Back-calculated individual growth of long rough dab (*Hippoglossoides platessoides*) in the Barents Sea

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Long rough dab, *Hippoglossoides platessoides* (Fabricius, 1730), of the Barents Sea shows great individual variation in growth rate and age at maturity. In this paper we compare the mean length-at-age of long rough dab at capture with growth curves back-calculated from digitized otoliths. Back-calculated individual growth did not show any abrupt changes in growth rate that might be associated with maturation. Furthermore, the results suggest a correlation between slow growth, delayed maturation and high expected maximum age. This could explain the indications of Rosa Lee's phenomenon found in the material. This paper shows that the curvilinear relationship, from catch data on length-at-age, may not represent the growth of individual fish. Indications suggest that this may be a result of size-selective mortality, possibly related to maturation.

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Key words: *Hippoglossoides platessoides*, back-calculation, size-selective mortality, Rosa Lee's.

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Introduction

For several stocks of long rough dab (Hippoglossoides platessoides Fabricius, 1730), maximum age seems to be closely correlated to the age at sexual maturity (Walsh, 1994). The reasons for this correlation are not fully understood. Like other pleuronectids, a substantial part of available energy may be allocated from somatic to reproductive growth (Templeman and Andrews, 1956; Roff, 1982; Rijnsdorp et al., 1983; Rijnsdorp, 1990). Therefore it has been argued that the curvilinear relationship between mean length and age at capture may be due to ontogenetical reduction in somatic growth rate (Minet, 1973; Roff, 1983; Wooton, 1990; Rijnsdorp, 1993). However, increased stress due to spawning may also increase mortality from diseases and predation (Stearns, 1976; Roff, 1984; Rijnsdorp, 1990, 1994). The curvilinear length-at-age curve will not represent individual growth patterns if mortality of an age group varies with the fish length.

The onset of sexual maturity of fish is usually more a function of size than age (Stearns, 1976; Roff, 1982; Stearns and Crandall, 1984). If maturation and spawning result in increased mortality, than maximum age will be higher for slow-growing individuals than for the faster-growing conspecifics. This is one of the factors that will lead to Rosa Lee's phenomenon (Lee, 1912; Jones, 1958) when length-at-age is back-calculated from otoliths. In this paper we compare mean length-at-age of long rough dab at capture with back-calculated individual growth curves. The purpose of the study is to describe how the growth varies ontogenetically and how mortality is related to growth.

Materials and methods

Long rough dab were sampled with a modified shrimp trawl, Campelen 1800 with "rockhopper" gear (Engås and Godø, 1989), on a cruise with RV "Jan Mayen" in May 1994. Details of trawl equipment and procedures

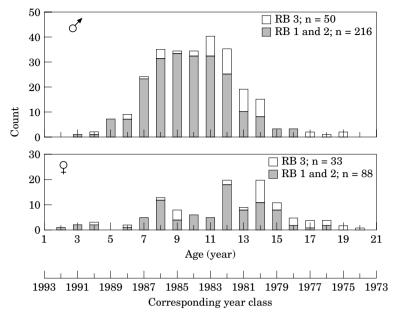


Figure 1. Age distribution with respect to sex. The year-class corresponding to the age is shown. RB=readability (Table 1), n=number of observations.

were given by Aschan and Sunnanå (1997). Trawls were made on 200–487 m depth within an area defined by northern latitudes 72°39′ and 74°42′ and eastern longitudes 17°20′ and 24°35′.

Total length, sex, and maturity stage were recorded and otoliths were collected for all or a subsample of all long rough dabs in each catch. Definition of maturity stages were as follows: Immature: small clear-reddish gonads, testes as a thin string; Mature: ripening, running or clearly spent; Uncertain: all other stages.

To estimate the age, M_{50} , where 50% of the long rough dabs had reached maturity a logistic model of maturity vs. age was used:

$$y=100/[1+e^{(a+bx)}],$$
 (1)

where y=percentage of mature individuals, x=age at catch, a+b=estimated parameters, and:

$$M_{50} = -a/b,$$
 (2)

Table 1. Index of readability, rewritten after Jensen (1965).

In the laboratory, the medial face of the acentric otoliths were digitized and analysed using the computer software NIH-Image 1.55.1 Only the acentric otoliths were used because the zonation pattern seemed to appear clearer in the acentric than in the centric otoliths. The otoliths were honed on the outside using abrasive paper (granulation 500) in water. This resulted in better light permeability and solved the problem related to the obscuring of the inner annulus in older otoliths. The age of fish younger than 8-9 years of age could usually be adequately determined using only the acentric otoliths. For older fish the acentric otolith was used as a control and for identifying the first or last annulus. The width of annuli appeared relatively similar throughout the otolith and very thin zones in older specimens were not observed. Therefore, the possibility of older fish being under-aged as a result of otolith growth not being visible on the medial face of the otolith is regarded as low, however, the possibility cannot be ignored.

