Sensitivity of copepod populations to bottom-up and top-down forcing: a modeling study in the Gulf of Maine region

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The spatio-temporal variability of marine copepods, like other aquatic and terrestrial organisms, is controlled by both bottom-up (through changes in food resource) and top-down (through changes in predation) forcing. Canonically, climate-related changes in hydrography, nutrient chemistry and circulation can modulate phytoplankton production, thus imposing a bottom-up control on marine copepods, whereas human activities such as fishing may affect the predation mortality of copepods through food-web re-organization such as trophic cascading. Evaluating the sensitivity of copepod populations to bottom-up and top-down forcing is an essential step toward the prediction of future marine planktonic ecosystem changes. In this study, we used a coupled hydrodynamics/food-web/population-dynamics model to identify the key processes controlling the observed seasonality and distributional patterns of two copepod groups in the Gulf of Maine (GoM) region, including *Pseudocalanus* spp. and *Centropages typicus.* Numerical experiments were conducted to assess the sensitivity of the modeled species to changes in phytoplankton biomass and bloom timing, as well as the changes in mortality regime. The results show that both copepod groups are more sensitive to changes in mortality rates than to food availability and peak timing. Bottom-up processes alone cannot explain the observed variability in *Pseudocalanus* and *Centropages* population sizes, while top-down controls play a critical role in copepod population dynamics in the GoM region.

INTRODUCTION

Copepods are the most abundant mesozooplankton in the North Atlantic Ocean and play a central role in marine food webs (e.g. Davis, 1987; GLOBEC, 1992; Mitra and Davis, 2010). Copepods are sensitive to environmental changes and are important climate indicators (e.g. Richardson, 2008). Increasing efforts have been made to develop the predictive capability of coupled biological–physical models in order to quantitatively assess the influence of climate change on plankton phenology and biogeographic boundaries (Ji *et al.*, 2010). Evaluating the sensitivity of copepod populations to bottom-up (through changes in food environment) and top-down (through changes in predation) forcing is an essential step toward building such predictive capacity.

In the Gulf of Maine (GoM) region (Fig. 1), *Centropages typicus* and *Pseudocalanus* spp. (the congeners *Pseudocalanus newmani* and *Pseudocalanus moultoni*) are among the dominant small-sized copepod species (Bigelow, 1926; Davis, 1982, 1984a; Kane, 2007). For simplicity purposes, these two species groups will be referred as CT for *C. typicus* and PS for *Pseudocalanus* spp. Although both CT and PS are exposed to the same physical environmental conditions, the timing of their seasonal abundance peaks differs. PS is a winter/spring species with a highest abundance between May and July, a few weeks after the spring bloom. In contrast, CT peaks during October–November, coinciding with the weaker fall bloom and the start of the seasonal temperature decline. The spatial distributions of these species differ as well (see Ji *et al.*, 2009), including a steeper decrease in the abundance from shallow to deep regions for PS than CT. These differences in spatio-temporal patterns suggest that their distributions are likely related to their unique life-history traits, with different development, growth, and reproduction regimes under the same external environmental forcing. Due to these differences, it is likely that they also respond differently when environmental conditions vary from year to year.

Long-term surveys reveal a strong inter-annual variability for both CT and PS (Fig. 2, top and middle panels). Their annual mean adult abundance was low in the early 1980s, followed by a significant increase in CT in the late 1980s, reaching ~ 300 inds. m^{-3} on Georges Bank (GB) and ~ 100 inds. m^{-3} in the deep GoM region, while PS increased in the late 1990s, reaching ~ 150 inds. m^{-3} on GB and ~ 50 inds. m^{-3} in
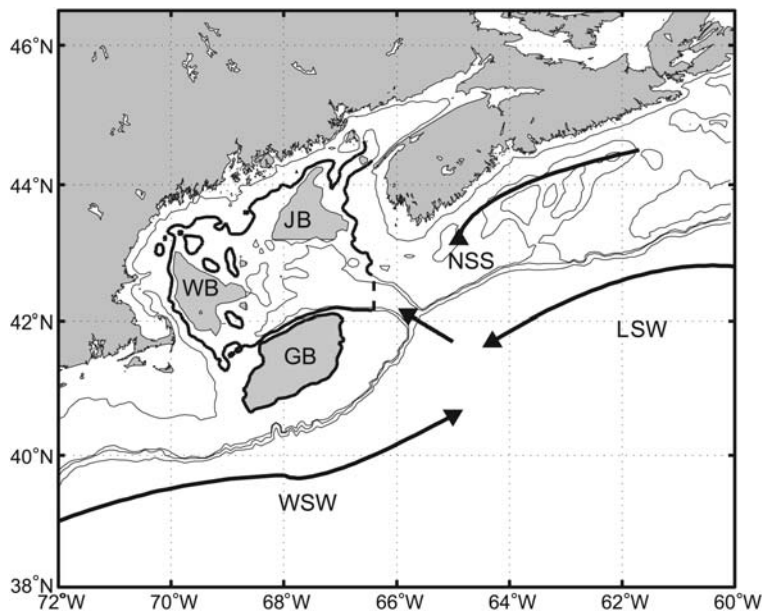

Fig. 1. Bathymetry of the GoM and Scotian Shelf ecosystem. Lines indicate the 60 m (light gray), 150 m (dark gray), 200 and 500 m isobath (black). Bold lines indicate the GB and GoM areas used in Figs 2 and 3 defined by the 60 and 150 m isobaths, while the gray shaded are the three areas referred to in Fig. 7. GB, Georges Bank; JB, Jordan Basin; WB, Wilkinson Basin; NSS, Nova Scotian Shelf, LSW, Labrador Slope Water; WSW, Warm Slope Water.
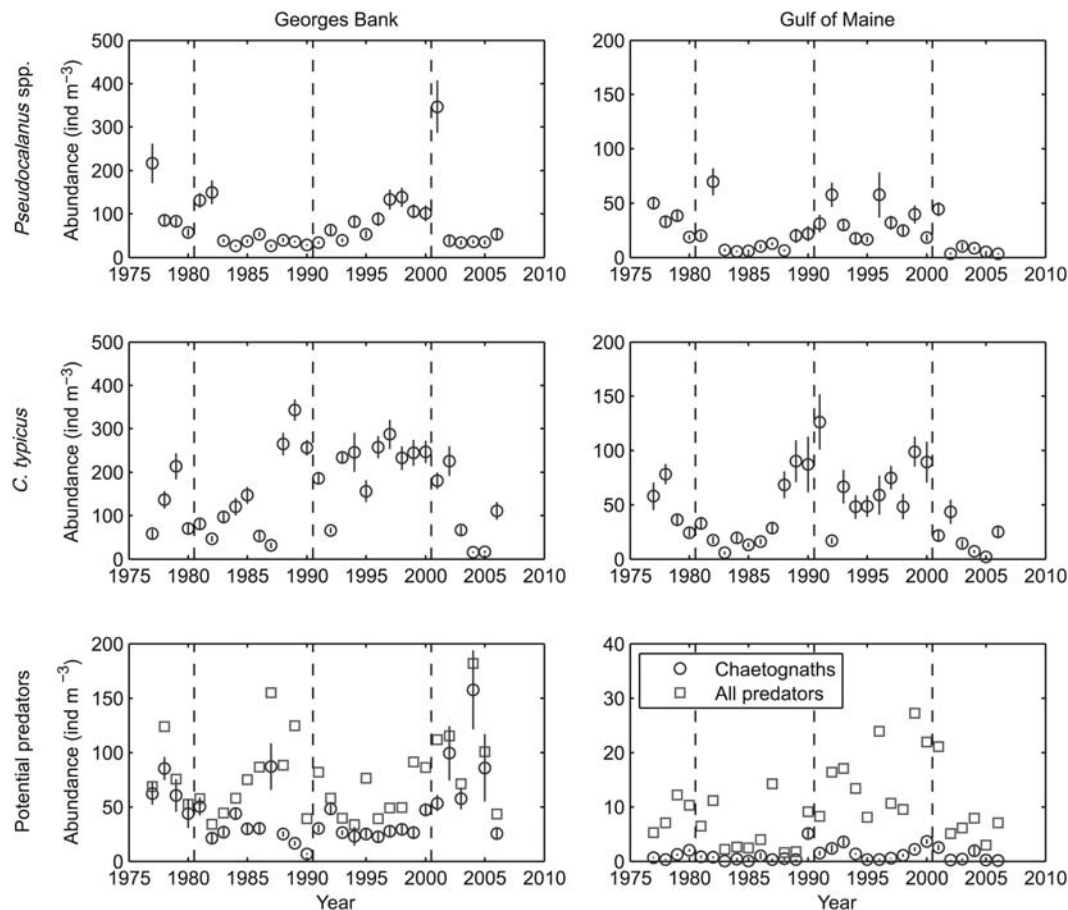
Fig. 2. Annual mean abundances for 1977–2006 for the copepods *Pseudocalanus* spp. and *Centropages typicus* as well as potential copepod predators in two different regions: GB <60 m (left) and GoM >150 m (right). Vertical bars indicate standard error. Copepod data: Adult inds. m^{-3}, predators: total abundances, all potential predators include: chaetognaths, hyperiids, gammarids, euphausiids, fish larvae and mysids; data from MARMAP/EcoMon surveys.

