish. Therefore, to obtain a general trend in community structure of the different sampling sites reference is made to the groups cichlid and non-cichlid species when referring to the species compositions of the different sampling sites. A taxonomic listing of all species collected during this study including trophic and reproductive guilds is given in Appendix 1.

RESULTS

THE OVERALL FISH FAUNA OF THE OKAVANGO DELTA

A total of 130908 specimens comprising at least 66 species with a combined mass of 3901 kg was collected in the Okavango Delta between November 1983 and December 1986 (Appendix 2). Numerically, the most important cichlid species included Oreochromis andersonii (8.0%), O. macrochir (3.0%), Tilapia sparrmanii (7.1%), T. rendalli (3.4%), Pseudocrenilabrus philander (4.6%), and Pharyngochromis darlingi (3.6%; Fig. 4.1a). Important non-cichlid species included Aplocheilichthys johnstoni (7.2%), Schilbe mystus (4.3%), Brycinus lateralis (6.1%) and Barbus barnardi (4.5%) and B. thamalakanensis (3.7%). The group "Others" (44.6%) represents a total of 55 additional species.

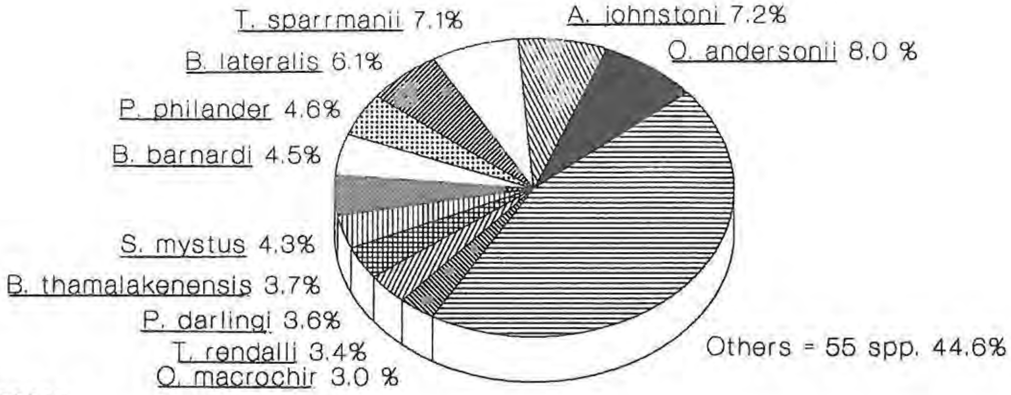
The results on mass composition of all Okavango fishes (Fig. 4.1b) indicates that important cichlid species included Oreochromis andersonii (12.3%), O. macrochir (4.6%), Serranochromis angusticeps (7.1%), Tilapia sparrmanii (3.3%) and T. rendalli (3.0%). Important non- cichlid species included Hydrocynus vittatus (12.8%), Clarias gariepinus (11.5%) and C. ngamensis (4.2%), S. mystus (10.3%), Hepsetus odoe (6.3%) and Synodontis nigromaculatus (3.7%). The group "Others" contributed 20.8% of the total mass value.

The five selected species are well represented comprising 53.2% of the overall fauna by mass and 16.9% by number (Table 4.1). The results on species diversity and relative abundance for the entire delta presented above can now be used as a foundation on which to compare interspecific variations in faunal associations between the different sampling sites.

Table 4.1 The percentage mass contribution for the five selected species for study for each sampling site in the Okavango Delta between November 1983 and December 1986.

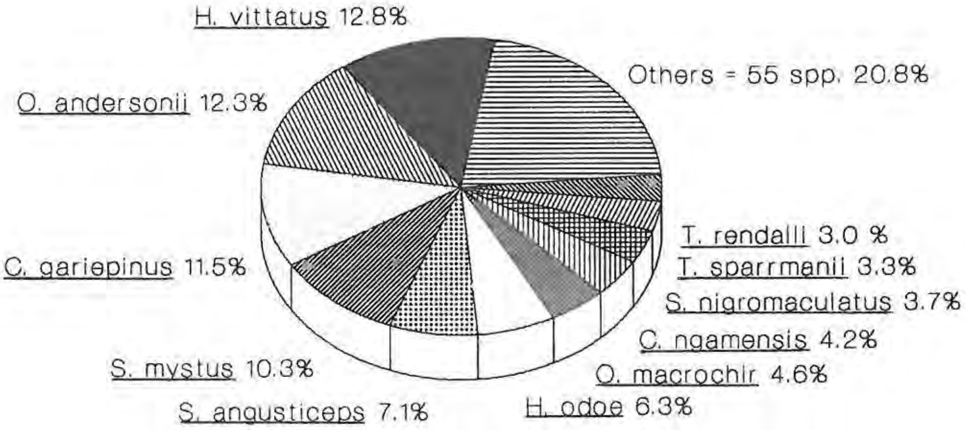
Species	1	2	3	4	5	6	7	8
Clarias gariepinus	5.3	8.2	7.0	15.1	11.8	8.9	15.3	16.3
Schilbe mystus	19.3	15.3	14.7	6.8	7.0	1.2	6.1	6.1
Hydrocynus vittatus	0.0	0.0	0.5	29.2	10.3	0.0	29.6	15.2
Hepsetus odoe	11.2	9.4	17.4	0.0	3.9	1.6	0.0	3.1
Oreochromis andersonii	15.2	14.2	9.8	7.4	13.8	37.5	8.7	12.9
Total	51.0	47.1	49.4	58.5	46.8	49.2	59.7	53.6

(a) NUMBER



n = 130908

(b) MASS



mass = 3901 kg

Figure 4.1. Total number (a) and mass (b) of fish collected using all sampling methods from the Okavango Delta, between November 1983 and December 1986.

DISTRIBUTION AND ABUNDANCE OF FISH SPECIES FOR EACH SAMPLING SITE

Chanoga Lagoon, Boteti River

A total of 26206 specimens, representing 46 species with a combined mass of 581 kg, was collected from this site (Appendix 2). Numerically, the most common cichlid species included Tilapia sparrmanii (10.8%), T. rendalli (3.6%), Oreochromis andersonii (8.3%), O. macrochir (5.0%), Pharyngochromis darlingi (5.9%) and Pseudocrenilabrus philander (5.7%; Fig. 4.2a). Important non-cichlid species included B. lateralis (7.8%), Rhabdalestes maunensis (5.5%), Barbus barnardi (7.7%), A. johnstoni (6.1%) and S. mystus (4.5%). The group "Others" comprised 35 additional species which contributed 29.1% to the total.

An analysis of the contribution by mass (Fig. 4.2b) indicates that important cichlid species included Oreochromis andersonii (15.2%), O. macrochir (6.1%), Tilapia sparrmanii (6.0%), Serranochromis codringtoni (2.8%), S. giardi (2.7%) and S. thumbergi (2.6%). Important non-cichlid species included S. mystus (19.3%), H. odoe (11.2%), C. gariepinus (5.3%), Synodontis leopardinus (3.9%) and S. nigromaculatus (3.5%). The group "Others" contributed 21.4% of the total mass value.

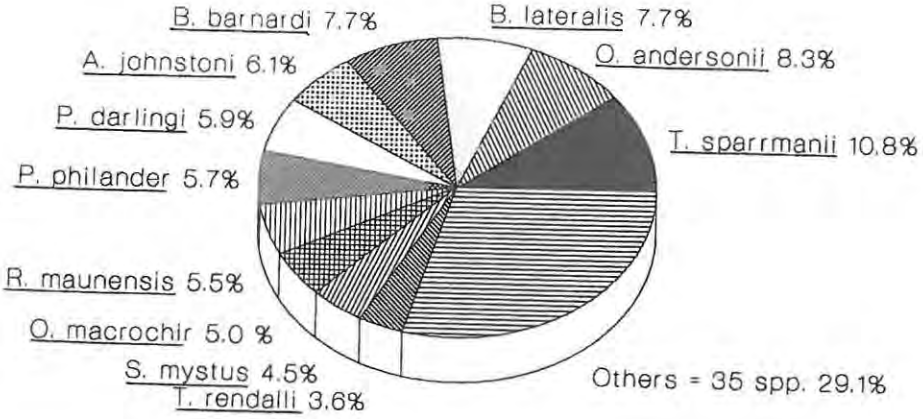
The species composition of this sampling site differs markedly from the overall Okavango fauna (see Fig. 4.a & b). Four of the five selected species were well represented in this sampling site comprising 51.0% of the overall mass and 14.5% of the numeric contribution (Table 4.1). H. vittatus was absent from all samples, although one individual was collected by staff of the Botswana Fisheries Unit in November 1984 (pers. observation).

Thamalakane River

A total of 23359 specimens, representing 56 species with a combined mass of 489 kg, was collected from this sampling site (Appendix 2). Important cichlid species in the numeric composition of the community included Tilapia sparrmanii (11.2%), T. rendalli (4.8%), Oreochromis andersonii (8.8%), O. macrochir (4.6%), Pharyngochromis darlingi (5.9%) and Pseudocrenilabrus philander (4.4%; Fig. 4.3a). Important non-cichlid species included Barbus barnardi (5.7%), B. thamalakanensis (3.9%), Brycinus lateralis (5.7%), A. johnstoni (7.2%) and S. mystus (4.5%). The group "Others" comprised 45 additional species which contributed 33.3% to the total.

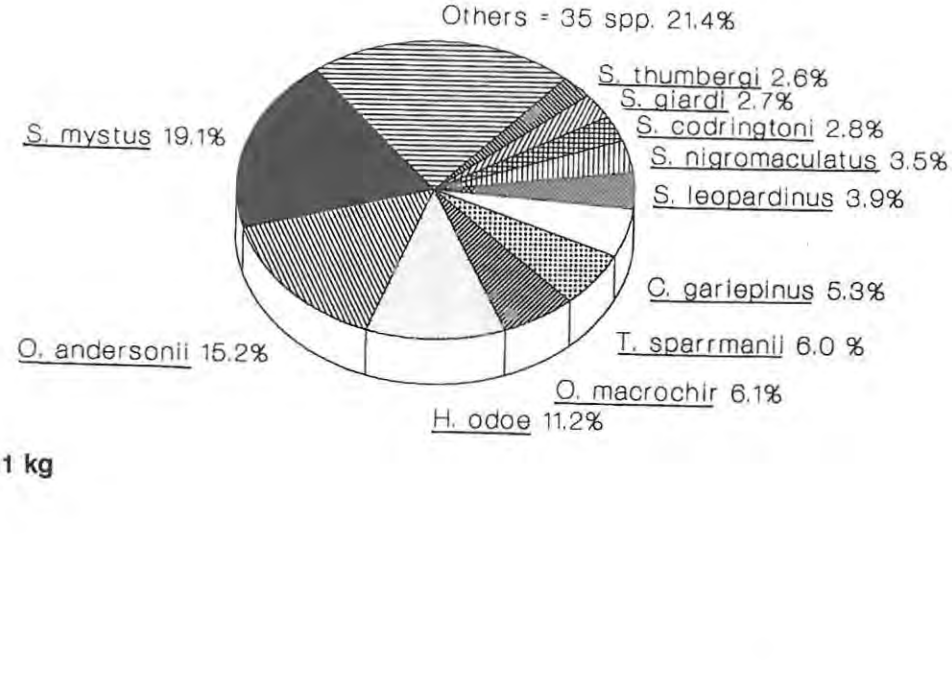
An analysis of the mass composition (Fig. 4.3b) indicates that important cichlid species included Tilapia sparrmanii (6.6%), T. rendalli (5.6%), Oreochromis andersonii (14.2%), O. macrochir (6.5%),

(a) NUMBER



n = 26206

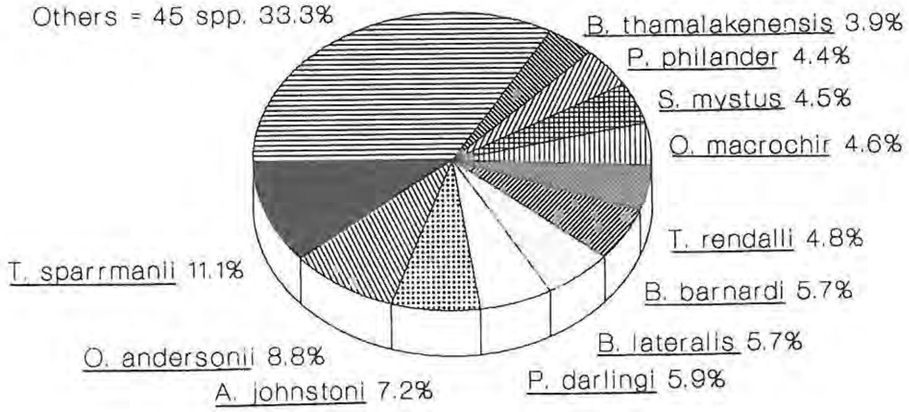
(b) MASS



mass = 581 kg

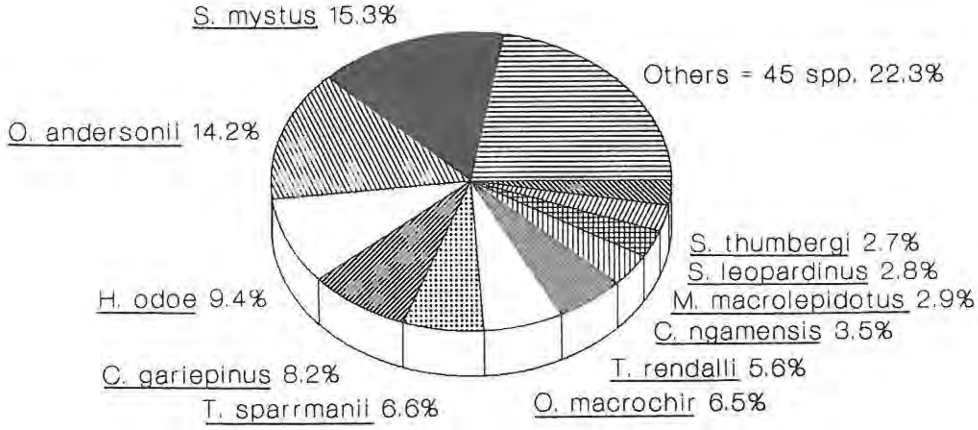
Figure 4.2. Total number (a) and mass (b) of fish collected using all sampling methods from Chanoga Lagoon, Boteti River, Okavango Delta, between November 1983 and December 1986.

(a) NUMBER



n = 23359

(b) MASS



mass = 489 kg

Figure 4.3. Total number (a) and mass (b) of fish collected using all sampling methods from the Thamalakane River, Okavango Delta, between November 1983 and December 1986.

and Serranochromis thumbergi (2.7%). Important non-cichlid species included H. odoe (9.4%), S. mystus (15.3%), Clarias gariepinus (8.2%), C. ngamensis (3.5%), Marcusenius macrolepidotus (2.9%) and Synodontis leopardinus (2.8%). The group "Others" contributed 22.3% of the total mass value.

It is apparent that the species composition and relative abundance of fish in this sampling site differs markedly from the overall Okavango Delta analysis (see Figs. 4.1a & b). With the exception of H. vittatus the four other selected species (e.g. C. gariepinus, S. mystus, H. odoe & O. andersonii) were well represented in this sampling site comprising 47.1% of the total mass and 15.9% of the numeric contribution (Table 4.1).

Southern seasonal swamp

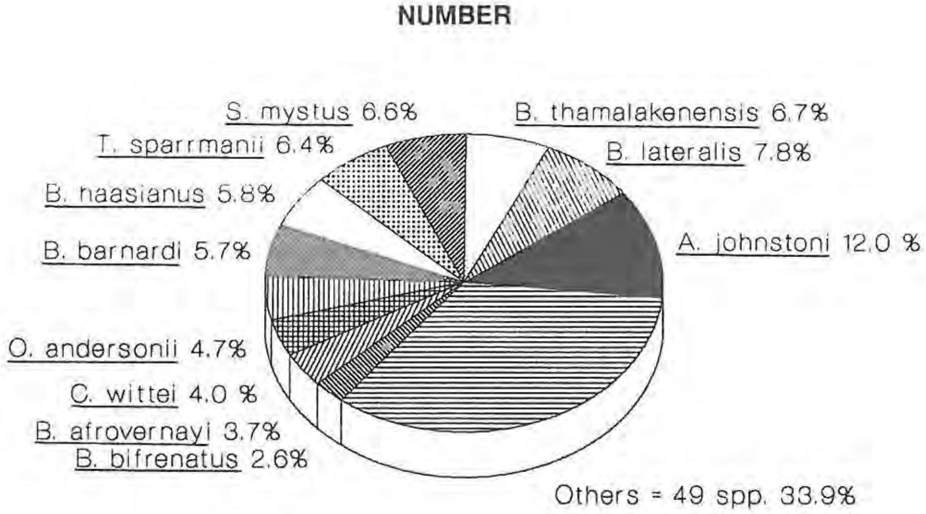
The southern seasonal swamp sampling site at Nxaraga Lagoon and the Boro River harboured a greater diversity of non-cichlid species when compared to either Chanoga Lagoon or the Thamalakane River. A total of 20188 specimens, representing 60 species with a combined mass of 481 kg was collected from this sampling site (Appendix 2).

Numerically, the community was dominated by non-cichlid species of which A. johnstoni (12.1%), Brycinus lateralis (7.8%), S. mystus (6.6%), Barbus barnardi (5.7%), B. thamalakanensis (6.7%), B. haasianus (5.8%), B. afrovernayi (3.7%), B. bifrenatus (2.6%) and Coptostomabarbus wittei (4.0%) were the most common (Fig. 4.4a). Only two cichlid species T. sparrmanii (6.4%) and O. andersonii (4.7%) were common. The group "Others" comprised 49 additional species which contributed 33.9% to the total.

In terms of mass contribution (Fig. 4.4b), important non- cichlid species included H. odoe (17.4%), S. mystus (14.7%), Clarias gariepinus (7.0%), C. ngamensis (3.4%), Synodontis leopardinus (4.2%) and S. nigromaculatus (5.8%). Important cichlid species included Oreochromis andersonii (9.8%), O. macrochir (2.8%), Serranochromis angusticeps (7.9%), S. robustus jallae (3.5%) and T. sparrmanii (4.7%). The group "Others" contributed 18.8% to the total.

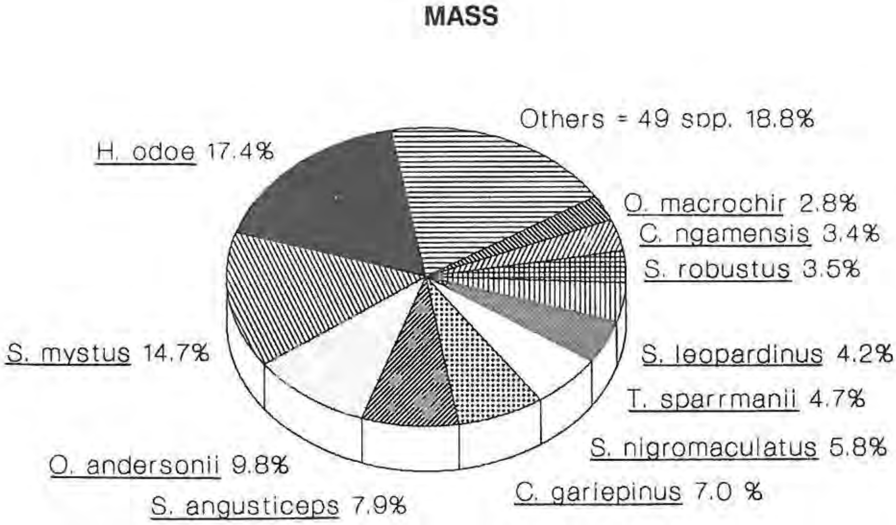
With the exception of H. vittatus, all other selected species featured prominently in this sampling site and comprised 49.0% of the total mass and 14.1% of the numeric composition (Table 4.1). H. vittatus was virtually absent from this sampling site with only two individuals recorded during the study period.

(a)



n = 20188

(b)



mass = 481 kg

Figure 4.4. Total number (a) and mass (b) of fish collected using all sampling methods from the seasonal swamp, Okavango Delta, between November 1983 and December 1986.

Northern perennial swamp

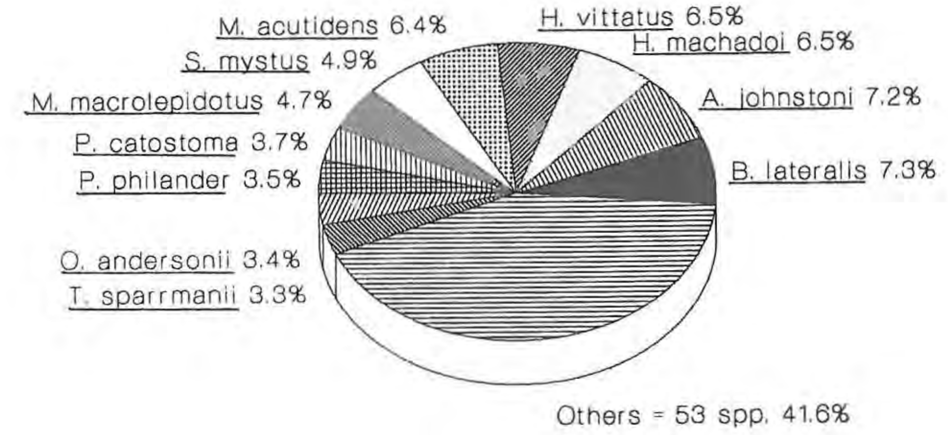
The perennial swamp habitat type was characterised by a community of many non-cichlid species, that were not recorded in the former sites. A total of 11327 specimens, representing 64 species with a combined mass of 599 kg was collected from this sampling site (Appendix 2). Both species diversity and the total mass catch was greater than that recorded in the previous sampling sites. Most noticeable was the appearance of large numbers of the rheophilic H. vittatus (Table 4.1).

Numerically, the most common fishes collected in the perennial swamp were non-cichlid species of which the following were the most important: B. lateralis (7.3%), A. johnstoni (7.2%), Hemigrammocharax machadoi (6.5%), H. vittatus (6.5%), M. acutidens (6.4%), S. mystus (4.9%), M. macrolepidotus (4.7%) and Petrocephalus catostoma (4.7%; Fig. 4.5a). The only common cichlids in the numeric analysis were Pseudocrenilabrus philander (3.5%), O. andersonii (3.4%) and T. sparrmanii (3.3%). The group "Others" comprised 53 additional species which contributed 41.6% to the total.

In terms of mass contributions (Fig. 4.5b), the most important non-cichlid species were H. vittatus (29.2%), Clarias gariepinus (15.1%), C. ngamensis (5.7%) and S. mystus (6.8%). Important cichlid species included S. angusticeps (8.9%) and O. andersonii (7.4%). The group "Others" contributed 12.8% of the total. The total cichlid proportion in the community was considerably less than the proportion found in the drainage river sampling sites or seasonal swamp (Appendix 2).

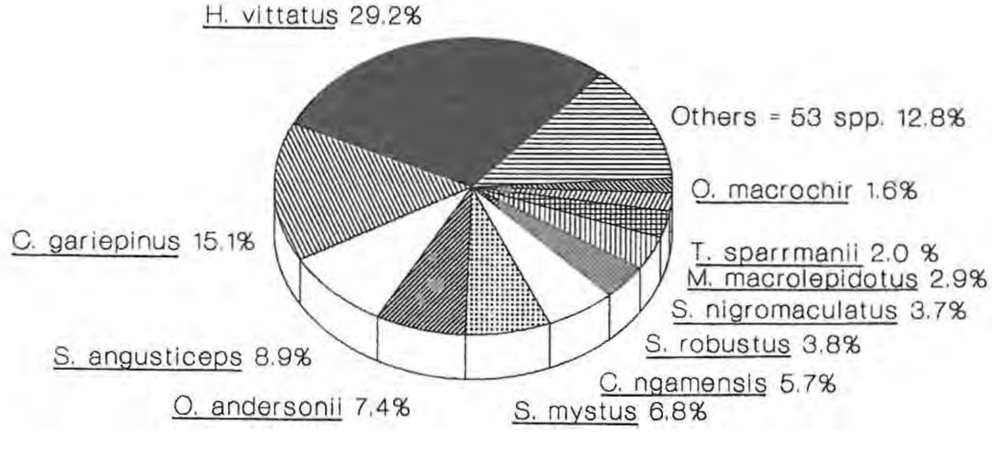
All five selected species were collected in this community and comprised 59.7% of the total mass and 17.5% of the numeric composition (Table 4.1). However, the percentage mass contribution of H. odoe and S. mystus was considerably lower than in the previous sampling sites.

(a) NUMBER



n = 11261

(b) MASS



mass = 599 kg

Figure 4.5. Total number (a) and mass (b) of fish collected using all sampling methods from the perennial swamp, Okavango Delta, between November 1983 and December 1986.

Perennial swamp floodplain-connected lagoons

A total of 11261 specimens, representing 62 species with a combined mass of 394 kg was collected from this sampling site. Numerically, the most important species were non-cichlids which included Barbus haasianus (10.8%), A. johnstoni (7.2%), Brycinus lateralis (5.9%), C. wittei (4.4%), S. mystus (4.2%), M. macrolepidotus (3.8%), Hydrocynus vittatus (3.7%) and Hemigrammocharax machadoi (3.3%; Fig. 4.6a). Important cichlid species were P. philander (6.3%), T. sparrmanii (3.2%) and O. andersonii (3.0%). The group "Others" comprised 51 species which contributed 44.2% to the total.

The most substantial mass contributions were recorded for the non-cichlid species of which Clarias gariepinus (11.8%), C. ngamensis (4.7%), Labeo lunatus (10.7%), H. vittatus (10.3%), Schilbe mystus (7.0%) and Synodontis nigromaculatus (3.5%) were the most common (Fig. 4.6b). Important cichlid species included Oreochromis andersonii (13.8%), O. macrochir (4.9%), Serranochromis angusticeps (11.3%) and T. rendalli (3.0%). The group "Others" contributed 15.0% of the total.

All five selected species were collected in this sampling site and comprised 46.8% of the total mass and 12.9% of the numeric composition (Table 4.1). However, the relative abundance and mass contributions of S. mystus and H. odoe were low when compared to the seasonal swamp and drainage river sampling sites.

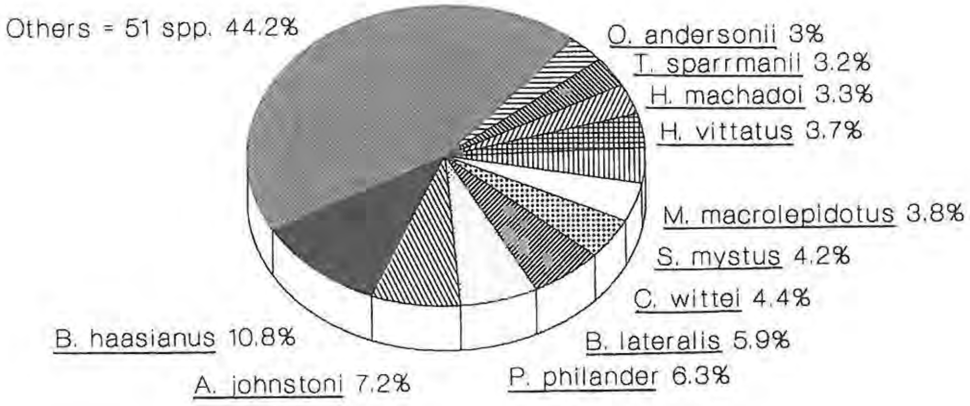
Rain pools

A total of 12345 specimens, representing 28 species with a combined mass of 102 kg was collected from this habitat type (Appendix 2). Numerically, the most important cichlid species included Oreochromis andersonii (26.9%), O. macrochir (6.4%), Tilapia rendalli (10.8%), T. sparrmanii (4.7%), T. ruweti (2.7%) and P. philander (8.2%; Fig. 4.7a). The non-cichlid, numeric composition of the fauna was represented by Barbus paludinosus (16.9%), B. thamalakanensis (6.3%), B. bifrenatus (2.7%), C. gariepinus (2.8%) and A. johnstoni (2.5%). The group "Others" comprised 17 additional species which contributed 9.1% to the total.

In terms of mass contributions (Fig. 4.7b), the most important cichlid species included Oreochromis andersonii (37.5%), O. macrochir (14.7%), Tilapia rendalli (17.3%), T. sparrmanii (4.3%) P. philander (1.4%) and S. codringtoni (1.1%). Important non-cichlid species included Clarias gariepinus (8.9%), C. ngamensis (3.5%), B. paludinosus (4.1%), S. mystus (1.2%) and H. odoe (1.6%). The group "Others" contributed 5.0% of the total.

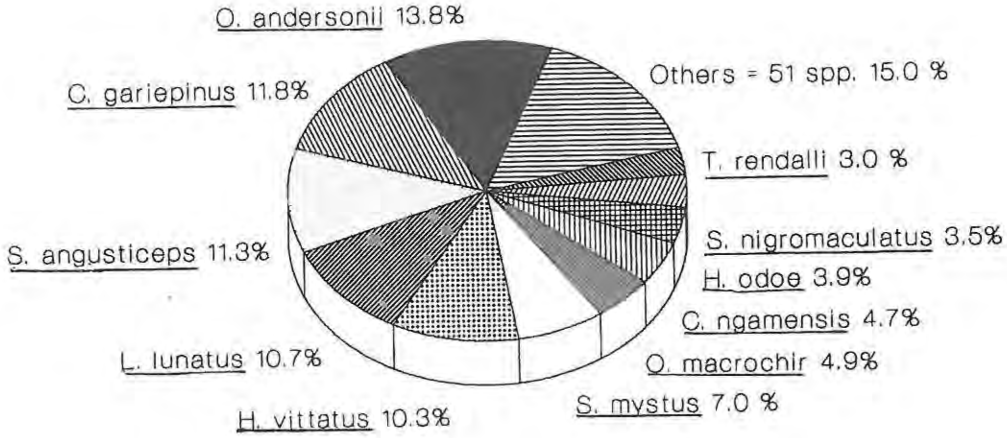
Of the five selected species, only O. andersonii and C. gariepinus featured prominently in this sampling site (Table 4.1). H. vittatus was absent from collections. The rain pool habitat type harboured a depauperate fauna with the community dominated by a few abundant, species.

(a) NUMBER



n = 11261

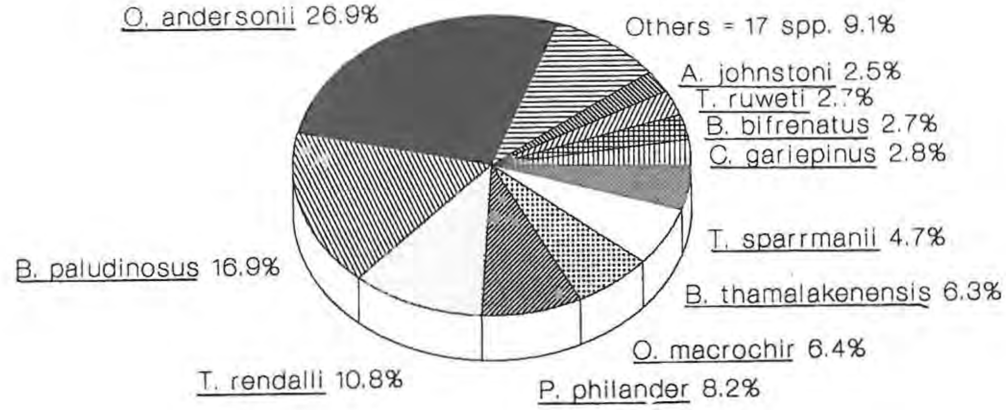
(b) MASS



mass = 394 kg

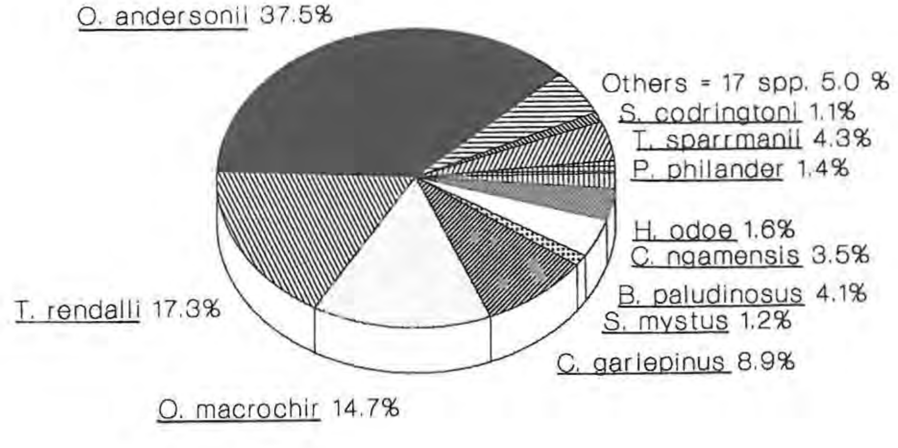
Figure 4.6. Total number (a) and mass (b) of fish collected using all sampling methods from the perennial swamp floodplain-connected lagoons, Okavango Delta, between November 1983 and December 1986.

(a) NUMBER



n = 12345

(b) MASS



mass = 102 kg

Figure 4.7. Total number (a) and mass (b) of fish collected using all sampling methods from the rain pool habitat type, Okavango Delta, between November 1983 and December 1986.

Riverine floodplain mainstream channel

A total of 10077 specimens, representing 66 species with a combined mass of 649 kg was collected from this sampling site (Appendix 2). Numerically, the community was dominated by non-cichlid species of which M. macrolepidotus (8.5%), Hemigrammocharax machadoi (8.0%), B. lateralis (5.2%), H. vittatus (4.9%), S. mystus (4.4%), M. acutidens (4.2%), P. catostoma (3.6%), C. gariepinus (3.5%) and S. nigromaculatus (3.3%) were the most common (Fig. 4.8a). Only two cichlid species, O. andersonii (3.8%) and T. sparrmanii (3.4%), were common. A total of 55 additional species in the group "Others" comprised 47.2% of the total.

The largest non-cichlid contributions to the mass composition (Fig. 4.8b) were from H. vittatus (29.6%), Clarias gariepinus (15.3%), C. ngamensis (4.0%), Schilbe mystus (6.1%), Synodontis nigromaculatus (4.2%) and M. macrolepidotus (2.6%). Common cichlid species included Serranochromis angusticeps (10.6%), S. robustus jallae (2.4%), S. giardi (1.4%), Oreochromis andersonii (8.7%) and O. macrochir (2.7%). The group "Others" contributed 12.4% to the total mass of fish.

The species composition of this sampling site was similar to that recorded for the perennial swamp and was characterized by a high diversity of species with large body size, such as H. vittatus. All the selected species were represented in this sampling site, comprising 60.1% of the total mass and 16.9% of the numeric composition (Table 4.1). The percentage contribution of H. odoe and S. mystus was, however, considerably less than in the seasonal swamp or drainage river sites.

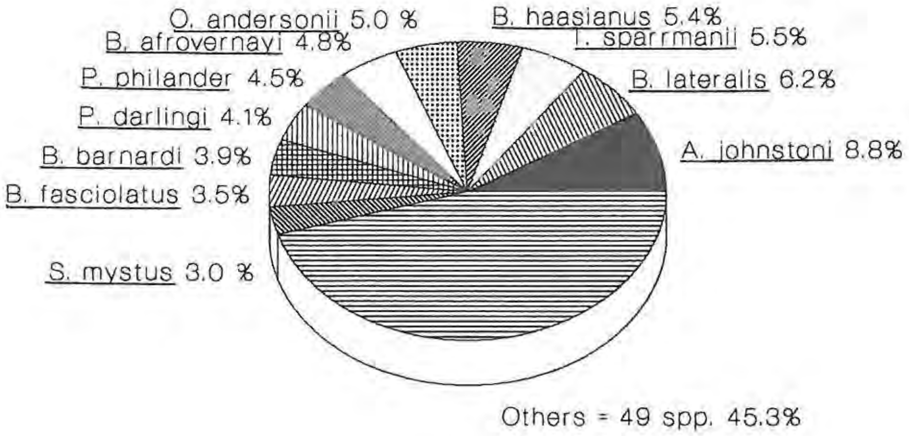
Riverine floodplain-connected lagoons

The species composition of this sampling site was also characterized by the large proportion of non-cichlid species. A total of 16145 specimens, representing 60 species with a combined mass of 605 kg was collected from this sampling site (Appendix 2).

Numerically important non-cichlid species included A. johnstoni (8.8%), Brycinus lateralis (6.2%), Barbus haasianus (5.4%), B. afrovernayi (4.8%), B. barnardi (3.9%), B. fasciolatus (3.5%) and S. mystus (3.0%; Fig. 4.9a). The most commonly encountered cichlid species included T. sparrmanii (5.5%), O. andersonii (5.0%), Pseudocrenilabrus philander (4.5%) and Pharyngochromis darlingi (4.1%). The group "Others" comprised 49 additional species which contributed 45.3% to the total.

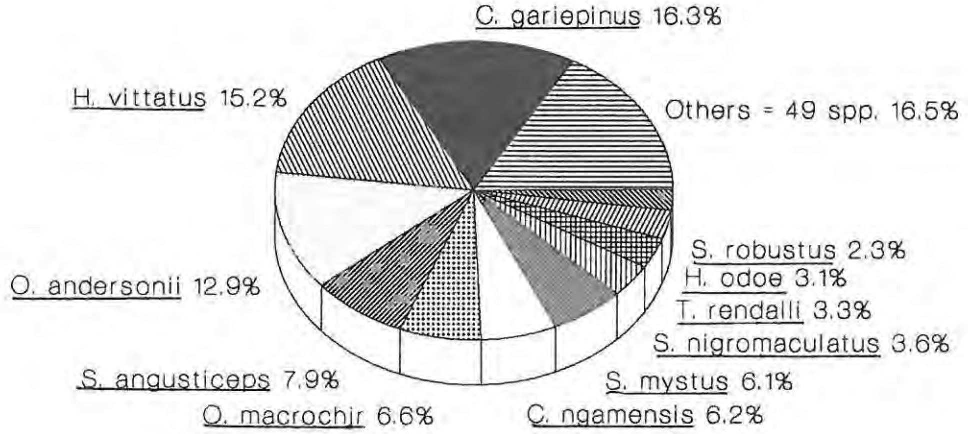
The largest non-cichlid contributions to the mass composition of the community (Fig. 4.9b) were from Clarias gariepinus (16.3%), C. ngamensis (6.2%), H. vittatus (15.2%), Schilbe mystus (6.1%),

(a) NUMBER



n = 10077

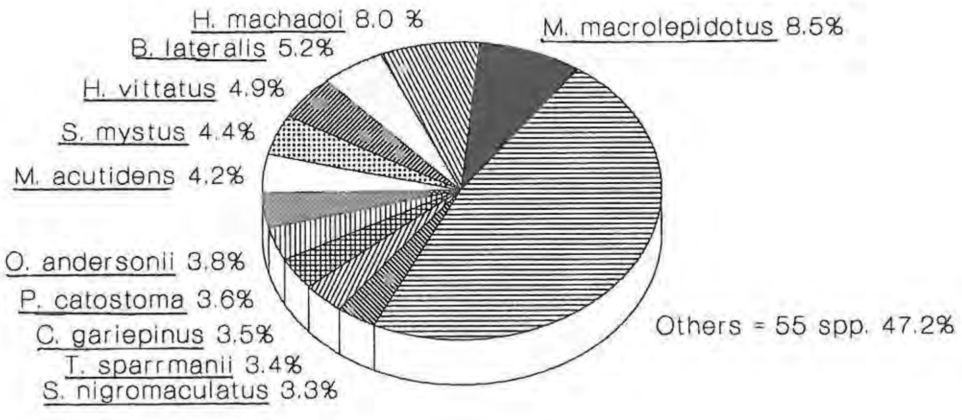
(b) MASS



mass = 649 kg

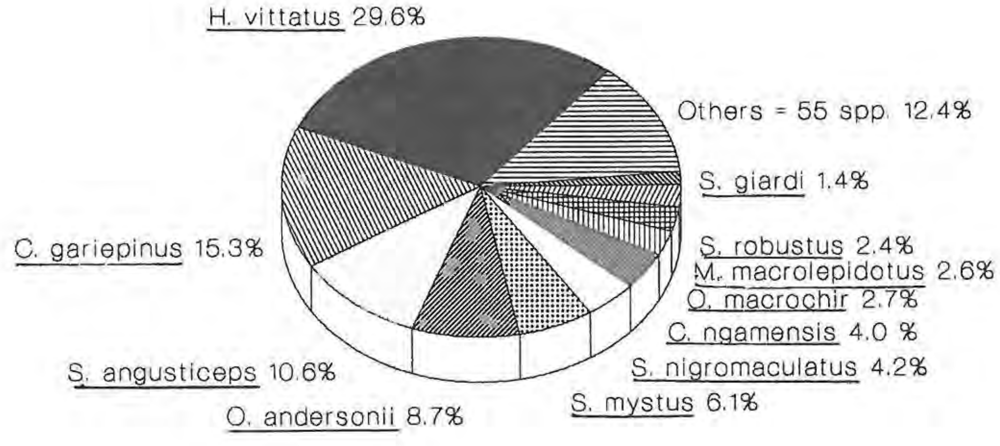
Figure 4.8. Total number (a) and mass (b) of fish collected using all sampling methods from the riverine floodplain mainstream channel, Okavango Delta, between April 1985 and December 1986.

(a) NUMBER



n = 16145

(b) MASS



mass = 605 kg

Figure 4.9. Total number (a) and mass (b) of fish collected using all sampling methods from the riverine floodplain-connected lagoons, Okavango Delta, between April 1985 and December 1986.

Synodontis nigromaculatus (3.6%) and H. odoe (3.1%). Important cichlid species included Oreochromis andersonii (12.9%), O. macrochir (6.6%), Serranochromis angusticeps (7.9%), S. robustus jallae (2.3%) and T. rendalli (3.3%). The group "Others" contributed 16.5% to the total.

All of the selected species featured in this sampling site, comprising 53.6% of the total mass and 12.9% of the numeric composition (Table 4.1). The relative abundance of H. odoe and S. mystus was, however, low when compared to catches in the drainage river and seasonal swamp sampling sites. The overall mass of fish collected, based on standardized catch and effort data, was also higher than in the seasonally fluctuating habitat types (Appendix 2).

COMMUNITY SIMILARITIES

Within the southern African geographic region, the Okavango Delta has a high diversity of fishes (66 species recorded during the present study period). However, the number of species and their relative abundance in different sampling sites varied markedly. Fish diversity and total catch, in mass, were highest in sampling sites within perennially flooded ecotones (e.g. riverine floodplain and perennial swamp), whereas diversity and total catch was lowest in sampling sites within seasonally flooded ecotones (e.g. seasonal swamp and drainage rivers; Appendix 2).

