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<th>Population Changes of Sardines in Northern Lake Tanganyika</th>
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<tr>
<td>Citation</td>
<td>African Study Monographs (1992), 13(1): 57-67</td>
</tr>
<tr>
<td>Issue Date</td>
<td>1992-06</td>
</tr>
<tr>
<td>URL</td>
<td><a href="https://doi.org/10.14989/68086">https://doi.org/10.14989/68086</a></td>
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<tr>
<td>Type</td>
<td>Departmental Bulletin Paper</td>
</tr>
<tr>
<td>Textversion</td>
<td>publisher</td>
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ABSTRACT Population changes of sardines, so called ndakala, in northern Lake Tanganyika and some possible causes of their decrease in catch in the 1980s were studied using the catch statistics of Zaire and Burundi from 1974 to 1987. Neither immigration nor emigration could be proved in the northern part of the lake. Yearly changes in catch and catch per unit effort suggested that the ndakala population size had mildly but steadily decreased since 1980 and the size in 1987 was about a half of that in 1980. Density dependence was detected and the mild population fluctuation might be related to recruitment compensation among the multiple cohorts born in the same year. A stable level of fishing effort in Burundi in the 1980s supported a view that the decrease in catch was caused by the population decrease. A hypothesis that an increase in predation pressure had caused the decrease was rejected. A preliminary analysis using simplified population dynamics models implied that the population had not been overfished, though consideration of overfishing will be still indispensable.

Key Words: Population change; Ndakala; Density dependence; Recruitment compensation; Predation; Overfishing.

INTRODUCTION

Lake Tanganyika, one of the world's oldest and largest lakes, contains many endemic fish species. But the fish fauna in the pelagic waters of the lake is rather simple: two planktivorous sardines, Stolothrissa tanganicae and Limnothrissa miodon, and four Centropomid fishes, Luciolates stappersii, Lates mariae, L. angustifrons and L. microlepis. These pelagic fishes are exploited and serve as important fishery resources for inhabitants near the lake. In the northern part of the lake (see Fig. 1(a)), sardines maintain the highest catch among fishes, suggesting that they are the most abundant. They are also prey for the Centropomid fishes. Studies on population dynamics of sardines will contribute to the sustainable use of fishery resources and a better understanding of the dynamics of the pelagic fish community.

A decrease in sardines' catch in the 1980s has been recognized in the northern part of the lake. More attention is paid to the management and conservation of sardines. Few studies on the population dynamics, however, have been carried out. The objective of this study is to clarify the population changes using the catch statistics and to give preliminary consideration on some possible causes of the
METHODS

Two species of sardines and a small-sized fish of *L. stappersii* are captured together by fishermen and are classified into a commercial category called "ndakala." Thus ndakala catch is a single entity recorded in the catch statistics. The species composition in a catch varied highly from boat to boat (Shirakihara, personal observation). It seems impossible to compile the statistics by species unless a well-designed sampling survey over the whole area in question is undertaken. This study treats ndakala as a single pelagic species. However, past studies (Ellis, 1971; Coulter, 1977; Roest, 1978) showed that *S. tanganicae* accounted for 70% or more of ndakala catch in weight.
The data used in this study were the catch statistics of Zaire and Burundi for the period of 1974 to 1987, which were obtained by the courtesy of the Environment Office, Zaire, and the Department of Water, Fisheries and Fish Culture, Burundi. The form of statistics differed between the two countries, but both recorded ndakala catch in weight by month and by landing beach (see Fig. 1(b)). The fishing effort measured by the number of fishing units which operated actually were available only in Burundi. The Zaire statistics were compiled on a calendar month basis whereas the Burundi statistics on a lunar cycle basis. For comparison, we converted the Burundi statistics into the calendar month version by proportional allotment.

Ndakala is exploited by three types of fisheries; rural, artisanal and industrial. Each type of fisheries should have a different catchability. Following Gulland (1983), the total effort was evaluated as follows:

\[
\text{Total effort} = \frac{\text{Total catch}}{\text{CPUE of the standard fishery}},
\]

where CPUE, an index of population size, stands for catch per unit effort. The artisanal fishery was chosen as the standard fishery for ndakala because of its highest dependence on ndakala: in Burundi, ndakala catch in weight accounted for more than 70% of the total catch of the artisanal fishery in each year. The industrial fishery was chosen as the standard fishery for predators for the same reason. The total catch divided by the total effort in terms of the standard fishery will be referred to as standardized CPUE or simply CPUE, which is equal to CPUE of the standard fishery.

