Life history traits and spatiotemporal distributional patterns of copepod populations in the Gulf of Maine-Georges Bank region

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ABSTRACT: Life history traits play a significant role in determining the spatiotemporal distributional patterns of marine zooplankton, but biological–physical mechanisms controlling the population dynamics need to be further examined. In the present study, we used a coupled biological–physical model to examine the processes controlling the observed distributional patterns of 3 representative copepod populations in the Gulf of Maine-Georges Bank region including *Pseudocalanus* spp., *Centropages typicus* and *C. hamatus*. The model reveals that the shorter generation time of *Pseudocalanus* spp. at cold temperatures, together with their egg-carrying strategy, allows an earlier population development compared to *Centropages* spp. The model further reveals that predation mortality plays an important role in the decline of *Pseudocalanus* spp. in the warm season, and that the resting egg strategy is crucial for the persistence of the *C. hamatus* population in the Gulf of Maine-Georges Bank region. Analyses of observational data and model results suggest that temperature- and food-dependent egg production and development rates, temporally and spatially varying mortality rates and physical transport are important contributors to the formation of characteristic distributional patterns for the copepod populations in the system.

KEY WORDS: Life history traits · Modeling · Zooplankton · Copepod · Population dynamics

INTRODUCTION

Life history theory predicts that organisms develop different life history strategies to maximize their fitness in environments (Pianka 1976, Stearns 1976, 1989, Fiksen & Carlotti 1998). Thus, organisms have different life history traits as a result of trade-offs among reproduction, growth and survival (Stearns 1989, Roff 1992) under environmental conditions that differ in resource availability, predation pressure and spatiotemporal variation in physical/chemical factors (e.g. temperature, salinity, oxygen, etc). As far as reproductive strategy is concerned, the classic *r/K*-selection theory (MacArthur & Wilson 1967, Pianka 1970) has often

been used to categorize different organisms: *r*-strategists (also called opportunistic species) are characterized by high fecundity, high mortality rates, small body size, small generation time and high dispersion possibility; whereas *K*-strategists usually have the opposite characteristics. Species that are *r*-strategists are usually dominant in highly disturbed and/or stressed environments, and *K*-strategists are typically dominant in stable environments. Most organisms fall between the 2 ends of the *r/K* continuum and can be categorized based on whether they have more elements of *r*- versus *K*-strategy.

Copepods in the Gulf of Maine-Georges Bank (GoM-GB) region (Fig. 1), as in many other coastal/ shelf sys-
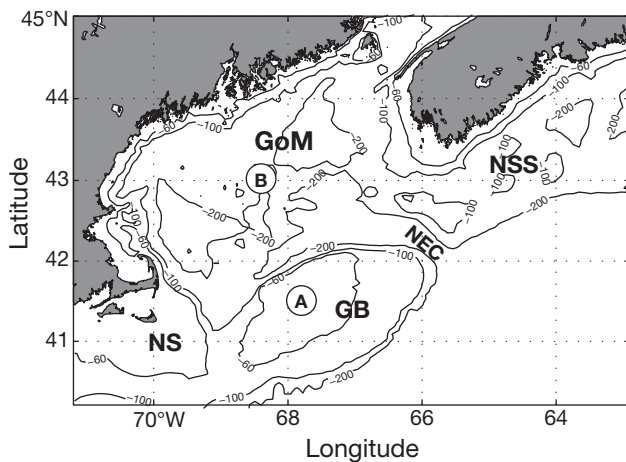
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Fig. 1. Bathymetry map. GoM: Gulf of Maine; GB: Georges Bank; NSS: Nova Scotian Shelf; NEC: Northeast Channel; NS: Nantucket Shoals; Stns A and B are locations for plotting the time series data on the crest of GB and in the central GoM, respectively. Relatively cold and low salinity water enters the GoM from the NSS at the surface, while warmer and more saline slope water enters the GoM along the bottom through the NEC. These 2 water masses progressively mix as they move in a general counterclockwise pattern around the GoM before they turn clockwise around GB and continue southwestward

tems, have different life history strategies (especially in terms of reproduction) that maintain their local populations. Some species, such as *Pseudocalanus* spp. and *Oithona* spp., carry their eggs in egg sacs attached to the adult females (egg-carrying strategy), while other species, such as *Calanus finmarchicus* and *Centropages* spp., utilize a free spawning strategy (also called broadcasting). Further species, including *Centropages hamatus* and *Temora longicornis*, have a resting-egg strategy that allows the population to survive during unfavorable environmental conditions. These life history traits, interacting with surrounding environmental conditions, might be responsible for the characteristic spatiotemporal distributional patterns exhibited by copepod populations in the GoM-GB region (e.g. Davis 1987b, Durbin & Casas 2006). In the next section, we will demonstrate this concept by comparing and contrasting the distributional patterns of 3 representative copepod species in this region, *Pseudocalanus* spp. (egg-carrying), *Centropages typicus* (broadcasting) and *Centropages hamatus* (resting-egg), using climatological data collected in this region.

It is important to be aware that in many cases the relationships between the distributional patterns of copepod populations and their life history characteristics are derived from empirical analysis (e.g. correlative analysis of field data), and a good understanding of many aspects of population dynamics remains elusive. One of the key questions is: What is the relative

importance of life history traits versus environmental factors in determining spatiotemporal distribution patterns? This question can be broken down further: (1) How sensitive are the distribution patterns to changes in life history traits? (2) How does physical transport or circulation pattern affect population distribution and persistence? and (3) What kind of different distributional patterns can be generated by copepod species with different life history traits but under the same physical regime? Due to the strong non-linearity of multiple biological–physical interactions in the GoM-GB region, empirical analyses of observational data alone are not sufficient. Therefore, in addition to analyses of observational data, we also applied a 3D coupled biological–physical model to address the above questions and to provide insights into possible responses of copepod populations in this region to local and remote environmental changes. Specifically, the present study focused on the following 4 questions: (Q1) What controls the seasonal cycle and spatial gradients of the *Pseudocalanus* spp. population in the GoM-GB region? (Q2) How does the change in temperature-dependent development rate affect the seasonal cycle and persistence of the copepod populations? (Q3) What is the effect of reproductive strategy (egg-carrying vs broadcasting) on the growth rate and spatial distribution of the copepod populations? (Q4) How important is the resting-egg strategy for the generation and maintenance of the *Centropages hamatus* population on GB?

Distributional patterns of copepod populations

A considerable amount of zooplankton data has been accumulated for the GoM-GB region since the 1930s. Here the analyses are based primarily on bimonthly survey data collected in the Marine Monitoring Assessment and Prediction (MARMAP, 1977 to 1987) and the subsequent Ecosystem Monitoring (EcoMon, 1988 to present) programs (see Sherman 1980, Meise & O'Reilly 1996 for program details and survey protocols, and Kane 2007 for an analysis of the combined MARMAP and EcoMon data). The climatology of bimonthly distribution for *Pseudocalanus* spp., *Centropages typicus* and *C. hamatus* adults were generated by averaging the abundance of adult populations from 1977 to 2006. Specifically, the observation data collected from each year's survey were binned into 2 mo periods and linearly interpolated into a regular grid; the arithmetic means were then computed using the gridded data to represent the climatology. Other copepod distribution patterns derived from historical data (e.g. Davis 1987b) and more recent US GLOBEC Georges Bank program data (monthly surveys from

January to June 1995 to 1999, details in Durbin & Casas 2006) were also used as auxiliary information.

Observational data have shown that copepod populations in the GoM-GB region exhibit characteristic distributional patterns, due in some way to their unique life history traits interacting with surrounding environmental conditions, including the temperature- and food-dependent egg production and development/growth rates, temporally and spatially varying mortality rates caused by predation and/or starvation and the interaction between physical transport and biological behaviors. In the following paragraphs, we describe the system-wide distributional patterns of 3 representative copepod species and the presumed life history traits and environment factors that control the generation of these patterns.

Pseudocalanus in the GB-GoM region features mainly 2 sibling species, *P. moultoni* and *P. newmani* (Frost 1989, Bucklin et al. 1998, 2001). The abundance of adult populations (pooled species) shows a clear seasonal variation on GB and in most of the GoM region (Fig. 2) with large spring populations, but much lower abundance in the warm-water environment (>10 to 12°C) during later summer and fall. Spatially, the abundance of *Pseudocalanus* spp. is higher in shallower areas (<100 m) with a peak on the GB crest in May–June. The distributional pattern for the abundance of nauplii or copepodite stages is less clear due to the lack of data in MARMAP and EcoMon (which collected only individuals retained in the 330 µm mesh), but a similar spatial and temporal pattern is
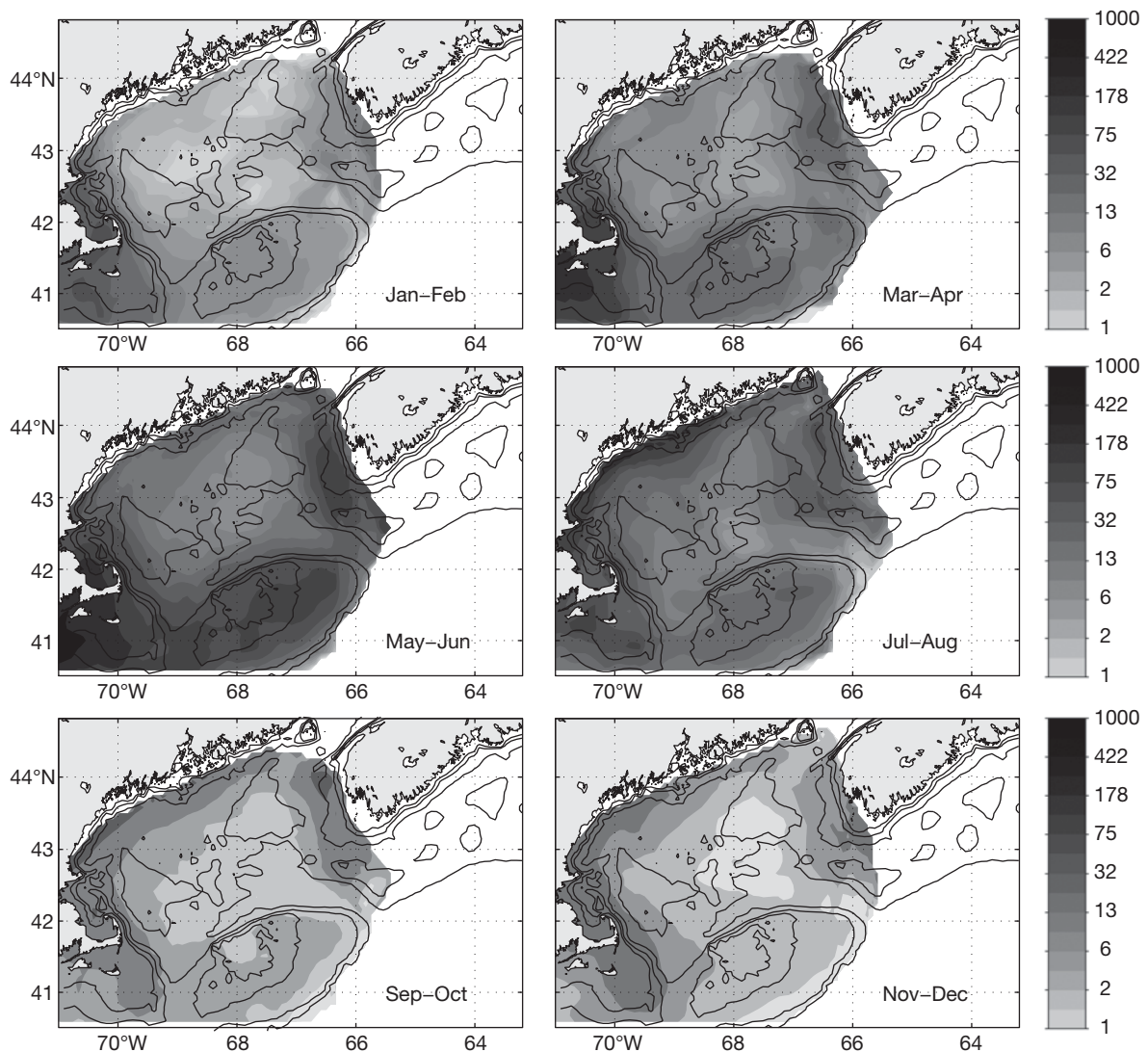

