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**Modeling growth of larval cod and haddock on Georges Bank:
a synthesis of observations and model results for Spring 1995**

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Abstract

Surveys conducted as part of the U.S. GLOBEC/NW Atlantic program from March-June 1995, encountered a large number of cod and haddock eggs and larvae on the Northeast Peak and southern part of Georges Bank. Detailed information was obtained on larval abundance and growth, and the space-time structure of the zooplankton prey field and hydrography. These data are being synthesized and interpreted using spatially-explicit physical and biological models. We present preliminary results of our efforts examining the growth and survivorship of the larval fish cohorts using individual-based models (IBM) embedded in realistic prey fields and physical environments. Our larval fish IBM includes considerations of turbulence, light, prey choice and behavior. Our copepod prey field includes naupliar and copepodite stages of major species of copepods on the Bank (including *Pseudocalanus* spp., *Calanus finmarchicus* and *Oithona* spp.).

Introduction

During the past decade, we have conducted a series of studies using spatially explicit individual-based models of larval fish trophodynamics to explore the relative importance of biological and physical variables on Georges Bank cod and haddock larval growth and survival (e.g., Werner et al. 1993, 1996 and 2000; Lough et al. 1994; Page et al. 1999; and Lynch et al. 2001). Conceptually, larvae in high growth and survival areas could make a greater contribution to the recruiting population if these areas also have longer retention time-scales than poor growth and survival areas. Alternatively, larvae in poor growth areas could make a greater contribution if these areas have longer retention time-scales, compared to areas of good growth but high advective through-flows.

The problem is to determine the relative magnitudes of growth rates and retention times. To answer both components we must be able to accurately prescribe the physical and feeding environments of the larval fish. While the physical environment is relatively advanced and includes spatial and temporal circulation, turbulence and baroclinicity (e.g., Naimie, 1996), the feeding environment has been idealized and prescribed as depth-independent and temporally-constant based on averaged or multi-year composite observations (e.g., Werner et al. 1996 and 2000; and Lynch et al. 2001). As such, our results to date have not been able to quantitatively address inter-seasonal or inter-annual variability of larval fish populations.

In this paper, using preliminary data on larval prey-fields collected during the broad scale surveys on Georges Bank U.S. GLOBEC/NW Atlantic 1995, we take a first look at the possible bank-wide variability in larval cod growth based on observed variability in larval prey. In a companion paper, Runge et al. (2000) compare the potential effect on larval cod growth resulting from the observed variability of certain larval prey for two different years.

Methods

Trophodynamic model. We use the model described in Werner et al. (1996 and 2000) with extensions to include temperature on metabolic costs as in Buckley et al. (2000a). The core of our larval fish model is the standard bioenergetic supply-demand function, in which growth is represented as the difference between the amount of food assimilated by a larva and the metabolic costs of its daily activities. The formulation used herein is an elaboration of Laurence's (1985) model, with key enhancements as described in Werner et al. (2000) and Buckley et al. (2000a) including: (i) prey encounter and ingestion modified by local turbulence; (ii) prey selection specified based on observations on prey-in-gut of cod larvae sampled in the field; (iii) light limitation, based on studies on the effect of light on prey ingestion rates in the laboratory (Huse, 1994) that show a decrease in ingestion at low and at high light intensities, (iv) temperature, since optimum growth for larval cod and haddock is temperature dependent (e.g., Campana and Hurley, 1989); and (v) food satiation, whereby a limitation is placed on the food ingested depending on the gut volume, prey ingested and a 4-hour gut evacuation.

Physical environment. In this paper, to focus on the effect of prey variability on potential larval growth, we simplify the physical environment to include only model-computed turbulence and temperature fields for the March-April and May-June bi-monthly periods computed by Naimie (1996). Light penetration in the water column is specified as exponentially decaying as a function of depth (see Figure 1.)