RESULTS AND DISCUSSION

I. Some Considerations on Distribution and Seasonal Movement

Fig. 1(b) shows the mean monthly catch of ndakala by landing beach. The fishing places for the fish were not recorded in the statistics, but they were considered to be near the landing beaches (Mambona, personal communication). Ndakala was landed at all the beaches. This indicates that ndakala is distributed widely in the northern waters. No available statistics could prove any geographical discontinuity in the distribution.

Fig. 2 and Fig. 3 show the monthly changes in catch and CPUE by beach, respectively. There were periods with an increase in catch or CPUE. A plausible explanation is that seasonal movement from the central or southern parts of the lake into the northern part may occur. If ndakala has such a latitudinal movement pattern, monthly changes in catch or CPUE within the northern part are expected to reflect the pattern: when the fish move northward in a specific season, a peak of catch or CPUE should occur earlier at a southern beach than at a northern beach. The observed data, however, did not support a clear geographical shift in the peak month. The data, rather, showed some peaks occurred almost simultaneously at several beaches. Available daily catch data in Zaire suggested a similar pattern (Fig. 4) even after considering that the daily change in catch depended on the lunar
cycle because of night fishing with lamp. Our analysis could not find any indication of the seasonal movement, though rapid and extensive movement of *S. tanganicae* has been pointed out by Chapman & Well (1978). Mature fish and larvae of *S. tanganicae* were collected in the northwestern part (Mulimbwa, personal communication; Tshibangu & Kinoshita, personal communication), indicating that the fish actually reproduce there. Hereafter we will assume that ndakala in the northern part of the lake constitute a closed population.

The above consideration may lead to the following hypothesis. The population defined here is a continuum of many local populations. Each local population shows a common response to environment fluctuations in the northern part of the
II. Population Changes

The CPUE in Burundi showed a yearly decreasing trend (Fig. 5(a)). The yearly changes in catch were similar between the Uvira zone in Zaire and Burundi (Fig. 6, $r=0.78$, $n=10$): there were peaks in 1980 and declines thereafter. Such a decline was also observed in the Fizi zone after 1982. The population in the northern part of the lake had decreased in size. The population size in 1987 was estimated to be about a half of that in 1980 (Fig. 5(a)). Because fishing effort had been kept rather
stable, except for the two years of 1975 and 1976 (Fig. 5(a)), the decrease in catch can be considered to have been caused by a population decrease.

Coulter et al. (1965) stated that natural fluctuation in tropical fish populations appears to be more marked than in the temperate zones. But contrary to expectation, the fluctuation of the ndakala population appeared to be mild. The maximum/minimum ratio in population size was 2 for this population with a decreasing trend, whereas the ratio was 6 for Ayu, Plecoglossus altivelis, in Lake Biwa, Japan, for the period of 1915 to 1937. Ayu is comparable with S. tanganicae in that it lives in fresh water lake for about one year and eats plankton (Miura, 1977).

III. Detection of Density Dependence

One possible cause of the mild fluctuation would be that the population has a
Fig. 5. (a) Yearly changes in the ndakala standardized CPUE (artisanal fishery's CPUE) and the standardized fishing effort for the fish. (b) Yearly changes in the predators standardized CPUE (industrial fishery's CPUE).

Fig. 6. Yearly changes in total catch of ndakala in the northern part of the lake.

mechanism to regulate its size. Density dependence was examined by the following procedures. The observed CPUE was assumed to be proportional to the population size. Then the annual rate of population change, $CR_t$, can be defined as:

$$CR_t = (\text{CPUE}_{t+1} - \text{CPUE}_t)/\text{CPUE}_t.$$ (1)
where \( t \) is the year. The rate \( CR_t \) was negatively correlated with \( CPUE_t \) (Fig. 7, \( r = -0.566, P < 0.05 \)), which implies that the population tends to stabilize its size.

IV. Recruitment Seasons and Compensation by Multiple Cohorts

The longevity of \( S. tanganicae \) is about one year (Matthes, 1967). Thus the ndakala population size can be expected to be changeable, depending on the yearly success in recruitment. The actual situation seemed not so.

Among several beaches in Burundi, peaks of CPUE occurred in the same months (Fig. 3). The peaks should be caused by recruitment, under a hypothesis of no seasonal latitudinal movement and no marked seasonal changes in growth. The common peaks were observed during February to April, July to September and November to December, though yearly variations in peak months were observed. These months were estimated to be the main seasons of recruitment to the fishing ground. These multiple seasons correspond to multiple spawning seasons in a year (Ellis, 1971).

