



Model-based estimates of *Calanus finmarchicus* abundance in the Gulf of Maine

Andrew J. Pershing^{1,2,*}, Nicholas R. Record^{1,2}, Bruce C. Monger³,
Daniel E. Pendleton^{1,2,4}, Linda A. Woodard⁵

¹School of Marine Science, University of Maine, Orono, Maine 04469, USA

²Gulf of Maine Research Institute, 350 Commercial St., Portland, Maine 04101, USA

³Ocean Resources and Ecosystem Program, Snee Hall, Cornell University, Ithaca, New York 14853, USA

⁴Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, New York 14853, USA

⁵Center for Advanced Computing, Frank H. T. Rhodes Hall, Cornell University, Ithaca, New York 14853, USA

ABSTRACT: Ocean observing systems and satellites routinely collect a wealth of information on physical conditions in the ocean. With few exceptions, such as chlorophyll concentrations, information on biological properties is harder to measure autonomously. Here, we present a system to produce estimates of the distribution and abundance of the copepod *Calanus finmarchicus* in the Gulf of Maine. Our system uses satellite-based measurements of sea surface temperature and chlorophyll concentration to determine the developmental and reproductive rates of *C. finmarchicus*. The rate information then drives a population dynamics model of *C. finmarchicus* that is embedded in a 2-dimensional circulation field. The first generation of this system produces realistic information on interannual variability in *C. finmarchicus* distribution and abundance during the winter and spring. The model can also be used to identify key drivers of interannual variability in *C. finmarchicus*. Experiments with the model suggest that changes in initial conditions are overwhelmed by variability in growth rates after approximately 50 d. Temperature has the largest effect on growth rate. Elevated chlorophyll during the late winter can lead to increased *C. finmarchicus* abundance during the spring, but the effect of variations in chlorophyll concentrations is secondary to the other inputs. Our system could be used to provide real-time estimates or even forecasts of *C. finmarchicus* distribution. These estimates could then be used to support management of copepod predators such as herring and right whales.

KEY WORDS: *Calanus finmarchicus* · Population dynamics · Model · AVHRR · SeaWiFS · MODIS

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INTRODUCTION

The amount of oceanographic data increases every year. Advances in computing and communication mean that much of this data is available within a few hours of collection. The majority of near realtime data comes from satellites, although data from moored instruments (Schofield et al. 2005), drifters (Schmid et al. 2007), gliders (Schofield et al. 2007) or even tagged animals (Block et al. 2002) are becoming more prominent.

There has been considerable success using realtime data to provide information on physical processes in the ocean. For example, the Tropical Ocean Global Atmosphere-Tropical Ocean Atmosphere (TOGA-TAO) array in the equatorial Pacific provides early warning of El Niño Southern Oscillation (ENSO) events (McPhaden 1993), while satellite sea surface temperature (SST) measurements are a routine input into weather forecast models. However, many of the problems of interest to society are biological in nature; for example, detecting harmful algal blooms or estimating fish recruitment and

*Email: andrew.pershing@maine.edu

biomass. Unlike physical variables, most biological variables are difficult to sense electronically. The main exceptions are the local and global estimates of chlorophyll concentrations from fluorometers or satellite-based color sensors. The abundance of zooplankton and fish can be measured with moored or towed acoustic transducers (Greene et al. 1998, Wiebe et al. 2002) or instruments such as the optical plankton counter (Herman 1988) or video plankton recorder (Davis et al. 1996); however, the spatiotemporal coverage achieved with these methods is limited.

The question facing the marine science community is how can we provide information on higher trophic level properties in the ocean using the available, and largely physical, data? The problem amounts to understanding how the conditions we measure are related to the properties we seek. Physical–biological interactions have been the subject of intense research (e.g. Robinson et al. 2002, Mann & Lazier 2006), and, while our knowledge is imperfect, we are not completely ignorant. What we require are quantitative relationships, i.e. models that capture these physical–biological interactions. By combining large-scale remote observations of chlorophyll concentration and a range of remotely sensed physical variables with knowledge of biological–physical interactions, we can simulate how observed variations in phytoplankton abundance and physical conditions propagate upward through the consumer community.