Feeding environment. We specify the feeding environment for March, April and May of 1995 based on field data collected for three zooplanktonic species: *Calanus finmarchicus*, *Pseudocalanus* spp., which were sorted and staged into six naupliar and six copepodite stages, and *Oithona* spp., which were grouped as nauplii, copepodites, and adults (Durbin et al., in press). These were the three principal prey species found in the stomach contents of cod larvae for this time period (Lough, unpublished data). The zooplankton data were collected using MOCNESS (153 μ m mesh) and pump samples (50 μ m mesh). The depth intervals of the sample collection was 0-15m, 15-40m, 40-100m and 100m to the bottom. A typical broadscale survey cruise track is shown in Figure 2. Samples for this analysis are from Priority 1 stations (3, 7, 9, 12, 16, 18, 20, 29, 36 and 38). The data were objectively analyzed onto a three-dimensional finite element grid (see Werner et al. 1996) using the method described by Hendry and He (1996). The model mesh has 1200 non-uniformly spaced grid-points in the horizontal (grid spacing of 2-10 kms) and 21 non-uniformly spaced grid points in the vertical (grid spacing of 1-5 m). Figures (3 and 4) show the concentration of the zooplanktonic species at three depth levels for the months of March and

April respectively. The biomass of *Pseudocalanus* and *Oithona* includes all naupliar and copepodite stages; the biomass of *Calanus* only includes the naupliar stages.

Results

The 24-hour growth rates of cod larvae were computed at each of the model grid points. The larvae were fixed at each location, i.e., they were not allowed to swim or be advected by currents. Growth rates based on 24-hour exposure to prey, light, turbulence and temperature were computed for 6mm cod larvae in March, 8mm cod larvae in April and 10 mm larvae in May. The chosen 6-10mm variation in length from March to May is in keeping with the observed modal length of cod larvae on Georges Bank during these months. Based on observed gut-contents, 6 to 10 mm larvae are allowed to feed on all stages of *Oithona* and *Pseudocalanus*, but only on *Calanus* naupliar stages.

To assess the relative contribution of the major components of the prey field, growth rates were first calculated assuming cod larvae fed only on *Calanus* nauplii (Figure 5); *Oithona* nauplii and copepodites in Figure (6); and *Pseudocalanus* nauplii and copepodites in Figure (7). Feeding on *Calanus* and *Oithona* alone resulted in weak growth. Maximum larval cod growth rates for the *Calanus* prey field were approximately 5% per day (Fig. 5) and were negative in all cases for *Oithona* (Fig. 6). Larval cod growth rates in the presence of *Pseudocalanus* only (Fig. 7) were the greatest, reaching peak values of 15% per day near the crest of the Bank. Some of these high values are a result of the increased encounter rate due to the high turbulence in this region and may be overestimated. In any event, cod and haddock larvae are not generally found in abundance over the Bank's crest.

The growth rate of cod larvae feeding on the combined prey fields of the three species is shown in Fig. (8). The incremental effect of including all three prey species is clear; growth is raised at all levels and for all months relative to the highest rates observed in the *Pseudocalanus* alone case.

A comparison of observed (Buckley et al. 2000b) versus modeled growth rates is provided in Figs. (9) and (10) for the southeastern section of the Bank (away from the zone of high turbulence noted above). Observed rates are based on measured water temperature and larval RNA-DNA ratios (Buckley et al. 2000b). The magnitude of modeled and observed growth rates of 4-8% per day (or fractional growth of 0.04-0.08 per day) are in reasonable agreement inside the 60m isobath. However, between the 60 and 100 m isobath, the modeled growth rates are a factor of two to three lower than the observed values. Detailed agreement should not be expected as larval collections and prey field estimates were made on different cruises separated by about two weeks.

Concluding Remarks

We examined the broadscale field data for key zooplanktonic prey of larval cod for the months of March-April 1995 and found that for this time period, *Pseudocalanus* may provide the highest growth rates for 6-10 mm larval cod. The inclusion of *Oithona* and *Calanus* in the prey field increases the larval fish growth rates to values that are comparable to those observed in the field. While these results are encouraging, it should be stressed that they are preliminary. Additional work and analyses are required before a conclusive evaluation of cod growth in 1995 on Georges Bank is possible.