The use of the TWIN-SPAN multivariate community classification further revealed a clear distinction, at the first level of division, between the species composition of sampling sites in perennially or seasonally flooded ecotones (Fig. 4.10).

At the second level of division a clear distinction was again made between the species composition of perennially flooded, fast flowing (> 1 m/sec) sampling sites and perennially flooded, moderately flowing (0.5 m/sec) sampling sites. The species composition of fast-flowing sampling sites formed a group on the left side of the dichotomy; whereas the species composition of perennially flooded, moderately flowing sampling sites formed a group on the right hand side of the dichotomy. Within the seasonally flooded ecotones the species composition of the rain pool sampling site formed a group on the left hand side of the dichotomy. Rain pools had no measurable flow and as previously stated harboured a depaurperate fauna. The species composition of seasonally flooded, slow-flowing sampling sites (< 0.3 m/sec) were grouped on the right hand side of the dichotomy.

It should be stressed that this is a simplistic interpretation at present but that these two parameters (e.g. perennial versus seasonal and having a flow or not) affect everything else such as substrate type and presence of aquatic vegetation, which in turn influence the community structure.

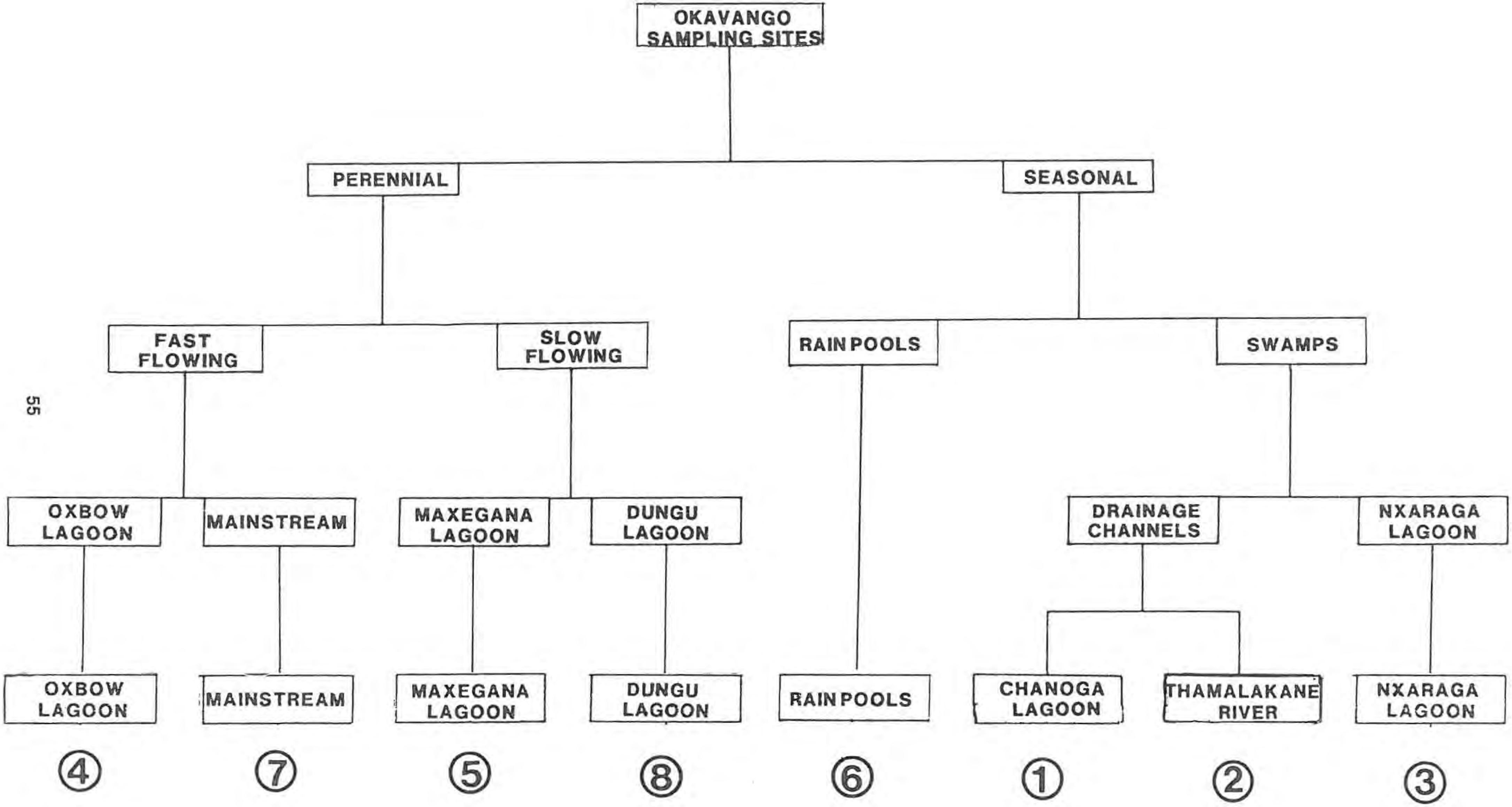


Figure 4.10. TWIN-SPAN community classification based on the grouping of all fish collections and sampling sites in the Okavango Delta, between the period November 1983 and December 1986. Sampling site numbers are given in Table 4.1.

The third dichotomy further subdivides the sampling sites. The species composition of the perennial swamp at Xakanixa Lagoon (site 4) and the riverine floodplain mainstream channel (site 7) formed a group on the extreme left side of the perennially flooded, fast flowing division. The species composition of perennial swamp floodplain-connected lagoons (e.g. Maxegana Pools; site 5) and the riverine floodplain-connected lagoons (e.g. Dungu Lagoon; site 8) were grouped together under perennially flooded, moderately flowing sampling sites.

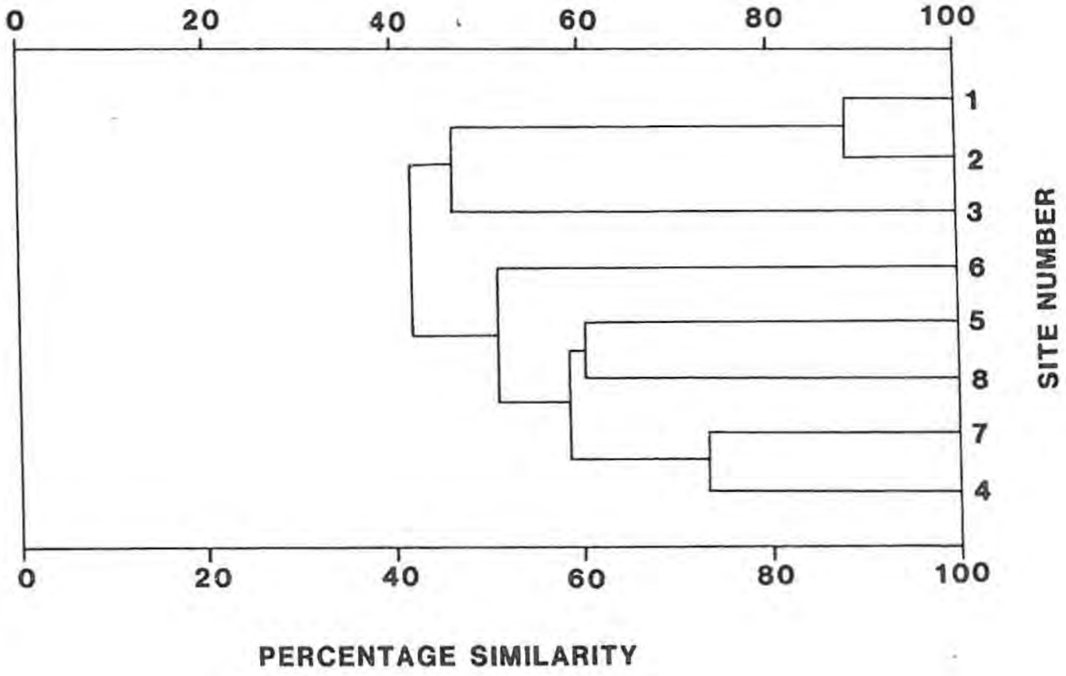
Although the riverine floodplain mainstream and floodplain-connected lagoons (e.g. sites 7 and 8) were immediately adjacent to one another, the species composition of the riverine floodplain mainstream (e.g. site 7) showed a stronger affinity to the perennial swamp fauna at Xakanixa Lagoon (e.g. site 4). It should be noted that although both of these sampling sites were in different ecotones, the riverine floodplain mainstream and perennial swamp sampling sites were within habitats with a continual flow of water. The perennial swamp floodplain-connected lagoons (e.g. site 5), on the other hand, was more closely aligned with the riverine floodplain-connected lagoons (e.g. site 8). Both these sites were perennial floodplain lagoon habitat types that are connected to the larger river channels during flooding.

Within the seasonally flooded, slow flowing habitat types, the species composition of Nxaraga Lagoon (e.g. site 3) formed a group on the right side of the dichotomy. The species composition of the drainage river sites were grouped on the left side of the dichotomy. No further distinction was made for the rain pool sampling site.

The fourth dichotomy further subdivides the drainage rivers sampling sites (e.g. Chanoga Lagoon; site 1 & the Thamalakane River; site 2) into distinct groups. The species composition in all other sampling sites also formed closely similar groups on their own (Fig. 4.10).

For the most part the species assemblages and corresponding sampling sites formed a fairly well defined sequence from those clustered on the left side of the dichotomy (e.g. perennial habitat types) to those clustered on the right side of the dichotomy (seasonal swamp and drainage river habitat types). These differences can be associated with the difference in physical, chemical and biological characteristics between the respective sampling sites such as the permanence of water, flow rates, depth, substrate and aquatic macrophyte cover.

CANACO similarity ordination further revealed two distinct groups of sampling sites (e.g. perennial versus seasonal swamp habitat types) that can be separated at a similarity level of 40% (Fig. 4.11). The drainage river and seasonal swamp sampling sites (e.g. site 1, 2 & 3) formed one stem, while the perennial swamp and riverine floodplain sampling sites (e.g. sites 4, 5, 6, 7 & 8) formed another stem. The relatively long stems of the dendrogram giving rise to perennial and seasonal sites indicate that these two groups are quite distinct. The drainage river sampling sites (e.g. 1 & 2) had a 90% similarity, but only a 50% similarity to the seasonal swamp. These results are supported by the above TWIN-SPAN dichotomies (Fig. 4.10). The rain pool habitat type (e.g. site 6) formed its own grouping, with a 50% similarity value. Species which occurred in all sites in perennially flooded habitats (i.e. indicator species) included H. vittatus, M. acutidens and S. robustus jallae, and those for the seasonally flooded habitats included H. odoe, S. mystus and B. lateralis.



*sampling site 1 = Chanoga Lagoon; site 2 = Thamalakane River; site 3 = Nxaraga Lagoon; site 4 = Xakanixa Lagoon; site 5 = Maxegana Pools; site 6 = Rain Pools; site 7 = Okavango mainstream channel; site 8 = Dungu Lagoon

Figure 4.11. CANOCO similarity ordination based on all collections and sampling sites grouped together in the Okavango Delta, between the period November 1983 and December 1986.

DISCUSSION

It is apparent that each of the various major sampling sites within the different ecotones in the Okavango has a unique combination of hydrological fluctuations and other pertinent physical features. A general relationship between the degree of fluctuation and the diversity of forms, total catch and similarity of sampling sites (ecotones) can be made. A greater diversity and overall catch, particularly of larger non-cichlid species (e.g. H. vittatus), was found in the more hydrologically stable riverine floodplain and perennial swamp ecotones relative to the hydrologically unstable seasonal swamp and drainage rivers ecotones. This trend may be attributed to the greater habitat heterogeneity resulting in a wider range of microhabitats (e.g. dense papyrus roots, mainstream channel, floodplain lagoons) in the riverine floodplain and perennial swamp ecotones which enable more stenotopic non-cichlid species to proliferate relative to the cichlid species. It is reasonable to assume that the degree of stability of the annual flood cycle is negatively correlated with species diversity.

During the course of this study there was both lateral and longitudinal zonation from a relatively predictably perturbed (stable) rheophilic state to an unpredictably perturbed (unstable) palustrine state. The seasonal swamp and drainage river communities were dominated by a large number of smaller species (< 200 mm SL) such as B. lateralis, S. mystus and M. macrolepidotus. In contrast, the community structure in the perennial swamp and riverine floodplain was dominated by a high diversity of many large fish (> 200 mm SL) such as H. vittatus, Serranochromis angusticeps and S. robustus jallae.

Based on standardized CPUE figures for the mass contribution to individual sampling sites (Appendix 2), the catch was highest in the riverine floodplain and perennial swamp and lowest in the seasonal swamp and drainage rivers. In addition, a greater mass of fish in the riverine floodplain and perennial swamp were collected in larger mesh nets (e.g. 96, 110 & 118 mm stretch-mesh) whereas smaller mesh nets (e.g. 24, 40 & 50 mm stretch-mesh) caught the greatest mass of fish in the seasonal swamp and drainage rivers.

The major factor determining the distribution and abundance of fishes in the Okavango Delta appears to be habitat preferences, with the physical characteristics of the environment playing a major role. The permanence of the water (i.e. retention time) and the nature of its flow properties are two of the most obvious ecological factors influencing community structure in the Okavango. These two factors influence all other physico-chemical parameters in the Okavango, such as substrate type, extent of emergent, submergent and floating macrophyte cover, dissolved oxygen values, water temperatures, etc.

The TWIN-SPAN community classification and CANOCO similarity analysis did separate the major components of the fauna into perennial and seasonal swamp habitat types. However, it should be stressed that this is not an absolute criterion as, even within the perennial, riverine reaches of the system, seasonal floodplains and marsh conditions were found, and within the seasonal swamp, perennial water bodies were found.

Based on the results presented in this Chapter, the specialized rheophilic species such as *H. vittatus*, *Nannocharax macropterus* and *Barbus eutaenia* were restricted to the riverine floodplain and perennial swamp. In the seasonal swamp many of the species were widely distributed in floodplains and channels throughout this ecotone. Species in this category included *H. odoe*, *Mormyrus lacerda*, *T. ruweti*, *S. giardi*, *Clarias theodorae*, *A. hutereaui* and *Ctenopoma multispinis*.

A large number of species also have sufficiently generalized habitat preferences to be widespread and relatively common throughout all sampling sites. The most obvious of these were several small *Barbus* species, including *B. barnardi*, *B. radiatus* and *B. thamalakanensis*, as well as *Petrocephalus catostoma*, *M. macrolepidotus*, *Pseudocrenilabrus philander*, *O. andersonii* and *C. gariepinus*.

Four of the five selected species (e.g. *C. gariepinus*, *S. mystus*, *H. odoe* & *O. andersonii*) appeared in the catches of almost all the sampling sites. However, only two specimens of *H. vittatus* were collected from the seasonal swamp, and none were collected in the drainage rivers (e.g. Chanoga Lagoon and Thamalakane River). The virtual absence of this species from these sampling sites can be related to its preference for large, relatively clear water bodies. *H. odoe*, on the other hand, was more common in the drainage rivers and seasonal swamp than in the perennial swamp or riverine floodplain. The habitat preferences of *H. odoe* are well-vegetated areas. Being an ambush predator, *H. odoe* relies on dense vegetation for cover while waiting for prey (Chapter 7). In the perennial swamp the fast-flowing mainstream channel was relatively deep and void of submergent vegetation where *H. vittatus* were common. In contrast, the seasonal swamp and drainage river habitats were characterized by slow-flowing channels and extensive floodplains with abundant submerged vegetation. These observations on habitat preference for the above selected species are in agreement with the findings in other similar African wetland systems such as the Zambezi River system (Jackson, 1961a) and Kwando-Linyanti-Chobe River systems (van der Waal, 1985; Merron 1990). The relative increase of *S. mystus* in the seasonal swamp and drainage rivers is also noteworthy, particularly for the long-term development of the commercial fishery (Chapter 8).

CHAPTER 5

SEASONAL ANALYSIS OF FISH COMMUNITIES AND THEIR RESPONSE TO THE ANNUAL FLOOD REGIME

INTRODUCTION

Chapter 4 revealed that there are distinct communities of fish in the Okavango Delta that can be separated from each other by the physical conditions (e.g. water retention and flow rates) within the different sampling sites. This chapter assesses the seasonal responses of these fish communities, particularly the selected species, to the annual flood cycle. This was essential for determining the importance of the role of the floods in maintaining these communities. This chapter attempts to quantify whether or not large scale intra- and inter-sampling site migrations existed and to assess the significance of these movements in relation to the annual flood regime.

It has been well established that African floodplain fish populations move in response to the annual flood regime (Jackson, 1961a; Lowe-McConnell, 1979; Welcomme, 1979; Kok, 1980). Many fish move to more favourable breeding and feeding sites. This trend has also been found in many other wetland areas of the world. Kushlan (1976, 1980) found that the seasonal fluctuation in water level in the Everglades Swamp in the USA was the most critical environmental factor affecting the demography of the fish community. Goulding (1980) discusses the role of fishes of the Amazon basin in South America as organisms of dispersal for aquatic and terrestrial plant seeds during flooding.

An important question which needed to be addressed in this thesis is the degree of biotic interaction between peripheral floodplain-connected lagoons and the mainstream channels. Floodplain-connected lagoons occur throughout the Okavango system, but with a greater frequency in the riverine floodplain ecotone.

MATERIALS AND METHODS

The standardized gillnet, seine net and rotenone sampling results described in Chapter 4 were analysed on a seasonal basis to determine the species diversity, relative abundance and mass composition of the fish commmunities under different flood regimes.

This analysis entailed grouping each collection of fish made within each sampling site according to four distinct flood levels (i.e. receding, low, filling and high water levels). Each site at which collections were made was then assigned a habitat code. For example, Chanoga Lagoon during the receding water level was assigned habitat code 1R; during the low water level habitat code 1L; during the the arrival of the floods (i.e. filling phase) habitat code 1F; and at high water level habitat code 1H. This process was repeated for all 8 major sampling sites. A total of 32 different habitat codes was assigned. Table 5.1 shows all the habitat codes assigned to the different sampling sites.

Multivariate (TWIN-SPAN) community analysis was again performed to determine whether or not differences existed in the species composition at various flood levels between the different sites. The catch per unit effort (CPUE) for each sampling site and quarterly survey was established to ascertain the demography of the population in response to the annual flood. It should be emphasized that the CPUE was calculated based on the combined sampling methods using identical gear. The quarterly surveys were conducted in such a way that the different techniques and efforts in different sampling sites are believed to be as comparable in the present context as possible. In addition, computer-smoothed trends of the amplitude of change for the CPUE in each sampling site are also shown. The collections of fish recorded in August 1984 were done by courtesy of the Botswana Fisheries Unit, but all other collections from November 1983 to December 1986 were carried out by the author.

Table 5.1. The habitat codes assigned to four distinct flood levels for each sampling site based on all fish collections in the Okavango Delta, between November 1983 and December 1986.

Sampling site	Flood cycle			
	Receding	Low	Filling	High
Chanoga Lagoon, Boteti River	1R	1L	1F	1H
Thamalakane River	2R	2L	2F	2H
Seasonal swamp, Nxaraga Lagoon	3R	3L	3F	3H
Perennial swamp, Xakanixa Lagoon	4R	4L	4F	4H
Perennial swamp floodplain lagoons	5R	5L	5F	5H
Rain pools	6R	6L	6F	6H
Riverine floodplain mainstream	7R	7L	7F	7H
Riverine floodplain lagoons	8R	8L	8F	8H

RESULTS

Chanoga Lagoon, Boteti River

The TWIN-SPAN community classification for all 32 different habitat codes was identical to that presented in Figure 4.10 and revealed that the fish fauna of Chanoga Lagoon was more similar within this site than to any other sampling site irrespective of flood level (e.g. receding, low, filling and high water level; see Appendix 3). Although the species composition over the flood regime remained relatively constant, large scale annual changes in CPUE occurred in this sampling site according to the prevailing flood level. The highest catches were recorded during low water level while the lowest catches were taken at high water levels (Fig. 5.1a). Four of the five selected species (e.g. C. gariepinus, S. mystus, H. odoe & O. andersonii) featured prominently in this sampling site contributing more than 50% of the total mass of fish collected during all flood levels (Appendix 3). H. vittatus was absent from this sampling site.

Chanoga Lagoon was first surveyed in November 1983 during the receding water phase. The CPUE based on all sampling methods was 52.2 kg. Chanoga Lagoon was next surveyed in March 1984 during the low water level. The CPUE was slightly higher than that recorded for November 1983 with 53.5 kg collected (Fig. 5.1a).

Chanoga Lagoon began to receive flood waters in late June 1984. In July 1984 the CPUE declined sharply to 32.1 kg. By August 1984 the lagoon was at its highest annual level, and the CPUE was lower than that previously recorded for any flood level (28.1 kg; Fig. 5.1a).

Similar changes in CPUE were apparent in 1985 and 1986, with the highest catch recorded in March 1986 (Fig. 5.1a). The computer-smoothed changes in annual catch indicates that the catch was not constant and the amplitude between peaks varied markedly depending on the flood cycle (Fig. 5.1b). The highest CPUE was recorded during low water with the lowest CPUE recorded at high water. These changes most likely reflect the concentrating and diluting effects of fish stocks in relation to the flood level.

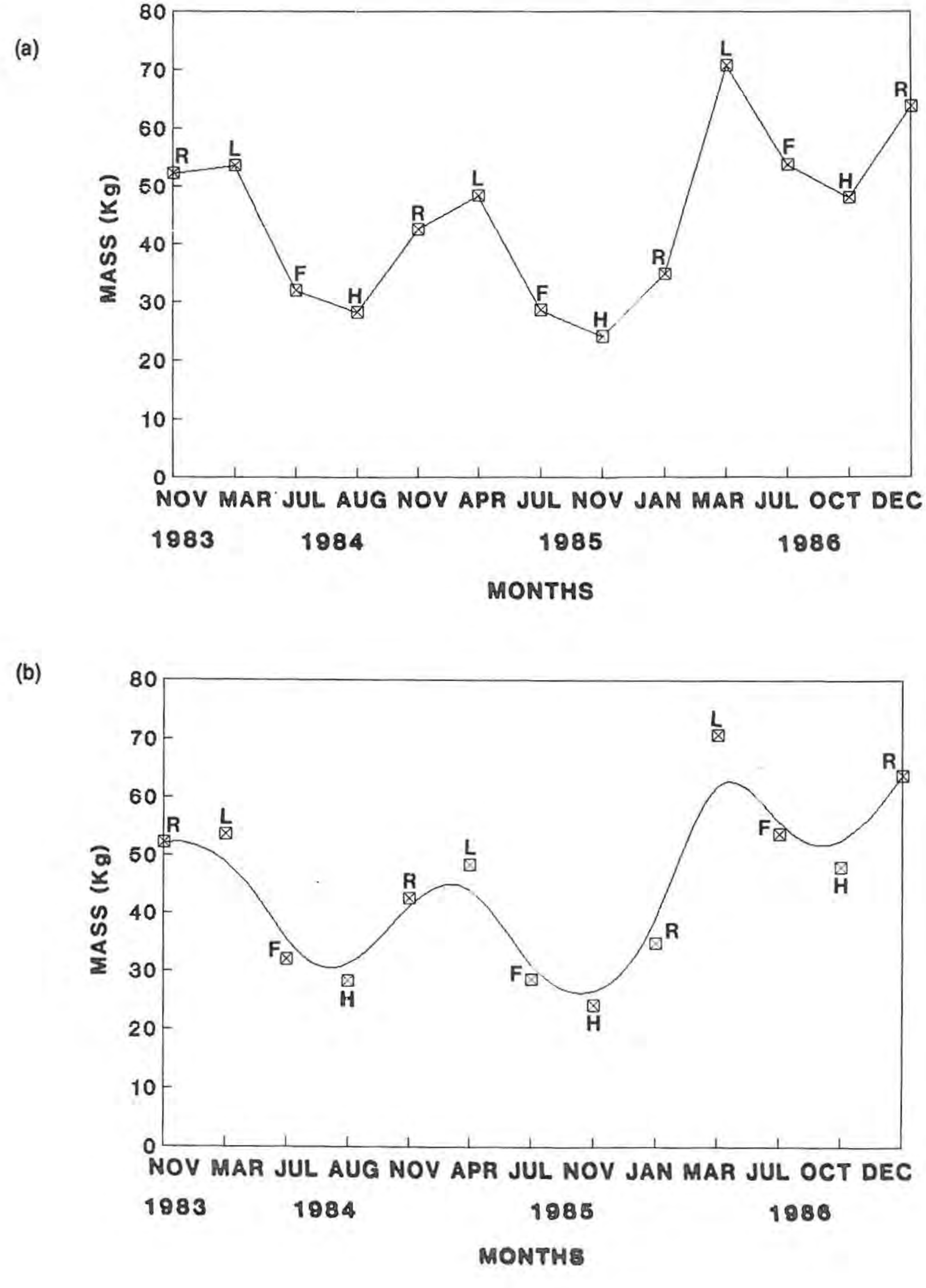


Figure 5.1. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for different flood levels in Chanoga Lagoon, Boteti River, Okavango Delta, between November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

Thamalakane River

The annual changes in species composition indicate that this sampling site also was more similar to itself at different flood levels than to any other sampling site irrespective of the flood level (see Fig. 4.10; Appendix 4). Four of the five selected species (e.g. C. gariepinus, S. mystus, H. odoe & O. andersonii) contributed more than 40% of the mass composition during all flood levels (Appendix 4). H. vittatus was again absent from this sampling site. The CPUE (Fig. 5.2a) indicates that the catch was not constant and that large scale annual changes in CPUE occurred in this sampling site according to the prevailing flood level. The highest catches were recorded during low water level while the lowest catches were taken at high water levels (Fig. 5.2a).

In November 1983 the Thamalakane River was limited to a narrow channel, about 10 m wide on average and less than 1.0 m deep. Aquatic macrophytes were scarce and limited to the extreme margins of the river. The combined CPUE based on all sampling methods was 56.7 kg (Fig.5.2a).

By March 1984 the Thamalakane River was reduced to a series of shallow (< 1 m) turbid, disjunct pools void of aquatic macrophytes. The density of fishes per unit sampling effort was higher than that recorded in November 1983 with a total catch of 95.7 kg (Fig. 5.2a). This reflects the concentrating effect on the fish stocks during the annual drawdown of flood waters. Although the CPUE was higher than that recorded in November 1983, many of the species succumb to natural mortality during the annual low water level. Pelicans and maribou storks fed heavily in the drying up pools each year (pers. observation). In many of the smaller isolated remnant pools the community was reduced to mainly three species (i.e. O. andersonii, C. gariepinus and B. paludinosus). This finding is similar to that found by Skelton et al. (1983) and Bruton and Jackson (1983) for Lake Ngami, Merron et al. (1987) for the Pongolo floodplain and Jackson (1989) for Lake Mweru.

Except for a small 50 x 50 m pool below Matlapaneng (Fig. 3.1), the entire Thamalakane River dried up by late April 1984 (P. A. Smith, Department of Water Affairs, Maun, Botswana, pers. communication). Flood waters began to fill the river in June 1984. The river rose rapidly with the initial pulse of flood waters and continued to fill for the next month. By the end of July 1984 the area of the Thamalakane River was greatly expanded in size, up to 100 m wide in some areas, with extensive areas of terrestrial vegetation now inundated. The CPUE of 35.8 kg was lower than in either November 1983 or March 1984 (Fig. 5.2a). This suggests that movement of fish occurred from upstream areas and indicates the resilience of the fish community in this sampling site, as the river had virtually dried up in April 1984. During the height of the flood in August 1984 the CPUE was at its lowest level with a total catch of 30.0 kg (Fig. 5.2a).

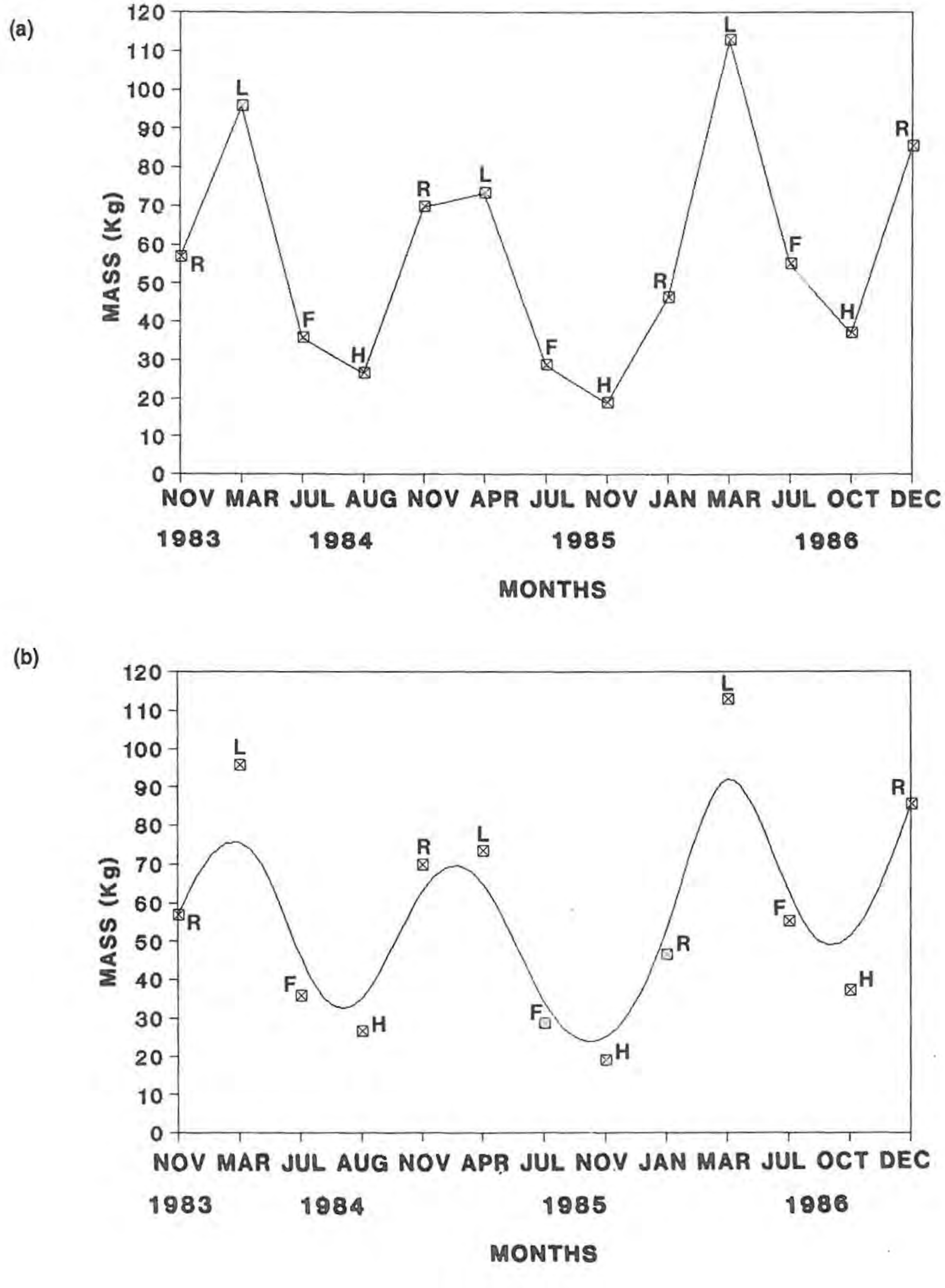


Figure 5.2. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for different flood levels in the Thamalakane River, Okavango Delta, between November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

When compared to the same time period in 1983, the Thamalakane River in November 1984 maintained a considerably higher water level. The CPUE of 69.6 kg was higher than for the same period in 1983 (Fig. 5.2a). This indicates the difficulty of assigning specific months to different flood levels. Although the river in November 1984 was in a receding stage, the magnitude of the annual flood made it resemble the high water level condition of 1983 (P.A. Smith, pers. communication).

The Thamalakane River was also subjected to wide annual fluctuations in water level during the 1985 and 1986 sampling periods. Similar patterns of CPUE changes were apparent (Fig. 5.2a) with the highest catches recorded during low water levels. The computer smooth trends for CPUE also indicate that marked changes in the amplitude of the catch is influenced by the magnitude of previous and present flood conditions (Fig. 5.2b).

The highest CPUE recorded was in 1986 and an overall increase in CPUE of 20% was apparent between 1983 to 1986 (Fig. 5.2a). The catch in 1986 is believed to be a result of large scale movement of fish spawned during the relatively high 1984 flood in the seasonal swamp. Similar changes in CPUE have been recorded by Welcomme (1979) who states that the recruitment and catch in a given year x is determined largely by the magnitude of the flood in year x-2. Although a longer time series of data are needed to quantitatively model yield in the Okavango, the preliminary results suggests that a similar pattern of flood related increases in catch was evident in the Okavango between 1983 and 1986. This observed increase in catch could also be an artifact of increased sampling efficiency which undoubtedly occurred during the course of this study. However this bias was kept to a minimum and it is believed that the overall increase in CPUE during this study more closely reflects the magnitude of the various annual flood cycles.

There was also a succession of species which recolonized the Thamalakane River from upstream areas. The primary colonizers were small fish species (< 50 mm SL) such as A. johnstoni and various Barbus spp. followed by large fish species (> 200 mm SL) such as C. gariepinus and S. mystus. As the system stabilized (i.e. within 2 - 4 weeks of flooding) other large fishes, such as H. odoe and Serranochromis species, were represented in the catches. The catfishes C. gariepinus and S. mystus were the first larger species to migrate as they can take advantage of the increase in allochthonous food sources, such as drowned terrestrial insects and small mammals (see Chapter 7). It is believed that the cichlids are not able to take immediate advantage of the rising flood waters to feed as the detritus food web takes longer to develop. These observations for the Okavango are similar to recolonization patterns observed for recently inundated areas of the Pongolo floodplain in Zululand (Merron et al., 1987).

Seasonal swamp

The species composition of the seasonal swamp also was more similar within this site than to any other sampling site regardless of the flood level (see Fig. 4.10; Appendix 5). The species composition of the seasonal swamp does, however, have a closer affinity to Chanoga Lagoon and the Thamalakane River than to the other sampling sites (see Chapter 4).

With the exception of H. vittatus, of which only two individuals were caught during the high water phase in 1984, the four other selected species featured prominently in this community, contributing greater than 40% to the total mass during all flood levels (Appendix 5).

In November 1983 the water level in the seasonal swamp at Nxaraga Lagoon was in full recession. The surrounding floodplains were drying and the Boro River averaged 7 m wide and 0.5 m deep. The CPUE at Nxaraga Lagoon of 36.2 kg (Fig. 5.3a) was lower than that recorded for either the Thamalakane River or Chanoga Lagoon during the same time period. In March 1984 the Boro River leading into Nxaraga Lagoon averaged 3 m wide and less than 0.3 m deep and all the surrounding floodplains were dry. Fish populations in Nxaraga Lagoon were concentrated and a high CPUE of 53.8 kg was recorded (Fig. 5.3a).

The seasonal swamp was next sampled in July 1984, after the relatively large flood which reached this area in May 1984. The CPUE in Nxaraga Lagoon had dropped markedly to 25.5 kg, lower than either the November 1983 or March 1984 values (Fig. 5.3a). During the period of high water level in August 1984, the CPUE dropped slightly, relative to that recorded in June 1984 to a value of 13.5 kg (Fig. 5.3a). By November 1984 the water level at Nxaraga Lagoon was again receding. The CPUE of fish (41.4 kg) was higher than the same time period in 1983 (Fig. 5.3a). A similar pattern of changes in CPUE was evident in the 1985 and 1986 sampling periods with an overall increase in CPUE recorded between 1983 and 1986.

The amplitude of change in CPUE recorded for the seasonal swamp was similar to the drainage river sites with the highest CPUE recorded during the receding and low water levels when stocks were concentrated (Fig. 5.3b; Appendix 5). However, the species composition of the catch at low water level in the seasonal swamp was dominated by a greater percentage of larger fish whereas in the drainage rivers it was dominated by a greater percentage of smaller fish species.

An increasing importance of lateral and longitudinal movements of fish in the seasonal swamp was evident when compared to the former sampling sites. In general the drainage rivers received an annual influx of fish whereas refuges in the seasonal swamp, such as Nxaraga Lagoon, harboured important inocula which recolonized the floodplains and drainage rivers during the flood.

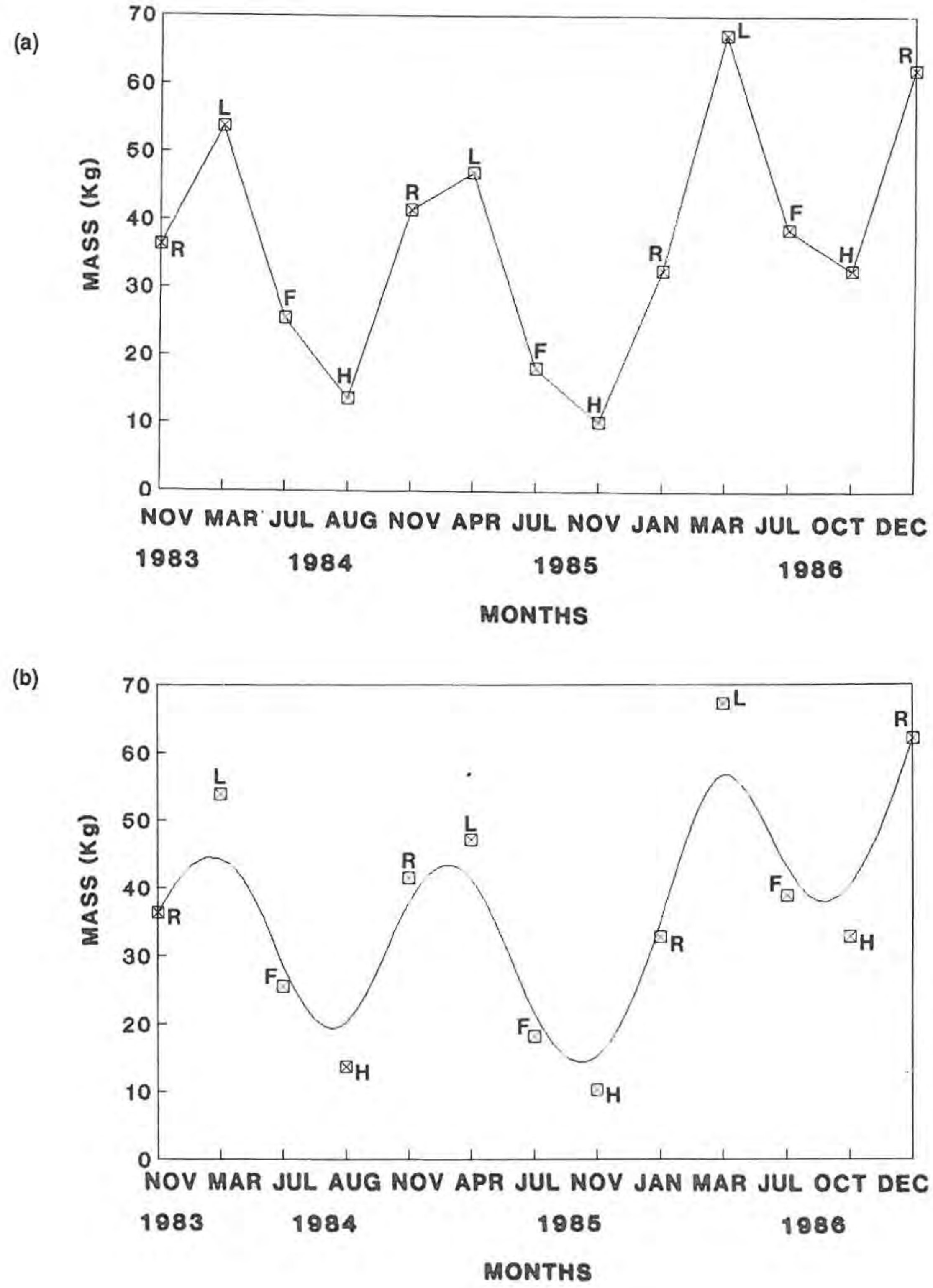


Figure 5.3. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the seasonal swamp, Okavango Delta, between the period November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

Perennial swamp

The seasonal changes in species composition of the perennial swamp at Xakanixa Lagoon indicate that the fauna was more similar throughout the flood cycle than to any other sampling site regardless of the flood level (see Fig. 4.10; Appendix 6). The perennial swamp sampling site does, however, share some similarities with other northern Okavango sampling sites (e.g. riverine floodplain mainstream channel; see Chapter 4).

Of the five selected species, H. vittatus, O. andersonii and C. gariepinus contributed the greatest mass proportion during all flood levels (Appendix 6). There was a noticeable decrease in mass contribution for the other two keynote species (e.g. H. odoe and S. mystus) during all flood levels when compared to the former sampling sites (Appendix 6).

The perennial swamp was first surveyed during the receding water level in November 1983. The CPUE, based on all sampling methods, was 43.8 kg (Fig. 5.4a). During the low water level in March 1984 a higher CPUE of 53.8 kg was recorded compared to November 1983 (Fig. 5.4a). During the filling phase in July 1984 the CPUE was 54.5 kg (Fig. 5.4a). The CPUE for August 1984, during the high water level, was the highest recorded for the 1983/84 flood season with 61.9 kg collected (Fig. 5.4a). This is in sharp contrast to the finding in the former sites where an increase in CPUE was recorded during the receding and low water levels.

In November 1984, during the receding flood level, a decrease in the CPUE was recorded (35.9 kg, Fig. 5.4a). Similar results for CPUE were observed during the 1985 and 1986 sampling periods (Fig. 5.4a). An increase in catch between 1983 and 1986 was recorded and agrees with the findings for the former sampling sites (Fig. 5.4a).

It is apparent that, although diversity did not change throughout the flood cycle, the catch composition changed between the selected species. At high water levels a greater mass contribution of H. vittatus and C. gariepinus was recorded in the catches while during the receding and low water levels the mass contribution of O. andersonii increased (Appendix 6).

During the receding and low water levels C. gariepinus and H. vittatus appear to undergo potamodromic movements out of this habitat type and more cichlids, particularly O. andersonii, appeared in the catch (Appendix 6). A more consistent CPUE was recorded in the perennial swamp with the degree of amplitude in the CPUE not as marked as for the seasonal swamp or drainage river sampling sites (Fig. 5.4b).

