Density-dependent growth and cannibalism in Northeast Arctic cod: Some implications for fishing strategies

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ABSTRACT

Density-dependent growth of Northeast Arctic cod is studied empirically by regressing (i) the growth of different age groups of fish and (ii) the weight at age on the number of fish in the same and adjacent age groups. Density dependence is found for almost all age groups, but with the two approaches giving a somewhat contradictory evidence; using weight at age gives a correlation that rises with age, while growth gives the opposite result. The von Bertalanffy growth function is used to model fish growth, with density dependence modelled as affecting asymptotic weight. Cannibalistic mortality for younger cohorts is regressed on the number of fish in older cohorts, with a significant relationship found for fish over a certain age. Implications for catch-maximizing fishing mortality and gear selectivity are studied by examining the life history of normal versus large year classes. Fishing young age groups of large year classes to improve growth would not increase fish catches while increasing fishing mortality for older and cannibalistic year classes would increase catches by increasing the survival of young fish.

1. Introduction

In age-structured fishery models, natural mortality and weight at age are critical quantities. They have traditionally been assumed constant. Weight at age is, however, known to vary considerably from year to year, presumably due to varying environmental conditions, in particular availability of food; the maximum reported weight at age for an age group of Northeast Arctic cod 1946–2015 is two to three times greater than the minimum. Natural mortality for the youngest age groups (1–6 years old) is known to depend on predation from older age groups of cod (cannibalism), and since the early 1980s this phenomenon has been studied extensively by investigating the stomach content of cod captured in stock surveys. Assessment reports on the Northeast Arctic cod stock now include detailed tables of estimated cannibalistic mortality of young age groups of cod.

Variations in weight at age could be caused not only by variations in the availability of food, but also by variations in the abundance of the age groups, due to density-dependent growth. If food is a limiting factor, each individual fish in a large cohort would find it more difficult to obtain food and hence would grow more slowly. We investigate this by regressing growth of fish of any given age on the number of fish in age groups that might be its competitors for food. Other investigators (Kovalev and Yaragina, 2009) have investigated density dependence by relating weight at age to competing age groups. We do this here as well and find that these two methods give somewhat different results, for which we offer plausible explanations.

Density dependence is found for almost all age groups, but with the two approaches giving a somewhat contradictory evidence; using weight at age gives a correlation that rises with age, while growth gives the opposite result. The von Bertalanffy growth function is used to model fish growth, with density dependence modelled as affecting asymptotic weight. Cannibalistic mortality for younger cohorts is regressed on the number of fish in older cohorts, with a significant relationship found for fish over a certain age. Implications for catch-maximizing fishing mortality and gear selectivity are studied by examining the life history of normal versus large year classes. Fishing young age groups of large year classes to improve growth would not increase fish catches while increasing fishing mortality for older and cannibalistic year classes would increase catches by increasing the survival of young fish.

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1 The classic reference to age-structured models is Beverton and Holt (1957).
2 See the annual reports of the Arctic Fisheries Working Group of the International Council for the Exploration of the Sea (ICES), the latest of which at the time of writing is ICES (2016a).
3 See Yaragina et al. (2009).
4 ICES (2016a).
effects, while the practicality of changing fishing strategy (fishing mortality or selection pattern) would require a fully-fledged age-structured model with year classes of varying strength.

2. Materials and methods

The data used in this study were taken from the 2016 report from the ICES working group on Arctic fisheries (ICES, 2016a). They comprise (i) weight at age of individuals in the stock (Table 3.9), (ii) number of fish in the stock for age groups 3 to 12+ (Table 3.21, final VPA run), and (iii) number of individuals in age groups 1–6 consumed by older cod (Table 3.12).

The reported weight at age in the stock each year is calculated as a weighted average of Norwegian and Russian stock surveys; the formula is given in ICES (2016a, p. 175). This applies to data from 1983 and later; the older data are discussed in ICES (2001, pp. 353–4). These surveys are undertaken each year at about the same time (October–December for Russia and January–March for Norway). The length of each fish is measured, and a sub-sample, one fish per 5 cm length interval, is further analyzed (weight, age, sex, maturity, and stomach content). Weight at age data on older cod than 11 years are too scarce to be reliable. Number of cod consumed by cod is estimated from the sample of stomach contents; each year about 9000 stomachs are analyzed (ICES, 2016a, p. 176). The methodology is described in Bogstad and Melh (1997) and Melh and Yaragina (1992).