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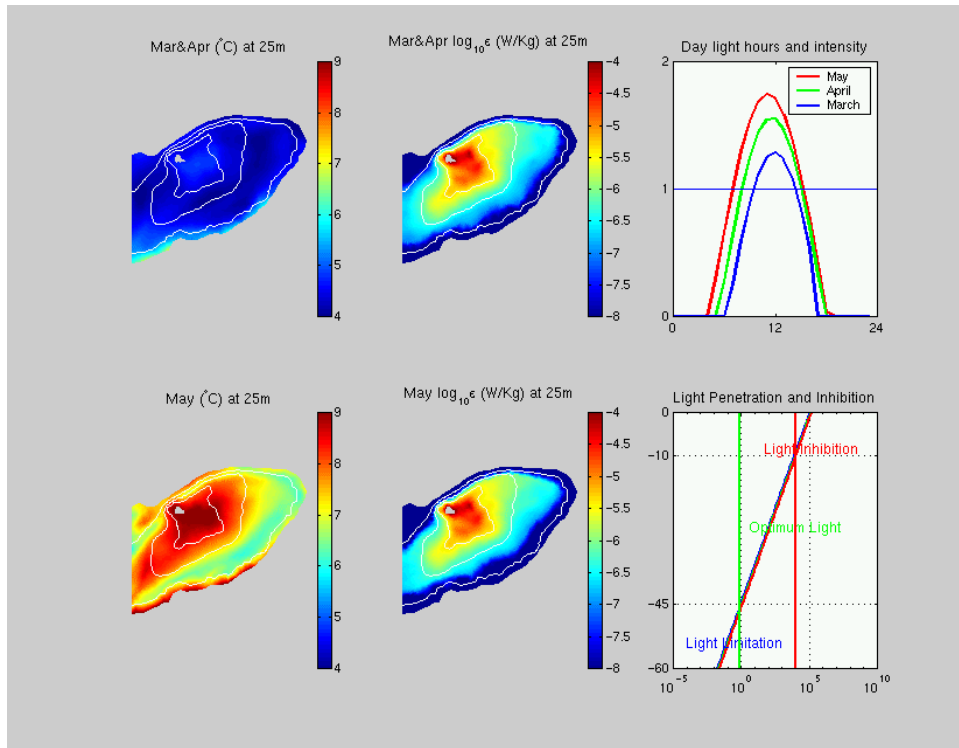


Figure 1. Georges Bank temperature, turbulence and light intensity, duration and penetration used in the trophodynamic computations of larval growth.

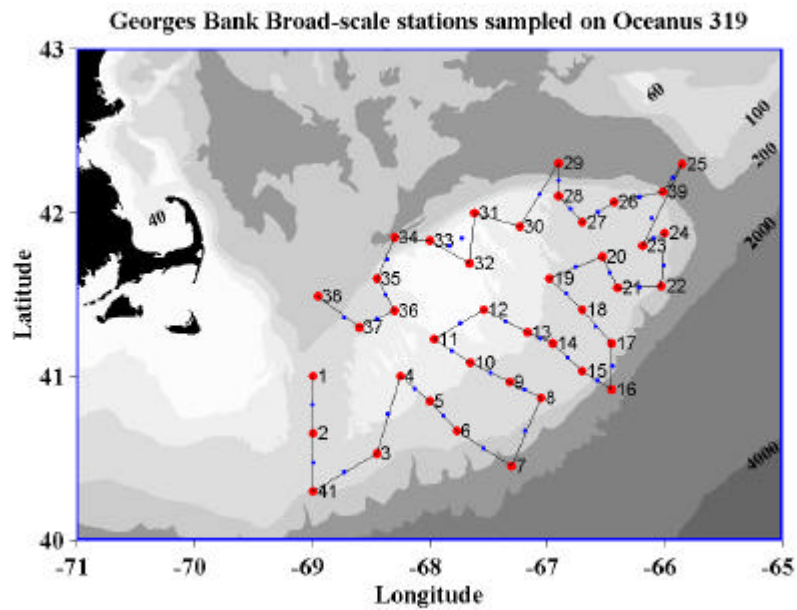


Figure 2. Sample broadscale cruise track. Numbers refer to station locations.

