Dynamic age-length keys

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Information about age composition is important when analyzing fish population dynamics. Age determination of individual fish is more difficult and time consuming than the recording of length measurements but by using age-length keys, age distributions can be estimated without much difficulty from length distributions (Fridrikson, 1934). Knowledge of the age-length composition in the population or in a given subgroup of the population is required for constructing adequate age-length keys. Various methods for construction and evaluation of age-length keys are described in the literature (see e.g. Fridrikson, 1934; Macdonald and Pitcher, 1979; Schnute and Fournier, 1980; Kimura and Chikuni, 1987; Hayes, 1993; Terceiro and Ross, 1993; Goodyear, 1997). Because of individual variation in growth rates and the variation in mortality rates at different ages and sizes, the age and length composition of a fish stock are constantly changing. With sufficient information about a fish stock, the change in the age-length composition can be modeled and theoretical age-length keys can be constructed for specific time periods. Age distributions can then be estimated from length distributions taken at different times of the season. In this work, a simple but useful modeling approach for constructing dynamic age-length keys is described and applied to data from the Atlantic cod (Gadus morhua) stock in the Barents Sea.

Material and methods

The model is based on principles described by Schnute and Fournier (1980) and Fournier et al. (1990). In an age-structured fish population, the proportion of an individual being a certain length (l) within an age group (a) at a given time is assumed to follow a normal probability density function (Fig. 1A), N(µa, σa), with expectation s and standard deviation σa. When lengths of individual fish are recorded, they are normally classified as discrete length groups (e.g. 1-cm or 5-cm length intervals). The probability (P) for an individual in age group a to belong in a discrete length group, s, at a given time is then given by

\[ P_{as} = \int_{l_{ma,s}}^{l_{ma,s}} N(\mu_s, \sigma_s) \, dl \]  

where \( l_{ma,s} \) and \( l_{ma,s} \) are the upper and lower length limits of length group s, respectively.

Because the normal distribution is defined on the interval \((-\infty, \infty)\), it has mass below zero which may not be negligible for distributions centered near zero or with large variance. Thus, the \( P_{as} \)'s should be normalized across length groups for each age, i.e.

\[ P_{as} \rightarrow P_{as} / \sum P_{as} \]

so that

\[ \sum P_{as} = 1. \]

The theoretical number of individuals in age group a and length group s, \( N_{as} \), can then be found (Fig. 1B):

\[ N_{as} = P_{as} \cdot N_a \]  

where \( N_a \) is the number of individuals in age group a.

The proportion of individuals from age group a in length group s, \( Q_{as} \), is consequently found by dividing the number of individuals in age group a and length group s by the total number of individuals in the length group (Fig. 1C):

\[ Q_{as} = \frac{N_{as}}{\sum_{a} N_{as}} \]  

The total number of individuals in length group s (denominator) is found by summarizing the individuals from all age groups (a) in the length group. Note that an index of abundance (i.e. a relative measure) can be used as the estimated number of individuals in an age group (\( N_a \)). The expectation (\( \mu_a \)) and standard deviation (\( \sigma_a \)) increase with time as the individuals grow larger at different growth rates. By analyzing age and length data from a fish stock, \( \mu_a \) and \( \sigma_a \) can be estimated from observed data or models.

The method was applied to data on the Atlantic cod (Gadus morhua) stock in the Barents Sea from the period 1981 to 2000. Data from the annual bottom trawl surveys in the Barents Sea, which is conducted by the Institute of Marine Research in Bergen (Norway) around February (see e.g. Jakobsen et al. 1, was used to estimate the parameters in the model (\( N_a \), \( \mu_a \) and \( \sigma_a \)) for each month by interpolating between annual estimates (described later). Monthly age-length keys (\( Q_{as} \)) from the model were then tested by comparing predicted and observed age distributions in samples from commercial catches where the individual fish were both age and size measured. Note that the data used to estimate parameters and the data used to test the model were from different sources.