3. Results

3.1. Density-dependent growth

3.1.1. Statistical analysis

The effect of density (population number) on growth was studied by (i) regressing weight increment (growth) and (ii) regressing weight at age on the number of individuals. The first approach seems intuitively more appealing; the effect on weight at age presumably comes through the effect on growth, with greater availability of food generating more growth. Table 1 shows the results of regressing growth (\(w_{a+1} - w_a\)) of fish of age \(a\) on the number of fish in the age groups in year \(t\) that are potential competitors for food with fish of that particular age. The competing age groups were determined by adding age groups until the p-value of the explanatory variable (N) was minimized. The results make sense; as fish grow older, they compete with progressively older fish; 3 and 4 years old fish (a = 3, 4) compete with fish 3–6 years old; 5 years old fish (a = 5) compete with fish 4–7 years old, and so on.

Somewhat surprisingly, regressions with the relative growth rate (\(\ln w_{a+1} - \ln w_a\)) as dependent variable gave different results, producing significant correlation only for 3 and 4 years old fish, with the number of 3 and 4 years old fish as explanatory variable in both cases. A possible explanation is that living organisms need a certain intake of food to maintain their body weight and that all intake beyond

<table>
<thead>
<tr>
<th>(a)</th>
<th>3 to 6</th>
<th>4 to 7</th>
<th>5 to 7</th>
<th>6 to 13+</th>
<th>7 to 13+</th>
<th>8 to 13+</th>
<th>9 to 13+</th>
<th>10 to 13+</th>
</tr>
</thead>
<tbody>
<tr>
<td>(w_{a+1} - w_a)</td>
<td>0.1240</td>
<td>0.1135</td>
<td>0.1654</td>
<td>0.1017</td>
<td>0.1120</td>
<td>0.0906</td>
<td>0.0123</td>
<td></td>
</tr>
<tr>
<td>(w_a)</td>
<td>0.0030</td>
<td>0.0046</td>
<td>0.0005</td>
<td>0.0706</td>
<td>0.0499</td>
<td>0.0119</td>
<td>0.3652</td>
<td></td>
</tr>
<tr>
<td>(R^2)</td>
<td>0.0023</td>
<td>0.3652</td>
<td>0.0000</td>
<td>0.3277</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.3451</td>
<td></td>
</tr>
<tr>
<td>p-value</td>
<td>0.1853</td>
<td>0.2439</td>
<td>0.2994</td>
<td>0.3177</td>
<td>0.3837</td>
<td>0.3827</td>
<td>0.0000</td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Results from regressing growth (\(w_{a+1} - w_a\)) versus weight at age (\(w_a\)) on the number of fish (N) in selected age groups in year t. Only p-values and \(R^2\) are shown.

3.1.2. Modeling density-dependent growth

We use the von Bertalanffy growth function, which is widely used for fish growth. The growth function is (Beverton and Holt, 1957, p. 33–34):

\[
\frac{dW}{dt} = w_0 \left(1 - e^{-K(a-a_0)}\right)
\]

where \(a_0\) in this formulation is the theoretical age when \(w = 0\) (not necessarily \(a_0 = 0\)). If some of the parameters of the growth function change over time, we need to update the intercept (\(a_0\)), in which case we get (cf. Beverton and Holt, 1957, p. 36, equation (3.6)):\n
\[
\frac{dW}{dt} = \left[w_0^{1/3} + \left(w_0^{1/3} - w_0^{1/3}\right)e^{-K(a-a_0)}\right]^{1/3}
\]

At any given age \(a\) the growth rate is

\[
\frac{dW}{da} = -3K\left(w_0^{1/3} - w_0^{1/3}\right)e^{-K(a-a_0)}\left[w_0^{1/3} + \left(w_0^{1/3} - w_0^{1/3}\right)e^{-K(a-a_0)}\right]^{1/3}
\]

If the growth rate depends on density, it would presumably be reflected in the parameter \(w_0\). A change in \(K\) would not be consistent with the meaning of \(K\) as a physiological parameter reflecting the maintenance need of accumulated weight.\(^5\) It seems to make more sense to relate density-dependent growth to the changes in the uptake of food; the more fish there are in an age group the less the uptake of

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\(^5\)This is discussed at some length in Beverton and Holt (1957), pp. 105–108.
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