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# POSSIBLE FISH STOCK SIZE ASSESSMENT AND AVAILABLE PRODUCTION SURVEY AS DEVELOPED ON LAKE KARIBA 

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#### Abstract

This paper is an outline of methods practically useful for the evaluation of ichthyomass, fish abundance, available production and yield in lakes and rivers. Terms and concepts are reviewed, and difficulties stemming from the use of "predetermined" mathematical models are discussed. Sampling with toxicants in blocked-off areas was found to be the most practical method and is described in detail. For the total estimation of ichthyomass the spatial ranges of fish distribution must be determined; the results of echo-sounding surveys for horizontal, vertical, topographical, seasonal and diel fish distribution are given.

Some of the most important methods for computing available production are listed and applied to Lake Kariba as an example. In particular, a method based on the balance between the main predator and prey species is reviewed. The ecological production survey concept is finally stressed as applied to multispecies fish stocks.

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"It cannot be over-emphasized that no matter how the data are tabulated (machine, desk calculator or by hand), the tabulations can be no more accurate than the original observations. Erroneously or sloppily collected data will always be erroneous and inaccurate no matter how refined the methods of tabulating or analyzing the data are. Statistical results can never be better than the data they are based on" (LAMBOU 1959).
There are different meanings for terms developed in fish population analysis (HOLT et al. 1959; HOLT 1960). A stock is part of a population and both terms have been clearly
defined in biology (e.g. MARR 1957; MAYR 1963). A stock is usually considered as a topographical part but not an isolated part of the population (the fish stock of a cove is part of the whole lake fish population). In an ecological sense stock may be equal to taxocene (CHODOROWSKI 1959; HUTCHINSON 1967; HANDLER 1970) in which case the stock includes members from a number of species. The terms spawning stock, usable stock, fishable stock, adult stock and unit stock (e.g. HOLT 1958; RICKER 1958b; GULLAND 1967, 1969) always refer to some definite part of all the fish inhabiting a certain area; they must be defined precisely
and differentiated by a special adjective. Stock or population sample is different from catch sample. Catch and landing are equal neither to ecological production nor to yield. They represent the part of production and yield which is caught and landed by fishermen. The quantitative values of stock or population represent abundance of fish and ichthyomass (if applied to all fish taxa present) or standing crop or standing stock. If applied to single species we may prefer the terms biomass or mass of species under study. The meaning of other terms will be clear from the following text (Fig. 1). We also simplify the terms applied in this fish production survey, as opposed to rather welldefined uses by some ecologists.

Parallel with the development of the fish production concept new terms were invented, defined and modified by various adjectives such as: actual, whole, gross, net, global, primary, potential, real, total, secondary, community, effective, etc. Such proliferation may finally lead to misunderstanding and misinterpretation of the production concept, if the latter is used without explanation.

Recently the most correct interpretation of fish production is that "Production is defined as the total elaboration of fish tissue during any time interval $\Delta \mathrm{t}$, including what is formed by individuals that do not survive to the end of $\Delta \mathrm{t}$ (IVLEV 1945)" or "regardless of the ultimate fate of that tissue" (CHAPMAN 1967, 1968). It is formulated in simplified from by RICKER (1946):

$$
\begin{equation*}
\mathbf{P}=G \overline{\mathbf{B}} \tag{1}
\end{equation*}
$$

Here $P$ is production per unit time, $G$ is a coefficient of biomass growth, and $\overline{\mathrm{B}}$ is the mean biomass during the unit time interval. Based on this formula the original numerical estimation of production proposed by Ricker was later developed into a simple graphical method by ALLEN (1951). Although many authors have used this method of estimating fish production, it is also subject to some criticism on the question of realism and
precision (CHAPMAN 1968; NIKOLSKIJ 1965). Nevertheless it is the simplest method so far available to estimate the production as meant by Ivlev's definition.

From the fishery management point of view we may consider the part of production represented by the total elaboration of fish tissue during any time interval $\Delta \mathrm{t}$ by fish surviving to the end of $\Delta \mathrm{t}$. In case the ratio between the instantaneous growth and mortality rates ( $\mathrm{G} / \mathrm{Z}$ ) is constant and no immigration or emigration of fish occurs in the evaluated stock, this part also represents production in the sense of Ivlev (RICKER 1958a; NEESS and DUGDALE 1959). This production value can be estimated "by multiplying individual weight increases by the mean number of fish present in each interval of interest" (CHAPMAN 1967). It was used by BURMAKIN and ZHAKOV (1961), HOLCIK (1970a, 1970b) and by myself.
"Production" here is akin to the "net production" of some ecologists and would equal the "available production" of a population, untouched by death, predation or exploitation during the specified time interval. Normally it is a part of Ivlev's production. The latter incorporates also the various increments of the tissue of fish that have died from natural causes, or have been eaten by predators, or caught by fishermen at different times within the time interval of interest. The available production is that mass of fish which may be taken through increased exploitation in addition to existing levels. Thus yield can be interpreted as being a harvestable part of production.

More work has been done on ocean or anadromous fish population analysis with hypothetical mathematical models (BARANOV 1918; DERZHAVIN 1922; RICKER 1954, 1958a, BEVERTON and HOLT 1957; DOI 1959; HEMPEL and SAHRHAGE 1961; GULLAND 1962, 1965, 1968a, 1968b, 1969; IVANOV 1961; LARKIN and HOUS-

Fig 1. The simplified population analysis concept and terminology used.

TON 1964; PELLA and TOMLINSON 1969; FOX 1970) than has been done on fresh water fish populations. The reason for this is that the ocean environment is more difficult to sample than a smaller fresh water area (REGIER 1970a). The open water habitat of a large lake and that of an ocean are similar, however, and sampling methods for population analysis used in ocean fishery research are equally valid for shoaling open water fish without respect to salinity or the size of environment. Furthermore, methods of fresh water fish population analysis stressed here are fully applicable for lagoons, reefs, or inshore marine populations (BALON and SENES 1967; HOLCIK 1970b).

We may identify the role of models and distinguish between roles as follows. Methodological models are those which help to programme the research and state in advance the number of samples required for certain variability coefficients and confidence limits. These models are clearly useful. Models that seek to define the interrelationships of a series of variables rather precisely, as opposed to general semi-quantitative research concepts, should not be assumed uncritically (VARLEY'S comment, 1962), particularly in work which tries to generalize and predict theoretical conclusions. A model must not be accepted and applied before the collection of sufficient data to indicate its degree of realism. The steps might be formulated as follows:
1 Field data collection (measurements) on variables thought to be closely related to the question under consideration.
2. Summary calculations (perhaps with the help of computers, e.g. GERKING 1965; ALLEN 1966; SWINGLE and SWINGLE 1966; LEEPER, STERN and LAMBOU 1958; LAMBOU 1959, recognizing that computers cannot improve bad data or replace missing data).
3. Construction of working models.
4. Completion of field data collection.
5. Tests of models thought to be appropriate.
6. Formulation of theoretical generalization and construction of models that will yield predictions.
The rigorous purist would argue that a model is to be constructed separately for every case of data collection and in respect to the specific situation. If not, the influence of predetermined mathematical models on data collection and resulting calculation can lead to quite erroneous conclusions; empiric real data cannot be selected ultimately, but must be collected. Similar views have been expressed by VARLEY, PEARSALL, GRAHAM (1962), NIKOLSKIJ (1965), KNIGHT (1968) and others. Furthermore, no model constructed in advance is able to predict species inter-relationships and such model construction for a single or a few equalized species is the source of unrealistic results and erroneous conclusions (NIKOLSKIJ 1964; HOLCIK; 1970a).

Difficulties with overly simplified mathematical models may be illustrated by the trend in estimates of maximum sustained yield of the Peruvian anchoveta, Cetengraulis mysticetus as more data become available (SCHAEFER 1967, 1970). Alternative estimates could have been obtained employing simple calculations and evaluations of empiric variables from the fish biology, e.g. relation of mortality rates (man and birds) to fecundity and growth increases of the exploited anchoveta population. But this may mean more field data sampling. "It is clear that our mathematical models are not yet adequate for the complexity of natural systems" was the conclusion of a panel of ecologists under A. D. Hasler's chairmanship. It continued as follows: "Computer simulation is a promising technique for understanding such matters, but computer models need both adequate formulation, or programming, and higher quality data . . ." (HANDLER 1970).