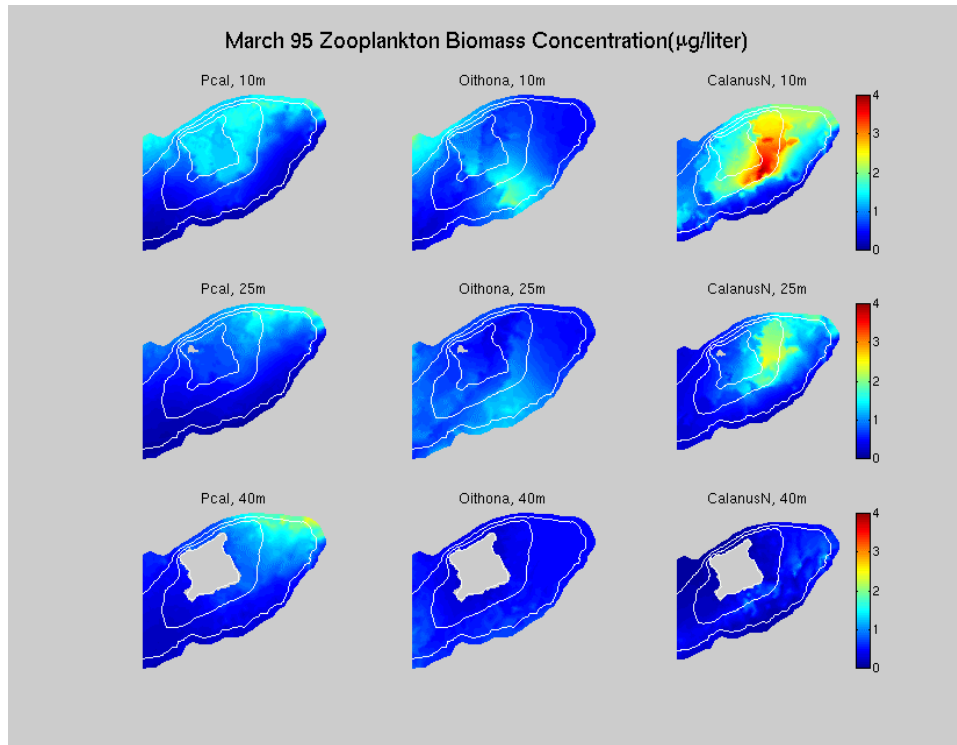


Figure 3. March 1995 biomass ($\mu\text{g/liter}$) of *Pseudocalanus* and *Oithona* (nauplii and copepodites), and *Calanus* (nauplii) at 10, 25 and 40m. Data were objectively analyzed from broadscale survey locations (Figure 2) onto a finite element mesh.

