DIFFERENTIATION OF BODY SIZE IN TWO COREGONID SPECIES UNDER CONDITIONS OF LONG-TERM CULTURE IN ILLUMINATED CAGES

RÓŻNICOWANIE SIĘ ROZMIARÓW CIAŁA DWU GATUNKÓW RYB GŁĘBIELOWATYCH (COREGONIDAE) W WARUNKACH DŁUGOTRWAŁEGO CHOWU W SADZACH OŚWIETLONYCH

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Changes in population structure of two coregonid species (Coregonus lavaretus L. and C. peled Gmel.) kept in illuminated cages from hatching until maturity are a result of concerted action of a number of ecological factors, food resources playing the key role. The analysis of long-term trends in body size variability and in changes within each stock allows to reconstruct the conditions of growth in cages and to indicate certain critical periods in fish life.

INTRODUCTION

The phenotypic variability, i.e. the level of differentiation in a natural or experimental population, observed under certain conditions and in a defined period of time results from a number of processes which are an effect of a combination of genetic and environmental factors (Sluckij, 1978). Differences between individuals are affected by processes governing the mortality level in a population. Variability is more and more frequently considered a control mechanism of population dynamics (Łomnicki, 1980). A number of within-population phenomena such as hierarchy and competition for food and space influence the variability to a significant degree (Poljakov, 1960; Yamagishi, 1969; Mashiko, 1976; Nakamura and Kasahara, 1977a, b, c, d; Wohlforth, 1977; Ruban, 1977; Geršanovič, 1983). So far, body size differentiation in plankton-feeding coregonids in intensive cultures has not been dealt with. First attempts to study coregonid variability in cage culture were made in the early 80's only (Tisčenko, 1981).
In 1977–1980, the first Polish attempt to keep Goregonus spawners in fully controlled illuminated cage cultures was made (Mamcarz and Szczerbowski, 1984). Apart from a number of results showing the culture output, the 4-yr period of culture yielded also preliminary data on size differentiation in Coregonus lavaretus L. and C. peled Gmel. Their presentation is the author’s aim in this paper.

MATERIALS AND METHODS

Both species were kept under controlled conditions in cages placed in the Legińska Lake situated upstream the river Sajna (the Łyna-Pregoła drainage). Culture methods, fish growth and survival as well as environmental conditions and techniques used to monitor them were discussed earlier (Mamcarz and Szczerbowski, 1984; Szczerbowski and Mamcarz, 1984).

The experiment involved 8 m$^3$ capacity cages. At the first stage, 1.0 and 1.8 mm mesh size polyethylene netting was used in cage construction. After 5 months, the fish were transferred to 5.5 mm mesh size net cages where they were kept until the experiment was terminated. Photocell-controlled illumination (24 V/60 W) inside the cage was used to bait natural food. The fish were wintered in the same cages, under ice, at 24 h illumination. To analyse size differentiation of fish during a long-term cage culture, data on 3 stocks (2 cages with C. peled and one with C. lavaretus) with no marked changes introduced to the stocking density were used. The initial C. lavaretus stocking density was 5,832 larvae per m$^3$. The density in the cage was not interfered with throughout the entire experiment. One cage was stocked with C. peled at a density of 12,500 ind./m$^3$. Two months later the stock was divided into 3 cages with densities of 1,969; 1,313; and 657 ind./m$^3$. A detailed description of stocking density-dependent size variability of C. peled during the first year was given in a separate paper (Mamcarz, 1984). The present paper is restricted to a brief characteristics of changes in extreme densities over the same period of time. As of the second year until the end of the experiment, stock densities in the two cages with C. peled maintained a ratio of 1 : 4 (Fig. 1).

The larvae and O+ fry were sampled every week, while samples of older fish were collected once or twice a month. The fish were weighed to 1 mg (larvae) and 1 g (older fish). Total fish length was measured to 0.1 mm. A total of 814 and 3,204 individuals of C lavaretus and C. peled were examined, respectively.