Here, we apply a model-based approach to provide estimates of *Calanus finmarchicus* abundance in the Gulf of Maine using satellite measurements of SST and chlorophyll. Although *C. finmarchicus* dominates the spring–summer zooplankton biomass over many regions in the North Atlantic, including the Gulf of Maine (Mauchline 1998), societal interest in copepod abundance is limited. However, *C. finmarchicus* is an important prey item for many species that are of interest, for example larval cod and haddock (Kane 1984), Atlantic herring (Darbyson et al. 2003) and North Atlantic right whales (Mayo & Marx 1990). The ability to estimate or even forecast right whale distributions from fields of *C. finmarchicus* abundance is a main motivator of our work and is explored in a companion paper (Pershing et al. 2009, this volume).

Our project's main challenge was to estimate the abundance of *Calanus finmarchicus* on time scales of days to weeks using measurable properties. Three facts are at the center of our solution: *C. finmarchicus* development rate is largely a function of temperature (Campbell et al. 2001); egg production rate is largely a function of food availability expressed as chlorophyll concentration (Runge & Plourde 1996, Durbin et al. 2003); and both temperature and chlorophyll can be measured by satellites. Although our model attempts to provide accurate estimates of *C. finmarchicus* abundance, we recognize

that uncertainties in model inputs (e.g. initial and boundary conditions) and parameterization (e.g. mortality) will introduce uncertainty into our abundance estimates. However, our hypothesis is that model-based estimates of *C. finmarchicus* abundance can provide a meaningful index of interannual variability in this species, and furthermore, that this index can provide unique information on higher trophic levels.

All models are approximations, and it is the job of the modeler to identify the processes that must be represented explicitly, those that must be parameterized in some way and those that can be ignored. For our work, *Calanus finmarchicus* life history and population dynamics lead to a clear set of processes that must be included. The modeler is also constrained by the information available to force the model and to assess its reliability. Our focus on using satellite data to drive the model provides an additional set of constraints on our model specification.

The first step in our model development is to identify the aspects of *Calanus finmarchicus*'s life history that will be included in the model. Development in *C. finmarchicus* follows the pattern of all calanoid copepods. After hatching, *C. finmarchicus* transitions through 6 naupliar stages (designated N1–N6) followed by 5 copepodid stages (C1–C5) before reaching adulthood (C6). The 13 life stages of *C. finmarchicus* are a natural starting point for the model. The rate at which individuals transition through the stages determines the generation time, and thus, how fast the population can increase. Stage durations are largely a function of temperature (Campbell et al. 2001), with an individual taking 56 d to reach stage C5 at 4°C, and 30 d at 12°C. This delay will cause *C. finmarchicus* abundance patterns to deviate from anomalies in the satellite data; therefore, satellite data alone will be an inadequate proxy for *C. finmarchicus* abundance. Other properties, notably mortality rate, also change with stage (Eiane et al. 2002, Ohman et al. 2004), underscoring the need for the model to resolve stage structure.

Calanus finmarchicus has a well-defined phenology that must be captured by the model. Beginning in early summer, some C5s delay their development and enter a state of reduced activity known as diapause. Diapausing C5s descend to depth, below 100 m in the Gulf of Maine (Durbin et al. 1997), and up to 1000 m in the Norwegian Sea (Heath 1999), where they remain for several months. The dynamics of diapause impose constraints on both the spatial and temporal distribution of this species, constraints that can be exploited in developing a model. Because *C. finmarchicus* requires deep water during diapause, its distribution during autumn and winter in the Gulf of Maine is limited to the deep basins (Meise & O'Reilly 1996). Thus, the end of the diapause period is a natural time to begin a model, with the added benefit

that we have a reasonable estimate of the initial distribution, both in space and across stages, for the population.

