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GROWTH, MORTALITY, AND PRODUCTION OF FIVE FISH SPECIES OF THE KAFUE RIVER FLOODPLAIN, ZAMBIA

by
James McDaid Kapetsky

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Fisheries)
in The University of Michigan
1974

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CHAPTER I

INTRODUCTION

Background and Objective

The major tropical rivers of the world and many of their tributaries incorporate floodplain ecosystems which are usually of great expanse in relation to the surface areas occupied by the rivers themselves (Table 1).

From an ecological viewpoint these tropical floodplain ecosystems are unique. Only a relatively small proportion of the total area of the ecosystem is permanently terrestrial or entirely aquatic, and most of the system is in a continuous state of flux due to the seasonal rise and fall of water levels. Therefore the floodplain biota are adapted to high amplitude fluctuations in environmental conditions, particularly those of varying moisture for the flora of the terrestrial community and of varying living space for fauna for both the terrestrial and aquatic communities.

Viewed as exploitable natural resources, floodplains have potential for cultivation, grazing of domestic animals, game parks, and fisheries. Further, floodplains may serve as the reservoirs for impoundments which, in addition to electrical power generation, have potential for irrigation and for fisheries.

TABLE 1. Names, locations and area characteristics of some of the tropical floodplains of the world.

Continent	Floodplain	River	Country	Area Inundated km^2[1]	Source
South America	Rupununi	Rupununi	Guyana	12,000?	Lowe-McConnel, 1964
	Chaco	Paraguay/Parana	Paraguay/Argentina	?	Carter & Beadle, 1930
	Amazon, tributaries	Amazon, tributaries	Brazil	?	Soli, 1958
Asia	Mekong	Mekong, tributaries	Cambodia/Viet-Nam	53,600	UN/ECAFE, 1970
	Ganges	Ganges	India	?	Gresswell & Huxley, 1965
Africa	Sudd	White Nile, tributaries	Sudan	92,000	Rzoska, 1974
	Gambia	Gambia	Gambia	?	Johnels, 1954
	Central Delta	Niger	Mali	17,000	Welcomme, 1972
	Niger	Niger	Niger	907	Welcomme, 1972
	Niger	Niger	Dahomey	274	Welcomme, 1972
	Niger	Niger	Nigeria	6,600	Motwani, 1970
	Benue	Benue	Nigeria	4,390	Motwani, 1970
	Oueme	Oueme	Dahomey	960	Welcomme, 1972
	Yaeres	Chari/Logone	Cameroon/Chad	63,000	Blache, 1964
	Senegal	Senegal	Mauritania/Senegal	4,560	Welcomme, 1972
	Barotse	Zambezi	Zambia	10,900	Duerre, 1969
	Kafue	Kafue	Zambia	4,340	herein

[1] Includes areas which remain inundated throughout the year.

Floodplains have received little study and therefore the ecological dynamics of these systems are poorly understood. With only a few exceptions knowledge of the dynamics of floodplain fish populations has come as a by-product of taxonomic investigations or from surveys directed toward development of floodplain fisheries. Only recently an effort has been made to gather and compile fish catch estimates from floodplain-river systems. Although still incomplete, these data indicate that floodplain fisheries in Africa provide about 40 percent of the riverine fish harvest and about 17 percent of the continent's total inland catch (Welcomme, 1972).

As a contribution to the knowledge of the ecology of floodplains and as a measure of the as yet undetermined fishery potential of these systems, the objective here is to estimate the annual rate at which fish flesh is produced by selected species in a tropical floodplain-river system. The approach is straightforward. Population numbers were estimated and life history information was collected while the author was employed by The University of Michigan on a pre-impoundment investigation of the fishes and fishery of the Kafue River floodplain, Zambia, Africa, in 1969 and 1970. Growth and mortality rates have been derived herein for selected species, and annual production is estimated with these data. As used herein the term "production" should not be confused with catch, yield, or harvest. By production is meant the total amount of fish tissue

elaborated in a unit of time regardless of whether or not the tissue survives to the end of that time (Ricker, 1946; Chapman, 1967, 1968).

Since completion of the field work the Kafue River has been impounded about 35 km downstream from the floodplain. In this thesis we are concerned with fish population dynamics under the natural hydrological regime which existed through 1970.

The remainder of this chapter is devoted to the integration of knowledge on the dynamics of the Kafue floodplain ecosystem. The topography, climate, hydrological regime, limnology, vegetation, and terrestrial and aquatic fauna of the system are discussed. Similar aspects of other floodplain-river systems are presented. Background information on the five species selected to serve as "models" for the growth, mortality, and production estimates completes this chapter.

The subject of Chapter II is the growth of the five selected fish species. The growth of each species is represented in a composite form which enables comparisons of the growth of Kafue fishes with conspecifics from other nearby systems. Variation in annual growth is demonstrated, and this variation is shown to be related to corresponding annual variations in the hydrological regime.

In Chapter III the results of the population estimates are presented. These estimates are then used to characterize the numbers and weights of fishes in the principal types

of floodplain habitats. The age structure of each population of the five "model" species is determined and this information provides the basis for the mortality computations. The effects of seasonal variations in growth and mortality are considered and the growth information of Chapter II and the mortality estimates of Chapter III are used to compute estimates of annual rates of production. Finally, the capacity of the floodplain ecosystem to yield fish flesh is estimated through the use of a morpho-edaphic model.

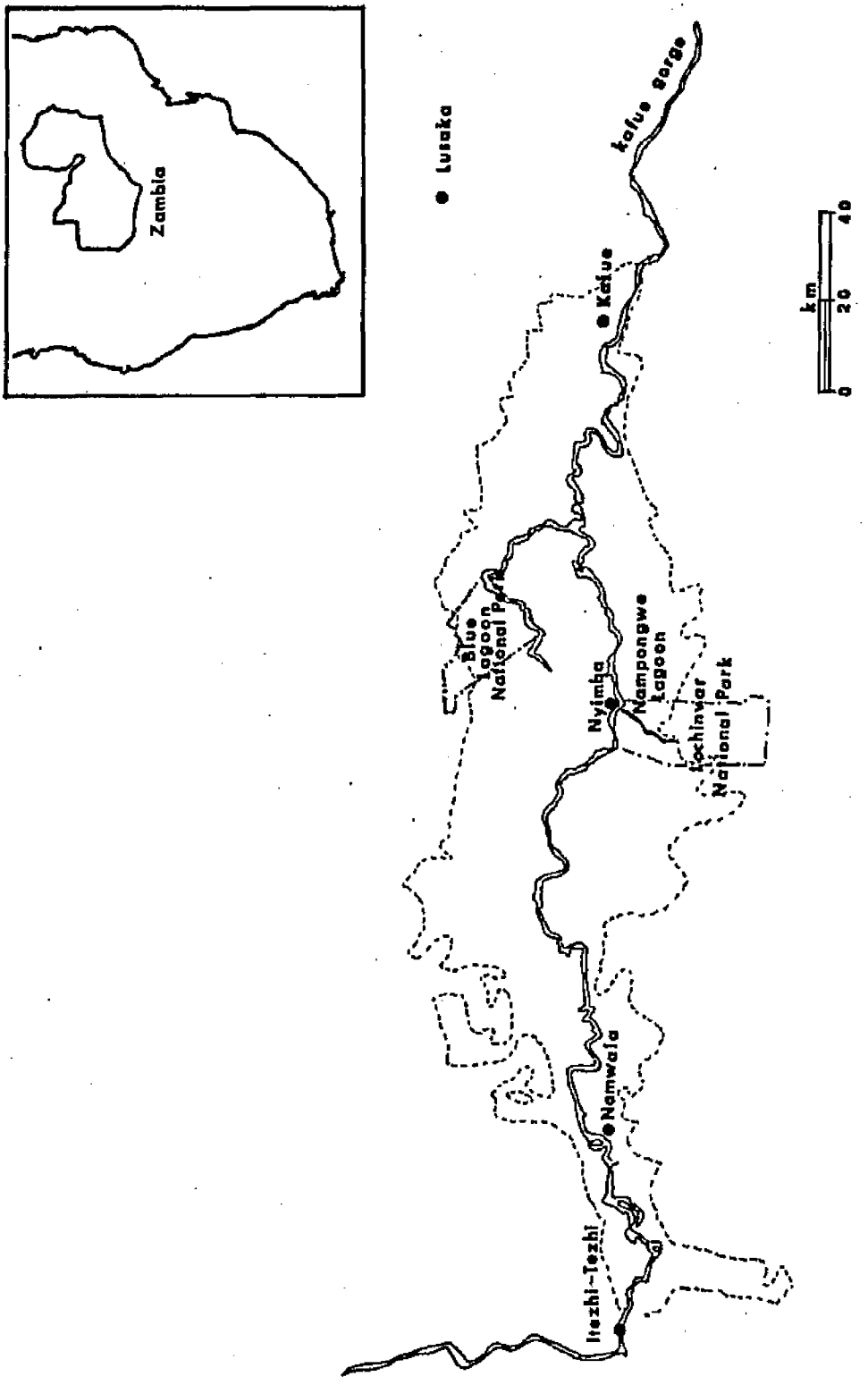
In the discussion, Chapter IV, the growth, population, mortality and production estimates are evaluated. Floodplain fish production and fishery yield are discussed in relation to the influence of man on the system, and in terms of factors which may limit fish production in the Kafue River floodplain.

The Kafue Floodplain Ecosystem

Location and Topography

The Kafue River rises in northwest Zambia and for most of its course flows through the Central African Plateau. For the initial 1,100 km the gradient is relatively steep; however, as it turns eastward at Itezhi-Tezhi it emerges onto the Kafue Flats, a vast area of about 14,000 km^2. The lower lying area of the Kafue Flats comprises the Kafue floodplain which extends over an area of 6,600 km^2 at an altitude of 975 m above sea level (Figure 1). The geology of the area is suggestive of a lacustrine origin for the

FIGURE 1. The Kafue River floodplain in Zambia.


Zambia
Lusaka
Kalue Gorge
Kalue
Blue Lagoon National Park
Nyimba
Nampongwe Lagoon
Lochinvar National Park
Namwala
Itezhi-Tezhi
km
0
20
40

floodplain. The river meanders 400 km through the 250 km length of the floodplain, and in this distance drops only about 10 m. At the eastern end of the floodplain the river begins an abrupt descent of about 600 m in 24 km in the Kafue Gorge and then becomes confluent with the Zambezi River about 60 km further downstream (FAO, 1968, Vol. I).

The region of inundation, on the average 4,300 km^2 (FAO, 1968, Vol. III), is essentially featureless and is interrupted only by the river channel, and by river backwaters and other open water areas collectively called lagoons. During inundation the floodplain is covered with grasses which emerge above the floodwaters, and as the flood recedes these grasses collapse forming a mat of dry vegetation part of which may be burned by the inhabitants. The banks of the river have been raised by deposition to form levees which are higher than the surrounding floodplain. The levees are broken in some areas by former river channels which have remained confluent with the river. Tributary streams arising in the upland regions of the Kafue Flats end in deltas at the floodplain periphery (FAO, 1968, Vol. I).

Climate

Although the Kafue floodplain lies within the limits of the tropical regions of Africa, its location on the Central Plateau of southern Africa has a moderating effect on the climate. October is usually the warmest month with daily maximum temperatures of about 32° C and lows of about

17° C. The rainy season begins in late October or early November and it extends to late March or early April. Average rainfall in the Kafue Flats area is about 81 cm. The remainder of the year is dry. Temperatures continue to decrease from October through June and July when daily maxima are about 24° C and minima about 4° C, rarely falling to 0° C (FAO, 1968, Vol. III).

Hydrological Regime

The timing, extent, and duration of the annual flood in the Kafue system depend on three hydrological inputs--local rainfall directly over the plain, inflows from tributaries within the 45,000 km^2 subcatchment surrounding the Kafue Flats, and overflow from the Kafue River which drains an area of 106,000 km^2 above the Kafue Flats catchment. In the usual sequence of events, local rainfall and flows from tributaries result in partial flooding of the plain in early December (FAO, 1968, Vol. III). The river is increasingly swollen by runoff from rains in its upper catchments and eventually reaches a bankfull flow rate of about 340 m^3/s in the western floodplain area and 170 m^3/s further downstream at which point the floodwaters overflow onto the plain (SWECO, 1967). The flood crest requires several months to traverse the plain, reaching a peak about February or March in the western portion and in April or May at the eastern terminus. The mean maximum area inundated over a period of 10 years was 434,000 ha and it

varied from 320,000 ha to 550,000 ha (FAO, 1968, Vol. III, Table 27). The maximum area of inundation is transitory, perhaps lasting for only a few days, but on the average an area of about 280,000 ha is flooded for four months (SWECO, 1967). The depth of flooding is up to 6 m.

The flood recedes at about the same rate at which inundation occurs. By July or August most of the plain is dry and only the river channel, backwater lagoons, isolated lagoons, and swampy depressions remain inundated. Together these areas total about 121,000 ha (FAO, 1968, Vol. III). As shown on 1:50,000 scale maps the open water areas comprise about 16,000 ha (derived from planimeter measurements).

The annual variability in the timing, extent, and duration of the flood results from variations in the hydrological inputs as well as from the "moisture debt" of the floodplain and catchment soils, and from the volume of water remaining from the previous year's flood. The flood regime is modified further by variations in rates of evaporation and transpiration (FAO, 1968, Vol. III).

Vegetation

The Kafue floodplain alluvium is montmorillonite clay which supports mostly grassland communities. These are distributed according to the depth of inundation and by variations in soil chemistry. Of the grasses, Oryza barthi is the most widespread occupying an area of about 220,000 ha

in depths from 1.5 m to 6 m. Vossia cuspidata, Echinochloa stagnina, and E. pyramidalis are characteristic of the peripheries of areas which are permanently inundated, and Cyperus papyrus is common around the edges of isolated floodplain lagoons. The reed, Phragmites mauritianus, grows on riverbank levees. In areas at the floodplain margin which become only shallowly inundated in some years a different plant community exists consisting mostly of Hyparrhenia rufa (Van Rensburg, 1968, FAO, Vol. IV). Lilies, Nymphaea capensis, and a legume, Aeschenomene fluitans, occur along the edge of the inundation zone in some areas. The true aquatics of permanently inundated areas are for the most part Ceratophyllum demersum and Trappa natans.

Production of vascular plants is most rapid early in the flood with the vertical growth of grasses keeping pace with the rise in water levels on the floodplain. Cuttings taken from five types of grass communities after about five weeks of flooding had a mean wet weight equivalent to about 16,000 kg/ha. The estimates for two of the most common species, Vossia cuspidata and Echinochloa pyramidalis, were 35,000 kg/ha and 3,900 kg/ha, respectively (derived from Table 5, Van Rensburg, 1968, FAO Vol. IV).

A succession of vegetation types takes place within hydrological cycles and from one hydrological cycle to the next. For example, one area that was exclusively water lilies at the height of the flood in March, 1969 consisted of about one-half water gentia, Ottelia exserta, by July.

Later, Aeschenomene fluitans also invaded the area. In the subsequent flood cycle, the latter two plants reappeared, but the lilies did not (Scully, 1972). Differing distributions of Oryza barthi which were related to annual variations in the depth of flooding have been noted by Van Rensburg (1968, FAO Vol. IV).

Terrestrial Community

The terrestrial and amphibious faunas of the Kafue floodplain have been changed by human influences in the present century. Intensive hunting has resulted in a reduction of economically important populations such as those of antelopes, and of the crocodile (Sheppe and Osborne, 1971; J. Butts and A. Jones, pers. comm.). The range of the most numerous antelope species has been reduced (Bell et al., 1973). Further, wild ungulates have been replaced to some extent by cattle (Van Rensburg, 1968, FAO Vol. IV), and as one consequence of the introduction of cattle, a disease of domestic cattle now afflicts one of the wild ungulate populations (Gallagher et al., 1972).

Although the floodplain is considered to be the most productive region of the Kafue Flats, relatively few large animal spcies utilize the floodplain (Sheppe and Osborne, 1971). Most numerous of the wild ungulates is the endemic Kafue lechwe, Kobus leche kafuensis, numbering about 93,000 on the central floodplain (Bell et al., 1973). It is a semi-aquatic grazer in depths of about 0.5 m, and rarely

is found more than 5 km from the water. As the floodwaters recede the lechwe occupy more and more of the floodplain where they graze on newly exposed grasses. Primary production is at its highest rate when the terrestrial system is rapidly contracting, but the period of greatest nutritional stress occurs for the lechwe at peak flood when herds are compressed in an area of poor grazing quality between the inundated plain and the adjacent woodlands. At this time deaths from starvation and diseases are most prevalent (Gallagher, et al., 1972; Bell et al., 1973).

About 250,000 cattle are driven to the floodplain for grazing during the low-water phase of the hydrological cycle. In contrast to the lechwe, cattle are selective in feeding and are unable to utilize most of the floodplain grasses. After several months of grazing on the floodplain cattle are often in poor condition (Van Rensburg, 1968, FAO Vol. IV).

Birds, of which 337 species inhabit the Kafue Flats area (Dowsett, 1966), are abundant as seasonal and permanent inhabitants of the floodplain.

The only amphibious ungulate is the hippopotamus. Populations of this animal have been reduced by hunting (Sheppe and Osborne, 1971; J. Butts, pers. comm.) so that at present it numbers only about 2 to 3 individuals per kilometer of river (Van Lavieren, pers. comm.).

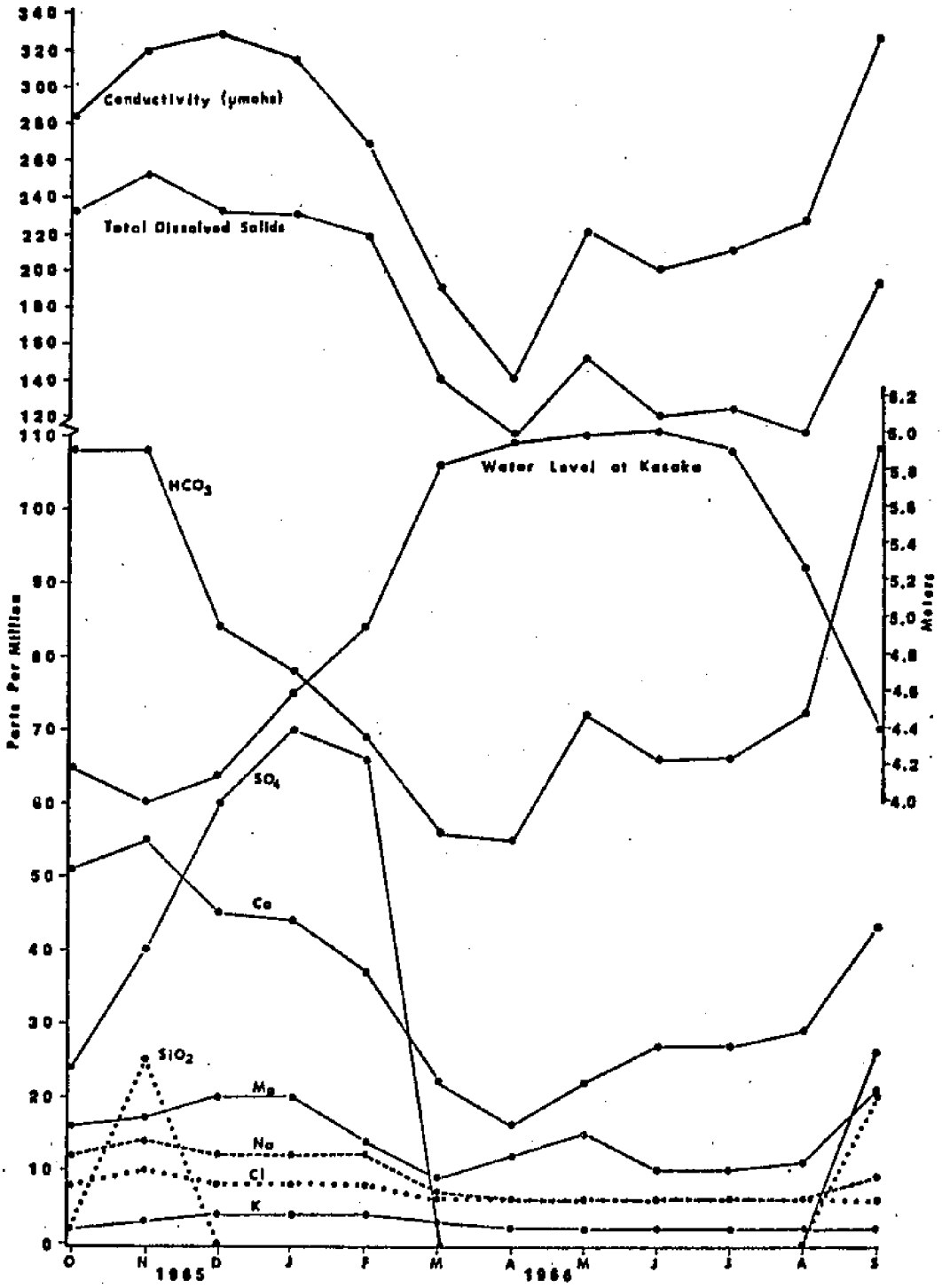
Limnology

The chemical composition of Kafue River and floodplain waters varies approximately inversely with water level (Figure 2), but it is probably also influenced by seasonal variations in the rate of primary production. Maximum nutrient uptake may occur early in the flood when the growth of vascular plants is rapid. As the flood waters recede, the vegetation decomposes and the concentration of nutrients in solution increases. The disappearance of silicon dioxide early in the flood may indicate uptake by diatoms, and the apparently rapid reduction in the concentration of sulphate may be due to its use by vegetation or by bacteria (Figure 2). A similar decrease in the concentration of sulfate was noted by Talling (1958) as the waters of the White Nile flowed through the Sudd swamp of the Sudan.

The Karoo rocks underlying parts of the Kafue River catchment cause a relatively high concentration of calcium in Kafue waters which is not characteristic of waters elsewhere in Africa (P. Kilham, pers. comm.). In terms of concentrations of major chemical constituents, the Kafue waters are similar to median values of the river waters of the United States (see, for example, Warren (1971), Table 5-2).

Water temperatures on the Kafue floodplain are similar to air temperatures--from 18° C to 29° C when averaged through the water column (Chapman et al., 1971); however,

FIGURE 2. Variations in the concentrations of major constituents of Kafue River waters as measured 15 km downstream from the floodplain (source: SWECO, 1967, Appendix II.7).


Conductivity (μmohs)
Total Dissolved Solids
Water Level at Kasaka
HCO3
SO4
Ca
SiO2
Mg
Na
Cl
K
Parts Per Million
Meters
O
N
D
J
F
M
A
M
J
J
A
S
1965
1966

maximum water temperatures have been recorded in January (Carey, 1971) and in February (Chapman et al., 1971) rather than in October when air temperatures are highest (FAO, 1968, Vol. III).

Variations in conductivities similar to those depicted in Figure 2 have been observed by Tait (1967a) and by FAO (1968, Vol. II). Hydronium ion concentration varies over time and by location with extremes from 6.3 to 8.4 (Tait, 1967a; Chapman et al., 1971). Depth of visibility is maximum at highest water levels, about 4.6 m, and reaches a minimum value of about 1 m prior to and during the early stages of flooding (Chapman et al., 1971).

Phytoplankton blooms were noted in 1965 in lagoons nearly isolated from the river by Carey (1971). A dense bloom occurred in the river channel during the recession of the flood in 1970; however, waters draining the floodplain were clear at this time. Phytoplankton blooms probably do not occur on the floodplain because the necessary nutrients are locked up in vascular plants and because the stems and leaves of these plants also limit light penetration. Carey (1971) also observed zooplankton in lagoons in 1965 and 1966. When the floodwaters were receding in 1969, zooplankters, mostly Cyclops, were dense in the Nampongwe Lagoon and were being cropped by Clarias (catfishes).

Contrary to my own observations and those of D. J. Stewart (pers. comm.), Carey (1971) states that epiphytic algae are abundant on grass stems and leaves. This seems

to be true only of the open water-vegetation interface where vegetation is less dense than elsewhere and light penetration is maximum.

Dissolved oxygen concentration, an important factor in fish distribution, is considered in the next section.

Kafue Floodplain Fish Populations

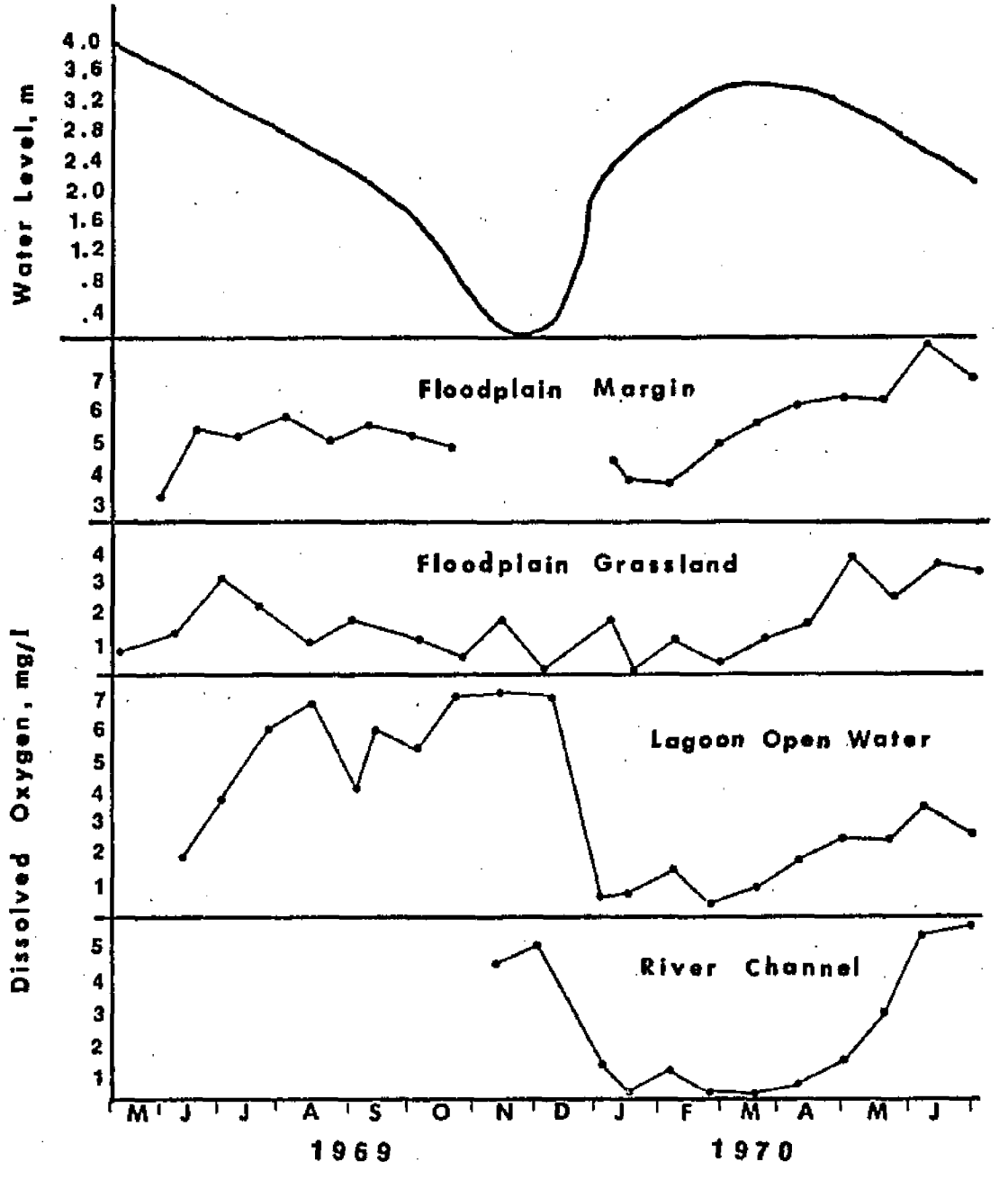
The Kafue River fish fauna consists of 67 species in 14 families (Bell-Cross, 1972). Although the Kafue River is a tributary of the middle Zambezi, the rapids of the Kafue Gorge below the floodplain probably block movements of Zambezi fishes further into the Kafue system. The Kafue fish fauna is similar to that of the upper Zambezi (Bell-Cross, 1968, 1972).

The distribution of Kafue fishes is closely related to the hydrological regime, and for non-air breathing fishes also is influenced by spatial variations in dissolved oxygen concentrations (Chapman et al., 1971). In other floodplain systems when fishes are released from their confinement in the river channel and lagoons by rising floodwaters they traverse the floodplain on spawning movements (Johnels, 1954; Sao-Leang, 1955: Van Someren, 1961; Blache, 1964; Lowe-McConnel, 1964; Motwani, 1970); however, in the Kafue system this also may be an obligatory movement of those fishes which are not adapted to use atmospheric oxygen.

As the floodwaters rise, decaying vegetation and animal wastes are accumulated by inundation and by rainfall runoff and cause a high biochemical oxygen demand in the organically laden waters. In the course of satisfying this oxygen demand large areas of the floodplain may become deoxygenated during the early stages of the flood. For example, as the rising floodwaters flushed through a previously isolated lagoon the dissolved oxygen concentration plummeted from 7.5 mg/l to 0.5 mg/l over a period of three weeks, and a similar decrease was recorded in the river channel (Chapman et al., 1971; Scully, 1972) (Figure 3). The decrease in dissolved oxygen in the lagoon coincided with observations of large numbers of dead and moribund fishes there. In laboratory tests Chapman et al. (1971) have shown that eight common species of Kafue fishes can tolerate dissolved oxygen concentrations of less than 1 mg/l although at this concentration stress is evident in their behavior. These fishes died at concentrations of 0.3 to 0.6 mg/l.

A distinct order in the movement of various species onto the floodplain has been noted by Williams (1971). Mouthbrooding cichlids, Sarotherodon, Serranochromis, and possibly Haplochromis, may reproduce before the flood and carry eggs or fry onto the floodplain (Williams, 1971; Chapman et al., 1971; Dudley, 1972). Clarias partly swim and partly "walk" up shallow rivulets draining onto the floodplain and spawn in rain-filled depressions. The period of reproduction of most of the other species has its peak during the early

FIGURE 3. Changes in dissolved oxygen concentrations in four habitat types of the Kafue River floodplain. (After Scully, 1972).


Water Level, m
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
.8
.4
Floodplain Margin
Floodplain Grassland
Lagoon Open Water
River Channel
Dissolved Oxygen, mg/l
M J J A S O N D J F M A M J
1969
1970

stages of the flood (Carey and Bell-Cross, 1967; Carey, 1971; Williams, 1971).

The floodplain margin provides optimal conditions for reproduction of many species. Fry are sheltered by the newly emergent vegetation, and the plants provide a substrate for the growth of periphyton and other fish-food organisms.

Clarias, obligate air breathers, are the only fishes to reinhabit the floodplain during the period of minimal dissolved oxygen concentrations (Scully, 1972). Evidently their food at this time is primarily aquatic insects. Most of the common insects listed by Carey (1967) (Ephemeroptera, Odonata, Hemiptera, Diptera and Trichoptera) include species which are adapted to breath atmospheric oxygen.

As indicated by changes in gill net catches at four stations, adults of species other than Clarias began to move away from the floodplain periphery as dissolved oxygen concentrations increased in February and March, 1970 (Figure 3). By the time of peak flood in April, fishes were redistributed in all floodplain habitats (Scully, 1972). Predators may be the first species to leave the flood plain margin (Carey, 1971); juveniles of larger species and diminutive species are probably the last fishes to move toward the river (Williams, 1971) as is the situation on the Barotse floodplain (Kelley, 1968; Duerre, 1969).

The movements of fishes from the floodplain margin occur at a time when they are increasingly liable to predation

by piscivorous birds. Shelter decreases as vegetation dies, and depths on the floodplain become more shallow. White pelicans, Pelecanus onocrotalus, arrive in large numbers on the floodplain at this time. A consumption rate of one to two tons per day has been estimated for a group of 500 pelicans by Tait (1967b). I observed at least 2,000 of these birds in the same area in 1970, and as did Tait I noted that some were so gorged on fish that they were unable to fly. Williams (1971) lists eight species of birds in addition to the white pelican which are piscivores on the Kafue floodplain. One population of these piscivores, the reed cormorant, Phalacrocorax africanus, is believed to consume about 260 mt of fish per year on the 8,000 km^2 Bangwelu swamp (Bowmaker, 1963).

Although dissolved oxygen concentrations have usually moderated throughout the floodplain area by the time of maximum inundation (Figure 3), fish mortalities may occur as the floodwaters recede due to the combined effects of low temperatures and locally low dissolved oxygen concentrations. In June and July low water temperatures are accompanied by high wind velocities and at this time decaying vegetation may give rise to open water areas on which winds may act. The wind action cools the water and at the same time wind-generated currents carry bottom sediments into the water column which depletes the dissolved oxygen. Tait (1967c) observed one such mortality which coincided with oxygen concentrations as low as 0.9 ppm and a temperature of 13° C.

Mortalities of Tilapia caused by wind-generated overturn have occurred on the shallowly inundated Lake Chilwa in Malawi (Morgan, 1971).

After the floodwaters have receded from the inundation zone, fishes are isolated in the river channel, in lagoons, and in adjacent swampy areas most of which lose their high-water connections with the river. Usually this period has a duration of about three months, but in some low-flood years it may be nearly twice as long. Evaporation and transpiration further decrease the volume of water available to fishes as the dry season progresses, and some isolated lagoons may dry completely. As is the case with the lechwe when they are compressed at the floodplain margin, the time when fishes are most concentrated is recognized as one of nutritional stress (Johnels, 1954; Lowe-McConnel, 1964; Blache, 1964; Lagler et al., 1971).

Some fishes may undertake long-range movements while isolated in the river channel and confluent lagoons. Returns of tags indicate that Hepsetus odoe may travel 60 km upstream and as much as 120 km downstream from the central floodplain area. Tags from Clarias ngamensis and Sarotherodon macrochir were recovered from as far as 70 km downstream (Williams, 1971, Table 1).

