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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.[1] 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.[2] 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.[3] Assessment reports on the Northeast Arctic cod stock now include detailed tables of estimated cannibalistic mortality of young age groups of cod.[4]

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. This investigation, as well as that of Kovalev and Yaragina, consider fish 3 years and older. Ottersen et al. (2002) analyzed growth of juvenile cod (1–4 years) and concluded that variations in growth were not due to density dependence.

Cannibalistic mortality of young fish is presumably related to the abundance of older fish. We analyze statistically how cannibalistic mortality is related to the size of older age groups. The purpose of this, and the study of density-dependent growth, is to investigate what the implications might be for the fishing strategy, both fishing mortality and how it affects different age groups of fish (selectivity). We do this for a single cohort of fish, assumed to be either average or large. Looking at one cohort in isolation makes it easier to isolate the principal

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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).

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Table 1
Results from regressing growth ($w_{a+1,t+1} - w_{a,t}$) 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.

	$w_{a+1,t+1} - w_{a,t}$			w_a		
a	Age groups for N	R^2	p-value	Age groups for N	R^2	p-value
3	3 to 6	0.1308	0.0023	3 to 7	0.0935	0.0106
4	3 to 6	0.1240	0.0030	4 to 6	0.1853	0.0002
5	4 to 7	0.1135	0.0046	5 to 7	0.2439	0.0000
6	4 to 13+	0.1654	0.0005	6 to 13+	0.2994	0.0000
7	4 to 13+	0.1017	0.0076	6 to 13+	0.3177	0.0000
8	4 to 13+	0.1120	0.0049	8 to 13+	0.3837	0.0000
9	8 to 13+	0.0906	0.0119	9 to 13+	0.3827	0.0000
10	10 to 13+	0.0123	0.3652	10 to 13+	0.3451	0.0000

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 fish 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 Mehl (1997) and Mehl 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 ($w_{a+1,t+1} - w_{a,t}$) 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 ($\ln w_{a+1,t+1} - \ln w_{a,t}$) 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 that will augment the weight gram for gram and not in relation to the body weight, which would make $w_{a+1,t+1} - w_{a,t}$ dependent on the number of fish in the relevant cohorts. Furthermore, if the weight increment at a certain age depends on the number of fish in relevant cohorts it will have repercussions for the weight of fish at later ages. If the weight increment and the weight at age depend on the number of fish in the same way, the ratio $(w_{a+1,t+1} - w_{a,t})/w_{a,t} \approx \ln w_{a+1,t+1} - \ln w_{a,t}$ would be independent of the number of fish.

Others (Diekert, 2014; Kovalev and Yaragina, 2009; ICES, 2016b) have investigated density-dependent growth by relating weight at age to the size of the stock or the size of relevant year classes. Kovalev and Yaragina found a high correlation between weight at age and the number of fish competing for food, the higher the older the fish. A recent report on harvest control rules (ICES, 2016b) regresses weight at age on total stock biomass the year before and finds insignificant correlation (at the 1% level) for fish 3–5 years old, but significant for older fish. This is explained by different feeding habits of the younger age groups. Here we take a different approach and try to identify age groups of competitors with a given age group. Table 1 also shows the results of regressing weight at age on the number of fish in the age groups that appear to compete most for food, again adding age groups to the explanatory variable (number of fish competing for food) until the significance of the correlation has been maximized. Because the p-value is in most cases extremely low it is no longer a useful criterion, so instead we use R^2, also shown in the table. The overall picture is much the same as when looking at growth; as the fish grow older the age of the competitors also increases.

There is, however, one difference between using growth and weight at age as dependent variable. The significance of the correlation with the number of fish competing for food declines with age when we use growth, but increases when we use weight at age. Furthermore, the significance level of the correlation is always higher when using weight at age, except for the youngest age group. This is a bit surprising, since food availability affects growth directly and weight at age only indirectly through growth. The reason why we nevertheless get a more significant correlation for weight at age is that a change in growth at a certain age increases the weight at age at later ages as well. An experiment where only growth of fish at age 3 and 4 is density dependent produced significant correlations between weight at age and the number of fish at some later ages.

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):

$$w_a = w_\infty \left[1 - e^{-K(a-a_0)}\right]^3 \tag{1}$$

where a_0 in this formulation is the theoretical age when $w = 0$ (not necessarily age $a_0 = 0$). 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)):

$$w_a = \left[w_\infty^{1/3} + \left(w_{a_0}^{1/3} - w_\infty^{1/3}\right)e^{-K(a-a_0)}\right]^3 \tag{1'}$$

At any given age a_0 the growth rate is

$$\frac{dw}{da} = -3K\left(w_{a_0}^{1/3} - w_\infty^{1/3}\right)e^{-K(a-a_0)}\left[w_\infty^{1/3} + \left(w_{a_0}^{1/3} - w_\infty^{1/3}\right)e^{-K(a-a_0)}\right]^2 \tag{2}$$

If the growth rate depends on density, it would presumably be reflected in the parameter w_∞. 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

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