Fig. 8 shows the monthly changes in CPUE in all the waters of Burundi. A peak in CPUE was observed in February, 1980. A peak in this month also occurred at most beaches of Burundi (Fig. 3). This peak can be considered as having derived from the successful recruitment of a cohort produced in a spawning season. Note that the peak in February disappeared in 1983 and 1986 and, instead, peaks occurred in other months. A recruitment failure of a cohort may be compensated by a success of the other cohorts. This may be one explanation why the population tended to remain stable from 1980 to 1986 (Fig. 5(a)), in spite of yearly variation in the monthly changes in CPUE for this period (Fig. 8).

![Graph showing correlation between CPUE and change rate]

Fig. 7. Correlation between the ndakala standardized CPUE in a year and its change rate until the next year (\( CR \)) for the period of 1974 to 1986. The regression analysis derived an equation: \( CR_t = 0.57 - 0.0078 CPUE_t \), where \( t \) is the year.
V. Effect of Predation

Many plausible causes of the decrease in the ndakala population can be pointed out: an increase in predators, overfishing, a decreasing period in the natural long-term population fluctuation, a decrease in food organisms, deterioration of physical or chemical conditions of the habitat due to human activities such as pollution. We considered only the first two, because some analyses can be made using the available catch statistics.

The predator population decreased after 1977 (Fig. 5(b)). Thus we rejected the hypothesis of an increase in predation pressure as a cause of the decrease of the ndakala population.

VI. Effect of Exploitation

If an increase in the fishing effort leads to a decrease in catch, the population may be overfished. But in Burundi, the decrease in catch was observed under the sustained level of the fishing effort (Fig. 5(a) and Fig. 6).

Using the simple models, a preliminary analysis was made to examine whether the population was overfished. The population dynamics was assumed to be expressed by the following equation.
\[ N_{t+1} = N_t + V_t - C_t, \]  
(2)

where \( N_t \) is the population size in weight in year \( t \), \( V \) is the amount of natural increase in weight, and \( C \) is the catch in weight. The catch is:

\[ C_t = qX_tN_t \]  
(3)

or

\[ \text{CPUE}_t = qN_t \]  
(4)

where \( X \) is the fishing effort and \( q \) is the constant referred to as the catchability coefficient. In general, \( V \) is a function of \( N \): \( V \) is small when the population is depleted or overcrowded. Let us define overfishing as the situation where population is so depleted by exploitation that a decrease in the population size only leads to a decrease in the amount of natural increase. Then, \( dV/dN \) shows a positive value.

Differentiating both sides of (2) by \( N_t \) and rearranging the equation,

\[ dV_t/dN_t = dN_{t+1}/dN_t + dC_t/dN_t - 1. \]  
(5)

As for the first term of the right side,

\[ dN_{t+1}/dN_t = 1.57 - 0.016\text{CPUE}_t. \]  
(6)

This was obtained from (4) and the observed relationship between \( CR \) and CPUE (Fig. 7):

\[ (\text{CPUE}_{t+1} - \text{CPUE}_t)/\text{CPUE}_t = 0.57 - 0.0078\text{CPUE}_t. \]

From (3), we have

\[ dC_t/dN_t = qX_t. \]  
(7)

Substituting (6) and (7) into (5),

\[ dV_t/dN_t = 0.57 - 0.016\text{CPUE}_t + qX_t. \]  
(8)

The catchability coefficient \( q \), rate of exploitation by an one-night operation of the standard fishery (artisanal fishery) in the waters of Burundi, was estimated to be \( 0.20 \times 10^{-5} \) based on the acoustic estimates of \( N \) in 1974-76 (Roest, 1978). The values of \( dV_t/dN_t \) calculated using the observed catch statistics were negative in all the years. Our analysis implied that the population had not been overfished yet. But note that our results depend critically on oversimplified models and the results may be too optimistic if the recorded total catch had been underestimated.

ACKNOWLEDGMENTS We are grateful to H. Kawanabe of Kyoto University and M. Nagoshi of Nara Women's University for their invaluable advice. We thank the directors of the Environment Office, Zaire and the Department of Fisheries and Fish Culture, Burundi for their permission to use the catch statistics. We also thank the staffs of the two offices, especially B. Sylvestre of the latter office, for their assistance in collecting the statistics. We are indebted to M. K. Kwetuenda, M. M. Gashagaza and other members of C. R. S. N./Uvira for their support to our work. This work was supported by the Japan International Cooperation Agency (No. 4860445) and the Ministry of Education, Science and
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---Received January 7, 1992