Kafue Fishery

The Kafue floodplain fishery is one of the most important in Zambia. From 1956 through 1970 the harvest has

averaged 5,600 mt per year, about 22 percent of the total catch from all of Zambia's fisheries, (Central Statistical Office, Lusaka, 1966, 1971). The fishery resource consists of about 19 species which are exploitable with gill nets and seines of 7.6 cm stretched mesh. The cichlids are the most important group in the catch, and of these Sarotherodon andersoni, S. macrochir, and Tilapia rendalli predominate. Two Clarias species form the second most important stock.

Before the mid-1950's the history of the Kafue fishery is obscure. Lozi people from the Central Barotse floodplain came to the Kafue in 1942 when their Paramount Chief laid claim to fishing rights in some areas of the floodplain (Brownridge, 1968). Fishing was a seasonal occupation carried out only during the time of lowest water levels (Sklower, 1951). In those times seine nets were laboriously constructed from the cords of discarded automobile tires (Everett, 1969), but traditional methods of fishing with baskets, spears, weirs, and hooks were still practiced by local peoples (Anon., 1955). The principle fishing craft of the Kafue were, and still are, hollowed-out log canoes.

The contemporary history of the Kafue fishery began in the mid-1950's as the result of two circumstances. Relatively inexpensive nylon gill nets became available (Williams, 1960), and there was also an increasing demand for fish in the population centers near the copper mines. By 1954, 1,200 fishermen were operating from 114 camps on the Kafue (Anon., 1955). A further stimulus for the Kafue

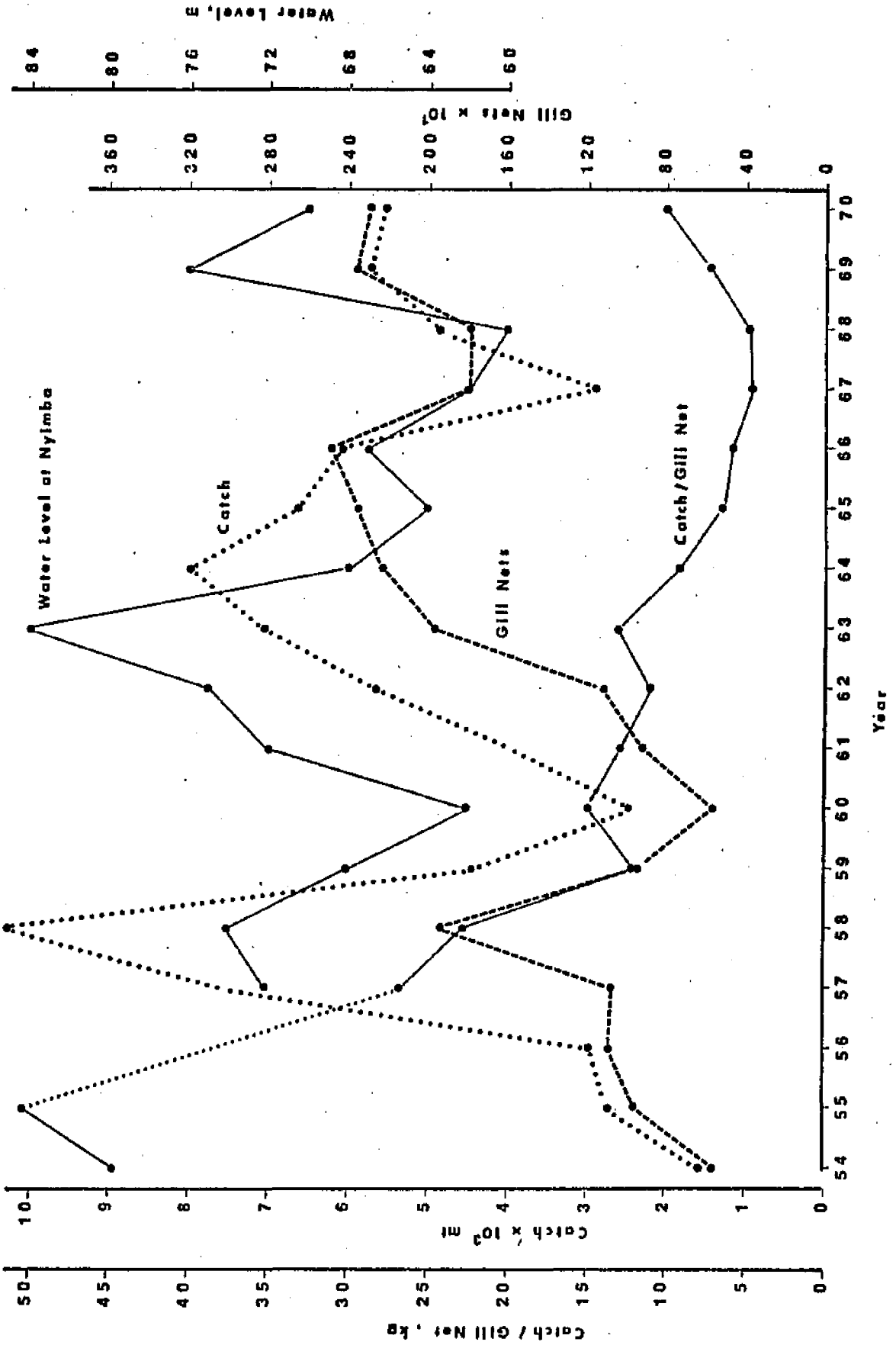
fishing industry occurred when fish traders temporarily lost access to fisheries in northern Zambia and their attention was then turned to the Kafue where fishermen were quick to respond to the increased demand (Anon., 1958).

Fishing, formerly a seasonal occupation, became a year around endeavor between 1955 and 1958. Gill nets were used at the floodplain periphery during high water when seining beaches along the river and lagoons were inundated (Pike and Carey, 1965), and seines were constructed by attaching gill nets end to end. Prior to 1955 the annual catch was probably about 1800 mt, but with the expansion of effort the catch increased in three years from about 2700 mt in 1956 to 10,000 mt in 1958 (Figure 4).

The increasing, then decreasing yield was accompanied by lower catches per net (Figure 4); however, fishing effort decreased along with decreasing catches in the period from 1958 to 1960, probably due to competition with Lake Kariba which was just then beginning as a fishery (Anon., 1960, 1961).

The low water levels that accompanied the decrease in catch and effort favored the use of seine nets. Fears of overfishing were compounded when the catch reached its low of 2,400 mt in 1960. Seining was thought to interfere with spawning activity and to cause overharvest of spawning stocks, and a ban was placed on seining in 1961 (Pike and Carey, 1965).

FIGURE 4. Catch, catch per standard gill net, and number of gill nets for the Kafue River floodplain fishery.


Water Level, m
Gill Nets x 10²
Catch / Gill Net , kg
Catch x 10³ mt
Year
Water Level at Nyimba
Catch
Gill Nets
Catch/Gill Net

The catch of 1962, 5,400 mt, included an estimated 1800 mt of Marcusenius macrolepidotus taken in dip net fisheries at the head of the Kafue Gorge located several kilometers downstream from the floodplain. Usually the Marcusenius fishery was small and seasonal, yielding perhaps 180 mt per year, but the 1962 run was the largest in memory (Anon., 1963).

A number of fishermen live on the higher riverbank levees the year around, but in some years, such as during the record flood of 1963, these fishermen also are forced to fish along the floodplain margin. Illegal seine netting was prevented by the high water levels of 1963, but increased in 1964 (Anon., 1965), and the gill net catch estimates were doubled for the latter months of the year in 1964, 1965 and 1966 to account for the additional catch made by this method (Central Statistical Office, Lusaka, 1965, 1966; Anon., 1967). The seine net ban, largely unenforceable (Anon., 1965, 1966), was lifted in 1967.

It long has been recognized that the yield potential of the Kafue fishery is related to the hydrology of the system, which in turn affects not only the fish populations, but also the spatial distribution of fishing effort and its intensity and duration. This is particularly true in the case of the seine net fishery which is dependent on the availability of suitable net-landing beaches along the river and in backwater lagoons.

Attempts to quantify the relationship between variations in annual catch and corresponding variations in the hydrological regime have been made by Chapman et al. (1971), Lagler et al. (1971), and by Muncy (1973). Statistically significant correlations between annual catch and an index of the annual flood based on water level data in the previous year ($r = 0.72$) and in two previous years ($r = 0.56$) were found by Chapman et al. (1971) for the period 1954 to 1969. Using data from the same period no statistically significant relationship between catch in one year and catch in the previous year was obtained, nor was there any apparent relationship when the catches from the two previous years were averaged and correlated with catch in the subsequent year.

The relationship between annual catch and hydrology was examined in more detail by Lagler et al. (1971). The area inundated and the volume of the flood from the previous year were well correlated with catch in the subsequent year for the period from 1957 to 1968 with $r = 0.70$ and 0.65, respectively. Essentially the same results as those obtained by Chapman et al. (1971) were found in correlations of catch with the subsequent year's catch.

Lagler et al. (1971) sought an index of hydrological conditions from within a hydrological year that would provide a high correlation coefficient with catch in the subsequent year. Water levels from different times of the year were used as independent variables. The phase of the hydrological regime which provided the highest correlation coefficient

with catch in the following year was the time of falling water levels, and an index called the "Draw Down Factor" (DDF) was developed to describe the apparent catch-hydrology relationship. The DDF was computed as the sum of flood storage volume on the floodplain from September to December. Plotting the DDF against catch in the subsequent year suggested that the relationship was exponential. The logarithm of DDF versus the catch provided a correlation coefficient of 0.77 (Lagler et al., 1971).

Muncy (1973) adopted the DDF concept of Lagler et al. (1971), but substituted the volume of flow at Kasaka (near Kafue) for flood storage as the independent variable. For his correlations Muncy had three additional years of data available, from 1970 to 1972, and he also incorporated the catch data from the early years of the fishery (1954 to 1956) which were not used by Lagler et al. (1971) because of their questionable accuracy.

Using these data, Muncy's correlation coefficients were somewhat different from those obtained either by Chapman et al. (1971) or by Lagler et al. (1971). Muncy concluded that catch was depressed by high water levels in the same year and that catch also could be depressed in the following year if water levels remained high due to the high flood of the previous year. Based on his hypotheses concerning the effect of the hydrological regime on fish stocks (largely unexplained) and of the time required for recruitment Muncy also concluded that the hydrological regime in one year has

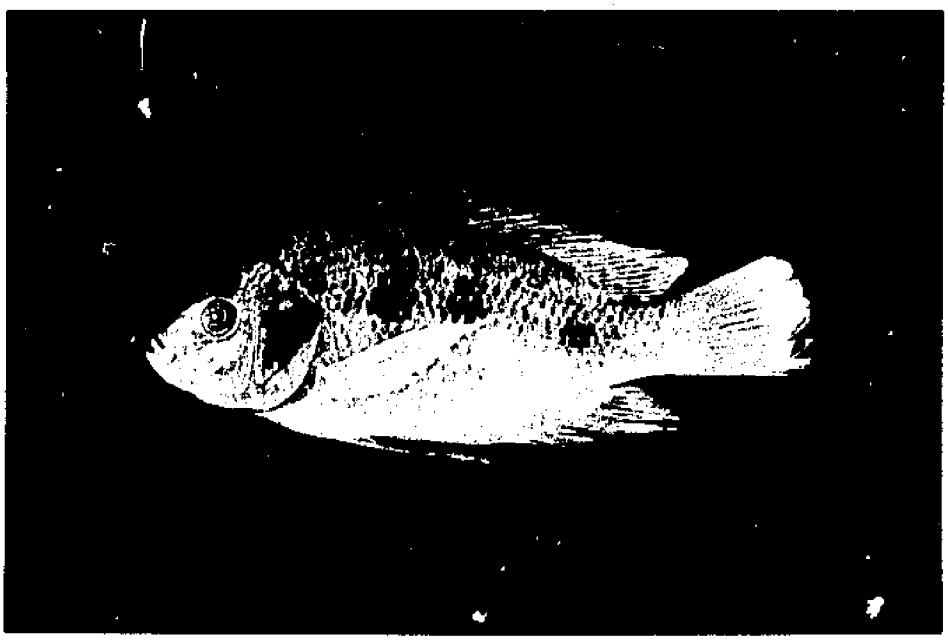
an effect on catch two years later. He further suggested that the correlation coefficients of hydrological factors with catch one year later, which were higher than with catch two years later, might be explained by "carry over" of fish stocks from one year to the next because the removal of fishes would be reduced by the interference of high water levels with fishing activity.

Life Histories of Selected Species

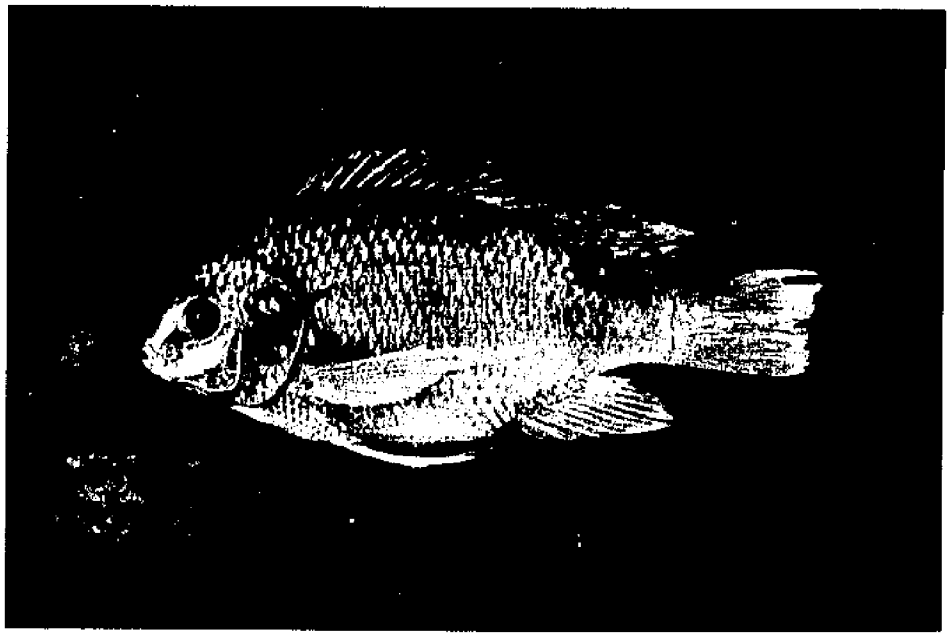
Five of the more than 30 species which were encountered in the Kafue River and floodplain have been selected for detailed studies of growth and mortality and to serve as the "model" species for production estimates. The criteria for selection were the types of ecological niches occupied by each species, their economic importance in terms of catch and of consumer preference, availability of data for growth, mortality, and production computations, and availability of supportive life history information. Accordingly, the species selected were Sarotherodon andersoni (Castelnau), S. macrochir (Bouleger), Tilapia rendalli (Dumeril), Serranochromis angusticeps (Boulenger), all of the family Cichlidae, and Hepsetus odoe (Bloch), family Hepsetidae (Figure 5).

S. andersoni, s. macrochir, (both formerly Tilapia, (Trevawas, 1973)) and S. angusticeps are fishes of the Upper Zambezi system (Jubb, 1967), but S. andersoni is also found in Lake Kariba (Bell-Cross, 1972). T. rendalli (formerly

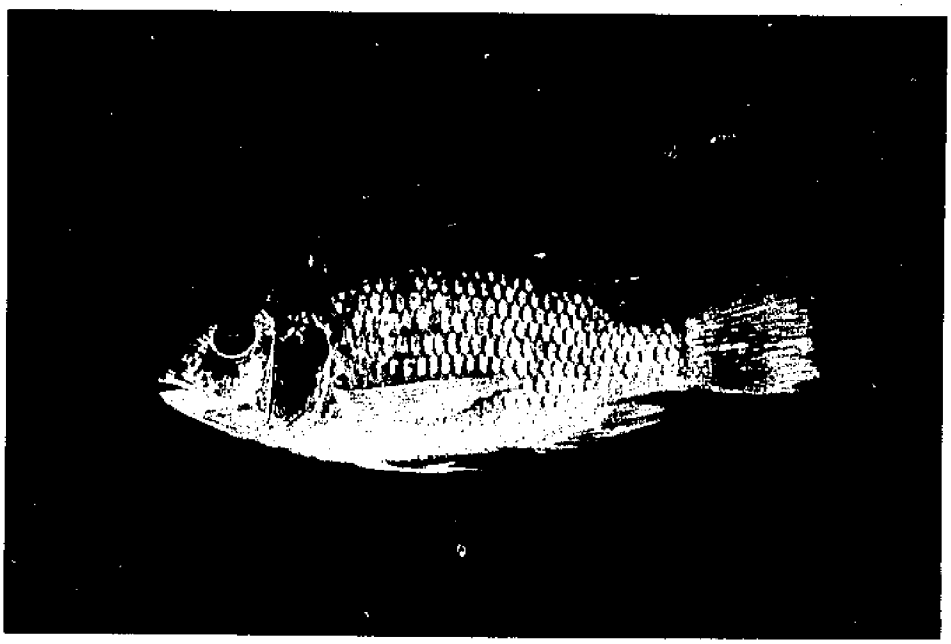
FIGURE 5. S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe of the Kafue River floodplain (Photos by D. J. Stewart).



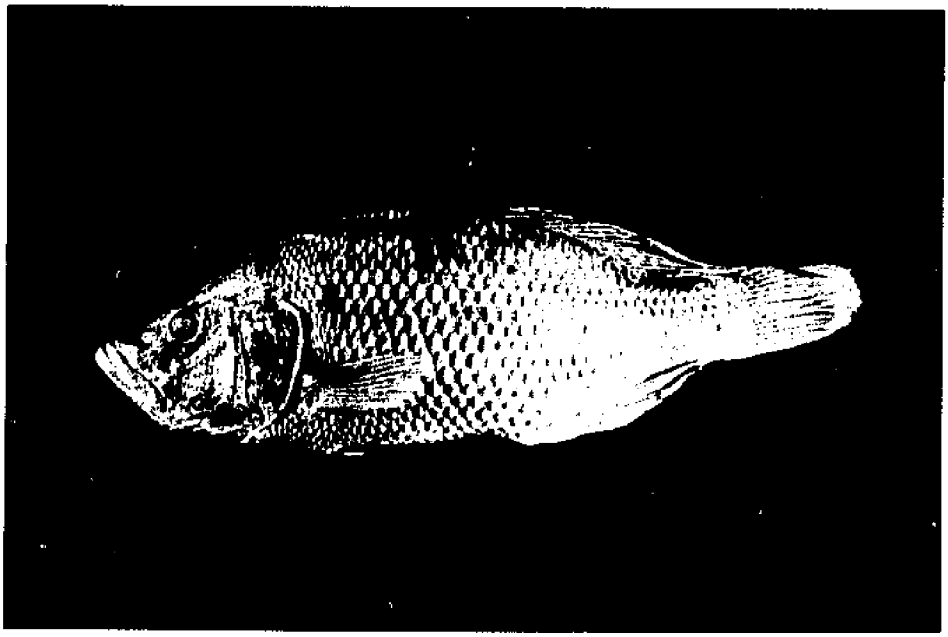
Sarotherodon andersoni



Sarotherodon macrochir



Tilapia rendalli



Serranochromis angusticeps



Hepsetus odoe

melanopleura) and H. odoe have much wider distributions. T. rendalli occurs throughout the Zambezi system and H. odoe is found in the Zambezi, Congo (Jubb, 1967), Niger (Reed, 1967), and Gambia Rivers (Johnels, 1954), and also in the Lake Chad drainage (Blache, 1964).

S. andersoni, S. macrochir (Mortimer, 1960), and S. angusticeps (Trevawas, 1964) are mouthbrooders, and T. rendalli is a substrate spawner (Mortimer, 1960). Evidence from the pond culture of S. andersoni indicates that this species is not usually a multiple spawner (Mortimer, 1960). A female S. angusticeps brooding young in the buccal cavity was found in a ripe condition (personal observation), and therefore this species may reproduce more than one time in each spawning period. H. odoe builds a bubble nest in which the eggs are deposited (Budgett, 1901; Johnels, 1954) and one or both parents may guard the nest (Jubb, 1967).

The spawning season of Sarotherodon andersoni, S. macrochir and T. rendalli coincides with the warm season and the beginning of the rains in October. The reproductive period lasts for about three months (Dudley, 1972). Eggs or young may be carried onto the floodplain by the former two species (Williams, 1971), as also may be the case for S. angusticeps which spawns from October to February (personal observation). H. odoe begins to reproduce in December and the spawning period extends over two months (Carey and Bell-Cross, 1967). S. macrochir and T. rendalli attain sexual maturity the end of the second year of life (Dudley,

1972) as do S. angusticeps (personal observation) and H. odoe (Chapman et al., 1971); however S. andersoni reproduces at not less than three years of age and usually not until four years old (Dudley, 1972).

S. andersoni, S. macrochir and T. rendalli are primarily herbivores. Study of the food of S. andersoni raised in ponds indicated that it is a bottom feeder. Observations on the feeding habits of S. macrochir and T. rendalli in aquaria suggested that S. macrochir feeds mainly at the surface and that T. rendalli feeds in the mid-water column (Mortimer, 1960). In the Kafue T. rendalli is the only species of the three that feeds on vascular plants (Dudley, 1972); however, all three species feed to some extent on crustaceans (Carey and Bell-Cross, 1967).

S. angusticeps is carnivorous, eating zooplankton and aquatic and terrestrial insects as well as a variety of fishes (Carey and Bell-Cross, 1967). My analysis of the contents of 31 stomachs suggests that adult S. angusticeps fed primarily on young Tilapia and Sarotherodon of about 10-20 mm in length just after the spawning period of these species, but later in the year S. angusticeps preyed on Alestes lateralis and Barbus spp. Stomach contents of 41 juveniles of about 40 mm to 60 mm in length indicated that fish of this size fed most extensively on aquatic insects (Ephemeroptera, Hemiptera), but also on small individuals of Barbus spp.

Hepsetus odoe is the only Kafue species that is entirely piscivorous, consuming at least 12 prey species (Carey and Bell-Cross, 1967; Carey, 1971; Scully, 1972).

Collectively, the five-species group accounted for 58 percent of the weight of the high-water standing stock in 1970, of which the three herbivorous species totaled 52 percent and the two carnivorous fishes the remaining 6 percent (derived, Lagler *et al.*, 1971, Table 5.3). Although the proportion in the catch is variable throughout the fishery area, *Sarotherodon* and *Tilapia* account for more than one-half of the catch from seine nets, but only up to about 30 percent of the catch from gill nets (Central Statistical Office, Lusaka, 1961-1970). These species are highly prized by fishermen, traders, and consumers in comparison with the catfish (*Clarias*) which are also abundant in the catch.

CHAPTER II

GROWTH

Introduction

The principal objective in this chapter is to estimate the mean weight for each year of life of five species of Kafue fishes. This information serves as one of the bases for the production estimates. A comparison of the annual growth in length and weight of Kafue fishes with conspecifics from other ecosystems is an additional objective. These comparisons provide a means of evaluating the fish productive potential of the Kafue floodplain relative to other systems. In order to better understand the dynamics of Kafue fish populations from the standpoint of annual variations in fish production, evidence for seasonal differences in growth rates is presented, and annual variations in growth increments are examined in relation to annual variations in environmental factors which may directly or indirectly affect the growth of fishes. Finally, annual growth in weight is approximated as a function of age.

Methods

Scale samples, lengths, weights, and sex data for the assessment of the growth of S. andersoni, S. macrochir,

T. rendalli, S. angusticeps and H. odoe were obtained in conjunction with population estimates made by chemofishing and seining in the principal fish habitats of the eastern floodplain and river area from June to November, 1970 (Table 2). The materials and data collected in this way were supplemented with some additional scale samples taken from gill-netted fish (Table 2).

For each collection of fishes obtained by seining or chemofishing the individuals of each species were separated by sex and key scales were removed from five randomly selected males and females in each one-centimeter length interval. For the cichlids the scales were taken from areas similar to those used by Balon (1972), but for H. odoe scales were removed from the first two scale rows above the lateral line in the area ventral to the adipose fin on the left flank. Total lengths were measured to the nearest millimeter, to the end of the median caudal ray with the caudal fin spread for the cichlids, and with the lobes of the caudal fin brought together for Hepsetus odoe.

One year old fish of each species were relatively abundant in each of the collections and only one scale sample from each sex in each one-centimeter length interval from each collection was randomly selected for annular and scale radius measurements. Fishes of two years of age and older were much less abundant and all scale samples, up to five for each sex in each centimeter length interval from each collection, were measured.

TABLE 2. Localities, dates, methods of capture, and numbers of scales measured for each collection of S. andersoni, S. macrochir, T. rendalli, S. angusticeps and H. odoe.

Location	Dates 1970	Method of Capture	Number of Scales Measured				
			S. andersoni	S. macrochir	T. rendalli	S. angusticeps	H. odoe
Kalilabuchende Lagoon	22-24 VI	C[1]	19	30	34	26	25
Chendelelo Lagoon	12-15 VII	C	8	12	--	--	5
Chinuka Pan	16-21 VII	C	17	9	39	70	21
Chanyanya Lagoon	22-30 VII	C	26	55	30	38	15
Nampongne Lagoon	17-19 VIII	S	39	86	11	28	72
Kafue River Section	22-24 VIII	S	32	61	42	--	20
Ceres River Section	26-28 VIII	S	40	55	30	--	14
Luwato Lagoon	4-7 IX	S	23	55	29	29	32
Chikunka River Section	9-12 IX	S	82	91	14	29	28
Kalilabuchende Lagoon	20-24 IX	C	29	17	--	--	--
Shimwaikila	21-23 IX	S	27	43	18	13	14
Chanyanya Lagoon	7-9 X	C	57	42	13	16	--
Kafue River Section	9-14 X	S	24	46	20	12	23
Ceres River Section	15-17 X	S	23	49	23	19	12
Chikunka River Section	7-11 XI	S	77	62	21	--	20
Unnamed Lagoon	12-14 XI	C	71	--	28	10	6
Luwato Lagoon	13-14 XI	S	15	20	28	25	12
Lochinvar	I - VI	G	--	--	2	54	--
TOTALS			609	733	395	369	319

[1]C - chemofishing; S - seining; G - gill netting.

Scale samples were mounted dry between glass slides or impressed on cellulose acetate and the scales were read on an Eberbach projector at 40 magnifications. In order to minimize measurement error scale radii along which annular measurements were made were selected to provide the maximum scale distance through which annuli were readily discernable. Accordingly, the scale radii for S. andersoni, S. macrochir, and T. rendalli extended from the focus to the ventral margin of the scale along a line perpendicular to the antero-posterior axis. For S. angusticeps and H. odoe the scale radius intersected the scale margin at the antero-ventral lobe. Plots of total lengths on corresponding scale radii measurements indicated that the relationships were linear for each of the five species. The total length-scale radius relationships were described using geometric mean regressions (Ricker, 1973) (Table 3); however, the standard errors of regression ($s_{y \cdot x}$) and coefficients of determination (r^2) are from the predictive regressions of total lengths on scale radii. Because of the good fits between the dependent and independent variables for these and other regressions (Table 3), the predictive and geometric regression parameters differed very little.

Weights, standard lengths, and total lengths of individual fish were measured on five males and five females randomly selected from each one-centimeter length interval throughout the total length range of each species to obtain data for weight and length relationships. These relationships

TABLE 3. Relationships of total length to scale radius, standard length to total length, and weight to total length for S. andersoni, S. macrochir, T. rendalli, S. angusticeps and H. odoe.

Species	Geometric Mean Regressions	n	$Sy \cdot x^1$	$r^{2\,1}$
S. andersoni	Total length(mm) = 12.54 + 1.22 (Scale radius x 40)	617	12.04	0.97
	Standard length(mm) = -1.67 + 0.80 (Total length(mm))	220	6.56	0.99
	Log_{10} weight(g) = -4.91516 + 3.07986 (Log_{10} total length(mm))	220	0.04524	0.99
S. macrochir	Total length(mm) = 5.81 + 1.12 (Scale radius x 40)	733	10.85	0.95
	Standard length(mm) = -5.02 + 0.82 (Total length(mm))	226	2.07	1.00
	Log_{10} weight(g) = -5.07125 + 3.17372 (Log_{10} total length(mm))	226	0.06901	0.99
T. rendalli	Total length(mm) = 0.41 + 1.12 (Scale radius x 40)	395	10.33	0.96
	Standard length(mm) = -3.07 + 0.81 (Total length(mm))	173	4.26	0.99
	Log_{10} weight(g) = -5.04972 + 3.15923 (Log_{10} total length(mm))	173	0.05804	0.99
S. angusticeps	Total length(mm) = 16.64 + 1.55 (Scale radius x 40)	366	13.00	0.98
	Standard length(mm) = -5.30 + 0.83 (Total length(mm))	136	3.32	1.00
	Log_{10} weight(g) = -5.62853 + 3.32277 (Log_{10} total length(mm))	272	0.04600	0.99
H. odoe	Total length(mm) = 59.53 + 2.23 (Scale radius x 40)	319	17.58	0.91
	Fork length(mm) = -6.96 + 0.92 (Total length(mm))	137	2.09	1.00
	Standard length(mm) = -9.28 + 0.85 (Total length(mm))	136	2.42	1.00
	Log_{10} weight(g) = -5.87510 + 3.31747 (Log_{10} total length(mm))	136	0.03163	0.99

[1]These statistics pertain to the predictive regressions of Y on X.

also were described using geometric mean regressions (Ricker, 1973) (Table 3).

Annulus Formation and Validation of Annuli

Annular marks on the scales of each of the five species were readily discernable. Cutting over of older circuli by newly formed circuli in the dorsal and ventral fields of the scale was the most prominent feature of the annulus for the cichlids, and broken circuli along the anterior field and cutting over in the postero-dorsal and postero-ventral fields were the principal criteria for annulus recognition on the scales of H. odoe. False annuli, which occurred on the scales of older fishes, were identified according to the criteria of Chugunova (1963).

The scale method of aging Kafue S. andersoni, S. macrochir, and T. rendalli has been validated by Dudley (1972) through the use of plots of length frequencies and observations on the number of marks on the scales of a sample of the fish whose lengths were plotted. The scale method was also validated by observations on the seasonal occurrence of mark formation.

In 1969 annulus formation began on the scales of S. andersoni, S. macrochir, and T. rendalli from the central floodplain in October. It continued into January 1970. The largest proportion of new marks were found in November for S. andersoni and T. rendalli, and in December for S. macrochir (Dudley, 1972, Table 1). Observations on

the occurrence of annulus formation on the scales of the same species which I collected one year later in the eastern floodplain area indicated that annulus formation began in mid-October, 1970, for S. andersoni and S. macrochir, but not until mid-November for T. rendalli (Table 4).

Annulus formation on the scales of S. angusticeps and H. odoe did not occur by the time of the final collections in mid-November, 1970; however, the scale method was validated for these species by observations of the timing of annulus formation during the latter months of 1969 and the early months of 1970 (Table 5). In comparison with annulus formation by Sarotherodon and Tilapia, annulus formation occurred somewhat later for H. odoe and much later for S. angusticeps.

No mention is made of the occurrence of juvenile marks on the scales of Kafue Sarotherodon or Tilapia by Dudley (1972); however, among my collections juvenile marks were clearly discernable on the scales of T. rendalli. These marks were formed at a mean total length of 42 mm. Juvenile marks at a mean total length of 45 mm were also found on the scales of S. andersoni, but at a much lower frequency of occurrence than among the scales of T. rendalli.

Composite Growth Representation

In order to facilitate the production computations and to permit comparisons of the growth of Kafue fishes with conspecifics from other ecosystems, annual growth in length

TABLE 4. Occurrence of new annuli on the scales of S. andersoni, S. macrochir and T. rendalli in the eastern floodplain area during October and November, 1970.

	Ceres Section 15-17 X 1970		Chikunka Section 7-12 XI 1970		Luwato Lagoon 13-14 XI 1970	
	Percentage of new annuli	Total sample	Percentage of new annuli	Total sample	Percentage of new annuli	Total sample
S. andersoni	2.8	72	39.5	129	31.1	61
S. macrochir	7.6	66	52.8	74	82.1	28
T. rendalli	0.0	88	0.0	77	7.6	118

TABLE 5. Occurrence of new annuli on the scales of S. angusticeps and H. odoe from the central flood-plain area.

Dates of Collections	Percentage of New Annuli	Total Sample
	S. angusticeps	
4-5 XII 1969	3.5	57
19-22 XII 1969	13.5	52
27-30 I 1970	32.1	53
3-6 III 1970	75.5	53
	H. odoe	
8-9 XII 1969	23.5	51
31 XII 1969 - 2 I 1970	63.3	49
20-23 I 1970	90.2	51

and weight has been represented in a composite form (Table 6).

In forming the composite for each species all of the growth measurements for a given year of growth were pooled regardless of sex and of calendar year during which the annuli were laid down. The mean scale measurement for a given year of growth was then computed, and the mean total length and corresponding weight were calculated using the length-scale radius relationships and weight-length relationships of Table 3. Confidence limits ($\alpha = 0.10$)[1] on mean total lengths expressed as percentages of the means were usually within $\pm$ 5 percent of the means except for the latter years of growth for which sample sizes were small (Table 6).

Two types of biases are involved with the composite growth representation. One of these is related to the decreasing number of growth determinations available from older fishes for any given year of growth. For example, of the 585 first year growth measurements available for S. andersoni 45 percent were from one year old fish whose first year of growth was in 1969, 17 percent were from two year old fish whose first year of growth was in 1968, and so on in decreasing percentages back to 1959 for which only one first year

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[1] A significance level (α) of 0.10 has been used in all statistical procedures throughout this paper. From a statistical viewpoint the sample sizes are relatively small and therefore, a level of significance of 0.10 increases the power of detecting differences.