Fig. 2. *Pseudocalanus* spp. Bimonthly climatology for the distribution of adult abundance (vertically averaged; no. m^{-3}) in the Gulf of Maine-Georges Bank region

expected (inferred from the pump data on GB described by Durbin & Casas 2006).

Compared to the *Pseudocalanus* spp., *Centropages typicus* has a very different distributional pattern (Fig. 3). It is a characteristic warm-water species, with peak abundance occurring in September–October and much lower abundance in winter and spring months (from January to June). Spatially, it has high abundance on GB and around the coastal GoM region during the warm half of the year, with high abundance extending into the interior of the GoM and not restricted to the shoaler areas like *Pseudocalanus*. The abundance near the southwest coast appears to be slightly higher than that in the northeast (upstream region) in all seasons. This feature is less apparent

from the plots in Fig. 3, but may be well established due to the fact that the southward increase of surface water temperature favors the population growth of *C. typicus* (as a warm-water species) in the southwest.

Centropages hamatus, on the other hand, has a markedly different distributional pattern compared to its congener *C. typicus*. For most of the year it has a very well-defined adult population on the crest of GB and near Nantucket Shoals (Fig. 4), matching the patterns described by Davis (1987b) and Sherman et al. (1987). Only during the peak months (July and August) does the population appear to have a relatively wider spatial distribution, extending beyond the edge of GB into adjacent GoM waters (note log scale). The population is almost undetectable in the northeastern GoM
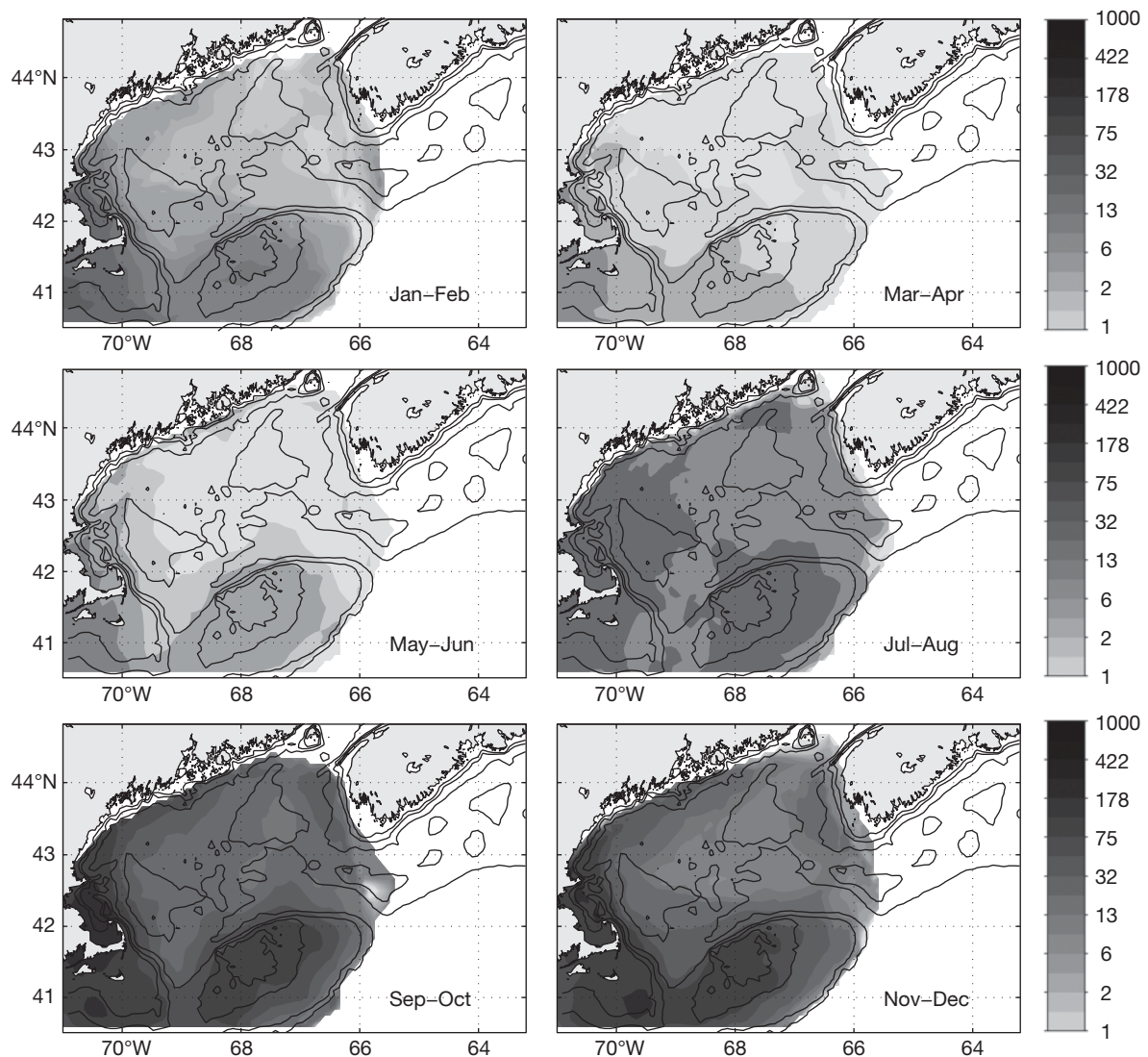

Fig. 3. *Centropages typicus*. Bimonthly climatology for the distribution of adult abundance (vertically averaged, no. m^{-3}) in the Gulf of Maine-Georges Bank region
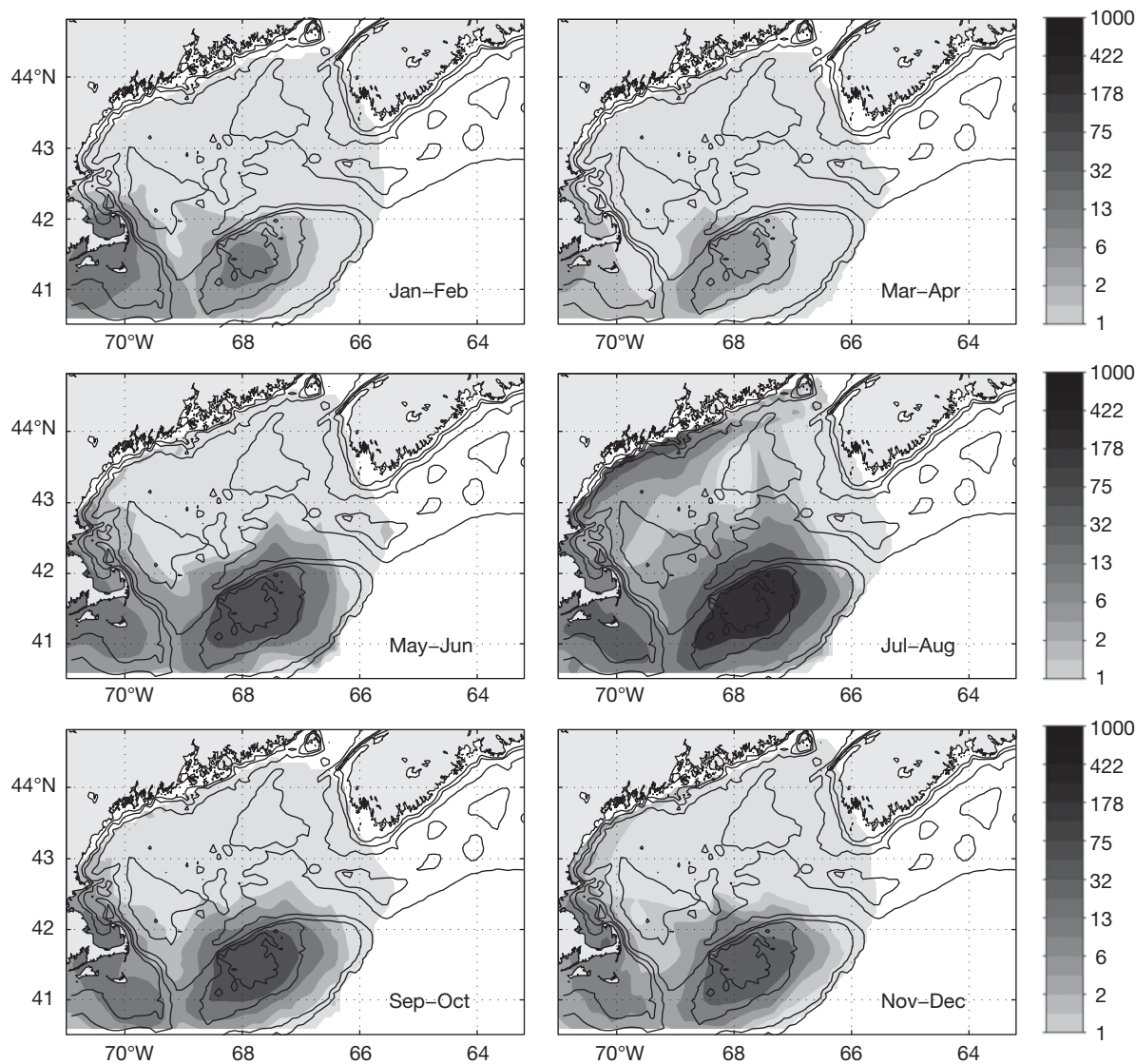
Fig. 4. *Centropages hamatus*. Bimonthly climatology for the distribution of adult abundance (vertically averaged, no. m^{-3}) in the Gulf of Maine-Georges Bank region

throughout the year, indicating a limited capability of the population to intrude into upstream regions, which also means that there is no obvious upstream supply for the local population.