The usual starting point in a quantitative
population analysis is to count or estimate the total stock or, more commonly, to obtain representative samples of it. If devices used to sample fish for such purpose are the same devices used to capture fish for food or sport, they are highly selective and the whole history of their use proves them to be unpractical if used uncritically. To estimate the gear's selectivity to limits of usable precision requires special studies, that have been undertaken for only a few species and gears. Some devices can be used successfully in specific cases without explicit selectivity estimates, e.g. use of the purse seine with single species stocks with schooling habits.

The capture-mark-recapture methods also are biased in that they evaluate only part of the stock (BASTL, HOLCIK and KRUPKA 1969) selected by gear in use. The LeslieDeLury and other similar methods (CHAPMAN 1948) are applicable mainly for smaller stream habitats and are also affected by gear selectivity. In some cases where production by juveniles can be ignored, the latter method can yield sufficiently good data for practical management purposes (HOLCIK 1970a; MARTEN 1970). Combined with juvenile capture devices (BREDER 1960) this method could in some cases replace chemical sampling.

The Lake Kariba programme has been based upon the above eonsiderations. Futhermore, it has been assumed that the most important aspect of fishery research and development in early stages should be the evaluation of the protein reserves, employing a well planned study of the production and yield of fish (HOLT 1967). Otherwise there would be nothing to guide the gear and processing technologists in planning the size and composition of fish catches, the scope of the processing plants, marketing systems, etc. Data on fish catches or landings and fishing effort statistics cannot provide estimates related to ecological production nor its relationship to the magnitude of
potential catches early in the development process. Available mathematical models proposing to do so may yield only very approximate estimates applicably only to dominant species.

It was decided that the main data to be collected were: relative abundance of fish and relative biomass by species, relationships and balance between various species, age composition and mortality rates of various species, and annual weight growth increments.

One of the most adaptable survey methods for shallow waters is sampling by eradicants in blocked-off areas. Since TARZWELL's (1940) first trials in 1939 in the Tennessee Valley, and ESCHMEYER'S (1943) programme, the method has been greatly improved and has been in general use in freshwater reservoir population studies (CARTER 1958; CHANCE 1958); and LAMBOU and STERN 1958; SWINGLE 1958; SURBER 1959). Some experiments have also been started in the sea (HIATT and STRASBURG 1960; RANDALL 1963). After this method was used for the first time in Africa on Lake Kariba, the results of an experiment on the Douglas Reservoir in the U.S.A. were published which discuss the significance of such sampling for an entire lake (HAYNE, HALL and NICHOLS 1967). The Lake Kariba work has utilized experience with different toxicants in population studies on the Elbe and Danube riverine lakes of Czechoslovakia (OLIVA 1955, 1960; BALON 1963, 1966a, 1966b, 1966c, 1967, 1968b); and this experience was adapted to African conditions.

The selection of the method of application depends upon the topography and maturity of the reservoir treated. If the lake is shallow and old with well developed open water ichthyofauna, the sampling area should be established away from the shore by blocking off square or circular areas. This should also be the case on most natural lakes, such
as Lake Mweru. Some deep lakes, however, have more or less separate inshore and open water fish fauna. This is the case of Lake Tanganyika, Lake Victoria, etc. Here blocked offshore areas as well as coves should be sampled. At Lake Kabira our original presumption was that the entire fish population was of riverine origin and that there had not yet been time to develop an open water fish fauna. After testing this by echosounding and gillnets set in different arcas it became evident that cove and inshore sampling should be representative enough. Stream and river sampling is simpler between two blocking nets and the chemical can be neutralized downstream.

## ECHO-SOUNDING SURVEY FOR RANGES OF FISH DISTRIBUTION

To test whether the fish fauna was essentially an inshore one, and to find ranges of fish distribution, a large scale echo-sounding survey was begun on Lake Kariba. With few exceptions, records from open water areas showed practically no fish. Closer to shore, in depths less than 30 m , the abundance of fish appeared to increase, the maximum being at 5 m during daytime and about 10 m at night. This generalization was equally valid for cleared bottom areas and for areas with submerged trees. Without exception the records showed that the main fish distribution was limited to shallow water close to shore and mainly to bays and coves.

Fish seemed to concentrate in the evening along the shoreline and especially in bays and coves, being distributed in remarkably high density from the surface to 15 m depth with maximum density at 6 to 7 m depth. Only at places shallower than 15 m was the evening concentration of fish distributed from the surface to the bottom. At dawn in the same places the major concentrations of fish had changed to a less dense distribution extending further offshore to a distance of
about 2 km . Around islands with steep shores fish were found only in coves or in strips a few meters wide close to shore. In areas of the lake shallower than 15 m but far away from shore, fish were recorded only occasionally, as was the case in the deeper open water areas. These observations are partly confirmed by COKE'S (1968) results with gillnets set in different depths.

It is estimated, therefore, that the main average area of Lake Kariba inhabited by fish in 1968 and 1969 was 33,422 ha, which corresponded to the $0-20 \mathrm{~m}$ depth area at a normal water level of 485 m (COCHE 1968, and personal communication). This represents $6.2 \%$ of the total lake surface, 5,364 $\mathrm{km}^{2}$.

## SAMPLING METHOD

Lake Kariba, which has numerous bays and coves along the entire shoreline and which presents a fish distribution as mentined above, is one of the best impoundments for cove and shore-line sampling. On the average this method should provide representative samples of the whole fish population. In a three year period several 0.5 to 5 ha coves, stream estuaries and three-sided blocked shore-line areas were selected and treated. The blocking nets of 8 mm mesh were set at different hours of the day (Fig. 2). This was done to avoid fencing off the same concentration of fish in the cove or along the shore-line and to to avoid fencing off the highest evening concentration each time. The blocking nets should be, and usually were, checked by a diver, especially along the bottom leadrope.

Emulsifiable rotenone at $5 \%$ concentration, and $75 \%$ emulsifiable toxaphene sold locally as a cattle dip (firm name: Altik), were used (HEMPHILL 1954; HOOPER and GRZENDA 1957). The kind of eradicant used is, however, not important and availability (MALAISSE 1969) as well as effect-


Fig 2. Setting of a double blocking net in the mouth of Chikanka Island cove at Lake Kariba.
iveness, harmlessness to environment, and cost may be taken into account (LENNON 1966; HERR, GRESELIN and CHAPPEL 1967; POWERS and BOWES 1967). The concentrated solution was distributed by boat through a 5 mm hole made in the original 5 gallon drum and was mixed by the outboard engine propeller or by motor pump through perforated hose--in a manner similar to that of CHANCE (1958). The water volume within the blocked area was estimated roughly in order to calculate the necessary amount of toxicant. The minimum lethal dose (HENEGAR 1966; MAHDI 1966) was exceeded because it was essential to kill all fish at once and get the residual fish on the bottom to surface not later than
the third or fourth day. In present temperature conditions, the fish which appeared later had become so rotten that it was difficult to lift and measure them. Fast killing was also essential in order to limit the bias created by scavenging by birds, mammals, and occasionally crocodiles and monitor lizards. An average of 200 litres of Altik was distributed per hectare or per $20,000 \mathrm{~m}^{3}$ water which represented 7 ppm toxaphene. Even so, some Clarias were dying only the third day. The overdosing has a limited effect outside the cove. One month later the treated area was inhabited again and in one recorded case had a higher abundance and mass of fish (although by a smaller number of species) than it had prior to treatment.

Fish were collected in the deepest part by dip nets and along the shoreline by hand. All fishes including the smallest juveniles were collected. On some of the larger fish the necessary determinations and measurements were made on the spot. The majority were preserved in 4-10\% formalin for later treatment in the laboratory.

Before the end of the sampling and the lifting of the blocking net, the entire cove was measured using plane table and soundings (first by lead-and-line, later by echosounding). A detailed bathymetric map was made. The area, length of shoreline, maximum and average depths and volume of water were then calculated exactly. Finally the blocked cove bottom was checked by a diver for residual fish which were counted for predetermined strips of bottom area.