Beginning in early winter, individuals emerge from diapause, ascend to the surface waters and molt into adults. The adults from the over-wintering (or more appropriately, over-autumning) population are referred to as 'generation zero' (G0). As waters warm and phytoplankton abundance increases, *Calanus finmarchicus* egg production increases and the first generation (G1) is spawned. In the Gulf of Maine, G1 appears as an abrupt increase in the adult population around mid-April (Meise & O'Reilly 1996). Moving from spring into summer, a larger proportion of C5s transition to diapause and the abundance of *C. finmarchicus* at depth increases. Because of *C. finmarchicus*'s diapause dynamics, the abundance of C5s and adults in the surface waters begins to decline in mid-summer, reaching a minimum in early winter (Meise & O'Reilly 1996). Furthermore, as waters become stratified during the summer, the remaining surface population can exhibit diel vertical migration, although in the Gulf of Maine this migration is highly variable (Durbin et al. 1995). Thus, both ontogenetic and high-frequency vertical migrations mean that surface measurements of temperature and chlorophyll will be less representative of the conditions experienced by *C. finmarchicus* during the summer, and we elect to end our simulations in this period. For this reason, we also decided against a vertically resolved 3D model; instead, we focus on modeling the population of *C. finmarchicus* near the surface.

Based on our review of *Calanus finmarchicus* biology, we conclude that temperature-dependent growth and chlorophyll-dependent egg production should provide a good representation of the conditions affecting the *C. finmarchicus* population. Starting from the beginning of the year, when the spatial distribution and stage distribution are known, will simplify the modeling, especially in light of limited observational data. Finally, satellite data should provide a good characterization of the environmental conditions influencing *C. finmarchicus* during the winter and spring; however, diel and ontogenetic migrations will complicate the relationship between satellite data and *C. finmarchicus* dynamics in the summer.

METHODS

The main goal of the present study was to develop a model of *Calanus finmarchicus* abundance that can be driven by satellite data. The constraints imposed by *C. finmarchicus* life history and satellite data led to a specification for the model. Model implementation involves selecting parameterizations for processes that

cannot or will not be directly modeled, and specifying initial and boundary conditions. Before the model can be applied to higher trophic levels, we need to evaluate the accuracy of the model and understand its strengths and limitations through comparisons with available observations.

Satellite data. A main goal of our project was to use available information to characterize the development of the *Calanus finmarchicus* population in the Gulf of Maine. Satellites provide a synoptic view of ocean conditions at high spatial and temporal resolutions. Our project used sea surface temperature (SST) and chlorophyll data from 1998 to 2006 to simulate seasonal and interannual changes in the Gulf of Maine *C. finmarchicus* population.

SST data for 1998 to 2003 were derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor and for 2003 to 2006 from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on the Aqua satellite. AVHRR data were available at 4 km resolution and were downloaded from the NASA Jet Propulsion Laboratory's Physical Oceanography Distributed Active Archive Center (PO-DAAC). Data with quality level less than 5 were masked. The Aqua MODIS SST data were downloaded as Level 2 local area coverage (1 km resolution) files from the Ocean Color Web (Feldman & McClain 2007a) and mapped to a cylindrical coordinate system. Quality control flags and masks used in the present study were the same as those used in the standard processing stream employed by the Ocean Biology Processes Group (OBPG) at NASA Goddard Space Flight Center.

As with SST, we used the MODIS instrument on the Aqua satellite for chlorophyll data for the period 2003 to 2006, while data prior to 2003 were obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). For both instruments, daily Level 2 local area coverage (1 km resolution) files were downloaded from the Ocean Color Web (Feldman & McClain 2007a,b) and mapped to a cylindrical coordinate system. SeaWiFS standard chlorophyll was derived using the OC4v4 pigment algorithm (O'Reilly et al. 1998, 2000), and chlorophyll values from MODIS were computed with the OC3 pigment algorithm (O'Reilly et al. 2000). Quality control flags and masks were the same as those used in the standard processing stream by OBPG.

