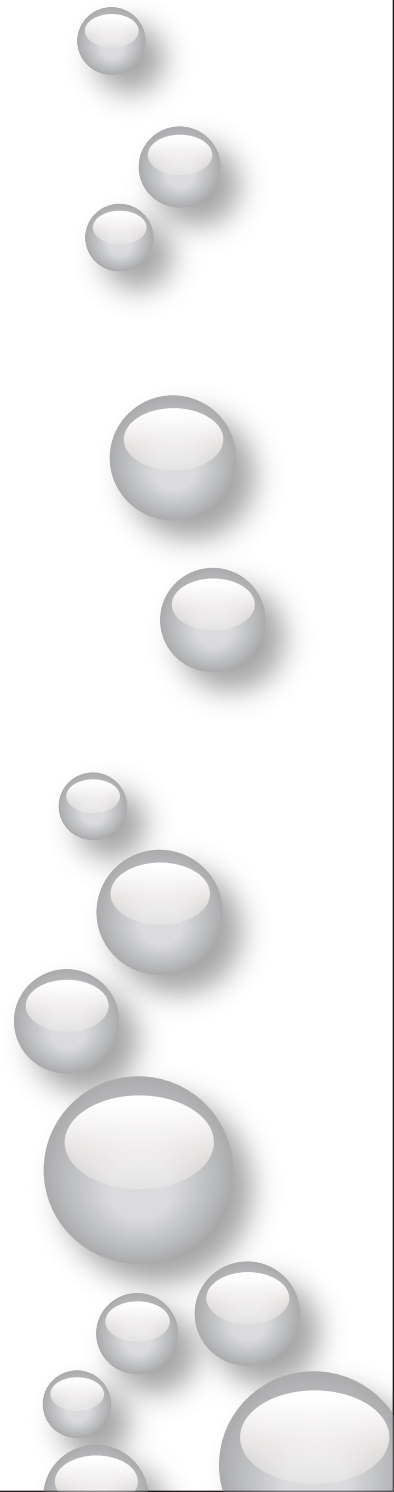# Paper 4

Modeling prey selection and growth of larval cod on Georges Bank

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Abstract

Larval cod (*Gadus morhua*) feeding ecology was investigated using a recently modified mechanistic individual-based model (IBM) incorporating metabolic parameters and prey selection based on their ability to perceive prey. Observed environmental conditions and prey abundance on Georges Bank (4 species, 13 stages) for May 1993 and 1994 provided forcing to the model. Larval cod on Georges Bank feed primarily on specific prey species. Whether this is a result of the prey abundance and visibility in the water column or an active selection was explored by explicit simulations of the diet of 5, 7, 9, and 11mm larval cod. The distribution of prey in the water column and the possible overlap with larval cod could be analyzed from observations. The highly stage-resolved prey fields allowed for analysis on how prey size composition was reflected in the observed and modeled growth rates.
Depth distribution of larval cod of various sizes overlaps with the distribution of their preferred nauplii and copepodite prey stages. The modeled growth rates were within a standard deviation of the observed field estimates. Highest growth rates were found in the surface layer (upper 30 meters), corresponding to the region of maximum abundance of observed larval cod. Total zooplankton biomass increased 170% from May 1993 to 1994, but observed growth rates were 1-2%·d^{-1} higher on average in 1993. The IBM predicted higher growth rates in May 1994 than in May 1993, contrary to field observations. Potential prey size availability between years was not found to account for the observed field growth difference so that other explanations were considered. Chessons' selectivity index provided a measure for modeled and observed prey selectivity. Prey selection on Georges Bank appears to be determined by the abundance of suitable sized prey and their visibility to larval cod. Modeled prey selection indicated *Pseudocalanus* spp. to be the preferred prey species for larval cod because of their abundance in the water column, and their image area (length times width), which makes them more vulnerable to predation. Simulation results suggest that *Pseudocalanus* spp., *Oithona* spp. and *Centropages* spp. are important prey items for 5-11mm larval cod. However, stomach content analyses revealed that *Centropages* spp. were seldom found in the stomach of these larvae, suggesting that *Centropages* spp. were not a preferred prey for the larvae in May 1993 and 1994.

Introduction

The larval marine habitat is a dynamic place where light changes through the day and the prey availability may vary both spatially and temporally. Most marine fish larvae drift passively with the prevailing ocean circulation, and their chances of survival are closely linked to food abundance and growth (Miller et al. 1988, Sundby et al. 1989, Hare & Cowen 1997). Growth of cod therefore depends on prey availability (Hjort 1914, Cushing 1990), and particularly planktonic crustaceans (Beaugrand et al. 2003). However, first-feeding larvae have functional constraints that limit potential prey sizes. Such constraints are swimming- (Peck et al. 2006), perception- (Hunter 1981, Aksnes & Utne 1997) and swallowing-capabilities (Puvanendran et al. 2004). As larvae grow their performance towards pursuit and capture of larger prey increases (Kane 1984, Puvanendran et al. 2004), while the relative size spectrum between predator and prey remains constant (Munk 1992). Habitats with abundant prey of favorable size provide conditions for rapid growth, and thereby increased survival (Miller et al. 1988, Hare & Cowen 1997). Larval cod may then grow and sustain increasing energy demands by selecting increasingly larger prey (Pope et al. 1994).

Lough et al. (2005) simulated growth rates of larval cod on Georges Bank for May 1993 and 1994 using an individual-based model (IBM) with prey selection specified from larval gut contents. Field estimated growth rates were lower on average in May 1994 than in May 1993 despite higher zooplankton biomass and warmer water (1ºC on average) (Lough et al. 2005). Simulations using all the potential prey field and larval positioned at fixed depths resulted in mean growth rates higher in May 1994, the opposite of the field estimated growth rates. Other simulations that only used their preferred prey *Pseudocalanus* and followed the field-derived weighted-mean depths over the sampling period resulted in growth rates close to the field estimates. Lough et al. (2005) argue that the observed growth rates were a result of depth-dependent food limitation, and selection of *Pseudocalanus* spp. as prey (from here on we skip spp notation). Still, Lough et al. (2005) did not address whether prey selection is a consequence of: (1) the relative frequency of prey in the water column; (2) their size-range, or (3) an active selection of particular species. In water of high

prey abundance, Munk (1995) observed larval cod to forage primarily on prey of size about 5% of larval size, whereas prey selectivity decreased with decreasing prey density. The results of Munk (1995) imply a selective ability of larval fish to maximize their proxy for fitness (here: weight) when prey are abundant. On Georges Bank *Pseudocalanus* is the most important prey item for larval cod (Lough et al. 1996, Lough & Mountain 1996) , together with *Oithona* spp., *Calanus finmarchicus*, and *Centropages* spp. (Kane 1984). The vertical and temporal distribution of these prey species differed between May 1993 and 1994. For both years, nauplii stages of *Pseudocalanus* spp. dominated the numbers of prey items in the water (30.7% and 23.7%), at least twice the numbers of *Centropages* (13.7 and 7.3%), *Oithona* (8.0 and 11.1%). *C. finmarchicus* were low in numbers, but high in total biomass (Lough et al. 2005). Based on the earlier model results of Lough et al. (2005), and our knowledge of the environmental conditions on Georges Bank in May 1993 and 1994, an IBM (Fiksen & MacKenzie 2002, Kristiansen et al. in press) was used to explore what regulates the larval preference for *Pseudocalanus*. If the preference for *Pseudocalanus* spp. is based on their characteristics (size, width, swimming speed) and abundance, the selection is passive, contrary to an active selection where larval cod search for this specific prey item. The IBM included a mechanistic feeding component which enabled explicit modeling of larval encounter, pursuit, and capture success of prey items (4 species, 13 stages each). The modeled larval habitat was identical to the one used in Lough et al. (2005) and consisted of zooplankton, temperature, and turbulence data from 22nd to 27th of May 1993 and 1994. Observations of the vertical distribution as well as gut samples of larval cod and haddock facilitated direct comparisons between observed and modeled diet and growth. Based on the results we explored; (1) the importance of not only total prey abundance, but also how vertical distribution of prey stages (sizes) affects the growth and prey selection of larval cod. (2) The relation between observed and modeled growth rates and diet selection in May 1993 and 1994. (3) The difference between modeled and observed prey selection of various sizes of larvae.

Materials and methods

Purpose

Our hypothesis was that the larval preference for the prey species *Pseudocalanus* results from passive selection determined by prey encounter. Here, passive selection means a preference for prey species based on their abundance and visibility (image area) in the water column. Passive selection is then a result of physical and biological characteristics of prey, predator, and the habitat, contrary to an active selection where particular prey items are pursued while others are ignored.

Prey, temperature, and turbulence measurements

The larval habitat was modeled using temperature, turbulence, and zooplankton data described by Lough et al. (2005), and modeled estimates of light as a function of day of the year, latitude, and depth (Skartveit & Olseth 1988). Environmental data are from two periods: 22-27 May 1993 and 22-27 May 1994. In both years, a cohort of larval cod was tracked using a drifter deployed at 13-m depth (Lough et al. 2005). Horizontal movements of larval fish are much less than the prevailing horizontal currents. Samples taken along the trajectory of the drifter resembles the habitat of the larval cohort. The location of the 1993 cohort was 40º43.0´N, 68º3.0´W and the 1994 cohort was 40º55.0´N latitude and 67º35.0´W longitude (Fig. 1). For both years the drifter was located in stratified water, and consequently all zooplankton (Fig. 2) and temperature data (Fig. 3) are from stratified sites. Zooplankton was sampled every 10-m using a $\frac{1}{4}$-m^2 MOCNESS with 64-µm mesh nets. *C. finmarchicus, Pseudocalanus, Oithona,* and *Centropages*, dominated the data and were identified to their 6 nauplii, 5 copepodite, and adult female and male stages. Turbulence was provided from a one-dimensional model, initialized by the observed wind conditions and hydrographic properties, and the M2 tide (Naimie 1996). RNA:DNA ratios estimated from samples of different size-classes of larval cod were from Lough et al. (2005), and provided data for comparison between observed and modeled growth rates.

