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Climatic effects filtered through the food web affect the dynamics of Arcto-Norwegian cod

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Abstract

The world's largest cod stock, the Arcto-Norwegian cod (a.k.a. North-East Arctic cod), is heavily influenced by temperature in two ways: First, cod recruitment tends to be high when Barents Sea temperature in the spawning year is high. Secondly, there is a more indirect effect of climate via herring and capelin: Warm conditions increase the chance of high recruitment of Norwegian Spring-spawning herring; 1-2 year old herring eat 0-year old capelin; and cod cannibalism increases when the biomass of 1-4 year old capelin is low. While these relationships have been shown separately and for the later years, we develop and parameterize models for the effects of herring (via capelin) and temperature on cod recruitment at age 3, using data from 1973 until present. Using data on cod, herring and temperature back to 1921 to verify the model,we find a significant relationship between predictions and data back to the 1950s, but before this, the predicted time-series pattern is not observed in the data.

Introduction

Fish stocks are affected by both climate, fisheries and interactions other species. Also, climate and fisheries can affect a stock indirectly with a time lag, by affecting other species that interact with the stock in question (through, e.g., predation). Here, we explore how the recruitment of Arcto-Norwegian (AN) cod (*Gadus morhua*) in the Barents Sea is influenced directly by temperature in the cod's spawning year, as well as indirectly, as temperature affects the recruitment of Norwegian Spring-Spawning (NSS) herring (*Clupea harengus*), which again affects the recruitment of Barents Sea capelin (*Mallotus villosus*).

Both AN cod and NSS herring prey on capelin, the main plankton-feeder of the Barents Sea; herring eat capelin larvae, cod eat 1-5 year old capelin. Data from the last 30 years show that a single large herring cohort may cause the capelin stock to collapse, which has happened three times since 1985 (Gjosaeter and Bogstad 1998; Hjermann et al. 2004b; Hjermann et al. 2004a). Data on cod stomachs collected since 1984 (Mehl 1991; Hamre 2003; ICES 2004a) show that when there is little capelin, piscivorous cod (mainly age 3-6; (Dolgov 2002)) increases its consumption of alternative prey, including young cod (mainly age 1-3), which again has a negative effect on the survival of young cod (Hjermann et al. 2004c). Here, we formulate a model for cod recruitment as a function of temperature (in the cod's spawning year) and the ratio between cod predators and capelin (when the recruiting cod is 1 and 2 years old). Since capelin abundance estimates is only available from 1973, we parameterize this model based on time series data from 1973 onwards. Thereafter, we formulate a model for capelin biomass as a function of the biomass of young herring, and a model for herring recruitment as a function of spawning stock and temperature. Putting these models together, we can then check whether the patterns predicted by this model fit the longer time series available for temperature, herring and cod (1921 till present).

The data

The cod and herring are age-specific abundance estimates derived from virtual population analysis (VPA), based on commercial catch statistics. The cod VPA estimates for 1946-2001 were taken from ICES (2004a), the estimates for the period 1921-1945 from Hylen (2002). We used traditional VPA calculated using a constant natural mortality (M=0.2) to avoid heterogeneity in the time series (the alternative VPA has constant M before 1984 and varying M from 1984 onwards). For herring, we used VPA estimates for 1921-1949 and SeaStar estimates for 1950-2003, taken from ICES (2002). Capelin abundance estimates, taken from ICES (2004b), are based on acoustic surveys performed in September-October by the Institute of Marine Research (IMR), Bergen, Norway and the Knipovich Polar Institute of Marine Fishery and Oceanography (PINRO), Russia. Capelin catch data were provided by Harald Gjøsæter (IMR). Temperature data from the Russian Kola meridian transect (33° 30' E, 70° 30'N to 72° 30' N) were provided by the PINRO. Monthly average values were calculated by averaging from 0 to 200 m depth vertically along the transect. Annual averages of these monthly values were used in our analyses.

Modelling cod recruitment taking the effect of capelin into account

Cod is recruited as a fishery resource at an age of 3, an age at which it attains fishable size, assuming a Beverton-Holt relationship between spawners and recruits. We modify this relationship by including the positive effect of temperature in the year of spawning and the negative effect of the ratio between predatory cod and capelin in years t-2 and t-1, which increases cannibalism on 1 and 2 year old cod. We used the observed abundance of capelin 1973-2000, modified by subtracting the biomass of capelin fished after the survey. We find significant effects of both factors. The resulting model, fitted to recruitment data for cod year-classes 1972-1998, was able to predict the major variations of cod recruitment in the same period.

Modelling the indirect effects of herring and temperature

In general, the major factor affecting capelin dynamics is the predation from young (age 1-2) NSS herring on capelin larvae (Gjøsæter and Bogstad 1998, Hjermann et al. 2004b). Thus, we used a weighted average of the biomass of young herring 1-4 years before as the predictor variable for capelin biomass. The relationship between the two was non-linear, i.e., there was little effect of herring when the weighted average of herring biomass was $< 0.25*10^6$ tons, but a sharp decrease when herring biomass exceeded this threshold. We found that using herring as a proxy for capelin in the model of cod recruitment of year-classes 1972-1998 was almost as good as using capelin biomass itself. However, NSS herring abundance-at-age has been estimated from 1907 onwards using VPA, so we could predict recruitment for cod from the year-class of 1921 (the start of the temperature time-series). Finally, we fitted a model for herring recruitment as a function of stock biomass and temperature, using data from 1921 to 2003. Using this model, we found a similar fit as we did using observed herring abundance. We find significant correspondence between observed and predicted fluctuations in cod recruitment in the 1950s and 1960s (Fig. 2). The model is better at predicting years of low recruitment than years with high recruitment.