TABLE 6. Composite representation of the growth of *S. andersoni*, *S. macrochir*, *T. rendalli*, *S. angusticeps*, and *H. odoe*.

	Year of Growth								
	1	2	3	4	5	6	7	8	9
S. andersoni									
Mean total length, mm	134±1%[1]	194±1%	242±1%	276±2%	307±2%	324±3%	338±3%	358±4%	389±7%
Length increment	134	60	48	34	31	17	14	20	31
Mean weight, g	43	135	267	400	556	656	747	892	1152
Weight increment	43	92	132	133	156	100	91	145	260
Sample size	585	321	220	114	68	37	24	18	8
S. macrochir									
Mean total length, mm	112±1%	172±1%	211±1%	231±1%	247±2%	262±2%	276±3%	295±7%	
Length increment	112	60	39	20	16	15	14	19	
Mean weight, g	27	106	202	269	333	402	474	585	
Weight increment	27	79	96	67	64	69	72	111	
Sample size	695	490	273	107	61	33	19	7	
T. rendalli									
Mean total length, mm	141±2%	212±2%	248±4%	277±6%	298±14%	310±16%	334±50%	344±55%	
Length increment	141	71	36	29	21	12	24	10	
Mean weight, g	55	199	327	464	585	662	838	920	
Weight increment	55	144	128	137	121	77	176	82	
Sample size	327	79	21	6	3	3	2	2	
S. angusticeps									
Mean total length, mm	187±2%	307±2%	372±3%	380±11%					
Length increment	187	120	65	6					
Mean weight, g	83	432	818	878					
Weight increment	83	349	386	60					
Sample size	255	103	25	4					
H. odoe									
Mean total length, mm	273±2%	333±1%	389±3%	414±11%	500±53%				
Length increment	273	60	56	25	114				
Mean weight, g	163	311	521	641	1199				
Weight increment	163	148	210	120	558				
Sample size	286	162	40	7	2				

measurement was available. Thus, the mean for any given year of growth is always biased toward the growth characteristic of the most recent growth year for which back-calculations were made, for my data, 1969.

The other source of bias in the composite representation of growth is related to sex. Ideally, the sex ratios existing in the populations of each species should be reflected in the sex ratios among the individuals whose growth was measured for the composite representations. In fact, the population-scale measurement sex-ratios were very close for S. andersoni, S. macrochir, and T. rendalli, but not for S. angusticeps and H. odoe (Table 7). Although male S. angusticeps were generally less abundant than females, two- and three-year old males spanned a greater length range than did females, and consequently the scales of more males than females were sampled. The opposite case pertained for H. odoe. For this species two- and three-year old females spanned a greater range in length than did the males. Thus, the composite representation of the growth of S. angusticeps is weighted toward the growth characteristic of males, and for H. odoe it is biased toward the growth patterns of females.

Comparative Growth

Comparative Growth of Kafue Floodplain Fishes

The growth of Kafue S. andersoni, S. macrochir, and T. rendalli was the subject of a recent doctoral dissertation

TABLE 7. Sex ratios among fish randomly selected for length measurements and sex ratios among fish randomly selected for scale samples.

	S. andersoni		S. macrochir		T. rendalli		S. angusticeps		H. odoe	
	n	Percentage Males	n	Percentage Males	n	Percentage Males	n	Percentage Males	n	Percentage Males
Sex Ratios for Length Measurements	11,239	52	11,910	54	5,613	48	1,547	41	4,460	46
Sex Ratios for Scale Samples	609	53	733	50	395	53	366	55	319	35

by Dudley (1972). Although his collections were made only in the vicinity of Lochinvar National Park in the central floodplain (Figure 1), and although he measured annular distances along a different scale radius than used herein and described the length-scale radius relationships with predictive regressions, his results are similar to mine (Table 8). For the comparisons I computed grand means for each year of growth from Dudley's (1972, Tables 6 to 8) data by weighting the means tabulated for each sex according to their respective sample sizes.

The largest differences between the results of the two investigations were generally for the middle-age years of growth of each species. These differences may be associated with geographical differences in size-selective mortality between the central floodplain area where Dudley's collections were made relative to the eastern floodplain area where most of my collections were made.

Dudley (1972) has shown that the growth rate of males of the above-mentioned species exceeds that of females. The same is true for S. angusticeps; however, the growth of female H. odoe exceeds that of males (Figure 6).

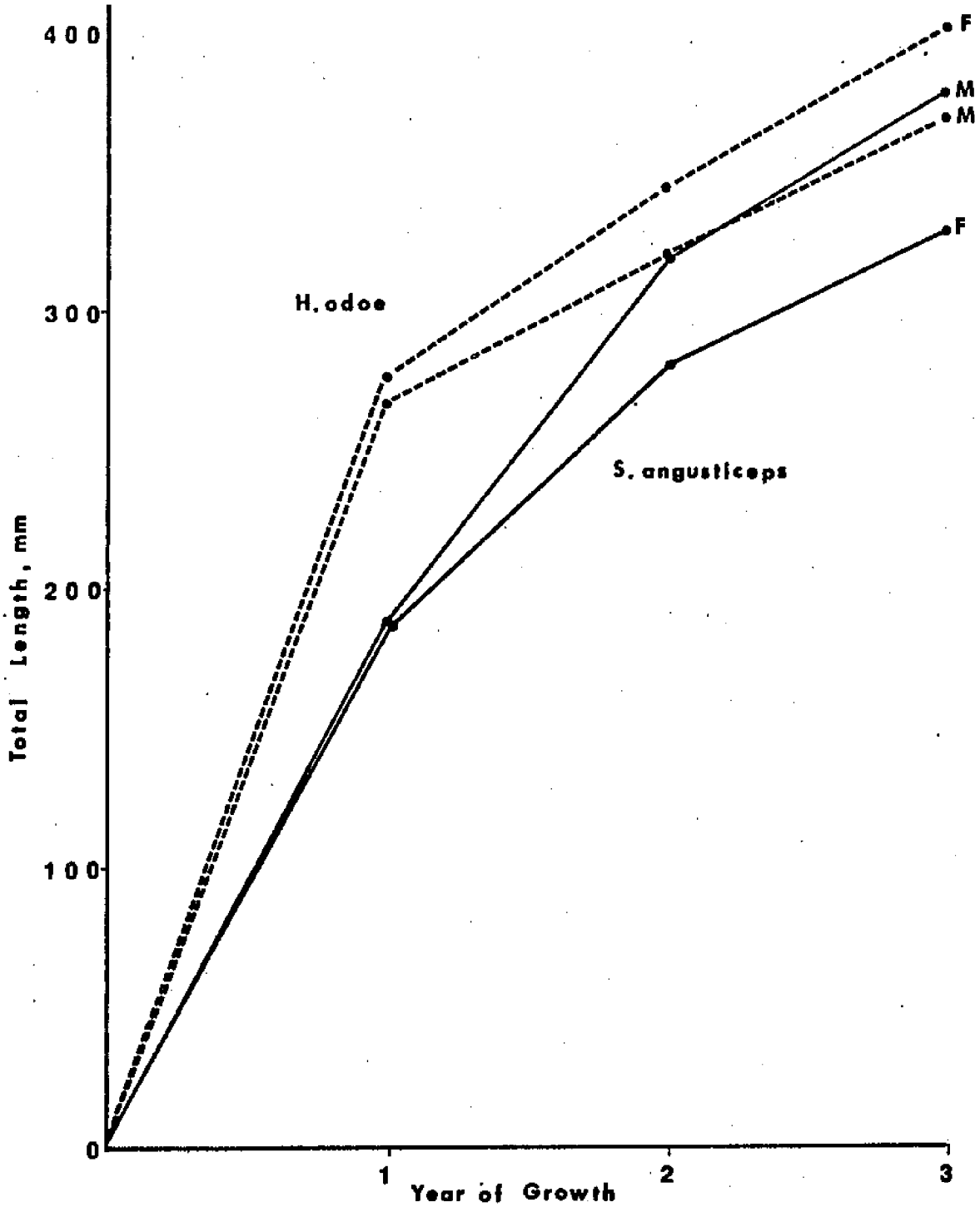
Comparative Growth of Kafue Floodplain, Barotse Floodplain, and Lake Kariba Fishes

Of the five species whose growth has been investigated herein, the growth of four conspecifics has also been studied in the Barotse floodplain of the upper Zambezi by Duerre (1969) and the growth of one of these fishes has also been

TABLE 8. Results of two investigations of the growth of S. andersoni, S. macrochir, and T. rendalli from the Kafue floodplain.

Year of Growth	1	2	3	4	5	6	7	8	9
					S. andersoni				
Sample size	585	321	220	114	68	37	24	18	8
Mean total length, mm (herein)	134	194	242	276	307	324	338	358	389
Difference (Dudley-herein)	+2	+11	+15	+12	+2	+6	+8	+1	-2
Mean total length (Dudley, 1972)	136	205	257	288	309	330	346	359	387
Sample size (Dudley, 1972)	440	465	364	223	162	130	93	44	11
					S. macrochir				
Sample size	695	490	273	107	61	33	19	7	
Mean total length (herein)	112	172	211	231	247	262	276	295	
Difference (Dudley-herein)	+6	+13	+13	+10	+3	0	-4	-27	
Mean total length (Dudley, 1972)	118	185	224	241	250	262	272	268	
Sample size (Dudley, 1972)	170	235	164	93	59	52	31	3	
					T. rendalli				
Sample size	327	79	21	6	3	3	2	2	
Mean total length (herein)	141	212	248	277	298	310	334	344	
Difference (Dudley-herein)	0	+9	+15	+12	+10	+20	+10	-14	
Mean total length (Dudley, 1972)	141	221	263	289	308	330	344	330	
Sample size (Dudley, 1972)	121	79	50	39	31	26	14	2	

FIGURE 6. Dimorphic growth of S. angusticeps and H. odoe.


400
300
200
100
0
Total Length, mm
H. odoe
S. angusticeps
F
M
M
F
1
2
3
Year of Growth

investigated in Lake Kariba, an impoundment of the middle Zambezi, by Bastl (in press).

In comparing the growth of the four Kafue species with that of their conspecifics from the Barotse floodplain, apparent differences in growth patterns exist (Figure 7); however, Duerre (1969) has emphasized that he did not validate the marks on the scales of Barotse fishes. Each of the four Kafue species attains a greater length in the first year of growth than does its conspecific of the Barotse floodplain; however, in subsequent years the growth in length of three of the Barotse species exceeds that of the Kafue species. The exception is S. angusticeps for which growth in the Kafue floodplain system is more rapid than growth in the Barotse system. It is interesting to note that Kafue S. angusticeps of more than three years of age were very rare; however, in the Baroste floodplain individuals of this species survive to an age of six years.

That growth in length is not a suitable criterion for comparisons of growth of conspecifics among systems is illustrated by comparisons of growth in both length and weight for Kafue floodplain and Lake Kariba T. rendalli (Figure 8). For this comparison the standard lengths tabulated by Bastl (in press, Table 33) have been converted to total lengths using my data for the relationship: Total length (mm) = 3.77 + 1.22 (Standard length (mm)), n = 177 ($s_{y \cdot x}$ = 5.16, r^2 = 0.99, for the predictive regression).

FIGURE 7. Growth in length of S. andersoni, S. macrochir, T. rendalli, and S. angusticeps from the Kafue floodplain and from the Barotse floodplain.

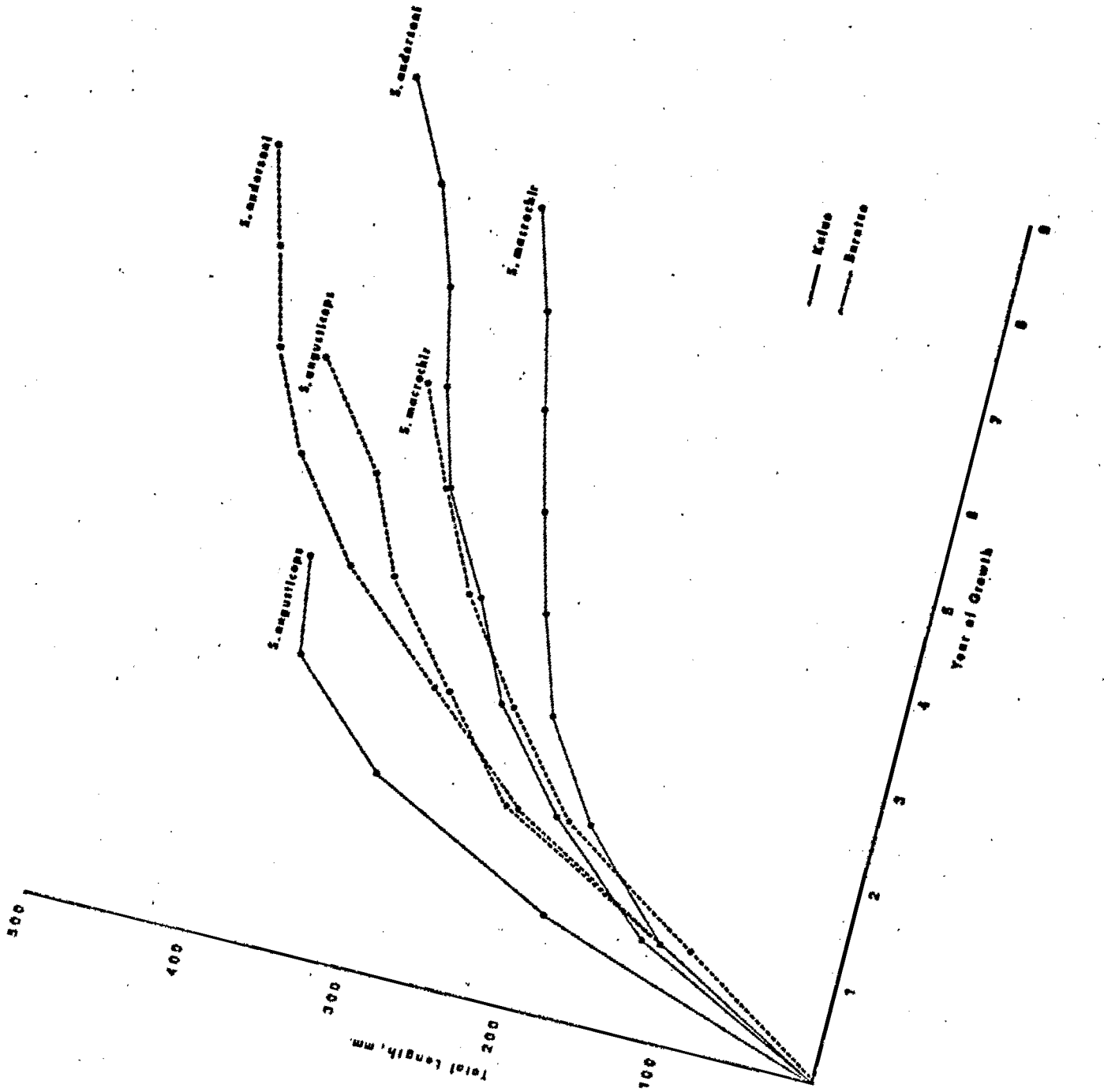
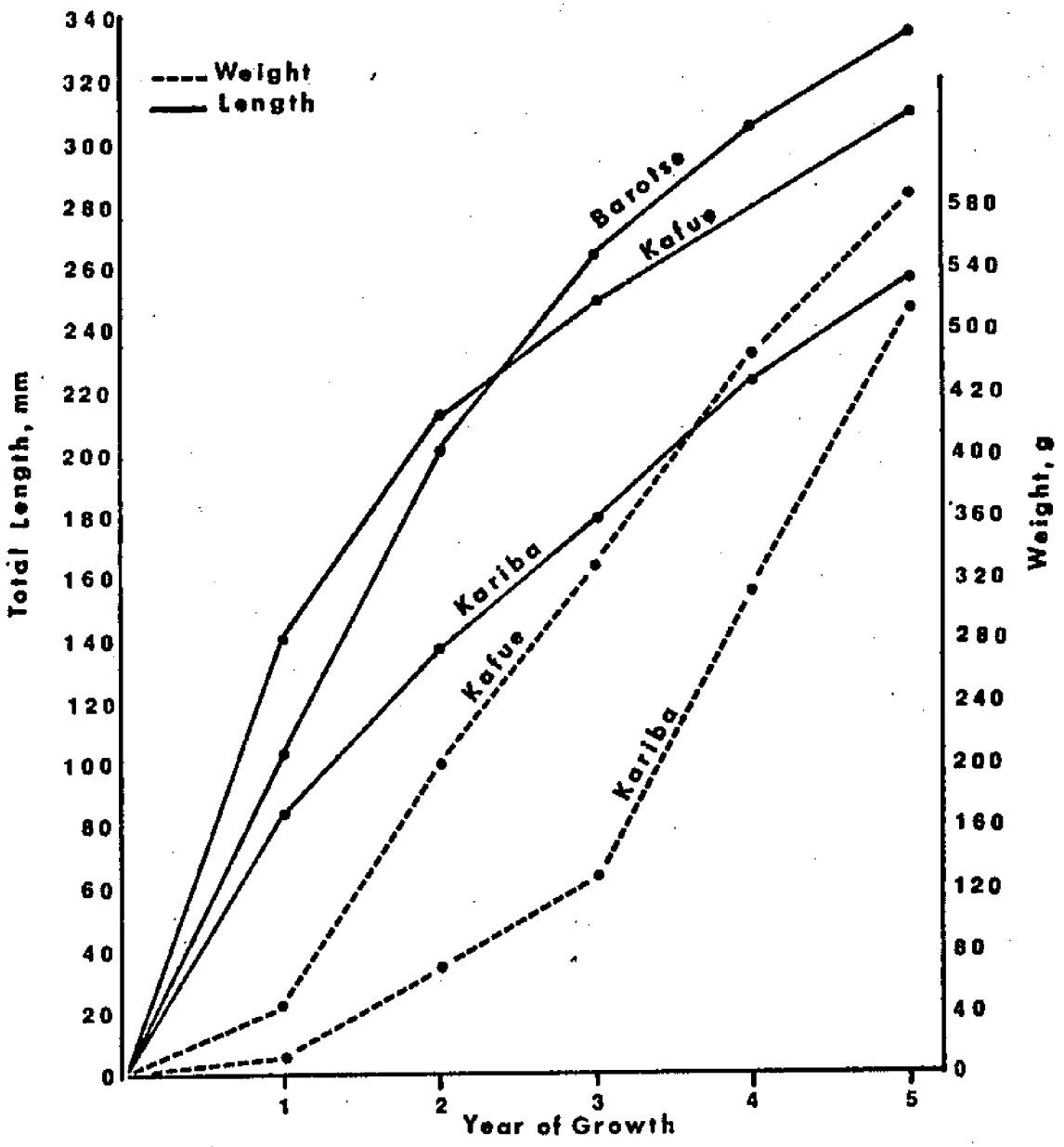

S. anderssoni
S. anguiticeps
S. macrochir
S. anderssoni
S. macrochir
S. anguiticeps
Kalgo
Baraka
Total length, mm
100
200
300
400
500
Year of Growth
1
2
3
4
5

FIGURE 8. Growth in length and weight of Kafue floodplain and Lake Kariba T. rendalli, and growth in length of Barotse floodplain T. rendalli.


Weight
Length
Barotse
Kafue
Kariba
Kafue
Kariba
Total Length, mm
Weight, g
Year of Growth
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
0
40
80
120
160
200
240
280
320
360
400
420
500
540
580
1
2
3
4
5

The length and weight plots (Figure 8) indicate that Kafue floodplain T. rendalli attain greater lengths and weights in each year of life than do the Lake Kariba fish; however, the plots also show that weights for the two populations converge with increasing age. For example, the weight of a Lake Kariba T. rendalli of 256 mm in total length is 510 g, (Bastl, in press, Table 33), but the weight of a Kafue floodplain T. rendalli of the same length is only 362 g, 71 percent of that of the Lake Kariba fish. The weight difference is too great to be accounted for by variations in condition between the two populations. Error in the weight-length relationship can be eliminated for the Kafue floodplain population because Dudley's (1972) predictive regression of weight on length provides an estimate of the weight of a fish 256 mm in length within 2 g of that predicted by my weight-length relationship. Thus, for this species it appears that real differences exist between Lake Kariba and Kafue floodplain growth patterns which are not evident from a comparison of lengths alone. Unfortunately, Duerre (1969) did not provide any weight data from which to extend the comparison; however, his length data for T. rendalli of the Barotse floodplain suggest that growth in length is more rapid after the first year of life than for the Kafue floodplain and Lake Kariba fish.

Variations in Growth

Seasonal Variations in Growth

It is reasonable to assume that the growth rates of fishes change throughout the year because of changes in the rate of primary production, because of the cyclical expansion and contraction of the aquatic environment, and because of seasonality of temperatures and of rainfall. Dudley (1972) has shown that juvenile S. andersoni and S. macrochir attained about 75 percent of the expected first year growth in length (mean for all years) by mid-May, 1970, about six weeks after peak inundation. Assuming that these fish were spawned in the beginning of December, 1969 (derived from Table 15, Dudley (1972)), then they would have been about 6½ months of age in mid-May. If growth in length were a linear function of time, then only about one-half of the first year growth increment would have been expected by mid-May.

Mean lengths computed from length frequency data with 10 mm class intervals (Snedecor and Cochran, 1967) for age group 0 and age group 1 fish during three periods from June to November, 1970, indicated that there was relatively little growth in length during this time (Table 9). The first period, from the third week of June to the end of July corresponded to the recession of the flood. During the second period, from mid-August to the third week of September, the floodplain had become dry and fishes were isolated in the river, marshes, and lagoons. The last period, from early

TABLE 9.--Mean lengths of S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe during three sampling periods in 1970.

		Period 1 22-VI - 30-VII 1970			Period 2 17-VIII-24-IX 1970			Period 3 7-X - 14-XI 1970			Expected Length (Table 6)		
	Age	x(mm)	s[1]	n	x(mm)	s	n	x(mm)	s	n	x(mm)	s	n
S. andersoni	1	179	16	1521	190	21	5049	185	14	3811	194	20	585
S. macrochir	0	-	-	-	89	11	71	97	15	57	112	21	695
	1	156	13	1684	161	15	5356	157	17	3653	172	19	490
T. rendalli	0	135	16	87	131	10	112	147	14	294	141	28	327
	1	173	14	1830	197	16	2076	181	13	1135	212	28	79
S. angusticeps		129	9	260	174	12	87	177	9	104	187	33	255
	1	243	14	272	253	20	580	240	12	139	307	39	103
H. odoe	0	224	19	55	243	23	123	-	-	-	273	34	286
	1	301	12	489	305	16	1985	315	17	1231	333	26	162

[1]Standard deviation.

October to mid-November, spanned the time when riverine, marsh, and lagoon habitats were approaching their minimum sizes during the 1970 hydrological cycle.

Length data were incomplete or represented by small sample sizes for the age group 0 fishes; however, there is some indication that growth in length was ongoing from the first to the second period, particularly for S. angusticeps, and from the second to third period, particularly for T. rendalli (Table 9). The mean lengths attained by age group 0 S. macrochir and S. angusticeps (Table 9) were less than the average first year growth increments for these two species (Table 6); however, T. rendalli exceeded the expected (mean) first year growth.

A comparison of the first period means for age group 1 fishes with those of the second period suggests that some growth in length occurred during this interval; however, there was a decrease in length for each species, except H. odoe, from the second to the third period. This may indicate that faster growing fishes were being selectively cropped by gill nets and seines. The mean lengths attained by age group 1 fishes during the first period exceeded the minimum length for harvest by 7.6 cm gill nets and seines (Lagler et al., 1971, Table 5.4).

The third period coincided with the beginning of annulus formation for S. andersoni, S. macrochir and T. rendalli, and therefore the mean lengths of fishes at that time should have corresponded to the lengths attained at

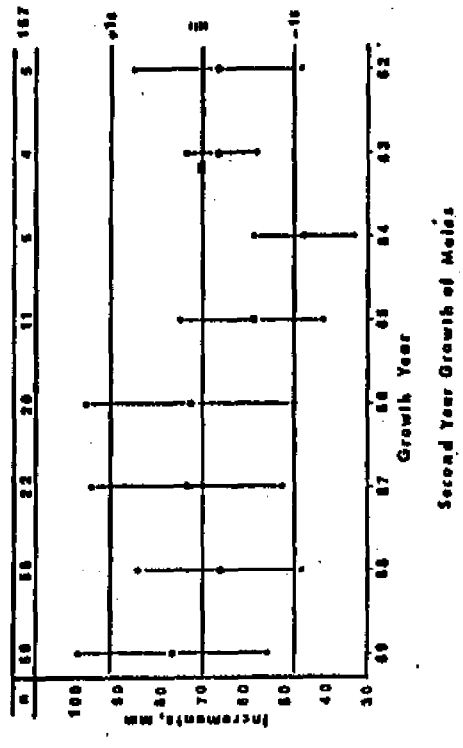
the end of the 1970 growth year. Comparisons of the means from the length frequency computations (Table 9) with the first and second year growth means from Table 6 for these three species suggest that 1970 was a below-average growth year.

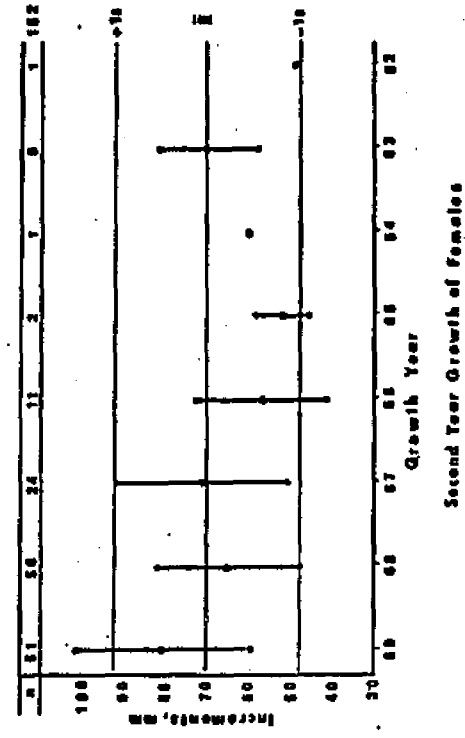
Annual Variations in Growth

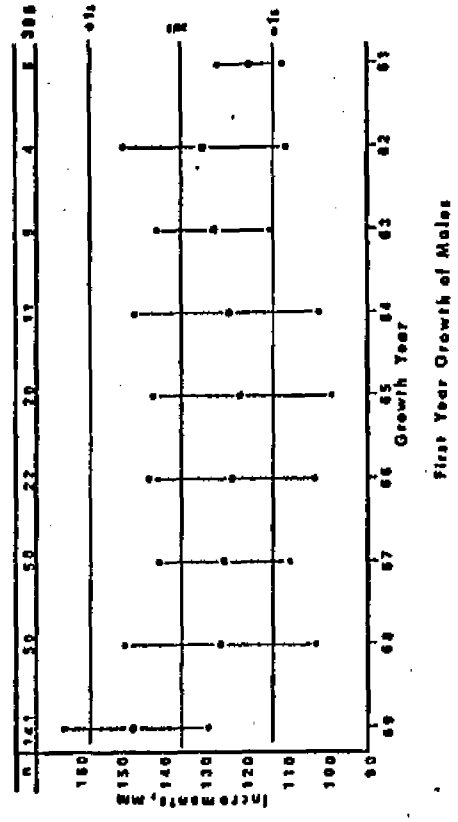
Physical conditions of environment such as the extent and duration of inundation, amount of rainfall, and seasonal temperatures vary from year to year in the floodplain ecosystem. Undoubtedly these annual variations in physical conditions engender corresponding variations in chemical and biological components of the system which, in turn, affect the dynamics of fish populations. Non-random annual variation in growth is one aspect of the dynamics of fish populations which appears to be characteristic of at least two species of Kafue floodplain fishes as shown by the similarity of the plots of mean length increments attained during the first and second years of growth (Figures 9 and 10). Along with annual variations in the numbers of fishes, annual variations in growth have important implications for fish production and fishery yield.

Results of Dudley's (1972) simple linear and partial correlations of annual growth with the annual duration and extent of inundation, cold season temperatures, and density of fishes suggest that these factors could account for much of the annual variation in the growth of some Kafue floodplain fishes.

FIGURE 9. Time plots of first and second year growth increments of male and female S. andersoni.


Second Year Growth of Males
Growth Year
Increments, mm


Second Year Growth of Females
Growth Year
Increments, mm


First Year Growth of Males
Growth Year
Increments, mm

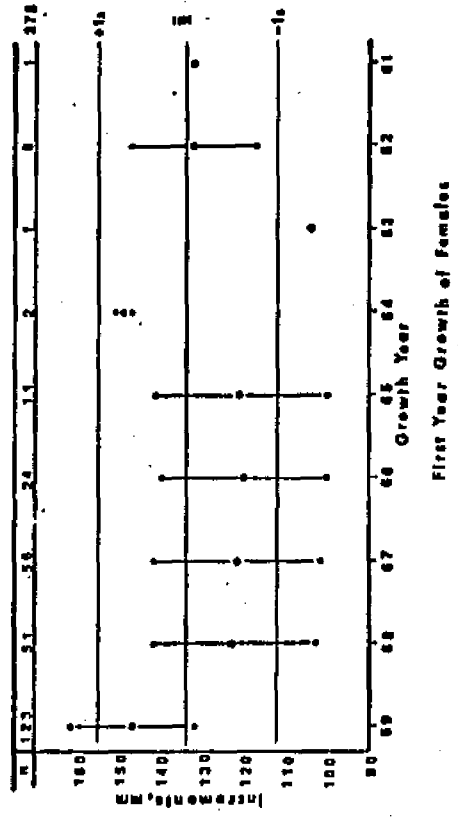
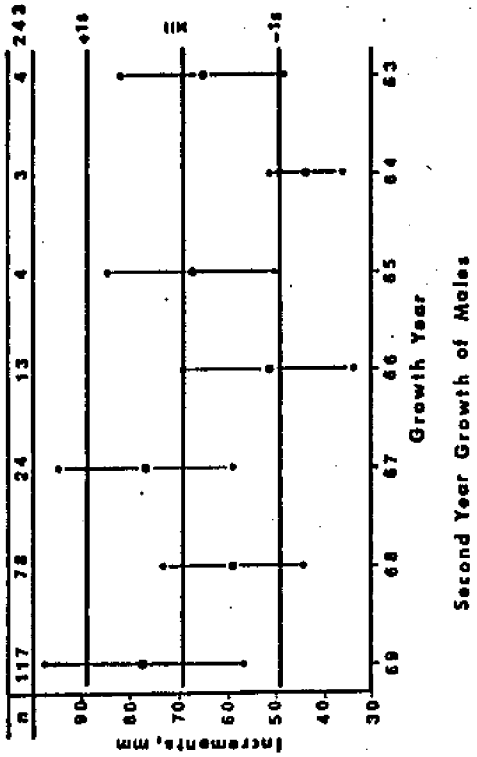
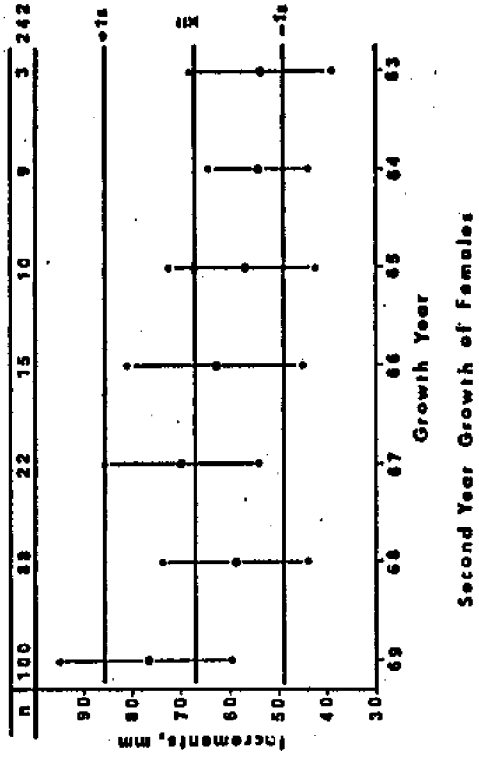
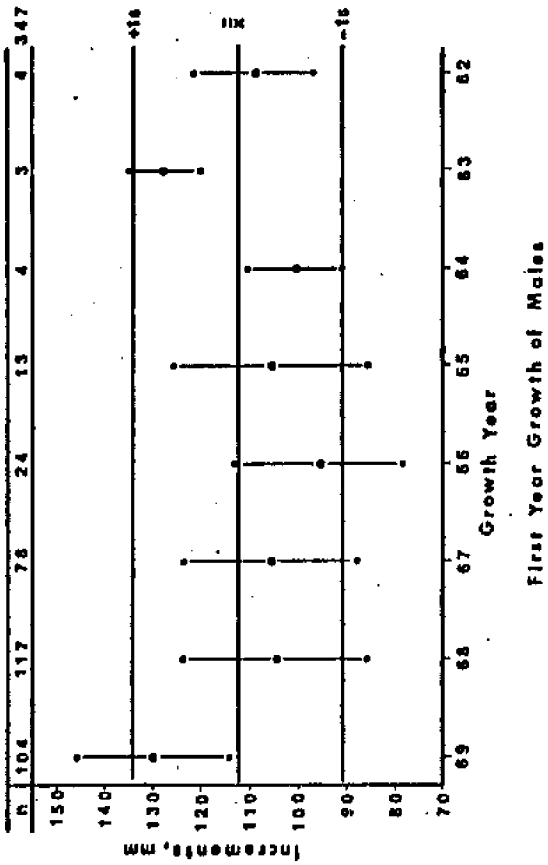
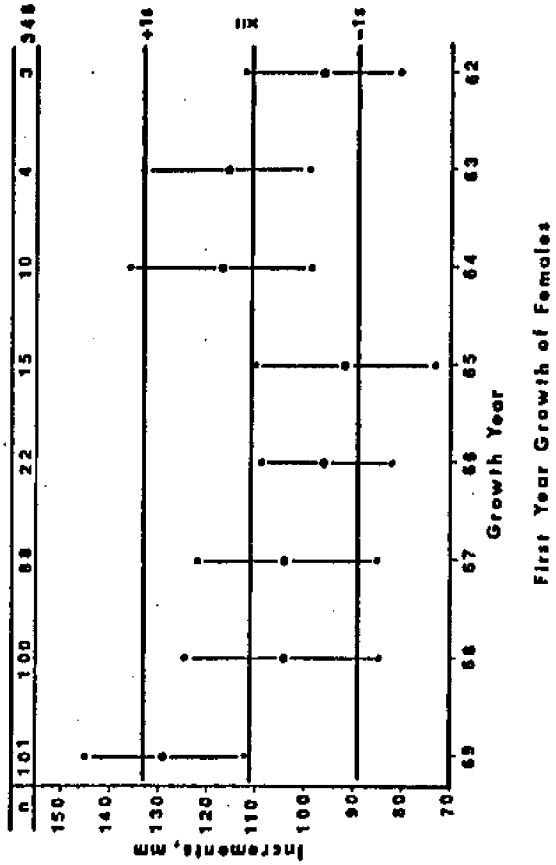

First Year Growth of Females
Growth Year
Increments, mm

FIGURE 10. Time plots of first and second year growth increments of male and female S. macrochir.


