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An Individual Based Model of Arctic cod (*Boreogadus saida*) early life in Arctic polynyas: I. Simulated growth in relation to hatch date in the Northeast Water (Greenland Sea) and the North Water (Baffin Bay)

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ABSTRACT

A bioenergetics Individual Based Model (IBM) is developed to simulate the early growth (age 0 to 43 d) of Arctic cod hatched from mid-May to mid-July in the Northeast Water (NEW) in 1993 and the North Water (NOW) in 1998. In the model, the growth of a virtual larva is forced by observed temperature and prey concentrations as dictated by its hatch date. The functional response of food consumption to temperature in the range −1.8 to +1.6 °C was estimated based on the gut content of field-captured larvae. A sensitivity analysis indicated that high prey concentrations could compensate the depressing effect of low temperature on growth and vice-versa. The IBM reproduced well the observed differences in mean length-at-age between the two polynyas/years, in particular the poor growth in the North Water. In the NEW, a temporal match between yolk exhaustion and good feeding conditions occurred for early hatchers (abundant prey — medium temperature) and mid-season hatchers (medium prey — high temperature), which reached the largest sizes. In the NOW, prey concentrations were generally low at yolk exhaustion and variations in growth among cohorts depended essentially on temperature. Sub-sampling the model output to mimic the limited temporal resolution of sampling at sea reduced the variability in virtual growth and increased the match between simulated and observed variances in length-at-age. The IBM nevertheless underestimated the observed exceptional growth during match events.

1. Introduction

In Arctic seas, the Arctic cod (*Boreogadus saida*, Lepechin 1773, also known as polar cod) channels the bulk of the energy flux between plankton and vertebrates (Welch et al., 1992). Adaptations such as large eyes, large liver reserves, and antifreeze proteins enable Arctic cod to survive the low light regime, sub-zero temperatures, and extreme seasonality of biological production that prevails under the quasi-permanent ice cover (Gradinger and Bluhm, 2004; Hop et al., 1997). As the Arctic Ocean warms (Belkin, 2009) and the sea ice cover retreats over Arctic shelves (Serreze et al., 2007; Stroeve et al., 2007), boreal generalists such as the capelin (*Mallotus villosus*) may displace the hyper-specialized Arctic cod as the main forage fish in the ecosystem (Bouchard and Fortier, 2008; Gaston et al., 2005; Mueter et al., 2009).

Long-standing hypotheses on the reproduction of fish in temperate and Nordic seas assume that spawning is timed to match the hatching and first feeding of fish larvae with the phytoplankton bloom and the period of availability of suitable zooplankton prey in spring (e.g. Anderson, 1988; Cushing, 1974; Hjort, 1914). This temporal match should be particularly evident in polar seas where the season of production of copepod nauplii (the main prey of fish larvae) is short. At odds with this paradigm, the hatching of Arctic cod larvae starts as early as January and extends over several months in some arctic and sub-arctic seas (Bouchard and Fortier, 2008, 2011). In the Northeast Water (Greenland Sea) and the North Water (Baffin Bay), the larvae hatch from mid-May to mid-July, a period saddling the ice break-up (Bouchard and Fortier, 2011; Fortier et al., 2006). In the Northeast Water in 1993, an important fraction of the larval population hatched under the sea ice, several weeks in advance of the spring bloom and the maximum production of copepod nauplii prey. Larvae hatched under the ice in spring survived poorly relative to summer hatchers, but reached a significantly larger pre-winter size than summer hatchers (Fortier et al., 2006). However, the growth and fate of the spring cohort hatched under the ice is difficult to track since few early hatchers survive the first weeks of life and are consequently almost absent in field samples.

In this study, an Individual Based Model (IBM) of Arctic cod early bioenergetics is used to simulate the observed growth of larvae collected in the Northeast Water in 1993 and the North Water in 1998. Food consumption during the life trajectory of a modeled larva hatched on a given date is forced by observed temperature and prey

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concentration. For each study area, the simulated lengths-at-age of larvae are compared to observations for the amalgamated population and for daily sub-cohorts. To assess the impact of the unavoidable spatio-temporal limitation of ship-based sampling on growth estimates, a sub-sample of the model based on the age and hatch date of individuals captured in the field is compared to the full model output.

2. Sampling and aging of larvae

Arctic cod larvae were sampled from 23 May to 2 August 1993 in the Northeast Water (NEW) and from 29 April to 20 July 1998 in the North Water (NOW) (Fig. 1). The sampling methodology used in both polynyas was similar and is detailed elsewhere for the NEW (Fortier et al., 2006; Michaud et al., 1996). In summary, zooplankton and fish larvae were collected with a bongo sampler (200 and 500 μm mesh) deployed vertically and a Rectangular Mid-water Trawl (330 and 2000 μm meshes) deployed in a double-oblique tow at 240 stations in the NEW, 61 of which yielded Arctic cod larvae from 26 May to 27 July. In the NOW, vertical tows of 1-m^2 aperture nets (200 and 500 μm meshes) and oblique tows of 1-m^2 aperture double nets (500 μm meshes) were used at 145 stations, 44 of which yielded larvae from 29 April to 20 July. All samplers were equipped with an additional 10-cm diameter cylindrical net of 64-μm mesh (NEW) and 50-μm mesh (NOW) to sample copepod eggs and nauplii, the main prey of Arctic cod larvae. At each sampling station, a temperature profile was recorded with a CTD–rosette system. The notochord length of Arctic cod larvae ($n = 819$ in the NEW; $n = 1086$ in the NOW) was measured and corrected for shrinkage due to preservation. The gut of undamaged larvae ($n = 687$ in the NEW; $n = 1047$ in the NOW) was dissected under the microscope and prey were identified and measured (length and width).