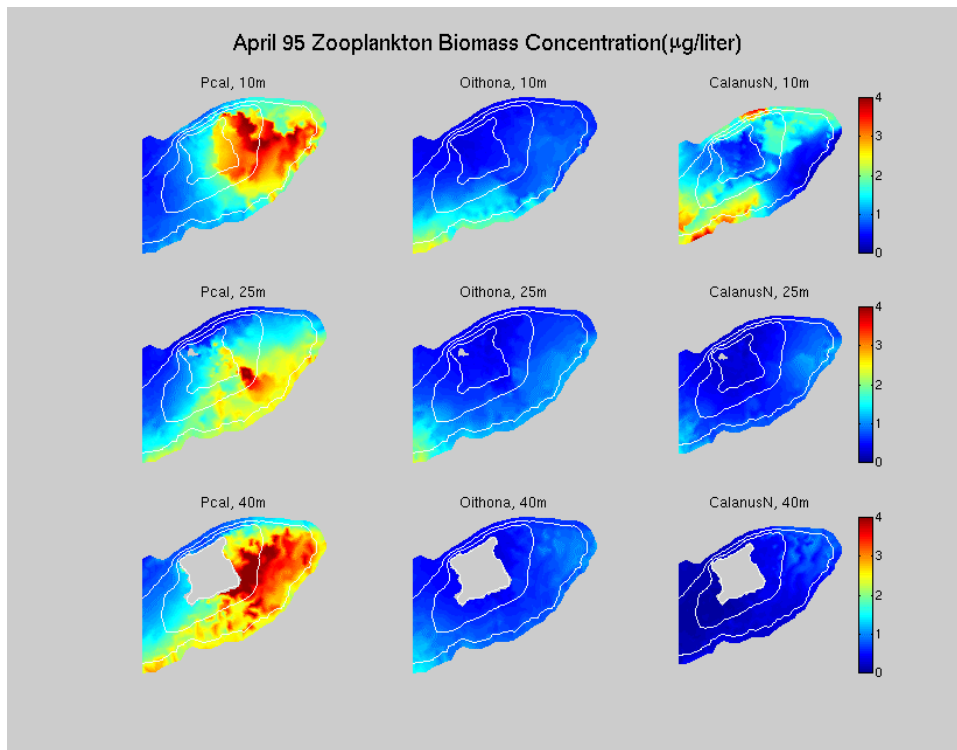


Figure 4. As in Figure (3), for April 1995.

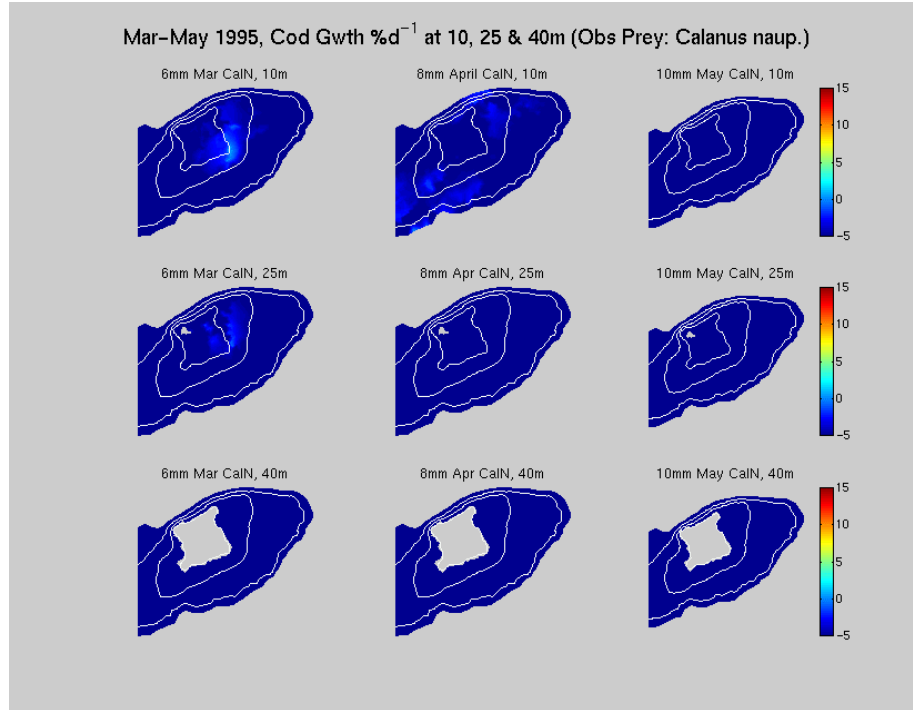


Figure 5. 24-hour growth rates for larval cod in response only to observed *Calanus finmarchicus* naupliar concentrations. Left column is for 6mm larvae in March at 10, 25 and 40 meters (top to bottom); middle column is for 8mm larvae in April; and right column is for 10 mm larvae in May.