Satellite images of the Gulf of Maine are frequently obscured by clouds. To provide a complete estimate of surface conditions for our *Calanus finmarchicus* model we developed a robust interpolation procedure. First, composite images for each data type (SST and chlorophyll) were created by averaging over all images collected during each 8 d period. The 8 d interval is several times shorter than the copepod generation

times in Campbell et al. (2001), and thus, should adequately resolve the influence of temperature and chlorophyll on copepod population dynamics. The composite images were then smoothed by replacing each pixel by the median of the 3×3 pixel block surrounding it. Then, we used a statistical interpolation procedure, analogous to objective analysis, to fill for the cloud-obscured pixels. The interpolation merges an incomplete set of observations (the smoothed 8 d composites), with a prior estimate of the data (the interpolated field from the previous 8 d) into an analyzed field. The interpolation procedure is based on a multi-grid implementation of a Markov random field image restoration algorithm (Felzenszwalb & Huttenlocher 2006). This procedure produces analyzed fields comparable to standard objective analysis but requires only a fraction of the computer time. The satellite data were then projected on to the finite element mesh by extracting the satellite observation closest to each mesh node.

For our model, we wanted a temperature value that represents the average conditions experienced by the *Calanus finmarchicus* population in the surface mixed layer. However, satellite SST data only represents the ocean skin temperature. To obtain an estimate of mixed-layer temperature (T) from the satellite estimates (SST), we fit a function to vertical distributions of temperature from the deep areas of the Gulf of Maine for 1 January to 1 June obtained from the Bedford Institute of Oceanography's Climate Database. The function:

$$T(z, \text{SST}) = c_1 + c_2 \text{SST} + c_3 \text{SST}^2 + z(c_4 + c_5 \text{SST} + c_6 \text{SST}^2)$$

accurately captures the relationship between skin temperature and temperature at depth z ($r^2 = 0.83$, $p < 0.01$). This equation was then used to estimate the average temperature between 0 and 50 m.

Calanus finmarchicus data. Two *Calanus finmarchicus* datasets were used to ground truth the model. In both datasets, stages C5 and C6 (adults) were binned together. Between 1977 and 1987, the US National Marine Fisheries Service (NMFS) conducted plankton surveys across the NW continental shelf as part of the Marine Resources Monitoring, Assessment and Prediction program (MARMAP) (Meise & O'Reilly 1996). Samples were collected every 1 to 2 mo at approximately 25 km intervals using 333 μm bongo nets. The nets were towed obliquely to within 5 m of the bottom or to 200 m in deeper areas. To compare with our 2D model, we adjusted the MARMAP concentrations under the assumption that all of the copepods were captured within the top 10 m. The 1977–1987 MARMAP dataset provides an excellent summary of the spatial pattern and seasonal evolution of the zooplankton community and has become the standard ref-

erence dataset for zooplankton models in the Gulf of Maine (Lynch et al. 1998, McGillicuddy & Bucklin 2002). In keeping with these studies, we used the MARMAP data to quantify the model's ability to capture the seasonal cycle in our reference regions. This dataset was also used as a reference when tuning the mortality parameters.

Although MARMAP-style bongo net surveys have continued under the Ecosystem Monitoring (ECOMON) program, the temporal resolution of this survey (4 times per year) does not support an effective evaluation of our model's ability to capture interannual changes. For interannual changes, we used data from NMFS's continuous plankton recorder (CPR) survey (Jossi & Goulet 1993). The CPR instrument is towed behind a commercial ship and samples the top ~10 m of the water column. The survey, which began in 1961 and continues to this day, is conducted approximately monthly along a transect from Boston, Massachusetts, to Yarmouth, Nova Scotia, and samples are processed according to the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) protocols (Warner & Hays 1994). We divided the 1998–2006 CPR data into 6 regions based on bathymetry (Fig. 1a). CPR samples within each reference region were log-transformed and binned into 50 d intervals for graphical comparisons. All statistics were conducted using individual samples. We specifically avoided adjusting the model parameters to fit the CPR data so that these data could be used to evaluate the ability of the model to capture interannual changes in *Calanus finmarchicus*.