## PRIMARY LABORATORY PROCESSING OF FIELD SAMPLES

The majority of fish sampled, and particularly the smallest ones, were transported to the laboratory in formalin solution. Every specimen was identified and standard length recorded. The weight and the total
length were also recorded for the hirst tew
hundred fish of every species and correction factors for weight differences of fresh, rotten and preserved fish determined. Conversion diagrams and tables for total length and fresh weight were calculated which simplified processing of later experiments based on standard length measurements only (Table 1).

The symbols used are those suggested in the IBP Handbook No. 3 (RICKER 1968). The standard length (1) and the total length (L) were measured with an accuracy of 1 mm ; the weight ( $w$ ) of fresh fish or of fish fixed in formalin was obtained to the nearest 0.1 g (small) or 1 g (large fish). The entire material was put into groups of 10 mm length intervals. The basic table of abundance and biomass was then constructed and the length-frequency distributions were calculated. Then from each " 10 -mm-length-group" a maximum of 10 specimens ( 5 females and 5 males) were selected, their sex was determined and key scales or vertebrae removed.

In this paper there will not be a list of all processes and methods used but only those of special importance for the main outline of the fish population production study. Concrete cases have been published (BALON 1971c, 1971d), and will be described in the future. Here, a single example will be used throughout to illustrate the problems being discussed.

## STOCK COMPOSITIONS, ABUNDANCE AND ICHTHYOMASS

The composition of the samples was listed by species, with the numbers and weights of specimens in each 10 mm length-group. Relating the results to the area treated it was possible to calculate the abundance (relative number of fish per hectare) and the biomass (relative weight of fish per hectare) for every species and for the entire stock sampled (Table 2).

To estimate how close these values repre-
sented the whole lake hish population, corrections had to be applied for all possible sampling biases. Most of them were usually difficult to perform and have not been presented in detail here. HAYNE et al. (1967) proposed a simple ratio called "bias in cove samples". It is the "quotient when the sample mean value is divided by the population mean. If this ratio is 1.0 , then the cove samples are a good representation of the whole arm. If this measure of bias exceeds 1.0 , then the use of cove samples will overestimate the true value, and when the bias is less than 1.0 , then cove samples produce an underestimate". But because of topographical, seasonal and diel variances even an unbiased cove will vary and such a ratio cannot be considered as a precise measure of this bias. The only important "bias" within single locality treated by piscicide and blocking net is due to bird and mammal pick-up of the dead fish. We expect therefore that the bias should generally be one of underestimation.

Ignoring the question of bias, LAMBOU and STERN (1958) and HAYNE et al. (1967) estimated the number of coves to be sampled to give abundance and biomass estimates of required precisions (Table 3). Recalculated on the basis of local samples, such a table would help in planning and evaluating a particular sampling scheme. Bearing the above considerations in mind, the total average of stock abundance and ichthyomass sample data thus yield corrected estimates of the population abundance and ichthyomass for each species. Separate estimates can be made in respect of topographical, seasonal and diel strata. ${ }^{1}$

From the present data we may calculate

1. LOUBENS (1969) made different sample comparisons with the rank correlation coefficient of Kendall. He also discussed the different bias involved in piscicide sampling in the Lake Tchad basin.

Table 1. Conversion table of Hydrocynus vittatus observed mean standard length, calculated total length and geometric intercepted mean weights.

| Standard length in mm | Total length in mm | Weight in g | Standard length in mm | Total length in mm | $\begin{gathered} \text { Weght } \\ \text { in } \\ \mathrm{g} \end{gathered}$ | Standard length in mm | Total length in mm | $\begin{gathered} \text { Weight } \\ \text { in } \\ g \end{gathered}$ | $\begin{aligned} & \text { Standard } \\ & \text { length } \\ & \text { in } \mathrm{mm} \end{aligned}$ | Total length in mm | Weight in g | Standard length in mm | Total length in mm | Weight in g |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 15 | 18 | 0.045 | 155 | 195 | 74 | 295 | 377 | 530 | 435 | 548 | 1900 | 575 | 724 | 4600 |
| 20 | 24 | 0.11 | 160 | -202 | 80 | 300 | 378 | 555 | 440 | 554 | 1950 | 580 | 731 | 4800 |
| 25 | 30 | 0.23 | 165 | 208 | 86 | 305 | 384 | 580 | 445 | 561 | 2050 | 585 | 737 | 4850 |
| 30 | 36 | 0.40 | 170 | 214 | 94 | 310 | 390 | 620 | 450 | 567 | 2100 | 590 | 743 | 5000 |
| 35 | 42 | 0.66 | 175 | 221 | 105 | 315 | 397 | 650 | 455 | 573 | 2200 | 595 | 750 | 5200 |
| 40 | 48 | 1.0 | 180 | 227 | 110 | 320 | 403 | 675 | 460 | 579 | 2300 | 600 | 756 | 5400 |
| 45 | 54 | 1.3 | 185 | 233 | 125 | 325 | 409 | 730 | 465 | 586 | 2350 | 605 | 762 | 5500 |
| 50 | 60 | 2.0 | 190 | 239 | 130 | 330 | 416 | 740 | 470 | 592 | 2400 | 610 | 768 | 5600 |
| 55 | 66 | 2.6 | 195 | 246 | 142 | 335 | 422 | 790 | 475 | 598 | 2500 | 615 | 775 | 5700 |
| 60 | 72 | 3.5 | 200 | 252 | 155 | 340 | 428 | 820 | 480 | 605 | 2600 | 620 | 781 | 5800 |
| 65 | 78 | 4.5 | 205 | 258 | 172 | 345 | 435 | 850 | 485 | 611 | 2700 | 625 | 787 | 6000 |
| 70 | 84 | 5.6 | 210 | 265 | 180 | 350 | 441 | 900 | 490 | 617 | 2800 | 630 | 794 | 6200 |
| 75 | 91 | 7.2 | 215 | 272 | 198 | 355 | 447 | 950 | 495 | 624 | 2850 | 635 | 800 | 6350 |
| 80 | 97 | 8.8 | 220 | 278 | 210 | 360 | 453 | 1030 | 500 | 630 | 2950 | 640 | 806 | 6500 |
| 85 | 103 | 10.2 | 225 | 285 | 228 | 365 | 460 | 1080 | 505 | 636 | 3100 | 645 | 813 | 6600 |
| 90 | 109 | 12.5 | 230 | 291 | 240 | 370 | 466 | 1120 | 510 | 642 | 3200 | 650 | 819 | 6800 |
| 95 | 121 | 14.6 | 235 | 297 | 260 | 375 | 472 | 1170 | 515 | 649 | 3250 | 655 | 825 | 7000 |
| 100 | 128 | 17.5 | 240 | 304 | 280 | 380 | 479 | 1220 | 520 | 655 | 3400 | 660 | 831 | 7200 |
| 105 | 134 | 21.0 | 245 | 310 | 298 | 385 | 485 | 1270 | 525 | 661 | 3500 | 665 | 838 | 7400 |
| 110 | 140 | 24.0 | 250 | 316 | 310 | 390 | 491 | 1330 | 530 | 668 | 3600 | 670 | 844 | 7600 |
| 115 | 147 | 28.5 | 255 | 321 | 335 | 395 | 498 | 1400 | 535 | 674 | 3650 | 675 | 850 | 7700 |
| 120 | 153 | 30 | 260 | 327 | 350 | 400 | 504 | 1440 | 540 | 680 | 3800 | 680 | 857 | 7800 |
| 125 | 160 | 36 | 265 | 334 | 370 | 405 | 510 | 1500 | 545 | 687 | 3900 | 685 | 863 | 7900 |
| 130 | 166 | 40 | 270 | 340 | 400 | 410 | 516 | 1550 | 550 | 693 | 4000 | 690 | 869 | 8000 |
| 135 | 170 | 44 | 275 | 346 | 425 | 415 | 523 | 1650 | 555 | 699 | 4100 | 695 | 876 | 8200 |
| 140 | 176 | 52 | 280 | 353 | 450 | 420 | 529 | 1700 | 560 | 705 | 4250 | 700 | 882 | 8500 |
| 145 | 183 | 56 | 285 | 359 | 475 | 425 | 535 | 1760 | 565 | 712 | 4400 | 705 | 888 | 8800 |
| 150 | 189 | 62 | 290 | 365 | 500 | 430 | 542 | 1830 | 570 | 718 | 4500 | 710 | 894 | 9000 |