Second Year Growth of Males
Growth Year
Increments, mm
n
117 78 24 13 4 3 4 243
+1s
-1s
69 68 67 66 65 64 63


Second Year Growth of Females
Growth Year
Increments, mm
n
100 88 22 15 10 9 3 242
+1s
-1s
69 68 67 66 65 64 63


First Year Growth of Males
Growth Year
Increments, mm
n
104 117 78 24 13 4 3 4 347
+1s
-1s
69 68 67 66 65 64 63 62


First Year Growth of Females
Growth Year
Increments, mm
n
101 100 88 22 15 10 4 3 348
+1s
-1s
69 68 67 66 65 64 63 62

The objective here is to expand on the work begun by Dudley (1972) by using regression techniques to examine the apparent relationships between annual variations in growth and annual variations in abiotic and biotic factors of the environment. It is reasonable to assume that the entire sequence of environmental conditions throughout the year affects fish growth. Therefore, in addition to the single hydrological measure used by Dudley (1972) which represented the extent and duration of inundation, I have hypothesized that fish growth is also influenced by the hydrological conditions which prevail after the floodplain has become dry, and accordingly, two indices have been developed to reflect hydrological conditions during this period. Further, as a measure of the effect of temperature on fish growth Dudley (1972) used an independent variable which represented only the temperature conditions which prevailed during the cold season of each year. In addition to an index of the temperatures during the cold season, I have computed two other temperature indices which incorporated seasonal temperature conditions during the cool season and during the warm season of each year. Finally, as an indication of the effect of interspecific competition on growth, Dudley (1972) used annual fishery yield as an independent variable. Along with this type of measure of the density of the entire fish stock, I have computed two indices which permit evaluation of the effects of density on growth at the species level.

Hydrological Indices.--Estimates of the areas of the floodplain which were inundated during each hydrological cycle after 1964 were not available and therefore it was necessary to find another means to approximate these quantities. Dudley's (1972) "Flood Index" was based on a plot of water level observations taken at the Kasaka gauge station near Kafue at the eastern terminus of the floodplain (Figure 1). Values for this index were computed as the areas under the water level curves above a depth of 4.88 m. No reason was given for the selection of this depth. I have adopted Dudley's (1972) method, but I have attempted to make the measurements more realistic by using estimates of the water levels at which the floodplain initially becomes inundated and at which it finally becomes dry during each hydrological cycle. Furthermore, it cannot be assumed that water level data taken from one location on the floodplain, particularly at its extremity, best represents hydrological conditions throughout the floodplain. Therefore, in addition to the water level data from the Kasaka gauge station, I also have used water level data from the Nyimba gauge station on the central floodplain (Figure 1) to compute another set of hydrological indices. Geographically, the two gauge stations are located at the peripheries of the areas in which my fish collections were made.

Water level heights at each gauge station which corresponded to the initial inundation and final recession of the flood from the floodplain served as the basis for the

computation of the hydrological indices. These water level heights were determined by matching water level observations taken on the first day of each month with estimates of the area inundated on the floodplain during these same months from January, 1957 to October, 1964.[2] At the Kasaka gauge station the mean water level at which the floodplain became inundated was 5.18 m and the water level at which the floodplain became dry was 5.93 m. The respective estimates for the Nyimba gauge station were 4.42 m and 5.03 m. Water level data were obtained from the Department of Water Affairs, Lusaka.

Hydrological Index 1 is defined by the area above the water level curve at which the floodplain initially becomes inundated and at which it finally becomes dry (Figure 11). Values for this index for each hydrological cycle were computed by plotting water level observations taken on the first day of each month at the Nyimba and Kasaka gauge stations. The area under the curve was estimated by using a planimeter (Table 10). With water level as the ordinate and time as the abscissa, Hydrological Index 1 is a measure of the annual extent and duration of the inundation

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[2]The estimates of the area inundated in each month were taken from a copy of a computer printout. The data were generated in connection with a background study for the Multipurpose Survey of the Kafue River Basin (FAO, 1968) entitled "Study No. 6, Water Balance of the Kafue Flats." Attempts to obtain a copy of this study in Stockholm, London, Lusaka, and Rome failed.

FIGURE 11. Derivation of three hydrological indices from monthly water level observations at the Nyimba gauge station.

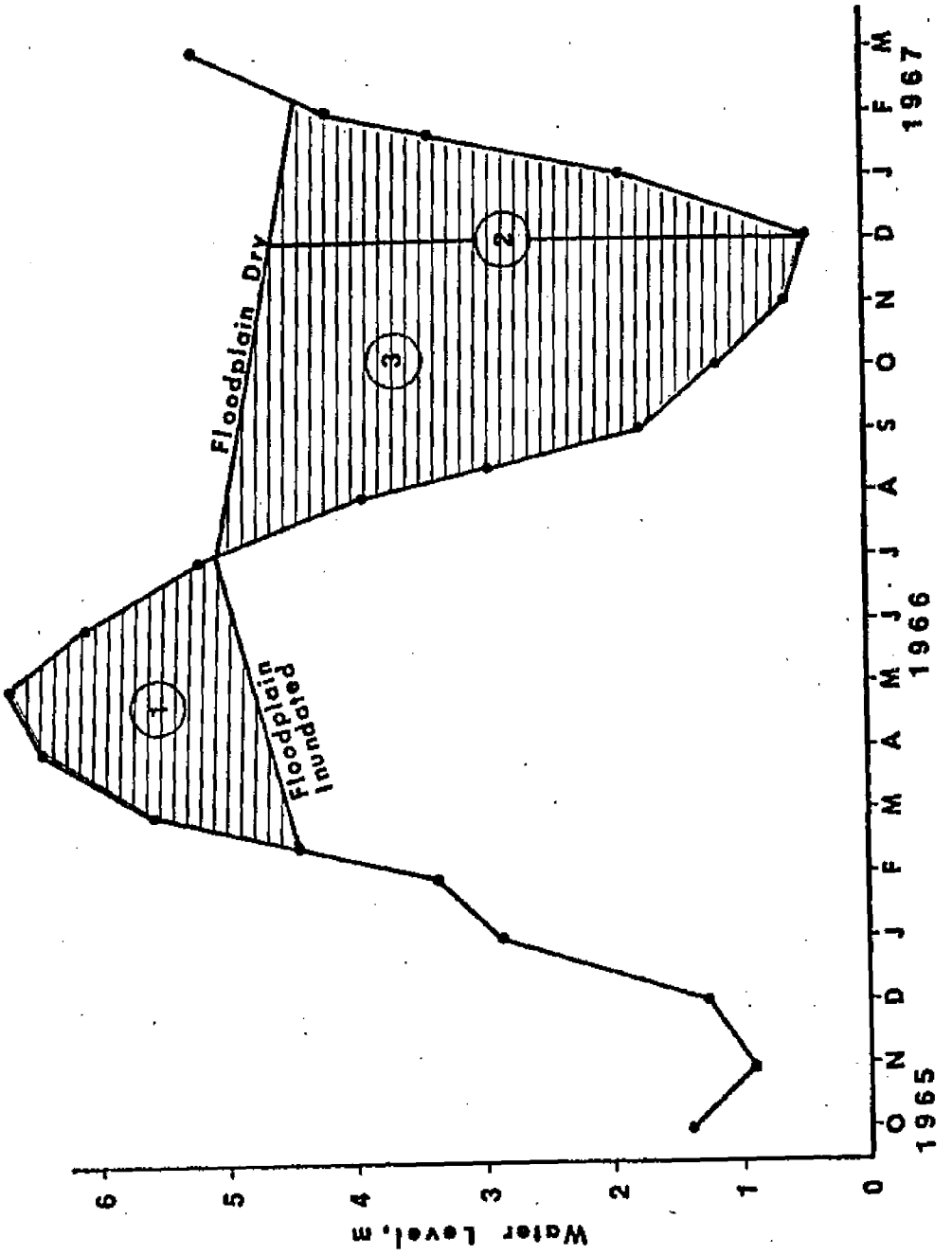

Floodplain Dry
Floodplain Inundated
1
2
3
Water Level, m
0
1
2
3
4
5
6
O N D J F M A M J J A S O N D J F M
1965
1966
1967

TABLE 10. First and second year length increments of S. andersoni, and of S. macrochir and values of temperature, hydrological, and density indices.

	Length Increments (mm)								Temperature Indices		
	S. andersoni				S. macrochir				Cool Season	Cold Season	Warm Season
	First Year		Second Year		Firts Year		Second Year				
Year	M	F	M	F	M	F	M	F	Dec.-Apr.	May-Aug.	Sep.-Nov.
1969	146.6	147.0	77.1	80.8	130.2	128.8	77.5	77.3	55.8	53.6	27.2
1968	126.3	122.5	65.6	65.1	105.1	104.3	59.2	58.7	58.0	46.8	23.8
1967	125.1	122.0	73.9	71.2	106.3	103.6	71.8	69.7	62.5	49.7	24.0
1966	122.9	120.5	72.9	57.2	95.6	95.9	51.5	62.9	59.5	52.8	27.2
1965	120.6	120.8	57.7	51.9	106.1	91.7	67.5	57.3	50.9	44.7	22.2
1964	124.5	148.6	45.6	59.8	101.3	117.5	43.7	53.9	56.2	38.7	21.3
1963	127.2	104.0	65.6	69.7	127.9	116.5	65.0	53.8	53.6	47.4	24.3
1962	129.5	132.3	66.4	48.8	109.4	96.2	-	-	55.1	51.1	18.2
1961	118.7	132.1	-	-					55.5	55.5	16.2

	Hydrological Indices						Density Indices			
	Kasaka			Nyimba					Kafue Camp Number/gill net	
Year	1	2	3	1	2	3	Fishery Area lbs/gill net	Lusaka District lbs/gill net	S. andersoni	S. macrochir
1969	161	7	7	215	10	8	15.8	14.9	0.68	0.32
1968	3	78	51	41	199	127	10.7	9.3	5.43	3.20
1967	5	80	39	68	179	95	10.6	7.8	0.25	0.14
1966	21	104	80	72	243	185	13.8	6.8	0.53	0.51
1965	8	106	71	87	226	119	14.8	11.8	0.11	0.42
1964	21	71	38	130	172	88	19.6	11.8	0.64	0.68
1963	263	26	15	294	19	14	29.2	15.0	1.03	0.35
1962	115	3	3	233	10	9	25.2	13.8	-	-
1961	67	41	14	134	112	56	28.4	18.6	0.26	0.32

of the floodplain. A positive effect on annual growth is hypothesized for this index because the duration and extent of inundation should indirectly, but positively affect the availability of food and of living space. Hydrological Index 2 is the area above the water level curve from the time when the floodplain finally becomes dry until it is once more inundated (Figure 11, Table 10). This index is a relative measure of the extent of the aquatic environment when the floodplain is dry and it also measures the duration of the period during which fishes are confined to the river channel, lagoons and marshes. The Index 2 - growth relationship is hypothetically negative because during this period food resources and living space are at a minimum. Index 3 is similar to Index 2 but includes the area above the water level curve only to the time when minimum annual water levels occur (Figure 11, Table 10). Thus this index is a measure of the extent and duration of the contraction of the aquatic environment after the floodplain has dried. The hypothesized relationship with growth is negative for the same reason as was suggested for Index 2.

Temperature Indices.--Three indices were computed to represent annual variations in seasonal temperatures. These were for the warm season from September to November, the cool season from December to April, and the cold season from May to August (Table 10). The latter corresponds approximately to Dudley's (1972) cold season temperature index.

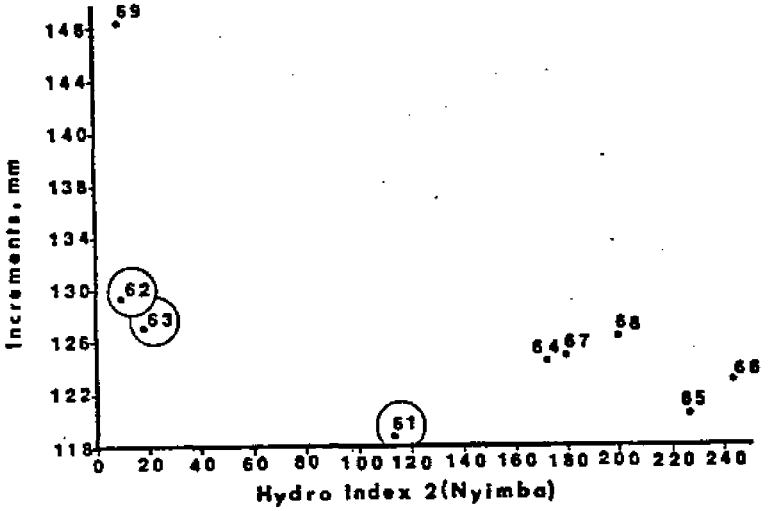
Values of indices were calculated as the sums of mean monthly air temperatures minus a constant as measured at Kafue Polder in the eastern floodplain area (Department of Meterology, Lusaka). A positive relationship of temperatures with growth is hypothesized because S. andersoni and S. macrochir in the Kafue are near the southern limits of their respective ranges.

Density Indices.--Values for four density indices were computed to represent likely intra- and interspecific competition for food and space. The first density index is a measure of the annual variation in the density of the entire exploited stock which includes about 19 species. It was computed as the mean annual catch per gill net (in lbs) for the entire fishery area (Anon., 1962, 1963; Central Statistical Office, Lusaka, 1965-1970) (Table 10). Density Index 2 was similar, but was computed for the Lusaka District of the fishery which encompasses most of the eastern floodplain area. The third and fourth density indices were, respectively, the mean annual catches per gill net (in numbers) of S. andersoni and of S. macrochir at Kafue Fish Camp at the eastern end of the floodplain (unpublished data of the Department of Wildlife, Fisheries, and National Parks, Chilanga, and of the Central Statistical Office, Lusaka) (Table 10). Density-dependent effects were expected and therefore the growth-density relationships were hypothesized to be negative.

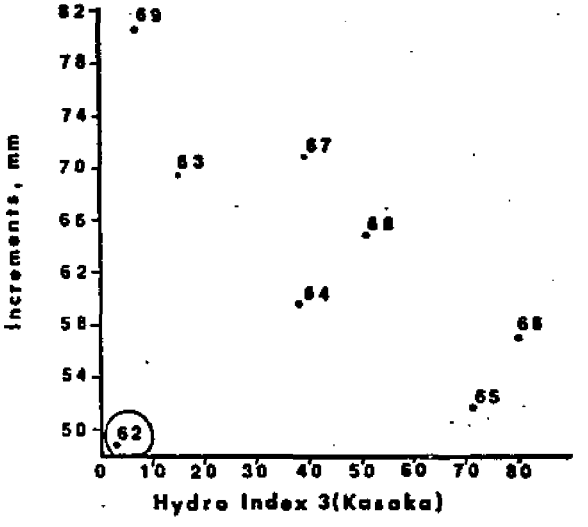
Dependent Variables.--Annual variations in growth were represented by back-calculated first and second year mean growth increments of S. andersoni and of S. macrochir (Table 10, Figures 9 and 10). Too few growth observations were available from older-aged T. rendalli, and the relatively short life spans of S. angusticeps and of H. odoe precluded the use of growth data for these species.

Growth Models.--As the initial step in the model building process, dependent variables were plotted with independent variables and the forms of likely relationships were identified (e.g., Figures 12 and 13). The relationships were apparently linear, or no discernable relationships existed. A correlation matrix of dependent and independent variables was also examined to confirm the results of visual examination and to insure that multicolinearity was not serious in multiple linear regressions. Dependent variables were regressed on the most likely indpendent variables or combinations of independent variables as determined from the plots and correlation matrices. The relatively high correlation coefficients among hydrological variables ($r = 0.70 +$) precluded the use of more than one in any regression. A check on the underlying assumptions of the models was conducted by examination of the plots of the residuals with the independent variables, and with the predicted values. Normal plots were also made and these were compared with those of Daniel and Wood (1971) for similar sample sizes. The results

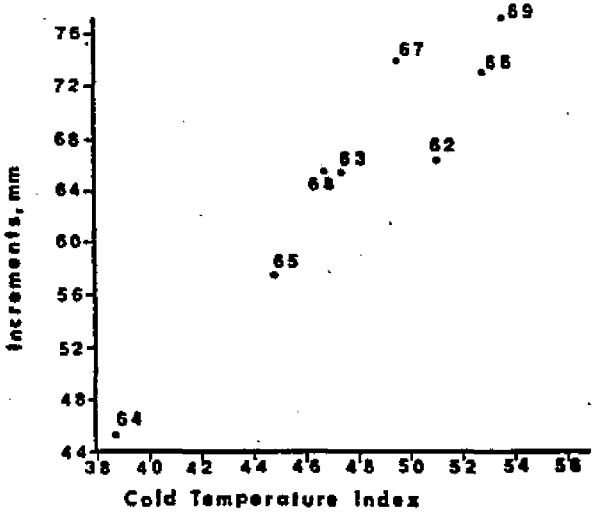
FIGURE 12. Plots of first and second year growth increments of male and female S. andersoni with hydrological and temperature indices. Outliers not used in regressions are circled.



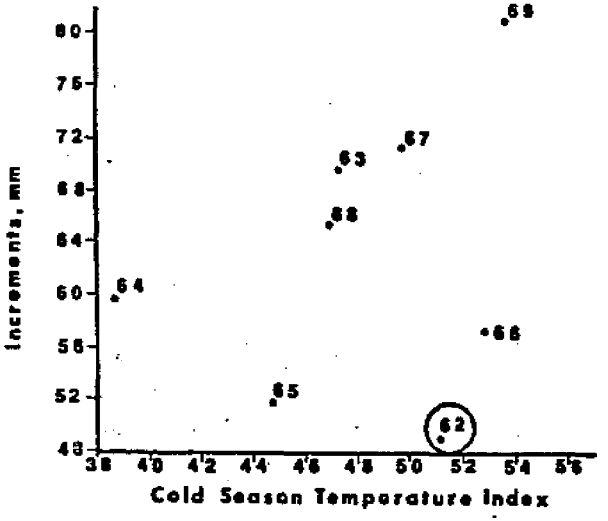
First Year Growth of Male S. andersoni



Second Year Growth of Female S. andersoni

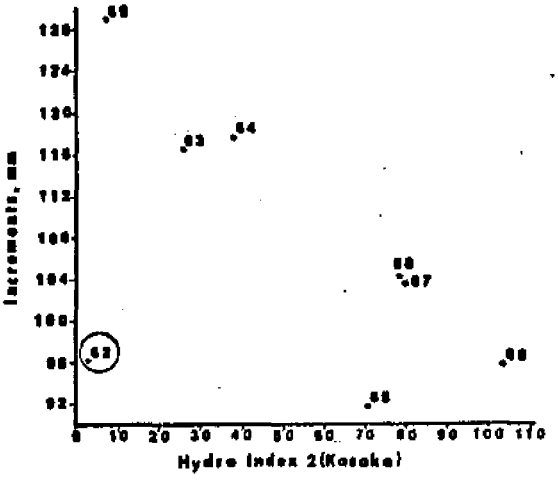


Second Year Growth of Male S. andersoni

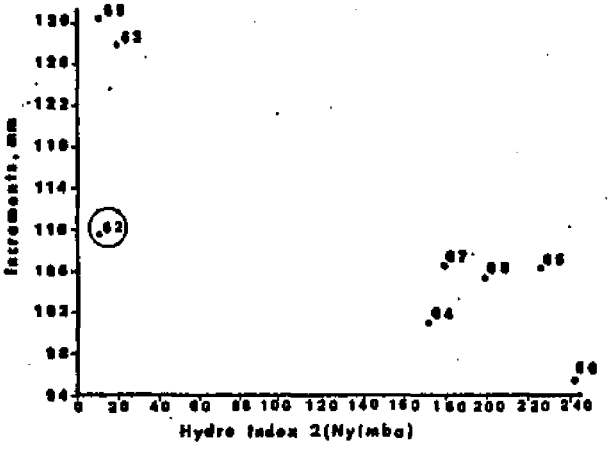


Second Year Growth of Female S. andersoni

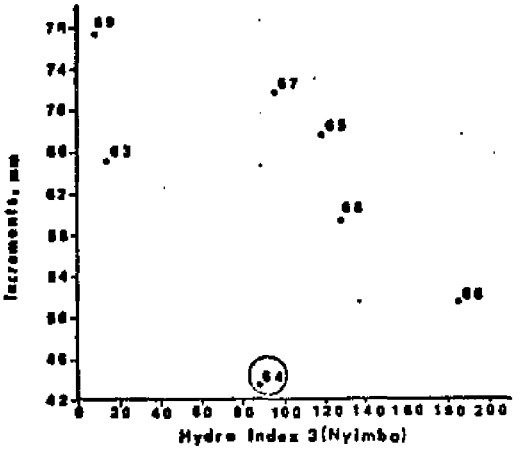
FIGURE 13. Plots of first and second year growth increments of male and female S. macrochir with hydrological and temperature indices. Outliers not used in regressions are circled.



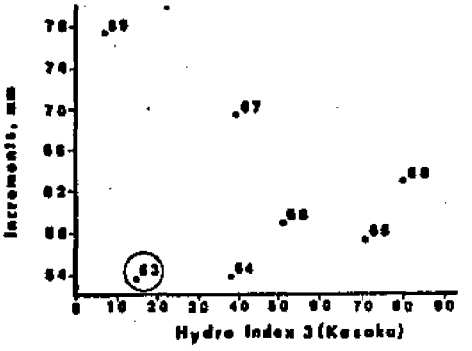
First Year Growth of Male S. macrochir



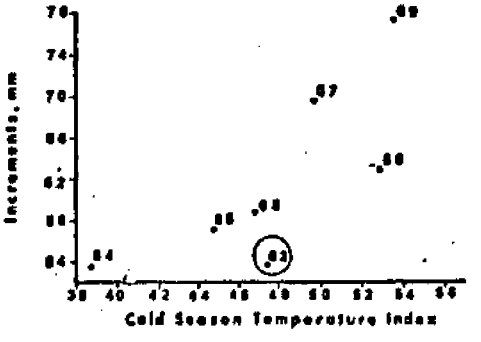
First Year Growth of Female S. macrochir



Second Year Growth of Male S. macrochir



Second Year Growth of Female S. macrochir



Second Year Growth of Female S. macrochir

of these checks suggested that the assumptions of the models were not seriously violated. The level of significance of F-statistics for regression and of t-statistics for intercepts and slopes was set at $\alpha = 0.10$ as elsewhere throughout this paper. This level was adhered to with one exception.

The results of the model building, in themselves, and their similarity to the results of Dudley's (1972) correlations, support the hypothesis that annual variations in the hydrological regime exert significant, but probably indirect, effects on annual variations in the growth of floodplain fishes. These results also support Dudley's (1972) hypothesis that annual variations in temperatures during the cold season affect fish growth. Probabilities of higher values of F for regressions ($\hat{P}_F$) were less than 0.001 in five of the seven relationships and for the other two were less than 0.011 and 0.078 (Table 11). Plots of observed and predicted growth increments on time illustrate the generally good fits obtained (Figures 14 and 15).

No logical relationships existed between fish growth and my density indices. Dudley (1972) found one significant ($\alpha = 0.10$) negative correlation between the third year growth and of male S. macrochir and an index of the total annual catch.

Hydrological Indices 2 and 3, representing conditions in the aquatic environment after the floodplain had dried, provided the best relationships with my growth data (Table 11). Index 3, representing the duration and extent of contraction

TABLE 11.--Parameter estimates for simple and multiple linear regressions of first and second year growth increments of S. andersoni and of S. macrochir on temperature and hydrological indices.

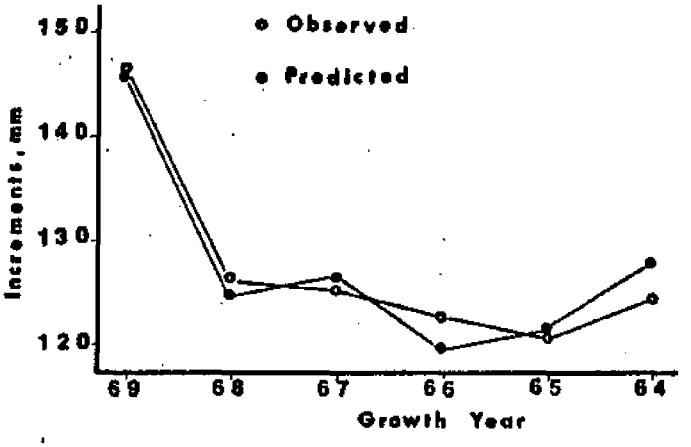
Year of Growth	Sex	Years	Model	R^2	$s_{y \cdot x}$	$\hat{P}_R$ [1]	$\hat{P}_I$ [1]	$\hat{P}_{X_1}$ [1]	$\hat{P}_{X_2}$ [1]
			S. andersoni						
First	M	1964-69	T.L.(mm)=146.51-0.11(H.I.[2](N)[3])	0.94	2.63	0.0014	0.0000	0.0014	-
Second	M	1962-69	T.L.(mm)=-29.47+1.98(T.I.2)	0.90	3.39	0.0003	0.0596	0.0003	-
Second	F	1963-69	T.L.(mm)=38.24-0.30(H.I.3(K))+0.83(T.I.2)	0.93	3.16	0.0049	0.0377	0.0034	0.0305
			S. macrochir						
First	M	1963-69	T.L.(mm)=130.39-0.13(H.I.2(N))	0.92	4.02	0.0006	0.0000	0.0006	-
First	F	1963-69	T.L.(mm)=130.13-0.32(H.I.2(K))	0.85	5.54	0.0030	0.0000	0.0030	-
Second	M	1963,65-69	T.L.(mm)=74.72-0.10(H.I.3(N))	0.58	6.66	0.0778	0.0001	0.0078	-
Second	F	1964-69	T.L.(mm)=14.69-0.18(H.I.3(K))+1.20(T.I.2)	0.95	2.48	0.0106	0.2389	0.0251	0.0094

[1] Probabilities of higher values of F for regressions, of t for intercepts, and of t for the slopes of the first and second independent variables.

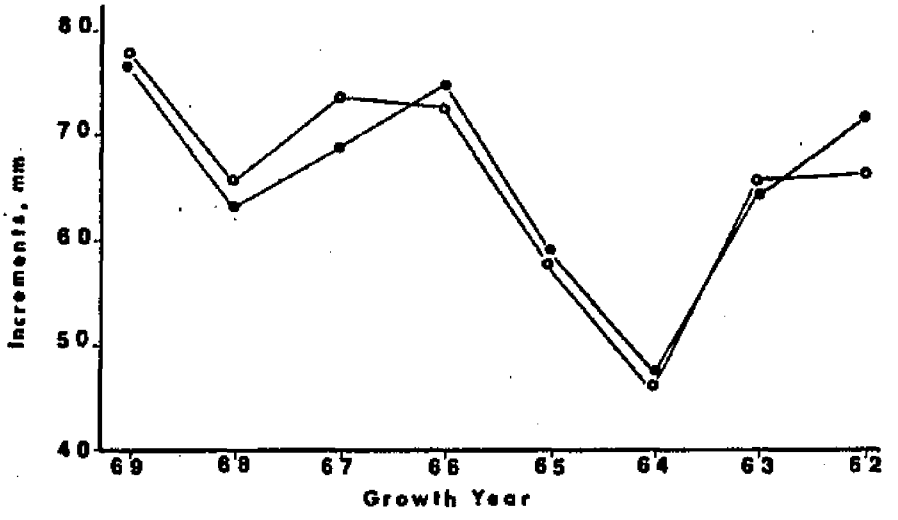
[2] H.I. - Hydrological Index; T.I. - Temperature Index.

[3] N - Nyimba; K - Kasaka.

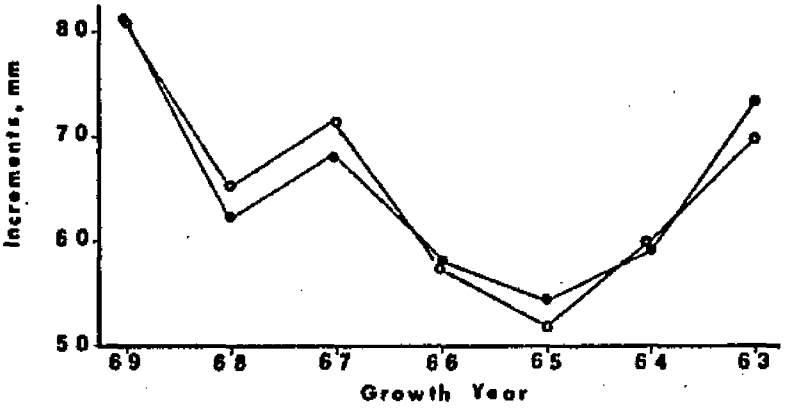
FIGURE 14. Observed values, and predicted values from regressions of first and second year growth increments of male and female S. andersoni on temperature and hydrological indices.



First Year Growth of Males on Hydro Index 2(Nyimba)

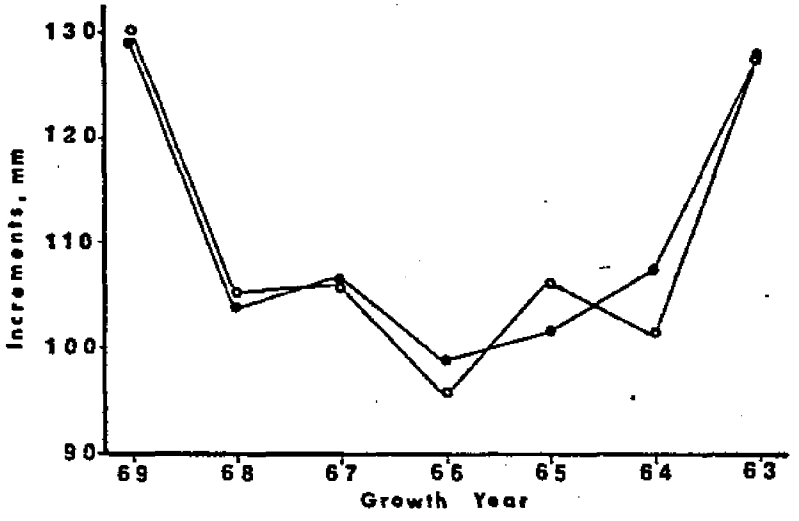


Second Year Growth of Males on Temperature Index 2

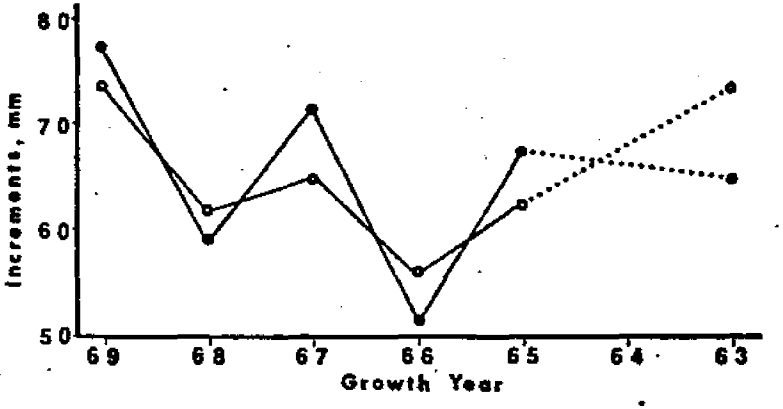


Second Year Growth of Females on Hydro Index 3(Kasaka) and Temperature Index 2

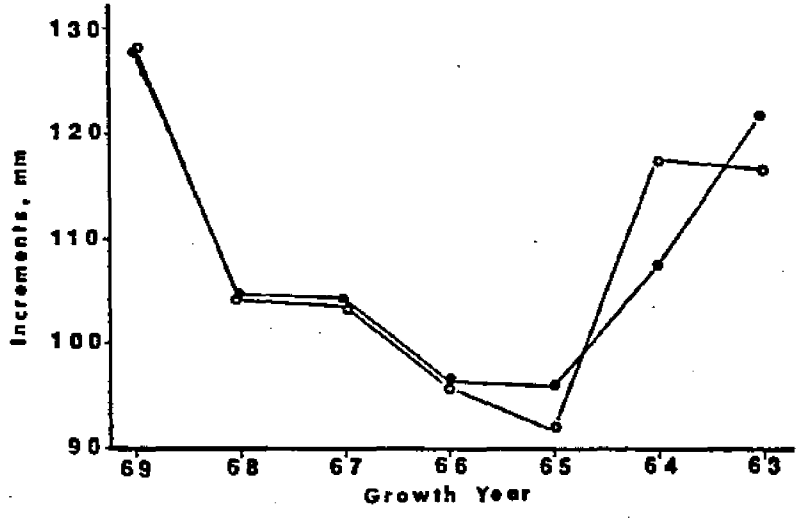
FIGURE 15. Observed values, and predicted values from regressions of first and second year growth increments of male and female S. macrochir on temperature and hydrological indices.