the deeper GoM region. The annual mean abundance dropped significantly in the 2000s, reaching a level similar to that in the 1980s. The causes of the observed variability are difficult to determine, and they could be through bottom-up forcing, top-down forcing or a combination of the two.

It has been suggested that climate forcing could have impacted the copepod populations through bottom-up processes (e.g. Greene and Pershing, 2007). Decadal-scale variability of sea surface salinity in the GoM region has been observed, with a general freshening from the 1990s compared with the 1980s (Smith et al., 2001; Mountain, 2003; Belkin, 2004; Mountain and Kane 2010). The change in surface salinity can affect water column stability and mixed layer depth (e.g. Taylor and Mountain, 2009) and likely caused phytoplankton phenological shifts and changes in productivity in this region (Ji et al., 2007, 2008b; Song et al., 2010, 2011). In addition, the North Atlantic Oscillation (NAO)-dependent intrusions of Labrador Slope Water

(LSW) and Warm Slope Water (WSW) through the Northeast Channel may influence nutrient supply to the GOM–GB regions and subsequently overall primary production (Thomas et al., 2003; Townsend et al., 2010). Changes in phytoplankton phenology and productivity have been related to inter-annual variability of copepod abundance, and the intensification of the fall-winter bloom has been hypothesized as the main driver for the increase in small-sized copepods in the 1990s (e.g. Durbin et al., 2003; Durbin and Casas, 2006; Greene and Pershing, 2007).

A top-down control (abundance regulation through predation), though less studied, has also been considered as a possible cause of variation in the zooplankton abundance. Frank et al. (Frank et al., 2005, 2011) proposed a trophic cascade hypothesis in the Nova Scotian Shelf (NSS) region, whereby overfishing of large-bodied demersal fishes (and their subsequent population collapses) resulted in the dominance of planktivorous forage fishes that reduced the abundance of large-sized

(≥2 mm) zooplankton in the region. The small-sized (<2 mm) zooplankton, however, increased with the increase in forage fish, highlighting the complexity of trophic interactions among pelagic food-web components. This trophic cascade hypothesis was derived from the regression analyses of fish and plankton time series data. Further evaluation based on the food-web dynamics is needed to quantify the predator–prey interaction and the relative importance of top-down vs. bottom-up processes. Data from the GoM–GB regions also revealed a strong inter-annual variability of the mean abundances of potential copepod predators (chaetognaths, hyperiids, gammarids, euphausiids, fish larvae and mysids; Fig. 2, bottom panel). A low (high) predator abundance in the early 1990s (2000s) coincided with a high (low) abundance of PS and CT on GB (but not in the GoM), suggesting a possible top-down control in some regions. It is worth noting that gelatinous zooplankton such as ctenophores and cnidarians (medusa and pelagic hydroids) are considered to be major predators of copepods in the GoM–GB regions, but they are not included in the time series. This is because the distribution pattern of gelatinous zooplankton is often characterized by the high degree of spatial and temporal variability (Hamner *et al.*, 1975; Monger *et al.*, 1998) and therefore data collected using traditional sampling methods are unreliable. Specifically, the zooplankton sampling protocol based on bongo net tows did not target gelatinous zooplankton in the GoM nor treat the process of such organisms consistently over time (Link and Ford, 2006).

The objective of this study was to assess the relative importance of bottom-up and top-down controls of different copepod species in different areas of the GoM–GB regions. Earlier life-table analysis by Kiørboe and Sabatini (Kiørboe and Sabatini, 1994) has suggested that copepod populations are more sensitive to post-hatching mortality than to reproduction. Previous studies in mortality estimations of copepod species also showed that the variability in mortality may be at least as important as the variability in birth rates in explaining the fluctuations of copepod abundances in coastal oceans (e.g. Ohman and Wood, 1996; Ohman and Hirche, 2001; Ohman *et al.*, 2002). Given that the food concentration on the crest of GB is high (or nearly saturated) due to high primary productivity, we expect that zooplankton populations are then more likely to be subjected to the top-down controls than the bottom-up controls in this shallow area (Davis, 1984b), whereas in the GoM region, the food concentration is much lower, and the bottom-up controls are likely more important. Empirical evidence indicates that neither species is likely to be food-limited in the food-rich crest of GB

(Davis, 1984a), but CT may be food-limited on the flank of GB (Davis and Alatalo, 1992). To further explore the potential for the bottom-up vs. top-down controls, we conducted a sensitivity analysis based on copepod population dynamics models developed and calibrated for PS and CT in the GoM–GB regions (Ji *et al.*, 2009; Stegert *et al.*, 2012).

METHOD

Details for the 3-D coupled model implementation of the mean-age population model can be found in Ji *et al.* (Ji *et al.*, 2009) and Stegert *et al.* (Stegert *et al.*, 2012). Briefly, we use the Finite Volume Coastal Ocean Model (FVCOM) framework, which includes a hydrodynamic model, a food web (Nutrient-Phytoplankton-μZooplankton-Detritus, NPZD) model and a stage-based copepod population model. The hydrodynamic model is described by Chen *et al.* (Chen *et al.*, 2003). The NPZD model simulates the nitrogen cycle with the uptake of inorganic nutrients by phytoplankton, grazing by microzooplankton and remineralization by detritus as described by Ji *et al.* (Ji *et al.*, 2008a,b). For the copepod population model, we followed a process-oriented approach. This involves a simple population dynamics model that simulates key life-history processes including development and reproduction as a function of temperature and food concentration and mortality as a function of temperature.

Model runs for the following four cases are conducted to examine the copepod population responses to changes in the magnitude and timing of both food concentration and mortality. It should be noted that we consider the mortality rate variation as a result of the change in the predator abundance. In this sense, we are comparing the change in the biomass (of phytoplankton) with the change in the biomass (of predator), not the biomass with rate. Therefore, when we mention the change in the mortality rate in the following text, it can be viewed as the change in the predator abundance:

Case 1. Change in phytoplankton concentrations: a 20% increase/decrease in the phytoplankton (P) concentration derived from the baseline run of the NPZD model. The increase/decrease was applied to the entire time series (including phytoplankton blooms) throughout the domain.
Case 2. Change in mortality rates: a 20% increase/decrease in baseline mortality is adjusted directly in the copepod population model for all stages.
Case 3. Change in phytoplankton bloom timing: based on the baseline NPZD model run, the spring bloom
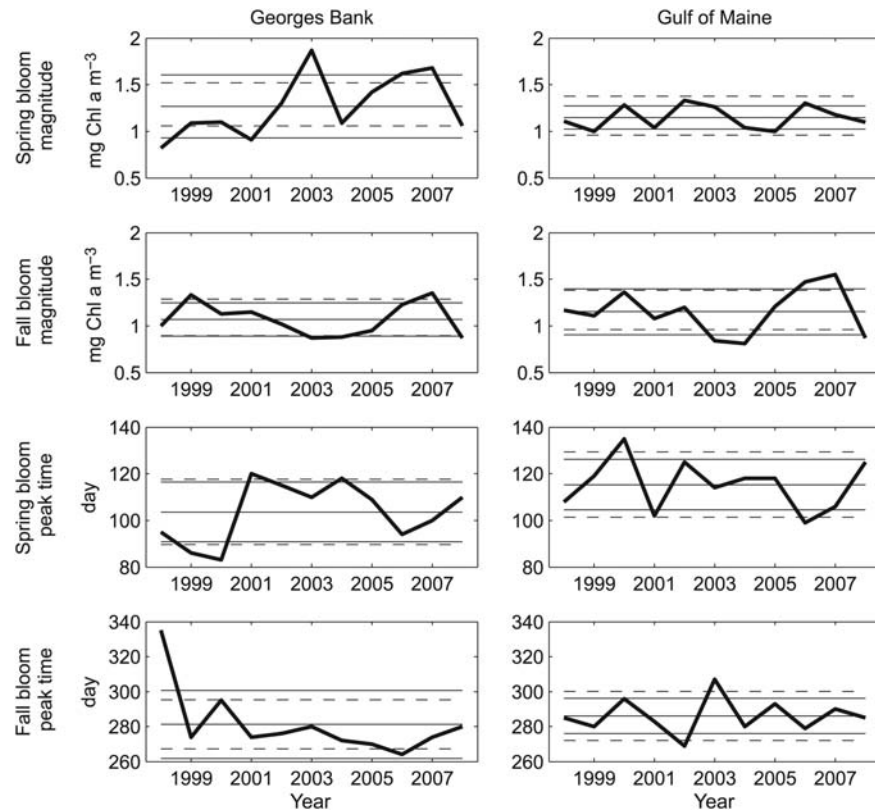
Fig. 3. Annual mean magnitude and peak timing of the spring and fall phytoplankton blooms for 1998–2007 in two different regions: GB (<60 m, left column) and GoM (>150 m, right). Black lines indicate the mean value and standard deviations, red lines indicate a change by 20% (for magnitude) and 14 days (for timing), respectively, as used for scenarios in the model.

timing is shifted earlier by 2 weeks and the fall bloom delayed by 2 weeks.

Case 4. Change in mortality timing: the temperature-dependent coefficient Q_{10} for mortality is increased (decreased) by 20%, resulting in lower (higher) mortality in spring and higher (lower) mortality in the fall.

The changes in the phytoplankton bloom magnitude and timing are based on the observed variability. Analysis of SeaWiFS ocean color data for 1998–2008 (Song *et al.*, 2010) showed that for five stations in the GoM (including GB and the deep basins), the standard deviation (SD) varies from 10 to 26% (mean SD = 17.5%) for the spring bloom magnitude and 16–21% (mean SD = 19.2%) for the fall bloom magnitude. Thus, we chose 20% deviation for the sensitivity analysis indicating a change by 1 standard deviation from the mean magnitude (Fig. 3). For the timing of blooms, the mean standard deviation for the five stations was 11.4 and 13.5 days for the spring and fall blooms, respectively. We used a value of 14 days to simulate the possible variability within 1 standard deviation (Fig. 3).

Since the timing of spring and fall blooms appears to be negatively correlated in specific locations (Song *et al.*, 2010), a simulation with an earlier spring bloom also includes a later fall bloom and vice versa. For mortality we chose the same factor (20%) as for the variability in food concentrations, though the predator abundance could vary significantly, up to 2- or 3-fold or even higher (Fig. 2). We chose a similar magnitude of variation in the model, so that the sensitivity can be better compared with a normalized scale.

The control simulations are based on published model runs: the parameterization for CT is identical to simulation S-4 in Stegert *et al.* (Stegert *et al.*, 2012), describing CT as an omnivorous species and includes cannibalism by females on eggs (cf. Davis and Alatalo, 1992) and young nauplii and vertical swimming toward a higher food concentration. The parameterization for PS is similar to the simulation published in Ji *et al.* (Ji *et al.*, 2009), but considers the influence of food on developmental time as in CT and slightly revised base mortality rates. An overview of the model formulations and the corresponding parameter values are given in Table I. We used the vertically averaged adult

Table I: Population dynamics equations as functions of temperature T *(°C), phytoplankton* P *(mg Chl m^{-3}) and parameter values for different stages: (e)ggs, (n)auplii, (c)opepodites and (a)dults*

Process	Development D (days)			Reproduction R (egg/female/day)			Mortality M (day^{-1})		
Formula	$D = a(T − \alpha)^{−2.05}/F_1$ $F_1 = 1 − \exp(−qT^s P)$			$R = r_o \exp[(T − T_1)^2/2r_1^2]F_2$ $F_2 = P^2/(k^2 + P^2)$			$M = m_o Q^{(T−T_o)/10} M_n$ $M_n = 1 + N_{adult}/K_m$		
Species		PS	CT		PS	CT		PS	CT
Parameter values	$a(e)$	2312.0	921.8	r_o	17.56	46.63	$m_o(e)$	0.040	0.350
	$a(n)$	8861.0	4221.6	T_1	42.83	18.65	$m_o(n)$	0.040	0.090
	$a(c)$	11560.0	5217.4	r_1	19.48	7.62	$m_o(c)$	0.025	0.060
	A	13.87	5.3	k	0.50	1.50	$m_o(a)$	0.030	0.040
	$q(e)$	1.00	1.00				Q	6.000	1.900
	$q(n)$	0.05	0.60				T_o	7.000	10.000
	$q(c)$	0.26	0.40				K_m	inf	750.00
	$s(e)$	0.0	0.00						
	$s(n)$	−0.58	−0.40						
	$s(c)$	−1.14	−1.00						

α, T_1 and T_0 are respective reference temperatures (°C), a and m_0 are baseline development and mortality parameters, k and K_m are half-saturation constants for reproduction (mg Chl m^{-3}) and mortality (ind. m^{-3}), respectively, while q, s, r_0, r_1 and Q are dimensionless.

abundance from four seasons (winter: January−March, spring: April−June, summer: July−September, autumn: October−December) to evaluate the simulation results.

The effect of the bottom-up and top-down controls is assessed for each species by comparing the adult abundance in different case runs (N_{sim}) to the control run (N_{ctrl}). The log-transformed ratios, log$_{10}$ (N_{sim}/N_{ctrl}) are computed for different seasons and plotted for the entire model domain. In each case we found a cumulative effect, i.e. the ratio of the abundance change increased from January to December. Very low abundances, as found for PS in the fall, and small abundance changes can have a significant influence on the ratios, which does not necessarily reflect the changes in the overall population size. For this analysis, we compare the ratios during the population abundance peak season (April−June for PS and October−December for CT) to evaluate the respective influences.

RESULTS

Baseline model runs

The model simulations for both PS and CT reproduced the general spatio-temporal patterns derived from the MARMAP/EcoMon [The MARMAP/EcoMon data set used here includes stage-specific PS and CT abundances from the Marine Resources Monitoring, Assessment and Prediction program and the ECOsystem MONitoring program by the National Oceanic and Atmospheric Administration (NOAA)] data set in the GoM−GB regions (Fig. 4). In winter the abundance of PS adult population is <10 inds. m^{-3} in the deep GoM basins but higher on GB. Abundances near the southwest GoM are >100 inds. m^{-3}. In spring the population increases throughout the area with abundances >200 inds. m^{-3} on GB, near the southwest GoM and along the NSS. During the fall, the overall abundance decreases with relatively higher abundance in the shallower areas. Differences between the baseline model run and the observation data exist. For instance, the adult abundances off the western NSS are significantly lower than in observations (20 compared to ca. 200 inds. m^{-3}), and the GB population remains high throughout summer in the model, while observations show a faster decline.

Both modeled and observed CT abundances decrease in the beginning of the year to numbers similar to those of PS in winter and remain low throughout spring (<10 inds. m^{-3} in the basins, <50 inds. m^{-3} on GB). In summer the overall abundance increases significantly and exceeds 100 inds. m^{-3} in most areas, with values over 500 inds. m^{-3} on GB and in the western GoM. After its abundance peak in October, the CT abundance decreases in the deep GoM, while numbers in the shallower areas (<60 m) remain above 200 inds. m^{-3} until the end of the year. The model-computed population takes longer to decline in winter throughout the investigated area, while in summer abundances in the deep GoM increase later and are lower than the observed abundance.