Temperature, salinity, and water types

In 1993 temperature ranged from 5.5 to 8.5°C and salinity sigma-t (σ_t) from 25 to 26 (Figure 3a, b). In 1994 temperature ranged from 7.2 to 9.5°C and salinity sigma-t (σ_t) from 23 to 26. On average temperature was 1°C higher in May 1994.

Observations of larval vertical distribution

The depth distribution of larval cod and haddock was sampled, both in stratified (during drifter study) and mixed (after drifter study) water. Samples were from every 10-m at various locations (Fig. 1) using 1-m^2 MOCNESS nets with nine 333-µm mesh nets. Cod and haddock observations were combined because the two species have comparable vertical behavior (Lough & Potter 1993). In Lough et al. (2005) only mean vertical profiles over the sampling period were shown.

Model initialization

All individuals were initialized at 15-m depth with a 10% full stomach, at sizes 5 (86-µg), 7 (285-µg), 9 (705-µg), and 11 (1450-µg) mm. For both years, individuals were modeled from 22 May at 13:00, to 27 May 24:00.

Simulation runs

Two main types of model runs were performed: (1) Individual larvae were fixed at a 1-m depth interval, and growth rates and stomach content were tracked for 5 days. Average observed depth distribution of size classes (2-5mm, 6-8mm, 9-13mm) of larvae (Lough et al. 2005) made it possible to estimate weighted mean depth (WMD) growth rates. (2) Simulations of growth and stomach content over 5 days were conducted for vertically migrating larvae under different scenarios. We first modeled growth and ingestion of individuals that optimized their vertical position (OPT) by trading off the local ingestion and mortality rate within one-hour swimming range, next we assumed unlimited food supply (temperature-dependent growth, TDG) for individuals following the optimized trajectory, and finally we assumed that

individuals did not forage on *Centropages* (NOC), but still followed the optimized trajectory.

Prey selectivity

Chesson's (1978) prey preference index α_i was applied to estimate prey selectivity. The index is a ratio between selected prey items r_i relative to their frequency in the environment (n_i) and the ratio of the sum of prey items in the stomach and the environment. Neutral selection (Chesson 1978) is defined as $\alpha_{neutral}=1/m$ where m is the number of prey types and stages considered. If values $> \alpha_{neutral}$ are prey is actively selected as they appear more often in the diet compared than expected from their abundance. The model evaluates the index over 4 prey species and 13 stages (neutral selection, $\alpha_{neutral}=0.0192$).

$$\alpha_i = \frac{\dfrac{r}{n_i}}{\displaystyle\sum_{j=1}^{m} \frac{r_j}{n_j}}$$

Description of sub-models

The IBM has been described in earlier papers (Fiksen & MacKenzie 2002, Kristiansen et al. in press), and only a short outline will be given here. The IBM estimates five sub-models sequentially per time-step (one hour); (*i*) prey encounter, (*ii*) prey pursuit and capture, (*iii*) ingestion, (*iv*) growth and stomach dynamics, (*v*) update of variables and continue to next time-step.

(*i*) Larval cod are pause-travel, visual predators (Hunter 1981, O'Brien et al. 1989) and prey encounter depends on the larval visual ability to perceive prey (Aksnes & Utne 1997), turbulence (prey swept into view) (Fiksen & MacKenzie 2002), prey swimming speed (prey swim into larval perception area) (MacKenzie & Kiørboe 1995).

(***ii***) Successful approach of prey is achieved if the swimming speed of the larva is below the threshold value that creates a deformation rate in the water that alarms the prey (Kiørboe & MacKenzie 1995). The IBM described here, allows the larva to always swim below the threshold value, but the distance from the larva to the prey (distance of perception) must be reached within 10 seconds or else the approach fails (e.g., if a small larva detects a large prey, the distance is too far, and the prey is too large). If the turbulence level is high, prey may be swept out of the perceptive area of the larva (Fiksen & MacKenzie 2002), resulting in unsuccessful approach (MacKenzie & Kiørboe 2000). Prey behavior is restricted to swimming speed which proportional to length. The handling time spent on the unsuccessful approaches was included in total handling time (Fiksen & MacKenzie 2002). If the approach is successful; the larva reaches attack position, and may elicit a capture attempt.

(***iii***) Capture success is a function of the relative attack speed of predator and escape speed of prey, the jump angle of prey, and mouth size of larva (Caparroy et al. 2000, Fiksen & MacKenzie 2002).

(***iv***) Procedures *i-iii* are repeated for all prey species (4) and stages (13) (in total 52). Total captured biomass was estimated every time-step (one-hour) using Hollings' disc equation (Holling 1966). Metabolism of larval cod was parameterized from Finn et al. (2002). Active metabolism increases by a factor of 2.5 (1.4 for SL<5.5) (Lough et al. 2005) routine metabolism during hours of the day when light is above a threshold ($Eb > 0.01 \ \mu mols^{-1}m^{-2}$). Growth per time step is then the increase in weight corresponding to total biomass digested (ingested biomass modified by assimilation efficiency (Buckley & Dillmann 1982)) within the last hour plus the stomach content, minus the energy needed for metabolism (active and routine) (Kristiansen et al. in press). The amount of food in the stomach determines whether the larvae will grow at a maximal (size- and temperature-limited as in (Otterlei et al. 1999, Folkvord 2005) or food-limited rates (Kristiansen et al. in press).

Strategy for vertical behavior

Larval behavior is given as 'rules-of-thumb' (Gilliam & Fraser 1987), where each larva uses a strategy that maximizes ingestion rate relative to stomach fullness, and minimizes exposure to ambush and visual predators, and to starvation mortality (Kristiansen et al. in prep.). Willingness to take risk was determined by a functional relationship between larval condition (stomach fullness, larval size), and local mortality and ingestion rates within one-hour swimming distance away from current depth location. Choice of depth within swimming distance, z*(t) is then determined by maximizing,

$$z^*(t) = \max_z \left[(1 - \pi_i) i_z - \pi_i m_z \right]$$

where $\pi_{i,t} = \begin{cases} \left(\dfrac{s_{i,t} - STV}{1 - STV} \right)^{\beta_i}, & s_{i,t} > STV \\ 0, & s_{i,t} \leq STV \end{cases}$

$\beta = 5$, s is stomach fullness, $STV(SL) = 0.3 + 10^3 (1 + SL \cdot e^{SL})^{-1}$ is the size-dependent (SL is length) stomach threshold value (STV) which defines the hunger level. STV ranges from 0.7 (6mm) to 0.3 (18mm)) (see Kristiansen et al. (in prep.) for details).

Results

Zooplankton biomass and size distribution

Between May 1993 and 1994, there was 170 % increase in total zooplankton biomass. In both years, *C. finmarchicus* (Fig. 2 a, b) was located primarily in the upper 30-m, while *Pseudocalanus* (Fig. 2 c, d) biomass increased below 20-m, the depth of the thermocline. *Pseudocalanus* biomass increased by a factor of 1.3 from May 1993 to 1994 and most of the elevated biomass occurred between 50 and 70-m depth. *Oithona* (Figure 2 e, f) did not contribute significantly to the total biomass (3.1% in 1993 and 9.2% in 1994) because of low specific weight. *Oithona* was

mainly found in the upper 10-m. *Centropages* (Fig. 2 g, h) biomass was 43% of *Pseudocalanus* biomass for both May 1993 and 1994, with maximum biomass located in the upper 30-m (for further details see Table 1 in Lough et al. (2005)).

The prey field was further divided into three size ranges based on the prey width (dp < 0.15-mm, $0.15 \leq dp$ < 0.3-mm, and dp > 0.3-mm) (Fig. 4) which limits swallowing probability. Total number of nauplii in the water column varied with depth and between years (Fig. 4). Maximum abundance of all size groups occurred in the upper 40-m with values between 1.5 and 15 L^{-1} (Fig. 4 a, b) for the smallest size group and significantly lower (0-2 L^{-1}) for the two largest size groups. Patches of high densities of nauplii (smallest size group) and copepodites (the two largest size groups) co-occurred (Fig. 4). Copepodites were distributed throughout the water column, although maxima were found at 10 and 30-m in May 1993 and at 10-m in 1994.

Modeled behavior

Vertical variation of prey abundance, temperature, and predation rate influenced modeled growth and foraging of larval cod. In this model study, state-dependence (stomach fullness, size) determined the trade-off between ingestion and mortality, and the subsequent vertical behavior. Diel vertical migration (DVM) emerged from this trade-off and larvae moved downward during day and towards the surface during night (Fig. 5). Modeled larvae of size 5-mm were mostly located in the upper layer of the water column between the surface and 20-m depth. The individuals followed the local maximum of nauplii (upper 15-m) in May 1993, while in 1994, the nauplii were more homogenously distributed and the larvae migrated deeper (Fig. 5). The increased swimming ability of 9-mm individuals extended the DVM range (Fig. 5), which may have allowed the larger larvae to avoid predators in the surface layer at daytime. Average modeled depth position through 5 days (Fig. 5) was 9.1-m and 24.3-m for 5 and 9-mm in May 1993, and 7.8-m and 26.5-m for 5-mm and 9-mm in May 1994, respectively.

Observed larval distribution

The 2-5-mm larvae from the stratified and mixed (Fig. 7) locations were distributed in the upper 30-m of the water column. No clear pattern was apparent from the data, except the broader vertical distribution at mixed stations compared to the near surface distribution at stratified stations. Depth-integrated values of larval abundance differed with time of sampling, which could indicate sampling of different larval cohorts.

Larval cod and haddock 6-8-mm generally remained in the upper 30-m by day and night (Fig. 8), with maximum abundance around 20-m. Larvae of 6-8-mm were distributed throughout the water column at the mixed site, while at the stratified site they were closer to the surface.

Most of the 9-13-mm larvae at the stratified site were located in the upper 40-m, compared to the mixed site where larvae were more distributed towards the bottom (Fig. 9). Still, the data suggests that larvae move throughout the water column and that depth distribution change rapidly.