It is likely that certain life history characteristics contribute significantly to the formation of the above-described distributional patterns. The cold-water species, *Pseudocalanus* spp., have increasingly shorter life-stage durations than the other 2 species for egg, nauplii and copepodite stages as the temperature drops below 10°C (Fig. 5a–c; detailed parameter values and their sources are listed in Table 1). At 5°C, the total duration of copepodite stages for *Pseudocalanus* spp. is only a little more than half that of *Centropages typicus* and *C. hamatus*. This observation might par-

tially explain why *Pseudocalanus* spp. peak in spring whereas *Centropages* spp. peak in summer and fall. When the temperature is above 10°C, the 3 species have a very similar development rate. Thus the development of *Pseudocalanus* spp. is less sensitive to temperature variation than the other 2 species, and temperature-dependent development alone cannot explain the decline of *Pseudocalanus* spp. in late summer. Other factors, including the reproduction and mortality rates, must play more important roles. These factors will be examined in the numerical experiments below.

From the plot of egg production rates (EPR) at different temperatures (Fig. 5d; detailed parameter values and their sources are listed in Table 2), *Centropages*
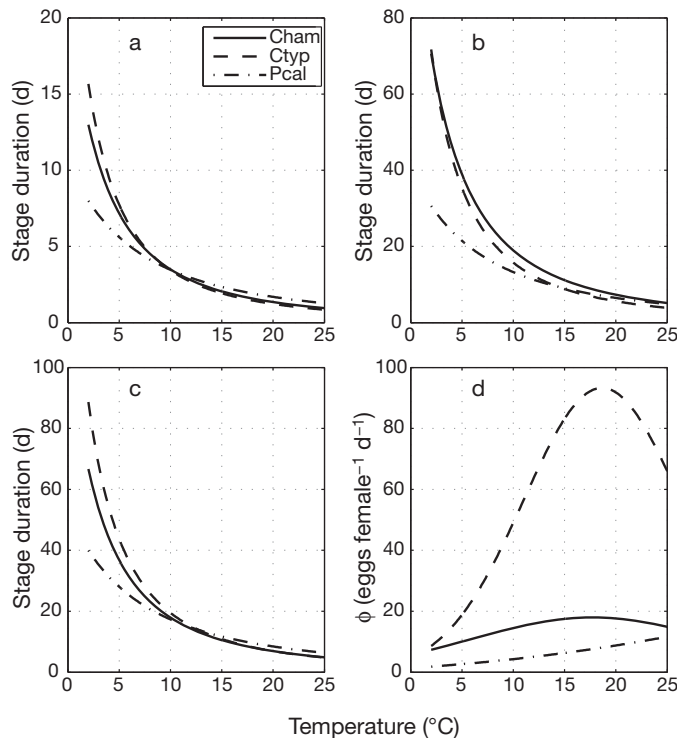
Fig. 5. *Pseudocalanus* spp. (Pcal), *Centropages typicus* (Ctyp) and *C. hamatus* (Cham). Temperature-dependent stage duration and egg production rate (φ) of 3 species. (a,b,c) Bêlehrádek curves for temperature-dependent stage duration for egg, nauplii and copepodite stages, respectively. (d) Egg production rate as a function of temperature. Parameters are listed in Tables 1 & 2

Table 1. *Pseudocalanus* spp., *Centropages typicus* and *C. hamatus*. Bêlehrádek parameters for Eq. (7)

Species	a_1	a_2	a_3	α	β
Pseudocalanus spp.[a]	2312.0	8861.0	11560.0	13.87	−2.05
C. typicus[b]	921.8	4221.6	5217.4	5.3	−2.05
C. hamatus[c]	1148.0	6237.0	5894.0	6.9	−2.05

[a]Davis (1984b)
[b]a_1 is from Carlotti et al. (2007); all others are derived from Fryd et al. (1991)
[c]a_1 is from Halsband-Lenk et al. (2002); all the others derived from Fryd et al. (1991)

typicus is much more productive across the entire temperature range, and its EPR may be more sensitive to the change in temperature than the other 2 species. This feature is typical for broadcasters (Hirche 1992) and is likely to be the reason for the population peaking during summer and fall seasons. On the other hand, *C. hamatus* also employs a broadcasting strategy, yet its EPR may be lower, based on limited experimental data (Halsband-Lenk et al. 2002). However, this low EPR may be a seasonal effect, as *C. hamatus*

used in these experiments were collected in late summer when fecundity is lower than during peak spawning season (Halsband & Hirche 2001, Halsband-Lenk et al. 2004). Nonetheless, additional strategies, such as the production of resting eggs, may be needed for this population to persist in a highly advective and diffusive system. These strategies will be further explored in the following numerical experiments.

NUMERICAL MODEL

To examine the interaction between copepod life history characteristics and the physical and biological environment, we used a 3-dimensional (3D) high-resolution biological–physical coupled model. The system includes a hydrodynamics model — the finite-volume coastal ocean model (FVCOM) — along with a 4-compartment (nitrogen-phytoplankton-microzooplankton-detritus, NPZD) lower food web model (to supply food for the copepod species) and a 4-stage (mean-age) concentration-based copepod population dynamics model (Hu et al. 2008). The general modeling framework is shown in Fig. 6 and the FVCOM model grid is shown in Fig. 7. Here we present a brief summary of FVCOM and NPZD coupling (details in Ji et al. 2008a), along with a detailed description of the copepod population dynamics model.

The physical modeling system consists of (1) a nested regional community atmospheric mesoscale model (MM5) that provides surface wind stress and heat flux for the ocean model and (2) an ocean model (FVCOM) driven by realistic surface and boundary forcing with assimilation of satellite/buoy data. The system is designed with a flexible modular structure, such that many third-party model components and data assimilation modules can be easily incorporated (see http://fvcom.smast.umassd.edu for a complete list of modules and functions that have been implemented). The integrated model system can also run with idealized forcing and boundary conditions to investigate specific processes. As the central component of the modeling system, FVCOM is a prognostic, unstructured-grid, finite-volume, free-surface, 3D, primitive equation coastal ocean circulation model (Chen et al. 2003, 2007). The model is solved numerically by a second-order accurate discrete flux calculation of the integral form of the governing equations over an unstructured triangular grid.

The NPZD model coupled with FVCOM contains key aspects of lower trophic-level food web dynamics and is used to provide a food source for the modeled

Table 2. *Pseudocalanus* spp., *Centropages typicus* and *C. hamatus*. Egg production rate (ϕ, no. eggs female^{-1} d^{-1}) as a function of temperature (T, °C)

Species	Function
Pseudocalanus spp.[a]	$\phi = 0.00641 \times (T+13.87)^{2.05}$
C. typicus[b]	$\phi = 93.3 \times \exp\left(-\dfrac{(T+18.65)^2}{2 \times 7.63^2}\right)$
C. hamatus[b]	$\phi = 18.0 \times \exp\left(-\dfrac{(T+17.73)^2}{2 \times 11.78^2}\right)$

[a]Davis (1984b)
[b]Based on Halsband-Lenk et al. (2002) for Gaussian fit, but double the value of ϕ to reconcile much higher egg production rates reported elsewhere (e.g. Bonnet et al. 2007)
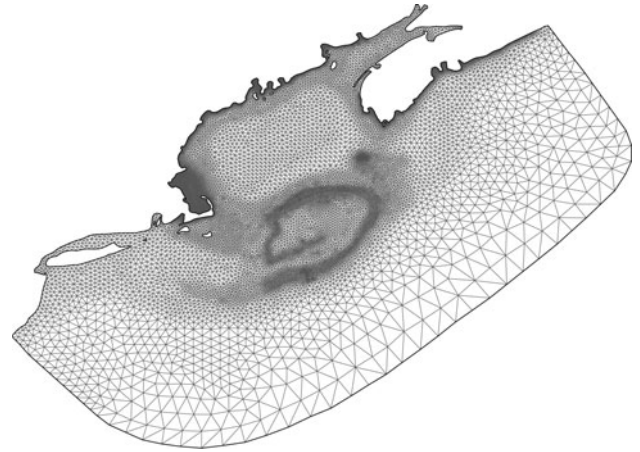

Fig. 7. The finite-volume coastal ocean model (FVCOM) model grid

copepod species. The coupled FVCOM-NPZD model proves to be capable of capturing major seasonal and 3D spatial distributions of nutrient and phytoplankton dynamics across the GoM-GB region as a function of local and remote forcing (Ji et al. 2008a,b). In addition, the simplicity of this biological model allows us to examine the response of the food web to different forcing while avoiding large uncertainties in the model parameterization.