Table 2. Abundance of fish stock and ichthyomass in cove of Lake Kariba Chikanka Island (No. 16 —surface $12100 \mathrm{~m}^{2}$, shore line 680 m ) on 21 June 1968

| 28 Species | Standard length ranges in mm | Average length of 1 sp . in mm | Number of specimens | Relative |  |  | Total weight in $g$ | Relative |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Number of fish per I ha <br> ABUN | Number of fish per 100 m shore line DANCE | Average weight of 1 sp . in $g$ |  | Weights in kg per ha ICHTH | Weights in kg per 100 m shore line OMASS |
| Tilapia rendalli gefuensis Thys, 1964 | 37-425 | 126 | 582 | 481 | 85 | 177 | 103281 | 85.35 | 15.19 |
| Clarias gariepinus (Burchell, 1822) | 30-710 | 334 | 89 | 73 | 13 | 812 | 72246 | 59.70 | 10.62 |
| Tilapia mossan:: ica mortimeri Trewavas, 1966 | 35-299 | 101 | 479 | 396 | 70 | 78 | 37350 | 30.86 | 5.49 |
| Hydrocynus vittatus Castelnau, 1861 | 48-420 | 131 | 296 | 245 | 43 | 126 | 37264 | 30.79 | 5.48 |
| Marcusenius discorhynchus (Peters, 1852) | 33-185 | 125 | 329 | 272 | 48 | 42 | 13706 | 11.32 | 2.01 |
| Heterobranchus longifilis Val, 1840 | 103-963 | 400 | 7 | 6 | 1 | 1927 | 13487 | 11.14 | 1.98 |
| Sargochromis codringtoni (Boulenger, 1908) | 72-270 | 157 | 45 | 37 | 7 | 205 | 9247 | 7.64 | 1.36 |
| Synodontis zambezensis Peters, 1852 | 26-278 | 158 | 60 | 49 | 9 | 129 | 7721 | 6.38 | 1.13 |
| Distichodus schenga Peters, 1852 | 63-230 | 191 | 28 | 23 | 4 | 227 | 6367 | 5.26 | 0.94 |
| Labeo altivelis Peters, 1852 | 57-315 | 210 | 10 | 8 | 1 | 569 | 5690 | 4.70 | 0.84 |
| Alestes lateralis (Boulenger, 1900) | 22-60 | 40 | 1759 | 1454 | 259 | 1.3 | 2271 | 1.87 | 0.33 |
| Haplochromis carlottae (Boulenger, 1905) | 200-250 | 225 | 4 | 3 | 0.5 | 542 | 2167 | 1.78 | 0.32 |
| Malapterurus electricus (Gmelin, 1789) | 380 | 380 | 1 | 0.8 | 0.1 | 1272 | 1272 | 1.05 | 0.19 |
| Serranochromis macrocephalus (Boulenger, 1899) | 162-225 | 189 | 4 | 3 | 0.5 | 260 | 1039 | 0.85 | 0.15 |
| Synodontis nebulosus Peters, 1852 | 34-121 | 94 | 34 | 28 | 5 | 21 | 711 | 0.58 | 0.10 |
| Brachyalestes imberi imberi (Peters, 1852) | 60-150 | 103 | 11 | 9 | 2 | 45 | 495 | 0.40 | 0.07 |
| Eutropius depressirostris (Peters, 1852) | 18-179 | 74 | 30 | 25 | 4 | 13 | 391 | 0.32 | 0.06 |
| Haplochromis darlingi (Boulenger, 1911) | 24-88 | 42 | 165 | 136 | 24 | 2.3 | 386 | 0.31 | 0.06 |
| Barbus unitaeniatus Günther, 1866 | 35-58 | 47 | 79 | 65 | 12 | 2.5 | 199 | 0.16 | 0.03 |
| Hippopotamyrus macrolepidotus (Peters, 1852) | 165-191 | 178 | 2 | 2 | 0.3 * | 100 | 201 | 0.16 | 0.03 |
| Schilbe mystus (Linnaeus, 1762) | 75-139 | 100 | 13 | 11 | 2 | 15 | 190 | 0.15 | 0.03 |
| Micralestes acutidens (Peters, 1852) | 36-53 | 44 | 44 | 36 | 6 | 1.9 | 83 | 0.07 | 0.01 |
| Hemihaplochromis philander (Weber, 1897) | 24-58 | 42 | 22 | 18 | 3 | 2.8 | 61 | 0.05 | 0.01 |
| Sargochromis giardi (Pellegrin, 1904) | 109 | 109 | 1 | 0.8 | 0.1 | 64 | 64 | 0.05 | 0.009 |
| Barbus fasciolatus Günther, 1868 | 28-35 | 31 | 52 | 43 | 8 | 0.7 | 38 | 0.03 | 0.005 |
| Labeo lunatus Jubb, 1963 | 92 | 92 | 1 | 0.8 | 0.1 | 20 | 20 | 0.02 | 0.003 |
| Labeo congoro Peters, 1852 | 70 | 70 | 1 | 0.8 | 0.1 | 9.5 | 9.5 | 0.008 | 0.001 |
| Barbus poechii Steindachner, 1911 | 53 | 53 | 1 | 0.8 | 0.1 | 3.4 | 3.4 | 0.003 | 0.0005 |
| Total |  |  | 4149 | 3427 | 609 |  | 315963 | 261 | 46 |

Table 3. Number of cove samples necessary to produce confidence limits $\pm 20 \%$ of the mean with given values of coefficient of variability

| Coefficient of variability | Statistical confidence level used |  |  |
| :---: | :---: | :---: | :---: |
|  | $80 \%$ | $95 \%$ | $99 \%$ |
| 0.20 | 3 | 7 | 11 |
| 0.55 | 14 | 32 | 55 |
| 1.00 | 42 | 100 | 169 |

various relationships and "balance" between the various species, e.g. by applying the ratios $F / C, Y / C, A_{T}$ and the values $A_{F}$, $\mathrm{I}_{\mathrm{F}}, \mathrm{S}_{\mathrm{F}}$ and E as proposed by SWINGLE (1950). Together with echo-sounding records showing vertical and horizontal fish distribution, they can lead directly to conclusions valuable for fishery management and direct attention to locations and species sizes to be fished. SWINGLE (1961) has proposed the equation $\hat{Y}=151.1+0.638 \mathrm{~A}_{\mathrm{T}}+6.212 \mathrm{~F} / \mathrm{C}+2.79$ $S_{F}$ (2) for the estimation of ichthyomass (standing crop) in some reservoirs of the U.S.A. The value $\hat{Y}$ expresses pounds per acre, $A_{T}$ the percentage of the total weight of a fish stock composed of fish of harvestable size, F/C is the ratio of the total weight of all forage fishes to the total weight of all piscivorous fishes in a stock, and $S_{F}$ the percentage of total weight of forage species composed of fish available to the average-size piscivorous fish. So far the estimates of ichthyomass derived from the mentioned equation have been in reasonably good agreement with the sampling averages found by SWINGLE and SWINGLE (1968). But more data and tests are needed to estimate a corresponding equation for Zambia or other waters. Further elaboration of the concepts involved (SWINGLE 1968) would appear to be useful.

Further tests of the general validity of our direct estimates can be sought by applying RYDER's (1965) morpho-edaphic index or similar approaches which may be elaborated later (JENKINS 1968). If the relationship between direct estimates of ichthyomass,
production and yield and these indices become well established, much labour can be eliminated and the data needed for initial research and development obtained and applied more rapidly and less expensively.

## AGE COMPOSITION, GROWTH AND MORTALITY RATES

For estimating age composition, growth and mortality rates, it is necessary to know the correct time of the annulus appearance (BERG and GRIMALDI 1967). In north temperate regions many authors find the annulus to be formed in April to July, less often in March to August. Findings in subtropical regions to date have pointed to a time of annulus formation between December and April (EL ZARKA 1961; VAN RENSBURG 1966a; BALON 1971c), after the rainy season had gotten well under way and when the main spawning period of many species was observed (JOHNELS 1952). In tropical regions with two rainy seasons and repeated spawning in the same year the situation seems to be more complicated. I suspect that there will be one main rainy season and one main spawning period, to which the annulus appearance can be related (VAN SOMEREN 1950, 1952). Repeated spawning is also known in fish of temperate regions. The time of annulus formation in all regions seems to be connected with the main spawning period and with the main vegetation growth period.