Modeled and observed growth rates

Average field-derived larval growth rates (RNA:DNA) for all sizes (5-9-mm) were 10.6 %·d^{-1} in May 1993 and 9.9 %·d^{-1} in May 1994 (Table 1), despite a 1.5 fold increase in plankton biomass in 1994. Estimated modeled growth of 5-mm larval cod in May 1993 at fixed depths and weighted for observed vertical abundance (WMD), was 8.2 %·d^{-1}. Larval cod that exhibited vertical behavior (OPT), experienced growth rates of 9.6 %·d^{-1}. Field observations for 5-mm larvae revealed mean growth (plus minus standard deviation, SD) rate of 7.6±2.4 %·d^{-1}. For 1994, modeled growth rates for 5-mm larvae were 7.8 %·d^{-1} for WMD and 10.3 %·d^{-1} for OPT, compared to the observed field mean of 9.4±0.0 %·d^{-1} (only one larva sampled) (Table 1). Observed growth rates increased with larval size with maximum of 12.9±1.6 %·d^{-1} for a 9-mm larvae in 1993 (10.4±2.0 %·d^{-1} in 1994). With the exception of 5-mm larva (WMD), the simulated growth rates were slightly higher in 1994 compared to 1993 due to the increased temperature and abundance of prey. This suggests that the number of

potential prey available to first-feeding larvae in 1994 provided enough energy for the larvae to sustain the elevated metabolic cost caused by increased temperature.

Temperature dependent, but food unlimited, growth (TLG) was higher for all sizes of larvae compared to the growth depending on prey density (OPT and WMD). Consequently, even vertically migrating larvae are food limited (Table 1). Maximum growth rate of 13.5 %·d^{-1} was achieved by 9-mm larvae in 1994. Lowest modeled and observed growth rates were found for 5-mm larvae.

Modeled prey selection at constant prey densities

Predicted mechanistic capture success was comparable to stomach observations (Fig. 6), except for small differences for the largest prey items available to 5 and 9-mm larval cod. The species-specific length and width (Fig. 10 a) of the prey represent characteristics that determine the conspicuousness to larval cod, while prey swimming speed and jump angle affect larval capture success. Given equal densities of the four prey species, *Oithona* was the preferred simulated prey species for 5 and 9-mm larva (Fig. 10). This is a result of the relatively large width to length ratio of *Oithona* which increases their visibility (image area) and thus encounter rate with larval cod. Overall, modeled preferred ratio between prey and predator length is 0.06 for 5-mm larva and 0.05 for 9-mm larva (Fiksen & MacKenzie 2002).

Modeled and observed prey selection with varying prey densities

When the observed prey densities are used, *Pseudocalanus* and *Centropages* are the most important modeled prey items regardless of larval size (Table 2). The two species accounted for 60-80 % of the prey items in the modeled gut for both 1993 and 1994. *Pseudocalanus* nauplii were 2.2-fold more abundant than *Centropages* nauplii in 1993, and 3.2-fold more abundant in 1994. The abundance of *Pseudocalanus* partly explains why they are preferred. Contrary to modeled prey selection, stomach samples showed a clear preference for *Pseudocalanus* for all larval sizes, and low (0-19 %) values of *Centropages* (Table 3). *Oithona* accounted for 12-30 % of prey in the modeled diet for all larval sizes (Table 2), comparable with stomach samples (Table

3). Low preference for *C. finmarchicus* is predicted from both modeled (0-7 %) and observed (0-1 %, valid for 6-8-mm) stomach content (Table 2 and 3). *C. finmarchicus* is by far the largest copepod prey available and prey width, length, and swimming speed constrain modeled capture efficiency (Fig. 6).

Table 2 summarizes the Chessons prey preference index of all stages, whereas Figure 11 reveals the preference for both prey stages and species. Modeled 5-mm larvae forage mainly on nauplii stages, however for *Pseudocalanus*, *Centropages*, and *Oithona*, the smallest copepodites stages are also be preyed upon (Fig. 11). *C. finmarchicus* is nearly absent as prey for 5-mm larvae with exception of the smallest nauplii stages (Fig. 6 and 11).

Simulated larval cod of size 9mm forage on nearly all available prey items (Fig. 11), with the exception of the largest *C. finmarchicus*. Modeled gut content indicated high selection for *Pseudocalanus* and *Centropages* with a preference for copepodite stages CI-CIV (Fig. 11). Observed stomach content values 6-8-mm larva showed the same pattern seen in the modeled results, with the exception that *Centropages* was close to absent from the diet. Instead, the larvae must have compensated for the absence of *Centropages* by foraging on *Pseudocalanus*, which accounted for 46-92 % of the observed stomach content (Table 3).

Observed gut content of 6-8-mm larval cod showed low numbers of *Centropages*. If we assume that *Centropages* is negatively selected (for unknown reasons) and remove *Centropages* as potential prey in the model, the modeled number of *Pseudocalanus*, and *Oithona* in the stomach increased (Fig. 12 and Table 4). The larval selection on *C. finmarchicus* did not increase as abundance was generally low and also difficult to capture for the larvae. With the absence of *Centropages*, small larvae (5-7-mm) increased their numbers of *Oithona* in the stomach, while larger larvae (9-11mm) mainly fed on *Pseudocalanus* (Fig.12 and Table 4).

Discussion

The spatial overlap between larval fish and their prey increases larval survival probability and can have significant impact on determination of year-class strength (Cushing 1990). Platt et al. (2003) were able to connect the timing of the phytoplankton bloom to recruitment strength of the Nova Scotia haddock population. The authors correlated year-class abundance of haddock to satellite data of chlorophyll, thereby providing evidence for the match-mismatch theory of Cushing (1990). However, the quality of the prey may prove to be equally important as the quantity of prey to ensure larval and juvenile survival. Beaugrand et al. (2003) observed a two-fold decrease in the mean size Calanoid copepods in the North Sea in the mid 1980s. Estimates were based on extensive time series of zooplankton abundance from continuous plankton recorder measurements. A combination of increased temperature and decrease in prey-predator length ratio resulted in low growth of North Sea juvenile cod, and consequently low survival and recruitment. Survival and growth is inter-linked in larval fish ecology (Houde 1987, Bailey & Houde 1989, Gallego & Heath 1997), and recruitment in fish populations is therefore correlated to prey availability and quality. For larval cod on the Georges Bank and the Western Bank of Nova Scotia, *Pseudocalanus* is the main prey item (Kane 1984, McLaren & Avendaño 1995, Lough et al. 1996, Lough & Mountain 1996, McLaren et al. 1997, Reiss et al. 2005). Based on the model results shown in this work it seems likely that this preference is passive and a consequence of *Pseudocalanus* visibility and abundance in the water column. *Pseudocalanus* is also energy rich due to the high lipid content (Reiss et al. 1999) and thereby a quality prey item for larval cod. Luo et al. (1996) modeled prey selection of bay anchovy of Chesapeake Bay and concluded that behavioral choice is of minor importance. This conclusion was based on simulation results from a mechanistic model, not too different from the one described in this work. Luo et al. (1996) stated that to understand prey selection of larval fish it is necessary to observe the prey availability through the visual perception of the larva. This is achieved by the use of a mechanistic model that resembles the visual perception of the larva, which is modified by the current light

intensity and water quality. All of these processes combined with the prey distribution determine the prey-predator encounter rate, and consequently the passive selection of prey. Here, the passive selection of prey in the diet is consistent with stomach samples, a fact that increases the viability of the result. However, the potential prey field on Georges Bank is diverse, and this model effort has only considered 4 main species found in the diet of larval cod. At times when prey abundance is low it is likely that other species may provide energy for larvae, perhaps with the effect of decreased prey quality, growth, survival, and recruitment success (Beaugrand 2003).

There was a difference between the modeled and observed diet abundance of *Centropages*. Only few prey items of *Centropages* were found in stomach samples, but the model predicted this prey species as an important part of the diet. Some *Centropages* were found in observations in May 1994, but mainly the naupliar stages. *Centropages* is an omnivorous predator and has a behavior, which differs from the (mainly) herbivorous *Pseudocalanus* (Davis 1987), e.g. a faster reaction pattern and improved swimming abilities (Tiselius & Jonsson 1990, Titelman 2001). If the behavior of *Centropages* is mainly ambush or tactile, encounter between larval cod and *Centropages* may be lower compared to the suspension feeding *Pseudocalanus*. In a recent laboratory experiment, larval cod successfully preyed on *Centropages* (Seljeset 2006), however the behavior of the prey in natural and laboratory conditions may differ significantly (Munk 1995). Still, Reiss et al. (2005) studied the feeding ecology of Atlantic cod larvae on the Western Bank of Nova Scotia and found 80 % of the larval diet consisted of *Pseudocalanus* and *Centropages* prey items. When *Centropages* was removed as a potential prey item, the modeled (Table 4) and observed (Table 3) prey selection agreed well, and the modeled growth rates were within standard deviation of the observed.

The mechanistic component of the IBM described here did not include any species-specific behavior of the prey items. Modeled evasiveness of the prey was determined solely by the size of the prey (jump speed scaled to prey length). In future work

differences between species should be included as predators may react both to prey visibility and behavior (Utne-Palm 2000). Behavioral differences between prey species (Buskey et al. 2002, Titelman & Kiørboe 2003) may also shed increased light on prey selection of larval fish.

Larval feeding is dependent on ambient light (Blaxter 1986) and prey abundance within the preferred size range (Munk 1992). Most of the prey items within edible size of larval cod where distributed in the upper 40-m in May 1993 and 1994, and overlapped with the larval distribution. From the interaction between larval phenotypical traits and local mortality sources, individual behavior emerged (Kristiansen et al. in prep.), and the larvae moved up or down in water column. The modeled and observed larval depth distributions are difficult to compare given the inherent sampling variability. Still, observations indicate that significant vertical movements may occur in the upper 40-m, which corresponds to where the modeled larvae feed. This is not surprising since small (5-7-mm) larvae need to stay in this surface layer to visually hunt for prey. Larger individuals (9-11-mm) larvae may utilize a wider range of the water column as their visual abilities improve with ontogeny (Blaxter 1986). Lough et al. (1996) observed homogenous distribution of 7-8-mm larval cod in mixed water on Georges Bank during night, and a deepening of the distribution towards 30-40-m at day. Lough and Mountain (1996) found lowered feeding incidence (number of prey in gut) for larvae sampled deeper than 30-m, increasing towards the surface in non-stratified water. The authors also observed larval cod (7-8-mm) distributed throughout the water column with maximum abundance around the thermocline (15-30-m). The majority (60 %) of 9-10-mm larvae occurred below the thermocline during day, and 80 % within or above thermocline during night. Observations have also revealed that larval cod probably initiate vertical migration at the size range 6-8-mm, and at the size 9-13mm have a distinct day-night migratory pattern (Lough & Potter 1993). Modeled behavior exposes larvae to various depths of the habitat through the day, consequently to different prey availability and temperatures. Modeled growth and diet selection resulting from the imposed behavioral constraints are close to observed values, and

suggests that the behavior overlaps with the actual larval distribution. Implementing physiological and environmentally regulated vertical behavior seems to provide reasonable behavioral response. Behavioral dynamics is especially important in IBMs that are coupled to physical models where dispersal and advection of particles may differ considerably with the depth position of the larvae (Vikebø et al. 2005).