A 4-stage (egg-nauplii-copepodite-adult, ENCA) mean-age model (Hu et al. 2008) is used to simulate the
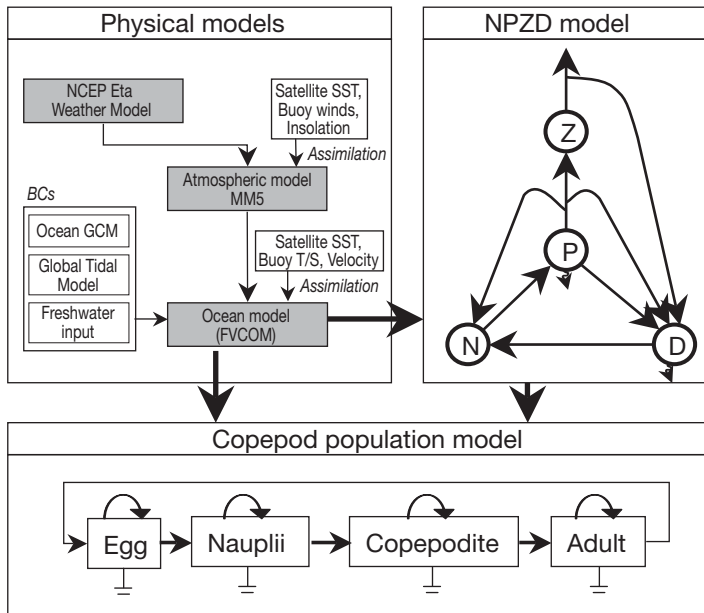

Fig. 6. Schematic diagram of the biological–physical coupled modeling system. NPZD: nitrogen–phytoplankton–microzooplankton–detritus model; MM5: Fifth-Generation NCAR/ Penn State Mesoscale Model; GCM: general circulation model; FVCOM: finite-volume coastal ocean model; BC: boundary condition; SST: sea surface temperature; T/S: temperature/salinity

copepod population dynamics. This model has been tested in a 0-dimension configuration (spatially non-explicit, time varying only), and it effectively removes the numerical diffusion problem, a problem caused by insufficient resolution of the population structure on time scales of the temporal forcing, leading to artificially short generation times (Davis 1984a), and reproduces observed median development times (MDTs) without the need for a high-resolution age-stage structure. Thus it is well suited for finding solutions of concentration-based zooplankton models in complex biological–physical models. The basic concept of this modeling approach coincides with the mean individual mass approach used for modeling *Pseudocalanus elongates* in the North Sea (Fennel 2001, Moll & Stegert 2007, Stegert et al. 2007).

For copepods in a given life-stage (i), the abundance (C_i) and mean age (A_i) at each model grid point is denoted by:

$$[C_i, A_i],\ i = 1{:}N \tag{1}$$

where N is the total number of stages and equals 4 for the 4-stage mean-age model. C_i can be scaled to a dimensionless value C_i^* by normalizing C_i to an arbitrary value (in the present study, the mean initial abundance of the adult population on the crest of GB was chosen) to make the model more generic for different copepod species (we omit the $*$ in the equations below). The governing advection-diffusion-reaction equations can be written as follows:

$$\frac{\partial C_i}{\partial t} = \psi_{C_i} - \vec{v} \cdot \nabla C_i + \nabla \cdot (K \nabla C_i) \tag{2}$$

$$\frac{\partial (A_i C_i)}{\partial t} = \psi_{A_i C_i} - \vec{v} \cdot \nabla (A_i C_i) + \nabla \cdot (K \nabla (A_i C_i)) \tag{3}$$

where ψ_{C_i} and $\psi_{A_iC_i}$ are the biological source/sink terms for the change of abundance and total mean age (A_iC_i) for stage i, respectively. The term ψ_{C_i} can be computed using:

$$\psi_{C_i} = \begin{cases} \phi C_N - (\mu_i + m_i)C_i, & i = 1 \\ \mu_{i-1}C_{i-1} - (\mu_i + m_i)C_i, & 1 < i < N \\ \mu_{i-1}C_{i-1} - m_iC_i, & i = N \end{cases} \quad (4)$$

where ϕ, μ_i and m_i are EPR, molting and mortality rates at stage i, respectively. The derivation of these variables will be discussed below. The change of total mean age, $\psi_{A_iC_i}$, is a function of the changes in A_i and C_i. For the individuals newly molted into the stage i, the age is set to 0. Therefore, $\psi_{A_iC_i}$ can be calculated as:

$$\psi_{A_iC_i} = [1 - (\mu_i + m_i)A_i]C_i \quad (5)$$

The molting rate, μ_i, can be estimated based on the observed molting probability function of the original population at time t, $f_o(t)$ (Hu et al. 2008), in the following form:

$$\mu = \begin{cases} \dfrac{f_o(t)}{\left(1 - \int_{-\infty}^{1} f_o(x)\mathrm{d}x\right)}, & i < N \\ 0, & i = N \end{cases} \quad (6)$$

Typically, $f_o(t)$ has an asymmetric distribution that can be described as a log-normal or gamma distribution, but a normal distribution or a piece-wise linear function will produce very similar results (Hu et al. 2008). In the present study, a trapezoid-shape piece-wise linear function is used for $f_o(t)$ (Fig. 8), which is a function of mean stage duration at each stage i (MSD_i).

MSD_i has a Bêlehrádek-type temperature-dependency as shown in the following:

$$MSD_i = a_i(T + \alpha)^\beta \quad (7)$$

where a_i is a stage-dependent parameter, T is temperature and α and β are constants determined by empirical fitting (see Table 1 for parameter values used for different species).

The model sets the reproduction rate (ϕ) to be both temperature- and food-dependent. The temperature dependency is in Bêlehrádek form for *Pseudocalanus* spp. (Davis 1984b) and has Gaussian fits for *Centropages* spp. (see Fig. 5d) based on observation data (see Table 2). The Bêlehrádek parameter values used in Davis (1984a) for *Pseudocalanus* fall between those found for *P. newmanii* and *P. moultoni* (McLaren et al. 1989b) and represent a reasonable approximation for *Pseudocalanus*

spp. For food dependency, a Holling Type-III form is used, with different half saturation constants for *Pseudocalanus* (1.0 µg chl *a* l^{-1}) and *Centropages* (1.5 µg chl *a* l^{-1}), reflecting different degrees of food limitation on egg production rates (Jonasdottir 1989, Davis & Alatalo 1992). The parameter values used for *Pseudocalanus* approximate laboratory data for *P. moultoni* and *P. newmani* (Jonasdottir 1989).

Mortality rate is very difficult to measure in the field, given the fact that there are significant spatial and temporal variations in predator distribution and varying sources of predators for copepods at different stages. Many attempts have been made to assess mortality rates using different approaches, including life tables (e.g. Aksnes & Ohman 1996, Ohman et al. 2002) and adjoint data assimilation (McGillicuddy et al. 1998). Yet these estimates are most likely space- and time-specific and should not be used for different regions and/or seasons. In the present study, we made no attempt to simulate the detailed variation of mortality rate in space and time, due to the lack of predator information. Instead, we used a simple temperature-dependent function to reflect that: (1) predators have higher predation rate as temperature increases, (2) predator abundance increases in warm seasons (e.g. Sullivan & Meise 1996), and (3) visual predators exert higher predation pressure on prey in warm seasons due to the increase in daylight length. The following Q_{10} relationship is used in our model for this purpose:

$$m_i = m_i^b Q_{10}^{[(T - T_b)/10]} \quad (8)$$

where m_i^b is a stage-dependent mortality rate at base temperature (5°C). For *Pseudocalanus* spp., m_i^b is set to 0.03, 0.045, 0.02 and 0.03 ($i = 1:4$); whereas for *Centropages* spp., only the value of m_i^b is increased to 0.15 to represent a higher egg mortality rate for broadcasters. Due to the uncertainty in mortality rate, the sensi-
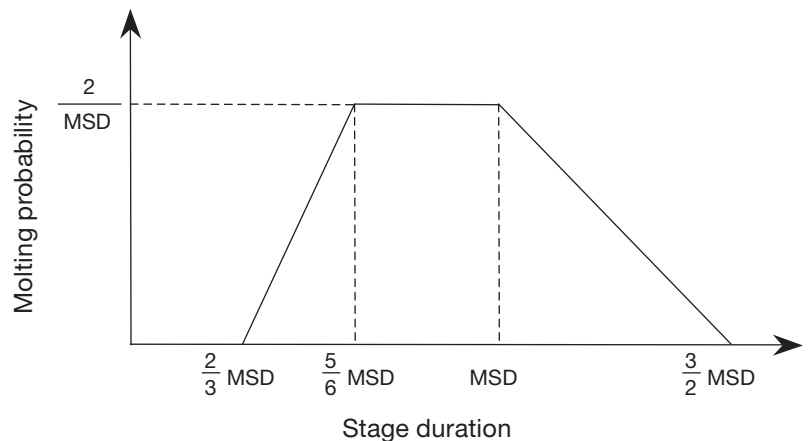

Fig. 8. Model-specified molting probability of the original population as a function of mean stage duration (MSD)

tivity of the model results to the parameters in Eq. (8) was examined in the numerical experiments and will be discussed in the 'Discussion' with regard to the factors affecting the seasonality of copepod populations.

The general modeling strategy is to use a process-oriented modeling approach rather than realistic simulations. We start the numerical experiments with the base model run for *Pseudocalanus* spp. to obtain reasonable temporal and seasonal distributional patterns, and then modify the vital rates to model other species and examine the consequent changes in population dynamics and distributional patterns. The case name and vital rate configuration is listed in Table 3, with each model run to address the first 3 questions (Q1–Q3) listed in the 'Introduction' (Q4 is addressed separately in 'Model runs and results'). We set the initial copepod concentration based on the observed December climatological distribution pattern, with high and low concentrations in shallower and deep regions, respectively. For the hydrodynamic model, December monthly averaged climatological temperature and salinity fields (retrieved from the National Oceanographic Data Center [NODC] Ocean Climatology database) were used as initial conditions, and the model was integrated over 1 yr using surface (heat and wind) and boundary forcing in 1999 (represents typical forcing condition in the 1990s). This baseline hydrodynamics model run is the same as the baseline run presented in Ji et al. (2008b).

MODEL RUNS AND RESULTS

Water temperature is a key environmental factor that directly affects the growth and development of copepods with varying degrees of intensity. The model-computed sea surface temperature (SST) (Fig. 9) has a strong annual signal across the Nova Scotian Shelf (NSS) and GoM-GB region, with the lowest bimonthly mean temperatures in March–April and highest in July–August (range of 0 to 20°C). Temperature in the NSS region is on average lower than the central GoM, especially during the winter season when cold, low-salinity water inflow reaches its maximum (Smith 1989). The SST near the coast is lower than that in the

offshore region, most likely due to the influence of the coastal current that carries colder water from the NSS as well as stronger nearshore mixing that prevents the formation of warm surface layer as in the deep region.

Another important factor affecting copepod population dynamics is the food availability. Here the model-computed chl *a* distribution (Fig. 10) can be considered as a proxy of food availability for copepods, with an understanding that species like *Centropages typicus* and *C. hamatus* are omnivores (Conley & Turner 1985, Calbet et al. 2007). In other words, the chl *a* concentration serves as an index of overall food concentration including phytoplankton, microzooplankton and other possible food sources. Copepod egg production has been shown to be strongly associated with field chlorophyll levels (e.g. Davis & Alatalo 1992, Kiørboe & Nielsen 1994). The model produces the basic seasonal and spatial patterns of phytoplankton distribution in the NSS and GoM-GB region, featured by a strong spring phytoplankton bloom in March–April and a relatively weak autumn phytoplankton bloom (Fig. 10). The phytoplankton concentrations on GB and around Nantucket Shoals are generally higher than in the rest of the system throughout the year. Other features like the formation of the subsurface chl *a* maximum in stratified seasons are also reproduced. Our previous papers (Ji et al. 2008a,b) show that the model captures the general patterns reasonably well, based on comparisons with both SeaWiFS and water sample data, thus providing a good first-order approximation of food availability for the copepod model.