Calanus finmarchicus model implementation. Our model implementation builds on previous zooplankton modeling work in the Gulf of Maine (Lynch et al. 1998, McGillicuddy et al. 1998). As in those studies, we envision *C. finmarchicus* distributed evenly in a layer, which in our case is 0 to 10 m. The rate of change of abundance (C) at any point in space can be described by a 2D advection-reaction-diffusion equation:

$$\frac{\partial C}{\partial t} = -\mathbf{u} \cdot \nabla C + \frac{1}{h} \nabla(kh \nabla C) + R(C, \mathbf{x}, t) \quad (1)$$

where $u(x, y, t)$ and $k(x, y, t)$ are the velocity vector and horizontal diffusivity integrated over the layer $h(x, y)$, respectively. Thus, the first term represents advection, the second term diffusion, and the third term the reactions, i.e. the biology. We approximated the fields C , u and k on an unstructured mesh of triangles (Fig. 1b; see also Fig. 4 in Lynch et al. 1998). The unstructured mesh allows for higher spatial resolution in areas of sharp gradients (e.g. the frontal region around Georges Bank). The diffusion term in Eq. (1) is solved implicitly using Galerkin finite elements, while the advection term is solved explicitly using a first order

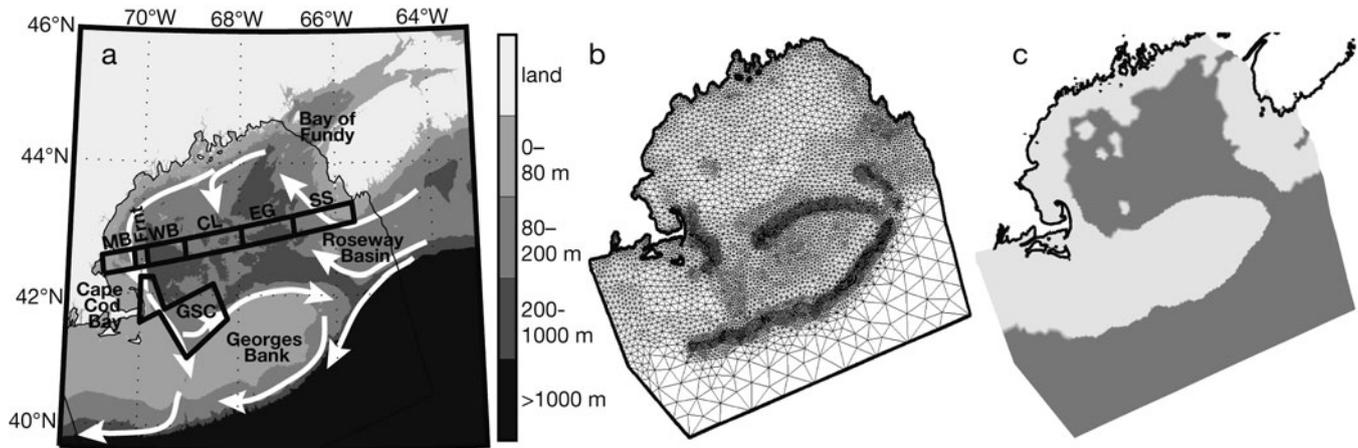


Fig. 1. (a) Bathymetry (shading) and circulation (arrows) of the Gulf of Maine. Regions referenced in the present study are indicated by black polygons. The Great South Channel (GSC) is the major late-spring–early summer right whale feeding ground. The Gulf of Maine continuous plankton recorder (CPR) survey route was divided into 6 regions based on bathymetry: MB (Massachusetts Bay), Frnt (Front Region), WB (Wilkinson Basin), CL (Central Ledges), EG (eastern Gulf of Maine) and SS (Scotian Shelf). (b) Boundary of the finite element mesh (thin black line) used by the model, the same mesh used in Lynch et al. (1998). (c) Distribution of C5 and adult *Calanus finmarchicus* concentration at the beginning of the simulation: (Dark gray regions) 25 m⁻³; (light gray regions) 1 m⁻³. Concentrations over the deep basins were adjusted in each year according to the winter CPR values

semi-Lagrangian method (Durrant 1999). The reaction term is solved using a first order (Euler) method.

The advection-reaction-diffusion framework requires the user to specify the physics (advection and diffusion) and the biology (reaction). Together, these terms determine the internal dynamics of the model. In addition to the internal dynamics, external factors influence the model in the form of the distribution of copepods at the start of the simulation and the copepod abundances at the inflow boundaries.