Many authors have found that the annulus appearance is delayed as age increases
Table 4. Age group nomenclature related to seasonal appearance of annuli

| Age groups |  | 0 | 1 | II | III |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Number of annuli and occurence of additional sklerits after last one ( + ) |  | 0 | $0,1,1+$ | $1+, 2,2+$ | $2+, 3,3+$ |
| Name of age groups Number of annuli | at beginning of year | - | yearling $0,1,1+$ | $\begin{aligned} & \text { 2-year-old } \\ & 1+, 2,2+ \end{aligned}$ | $\begin{aligned} & 3 \text {-year-old } \\ & 2+, 3,3+ \end{aligned}$ |
| Name of age groups Number of annuli |  | young-of-year <br> 0 | 2-summer-old $1+$ | 3-summer-old $2+$ | 4-summer-old $3+$ |

(ZAWISZA 1951; BALON 1955). In most cases, therefore, the growing seasons of fish are not related in the most simple manner to the calendar year. To bring the growth nomenclature of fish under the calendar year, it is always necessary to check carefully the time of capture with annulus appearance (Table 4). The age groups should agree with calendar years; for example Group O normally includes fish within the year of hatching. For latespawning fish of the temperate zone this means only half a year, for brown trout and tropical late spawners an entire year, and for some early spawners of the tropical region it may only mean a few weeks. The next age-groups I, II, III, IV, etc., always include a full calendar year. To avoid the O age-group paradox when fish juveniles from a December spawn are graduated a few weeks later from $O$ to the I age-group, some authors prefer to use the symbols $0+, 1+, 2+, 3+, 4+$ etc. in age-group designation, according to the number of annuli present.

For the time being no unbiased evidence is available to oppose the objections made by DE BONT (1967) on the validity of the annuli, especially with tropical fish, so it is necessary to rely on experience with the aging of fish in temperate zones (BALON 1953, 1955, 1957, 1962a, 1962b, 1965). Moreover, it is necessary to differentiate the real tropical areas where the formation of annuli is still questionable (BERTRAM, BORLEY and TREWAVAS 1942; DE BONT 1950; JOHNELS 1952; HOLDEN 1955; GARROD 1959; FRYER 1961; OKEDI 1969) from the sub-tropical areas with more pronounced seasons where evidently annuli are formed (LOWE 1952; JENSEN 1957; KOURA and EL BOLOCK 1958; EL BOLOCK and KOURA 1960, 1961 ; EL-ZARKA 1961 ; VAN RENSBURG 1966b) as in temperate regions. Consequently, I can only repeat with DE BONT (1967)
that "There is first of all the presence of different kinds of marks which are not necessarily present on all scales of the same fish, nor on all scales of the same species. Secondly, the time of the year that the marks are laid down may be different from one species to another, from region to region for the same species, and variable from one year to another. There are nearly as many explanations proposed as cases studied. The main factor involved may be one or a combination of the following: drop in temperature, decrease in available food, photoperiod, reproduction, migration, internal physiological rhythm, etc." But still I have the impression that all this is valid for both cold and warm regions. We encounter the problem of false annuli in the American or European pikes as well as in the subtropical tiger-fish. They are, however, always differentiable by their singular appearance and especially by their incomplete course as described in details elsewhere (CHUGUNOVA 1952, 1959 ; BALON 1963).

Therefore, I believe it more reasonable to consider the marks observed on tropical fish scales as similar to the annuli of temperate fish and of possible use as year marks if there is no strong evidence to the contrary. In order to speculate about the intervals in organism development (BALON 1960, 1971a) it can be assumed that the combination of the quoted factors in tropical regions also affects the intervals of seasonal development and that also here the "planetary yearly system"' is recorded on the structure of the scales. As it was correctly remarked by DE BONT (1967) not even in temperate regions do we yet know which of the factors or which combination of them causes the phenomenon of the annulus formation. It is obvious that the "complete cessation of growth during winter" cannot be generalized as the only reason of annulus formation (BERG and GRIMALDI 1967).

In the Lake Kariba studies, the key scales


Fig 3. Key scales sampling scheme of Lake Kariba fishes.
(Fig. 3) or vertebrae sampled following the length-frequency distribution were used for age determination. The latter, after having been adjusted to the total number of specimens present in the sample of each species (Table 5) were used for calculating mortality
rates. The instantaneous rate of total mortality ( $Z$ ) can be calculated according to RICKER 1958a); the seasonal total mortality rate $(A)$ and the survival rate $(S)$ have to be determined for the given $Z$ ( $i$ for RICKER) from his tables of exponential

Table 5. Age composition of Hydrocynus vittatus, Chikanka Cove sampled stock. Calculated from the same relation by age determined part $(\mathrm{n}=160)$

| Standard | O |  | I |  | II |  | III |  | IV |  | VI |  | $\Sigma \mathrm{n}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| groups in mm | n | \% | n | \% | n | \% | n | \% | n | \% | n | \% |  |
| 41-50 | 3 | 1.0 |  |  |  |  |  |  |  |  |  |  | 3 |
| 51-60 | 26 | 8.6 |  |  |  |  |  |  |  |  |  |  | 26 |
| 61-70 | 30 | 10.0 |  |  |  |  |  |  |  |  |  |  | 30 |
| 71-80 | 23 | 7.6 |  |  |  |  |  |  |  |  |  |  | 23 |
| 81-90 | 27 | 9.0 |  |  |  |  |  |  |  |  |  |  | 27 |
| 91-100 | 18 | 6.0 |  |  |  |  |  |  |  |  |  |  | 18 |
| 101-110 | 23 | 7.6 |  |  |  |  |  |  |  |  |  |  | 23 |
| 111-120 | 24 | 8.0 |  |  |  |  |  |  |  |  |  |  | 24 |
| 121-130 | 17 | 5.6 |  |  |  |  |  |  |  |  |  |  | 17 |
| 131-140 | 7 | 2.3 |  |  |  |  |  |  |  |  |  |  | 7 |
| 141-150 | 2 | 0.7 |  |  |  |  |  |  |  |  |  |  | 2 |
| 151-160 | 5 | 1.6 |  |  |  |  |  |  |  |  |  |  | 5 |
| 161-170 | 6 | 2.0 |  |  |  |  |  |  |  |  |  |  | 6 |
| 171-180 | 2 | 0.7 |  |  |  |  |  |  |  |  |  |  | 2 |
| 181-190 | 1 | 0.3 |  |  |  |  |  |  |  |  |  |  | 1 |
| 191-200 | 4 | 1.3 |  |  |  |  |  |  |  |  |  |  | 4 |
| 201-210 | 3 | 1.0 |  |  |  |  |  |  |  |  |  |  | 3 |
| 211-220 | 1 | 0.3 | 4 | 1.3 |  |  |  |  |  |  |  |  | 5 |
| 221-230 |  |  | 11 | 3.6 |  |  |  |  |  |  |  |  | 11 |
| 231-240 | 3 | 1.0 | 7 | 2.3 |  |  |  |  |  |  |  |  | 10 |
| 241-250 |  | - | 4 | 1.3 |  |  |  |  |  |  |  |  | 4 |
| 251-260 |  |  | 4 | 1.3 | 5 | 1.6 |  |  |  |  |  |  | 9 |
| 261-270 |  |  | 2 | 0.7 | 3 | 1.0 |  |  |  |  |  |  | 5 |
| 271-280 |  |  | 2 | 0.7 | 3 | 1.0 | 2 | 0.7 |  |  |  |  | 7 |
| 281-290 |  |  |  |  | 3 | 1.0 | 3 | 1.0 |  |  |  |  | 6 |
| 291-300 |  |  |  |  | 5 | 1.6 |  |  |  |  |  |  | 5 |
| 301-310 |  |  |  |  | 2 | 0.7 |  |  |  |  |  |  | 2 |
| 311-320 |  |  |  |  | 1 | 0.3 |  |  |  |  |  |  | 1 |
| 321-330 |  |  |  |  | 2 | 0.7 |  |  |  |  |  |  | 2 |
| 331-340 |  |  |  |  |  |  | 3 | 1.0 |  |  |  |  | 3 |
| 341-350 |  |  |  |  | 1 | 0.3 | 1 | 0.3 | 1 | 0.3 |  |  | 3 |
| 351-360 |  |  |  |  |  |  | 2 | 0.7 |  |  |  |  | 2 |
| 381-390 |  |  | 1 | 0.3 |  |  |  |  |  |  |  |  | 1 |
| 411-420 |  |  |  |  |  |  | 1 | 0.3 |  |  |  |  | 1 |
| 501-510 |  |  |  |  |  |  | 1 | 0.3 |  |  | 1 | 0.3 | 2 |
| 511-520 |  |  |  |  |  |  |  |  |  |  | 1 | 0.3 | 1 |
| Totals | 225 | 75 | 35 | 12 | 25 | 8 | 13 | 4 | 1 | 0.3 | 2 | 0.6 | 301 |