A more quantitative assessment of the model's skill was conducted using an approach designed to compare ecosystem model results and observational data (Radach and Moll, 2006). The idea is to compute cost function (CF) for each model grid bimonthly by dividing the absolute difference between the mean values of model results and observation data by the standard deviation of the observation data. An annually averaged CF value can be derived for the entire model domain. The model is considered to have "very good" skill if CF <1, and "good" skill if 1 < CF < 2 (Radach and Moll,
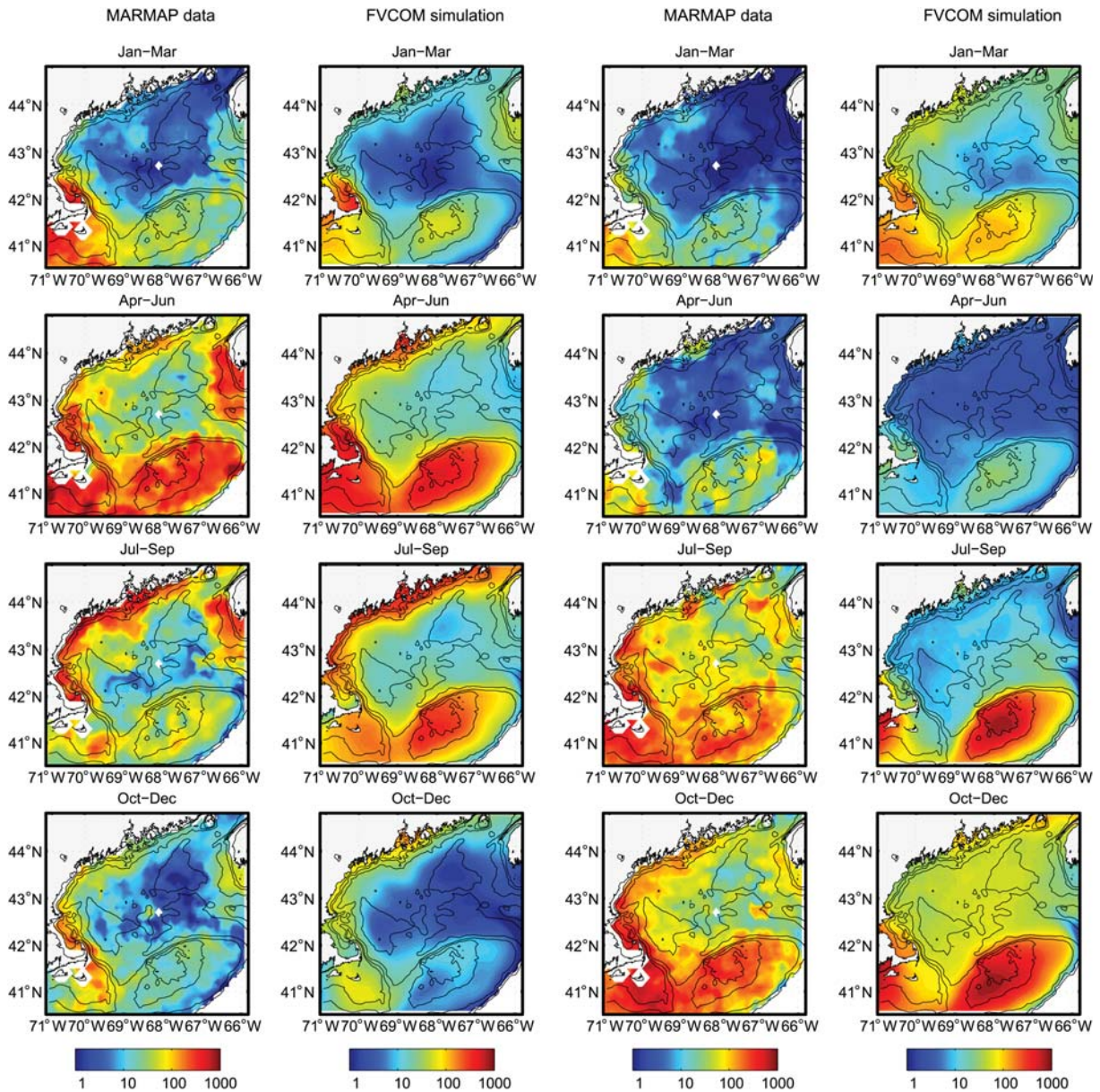
Fig. 4. Comparison of control simulation with the MARMAP/EcoMon data (1977–2006 climatology) of seasonal adult abundances of *Pseudocalanus* spp. and *Centropages typicus* (inds. m^{-3}).

2006). The CF values for CT and PS simulations in this study are 1.138 and 0.861, respectively, which indicates that our model has a reasonably good skill for simulating both species.

Model case runs

In Case 1 (with changes in phytoplankton concentration), an increase of 20% for the overall phytoplankton concentration generally leads to an increase in the copepod population for both species, while the opposite is found for both copepod species at a 20% lower phytoplankton concentration. However, there are spatial differences in the changes. In the GoM the effect of phytoplankton increase or decrease on PS (Fig. 5, upper panel) is generally more homogenous compared with that on CT (Fig. 6, upper panel), which shows opposite spatial patterns when the overall phytoplankton concentrations are increased vs. decreased. A 20% increase of phytoplankton leads to a 2- to 4-fold increase in the peak CT adult abundance in the southern part of the GoM (including GB) but almost no change in the
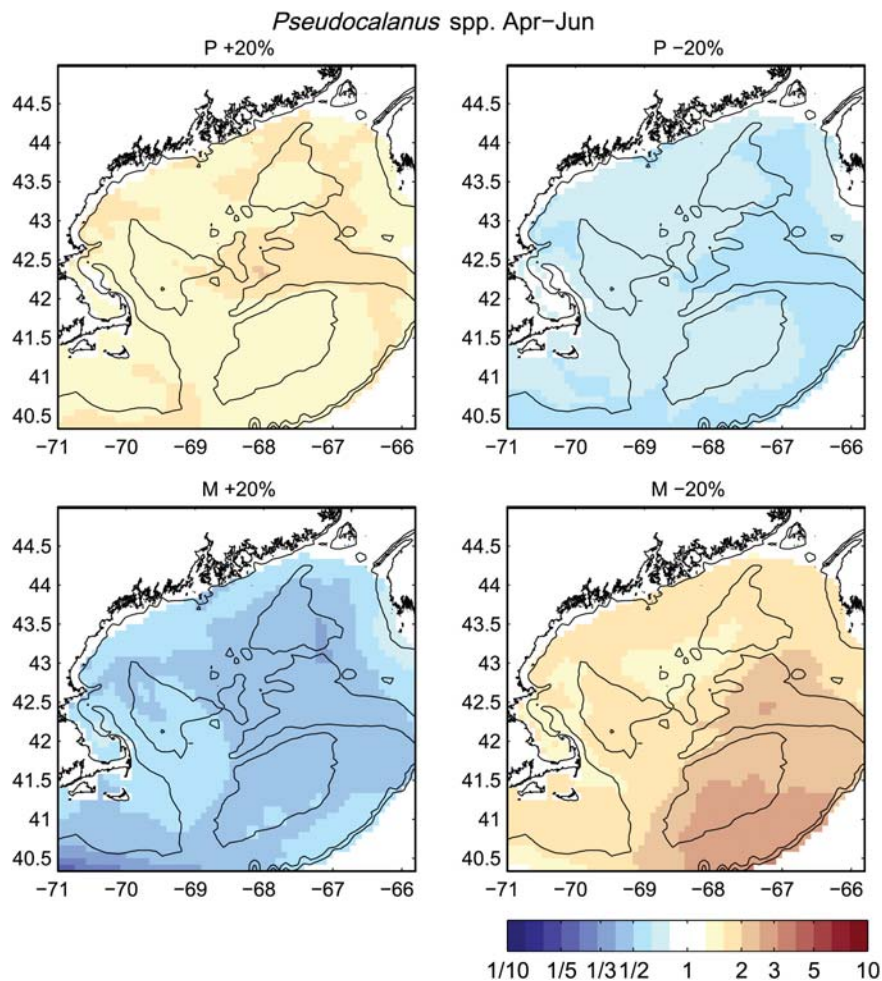
Fig. 5. The effect of changes in the magnitude of food availability (top row) and (predation) mortality (bottom row) on adult abundances of PS comparing simulations N_{sim} with $\pm 20\%$ phytoplankton and $\pm 20\%$ mortality rates with control simulation N_{ctrl}. Colour contour shows the value of $\log_{10}(N_{sim}/N_{ctrl})$ during the population peak season (April–June).

northeastern part. A 20% decrease of phytoplankton leads to 2- to 4-fold decrease in the peak CT abundance in the GoM but much smaller changes on GB.