The physical fields (u and k) were taken from the bimonthly climatology of Naimie (1996). These 3D flow fields capture the essential features of the Gulf of Maine circulation and include realistic tidal forcing, bimonthly temperature and salinity fields, and forcing from climatological heating and winds. These fields are a good representation of the Gulf of Maine circulation, especially on time scales of several weeks (Lynch & Naimie 2002), but do not capture weather-band forcing or persistent deviations from the climatology.

One of the main limitations of the Naimie (1996) fields is that the model domain is cut at the mouth of the Bay of Fundy. For our purposes, this means that we are unable to track the development of the *Calanus finmarchicus* community as it enters the Bay of Fundy. Rather than specify boundary conditions in this domain, we chose to modify the flow field to simulate a land boundary at the Bay of Fundy by eliminating the velocity component perpendicular to the boundary. Thus, rather than entering the Bay of Fundy, copepods slide along the boundary. Although clearly unphysical, this compromise allows abun-

dance anomalies to propagate through the entire domain rather than being erased at the Bay of Fundy boundary.

Following Lynch et al. (1998), we use a 13 component (egg + 6 naupliar stages + 5 copepodid stages + adult) reaction term. The reaction term (R in Eq. 1) for stage j is given by:

$$R_j = g_{j-1}C_{j-1} - g_jC_j - m_jC_j \quad (2)$$

where $g_j(x, y, t)$ is the rate at which individuals develop from stage j to stage $j + 1$ and $m_j(x, y, t)$ is the mortality rate. The first term is the number of individuals molting into stage j from stage $j - 1$, the second term is the number molting to the next stage and the third term is the number dying. Since adults do not molt, g_{13} is 0. For eggs, the first term is replaced by the egg production rate, $EPR(x, y, t)C_{13}$.

If the time-step of the simulation is smaller than the stage duration ($1/g$), then the model will have a tendency to prematurely leak individuals to advanced stages, a process known as developmental diffusion (reviewed in Gurney et al. 2001). To accurately represent advection, we used a time step of 1200 s (20 min); however, stage-durations in *Calanus finmarchicus* (see below) are on the order of several days (Campbell et al. 2001). To minimize developmental diffusion, we followed the approach of Davis (1984) and divided each stage into several substages. We experimented with a range of substage resolutions and found that the seasonal development converged at around 5 substages per life stage. Further increasing the number of substages did not lead to any noticeable changes in the population's seasonal development.

Development and egg production rates in *Calanus finmarchicus* are known to vary as functions of both temperature and food availability, with chlorophyll concentration a standard proxy for food. From lab experiments, Campbell et al. (2001) measured stage durations (D) at a series of temperatures (T) and fit a Belehrádek function (parameters a_j , β and T_d) (Belehrádek 1935) for each stage:

$$D_j = a_j(T + T_d)^\beta \quad (3)$$

The Campbell et al. (2001) parameter values serve as the basis of most *C. finmarchicus* models (Lynch et al. 1998, Zakardjian et al. 2003, Speirs et al. 2006), including ours (Table 1). At maximum temperature, development rate varies in proportion to chlorophyll (F in mg m^{-3}) as an Ivlev function (Ivlev 1961), representing the proportion of maximum development rate:

$$S_j = 1 - e^{-qFb_j} \quad (4)$$

where q is the carbon:chlorophyll ratio and b_j is the food dependence. The Ivlev function increases more slowly as F increases and approaches 1 in the limit. Using the values in Tables 1 & 2, S reaches 0.95 at chlorophyll values of 0.46 mg m^{-3} in nauplii and 0.45 mg m^{-3} in copepodids. To get the development rate, we multiplied S_j by the maximum growth rate, $1/D_j$.

Field measurements by Durbin et al. (2003) suggest that *Calanus finmarchicus* egg production in the Gulf of Maine depends strongly on food availability (e.g. chlorophyll) and only weakly on temperature. Based on their results, we computed EPR as an Ivlev function:

$$EPR_j = EPR_{\max}(1 - e^{-qFb_{EPR}}) \quad (5)$$

With $b_{EPR} = 0.0069$, egg production reaches 95% of the maximum at 2.2 mg m^{-3} , and is 75% of the maximum at 1 mg m^{-3} .