functions and derivatives. The estimate of mean seasonal survival survival rate ( $\hat{S}$ ) should be calculated according to

$$
\begin{equation*}
\hat{\mathbf{s}}=\frac{\mathrm{n}_{2}+\mathrm{n}_{3}+\mathrm{n}_{4}+\mathrm{n}_{5}+\ldots+\mathrm{n}_{\mathrm{i}}}{\mathrm{n}_{1}+\mathrm{n}_{2}+\mathrm{n}_{3}+\mathrm{n}_{4}+\ldots+\mathrm{n}_{\mathrm{i}-1}+} \tag{3}
\end{equation*}
$$

where there are $i$ age groups and $n_{i}$ fish in the ith group. The estimate of mean seasonal total mortality (A) can be derived from Ricker's table and the mean daily rate of mortality is $\frac{\mathrm{Z}}{365}$ (HOLCIK 1966).
$S$ and $A$, however, can be directly read from the semilogarithmic diagram of the stock curves (BALON 1971c, Fig. 9, BALON 197ld, Fig. 14) and estimated by some kind of mechanical means from the resulting slope if a certain relationship of units on ordinate and abscissa is maintained. This approach is arithmetically well elaborated by REGIER's (1962) models of mortality coefficients under various fishing pressures. However, empirical data so far obtained for different population curves present a proportional distribution of mortality in annual intervals. It can be infurred that the coefficient of natural mortality is not constant, as assumed by REGIER (1962) but changing with every change of fishing mortality as some kind of density dependant, etc. feedback. It explains the proportional total mortality rates within successive years in a "stable" population, in spite of varying actual catch (ROBSON and CHAPMAN 1961).
Concerning the methods of back calculation of growth of fish from annuli measurements on scale and bones it can be repeated that "Each method is accurate which calculates corrections based on one of the objectively determined relations of body length to the observed scale-radius measurement. It is impossible to make methods more exact because the chief cause of error, as indicated previously, lies in the subjective inaccuracy of measurements. There is, hence, only a single further course to follow; the
seasonal and yearly rhythm of scale growth in relation to the body growth of fish must be empirically determined" (BALON 1963). Any method which follows this view is, therefore, correct (e.g. MONASTYRSKY 1926; SEGERSTRÅLE 1933; HILE 1941, 1970; RICKER and LAGLER 1942; VOVK 1956). However, the effect of size selective mortality bias has to be taken into account (RICKER 1969).
For the calculation of production we need to know the annual increment of growth for all species. As the determination of age is part of the growth study it can be used to establish the age compostition and the mortality rates of each studied taxa stock (Table 6). This has provided some very interesting results. The mean seasonal total mortality rate for tiger-fish was calculated as $71 \%$ and the mean seasonal survival rate as $29 \%$. Using rough mortality values it was calculated that in order to produce one 6 -year-old tiger-fish weighing more than $2 \mathrm{~kg}, 4,000$ specimens were required in the first growth season, weighing 640 kg total (Table 7). In the same way it was determined how many juveniles were necessary to produce one first mature female, or male, etc. There seems to be no need to use mortality rates for correction of production sensu lato. It was proved that in normal conditions the recruitment and mortality are in balance (OLIVA 1960; ROBSON and REGIER 1968; HOLCIK 1970a); and we meant by 'normal' when the population's adaptive mechanisms are not yet "pushed beyond the range of their effectiveness and systems will become unstable and will begin to transform" (REGIER 1970a). The calculation of production dates, however, should take into consideration the time difference between the annulus formation and sampling date (HOLCIK personal communication February 18, 1971). We cannot use the increments from back calculated growth rates which are related to

Table 6. Age compositions, seasonal total mortality rates (A), survival rates (S) and instantaneous rates of total mortality (Z) for $H$. vitatus


Table 7. Relative mass of Hydrocynus vittatus after mean seasonal total mortality rate ( $\hat{\mathrm{A}}$ ) and mean seasonal survival rate ( $\hat{\mathrm{S}}$ )

| Growth seasons | Number of specimens dead after$\hat{\mathrm{A}}=75 \%$ | Number of surviving specimens $\hat{\mathrm{S}}=25 \%$ | Standard length in cm of one specimen |  | Weight in $g$ of one specimen |  | Mass of survivals Weight of growth season |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | range | mean | range | mean | $\begin{gathered} \mathrm{kg} \\ \text { minimum-maximum } \end{gathered}$ |
| 1 | 3000 | 1000 | 18 | 9.3-29 | 160 | 14-460 | 160 | 14-460 |
| 2 | 750 | 250 | 28 | 15-39. | 420 | 60-1150 | 105 | 15-287 |
| 3 | 188 | 62 | 35 | 22-45 | 800 | 193-1800 | 50 | 12-112 |
| 4 | 46 | 15 | 39 | 34-48 | 1150 | 750-2100 | 17 | 11-31 |
| 5 | 11 | 4 | 48 | 47-50 | 2110 | 2050-2480 | 8 | 8-10 |
| 6 | 3 | 1 | 49 |  | 2300 |  | 2 |  |

the time of annulus formation and multiply it simply by the assessed abundance, which is related to the time of sampling. We have to adjust the abundance at time of capture ( N ) to the time of the annulus formation ( $\mathrm{N}^{\prime}$ ) according to the mean daily rate of mortality (instantaneous rate of total mortality) as

$$
\begin{equation*}
\mathrm{N}^{\mathrm{I}}=\mathrm{N}\left(1+\frac{\mathrm{Zt}}{365}\right) \tag{5}
\end{equation*}
$$

where $t$ expresses the number of days elapsed from the time of annulus formation to the date of sampling of the given locality, $Z$ is the mean instantaneous mortality rate for the species in a particular locality and $N$ is the number of fish in an age-group. Futhermore, some corrections should be made for the same time differences in fish weight and to young-of-year fish, which exist at time of the sample but not in the time of annulus formation (HOLCIK 1971).

In a study of fish production it is useful to calculate relative values of growth (BALON 1968a). For example, we may calculate the absolute increment

$$
\begin{equation*}
\mathrm{h}_{\mathrm{i}}=\mathbf{1}_{\mathrm{i}}-1_{\mathrm{i}-1} \tag{6}
\end{equation*}
$$

and the index of the species average size

$$
\varnothing \mathrm{H}=\underset{\mathrm{i}=1}{\mathrm{i}=\mathbf{i}+\mathrm{a}} \mathrm{~h}_{\mathrm{i}}
$$

in order to separate the fish into classes of economically preferred species ( $\varnothing \mathrm{H}>5$ ), partly exploited secondary species ( $5>\varnothing \mathrm{H}>2$ ), and unexploited accompanying species ( $\varnothing \mathrm{H}<2$ ). In these formulae 1 is the fish length during various $i$ th years of growth, $j$ for juvenile and $a$ for adult period (BALON 1971a). Weight indices are obtained by replacing the symbol 1 by $w$.