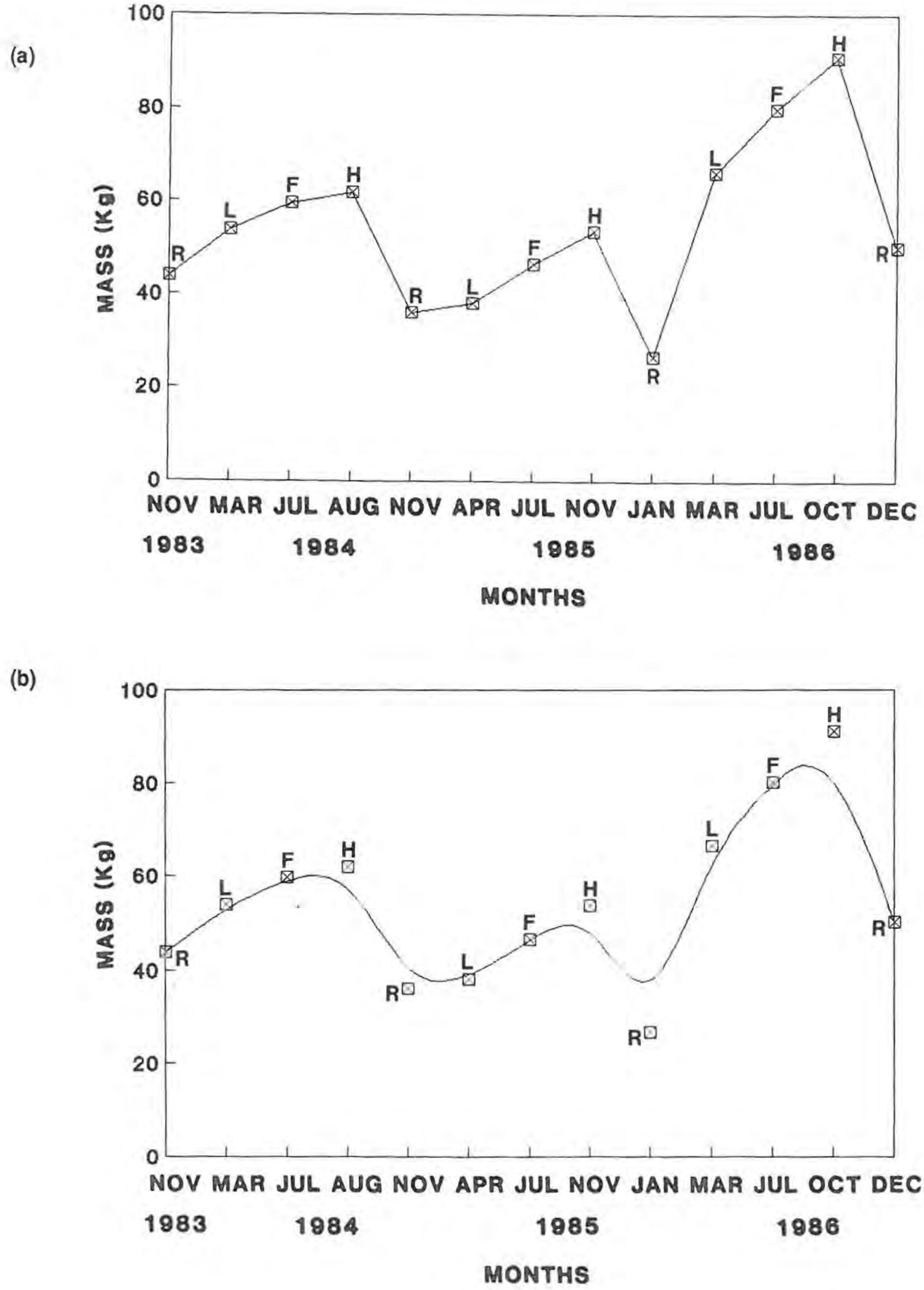


Figure 5.4. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the perennial swamp, Okavango Delta, between November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

Perennial swamp floodplain-connected lagoons

The seasonal changes in the relative abundance and mass composition of the fish fauna in the perennial swamp floodplain-connected lagoons at Maxegana Pools were more similar during all flood levels than to any other sampling site irrespective of the flood level (see Fig. 4.10; Appendix 7). This sampling site does, however, share some similarity with other northern Okavango sampling sites (see Chapter 4).

All five selected species were common during all flood levels. During the receding and low water levels the mass contribution of O. andersonii in the catch increased while H. vittatus and C. gariepinus were more common from catches during the filling and high water levels (Appendix 7). Both H. odoe and S. mystus did not feature as strongly in the mass composition of this sampling site as they did in the seasonal swamp and drainage rivers sampling sites (Appendix 7).

The perennial swamp floodplain lagoons were first surveyed during the receding water level in November 1983. The CPUE, based on all sampling methods, was 20.8 kg (Fig. 5.5a). During the low water level in March 1984 an increase in the CPUE to 34.8 kg was recorded (Fig. 5.5a).

During the arrival of the flood waters in July 1984 (i.e. filling phase) the CPUE decreased to 27.7 kg (Fig. 5.5a). During the high water level in August 1984, the CPUE was 25.8 kg (Fig. 5.5a). In November 1984, the water level was again receding and the CPUE increased to 32.4 kg (Fig. 5.5a).

Similar changes in CPUE were apparent during the 1985 and 1986 sampling periods (Fig. 5.5a). The degree of change in the amplitude of the CPUE (Fig. 5.5b) was more uniform over time than that found for the seasonal swamp and drainage river sites. An increase in CPUE during the course of this study period was also evident in the perennial swamp floodplain-connected lagoons and agrees with the findings recorded for the other sampling sites.

Rain pools

The species composition of rain pools was more similar within this sampling site regardless of flood level than to the other sampling site (see Fig. 4.10; Appendix 8). Of the five selected species, H. vittatus was absent from the rain pool sampling site. O. andersonii and C. gariepinus were the most common species during all flood levels but the proportions of H. odoe and S. mystus were the lowest recorded for any sampling site (Appendix 8).

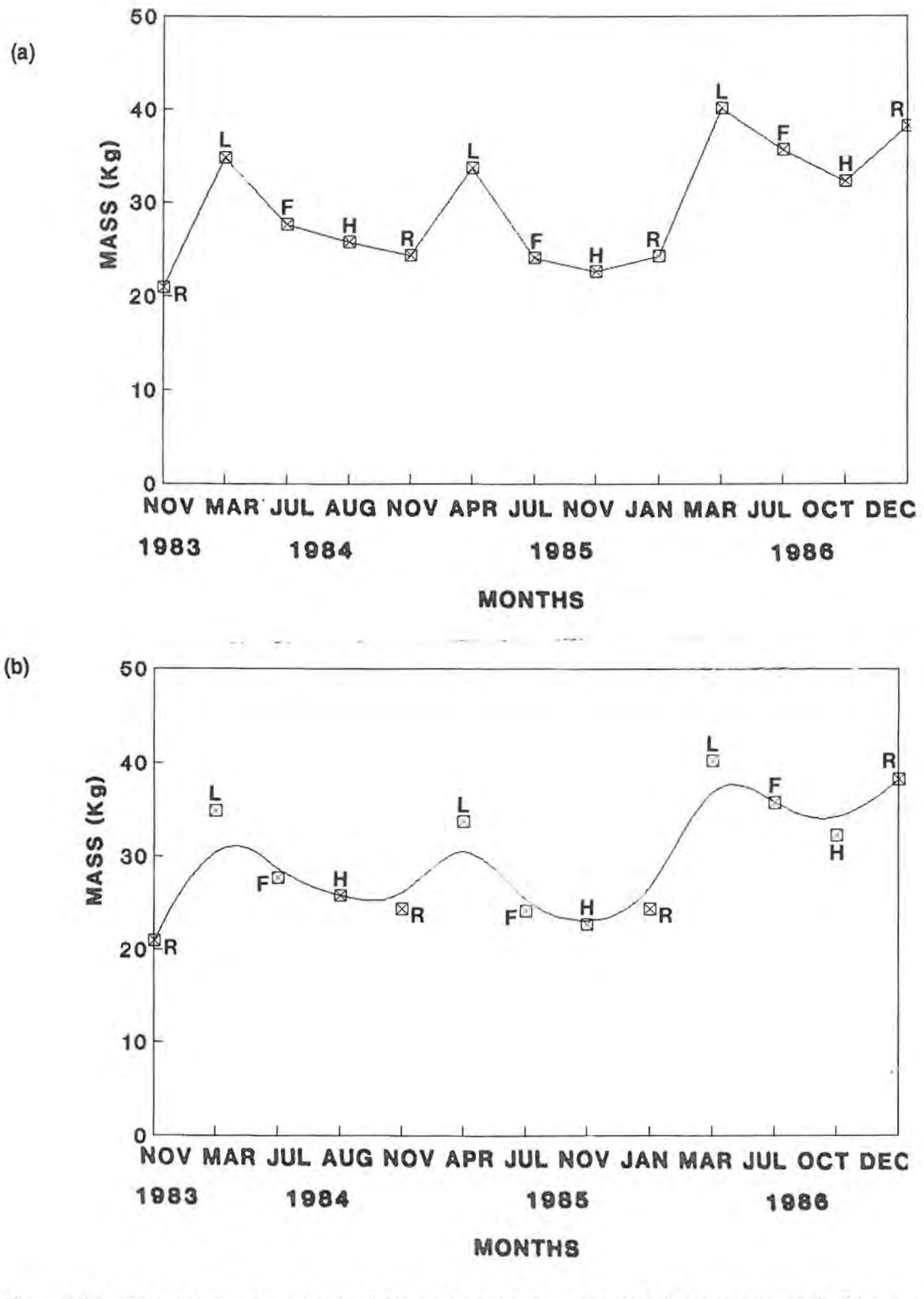


Figure 5.5. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the perennial swamp floodplain-connected lagoons, Okavango Delta, between the period November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

The rain pool habitat type was first surveyed during the receding water phase in November 1983. The CPUE, based on all sampling methods, was 7.0 kg (Fig. 5.6a). This was the lowest CPUE recorded for any previous sampling site. During the low water level in March 1984 the CPUE was slightly higher (8.4 kg; Fig. 5.6a). In July 1984 the rain pools were connected to the main floodplain and a slight decrease in CPUE was apparent (7.4 kg; Fig. 5.6a), possibly due to dispersal. In August 1984, during the high water level, the CPUE was 7.8 kg (Fig. 5.6a) whereas in November 1984, during the receding water level, a CPUE of 7.7 kg was recorded (Fig. 5.6a).

Similar results were obtained during the 1985 and 1986 sampling periods (Fig. 5.6a). The movement patterns of fish in this sampling site were relatively simple and included fish which immigrated or emigrated only during periods of connection. The amplitude of change in the CPUE was minimal (Fig. 5.6b) although this may be an artifact of the ease of collecting fish within rain pools.

Riverine floodplain mainstream channel

The species composition of this sampling site was also more similar within this sampling site than to any other sampling site irrespective of the flood level (see Fig. 4.10; Appendix 9). The riverine floodplain mainstream channel fauna shared its closest affinities with the perennial swamp fauna (see Chapter 4).

As stated in Chapter 3, quantitative quarterly sampling was only initiated in this sampling site in April 1985. However, a number of "ad hoc" collections were made in this habitat type (Merron *et al.*, 1983; 1985). This area has also been resurveyed by staff of the J.L.B. Smith Institute of Ichthyology between September and December 1987, 1988, 1989 and 1990 (Merron, *in press*). With the exception of *H. odoe*, the four other selected species (e.g. *C. gariepinus*, *S. mystus*, *H. vittatus* and *O. andersonii*) featured prominently in this sampling site contributing more than 50% to the mass composition during all flood levels (Appendix 9).

During the arrival of the annual floods in April 1985, the CPUE based on all sampling methods was 47.5 kg (Fig. 5.7a). During the high water level in July 1985 the CPUE decreased to 31.4 kg (Fig. 5.7a). This was slightly lower than that recorded in April 1985 (Fig. 5.7a) and possibly a result of the dilution of the fish stocks brought about by increased water levels.

In November 1985, during the receding water levels, a dramatic increase in CPUE was apparent rising to 83.5 kg (Fig. 5.7a). Towards the end of the low flood in February 1986, the CPUE was greater than that recorded in former sampling periods with a total of 99.2 kg (Fig. 5.7a).

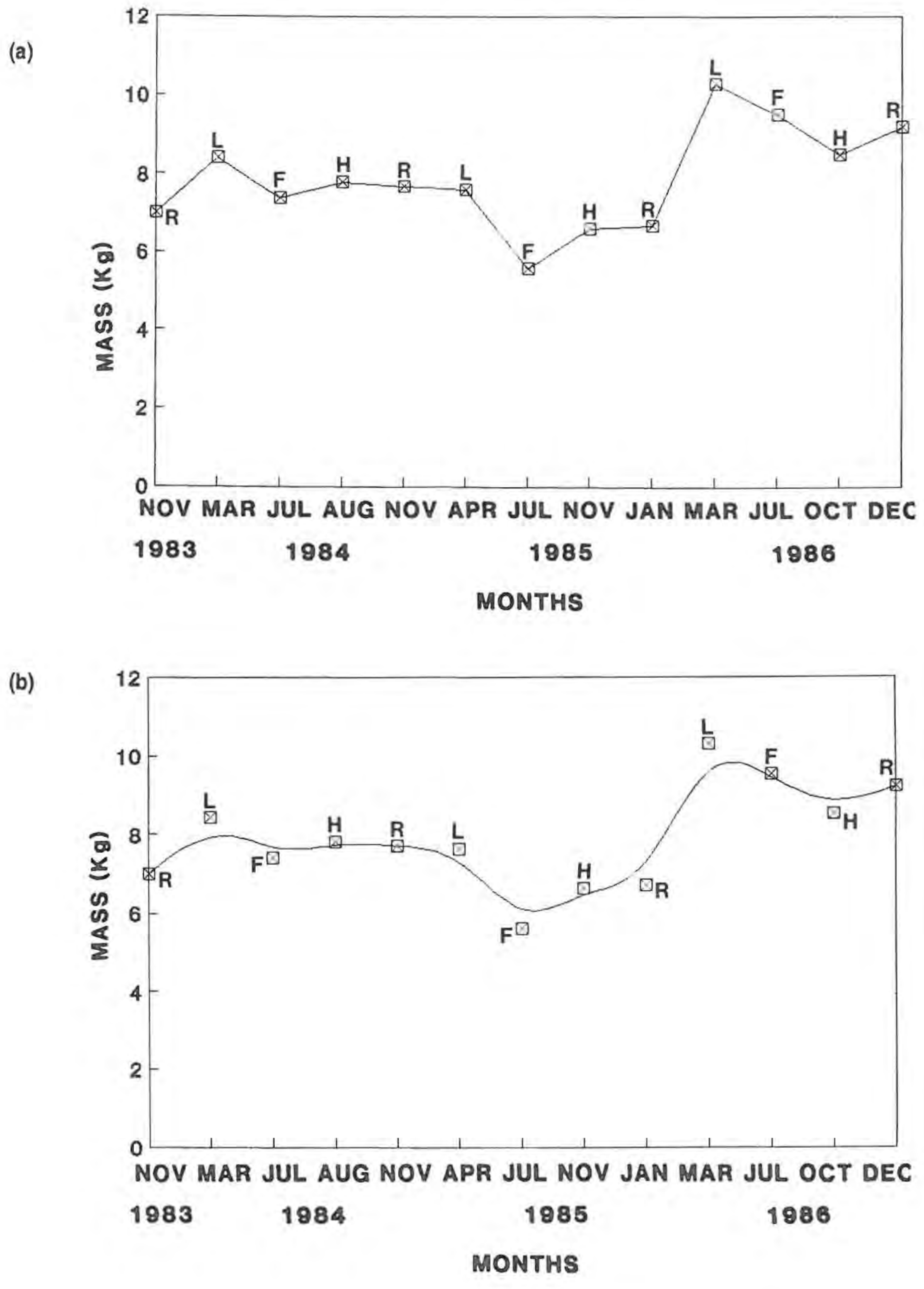


Figure 5.6. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the rain pool habitat type, Okavango Delta, between the period November 1983 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

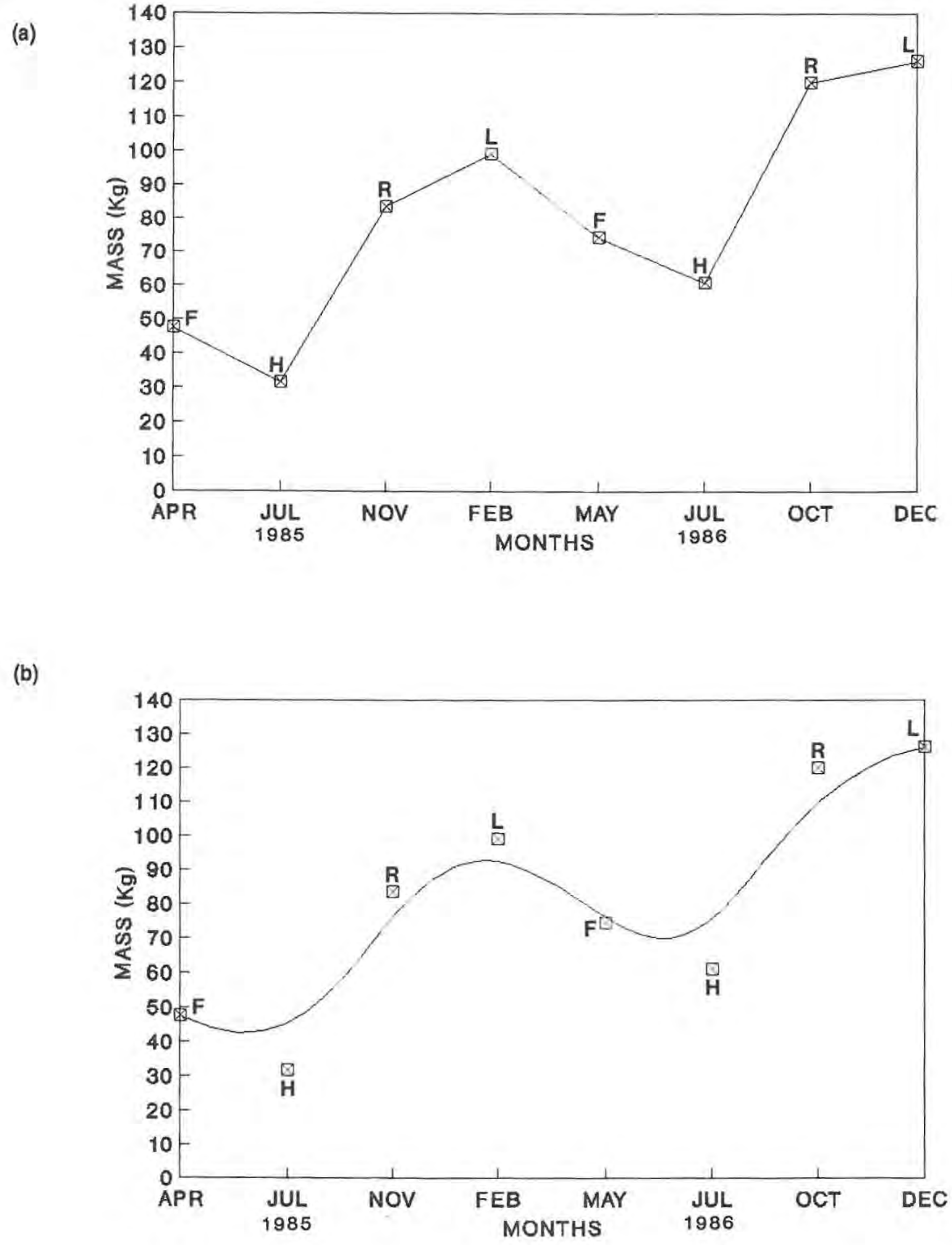


Figure 5.7. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the riverine floodplain mainstream channel, Okavango Delta, between the period April 1985 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

A similar pattern of reduced catches was evident in May and July 1986 with a CPUE of 74.3 and 61.0 kg (Fig. 5.7a). However, during the receding and low water levels in October and December 1986 an increase in CPUE was again apparent with values of 120.1 and 126.2 kg (Fig. 5.7a).

Of particular interest in the November 1985 and October 1986 collections was the appearance in catches of large numbers of the catfish Clarias gariepinus in the mainstream channel. This trend was the result of an annual mass congregation of this species which pack-hunt at this time of year in the mainstream channel. This phenomenon is explained in greater detail in Chapter 7. It is, however, important to stress here that these aggregations are a predictable response to the receding and low water levels each year (Merron, in press).

The changes in CPUE throughout the year in the riverine floodplain mainstream channel were relatively more stable and predictable, with the amplitude of change considerably less than in the seasonal swamp or drainage rivers (Fig. 5.7b). The overall catch in 1986 in the riverine floodplain mainstream channel was also higher than that recorded for 1985 and in this respect agrees with the findings for the other sampling sites.

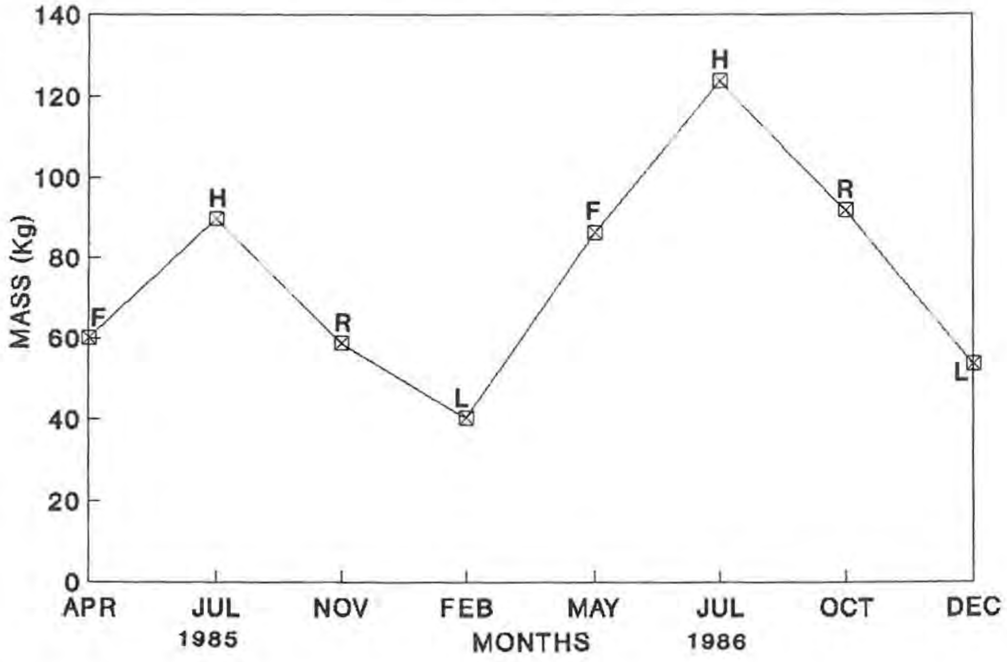
Riverine floodplain-connected lagoons

The species composition of the fish fauna inhabiting the riverine floodplain-connected lagoons was also more similar within the group of samples for this sampling site than to any other sampling site irrespective of the flood level (see Fig. 4.10; Appendix 9). The community does share some similarities with the riverine floodplain mainstream channel and perennial swamp sampling sites (Chapter 4).

During the filling and high water levels the mass composition was dominated by H. vittatus and C. gariepinus while during receding and low water levels O. andersonii contributed a larger percentage to the mass composition (Appendix 9). The two other selected species (e.g. S. mystus and H. odoe) were common although their contribution to the mass composition was lower than that recorded in the seasonal swamp or drainage rivers.

In April 1985, during the filling phase, a CPUE of 60.0 kg was recorded (Fig. 5.10a). In July 1985, during the high water level, the CPUE was 89.6 kg and was higher than that recorded in April 1985 (Fig. 5.10a). This pattern of increased CPUE of fish during high water levels was similar to that observed in the perennial swamp sampling site at Xakanixa Lagoon where high water levels also resulted in the highest CPUE of fish (see Fig. 5.4a).

(a)



(b)

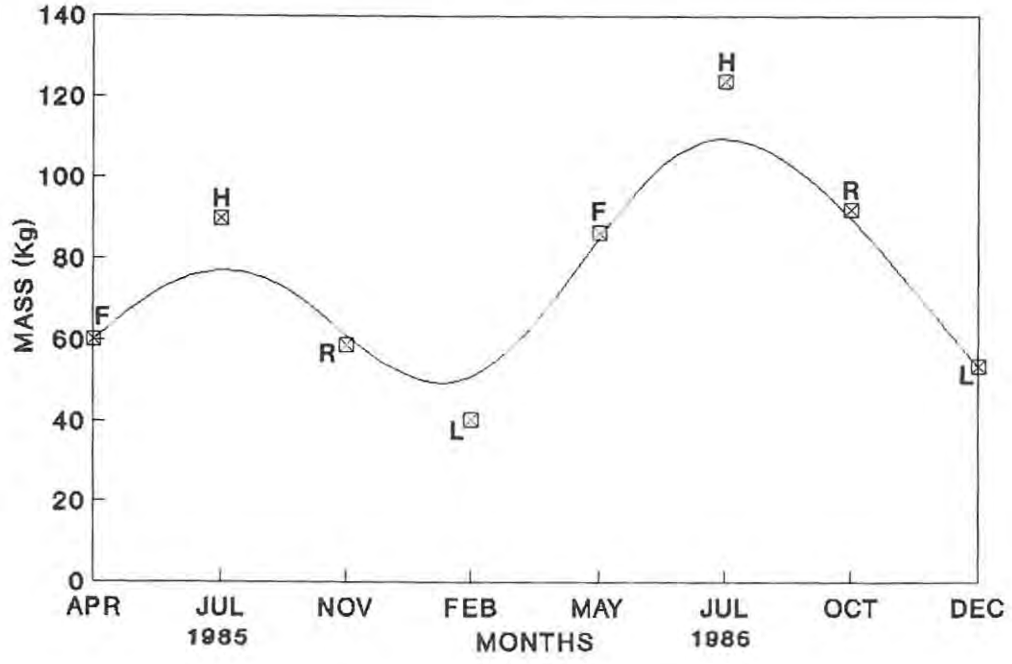


Figure 5.8. The catch per unit effort (a) and computer-smoothed trends in catch (b) based on all sampling methods for the riverine floodplain-connected lagoons, Okavango Delta, between the period April 1985 and December 1986. The various flood levels are R = receding, L = low, F = filling and H = high flood levels.

In November 1985 and February 1986 during the annual drawdown of flood waters, a lowered CPUE was apparent with values of 58.7 and 40.2 kg respectively (Fig. 5.10a). A similar pattern of progressive increases in CPUE with higher flood levels was evident for the May and July 1986 sampling periods with the overall catch higher than that recorded during the same time periods in 1985 (Fig. 5.10a). The amplitude of change in CPUE was also less severe than in the seasonal swamp and drainage rivers (Fig. 5.10b).

DISCUSSION

The results presented in this Chapter indicate that different degrees of change occurred within the mass and abundance data for fish communities in each sampling site at different stages of the annual flood cycle. These differences were, however, more similar within the particular sampling site than to any other sampling sites flood level. It is possible that because of a relatively short sampling period (e.g. November 1983 to December 1986) that was conducted during the height of a drought, the data and interpretations based on quarterly surveys, may not have detected all the changes which occur annually within a sampling site. Although the total catch varied throughout the year in all sampling sites, the proportions of certain fish species within the community did not change. The results presented here serve, however, as a first attempt to quantify the dynamics of the fish population and lay a foundation for further scientific investigations.

The widely fluctuating drainage rivers can be characterized by relatively simple movement and recolonization patterns, primarily from refuge areas in the seasonal swamp (e.g. Nxaraga Lagoon). This is an obvious conclusion as the drainage rivers, except for Chanoga Lagoon on the Boteti River (see Fig. 3.1), either dried up completely or were reduced to a series of isolated pools following low floods during the course of this study. Chanoga Lagoon retained water and a relatively diverse and abundant fish fauna throughout the drought and was likely of considerable importance in recolonizing the lower half of the Boteti River when the annual flood waters arrived. Although the colonization ability of fish into the drainage rivers appears to be high, the mortality rate of these species was also high when conditions deteriorated in the rapidly drying drainage river channels. Many fish become trapped in isolated pools which suggests that upstream movement into the seasonal swamp refuges when water levels recede does not appear to be as important as downstream movements. The fact that the Okavango system also recedes in a downstream direction may also create physical barriers to upstream movement during the low water level each year. It should also be stressed that the Thamalakane River was surveyed during the height of the drought when fish communities were naturally stressed. The absence of H. vittatus and the low frequency of other rheophilic forms (e.g. M. acutidens) suggests that recruitment from the perennial swamp into the drainage rivers was minimal during the course of this study. This supports the contention that the main movement and recruitment during the course of this study was by species and individuals from the seasonal swamp to the drainage rivers. However, movements of fish from the perennial swamp to the seasonal swamp and drainage rivers under high flood conditions may occur during an extended wet cycle.

The changes which occurred in Lake Ngami (Fig. 2.3) on a relatively short time scale, described below, also serve as a microcosm of what can happen to the communities of fish in the drainage rivers. In 1979 when the lake was > 150 km^2 in area, a total of 49 species was recorded (Bruton, 1979c; Bruton & Jackson, 1983). In late 1982, when the lake was drying, the community was reduced to two species of catfish, Clarias gariepinus and C. ngamensis (Skelton et. al., 1983). In 1984 the lake received flood waters via the Kunyere River (Fig. 2.3). There was a large migration of fish into the lake from the refuges of the seasonal swamp. By mid-1985 Lake Ngami once again dried until 1989 when flood waters re-entered the lake (pers. observation).

A similar pattern has also been recorded for Lake Chilwa, Malawi. During the years 1965 to 1968 the lake was transformed from a large body of open water to a dry lake basin. As soon as the lake was reflooded fish catches rose dramatically (Furse et al., 1979). Wide fluctuations in catch in relation to changing water levels have also been reported for Lake Mweru, Zambia (Jackson, 1989), Lake Chad, Chad (Durand, 1980; Benech et al., 1983), Lake Rukwa, Tanzania (Mann, 1967) and the Pongolo floodplain in South Africa (Kok, 1980; Merron et al., 1987).

During this study, permanent water bodies in the seasonal swamp, such as Nxaraga Lagoon served as refuges which harboured dense concentrations of fish stocks during the drying down phase. These fish dispersed laterally at high water level to recolonize the previously dry surrounding floodplains and longitudinally into the drainage rivers.

The seasonal swamp community thus has a resident fish fauna with recolonization taking place mainly from within this ecotone. Minshull (1985) also found that refuges in the seasonal swamp play a crucial role in repopulating the adjacent floodplains during the flood. This conclusion is also based on the finding that very few H. vittatus and M. acutidens, were collected, which would indicate a greater movement from perennial swamp to seasonal swamp. However, these species were insignificant in the catch (see Appendix 5). Many of the other smaller rheophilic species (e.g. the mastacembelid eel, Afromastacembelus frenatus) found in the perennial swamp were also rare in the seasonal swamp and further supports the finding that minimal movement occurred between the perennial swamp and seasonal swamp during the study period. If large scale longitudinal movement existed a greater number of these rheophilic species would have been expected. It must also be stressed again that this study was performed during a period of extreme drought and lowered water levels which may have enhanced the formation of physical isolating mechanisms between different sampling sites. Many species may be prevented from migrating from the perennial to the seasonal swamp, except during exceedingly high floods. This is especially important with regard to predation by raptorial birds such as the fish eagle, particularly on larger species such as H. vittatus.

The two H. vittatus recorded from the seasonal swamp during the relatively large flood of 1984 (see Fig. 2.2) are, however, believed to have originated further upstream. The presence of this species supports the finding that the movement of more specilialized forms at high water level does occur at certain times. This finding suggests that encroachment of the perennial swamp fauna may occur, although it must be stressed that the magnitude of this encroachment is likely to depend on repetitive years of high flood levels. For example, the rheophilic H. vittatus was collected from Lake Ngami in 1858 by Frederic Daviaud who described the Lake as a "Grand Lac" over 200 km long (see Jubb & Gaigher, 1971). During this period the Okavango experienced prolonged years of high floods (Shaw, 1984). This, undoubtedly, allowed a greater movement of rheophilic species from the riverine floodplain and perennial swamp that colonized the seasonal swamp, drainage rivers and sump lakes.

The seasonal swamp fish community exhibited both lateral movement of certain species onto the adjacent floodplains, and a succession of longitudinal movements of certain species into the drainage rivers. The reason why some fish have different movement patterns may be related to their trophic or spawning requirements. For example, the cichlid Serranochromis giardi displayed a greater degree of lateral movement, possibly because its preferred food supply, molluscs, was more abundant on the floodplains (pers. observation). Predatory species such as C. gariepinus and S. mystus exhibited a greater degree of longitudinal movement.

During the filling and high water levels in the perennial swamp, a larger mass contribution of H. vittatus and C. gariepinus was recorded. Conversely, during the receding and low water levels the mass contributions of these two species was considerably lower. This may suggest that these species, which are known to be potamodromous, may be migrating out of the perennial swamp and upstream into the riverine floodplain at this time of year. This migration is believed to result from fish seeking more favourable spawning (e.g. H. vittatus; Chapter 6) and feeding sites (e.g.C. gariepinus; Chapter 7).

It is also believed that both C. gariepinus and H. vittatus return to the perennial swamp during the filling and high water level. This theory is supported by the increased catches of these species in the perennial swamp when water levels were high (see Appendix 6). The overall increase in CPUE of all species during the filling and high water levels in the perennial swamp was in contrast to that recorded for the seasonal swamp and drainage rivers where an increase in CPUE was apparent during the receding and low water levels.

There was also a large degree of lateral movement at high water level in the perennial swamp to the floodplain-connected lagoons such as Maxegana Pools. Maxegana Pools is a complex of relatively stable perennial floodplain lagoons with a large resident population of fish. The relatively stable CPUE may reflect the presence of large numbers of hippopotami in this lagoon which serve to enrich the system by defaecating in the water.

The greatest complexity of seasonal movement of fish was documented between the riverine floodplain and perennial swamp. This was particularly evident in the seasonal, low water aggregation of the catfish Clarias gariepinus in the mainstream channel which is explained in greater detail in Chapter 7. Another important interaction, documented by Merron & Bruton (1988), was the degree of annual size segregation among predator and prey species between the mainstream channel and floodplain-connected lagoons, i.e. large predators-small prey in the mainstream channel and small predators-large prey in the floodplain lagoons. Size segregation between different species may indicate a more stable, biotically interactive community.

The riverine floodplain and perennial swamp should be classified as the definitive refuge for fish of the Okavango Delta. The seasonal swamp and drainage rivers ecotones depend, ultimately, on these refuge stocks for re-inoculation. However, during the course of this study, fish in the perennial swamp moved upstream to the riverine floodplain, whereas fish in the seasonal swamp moved downstream to the drainage rivers. Very few fish species were recorded moving from the perennial swamp into the seasonal swamp. This apparent paradox in movement patterns between refuges during this study is probably due to the extreme low water levels during the drought stricken 1980's. It is apparent that a longer time-series is needed, particularly during a prolonged wet cycle, to quantify the importance of movement and recolonization between ecotones.

It is concluded that the degree of biotic interdependence exhibited in both lateral and longitudinal movements progressively diminishes in a downstream direction from the perennial to the seasonal habitat types. In the seasonal swamp relatively simple lateral and longitudinal movements of fish replace the relatively complex movement patterns of fish from the perennial swamp and accounts for the recolonization of fish into the drainage rivers.

The wide oscillations in species composition and relative abundance, based on CPUE, from the north to the south in the delta was another significant trend apparent in the results. A greater and more consistent CPUE was recorded for the northern Okavango relative to the southernmost sampling sites.

Because the total ichthyomass of the delta varies considerably in relation to fluctuations in water level, it follows that the yield fluctuates widely, from low catches in extremely dry years to very large catches shortly after periods of large floods. Welcomme (1979) showed that the yield from a river-associated wetland fishery is reasonably well correlated with the flood history of the previous two years. This is due to the flood-dependent spawning behaviour of many of the fish species. Periods of high water level result in a greater percentage of the population being able to spawn successfully and also create vast nursery areas for the young. Although a longer time series of data are required to accurately predict yields in the Okavango, the preliminary results presented in this Chapter support Welcomme's (1979) finding, with a 20% increase in catch in November 1986 compared to November 1983. This is two years after the relatively high flood of 1984.

Yield is also correlated with the flood level in a given year. Higher relative yields are obtained in the riverine floodplain, seasonal swamp and drainage rivers under low water conditions when fish stocks are more concentrated. Conversely, lower relative yields are obtained under high water levels when fish stocks are diluted. In contrast, in the perennial swamp and riverine floodplain-connected lagoons a greater yield was recorded at high water levels.

CHAPTER 6

THE REPRODUCTIVE BIOLOGY OF SELECTED FISH SPECIES AND THEIR RESPONSE TO THE ANNUAL FLOOD REGIME

INTRODUCTION

Floodplain ecosystems are often inhabited by fish which synchronize their entire reproductive biology to the flood cycle (Lowe-McConnell, 1975; Welcomme, 1976). Many floodplain fishes have been reported to spawn during the flood season. This finding has been shown in the fish of the middle Zambezi River (Jackson, 1961a), the Kafue floodplain (Chapman et al., 1971), the Pongolo floodplain (Kok, 1980; Merron et al., 1987, 1989) and the Kwando- Linyanti swamp and Lake Liambezi (van der Waal, 1985; Merron, 1990).

The flood cycle and associated environmental changes tend to occur seasonally in African swamps and therefore affect the onset of maturation of the gonads in a cyclical pattern (Lowe-McConnell, 1975, 1979; Welcomme, 1979). The environmental factors associated with a flood can be divided into biotic or abiotic factors. Biotic factors include population densities and the quality and quantity of food, while examples of abiotic factors are fluctuating water levels, water depth, temperature, onset of the rainy season and increasing photoperiod.

The floods in most African floodplains are synchronous with the warmer summer months and rainy seasons (Lowe-McConnell, 1975; Welcomme, 1979). In the Okavango Delta, however, the flood reaches a peak (in the greater part of the delta, particularly in the seasonal swamp and drainage rivers) during the coldest and driest part of the year when conditions are believed to be least conducive for spawning. This led Fox (1976) to speculate that breeding activity is not dependent on the floods in the Okavango as the main floods do not occur in summer. However, no quantitative studies had been conducted to test this hypothesis. The information collected during this study provided an opportunity to determine the interrelationships, if any, between the influence of floods and water temperature on the reproductive seasonality of the selected fish species.

An eco-ethological classification of fishes (Balon, 1975, 1981b) reveals that there are over 30 reproductive guilds divided into three main sections: non-guarders, guarders and bearers (Table 6.1).

Table 6.1. Summary of the reproductive guilds of fishes proposed by Balon (1975, 1981b)

Non-Guarders
- Spawners on open substrata (egg scatterers): seven guilds of pelagic, gravel, plant and sand spawners which produce buoyant or adhesive eggs and do not hide or guard the young
- Brood hiders: five guilds of beach, gravel, cave and other specialized spawners which hide the young but do not guard them

Guarders
- Substratum choosers: four guilds of pelagic, above water, rock and plant spawners whose young are tended by the parents
- Nest spawners: eight guilds of froth, gravel, plant, sand and other specialized spawners which make protective cavities in which they guard the young

Bearers
- External bearers: five guilds of mouth, gillchamber and pouch spawners which carry the young in a cavity opening to the exterior in order to protect them
- Internal bearers: four guilds of spawners which carry the young inside the body cavity where they may receive some nutrition from the parent

This classification distinguishes guilds of species which are similar in their use of the ecosystem and which have covergent behavioural, morphological and physiological adaptations, irrespective of phyletic origin. The eco-ethological classification of Balon thus bears no resemblance to the Linnean classification since some phylogenetically primitive fishes (e.g. coelacanth, mustelid sharks) are found in advanced guilds and vice-versa (Balon, 1985; Bruton & Merron, 1990; Compagno, 1990).

Of the five selected species, C. gariepinus, S. mystus and H. vittatus are egg-scattering non-guarders while H. odoe is a nest spawning guarder and O. andersonii is an external bearer.

MATERIALS AND METHODS

The present study was conducted over the period November 1983 to December 1986. A quarterly sampling schedule using a wide variety of gillnets was undertaken as explained in Chapter 3. In addition to collecting fish in gillnets, a 10 m seine net and rotenone ichthyocide were also used at all sampling sites throughout the study period to collect juvenile fish.

Because of the close similarities and interdependence of the riverine floodplain and perennial swamp, it is practical in this chapter to include these two ecotones together. The data for the seasonal swamp and drainage rivers ecotones have also been grouped for the present analysis.

Reproductive seasonality for the five selected species was determined by macroscopic examination of the gonads using a gonadal maturation index (GMI) of one to six from Nikolsky (1963). These gonad indices can be summarized as follows: 1 = inactive; 2 = active; 3 = developing; 4 = ripe; 5 = ripe-running; 6 = spent. These data are presented in tables for each sampling site and respective quarterly survey. In addition, all fish with a GMI > 4 were combined, using a standard arithmetic weighted means, over one calender year and graphically presented to indicate the trends in reproductive seasonality in relation to the annual flood in different parts of the Delta. Although minor variations in reproductive seasonality undoubtedly occur annually depending on the timing, magnitude and duration of the flood cycle, within the context of this chapter an overall trend was desired.

Data used to compute length at sexual maturity were taken from a sub-sample of fish during each quarterly survey. For the purpose of this study, the size at which 50% of the population have mature gonads has been taken to represent the average length at sexual maturity (Table 6.2).

In the present analysis fecundity is defined following Bagenal (1971) as the number of ripening eggs in the female prior to the next spawning period. This was necessary because H. odoe and O. andersonii showed a polymodal distribution in egg size and are multiple spawners. Ripening and ripe-running ovaries (GMI stages 4 & 5) were removed from selected fish and preserved in the field for laboratory inspection. For H. odoe and O. andersonii all eggs from one ovary were counted. For S. mystus 20% of the total ovarian weight was used to count the number of eggs and for C. gariepinus and H. vittatus 10%. This difference in egg counting procedure in the latter three species was necessary because of their high gonadal mass and fecundity. The counted eggs were weighed in the laboratory and then multiplied by the appropriate factor (e.g. two, five or ten) to determine fecundity.

The occurrence of juveniles < 50 mm SL, was also graphed over one calender year and flood cycle to substantiate the spawning periodicity for each species. Other species were qualitatively checked for reproductive condition during the course of the overall fisheries research programme (Merron & Bruton, 1988) and mention is made of these findings in the discussion.

Table 6.2. The total number, mean size (SL, mm), sex ratio and size at sexual maturity (SL, mm) of male and female fishes of the selected species between November 1983 and December 1986 in the Okavango Delta

Species	no.		mean size (mm SL)		sex ratio	size at sexual maturity (SL mm)	
	M	F	M	F	M:F	M	F
C. gariepinus	312	447	460	485	1:1.4	290	275
S. mystus	430	999	160	210	1:2.3	125	140
H. vittatus	857	256	310	380	3.3:1	190	260
H. odoe	371	677	241	279	1:1.8	140	160
O. andersonii*	338	248	240	210	1.4:1	110-140	105-155

*O. andersonii showed considerable variation in size at sexual maturity, as discussed below.