Variability in fish size was described by means of the coefficient of variation (CV) calculated from separated series generated with the Sterdges formula (Balicki and Bielecki, 1980). Changes in stock structure during the growth period in cages were assessed with the coefficient of skewness (Nakamura and Kasahara, 1977a) as follows:

$$\text{SK} = \frac{1}{\sigma^3} \cdot \frac{1}{N} \sum f_i (x_i - \bar{x})^3$$

where $\frac{1}{N} \sum f_i (x_i - \bar{x})^3 = \mu_3$ is the third order central moment. Since Sk has no defined
Body size of coregonids in illuminated cages

Fig. 1. Variability of length (L) and weight (W) of Coregonus lavaretus and C. peled kept in illuminated cages against the background of changes in stocking density and zooplankton biomass in Lake Legińskie within 1977–1980
1 and 2: cages with C. peled with initial densities of 1,969 and 657 ind./m³ in July 1977;
3: cage with C. lavaretus

Fig. 2. Changes in coefficient of skewness of C. peled length (L) and weight (W) distributions during culture in illuminated cages in Lake Legińskie within 1977–1980; for explanations see Fig. 1.
numerical range, the following modification of the formula proposed by Krzysztofiak (1966) was used to facilitate interpretation of the data:

$$SK = \frac{\mu_3}{\sigma^2 + |\mu_3|}$$

Owing to the module $u_3$ being added in the denominator, all SK values are in the range of $-1 < SK < 1$.

RESULTS

Size variability of *C. lavaretus* and *C. peled*

During the initial stage of growth in cages (until the yolk sac was resorbed), size differentiation of the larvae was similar between the two species. The CV values for *C. peled* and *C. lavaretus* body length were 3.5% and 4.5%, respectively. The respective mean lengths were 9.4 and 12.5 mm. Variability in body weight of *C. peled* was 13.5% (at a mean weight of 4.1 mg), while the corresponding CV value for *C. lavaretus* was 11.1% (mean weight of 9.8 mg). Once the larvae switched to the external food, their size underwent a considerable differentiation (Fig. 1). Toward the end of the larval period, size differentiation was 3–5 times greater than recorded initially. A sizeable increase in fish weight variability was observed as well. As soon as on the 40th day of culture, the weight CV exceeded 70% in *C. peled* and reached about 40% in *C. lavaretus*. The maximum variation in fish size occurred during the summer stagnation (July-August), when the zooplankton biomass decreased in the lake and a resultant growth retardation of the two species ensued. At that time, the *C. peled* growth variability in the highest-density cage (cage 1) reached 83.1% at a mean individual weight of 238 mg. The variability in *C. lavaretus* was lower by half. Regardless of stocking density, all the cages exhibited characteristic peaks of variability followed by a marked reduction in variation (Mamcarz, 1984). During the autumn growth acceleration, size variability was subject to a further slow decrease accompanied by oscillation in CV values as described by Sluckij (1978). In December (after 220 days of culture), the *C. peled* size CV ranged within 4.6–8.1% at a mean length range of 95–110 mm. The corresponding values for *C. lavaretus* were 4.8 and 117 mm. At the end of the first the body length variability became stabilised and remained virtually at the same level throughout the subsequent years of culture (Fig. 1).

Changes in the body weight CV values of *C. peled* and *C. lavaretus* showed a certain seasonal pattern, related also to cage stocking density. An intensified differentiation in winter was also followed in spring-summer 1978 by a decrease in CV down to 12–17%. The largest decrease was observed in the *C. peled* containing cage 1 with the lowest density (about 125 ind./m$^3$) (Fig. 1). The 1978 summer stagnation with its decrease in food biomass again yielded an increased variability in body weight of the two species. In
late August, the \textit{C. peled} CV ranged within 24–34\% (at a mean individual weight of 20–40 g). The pattern was repeated in 1979 (Fig. 1). Irrespective of the fish growth retardation, outbreak of an unknown disease lasting until the end of the summer stagnation, was observed (Waluga, 1980). In spite of the low density, the disease resulted in a 63\% loss of the stock. As late as at the end of September 16.4\% of the surviving fish showed open wounds and lesions, healing gradually (Mamcarz, 1982). The epizootics, showing symptoms of a prolonged bacterial invasion, caused the fish growth differentiation to increase out of proportion to the stock density in the cage (Fig. 1).