Discussion

These results confirm that the abundance of capelin affects the recruitment of AN cod, presumably by affecting cannibalism. Also, this study indicates that AN cod recruitment is significantly affected by a lagged negative effect of temperature on cod through the causal chain: temperature -> NSS herring -> capelin -> cod cannibalism -> cod recruitment. The modelling approach taken here is very quite simplistic; also, the coefficients of most equations are based only on the period for which we have capelin survey estimates (indicated by an arrow in Fig. 1). Taking these simplifications and assumptions taken into account, the model performs pretty well when it is extrapolated backwards, i.e., for cod before the 1972 year-class. This indicates that the chain of processes we have assumed to be important – herring predating capelin larvae, lack of capelin inducing cannibalism in cod – were important also before the recorded incidents of herring-capelin-cod chain reactions in the 1980s, 1990s and the 2000s. The reason that the model “breaks down” before 1950 may be (1) that data quality for the VPA (catch statistics, sampling of the catch, and age readings) is poorer as we go further back, and/or that (2) the mechanisms themselves may have changed. For instance, cod recruitment appears to have become more dependent on favourable climate in the spawning year over the years, possibly because the cod spawning stock has become younger, smaller and more uniformly aged (Ottersen et al. in press).

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References

Dolgov, A.V. 2002. The role of capelin (Mallotus villosus) in the foodweb of the Barents Sea. Ices Journal of Marine Science **59:** 1034-1045.

Gjosaeter, H. and Bogstad, B. 1998. Effects of the presence of herring (Clupea harengus) on the stock-recruitment relationship of Barents Sea capelin (Mallotus villosus). Fisheries Research **38:** 57-71.

Hamre, J. 2003. Capelin and herring as key species for the yield of north-east Arctic cod. Results from multispecies model runs. Scientia Marina **67:** 315-323.

Hjermann, D., Stenseth, N.C., and Ottersen, G. 2004a. Competition by fishermen and fish cause collapses of Barents Sea capelin. Proceedings of the national academy of sciences of the United States of America.

Hjermann, D., Stenseth, N.C., and Ottersen, G. 2004b. Indirect climatic forcing of the Barents Sea capelin: a cohort effect. Marine Ecology Progress Series **273:** 229-238.

Hjermann, D.O., Stenseth, N.C., and Ottersen, G. 2004c. The population dynamics of Northeast Arctic cod (Gadus morhua) through two decades: an analysis based on survey data. Canadian Journal of Fisheries and Aquatic Sciences **61:** 1747-1755.

Hylen, A. 2002. Fluctuations in abundance of Northeast Arctic cod during the 20th century. ICES Mar. Sci. Symp. **215:** 543-550.

ICES. 2002. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES CM **2002/ACFM:19**.

ICES. 2004a. Report of the Arctic Fisheries Working Group. ICES CM **2004/ACFM:28**.

ICES. 2004b. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES CM **2004/ACFM:24**.

Mehl, S. 1991. The Northeast Arctic Cod Stocks Place in the Barents Sea Ecosystem in the 1980s - an Overview. Polar Res. **10:** 525-534.

Ottersen, G., Hjermann, D.Ø., and Stenseth, N.C. in press. Changes in spawning stock structure strengthens the link between climate and recruitment in a heavily fished cod stock. Fish Oceanogr. **xx:** xxx-xxx.

Figure 1: Factors affecting the recruitment of North-East Arctic cod at age 3. Temperature (and cod SSB) affects the recruitment of cod zero-group (larval mortality), while the survival from age 0 to age 3 to some degree depends on cannibalism, which again depends on the availability of capelin for piscivorous cod. The recruitment of capelin is affected by herring (which eat capelin larvae). Finally, herring recruitment is positively correlated with temperature, which thereby has an indirect negative effect on cod recruitment. The capelin is also affected by a directed fishery.

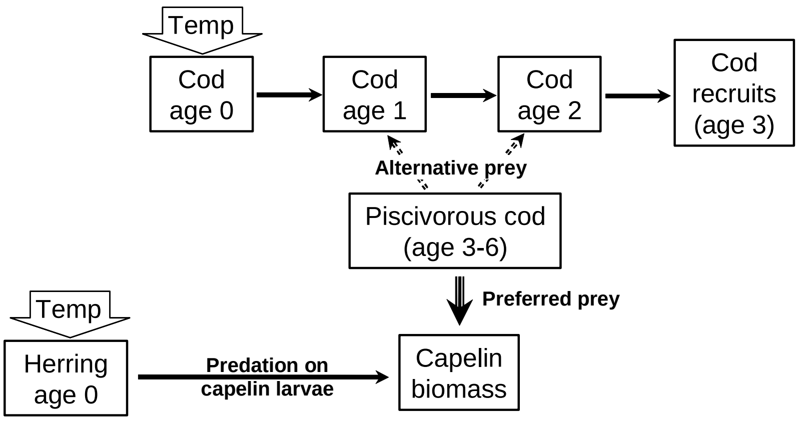

Fig. 2. Correlation between observed and predicted cod recruitment (log-transformed number of age 3 cod) for 21-year periods. The predictions were based on observed temperatures, as well as the observed spawner biomass of cod and herring. Cod recruitment was then predicted by first predicting capelin and herring abundances. The dotted lines show the 95% confidence interval of the correlations. The hatched square indicates the period that was used to estimate the parameters of the cod's recruitment function (age 3 cod 1975-2001).