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Fish biology

GROWTH OF THE BALTIC HERRING AS A FUNCTION OF STOCK
DENSITY AND FOOD RESOURCES

MODEL WZROSTU ŚLEDZIA BAŁTYCKIEGO JAKO FUNKCJA
ZAGĘSZCZENIA POPULACJI JEJ BAZY POKARMOWEJ

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A mathematical model has been used to describe growth of coastal herring caught in the Baltic Sea in the Subdivision 26 in 1984–1995. The ratio of food resources, represented by biomass of *Mysis mixta*, to stock density explained about 65–83% of growth variation. It is argued that the deteriorating food conditions for herring are one of the basic causes of high decrease of herring weight-at-age.

INTRODUCTION

Since the beginning of the 1980s a systematic decrease in growth rate of the Baltic herring has been observed. Mean weight-at-age of herring caught in ICES Subdivisions 25–29 + 32 (Fig. 1) decreased about twofold during fifteen years (Anonymous 1996). Stock of herring caught in Subdivisions 25–29 + 32 consists of many populations showing different degrees of mixing on the fishing grounds. Changes in the fishing intensity in different parts of the area of stock inhabitation could to some extent explain the changes in mean weight-at-age in the catch. However, similar decrease in weight has been observed in herring populations forming the herring stock in Subdivisions 25–29 + 32, e.g., herring in the Gulf of Riga (Kornilovs et. al. 1992), coastal spring spawning herring caught in the Gdańsk Bay (Wyszyński 1995), herring in the Gulf of Finland (Raid and Lankov 1993), and herring in Subdivision 29 (Parmanne 1992). This decrease in individual fish weight is a serious problem for herring fishery, as fishermen have been catching smaller and smaller herring of lower quality for fish processing. Diminishing herring weights are partly responsible for the decrease of stock biomass which from mid 1980s until now has been only about 50% of the value estimated in the mid 1970s. In the recent ten years, the decrease in herring weight has been compensated by the increase in herring survival, resulting from the low biomass of cod stock. As a final outcome in these years the stock biomass has been changing only slightly.