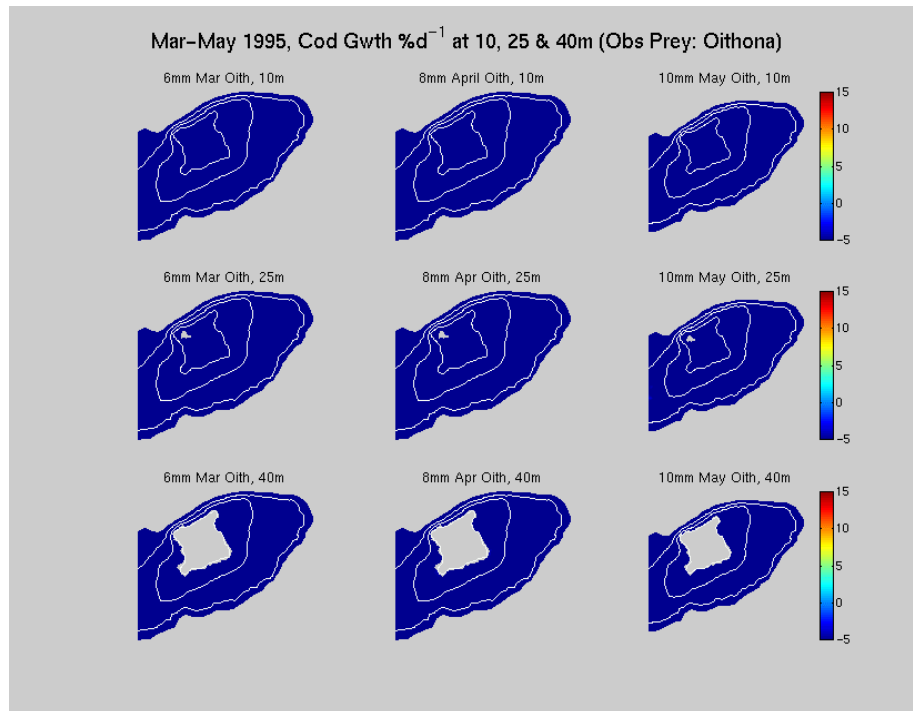


Figure 6. As in Figure (5), but including only *Oithona* nauplii and copepodites.

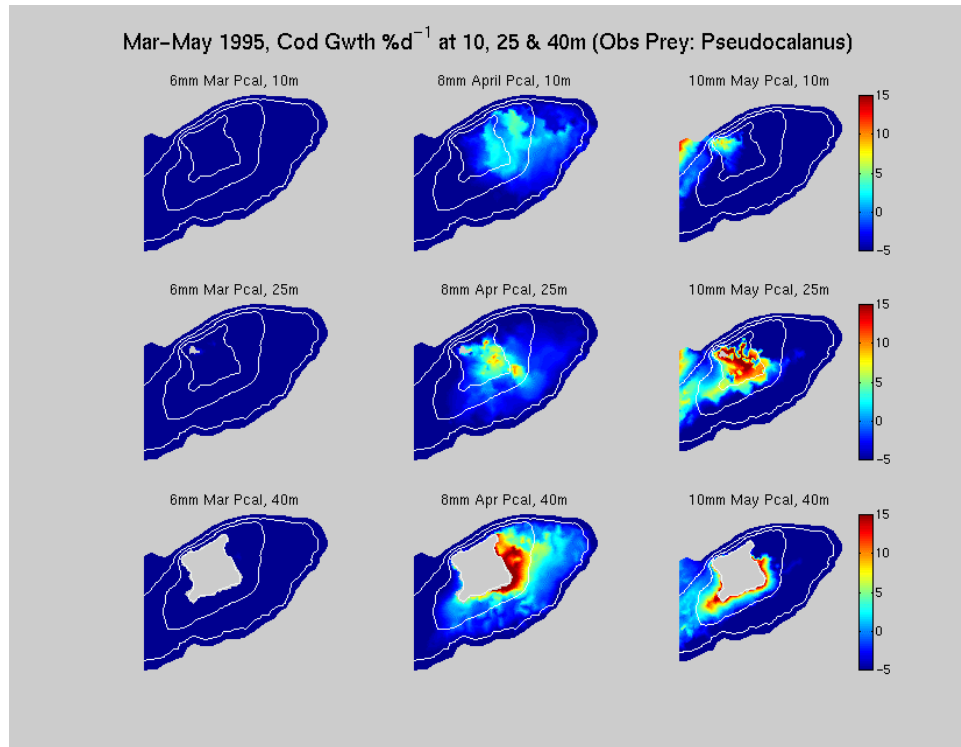


Figure 7. As in Figure (5), but including only *Pseudocalanus* nauplii and copepodites.