Equation 1 and 4 in Pennington et al. (2002) were used to estimate the average length (\( \mu_a \)) in February and

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Figure 1
Graphs of Equations 1–3 (A=Eq. 1; B=Eq. 2; C=Eq. 3) showing two different age groups with overlapping length distributions. Sections A, B, and C are referred to in the description of the model in the “Materials and methods” section of the paper.

the standard deviation of length in February ($\sigma_a$), respectively. A linear length increment between surveys was assumed for individuals in a cohort, and the average length in a given month was estimated by interpolating from the linear growth curve (i.e. the length corresponding to the mid-point of the month). Although the $\mu_a$'s were estimated from mean lengths specific to a given year, the standard deviation of length at age was assumed constant and to increase linearly with time (or age) for a cohort. A regression analysis of age and average standard deviation of length at age gave the fitted line in Figure 2. The equation from this regression was used to calculate $\sigma_a$ for a given age (where age is measured in months). Abundance indices (estimate of $N_a$) from the Norwegian bottom trawl survey in the Barents Sea were taken from ICES, and the relative number of individuals in each age group was assumed constant in the rest of the year. The size of the length group intervals ($l_{\text{min},s} - l_{\text{max},s}$ in Eq. 1) was 5 cm, and the number of length groups in the model was set to 30.

All recorded individuals of Northeast Arctic cod that were sampled randomly from commercial catches were pooled over each month (these data are available from 1985 onwards). Monthly length distributions (5-cm length groups) and corresponding (observed) age distributions were then constructed. The predicted proportion of each age group in a given month (based on the length distribution) was

$$P_{as} = \frac{\sum Q_{as}N_s}{N},$$

where $Q_{as} = $ the theoretical age-length key (from Eq. 3);
$N_s = $ the observed number of individuals in length group $s$; and
$N = $ the number of sampled individuals.
The corresponding observed proportion of each age group was $N_a/N$, where $N_a$ is the observed number of individuals in age group $a$. Only months with more than 300 sampled individuals were used in the testing of the age-length keys.

**Results**

The predicted age distributions from the model (based on monthly length distributions) were generally quite similar to the observed age distributions, although they varied between the investigated years (Fig. 3). Deviations from the observed age distributions were especially large in the years 1992–94. The commercial catches were dominated by the age groups 4–6, and there was a slight tendency that the model underestimated proportions. It is also worth noting that points from the same age group within years often seemed to form a line with a slightly different slope or intercept from the diagonal.

**Discussion**

The application and testing of the theoretical age-length keys is only an indication of the quality and usefulness of the method. An important assumption about the samples from the commercial catches is that individuals are sampled randomly within the 5-cm size groups from the population. If some age groups are over- or under-represented within size groups in the catches, in relation to the true population, there will be deviations in the proportion of age groups seen in Figure 3. Catches (and thereby the samples) are often taken from a restricted area within the total distributional area of the cod stock, where the length-at-age of individuals may differ from the rest of the population or where particular age groups dominate. In addition, errors in the age readings may occur.

The model’s potential inability to capture the true age-size structure in the population may also lead to deviations in Figure 3. The estimates of the parameter values may suffer from sampling error, and simplifying assumptions may lead to errors (e.g. linear length increment between years and equal mortality rates for all age groups within years). Monthly growth rates for gadoids in temperate areas often vary seasonally (Jørgensen, 1992; Hayes, 1993). In addition, both the fishing mortality and the natural mortality are expected to vary for different ages and sizes because of ecological factors, fishermen’s strategy, and the selection properties of commercial fishing gears.

By reading the age of a limited number of individuals at different times during the season, the resulting average lengths at age can be used to estimate the current value of $\mu_a$. Another solution is to model the dynamics in average length more exactly (see e.g. Schnute and Fournier, 1980). The seasonal change in the (relative) number of fish in each age group can be estimated by using available information about the fishing mortality. More complex modeling of structured populations than the approach described here, which is quite simple, can of course be used (see e.g. Tuljapurkar and Caswell, 1997). However, the main point is to use a method that gives a fairly accurate estimate of the age-length distribution in the population at a given time, and a complex model is not necessarily a better one in this respect.

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Figure 3

Observed and predicted proportions of different age groups in monthly samples (n>300) from commercial catches in the period 1985–2000. Each age group has its own symbol (see plot for 1985 and 1993). The diagonal is shown, which is where the points should lie. Note that the range on the axes varies between years according to the maximum values.
Figure 3 (continued)
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