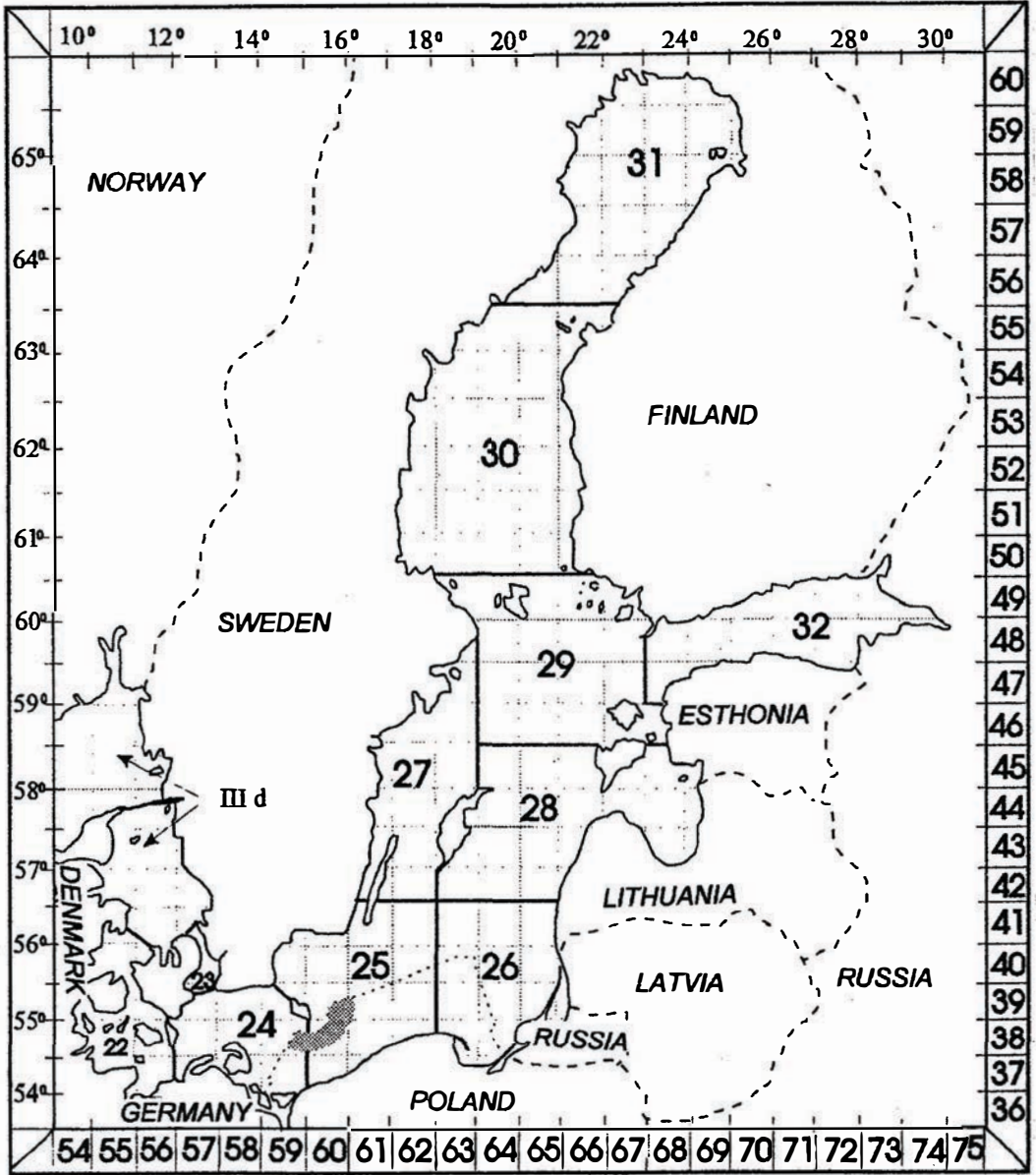


Fig. 1. The Baltic Sea with ICES Subdivisions

The changes in growth rate of fishes are observed often. Growth may depend on many factors e.g., stock density, availability of food, water temperature. In the present paper an attempt was undertaken to develop a model of herring growth in which the decrease of herring weight-at-age could be at least partly explained by changes in stock density and food resources.

MATERIAL AND METHODS

A. The model of herring growth

The growth of herring has been modelled by a method similar to the one presented by Horbowy (1983), and subsequently used by Horbowy and Swinder (1989) to describe the growth of sprat. The model is based on the von Bertalanffy's equation generalised by Andersen and Ursin (1977). In this equation the growth in weight, w , is expressed as

$$\frac{dw}{dt} = vh \frac{P}{P+Q} w^{2/3} - kw \quad (1)$$

where

$$Q = q \sum N_i w_i^{2/3} = qZ$$

and

v —fraction of food consumed, assimilated for growth,

h —species specific parameter,

P —available food,

Q —search rate,

k —coefficient of catabolism,

Z —index of food requirements of the population,

N_i —number of fish at age-group i ,

q —parameter,

t —time (age).

Food requirement of the population is defined as $\sum N w^{2/3}$ because it is assumed that the food consumption of an individual is proportional to its weight raised to 2/3 (Andersen and Ursin 1977).

To determine the unknown parameters of the model (1), we define the normalised increments, $\Delta w(t)^{1/3}$, as

$$\Delta w(t)^{1/3} = w(t+1)^{1/3} - e^{-K} w(t)^{1/3} \quad (2a)$$

which is approximately equivalent to

$$\Delta l(t) = l(t+1) - e^{-K}l(t) \quad (2b)$$

where

$$K = k/3,$$

$l(t)$ —length of an individual at age t .

It is easy to show that the right-hand side of equation (2a) is equivalent to (Horbowy 1983; Horbowy and Swinder 1989)

$$w(t+1)^{1/3} - e^{-K}w(t)^{1/3} = a \frac{P}{P+qZ} \quad (3)$$

where $a = vh(1-e^{-K})/(3K)$.