The base model run for *Pseudocalanus* spp. produced a similar spatiotemporal distributional pattern (Fig. 11) as that observed in the climatology (Fig. 2). The adult population has a relatively higher concentration in the shallow coastal regions and on GB than in the central GoM region. The abundances of other stages (egg, nauplii and copepodite) have a similar spatial gradient. As observed in the field data, the modeled population size on GB increases from the beginning of the year, reaches its peak in the end of June and drops to a low level after August (Fig. 12a). The model also shows that the population goes through 3 to 4 generations before it reaches the peak abundance in summer. The seasonality of *Pseudo-*

Table 3. List of numerical experiments. Questions are specified at the end of the 'Introduction'. Species listed indicate the parameters used for that species as specified in Tables 1 & 2 and Eq. (8)

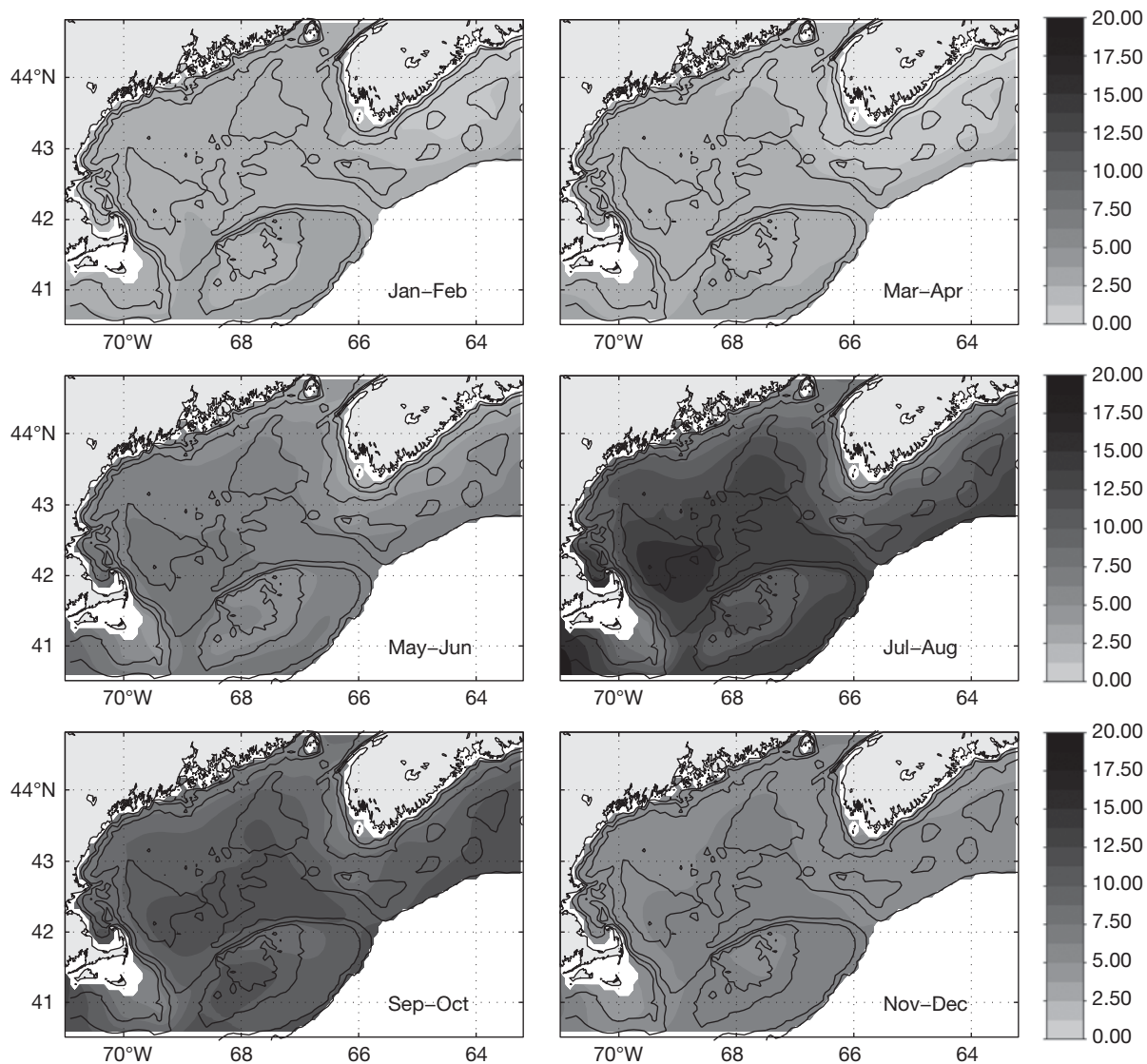| Runs	Questions	Bêlehrádek parameters	EPR parameters	Mortality parameters
Base	Q1	*Pseudocalanus* spp.	*Pseudocalanus* spp.	*Pseudocalanus* spp.
Case 1	Q2	*C. typicus*	*Pseudocalanus* spp.	*Pseudocalanus* spp.
Case 2	Q3	*C. typicus*	*C. typicus*	*Pseudocalanus* spp.
Case 3	Q3	*C. typicus*	*C. typicus*	*C. typicus*

Fig. 9. Model-computed bimonthly-averaged spatial distribution of sea surface temperature (SST, °C) in the Gulf of Maine-Georges Bank region

calanus is similar in the GB and central GoM regions, but the GB population has a slightly delayed abundance peak. The abundance in the deep central GoM is much lower than that in the shallow regions (Fig. 12b), with the peak abundance more than 1 order of magnitude lower than the peak on GB. It is difficult to validate the cohort structure shown in the model results with field data due to the coarse temporal resolution of zooplankton time series data (usually collected from monthly or bimonthly surveys).

For *Pseudocalanus* spp., a relatively rapid development rate in low temperature appears to be a key life history strategy for the population to develop and grow between winter and early summer. The effect of this life history trait was tested by replacing the Bêleh-

rádek parameter values of *Pseudocalanus* with those of *Centropages typicus* in the model (Case 1 in Table 3). The results clearly show that the population will not maintain itself either on GB or in the central GoM (Fig. 12c,d), even with a 10-fold increase of the initial population size. This result also suggests that, for warm-water species, the slower development rate in cold water is the major factor preventing the population from growing in cold seasons, even if they have the same reproductive strategy and were under the same predation pressure as the cold-water species.

For warm-water species like *Centropages typicus*, the model suggests the population size increases dramatically as the reproduction rate increases (without changing mortality parameter values, Case 2 in
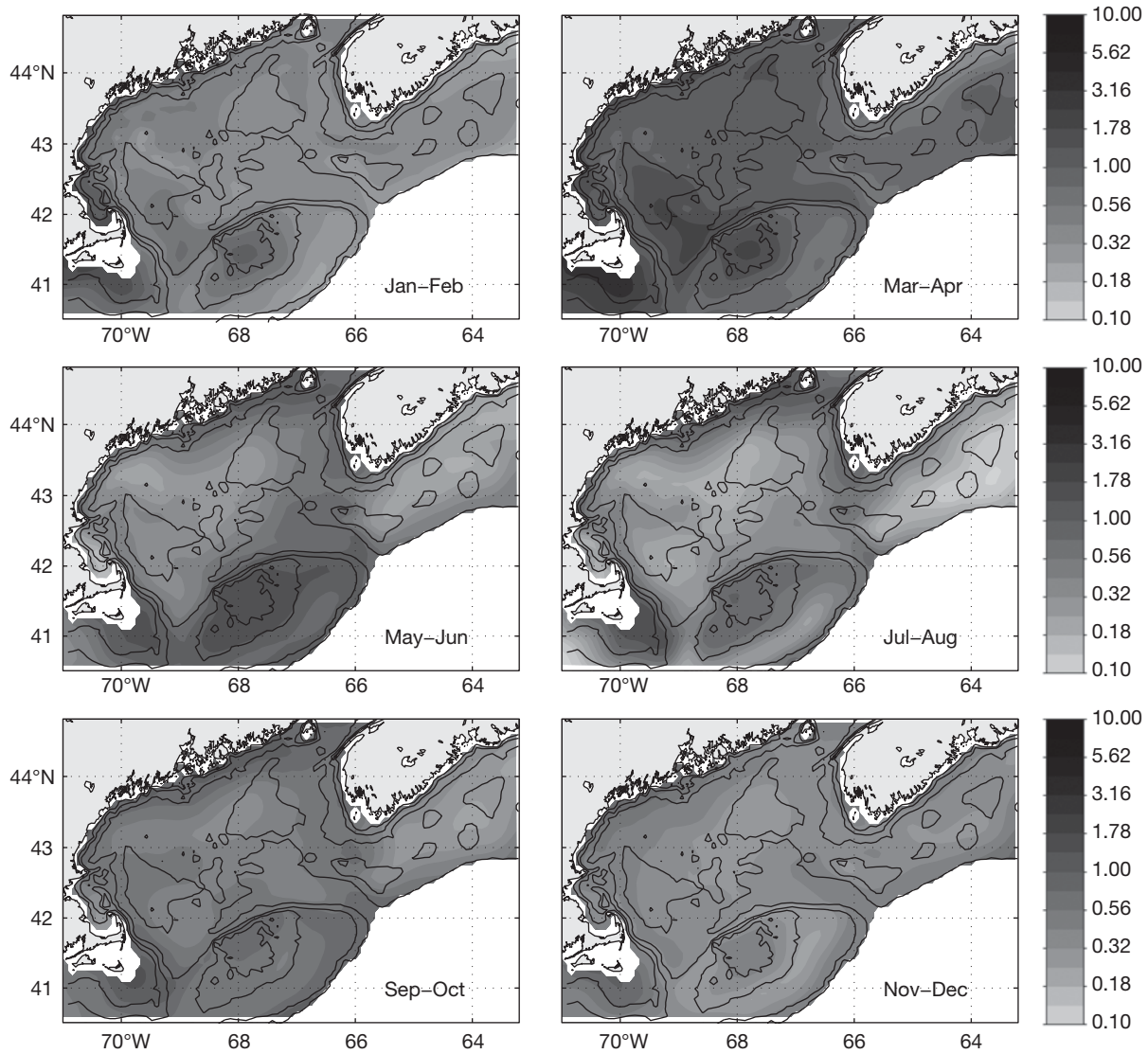
Fig. 10. Model-computed bimonthly-averaged spatial distribution of surface phytoplankton (µg chl *a* l^{-1}) in the Gulf of Maine-Georges Bank region

Table 3) and the peak occurs during fall months (Fig. 13a,b). Such an increase of nearly 3 orders of magnitude is unrealistic for *C. typicus*, as we have seen from the observation data. This population explosion has to do with the model configuration in which the mortality rates for all stages remain the same as *Pseudocalanus* spp. It is well known that the egg mortality rate could be 1 order of magnitude higher (Kiør-boe & Sabatini 1994) for broadcasters like *C. typicus* than egg-carriers like *Pseudocalanus* spp. By increasing the egg mortality rate from 0.03 to 0.15 d^{-1} in the model (Case 3 in Table 3), the peak population size comes back down to a reasonable range, but another issue appears: the timing of the peak occurs in summer months (Fig. 13c,d), a pattern similar to *Pseudocalanus* spp., but much earlier than the observed fall peak of the

C. typicus population. The mismatch between modeled and observed patterns is likely caused by the difference in mortality rates for *Pseudocalanus* and *Centropages* in different seasons; such a difference might have a good biological basis (as shown in the 'Discussion'), but the information is not yet available for incorporation into the model.