RESULTS

NON-GUARDERS

Clarias gariepinus

Mean size, sex ratio and size at 50% maturity

The mean size of C. gariepinus females (485 mm SL) was larger than males (460 mm SL; Table 6.2). The sex ratio (male:female) of C. gariepinus indicates that females were slightly more numerous than males with a male:female ratio of 1:1.4 (Table 6.2). These findings are slightly higher to those reported from Lake Sibaya (1:1.07; Bruton, 1979) and Lake Liambezi (1:1.1; van der Waal, 1985) and likely reflect the different environmental conditions which can influence the sex ratio at the various study sites.

On the basis of 50% maturity, C. gariepinus was found to mature at 290 mm SL for males and 275 mm SL for females (Table 6.2). These sizes agree with similar sizes at sexual maturity recorded by Bruton (1979; 340 mm TL for males & 330 mm TL for females) and van der Waal (1985; 270 mm TL for males & 300 mm TL for females). It should be noted that the abovementioned authors reported on total length (TL) of fish whereas the data presented here are reported as standard length (SL), for reasons explained in Chapter 3. However based on preliminary TL:SL conversions for Okavanga fishes these sizes are similar (D. Freer, pers. communication).

Spawning season and environmental influences at the time of spawning

Throughout the Okavango Delta the spawning periodicity of C. gariepinus was closely associated with the flood peak. In the seasonal swamp and drainage rivers all ripe-running and recently spent fish (i.e. GMI 5 & 6) were collected between July and December (Table 6.3). This spawning season encompasses the entire flood peak (Fig. 6.1) and both cooler (e.g. 20°C) and warmer (e.g. 30°C) water temperatures.

In the riverine floodplain and perennial swamp ripe-running and recently spent fish were collected between January and April (Table 6.4). The peak spawning period in these ecotones also corresponds with the rising flood waters (Fig. 6.2) and high water temperatures. The activities leading up to the spawning season in these ecotones, particularly the riverine floodplain, did however entail an intense feeding migration between September to December each year which is explained in greater detail in Chapter 7. This intense feeding migration was associated with an increase in reproductive condition at this time of year so that as soon as the flood arrives this species can take immediate advantage of the rise in water level. Intense feeding prior to the arrival of the flood in the seasonal swamp (i.e. Nxaraga Lagoon) and drainage rivers (i.e. Thamalakane River & Chanoga Lagoon) was not recorded during the course of this study period.

The observations on the spawning seasonality of C. gariepinus in the riverine floodplain and perennial swamp complement those of Bruton (1979), Kok (1980) and van der Waal (1985). These studies indicate that the spawning season extends from September to April-May, and that spawning is dependent on the incidence of rain and/or flood conditions. However, in the seasonal swamp and drainage rivers of the Okavango fish spawned in July which is earlier than these authors indicate and most likely reflects the variation in flood cycle between the different study sites.

Table 6.3. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Clarias gariepinus from the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	9	17	2	3	2	4	1	5	2	2	1	1	1	2
March 1984	11	23	2	3	6	5	1	9	2	6	0	0	0	0
July 1984	8	14	0	0	0	3	1	1	3	2	4	6	0	2
November 1984	12	24	0	0	0	3	3	6	2	3	2	5	5	6
April 1985	10	18	3	5	5	4	1	6	1	3	0	0	0	0
July 1985	14	23	0	1	1	3	2	7	4	5	5	4	2	3
November 1985	16	25	0	2	1	6	4	5	5	6	2	2	3	4
January 1986	16	21	4	6	8	7	2	5	2	3	0	0	0	0
March 1986	14	18	3	5	6	9	4	3	1	1	0	0	0	0
July 1986	11	13	0	0	1	1	2	2	2	3	4	6	2	1
October 1986	14	22	1	0	0	1	3	5	3	6	4	6	3	4
December 1986	15	26	3	2	5	7	2	4	2	5	1	2	2	6
Total	150	244												

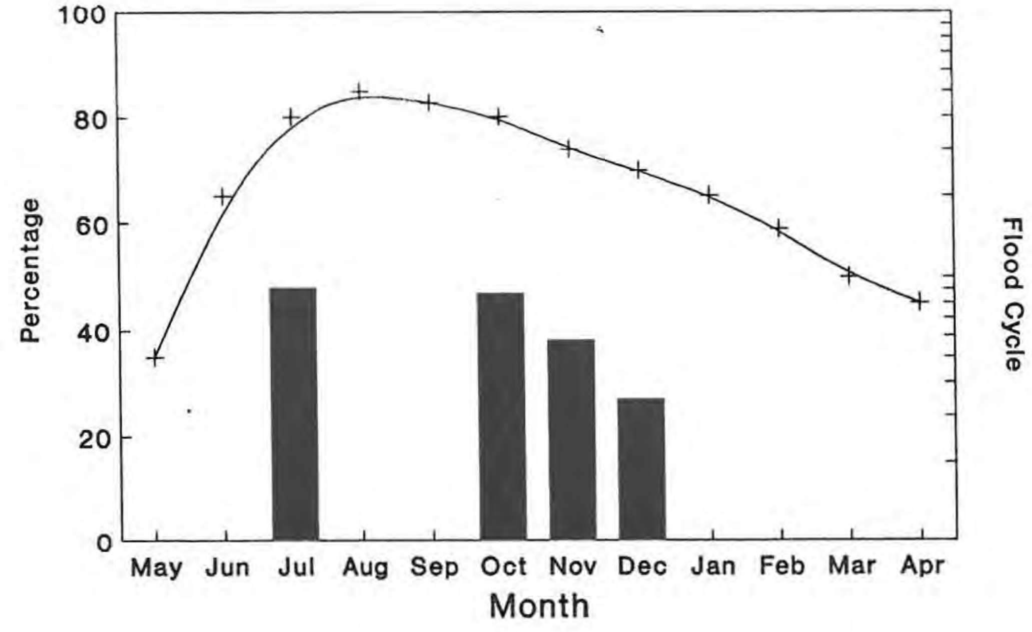


Figure 6.1. The combined monthly number and percentage of C. gariepinus with a GMI > 4 in the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Table 6.4. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) <u>Clarias gariepinus</u> from the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	7	11	0	0	0	0	3	5	4	6	0	0	0	0
March 1984	8	13	0	1	2	1	2	2	1	1	2	5	1	3
July 1984	10	9	1	2	4	5	2	2	3	0	0	0	0	0
November 1984	14	18	2	0	1	4	6	6	5	8	0	0	0	0
April 1985	8	11	0	2	3	2	1	1	0	0	0	1	4	5
July 1985	9	12	2	1	1	4	4	6	2	1	0	0	0	0
November 1985	15	27	2	0	4	2	4	12	5	13	0	0	0	0
January 1986	11	15	0	0	0	0	2	4	3	7	4	3	2	1
March 1986	5	14	0	1	1	2	0	3	0	1	3	3	1	4
July 1986	22	13	2	1	9	6	8	3	3	3	0	0	0	0
October 1986	29	33	0	1	4	6	19	16	6	10	0	0	0	0
December 1986	24	27	0	0	1	2	8	9	15	16	0	0	0	0
Total	162	203												

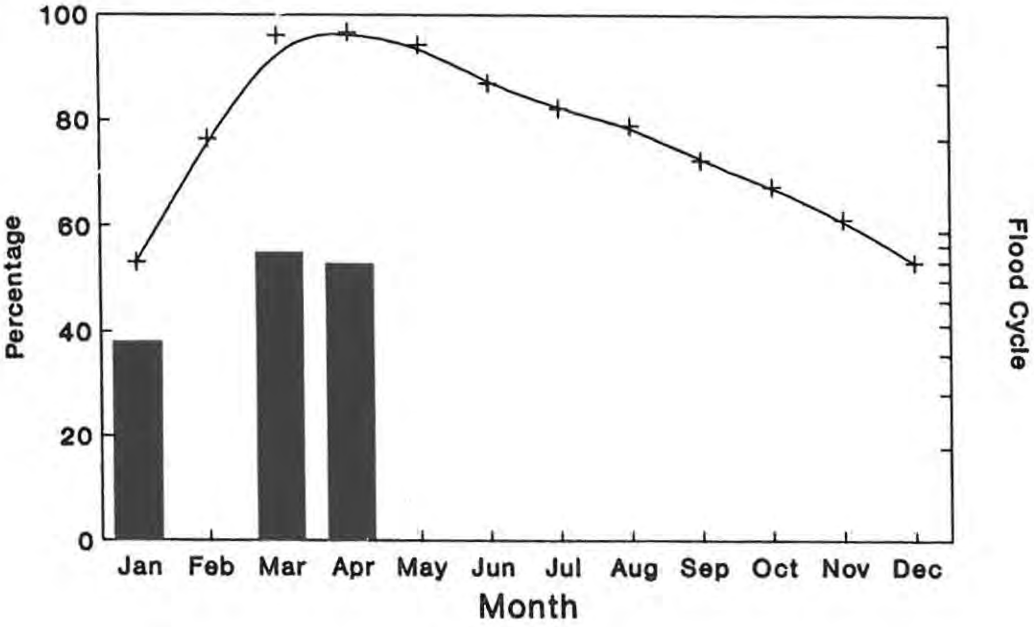


Figure 6.3. The combined monthly number and percentage of <u>C. gariepinus</u> with a GMI > 4 in the perennial swamp and riverine floodplain, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Monthly frequency of occurrence of juvenile fish

Juvenile < 50 mm SL C. gariepinus were mainly collected between July and December in the seasonal swamp and drainage rivers and between January and April in the riverine floodplain and perennial swamp (Fig. 6.3). This finding supports the above observations on spawning periodicity based on gonad maturation indices.

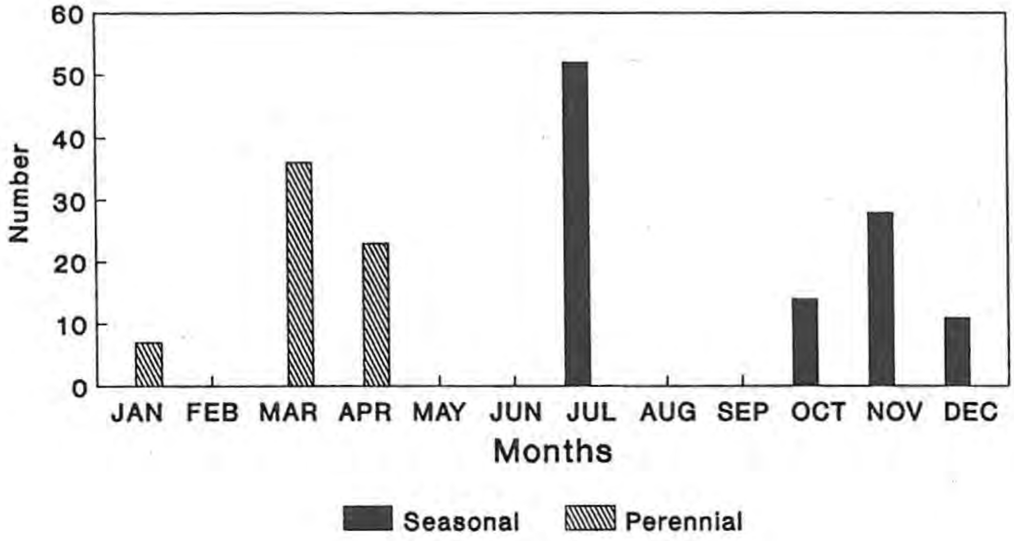


Figure 6.3. The combined monthly number of juvenile C. gariepinus (< 50 mm SL) collected in the seasonal swamp and drainage rivers (S), and the riverine floodplain and perennial swamp (P), Okavango Delta, between November 1983 and December 1986.

Fecundity

Fecundity estimates for C. gariepinus from the Okavango were as high as 34511 to 236000 eggs for females ranging from 436 mm to 770 mm SL (Table 6.5). Pott (1969) found that females of 670 and 1100 mm TL from the Pongolo floodplain have 293000 and 446000 eggs. These estimates are higher than the fecundities established for C. gariepinus in Lake Sibaya, where an average size female of 540 mm TL produced 50000 eggs and a female of 894 mm TL produced 163000 eggs (Bruton, 1979). In the Shire marshes, females of 300 and 400 mm TL produced 20000 and 160000 eggs respectively (Willoughby & Tweddle, 1978). From these wide ranging estimates it is apparent that egg production is high and that it increases with increasing size of the female. The different estimates also reflect the response of the populations to the prevailing environmental conditions in the different sampling sites. No obvious differences in fecundity between sampling sites were noted.

Spawning behaviour

The spawning behaviour of C. gariepinus has been described by Bruton (1979). This species spawns a relatively large number of eggs that are broadcast in shallow, well-vegetated water without any subsequent parental care.

Table 6.5. The fecundity of ripe (GMI stages 4 & 5) C. gariepinus in the Okavango Delta, between November 1983 and December 1986.

SL	Fish weight (g)	Gonad weight (g)	Total no. of ripe eggs
436 mm	970	49.2	34511
455 mm	1204	32.6	32929
490 mm	1346	56.7	50656
495 mm	1522	83.2	55716
495 mm	1470	85.9	47619
500 mm	1502	76.0	90764
530 mm	1696	76.2	107656
770 mm	4871	93.8	236000
mean no.			81981

Schilbe mystus

Mean size, sex ratio and size at 50% maturity

The mean size of female S. mystus was 210 mm SL while males had a smaller mean size of 160 mm SL (Table 6.2). The sex ratio of S. mystus was skewed towards females with a 1:2.3 (male:female) ratio (Table 6.2). This finding is slightly lower than that recorded for Lake Liambezi (1:2.7; van der Waal, 1985).

Male S. mystus matured at a smaller size than females (125 to 140 mm SL, respectively). These estimates fall within the range of sizes at 50% sexual maturity described by Kok (1980; 120 mm SL males & 160 mm SL females) and van der Waal (1985; 120 mm TL males & 140 mm TL females).

Spawning season and environmental influences at the time of spawning

In the seasonal swamp and drainage rivers, where floodwaters arrived in June (during the coldest time of year), an increase in the number of ripe-running and recently spent S. mystus occurred immediately after the arrival of the floods and extended until December (Table 6.6; Fig. 6.4). It is likely that the arrival of the flood stimulates gonad development which peaks as water temperatures increase. The results of Daget (1954) also indicate that the onset of flood conditions serves as an important cue for gonad development in S. mystus.

In the riverine floodplain and perennial swamp an increase in the number of ripe-running and recently spent S. mystus occurred in January with a peak in March and April (Table 6.7). This co-incides with the arrival of the flood (Fig. 6.5) and with high water temperatures.

This information is important for the management of S. mystus in the delta as their are two distinct spawning populations. Any formulation of fishing regulations, based on the spawning season of this species, should take into account the fact that the bulk of the S. mystus population spawns between January and April in the riverine floodplain and perennial swamp and between July and December in the seasonal swamp and drainage rivers.

Similar spawning activity of S. mystus and E. depressirostris (now synonomized with S. mystus; De Vos, 1984) has been recorded by Daget (1954), Groenewald (1967), Carey & Bell-Cross (1965), Gaigher (1969a), Olatunde (1978a), Hecht (1980), Kok (1980) and van der Waal (1985).

Monthly frequency of occurrence of juvenile fish

The majority of juvenile S. mystus (< 50 mm SL) were collected from the seasonal swamp and drainage rivers between July and December (Fig. 6.6). This further substantiates an earlier spawning season of this species in these regions of the Okavango. No juveniles were collected between January and June. In the riverine floodplain and perennial swamp the appearance of juveniles in catches occurred between January and April (Fig. 6.1) and further supports a later spawning season for these regions.

Table 6.6. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Schilbe mystus from the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November1983	23	59	3	12	6	17	6	10	3	8	2	5	3	7
March 1984	19	48	4	11	6	15	6	14	3	8	0	0	0	0
July 1984	27	57	0	0	5	6	4	11	8	18	7	14	3	8
November 1984	18	43	0	3	2	7	5	12	3	9	2	3	6	9
April 1985	25	58	9	17	11	15	3	22	2	4	0	0	0	0
July 1985	18	47	2	1	3	5	2	9	5	18	6	14	0	0
November 1985	29	44	5	5	4	10	6	10	4	3	2	9	8	7
January 1986	21	55	4	22	6	21	0	11	2	1	0	0	0	0
March 1986	17	41	2	5	9	19	4	13	2	4	0	0	0	0
July 1986	26	89	7	5	1	16	2	13	5	13	2	19	9	23
October 1986	17	31	1	1	2	5	2	4	1	5	3	4	8	12
December 1986	14	44	3	15	2	11	1	6	1	3	1	2	6	7
Total	254	616												

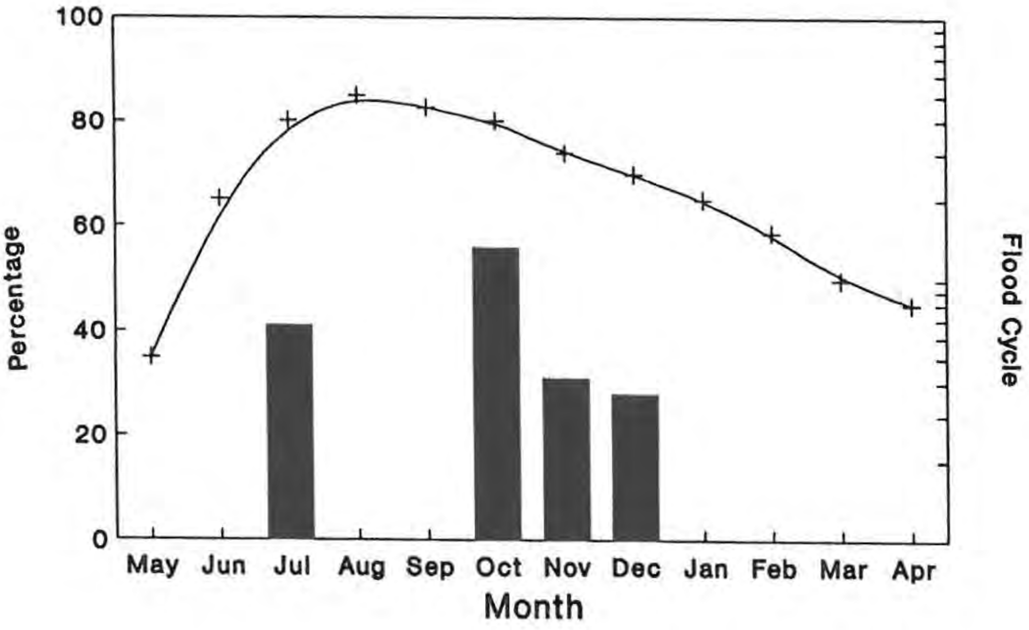


Figure 6.4. The combined monthly number and percentage of S. mystus with a GMI > 4 in the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Table 6.7. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Schilbe mystus from the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

Date	no.		Gonad Maturation Index 1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	11	27	0	2	2	4	4	9	5	12	0	0	0	0
March 1984	9	23	1	5	0	5	1	0	1	0	3	4	3	9
July 1984	17.	36	9	15	6	7	3	6	2	1	0	0	0	0
November 1984	14	35	0	3	2	3	5	11	7	18	0	0	0	0
April 1985	19	42	4	6	5	9	1	9	0	0	0	2	9	14
July 1985	8	27	3	11	1	7	2	6	2	3	0	0	0	0
November 1985	18	37	1	3	2	9	7	12	8	13	0	0	0	0
January 1986	8	29	0	0	1	1	1	6	3	17	3	4	0	1
March 1986	15	35	4	6	1	7	0	3	2	3	0	3	8	13
July 1986	26	41	9	7	8	13	7	16	2	5	0	0	0	0
October 1986	13	27	1	3	2	5	4	7	6	12	0	0	0	0
December 1986	18	24	0	1	3	3	7	6	8	14	0	0	0	0
Total	176	383												

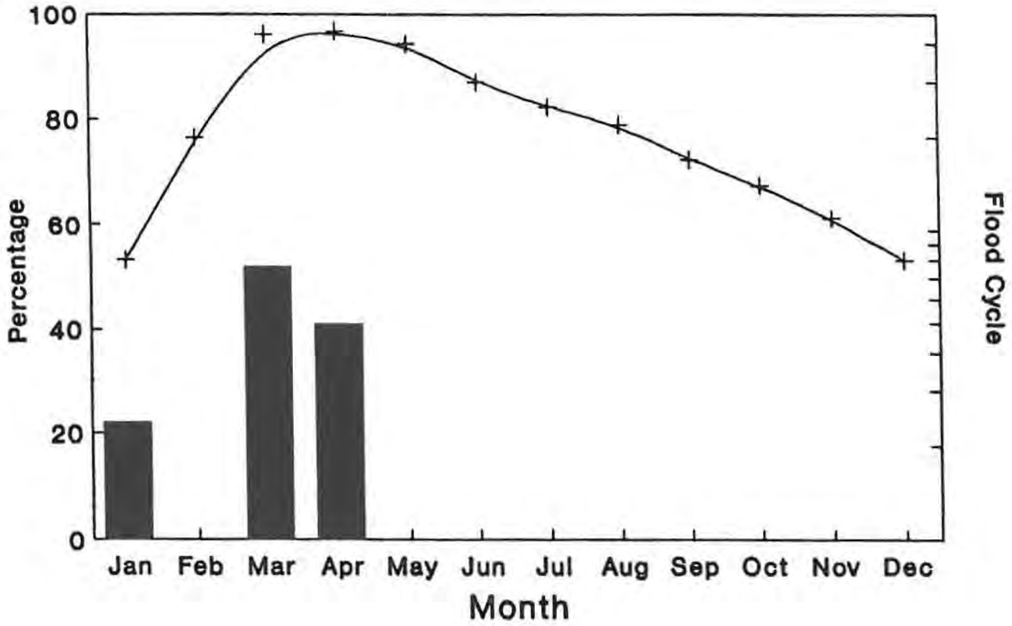


Figure 6.5. The combined monthly number and percentage of S. mystus with a GMI > 4 in the perennial swamp and riverine floodplain, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

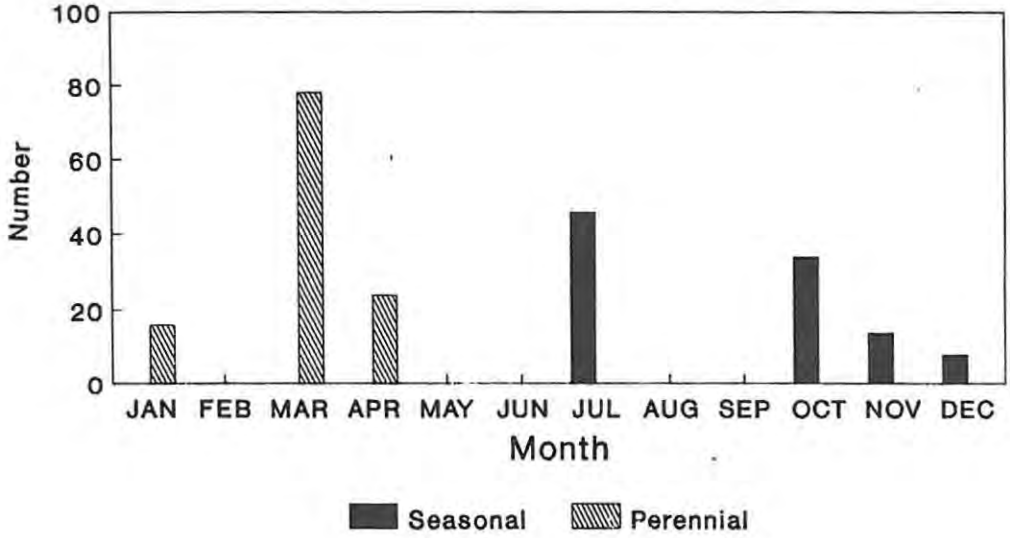


Figure 6.6. The combined monthly number of juvenile S. mystus (< 50 mm SL) collected in the seasonal swamp and drainage rivers (S), and the riverine floodplain and perennial swamp (P), Okavango Delta, between November 1983 and December 1986.

Fecundity

S. mystus has a relatively high fecundity which increases with length. Fish of 156, 221 and 253 mm SL produced 9408, 13500, and 34541 eggs respectively (Table 6.8). The eggs are small (650 um diameter) and of uniform size which suggests a single spawning season (i.e. monocyclic spawners) as reported by van der Waal (1985). The fecundity estimates of S. mystus in the Okavango agree with egg counts from the Kafue River (Carey & Bell-Cross, 1967) and Lake Liambezi (van der Waal, 1985) which range between 38500 and 67500 eggs for a body length range of 240-270 mm FL.

No difference in the egg size or number of eggs was apparent between the sampling sites. Relatively high fecundity and small egg size are features characteristic of S. mystus in the Okavango that help to explain the success of this species in the delta where the unpredictability of the flood regime may influence year class strength.

Table 6.8. The fecundity of ripe (GMI stages 4 & 5) S. mystus in the Okavango Delta, between November 1983 and December 1986.

SL	Fish weight (g)	Gonad weight (g)	Total no. of ripe eggs
156 mm	44	7.7	9408
196 mm	83	11.9	18935
220 mm	171	10.0	12380
221 mm	179	9.2	13500
239 mm	206	12.3	35900
249 mm	236	13.7	40800
253 mm	245	11.6	34541
mean no.			23638

Spawning behaviour

S. mystus is a broadcast spawner which places its eggs on submerged aquatic vegetation (Welcomme, 1979). Many tropical and sub-tropical riverine fishes migrate upstream during flood periods in order to spawn in areas removed from their dry-season habitats (Lowe-McConnell, 1975; Welcomme, 1979). During the summer flood, Whitehead (1959) observed the ascent of S. mystus from Lake Victoria up the Nzoia River in Kenya. They entered the river in fairly compact shoals and swam for 8-25 km up-river before moving laterally into floodwater pools to spawn. Potamodromic behaviour of S. mystus has also been recorded in the Niger River (Daget, 1954; Olatunde, 1978a) and on the Pongolo floodplain (Kok, 1980; Merron et al., 1987). The probable reasons for this behaviour are to provide a suitable physico-chemical environment for the development of eggs and larvae (Greenwood, 1965), to ensure dispersion of the species over the entire colonizable river course (Fryer, 1965), and to provide juveniles with adequate food and protection from predators (Jackson, 1961a).

There was no direct evidence of S. mystus undergoing potamodromic migrations in the Okavango Delta. However, in the riverine floodplain a large degree of lateral movement occurred, as indicated in Chapter 5.

Hydrocynus vittatus

Mean size, sex ratio and size at 50% maturity

The mean size of H. vittatus females (380 mm SL) was larger than males (310 mm SL; Table 6.2). Males attained sexual maturity at 190 mm SL while females matured at 260 mm SL (Table 6.2). Gaigher (1970) gives the size at sexual maturity for male H. vittatus in the Incomati River system at 200 mm SL, while that for females was 275 mm SL. Kok (1980) also quotes these latter sizes as the size at which H. vittatus in the Pongolo floodplain become sexually mature.

There was a skewed sex ratio in favour of males in the Okavango (3.3:1; Table 6.2). This sex ratio is similar to that reported for Lake Kariba (3:1; Kenmuir, 1973) and the Pongolo floodplain (3.2:1; Merron et al., 1987).

Spawning season and environmental influences at the time of spawning

The spawning season of H. vittatus has been well documented. In the Zambezi River (Jackson, 1961a; Bell-Cross, 1966), Lake Kariba (Badenhuizen, 1967; Kenmuir, 1973), Incomati River system (Gaigher, 1970) and Pongolo floodplain (Kok, 1980; Merron et al., 1987) spawning occurs during the flood or rainy season.

Based on the quarterly GMIs of both sexes from the riverine floodplain and perennial swamp, all ripe-running and recently spent H. vittatus were collected between October and December (Table 6.9). This is a relatively truncated spawning season and in the Okavango it is important to realize that spawning occurs before the arrival of the flood or the rainy season (Fig. 6.6). No data are available for H. vittatus from the seasonal swamp or drainage rivers as these areas are not preferred habitats of this species during the course of this study (see Chapter 4).

H. vittatus were found in an advanced reproductive condition (GMI 4) in winter (e.g. July), although no fish were recorded to spawn at this time (Table 6.9). Kenmuir (1973) found that many H. vittatus in Lake Kariba also ripened months before the spawning season.

Monthly frequency of occurrence of juvenile fish

Juvenile H. vittatus (< 50 mm SL) were only collected from the riverine floodplain and perennial swamp between October and December (Fig. 6.8). It was noted, however, that fewer juveniles were collected in the perennial swamp (e.g. Xakanixa Lagoon; see Fig. 3.1). This finding supports the observation made in Chapter 5 that H. vittatus undergoes potamodromic migrations to the riverine floodplain each year and, based on the above findings, probably to spawn.

Table 6.9. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Hydrocynus vittatus from the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	38	5	5	1	10	2	8	0	7	1	6	1	2	0
March 1984	40	7	17	2	22	5	1	0	0	0	0	0	0	0
July 1984	46	9	9	0	11	2	10	5	16	2	0	0	0	0
November 1984	61	26	8	1	4	3	9	4	18	5	14	10	8	3
April 1985	45	18	12	9	24	5	9	4	0	0	0	0	0	0
July 1985	71	16	19	2	14	7	17	3	21	4	0	0	0	0
November 1985	95	37	14	8	21	6	26	14	16	4	11	6	12	4
January 1986	85	24	29	8	41	14	11	0	4	2	0	0	0	0
March 1986	76	17	25	10	38	5	13	2	0	0	0	0	0	0
July 1986	91	26	16	11	26	5	33	2	16	8	0	0	0	0
October 1986	120	39	0	0	12	3	30	6	34	13	26	8	18	9
December 1986	89	32	22	0	21	5	24	10	13	2	3	4	16	11
Total	256	857												

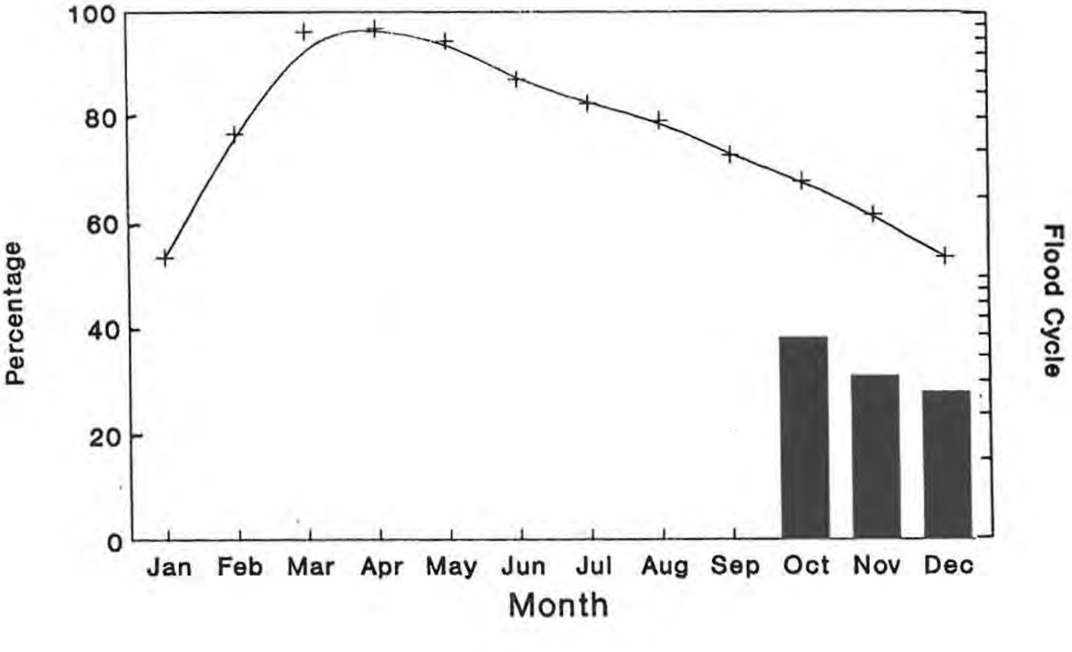


Figure 6.7. The combined monthly number and percentage of H. vittatus with a GMI > 4 in the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

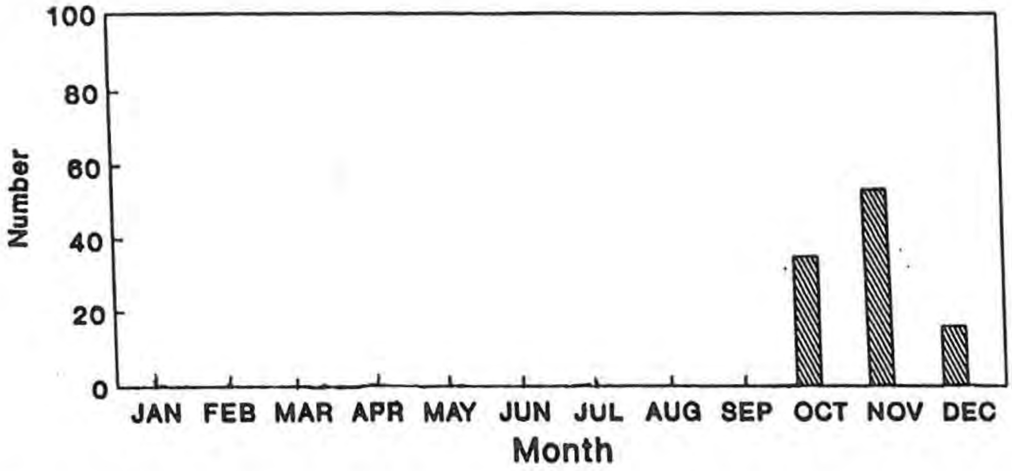


Figure 6.8. The combined monthly number of juvenile H. vittatus (< 50 mm SL) collected in the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

Fecundity

Fecundity estimates for H. vittatus in the Okavango (n = 6) indicate that fish of 410, 462 and 530 mm SL produced approximately 216970, 224865 and 429160 eggs respectively (Table 6.10). Fecundity estimates from Lake Kariba range from 78750 eggs for a female of 311 mm FL to 779590 eggs for a female of 685 mm FL (Kenmuir, 1973) while Pott (1969) records females from the Pongolo floodplain of 510, 525 and 630 mm FL producing 306000, 477000 and 873000 eggs respectively. Bowmaker (1973a) gives an egg production of 300000 for an average size adult female (400 mm FL).

Table 6.10. The fecundity of ripe (GMI stages 4 & 5) H. vittatus in the Okavango Delta, between November 1983 and December 1986.

SL	Fish weight (g)	Gonad weight (g)	Total no. of ripe eggs
410 mm	1279	22.5	216970
425 mm	1387	23.0	267580
462 mm	1843	19.4	224865
478 mm	2102	27.8	298515
495 mm	2470	31.8	360725
530 mm	3138	35.7	429160
mean no.			299636

Spawning behaviour

Direct observations of H. vittatus spawning were never made during the course of this study in the Okavango. Based on its fecundity and ecology, it would appear that H. vittatus is a broadcast spawner which releases large numbers of eggs into the environment with little or no parental care afforded to the young. This apparent spawning behaviour of H. vittatus in the Okavango is supported by observations on the spawning behaviour of this species in other ecosystems (Gaigher, 1970; Kenmuir, 1973; Kok, 1980).

Lowe-McConnell (1975) regards the characins as total spawners with seasonal spawning activity associated with floods. However, in the Okavango, the characin H. vittatus spawns at least two months before the floods and it would appear that some other regulatory mechanism determines the timing of spawning in this wetland system.

GUARDERS

Hepsetus odoe

Mean size, sex ratio and size at 50% maturity

The mean size of female H. odoe was larger than males (279 vs. 241 mm SL; Table 6.2). The sex ratio of H. odoe of 1:2.1 (male:female) indicates that females were twice as numerous as males (Table 6.2). This finding agrees with the sex ratio reported from Lake Liambezi (van der Waal, 1985) which was 1:2.5.

On the basis of 50% maturity, H. odoe was found to mature at approximately 140 mm SL for males and 160 mm SL for females (Table 6.2). These estimates are similar to those sizes at sexual maturity reported by van der Waal (1985) of 180 mm TL for males and 200 mm TL for females.

Spawning season and environmental influences at the time of spawning

The majority of ripe-running and recently spent H. odoe in the seasonal swamp and drainage rivers were collected between October and January (Table 6.11). Although this spawning period is after the peak flood conditions (Fig. 6.9), it does correspond to increased water temperatures.

Table 6.11. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Hepsetus odoe from the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	5	12	0	2	3	0	1	3	1	5	0	1	0	1
March 1984	31	89	2	7	7	31	14	20	3	18	0	0	5	13
July 1984	3	6	1	0	0	1	1	3	1	1	0	0	0	1
November 1984	17	20	2	0	4	6	0	1	2	1	3	2	6	9
April 1985	13	40	4	8	7	8	1	11	0	6	0	3	1	4
July 1985	30	41	18	9	6	14	2	10	4	2	0	1	0	5
November1985	17	31	0	0	3	5	2	4	2	5	4	8	6	9
January 1986	24	40	7	6	3	7	0	6	5	6	4	7	5	8
March 1986	21	51	2	8	14	22	1	6	0	6	1	6	3	3
July 1986	16	16	6	7	6	5	1	1	2	3	1	0	0	0
October 1986	55	88	0	0	6	10	5	10	21	15	17	31	6	22
December 1986	27	40	0	0	5	6	6	5	7	9	6	13	3	7
Total	313	557												

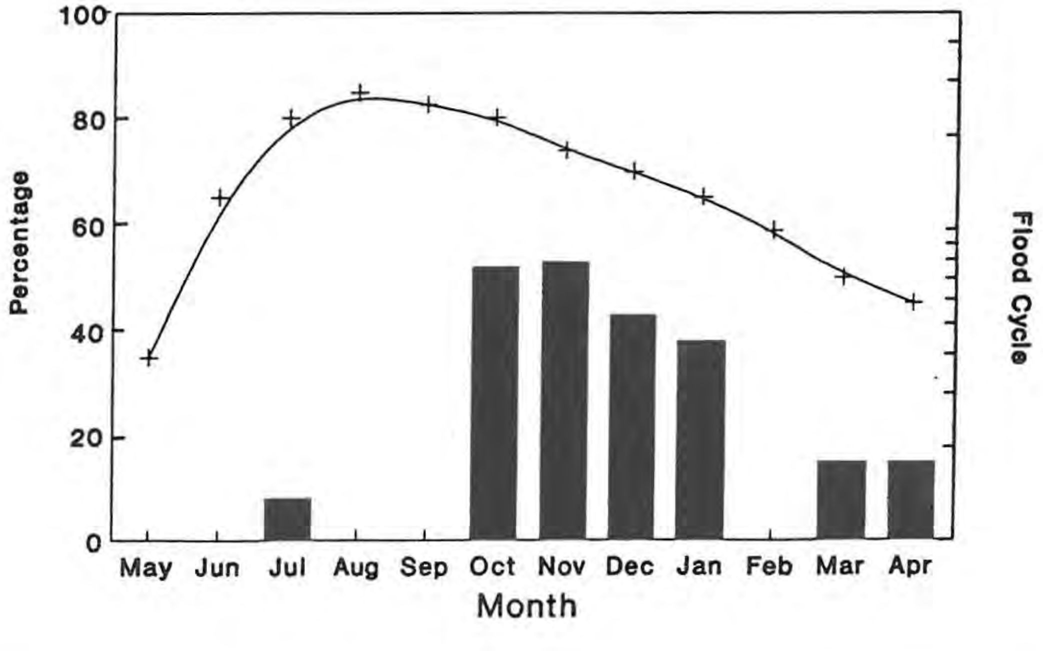


Figure 6.9. The combined monthly number and percentage of H. odoe with a GMI > 4 in the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

In the riverine floodplain and perennial swamp H. odoe was not a common species (Chapter 4; Table 4.1). Based on the limited data, a greater number of ripe-running and recently spent H. odoe were collected between October and April (Table 6.12). H. odoe spawned before and during the arrival of the annual flood (Fig. 6.10) when water temperatures were highest and can be classified as a facultative flood dependant spawner. This is in agreement with the findings of van der Waal (1985) for H. odoe in Lake Liambezi where water temperature changes have a marked influence on spawning periodicity.

These observations on the spawning season of H. odoe are in agreement with the spawning season for this species reported from the Gambia River (Budgett, 1901b; Svensson, 1933), Lake Chad (Blache, 1964), Kafue floodplain (Carey & Bell-Cross, 1967; Chapman et al., 1971) and Lake Liambezi (van der Waal, 1985).

Table 6.12. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Hepsetus odoe from the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	1	3	0	0	0	0	1	0	0	2	0	0	0	1
March 1984	3	4	0	1	0	0	0	2	2	1	0	0	1	0
July 1984	2	5	2	1	0	2	0	2	0	0	0	0	0	0
November 1984	4	8	0	0	0	0	1	2	2	3	1	2	0	1
April 1985	0	2	0	1	0	0	0	0	0	0	0	0	0	1
July 1985	7	2	2	0	4	1	1	1	0	0	0	0	0	0
November 1985	8	19	0	0	0	3	4	7	3	6	0	3	1	0
January 1986	7	15	0	0	2	3	1	2	2	2	1	6	1	2
March 1986	3	7	2	3	0	1	0	1	0	1	0	0	1	1
July 1986	8	21	8	5	0	14	0	2	0	0	0	0	0	0
October 1986	11	28	0	0	4	2	0	3	3	10	2	11	2	2
December 1986	6	4	0	0	0	0	0	0	2	1	4	3	0	0
Total	60	118												

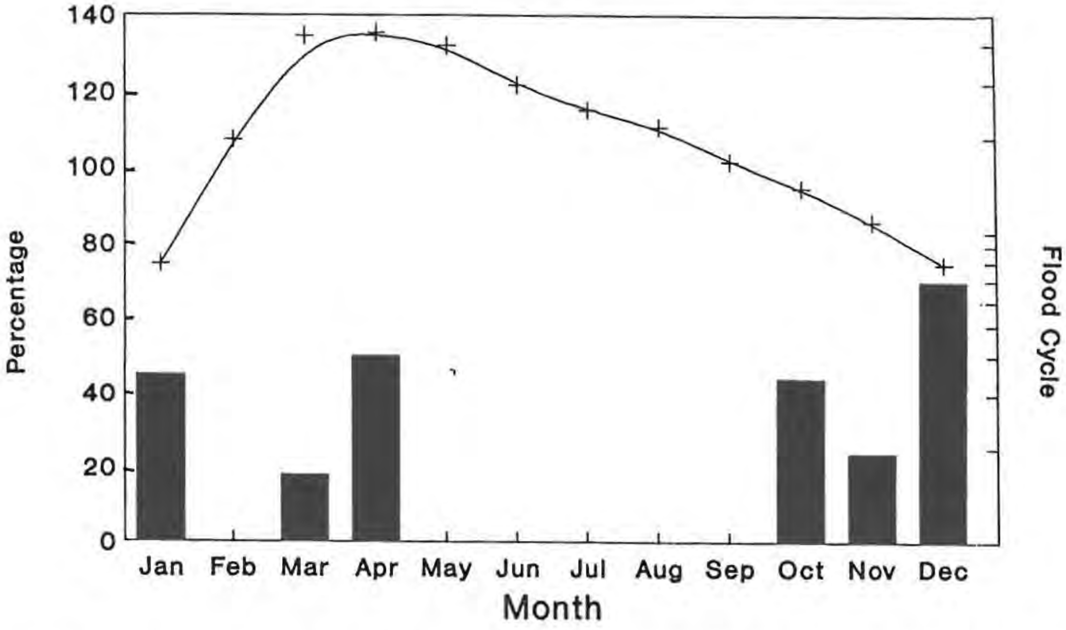


Figure 6.10. The combined monthly number and percentage of H: odoe with a GMI > 4 in the perennial swamp and riverine floodplain, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Monthly frequency of occurrence of juvenile fish

Juvenile H. odoe < 50 mm SL were mainly collected from the seasonal swamp and drainage rivers between the warmer months of October and December (Fig. 6.11). The majority of juvenile H. odoe were also collected in the riverine floodplain and perennial swamp between October and January (Fig. 6.11). It should be noted that juveniles were also collected in July 1984 (n = 1) and July 1986 (n = 4) although no ripe-running adults were collected. These findings support the above observations on spawning periodicity for this species from these sampling sites and indicates that spawning is not dependent on the arrival of the annual flood.