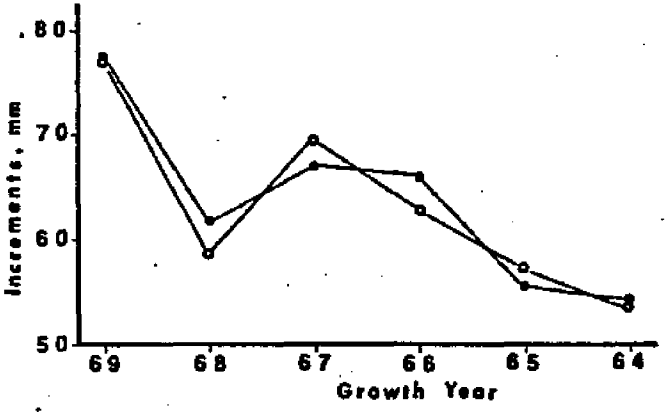
First Year Growth of Females on Hydro Index 2(Nyimba)



Second Year Growth of Males on Hydro Index 3(Nyimba)



First Year Growth of Females on Hydro Index 2(Kasaka)



Second Year Growth of Females on Hydro Index 3 (Kasaka) and Temperature Index 2

of the aquatic environment, was most closely related to second year growth increments and Index 2 gave the best fit with first year growth increments (Table 11). I selected the two sets of Dudley's (1972) growth data (from his Tables 3 and 4) that had the highest correlation coefficients with his own hydrological index ($r = 0.92$ and $r = 0.90$) and plotted these with my hydrological indices. The plots indicated that Dudley's (1972) data gave a slightly better fit to my hydrological Index 1 than to my Indices 2 and 3.

Outliers, suspect growth measurements, occurred in nearly all of the plots (e.g., Figures 12 and 13). These were mean growth measurements which were based on very small sample sizes for the period 1961 to 1964 and therefore were suspect from the outset. Apparent outliers were excluded from the regressions only after a number of plots with additional independent variables were examined and the suspected erroneous value was seen to consistently occupy a position other than that expected for it. In the case of the first year growth of male S. andersoni three outliers were identified (Figure 14). Here my suspicion that the 1961 and 1963 growth means were too low was confirmed by plots of Dudley's (1972, Table 3) growth data for males of this species for which he had sample sizes larger than mine for the years in question. The growth mean for 1962 was also an outlier in his data, and the means for this same year are also outliers among my data for the first year growth of male and female S. macrochir (Figure 13). Although the

growth measurements for this year might coincidentally be in error among males and females of these species in my data and also in Dudley's data, it may be that the growth of these fishes in 1962 did not respond, as usual, to factors associated with the hydrological regime.

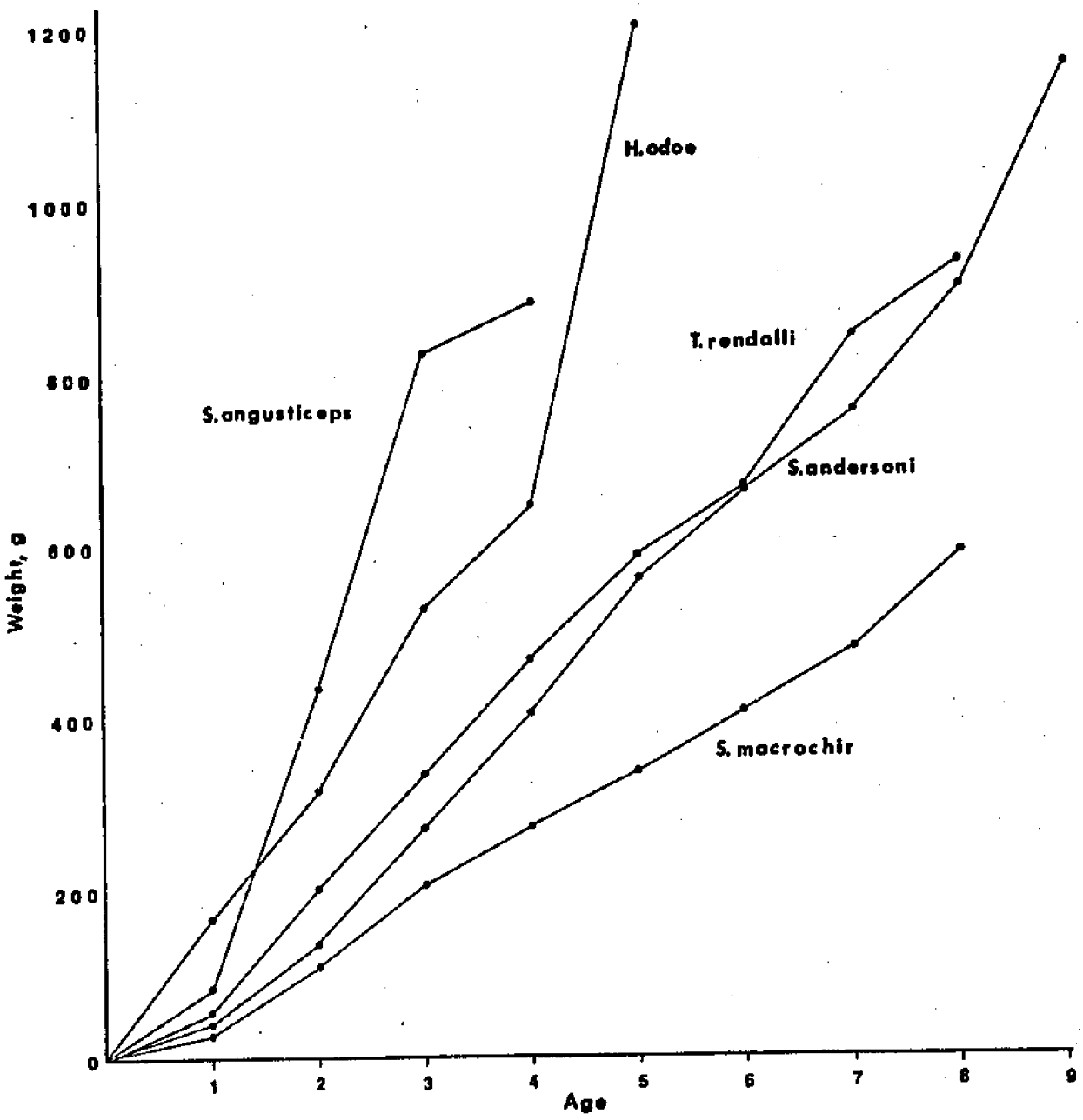
The growth models have been built in order to demonstrate one aspect of the dynamics of floodplain fish populations. Their use for predictive purposes is restricted on the one hand because of the relatively short span of years incorporated in the models and on the other hand by the nature of the independent variables, the values of which cannot be computed in advance of the growth process to which they are apparently indirectly related. Additional aspects of the growth - hydrological and growth - temperature relationships are discussed in Chapter IV.

Annual Growth in Weight

Production estimates for the five species are presented later in terms of "average" values for the Kafue River floodplain which involve the smoothing of annual growth and mortality curves for each species.

Plots of the mean weights attained at the beginning of each year of life (from Table 6) on age suggest that annual growth in weight from age 1 onward can be considered as approximately linear for the data available here (Figure 16). The largest deviations from the apparent linear trends occurred for older-aged fishes for which sample sizes were

FIGURE 16. Mean weights attained at the beginning of each year of life for S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe.


1200
1000
800
600
400
200
0
Weight, g
1
2
3
4
5
6
7
8
9
Age
H.odoe
T.rendalli
S.angusticeps
S.andersoni
S. macrochir

relatively small. For example, the final weights of S. andersoni and H. odoe were higher than would be expected, and the final weight of S. angusticeps was less than would be expected from the weight-age trends for earlier years of life (Figure 16).

The curves of annual growth in weight were smoothed by regression of the mean weights attained at the beginning of each year of life (from age 1 onward) on age (Table 12). Because of the possibility of bias in the weight estimates for the final years of life due to small sample sizes, final weight observations were eliminated from the regressions for each species where they departed from the apparent linear trends for the previous years of life. The predicted weights provided good fits to the observed weights (Table 12).

TABLE 12. Weights at the beginning of each year of life computed from mean lengths and weight-length relationships, and predicted weights from regressions of weight on age for S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe.

	Age								
	1	2	3	4	5	6	7	8	9
S. andersoni									
Observed Weight, g	43	135	267	400	556	656	747	892	1152
Predicted Weight, g	32	155	278	401	523	646	769	892	1015
Parameter Estimates	Weight = -91.18 + 122.93 (Age) (Ages 1-8; n = 8)								
S. macrochir									
Observed Weight, g	27	106	202	269	333	402	474	585	
Predicted Weight, g	38	112	185	259	333	406	480	554	
Parameter Estimates	Weight = -35.86 + 73.71 (Age) (Ages 1-7; n = 7)								
T. rendalli									
Observed Weight, g	55	199	327	464	585	662	838	920	
Predicted Weight, g	74	197	321	444	568	692	815	939	
Parameter Estimates	(Weight = -49.61 + 123.52 (Age) (Ages 1-8; n = 8)								
S. angusticeps									
Observed Weight, g	83	432	818	878					
Predicted Weight, g	77	444	812	1179					
Parameter Estimates	Weight = -290.67 + 367.50 (Age) (Ages 1-3; n = 3)								
H. odoe									
Observed Weight, g	163	311	521	641	1199				
Predicted Weight, g	162	327	491	666	820				
Parameter Estimates	Weight = -2.00 + 164.40 (Age) (Ages 1-4; n = 4)								

CHAPTER III

MORTALITY AND PRODUCTION

Introduction

The principal objective in this chapter is to estimate the annual production of the five Kafue floodplain fishes whose growth has been considered in the previous chapter. The results of population estimates in the principle habitat types of the eastern floodplain are presented and these provide the basis for determinations of the numbers of individuals of each age in the populations of each species. Annual mortality rates are estimated from the age structure data. Seasonal changes in mortality rates are then considered. The evidence for seasonal patterns of growth and mortality in the Kafue floodplain system has been brought together to propose a departure from the usual models for decrease in numbers and increase in weights for the computation of annual production. The production estimates from the Kafue floodplain are compared with those from other tropical and temperate waters. Finally, the apparent productivity of the Kafue River-floodplain, in terms of its fishery yield, is compared with that of African lakes by using morpho-edaphic criteria.

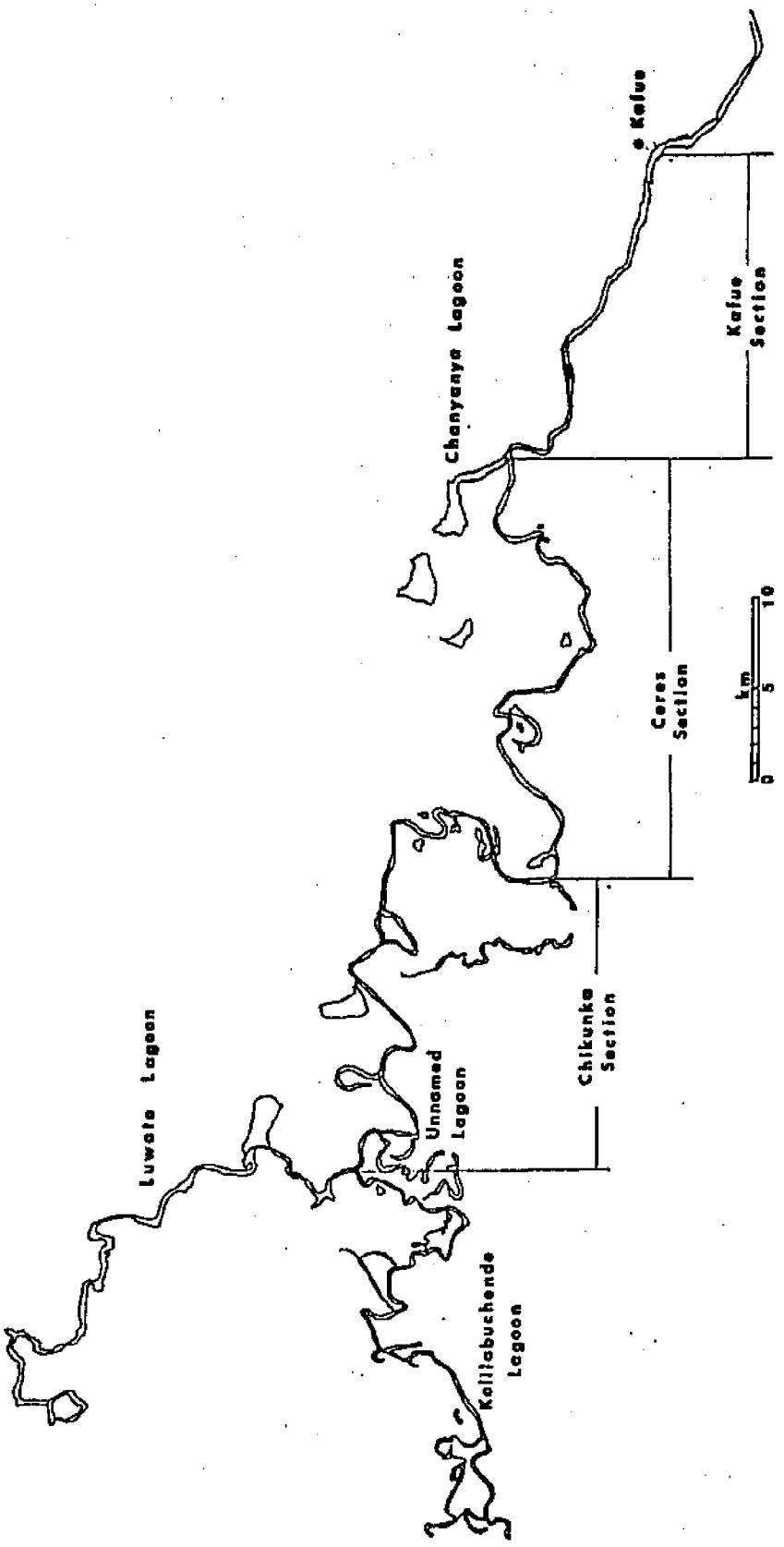
Population Estimates

Until 1969 there had been no attempt to estimate abundances or weights of Kafue floodplain fishes on a unit area basis although the distributions of fishes had been studied through gill net surveys (Carey, 1971; Williams, 1971; Chapman et al., 1971). Two series of fish population estimates in the principal fish habitats of the eastern floodplain area were made by Lagler et al. (1971) during the latter part of 1970 in connection with an investigation of the effects of impoundment on fish stocks and the commercial fishery. The first series was undertaken while much of the floodplain was still inundated in June and July, 1970, and the second series, in August and September, coincided with the recession of the floodwaters from the floodplain. The results of a third series of 26 population estimates, 24 of which were previously unreported, serve as part of the basis for the production computations herein. The third series of estimates was carried out in October and November, 1970, when riverine, lagoon, and marsh habitats were approaching their minimum expanses for the 1970 hydrological cycle.

Methods

The study area for the third series of population estimates encompassed the eastern floodplain from the Luwato Lagoon area to the eastern terminus of the floodplain near the town of Kafue (Figure 17). Based on experience from the two earlier series of population estimates, three types of

FIGURE 17. The eastern area of the Kafue River flood-plain.


Kafue
Chanyanya Lagoon
Luwato Lagoon
Unnamed Lagoon
Kallabuchende Lagoon
Kafue Section
Ceres Section
Chikunka Section
km
0
5
10

fish habitats were recognized in which abundances and weights of fishes were expected to be different. One type was the river channel of about 1300 ha in area, and a second type was the open water areas of lagoons that occupied an area of about 2240 ha. The third type of fish habitat was the densely vegetated (Ceratophyllum, Trappa) areas of lagoons, in total about 340 ha. Areas were derived from 1:50,000 scale maps and the distribution of vegetation was observed from aircraft and from the ground.

In the planning stage, sampling effort was to be allocated to the various types of habitats in proportion to their relative expanses in the study area; however, in practice, limitations of the fishing gears, interference with commercial fishermen, inaccessibility of some localities, and the time required for traveling between locations played a part in the actual choice of sample areas.

The river channel was sampled in three sections of approximately equal area--Kafue, Ceres, and Chikunka (Figure 17). Differences in stocks among the sections were expected because of the varying amounts of fishing pressure in each section and because of the differing expanses of adjacent floodplain. The Luwato Lagoon was selected to represent the lagoon open water type of habitat (Figure 17). The Luwato Lagoon is the largest lagoon on the floodplain and it alone accounted for about 40 percent of the total lagoon open waters in the study area. The lower reaches of this lagoon were extensively exploited by seine nets at the time of sampling.

The dense vegetation of lagoons was sampled in three localities. Chanyanya Lagoon was representative of the large "lake-like" lagoons, Kalilabuchende Lagoon was characteristic of the type which become isolated from the river, and an unnamed lagoon confluent with the Chikunka section of the river represented the narrow, vegetation-choked type (Figure 17). Densely vegetated areas of lagoons could not be fished with seine nets, but fishermen used gill nets in adjacent areas in Chanyanya Lagoon and in the unnamed lagoon.

Descriptions of fishing gears, methods of use, and evaluation of efficiencies have been presented in detail elsewhere (Lagler et al., 1971) and only a brief summary is given here. Population estimates were obtained using two methods--seining and chemical fishing. The seine, especially designed for riverine sampling, incorporated an acentric bag. The seine was 100 m x 6 m with mesh sizes of 7.6 cm (stretched) at the ends of the wings which decreased in 1.3 cm intervals to 2.5 cm at the jointure of the bag which was of 2.5 cm mesh. The seine was set from a boat upstream from the landing point and parallel to the shore. It was drawn to the beach with two 90 m ropes attached at the brails. The area through which the seine fished was estimated by plotting compass bearings and range measurements taken on the brails. The use of the 100-meter seine was limited to waters of less than 5 m in depth and to areas with firm substrates. In total, 12 population estimates were made using the 100-meter seine (Table 13).

TABLE 13. Dates, locations, and methods of population estimation in the eastern floodplain area from September 20 to November 14, 1970.

Kafue River Channel		Lagoon Vegetation		Lagoon Open Water	
Kafue Section	6; 100m seine 9-11 X	Kalilabuchende	1; chemofishing 20-24 IX	Luwato	4; 200m block net as a seine 13-14 XI
Ceres Section	3; 100m seine	Chanyanya	1; chemofishing 7-9 X		
	2; 100m seine and 200m block net 15-17 X	Unnamed	1; chemofishing 12-14 XI		
Chikunka Section	4; 100m seine				
	4; 100m seine and 200m block net 7-12 XI				
TOTALS	19		3		4

The seine was used in conjunction with a 200 m x 5 m block net of 2.5 cm stretched mesh to measure its efficiency. The block net was anchored in an inverted "U" shape against a seining beach and repeated hauls of the 100-meter seine were made within the block net. Based on the results of six such trials the efficiency of the seine was estimated at 92 percent with immigration and emigration removed as sources of error (Lagler et al., 1971). Accordingly, the 12 estimates obtained with the 100 m seine have been adjusted upward by a factor of 1.09. The results of the block net-seine net operations were also used as 6 additional population estimates (Table 12).

Chemical fishing was the other method employed for population estimates. It was used on three occasions (Table 13). The 200 m x 5 m block net was set in a square shape enclosing an area of about 2500 m^2 for two of the estimates. Cattle dip containing 75 percent emulsifiable toxaphene was pumped into the enclosed area to make a final concentration of approximately 7.5 ppm. Moribund fishes were collected within the first few hours after treatment, and as "bloaters" on subsequent days. On the final day, usually the fourth, fishes clinging to submerged vegetation and lying on the bottom were dislodged by repeatedly dragging cement weights through the sample area. At the end of an earlier chemical fishing operation (Lagler et al., 1971) the weight of unrecovered fishes was estimated by a SCUBA diver who collected fishes on several transects across the sample area. Expanded

to include the entire sample area, the weight of unrecovered fishes amounted to less than 2 percent of the total weight of recovered fishes. Accordingly, no upward adjustment has been made in the estimates made by chemical fishing.

Although the chemofishing method could be used in areas not accessible with the seine, it was limited by the depth of the block net, by the flushing action of currents, and by dense vegetation which could have prevented the net from reaching the bottom in some areas.

One of the three chemical fishing operations, in an unnamed lagoon (Figure 17), was conducted without the use of the block net. In this case the sample area was narrowly constricted at both ends and dense "curtains" of rotenone were first laid down at these points to prevent emigration, after which the remainder of the sample area was treated.

Fishes captured during seining and chemofishing operations were sorted by species, counted and weighed in aggregate.

Results of the Population Estimates

The results of the riverine population estimates suggested that the hypothesized differences among river sections were real (Figure 18, Table 14). Numbers of four of the five species and the total stock weight[3] followed the same trends from section to section with the largest numbers of S. andersoni, T. rendalli, S. angusticeps, and H. odoe in

[3]The combined weight of all species in addition to the weight of the five under special consideration herein.

FIGURE 18. Mean numbers per hectare of S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe, and mean kilograms per hectare of the total stock in the Kafue, Ceres, and Chikunka river sections.

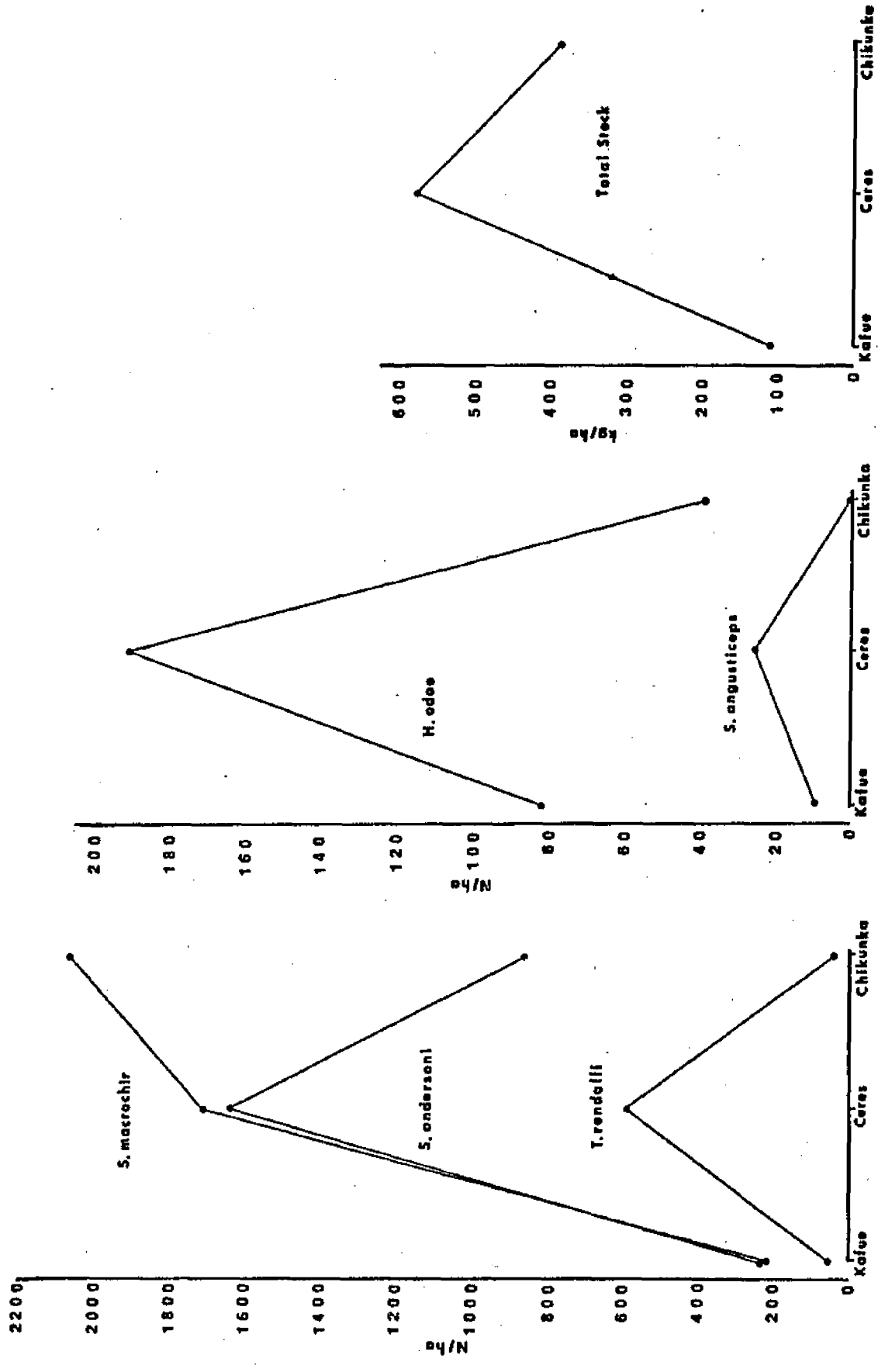

S. macrochir
S. andersoni
T. randalli
H. odae
S. angusticeps
Total Stock
N/ha
kg/ha
Kafue
Ceres
Chikunka
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
20
40
60
80
100
120
140
160
180
200
100
200
300
400
500
600

TABLE 14. Mean numbers per hectare of S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe, and mean kilograms per hectare of the total stock in the Kafue, Ceres, and Chikunka river sections.

	Kafue (n = 6)		Ceres (n = 5)		Chikunka (n = 8)		Pooled Estimates (n =19)	
	$\bar{N}$/ha	$s_{\bar{x}}$	$\bar{N}$/ha	$s_{\bar{x}}$	$\bar{N}$/ha	$s_{\bar{x}}$	$\bar{N}$/ha	$s_{\bar{x}}$
S. andersoni	227.7	58.9	1643.0	557.1	861.7	213.0	867.1	213.3
S. macrochir	210.4	58.8	1706.5	369.2	2062.1	729.1	1383.8	348.0
T. rendalli	55.0	18.5	597.1	138.4	48.3	7.3	194.9	66.1
S. angusticeps	9.2	2.5	25.5	13.4	1.0	0.7	10.0	4.1
H. odoe	81.7	36.6	191.4	27.1	38.3	11.1	92.34	19.9
	$\bar{kg}$/ha	$s_{\bar{x}}$	$\bar{kg}$/ha	$s_{\bar{x}}$	$\bar{kg}$/ha	$s_{\bar{x}}$	$\bar{\bar{kg}}$/ha	$s_{\bar{x}}$
Total Stock	106.5	29.2	576.7	129.2	386.6	63.9	348.2	59.5

the Ceres section. Only S. macrochir was greater in numbers in the Chikunka section than elsewhere. The relative stock weights among river sections and the relative numbers of each species, except S. macrochir, conformed to the relative amounts of fishing effort observed in each section during the time when the population estimates were made. The Kafue section was classified as one of heavy fishing effort and the stock weight was lowest there. The Ceres section was one of light fishing effort and had a relatively high stock weight, and the Chikunka section of intermediate fishing pressure had an intermediate stock weight (Figure 18, Table 14).

The results of one-way analyses of variance on the numbers of each species and on the stock weights supported the hypothesis of differences among river sections with probabilities of higher values of F ($\hat{P}_F$) of 0.03 for S. andersoni, 0.06 for S. macrochir, 0.00 for T. rendalli, 0.04 for S. angusticeps, and 0.00 for H. odoe.

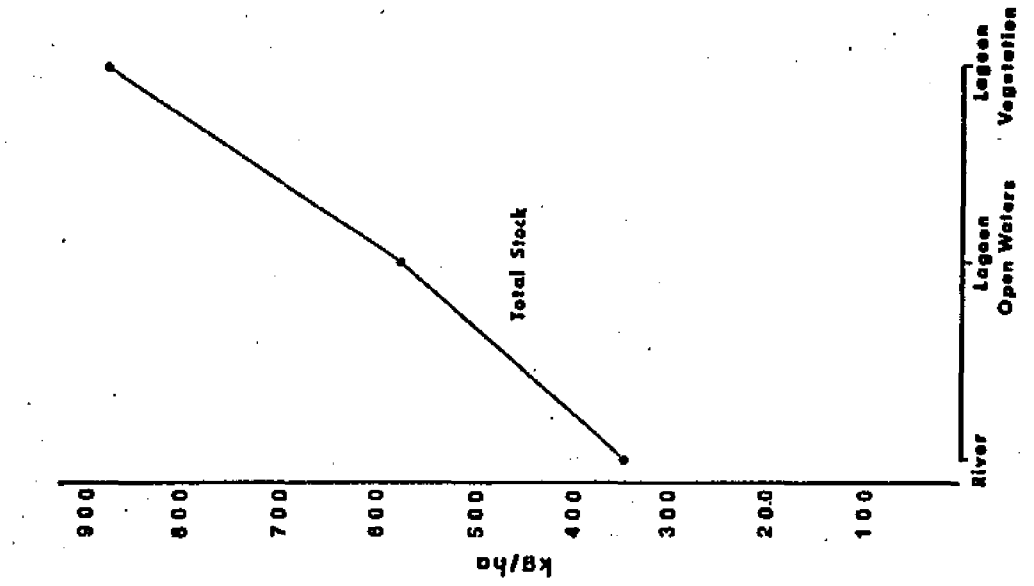
Because the surface areas of the river sections were approximately equal, the riverine population estimates have been pooled to enable comparison with the population estimates from other habitat types in the eastern floodplain area.

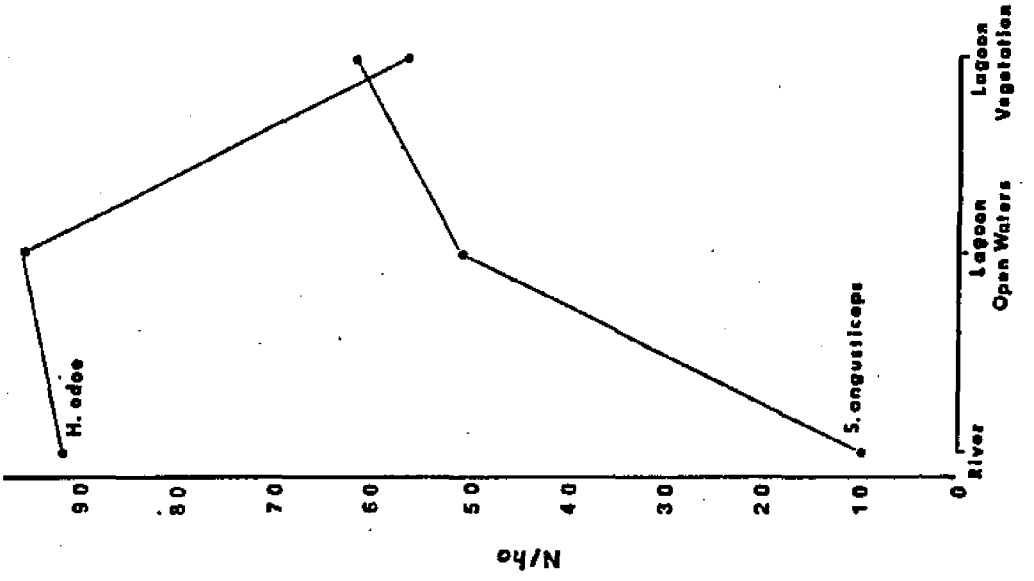
Apparent differences in numbers of fishes and in total stock weights in the principal floodplain habitats which were observed during an earlier series of population estimates (Lagler et al., 1971) were also apparent from this

series and followed the same trends (Figure 19, Table 15). The largest concentration of fishes, 879 kg/ha, was encountered in lagoon vegetation, the open water areas of lagoons were intermediate with 575 kg/ha, and the river channel was lowest in stock weight with 348 kg/ha. Apparent differences in numbers among all habitat types existed for S. andersoni and S. macrochir and differences were apparent between two of three of the habitat types for T. rendalli, S. angusticeps, and H. odoe. Because of the small number of estimates and the large standard errors of the means from the lagoon open water and lagoon vegetation habitats, hypothesized differences for S. andersoni, S. macrochir, and H. odoe were not detectable in one-way analyses of variance of the population estimates from the three types of habitat ($\hat{P}_F$'s of 0.31, 0.31, and 0.80, respectively); however, the hypothesized differences for T. rendalli, S. angusticeps, and the total stock weight were statistically detectable ($\hat{P}_F$'s of 0.02, 0.01, and 0.01, respectively).

The mean stock weights for the riverine and lagoon open water habitats from this series of population estimates (Table 15) exhibited similar trends among habitats, but were considerably higher than the estimates for the same areas made by Lagler et al. (1971, Table 4.3) during their second series which was conducted about 8 weeks prior to this one. Their estimate for the river channel was 216 kg/ha and for the Luwato Lagoon it was 426 kg/ha. The corresponding estimates herein (Table 15) were 348 kg/ha and 575 kg/ha.

FIGURE 19. Mean numbers per hectare of S. andersoni, S. macrochir, T. rendalli, S. angusticeps and H. odoe, and mean kilograms per hectare of the total stock in the river, lagoon open waters, and in lagoon vegetation.