Centropages hamatus has a spatial distribution pattern significantly different from that of *C. typicus*, although they both have similar temperature-dependent development rates at all stages (Fig. 5a,b,c) and use the broadcast spawning strategy. *C. hamatus* may have a much lower egg production rate during late summer, more like *Pseudocalanus* (Kiørboe & Sabatini 1994, Halsband-Lenk et al. 2002) (Fig. 5d). Data on *C. hamatus* EPR is variable, however, as it appears to
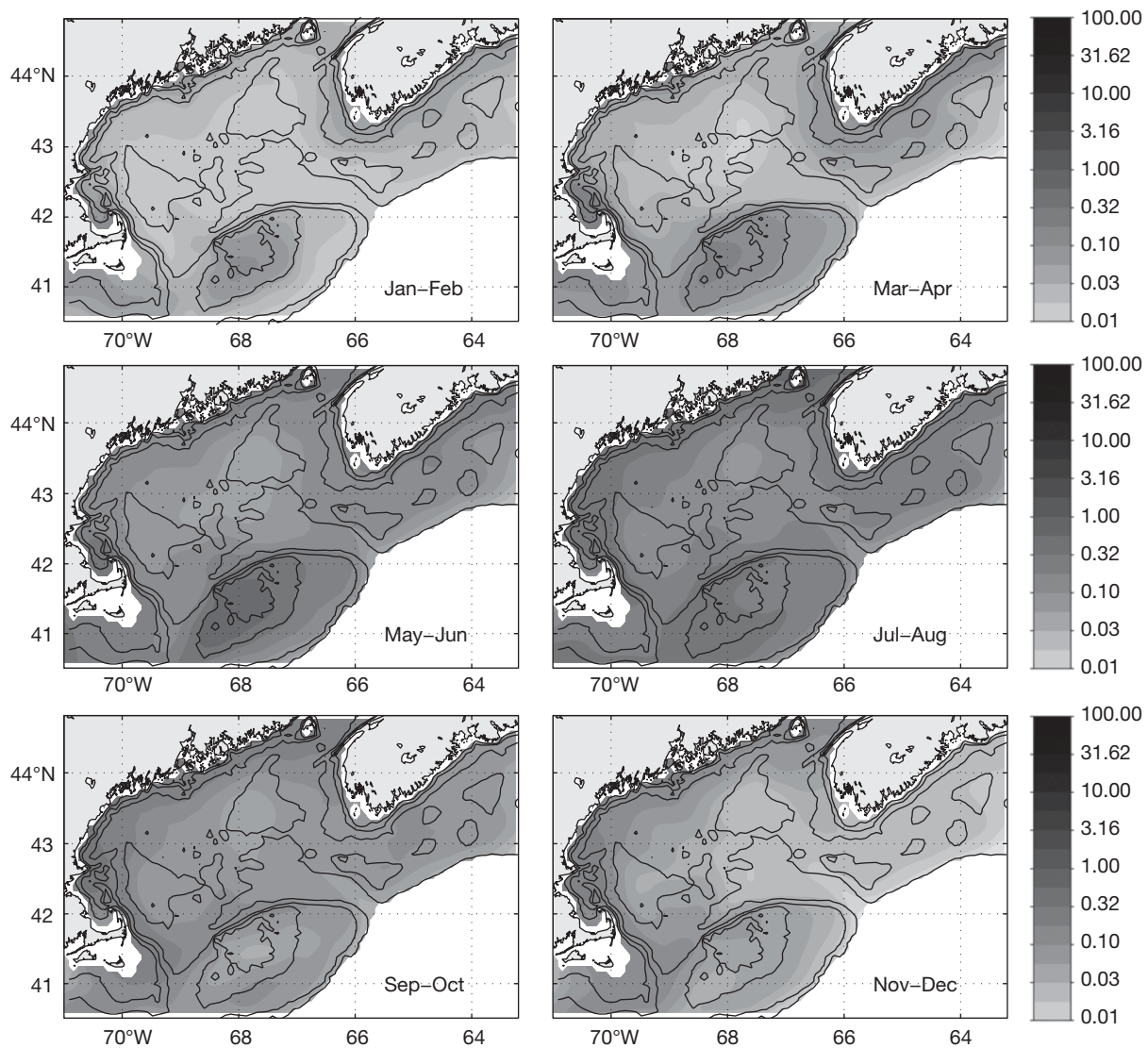
Fig. 11. Model-computed bimonthly-averaged spatial distribution of adult *Pseudocalanus* spp. (vertically averaged, dimensionless) in the Gulf of Maine-Georges Bank region

be highly fecund in early summer (Halsband & Hirche 2001, Halsband-Lenk et al. 2004). Assuming the EPR is low (i.e. Fig. 5d), and assuming the same egg mortality rate as *C. typicus*, the model run suggests that the population is not capable of maintaining itself in the system (results not shown). On the other hand, assuming the EPR values are as high as *C. typicus*, the population is easily self-sustaining (Fig. 13a,b). This points to the need for further experimental data on the food and/or temperature dependence of *C. hamatus* EPR.

A numerical experiment was conducted to test whether laying resting eggs is a possible life history strategy for *Centropages hamatus* to generate the restricted distributional pattern. From the observational data, the adult population increased its size sub-

stantially from the seasonal minimum in March–April to much higher levels in May–June and peak abundance in July–August, with the population restricted to shoaler regions (especially the GB crest). We can infer that the eggs start hatching in March, given the ambient water temperature of 5°C and the 2 mo generation time (derived from the Bêlehrádek equation without considering food limitation on development rates). In the model, a cohort of eggs were released only on the GB crest in the middle of March (Fig. 14a). The ages of released eggs have a uniform–random distribution with a mean of 5 d, so all the eggs hatch within 10 d. After running the model for about 2 mo, we can see that the adult population remains well confined within the crest (Fig. 14b,c). Even without mortality, the
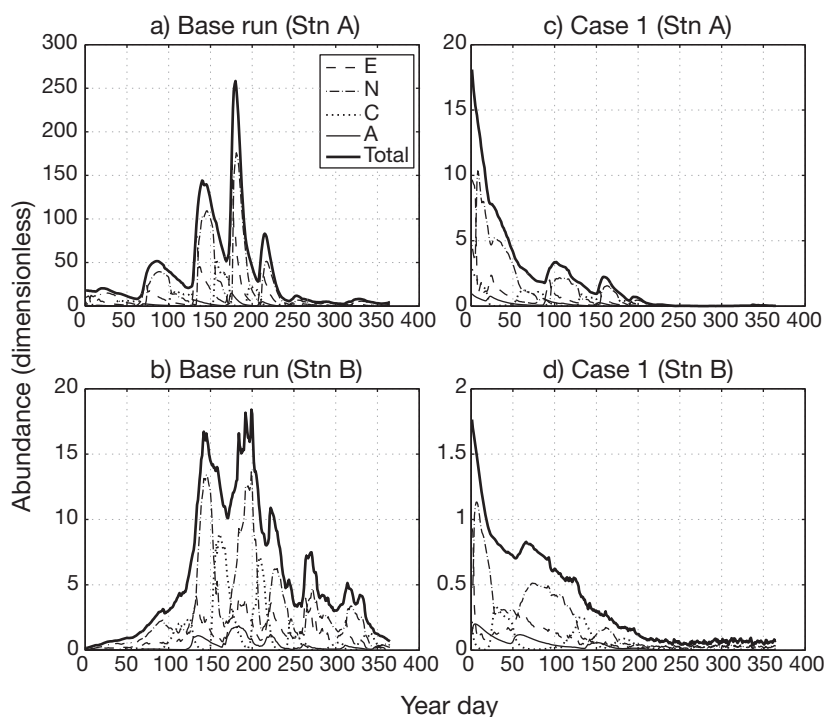
Fig. 12. Model-computed time series (dimensionless) for the abundance of *Pseudocalanus* spp. populations. (a,b) Base model run at Stns A and B, respectively. (c,d) Case 1 run (see Table 3 for case number details) at Stns A and B, respectively. E: egg; N: nauplii; C: copepodite; A: adult. See Fig. 1 for station locations
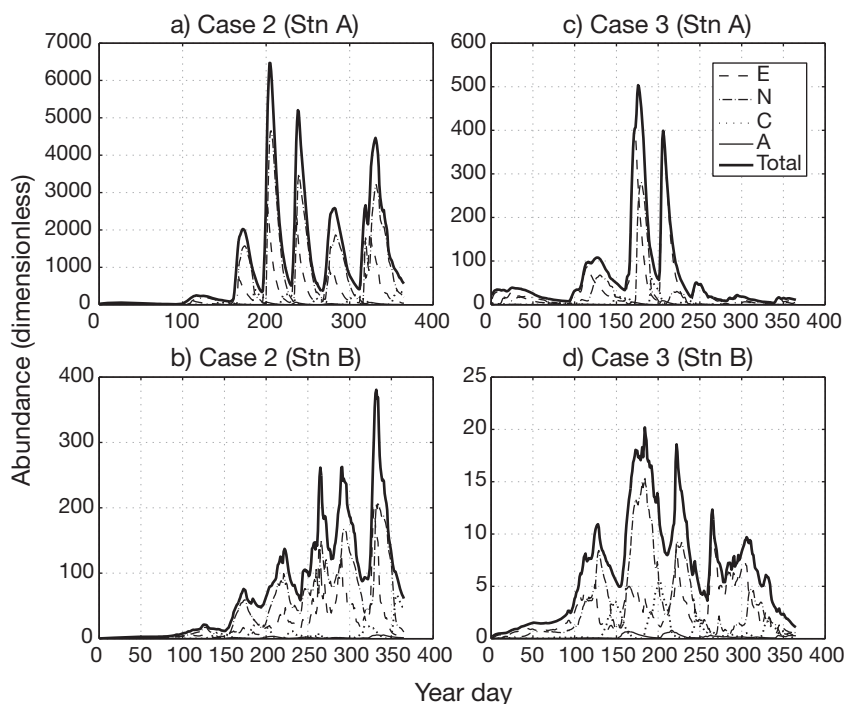