To compare the growth rates of different species or the same species in different lakes it is best to calculate the specific weight rate of growth

$$
\begin{equation*}
\mathrm{cw}=\frac{\mathrm{w}_{\mathbf{i}}-\mathrm{w}_{\mathbf{i}-1}}{\mathrm{w}_{\mathbf{i}}-1} .100 \tag{8}
\end{equation*}
$$

and the index of population weight growth intensity

$$
\varnothing \mathrm{C}_{\mathrm{w}}=\begin{gather*}
\mathrm{i} \mathbf{j}+\mathrm{a} \\
\mathrm{I}_{\mathrm{w}}=1  \tag{9}\\
\mathrm{Cw}_{\mathrm{i}}=1
\end{gather*}
$$

From the relative indices of growth mentioned it is possible to determine the mean age of first maturity of the species stock or population (BALON 1964, 1968a). But for the evaluation of the seasonal changes in species stock it is more useful to calculate the relative condition index (LE CREN 1951).

## PRODUCTION AND YIELD

For illustrating the results we have selected here one of the main predator species (Hydrocynus vittatus) and one main prey species (Alestes lateralis) living in Lake Kariba. The calculations are based on the methods previously mentioned. The calculated lengths for previous years of life are used to estimate mean lengths and increments (BALON 1971c, Fig. 10, Table 8). The minimum harvestable size in relation to the first spawning and especially to economical increments can be established from the crossing point of length increment in percent of length of the first growth season curve and length in percent of length of the final growth season curve (BALON 1971c). HOLCIK (1970 a) assumed furthermore that from "the relation of production to ichthyomass it is possible to compute the best minimum size if we subtract the amount equal to the total production from the total ichthyomass by age groups". In our case both methods gave similar results.

According to the population estimated and the growth analysis the yearly available production ${ }^{2}$ of tiger-fish in Lake Kariba
2. The production values are given the simplest way. No corrections on annulus formation and sampling time differences were made. As already stated all our production values express the annual biomass increments of surviving fish only-the available production.

Table 8. Available production computation of Hydrocynus vittatus in Lake Kariba

| Age groups | Number of fish $n / \mathrm{ha}$ | Sample curve intercepted $\hat{\mathbf{n}} / \mathrm{ha}$ | Mean weight in $g$ of one specimen w | Mean weight increments in $g$ of one specimen h | Total increments of age group per year in $\mathrm{kg} \mathrm{h} \hat{\mathrm{n}} / \mathrm{ha}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 186 | 116 | 140 | 140 | 16.2 |
| I | 29 | 55 | 590 | 450 | 24.7 |
| II | 21 | 27 | 1050 | 460 | 12.4 |
| III | 11 | 12 | 1530 | 480 | 5.3 |
| IV | 1 | 6 | 2000 | 470 | 2.8 |
| v | - | 2 | 2400 | 400 | 0.8 |
| VI | 2 | 2 | 3000 | 600 | 1.2 |
| Relative | production in $\mathrm{kg} / \mathrm{ha} / \mathrm{yr}$ <br> production in percent of biomass ( 30.8 kg ) production for 33,422 of fish inhabited lake area |  |  | $\mathrm{Pa}_{\text {A }}$ | 63.9 |
| Relative |  |  |  | $\mathrm{P}_{\mathrm{A}} / \mathrm{B}$ | 207.5 |
| Relative |  |  |  | $\hat{P}_{A}$ | 2119 metric tons |

equals at the time recorded $12 \%$ of the ichthyomass and $207.5 \%$ of the tiger-fish biomass (Table 8). If we consider that the tiger-fish habitat corresponds with general fish distribution recorded $(33,422$ ha or $6.2 \%$ of the lake surface) its yearly production for the lake would be 2,119 metric tons. From this estimated production the yield or quantity of tiger-fish which can be removed yearly by fishing in the most economical size and without deleterious effect on the present stock, can be calculated. If we determine the harvestable size to belong in average to the II-age group (mean weight about 1 kg or 1.3 kg and 38 cm according to HOLCIK's method), the yield or annual production of harvestable size would be $22.5 \mathrm{~kg} / \mathrm{ha}$. It is possible, therefore, to crop annually a total of 742 metric tons of tigerfish more. This tonnage represents already $70 \%$ of the prcsent annual harvest of all fish from the Zambian part of Lake Kariba.

Alestes lateralis is the most abundant fish: $59 \%$ of the total. Because of its small size its share in the ichthyomass is low, only a little over $0.7 \%$. Its annual available production has been calculated for the same $6.2 \%$ inhabited area of Lake Kariba as 169 metric tons (Table 9). As we later found
that this species is the first to colonize the free open lake area, this production value might be underestimated. From the analysis of the length frequency, the largest specimens of $A$. lateralis are small enough to be eaten by tiger-fish in the most numerous size range. A. lateralis will obviously also be eaten by other predators, but on this issue there is no knowledge up to now. As we have been treating only the data for $A$. lateralis and tiger-fish, let us consider the interrelation of these fish as an example of yield estimates for prey species.

How is the calculated annual production of $A$. lateralis related to the food ration of the main predator? In a paper on tiger-fish (BALON 1971c) attention was drawn to the similarity in many aspects of the biology of the tiger-fish and the European pike. Here-because of shortage of values for the tiger-fish we shall try to use the values found for the annual food ration of the pike in the Volga Delta mentioned by POPOVA (1967); an average value of 3 kg per kilogram of body weight. This lies roughly between POPOVA's (1967) and MUNRO's (1967) "daily ration" 5 ml of food per kg of tiger-fish (calculated as "annual ration" it is $5 \times 365=$ $1,825 \mathrm{ml} / \mathrm{kg}$ ). The mass of tiger-fish per
Table 9. Available production computation of Lake Kariba Alestes lateralis

| Age groups | Number of specimens per 1 ha | Absolute mass per 1 ha |  |  | Relative mass per survival |  |  | Mean weight increment in $g$ of 1 specimen | Total increment of age group per year in kg | Production |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | rate |  |  |  | abs | ute | p |
|  |  | Standard length in cm of 1 specimen | Mean weight in $g$ of 1 specimen | Mass (weight of age group in kg ) | Number of of specimens dead after $\hat{A}=$ 85\% | Number of survived specimens after $\dot{\mathbf{S}}=$ 15 | Mass in kg |  |  | in kg | in \% <br> ichthy- <br> omass | inshore 34298 ha area of lake |
| 0 | 1232 | 4.6 | 2 | 2.46 | 850 | 150 | 0.30 | 2 | 2.46 |  |  |  |
| I | 206 | 7.7 | 12 | 2.47 | 128 | 22 | 0.26 | 10 | 2.06 | 4.90 | 1.88 | metric |
| II | 16 | 10.6 | 36 | 0.58 | 19 | 3 | 0.11 | 24 | 0.38 |  |  |  |

inhabited $6.2 \%$ area of Lake Kariba was calculated as $1,056,000 \mathrm{~kg}$. This quantity of tigerfish requires $3,168,000 \mathrm{~kg}$ of food, so the annual production of 169 tons of A. lateralis covers $5.3 \%$ of the annual food requirement of the Kariba tiger-fish population. MATTHES (1968) found that $5.3 \%$ of the stomach contents of the tiger-fish was $A$. lateralis, which is a very striking agreement for such speculative calculations. At the same time it probably proves that in this case available production estimation is equal to the total production in Ivlev's meaning (see p. 44).

To calculate uniform data for every species living in the studied impoundment (Lake Kariba with 40 species) is a very long lasting project indeed. It could only be effectively accomplished by the cooperation of several institutions working on individual species production and yield to obtain the total annual fish production and yield.

If the maximum sustainable yield is obtained from the natural balanced fish population the fishery management should then look for ways to increase the production and yield by changing the species composition, their relationship, and balance following SWINGLE's (1950) others criteria, according to the carrying capacity of the lake. In Lake Kariba the Tanganyika sardine Limnothrissa miodon was successfully introduced (BELL-CROSS and BELL-CROSS 1971; BALON 1971e) to utilize the uninhabited open lake area, and a large eel stock inhabiting the $20-45 \mathrm{~m}$ depth area was later discovered (BALON 1971b). Assessment of these stocks is done with different methods. The sardine is studied using a combination of determined echo-traces, ring-net hauls and underwater photography, the eels with capture-markrecapture method. Both will add to the already estimated ichthyomass and production of the shore-line fish population, though the addition may not be so simple
in view of the newly developed interactions in relation to the available nutrients.
If there is a shortage of time the production evaluation of the economically preferred species and of the secondary species should be sufficient (Table 10); often the accompanying species do not represent an appreciable part of the ichthyomass and production.