Total Stock
kg/ha
900
800
700
600
500
400
300
200
100
River
Lagoon Open Waters
Lagoon Vegetation


H. edoe
S. angustilcaps
N/ha
90
80
70
60
50
40
30
20
10
0
River
Lagoon Open Waters
Lagoon Vegetation

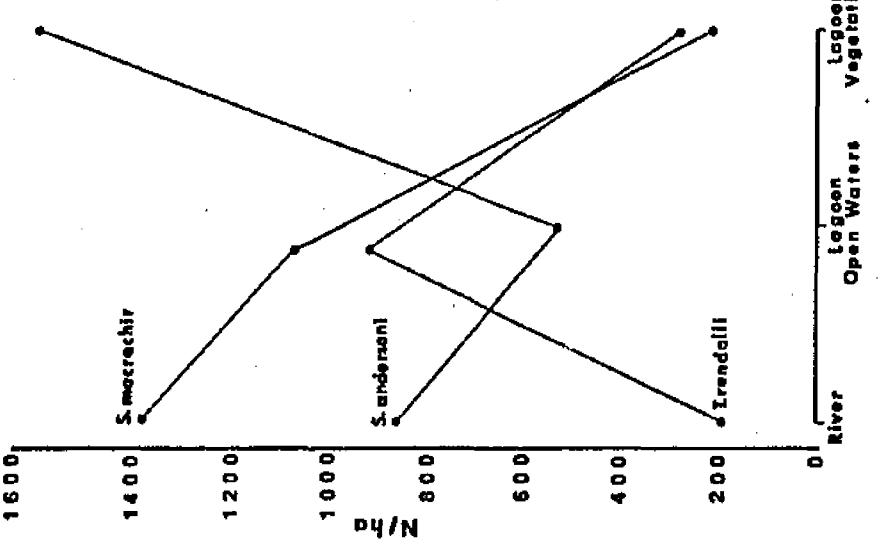

S. macrochir
S. andersani
I randalli
N/ha
1600
1400
1200
1000
800
600
400
200
0
River
Lagoon Open Waters
Lagoon Vegetation

TABLE 15. Mean numbers per hectare of S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe, and mean kilograms per hectare of the total stock in the river, in lagoon open waters, and in lagoon vegetation.

	River (n = 19)		Lagoon Open Waters (n = 4)		Lagoon Vegetation (n = 3)	
	$\bar{N}$/ha	$s_{\bar{x}}$	$\bar{N}$/ha	$s_{\bar{x}}$	$\bar{N}$/ha	$s_{\bar{x}}$
S. andersoni	867.1	213.3	530.9	251.9	1598.4	629.3
S. macrochir	1383.8	348.0	1078.1	236.5	210.2	60.6
T. rendalli	194.9	66.1	921.0	455.7	282.8	142.3
S. angusticeps	10.0	4.1	51.2	25.4	62.0	34.7
H. odoe	92.3	19.9	96.1	52.5	56.5	42.5
	kg/ha	$s_{\bar{x}}$	kg/ha	$s_{\bar{x}}$	kg/ha	$s_{\bar{x}}$
Total Stock	348.2	59.5	575.1	122.8	879.4	267.9

Although the comparison at first appears to be quite anomalous since lesser weights would have been expected from the present series than from the former series, at least part of the apparent difference can be accounted for.

Based on the assumption of an average 45 degree slope on the river banks it can be shown that over the two-month period between the two series of population estimates the reduction in surface area of the river channel was slight, perhaps as little as 2 percent; however, during the same period the reduction in volume was probably substantial, both in the river channel and in the Luwato and other confluent lagoons. Using the average of the decreases in water levels at the Nyimba and Kasaka gauage stations as a measure of the decrease, 1.75 m, the reduction in volume was about 29 percent. This corresponds to a "concentration factor" of 1.4 (1/(1 - 0.29)). Thus, if there were no fishing or natural mortality between the two series, the expected increase in the total stock from the second series to third series based solely on the decrease in volume would be 300 kg/ha x 1.4 = 420 kg/ha with the riverine and Luwato Lagoon means weighted for the relative expanses of each habitat type in the eastern floodplain area. This result is very close to the weighted mean of 439 kg/ha which was observed from the final series of population estimates.

That no natural mortality or fishing occurred between series is, of course, not a valid assumption. For example, the catch from the eastern floodplain study area,

estimated as the catch for September and one-half of the catch for October from the Lusaka and Mumbwa Districts (Central Statistical Office, Lusaka, 1971), is equivalent to a removal of about 107 kg/ha. Therefore, it seems that the riverine and Luwato Lagoon estimates of Lagler et al. (1971) were underestimates.

Mortality

Information on numbers of fishes per unit area from the previous section and the results of aging of individuals of sample populations have been brought together to determine the age structure and annual mortality rates for each of the five species. The mortality rates are apparent. That is, they are based on cross sections of the population of each species with the cross sections taken during only one period of the year.

Annual Mortality Rates

The population estimates coincided with the beginning of annulus formation on the scales of three of the five species (Table 4), and from the information on the timing of annulus formation in 1969 for the other two species (Table 5) annuli would have been laid down by these fishes shortly after the termination of the population estimates in 1970. For convenience and to avoid confusion in presenting age-specific mortality estimates, annulus formation has been assumed to occur simultaneously for each species. For example,

fish of the same year class that were of ages 1+, 2, and 2+ at the time of capture have been designated as age 2.

The numbers of individuals of each age of each of the five species were estimated for the principal habitat types using aging and length frequency data in conjunction with the population estimates for each habitat type (method Ketchen, Ricker, 1958). The age structure of each species characteristic of the eastern floodplain area was then estimated by weighting the number of individuals of each age from each habitat type by the relative expanses of that habitat type in the eastern floodplain area, 33 percent for the vegetated areas of lagoons, 54 percent for the open water areas of lagoons, and 13 percent for the vegetated areas of lagoons (Table 16).

The number of individuals per hectare of each age have been plotted as "catch curves" (the common logarithm of numbers on age) to illustrate the apparent course of annual mortality for each of the species (Figures 20 to 24). The rising left sides of the curves indicate that the numbers of age 1 fishes were not estimated in relation to their actual abundance and therefore age 1 fishes have not been used in mortality computations. The forms of the curves suggest that annual mortality is nearly constant for fishes of age 3 and older. S. macrochir (Figure 21) provides the best example, but similar trends are also evident for T. rendalli (Figure 22) and for H. odoe (Figure 24).

The catch curve for S. andersoni (Figure 20) indicates that the number of fish of age 3 were less than would have been expected from the apparent trends in mortality for fish

TABLE 16. Mean numbers of fish per hectare of each age in each of three habitat types, and weighted mean numbers per hectare for the eastern floodplain area for S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe.

Habitat Type	Age 1	2	3	4	5	6	7	8	9	Totals
S. andersoni N/ha										
River	0.6	846.5	9.2	8.2	1.4	0.5	0.7	-	-	867.1
Lagoon Open Waters	0	528.1	1.4	1.4	-	-	-	-	-	530.9
Lagoon Vegetation	14.8	1018.3	146.5	221.1	110.0	66.1	10.6	4.9	3.7	1596.0
Eastern Floodplain	2.1	696.9	22.8	32.2	14.8	8.8	1.6	0.6	0.5	780.3
S. macrochir N/ha										
River	8.9	1296.6	42.1	24.4	8.3	1.6	1.1	0.8		1383.8
Lagoon Open Waters	113.3	962.4	2.4	-	-	-	-	-		1078.1
Lagoon Vegetation	-	145.3	17.4	18.7	9.2	11.3	6.1	-		208.0
Eastern Floodplain	64.1	966.5	17.5	10.5	3.9	2.0	1.2	0.3		1066.0
T. rendalli N/ha										
River	19.2	172.4	2.3	1.0	-	-	-	-		194.9
Lagoon Open Waters	241.7	679.3	-	-	-	-	-	-		921.0
Lagoon Vegetation	103.5	138.0	32.2	4.1	2.5	-	-	-		280.3
Eastern Floodplain	150.3	441.7	4.9	0.9	0.3	-	-	-		598.1
S. angusticeps N/ha										
River	4.3	5.6	0.1	-						10.0
Lagoon Open Waters	24.9	26.3	-	-						51.2
Lagoon Vegetation	21.7	32.3	7.0	1.0						62.0
Eastern Floodplain	17.7	20.3	0.9	0.1						39.0
H. odoe N/ha										
River	0.4	85.3	4.9	1.3	0.4					92.3
Lagoon Open Waters	10.7	104.8	1.5	-	-					96.1
Lagoon Vegetation	-	43.1	12.1	1.3	-					56.5
Eastern Floodplain	5.9	90.3	4.0	0.6	0.1					100.9

FIGURE 20. Catch curve for S. andersoni.

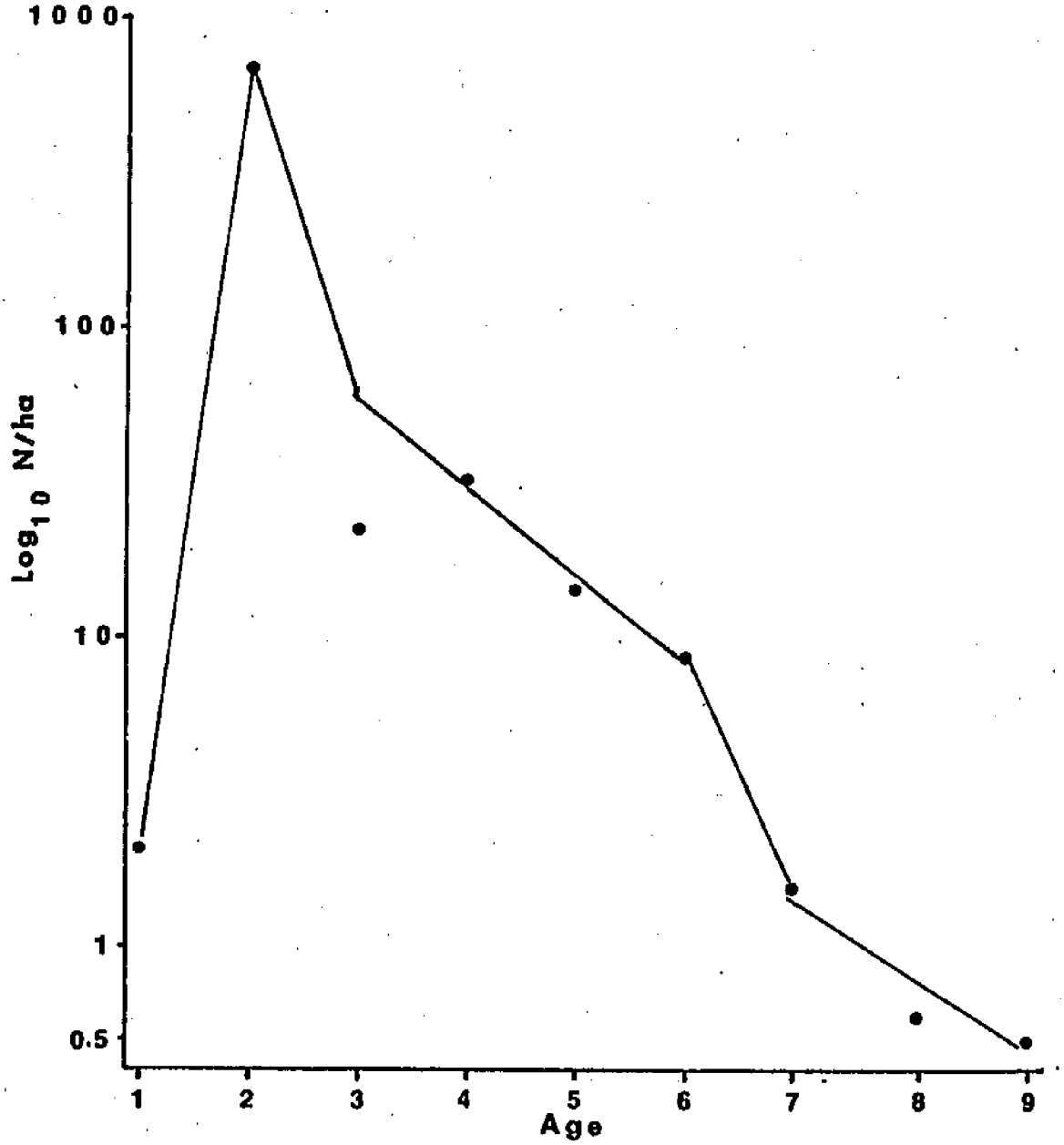

1000
100
10
1
0.5
Log10 N/ha
1
2
3
4
5
6
7
8
9
Age

FIGURE 21. Catch curve for S. macrochir.

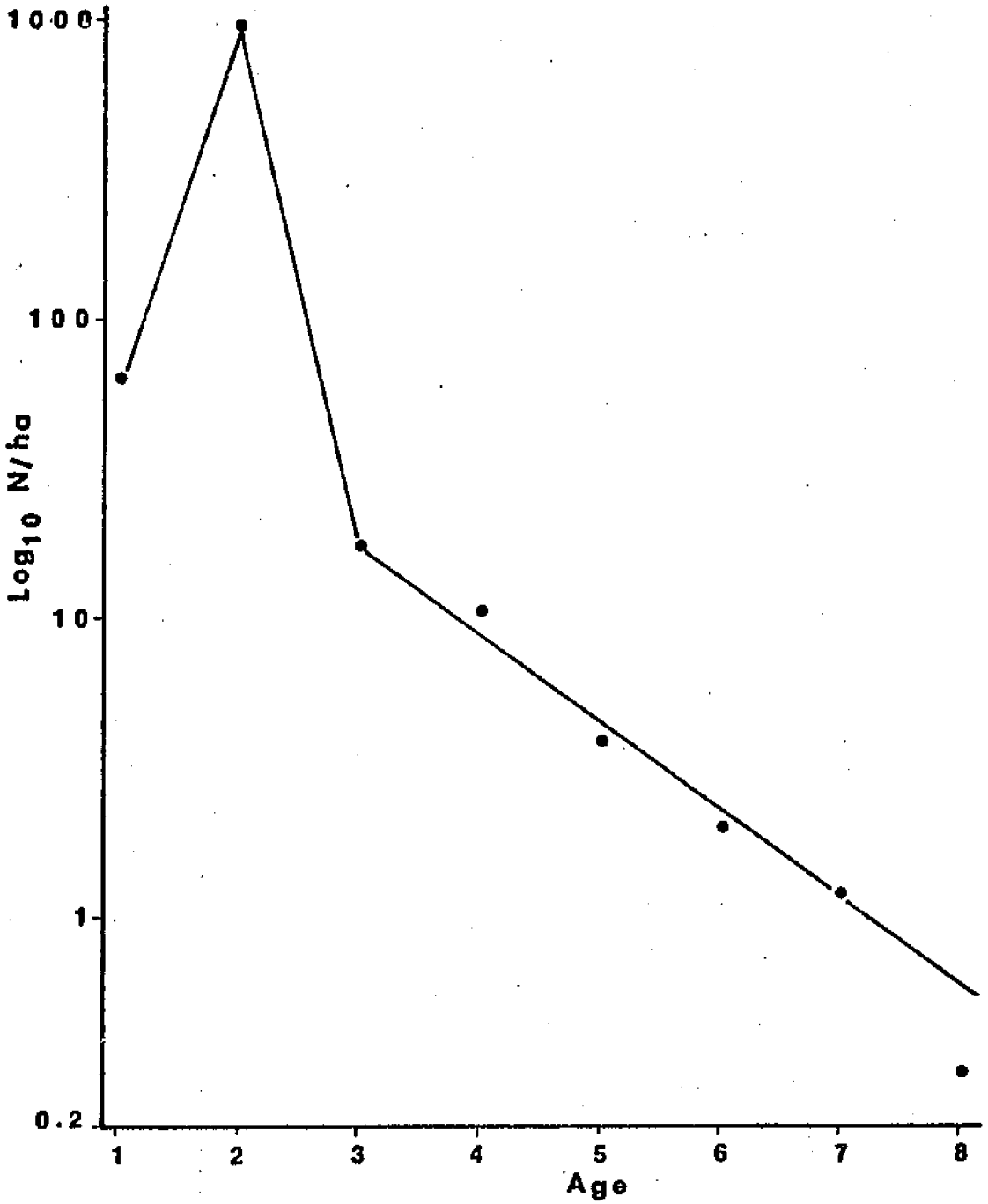

1000
100
10
1
0.2
Log10 N/ha
1
2
3
4
5
6
7
8
Age

FIGURE 22. Catch curve for T. rendalli.

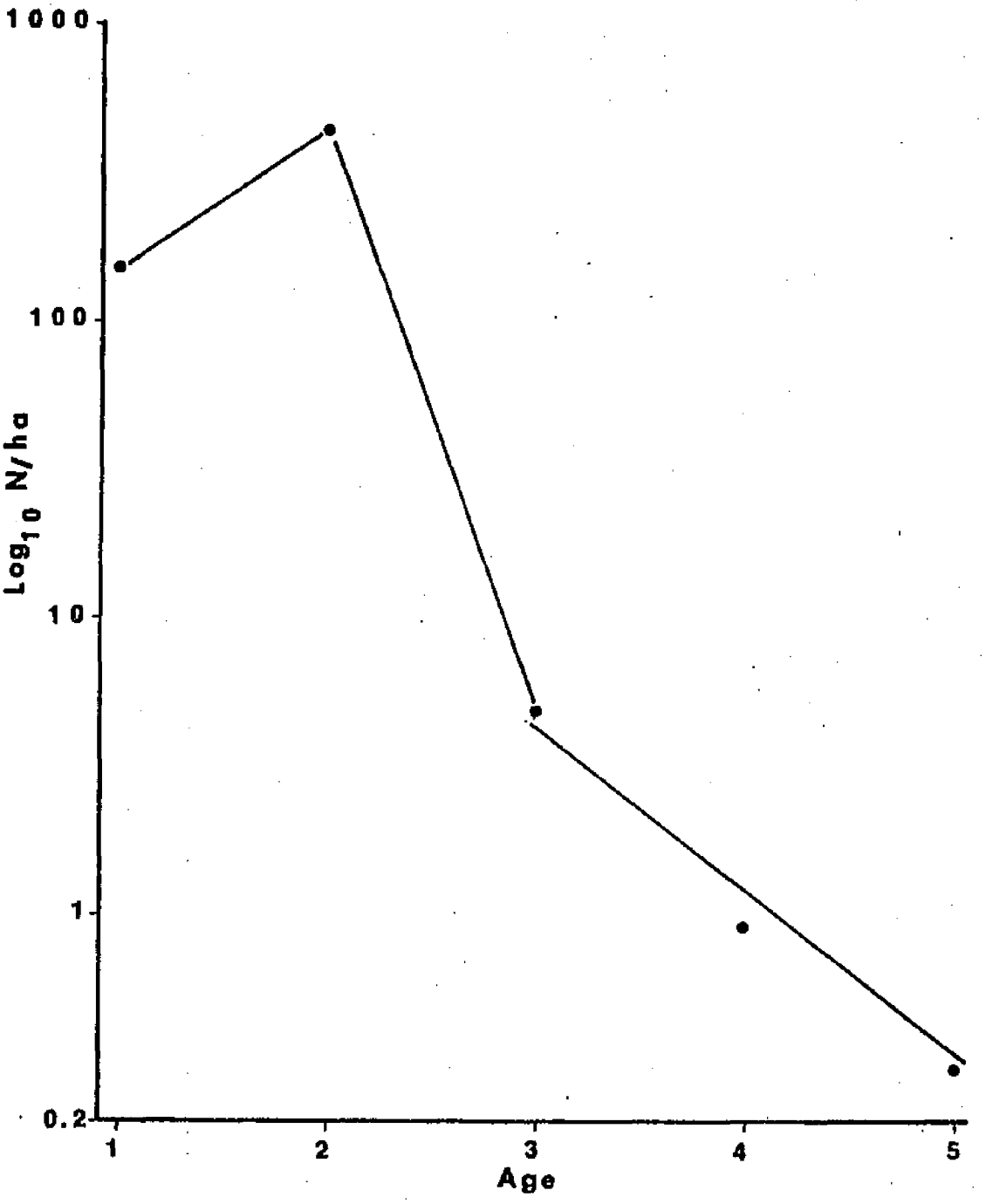

1000
100
10
1
0.2
Log10 N/ha
1
2
3
4
5
Age

FIGURE 23. Catch curve for S. angusticeps.

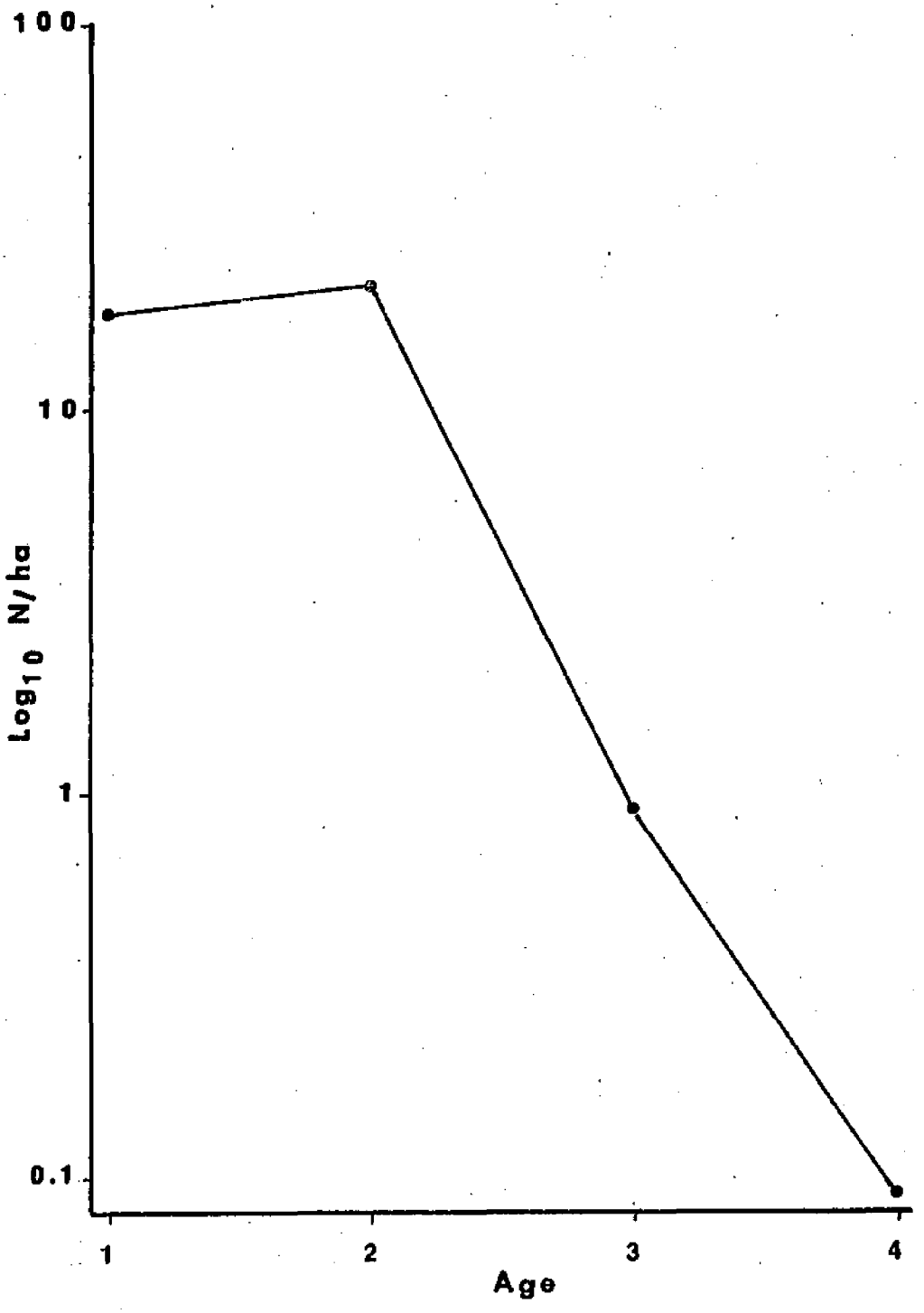
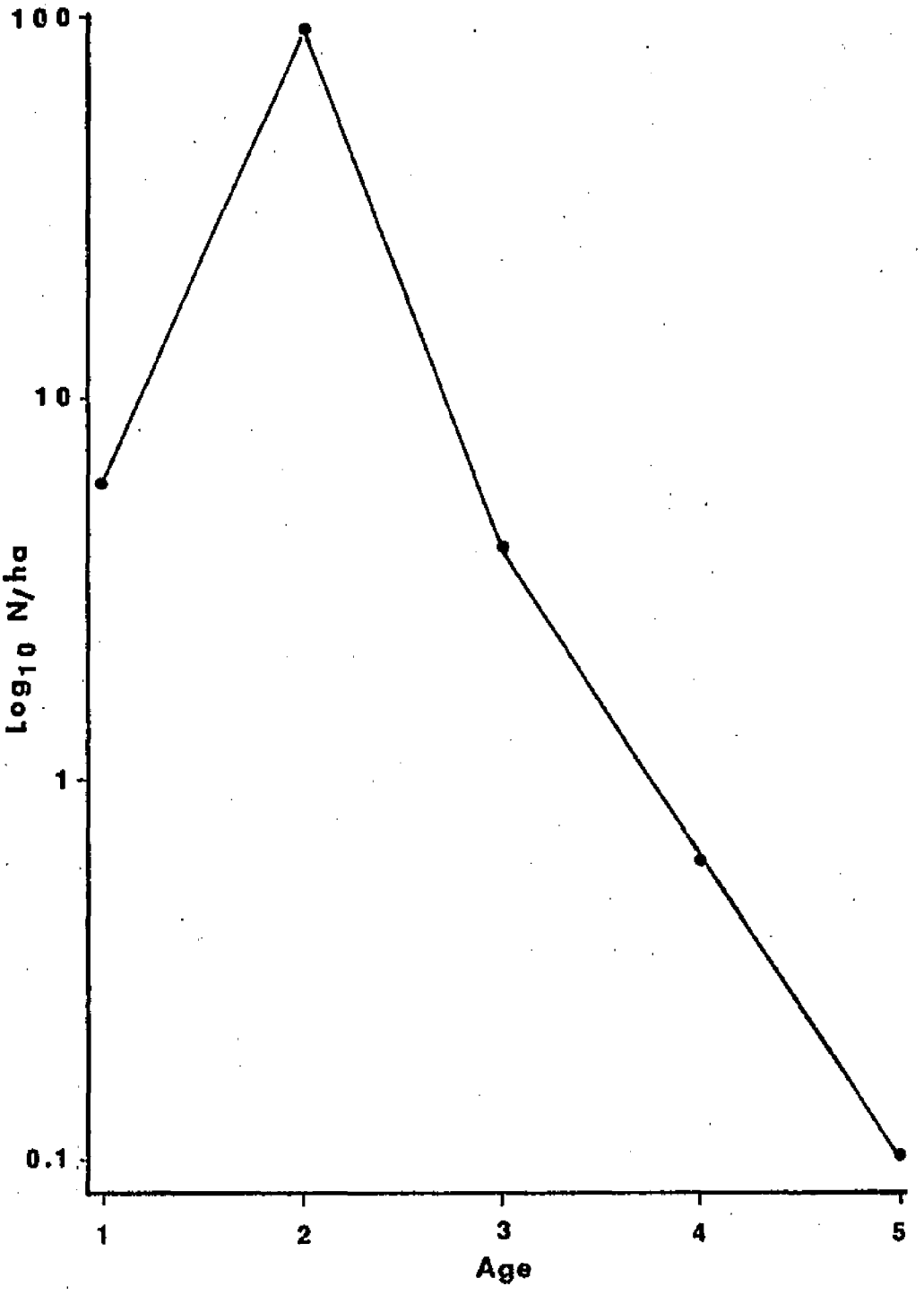

100
10
1
0.1
Log10 N/ha
1
2
3
4
Age

FIGURE 24. Catch curve for H. odoe.


100
10
1
0.1
Log10 N/ha
1
2
3
4
5
Age

of ages 4 to 6. The trend in mortality for fishes of 7 to 9 is similar to the trend exhibited by fish of ages 4 to 6.

Apparent trends for constant mortality among years have been smoothed by regressions of the common logarithms of numbers of fish per hectare on age. For S. macrochir ages 3 to 7 were used for the regression and for H. odoe and T. rendalli ages 3 to 5 were used. Two regressions were employed for S. andersoni, one for ages 4 to 6 and the other for ages 7 to 9. With fish of only 3 ages available, no regressions were used for S. angusticeps.

The parameter estimates from the regressions have been used to interpolate numbers of individuals of each age for four of the species (Table 17). Comparisons of the predicted and observed numbers per hectare indicate that the fit was quite good with differences of less than one individual per hectare in most cases (Table 17).

Total annual mortality rates in finite terms (a) and in the instantaneous form (Z) were based on the predicted numbers of individuals per hectare (Table 17). The latter rate was computed as 2.3026(b) where b was the slope of the regression for the portions of the curves where mortality was assumed to be constant. For computations of annual mortality for the third year of life (ages 2 to 3) the estimates of the numbers of age 2 fishes were accepted at face value because no reliable data were available for numbers of fish of age 1 from which the pattern of mortality during the early years of life could be determined; however, it

TABLE 17. Observed and predicted numbers per hectare and annual mortality rates for S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe.

	Age							
	2	3	4	5	6	7	8	9
S. andersoni								
Observed N/ha	696.9	22.8	32.2	14.8	8.8	1.6	0.6	0.5
Predicted N/ha		59.0	30.8	16.1	8.4	1.4	0.9	0.4
Annual Mortality ^a_z		0.92 2.4691	0.48 0.6486		0.33 1.7918		0.44 0.5816	
S. macrochir								
Observed N/ha	966.5	17.5	10.5	3.9	2.0	1.2	0.3	
Predicted N/ha		18.1	9.0	4.4	2.2	1.1	0.5	
Annual Mortality ^a_z		0.98 3.9778	0.50 0.7018					
T. rendalli								
Observed N/ha	441.7	4.9	0.9	0.3				
Predicted N/ha		4.4	1.1	0.3				
Annual Mortality ^a_z		0.99 4.6090	0.75 1.3966					
S. angusticeps								
Observed N/ha	20.3	0.9	0.1					
Annual Mortality ^a_z		0.96 3.1160	0.89 2.1972					
H. odoe								
Observed N/ha	90.3	4.0	0.6	0.1				
Predicted N/ha		3.9	0.6	0.1				
Annual Mortality ^a_z		0.96 2.7357	0.84 1.8444					

seems likely that the mortality estimates for the third year of life, ranging from 92 percent for S. andersoni to 99 percent for T. rendalli (Table 17), have been over-estimated. It has been shown that 1969 was an exceptionally good growth year for the first year growth of S. andersoni and for S. macrochir (Figures 9 and 10), and it is reasonable to believe that conditions that promote exceptional growth also give rise to exceptional survival. Therefore, it follows that the 1969 year classes (fishes of age 2 herein) may have been relatively large ones, and derivations of the mortality rates for the third year of life through the use of the numbers of the 1969 year classes with the numbers of the 1968 year classes would overestimate the actual mortality rates if the 1968 year classes were of "average" size.

Relatively high mortality rates throughout life are evident for the predators, S. angusticeps and H. odoe (Table 17), but not for the mainly herbivorous S. andersoni and S. macrochir for which mortality is relatively moderate. T. rendalli is intermediate in this respect (Table 17).

Seasonal Mortality

The point estimates of the abundances of fishes at the beginning of each year of life from the previous section indicated that numbers decrease exponentially throughout life when considered on an annual basis; however, this does not necessarily imply that mortality rates follow the same exponential pattern within each year of life. In fact, the

available evidence suggests that mortality rates are highest during the latter six months of each hydrological cycle.

During the period when the floodwaters recede from the floodplain, fishes are increasingly liable to predation by piscivorous birds (Tait, 1967b; Williams, 1971). As fishes become more and more concentrated during this period and the availability of shelter decreases, fishes are intensively preyed upon by the larger predatory fishes as they move from the floodplain periphery to deeper waters (Tait, 1967b; Carey, 1971; pers. obs.). Further, mass mortalities of fishes may occur during this period through deoxygenation which may be brought about by decomposition of vegetation, or through a combination of the effects of deoxygenation and low temperatures (Tait, 1967c).

The results of two series of population estimates which were made in the same two lagoons by Lagler et al. (1971) are illustrative of the relatively high mortality rates which apparently prevail during the period when the flood waters are receding from the floodplain. One of the lagoons was sampled in late June, 1970, when it was about to become isolated from the surrounding floodplain. The biomass estimate was 2693 kg/ha. Resampled about three months later after about two and one-half months of isolation, the biomass was 684 kg/ha which indicates an apparent mortality rate of about 75 percent. In another lagoon, this one continually open to the river channel, the biomass estimate from the first sampling in late July, 1970, was

3306 kg/ha and from the second sampling about 10 weeks later it was 501 kg/ha. In this case the apparent mortality rate was 85 percent, although emigration from the lagoon could not be ruled out as a possible source of bias. Overall, Lagler et al. (1971) estimated a 40 percent decrease in biomass for the approximately three-month period from June-July to August-September, 1970.

Mortality also appears to be relatively severe during the phase of the hydrological cycle which begins with the final recession of the floodwaters from the floodplain and ends when water levels begin to rise at the beginning of the next hydrological cycle. The aquatic environment continues to contract in area and in volume and some of the lagoons which become isolated from the surrounding floodplain and the river channel may go completely dry with the loss of all fish confined in them. For example, a lagoon which had a biomass estimated at 610 kg/ha in early June, 1970 (Lagler et al., 1971), was completely dry by mid-November. This phase of the hydrological cycle has been recognized as one of high mortality in other floodplain-river systems, in the Gambia floodplain by Johnels (1954), and in the Zambezi River by Roberts (1972).

In contrast, it is likely that the period of expanding floodplain environment is one of relatively low mortality for fishes of age 1 and older. At this time shelter is abundant, and except at the beginning of the period when mortalities associated with low dissolved oxygen concentrations

may occur (Chapman et al., 1971; Scully, 1972; personal observations), the aquatic environment becomes increasingly more favorable both chemically and physically.