Fig. 13. Model-computed time series (dimensionless) for the abundance of *Pseudocalanus* spp. and *Centropages typicus*. (a,b) Case 2 run at Stns A and B, respectively. (c,d) Case 3 run (see Table 3 for details) at Stns A and B, respectively. E: egg; N: nauplii; C: copepodite; A: adult. See Fig. 1 for station locations

advection and diffusion processes, acting together with the crest egg source and subsequent population growth, lead to an adult population distribution that is restricted to the shoaler region of the bank, agreeing with the field data (cf. Fig. 4). In the case of 'including spatially and temporally uniform mortality' (Fig. 14c), the pattern is similar to that in the case of 'no mortality' (Fig. 14b), but the overall population size is reduced, suggesting that it is possible for the *C. hamatus* population to generate the observed distribution patterns with population recruitment through resting eggs hatching on the GB crest, population loss due to uniform mortality and physical transport featuring around-bank circulations and mixing (Naimie et al. 1994, Limeburner & Beardsley 1996, Chen et al. 2001).

DISCUSSION

r- versus *K*-strategy

Egg carriers such as *Pseudocalanus* spp. have relatively lower fecundity and egg mortality rates (similar to the mortality rate of the females), whereas broadcasters such as *Centropages typicus* usually have higher fecundity as an adaptation to the much higher mortality rates experienced by suspended eggs (Kiørboe & Sabatini 1994). Therefore, the former contain more elements of *K*-strategy than the latter. It is difficult to categorize the other broadcaster, *C. hamatus*, as an *r*- or *K*-strategist since it has a relatively lower fecundity rate than *C. typicus* during late summer but appears to have high fecundity during spring/early summer (Halsband & Hirche 2001, Halsband-Lenk et al. 2002, 2004). The production of resting eggs by *C. hamatus* enables its population to persist in shallow regions. The turbulent environment in these shallow areas causes turnover of the bottom sediments, allowing bottom resting eggs to be exposed to the water–sediment interface rather than being permanently buried as in less turbulent environments (Marcus & Taulbee 1992).
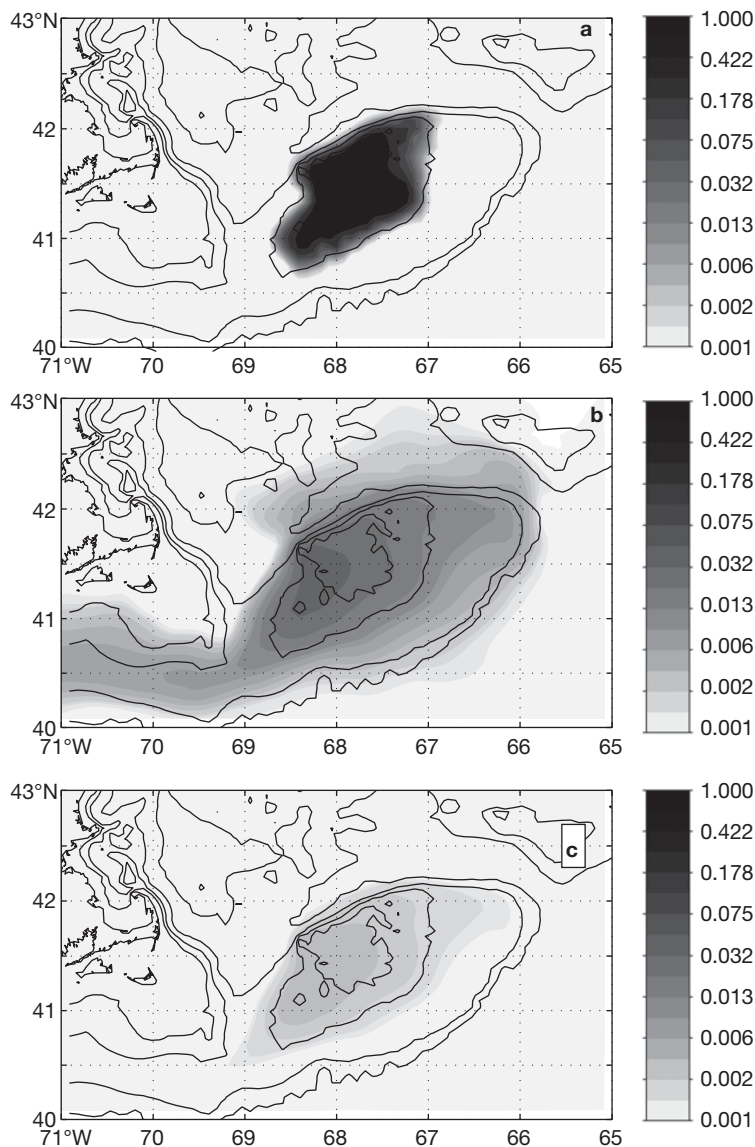
Fig. 14. *Centropages hamatus*. (a) Distribution of eggs released in the middle of March, and the eventual distributions of adults 2 mo later in the cases of (b) no mortality and (c) including mortality. Initial abundance on the crest is 1 (dimensionless)

While our initial distribution of resting eggs on the crest region yielded high crest populations of adults, agreeing with the observed data (Fig. 4), initializing with a bank-wide (shallow and deep) distribution of resting eggs would yield a much broader distribution. Thus, the deeper regions surrounding the GB crest are likely to serve as a sink for bottom resting eggs of *C. hamatus*. Consequently, the dispersion capability of *C. hamatus* in the spatial domain is much weaker than that of *C. typicus*, and the *C. hamatus* population is much more confined in areas where the resting eggs can be resuspended. Both the observational data

and our numerical experiments support this argument.

It remains unclear whether higher fecundity and broadcast spawning by *r*-strategists can lead to a higher dispersion capability. Other life history characteristics, including mortality, food and temperature effects on development and reproduction, can significantly influence the eventual distributional patterns in space. For instance, it appears from the field data (Figs. 2 & 3) that the gradient of vertically averaged abundance, from the shallow coastal regions to the deep central GoM region, is similar between *Pseudocalanus* spp. (May–June) and *Centropages typicus* (September–October), even though they have significantly different reproductive strategies. This seems to suggest that the dispersion capability of *C. typicus* might be hindered by other factors, possibly the higher food limitation in deeper regions where the food availability is relatively lower (especially in non-bloom time periods). However, the shorter generation time also increases overall population size and may lead to greater spread of the *C. typicus* population. It should be pointed out that the integrated abundance data (Figs. 2 & 3) includes the deep water column below the mixed layer, whereas we know from prior field studies that *C. typicus* is restricted to the warm upper layer (e.g. Davis 1987b). If we allow *C. typicus* to stay in the mixed layer in the model and plot the model results only for the surface layer, then the horizontal gradients for *C. typicus* are weaker. On the other hand, it is well known that *Pseudocalanus* spp. are much more abundant in regions where bottom depth is less than 100 m. Although the *K*-strategy may help explain reduced dispersion in *Pseudocalanus* spp., it does not explain why these species are restricted to shallower regions. Our modeling suggests that food-limited conditions in deeper regions limit *Pseudocalanus* spp. population growth there.

It has been argued that the seasonal resource partitioning by *r*- and *K*-strategists is probably related to their response to temperature variation, as suggested in a case study by Hirche (1992), with *r*-strategists being relatively more competitive during summer than *K*-strategists. The fecundity of *r*-strategists (e.g. *Centropages typicus*) appears to be more sensitive to seasonal temperature variation than *K*-strategists (e.g. *Pseudocalanus* spp.). Assuming the same predation pressure, one would expect to see the above-described

seasonal alternation in dominance between *r-* and *K*-strategists. The question becomes: Can the reproductive strategy alone can completely control the seasonality? Our model results suggest that, if the same mortality function is used for both *Pseudocalanus* spp. and *C. typicus*, the *C. typicus* population peaks at almost the same time as *Pseudocalanus* spp. (instead of a late summer–fall peak, as field data show). This numerical experiment indicates that predation mortality, in addition to fecundity, could play a critical role in controlling the seasonality of populations (discussed below).

Factors affecting the seasonality of copepod populations

The relatively short stage duration time of *Pseudocalanus* spp. in cold water, along with their egg-carrying strategy, appear to be the major reasons for their peak in abundance during spring and early summer. However, it is much less intuitive to understand the observed population decline in the warm season. From the Bêlehrádek curves at warm (>10°C) temperatures (Fig. 5a,b,c), it appears that *Pseudocalanus* spp. have very similar stage durations as the 2 *Centropages* species, suggesting that development rate alone is probably not the reason for the decline of *Pseudocalanus* spp. population in summer (since *Centropages* spp. can still bloom even though they have similar development rates).

It is also unlikely that the summer decline in the *Pseudocalanus* spp. population is caused by a decrease in reproduction. McLaren (1965) found that reproductive rates in *Pseudocalanus* are not impeded when the temperature is lower than 15°C, which is within the range of maximum temperature on GB and many parts of the GoM. In addition, food concentrations on the GB crest are high throughout the year, peaking in March, whereas the *Pseudocalanus* spp. population peaks in June.