The increments defined in (2) depend on population density (or its requirements for food) and available food resources, while they do not depend on the age of fish. Therefore, the mean annual increment may be determined because increments at age, being not age dependent, have comparable values. Taking reciprocals of equation (3) one obtains

$$\frac{1}{w(t+1)^{1/3} - e^{-K}w(t)^{1/3}} = \frac{1}{a} + \frac{q}{a} \frac{Z}{P}$$

When treating the left-hand side of the above equation as a dependent variable (reciprocal of normalised increment), and taking the ratio Z/P as an independent variable, one can fit linear regression to the observed data, and determine the parameters a and q .

To calculate the normalised increments, the estimate of K is needed. To obtain such estimate the parameters of the standard form of the von Bertalanffy's equation were determined

$$w(t) = W_{\infty} (1 - e^{-K(t-t_0)})^3$$

where

W_{∞} —asymptotic weight in the population,

t_0 —theoretical age at which weight is zero.

The parameters of the above equation were calculated by minimalization of the sum of squares of differences between the observed and modelled weights.

Having parameters a , q and K determined, the product vh can be easily obtained. The separation of the values of v and h from the product vh is not needed to model the growth.

B. The data for modelling herring growth

The weight-at-age of herring caught in the Gdańsk Basin in 1984–1993 can be found in Wszyński (1995). These data, however, are yearly means while for calculation of the growth increments referring to consecutive years it would be more appropriate to use data from the first quarter. Such data were made available by Wszyński (personal communica-

tion). Therefore, the normalised increments were calculated for ages 2–6 on the basis of weight-at-age of herring caught in the first quarter of each year of the period 1984–1995 in the Gdańsk Basin (Subdivision 26). Age 1 was excluded from the analysis as fish are not fully recruited to the fishery at this age. Ages older than 6 were also excluded because in some years the weight estimates for these ages were lacking. The parameters of the standard form of the von Bertalanffy's equation were determined on the basis of weight-at-age for age 2–7, averaged over the years 1984–1995. In this case the inclusion of age 7 made it easier to realistically estimate W_{∞} .

It was assumed that the number of herring utilising the same food resources as coastal herring in Subdivision 26 is proportional to the yearly mean number of herring stock in Subdivisions 25–29 + 32. The reason for that is the mixing of coastal herring from Subdivision 25 and 26 with, so-called, sea herring from Subdivision 27 on the feeding grounds in the summer and autumn. The numbers of herring in Subdivisions 25–29 + 32 were taken from Horbowy (1997).

The biomass of *Mysis mixta* (Shvetsova et al. 1992) was taken as an indicator of the quantity of food resources. These data present the biomass dynamics of *Mysis mixta* in the Baltic in 1979–1990. For the period of 1991–1995 the average of the values from previous years was accepted as the *Mysis mixta* biomass.

RESULTS AND DISCUSSION

The weight-at-age of herring in the first quarter in 1984–1995 is presented in Fig. 2. The weights show a decreasing trend, especially after 1990. The parameters of the von Bertalanffy's equation are: $W_{\infty} = 187.9$ g, $K = 0.226$, and the variance of observed values along the fitted growth curve is 13.8 g². In the late 1980s the mean normalised increments fluctuated without a clear trend (Fig. 3), but they decreased significantly in the 1990s.

The dependence between the reciprocal of mean normalised increments, $1/\Delta w^{1/3}$, and the ratio of food requirements of herring to the biomass of *Mysis mixta*, Z/P , is presented in Fig. 4. The relationship is approximately linear which is in agreement with the developed theory. The coefficient of correlation between the above variables is 0.82 ($p < 0.0034$). In 1987, there was a very severe winter which could be an additional factor influencing growth rate. When the data point referring to that year is omitted then the correlation coefficient increases to 0.91. Thus the model explains 65–83% of herring growth variation. After fitting linear regression to points $(Z/P, 1/\Delta w^{1/3})$ the estimates of the parameters a and q , and the product vh were found. They are equal to 2.49 g^{1/3}, 0.0455 g^{1/3}, and 8.33 g^{1/3}, respectively.