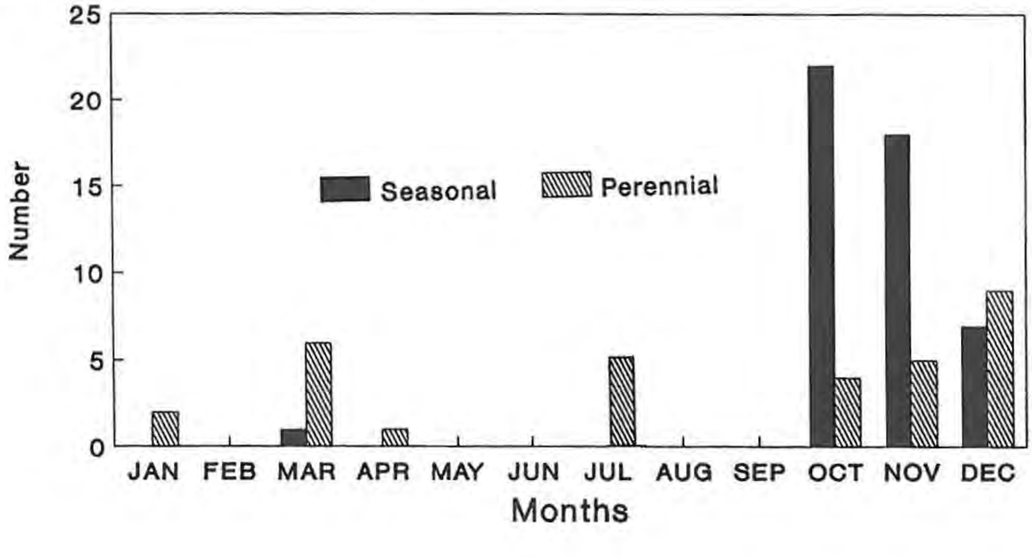


Figure 6.11. The combined monthly number of juvenile H. odoe (< 50 mm SL) collected in the seasonal swamp and drainage rivers (S), and the riverine floodplain and perennial swamp (P), Okavango Delta, between November 1983 and December 1986.

Fecundity

The fecundity of H. odoe is relatively low, with an average total number of 2627 eggs (n = 17; Table 6.14). Ripe eggs are large (2.5 to 2.9 mm diameter), and ovaries contained eggs of different sizes which suggests a multiple spawning habit.

Table 6.14. The fecundity of ripe (GMI stages 4 & 5) H. odoe from the Okavango Delta, between November 1983 and December 1986.

SL	Fish weight (g)	Gonad weight (g)	Total no. of ripe eggs
257 mm	351	33.2	3715
258 mm	342	23.4	3091
275 mm	416	10.5	2186
288 mm	377	15.8	1714
305 mm	492	22.5	3128
307 mm	526	22.4	3092
310 mm	496	13.0	1998
310 mm	520	25.7	3177
312 mm	516	17.8	1743
314 mm	507	23.9	2519
323 mm	551	28.5	3823
324 mm	559	25.9	3431
325 mm	605	17.4	1502
326 mm	582	31.0	2320
327 mm	558	11.6	1986
335 mm	628	15.3	2347
340 mm	670	22.4	2891
mean no.			2627

Spawning behaviour

H. odoe belongs to the aphrophilic nest-guarding breeding guild of Balon (1975, 1981b), which is characterised by a moderate parental investment in relatively few young, the construction of a nest for guarding the young and the provision of an oxygen-rich environment. Other features of this group are the deposition of eggs in clusters of mucous bubbles, and embryos which typically have a cement gland and well-developed respiratory structures. At least 23 species of fishes in three families have been reported to produce foam nests (Breder & Rosen, 1966; Axelrod & Vroderwinkler, 1974). The aerial mode of protection of the young in H. odoe is similar to that exhibited by various anuran Amphibia which also attain some independence from the water and the risks associated with it (Duellman, 1985, 1989). The trend in anuran life-history evolution has been towards the placement of the eggs in situations which are increasingly independent of water, whereas this is a relatively rare behaviour in fishes.

In the Okavango Delta, H. odoe built foam-bubble nests among dense emergent reeds and sedges along the reed fringe of lagoons, mainstream channels and shallow floodplains (Fig. 6.12). The nests were generally well hidden from view.

Figure 6.12. A H. odoe nest in the seasonal swamp of the Okavango Delta, November 1986.

H. odoe nests, when newly formed, consist of a firm high dome of tightly packed foam-bubbles with embedded eggs. Older nests have a more flattened configuration whereas abandoned nests consist of a few loosely-packed bubble rafts. The nests have a roughly circular base and vary in diameter and height according to their age. The nests are pierced to varying degrees by plant stalks which may serve to stabilize their location when they are subjected to wind-induced wave action. Older nests were typically covered with leaf and stalk debris, which soils the bright white foam and creates a more cryptic colour. Upon hatching the embryos wriggle their way down through the foam nest and continue their early development suspended from their cement glands on the lower row of bubbles. Embryos removed from two nests totalled 1604 and 1844 in number (Merron et al., 1990). Early development is rapid with fry of 28 mm SL morphologically similar to adults.

Although the construction of the foam nests was not observed, the presence of eggs in the foam nest above the water line and their absence from the upper stratum of the nest suggests that the nests are partially built prior to spawning. Johnels (1954) came to the same conclusion when he found fully formed nests devoid of eggs and later found eggs embedded in these same nests. Adults exhibit territorial behaviour in the vicinity of the nests.

H.odoe has an interesting spawning behaviour which was relatively easy to observe under field conditions in the Okavango Delta. Their spawning behaviour allows them to take full advantage of the fluctuating water levels in the Okavango, particularly in the seasonal swamp and drainage rivers, where they are abundant (see Chapter 4; Appendix 3). H. odoe has also been the focus of a detailed reproductive and embryonic development study (Merron et. al, 1990). A diagrammatic illustration of its life cycle in the Okavango has been published by these authors and is useful to include in the present context (Fig. 6.13).

Because the spawning season occurs mainly during low water and oxygen levels, H. odoe has to overcome a number of threats to the survival of their offspring. The likely advantages of their foam-nesting habit can be summarized as follows:

(a) The dense vegetation cover around the nests affords protection to the embryos from aerial, aquatic and terrestrial predators as well as from the intense tropical heat. The nest also serves as an aggregating device to facilitate more effective parental care.

(b) By placing the eggs out of the water and the embryos at the air/water interphase, a hospitable oxygen environment is provided for the young. This is especially important at low water levels when there are reduced oxygen concentrations (Chapter 2).

(c) The nest affords flotation during periods of changing water levels.

(d) The nest may provide food for the embryos at the start of first exogenous feeding. Wunder

(1931) found that bubbles in the foam nests of fishes may contain dead bacteria and saliva from the adult fishes.

(e) Foam nests act as an anchor to which the embryos can attach before they are able to swim and hunt independently. In this respect, the cement gland on the head is an important adaptation of the embryos. These glands allow the embryos to remain attached to the nest and to the water surface where oxygen is relatively abundant.

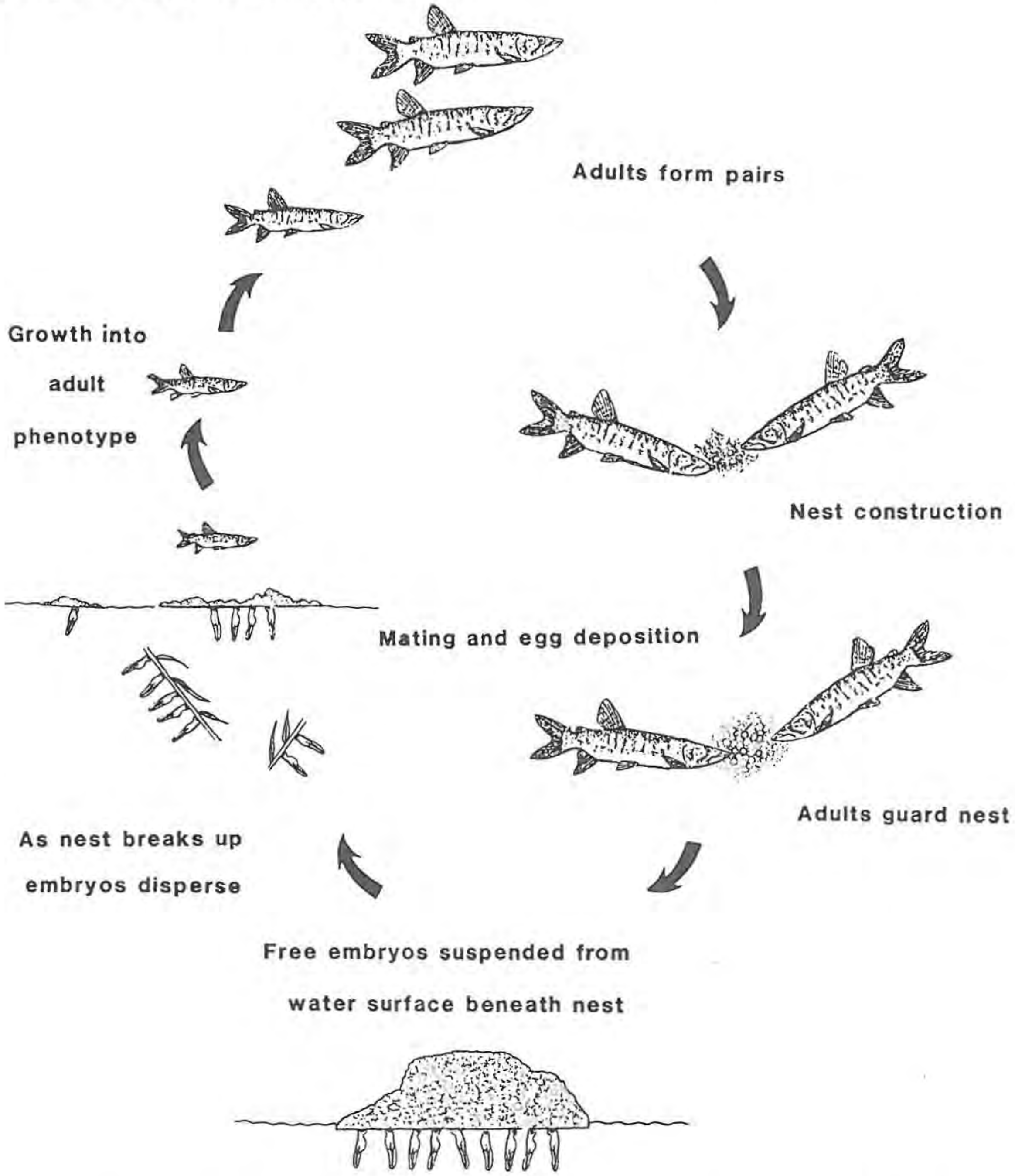


Figure 6.13. Diagrammatic illustration of the life cycle of H. odoe in the Okavango Delta (from Merron et al., 1990).

However, there are certain disadvantages associated with foam nesting. Most obvious is a foam nests conspicuous microhabitat appearance within the reed beds which results in increased predation on eggs by reed ants and various species of spiders (pers. observation). Aerial predation on the young may also be a threat in certain instances. However, many of the fish eating birds inhabiting the Okavango such as the giant kingfisher (Ceryle maxima) and African fish eagle (Haliaeetus vocifer) prey mainly on larger size fish, such as tilapia and tigerfish.

Kryzhanovsky et al. (1953) and Balon (1975) have proposed that two factors play leading roles in determining the nature and course of embryonic development in fishes: predation pressure and the availability of oxygen. These factors appear to be associated with the foam nesting habit of H. odoe, although additional observations relating to predation pressure are needed.

Oreochromis andersonii

Mean size, sex ratio and size at 50% maturity

O. andersonii males were larger than females (240 vs. 210 mm SL; Table 6.2). Males were also slightly more numerous (1.4:1), as found by van der Waal (1:0.6; 1985).

O. andersonii is one of the most widely distributed cichlids in the Okavango Delta. The size at 50% sexual maturity was attained between 110-140 mm SL for males and 105-155 mm SL for females depending on site. In the perennially flooded habitats the size at sexual maturity for both sexes was significantly larger ($P < 0.05$) than in areas of seasonally fluctuating water levels where sexual maturity was attained at a smaller size.

Spawning season and environmental influences at the time of spawning

The quarterly GMI's of male and female O. andersonii from the seasonal swamp and drainage rivers indicates that the majority of ripe-running and recently spent fish were caught mainly betweeen October and January (Table 6.14). This is after the arrival of the annual flood but corresponds to relatively high water levels (Fig. 6.14) and increased water temperatures. In the riverine floodplain and perennial swamp the majority of O. andersonii with ripe-running and recently spent gonads were also collected between October and April (Table 6.15). This spawning season coincides with both low and high flood levels (Fig. 6.15) and increased water temperatures.

Table 6.14. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Oreochromis andersonii from the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986.

Date	no.		Gonad Maturation Index 1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	8	3	1	0	2	0	4	2	0	1	0	0	1	0
March 1984	18	12	2	1	6	3	6	4	3	2	0	2	1	0
July 1984	6	5	0	2	3	1	2	0	0	1	1	0	0	1
November 1984	21	14	3	0	4	3	2	1	7	2	2	4	3	4
April 1985	8	10	1	4	5	2	1	3	0	0.	0	1	1	0
July 1985	12	11	3	2	3	3	3	4	2	2	0	0	1	0
November 1985	28	17	4	0	6	3	5	3	6	2	4	4	3	2
January 1986	11	16	2	4	1	3	0	1	2	1	2	2	3	6
March 1986	21	7	5	0	7	5	3	1	5	0	0	1	1	0
July 1986	11	14	1	3	3	3	3	6	2	1	2	0	0	1
October 1986	24	10	0	0	2	3	4	1	4	3	6	0	8	3
December 1986	15	19	0	0	5	3	3	4	3	4	4	3	3	5
Total	183	138												

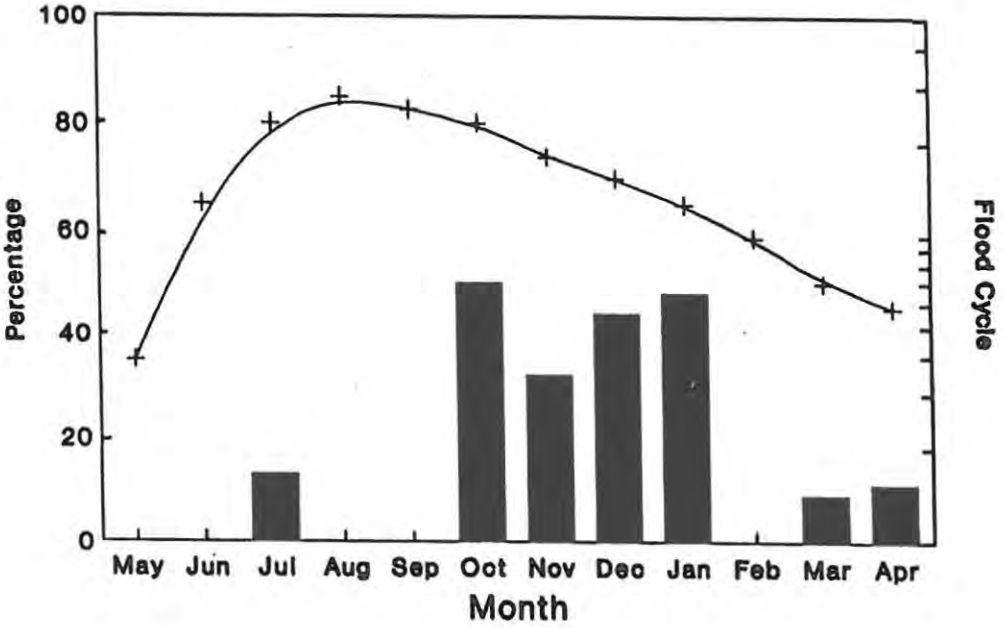


Figure 6.14. The combined monthly number and percenatge of O. andersonii with a GMI > 4 in the seasonal swamp and drainage rivers, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Table 6.15. The number of individuals and corresponding Gonad Maturation Index (GMI) of male (m) and female (f) Oreochromis andersonii from the riverine floodplain and perennial swamp, Okavango Delta, between November 1983 and December 1986.

			Gonad Maturation Index											
Date	no.		1		2		3		4		5		6	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
November 1983	11	4	1	1	3	0	4	2	0	1	2	1	1	0
March 1984	11	5	2	1	1	2	3	0	2	1	2	0	1	1
July 1984	14	7	2	1	4	3	4	2	2	1	1	0	1	0
November 1984	19	15	2	1	2	3	4	1	3	2	5	3	3	4
April 1985	8	5	1	2	3	1	1	1	1	0	1	1	1	0
July 1985	13	8	3	2	4	1	3	3	2	1	0	0	1	0
November 1985	18	17	1	0	2	3	4	3	2	3	4	4	5	4
January 1986	12	15	1	1	1	3	3	1	2	3	2	1	3	3
March 1986	7	5	0	1	5	2	0	1	0	0	1	3	1	1
July 1986	19	6	2	1	4	2	5	2	3	0	2	1	2	0
October 1986	11	14	2	1	3	2	0	2	1	3	2	4	3	2
December 1986	12	9	0	0	4	1	2	1	2	2	2	3	2	2
Total	155	110												

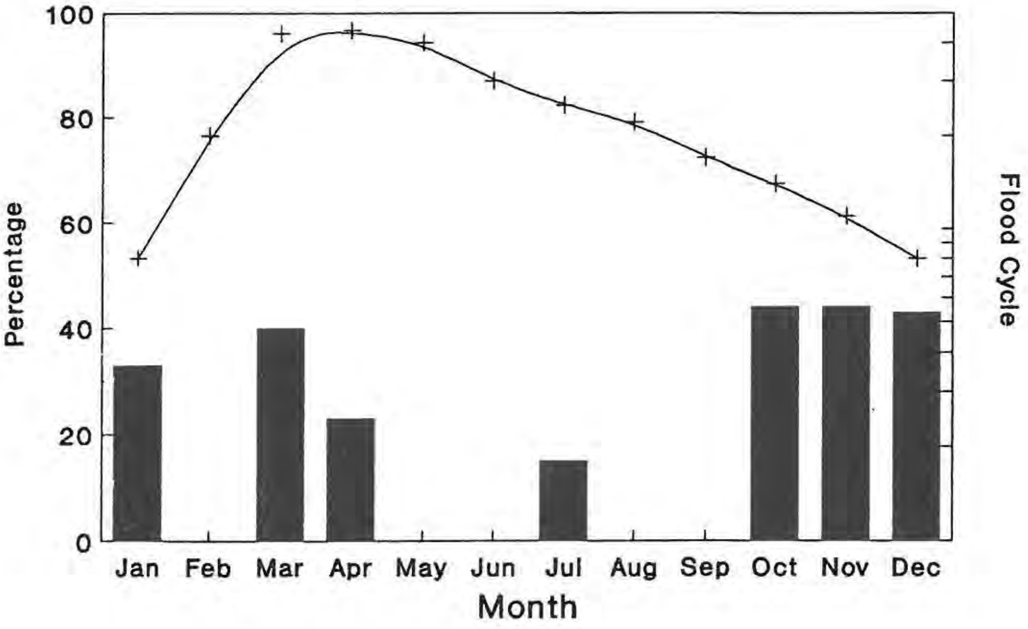


Figure 6.15. The combined monthly number and percentage of O. andersonii with a GMI > 4 in the perennial swamp and riverine floodplain, Okavango Delta, between November 1983 and December 1986. An indication of the annual flood regime is also shown.

Monthly frequency of occurrence of juvenile fish

Juvenile O. andersonii < 50 mm SL occurred throughout the year in all regions (Fig. 6.16). This feature, together with the relatively wide distribution of sexually mature fish throughout the year, is indicative of the extended spawning season of this species relative to the non-substrate spawners (e.g. C. gariepinus, S. mystus and H. vittatus).

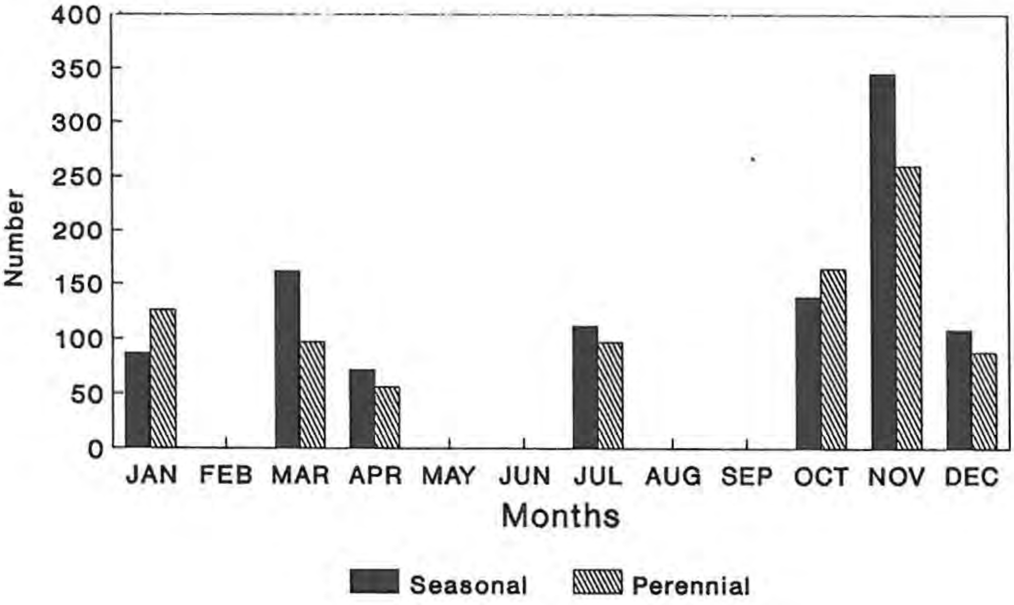


Figure 6.16. The combined monthly number of juvenile O. andersonii (< 50 mm SL) collected in the seasonal swamp and drainage rivers (S), and the riverine floodplain and perennial swamp (P), Okavango Delta, between November 1983 and December 1986.

Fecundity

Of the selected species chosen for detailed study, O. andersonii exhibited a significant difference ($P < 0.05$) in size at sexual maturity between perennially and seasonally flooded areas. Therefore, fecundities were determined separately for these areas. Overall, the fecundity of O. andersonii was relatively low, with an average total number of 3270 eggs ($n = 9$) and 1756 eggs ($n = 11$) for fish in the seasonally and perennially flooded sampling sites respectively (Table 6.16).

Table 6.16. The fecundity of ripe (GMI stages 4 & 5) O. andersonii from perennially and seasonally flooded sampling sites in the Okavango Delta, between November 1983 and December 1986.

	SL (mm)	Fish weight (g)	Gonad weight (g)	Total no. of ripe eggs
Seasonally flooded	155	110	2.64	1948
	160	116	2.86	2209
	221	302	3.21	2592
	230	360	5.10	3546
	232	356	5.24	3655
	240	397	8.50	4031
	247	440	6.01	3971
	250	504	10.10	3794
	255	512	8.47	3684
mean no.				3270
Perennially flooded	210	340	3.80	1223
	215	372	4.21	1172
	221	392	7.53	1486
	225	408	3.56	1050
	234	461	9.70	1362
	238	468	8.64	1378
	256	553	10.60	1712
	258	597	12.65	1740
	263	624	8.31	1354
	323	1160	14.31	3468
	330	1349	13.90	3369
	mean no.			1756

The lowered fecundity of this species is related to the mouth-brooding activity of the female in which the eggs and resulting fry are retained in the mouth cavity until those large enough to be independent of parental care are released. Ripe eggs were found to vary in size between 0.8 and 2.4 mm diameter, with larger eggs recorded from perennially flooded areas. Although the sample size is relatively low, fish from perennially flooded areas also had fewer eggs relative to those collected in seasonally inundated areas. This change in egg size and number for fish of a given length group does not appear to be attributed to an allometric change in the size of the individuals between these sites. The linear regressions for the relationship between fecundity and fish size (Fig. 6.17) from perennially and seasonally sites indicates that there is a significant difference in the slopes and intercepts for these two regression lines ($P < 0.05$)

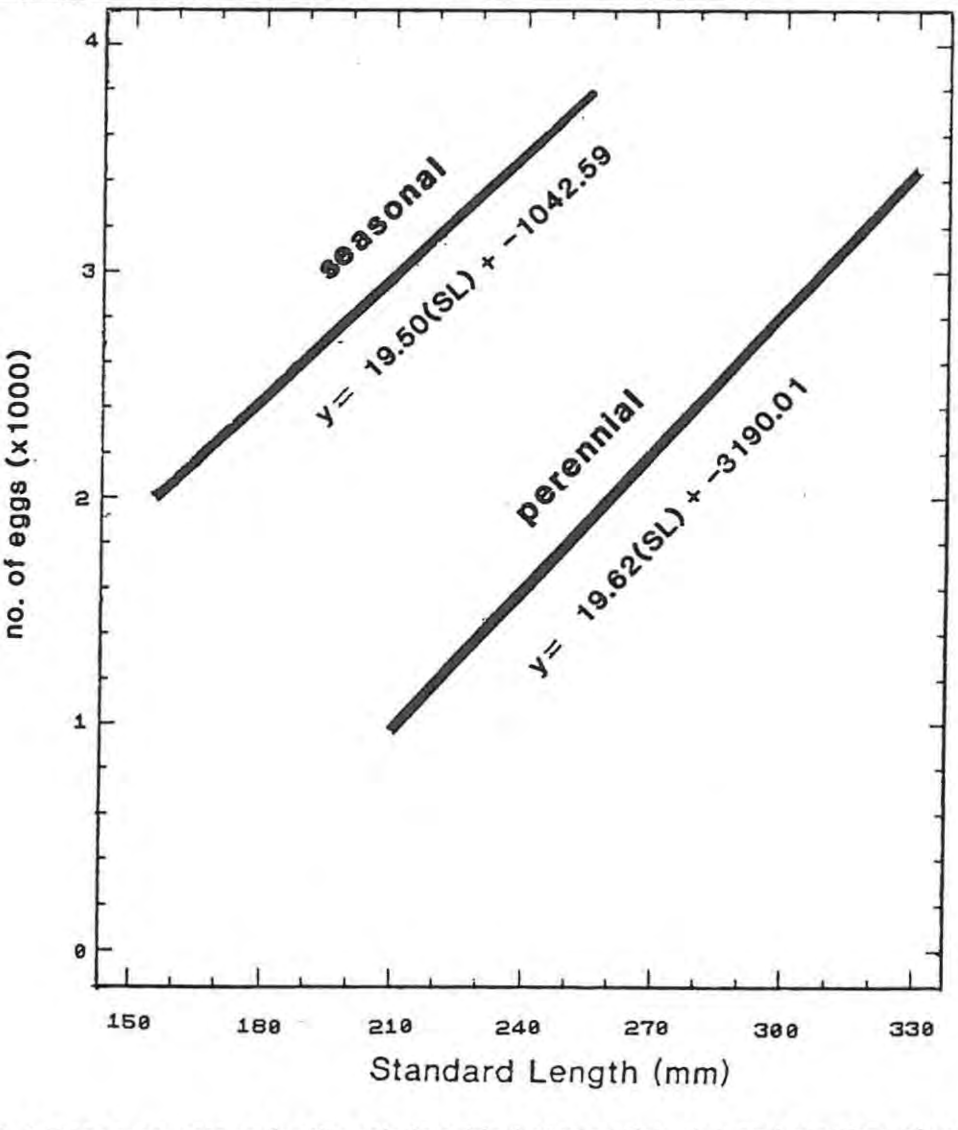


Figure 6.17. Linear regressions for the relationship between fish size and number of eggs in the ovaries of O. andersonii in seasonally and perennially flooded areas of the Okavango Delta, between November 1983 and December 1986.

Spawning behaviour

The spawning behaviour of O. andersonii has been adequately described (Bell-Cross, 1976). In summary, spawning involves the male setting up territories in arenas or "leks" and preparing nests in which mating occurs with a succession of receptive females. The male attracts a female which then lays her eggs in the nest for the male to fertilize. The female then picks up the eggs in her mouth where they are incubated for about one month after which the juveniles move away into the very shallow margins of the floodplains.

DISCUSSION

The research on reproductive biology was designed to assess the influence of the flood cycle on spawning behaviour. The results presented in this Chapter, and given by Merron and Bruton (1988), indicate that the flood cycle does influence the spawning periodicity of many Okavango fishes.

In the riverine floodplain and perennial swamp many species, particularly non-guarding, egg-scattering fishes, synchronize spawning with the initial arrival of the flood in February and March. The information obtained on S. mystus and C. gariepinus from the riverine floodplain is an example of this pattern. The advantages attached to this synchronized spawning are obvious. The recently inundated vegetated areas provide cover for the spawning fishes and for the juveniles. In addition, the conditions for adult and larval growth are favourable since the floods cause an injection of nutrients and stimulate a rapid growth of micro-organisms and small invertebrates. This newly produced micro-fauna serves as a food source for many of the juveniles (Lowe-McConnell, 1979; Bruton & Jackson, 1983). However the non-guarding, egg-scattering H. vittatus has a truncated spawning season prior to the arrival of the flood and may be selecting this strategy in the Okavango to ensure that their young are sufficiently large to take advantage of fry of species which spawn during the floods.

Although the arrival of the flood waters in the riverine floodplain and perennial swamp is associated with spawning in most non-guarding species of fish, the results also indicate that certain fish species, particularly within the guarding reproductive guilds such as O. andersonii and H. odoe, have an extended spawning season before, during and after the arrival of the annual floods.

The reason for the difference in sexual activity between the majority of non-guarders and guarders can possibly be ascribed to the difference in spawning pattern of these species. In the riverine floodplain and perennial swamp, the non-guarding spawners, such as C. gariepinus and S. mystus are dependent on the right physico-chemical conditions before they spawn. These species have adopted a high fecundity and high risk strategy. The guarders and mouthbrooders like H. odoe and O. andersonii seek and create suitable conditions for spawning in the nest and/or mouth and have an extended spawning season which is relatively independent of physico-chemical conditions when compared to the non-guarders.

In the seasonal swamp and drainage rivers, where the floodwaters arrive, on average, in June (during the coldest time of year), both C. gariepinus and S. mystus spawned in July, shortly after the arrival of the floods. O. andersonii and H. odoe spawned during spring with a peak between October and November, which was after the initial flood pulse but did coincide with relatively high water levels and temperatures. During January to May the water level in the seasonal swamp and drainage rivers was at its lowest level.

It is therefore concluded that both the arrival of the flood and an increase in water temperature are major ecological factors determining spawning periodicity of fish in the Okavango Delta. It is believed that a combination of these two environmental variables is the primary stimulus determining the success of respective year classes of fish.

Of particular interest in the present discussion is that, within the reproductive guild category of bearers, differences in reproductive characteristics are apparent. In O. andersonii individuals reached sexual maturity at a larger size and attained a greater maximum size in relatively hydrological stable environments (e.g. the perennial mainstream channel) relative to unstable environments (e.g. drainage rivers). It appears reasonable to suggest that, in the stable areas of the Okavango, more energy is directed into growth as the selection pressures in these areas probably favour a large "experienced" parent which produce fewer, larger young. Alternatively, in areas which are subject to wide fluctuations in flood inundation, O. andersonii spawns at a smaller mean size and more energy is shunted into reproductive effort to counteract the relative unpredictability of the varying flood cycle.

The reproductive guilds of Balon (1975, 1981b; Table 6.1) may be represented as alternative states from generalized to specialized forms (Bruton, 1989). The most generalized forms such as C. gariepinus, S. mystus and H. vittatus belong to non-guarders which have a high fecundity and scatter their eggs on open substrata and perform no parental care. They invest a relatively small amount of energy in each of the large number of young. The more specialized reproductive guilds belong to the guarders and bearers. In the Okavango, species such as H. odoe and O. andersonii spawn in specially prepared nests and/or carry the young internally. These fish exercise intensive parental care, have a low fecundity but large-yolked ova and invest a large amount of energy in each of a small number of young.

Superimposed on this genotypic state is a phenotypic one whereby a fish can alter its life-history style by shifting its relative position on an altricial/precocial continuum in response to the environment (Balon, 1989b; Bruton, 1989). The terms altricial and precocial were first described for birds (Rickleffs, 1973) and later adopted for fish (Balon, 1985). With reference to O. andersonii, fishes which have altricial suites of characters produce relatively small, incompletely developed young and are capable of surviving in an unstable environment in which they are mainly subjected to density-independent mortality. O. andersonii exhibiting precocial suites of characters produce large, well-developed young and are adapted to survive in a stable environment which is subject to density-dependent mortality. The interaction between the genotypic and phenotypic states allows the fish to change its relative position on the continuum in response to different environmental stimuli. Kok (1980) and Merron et al. (1987) found that the resident stock of Oreochromis mossambicus, a closely related species to O. andersonii, in Nhlanjane pan on the Pongolo floodplain in South Africa also exhibited suites of altricial characters. Nhlanjane is usually separated from the Pongolo River for several consecutive seasons before the pan is flooded again. The spawning size of O. mossambicus is affected by the unstable environmental factors in this pan when compared with the more stable environments (i.e. pans which annually connect to the river). These populations of fish appear to display different phenotypic, altricial traits when compared to populations in more stable environs. These traits include earlier maturity, decrease in egg size, and decrease in mean adult size.

It is apparent that different life styles exist within O. andersonii in perennially flooded or seasonally flooded sampling sites in the Okavango and is an exciting area for future research. A summary of the preliminary data on life- history characteristics typically associated with these habitat types is given in Table 6.19.

It would be useful in the future to determine whether or not there is a genetic mixing between the two "apparent" populations of O. andersonii during high water levels, and to determine whether the above traits are genotypic or phenotypic. It is my belief that the environment can have a marked effect on the phenotype of many Okavango fishes and that the phenotype, if not the genotype, is flexible. Similar changes in the phenotype in response to changing environmental conditions for other plant and animal groups (Balon 1980, 1985; Via & Lande 1985; Bruton, 1989) appear to support the above idea.

Table 6.19. Various reproductive parameters for O. andersonii from the predictably perturbed (i.e. perennially flooded) and unpredictably perturbed (i.e. seasonally flooded) sampling sites in the Okavango Delta.

	Unpredictably perturbed	Predictably perturbed
Life history	exhibit altricial traits	exhibit precocial traits
Egg no.	3270	1756
Egg size	0.8 mm diameter	2.4 mm diameter
Size at first maturity (females)	105 mm SL	155 mm SL
Final size	< 200 mm SL	> 135 mm SL

CHAPTER 7

FEEDING BIOLOGY OF SELECTED FISH SPECIES

INTRODUCTION

The Okavango Delta, with its densely-vegetated swamps, has much of its nutrients locked up in papyrus and reed mats and associated epiphytes and detritus. The annual inundation of the floodplain results in an allochthonous nutrient pulse into the aquatic system. Extensive tracts of semi-terrestrial vegetation are submerged, and leaves, fruits, seeds and the dung of antelope, elephants, other wild game and cattle are carried into the water. A rich invertebrate fauna develops which provides food for young fishes. Daily, small water level changes caused by wind-induced seiches also enrich the system by carrying game and cattle manure into the waterbodies (Allanson, 1980; Merron & Bruton, 1989).

A quantitative assessment of the feeding habits of the selected fish species was essential in order to obtain an understanding of the feeding response of these species to the annual flood regime. Since the Okavango experiences cyclical floods and seasonal environmental fluctuations, temporal and spatial feeding variations within the community may be expected. An indication of the respective feeding niches and trophic relationships can show how the food chain of this community, on a broad scale, responds to the annual flood cycle. It is not the intention of this chapter to elucidate all the trophic pathways in the Okavango Delta but to determine the broad changes in diet for the selected species in response to the flood.

MATERIALS AND METHODS

From November 1983 to December 1986 at least twenty-five stomach samples from each selected species were collected from quarterly gillnet catches. The specimens chosen for study were the same as those analysed for reproductive biology (Chapter 6). However, the data presented for C. gariepinus include an additional 317 fish from the riverine floodplain which were examined for stomach contents during October to December 1986. This was during the annual catfish migrations, explained in greater detail in this Chapter. The selected species represent all major trophic groups in the Okavango (Table 3.4). These include an omnivore/predator (C. gariepinus), insectivore/predator (S. mystus), piscivores (Hydrocynus vittatus and Hepsetus odoe), and detritivore (O. andersonii). These five species comprised 53.2% of the total mass of fish collected during this study (see Table 4.1). None of the species found in the Okavango can be regarded as a strict planktivore and only one species, T. rendalli, is a strict herbivore (Merron & Bruton, 1988). Phytoplankton production appears to be inhibited in most wetlands by the shallowness of the system and seasonal fluctuations in water level which may be faster than the growth rate of the phytoplankton, as has been proposed for estuaries (McLusky, 1981). It should be emphasized that the stomach contents of the majority of other species have been qualitatively assessed in a separate study (Merron & Bruton, 1988).

The stomachs of whole fish were dissected out by cutting through the oesophagus above the stomach and below the pyloric sphincter. After fixation, the stomachs were opened and their contents washed into a glass petri dish for sorting under a dissecting microscope. Each food item was assigned to its broad taxonomic grouping i.e. fish, terrestrial insects, aquatic and larval insects, bivalve molluscs, gastropods, detritus and algal material. These data were firstly combined to obtain an overall indication of the dietary preferences of each species and, secondly, according to their broad habitat types. Seasonal and size-related changes in diet in relation to the flood cycle were than assessed.

The number of stomachs in which each food item occurred was recorded and expressed as a percentage of the total number of stomachs examined. A quantitative volumetric ranking index was determined for each stomach. The volumetric ranking index entails a volumetric assessment of the diet categories weighted by a stomach fullness index. This method most closely resembles the Hynes (1950) method whereby values (e.g. 10%, 20%) are ascribed volumetrically to individual food items. The value ascribed to a particular food item was multiplied by the degree of stomach fullness. The importance of each diet category was then calculated by expressing the summation of multiplied values for each food item for all stomachs as a percentage of the total values. This method should be treated with caution when specimens are captured in gillnets as stomach contents may be digested or regurgitated by the time the fish are removed from the net. However, as this variable remained constant throughout the study period, a relative indication can be obtained. Fish prey that were undigested and could be identified were measured using standard length. All samples have been housed in the J.L.B. Smith Institute of Ichthyology for further analysis.

All methods of stomach content analysis have certain advantages and disadvantages (Hynes, 1950; Hyslop, 1980). For the purpose of this thesis, the occurrence of the dominant food items and the response of the selected species to the annual flood regime was of most importance. In this respect it is believed that the data presented here is an accurate indication of the diet based on a volumetric assessment.

RESULTS

Clarias gariepinus

General feeding biology and size-related changes in diet

A total of 759 sharptooth catfish in the size range 200 to 940 mm SL was examined for stomach contents (Table 7.1). A large number of the stomachs were empty (i.e. 243 or 32%). The overall composition of all catfish stomachs throughout the Okavango indicates that the most important dietary items were fish (27%) of which cichlids, characins, mormyrids and cyprinids were the most common. Other important components of the diet were detritus and algal material (19%), molluscs (10%), adult aquatic insects (10%), larval aquatic insects (4%), terrestrial insects (9%), gastropods (4%), crustaceans (2%), seeds and fruit (7%) and aquatic macrophytes (3%). C. gariepinus was also found to have amphibians (i.e. frogs) (2%), small mammals (2%) and bird hatchlings (1%) in their stomachs (Table 7.1). It was noted that smaller C. gariepinus (< 300 mm SL) fed mainly on insects, detritus and algal material and that larger C. gariepinus (> 300 mm SL) fed proportionately more on fish.

The overall prey composition reveals that C. gariepinus is an omnivorous predator. The gross composition of the diet of C. gariepinus in the Okavango approximates the diets established for this species in other systems such as Lake Liambezi, Namibia (van der Waal, 1976), Shire River, Malawi (Willoughby & Tweddle, 1978), Lake Sibaya, South Africa (Bruton, 1979a) and the Pongolo Floodplain, South Africa (Kok, 1980).

This species is morphologically well-adapted to feed on a wide range of foods. The circum-oral barbels function as mechano-, electro- and chemoreceptors that enable the catfish to feed at night and in turbid waters (Bruton, 1979a). The mouth is terminal with a wide gape and the jaws are equipped with numerous small teeth. In addition, there is a vomerine band of small teeth as well as paired pharyngeal tooth pads. This buccal structure enables C. gariepinus to capture and swallow large prey items whole. The stomach is thick-walled and muscular with the intestine thin-walled and moderately short, as is common in many predatory fish.

Seasonal changes in diet in relation to the annual flood

Temporal and spatial changes in prey choice have been recorded for other populations of C. gariepinus (Bruton, 1979a; van der Waal, 1985). The most dramatic seasonal change in diet of C. gariepinus in relation to the annual flood regime in the Okavango was demonstrated in the riverine floodplain mainstream channel.

Table 7.1. The percentage importance of diet items according to a weighted, volumetric method for five selected species in the Okavango Delta, between November 1983 and December 1986. The underlined figures indicate the major dietary items.