Despite the differences between the IBM presented in Lough et al. (2005) and the IBM presented here, both models produced growth rates comparable to observations, However, it might be asking too much of the models used with limited field data to detect small population differences in field-estimated growth rates. The major difference between the two models is the statistical approach to capture success taken in Lough et al. (2005), and the mechanistic approach taken here. Lough et al. (2005) used gut evacuation rate while we have used a stomach for energy storage, however testing revealed comparable amounts of biomass ingested by various sizes of larvae in both models. This suggest that the models simulate energy intake and energy flow quite comparable, however the mechanistic approach taken in this model setup allows for a more detailed study of the feeding ecology of the larvae.

Conclusion

In conclusion, larval cod on the Georges Bank passively select *Pseudocalanus* as a consequence of their visibility in the water column and their abundance. First-feeding larvae are able to capture nauplii stages of *Pseudocalanus*, *Oithona*, *Centropages*, and to some extent the smaller *C. finmarchicus*. With the exception of the nauplii stages, *Centropages* were seldom found in stomach samples of larval cod, probably because of species specific behavior. The observed and simulated larval diet lacked *C. finmarchicus* because of their large size which limits larval capture success and ingestion. Larval cod did not achieve maximum growth rates as the prey densities were too low, however, modeled larval growth were still high and close to observed values. Prey size composition and prey depth distribution was favorable for small (<7mm) larvae, as most of the prey edible by small larvae were located in the upper 40-m. Future model attempts to explore the feeding ecology of larval fish would

benefit from including species-specific characteristics of prey, such as escape speed, behavior, prey contrast in the water column, and the threshold level of reaction when approached by a predator.

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Table 1 Mean observed growth rates (%•d^{-1}) from RNA/DNA measurements (Lough et al. 2005) for 4 sizes of larval cod compared to modeled growth rates for May 1993 and 1994. Simulated growth rates for larval cod averaged throughout the water column and weighted by observed (Lough et al. 2005) abundance at depth (weighted mean depth, WMD). Also shown are averaged growth rates (100ind.) for individuals with vertical behavior that optimize (OPT) ingestion rate and minimize mortality risk. Temperature-limited growth rate (TLG) was estimated assuming unlimited amounts of food, restricting larval growth to their physiological maximum (Folkvord (2005)). Simulations where *Centropages* were excluded as potential prey are denoted NOC. The vertical behavior of TLG and NOC was identical to OPT behavior.

	1993					1994				
	Obs.	WMD	OPT	TLG	NOC	Obs.	WMD	OPT	TLG	NOC
	(mean,SD,N)					(mean,SD,N)				
5mm	7.6 (2.4,11)	8.2	9.3	9.7	8.9	9.4 (0.0,1)	7.8	10.3	10.6	9.5
7 mm	11.3 (3.3,60)	8.8	10.2	12.0	11.0	9.8 (1.9,83)	10.1	11.2	13.3	11.8
9 mm	12.9 (1.6,270)	10.9	10.6	12.2	11.5	10.4 (2.0,46)	11.6	11.9	13.5	12.4
11mm	-	10.9	11.5	11.6	11.4	-	12.0	12.4	12.8	12.3

Table 2 Simulated Chessons' alpha values for the environmental conditions in May 1993 and 1994 for 4 sizes of larval cod (5, 7, 9, 11mm). Modeled larvae performed vertical behavior in the upper 40m of the water column (OPT). All prey stages within species was added, and the level of neutral selection was $\alpha_{neutral}$=0.25.

	1993				1994			
	5 mm	7 mm	9 mm	11 mm	5 mm	7 mm	9 mm	11 mm
Calanus finmarchicus	0.00	0.03	0.04	0.05	0.00	0.04	0.07	0.06
Pseudocalanus spp.	0.38	0.47	0.52	0.53	0.35	0.39	0.49	0.53
Oithona spp.	0.25	0.15	0.12	0.13	0.32	0.30	0.15	0.12
Centropages spp.	0.36	0.35	0.33	0.28	0.32	0.27	0.30	0.30

Table 3 Observed Chesson's alpha index at mixed and stratified locations for May 1993 and 1994 including the 4 most important prey species for larval cod (6-8mm) on Georges Bank; *C. finmarchicus*, *Pseudocalanus*, *Oithona,* and *Centropages*. Numbers of stomach samples (N) are shown below sampling site. Neutral selection was $\alpha_{neutral}$ =0.25.

Year	1993		1994	
Sampling site	Mixed	Stratified	Mixed	Stratified
N	189	59	28	41
Calanus finmarchicus	0.01	0.00	0.00	0.00
Pseudocalanus spp.	0.80	0.82	0.92	0.46
Oithona spp.	0.18	0.18	0.0	0.35
Centropages spp.	0.00	0.00	0.08	0.19

Table 4 Simulated Chessons' alpha values for the environmental conditions in 1993 and 1994 for 4 sizes of larval cod. All prey stages within species was added, except for Centropages, and the level of neutral selection was $\alpha_{neutral}$=0.33.