The fish population is a complicated community. Different species are not equal. Their inter-and intra-relationships are as different as those taxonomical characters from one species to another. Furthermore, every species is related in various ways to the environmental factors. We are able to recognize several types of single species stock, eg.:

$$
\begin{array}{r}
\text { I. } \mathrm{A}: \mathrm{X}=\mathrm{a}: \mathrm{y} \\
\text { II. } \mathrm{A}: \mathrm{Y}=\mathrm{a}: \mathrm{x} \\
\text { III. } \mathrm{B}: \mathrm{X}=\mathrm{b}: \mathrm{y} \\
\text { IV. } \mathrm{B}: \mathrm{Y}=\mathrm{b}: \mathrm{x} \tag{11}
\end{array}
$$

where $A$ is a high and $B$ a low amount of food within easy reach, $X$ is the high and $Y$ the low stock density, $a$ is the fast and $b$ the slow growth rate, $x$ is the early and $y$ the late sexual maturity (BALON 1963). By changing the above mentioned relationship (e.g. by fishing or dam building), one species stock change over to another species stock type. Not always does fishing result in a reduction of the abundance or the ichthyomass. KESTEVEN (1962) was not precise on this point even when he later described the situation very well: "The reduction is not equal to the catch, since part of what is caught would have died from natural causes. The reduction of community biomass may be even less than catch-minus-some-proportion-of-it that would have gone to natural mortality, since removal of the catch means presumably greater survival of the organisms on which the caught fish had fed, except that the surviving members of the exploited population may each eat slightly more

Table 10. Recent (1968-1971) list of Lake Kariba fish species in economical order according to the species average size, abundance, topographical frequency of occurrence and mean percentage of total number of specimens.

| Order number | ECONOMICALLY PREFERRED SPECIES | Frequency of occurrence | Mean percentage of total number |
| :---: | :---: | :---: | :---: |
| 1 | Tilapia mossambica mortimeri Trewavas, 1966 | 8 | 10.00 |
| 2 | Tilapia rendalli gefuensis Thys, 1964 | 8 | 3.62 |
| 3 | Hydrocynus vittatus Castelnau, 1861 | 8 | 2.48 |
| 4 | Clarias gariepinus (Burchell, 1822) | 6 | 2.00 |
| 5 | Sargochromis codringtoni (Boulenger, 1908) | 6 | 1.10 |
| 6 | Heterobranchus longifilis Val., 1840 | 6 | 0.09 |
| 7 | Mormyrops deliciosus (Leach, 1818) | 5 | 0.47 |
| 8 | Labeo altivelis Peters, 1852 | 5 | 0.18 |
| 9 | Mormyrus longirostris Peters 1852 | 4 | 0.05 |
| 10 | Distichodus schenga Peters, 1852 | 3 | 0.28 |
| 11 | Labeo congoro Peters, 1852 | 3. | 0.02 |
| 12 | Tilapia andersonii (Castelnau, 1861) | 2 | 0.85 |
| 13 | Sargochromis giardi (Pellegrin, 1904) | 2 | 0.16 |
| 14 | Haplochromis carlottae (Boulenger, 1905) | 1 | 0.10 |
| 15 | Serranochromis robustus jallae (Boulenger, 1896) | 1 | 0.04 |
| 16 | Serranochromis macrocephalus (Boulenger, 1899) | 1 | 0.04 |
| 17 | Distichodus mossambicus Peters, 1852 | 1 | 0.03 |
| SECONDARY SPECIES |  |  | 21.51 |
| 18 | Alestes lateralis (Boulenger, 1900) | 8 | 58.78 |
| 19 | Hippopotamyrus discorhynchus (Peters, 1852) | 6 | 7.94 |
| 20 | Eiltropius depressirostris (Peters, 1852) | 5 | 0.74 |
| 21 | Marcusenius macrolepidotus (Peters, 1852) | 5 | 0.12 |
| 22 | Malapterurus electricus (Gmelin, 1789) | 5 | 0.07 |
| 23 | Schilbe mystus (Linneaus, 1762) | 3 | 0.13 |
| 24 | Anguilla nebulosa labiata Peters, 1852 | - | - |
| 25 | Limnothrissa miodon (Boulenger, 1906) | - | - |
| ACCOMPANYING SPECIES |  |  | 67.78 |
| 26 | Haplochromis darlingi (Boulenger, 1911) | 8 | 5.20 |
| 27 | Barbus fasciolatus Günther, 1868 | 5 | 4.64 |
| 28 | Barbus unitaeniatus Günther, 1866 | 8 | 1.80 |
| 29 | Hemihaplochromis philander (Weber, 1897) | 7 | 1.28 |
| 30 | Synodontis zambezensis Peters, 1852 | 6 | 1.02 |
| 31 | Micralestes acutidens (Peters, 1852) | 6 | 0.41 |
| 32 | Synodontis nebulosus Peters, 1852 | 5 | 0.33 |
| 33 | Brachyalestes imberi imberi (Peters, 1852) | 5 | 0.28 |
| 34 | Aplocheilichthys johnstonii (Günther, 1893) | 5 | 0.04 |
| 35 | Labeo cylindricus Peters, 1852 | 3 | 0.01 |
| 36 | Barbus lineomaculatus Boulenger, 1903 | 2 | 0.02 |
| 37 | Barbus poechii Steindachner, 1911 | 2 | 0.02 |
| 38 | Labeo lunatus Jubb, 1963 | 1 | 0.02 |
| 39 | Barbus paludinosus Peters, 1852 | - | - |
| 40 | Barilius zambezensis (Peters, 1852) | - | - |
|  |  |  | 15.07 |

and take up the spare food left by those that have been caught. By eating more, the surviving fish could grow more, and further offset the removal by the catch. Again, if the fishing removes older fish, the growing potential and efficiency of food utilization of the population can increase". A reduction of the ichthyomass is then usually not the immediate result of fishing (if this does not extend beyond "normal" population adaptability). Even reduction of economically preferred species does not necessarily mean a reduction of total fish production (TSAI 1970). More often fishing results in an increase of production, especailly in shortliving and early maturing fish species. It takes very long continuous fishing with intensive methods leading to a high catch increase to reduce the ichthyomass. Even in the Danube River (high populated shores) it has taken centuries to overfish easy-to-catch giant huso, maturing for the first time at 20 years of age (BALON 1967). Overfishing of short-living and early-maturing bleak was found to be impossible (ENTZ 1952) and I have to agree with MESECK (1962) that usually bad landings "caused by a wrong fishing technique are frequently explained as overfishing".

If we take into consideration all the complicated relationsships between different species in a stock and the environmental factors (e.g. HANDLER 1970) where we usually find a strong trend to balance the community, there is really very little fishing influence to be expected especially in a subsistence fishery. More harm is to be expected (and was proved, e.g. MILLER 1961; BALON 1967) from dam building and pollution where irreversible changes occur. Furthermore, this stands also in case of intensive fishing industries with catches over maximum sustainable yield. Continuous overfishing usually terminates the economy of a catch before the species affected is in danger of extinction. Then regulations
become a perpetual interest of exploiting insititutions and they may be effective if no other factors interfere. As the latter is usually the case (e.g. pollution and lampreys in the Laurentian Great Lakes, river bank regulations and dam building on Europe main streams) preventive measures to forbid overfishing are vital. As empiric fish production data and maximum sustainable yield data are lacking, intensive research should be developed in this direction.

As REGIER (1970b) expressed so excitingly in his address to the Centennial Meeting of the American Fisheries Society in relation to pollution: "We have fought to have corrective technology applied to this or that case of pollution. We have won many small battles, but have been losing the war'. Similar statements have been made in relation to water buildings equally by myself (BALON 1967). But still COUSTEAU (1964) is right in stating: "In our times the technocrats are at the summit. Almost everywhere they have powerful contact with politicians. It is clear that this will change again. Biological sciences will again be in the fore because without life even science cannot exist'. Let's hope it will not be too late then. If we like to find out how our recent fish production studies are related to the much preferred fish yield predictions, "then the only logical conclusion is that the biomass of the future is likely to be just so much more or less than it is now, as man makes it to be" KESTEVEN 1962).

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