In Case 2, the change in mortality rates by 20% generally has a stronger effect on both species when compared with the 20% change in the phytoplankton concentration (see Figs 5 and 6 bottom panels for the effect of changes in the mortality rate). Comparing CT with PS, the CT population appears to be more sensitive to mortality changes, as the peak abundance changes by 5- to 10-fold for CT (smallest changes on GB), but only 1- to 3-fold for PS. Spatially, the GoM−GB contrast is less apparent for the PS population when the mortality is increased by 20%, but stronger if decreased by 20% (higher impact on GB than the GoM) (Fig. 5, bottom panel). In contrast, the CT population is less sensitive to mortality changes on the crest of GB compared with most of the GoM system (Fig. 6, bottom panel).

In Case 3 (with changes in the phytoplankton bloom timing) and Case 4 (with changes in the mortality timing), both PS and CT populations are much less sensitive than that in Cases 1 and 2. The spatial distribution of population responses for Cases 3 and 4 is not plotted here. Instead, the results are summarized in a bar plot in Fig. 7, showing a model comparison in different regions, including GB, Wilkinson Basin and Jordan Basin.

The relative sensitivity of the PS and CT population to bottom-up and top-down forcing can be further analyzed (Fig. 7). Three population abundance features were compared between the baseline and case runs, including: (i) the annual mean abundance, (ii) the mean abundance during peak season (April−June for PT and October−December for CT) and (iii) the ratio of abundance in the end (year day 365) vs. the beginning (year day 1) of model runs. For all three abundance features, both species are much more sensitive to changes in
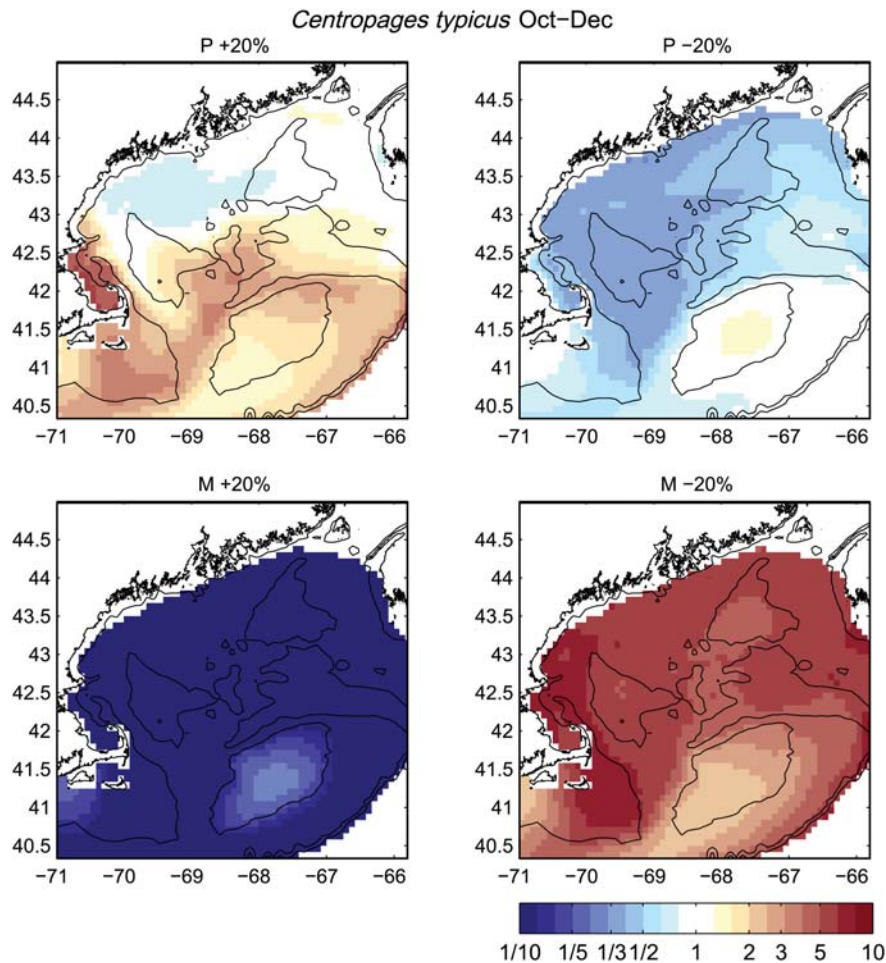
Fig. 6. The effect of changes in the magnitude of food availability (top row) and (predation) mortality (bottom row) on adult abundances of *Centropages typicus* spp. comparing simulation N_{sim} with $\pm 20\%$ phytoplankton and $\pm 20\%$ mortality rates with the control simulation N_{ctrl}. Colour contour shows the value of $\log_{10}(N_{sim}/N_{ctrl})$ during the population peak season (October–December).

mortality rates in all three of the regions we compared, including the shallow GB and two deep basins in the GoM. However, when comparing the two species, phytoplankton changes had a stronger influence on the abundance of PS than CT, while the changes in mortality rates had a stronger influence on CT than PS except on GB. In addition, the changes in the magnitude of phytoplankton concentration and mortality rate have higher impacts on the population than the timing shift of phytoplankton and mortality cycles.

DISCUSSION

Dynamic model vs. static life-table analysis

Our model result shows, as we expected, that both PS and CT populations are more sensitive to changes in