	1993				1994			
	5 mm	7 mm	9 mm	11 mm	5 mm	7 mm	9 mm	11 mm
Calanus finmarchicus	0.00	0.0	0.02	0.07	0.00	0.07	0.08	0.09
Pseudocalanus spp.	0.55	0.63	0.80	0.75	0.58	0.53	0.69	0.74
Oithona spp.	0.45	0.36	0.18	0.18	0.42	0.40	0.23	0.17
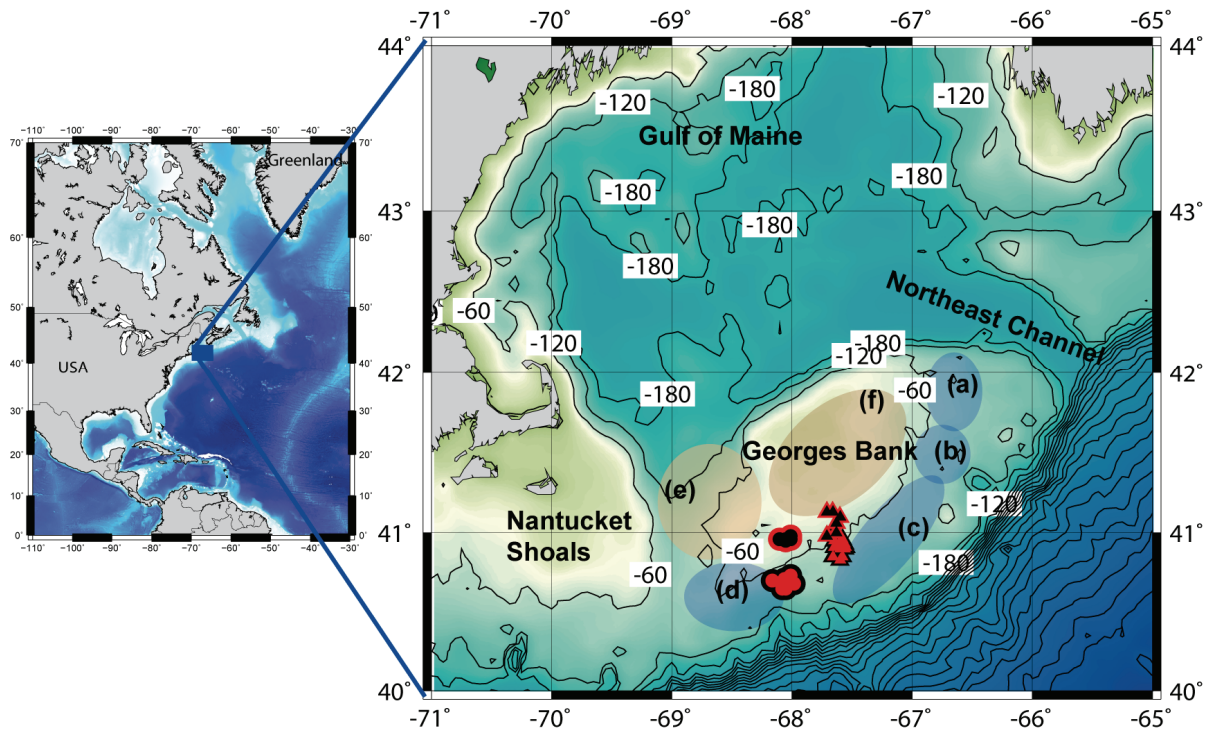
Figure 1 A map of Georges Bank with red and black circles denoting stratified and mixed sampling sites in May 1993. Red and black triangles mark the positions of stratified and mixed sampling sites for May 1994. Main spawning of Atlantic cod occurs in February-April around the Northeast Peak (a), and larvae and eggs passively drift with the circulation southwards, along the slope of the bank (b, c, and d). Larvae reach the western end of Georges Bank by June-July, and may enter the summer and autumn nursery habitats (e and f) (Based on Lough et al. (2005) Fig. 1). Depth contours are in meters.
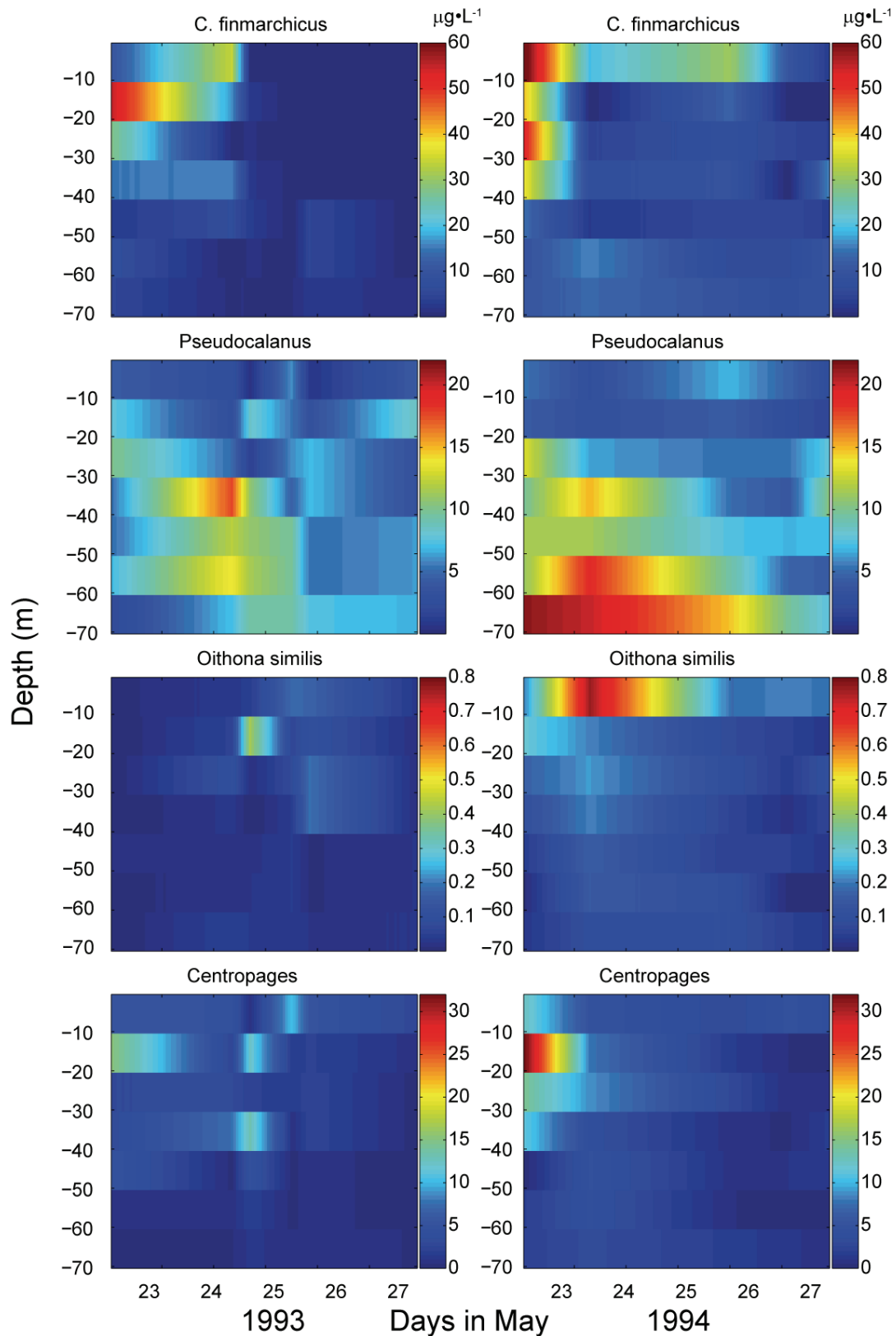
Figure 2 Zooplankton biomass (µgL⁻¹) distribution sampled in stratified water during May 1993 (left) and 1994 (right) from Lough et al (2005) (see map in Fig. 1 for details of the positions) for the four species *C. finmarchicus*, *Pseudocalanus*, *Oithona*, and *Centropages*.
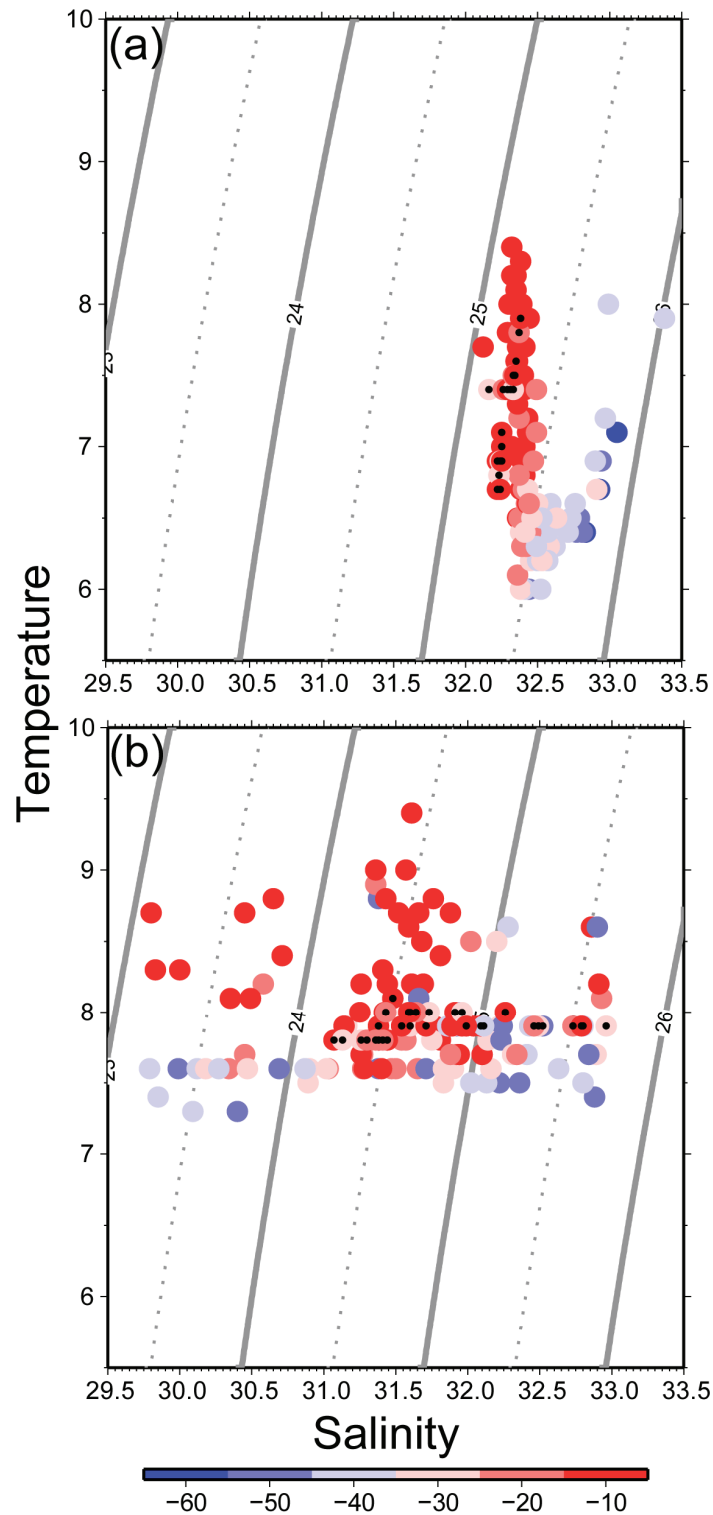