Age was determined both with the use of digitized pictures and with a stereomicroscope. The precision of the age readings were higher when using digitized pictures and these estimates were used in this paper. Each otolith was also given an index of readability (Table 1). Low readability was associated with low

⁽¹⁾ Believed to be reliable, good definition between hyaline and opaque zones.

⁽²⁾ Relatively clear zonation but not well defined, the error margin is expected to be ± 1 year.

⁽³⁾ The zones are vaguely marked, and the error margin may be ± 2 years or more.

¹NIH Image 1.55. is written by Wayne Rasband at US National Institutes of Health and is accessible online through anonymous ftp zippy.nimh.nih.gov or on floppy disc at NTIS, 5258 Port Royal Road, Springfield, VA 22161, USA, part number PB93-504868.

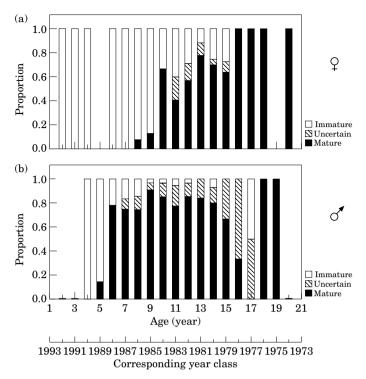


Figure 2. Proportion distribution of maturity of each sex and age group, (a) females and (b) males.

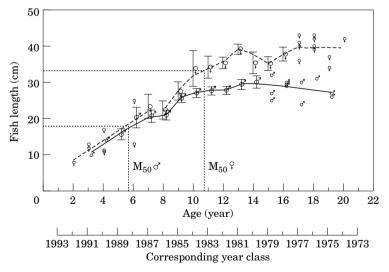


Figure 3. Mean length ($\pm 95\%$ CI) with respect to age and sex. Small symbols: age groups with less than five observations. Smoothing (lowess) based on raw data (Clevland, 1979). M_{50} and the corresponding length are also shown in the figure.

precision. For the purpose of this paper otoliths with a readability index of three were excluded from the analyses. The width of each annual growth-zone along the longest otolith radius was also recorded.

The slope in the log-transformed relationship between fish length and otolith radius did not differ significantly from 1 (slope of females=1.05; $F_{1,118}$ =1.29; p=0.258 and slope of males=1.01; $F_{1,263}$ =0.92; p=0.762). This relationship can therefore be treated as proportional. We used Campana's (1990) biological intercept procedure to perform the calculation of length-at-age (3). The average length of fish at time of otolith formation,

the biological intercept, was set to 0.7 cm (Powles, 1966; Walsh, 1994).

$$L_a = L_c + (O_a - O_c) (L_c - L_0) (O_c - O_0)^{-1}$$
(3)

where L=fish length, O=otolith, c=at catch, a=a given age, 0=biological intercept.

Results

Population structure

The age range of long rough dab was 2–20 years (Fig. 1). Males were most numerous in age-groups 7–13, whereas females were recorded more evenly across a wider age span. The proportion of otoliths that were classified as "bad" (readability index of three) increased with age.

Males matured at a younger age than females (Fig. 2) and estimated M_{50} (with 95% confidence intervals) was 5.7 (\pm 0.12) and 10.8 (\pm 0.24) years, respectively. The percentage of the total catch of each sex that was classified as "mature" was 89% for males and 57% for females. There was a significant predominance of males (χ^2 -test, d.f.: 1, p<0.001), which contributed to 68.0% of the total catch.

Length-at-age

Mean length-at-age was similar for male and female long rough dab up to age 9 (Fig. 3). For older fish, females were, on average, larger than males. The increments in mean length were relatively constant up to age 10 for males and 13 for females. Reduced increments above this age produced a curvilinear relationship between mean length and age. The resulting curves resemble "typical" growth curves for fish. Eliminating otoliths classified as "bad" did not change the curves in any consistent manner.