mortality rates than phytoplankton concentrations throughout the model domain. This result supports prior work on GB (Davis, 1984b) as well as the basic conclusions derived from the life-table analysis by Kiørboe and Sabatini (Kiørboe and Sabatini, 1994). For a direct comparison, we inserted our values for vital rates specific to PS and CT and the temperature/food environment specific to the GoM–GB regions into Kiørboe and Sabatini's (Kiørboe and Sabatini's, 1994) population growth rate equation. Temperatures were taken from monthly climate model output and food concentration was based on climatological SeaWiFS data as described by Stegert et al. (Stegert et al., 2010). Results show that the change in the mortality rate is the dominant driver for the population growth rate variability, whereas there was no significant change in the population growth rates for both species with a change in chlorophyll concentrations (Table II). It is worth
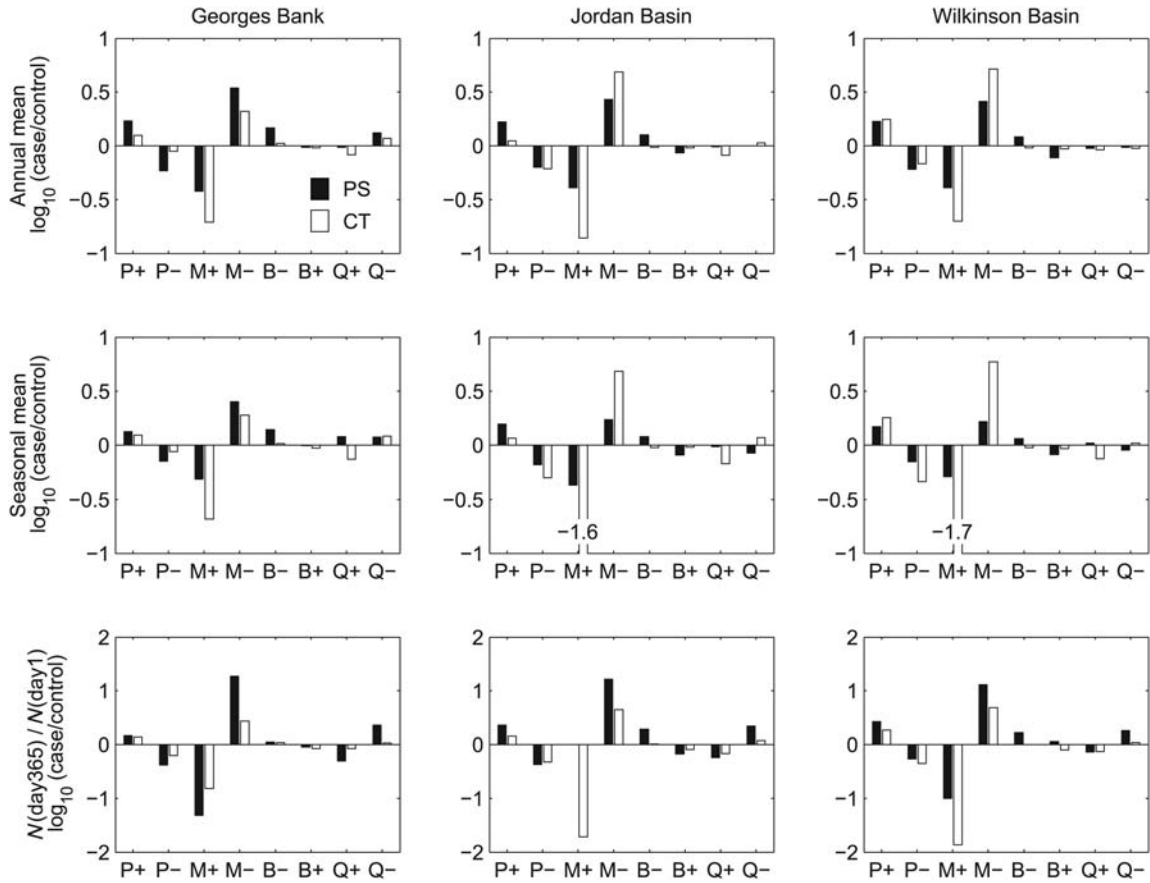
Fig. 7. Deviations for each case scenario from the control simulation (N_{sim}/N_{ctrl}) in three regions (GB, Jordan Basin and Wilkinson Basin), from top to bottom: annual mean abundance, seasonal mean abundance (April–June for PS, October–December for CT), ratio of the abundance in the end of the year [N(day365)] to the abundance in the beginning of the year [N(day1)]. *Notes*: cases are for changes in P, phytoplankton; M, mortality; B, bloom timing and Q, mortality timing (changing Q_{10}, see text for details); *Note*: in the 'M+' case for PS in Jordan Basin, the population abundance $N(d_{365}) = 0$.

Table II: Population growth potential in May and October as estimated by the equation from Kiørboe and Sabatini (Kiørboe and Sabatini, 1994) for our control simulations of PS and CT and percentage deviation from these controls by our case scenarios.

Scenario	PS May	PS Oct	CT May	CT Oct
Control	0.0455	0.0297	0.0372	0.0817
P −20%	−2.0	−7.7	−4.3	−2.6
P +20%	1.3	4.7	3.2	1.8
M −20%	26.6	82.2	61.3	34.1
M +20%	−35.4	−105.1	−79.6	−45.8
M_{nc} −20%	24.4	75.8	40.6	22.0
M_{nc} +20%	−32.3	−96.6	−52.2	−29.7
SB −14 days	nd	nd	nd	nd
SB +14 days	nd	nd	nd	nd
Q −20%	9.7	65.7	21.8	27.4
Q +20%	−10.5	−79.5	−23.7	−34.5

Note: for the monthly model data, no 14-day shift in the food concentration could be included. In the case of M_{nc}, only the naupliar and copepodite (i.e. post-hatching) mortality has been changed.

noting that our model result shows a higher sensitivity to food concentration (although still lower than mortality) than the results based on this static life-table based analysis. This is likely due to the fact that our model not only considers the instantaneous effect of food conditions on reproduction, but also its cumulative effect on development time of the populations at various life stages, which in turn can change the total duration of life cycle and the duration exposed to mortality loss.

The coupled model with full population dynamics goes beyond the static life-table analysis, and assesses population-specific sensitivities at different locations to spatially and temporarily varying forcing. It is noticed from our model results that the CT and PS populations respond to changes in food and mortality differently. First of all, the PS population (Fig. 5), in terms of the peak season abundance, responds to phytoplankton changes more homogenously than the CT population (Fig. 6), with a slightly less effect on GB and the western

GoM. For the CT population, an increase in phytoplankton induces a strong population increase around the edge of GB, but very little impact in the upstream regions (eastern GoM), whereas a decrease in phytoplankton leads to a strong decline in the population in the GoM but has little impact on GB. This spatial pattern is much more complex than the initially expected pattern where higher food concentration on GB makes the population less sensitive to food than in the GoM (see the Introduction). The PS population responds more or less equally to phytoplankton changes throughout the domain. This uniformity is mainly due to the fact that food concentration is sufficiently high during spring throughout the region, and a small change in food has little regional impact on reproduction and development. For the CT population, which peaks during the fall, a 20% decrease in phytoplankton has little impact on peak population size on GB. Also, the dilution effect on the GB population by the lower population abundance from the (upstream) GoM is not significant, since the *in situ* population growth dominates the population dynamics. It is less intuitive in terms of how the population responds to a 20% increase in phytoplankton, as it shows an opposite spatial pattern compared with the case of 20% decrease in phytoplankton. Apparently, the phytoplankton concentration is near a critical threshold in the GoM region, such that a 20% increase has no significant effect on CT population size, but a 20% decrease does. Also, changes in phytoplankton concentrations have shifted the CT population seasonality slightly, so the mean seasonal abundance peak in the fall may decrease (increase) with food increase (decrease). Nevertheless, the overall sensitivity of the CT population to changes in food concentrations is weaker than changes in mortality rates throughout the region.

Our model shows that the CT population responds to changes in mortality rates more strongly than the PS population throughout the domain. This is largely due to the difference in the timing of peak abundance seasons (spring for PS and fall for CT), i.e. the longer duration from the beginning of model runs induces a more severe cumulative effect on CT. It is however interesting to see that mortality changes have less effect on the GB population than that in the GoM for CT (again, this is different from our initial expectation described in the Introduction section). This spatial difference is likely due to the negative feedback caused by cannibalism, an important feature of the CT population (Stegert *et al.*, 2012). For the CT population on GB, the increase in mortality causes the decline in the population size, which then alleviates the intensity of cannibalism, and therefore negates the effect of enhanced base mortality. This negative feedback is more significant in a high abundance region such as GB than in the low abundance GoM region, as the cannibalism is a density-dependent function of the population size (Miralto *et al.*, 1996; Ohman *et al.*, 2002).

Small timing shifts (± 2 weeks) of the phytoplankton peaks appear to have much less impact than a 20% change in phytoplankton concentrations. This finding is very different from the traditional view of the phytoplankton–zooplankton interactions, from which it is expected that a slightly earlier phytoplankton peak can boost the population increase at a time when the zooplankton mortality are still low. This effect is not evident in our model simulation, possibly because the population does not have enough time to respond to bloom timing shifts for a 1-year simulation. However, a multi-year cumulative effect from a phytoplankton peak-timing shift is likely to be weaker compared with the effect of changes in the phytoplankton concentration or mortality rates (Fig. 7, bottom panel). Thus, the shifts in the phytoplankton bloom timing play a second-order role in controlling the abundance variability of the copepod populations examined in this study.

We intentionally limited our model to one-way coupling of the copepod model to the NPZD model (i.e. no feedback on P or Z). The same approach was applied to the copepods – predator linkage: changes in copepods do not affect predators (hence the mortality rate). The Z in the NPZD model is parameterized for microzooplankton, and the NPZD dynamics are robust, resulting in temporal-spatial patterns that are consistent with field observations. The lack of two-way coupling prevents us from assessing the dynamic feedback of copepods to their food (phytoplankton and microzooplankton) and to their predator, which will in turn affect the copepod populations. Development of a full two-way coupled model requires that we explicitly model the copepod species of interest plus other zooplankton components. This will definitely increase model complexity (and associated uncertainty) and require significant additional effort that is needed for future modeling studies.