The age and hatch date (capture date–age) of a stratified subset of larvae ($n = 444$ in the NEW; $n = 459$ in the NOW) were determined through otolith analysis. The hatch date frequency distribution (HFD) of each larval population was built by summing the number of fish hatched in a given 3-day period and dividing this sum by the total number of fish aged. In the NEW, the HFD was corrected for mortality and dispersal (Fortier and Quiñonez-Velazquez, 1998) using distinct catch-curves to estimate mortality for the observed spring and summer cohorts (Fortier et al., 2006). In the NOW, the more continuous HFD was corrected using the mortality rate estimated from the catch-curve for the overall population ($\text{catch} = 755\ e^{-0.145\text{age}}$; $r^2 = 0.95$, $p < 0.0001$).

For each region, 3×10^6 virtual larvae were hatched over the hatching season in pro rata to the corrected HFD. The simulation ended ten days after the last date on which larvae were captured, i.e. 6 August in the NEW and 30 July in the NOW. Arctic cod larvae are visual feeders and were assumed to distribute primarily in the 0–30 m surface layer. Observed temperature integrated over the 0–30 m layer was used as an estimate of the temperature experienced by the larvae on a given date in each region. Assuming that prey were distributed primarily in the 0–30 m layer, the abundances of copepod nauplii and eggs per m^{-2} from the vertical net tows were transformed into concentrations (l^{-1}) to estimate prey concentration at date. When more than one station was sampled on a given day, the temperature and prey concentration data were averaged. Missing daily data were calculated by linear interpolation between the nearest dates for which data were available.

3. Numerical model of Arctic cod early growth

The IBM is based on a temporally explicit framework (Roy et al., 2004; Tyler, 1998) with age 0 corresponding to hatch and a time-step of one day (Fig. 2). The central bioenergetics equation calculates individual daily growth in weight per unit weight (g g^{-1} d^{-1}) as gains by food consumption minus losses by respiration, specific dynamic action, egestion, and excretion (e.g. Megrey et al., 2007). Each of these processes is directly or indirectly affected by temperature and related to weight by allometric relationships (e.g. Carlotti et al., 2000). The parameters of most of these relationships have been estimated in the laboratory for juvenile and early adult Arctic cod (Hop and Graham, 1995; Hop et al., 1997) and are used in the model. Arctic cod is characterized by low rates of food consumption, digestion, and respiration that result in slow growth and high resistance to starvation (Aronovich et al., 1975; Hop and Graham, 1995; Hop and Tonn, 1998). Low feeding activity is balanced by high assimilation efficiency, which stresses the importance of prey size and nutritional value (Hop et al., 1997).

3.1. Sub-model of prey consumption

The potential daily food intake per unit weight of a larva or potential consumption C_{pot} (g g^{-1} d^{-1}) is given by (adapted from Roy et al., 2004):

$$C_{pot} = VS \cdot (Cn \cdot Ceffn + Ce \cdot Ceffe) \cdot (CDp / CD) \cdot (Wp / W), \qquad (1)$$

Where VS is the volume searched (l d^{-1}), Cn and Ce are the concentration of copepod nauplii and copepod eggs (l^{-1}) respectively, $Ceffn$ and $Ceffe$ are the capture efficiency (ratio of prey captured to

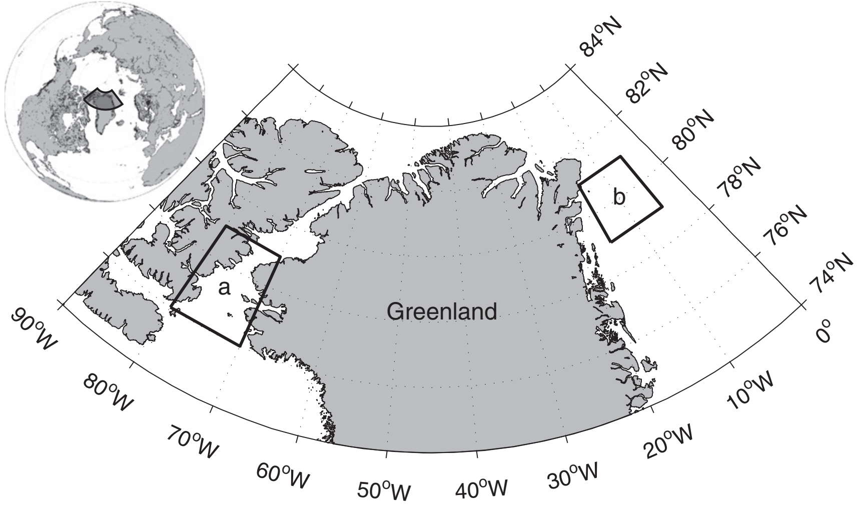

Fig. 1. Location of (a) the North Water (NOW) and (b) Northeast Water (NEW) study areas.