Figure 3 Temperature and salinity plot for May 1993 (a) and May 1994 (b). Density contours are shown as grey lines. Sampling depth for temperature, and salinity measurements are indicated by color (see scale). Sampling location is featured by single colored (stratified site) and single colored with black dot (mixed site): however only temperature data from the stratified locations were used as model input.
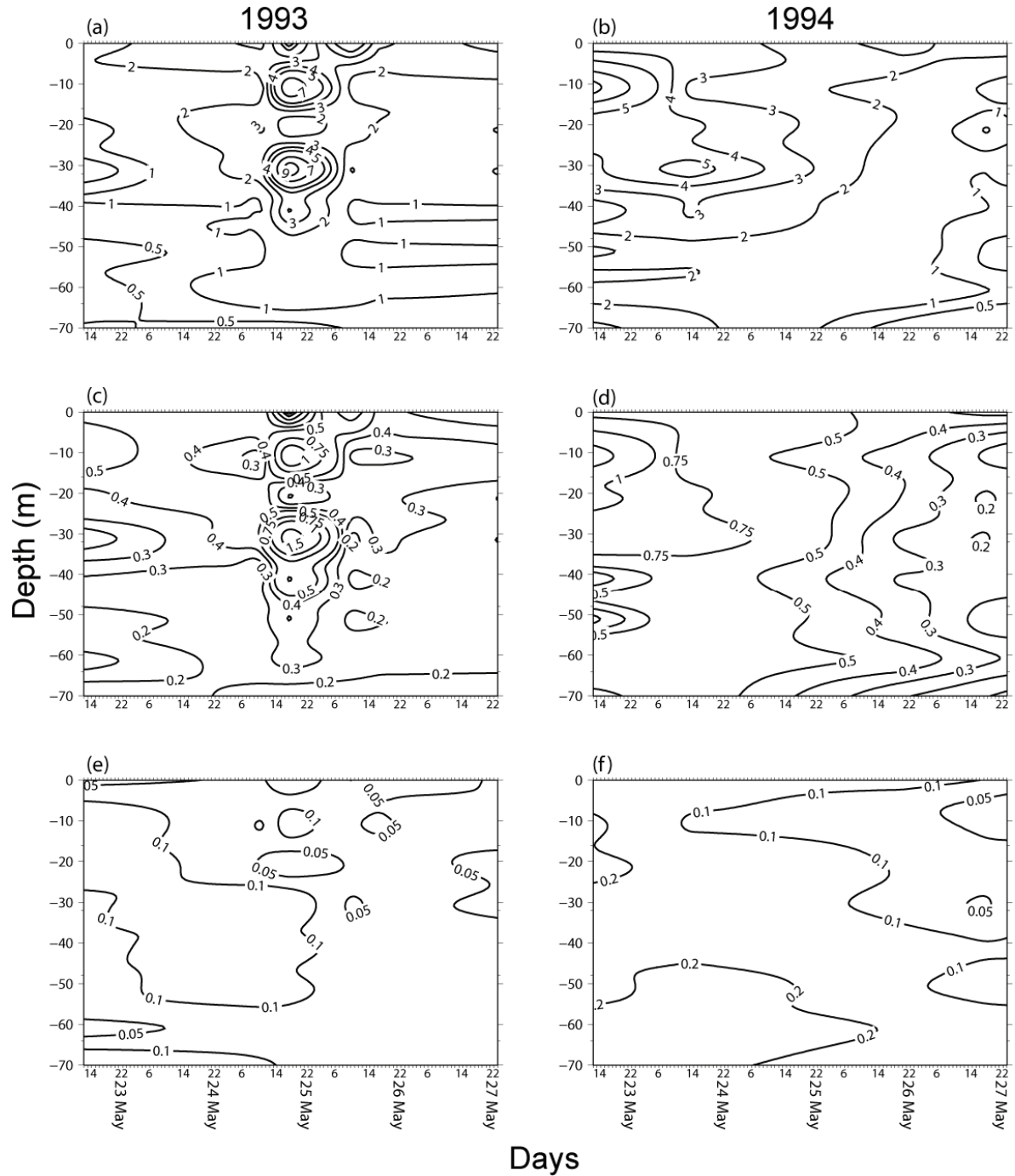
Figure 4 Distribution of three size classes of prey (prey·L^{-1}) in May 1993 (left) and May 1994 (right) from stratified sites (Fig. 1). Prey were divided into sizes based on their width (*dp*); *dp* < 0.15-mm (a, b), 0.15 ≤ *dp* < 0.3-mm (c, d), and *dp* > 0.3-mm (e, f).
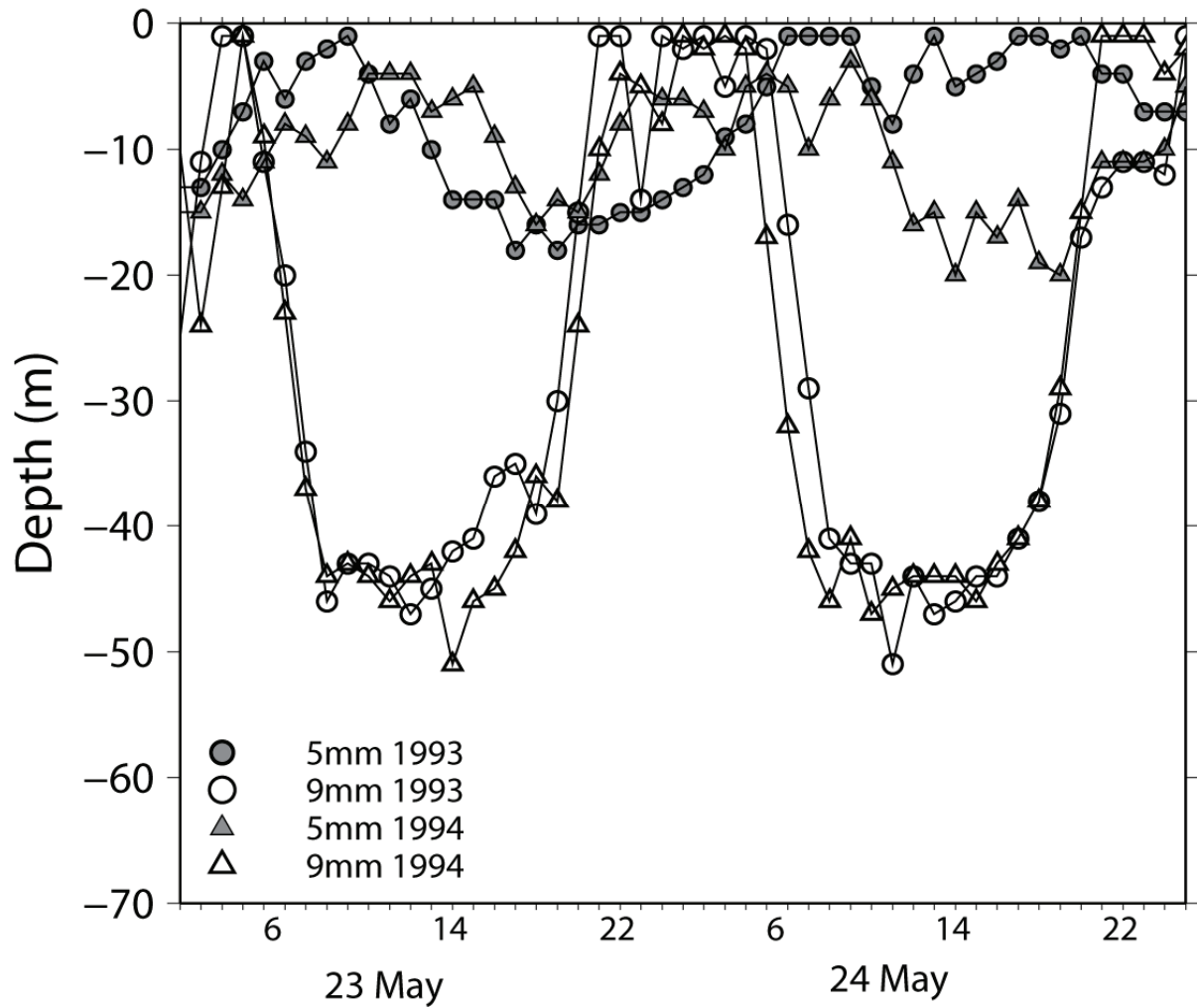
Figure 5 Depth position of two sizes (5 and 9-mm) of larval cod with vertical behavior modified by the local mortality and ingestion rates, and their state dependence (stomach fullness, size). Hour of the day and the date are labeled on the x-axis, and restricted to a 48·h period.
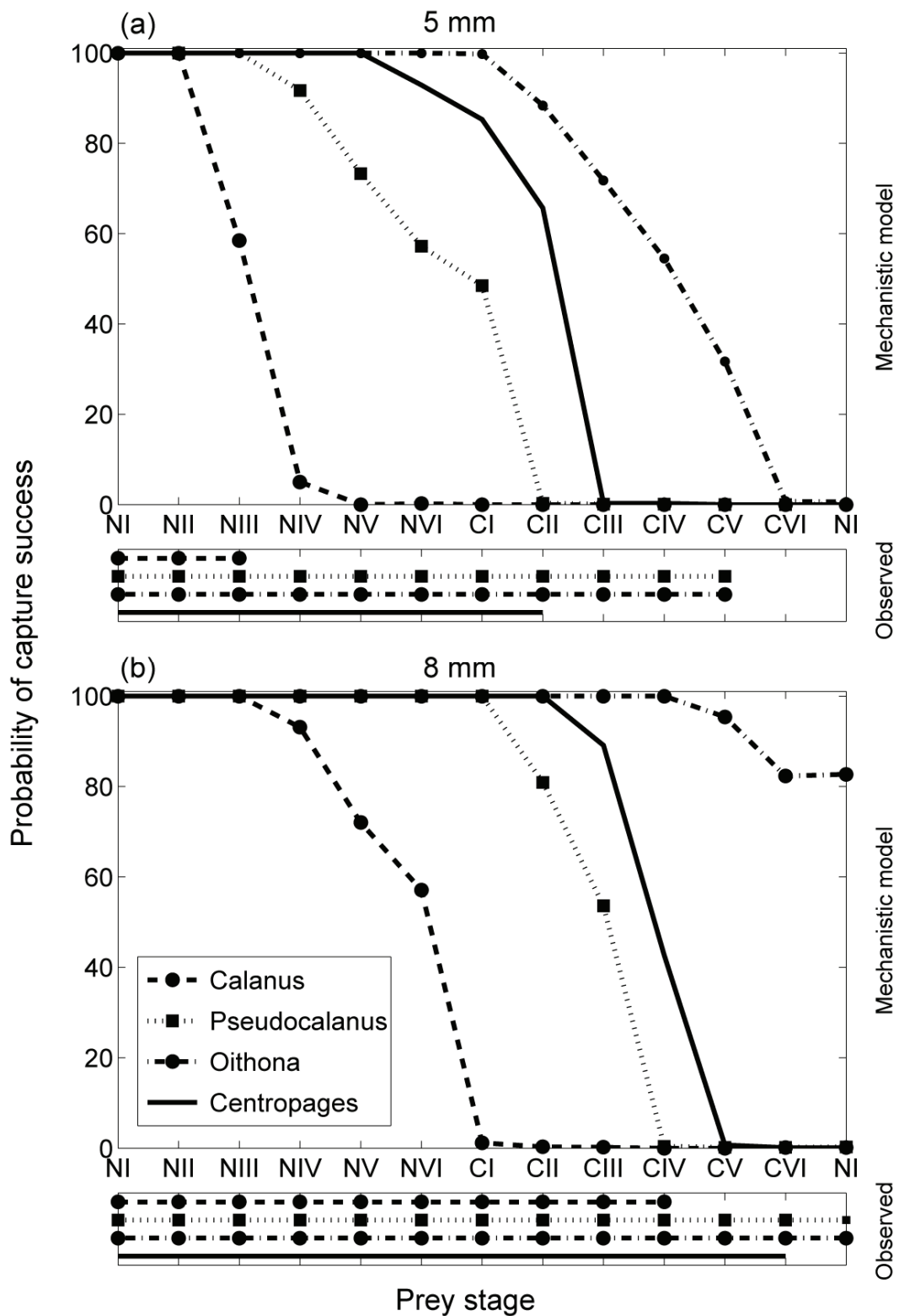
Figure 6 Modeled and observed probability (%) of capture success for 5 (a) and 8 (b) mm larvae. Modeled values were averaged over 1000 capture attempts per prey species and stage. Observed values (bottom lines) from Lough et al. (2005) were based on stomach samples of 2-5-mm and 6-8-mm larval cod.