Mortality rates are notoriously difficult to measure in wild populations, yet they are a critical component of population models. For our model, we needed a mortality function that captures ontogenetic and seasonal changes in mortality. The function should also incorporate an element of density dependence. Speirs et al. (2006) developed a temperature and food-dependent mortality function that has many of these qualities. Having mortality change with temperature provides seasonal variability, but tied to conditions in the water rather than to the calendar. Speirs et al. (2006) inferred parameter values by comparing their model to *Calanus finmarchicus* abundance across the North Atlantic. For the present study, we assume that the functional form of their

mortality function is correct but that the parameter values may need adjustment to simulate conditions in the Gulf of Maine.

The Speirs et al. (2006) formulation imagines a baseline mortality value, ϕ_j , for each stage. This value is scaled by an increasing function of temperature, $\gamma(T)$, and an additional density dependent term $\kappa\bar{C}$, where \bar{C} is the total *Calanus finmarchicus* biomass. Additional mortality $\mu(F)$ is added when food is low. Together, the total mortality is given by:

$$M_j(T, F) = \gamma(T)\phi_j(1 + \kappa\bar{C}) + \mu(F) \quad (6)$$

Speirs et al. (2006) used stage-based mortalities (ϕ_j) from Eiane et al. (2002).

The temperature dependence function

$$\gamma(T) = \gamma_0 + (1 - \gamma_0)(T / T_c)^n \quad (7)$$

is < 1 if temperature is below the threshold temperature T_c (assuming $\gamma_0 < 1$). As temperature increases beyond T_c , mortality increases rapidly. In the North Atlantic context described by Speirs et al. (2006), the threshold temperature restricts *Calanus finmarchicus* to cooler waters. In our model, the function keeps the population from growing unrealistically in the warmer slope waters. The function also serves to increase mortality during the summer.

The Speirs et al. (2006) mortality function adds additional mortality if food is less than some critical value F_c :

$$\mu(F) = \mu_{\max}(1 - F / F_c) \quad (8)$$

As food increases, the food dependent mortality falls, and is held at zero if $F > F_c$. Finally, we added an additional mortality of 0.04 d^{-1} in regions shallower than 40 m. This provided more realistic spatial patterns and

Table 1. Stage-dependent variables used in the *Calanus finmarchicus* model. The base configuration of the model used stage-based mortality rates (ϕ_j) from Eiane et al. (2002). These values were reduced for 3 stages (N3, C5 and adult) to produce a better agreement with the MARMAP data. a_j and b_j values from Campbell et al. (2001); w_j values from Speirs et al. (2006)

Stage	Index j	Belehrádek a_j (d)	Mortality ϕ_j (d^{-1})	Ivlev b_j	Dry weight w_j (μg)
Egg	0	595	0.182	0.0329	0.50
N1	1	388	0.336	0.0329	0.33
N2	2	581	0.336	0.0329	0.49
N3	3	1387	0.149/0.026	0.0329	1.0
N4	4	759	0.026	0.0329	1.5
N5	5	716	0.026	0.0329	2.1
N6	6	841	0.026	0.0329	2.8
C1	7	966	0.015	0.0333	4.2
C2	8	1137	0.015	0.0333	13
C3	9	1428	0.02	0.0333	23
C4	10	2166	0.02	0.0333	64
C5	11	4083	0.15/0.02	0.0333	170
Adult	12		0.01/0.0001		276