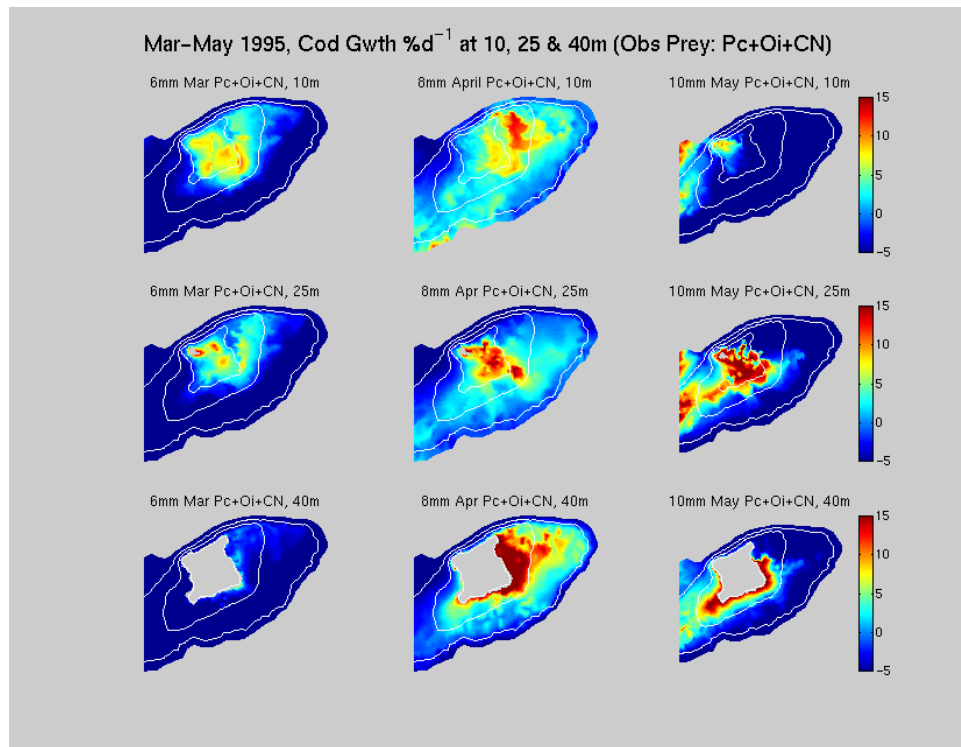


Figure 8. As in Figure (5), but including all three prey: *Oithona* and *Pseudocalanus* nauplii and copepodites, and *Calanus* nauplii.