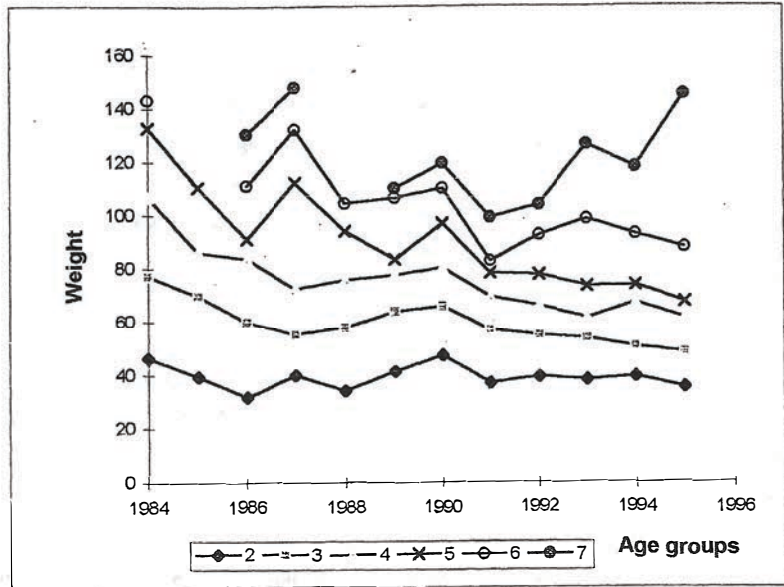


Fig. 2. Mean weight-at-age (g) of herring caught in Subdivision 26 in the first quarter of 1984–1995 (according to Wszyński, personal communication)

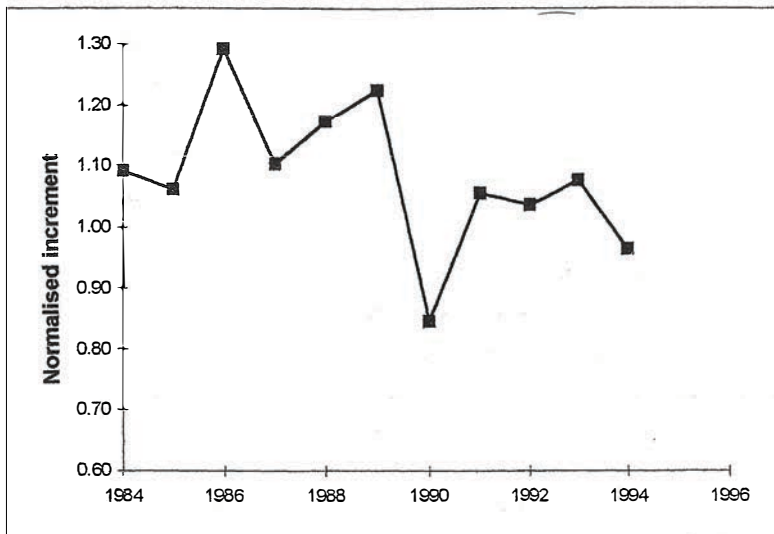


Fig. 3. Mean, over age 2–5, normalised increment of size ($g^{1/3}$) of herring 1984–1994