Species *	1	2	3	4	5
No. examined	759	1429	1113	1048	586
No. empty	243	529	479	545	70
Fish	27	21	79	72	
Fish scales		9			
Adult aquatic insects	10	14	5	7	
Larval aquatic insects	4	7	3	3	
Terrestrial insects	9	24	4	9	
Bivalve molluscs	10	3			
Gastropods	4				
Detritus and algal material	19	8			95
Crustaceans	2	6	4	5	
Seeds and fruit	7	5			
Aquatic macrophytes	3	1	2	4	5
Amphibians	2	1			
Reptiles			3		
Birds	1				
Mammals	2	1			

* 1 = C. gariepinus; 2 = S. mystus; 3 = Hydrocynus vittatus; 4 = Hepsetus odoe; 5 = O. andersonii

Each year mass aggregations of C. gariepinus occur in this habitat type during the low flood level between October and January (see Fig. 7.1). In an attempt to quantify the reasons why these catfish congregate at this time of year an intensive survey was launched in the riverine floodplain mainstream channel between Shakawe and Seronga (see Fig. 3.1) in 1986. During this intensive survey an additional 317 C. gariepinus were dissected to assess the stomach contents and reproductive condition of fish.

Although 34% of C. gariepinus stomachs were empty, those with contents revealed that the majority of prey items consumed during this time were mormyrids, particularly M. macrolepidotus and P. catostoma (Table 7.2). C. gariepinus contained an average of 2.48 prey items per stomach.

The highest number recorded was from a 520 mm SL C. gariepinus which had 8 M. macrolepidotus and 2 P. catostoma in its stomach (Fig. 7.2).

Whilst feeding, the catfish make a distinctive slurping sound, believed to be the result of suctorial feeding and surface breathing. Many catfish were observed with fresh lesions on and around the caudal fin. It is likely that these lesions are caused by catfish beating the densely rhizomed papyrus mats with their tails to chase fish into the open water. Figure 7.3 provides a diagrammatic illustration of catfish pack-hunting. As water levels recede in September a larger number of M. macrolepidotus move into the mainstream. During October and December, catfish form pack-hunting groups in which it appears all the individuals benefit.

Table 7.2. Species composition and numerical abundance of prey items in the stomach contents of 317 Clarias gariepinus caught during pack-hunting in the riverine floodplain mainstream channel of the Okavango Delta, between October and December 1986. The underlined figures indicate the major dietary items.

Species	no.	% contribution
Hippopotamyrus discorhynchus	5	0.6
Marcusenius macrolepidotus	423	53.9
Mormyrus lacerda	6	0.8
Petrocephalus catostoma	196	25.0
Pollimyrus castelnaui	57	7.3
Brycinus lateralis	11	1.4
Schilbe mystus	32	4.1
Synodontis spp.	3	0.4
Clarias theodorae	1	0.1
Hepsetus odoe	1	0.1
Barbus poechii	7	0.9
Barbus spp.	16	2.0
Labeo lunatus	1	0.1
Pseudocrenilabrus philander	9	1.1
Serranochromis angusticeps	3	0.4
S. macrocephalus	2	0.2
S. robustus jallae	1	0.1
Tilapia sparrmanii	11	1.4
Total	785	99.9

Figure 7.1. A mass aggregation of C. gariepinus along the riverine floodplain mainstream channel, November 1986.

Figure 7.2. Stomach contents of a C. gariepinus showing eight M. macrolepidotus and two P. catostoma taken during pack-hunting in the riverine floodplain mainstream channel, October 1986. Photo by R. Stobbs.

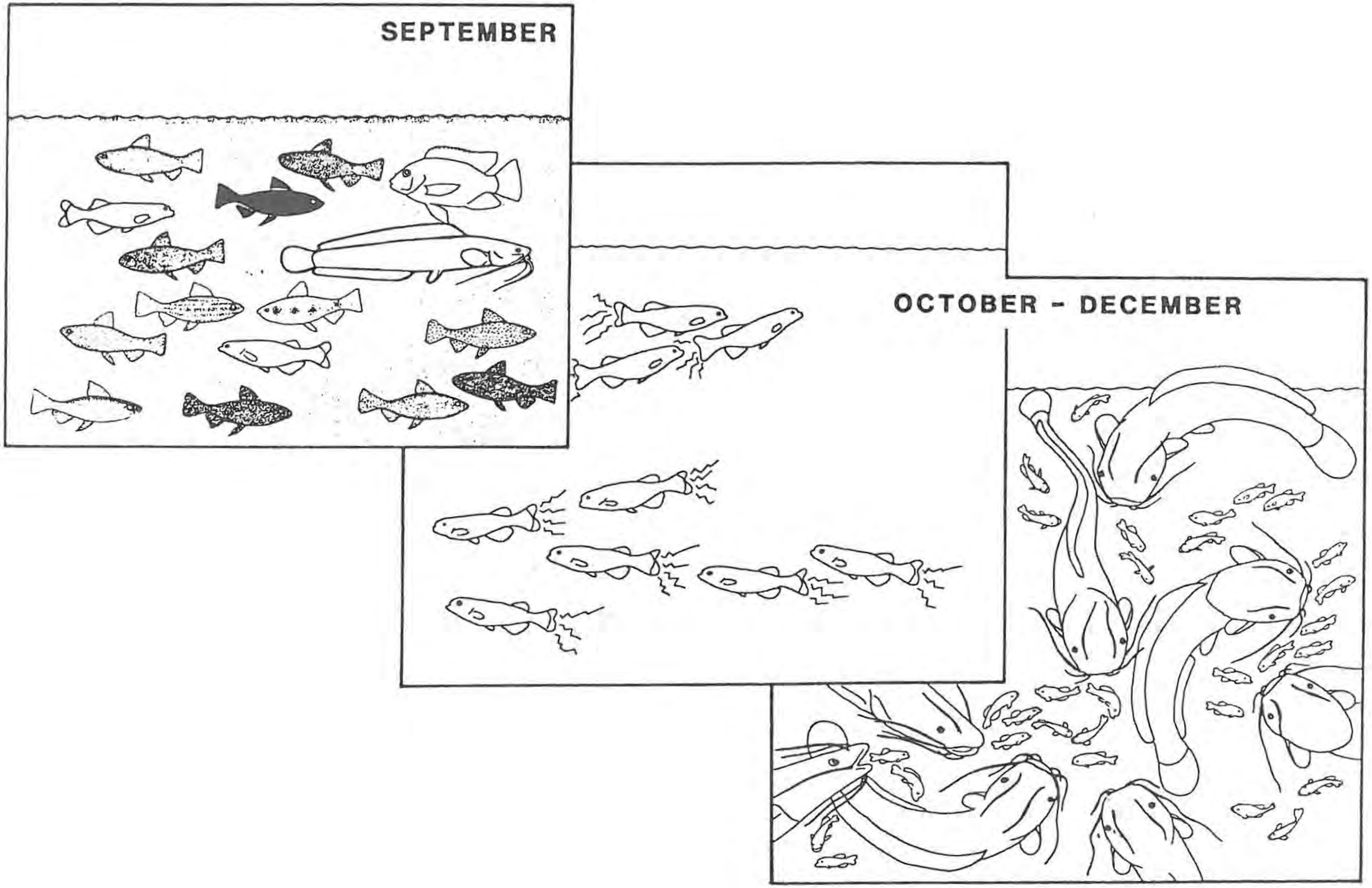


Figure 7.3. A diagrammatic illustration of catfish pack-hunting in the riverine floodplain mainstream channel.

Pack-hunting catfish fed in and amongst the papyrus fringe, while others, some satiated with mormyrids, drifted passively downstream. Once the catfish were located it was possible to follow them on a daily basis and to determine the direction of travel and distance covered. Visual observations indicate that the overall movement was upstream at a speed of 2 - 4 km per day despite some downstream drifting.

In an attempt to substantiate the diel periodicity of feeding activity,nocturnal observations were made on five occasions between October and December 1986. It should be mentioned that the presence of both crocodiles and hippopotami in the river restricts night research. The limited nocturnal observations revealed that the catfish were actively feeding along the fringe of the mainstream throughout the night. Catches from gillnets set approximately 500 m upstream of the shoal at dusk and retrieved at dawn also demonstrate an upstream movement during the night. Further evidence of nocturnal feeding activity by catfish in the Okavango is provided by Donnelly (1966).

There were at least four distinct pack-hunting shoals operating simultaneously at different places in the river each day. The average length of the pack-hunting shoals studied was approximately 250 m, with a range between 50 m and 1.5 km. The average water depth at which the catfish fed was found to be 0.5 m and the width of the shoal extended approximately 20 m into the papyrus fringe.

Stomach content analysis revealed that C. gariepinus that were pack-hunting fed predominantly on mormyrids (86%), especially M. macrolepidotus (Table 7.2). It is useful in the present context to describe briefly the movement patterns of this prey species to fully appreciate the biotic inter-relationship of catfish pack-hunting in response to the annual flood levels in the northern perennial areas of the Okavango.

The length frequency of M. macrolepidotus taken from C. gariepinus stomachs was plotted and compared with the length frequency of M. macrolepidotus collected in gillnets set along the mainstream channel and in Dungu Lagoon, a floodplain-connected lagoon (Fig. 7.4). The modal lengths of fish collected from stomach contents was 130 mm SL, those from gillnets set in the mainstream channel and Dungu Lagoon 130 mm and 160 mm SL respectively. These figures suggest that the catfish were feeding on the same size class of fishes as that available in the mainstream channel. However, when the length-frequency for fish collected in C. gariepinus stomachs or gillnets set in the mainstream channel are compared with those for fishes collected in Dungu Lagoon, a very interesting contrast emerges. It appears that there is a segregation in the size classes of M. macrolepidotus between these two main sampling sites (i.e. habitat types) in the riverine floodplain. A higher proportion of larger individuals was found in the floodplain lagoons than in the stomachs of C. gariepinus or caught using gillnets in the mainstream channel at this

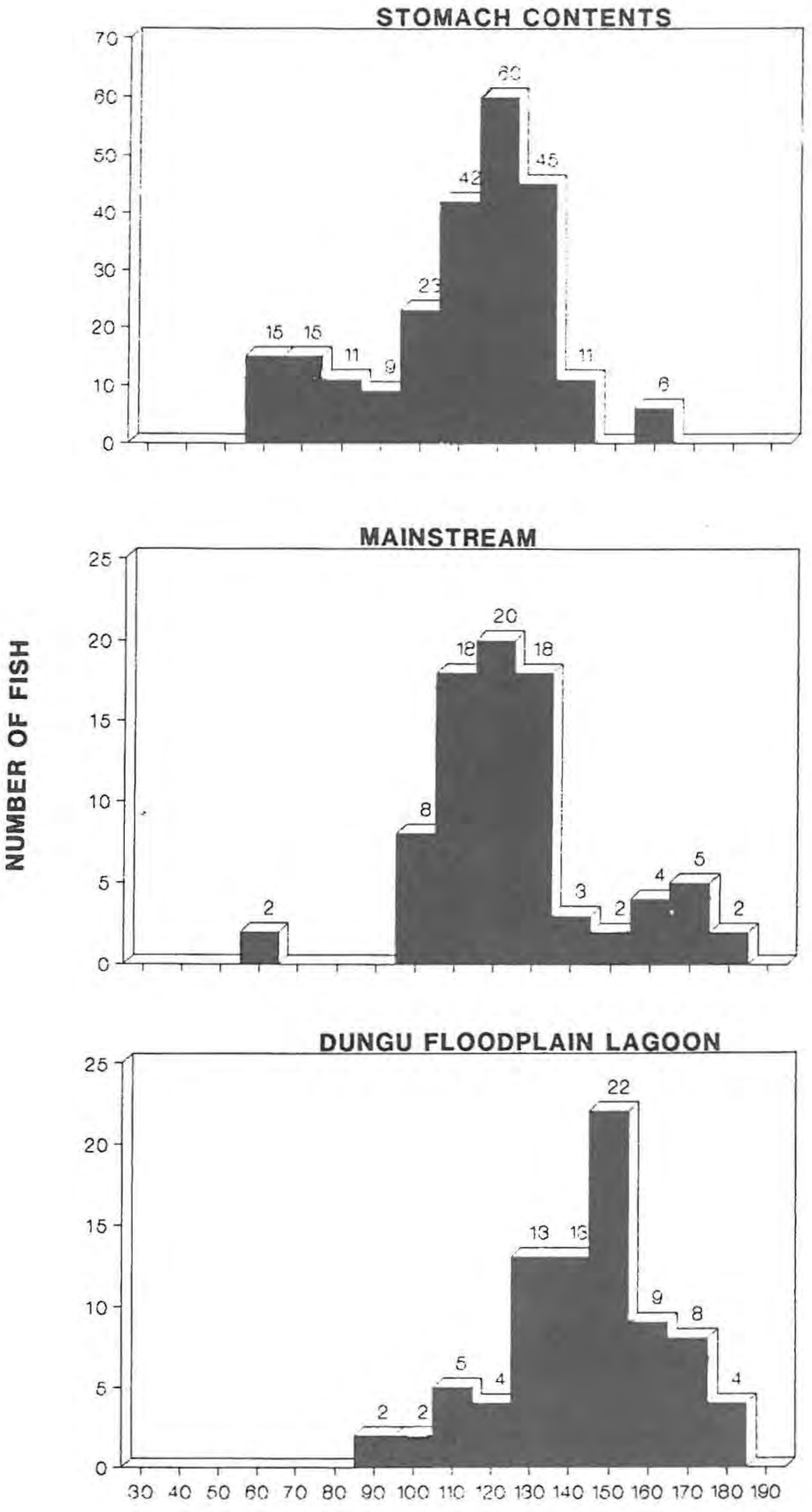


Figure 7.4. Length-frequency histograms for M. macrolepidotus taken from catfish stomach contents, mainstream and Dungu floodplain lagoon gillnet catches between October and December 1986 in the Okavango Delta.

time of year. Although the student "t" test showed that there was no significant difference between the three samples (P > 1.0), the mode of the standard length for Dungu (i.e. 160 mm SL) was greater than that for the mainstream (i.e. 130 mm SL) and from catfish stomach contents (i.e. 130 mm SL; Table 7.3). This finding of similar size M. macrolepidotus in the mainstream channel and catfish stomach contents compared with the size of M. macrolepidotus in the floodplain- connected lagoons such as Dungu Lagoon warrants further investigation. It is, however, important to realize that this trend of apparent size-segregation is similar to the observations made by Merron and Bruton (1988) for S. mystus and H. vittatus in the riverine floodplain ecotone.

Table 7.3. Comparisions of modal length and standard deviation for M. macrolepidotus taken from catfish stomach contents, mainstream and Dungu floodplain lagoon gillnet catches between October and December 1986 in the Okavango Delta.

variable	stomach contents	mainstream gillnets	Dungu lagoon gillnets
Sample size	237	83	82
Modal length of prey (mm)	130	130	160
Standard deviation of prey (mm)	23.2	22.4	22.1

Schilbe mystus

General feeding biology and size-related changes in diet

A total of 1429 S. mystus over a size range of 105 to 260 mm SL was examined for stomach contents (Table 7.1). A large number of the stomachs were empty (529 or 37%). The overall prey composition based on all fish in the Okavango indicates that insects were the most important component of the diet with terrestrial insects (22%), adult aquatic insects (14%) and larval aquatic insects (7.0%) forming the major components of the diet. Fish prey, including cichlids, characins and cyprinids, were also important in the diet (24%). Other food items in the diet included fish scales (9%), molluscs (3%), crustaceans (Caridina nilotica) (6%), detritus and algal material (8%), unidentified seeds and Ficus sycamorus fruits (5%), aquatic macrophytes (1%), amphibians (1%), and mammals (i.e. small rodents; 2%). Plant fragments found in the stomach contents were considered to have been ingested accidentally when S. mystus fed on fish amongst the dense beds of aquatic macrophytes as all the stomachs which contained macrophytes also contained fish.

The diet of this species from the Okavango generally agrees with that found for S. mystus in other systems (Corbet, 1961; Groenewald, 1964; Gaigher, 1969b; Gilmore, 1979a; van der Waal, 1985).

S. mystus is an opportunistic, generalized insectivore and piscivorous predator as shown by the wide range of food items consumed (Table 7.1). It differs from other catfish species by being morphologically adapted to a more pelagic mode of life. The head is smaller and less ossified, and the abdominal viscera are compressed within the anterior one-third of the body, thus moving the center of gravity forward. The long post-anal body segment is laterally flattened and muscular, forming a large power unit for active swimming. The comparatively larger and more anteriorly orientated eyes are also indicative of active hunting habits. The body is equipped with sensory barbels, a large mouth, jaws armed with numerous small teeth and with a short alimentary tract that is typical of a predatory fish. Prey appears to be swallowed whole, often resulting in gross distension of the stomach, as witnessed in Cahora Bassa, Mozambique (Jackson & Rogers, 1976).

Smaller S. mystus (< 150 mm SL) fed proportionately more on aquatic insects, mainly ephemeropteran, dipteran and trichopteran nymphs, and the larger fish (> 150 mm SL) predominantly on larger prey, such as fish and terrestrial insects.

The importance of aquatic nymphs decreases with increasing size of S. mystus, possibly because individual prey organisms are extremely small and the energy expenditure required in capturing sufficient bulk of these organisms is generally not warranted. It was also observed that insect prey size tended to increase with increasing predator length so that aquatic larvae found in large specimens of S. mystus consisted almost entirely of odonatid nymphs rather than smaller ephemeropteran and dipteran larvae found in smaller S. mystus.

The success of S. mystus as a predator in the Okavango can be attributed to its ability to feed on a wide selection of prey. S. mystus is abundant in the delta, especially in the seasonal swamp and drainage rivers (Chapter 4; Table 4.1), and thus the importance of its role in community dynamics, in these ecotones, must be considerable.

Seasonal changes in diet in relation to the annual flood

Throughout the Okavango Delta this species is one of the few predators which fed extensively on terrestrial winged insects, especially flying termites when they hatch after heavy summer rains (Fig. 7.5). Other insects such as grasshoppers and crickets (Orthoptera), beetles (Coleoptera) and termites (Isoptera) in addition to small mammals were recorded in highest numbers as flood waters rose over the floodplains. Because S. mystus feeds heavily on allochthonous resources, it represents a major pathway by which exogenous energy is introduced into the aquatic system.

Figure 7.5. The stomach contents of one S. mystus (bottom) showing at least 35 terrestrial flying termites in November 1984. The specimen on top shows gross distention of the stomach. Note the damaged caudal fin on the bottom specimen.

Hydrocynus vittatus

General feeding biology and size-related changes in diet

A total of 1113 H. vittatus between the size range 220 to 620 mm SL was examined for stomach contents (Table 7.1). A large number of the stomachs were empty (i.e. 479 or 43%).

The proportions of dietary items in the stomachs of H. vittatus confirm that this species fed almost exclusively on fish (79%). Other less important components of the diet included adult aquatic insects (5%), larval aquatic insects (3%), terrestrial insects (4%) and crustacea (4%). The prey species that occurred most frequently in H. vittatus stomachs were open water shoaling fishes such as the small characins, B. lateralis and M. acutidens. During the annual pack-hunting catfish migrations between October and December, M. macrolepidotus and S. mystus featured strongly in their diet.

Some species are less susceptible to H. vittatus predation than others, which may be a result of their morphology (e.g. the large dorsal spines of Synodontis spp.) or behaviour (e.g. the nocturnal behaviour of Barbus radiatus). The insects recorded from H. vittatus stomach contents were mainly odonatid nymphs and aquatic hemipterans. Freshwater shrimps (Caridina nilotica) formed the crustacean component of the diet. Two stomachs also contained intact snakes (3%), one a night adder (Causus rhombeatus) and the other unidentifiable.

Although aquatic macrophytes comprised 2% by volume of the dietary items, plant material should not be regarded as making a substantial contribution to the diet of H. vittatus. Aquatic macrophytes were never found in significant quantities in any single stomach. Generally, plant material was found in small fragments in stomachs that also contained fish prey either picked up incidentally or regurgitated by prey.

Insect remains and crustacea were more important in the diet of fish less than 300 mm SL. In addition, B. lateralis, M. acutidens, S. mystus, M. macrolepidotus and Serranochromis spp. were almost exclusively consumed by H. vittatus individuals greater than 300 mm SL. H. vittatus less than 300 mm SL exerted the greatest predation pressure on the smaller size Barbus populations. This can be explained by the fact that smaller H. vittatus occupy a similar habitat (i.e. relatively sheltered areas) to that of Barbus species.

The diet and relative abundance of different prey items consumed by H. vittatus largely reflects the findings of other workers (Jackson, 1961a; Munro, 1967; Matthes, 1969: Gaigher, 1970; Kenmuir, 1973, 1975; Kok, 1980).

Seasonal changes in diet in relation to the flood regime

A greater number of M. macrolepidotus and S. mystus was recorded from stomachs during October and December. This coincides with the annual catfish feeding migrations. It was observed that H. vittatus also shoal and feed heavily on these species at this time. The degree of stomach fullness was also highest during the annual catfish feeding migrations.

The impact of H. vittatus predation on the community dynamics of tropical rivers and floodplains has been extensively discussed by Jackson (1961b) and Fryer (1965). It is beyond the scope of this discussion to comment on whether H. vittatus predation is responsible for spawning migrations of other fish species as Jackson (1961b) suggests. The presence of H. vittatus in a fish community does appear to have a considerable impact upon the behaviour of smaller fish. This observation is supported by diurnal-nocturnal seine netting which reveals that the species composition and relative abundance of the inshore littoral community is much richer at night when H. vittatus are less active (Skelton & Merron, 1984). Social hunting by H. vittatus (approximately

200 mm SL) was recorded by Skelton & Merron (1984) on small fish species leaving the floodplain at the confluence of the Okavango/Omatako Rivers in Namibia (see Fig. 1.1).

Hepsetus odoe

General feeding biology and size-related changes in diet

A total of 1048 H. odoe between the size range 125 to 475 mm SL was examined for stomach contents (Table 7.1). A large number of the stomachs were empty (545 or 52%). The results indicate that H. odoe fed almost entirely on fish (72%; Table 7.1). The majority of prey fish taken were small cichlids, cyprinids and characins. Other important dietary items included terrestrial insects (9%), adult aquatic insects (7%), larval aquatic insects (3%) and crustaceans (5%). Aquatic macrophytes were also recorded (4%) but are likely to have been bitten off when consuming smaller prey species in the dense macrophyte beds. The diet of H. odoe from the Okavango closely approximates that reported for the Kafue floodplain (Chapman et al., 1971) and for Lake Liambezi (van der Waal, 1985).

Size differences were also noted with smaller size groups (i.e. < 200 mm SL) feeding predominantly on smaller fish and insects, as recorded for H. vittatus, S. mystus and C. gariepinus. H. odoe greater than 200 mm SL fed predominantly on fish.

Seasonal changes in diet in relation to the annual flood

H. odoe exhibited a higher percentage of stomach fullness during the receding and low water levels, similar to H. vittatus. During the receding water level H. odoe was observed at floodplain drainage channels in the seasonal swamp, feeding mainly on A. johnstoni moving off the floodplain. At most other times of the year cyprinids and cichlids made up the majority of the fish prey.

Oreochromis andersonii

General feeding biology and size-related changes in diet

A total of 586 O. andersonii between the size range 50 to 390 mm SL was examined for stomach contents (Table 7.1). A relatively small number of stomachs were empty (70 or 12%). O. andersonii fed almost entirely on detritus (95%; Table 7.1). The low incidence of empty stomachs (12%) can be attributed to the high bulk intake of detritus in this species which may be due to the low nutritional value per unit volume of food eaten.

The dietary importance of detritus (silt and fine sand grains with its associated microfauna and microflora) and algal material (diatoms, desmids and filamentous blue-green algae) attest to the benthic feeding habits of this fish. Bowen (1981) has shown that a closely related species, O. mossambicus, digests heterotrophic micro-organisms which are associated with the detritus. Living vascular plant material (both aquatic and emergent) was of relatively minor importance, comprising 5% of the diet. No apparent size-related change in diet was observed using the volumetric analysis.

Young O. andersonii showed a diurnal preference for the shallowest vegetated margins where water temperatures were considerably higher (35°C) than in the deeper open waters (25°C). This has also been noted by Welcomme (1964) and Bruton & Boltt (1975), who suggest that diurnal movement results from the young fish seeking out the warmer waters during the day, then returning to deeper waters at night as the shallows cool off. This habitat preference enables the young fish to utilize the rich marginal waters during the day, and to benefit from a lower metabolic cost in cooler, deeper water at night when this species (like most cichlids) rests on the substrate. Jackson (1961a) has also stated that, in the presence of predators, fry and juveniles seek refuge in shallow vegetated waters. Therefore, because of the many piscivores in the Okavango, a preference for shallow water serves a dual purpose, namely for protection and feeding. Because one of the main energy pathways of the Okavango system is detritus-based, especially in the seasonal swamp and drainage rivers, O. andersonii is one of the major primary consumers.

Seasonal changes in diet in relation to the annual flood

No apparent dietary changes were recorded between the various sampling sites, although it was observed that a decrease in stomach fullness occurred during colder water periods (e.g. May, June & July).

DISCUSSION

Food chain dynamics

One of the main ecological roles of wetland fishes is to convert the resources at the base of the food chain, i.e. detritus, epiphytes and plants, into food for higher trophic levels (Bruton & Jackson, 1983). In the fast-flowing waters of the riverine floodplain and perennial swamp, where a rich invertebrate community exists under the floating papyrus mats, an insectivore-predator food chain appears to be the main food pathway. This finding is exemplified by the annual catfish pack-hunting event where M. macrolepidotus, an insectivore, is fed on by C. gariepinus, an omnivorous predator. The qualitative feeding accounts of other Okavango fish species (Merron & Bruton, 1988) also support the above finding.

In the slow-flowing waters of the seasonal swamp and drainage rivers, a high degree of settling occurs. A detritus-fish, and to a lesser degree an epiphyte-fish, food chains are the main food pathways.

Seasonal changes in trophic dynamics

During flooding a greater percentage of allochthonous material was consumed and the diets of four of the five selected species indicate that they became more generalized feeders. The detritivore, O. andersonii, showed no obvious change in diet. During the low water level, however, the selected species specialized in their dietary preferences. This was recorded for C. gariepinus which fed predominantly on M. macrolepidotus during the low water level. Hydrocynus vittatus also fed proportionately more on M. macrolepidotus, while Hepsetus odoe fed largely on A. johnstoni moving off the floodplains. At high water level these species were more generalized piscivores. These data support the well-substantiated tenet of Lowe-McConnell (1975) that species with specialized diets in low water conditions become more generalized feeders in high water periods. Low water levels have a concentrating effect on the fish species and lead to increased predation on selected smaller fish species.

Pack-hunting catfish

The most significant finding with regard to the response of fish, in terms of feeding, to the changing water levels was the annual congregation of pack-hunting catfish in the riverine floodplain. Pack-hunting by catfish in the Okavango was a regular response to the annual fluctuation in water level in which it appears that all the individuals in the group benefit. Bruton (1979a) found that C. gariepinus in Lake Sibaya, South Africa, herded small cichlids, predominantly Oreochromis mossambicus, into the shallow littoral areas where they were heavily preyed on. This activity was more commonly seen at low water levels when prey were concentrated. Van der Waal's (1976) account of catfish feeding frenzies in Lake Liambezi, Namibia, most closely resembles the Okavango event. He states that thousands of C. gariepinus hunt in packs and chase fish to the water surface as the lake and surrounding floodplains recede. The main prey items found in van der Waal's (1976) study were the small cyprinids Barbus paludinosus and B. haasianus, the distichodontid Hemigrammocharax spp. and small cichlids. Although most of these species were present in significant numbers in the papyrus mats in the Okavango, they were not preyed on by the catfish (Merron, 1987).

During pack-hunting, catfish fed predominantly on mormyrids. It is possible that, because of their size and abundance, they are a preferred food source. However, the mean size of other abundant species in the community such as Brycinus lateralis and Schilbe mystus (95 mm & 135 mm SL respectively, Merron in press) would also be ideal to consume. The dorsal and pectoral fin spines of Schilbe mystus may be a deterrent to C. gariepinus predation, and they may therefore not be preferred by these predators when other less defensively armed fish such as M. macrolepidotus are available. It was observed, however, that H. vittatus consumed large numbers of S. mystus during these periods.

It is known that mormyrids generate a weak electrical field (Bullock, 1973) and that catfish are electro-receptive (Lissman & Machin, 1963). Although additional data are needed, the results on pack-hunting catfish may be interpreted as a preference by catfish for feeding electro-receptively on mormyrids, particularly M. macrolepidotus.

One of the ways in which the population of M. macrolepidotus can withstand such an intense predation pressure and still maintain viable population levels may be by size-selective habitat preferences. It is postulated that, as the flood begins to recede, a large percentage of smaller-sized M. macrolepidotus respond by moving out of the floodplain lagoons into the mainstream river channel. This is believed to be a dispersal mechanism by smaller, more abundant fish and possibly relates to the limited niche space available for fish in the few remaining floodplain lagoons as the water level recedes.

The larger and older M. macrolepidotus remain in the floodplain lagoons. The relatively high fecundity coupled with an extended spawning season and early maturation are all attributes which enable this species to withstand this high degree of predation pressure. The heaviest mortality from catfish in the mainstream is then exerted on the smaller and younger fish. As the flood penetrates the delta, predation pressure on the remaining fish in the mainstream would be minimal due to a dilution effect on the fish stocks and lateral migration of catfish onto the floodplains to spawn.

There appears to be a great deal of size selective movement in response to the fluctuating water levels for many other Okavango fish species. This concept is of fundamental importance when understanding predator-prey interactions in this ecosystem, particularly in the riverine floodplain ecotone. It was noted in seine net and rotenone collections that large numbers of small cyprinids such as Barbus haasianus and Coptostomabarbus wittei, appeared with a greater frequency in mainstream sites as a result of movement off the floodplains during the receding water level. It is postulated that sufficient numbers of larger individuals exist, however, in the few remaining isolated floodplain lagoons to repopulate the area once the floods arrive. The isolated lagoons remaining on the floodplain are thus important refuges that harbour inocula of sexually mature fishes at low water level. Kushlan (1980), Howard-Williams and Ganf (1981) and Bruton and Jackson (1983) have emphasized the importance of inocula in wetland conservation and management. During the dry-down it is thus essential to avoid the temptation to exploit the inocula in these peripheral floodplain lagoons.

CHAPTER 8

FLOODPLAIN ECOLOGY: A CONCLUDING DISCUSSION

The fishes of the Okavango Delta are an important renewable resource for Botswana. Over the last decade the increased levels of commercial gillnetting concurrent with increased levels of recreational fishing on selected species (e.g. H. vittatus) have placed considerable pressure on the resource. In other wetlands, selective fishing pressure has resulted in the decline of stocks of the large species, which are replaced by smaller and less desirable species (Welcomme, 1979).

Other natural and artificial perturbations such as extended periods of low water level as a result of drought, and ultra-low-volume continual insecticide spraying have contributed to these pressures. In addition, plans to increase the utilization of the Okavango's waters in order to develop the mineral and agricultural potential of northern Botswana and Namibia have been developed and are presently being implemented. The exotic water plant Salvinia molesta has also been found in the Okavango Delta (pers. observation). This plant is an extremely hardy aquatic macrophyte with a rapid growth rate and can cover an entire lagoon in a few months. The establishment of S. molesta mats leads to the exclusion of light, which can result in a reduction of primary productivity and lowered fish densities (Merron, 1990).

It is apparent that quantitative scientific information on the fish communities was needed in order to make rational recommendations on the long term sustainable utilization of this resource. This concluding discussion is an attempt to define the ecological dynamics of the Okavango system and place into perspective the relative environmental components of this unique and increasingly threatened wetland system.

COMMUNITY CHANGES AND ECOSYSTEM STABILITY

The results presented in Chapter 4 on community similarities showed that marked differences in fish populations existed between different areas of the Okavango Delta while other areas were not as different. These communities of fish can be separated from each other by the degree of stability in the annual flood cycle and their response to the co-evolving environment. The riverine floodplain and perennial swamp ecotones experience a relatively stable flood cycle and harbour a similar species composition which was more closely related than the seasonal swamp and drainage rivers (see Chapter 4). These two latter ecotones experience a widely fluctuating flood cycle and share similar compositions of fish. In Chapter 5 it was shown that these fish communities differ widely in the extent of their population fluctuations, and consequently, in their degrees of movement and stability.

The complexity of both lateral and longitudinal movement was greater in the riverine floodplain and perennial swamp than in the seasonal swamp and drainage rivers. It is apparent that the annual flood regime has an important role in regulating the fish populations in the Okavango Delta. Welcomme (1979) showed that the higher the magnitude of the annual flood the longer its duration on the floodplains and the greater the overall production of fish. It would appear that the most important regulatory mechanism controlling the fish populations in the Okavango is also the magnitude of the annual flood. During the course of this study, the timing of the flood did not appear to be as decisive a factor as the magnitude of the flood. This conclusion is based on the fact that the flood arrives in the riverine floodplain and perennial swamp after the warmer summer months and in the seasonal swamp and drainage rivers before the warmer summer months, which is characteristically the optimum time for fish spawning and growth. The critical parameter of the annual Okavango flood cycle is the magnitude of the flood, particularly in the seasonal swamp and drainage rivers. If the magnitude of the flood is high, the water retention time will be longer and may lead to a longer spawning period with a greater percentage of the population spawning (Chapter 6). The duration and water retention time of flood waters in the Okavango Delta is characteristically long, when compared to intense but short periods of water retention as a consequence of flash flooding, such as in the Pongolo Floodplain (Merron et al., 1989).

The degree of stability of the Okavango flood cycle in the different ecotones is a major determinant of the nature of the fish community that inhabits that ecotone. Relatively stable ecotones, taken as representing the riverine floodplain and perennial swamp, enable the fish community to reach a higher level of complexity and biotic interdependence. The fish community achieves its stability through a relative constancy, which in these ecotones is a greater predictability in the degree of fluctuation in the annual flood cycle. Relatively unstable ecotones, such as the seasonal swamp and drainage rivers, are characterized by a fish community which exhibits a lower level of complexity and biotic interdependence. The fish community achieves only a short burst of stability each year which is directly influenced by the magnitude of the annual flood cycle.

In a broad ecological context, the Okavango Delta can be considered to be a sub-climax ecosystem that is maintained by the annual flood regime. It is important to realize that, although there are wide oscillations with regard to the timing, magnitude and duration of the annual flood, the Okavango receives a flood each year and a broad pattern over time is apparent. In this respect the Okavango Delta can be considered to be stable, though changeable. However, some areas within the Okavango (i.e. riverine floodplain and perennial swamp) are relatively more stable than others (i.e. seasonal swamp and drainage rivers).

The stability of an ecosystem, or in the present context an ecotone, usually refers to a tendency to remain near an equilibrium point or to return to it after a disturbance. Margalef (1969) and Jacobs (1975) have defined stability as the persistence of a given state or range of states in time. The word "stability" can, however, mean many things such as constancy, persistence, inertia, elasticity, cyclical and trajectory stability (Orians, 1975). However, the dual aspects "resistance" (constancy) and "resilience" (return after perturbation) adequately describe the main aspects of stability for most uses in ecology (Patten, 1975) and are mentioned in this discussion to describe the dynamics of the fish communities inhabiting the Okavango.

By measuring (albeit qualitatively) the degree of water level change in all major sampling sites throughout the delta, the relative stability of the flood cycle in the different sampling sites and ecotones was ascertained. By measuring the response of the fish populations in these habitats to the various flood cycles (Chapter 5) their resilience and/or resistance was assessed. In the Okavango, the riverine floodplain and perennial swamp fish community can be classified as a resistant fauna, whereas the fish community inhabiting the seasonal swamp and drainage rivers can be classified as a resilient fauna. However, this is not an absolute criterion as even within the seasonal swamp, the fauna inhabiting refuge lagoons such as Nxaraga (Fig. 3.1) should be classified and managed as a resistant community.

The main determinants of fish communities in the Okavango appear to be a combination of the extent of time the water is present and the nature of its flow in the different ecotones. Undoubtedly there are a host of other interconnected environmental parameters, but these two broad and obvious parameters separate much of the variation in fish communities between sampling sites. Where there is greater water flow, as in the riverine floodplain and perennial swamp mainstream channels, the water constantly flushes the system, creating a sandy substrate. This prevents the accumulation of detritus which is the basis of the food chain for many fish species. In these habitat types the food chain is based, predominantly, in the sub-surface (< 1 m) papyrus roots with associated epiphytes and aquatic invertebrates.

In the slower flowing channels of the seasonal swamp and drainage river ecotones, the water retention time is of a relatively short duration and flow rates are at times imperceptible. The food chain is simple and dominated by a few links of which the detritivore/omnivore/predator chain is most apparent. The floodplains, however, have an epiphyte- and mollusc-based food chain. This is mainly because these areas are not inundated for sufficient time to allow the formation of a rich detritivore based food chain. Many of these areas are utilized by game (or cattle) which release large amounts of dung on the floodplains during the annual drying phase. This dung becomes inundated during the next flood cycle, most likely resulting in a surge in nutrients into these habitats.

It is my conclusion that the main flow of biotic and abiotic stimuli within the Okavango Delta originates from the riverine floodplain and perennial swamp to the seasonal swamp and drainage rivers (i.e. from a predictably perturbed area to a unpredictably perturbed one). A simple analogy may be made with a lightning bolt. The energy of the bolt widens and dissipates in force as it moves further away from its epi-center.

In the relatively stable riverine floodplain and perennial swamp ecotones a resistant and delicately balanced community has evolved, whereas in the unstable seasonal swamp and drainage river ecotones a resilient and robust community exists. All the fish species in the Okavango which have a limited distribution, such as H. vittatus, M. acutidens, C. intermedium, and B. euteania, were found in the stable ecotones (see Appendix 2). These fishes have narrow tolerance limits and specific habitat requirements. More ubiquitous fishes, such as C. gariepinus, S. mystus and O. andersonii were found in all ecotones and have broader tolerances and more flexible habitat requirements.

The Okavango Delta can be regarded as a changeable ecosystem characterized by predictably wide temporal and spatial fluctuations (e.g. timing and magnitude of the flood). The closer the system approximates equilibrium (taken as representing the riverine floodplain and perennial swamp), a more diverse and resistant fish fauna is apparent. In addition, it is predicted that a loss of resilience in these ecotones will result from perturbations originating from outside the co-evolved system.

In the predictably perturbed riverine floodplain and perennial swamp, the community becomes more speciose and interspecific connections assume increasing importance (e.g. seasonal movements and feeding relationships, such as catfish pack-hunting) which extend both temporally and spatially. It is postulated that the reason why complex inter-relationships are only likely to develop in relatively stable ecotones is that these interactions are finely in tune with the relatively minor hydrological changes within these ecotones. The widely fluctuating seasonal swamp and drainage rivers ecotones do not permit the time necessary for complex interactions to develop.

The evolution of an ecosystem has been described as a process of information accumulation; succession proceeds in a direction which maximizes information or order (Margalef, 1958, 1963, 1968; Connell & Slatyer, 1977). Successions typically lead towards an increasingly mature community, but may be halted or slowed by biotic or abiotic factors. Since the annual flood regime is the basic independent (abiotic) variable influencing the distribution and abundance of fish in the Okavango, its relative constancy is an important determinant of the characteristics of the fish communities and how they respond to perturbations. Low maturity, relatively unstable ecotones such as the seasonal swamp and drainage rivers, which are subject to wide natural fluctuations, are predicted to be able to sustain a greater degree of human exploitation. It is also predicted that the relatively mature and complex relationships of the fish fauna in the riverine floodplain and perennial swamp would initially be resistant to low level exploitation and small perturbations. However, the fish fauna is believed to be very vulnerable to the introduction by man of major, unnatural perturbations and human exploitation. The complex biotic relationships of the riverine floodplain and perennial swamp fish communities would be reconstituted less easily than the simpler relationships of the less diverse communities of the drainage rivers and, depending on the degree of perturbation, could be irreversible.

The Okavango system harbours a dynamic and co-evolving fish fauna. Although the Okavango is regulated by an abiotic factor (e.g. flood regime), the response of fish to the annual flood regime in the riverine floodplain and perennial swamp is based on complex biotic interactions with other species and, to a lesser degree, in response to abiotic factors that are characteristic regulatory mechanisms in the seasonal swamp and drainage rivers.

Numerous studies suggest that, as a system becomes more complex in the sense of having more species and a richer structure of interdependence, it becomes more dynamically fragile, i.e. has a narrower amplitude of stability (May, 1973, 1975; Whittaker, 1975; Bruton, 1989). Based on hydrological characteristics, the relatively stable riverine floodplain and perennial swamp fish community need only cope with relatively minor annual hydrological changes in comparison with the seasonal swamp and drainage rivers fish community where hydrological changes are more severe. The riverine floodplain and perennial swamp fish community can therefore achieve a dynamically fragile complexity and persist relative to the seasonal swamp and drainage rivers which are characterized by a less diverse but resilient fish community.

Large scale fluctuations, such as a markedly different hydrological regime due to water abstraction schemes in the headwaters of Angola and/or Namibia, indiscriminant gillnetting and recreational fishing, and long-term pesticide spraying operations, may interfere with the integrity of the riverine floodplain and perennial swamp by causing species that are finely in tune with their environment to become threatened and possibly extinct. For example, there exists the possibility that large scale water abstraction via the Eastern National Water Carrier in Namibia might prevent the annual connection of the riverine floodplain mainstream channel with the floodplain-connected lagoons in northern Botswana. This may prevent the movement of predators and prey and break down essential, complex biotic interactions in this region of the Okavango. Ultimately, it is possible that the demise of annual events such as catfish pack-hunting might occur as the spawning population of the preferred prey species, M. macrolepidotus, may be affected.

Such extreme cases have already been observed in other systems which have approached their equilibrium state and have been disturbed as a result of man's inadvertent or often haphazard intervention. The drastic decline of the indigenous lake trout (Salvelinus namaycush) and burbot (Lota lota) populations which today have been replaced by exotic salmonids (Oncorhynchus spp.), sea lampreys (Petromyzon marinus) and alewifes (Alosa psuedoharengus) in the North American Great Lakes (Christie, 1974) is a classic example of major changes in a relatively stable or predictably perturbed ecosystem. The decimation of the cichlid fish species flocks of Lake Victoria in east Africa through the introduction of Nile perch (Lates niloticus; Coulter et al., 1986) is another example of a major alteration in the community structure of this once "stable" lake.

Man-made hydrological changes to wetland ecosytems have generally reduced the amplitude of oscillation in the annual water level fluctuations. The study on a riverine floodplain system such as the Pongolo floodplain in South Africa (see Merron et. al., 1989) shows that the timing, magnitude and duration of floods released from the Pongolapoort Dam is now largely asynchronous with the normal flooding cycle. This unnatural change has had a severe impact on the downstream fish fauna, especially the highly obligatory potamodromic species such as Labeo rosae which are now prevented from reaching their headwater spawning sites.

The traits exhibited by an ecotone and its fish community, be they 'resistant' or 'resilient' are very important factors to be considered when formulating a long term management strategy for the fishes of the Okavango. Developers will need to determine whether the effect of a given action by man is likely to result in a long term disturbance or merely in an elastic recoil to a more or less similar state. Clearly, conservation and resource management strategies will differ depending on whether the perennially or seasonally flooded ecotones of the Okavango are being investigated for potential development.