After 3 years of keeping \textit{C. peled} in strongly differentiated a marked deviation in growth of the two populations was observed (Mamcarz, 1982). In spring 1980, the \textit{C. peled} individuals in cage 1 attained 134 g mean individual weight, as little as 52,4 g being reached by the fish in cage 2. At the same time, the corresponding value for \textit{C. lavaretus} was 111 g. Similarly to previous years, fish weight variability during the spring growth tended to decrease. In June, the \textit{C. peled} CV values ranged, depending on density, within 12.1–22.3\%, while the \textit{C. lavaretus} body weight CV was 24.4\%. The 1980 summer stagnation was accompanied by a renewed increase in weight variability, the variability being gradually reduced in autumn (Fig. 1).

Changes in \textit{C. lavaretus} and \textit{C. peled} stock structure during cage growth

Panmictic populations existing under natural conditions show most of their quantitative characters to be distributed in a manner approaching the normal distribution. As a result of a non-uniform growth of various individuals in culture, resulting from a number of processes taking place within a stock, the “normality” may become strongly altered, which leads to the distributions being skewed to the left or to the right.

During the cage culture of \textit{C. lavaretus} and \textit{C. peled}, the structure of their stocks changed several times as reflected in oscillations of the skewness coefficient SK. The oscillations showed similar trends with respect to body length and weight. Moreover, in spite of considerable differences between the SK values of the two \textit{C. peled} stocks, the trends in this case were similar as well (Fig. 2). On the other hand, the course of changes differed somewhat between the \textit{C. lavaretus} and \textit{C. peled} stocks (Figs. 2 and 3).

During the first year of culture, the \textit{C. peled} length distribution showed a clear-cut positive asymmetry (SK > 0.5) as early as after the first month. As of June, until the end of the year, extensive SK oscillations and changes in the direction of skewness of length distributions in both stocks were observed. The oscillations in the \textit{C. peled} weight SK had a smaller amplitude; the distributions were positively asymmetric almost throughout the year. At the initial stage of keeping \textit{C. lavaretus} in cages their distributions were skewed to the left (SK < -0.5 for body length). In August, the distributions became skewed to the right, while in autumn the skewness was similar to that observed in \textit{C. peled}.

In the second year of the cage culture, the body dimensions distribution skewness in the two species continued to oscillate between negative and positive values within a broad range of \(-0.5 < SK < 0.5\), which was particularly evident during the summer stagnation.
Fig. 3. Changes in coefficient of skewness of *C. lavaretus* length (L) and weight (W) distributions during culture in illuminated cages in Lake Legińskie within 1977–1980

It was only the *C. lavaretus* length distribution that showed a positive asymmetry throughout most of the year (Fig. 3).

In the third and fourth year of cage culture, the length and weight distributions of the two *C. peled* stocks showed certain differences (Fig. 2). In 1979, the length distribution of the cage 1 individuals subject to the disease had a lower skewness than that in cage 2, a reverse situation being observed in weight distributions. The situation seems to reflect changes in fish condition, the changes being brought about by the disease which caused growth retardation in some individuals. The different nature of asymmetry in both *C. peled* stocks was observed in 1980 as well: distributions in cage 1 were definitely skewed to the left, which probably resulted from differing growth and maturation rates in the stock affected by the disease. An increased negative asymmetry in distributions in the two stocks was particularly marked in autumn 1980 when the gonadosomatic coefficients were strongly variable within the two stocks.