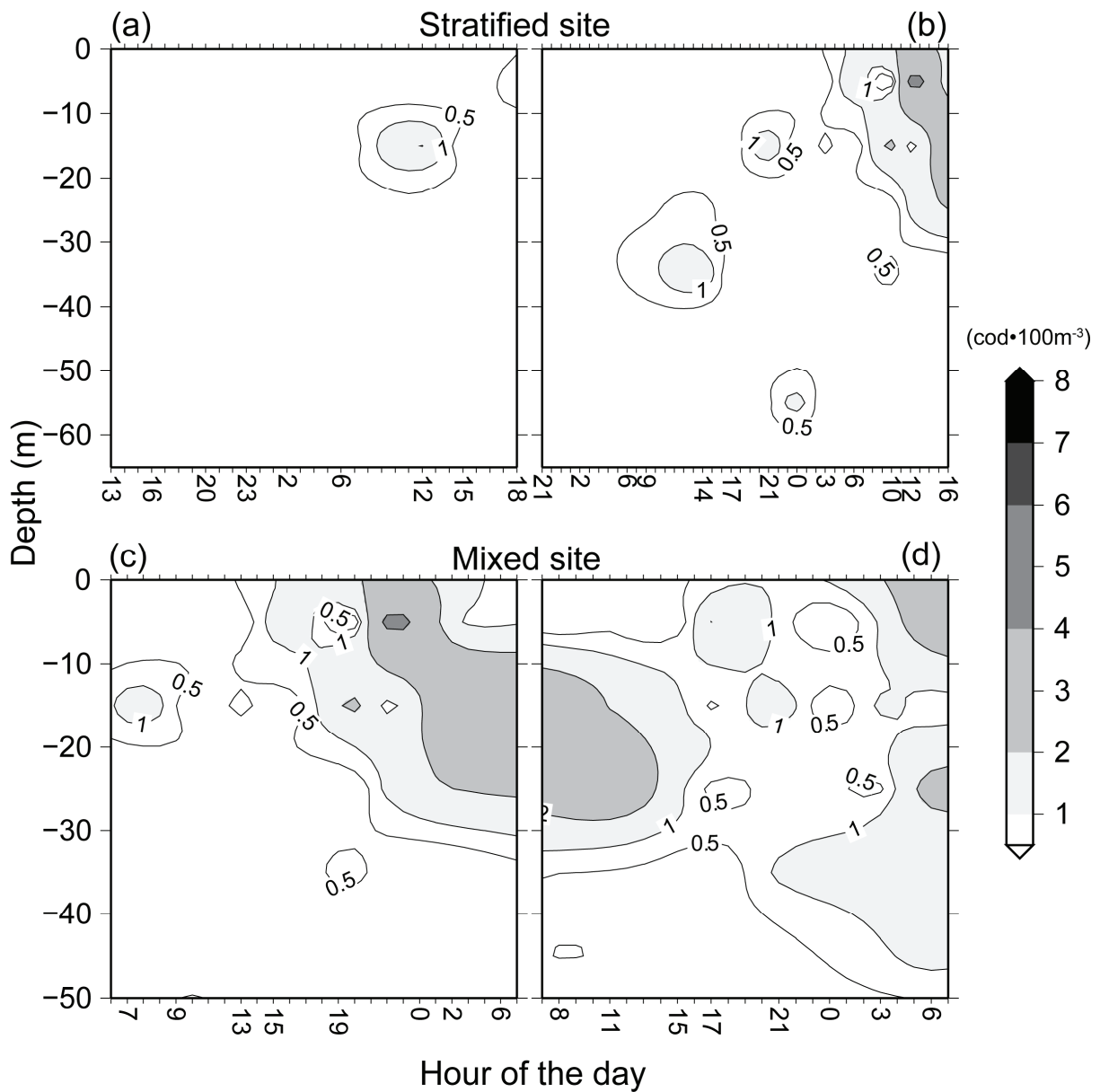
Figure 7 Distribution of larval cod and haddock (2-5-mm) at stratified (a, b) and mixed (c, d) sites during May 1993 (a, c) and 1994 (b, d). The x-axis indicate hour of the day and each label denotes one sampling station. The mixed sampling site on Georges Bank was 50-m deep, while the stratified locations were located along the flank of the Bank at depths > 70-m.
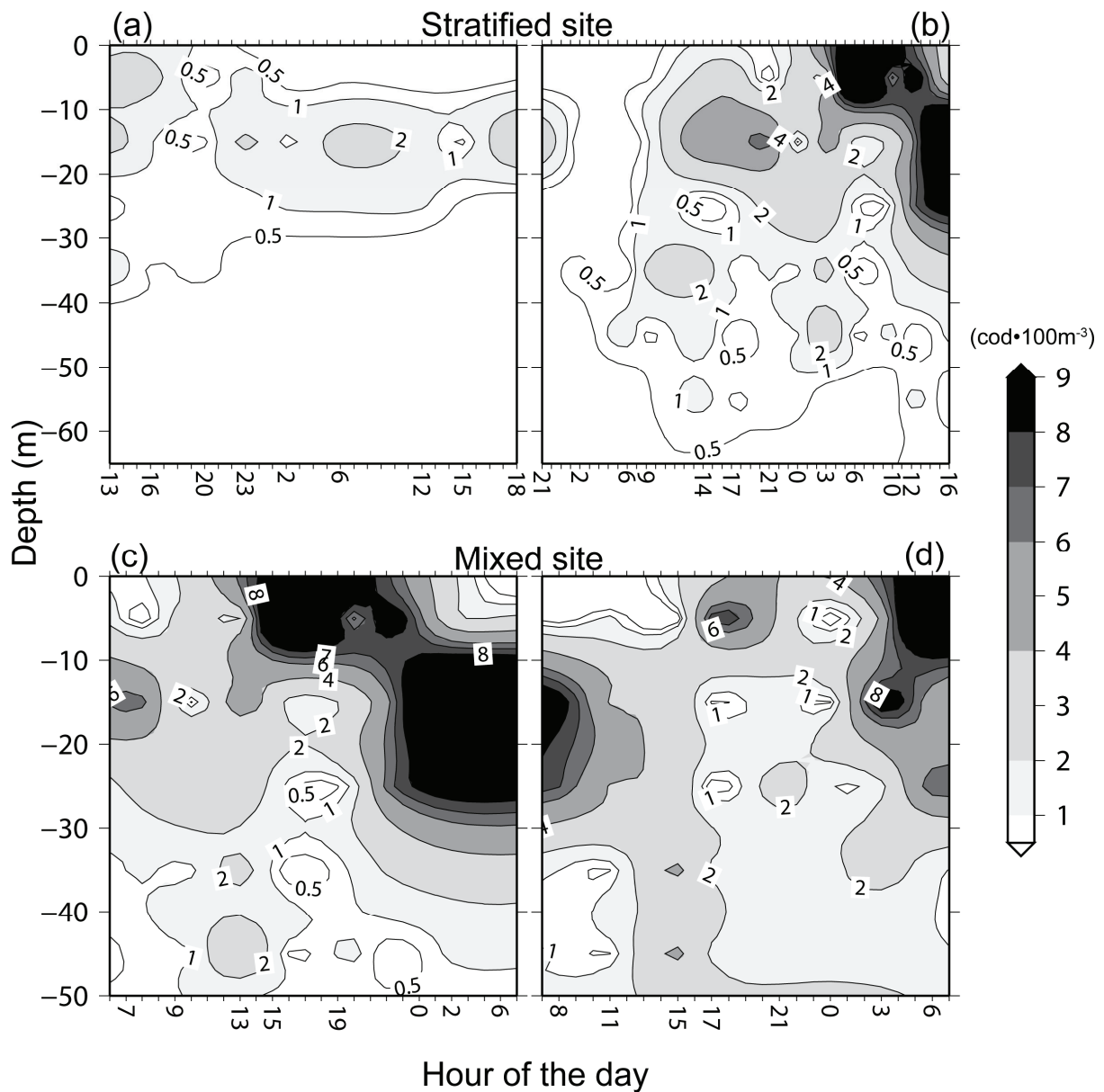
Figure 8 Distribution of larval cod and haddock (6-8-mm) at stratified (a, b) and mixed (c, d) sites during May 1993 (a, c) and 1994 (b, d). The x-axis indicate hour of the day and each label denotes one sampling station. The mixed sampling site on Georges Bank was 50-m deep, while the stratified locations were located along the flank of the Bank at depths > 70-m.
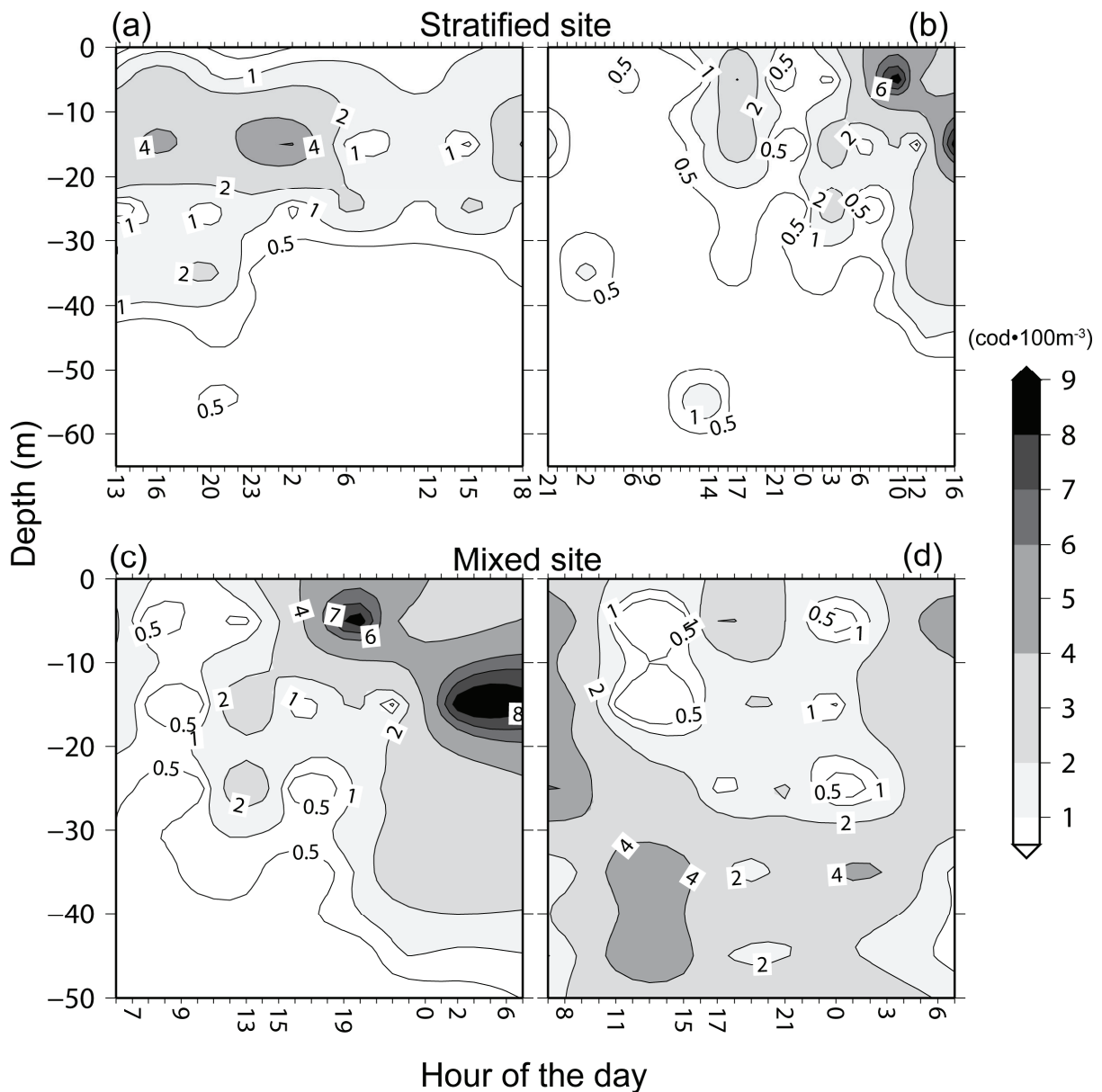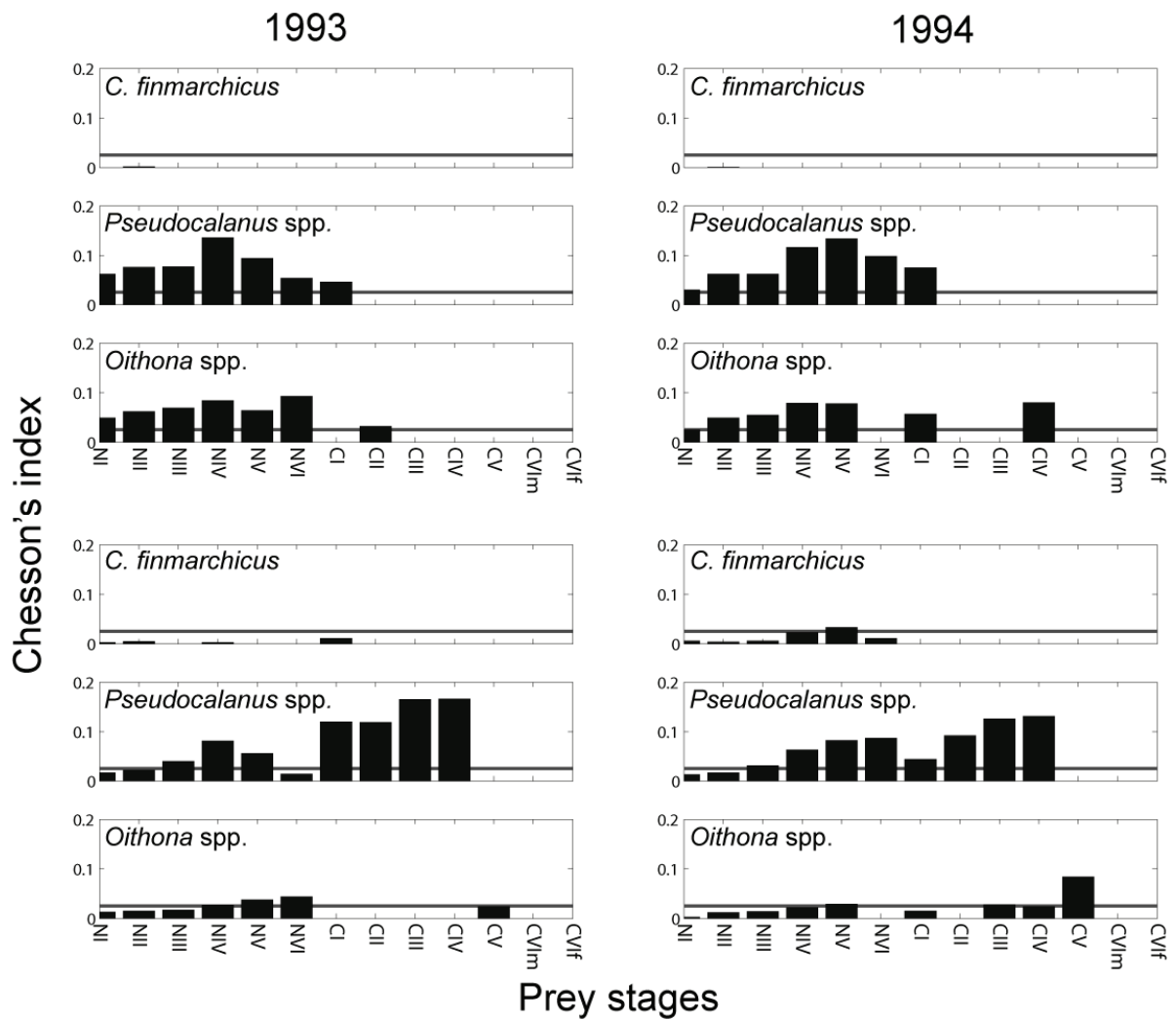
Figure 9 Distribution of larval cod and haddock (9-13-mm) at stratified (a, b) and mixed (c, d) sites during May 1993 (a, c) and 1994 (b, d). The x-axis indicate hour of the day and each label denotes one sampling station. The mixed sampling site on Georges Bank was 50-m deep, while the stratified locations were located along the flank of the Bank at depths > 70-m.