It would seem that fishing mortality rates would increase throughout the year as the numbers of fishes are successively reduced by both natural and fishing mortality and as fishes become increasingly concentrated, particularly when seining beaches are exposed and both seines and gill nets are used for fishing during the latter part of the year. However, this hypothesis is difficult to demonstrate directly. For the three years during which both the catch from gill nets and draw nets were directly estimated, 1967 to 1969, only the 1969 data show large increases in monthly catches when both seine nets and gill nets were in use (Central Statistical Office, Lusaka, 1968-1970).

Production

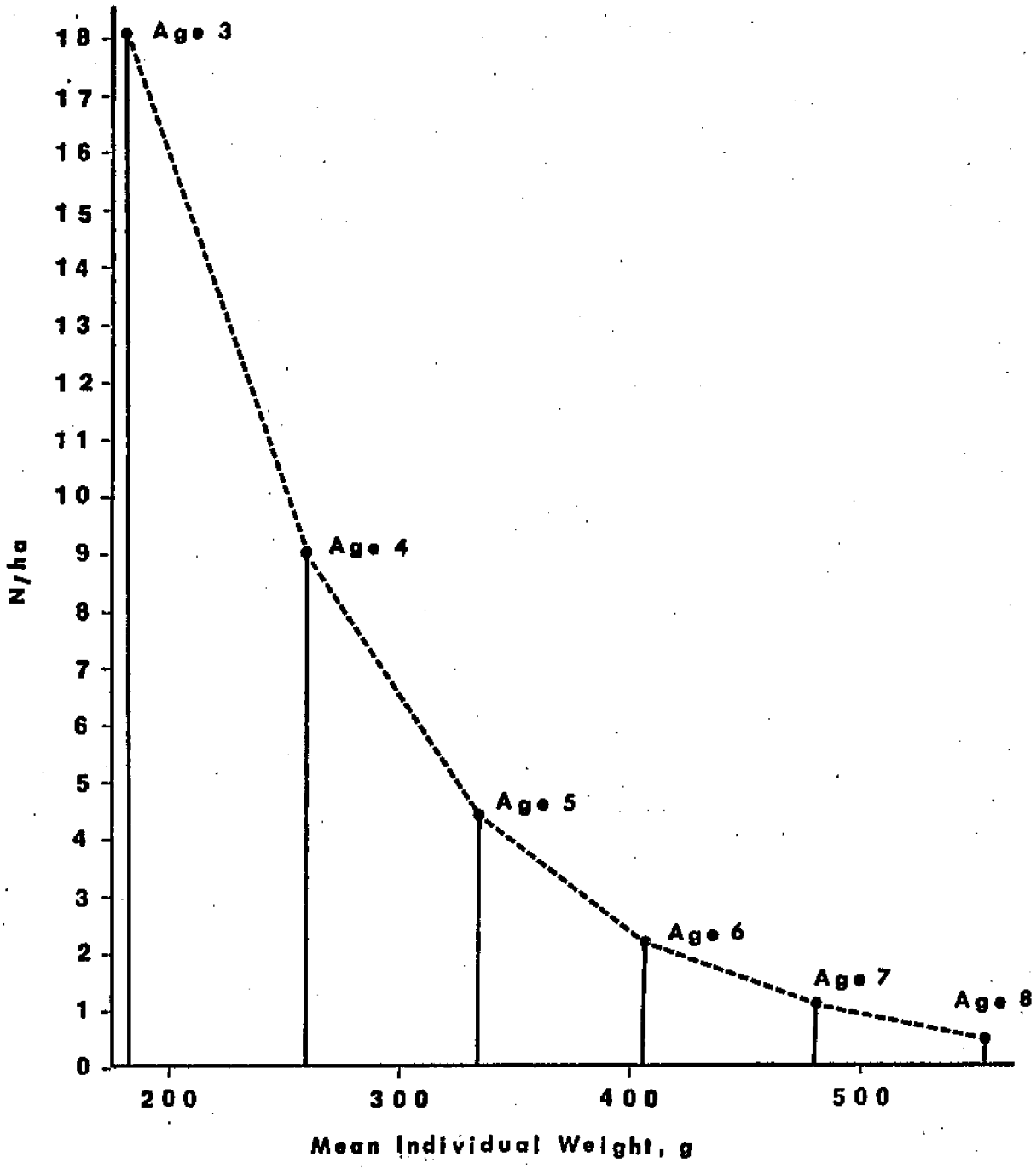
The information previously presented on annual and seasonal growth and mortality and populations has been brought together in this section to estimate annual rates of production for S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe. Production as used herein is the annual rate at which the wet weight of fish tissue is fixed regardless of the fate of the fish tissue (Ricker, 1946, 1958; Chapman, 1967, 1968).

Rationale and Methods

In estimating production for each year of life for each species it has been necessary to hypothesize seasonal patterns for mortality and growth. The problem is best illustrated in terms of an Allen (1951) curve which provides a graphical means of estimating production. For the Allen method, a plot is made of the estimated numbers of fish and their corresponding mean individual weights as shown here for the fourth to eighth years of life of S. macrochir (Figure 25) using the predicted numbers of individuals of each age from Table 17 and their corresponding predicted weights from Table 12. Usually number and weight data forming the points on an Allen curve are obtained at relatively short intervals of time and the points on the curve may be connected by straight lines with little effect on the resulting production estimates. Production is estimated as the area under the curve connecting the points for any appropriate interval of time.

In the present case, the estimates of numbers of fishes and their corresponding mean individual weights were separated, in essence, by "one-year" intervals because cross-sectional samples of populations have been used to estimate annual growth, and the population estimates from which numbers of fish and mortality rates were computed were made at one point in time. Thus the problem is one of logically interpolating between points so that the resulting curve will provide an accurate representation of seasonal patterns of

FIGURE 25. An Allen curve for the fourth to eighth years of life of S. macrochir. Dashed lines are shown connecting the points to emphasize the uncertainty about seasonal patterns of growth and mortality. Production during each year of life is defined by the area under the curve between vertical lines.


Age 3
Age 4
Age 5
Age 6
Age 7
Age 8
N/ha
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
200
300
400
500
Mean Individual Weight, g

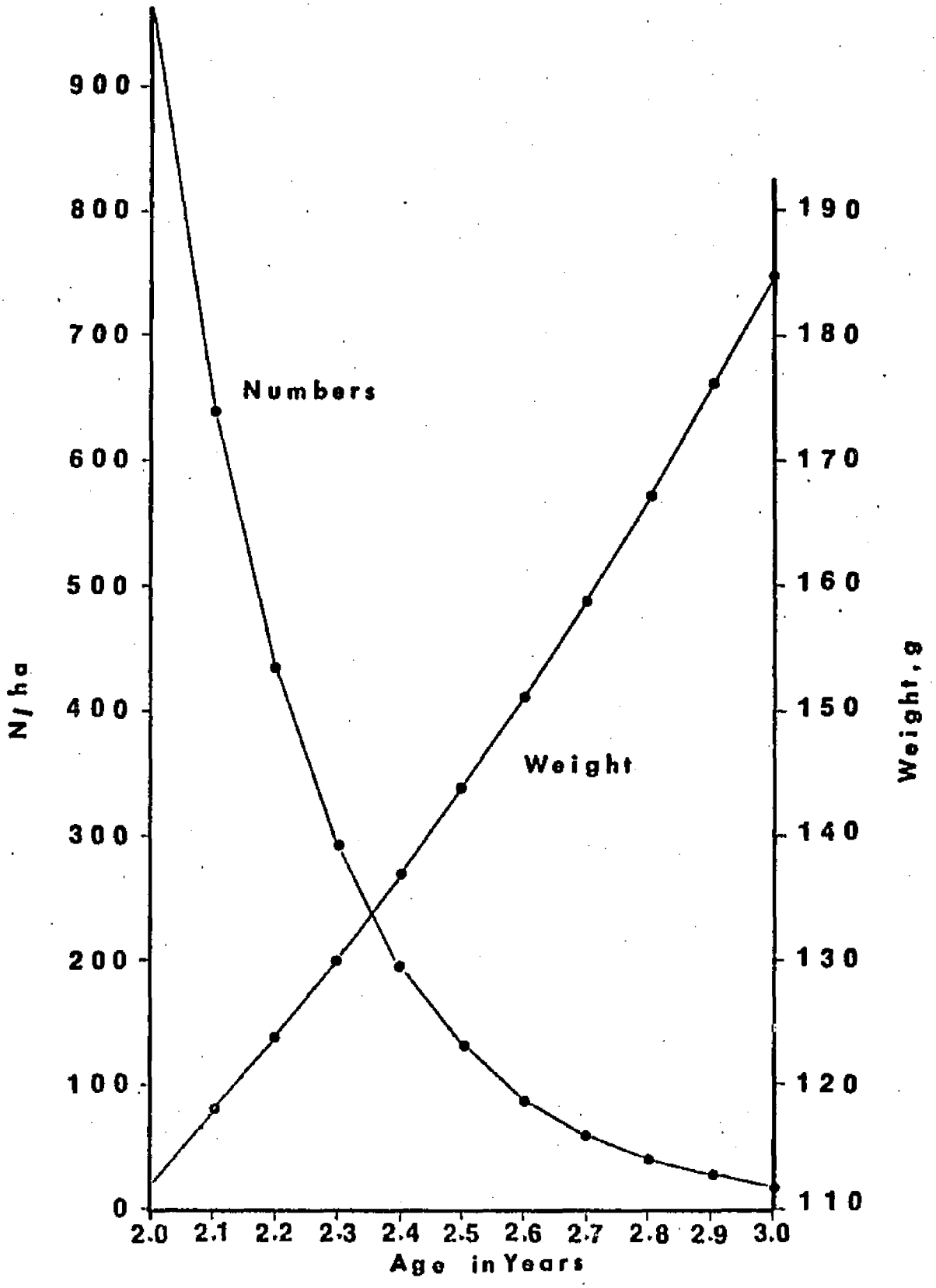
growth and mortality (and therefore production) during the "one-year" span between estimates of numbers of fish and their corresponding mean individual weights at successive ages.

Chapman (1968) has presented several combinations of linear and exponential models to portray decrease in numbers and increase in weight. Among these he suggests that exponential decrease in numbers may have some universal application. A plot of exponential decrease in numbers is illustrated for the third year of life of S. macrochir (Figure 26). Numbers of fish at the beginning and end of this year of life were obtained from the predicted values in Table 17, and the points for the curve at one-tenth year intervals were computed from the relationship:

$$N_t = N_o \, e^{-Zt} .$$

If it is assumed that the "production" year for floodplain fishes begins with the commencement of a new growth year (annulus formation), the appearance of a new generation (reproduction), and the start of a new hydrological cycle (rise in water level), with all of these events occurring in the period from October to December, then the curve of exponential decrease (Figure 26) seems to have little applicability to the dynamics of Kafue floodplain fish populations, except for the fishes of less than one year of age. As has been indicated in the previous section, all of the available evidence from the Kafue floodplain, and from other floodplains, points to the latter six months of the year as the

FIGURE 26. Curves of exponential decrease in numbers and exponential increase in weight for the third year of life of S. macrochir.


900
800
700
600
500
400
300
200
100
0
N/ha
Numbers
Weight
190
180
170
160
150
140
130
120
110
Weight, g
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
Age in Years

period of the greatest decrease in numbers, but the exponential model of decrease gives the opposite effect. With it numbers are rapidly reduced early in the production year (Figure 26). Further, although a model of linear decrease in numbers would more realistically describe the situation than an exponential model, it would tend to provide overestimates of the numbers of fishes surviving during the latter part of the year and underestimate numbers in the beginning of the year. Clearly, based on the available evidence, a model is required which would take into account the relatively high survival associated with the time of expanding floodplain environment and the relatively low survival which appears to be characteristic of the period of contracting floodplain environment.

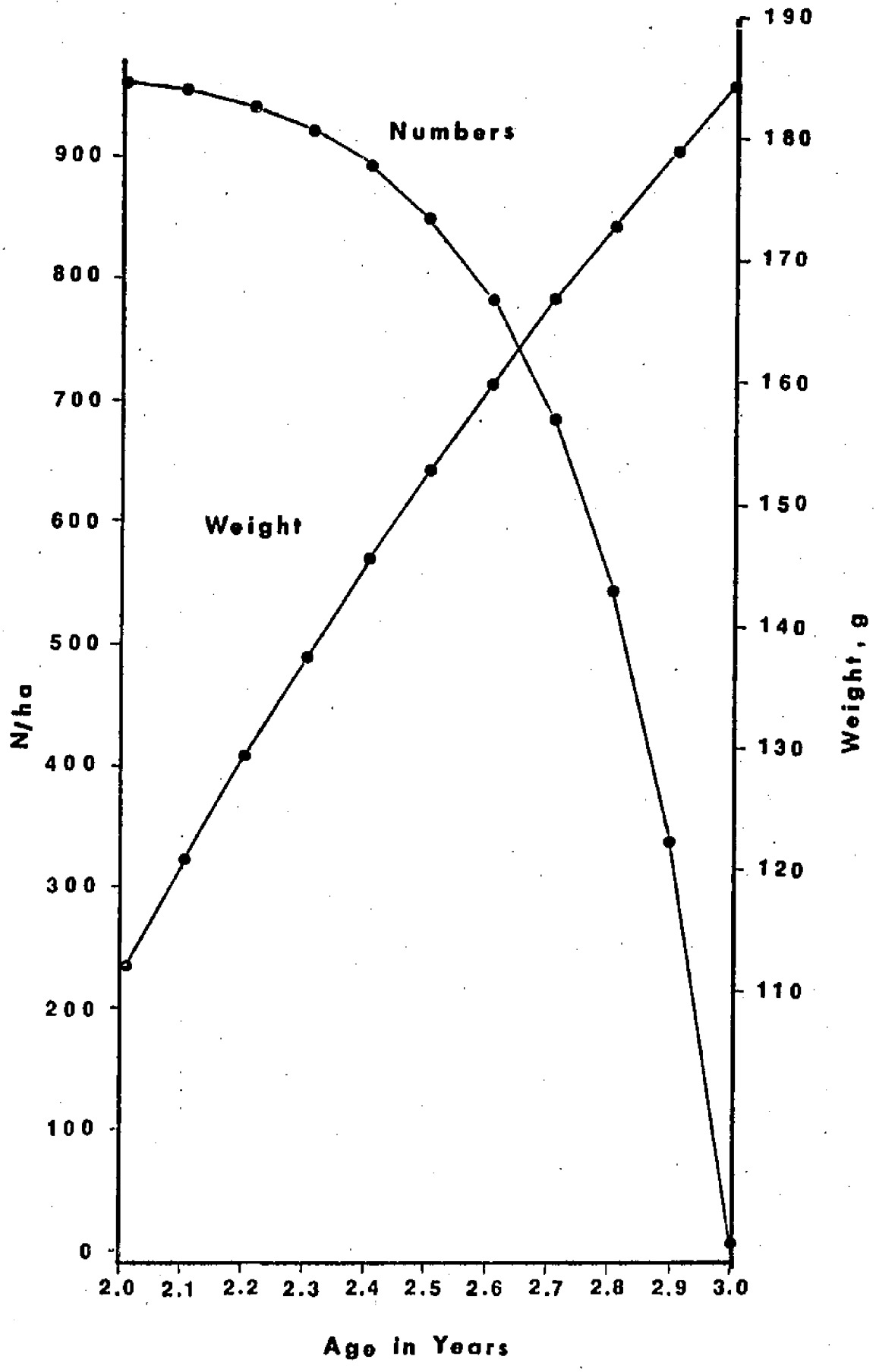
With regard to growth, neither the exponential model of increase in weight nor the model of linear increase in weight seem to fit the seasonal pattern of growth in the Kafue floodplain system. In the case of the exponential model of growth, increase in weight is relatively slow through mid-year and more rapid thereafter to the end of the year as shown for the third year of growth of S. macrochir (Figure 26). The weights for the beginning of and end of the third year of growth were taken from Table 12 and the points for the curve, at one-tenth year intervals, were obtained using the relationship:

$$W_t = W_o \, e^{Gt} \quad .$$

As has been shown earlier, Dudley's (1972) data on the growth of S. andersoni and S. macrochir during the time when the floodplain environment was expanding indicated that growth was rapid, and my data (Table 9) for the latter half of the year suggest that growth was relatively slow while the floodplain environment was contracting. Therefore, the model of exponential growth, if considered on a seasonal basis, would underestimate growth during the first part of the year and overestimate it during the latter part. A linear model of growth would have biases in the same directions. The growth model required for the floodplain situation, it seems, would be one for which growth was rapid during the time when the floodplain environment was expanding and primary production was high, and for which growth would decrease during the latter part of the hydrological cycle when food resources became increasingly scarce.

A straightforward solution is proposed for depicting the seasonal course of growth and mortality of floodplain fishes inorder to most realistically estimate annual rates of production. If the curves of exponential decrease in numbers and exponential increase in weight (Figure 26) are rotated on their diagonal axes and then reversed, the resulting curves (Figure 27) give reasonable approximations to the likely patterns of seasonal growth and mortality of floodplain fishes when the "growth" and "mortality" years are assumed to begin and end with the low-water point of the hydrological cycle. Numbers of fish and

FIGURE 27. Hypothetical curves for decrease in numbers and increase in weight for the third year of life of S. macrochir.


Numbers
Weight
N/ha
Weight, g
900
800
700
600
500
400
300
200
100
0
190
180
170
160
150
140
130
120
110
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
Age in Years

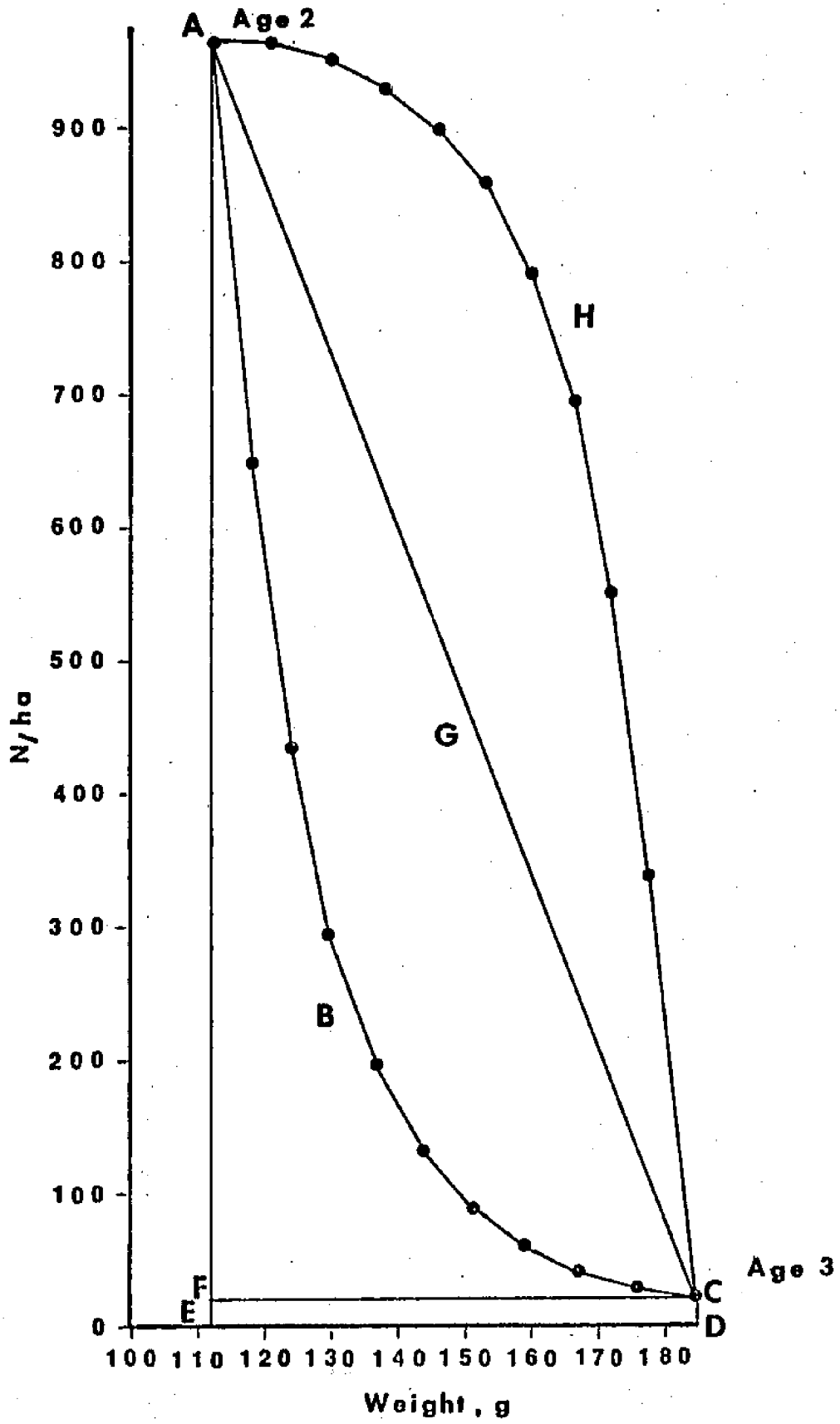
corresponding mean individual weights for the third year of life of S. macrochir have been combined to show the effect of the "floodplain" curves of growth and survivorship in terms of the Allen curve, AHC, in Figure 28.

It is not implied here that the "floodplain" curves of growth and mortality necessarily fit the situation for fishes of less than one year of age. Rather, the curves are for fishes of age 2 and older for which some growth and mortality information is available on a seasonal basis.

Although it is realized that the "floodplain" models of growth and mortality are highly sepculative because of the inadequacies of seasonal growth and mortality data, nevertheless they do appear to fit the available information. Therefore, production for each year of life of each of the five species has been estimated using these models. The estimates have been computed mathematically, but the method of computation can be best understood in terms of the Allen curve, AHC, shown in Figure 28.

Production during a given year of life using the floodplain models of decrease in numbers and increase in weight is equivalent to the area defined by AHCDEF (Figure 28). Geometrically, this area consists of the sum of the sub-areas defined by AHCG, ABCG, and ABCDEF; however, because the curve AHC is the rotated, reversed version of the curve ABC, and because AC is the common axis, then AHCG and ABCG are identical in area. Therefore, production during a given year of life

FIGURE 28. An Allen curve for the third year of life of S. macrochir. Annual production is defined by the area AHCDEF.


A
Age 2
900
800
700
600
500
400
300
200
100
0
N/ha
H
G
B
F
E
C
D
Age 3
100 110 120 130 140 150 160 170 180
Weight, g

is equivalent to ABCDEF + 2(ABCG). Geometrically, the area defined by ABCDEF is equivalent to an estimate of production during a given year of life if exponential models of decrease in numbers and increase in weight are assumed (Ricker, 1946; Chapman, 1967, 1968). Mathematically this is:

$$P = G\overline{B}$$

where P is the annual rate of production, G is the instantaneous growth rate, and for which the mean biomass, $\overline{B}$, is computed as:

$$\overline{B} = \frac{B_1(1 - e^{-(Z-G)})}{-(Z-G)} .$$

The initial biomass is B_1, and Z is the instantaneous rate of total mortality. As the first step in computing the production estimates using the floodplain models of decrease in numbers and increase in weight, computations of production using exponential models of growth and mortality (the above formulae) have been made for each year of life of each of the five species (Tables 18 to 22). Abundance and mortality estimates were taken from Table 17, and growth estimates were taken from Table 12.

With the area defined by ABCDEF known (Figure 28), which is equivalent to the production estimates for each year of life in Tables 18 to 22, it is a relatively simple matter to complete the production computations mathematically. The area defined by ABCF can be obtained as ABCDEF - (EF X ED),

TABLE 18. Production computations for S. andersoni based on exponential models of decrease in numbers and increase in weight.

Parameters		Age 2	3	4	5	6	7	8	9	Totals
Numbers per Hectare	N	696.9	59.0	30.8	16.1	8.4	1.4	0.9	0.4	813.9
Mean Weight, g	$\bar{w}$	155	278	401	523	646	769	892	1015	
Initial Biomass, kg/ha	B_1	108.02	16.40	12.35	8.42	5.43	1.08	0.80	0.41	152.91
Instantaneous Growth Rate	G	0.5842	0.3663	0.2656	0.2112	0.1743	0.1484	0.1292		
Instantaneous Mortality Rate	Z	2.4691	0.6486	0.6486	0.6486	1.7918	0.5816	0.5816		
Rate of Change in Biomass	-(Z-G)	-1.9119	-0.2823	-0.3830	-0.4374	-1.6175	-0.4332	-0.4524		
Mean Biomass, kg/ha	$\bar{B}$	48.15	14.29	10.26	6.82	2.69	0.88	0.64		83.73
Production, kg/ha/yr	P	28.13	5.23	2.73	1.44	0.47	0.13	0.08		38.21

TABLE 19. Production computations for S. macrochir based on exponential models of decrease in numbers and increase in weight.

Parameters		Age 2	3	4	5	6	7	8	Totals
Numbers per Hectare	N	966.5	18.1	9.0	4.4	2.2	1.1	0.5	1001.8
Mean Weight, g	$\bar{w}$	112	185	259	333	406	480	554	
Initial Biomass, kg/ha	B_I	108.25	3.35	2.33	1.47	0.89	0.53	0.28	118.35
Instantaneous Growth Rate	G	0.5019	0.3365	0.2513	0.1982	0.1674	0.1434		
Instantaneous Mortality Rate	Z	3.9778	- - - - -	0.7018	- - - - -				
Rate of Change in Biomass	-(Z-G)	-3.4759	-0.3654	-0.4506	-0.5037	-0.5345	-0.5585		
Mean Biomass, kg/ha	$\bar{B}$	30.18	2.81	1.88	1.15	0.69	0.41		37.12
Production, kg/ha/yr	P	15.15	0.95	0.47	0.23	0.12	0.06		16.98

TABLE 20. Production computations for T. rendalli based on exponential models of decrease in numbers and increase in weight.

Parameters		Age 2	3	4	5	Totals
Numbers per Hectare	N	441.7	4.4	1.1	0.3	447.5
Mean Weight, g	$\bar{w}$	197	321	444	568	
Initial Biomass, kg/ha	B_1	87.01	1.41	0.49	0.17	89.08
Instantaneous Growth Rate	G	0.4882	0.3244	0.2463		
Instantaneous Mortality Rate	Z	.46090	1.3966	1.3966		
Rate of Change in Biomass	-(Z-G)	-4.1208	-1.0722	-1.1503		
Mean Biomass, kg/ha	$\bar{B}$	20.77	0.87	0.29		21.93
Production, kg/ha/yr	P	10.14	0.28	0.07		10.49

TABLE 21. Production computations for S. angusticeps based on exponential models of decrease in numbers and increase in weight.

Parameters		Age 2	Age 3	Age 4	Totals
Numbers per Hectare	N	20.3	0.9	0.1	21.3
Mean Weight, g	$\overline{w}$	444	812	1179	
Initial Biomass, kg/ha	B_1	9.01	0.73	0.12	9.86
Instantaneous Growth Rate	G	0.6037	0.3729		
Instantaneous Mortality Rate	Z	3.1160	2.1972		
Rate of Change in Biomass	-(Z-G)	-2.5123	-1.8243		
Mean Biomass, kg/ha	$\overline{B}$	3.30	0.34		3.64
Production, kg/ha/yr	P	1.99	0.13		2.12

TABLE 22. Production computations for H. odoe based on exponential models of decrease in numbers and increase in weight.

Parameters		Age 2	3	4	5	Totals
Numbers per Hectare	N	90.3	3.9	0.6	0.1	94.9
Mean Weight, g	$\overline{w}$	327	491	666	820	
Initial Biomass, kg/ha	B_1	29.53	1.91	0.40	0.08	31.92
Instantaneous Growth Rate	G	0.4065	0.3048	0.2080		
Instantaneous Mortality Rate	Z	3.1422	1.8444	1.8444		
Rate of Change in Biomass	-(Z-G)	-2.7357	-1.5396	-1.6364		
Mean Biomass, kg/ha	$\overline{B}$	10.09	0.97	0.20		11.26
Production, kg/ha/yr	P	4.10	0.30	0.04		4.44

and therefore the area defined by ABCG is equivalent to the area of the right triangle, ACF, minus the area ABCEF. Production during each year of life is then estimated as:

$$P = AHCDEF = ABCDEF + 2\ (ABCG).$$

For comparative purposes annual rates of production for each year of life have also been estimated by assuming a linear decrease in biomass (Ricker, 1958; Chapman, 1968) for which mean biomass is estimated as:

$$\overline{B} = \frac{B_1 + B_2}{2}$$

where B_2 is the final biomass at the end of one year. Further assuming an exponential increase in weight, the annual rate of production is thus $P = G\overline{B}$. All of the necessary data for these computations are given in Tables 18 to 22. The estimates of production using the floodplain models of decrease in numbers and increase in weight, the exponential models, and the linear decrease in biomass model are summarized in Table 23.

In practical terms it makes little difference which combination of models is used to estimate production for fishes of age 3 and older as is readily discernable from the comparisons of the production estimates obtained through the use of three different combinations of models for decrease in numbers and increase in weight (Table 23). For these years of life the production estimates are relatively small,

TABLE 23. Production estimates based on "floodplain" models of seasonal decrease in numbers and increase in weight, production estimates based on exponential models of decrease in numbers and increase in weight, and production estimates based on a linear decrease in biomass.

Year of Life	3	4	5	6	7	8	9	Totals
	kg/ha/yr							
S. andersoni								
Floodplain models	64.85	5.81	2.99	1.57	0.73	0.15	0.08	76.21
Exponential Models	28.13	5.23	2.73	1.44	0.47	0.13	0.08	38.21
Linear Model	36.34	5.27	2.76	1.46	0.57	0.14	0.08	46.62
S. macrochir								
Floodplain Models	56.73	1.05	0.52	0.25	0.12	0.06		58.73
Exponential Models	15.15	0.95	0.47	0.23	0.12	0.06		16.98
Linear Model	28.01	0.96	0.48	0.23	0.12	0.05		29.85
T. rendalli								
Floodplain Models	45.18	0.40	0.10					45.68
Exponential Models	10.14	0.28	0.07					10.49
Linear Model, kg/ha	21.41	0.31	0.08					21.80
S. angusticeps								
Floodplain Models	5.81	0.24						6.05
Exponential Models	1.99	0.13						2.12
Linear Model	2.94	0.16						3.10
H. odoe								
Floodplain Models	11.35	0.49	0.07					11.91
Exponential Models	4.1	0.30	0.04					4.44
Linear Model	6.39	0.35	0.05					6.79

and the differences among the three combinations of models are insignificant. In contrast, the production estimates for the third year of life of each species differ to a large extent when the three combinations of models for growth and mortality are used. The differences among the production estimates for the third year of life emphasize the consequences of adopting assumptions for the seasonal patterns of mortality in the floodplain situation during the years of life for which annual rates of mortality are apparently relatively high.

Relatively large production estimates for the third year of life of each species result from the use of the "floodplain" models of growth and mortality. Despite the departure from traditional models of growth and mortality and despite the speculative nature of the underlying assumptions, the available evidence suggests that the "floodplain" models provide reasonable approximations to seasonal patterns of growth and mortality. Therefore, the production estimates based on the "floodplain" models have been used in further comparisons of production estimates from other systems.

Comparative Production

Production estimates have been traditionally expressed in terms of units of area, either as $g/m^2/yr$ or kg/ha/yr; however, in the floodplain situation the extent of surface area is an ever changing quantity both within and among hydrological cycles. The unit of area basis for the

production estimates given here stems from the population estimates which were made in the eastern floodplain at the end of the 1970 hydrological cycle with an approximate area of inundation of 3880 ha. If the production estimates were to be given in terms of the average or maximum area inundated, they would, of course, have much lower numerical values.

The highest rates of production were obtained for the relatively abundant, long lived, herbivores, 76 kg/ha/yr for S. andersoni and 59 kg/ha/yr for S. macrochir (Table 23). The production estimates for the less numerous, short-lived predators were considerably less, 12 kg/ha/yr for H. odoe and 6 kg/ha/yr for S. angusticeps. The short lived, but relatively abundant and fast growing T. rendalli was intermediate in production with a value of 46 kg/ha/yr.

Comparison of the production computations for each year of life indicates that a very large proportion of the lifetime production by fish of age 2 and older occurs during the third year of life (Table 23). For S. andersoni third year production is 85 percent of the total, for S. macrochir it is 97 percent, for T. rendalli 99 percent, and for S. angusticeps and H. odoe it is 96 percent and 95 percent, respectively. Because individuals of each species are probably recruited to the 7.6 cm gill net and seine net fisheries at about 1½ to 2 years of age, the implication is that the portion of the fishery based on these five species is essentially dependent on the production from a single year class.

Of the numerous investigations of fish production only two have been completed in the tropics, one in Lake Kariba, an impoundment of the middle Zambezi, and the other in Cuba. Of the two, the former is of primary interest here because of the proximity of Lake Kariba to the Kafue floodplain and because of similarities of fish faunas. The production computations for the latter investigation (Holcik, 1970) did not include the elaboration of tissue by fish that died during the interval for which production was computed.

The production of 20 of the 40 species of Lake Kariba fishes has been estimated at 3648 kg/ha/yr which varied for individual species from 0.01 kg/ha/yr to 1242 kg/ha/yr (Balon, in press). Field methods were similar to those described herein, but production was computed by assuming exponential decrease in numbers and exponential increase in weight. For comparative purposes the production estimates from Lake Kariba are given hereafter for fishes of age 2 and older to conform with the estimates as presented herein for Kafue fishes in Table 23.

T. rendalli is the only species whose production has been estimated in both Lake Kariba and in the Kafue. The production of T. rendalli was computed for two locations in Lake Kariba with an estimate of 25.56 kg/ha/yr at one location and 8.31 kg/ha/yr at the other (Balon, in press) as compared with 45.68 kg/ha/yr for the Kafue floodplain. In the two population samples from Lake Kariba the numbers of T. rendalli of age 2 and older were similar

to those found in the Kafue, but the mortality rates for the Kariba population were lower, 59 percent and 70 percent from age 2 onward in comparison with rates of 99 percent for the third year of life and 75 percent for the remaining years for Kafue T. rendalli (Table 17). Although the weights of Lake Kariba T. rendalli were less than those of the Kafue conspecific at a given age, the annual growth rates were higher than those for the Kafue population, as has been previously illustrated (Figure 8).

