ICES CM 2013/M:03

Disentangling the effects of ocean transport, temperature and food concentration on the distribution of fish larvae

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Summary

The causes of the large interannual fluctuations in the recruitment to many marine fishes remain incompletely understood. Two complementary approaches to studying these causes are coupled physical-biological modelling of the behaviour and drift of the early life stages of the fish, and statistical modelling of the observed spatial and temporal variation in their abundances in relation to environmental factors. By *combining* these approaches, the effect of variable drift can be accounted for in the statistical modelling, allowing for increased statistical power to detect effects of covariates such as temperature and zooplankton abundance. We here show the results of such combined modelling approaches for studying the spatiotemporal distribution of larval Northeast Arctic cod, *Gadus morhua*. A coupled physical-biological model is used to simulate the transport and development of cod eggs and larvae from spring to summer. The predictions from this model are used as input in a statistical analysis of the summer data, to investigate effects of covariates thought to be linked to survival. The results shed new light on the roles of temperature and zooplankton in the early life stages of cod.

Introduction

The recruitment to the Northeast Arctic (NEA) cod stock, the currently largest stock of cod in the world, has fluctuated considerably the last century. Recruitment has generally been highest in the warmest periods, but the mechanisms behind this relationship remain unclear. The NEA cod spawn off the northern coast of Norway, from where the pelagic eggs and larvae drift into the Barents Sea nursery and adult feeding area. Higher temperature may lead to faster developmental rates of the cod eggs and larvae, which in turn may increase survival by allowing the eggs and larvae to grow more quickly out of the diet range of their main predators (Cushing 1995). High temperature for larval NEA cod is also associated with high availability of suitable prey (mainly copepod nauplii), as well as with favourable oceanographic conditions for the transport of cod eggs and larvae to Barents Sea nursery area (Ellertsen *et al.* 1989; Ottersen and Loeng 2000; Stige *et al.* 2010). The effects of temperature, food availability and ocean transport are therefore partly confounded, which complicate the statistical analyses of the factors influencing cod recruitment. We here combine statistical and mechanistic modelling to quantify the relative importance of temperature, food (nauplii) availability and ocean currents in explaining the temporal and spatial variations in the abundance of larval NEA cod.

Materials and Methods

Eggs and larvae of NEA cod and copepod nauplii were sampled during ichthyoplankton surveys by PINRO from 1959 to 1993 off the coasts of northern Norway and Russia (approx. 67.5 N - 74.5 N, 5.0 E

- 33.5 E) (Mukhina *et al.* 2003). For most years, a Spring survey (April-May; i.e., 0-2 months after peak spawning) and a Summer survey (June-July) were conducted.

We analysed the temporal and spatial variation in the abundance of cod larvae in the Summer survey using generalized additive models (GAMs). In order to capture the variability that was explainable through the distribution of cod eggs and larvae in the Spring survey, we simulated the drift of eggs and larvae from spring to summer using a coupled physical-biological model (Langangen *et al.* 2013). This simulation generated predictions of the abundance of cod larvae at each station sampled during the Summer survey. These predictions («Predicted ln(N)», Fig. 1b) were used as explanatory variable in a GAM, along with indices of temperature and nauplii abundance in Spring, at locations back-tracked from the Summer stations. Prior to the spatiotemporal analysis, we analysed time series of spatially aggregated data.

Results and Discussion

Interannual variability: The interannual variability in cod larval abundance in Summer was positively associated with the abundance of cod eggs and larvae in Spring, with weaker evidence for effects of mean ambient temperature and nauplii abundance in Spring (Fig. 1a).

Spatiotemporal analysis: Analysis of the spatially resolved data showed a significant role of both temperature and nauplii abundance: samples with high abundance of cod larvae in Summer were characterized by both above-average temperature and above-average nauplii abundance at the back-tracked locations in Spring (Fig. 1b). There were also indications of an interaction between the effects of temperature and nauplii, suggesting that high temperature only lead to improved larval survival in areas with good feeding conditions (not shown).

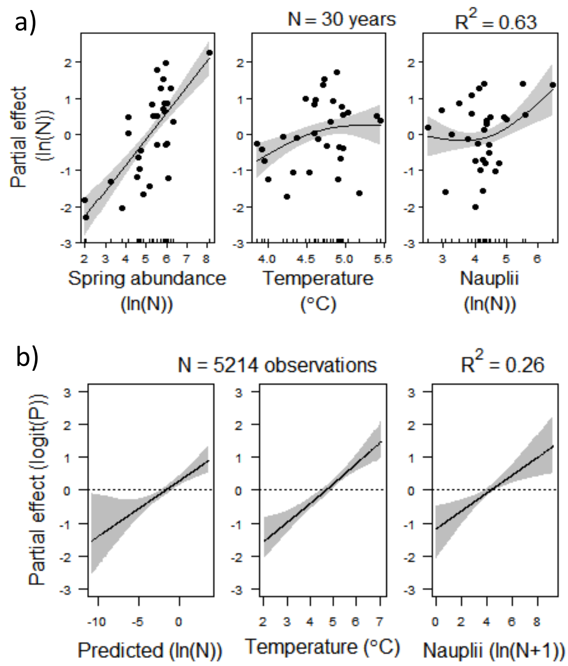

Figure 1. Effects of predictor variables on (a) interannual and (b) spatiotemporal variability in cod larval abundance in the Summer survey. Predictors were calculated from the Spring survey. A coupled physical-biological model was used to link observations from spring and summer in (b).

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