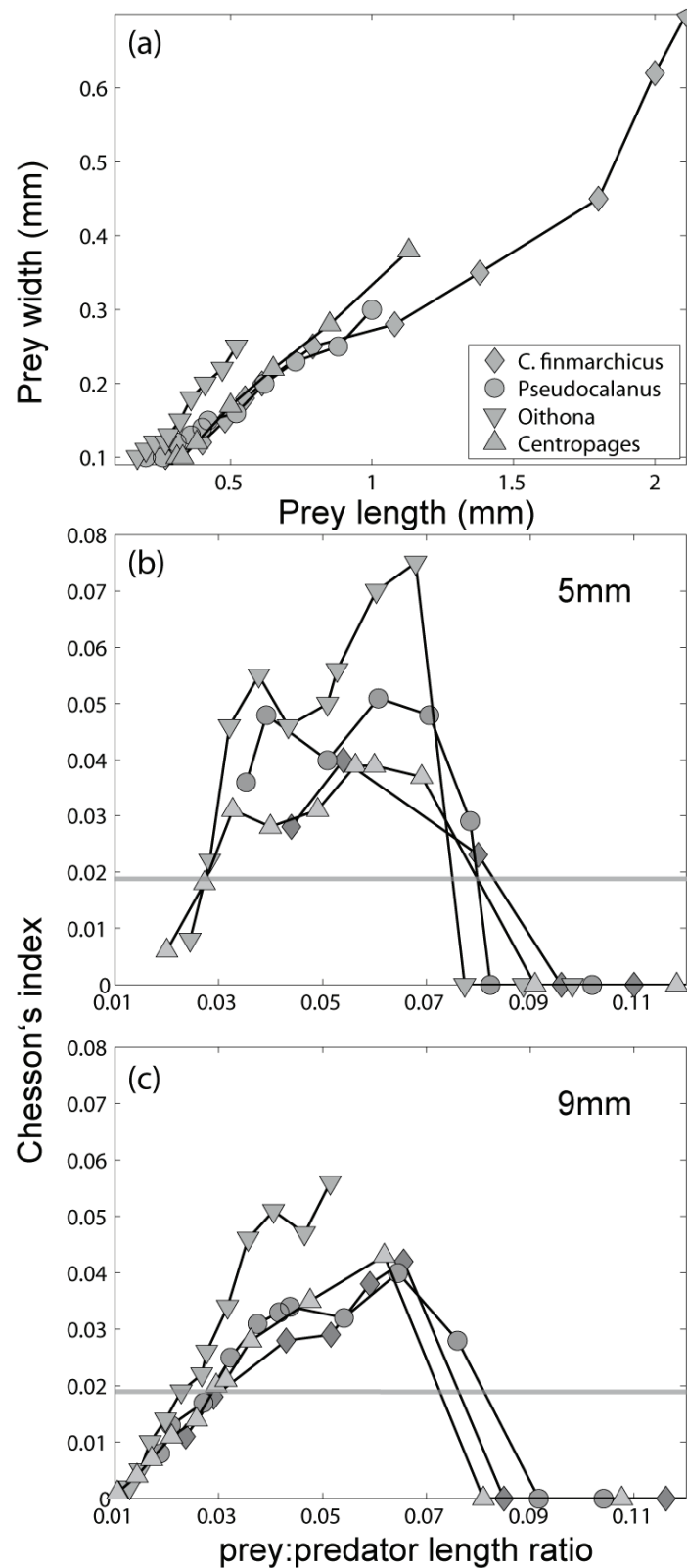
Figure 10 (a) Length and width of 13 developmental stages of *C. finmarchicus*, *Pseudocalanus*, *Oithona* and *Centropages* (Davis 1987). Using a mechanistic individual-based model we estimated average Chesson's prey preference index for all species and stages assuming constant and equal prey densities over 24·h for 100·ind. of 5-mm (b) and 9-mm (c) larval cod. Grey line (b, c) denote neutral selection.

Figure 11 Modeled average Chessons' prey preference index for 5 and 9-mm larval cod (100·ind.) in May 1993 (a, c) and May 1994 (b, d). Horizontal grey line denotes level of neutral selection ($\alpha_{neutral}=0.025$). Values above this line indicate a preference for these prey items as they are more frequently selected than they appear in the environment.

Figure 12 Modeled average Chessons' prey preference index for 5 and 9-mm larval cod (100·ind.) in May 1993 (a, c) and May 1994 (b, d) assuming *Centropages* is removed as available prey item. Horizontal grey line denotes level of neutral selection ($\alpha_{neutral}$=0.025). Values above this line indicate a preference for these prey items as they are more frequently selected than they appear in the environment.