The tigerfish, Hydrocyanus vittatus, is a relative of H. odoe, and in Lake Kariba the tigerfish occupies a niche similar to that of H. odoe in the Kafue floodplain. Production for H. vittatus in Lake Kariba has been estimated at 13.64 kg/ha/yr for fishes of age 2 to age 6 (Balon, in press) as compared with 11.91 kg/ha/yr for H. odoe of ages 2 to 5 in the Kafue. Annual mortality of the tigerfish, about 44 percent per year, is much less than the 96 percent for the third year of life of H. odoe and the 84 percent rate for older-aged fish. The tigerfish was more numerous in Lake Kariba than was H. odoe in the Kafue; however, growth rates were similar.

In total, the production of the five Kafue species for individuals of age 2 and older was 181 kg/ha/yr. If, as a general rule, production during the first two years of life contributes a substantial proportion of lifetime (cohort) production, as indicated by the results of several studies--58 percent for Lepomis macrochirus (Gerking, 1962), 80 to 95

percent for Salvelinus fontinalis (Hunt, 1966), and 90 percent and 80 percent, respectively, for Salmo salar and S. trutta (Egglishaw, 1970)--then the aggregate production of the Kafue species would be expected to be in the range of 430 kg/ha/yr to 1800 kg/ha/yr, assuming that first and second year production is 58 percent of the total production for the former estimate and that it is 90 percent for the latter. If this were the case, then the production of these five species on the Kafue floodplain would be within the range of the highest values yet known from temperate freshwaters, 1970 kg/ha/yr for 10 species of the River Thames, including the production of fishes of less than one year of age (Mathews, 1971), and 596 kg/ha/yr for the production of five species in a hardwater stream in southern England (Mann, 1971). However, it is reemphasized here that the production estimates for the Kafue River floodplain are based on the minimum area of inundation.

The five species together accounted for 61 percent (327 kg/ha) of the mean biomass of fishes (540 kg/ha) in the eastern floodplain area and about 32 percent (2574/ha) of the mean number of fishes (7960/ha), thus it is unlikely that production of all fishes in the Kafue floodplain system could be more than about twice as high as the maximum estimate for the five-species group with all ages included (1800 kg/ha/yr, above) or say, at most, 3600 kg/ha/yr for all of the species encountered.

Yield and Morpho-Edaphic Characteristics of the Kafue River Floodplain

In the previous section of this chapter fish production in the Kafue River floodplain has been estimated using the dynamics of the populations--their growth, numbers, and mortality--as measures of the productivity of the system and the results have been compared with production estimates from other systems. The results of a recent investigation of the relationship between the yield of African lakes and their morpho-edaphic characteristics (Henderson and Welcomme, 1974) permits an indirect comparison of the productivity of the Kafue floodplain system with that of a number of other African waters.

Methods

For the comparison of yield from the Kafue floodplain with the yield from African lakes using the Henderson-Welcomme (1974) models the information required consists of estimates of means for conductivity, depth, area inundated, and catch. Mean annual depths of inundation were computed by dividing monthly estimates of the volume of water on the floodplain by monthly estimates of the area inundated for each hydrological cycle from 1957 through 1968 (see footnote 2, p. 73). The grand mean depth of inundation was 1.36 m and it varied from 0.98 m to 2.13 m in 7 years. It was assumed that the depth of inundation in the river, lagoons, and marshes during the period when the floodplain was dry

was equal to the grand mean depth when the floodplain was inundated. The annual grand mean area of inundation for the same period was 263,187 ha. The smallest area was 180,411 ha and the largest area was 368,956 ha over a period of 7 years.

The mean annual conductivity was estimated by weighting monthly conductivity measurements taken at Kafue Road Bridge for the period October, 1963 to September, 1964 (FAO, 1968, Vol. II, Table 1A) by estimates of the monthly volumes of water on the floodplain for the same period (see footnote 2, p. 73). The weighted mean conductivity was 187 µmohs, considerably lower than the unweighted mean of 234 µmohs. The monthly variations were from 160 µmohs to 326 µmohs. The morpho-edaphic index for Kafue is thus estimated as 187 µmohs/1.36m = 137.5.

The mean annual catch from the Kafue for the period 1954 to 1970 was 5,085,560 kg (Williams, 1960; Central Statistical Office, Lusaka, 1965 to 1971). Divided by the mean annual area of inundation, 263,187 ha, the average yield for that period was 19.32 kg/ha/yr.

Yield as a Function of the Morpho-Edaphic Index

The Henderson-Welcomme (1974) model is based on yield-MEI relationships from 17 African lakes in which the intensity of exploitation was greater than one fisherman/km^2. Consideration of the yields from lakes with lower intensities of exploitation led them to believe that yields in these waters were limited by factors other than the productivities

of their waters. The model is:

$$\text{Yield (kg/ha)} = 14.3136 \times \text{MEI}^{0.4681}$$

$$(r = 0.69;\ \hat{P}_r < 0.01).$$

Using the Kafue floodplain MEI, 137.5, the predicted yield is 143.45 kg/ha/yr as compared with the average observed yield of 19.32 kg/ha/yr; however, the intensity of fishing on the Kafue is apparently somewhat less than for the set of lakes used to build the model. The grand mean of the number of fishermen on the Kafue for the years 1963 through 1970 was 928 (Central Statistical Office, Lusaka, 1965 to 1971). Divided by the mean annual area inundated this would provide an estimate of about 0.36 fishermen/km^2; however, the Government of Zambia estimates include only licensed fishermen (net owners) and not their unlicensed helpers. Thus the actual number of individuals engaged in fishing was somewhat higher than 0.36 fishermen/km^2.

For the parameter estimates of their first model, Henderson and Welcomme (1974) included data from 31 African lakes with no restriction on the intensity of fishing. This model,

$$\text{Yield (kg/ha)} = 8.7489 \times \text{MEI}^{0.3813}$$

$$(r = 0.51;\ \hat{P}_r < 0.01)$$

provides an estimate of 57.19 kg/ha/yr for the potential yield of the Kafue fishery which is much nearer the 19.37 kg/ha/yr observed value (with an average of 263,187 ha

inundated). If the yield per unit of area for the Kafue fishery is calculated for the minimum area of inundation, 121,000 ha (FAO, 1968, Vol. III), then the yield per hectare, 41.89 kg/ha/yr, approaches that predicted by the Henderson-Welcomme model.

Given that the estimates of the MEI and the average area of inundation for the Kafue are approximations, it seems that relative to African lakes, the Kafue floodplain has been less productive in terms of fishery yield than if it were a lake with the same morpho-edaphic characteristics.

In comparison with other African floodplains for which area and yield information are available (Welcomme, 1972, Table 2), the Kafue ranks sixth in size based on its mean maximum extent of inundation of 443,000 ha, but ranks ninth among a total of ten floodplains in terms of mean annual yield per hectare of the total area inundated (11.47 kg/ha/yr for the Kafue, with estimates of 3 kg/ha/yr to 65 kg/ha/yr for nine other floodplains).

CHAPTER IV

DISCUSSION

Introduction

Comparisons of the fish production estimates for the Kafue River floodplain with those from other waters suggested that the Kafue River floodplain is not as productive as might be expected. This contention was further supported on the basis of the Kafue floodplain-African lake yield comparisons. The objective in this chapter is to discuss some of the likely reasons for the apparently low productivity of the Kafue River floodplain.

Reasons for the apparently low fish production of the Kafue River floodplain are considered from three standpoints--biases in the growth, population, and mortality estimates; lowered production caused by recent man-induced changes in the system; and physical, chemical, and biological characteristics of the ecosystem which may inherently limit fish production.

Evaluation of the Growth, Population, Mortality and Production Estimates

The sources of biases in the growth, population, and mortality estimates, which result in error in the production estimates, are numerous, and many of the biases were "built

in" as a consequence of the methods. The purpose here is not to identify each source of error, but to discuss the direction of the biases which appear to have had the most serious effect on the estimation of fish production.

Evaluation of the Growth Estimates

The close correspondence between the growth determinations presented herein and those obtained by Dudley (1972) leaves little doubt concerning the validity of the scale method for aging Kafue floodplain fishes and for the use of the scales for back-calculation of annual length increments.

Back-calculated length measurements were pooled to form a composite representation of growth because the objective was to obtain production estimates which would approximate averages for each species over a long period of years. However, the back-calculated means for each year of growth were heavily weighted by the relatively large number of observations available for the 1969 growth year, a year of exceptionally good growth. Therefore, it is likely that annual growth rates were overestimated, and from this source of bias, the production estimates would be too high.

For the production computations it was assumed that seasonal growth patterns were the same for each species (Figure 27); however, it is likely that herbivores such as S. andersoni, S. macrochir, and T. rendalli and predators such as S. angusticeps and H. odoe have different patterns of seasonal growth. The apparent delay in the formation of

annuli on the scales of the predators relative to the herbivores lends some support to Johnel's (1954) hypothesis that predators are able to maintain relatively rapid growth rates during the low-water period when their prey is most concentrated, but when the floodplain environment is expanding and prey are dispersed, predators may experience difficulty in locating prey and, therefore, annuli on the scales of predators are laid down at approximately the time when the floodplain is inundated. In contrast, annuli are laid down on the scales of herbivores as the end of the low-water phase of the hydrological cycle approaches, when food resources are at a minimum.

If the curve for increase in weight (Figure 27) overestimates growth during the first one-half of each year, then the production estimates would be much too high for the third year of life, given the survivorship curve that has been used for the production computations (Figure 27). However, relatively few of the fish beginning the third year of life survive to the latter part of the year and, therefore, any deviation from the hypothesized pattern of growth during the latter part of the year would have little effect on the annual production estimate, assuming that the survivorship curve depicts the actual situation with regard to seasonal changes in abundance.

Biases in the growth estimates were the least critical of all of the likely sources of error associated with the production estimates.

The growth-hydrological relationships are of little practical value under the natural hydrological regime because the annual pattern of the hydrological regime cannot be adequately predicted in advance; however, growth-hydrological models could have utility after impoundment at Itezhi-Tezhi when the floodplain hydrological regime will be manipulated. Knowledge of the response of growth rates to variations in the hydrological regime could be used to predict the timing of recruitment, for example. However growth models would have to be based on observations for a greater span of years than were used for the growth models used herein.

Evaluation of the Population Estimates

Lagler et al. (1971) have attempted to measure the efficiency of the 100-meter seine through the use of the 200 m block net. The conditions of the trials were such that escapement from the area to be fished by the seine was partially prevented by the blocking net which surrounded the sample area. Thus, it is likely that their estimate of 92 percent efficiency is an overestimate and, therefore, the upward adjustment made in the population estimates herein on the basis of their estimate of efficiency probably only partially accounted for escapement.

Escape from the sample areas during the placement of the block net probably was also a source of error in the population estimates made by chemofishing. Additional

escapement may have taken place along the portions of the block net which were in the dense areas of vegetation because the leadline of the block net could not be forced tightly against the bottom in some instances. Emigration while the net was being set was probably a serious cause of underestimation. As previously mentioned, the results of Lagler et al. (1971) indicated that recovery of dead fishes was, for practical purposes, complete.

The principal difficulty with the population estimates was the small sample sizes from the lagoon vegetation and lagoon open water habitats. Doubtless, some of the variation among samples was associated with the methods used for the estimates, but it is also likely that the numbers and weights of fishes were quite variable within the same types of habitats. Data from Lagler et al. (1971) and from here, when combined, suggest that the variance on the mean of the estimates made in lagoon vegetation could have been reduced if the estimates were expressed in terms of volume rather than in units of surface area. For example, the mean of six chemofishing estimates was 0.18 kg/m^2 with 90 percent confidence limits of 50 percent of the mean, but if the same estimates are expressed in units of volume the mean is 0.30 kg/m^3 and the 90 percent confidence limit is 30 percent of the mean. Volume estimates were impractical because the volume of different habitat types could not be estimated, and in the case of seining, the shape of the area through

which the seine was fished could not be accurately related to the underwater topography.

It was determined from the standard deviations of the means from the series of population estimates described herein that to obtain population estimates of the total stock weight with 90 percent confidence limits within 10 percent of the means, 180 population estimates would have been necessary in the river channel, 58 would have been required for the lagoon open water habitat, and 65 would have been necessary in the lagoon vegetation.

Assuming that fishes were randomly distributed within the principal habitat types, it is likely that the population estimates are actually underestimates due to corresponding overestimates of the efficiencies of the fishing gears. Therefore, the production estimates may be low.

Evaluation of the Mortality Estimates

As was the case with the growth estimates, the objective was to determine "average" annual mortality rates for each year of life of each species. The two most likely sources of error were those associated with aging and those associated with the population estimates themselves. The probability of errors in aging increased with the ages of the fish under consideration, but as compared to the errors in the population estimates the errors in aging were probably not serious as is shown by comparisons with Dudley's (1972) results.

The mortality estimates were subject to the same types of errors as existed for the population estimates themselves, such as the error associated with the possible non-random distribution of various age groups of fishes within habitat types, and likely differences in catchability between younger and older fishes.

Regressions of the logarithms of numbers per hectare on age met the objective of smoothing the survivorship (catch) curves, however, the most remarkable result was that the among year mortality rates were, in fact, so similar. In the usual case, mortality would be expected to decrease in the later years of life as fishes outgrow size-selective fishing gears and small predators. Each of the five species considered are susceptible to 7.6 cm mesh gill nets and seine nets at from 1½ to 2 years of age; however, S. andersoni and S. macrochir, probably outgrow the commonly used mesh sizes of 7.6 cm and 10.2 cm by age 5 or 6 but H. odoe and S. angusticeps are vulnerable to these mesh sizes throughout the remainder of their lifespans. Thus it may be that mortality rates for older-aged fishes have been overestimated with consequent underestimates of production for the later years of life.

The problem of estimating mortality rates based on cross-sectional data already has been discussed in connection with the apparent high annual mortality rates for the third year of life of each of the five species. The result would

be to underestimate production if mortality rates for the third year of life have been overestimated.

Evaluation of the Production Estimates

On the basis of the downward bias which was likely for the population estimates and the upward bias which probably occurred for the annual mortality estimates for the third year of life, I conclude that production for fishes of age 2 and older was underestimated, assuming that the hypothesized patterns of seasonal growth and seasonal mortality accurately portrayed the actual growth and mortality situations.

Historical Changes in Fish Production

Probable changes in fish production can be traced to the direct and indirect influence of man on the terrestrial and aquatic portions of the Kafue River floodplain ecosystem. Among the hypothesized changes are those stemming from decreases in populations of wild ungulates and of the crocodile, and increased exploitation of the fishery resource.

Decreases in Wild Ungulates and Crocodiles

Populations of the primary users of floodplain vegetation, lechwe and hippopotami, have been reduced in range (Bell et al., 1972) or substantially reduced in numbers (Sheppe and Osborne, 1971; J. Butts, pers. comm.) during the present century. The semi-aquatic lechwe and the amphibious hippopotamus deposit at least part of their

wastes directly in the aquatic system and are dependent on the primary production of the floodplain during almost all phases of the hydrological cycle. Deposition of these wastes directly in the water enables rapid breakdown by aquatic decomposers and the recycling of nutrients, thereby decreasing the turnover time for primary production. At present the distribution of lechwe is confined to the central floodplain area and hippopotami have been reduced to densities of 2 to 3 per river km. Even so, the amount of vegetation consumed by the 90,000 lechwe and 500 or more hippopotami and the amount of nutrients recycled by them must be large. In contrast, the cattle, which have largely replaced the lechwe in many areas of the floodplain, do not deposit their wastes directly into the aquatic system, and therefore recycling of these materials must await the next flood. Further, cattle are seasonal inhabitants of the floodplain, and while they are on the floodplain they do not utilize the most abundant types of vegetation. Therefore, in terms of the potential rate of production in the aquatic system, cattle may be a poor substitute for the wild ungulates.

That there is a direct link between the presence of lechwe and the dynamics of fish populations of the Kafue is not a new idea. A fishery worker (Anon., 1956) sought to explain the relatively high catches per gill net in the Lochinvar area through the presence of the lechwe herd there. Everett (in press) has noted that fishes in the 1970

commercial catch were larger in the central floodplain area than elsewhere. The mean lengths of one year old S. andersoni, S. macrochir, S. angusticeps, and H. odoe were greater there than at any other location on the floodplain; however, fishing was restricted on Lochinvar National Park at the time of my observations and this may have had some effect of the size-frequencies of age 1 fishes. Substantially higher estimates of the production of Haplochromis darlingi and Sarotherodon mossambicus in some areas of Lake Kariba have been associated with the presence of high densities of game populations by Balon (in press).

The crocodile, which feeds on fishes when it is of intermediate size, has been severely reduced in numbers in the Kafue system. In 1950 when intensive hunting began an estimated 1,000 individuals were removed, in 1951 and 1952 a total of about 4,000 individuals were taken, and from 1953 to 1959 an additional 7,000 individuals were killed (J. Butts, pers. comm.). This decimation of crocodiles must have represented a substantial reduction in the rate of crocodile predation on fishes and may have increased survival of the species upon which the crocodiles fed producing an increase in the biomass of these species. Because crocodiles grow slowly, the effect of the decimation of the crocodile population on fish production would be expected to continue for many years after hunting had ceased.

The likely effects of the removal and restriction in range of wild ungulates probably have been to reduce

the production of fishes, all other contemporary changes aside.

Increase in the Intensity of Fishing

Prior to the introduction of modern fishing gears which occurred in the mid-1950's, the influence of subsistence fishing on Kafue floodplain fish populations was probably negligible. When fishing became economically important, but while it was still a seasonal occupation during the low-water period, fishing mortality was confined to the low-water period of the year when natural mortality was also high; however, large-mesh seines were in use then and the larger, older fishes were exploited.

When fishing began to increase in intensity in the mid-1950's in terms of more nets and year around activity the populations were probably characterized by large numbers of older-aged fishes. "Wonderful angling" in the Kafue River was mentioned for that period of time by Williams (1960) and J. Butts, a crocodile hunter on the Kafue River during the 1950's, stated that "There used to be thousands (of Sarotherodon and Tilapia) swimming in a line along the edge of the banks." Biomass was probably relatively high and the growth rates of fishes were probably relatively low as is the usual case with "virgin" stocks.

Comparisons of the average weights of individual fishes caught in seine nets in 1955, 1957, and 1970 support the hypothesis of a change in the age structures of the

exploited populations. In 1955 and 1957 the mean weights of S. andersoni, S. macrochir, and T. rendalli varied from about 0.4 kg to 0.6 kg in the Kafue and Namwala areas (Anon., 1956; Williams, 1960), but in 1970 in the Kafue area the mean weights varied from 0.12 kg to 0.15 kg based on modal lengths of these same species in the seine net catches (unpublished data obtained by D. J. Stewart).

Assuming for the moment that growth rates were the same in the period from 1955 to 1957 as they were in 1970, then, from the age-weight estimates in Table 6, S. andersoni and T. rendalli were probably about four years of age when they were recruited to the fishery and S. macrochir may have been about six years old when recruited. In 1970 recruits were one and one-half to two years of age.

If the catch per unit of effort of standard (91.4 m) gill nets is used as an index of stock abundance, then it is evident that the stock has been reduced to about one-tenth to one-fifth of its pre-1955 size (Figure 4). In the early years of fishing, in 1955, the gill net catch averaged 50.8 kg (Williams, 1960) and was as high as 81.2 kg per gill net in the Lochinvar area (Anon., 1956). In comparison, in 1969 the mean catch per gill net was 7.2 kg and in 1970 it was 10.0 kg, but the mean catch per gill net was as low as 4.8 kg in 1967 (Central Statistical Office, Lusaka, 1968, 1970). As is apparent from the curve of catch per unit of effort in Figure 4, about four to five

years of intensive fishing were required to reduce the stock size to about one-fifth of its 1954-1955 level.

Fish production in the Kafue River floodplain has been substantially reduced through the manyfold decrease in the biomass of fish stocks which followed intensive fishing. Although the decrease in the biomass of the stock was probably accompanied by an increase in the growth rates of fishes, this compensating factor was probably far outweighed by the effect of the decrease in the stock. Therefore, before intensive exploitation fish production was probably several times higher than it was during the period from 1960 to 1970.

Inherent Characteristics of the Kafue River-Floodplain Ecosystem Which May Limit Fish Production

Thus far it has been shown that the relatively low production estimates for the Kafue River floodplain could have been caused by downward biases in the population estimates which could have led to underestimates of annual production rates. It also is likely that commercial fishing has so depleted the stocks that production is considerably below its potential maximum. Nevertheless, it is worthwhile to consider several characteristics of the system which, in themselves or through interactions with other factors, may inherently limit annual rates of fish production.

Edaphic Characteristics of Kafue Waters

There is no apparent paucity of nutrients in the waters of the Kafue floodplain. The weighted conductivity for the Kafue River floodplain, 187 μmohs, compares

favorably with the median value of 223 µmohs for 31 African lakes with values from 27 to 3,000 µmohs (Henderson and Welcomme, 1974, Table 1). The conductivity of Kafue floodplain waters also is considerably higher than the unweighted average of 84 µmohs for the nearby Barotse floodplain which varies from 57 to 126 µmohs (Duerre, 1969, Table 1). Further, the concentration of total dissolved solids of the Kafue River floodplain (Figure 2) is much higher than the 46 ppm of total dissolved solids in Lake Kariba (Balon, in press).

Characteristics of Soils and of Vegetation

In general, the soils of the Kafue Flats area are of low fertility, and from the standpoint of agricultural potential the heavy clay soils of the floodplain have been classified as non-arable (FAO, 1968, Vol. II).

The dry weights of various grasses in the floodplain are an apparent indication of the relatively low fertility of the soils as shown by a comparison with the dry weights of grasses in warm-temperate salt marshes in the United States:

Kafue Floodplain
(Van Rensburg, 1968, Vol. IV, Table V)

Echinochloa pyramidalis	3230 kg/ha	(s = 3283, n = 4)
E. stagnina	4767 kg/ha	(s = 360, n = 4)
Vossia cuspidata	4875 kg/ha	(s = 1593, n = 4)

Warm-Temperate Salt Marshes
(Florida, North Carolina, Georgia, Virginia)
(Keefe, 1972, Table 1)

Spartina alterniflora *S. patens* *S. cynosuroides*	9632 kg/ha	(s = 3555, n = 7)

Taken together, the standing crops of the Kafue grasses are about 45 percent of the biomasses of Spartina.

Other aspects of the predominately grassland vegetation of the floodplain suggest that fish production might be negatively affected by its presence. Because the grasses are coarse they are not directly utilizable by fishes. Although some of the leaves die and fall into the water and then could be fed upon by aquatic herbivorous insects, most leaves remain aerial.

Even though the grass stems provide additional substrate for the growth of periphyton, because of the overhead shading by leaves and stems, this type of production may occur only on the near-surface portions of the stems. However, it seems that if the grasses were replaced with aquatic vegetation such as the Trappa and Ceratophyllum of lagoon areas, much more substrate would be available for aquatic primary and secondary production.

The largest concentrations of fishes were associated with the lagoon vegetation habitat as indicated by the results of my population estimates and those of Lagler et al. (1971). In addition, Carey (1967) found that aquatic insects also were more abundant in lagoon vegetation than in grassland areas.

Annual Variations in the Hydrological Regime and Corresponding Variations in Fish Production and Fishery Yield

For the most part, up to this point the Kafue River floodplain ecosystem has been discussed in terms of statics. In this section the objective is to consider the dynamic aspects of the relationships between the hydrological regime and variations in fish production and annual variations in fishery yield.

There is little doubt that variations in the hydrological regime produce corresponding variations in the chemical and biological components of the Kafue River floodplain ecosystem. Observations of Van Rensburg (1968, FAO Vol. IV), Chapman et al. (1971) and Scully (1972) indicate that the distribution and succession of floodplain grasses and other types of vegetation are closely related to variations in the depth, extent, and duration of flooding. Information on the lechwe population shows that its dynamics are affected by annual fluctuations in the hydrological regime (Gallagher et al., 1972; Bell et al., 1973) as are populations of less conspicuous terrestrial animals (Sheppe and Osborne, 1971).

With regard to fish populations, the growth-hydrological relationships illustrated the validity of the indirect relationship between the growth of Kafue floodplain fishes and variations in the hydrological regime. Results of the investigations of fishery yield in relation to variations in the hydrological regime by Lagler et al.

(1971), Chapman et al. (1971) and Muncy (1973) indirectly support the hypothesis that fluctuations in the hydrological regime result in corresponding variations in the sizes of fish populations, as has been demonstrated elsewhere in tropical and temperate waters (e.g., Morgan, 1971; Williams, 1972; Holcik and Bastl, 1973).

If both growth and numbers of fishes fluctuate annually in the Kafue River floodplain system as a function of the hydrological regime then it follows that production must also vary annually. As an example, it can be shown that if only growth rates were to vary annually, then the effect on production would be quite significant. Once more using for illustration the third year of life of S. macrochir, if the annual maximum observed growth increment, 123 g, is substituted for the average annual growth increment, 73 g (Table 19), and the initial numbers of fish and the mortality rate remain the same, then the resulting production estimate for the third year of life is 103 kg/ha/yr in comparison with 56 kg/ha/yr, if production is based on average growth. Because both growth and mortality vary simultaneously, but not necessarily in parallel among years, the annual variation in production rates must be quite high.

The basic hypothesis for the functioning of the production-hydrological regime relationship and the yield-hydrological regime relationship is that the carrying capacity of the aquatic environment during

the low-water stage of each hydrological cycle is the principal factor which determines the numbers of fishes which begin the subsequent "production" year and the numbers of older-aged fishes which will be available for harvest during that year. This is basically the relationship described mathematically by Lagler et al. (1971), but explained in more detail here. Recent man-induced changes in the system, principally fishing, have altered the relationship somewhat, but have not altered its basic validity.

If it is assumed that the carrying capacity of the Kafue River floodplain is directly related to the volume and area of the aquatic habitat, then the carrying capacity would be lowest during the low-water period. Further, low-water periods of long duration would result in high mortality rates and therefore, numbers of fishes surviving to the end of the low-water period would be relatively small. If this is the case, then it is not surprising that two of the lowest annual yields from the Kafue fishery, in 1967 and 1960, were preceded by low-water periods of the longest duration in recent years, of 5.2 and 4.6 months, respectively, as compared with an average of 3.4 months. (The durations of the low-water periods were determined from plots of monthly water levels for each hydrological cycle as shown in Figure 11.) Low-water years are also times when seining is most intensive because seining beaches become available earlier. After fishing became intensive fishing mortality could have played a significant part in the total mortality during the

low-water periods; however, the result would still remain the same--relatively small populations of exploitable-sized individuals would occur after an extended low-water period.

The apparent exception to the hypothesis of the low-water carrying capacity as the major factor in determining floodplain fish production and yield occurred in 1969, a year in which catch was above average, but the preceding low-water period was of long duration, 4.6 months. This apparent anomaly can be explained by considering the effect of a relatively large area of inundation on spawning success and fish growth.

The flood in 1969 was well above average, second only to the flood of 1963 in recent years. Apparently spawning success was greater than usual in 1969 as would be expected if a relatively large area was available to relatively small populations. A greater abundance in 1969 than in 1970 of fish of less than one year of age was noted by Dudley (1972), and his comparisons of length frequencies of S. andersoni and S. macrochir collected at various times during the first one-half of the 1969 hydrological cycle indicated that growth of young fishes was rapid. My back-calculations of the lengths attained by fish at the end of the first year of growth indicated that 1969 was an exceptionally good growth year, and Dudley's (1972) data give the same indication. The mean lengths attained at the end of the first year of growth of the 1969 year classes of S. andersoni, S. macrochir, and T. rendalli were close to, or

exceeded the minimum lengths for harvest of these species by 7.6 cm nets. Further, if seasonal growth patterns are considered, then many of individuals of the 1969 year classes would have attained a harvestable length before the onset of the low-water period. Thus, from the available evidence it seems that the above-average catch in 1969 can be explained on the basis of the early recruitment of 1969 year classes which were also larger than usual. Additional evidence for the early recruitment of the 1969 year classes comes from plots of monthly yields for the period from 1967 to 1970 (Central Statistical Office, Lusaka, 1968-1971). Only the plot for 1969 showed a large increase in catch during the latter months of the year, which would have been expected if large numbers of fishes became available for harvest at that time.

Assuming that the 1969 year classes of most of the exploited species were recruited in 1969, and assuming that the numbers of older fishes were depleted by natural mortality and by fishing during the long low-water period of the 1968 hydrological cycle, then an explanation is provided for the differences between the catch predicted for 1970 by Lagler et al. (1971), 7,850 mt, and the observed catch of 5553 mt (Central Statistical Office, Lusaka, 1971). If the 1969 year classes were depleted earlier than usual by fishing, and if the numbers of older fishes were already lower than usual due to a combination of severe hydrological conditions in 1968 and removal by fishing during 1968 and

1969, then the abundance of fishes available for harvest in 1970 could have been much lower than would have been expected on the basis of the high survival rates to be expected from the short duration of the low-water period in 1970.

Although I emphasized the importance of the varying expanse of the aquatic environment during the low-water period as the principal determinant of population size and therefore, of production and yield, the space limitation which apparently is imposed by deoxygenation of large areas of the floodplain during the rising water phase of the hydrological cycle also must be considered in its possible limitation on fish production. Although an area which is relatively large in comparison with that available during the low-water period becomes inundated during each hydrological cycle, not all of it can be occupied by non-air breathing fishes, and therefore, until reoxygenation occurs, it is not included in the productive substrate of the aquatic system, except for Clarias. Moreover, by the time when most of the floodplain is reoxygenated, the peak area of inundation has been attained and therefore the expanse of the aquatic environment is decreasing and the cold season is approaching.

The results of the Kafue floodplain-African lake yield comparisons provide some evidence for the contention that fish production and fishery yield in the Kafue River floodplain ecosystem are space-limited. Only when the observed

yield from the Kafue floodplain fishery was considered on the basis of the minimum area of inundation would the average yield approach the yield predicted for the Kafue floodplain system based on its morpho-edaphic characteristics.

Summary and Conclusions

1. Annually occurring marks on the scales of S. andersoni, S. macrochir, T. rendalli, S. angusticeps, and H. odoe, were reliable indicators of the ages of these fishes, and the marks can be used for the estimation of annual length increments.

2. Large proportions of the annual variations in the first and second year growth increments of S. andersoni and S. macrochir were accounted for by corresponding annual variations in the hydrological regime and by annual variations in cold season temperatures.

3. Rates of increase in length for the first year of growth were more rapid for four Kafue River floodplain fishes than for conspecifics in Lake Kariba and in the Barotse floodplain; however, the growth in length of three Barotse floodplain species surpassed that of Kafue floodplain fishes in subsequent years of life.

4. On an annual basis growth in weight from age 1 onward was approximately linear for each of the five species considered here when averages for several growth years were used. Information on seasonal patterns of growth indicated that growth was most rapid during the period when the floodplain environment was expanding, and that growth rates

decreased during the recession of the floodwaters from the floodplain.

5. The results of the population estimates indicated that fishes were not randomly distributed among the three principal low-water habitats. Fishes were most abundant in numbers and weight in lagoon vegetation, intermediate in numbers and weight in the open water areas of lagoons, and least abundant in numbers and weight in the river channel.

6. On an annual basis mortality rates were apparently relatively high during the third year of life for each of the species, but the annual mortality rates were lower and approximately constant for the remainder of the years of life. The evidence indicated that natural mortality rates were relatively high during the period when the aquatic environment was contracting.

7. Traditional models for decrease in numbers and increase in weight did not appear to fit the floodplain pattern of seasonal growth and mortality, and therefore, alternative models for the seasonal decrease in numbers and increase in weight were adopted for the estimation of annual production for each year of life of each of the five species. Comparisons of the results of the production estimates using the "floodplain" models for decrease in numbers and increase in weight with the results using traditional models indicated that there was no practical difference in the production estimates for fishes of age 3

and older; however, the "floodplain" models provided higher production estimates for the third year of life during which annual growth and mortality rates were higher than for the latter years of life.

8. Comparisons of the aggregate production estimates of fishes of age 2 and older with the results of production estimates from other tropical and temperate waters indicated that fish production in the Kafue River floodplain ecosystem was not as high as was hypothesized. Further, the yield from the Kafue River floodplain ranked ninth among the yields from ten African floodplains, and in comparison with African lakes the yield from the Kafue River floodplain was less than would have been expected on the basis of its morpho-edaphic characteristics.

9. Reasons for the apparently low production estimates were considered from the standpoint of errors in measurements, man-induced changes in the ecosystem which might affect fish production, and characteristics of the Kafue River floodplain ecosystem which might inherently limit fish production.

10. On the basis of an evaluation of the growth, population, and mortality estimates it was concluded that the production estimates were too low because numbers of fishes of all ages had been underestimated and because mortality rates had been overestimated for the third year of life of several of the species.

11. Fish production on the Kafue River floodplain may be limited inherently by fluctuations in the hydrological regime which cause variations in the carrying capacity of the aquatic environment during the low-water period. Fish production also may be limited by deoxygenation of large areas of the floodplain during the rising water phase of the hydrological cycle, and by the low fertility of the floodplain soils which support predominately grassland vegetation which is not directly utilizable by fishes.

12. Man has indirectly, but negatively, affected fish production through his reduction of the numbers and ranges of wild ungulates which appear to be more efficient in utilizing the floodplain than the cattle which have replaced them in most areas.

13. More than any other change the intensive exploitation of fish stocks has resulted in a substantial reduction in fish production in the Kafue River floodplain which accounts for the relatively low values of fish production which are presently characteristic of the ecosystem.

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