COMMENTS ON r- and K- SELECTION AND ALTERNATIVE LIFE- HISTORY STYLES

A wetland fish community such as in the Okavango Delta, with its varying ecotones and degrees of flood stability, requires a much longer data series to accurately describe the population dynamics of the fish communities and their response to the changing flood cycle. It must be emphasized again that this study was done during a period of prolonged drought and the interpretations are based largely on a community of fish sampled under extreme environmental conditions. It is apparent that a longer data series on the response of the fish communities during a prolonged wet cycle is needed. Notwithstanding this limitation, the theory of r- and K- selection, first proposed by MacArthur & Wilson (1967), can serve as a starting point when interpreting the response of fish communities to the annual flood regime. r- and K- selection were first defined in relation to natural communities which are subject to either density-dependent or density-independent mortality rates. The majority of wetland fishes exhibit r-selected traits (Lowe-McConnell, 1977; Welcomme, 1979). Wetland fish species live in an environment in which rapid colonization is favoured. Species with r-selected traits typically show rapid population growth, surplus production, early maturity and high fecundity. Species with K- selected traits show the opposite suite of characters, i.e. large size at sexual maturity, larger egg size and lower fecundity.

However, many of the typically non-guarding species in the Okavango with r-selected traits (e.g. H. vittatus) show a great deal of habitat specialization and narrow niche tolerance which are traits more closely associated with K- selection. On the other hand, many K-selected species (e.g. O. andersonii) exhibit some r-selected traits and depending on whether they inhabit seasonal or perennial flooded habitat types will exnibit varying reproductive styles. The difference in egg number presented for O. andersonii in Chapter 6 support this observation. r- and K- selection cannot fully describe the phenotypic plasticity exhibited by this species in response to different environmental stimuli in the Okavango.

Mann et al. (1984) found that the theory and concepts of r- and K- selection were too inflexible to explain their data and observations and proposed that genetically determined differences in life-history styles are overshadowed by environmental effects. Duellman (1989) states that although r- and K- selection adequately describes population demography, it does not explain the mechanism involved in phenotypic changes from one form to another.

An on-going debate regarding the importance of various patterns of bifurcation reflected in r- and K-selection, generalist and specialist, and altricial and precocial life histories, is resulting in new interpretations on the importance of density-independent and density-dependent control of populations (see Bruton, 1989). Much of the debate centers on the ability of an organism to keep open two or more life-history options, and allow the co-evolving environment to determine which one will be most successful.

Balon (1985) and Bruton (1989) prefer the ecological concept of altricial/precocial homeorhetic states (ALPREHOST) when describing an organisms response to environmental change. In altricial forms, the parental investment per individual young is different from precocial forms, which produce a few, large young as described in Chapter 6. The same thinking, developed by Hutchinson (1978) distinguished between "profligate" species, which lay a large number of small eggs, and "prudential" species, which raise a few, large young.

Species with altricial traits are characterized by rapid population growth during short favourable seasons, efficient dispersal abilities and density-independent mortality. Species exhibiting precocial traits, on the other hand, have characteristics which ensure their persistence and success in a strongly competitive, density- dependent environment (Bruton, 1989).

Based on the reproductive data presented for O. andersonii (Chapter 6), it appears that the prevailing environmental conditions in different habitat types have a marked effect on the phenotype of this species. Under a widely fluctuating flood cycle as in the seasonal swamp and drainage rivers, O. andersonii exhibits a greater degree of generalized, altricial traits. However, under relatively stable flood conditions in the riverine floodplain and perennial swamp, specialized, precocial traits are favoured. The phenotypic plasticity associated with either altricial or precocial life-history strategies is dependent on the degree of water retention in different habitats. Clearly, persistence in seasonally flooded habitats would require more resource allocation to survival and reproduction, whereas in perennially flooded habitats growth is emphasized.

Although alternative life-history styles such as r- and K- selection, generalist and specialist, and altricial and precocial forms represent patterns in nature, they do not adequately explain the process behind an organisms ability for phenotypic change under different environmental conditions. Bruton (1989) speculates on the mechanism which may produce the alternative life-history styles exhibited by many species, such as O. andersonii. He states that the concept of altricial-precocial homeorhetic states (ALPREHOST) is based on the principle that epigenetic processes are probably involved in the formation of these patterns. Bruton (1989) further states that the ALPREHOST may, therefore, be regarded as the means whereby generalist/specialist and other phenotype pairs are produced. He concludes that altricial and precocial forms represent the pattern, ALPREHOST the mechanism responsible for the formation of the pattern, and the predictability or unpredictability of the environment the causal factor both initiating the process and selecting the surviving form or forms.

Based on the results in this thesis and given by Merron & Bruton (1988), a greater percentage of species exhibiting precocial traits are associated with relatively hydrologically stable ecotones in the Okavango and which have the following kinds of flood stability: high constancy, low amplitude and high cyclical stability, as in the riverine floodplain and perennial swamp. In contrast, species exhibiting an altricial life-history trajectory are associated with resilient ecotones characterised by a flood cycle with a low constancy, high amplitude of change and low cyclical stability, as in the seasonal swamp and drainage rivers.

It is predicted that man-induced regulation of the flood regime in the predictably perturbed ecotones will result in a more unstable community composed of fishes exhibiting an altricial life-history style. Fish species exhibiting precocial traits suffer most from human interference because of their low rates of reproduction and specialized life styles which are intricately linked to, and dependent upon, other species (Norton, 1986).

It is also predicted that prolonged periods of high water level, as in the 1970's, will result in an encroachment of the resistant riverine floodplain and perennial swamp fauna into the resilient seasonal swamp and drainage rivers and that these fish communities will become inhabited by precocial forms. This is based on the assumption that fish communities, living under relatively stable environmental conditions (e.g. flood cycle) in the Okavango, will tend towards a more mature, diverse state through ecological succession, thus favouring a more precocial life form. An example of this succession is shown in Lake Ngami, where the stenotypic H. vittatus is found under more stable lake levels such as when the early explorer Frederic Daviaud visited this Lake in 1858 (see Jubb & Gaigher, 1971). Conversely, as the lake becomes increasingly perturbed (e.g. prolonged low water levels during a drought) there is a reduction of habitat specialists as found by Skelton et. al. (1983). It is predicted that these communities will be dominated by more eurytopic species (e.g. C. gariepinus and O. andersonii) which are tolerant of a wide range of environmental conditions. Although both of these species fall on opposite ends of the r- and K-continuum they are likely exhibiting altricial traits.

FISHERIES MANAGEMENT

In addition to the intrinsic scientific aspect of this research, it was necessary to provide relevant baseline biological data to the Botswana Fisheries Unit to enable this management authority to develop a clear understanding of the ecology and community structure of the fish populations.

An important finding regarding increased fisheries potential has been to identify the underexploitation of the prolific catfish S. mystus. This stock of fish represents a potentially large resource which is now being drawn on to increase the yield of fish to local fishermen (see Merron & Bruton, 1988). Targeting on this species also alleviates pressure on larger fish species, such as

O. andersonii and H. vittatus, which have been heavily exploited for over a decade by both commercial and recreational fishing activities. Fishermen are now encouraged through a monetary incentive programme to harvest S. mystus using smaller-mesh gillnets (e.g. 50-60 mm stretch mesh). In addition, recreational fishermen, realizing their own long-term interest in the resource, are beginning to practice a catch and release strategy.

Because of the relatively small size of S. mystus (e.g. 195 mm mean SL) it was not being caught because of the traditional use of only large-mesh gillnets (e.g. 96-118 mm stretch mesh). It was first thought that the use of smaller-mesh gillnets would harvest a variety of immature cichlids. Studies by Merron & Bruton (1988) showed, however, that very few immature cichlids were caught in small-mesh nets set in open water.

One of the reasons for the low numbers of immature cichlids in small-mesh gillnets is that the smaller cichlids inhabit the shallow littoral areas. The average length of various cichlid species which move into the open water limnetic zones is approximately 250 mm SL (Merron & Bruton, 1988). This pattern of low cichlid catches in small-mesh gillnets set in open water has also been reported for the Kafue floodplain (Lagler et. al., 1971) and Lake Liambezi (van der Waal, 1985).

Another important findings included the difference in catch between large-mesh (i.e. 96 mm) monofilament and multifilament gillnets. It was found that the monofilament nets caught a larger number of overexploited cichlid species and H. vittatus, whereas multifilament nets harvested a greater mass of underexploited Clarias gariepinus and C. ngamensis.

Increased fishing effort should be focussed on the drainage rivers, as this area has fish with life-history styles that allow a higher fishing pressure. There is a large annual movement of fishes from refuges in the seasonal swamp to repopulate previously dry areas in the drainage rivers. A large surplus of smaller fish is typically produced in each generation.

The northern perennial waters of the Okavango Delta should have restricted fishing activity and environmental changes imposed on it. The relatively resistant fish stocks might initially absorb considerable fishing pressure but these stocks may collapse suddenly as their life-histories are not suited to continual exploitation on a large scale. In addition, the complex predator-prey interactions such as the annual catfish pack-hunting migrations may be affected, as the components of these relationships are intricately interlinked. It is predicted that overfishing of one species may have a severe affect on the abundance of other species.

The data presented in Chapter 4 indicate that there was a greater mass of fish collected per unit effort in the riverine floodplain when compared with the seasonal swamp and drainage rivers. In addition, it was noted that there was a clear distinction in mass for individual mesh-size gillnets between the different sampling sites. In the riverine floodplain and perennial swamp, large-mesh gillnets (96 - 143 mm stretch mesh) harvested the highest percentage of fish mass whereas, in the seasonal swamp and drainage rivers small-mesh gillnets (24-60 mm stretch mesh) harvested the greatest percentage of mass. This difference in species composition of gillnets can be attributed to the degree of water level fluctuation between these sampling sites, which is the factor determining the nature of the fish community.

Plans to increase fishing activities must, furthermore, take into account the factors which limit the distribution and abundance of the fish populations, and the response of the fish populations to seasonal water level fluctuations. There is a potential to expand the fishery, although previous estimates, based on Welcomme's (1979) formula, in excess of 10,000 tonnes per annum (Skjonsberg & Merafe, 1987) appear to be inflated. Although the total surface area of the Okavango Delta is approximately 15,000 km^2, the surface area of the more productive perennial water is approximately 1,000 km^2. This is because many terrestrial areas in the Okavango (e.g. Chief's Island and the Sandveld tongue; see Fig. 2.3) are not flooded each year. This modified figure is probably a more realistic one to use in Welcomme's (1979) formula, and gives a yield of approximately 5,000 tonnes per annum. It must be pointed out that Welcomme's (1979) formula is of a very general nature. However, this simple formula has a relevance in third world situations until additional quantitative data are available to apply to more sophisticated yield models.

The commercial fishery presently harvests 1200 tonnes per annum and it would appear that the resource is under-utilized. There is a potential to increase the commercial fishery, but it must be realized that commercial fishing activities are not the only exploiters of the fish resource. Recreational fishing, makes an extremely important contribution to Botswana's lucrative tourist trade, and depends on the availability of popular angling species. Artisanal fishery practices, of which little is known, are also increasing as population density increases. Although no accurate figures are available on the magnitude of the artisanal fishery, it is believed to harvest 1000 tonnes per annum from the delta. The recreational fishery, centered largely in the riverine floodplain and perennial swamp, is estimated to harvest approximately 800 tonnes per annum. The total yield of the commercial, recreational and artisanal fishes is therefore about 3000 tonnes per annum and could be increased, with adequate management.

Clearly, commercial fishing is not the only pressure exerted on the fish stocks. Any management plan designed to increase the yield of fish in the Okavango must consider all the users of the resource, as well as the diversity of habitat types, the variations in species compositions and the life-history styles of the species within the habitat types.

Management strategies for African inland fisheries should be based on a life-history approach. Previous management strategies in many African wetlands have not taken into consideration the recommendations of biologists when exploitation schemes were designed and this has lead to the demise of many traditional inland fisheries (Jackson, 1989). Although the data presented in this thesis, and those provided by Merron & Bruton (1988), are being used to assist in refining potential yield estimates from the Okavango, it should be stressed that an on-going fisheries research programme is necessary to refine our knowledge of the ebb and flow of the fish communities in the Okavango.

CONCLUSION

The fish stocks in the Okavango Delta represent an important commercial, recreational and artisanal fishing resource. The fish species are also important in maintaining many ecological processes. Man-made manipulations of the Okavango Delta, such as large scale water extraction, will have a marked effect on the natural flood regime and on the fish populations living there. This thesis has tried to establish a fundamental understanding of the factors which limit the distribution and abundance of fish species. Based on this initial study, I accept the original hypothesis put forward in this thesis that the annual flood regime is important in maintaining the fish populations. In addition, the main factors determining the nature of the fish communities in the Okavango Delta are the retention time of water in particular habitats and whether or not the water is flowing.

Fisheries development in the Okavango Delta should be aimed at increasing the yield of fish to local fishermen. However, this can only be achieved if the fish communities are managed in such a way that they can sustain themselves, which in turn depends on the preservation of genetic diversity and the maintenance of essential ecological processes, such as flooding and draining.

In the Okavango, potential developers must strike an acceptable balance between the often conflicting needs of short term resource management and conservation. Long-term measures which safeguard the natural resource base and provide for the sustainable utilization of various plants and animals must be ensured. The ultimate aim should be to improve the quality of life of man by integrating conservation and development in such a way that the pace of change is dictated by the intrinsic strengths and weaknesses of the Delta. The preservation of the Okavango for its own sake is clearly not a viable option at present. However, it should be borne in mind that the present and potential natural productivity and diversity of the Okavango is the main working capital on which a natural-resource based economy can be sustained.

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Appendix 1. The different reproductive guilds (non-guarders, guarders and bearers) and trophic group for all species recorded from the Okavango Delta, Botswana between November 1983 and December 1986.

Species	Reproductive guild	Trophic group
Mormyridae		
Hippopotamyrus ansorgii	non-guarder*	insectivore
H. discorhynchus	non-guarder*	insectivore
Marcusenius macrolepidotus	non-guarder*	insectivore
Mormyrus lacerda	non-guarder*	insectivore
Petrocephalus catostoma	non-guarder*	insectivore
Pollimyrus castelnaui	non-guarder*	insectivore
Characidae		
Brycinus lateralis	non-guarder*	insectivore
Hydrocynus vittatus	non-guarder*	piscivore
Micralestes acutidens	non-guarder*	insectivore
Rhabdalestes maunensis	non-guarder*	insectivore
Hepsetidae		
Hepsetus odoe	guarder	piscivore
Distichodintidae		
Hemigrammocharax machadoi	non-guarder*	insectivore
H. multifasciatus	non-guarder*	insectivore
Nannocharax macropterus	non-guarder*	insectivore
Cyprinidae		
Barbus afrovernayi	non-guarder*	insectivore
B. barnardi	non-guarder*	insectivore
B. bifrenatus	non-guarder*	insectivore
B. eutaenia	non-guarder*	insectivore
B. fasciolatus	non-guarder*	insectivore
B. haasianus	non-guarder*	insectivore
B. multilineatus	non-guarder*	insectivore
B. paludinosus	non-guarder*	insectivore
B. poechii	non-guarder*	insectivore
B. radiatus	non-guarder*	insectivore
B. thamalakenensis	non-guarder*	insectivore
B. unitaeniatus	non-guarder*	insectivore
Coptostomabarbus wittei	non-guarder*	insectivore
Labeo cylindricus	non-guarder*	insectivore
L. lunatus	non-guarder*	insectivore
Opsaridium zambezensis	non-guarder*	insectivore
Bagridae		
Auchenoglanis ngamensis	guarder*	omnivore
Zaireicthys chobensis	guarder*	insectivore

Appendix 1 (continued). The different reproductive guilds (non-guarders, guarders and bearers) and trophic group for all species recorded from the Okavango Delta, Botswana between November 1983 and December 1986.

Schilbeidae		
Schilbe mystus	non-guarder*	omnivore
Clariidae		
Clarias gariepinus	non-guarder*	omnivore
C. ngamensis	non-guarder*	omnivore
C. stappersi	guarder*	omnivore
C. theodorae	guarder*	omnivore
Mochokidae		
Chiloglanis fasciatus	non-guarder*	insectivore
Synodontis leopardinus	non-guarder*	omnivore
S. macrostigma	non-guarder*	omnivore
S. nigromaculatus	non-guarder*	omnivore
S. woosnami	non-guarder*	omnivore
Poeciliidae		
Aplocheilichthys hutereaui	guarder*	insectivore
A. johnstonii	guarder*	insectivore
A. katangae	guarder*	insectivore
Cichlidae		
Hemichromis elongatus	bearer	piscivore
Oreochromis andersoni	bearer	detritivore
O. macrochir	bearer	detritivore
Pharyngochromis darlingi	bearer	insectivore
Pseudocrenilabrus philander	bearer	insectivore
Serranochromis (Serranochromis) angusticeps	bearer	piscivore
S. (Sargochromis) carlottae	bearer	molluscivore
S. (S.) codringtoni	bearer	molluscivore
S. (S.) giardi	bearer	molluscivore
S. (S.) greenwoodi	bearer	molluscivore
S. (Serranochromis) longimanus	bearer	piscivore
S. (S.) macrocephalus	bearer	piscivore
S. (S.) robustus jallae	bearer	piscivore
S. (S.) thumbergi	bearer	piscivore
Tilapia rendalli	guarder	herbivore
T. sparrmanii	guarder	detritivore
T. ruweti	guarder	detritivore
Anabantidae		
Ctenopoma intermedium	guarder*	insectivore
C. multispinus	non-guarder*	omnivore
Afromastacembelidae		
Afromastacembelus frenatus.	non-guarder*	insectivore

* Many of the species accounts are qualitative.

Appendix 2. Percentage number and mass (in parentheses) of fish collected from respective sampling sites in the Okavango Delta, between November 1983 and December 1986.

Species	Sampling site								Total
	1	2	3	4	5	6	7	8	Okavango
Mormyridae									
Hippopotamyrus ansorgii							0.01(<0.01)		0.01(<0.01)
H. discorhynchus	0.13(0.03)	0.16(0.07)	0.13(0.03)	0.10(0.01)			0.01(0.01)		0.01(0.02)
Marcusenius macrolepidotus	1.61(1.40)	2.42(2.90)	2.15(1.96)	4.67(2.90)	3.78(2.39)	0.03(0.07)	8.49(2.60)	2.65(1.29)	2.80(2.20)
Mormyrus lacerda	0.18(1.52)	0.16(1.76)	0.15(1.50)	0.08(0.62)	0.19(0.64)		0.15(0.72)	0.01(0.61)	0.13(1.01)
Petrocephalus catostoma	0.92(0.26)	1.18(0.39)	1.58(0.40)	3.67(0.47)	2.35(0.37)		3.55(0.36)	2.65(0.05)	1.76(0.38)
Pollimyrus castelnaui	0.21(0.04)	0.11(0.02)	0.43(0.07)	2.60(0.17)	1.94(0.22)		2.60(0.14)	1.58(0.12)	0.91(0.11)
Characidae									
Brycinus lateralis	7.72(0.76)	5.75(0.71)	7.79(0.74)	7.34(0.97)	5.87(0.34)	0.62(0.17)	5.15(0.61)	6.19(0.51)	6.13(0.66)
Hydrocynus vittatus			0.01(0.06)	6.45(29.20)	3.71(10.30)		4.93(29.60)	2.17(15.20)	1.53(12.80)
Micralestes acutidens		0.09(0.01)	0.15(0.02)	6.42(0.26)	2.82(0.14)		4.23(0.19)	1.50(0.09)	1.35(0.10)
Rhabdalestes maunensis	5.50(0.11)	3.55(0.11)	1.29(0.03)	1.88(0.02)	1.74(0.03)	0.28(0.01)	3.21(0.04)	2.00(0.06)	2.77(0.06)
Hepsetidae									
Hepsetus odoe	1.42(11.20)	1.89(9.40)	2.32(17.40)	0.29(1.20)	0.63(3.90)	0.13(1.60)	0.28(0.98)	0.61(3.10)	1.77(6.30)
Distichodontidae									
Hemigrammocharax machadoi	0.68(0.01)	0.88(0.01)	0.70(0.01)	6.47(0.05)	3.32(0.03)		8.04(0.04)	2.88(0.02)	2.22(0.02)
H. multifasciatus	0.05(<0.01)	0.06(0.01)	0.31(0.02)	1.56(0.04)	0.98(0.03)		2.41(0.08)	0.69(0.03)	0.56(0.03)
Nannocharax macropterus							0.06(<0.01)		0.01(<0.01)
Cyprinidae									
Barbus afrovernayi	1.84(0.05)	2.05(0.08)	3.73(0.12)	0.92(0.01)	0.79(0.02)		1.59(0.02)	4.79(0.11)	2.17(0.06)
B. barnardi	7.71(0.23)	5.72(0.19)	5.68(0.16)	2.02(0.02)	1.54(0.04)	1.38(0.07)	2.42(0.03)	3.88(0.07)	4.54(0.10)
B. bifrenatus	0.47(0.03)	1.26(0.12)	2.59(0.18)	1.05(0.04)	0.62(0.02)	2.71(0.35)	0.79(0.02)	1.91(0.06)	1.42(0.07)
B. eutaenia				0.11(<0.01)	0.04(<0.01)		0.47(0.01)	0.01(<0.01)	0.05(<0.01)
B. fasciolatus	0.80(0.03)	1.04(0.05)	0.53(0.02)	1.86(0.03)	2.79(0.07)		3.30(0.04)	3.53(0.08)	1.52(0.04)
B. haasianus		0.16(<0.01)	5.77(0.07)	3.09(0.01)	10.78(0.12)		1.88(0.01)	5.36(0.06)	2.92(0.03)
B. multilineatus	0.06(<0.01)	0.77(0.03)	1.11(0.03)	0.40(<0.01)	0.19(<0.01)	0.19(0.01)	1.31(0.01)	0.92(0.06)	0.60(0.01)
B. paludinosus	0.40(0.04)	1.10(0.16)	0.51(0.02)	0.11(<0.01)	2.05(0.04)	16.88(4.10)	0.29(0.01)	0.57(0.01)	2.22(0.14)
B. poechii	2.77(0.77)	3.05(1.05)	1.20(0.20)	1.44(0.11)	0.86(0.09)	1.11(0.40)	0.84(0.07)	1.32(0.19)	1.82(0.35)
B. radiatus	2.57(0.15)	2.97(0.27)	1.29(0.04)	2.54(0.06)	2.87(0.10)	0.76(0.21)	1.41(0.04)	1.28(0.03)	2.05(0.10)
B. thamalakenensis	2.53(0.05)	3.95(0.14)	6.73(0.20)	2.28(0.03)	2.92(0.05)	6.25(0.44)	2.25(0.03)	2.09(0.04)	3.72(0.08)
B. unitaeniatus	3.14(0.40)	2.30(0.51)	0.08(0.01)	0.02(0.01)	0.32(0.04)		0.07(<0.01)	0.24(0.02)	1.13(0.13)
Coptostomabarbus wittei		0.36(<0.01)	4.05(0.04)	0.86(0.01)	4.38(0.02)	0.38(0.02)	1.58(0.01)	2.61(0.02)	1.62(0.01)
Labeo cylindricus				0.06(<0.01)			0.12(<0.01)		0.02(<0.01)
L. lunatus			0.02(0.23)	0.10(0.27)	0.31(10.70)		0.10(1.04)	0.05(0.45)	0.05(1.39)
Opsaridium zambezensis				0.02(<0.01)	0.02(<0.01)		0.03(<0.01)	0.01(<0.01)	0.01(<0.01)
Bagridae									
Auchenoglanis ngamensis	0.07(0.15)	0.02(0.09)	0.21(0.19)	0.11(0.06)	0.01(0.01)		0.19(0.09)	0.02(0.01)	0.08(0.08)
Zaireicthys chobensis		0.01(<0.01)	0.24(0.01)	0.02(<0.01)	0.04(<0.01)		0.08(<0.01)	0.02(<0.01)	0.05(<0.01)
Schilbeidae									
Schilbe mystus	4.46(19.10)	4.54(15.30)	6.64(14.70)	4.92(6.80)	4.24(7.00)	0.36(1.20)	4.36(6.10)	2.98(6.10)	4.25(10.30)
Clariidae									
Clarias gariepinus	0.32(5.30)	0.64(8.20)	0.44(7.00)	2.42(15.10)	1.29(11.80)	2.83(8.90)	3.53(15.30)	2.09(16.30)	1.36(11.50)
C. ngamensis	0.11(2.21)	0.20(3.50)	0.28(3.40)	0.92(5.70)	0.35(4.70)	0.28(3.50)	0.82(4.00)	0.92(6.20)	0.41(4.20)
C. stappersi			0.01(0.01)	0.06(0.03)	0.01(0.04)		0.06(0.07)	0.05(0.08)	0.02(0.03)
C. theodorae	0.14(0.04)	0.16(0.05)	0.12(0.04)	0.17(0.02)	0.12(0.02)		0.28(0.04)	0.15(0.03)	0.14(0.03)
Mochokidae									
Chiloglanis fasciatus							0.06(<0.01)		0.01(<0.01)
S. leopardinus	1.36(3.90)	1.39(2.80)	1.31(4.20)	1.27(0.52)	0.46(0.48)		0.36(0.31)	0.38(0.64)	0.95(1.73)
S. macrostigma	0.35(0.90)	0.32(0.92)	0.55(0.88)	1.82(1.52)	0.61(0.58)		1.54(0.94)	0.45(0.67)	0.60(0.91)

Appendix 2. Percentage number and mass (in parentheses) of fish collected from respective sampling sites in the Okavango Delta between November 1983 and December 1986 (continued).

Species	Sampling site								Total
	1	2	3	4	5	6	7	8	Okavango
S. nigromaculatus	0.73(3.50)	0.72(2.49)	1.48(5.80)	2.69(3.70)	2.21(3.50)		3.31(4.20)	1.43(3.60)	1.36(3.70)
S. woosnami	0.59(0.95)	0.38(1.13)	0.59(0.95)	0.95(0.86)	0.64(0.38)		0.84(0.85)	0.24(0.63)	0.51(0.18)
Poeciliidae									
Aplocheilichthys hutereaui		0.09(<0.01)	2.36(0.02)	0.34(<0.01)	1.29(0.01)	0.36(0.01)	0.46(<0.01)	2.77(0.02)	0.93(0.01)
A. johnstoni	6.11(0.07)	7.24(0.11)	12.01(0.17)	7.25(0.04)	7.17(0.03)	2.49(0.14)	3.20(0.01)	8.77(0.08)	7.18(0.07)
A. katangae		0.01(<0.01)	0.20(<0.01)	0.11(<0.01)	0.23(<0.01)		0.42(0.01)	0.23(<0.01)	0.12(<0.01)
Cichlidae									
Hemichromis elongatus	0.05(0.06)	0.01(<0.01)	0.07(0.08)	0.16(0.09)	0.24(0.09)		0.26(0.11)	0.72(0.92)	0.16(0.20)
Oreochromis andersonii	8.30(15.20)	8.81(14.20)	4.72(9.80)	3.42(7.40)	3.01(13.80)	26.90(37.50)	3.79(8.70)	5.02(12.90)	7.96(12.30)
O. macrochir	5.04(6.10)	4.55(6.50)	1.39(2.80)	0.74(1.60)	0.99(4.90)	6.38(14.70)	0.90(2.70)	1.52(6.60)	3.04(4.60)
Pharyngochromis darlingi	5.90(0.56)	5.89(0.57)	1.91(0.18)	1.73(0.11)	1.37(0.07)	2.30(0.28)	1.01(0.05)	4.09(0.20)	3.59(0.25)
Pseudocrenilabrus philander	5.67(0.39)	4.38(0.43)	1.87(0.11)	3.53(0.19)	6.25(0.18)	8.24(1.40)	2.77(0.14)	4.52(0.36)	4.60(0.29)
Serranochromis (Sargochromis) carlottae	0.75(2.60)	0.57(2.05)	0.17(0.73)	0.44(1.25)	0.36(0.89)		0.51(1.23)	0.48(1.62)	0.44(1.48)
S. (Sar.) codringtoni	2.30(2.80)	1.05(1.60)	1.40(1.80)	0.26(0.46)	0.61(1.24)	0.29(1.10)	0.36(0.55)	0.72(1.69)	1.08(1.43)
S. (Sar.) giardi	0.74(2.70)	0.27(1.78)	0.53(2.53)	0.23(1.17)	0.35(1.73)		0.35(1.40)	0.27(0.93)	0.39(1.66)
S. (Sar.) greenwoodi	0.35(1.45)	0.16(0.68)	0.07(0.30)	0.03(0.06)	0.09(0.19)		0.09(0.20)	0.15(0.22)	0.15(0.43)
S. (Serranochromis) angusticeps	0.28(1.99)	0.19(2.28)	0.95(7.90)	1.97(8.90)	2.42(11.30)	0.15(0.64)	2.45(10.60)	1.65(7.90)	1.02(7.10)
S. (S.) longimanus	0.12(0.11)	0.03(0.09)	0.12(0.25)	0.03(0.02)	0.02(0.12)		0.04(0.08)	0.10(0.29)	0.07(0.13)
S. (S.) macrocephalus	0.30(0.56)	0.28(0.79)	0.30(0.60)	0.16(0.50)	0.23(0.79)		0.37(0.66)	0.32(0.80)	0.26(0.65)
S. (S.) robustus jallae	0.07(1.03)	0.06(1.52)	0.15(3.50)	1.21(3.80)	0.37(1.39)		1.03(2.40)	0.49(2.30)	0.33(2.27)
S. (S.) thumbergi	0.72(2.60)	0.87(2.70)	0.26(0.99)	0.05(0.15)	0.07(0.32)	0.11(0.76)	0.10(0.30)	0.19(0.81)	0.39(1.10)
Tilapia rendalli rendalli	3.64(2.36)	4.76(5.60)	1.73(2.66)	0.71(1.29)	2.66(3.00)	10.77(17.30)	0.63(1.14)	1.44(3.30)	3.38(3.00)
T. sparrmanii	10.75(6.00)	11.05(6.60)	6.36(4.70)	3.26(2.00)	3.24(0.03)	4.71(4.30)	3.35(1.07)	5.50(1.86)	7.05(3.30)
T. ruweti	0.04(0.01)	0.32(0.08)	1.04(0.11)	0.08(0.01)	1.05(0.19)	2.71(1.07)	0.03(<0.01)	0.48(0.12)	0.64(0.09)
Anabantidae									
Ctenopoma intermedium			0.07(0.01)	0.09(<0.01)	0.05(<0.01)		0.42(0.01)	0.07(<0.01)	0.06(<0.01)
C. multispinus		0.01(<0.01)	0.05(0.02)	0.02(<0.01)	0.01(<0.01)	0.38(0.41)	0.11(0.01)	0.12(0.02)	0.07(0.02)
Afromastacembelidae									
Afromastacembelus frenatus		0.01(<0.01)	0.08(0.01)	0.27(0.03)	0.12(0.02)		0.16(0.02)	0.05(0.01)	0.07(0.01)
Total no. species	46	56	60	64	62	28	66	60	66
Total no. specimens	26206	23359	20188	11327	11261	12345	10077	16145	130908
Total mass (kg)	581	489	481	599	394	102	649	605	3901

* 1 = Chanoga Lagoon; 2 = Thamalakane River; 3 = Seasonal swamp; 4 = Perennial swamp; 5 = Perennial swamp floodplain-connected lagoons; 6 = Perennial swamp rain pools; 7 = Riverine floodplain mainstream channel; 8 = Riverine floodplain-connected lagoons

Appendix 3. Percentage number and mass (in parentheses) of fish collected from Chanoga Lagoon, Boteti River, Okavango Delta, between November 1983 and December 1986 and grouped according to different flood levels.

Species	Sampling site 1 filling	 1 high	 1 receding	 1 low
Mormyridae				
H. discorhynchus	0.13(0.04)	0.13(0.03)	0.13(0.03)	0.13(0.03)
Marcusenius macrolepidotus	1.62(1.41)	1.61(1.41)	1.61(1.41)	1.61(1.41)
Mormyrus lacerda	0.19(1.53)	0.18(1.53)	0.19(1.51)	0.18(1.52)
Petrocephalus catostoma	0.92(0.26)	0.92(0.26)	0.93(0.26)	0.92(0.26)
Pollimyrus castelnaui	0.21(0.04)	0.22(0.04)	0.21(0.04)	0.20(0.04)
Characidae				
Brycinus lateralis	7.72(0.77)	7.71(0.77)	7.72(0.76)	7.72(0.76)
Rhabdalestes maunensis	5.49(0.11)	5.49(0.11)	5.51(0.11)	5.51(0.11)
Hepsetidae				
Hepsetus odoe	1.41(11.29)	1.43(11.28)	1.41(11.13)	1.41(11.22)
Distichodontidae				
Hemigrammocharax machadoi	0.67(0.01)	0.70(0.01)	0.67(0.01)	0.67(0.01)
H. multifasciatus	0.06(<0.01)	0.04(<0.01)	0.05(<0.01)	0.05(<0.01)
Cyprinidae				
Barbus afrovernayi	1.85(0.05)	1.84(0.05)	1.84(0.05)	1.84(0.05)
B. barnardi	7.71(0.23)	7.71(0.23)	7.72(0.23)	7.72(0.23)
B. bifrenatus	0.48(0.03)	0.47(0.03)	0.47(0.03)	0.47(0.03)
B. fasciolatus	0.80(0.03)	0.81(0.03)	0.79(0.03)	0.80(0.03)
B. multilineatus	0.06(<0.01)	0.07(<0.01)	0.06(<0.01)	0.06(<0.01)
B. paludinosus	0.40(0.04)	0.40(0.04)	0.41(0.04)	0.41(0.04)
B. poechii	2.77(0.78)	2.78(0.78)	2.78(0.78)	2.77(0.78)
B. radiatus	2.59(0.15)	2.60(0.15)	2.54(0.15)	2.58(0.15)
B. thamalakanensis	2.52(0.05)	2.53(0.05)	2.52(0.05)	2.53(0.05)
B. unitaeniatus	3.13(0.41)	3.14(0.41)	3.14(0.40)	3.14(0.40)
Bagridae				
Auchenoglanis ngamensis	0.08(0.15)	0.07(0.15)	0.07(0.15)	0.06(0.15)
Schilbeidae				
Schilbe mystus	4.46(19.23)	4.46(19.23)	4.47(19.23)	4.46(19.23)
Clariidae				
Clarias gariepinus	0.32(5.38)	0.31(5.37)	0.32(5.30)	0.33(5.35)
C. ngamensis	0.11(2.23)	0.11(2.22)	0.10(2.20)	0.11(2.21)
C. theodorae	0.13(0.04)	0.13(0.04)	0.14(0.04)	0.14(0.04)
Mochokidae				
Synodontis leopardinus	1.35(3.97)	1.37(3.97)	1.35(3.92)	1.36(3.95)
S. macrostigma	0.36(0.91)	0.36(0.91)	0.35(0.89)	0.36(0.90)
S. nigromaculatus	0.72(2.86)	0.72(2.91)	0.73(4.17)	0.72(3.41)
S. woosnami	0.59(0.96)	0.58(0.96)	0.59(0.94)	0.60(0.95)
Poeciliidae				
A. johnstoni	6.10(0.08)	6.10(0.08)	6.12(0.07)	6.12(0.07)
Cichlidae				
Hemichromis elongatus	0.04(0.06)	0.04(0.06)	0.05(0.06)	0.05(0.06)
Oreochromis andersonii	8.30(15.35)	8.30(15.34)	8.30(15.14)	8.29(15.26)
O. macrochir	5.04(6.10)	5.04(6.10)	5.05(6.02)	5.05(6.06)
Pharyngochromis darlingi	5.89(0.57)	5.90(0.56)	5.90(0.56)	5.90(0.56)
Pseudocrenilabrus philander	5.66(0.39)	5.67(0.39)	5.68(0.38)	5.67(0.39)
Serranochromis (Sargochromis) carlottae	0.74(2.65)	0.74(2.65)	0.75(2.62)	0.75(2.64)
S. (Sar.) codringtoni	2.31(2.86)	2.29(2.86)	2.30(2.82)	2.30(2.85)
S. (Sar.) giardi	0.74(2.69)	0.74(2.69)	0.74(2.65)	0.74(2.67)
S. (Sar.) greenwoodi	0.36(1.46)	0.36(1.46)	0.35(1.44)	0.36(1.45)
S. (Serranochromis) angusticeps	0.29(2.00)	0.29(2.00)	0.28(1.98)	0.28(1.98)
S. (S.) longimanus	0.11(0.11)	0.11(0.11)	0.13(0.11)	0.11(0.11)
S. (S.) macrocephalus	0.31(0.57)	0.29(0.57)	0.30(0.57)	0.31(0.57)
S. (S.) robustus jallae	0.08(1.04)	0.07(1.04)	0.06(1.02)	0.06(1.03)
S. (S.) thumbergi	0.72(2.66)	0.72(2.66)	0.72(2.63)	0.72(2.65)
Tilapia rendalli rendalli	3.64(2.37)	3.63(2.37)	3.64(2.34)	3.64(2.36)
T. ruweti	0.04(0.01)	0.04(0.01)	0.05(0.01)	0.04(0.01)
T. sparrmanii	10.76(6.09)	10.74(6.08)	10.77(6.00)	10.74(6.05)
Total no. species	47	47	47	47
Total no. specimens	5243	4460	8638	7865
Total mass (kg)	114	100	193	173

Appendix 4. Percentage number and mass (in parentheses) of fish collected from the Thamalakane River, Okavango Delta, between November 1983 and December 1986 and grouped according to four distinct flood levels.

Species	Sampling site			
	2 filling	2 high	2 receding	2 low
Mormyridae				
H. discorhynchus	0.16(0.07)	0.15(0.07)	0.16(0.07)	0.16(0.07)
Marcusenius macrolepidotus	2.41(2.82)	2.40(2.80)	2.42(2.84)	2.41(2.85)
Mormyrus lacerda	0.16(1.75)	0.15(1.73)	0.16(1.76)	0.16(1.77)
Petrocephalus catostoma	1.18(0.38)	1.18(0.38)	1.19(0.39)	1.18(0.39)
Pollimyrus castelnaui	0.28(0.06)	0.36(0.07)	0.03(0.01)	0.04(0.01)
Characidae				
Brycinus lateralis	5.72(0.70)	5.73(0.70)	5.76(0.71)	5.75(0.71)
Micralestes acutidens	0.26(0.03)	0.31(0.04)	0.01(<0.01)	0.01(<0.01)
Rhabdalestes maunensis	3.54(0.11)	3.53(0.11)	3.56(0.11)	3.56(0.11)
Hepsetidae				
Hepsetus odoe	1.88(9.39)	1.89(9.31)	1.89(9.46)	1.89(9.48)
Distichodontidae				
Hemigrammocharax machadoi	0.88(0.01)	0.87(0.01)	0.89(0.01)	0.89(0.01)
H. multifasciatus	0.07(0.01)	0.05(0.01)	0.06(0.01)	0.07(0.01)
Cyprinidae				
Barbus afrovernayi	2.04(0.08)	2.05(0.08)	2.05(0.08)	2.05(0.08)
B. barnardi	5.71(0.19)	5.70(0.19)	5.73(0.19)	5.73(0.20)
B. bifrenatus	1.27(0.12)	1.25(0.12)	1.26(0.12)	1.27(0.12)
B. eutaenia				
B. fasciolatus	1.04(0.05)	1.02(0.04)	1.04(0.05)	1.04(0.05)
B. haasianus	0.16(<0.01)	0.15(<0.01)	0.16(<0.01)	0.16(<0.01)
B. multilineatus	0.77(0.03)	0.77(0.03)	0.78(0.03)	0.77(0.01)
B. paludinosus	1.09(0.15)	1.10(0.15)	1.10(0.16)	1.09(0.16)
B. poechii	3.03(1.05)	3.04(1.04)	3.05(1.05)	3.05(1.06)
B. radiatus	2.96(0.26)	2.97(0.26)	2.97(0.27)	2.98(0.27)
B. thamalakanensis	3.94(0.13)	3.94(0.13)	3.96(0.14)	3.95(0.14)
B. unitaeniatus	2.29(0.51)	2.28(0.51)	2.30(0.51)	2.30(0.52)
Coptostomabarbus wittei	0.35(<0.01)	0.36(<0.01)	0.36(<0.01)	0.36(<0.01)
Bagridae				
Auchenoglanis ngamensis	0.02(0.10)		0.02(0.10)	0.02(0.10)
Zaireicthys chobensis		0.05(<0.01)		
Schilbeidae				
Schilbe mystus	4.53(15.18)	4.53(15.06)	4.55(15.30)	4.55(15.33)
Clariidae				
Clarias gariepinus	0.63(8.19)	0.64(8.13)	0.65(8.26)	0.65(8.28)
C. ngamensis	0.19(3.52)	0.20(3.50)	0.20(3.55)	0.20(3.56)
C. theodorae	0.16(0.05)	0.15(0.05)	0.15(0.05)	0.16(0.05)
Mochokidae				
Synodontis leopardinus	1.39(2.76)	1.38(2.74)	1.39(2.78)	1.39(2.79)
S. macrostigma	0.32(0.92)	0.31(0.91)	0.32(0.92)	0.32(0.93)
S. nigromaculatus	0.72(2.98)	0.72(3.82)	0.72(2.27)	0.72(2.09)
S. woosnami	0.39(1.12)	0.38(1.11)	0.38(1.13)	0.38(1.13)
Poeciliidae				
Aplocheilichthys hutereaui	0.09(<0.01)	0.08(<0.01)	0.09(<0.01)	0.09(<0.01)
A. johnstoni	7.22(0.11)	7.21(0.11)	7.25(0.11)	7.25(0.11)
A. katangae		0.03(<0.01)	0.01(<0.01)	0.01(<0.01)
Cichlidae				
Hemichromis elongatus			0.01(<0.01)	
Oreochromis andersonii	8.79(14.1)	8.77(13.99)	8.83(14.21)	8.82(14.24)
O. macrochir	4.54(6.44)	4.53(6.39)	4.56(6.49)	4.56(6.51)
Pharyngochromis darlingi	5.88(0.57)	5.86(0.57)	5.90(0.58)	5.90(0.58)
Pseudocrenilabrus philander	4.37(0.42)	4.37(0.42)	4.39(0.43)	4.39(0.43)
Serranochromis (Sargochromis) carlottae	0.56(2.04)	0.56(2.02)	0.57(2.05)	0.57(2.06)
S. (Sar.) codringtoni	1.04(1.59)	1.05(1.57)	1.05(1.60)	1.05(1.60)
S. (Sar.) giardi	0.28(1.77)	0.28(1.75)	0.27(1.78)	0.28(1.78)
S. (Sar.) greenwoodi	0.16(0.67)	0.15(0.67)	0.16(0.68)	0.16(0.68)
S. (Serranochromis) angusticeps	0.19(2.27)	0.20(2.25)	0.19(2.29)	0.19(2.29)
S. (S.) longimanus	0.04(0.09)	0.03(0.09)	0.04(0.09)	0.04(0.09)
S. (S.) macrocephalus	0.28(0.78)	0.28(0.78)	0.28(0.79)	0.29(0.79)
S. (S.) robustus jallae	0.07(1.51)	0.05(1.50)	0.06(1.52)	0.07(1.53)
S. (S.) thumbergi	0.86(2.67)	0.87(2.65)	0.87(2.69)	0.87(2.70)
Tilapia rendalli rendalli	4.74(5.61)	4.73(5.57)	4.76(5.66)	4.76(5.67)
T. ruweti	0.32(0.08)	0.31(0.08)	0.32(0.08)	0.32(0.08)
T. sparrmanii	11.02(6.54)	11.00(6.48)	11.07(6.59)	11.07(6.60)
Anabantidae				
C. multispinus			0.02(<0.01)	0.01(<0.01)
Afromastacembelidae				
Afromastacembelus frenatus			0.02(<0.01)	0.01(<0.01)
Total no. species	50	51	54	53
Total no. specimens	3748	2580	8165	8865
Total mass (kg)	144	208	154	99

Appendix 5. Percentage number and mass (in parentheses) of fish collected from the seasonal swamp, Okavango Delta, between November 1983 and December 1986 and grouped according to four distinct flood levels.