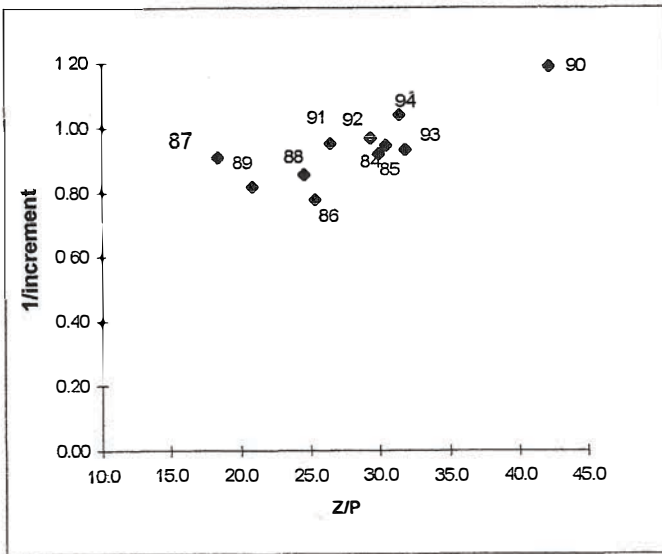


Fig. 4. The dependence of reciprocal of the mean normalised increment at age 2–5 ($g^{-1/3}$) on the ratio of index of population density to biomass of *Mysis mixta* (Z/P) in 1984–1994

The estimated value of q enabled the calculation of the ratio $P/(P + qZ)$ for 1984–1995 (Fig. 5). The values of this ratio do not fully reflect the dynamics of food conditions in 1991–1994 as for these years the biomass of *Mysis mixta* was assumed to be at average level. The changes in the normalised increments (Fig. 3) are in a very good agreement with the presented dynamics of food conditions. The lowest increment was observed in 1990, and then the food condition were the poorest. High increments in 1988–1989 reflect very good food conditions in these years. Only the data from 1987 are an exception from this consistent pattern but as it was mentioned earlier, there was a very severe winter in 1987 which could highly decrease growth rate.

Having determined all parameters of the model (1) and knowing the observed weight in 1984 and weight at age 2 in 1985–1994 (these weights were assumed to be the initial condition for model (1)), the weight-at-age for ages 3–6 for the period of 1985–1995 was calculated. The calculated weights differed from the observed weights by 9 percent on average, and the variance of the observed weights along fitted weights was $112.6 g^2$. When the ratio of food biomass to food requirements of the population was not taken into account in the model, then the modelled weights differed from the observed ones by 13 percentage points, and the variance of the observed weights along fitted weights was $182 g^2$. Therefore, the model enabled about a 40 percentage points reduction of the variance of the observed weight. It should be stressed, that the calculations which omit the ratio of food biomass to

food requirements of the population do not produce the constant weight-at-age values because the calculated weights depend on the observed weight at age 2 in 1985-1994 and the observed weight-at-age in 1984. Thus such approach also takes into consideration a part of the growth variation caused by difference in the observed weights assumed as initial conditions.

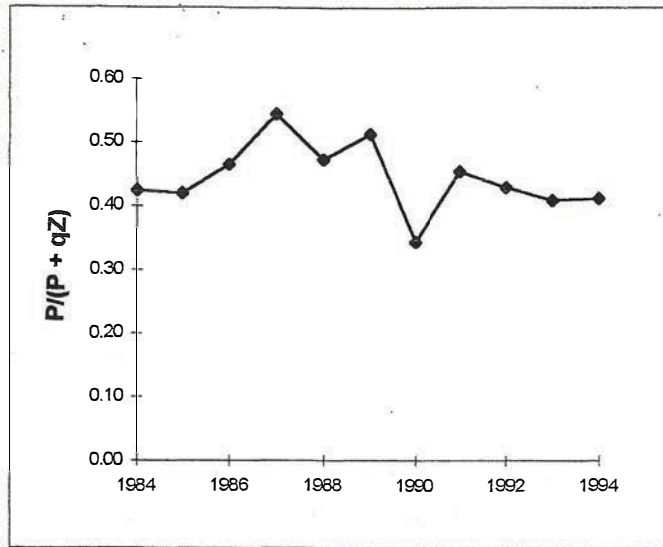


Fig. 5. The food condition of herring in 1984–1994, expressed by the ratio $P/(P + qZ)$

Next, the influence of changes in population density on coastal herring growth was projected. In these simulations the *Mysis mixta* biomass was assumed to be constant. According to the model, a decrease in population density by 10–30 percentage points would lead to the yearly increase in weight by 5–15 percentage points when compared with the weight modelled under constant population density (Fig. 6). With higher decrease in population density its influence on the growth rate was relatively higher: a decrease in population density by 60 percentage points led to an increase in growth increment by almost 50 percentage points. The presented results are slightly overestimated as the influence of increasing weight on food requirements of the population is neglected (Z is a sum of products of N and $w^{2/3}$, so Z will decrease less than N , because the decreasing density results in higher growth in weight compared to the growth for constant N).