Bottom-up vs. top-down control

Previously proposed mechanisms of the bottom-up control on zooplankton populations focus on two major pathways. The first proposed pathway is through the timing shift in phytoplankton blooms. Changes in surface shelf-water salinity can alter water column stability, leading to the timing shift in phytoplankton blooms (Durbin *et al.*, 2003; Ji *et al.*, 2007, 2008b), which can further affect the copepod populations along the shelf (Greene and Pershing, 2007; Head and Pepin,

2010; Pershing *et al.*, 2010). This pathway was considered to be the main driver for the observed strong decadal shift in the copepod community structure, with an increased ratio of small- vs. large-sized copepod species in the 1990s compared with that in the 1980s and 2000s (e.g. Mountain and Kane, 2010). However, a recent analysis (Hare and Kane, in press), with an expanded time series of observation data (by including data from late 2000s), found that the observed correlation between the salinity anomaly and copepod community structure does not persist into the 2000s, so salinity alone does not explain the changes in copepod dynamics. Our model result seems to support Hare and Kane's (Hare and Kane's, in press) analysis, although we do not model the full dynamic connection between salinity and copepod populations. Rather, we directly modify the bloom timing from the baseline model results to mimic the established link between changes in salinity and bloom timing. This approach allows us to exclude the potential impact of other biological and physical factors associated with salinity change and have a better assessment of the direct link between phytoplankton and copepod populations.

The second proposed pathway is through changes in the overall primary production and phytoplankton standing stocks, driven by changes in the slope-to-shelf nutrient supply. In the GoM, intrusions of deep slope water through the Northeast Channel and NSS surface water are the most important sources of nutrients supporting the strong biological productivity (Townsend, 1991). Flux of deep nutrients into surface layers is established in winter by wind and convective mixing and maintained throughout the year over shallow regions and along the eastern Maine coast by strong tidally forced vertical mixing. The deep nutrient input into the shelf is affected by intrusions of Slope Water along the shelf edge through the Northeast Channel. The slope water inflow to the GoM shifts between a WSW influenced by the Gulf Stream and a cooler and fresher LSW influenced by the Labrador Current in response to atmospheric forcing indexed by the NAO (MERCINA, 2001). This shift can potentially impact the nutrient budget of the GoM, as the LSW has ~50% lower dissolved inorganic nitrogen (Thomas *et al.*, 2003; Townsend *et al.*, 2006). This change in nutrient influx is hypothesized to cause major shifts in the ecosystem (Steele *et al.*, 2007; Townsend *et al.*, 2010). Based on a process-oriented numerical experiment by Ji *et al.* (Ji *et al.*, 2008a), a change of 50% nutrient concentration at the bottom layer of GoM led to a <10% change in the phytoplankton production and concentration on GB (and similar as in the GoM) throughout the year. This change is smaller than the 20% change in

the phytoplankton concentration we set for the present sensitivity analysis, suggesting that the second proposed pathway is also not the major process for the copepod variability.

The top-down control of copepod populations has been less examined, due to the difficulty in quantifying mortality rates in the field. Our model results suggest that mortality is a more sensitive term in controlling population dynamics than the other terms, including the magnitude and timing of food availability. It is worth noting that the inter-annual variability of potential predator abundance (Fig. 2) is significantly higher than the 20% mortality change specified in our numerical experiments, which would suggest that the model might respond even more dramatically assuming a linear relationship between the predator abundance and mortality rates. Although this assumption is likely to be too strong and over-simplified, it is not a surprise to see 2−3-fold changes of mortality rates from year to year for CT and PS (Ji *et al.*, 2009) and for *Calanus finmarchicus* (Plourde *et al.*, 2009) based on vertical life table calculations for copepods originally developed by Aksnes and Ohman (Aksnes and Ohman, 1996).

The question now becomes, what are the possible drivers for the variation in predators that impose mortality on copepod populations. The trophic cascading hypothesis proposed by Frank *et al.* (Frank *et al.*, 2005, 2011) offered a possible answer; overfishing of large bodied demersal fish populations in the Scotian Shelf (e.g. cod) leads to an increase in planktivorous, forage fish (e.g. herring), which feed on large-sized zooplankton. These large-sized zooplankton not only include the copepod *Calanus finmarchicus* but also predatory zooplanktons such as chaetognaths, amphipods, mysids and krill, which are known predators of small-sized copepods like PS and CT. The general pattern of decadal variation in forage fish biomass from high in the 1990s to low in the 2000s seems to correspond to the opposite shift in a large zooplankton abundance as shown in Frank *et al.* (Frank *et al.*, 2011). However, a solid relationship is yet to be further explored, mainly due to the lack in zooplankton data during the 1980s and forage fish data during the 1960s in the time series. Also, as MERCINA Working Group (MERCINA Working Group, 2012) pointed out, the herring population collapsed after the resurgence of large-size copepods in the 2000s, suggesting that the hypothesis of the top-down control through trophic cascading needs to be reconsidered. In the GoM−GB system, the pattern of high (in the 1980s)−low (in the 1990s) predator abundance (Fig. 2) generally matches the opposite shift in herring stocks (TRAC, 2009), but the predator abundance increased significantly (especially on GB, Fig. 2) even as

the herring population remained high in early 2000s. Therefore, a linear trophic cascading process (cod → herring → zooplankton) alone is not sufficient to explain the observed zooplankton variability. It is likely that the variability is a result of non-linear interaction between the bottom-up and top-down controls involving complex food-web dynamics. The inclusion of gelatinous predators also needs further study, but to date, these delicate organisms have not been well sampled.

CONCLUSIONS

The bottom-up and top-down controls are interactive and difficult to separate when examining the variability in a population within a marine food web. Although the bottom-up control is often hypothesized to be the dominant mechanism for the observed shift in the zooplankton community structure, the top-down control cannot be ignored and in some cases could be more important than the bottom-up control, as suggested by this study. Using a coupled hydrodynamics/food-web/population-dynamics model, we were able to assess the sensitivity of the modeled species (PS and CT) to changes in phytoplankton biomass and bloom timing, as well as the changes in mortality regime. We show that the bottom-up or top-down control alone is not sufficient to explain the observed zooplankton variability, and more attention needs to be paid to examine the mortality rate and associated predator variability, including gelatinous forms.

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REFERENCES

Aksnes, D. L. and Ohman, M. D. (1996) A vertical life table approach to zooplankton mortality estimation. *Limnol. Oceanogr.*, **41**, 1461–1469.

Belkin, I. M. (2004) Propagation of the "Great Salinity Anomaly" of the 1990s around the northern North Atlantic. *Geophys. Res. Lett.*, **31**, L08306.

Bigelow, H. B. (1926) Plankton of the offshore waters of the Gulf of Maine. *Bull. USA Bur. Fisheries*, **40**, 1–509.

Chen, C. S., Liu, H. D. and Beardsley, R. C. (2003) An unstructured grid, finite-volume, three-dimensional, primitive equations ocean model: application to coastal ocean and estuaries. *J. Atm. Ocean. Tech.*, **20**, 159–186.

Davis, C. S. (1982) Processes controlling zooplankton abundance on Georges Bank. Ph.D. Dissertation, Boston University.

Davis, C. S. (1984a) Food concentrations on Georges Bank: nonlimiting effect on growth and survival of laboratory reared *Pseudocalanus* sp and *Paracalanus parvus*. *Mar. Biol.*, **82**, 42–46.

Davis, C. S. (1984b) Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol.*, **82**, 31–40.

Davis, C. S. (1987) Zooplankton life cycles. In Backus, R. H. and Bourne, D. W. (eds), *Georges Bank*. MIT Press, Cambridge, MA, pp. 256–267.

Davis, C. S. and Alatalo, P. (1992) Effects of constant and intermittent food-supply on life-history parameters in a marine copepod. *Limnol. Oceanogr.*, **37**, 1618–1639.