Species	3	3	3	3
	filling	high	receding	low
Mormyridae				
H. discorhynchus	0.15(0.00)	0.12(0.00)	0.14(0.00)	0.13(<0.01)
Marcusenius macrolepidotus	2.16(1.87)	2.14(1.94)	2.15(1.91)	2.15(2.06)
Mormyrus lacerda	0.15(1.43)	0.16(1.49)	0.15(1.46)	0.16(1.58)
Petrocephalus catostoma	1.57(0.38)	1.57(0.40)	1.58(0.39)	1.59(0.42)
Pollimyrus castelnaui	0.44(0.07)	0.41(0.07)	0.43(0.07)	0.42(0.07)
Characidae				
Brycinus lateralis	7.78(0.71)	7.79(0.74)	7.79(0.72)	7.80(0.78)
Hydrocynus vittatus		0.08(0.05)		
Micralestes acutidens	0.15(0.02)	0.16(0.02)	0.18(0.02)	0.13(0.02)
Rhabdalestes maunensis	1.28(0.03)	1.28(0.03)	1.29(0.03)	1.30(0.03)
Hepsetidae				
Hepsetus odoe	2.33(16.64)	2.31(17.27)	2.32(16.98)	2.32(18.33)
Distichodontidae				
Hemigrammocharax machadoi	0.70(0.01)	0.70(0.01)	0.70(0.01)	0.7(0.01)
H. multifasciatus	0.32(0.02)	0.29(0.02)	0.30(0.02)	0.31(0.02)
Cyprinidae				
Barbus afrovernayi	3.73(0.11)	3.71(0.12)	3.73(0.11)	3.74(0.12)
B. barnardi	5.68(0.15)	5.65(0.16)	5.68(0.16)	5,68(0.17)
B. bifrenatus	2.59(0.17)	2.60(0.18)	2.59(0.18)	2.59(0.19)
B. fasciolatus	0.52(0.02)	0.54(0.02)	0.54(0.02)	0.54(0.02)
B. haasianus	5.77(0.07)	5.77(0.07)	5.76(0.07)	5.78(0.08)
B. multilineatus	1.11(0.03)	1.11(0.03)	1.11(0.03)	1.10(0.03)
B. paludinosus	0.50(0.02)	0.49(0.02)	0.51(0.02)	0.51(0.02)
B. poechii	1.19(0.19)	1.20(0.20)	1.20(0.19)	1.20(0.21)
B. radiatus	1.28(0.04)	1.28(0.04)	1.29(0.04)	1.29(0.04)
B. thamalakanensis	6.73(0.19)	6.72(0.20)	6.73(0.19)	6.74(0.21)
B. unitaeniatus	0.09(0.01)	0.08(0.01)	0.08(0.01)	0.08(0.01)
Coptostomabarbus wittei	4.05(0.03)	4.04(0.04)	4.04(0.03)	4.05(0.04)
L. lunatus		0.04(0.26)	0.04(0.41)	0.01(0.13)
Bagridae				
Auchenoglanis ngamensis	0.26(0.32)	0.21(0.21)	0.22(0.12)	0.17(0.18)
Zaireicthys chobensis	0.23(0.01)	0.25(0.01)	0.25(0.01)	0.24(0.01)
Schilbeidae				
Schilbe mystus	6.65(14.01)	6.64(14.54)	6.63(14.30)	6.64(15.44)
Clariidae				
Clarias gariepinus	0.44(6.66)	0.45(6.91)	0.44(6.79)	0.44(7.33)
C. ngamensis	0.26(3.23)	0.29(3.35)	0.28(3.29)	0.28(3.56)
C. stappersi	0.03(0.01)	0.08(0.04)		
C. theodorae	0.12(0.04)	0.12(0.04)	0.12(0.04)	0.13(0.04)
Mochokidae				
Synodontis leopardinus	1.31(5.33)	1.32(4.27)	1.31(4.78)	1.32(2.98)
S. macrostigma	0.55(0.84)	0.54(0.87)	0.55(0.86)	0.55(0.93)
S. nigromaculatus	1.49(8.85)	1.48(6.01)	1.47(7.43)	1.47(2.52)
S. woosnami	0.58(0.91)	0.58(0.94)	0.59(0.93)	0.59(1.00)
Poeciliidae				
Aplocheilichthys hutereaui	2.36(0.02)	2.35(0.02)	2.37(0.02)	2.36(0.02)
A. johnstoni	12.01(0.16)	12.00(0.17)	12.01(0.17)	12.02(0.18)
A. katangae	0.20(<0.01)	0.21(<0.01)	0.21(<0.01)	0.20(<0.01)
Cichlidae				
Hemichromis elongatus	0.06(0.07)	0.08(0.08)	0.07(0.08)	0.07(0.08)
Oreochromis andersonii	4.72(9.39)	4.70(9.75)	4.72(9.59)	4.72(10.35)
O. macrochir	1.40(2.70)	1.40(2.81)	1.39(2.76)	1.39(2.98)
Pharyngochromis darlingi	1.92(0.17)	1.90(0.18)	1.91(0.18)	1.91(0.19)
Pseudocrenilabrus philander	1.87(0.10)	1.86(0.10)	1.87(0.10	1.87(0.11)
Serranochromis (Sargochromis) carlottae	0.17(0.70)	0.16(0.72)	0.17(0.71)	0.17(0.77)
S. (Sar.) codringtoni	1.40(1.71)	1.40(1.78)	1.40(1.75)	1.40(1.89)
S. (Sar.) giardi	0.52(2.42)	0.54(2.51)	0.52(2.47)	0.52(2.66)
S. (Sar.) greenwoodi	0.09(0.29)	0.08(0.30)	0.07(0.29)	0.07(0.32)
S. (Serranochromis) angusticeps	0.93(7.54)	0.95(7.82)	0.95(7.69)	0.95(8.30)
S. (S.) longimanus	0.12(0.24)	0.12(0.25)	0.12(0.25)	0.11(0.27)
S. (S.) macrocephalus	0.29(0.57)	0.29(0.59)	0.30(0.58)	0.30(0.63)
S. (S.) robustus jallae	0.15(3.33)	0.16(3.46)	0.15(3.40)	0.16(3.67)
S. (S.) thumbergi	0.26(0.95)	0.25(0.98)	0.26(0.97	0.25(1.04)
Tilapia rendalli rendalli	1.72(2.54)	1.73(2.64)	1.73(2.5)	1.74(2.80)
T. ruweti	1.05(0.10)	1.03(0.11)	1.03(011)	1.05(0.11)
T. sparrmanii	6.35(4.50)	6.35(4.67)	6.35(4.0)	6.36(4.96)
Anabantidae				
Ctenopoma intermedium	0.06(<0.01)	0.08(<0.01)	0.07(<0.01)	0.07(0.01)
C. multispinus	0.06(0.02)	0.04(0.02)	0.06(0.02)	0.06(0.02)
Afromastacembelidae				
Afromastacembelus frenatus	0.09(0.01)	0.08(0.01)	0.08(0.01)	0.07(0.01)
Total no. species	57	59	57	57
Total no. specimens	3431	2425	7270	7062
Total mass (kg)	83	57	173	168

Appendix 6. Percentage number and mass (in parentheses) of fish collected from the perennial swamp, Okavango Delta, between November 1983 and December 1986 and grouped according to four distinct different flood levels.

Species	Sampling site 4 filling	 4 high	 4 receding	 4 low
Mormyridae				
Hippopotamyrus ansorgii			0.03(0.01)	0.03(<0.01)
H. discorhynchus	0.09(0.03)	0.11(0.03)	0.10(0.03)	0.08(0.04)
Marcusenius macrolepidotus	4.76(2.92)	4.73(3.06)	4.58(2.86)	4.58(2.90)
Mormyrus lacerda	0.09(0.61)	0.08(0.64)	0.04(0.60)	0.06(0.61)
Petrocephalus catostoma	3.74(0.47)	3.73(0.49)	3.61(0.46)	3.58(0.46)
Pollimyrus castelnaui	2.65(0.16)	2.63(0.17)	2.54(0.16)	2.56(0.16)
Characidae				
Brycinus lateralis	7.47(0.97)	7.46(1.01)	7.18(0.95)	7.20(0.96)
Hydrocynus vittatus	7.18(31.86)	7.07(31.03)	5.64(26.02)	5.70(26.92)
Micralestes acutidens	6.56(0.26)	6.51(0.27)	6.28(0.25)	6.30(0.25)
Rhabdalestes maunensis	1.91(0.02)	1.92(0.02)	1.84(0.02)	1.86(0.02)
Hepsetidae				
Hepsetus odoe	0.29(1.19)	0.29(1.25)	0.28(1.17)	0.29(1.18)
Distichodontidae				
Hemigrammocharax machadoi	6.59(0.05)	6.57(0.05)	6.35(0.05)	6.34(0.05)
H. multifasciatus	1.59(0.04)	1.58(0.04)	1.54(0.04)	1.54(0.04)
Cyprinidae				
Barbus afrovernayi	0.94(0.01)	0.95(0.01)	0.90(0.01)	0.90(0.01)
B. barnardi	2.06(0.02)	2.05(0.03)	1.97(0.02)	1.98(0.02)
B. bifrenatus	1.06(0.04)	1.08(0.04)	1.04(0.04)	1.02(0.04)
B. eutaenia	0.07(<0.01)	0.12(<0.01)	0.10(<0.01)	0.10(<0.01)
B. fasciolatus	1.88(0.03)	1.89(0.03)	1.84(0.03)	1.82(0.03)
B. haasianus	3.15(0.01)	3.13(0.01)	3.04(0.01)	3.04(0.01)
B. multilineatus	0.41(<0.01)	0.39(<0.01)	0.40(<0.01)	0.38(<0.01)
B. paludinosus	0.12(<0.01)	0.11(<0.01)	0.08(<0.01)	0.15(<0.01)
B. poechii	1.47(0.11)	1.47(0.12)	1.40(0.11)	1.41(0.11)
B. radiatus	2.59(0.06)	2.57(0.06)	2.47(0.06)	2.50(0.06)
B. thamalakanensis	2.32(0.03)	2.31(0.03)	2.24(0.03)	2.24(0.03)
B. unitaeniatus	0.21(0.01)	0.21(0.01)	0.20(0.01)	0.19(0.01)
Coptostomabarbus wittei	0.88(0.01)	0.87(0.01)	0.83(<0.01)	0.83(<0.01)
Labeo cylindricus	0.02(0.01)	0.11(0.01)	0.07(0.01)	0.03(<0.01)
L. lunatus	0.09(0.26)	0.11(0.28)	0.08(0.26)	0.10(0.26)
Opsaridium zambezensis	0.02(<0.01)	0.02(<0.01)		
Bagridae				
Auchenoglanis ngamensis	0.12(0.05)	0.11(0.06)	0.10(0.05)	0.10(0.05)
Zaireichthys chobensis	0.03(<0.01)	0.03(<0.01)	0.01(<0.01)	0.01(<0.01)
Schilbeidae				
Schilbe mystus	5.00(6.79)	4.99(7.10)	4.81(6.64)	4.83(6.72)
Clariidae				
Clarias gariepinus	3.06(18.68)	3.26(19.67)	1.70(10.80)	1.41(9.15)
C. ngamensis	1.24(7.45)	1.21(7.21)	0.57(3.55)	0.58(3.70)
C. stappersi	0.09(0.05)	0.03(0.01)	0.07(0.04)	0.04(0.05)
C. theodorae	0.18(0.02)	0.19(0.02)	0.17(0.02)	0.16(0.02)
Mochokidae				
Synodontis leopardinus	1.29(0.51)	1.29(0.54)	1.24(0.50)	1.25(0.51)
S. macrostigma	1.85(1.51)	1.84(1.58)	1.77(1.48)	1.79(1.50)
S. nigromaculatus	2.74(4.05)	2.73(2.92)	2.64(4.21)	2.66(3.90)
S. woosnami	0.97(0.86)	0.95(0.90)	0.94(0.84)	0.93(0.85)
Poeciliidae				
Aplocheilichthys hutereaui	0.35(<0.01)	0.34(<0.01)	0.33(<0.01)	0.32(<0.01)
A. johnstoni	7.38(0.04)	7.35(0.04)	7.11(0.04)	7.10(0.04)
A. katangae	0.12(<0.01)	0.13(<0.01)	0.10(<0.01)	0.13(<0.01)
Cichlidae				
Hemichromis elongatus	0.15(0.09)	0.16(0.09)	0.17(0.09)	0.19(0.09)
Oreochromis andersonii	2.32(5.00)	2.42(5.14)	4.68(10.44)	4.64(10.28)
O. macrochir	0.56(1.23)	0.55(1.20)	0.90(2.06)	0.99(2.32)
Pharyngochromis darlingi	1.76(0.11)	1.76(0.11)	1.70(0.10)	1.70(0.10)
Pseudocrenilabrus philander	3.59(0.19)	3.60(0.19)	3.47(0.18)	3.46(0.18)
Serranochromis (Sargochromis) carlottae	0.29(0.83)	0.32(0.88)	0.60(1.76)	0.58(1.74)
S. (Sar.) codringtoni	0.26(0.46)	0.26(0.48)	0.24(0.45)	0.26(0.45)
S. (Sar.) giardi	0.12(0.58)	0.13(0.64)	0.33(1.71)	0.38(2.02)
S. (Sar.) greenwoodi	0.03(0.08)		0.03(0.08)	0.03(0.08)
S. (Serranochromis) angusticeps	1.41(6.27)	1.47(6.47)	2.61(12.02)	2.56(12.11)
S. (S.) longimanus	0.03(0.04)	0.01(<0.01)	0.04(0.03)	0.04(0.03)
S. (S.) macrocephalus	0.18(0.49)	0.16(0.52)	0.17(0.48)	0.16(0.49)
S. (S.) robustus jallae	0.94(2.93)	0.97(2.99)	1.50(4.85)	1.50(4.98)
S. (S.) thumbergi	0.06(0.15)	0.03(0.16)	0.03(0.15)	0.03(0.15)
Tilapia rendalli rendalli	0.44(0.78)	0.45(0.78)	1.04(1.9)	1.02(1.93)
T. ruweti	0.07(0.01)	0.08(0.01)	0.07(0.01)	0.06(0.01)
T. sparrmanii	2.80(1.55)	2.84(1.56)	3.87(2.28)	3.92(2.32)
Anabantidae				
Ctenopoma intermedium	0.09(<0.01)	0.08(<0.01)	0.07(<0.01)	0.06(<0.01)
C. multispinus				0.06(,0.01)
Afromastacembelidae				
Afromastacembelus frenatus	0.26(0.03)	0.26(0.04)	0.27(0.03)	0.26(0.03)
Total no. species	61	60	60	61
Total no. specimens	2890	3236	2545	2656
Total mass (kg)	156	176	132	135

Appendix 7. Percentage number and mass (in parentheses) of fish collected from perennial swamp floodplain-connected lagoons, Okavango Delta, between November 1983 and December 1986 and grouped according to four distinct flood levels.

Species	Sampling site 5 filling	 5 high	 5 receding	 5 low
Mormyridae				
H. discorhynchus	0.02(<0.01)	0.02(<0.01)	0.02(<0.01)	0.02(<0.01)
Marcusenius macrolepidotus	3.77(2.79)	3.75(2.89)	3.81(3.07)	3.79(2.95)
Mormyrus lacerda	0.19(0.61)	0.18(0.63)	0.18(0.67)	0.19(0.65)
Petrocephalus catostoma	2.35(0.36)	2.34(0.37)	2.37(0.39)	2.36(0.38)
Pollimyrus castelnaui	1.92(0.21)	1.94(0.22)	1.94(0.23)	1.94(0.22)
Characidae				
Brycinus lateralis	5.85(0.32)	5.82(0.33)	5.90(0.36)	5.89(0.34)
Hydrocynus vittatus	5.23(14.15)	5.47(14.66)	2.49(7.13)	2.45(6.97)
Micralestes acutidens	2.81(0.13)	2.82(0.13)	2.83(0.14)	2.83(0.14)
Rhabdalestes maunensis	1.73(0.02)	1.72(0.02)	1.75(0.03)	1.75(0.03)
Hepsetidae				
Hepsetus odoe	0.62(3.73)	0.62(3.85)	0.65(4.10)	0.64(3.93)
Distichodontidae				
Hemigrammocharax machadoi	3.31(0.02)	3.31(0.03)	3.32(0.03)	3.34(0.03)
H. multifasciatus	0.96(0.03)	0.97(0.03)	0.98(0.03)	0.99(0.03)
Cyprinidae				
Barbus afrovernayi	0.77(0.02)	0.79(0.02)	0.80(0.02)	0.80(0.02)
B. barnardi	1.54(0.04)	1.54(0.04)	1.54(0.04)	1.53(0.04)
B. bifrenatus	0.62(0.02)	0.62(0.02)	0.61(0.03)	0.64(0.02)
B. eutaenia	0.04(<0.01)	0.04(<0.01)	0.03(<0.01)	0.03(<0.01)
B. fasciolatus	2.77(0.07)	2.78(0.07)	2.80(0.08)	2.80(0.07)
B. haasianus	10.74(0.11)	10.72(0.11)	10.82(0.12)	10.82(0.12)
B. multilineatus	0.19(<0.01)	0.18(<0.01)	0.18(<0.01)	0.19(<0.01)
B. paludinosus	2.04(0.04)	2.03(0.04)	2.06(0.04)	2.07(0.04)
B. poechii	0.85(0.08)	0.88(0.09)	0.86(0.09)	0.86(0.09)
B. radiatus	2.85(0.10)	2.87(0.10)	2.89(0.11)	2.86(0.10)
B. thamalakanensis	2.93(0.04)	2.91(0.05)	2.92(0.05)	2.93(0.05)
B. unitaeniatus	0.31(0.03)	0.31(0.04)	0.34(0.04)	0.32(0.04)
Coptostomabarbus wittei	4.35(0.02)	4.37(0.02]	4.39(0.02)	4.39(0.02)
Labeo cylindricus	0.01(<0.01)	0.01(<0.01)	0.01(<0.01)	0.01(<0.01)
L. lunatus	0.31(10.40)	0.31(8.76)	0.31(10.42)	0.32(12.65)
Bagridae				
Auchenoglanis ngamensis		0.02(0.01)	0.02(0.01)	0.02(0.01)
Zaireicthys chobensis	0.08(<0.01)	0.09(<0.01)		
Schilbeidae				
Schilbe mystus	4.23(6.63)	4.19(6.85)	4.24(7.29)	4.26(7.00)
Clariidae				
Clarias gariepinus	1.66(14.73)	1.72(15.18)	0.98(9.27)	0.99(9.24)
C. ngamensis	0.54(7.16)	0.62(8.14)	0.18(2.60)	0.16(2.23)
C. stappersi	0.01(0.15)			
C. theodorae	0.12(0.02)	0.13(0.02)	0.12(0.03)	0.13(0.02)
Mochokidae				
Synodontis leopardinus	0.46(0.46)	0.44(0.47)	0.46(0.51)	0.48(0.48)
S. macrostigma	0.62(0.55)	0.62(0.57)	0.61(0.60)	0.60(0.58)
S. nigromaculatus	2.19(3.25)	2.21(3.77)	2.21(3.79)	2.23(3.10)
S. woosnami	0.65(0.36)	0.62(0.37)	0.65(0.40)	0.64(0.38)
Poeciliidae				
Aplocheilichthys hutereaui	1.27(0.01)	1.28(0.01)	1.29(0.01)	1.30(0.01)
A. johnstoni	7.16(0.03)	7.10(0.03)	7.19(0.04)	7.19(0.03)
A. katangae	0.23(<0.01)	0.22(<0.01)	0.25(<0.01)	0.22(<0.01)
Cichlidae				
Hemichromis elongatus	0.23(0.08)	0.22(0.08)	0.25(0.09)	0.25(0.09)
Oreochromis andersonii	2.23(9.94)	2.12(9.35)	3.63(17.11)	3.66(17.15)
O. macrochir	0.81(3.92)	0.75(3.60)	1.14(5.84)	1.15(5.84)
Pharyngochromis darlingi	1.35(0.07)	1.37(0.07)	1.38(0.07)	1.37(0.08)
Pseudocrenilabrus philander	6.24(0.17)	6.22(0.18)	6.27(0.19)	6.27(0.18)
Serranochromis (Sargochromis) carlottae	0.35(0.85)	0.35(0.87)	0.37(0.93)	0.35(0.89)
S. (Sar.) codringtoni	0.62(1.19)	0.62(1.23)	0.61(1.30)	0.60(1.25)
S. (Sar.) giardi	0.35(1.65)	0.35(1.70)	0.34(1.81)	0.35(1.74)
S. (Sar.) greenwoodi	0.08(0.18)	0.09(0.18)	0.09(0.19)	0.10(0.19)
S. (Serranochromis) angusticeps	2.04(9.27)	1.94(8.75)	2.74(13.17)	2.74(13.09)
S. (S.) longimanus	0.03(0.12)		0.03(0.16)	0.03(0.15)
S. (S.) macrocephalus	0.23(0.75)	0.22(0.78)	0.25(0.83)	0.22(0.79)
S. (S.) robustus jallae	0.38(1.32)	0.35(1.37)	0.37(1.45)	0.38(1.40)
S. (S.) thumbergi	0.08(0.31)	0.09(0.32)	0.06(0.34)	0.06(0.32)
Tilapia rendalli rendalli	2.27(2.53)	2.21(2.43)	2.98(3.51	2.99(3.50)
T. ruweti	1.04(0.18)	1.06(0.18)	1.04(0.9)	1.05(0.19)
T. sparrmanii	3.23(0.89)	3.22(0.92)	3.26(0.9)	3.25(0.93)
Anabantidae				
Ctenopoma intermedium	0.04(<0.01)	0.04(<0.01)	0.06(<0.01)	0.06(<0.01)
C. multispinus		0.04(0.01)		
Afromastacembelidae				
Afromastacembelus frenatus	0.12(0.02)	0.13(0.02)	0.12(0.02)	0.13(0.02)
Total no. species	59	59	58	58
Total no. specimens	2598	2267	3254	3142
Total mass (kg)	94	82	111	107

Appendix 8. Percentage number and mass (in parentheses) of fish collected from the perennial swamp rain pools, Okavango Delta, between November 1983 and December 1986 and grouped according to four distinct flood levels.

	Sampling site			
Species	6 filling	6 high	6 receding	6 low
Mormyridae				
Marcusenius macrolepidotus	0.04(0.07)	0.04(0.07)	0.03(0.07)	0.03(0.07)
Characidae				
Brycinus lateralis	0.63(0.17)	0.61(0.17)	0.62(0.17)	0.63(0.17)
Rhabdalestes maunensis	0.29(0.01)	0.29(0.01)	0.27(0.01)	0.28(0.17)
Hepsetidae				
Hepsetus odoe	0.11(1.57)	0.14(1.57)	0.14(1.57)	0.13(1.57)
Cyprinidae				
B. barnardi	1.36(0.07)	1.37(0.07)	1.38(0.07)	1.39(0.07)
B. bifrenatus	2.72(0.35)	2.71(0.35)	2.72(0.35)	2.71(0.35)
B. multilineatus	0.18(0.01)	0.18(0.01)	0.19(0.01)	0.19(0.01)
B. paludinosus	16.89(4.15)	16.87(4.15)	16.89(4.15)	16.88(4.15)
B. poechii	1.10(0.40)	1.12(0.40)	1.11(0.40)	1.10(0.40)
B. radiatus	0.77(0.21)	0.76(0.21)	0.76(0.21)	0.76(0.21)
B. thamalakenensis	6.26(0.44)	6.25(0.44)	6.24(0.44)	6.27(0.44)
Coptostomabarbus wittei	0.37(0.02)	0.40(0.02)	0.38(0.02)	0.38(0.02)
Schilbeidae				
Schilbe mystus	0.37(1.21)	0.36(1.21)	0.35(1.21)	0.35(1.21)
Clariidae				
Clarias gariepinus	2.83(8.88)	2.82(8.88)	2.82(8.88)	2.83(8.88)
C. ngamensis	0.26(3.46)	0.29(3.46)	0.27(3.46)	0.28(3.46)
Poeciliidae				
Aplocheilichthys hutereaui	0.37(0.01)	0.36(0.01)	0.35(0.01)	0.38(0.01)
A. johnstoni	2.50(0.14)	2.49(0.14)	2.50(0.14)	2.49(0.14)
Cichlidae				
Oreochromis andersonii	26.90(37.47)	26.91(37.47)	26.91(37.47)	26.89(37.47)
O. macrochir	6.37(14.07)	6.36(14.07)	6.38(14.07)	6.39(14.07)
Pharyngochromis darlingi	2.28(0.28)	2.31(0.28)	2.31(0.28)	2.30(0.28)
Pseudocrenilabrus philander	8.24(1.38)	8.24(1.38)	8.23(1.38)	8.25(1.38)
S. (Sar.) codringtoni	0.29(1.15)	0.29(1.15)	0.30(1.15)	0.28(1.15)
S. (Serranochromis) angusticeps	0.15(0.64)	0.14(0.64)	0.16(0.64)	0.16(0.64)
S. (S.) macrocephalus			0.01(<0.01)	0.01(<0.01)
S. (S.) thumbergi	0.11(0.76)	0.11(0.76)	0.11(0.76)	0.13(0.76)
Tilapia rendalli rendalli	10.78(17.26)	10.77(17.26)	10.78(17.26)	10.77(17.26)
T. ruweti	2.72(1.07)	2.71(1.07)	2.72(1.07)	2.71(1.07)
T. sparrmanii	4.71(4.35)	4.70(4.35)	4.70(4.35)	4.69(4.35)
Anabantidae				
C. multispinus	0.37(0.41)	0.40(0.41)	0.38(0.41)	0.38(0.41)
Total no. species	28	28	29	29
Total no. specimens	2717	2768	3683	3176
Total mass (kg)	22	23	31	26

Appendix 9. Percentage number and mass (in parentheses) of fish collected from the riverine floodplain mainstream, Okavango Delta, between April 1985 and December 1986 and grouped according to four distinct flood levels.

Species	Sampling site			
	7 filling	7 high	7 receding	7 low
Mormyridae				
Hippopotamyrus ansorgii		0.14(<0.01)	0.03(<0.01)	0.08(<0.01)
H. discorhynchus	0.05(<0.01)	0.14(0.01)	0.13(0.01)	0.14(0.01)
Marcusenius macrolepidotus	8.53(2.26)	8.44(2.27)	8.52(2.25)	8.48(3.15)
Mormyrus lacerda	0.16(0.75)	0.14(0.75)	0.16(0.75)	0.14(0.75)
Petrocephalus catostoma	3.58(0.37)	3.57(0.38)	3.55(0.37)	3.53(0.37)
Pollimyrus castelnaui	2.58(0.14)	2.61(0.15)	2.61(0.14)	2.60(0.13)
Characidae				
Brycinus lateralis	5.16(0.64)	5.14(0.65)	5.16(0.64)	5.14(0.57)
Hydrocynus vittatus	4.95(30.89)	4.94(31.09)	4.94(30.79)	4.92(27.22)
Micralestes acutidens	4.26(0.20)	4.18(0.20)	4.25(0.19)	4.21(0.17)
Rhabdalestes maunensis	3.21(0.05)	3.22(0.05)	3.21(0.05)	3.19(0.04)
Hepsetidae				
Hepsetus odoe	0.26(1.03)	0.27(1.03)	0.28(1.02)	0.28(0.90)
Distichodontidae				
Hemigrammocharax machadoi	8.05(0.04)	8.02(0.04)	8.05(0.04)	8.02(0.04)
H. multifasciatus	2.42(0.08)	2.40(0.08)	2.42(0.08)	2.40(0.07)
Nannocharax macropterus	0.03(<0.01)	0.27(<0.01)	0.03(<0.01)	0.03(<0.01)
Cyprinidae				
Barbus afrovernayi	1.58(0.02)	1.58(0.02)	1.60(0.02)	1.58(0.02)
B. barnardi	2.42(0.03)	2.40(0.03)	2.42(0.03)	2.43(0.03)
B. bifrenatus	0.79(0.02)	0.82(0.02)	0.79(0.02)	0.79(0.02)
B. eutaenia	0.47(0.01)	0.48(0.01)	0.47(0.01)	0.45(0.01)
B. fasciolatus	3.32(0.04)	3.29(0.04)	3.30(0.04)	3.31(0.04)
B. haasianus	1.89(0.01)	1.85(0.01)	1.89(0.01)	1.86(0.01)
B. multilineatus	1.32(0.01)	1.30(0.01)	1.32(0.01)	1.30(0.01)
B. paludinosus	0.32(0.01)	0.27(0.01)	0.28(0.01)	0.28(<0.01)
B. poechii	0.84(0.07)	0.82(0.07)	0.85(0.07)	0.85(0.06)
B. radiatus	1.42(0.04)	1.37(0.04)	1.42(0.04)	1.41(0.04)
B. tangendensis	0.05(<0.01)	0.14(<0.01)	0.06(<0.01)	0.03(<0.01)
B. thamalakenensis	2.26(0.03)	2.26(0.03)	2.26(0.03)	2.23(0.03)
B. unitaeniatus	0.05(<0.01)	0.07(<0.01)	0.06(<0.01)	0.08(<0.01)
Coptostomabarbus wittei	1.58(0.01)	1.58(0.01)	1.57(0.01)	1.58(0.01)
Labeo cylindricus	0.02(<0.01)	0.21(0.01)	0.06(<0.01)	0.20(0.01)
L. lunatus	0.11(1.08)	0.07(1.09)	0.09(1.08)	0.11(0.95)
Opsaridium zambezensis	0.05(<0.01)	0.02(<0.01)	0.02(<0.01)	0.02(<0.01)
Bagridae				
Auchenoglanis ngamensis	0.11(0.05)	0.27(0.13)	0.16(0.07)	0.23(0.11)
Zaireicthys chobensis	0.08(<0.01)	0.08(<0.01)	0.06(<0.01)	0.08(<0.01)
Schilbeidae				
Schilbe mystus	4.37(6.41)	4.32(6.45)	4.37(6.39)	4.35(5.65)
Clariidae				
Clarias gariepinus	3.53(11.88)	3.50(10.38)	3.55(12.46)	3.53(21.78)
C. ngamensis	0.84(4.16)	0.82(4.18)	0.82(4.14)	0.82(3.66)
C. stappersi	0.05(0.08)	0.07(0.08)	0.06(0.07)	0.06(0.07)
C. theodorae	0.26(0.04)	0.27(0.04)	0.28(0.04)	0.28(0.04)
Mochokidae				
Chiloglanis fasciatus	0.05(<0.01)	0.07(<0.01)	0.06(<0.01)	0.06(<0.01)
Synodontis leopardinus	0.37(0.33)	0.34(0.33)	0.35(0.33)	0.37(0.29)
S. macrostigma	1.53(0.98)	1.58(0.99)	1.54(0.98)	1.53(0.86)
S. nigromaculatus	3.32(4.61)	3.29(5.43)	3.33(4.29)	3.31(3.39)
S. woosnami	0.84(0.87)	0.82(0.95)	0.85(0.87)	0.85(0.77)
Poeciliidae				
Aplocheilichthys hutereaui	0.47(<0.01)	0.48(<0.01)	0.44(<0.01)	0.45(<0.01)
A. johnstoni	3.21(0.01)	3.16(0.01)	3.21(0.01)	3.19(0.01)
A. katangae	0.42(<0.01)	0.41(<0.01)	0.41(<0.01)	0.42(<0.01)
Cichlidae				
Hemichromis elongatus	0.26(0.11)	0.27(0.11)	0.25(0.11)	0.25(0.10)
Oreochromis andersonii	3.79(9.07)	3.77(9.13)	3.81(9.04)	3.79(7.99)
O. macrochir	0.89(2.79)	0.89(2.81)	0.91(2.79)	0.90(2.46)
Pharyngochromis darlingi	1.00(0.05)	1.03(0.05)	1.01(0.05)	1.02(0.04)
Pseudocrenilabrus philander	2.79(0.15)	2.74(0.15)	2.77(0.15)	2.77(0.13)
Serranochromis (Sargochromis) carlottae	0.53(1.28)	0.48(1.29)	0.50(1.27)	0.51(1.13)
S. (Sar.) codringtoni	0.37(0.57)	0.34(0.58)	0.35(0.57)	0.37(0.51)
S. (Sar.) giardi	0.37(1.44)	0.34(1.45)	0.35(1.43)	0.34(1.27)
S. (Sar.) greenwoodi	0.11(0.21)	0.07(0.21)	0.09(0.21)	0.08(0.19)
S. (Serranochromis) angusticeps	2.47(11.07)	2.47(11.14)	2.45(11.03)	2.43(9.75)
S. (S.) longimanus	0.05(0.08)	0.04(0.09)	0.03(0.08)	0.03(0.07)
S. (S.) macrocephalus	0.37(0.68)	0.34(0.69)	0.38(0.68)	0.37(0.60)
S. (S.) robustus jallae	1.05(2.55)	1.03(2.57)	1.04(2.54)	1.02(2.25)
S. (S.) thumbergi	0.11(0.31)	0.07(0.32)	0.09(0.31)	0.11(0.28)
Tilapia rendalli rendalli	0.63(1.19)	0.62(1.20)	0.63(1.19)	0.62(1.05)
T. ruweti	0.03(<0.01)	0.03(<0.01)	0.03(<0.01)	0.03(<0.01)
T. sparrmanii	3.37(1.12)	3.36(1.13)	3.36(1.12)	3.33(0.99)
Anabantidae				
Ctenopoma intermedium	0.42(0.01)	0.41(0.01)	0.41(0.01)	0.42(0.01)
C. multispinus	0.05(<0.01)	0.07(<0.01)	0.06(<0.01)	0.20(0.01)
Afromastacembelidae				
Afromastacembelus frenatus	0.16(0.02)	0.14(0.02)	0.16(0.02)	0.17(0.02)
Total no. species	65	66	66	66
Total no. specimens	1900	1458	3180	3539
Total mass (kg)	123	93	205	228

Appendix 10. Percentage number and mass (in parentheses) of fish collected from the riverine floodplain-connected lagoons, Okavango Delta, between April 1985 and December 1986 and grouped according to four distinct flood levels.

Species	Sampling site			
	8 filling	8 high	8 receding	8 low
Mormyridae				
H. discorhynchus	0.03(<0.01)	0.01(<0.01)	0.02(<0.01)	0.08(0.01)
Marcusenius macrolepidotus	2.70(1.42)	2.69(1.43)	2.61(1.36)	2.57(1.31)
Mormyrus lacerda	0.10(0.63)	0.10(0.63)	0.10(0.60)	0.10(0.58)
Petrocephalus catostoma	2.70(0.51)	2.69(0.51)	2.61(0.49)	2.57(0.47)
Pollimyrus castelnaui	1.61(0.13)	1.61(0.13)	1.56(0.12)	1.53(0.12)
Characidae				
Brycinus lateralis	6.30(0.52)	6.28(0.52)	6.09(0.50)	5.99(0.48)
Hydrocynus vittatus	2.47(17.31)	2.38(16.89)	1.88(13.15)	1.70(11.62)
Micralestes acutidens	1.53(0.09)	1.53(0.09)	1.48(0.09)	1.46(0.08)
Rhabdalestes maunensis	2.04(0.06)	2.03(0.06)	1.97(0.06)	1.94(0.06)
Hepsetidae				
Hepsetus odoe	0.36(1.89)	0.44(2.34)	0.83(4,31)	0.97(4.90)
Distichodontidae				
Hemigrammocharax machadoi	2.93(0.02)	2.92(0.02)	2.83(0.02)	2.79(0.02)
H. multifasciatus	0.71(0.03)	0.70(0.03)	0.68(0.02)	0.67(0.02)
Cyprinidae				
Barbus afrovernayi	4.87(0.11)	4.86(0.11)	4.71(0.11)	4.64(0.10)
B. barnardi	3.95(0.07)	3.94(0.07)	3.82(0.07)	3.76(0.07)
B. bifrenatus	1.94(0.06)	1.93(0.06)	1.87(0.06)	1.85(0.05)
B. eutaenia	0.01(<0.01)		0.01(<0.01)	0.01(<0.01)
B. fasciolatus	3.59(0.08)	3.58(0.08)	3.48(0.08)	3.42(0.08)
B. haasianus	5.45(0.06)	5.44(0.06)	5.27(0.06)	5.19(0.05)
B. multilineatus	0.93(0.01)	0.93(0.01)	0.90(0.01)	0.89(0.01)
B. paludinosus	0.58(0.01)	0.58(0.01)	0.56(0.01)	0.55(0.01)
B. poechii	1.35(0.19)	1.34(0.19)	1.30(0.18)	1.28(0.18)
B. radiatus	1.30(0.03)	1.30(0.03)	1.26(0.03)	1.24(0.03)
B. thamalakenensis	2.13(0.04)	2.12(0.04)	2.06(0.04)	2.03(0.04)
B. unitaeniatus	0.24(0.02)	0.24(0.02)	0.23(0.02)	0.23(0.02)
Coptostomabarbus wittei	2.65(0.02)	2.64(0.02)	2.56(0.02)	2.52(0.02)
L. lunatus	0.08(0.85)	0.04(0.40)	0.02(0.15)	0.08(0.44)
Bagridae				
Auchenoglanis ngamensis	0.01(<0.01)	0.02(0.02)	0.01(<0.01)	0.08(0.04)
Zaireicthys chobensis	0.03(<0.01)	0.01(<0.01)	0.01(<0.01)	0.01(<0.01)
Schilbeidae				
Schilbe mystus	3.03(6.28)	3.02(6.32)	2.93(6.02)	2.88(5.80)
Clariidae				
Clarias gariepinus	2.39(18.69)	2.29(18.13)	1.81(14.09)	1.62(12.37)
C. ngamensis	1.20(8.03)	0.94(6.36)	0.66(4.42)	0.89(5.83)
C. stappersi	0.05(0.08)	0.05(0.08)	0.05(0.08)	0.05(0.07)
C. theodorae	0.16(0.03)	0.16(0.03)	0.15(0.03)	0.15(0.03)
Mochokidae				
Synodontis leopardinus	0.39(0.65)	0.39(0.66)	0.38(0.63)	0.37(0.60)
S. macrostigma	0.45(0.68)	0.45(0.68)	0.44(0.65)	0.43(0.63)
S. nigromaculatus	1.45(3.68)	1.45(3.70)	1.41(3.53)	1.38(3.40)
S. woosnami	0.25(0.32)	0.24(0.58)	0.24(0.91)	0.23(0.76)
Poeciliidae				
Aplocheilichthys hutereaui	2.81(0.02)	2.81(0.02)	2.72(0.02)	2.68(0.02)
A. johnstoni	8.93(0.08)	8.90(0.08)	8.63(0.07)	8.50(0.07)
A. katangae	0.23(<0.01)	0.23(<0.01)	0.23(<0.01)	0.22(<0.01)
Cichlidae				
Hemichromis elongatus	0.73(0.94)	0.73(0.95)	0.71(0.90)	0.70(0.87)
Oreochromis andersonii	4.06(10.41)	4.37(11.35)	5.92(15.13)	6.42(16.05)
O. macrochir	1.17(6.75)	1.28(6.79)	1.86(6.47)	2.05(6.23)
Pharyngochromis darlingi	4.16(0.20)	4.15(0.20)	4.02(0.19)	3.96(0.18)
Pseudocrenilabrus philander	4.60(0.37)	4.58(0.37)	4.44(0.35)	4.37(0.34)
Serranochromis (Sargochromis) carlottae	0.49(1.65)	0.49(1.66)	0.47(1.58)	0.47(1.52)
S. (Sar.) codringtoni	0.73(1.73)	0.731.74)	0.71(1.66)	0.70(1.60)
S. (Sar.) giardi	0.28(0.95)	0.28(0.96)	0.27(0.91)	0.26(0.88)
S. (Sar.) greenwoodi	0.15(0.22)	0.15(0.22)	0.15(0.21)	0.14(0.21)
S. (Serranochromis) angusticeps	1.30(6.22)	1.40(6.80)	1.98(9.45)	2.16(10.11)
S. (S.) longimanus	0.10(0.29)	0.10(0.29)	0.10(0.28)	0.10(0.27)
S. (S.) macrocephalus	0.32(0.82)	0.32(0.82)	0.31(0.78)	0.31(0.75)
S. (S.) robustus jallae	0.23(1.12)	0.32(1.56)	0.73(3.51)	0.85(3.99)
S. (S.) thumbergi	0.20(0.82)	0.19(0.83)	0.19(0.79)	0.19(0.76)
Tilapia rendalli rendalli	1.20(2.74)	1.28(2.96)	1.66(3.79)	1.78(3.97)
T. ruweti	0.48(0.13)	0.48(0.13)	0.47(0.12)	0.46(0.12)
T. sparrmanii	5.61(1.90)	5.59(1.91)	5.40(1.82)	5.30(1.75)
Anabantidae				
Ctenopoma intermedium	0.07(<0.01)	0.07(<0.01)	0.07(<0.01)	0.07(<0.01)
C. multispinus	0.13(0.02)	0.13(0.02)	0.12(0.02)	0.12(0.02)
Afromastacembelidae				
Afromastacembelus frenatus	0.05(0.01)	0.05(0.01)	0.05(<0.01)	0.05(<0.01)
Total no. species	60	59	60	60
Total no. specimens	3844	5623	4091	2587
Total mass (kg)	144	208	154	99