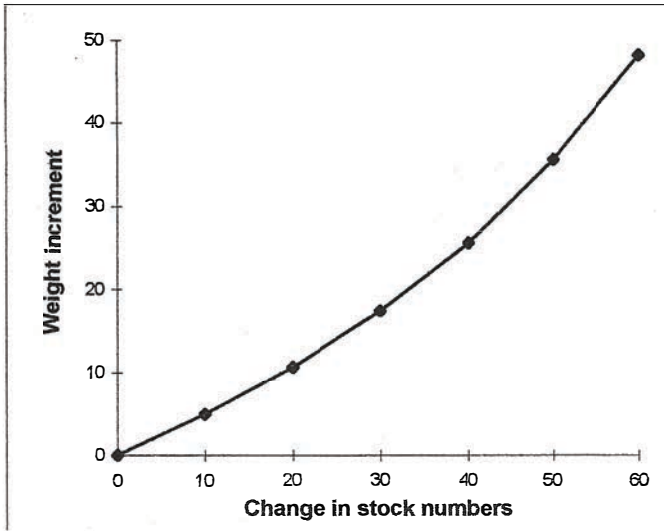


Fig. 6. The influence of decreasing stock density (%) on yearly growth rate; weight increment is presented in relation to weight increment for constant stock density (%)

The growth of herring can be influenced by three basic factors: stock density, availability of food and temperature. In this study only the first two factors have been considered. The food composition of herring has been investigated by many authors (Popiel 1951; Załachowski et. al. 1980, 1985; Szypuła 1992; Ostrowski 1993). It changes with age and season of the year. Generally, in summer *Mysis mixta* is a dominant species in food spectrum. Hence, the inclusion of this species into the presented model is justified. Other components of herring diet are mesoplankton forms like copepods *Pseudocalanus elongatus* and *Temora longicornis*. These two species may constitute up to 60% of herring stomach contents outside of summer season. According to Wolska-Pyś (1996) in 1984–1993 a sharp decrease in biomass of *Pseudocalanus elongatus* was observed while the biomass of *Temora longicornis* was increasing. Overall, the biomass of both species showed only a minor rate of decrease. The attempt was undertaken to include the dynamics of the two species in the presented model of herring growth. The results, however, were negative—replacing the *Mysis mixta* biomass by a biomass of one of the above species or by a sum of two biomasses led to a much worse and non-significant fit of the model.

The above analysis attempted to evaluate the influence of selected factors on herring growth. Its main weak point is the limited data on the biomass of *Mysis mixta* in the Baltic Sea. To continue the work on this model more data on the dynamics of herring food com-

ponents would be needed. An additional factor which may have impact on growth is temperature, and it was not taken into account in the model.

A lack of a relationship between herring growth and the biomass of Copepoda seems rather surprising. However, a similar lack of a relationship could be probably obtained for Baltic sprat as well. *Pseudocalanus elongatus* and *Temora longicornis* dominate sprat diet, constituting about 90% of it. The growth of sprat in the analysed years (Grygiel 1997) underwent much smaller changes than growth of herring, although the biomass of sprat was increasing sharply which in addition could negatively influence its feeding conditions.

An interesting hypothesis, offering different explanation of herring growth changes, is presented by Sparholt and Jensen (1992) and Beyer and Lassen (1994). They argue that the main reason for declining herring weight-at-age is decreasing predation by cod, caused by diminishing biomass of the predator. The simulation performed by Sparholt and Jensen (1992) showed that changes in predation mortality of herring observed in 1982–1988 may result in a reduction by 17 percentage points of the observed herring weight. Similar results were obtained by Beyer and Lassen (1994) who also showed that predation mortality of herring is inversely proportional to fish length raised to the power of about 0.5. Cod prefer to eat smaller herring, therefore a decreased predation by cod results in increased survival of smaller herring. This is then observed as a decreasing growth rate of herring population.