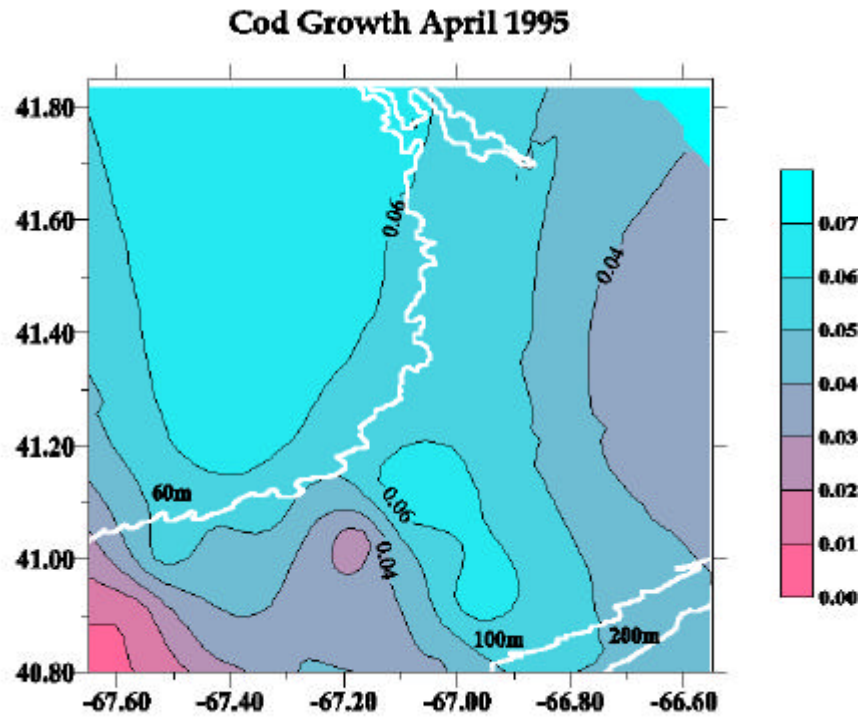


Figure 9. Observed growth on Southern Flank. See Buckley et al. (2000b).

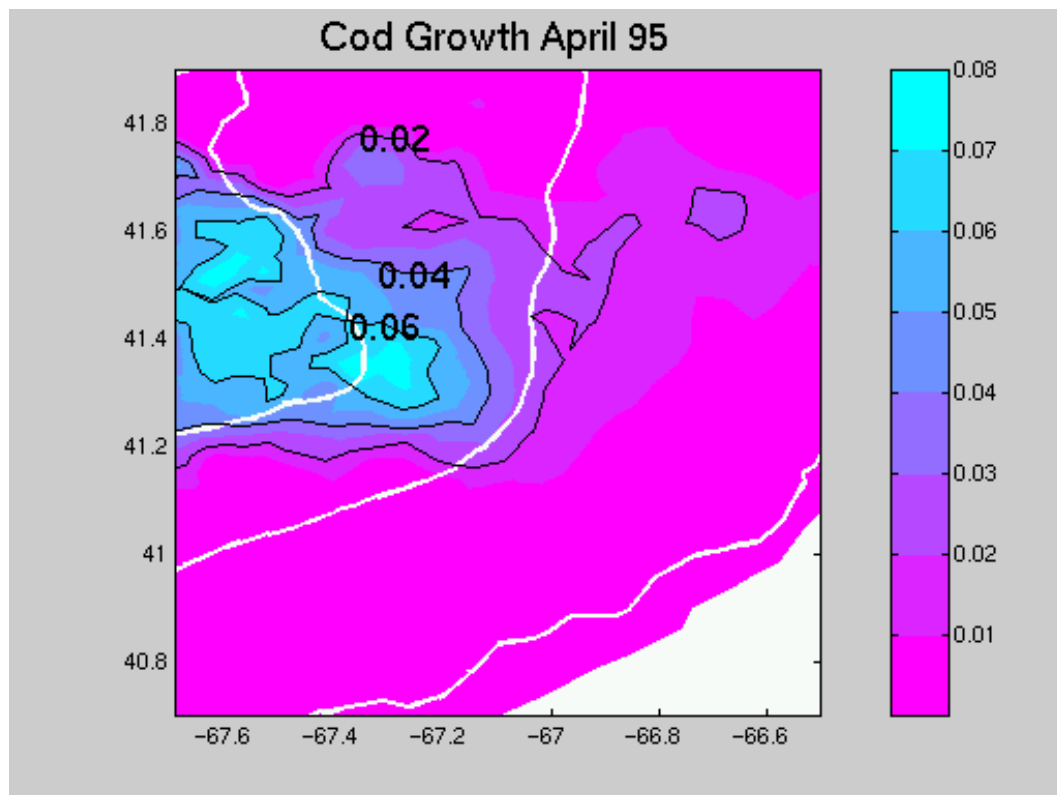


Figure 10. Modeled growth on Southern Flank; 40, 60 and 100m isobaths included for reference to Figure 9.