**DISCUSSION**

A number of reasons have been invoked to explain variability between individuals in a stock during the period of growth. The stock dynamics theory formulated by Nikolski (Lapin, 1981) is one of the most frequently quoted explanations. It assigns an adaptive value to the variability. According to Nikolski, an increase in variability, resulting from deteriorating conditions of the population's life, broadens the fish food spectrum and weakens the intraspecific competition. Studies of Suchanov (1981) demonstrate the presence of a certain feedback between the habitat and variability among individuals and allow to describe variability as a population's response to environmental stimuli. According to Łomnicki (1980), variability among individuals results from a non-uniform food resources partitioning in the population and is the prerequisite of its stability. The non-uniform growth of various length classes as measured with the coefficient of...
skewness reflects structural changes in a stock (Poljakov, 1970; Konikoff and Lewis, 1974; Mashiko, 1976; Kochanova, 1979). These, as a rule, are associated with changes in feeding conditions, which is expressed as asymmetry of size distributions in a stock consisting of individuals of equal age. At an extreme diet differentiation (e.g. in predatory fish), the distributions may become bimodal (Chodorowski, 1975). Additionally, ethologic phenomena like hierarchy, territorialism and others are of a paramount importance in shaping the stock structure (Yamagishi, 1969; Mashiko, 1976; Thorpe, 1977).

As demonstrated by observations made on coregonids confined to a restricted space, changes in stock structure result from a concerted action of a number of ecological variables. Due to the specific nature of fish culture in illuminated cages, food resources seemed to have played a key role. These effects were at their strongest during the period of larval growth (Mamcarz, 1984). Once the larvae switched to the food taken up from the water column, the competition between individuals led not only to differentiation of their size, but also retarded the development of some of them (Mamcarz, 1982). This was expressed by the negative asymmetry of the *C. lavaretus* larval size distributions and also by the “shoot carp” phenomenon, described by Wohlfarth (1977), in *C. lavaretus*. At the critical point, elimination of some of the weakest individuals brought the stock again to a certain equilibrium between the amount of food available and stock density. Against the background of food-density interactions, other processes played intermittently the key role, too. One may point to effects of diatom blooms on fish larvae (Mamcarz and Worniałło, 1986). A continuous pressure of various parasites and epizootics (Waluga, 1980) was an extra stimulus reinforcing the key factor. The summer stagnation, a period when effects of limiting factors were cumulated, played a particular role in the cage culture. All those processes were associated with an increased mortality or decreased condition of some individuals, expressed through increased size differentiation and structural changes in stocks. Sexual maturation was the only period of increased size variability without increased mortality. However, the abnormal course of the maturation, determined by conditions of cage culture, cannot be excluded (Worniałło and Mamcarz, 1985; Mamcarz and Worniałło, 1985). The complexity of limiting factors and their mutual modifications make the evaluation of their respective roles in shaping the stock size structure difficult. However, analyses of long-term trends in fish size variability and ratios between various length classes can be instrumental in approximating conditions of fish growth in cages and in defining certain critical periods in fish life.

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STRESZCZENIE

U dwóch gatunków Coregonidae (Coregonus lavaretus L. i Coregonus peled Gmelin), przetrzymywanych w sadzach oświetlonych od wyługu do dojrzewania płciowego, podjęto próbę obserwacji różnicowania się rozmiarów osobników oraz zmian wewnątrz stad w czasie długotrwałego chowu. Zróżnicowanie rozmiarów ryb określano współczynnikiem zmiennosci (CV), natomiast zmiany w strukturze stad – współczynnikiem skosnosći rozkładu (SK).

Stwierdzono, że zmiany w charakterze zróżnicowania rozmiarów ryb oraz różnice w charakterze rozkładów długości i masy osobników są przejawem pewnego mechanizmu regulacyjnego w stadach, będącego efektem kompleksowego oddziaływania szeregu czynników ekologicznych (baza pokarmowa, konkurencja o pokarm, zakwity okrzemek, pasożyty i epizootje). Czynniki te najsilniej wpływają na charakter stad ryb w pierwszym i drugim roku chowu, kształtując poziom śmiertelności Coregonidae w sadzach. U ryb starszych zmiany CV i SK są odbiciem niektórych zjawisk masowych jak długotrwałe epizootje lub dojrzewanie płciowe poszczególnych osobników.

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