The above phenomenon may be partly responsible for changes in herring growth. However, the increase in cod biomass, having been observed since 1993, did not result in a higher weight of the coastal herring. May be the predation pressure by cod is still too low to show its influence on the observed weight of herring. In summary, probably both factors, namely food resources in relation to stock density and predation by cod, influence the observed weight-at-age of herring. The impact of food and stock density is reflected not only in weight but in fat content of fish meat and Fulton condition factor as well. The fat content in herring has been decreasing from about 8–10% in 1980s to 2–5% in 1990s (Wyszyński 1997). Similarly, the Fulton condition factor has decreased by about 10 percentage points in the analysed period (Wyszyński 1997).

Also, in other areas of the Baltic changes in feeding conditions were blamed for a decrease of herring weight. Raid and Lankov (1993) suggest that changes in prey composition and the increasing number of herring with empty guts are the probable reasons of the declining growth rate of this fish in the north-eastern Baltic. Naglis and Siderevics (1993) found high correlation between herring weight sampled in Subdivision 28 and cod biomass as well as biomass of *Pseudocalanus elongatus*.

Davidyuk et. al. (1992) suggest that the composition of herring food plays a significant role in the growth rate. Arrhenius and Hansson (1993) noticed that diet of herring has shifted in 1980s from a mix of zooplankton, mysids and amphipods to zooplankton only.

They showed by simulations that a shift of diet could significantly reduce herring growth rate because zooplankton has lower calorific value than mysids and amphipods. This diet shift could decrease growth by about 25 percentage points for older age groups.

CONCLUSIONS

1. In the last several years, a significant decrease in the rate of growth of Baltic herring has been observed.
2. The ratio of food resources to the stock density (food requirements of the population) can explain about 65–83% of the variation of weight-at-age of coastal herring caught in Subdivision 26 in 1984–1995.

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MODEL WZROSTU ŚLEDZIA BAŁTYCKIEGO JAKO FUNKCJA ZAGĘSZCZENIA POPULACJI I JEJ BAZY POKARMOWEJ

STRESZCZENIE

Od początku lat osiemdziesiątych jest obserwowany systematyczny spadek mas osobniczych śledzi bałtyckich. Zjawisko to dotyczy zarówno śledzi wiosennych z południowego Bałtyku jak i śledzi odławianych w Zatoce Ryskiej, Zatoce Fińskiej czy w rejonie Morza Alandzkiego. Dwie główne hipotezy objaśniające powyższy proces to:

- spadek tempa wzrostu śledzi jest spowodowany zmniejszaniem się ich bazy pokarmowej,
- zmniejszyło się wyjadanie śledzi przez dorsze, co powoduje przeżywanie większej liczby śledzi małych niż w latach obfitości dorszy i objawia się w postaci zmniejszenia się średnich mas osobniczych w grupach wieku.

W pracy przedstawiono matematyczny model wzrostu śledzi, będący pewnym uogólnieniem równania von Bertalanffy'ego. W modelu wielkość wyrażenia określającego tempo anabolizmu osobnika jest zależna od wielkości zasobów pokarmowych oraz potrzeb pokarmowych populacji, będących pewną miarą jej zagęszczenia. Spośród organizmów składających się na dietę śledzi największy wpływ na objaśnienie zmian wzrostu miała biomasa *Mysis mixta*, będąca ważnym składnikiem pokarmowym w okresie lata. Natomiast biomasa Copepoda, stanowiąca także istotny składnik pokarmu śledzi, słabo korelowała ze zmianami wzrostu. W sumie biomasa *Mysis mixta* i zagęszczenie populacji wyjaśniały 65–83% wariacji mas osobniczych śledzi.

Obserwowany w ostatnich kilkunastu latach drastyczny spadek zawartości tłuszczu w mięsie śledzi oraz spadek współczynnika kondycji są kolejnymi przesłankami, sugerującymi decydujący wpływ zasobów pokarmowych na spadek tempa wzrostu śledzi.

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