Durbin, E. G. and Casas, M. C. (2006) Abundance and spatial distribution of copepods on Georges Bank during the winter/spring period. *Deep-Sea Res. II*, **53**, 2537–2569.

Durbin, E. G., Campbell, R. G., Casas, M. C. *et al.* (2003) Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. *Mar. Ecol. Progr. Ser.*, **254**, 81–100.

Frank, K. T., Petrie, B., Choi, J. S. *et al.* (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science*, **308**, 1621–1623.

Frank, K. T., Petrie, B., Fisher, J. A. D. *et al.* (2011) Transient dynamics of an altered large marine ecosystem. *Nature*, **477**, 86–89.

GLOBEC (1992) Northwest Atlantic Implementation Plan. U.S. Global Ocean Ecosystem Dynamics Report, vol. 6.

Greene, C. H. and Pershing, A. J. (2007) Climate drives sea change. *Science*, **315**, 1084–1085.

Hamner, W. M., Madin, L. P., Alldredge, A. L. *et al.* (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnol. Oceanogr.*, **20**, 907–917.

Hare, J. A. and Kane, J. (in press). Zooplankton of the Gulf of Maine—a changing perspective. *Am. Fisheries Soc. Symposium*. (in press).

Head, E. J. H. and Pepin, P. (2010) Spatial and inter-decadal variability in plankton abundance and composition in the Northwest Atlantic (1958−2006). *J. Plankton Res.*, **32**, 1633−1648.

Ji, R., Davis, C. S., Chen, C. *et al*. (2007) Influence of ocean freshening on shelf phytoplankton dynamics. *Geophys. Res. Lett.*, **34**, L24607.

Ji, R., Davis, C. S., Chen, C. *et al*. (2008a) Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: a 3-D biological-physical modeling study. *J. Mar. Sys.*, **73**, 31−47.

Ji, R., Davis, C. S., Chen, C. *et al*. (2008b) Modeling the influence of low-salinity water inflow on winter-spring phytoplankton dynamics in the Nova Scotian Shelf-Gulf of Maine region. *J. Plankton Res.*, **30**, 1399−1416.

Ji, R., Davis, C. S., Chen, C. *et al*. (2009) Life history traits and spatiotemporal distributional patterns of copepod populations in the Gulf of Maine-Georges Bank region. *Mar. Ecol. Progr. Ser.*, **384**, 187−205.

Ji, R., Edwards, M., Mackas, D. L. *et al*. (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.*, **32**, 1355−1368. doi:10.1093/plankt/fbq062.

Kane, J. (2007) Zooplankton abundance trends on Georges Bank, 1977−2004. *ICES J. Mar. Sci.*, **64**, 909−919.

Kiørboe, T. and Sabatini, M. (1994) Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *J. Plankton Res.*, **16**, 1353−1366.

Link, J. S. and Ford, M. D. (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. *Mar. Ecol. Prog. Ser.*, **320**, 153−159.

MERCINA (2001) Oceanographic responses to climate in the Northwest Atlantic. *Oceanography*, **14**, 76−82.

MERCINA Working Group (2012) Recent Arctic climate change and its remote forcing of Northwest Atlantic shelf ecosystems. *Oceanography*, **25**. http://dx.doi.org/10.5670/oceanog.2012.64.

Miralto, A., Ianora, A., Poulet, S. A. *et al*. (1996) Is fecundity modified by crowding in the copepod *Centropages typicus*? *J. Plankton Res.*, **18**, 1033−1040.

Mitra, A. and Davis, C. S. (2010) Defining the "to" in end-to-end models. *Progr. Oceanogr.*, **84**, 39−42.

Monger, B. C., Chinniah-Chandy, S., Meir, E. *et al*. (1998) Sound scattering by the gelatinous zooplankters *Aequorea victoria* and *Pleurobrachia bachei*. *Deep-Sea Res. II*, **45**, 1255−1271.

Mountain, D. W. (2003) Variability in the properties of Shelf Water in the Middle Atlantic Bight, 1977−1999. *J. Geophys. Res. Oceans*, **108**, C1, 3014.

Mountain, D. G. and Kane, J. (2010) Major changes in the Georges Bank ecosystem, 1980s to the 1990s. *Mar. Ecol. Progr. Ser.*, **398**, 81−91.

Ohman, M. D. and Hirche, H.-J. (2001) Density-dependent mortality in an oceanic copepod population. *Nature*, **412**, 638−641.

Ohman, M. D. and Wood, S. N. (1996) Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. *Limnol. Oceanogr.*, **41**, 126−135.

Ohman, M. D., Runge, J. A., Durbin, E. G. *et al*. (2002) On birth and death in the sea. *Hydrobiol.*, **480**, 55−68.

Pershing, A. J., Head, E. J. H., Greene, C. H. *et al*. (2010) Pattern and scale of variability among northwest Atlantic Shelf plankton communities. *J. Plankton Res.*, **32**, 1661−1674.

Plourde, S., Maps, F. and Joly, P. (2009) Mortality and survival in early stages control recruitment in *Calanus finmarchicus*. *J. Plankton Res.*, **31**, 371−388.

Radach, G. and Moll, A. (2006) Review of three-dimensional ecological modelling related to the North Sea shelf system. Part II: model validation and data needs. *Oceanogr. Mar. Biol.*, **44**, 1−60.

Richardson, A. J. (2008) In hot water: zooplankton and climate change. *ICES J. Mar. Sci.*, **65**, 279−295.

Smith, P. C., Houghton, R. W., Fairbanks, R. G. *et al*. (2001) Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993−1997. *Deep-sea Res. Pt. II*, **48**, 37−70.

Song, H. J., Ji, R. B., Stock, C. *et al*. (2010) Phenology of phytoplankton blooms in the Nova Scotian Shelf-Gulf of Maine region: remote sensing and modeling analysis. *J. Plankton Res.*, **32**, 1485−1499.

Song, H. J., Ji, R. B., Stock, C. *et al*. (2011) Interannual variability in phytoplankton blooms and plankton productivity over the Nova Scotian Shelf and in the Gulf of Maine. *Mar. Ecol. Progr. Ser.*, **426**, 105−133.

Steele, J. H., Collie, J. S., Bisagni, J. J. *et al*. (2007) Balancing end-to-end budgets of the Georges Bank ecosystem. *Progr. Oceanogr.*, **74**, 423−448.

Stegert, C., Ji, R. and Davis, C. S. (2010) Influence of projected ocean warming on population growth potential in two North Atlantic copepod species. *Progr. Oceanogr.*, **87**, 264−276.

Stegert, C., Ji, R., Li, N. *et al*. (2012) Processes controlling seasonality and spatial distribution of *Centropages typicus*: a modeling study in the Gulf of Maine/Georges Bank region. *J. Plankton Res.*, **34**, 18−35.

Taylor, M. H. and Mountain, D. G. (2009) The influence of surface layer salinity on wintertime convection in Wilkinson Basin, Gulf of Maine. *Cont. Shelf Res.*, **29**, 433−444.

Thomas, A. C., Townsend, D. W. and Weatherbee, R. (2003) Satellite-measured phytoplankton variability in the Gulf of Maine. *Cont. Shelf Res.*, **23**, 971−989.

Townsend, D. (1991) Influences of oceanographic processes on the biological productivity of the Gulf of Maine. *Rev. Aquat. Sci.*, **5**, 211−230.

Townsend, D. W., Rebuck, N. D., Thomas, M. A. *et al*. (2010) A changing nutrient regime in the Gulf of Maine. *Cont. Shelf Res.*, **30**, 820−832.

Townsend, D. W., Thomas, A. C., Mayer, L. M. *et al*. (2006) Oceanography of the Northwest Atlantic Continental Shelf. In Robinson, A. R. and Brink, K. H. (eds), *The Sea*. Vol. 14. Harvard University Press, pp. 119−168.

TRAC (2009) Transboundary Resources Assessment Committee Gulf of Maine/Georges Bank Atlantic Herring Stock Assessment Update. TRAC reference document 2009/04. http://www.mar.dfo-mpo.gc.ca/science/trac/rd.html.