It is therefore possible that the summer decline in *Pseudocalanus* spp. is mainly due to predation mortality, as has been indicated by previous field and modeling studies (Davis 1984a,b, Ohman et al. 2002). Predation rate is higher during the late summer and fall due to increases in gelatinous predators (ctenophores and chaetognaths) and *Centropages typicus* (which prey on younger stages of other copepods) as well as increased temperature-dependent predatory consumption rates (Davis 1984b, 1987b, Davis & Alatalo 1992). Our treatment of mortality as a simple Q_{10} temperature function gives a rough approximation to the increased predator abundance and consumption rates during warmer months and in shoaler regions. The model sug-

gests that a high Q_{10} (≥6) is required to reduce the *Pseudocalanus* spp. population to observed levels during late summer and fall. The same high mortality rate will decrease the *C. typicus* population even with higher fecundity as described above. The actual predation mortality is species- and life stage-specific, depending on abundance and consumption rates of particular predators (Davis 1984b). The predatory feeding behaviour of *C. typicus* on nauplii and copepodids of other species is also likely to play an important role (Davis & Alatalo 1992). In addition, consumption of broadcast eggs by a variety of copepod species is likely to be an important source of mortality and the main reason *Pseudocalanus* spp. are egg carriers (e.g. Ohman et al. 2008).

The model results are very sensitive to the mortality term formulation. The temperature dependency of mortality in the present study is probably oversimplified, but not totally unrealistic. Here we compiled all the available copepodite stage V (CV) and adult *Pseudocalanus* spp. and *C. typicus* abundance data and computed the mortality for CV–female pairs on Georges Bank using the vertical life table approach (Aksnes & Ohman 1996, Ohman & Hsieh 2008). The results (Fig. 15) suggest that the monthly mean mortality can be estimated using the temperature-dependent formulation reasonably well.

With the high Q_{10} value for temperature-dependent mortality, it is not surprising to see that the model is also sensitive to base mortality rate. For example, if we increase the mortality at the base temperature for nauplii and copepodite stages from 0.045 and 0.02 to 0.05 and 0.03 respectively, the peak abundance of adult *Pseudocalanus* spp. is approximately 5 times lower than the base run case, and the adult population dies out at the end of the year. Given the importance of mortality in controlling population dynamics, a complete retrospective analysis of predator abundances and consumption rates from this area is clearly needed to better understand the impact of predation on copepod populations.

Resting egg strategy

Centropages hamatus has, on average, lower fecundity during late summer than its congener, *C. typicus* (Halsband-Lenk et al. 2002). The former is capable of producing resting eggs that can survive environmental conditions unfavorable for population development (Pertzova 1974, Grice & Marcus 1981, Davis 1987b), including unfavorable temperatures, low food availability and high predator abundances (e.g. Marcus 1989, Engel & Hirche 2004). These eggs hatch once the environmental conditions are favorable or after the
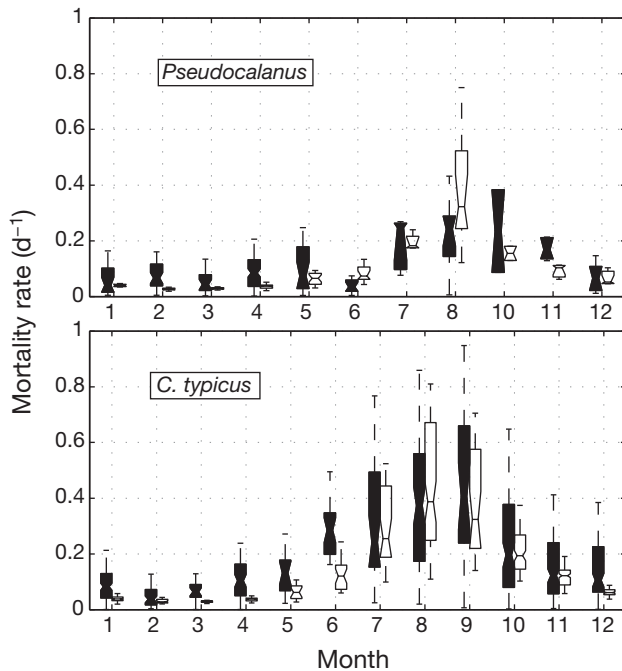
Fig. 15. *Pseudocalanus* spp. and *Centropages typicus*. Monthly averaged mortality rates of CV–adult female pairs for *Pseudocalanus* spp. (upper panel) and *C. typicus* (bottom panel) on Georges Bank. The results are presented using box-and-whisker plots. Filled boxes: mortality rates derived from the vertical life table method (Aksnes & Ohman 1996); open boxes: mortality rates derived from $Q_{10} = 6$ formulation (Eq. 8). Central mark: median, box: 25th and 75th percentiles: lower whisker: $1.5 \times$ interquartile range (IQR) lower than the low quartile; upper whisker: $1.5 \times$ IQR higher than the high quartile. We discarded negative mortality rates derived from the vertical life table method, with an understanding that negative values may indicate a violation of the primary assumption for that method (Aksnes & Ohman 1996)

completion of a refractory phase, depending on whether they are quiescent subitaneous or diapause (Chen & Marcus 1997). The tight distribution of *C. hamatus* in the well mixed area of Georges Bank, together with early evidence of resting eggs in this species in the White Sea (Pertzova 1974), led Davis (1982, 1987a,b) to suggest that this resting-egg strategy was a mechanism by which copepods could maintain their populations in regions of favorable growth, such as the food-rich, well-mixed crest of GB. Subsequently, *C. hamatus* resting eggs were found in Buzzards Bay, Massachusetts (Marcus 1984), on Georges Bank (N. H. Marcus unpubl. data), in the English Channel and North Sea (Lindley 1986) and in the northern Gulf of Mexico (Marcus 1989). Recently, Durbin & Kane (2007) suggested that the tight distribution of *C. hamatus* on the crest of GB may be due to either resting eggs or high food levels in this region. Results from the present study indicate that the tight

distribution of adult *C. hamatus* on the GB crest can be explained solely on the basis of resting eggs hatching from the sediments. The model also reveals that food-limited population growth does not yield such tight distributions on the crest, since the food source itself is more broadly distributed and non-resting egg laying copepod populations are more dispersive due to lack of a direct geographic anchor. This resting egg strategy is very successful for these copepods because it allows them to maintain their populations in shallow, well-mixed regions of the ocean, which typically have higher phytoplankton concentrations. These regions are characterized by low values of the Simpson-Hunter stratification index, h/u^3 (where h is bottom depth and u is vertically averaged M_2 tidal velocity, Simpson & Hunter 1974), which correspond to areas of high phytoplankton concentrations (Pingree 1978) and herring spawning grounds (Iles & Sinclair 1982). Such regions are well suited to copepod species that lay bottom resting eggs, due to the high turbulence and phytoplankton concentrations. Indeed, Lindley (1990) found a relationship between distribution of bottom resting eggs and bottom stress. On GB, copepods known to lay bottom resting eggs (*Labidocera aestiva*, *Temora longicornis* and *C. hamatus*) all have distributions that are restricted to the bank crest (Davis 1987b).

Model caveats

Although we have modeled the *Pseudocalanus* spp. population in the GoM-GB region as a single species, it actually comprises 2 species: *P. newmani* and *P. moultoni* (Frost 1989, McLaren et al. 1989a,b, Bucklin et al. 1998, 2001). Their vital rates appear similar, however, with large variation in laboratory data (McLaren et al. 1989a,b). Davis (1984a) modeled *Pseudocalanus* spp. transport around GB using a temperature-dependent molting rate that was an average of these 2 species. *P. moultoni* maybe a slightly colder water species and more abundant during winter/ spring, while *P. newmani* is more plentiful during spring/summer (McLaren et al. 1989a,b). *P. moultoni* may be a coastal species and *P. newmani* an offshore one (Frost 1989). Thus *P. moultoni* may be carried onto the bank from western GoM coastal waters (e.g. Cape Cod Bay), while *P. newmani* may have a source from Scotian Shelf water, either crossing over the Northeast Channel, or indirectly through the central GoM (McGillicuddy & Bucklin 2002). Inverse (adjoint) modeling, representing the biology by a single source/sink term, revealed that the 2 species may have different source locations on GB but intermingle by June (McGillicuddy & Bucklin 2002). These data are limited however, and we need to examine a more extensive

genetically resolved *Pseudocalanus* spp. data set developed for this region (A. Bucklin unpubl data). There also may be coastal refuges for *Pseudocalanus* spp. that are not captured by the model version used (or by field sampling programs), and in our future work we will use a much higher resolution grid in the coastal region to explore this possibility.

The impact of temperature on fecundity (EPR) of *Centropages hamatus* needs to be investigated at different times of the year instead of during late summer at the end of its growing season. Its EPR appears to be as high as that of *C. typicus* (Halsband-Lenk et al. 2004), and we examined both low and high EPR scenarios. It is also likely that its EPR changes with a seasonal switch from subitaneous to diapause eggs (e.g. Wu et al. 2007). In general, there is a need in zooplankton ecology to conduct more studies of the kind begun by Vidal (1980), which examined the effects of a matrix of temperature and food conditions on egg production, development and growth rate. Such studies should be done in collaboration with the modeling community to facilitate optimal knowledge exchange.

Further modeling studies are needed to examine how these species will respond to climate warming. From our results thus far, we can predict that warmer temperatures are likely to cause the seasonal growth of *Centropages typicus* and *C. hamatus* to occur earlier and *C. typicus* to extend its growing season. The observed freshening of the surface water in late winter (due to Arctic melting, Greene & Pershing 2007) may lead to an earlier spring phytoplankton bloom (Ji et al. 2007, 2008b) and earlier growth of *Pseudocalanus* spp. However, persistence of *C. typicus* (which preys on *Pseudocalanus* spp.) later into the year could limit the early growth of the *Pseudocalanus* spp. population. Future work will examine the effects of climate forcing and interspecific interactions among the copepod species.

Finally, future studies are required to obtain better data on predator abundances and consumption rates. We suggest that the interannual variability in top-down control (due to predation) plays an important role in controlling the copepod populations in the system. We are pursuing the compilation of the rich data set provided by the MARMAP, EcoMon and GLOBEC programs on copepod predators and their feeding rates.

CONCLUSIONS

Results of the numerical modeling experiments presented here reveal that the interaction between realistic ocean circulation/hydrography and the characteristic life history traits of the modeled copepod species can explain their observed abundance patterns in time and space. The *K*-selected *Pseudocalanus* spp. population is dominant in shoaler regions during the cold season due to its shorter generation time at low temperatures combined with the lower predation levels and higher food concentrations. In contrast, the *r*-selected *Centropages typicus* population, with its shorter generation time and high egg production during the warm season, is dominant during the late summer and is less restricted to the shoaler regions as it spreads out in the warm surface layer over the GoM-GB region. The modeled *C. typicus* population peaked during summer, earlier than the late-summer/fall peak observed in the field data, likely due to our treatment of predation mortality as a simple Q_{10} function. The model showed clearly that production of bottom resting eggs by *C. hamatus* is solely responsible for its restricted distribution on the crest of Georges Bank.

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