For each age group, Figure 4 shows back-calculated mean length-at-age vs. year class. For several age groups, a decreasing trend appeared when going from younger to older year classes. This trend was more pronounced for age-group 6 and older, but was not seen for age-groups 1–3. Between year-class difference in mean length was significant for males from age-group 4 ($F_{7,186}$; p<0.05) and for females from age-group 2 ($F_{8,68}$; p<0.05). Differences were particularly due to the 1986 year class, which was consistently small at age compared to other year classes. The other three of the four most recent year classes in the figure (1984, 1985, and 1987) were consistently larger at age than older year classes.

Length-at-age of capture was on average less for immature than for mature individuals (Fig. 5). Although these sample sizes were small and differences generally not significant, the tendency was consistent for both

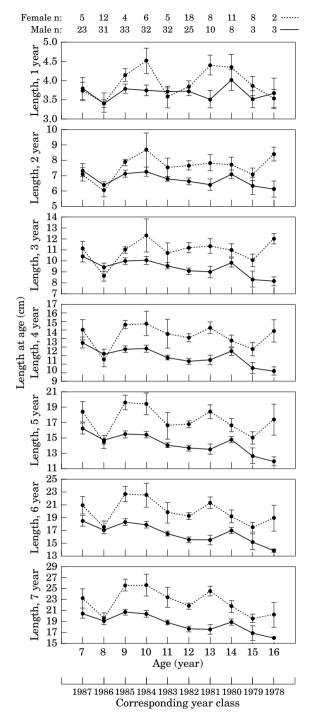
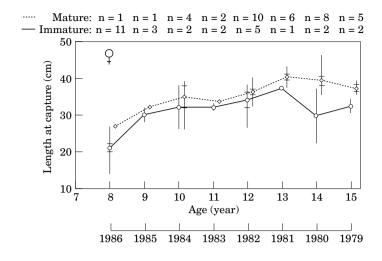


Figure 4. Back-calculated mean lengths (± 1 standard error) to seven different ages (1–7 years) of each sex, for the year classes between 1978 and 1987.

sexes and most age groups. Back-calculated lengths indicate that these differences had persisted throughout most of the life of the fish (Fig. 6).



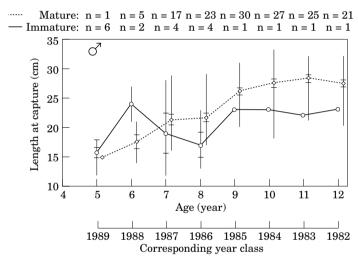


Figure 5. Mean length (range and standard error) at capture for mature and immature individuals in each age group/year class. Above, females aged from 8 to 15 years. Below, males from the age groups 5–12 years.

For the mature specimens in Figure 6, there were no indications of changes in growth rate that may be attributable to maturation. In order to see if these mean values may mask individual growth patterns, individual growth curves are shown in Figure 7. The oldest eight individuals of each sex were selected. Some of these may have been mature for several years. If marked ontogenetical changes in growth commonly apply to this stock, some sort of break in the curves should be expected to appear. However, the curves were mostly relatively linear and did not generally suggest any abrupt changes in growth.

The selected individuals in Figure 7 may not be representative for most individuals in the population. They may for example have reached an age due to slow growth and delayed maturation. To compare growth

curves of these older individuals with the younger ones, another selection of individual curves was made. These were selected so as to include as many individuals as possible from as few of the most recent year classes as possible. Thus, males from the 1987 year class and females from the 1983–1985 year classes were used. Figure 8 shows individual growth curves for the five largest and the five smallest individuals of each sex. These curves were also relatively linear without any marked changes in slope.

The range in length-at-age was much broader in this selection of young fish than for the older individuals in the first selection (Fig. 7). Males at age 7 ranged from 12 to 29 and 14 to 20 cm for the young and old group, respectively. Back-calculated length-at-age 7 were significantly higher for the ones that were 7 years at capture

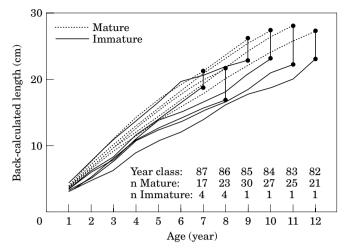


Figure 6. Back-calculated mean length-at-age of males from the year-classes 1982–1987 divided into mature and immature individuals. For each year class and stage, sample size is given in the figure.

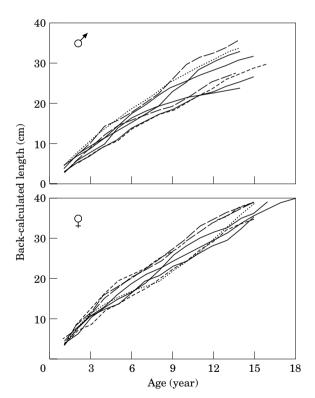


Figure 7. Back-calculated individual length-at-age curves for the oldest mature males and females.

(1987 year class) than for those that were 14 years or more (year-classes 1980 and earlier) (F-test, d.f. 1.36, p<0.05). Similarly, females at age 9 ranged from 25 to 35 and 22 to 27 cm for the young and old group, respectively. Back-calculated length-at-age 9 was significantly higher for the ones that were 9–11 years at capture

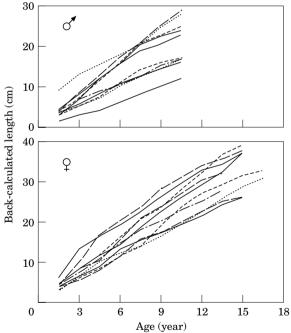


Figure 8. Back-calculated individual length-at-age curves for the five biggest and five smallest fishes from each sex. Males were taken from the 1987 year class and females from the year-classes 1983, 1984, and 1985.

(1983–1985 year classes) than for those that were 15 years or more (year-classes 1979 and earlier) (F-test, d.f. 1,26, p<0.01). Thus, the older individuals seem to have had a similar growth history to the smallest individuals of the younger age-groups. This can be an indication of what is known as Rosa Lee's phenomenon.

Discussion

Rosa Lee's phenomenon

It was found that back-calculated length-at-age of long rough dab decreased when age at capture increased. When this Rosa Lee's phenomenon is found for a single year class, three possible reasons are identified (Jones, 1958: Ricker, 1969). (1) The functional relationship between otolith radius and fish length may not be adequately represented in the back-calculation procedure. Given a linear fish-otolith relationship on an individual level this should not be a problem when using the back-calculation procedure used here (Ricker, 1969. 1992; Campana, 1990). (2) Size-selective sampling may give an under-representation of larger individuals in older age groups. The age and length distribution in this material contains, however, relatively old and large individuals compared to other areas of distribution (Albert et al., 1994). Although trawl gear is also sizeselective, the actual length range of long rough dab was relatively narrow and not all age groups were used. Ricker (1969) found that size-selective sampling by trawls had less influence on the occurrence of Rosa Lee's phenomenon when the oldest and/or youngest age groups were eliminated. (3) Size-selective mortality may also cause elimination of faster growing individuals from older age groups.

In the present work, it was not possible to sample a single year class for several years. Instead several age groups were sampled in one year. The observed reduced back-calculated growth rate for older year classes may thus also be explained by increased growth rate during the latest decade. If this was the case, one should also expect increased growth for the smaller individuals in the recent year classes. However, this has not been observed, neither for long rough dab or any other fish stock in the area (Mehl, 1986; Loeng, 1989; Loeng and Gjøsæeter, 1990; Bogstad and Mehl, 1991). The consistent pattern observed within and between year classes and sex indicates that a strong driving force is causing this pattern. Although selective sampling and interannual variations in growth conditions may influence the back-calculated growth curves, a more likely reason for the observed pattern is size-selective mortality.

Direct fishing for a long rough dab, which is the most abundant flatfish in the Barents Sea, is almost non-existent and the by-catch mortality is low, probably less than 0.2% (Albert *et al.*, 1994). Other causes for size-selective mortality may be related to differences between slow- and fast-growing individuals in metabolism, age at sexual maturity, and predator–prey interactions (Ricker, 1969; Wootton, 1990).

The results indicated that mature individuals tended to be larger than the immatures at the same age, and that older individuals were those that were relatively small at younger ages. This suggests a correlation between slow growth, delayed maturation, and high expected maximum age. The mechanism may well be that rapid growth results in early maturation, and that mature individuals are exposed to higher mortality rates (Stearns, 1976; Roff, 1984).

Growth patterns

Mean length-at-age at capture showed a curvilinear relationship. Back-calculated individual length-at-age curves, however, showed only a slight reduction in annual length increment with age both for individuals and in the mean for different year classes, but no abrupt and consistent ontogenetical changes were apparent. The back-calculated growth curves were based on discrete growth marks in the otoliths, and imprecision in the definition of these marks may have resulted in local break-points in some of the curves.

Length-at-age curves of long rough dab (fish) are often discussed in relation to ontogenetical processes (Minet, 1973; Pitt, 1975; Roff, 1982). This paper shows that the curvilinear relationship may not represent the growth of individual fish, but might primarily be a result of size-selective mortality, possibly related to maturation.

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