Table 2. Parameter values for the *Calanus finmarchicus* model

Parameter	Description	Value	Source
γ_0	Baseline temperature-dependent mortality	0.3	Chosen
T_c	Critical temperature for mortality	6°C	Chosen
η	Exponent for temperature-dependent mortality	7	Speirs et al. (2006)
κ	Density-dependent mortality	$3 \times 10^{-6} \text{ mg}^{-1}$	Speirs et al. (2006)
F_c	Starvation threshold	8 mg C m^{-3}	Speirs et al. (2006)
μ_{max}	Maximum food-dependent mortality	0.026 d^{-1}	Chosen
μ_{can}	Cannibalism	$0.033 \text{ d}^{-1} \text{ adult}^{-1}$	Ohman et al. (2004)
	Additional mortality in waters <40 m	0.04 d^{-1}	Chosen
EPR_{max}	Maximum egg production rate	50.7 d^{-1}	Durbin et al. (2003)
q	Carbon:chlorophyll ratio	100	Lynch et al. (1998)
b_{EPR}	Ivlev parameter for <i>EPR</i>	0.0138	Durbin et al. (2003)
β	Exponent for Belehrádek function	-2.05	Campbell et al. (2001)
T_d	Temperature standard for Belehrádek function	9.11°C	Campbell et al. (2001)

prevented unrealistically high values along the coast and on Georges Bank.

One of the most common predators on the eggs and early naupliar stages of *Calanus finmarchicus* are the adult stages of this species (Ohman & Hirche 2001). We simulated cannibalism by adding additional mortality to the egg and first naupliar stage equal to $\mu_{\text{can}} C_{13}$, where C_{13} is the adult abundance and μ_{can} is $0.033 \text{ d}^{-1} \text{ adult}^{-1}$ as in Ohman & Hirche (2001).

Simulations were started from an initial condition representing the *Calanus finmarchicus* distribution on 1 January and integrated for 150 d (through 30 May). Due to its preference for deep water during diapause, *C. finmarchicus* tends to be rare in shallow water in winter and more abundant over the deep basins on the Gulf of Maine (Meise & O'Reilly 1996). From this information, we created a simplified initial condition with 25 m^{-3} split evenly between C5s and adults over the deep basins and 1 m^{-3} over waters shallower than 150 m (Fig. 1c). However, the main purpose of the present study was to reproduce realistic variability in the abundance of *C. finmarchicus*. Starting from a climatological distribution ignores variability in the size of the overwintering population (e.g. Heath et al. 2004, MERCINA 2004). To examine the dependence of the spring *C. finmarchicus* population on the size of the overwintering stock, we created an initial condition for each year by scaling the deep water population in direct proportion to the ratio of the early abundance (Days 1 to 50) from the CPR survey to the climatological abundance during that period.

The other remaining external forcing is the abundance at the open boundaries. Surface waters enter the Gulf of Maine primarily along the eastern boundary on the Scotian Shelf. We used Dirichelet-type boundary conditions and specified the abundance of each stage at any point in time between Days 0 and 150. The stage structure was assumed to be dominated by C5s and

adults, with a peak in early May matching the G1 peak on the Scotian Shelf. This boundary condition time series was applied at any open water node, including those in the slope water. However, only the boundary conditions on the Scotian Shelf influenced the population in the Gulf of Maine.

Model fitting. There is considerable uncertainty with many of the parameters in the model. For example, the parameters in the Speirs et al. (2006) mortality formulation were developed using data from the entire North Atlantic, especially the eastern portion of the basin. It is likely that differences in the predator community and possibly the *Calanus finmarchicus* population in the Gulf of Maine will necessitate a change in the parameters to produce reliable estimates of *C. finmarchicus* in the Gulf of Maine. Starting from an initial configuration of the model using parameters from the literature, we began systematically varying different parameters in the mortality functions and comparing the output with the MARMAP climatology. We then selected a combination of parameter values that adequately captured the seasonal development of the *C. finmarchicus* population in the Gulf of Maine. These parameter values were used for subsequent model runs.

Model runs. After fitting, we conducted a full run of the model, using interannually varying initial conditions, SST and chlorophyll. In addition to the full run, we conducted 3 runs to evaluate the relative importance of these inputs as sources of interannual variability in *Calanus finmarchicus*. For each run, we replaced 2 of the inputs (either initial conditions, SST or chlorophyll) with their 1998–2006 climatologies. We did not test the influence of boundary conditions as we do not have a time series of *C. finmarchicus* concentration from the western Scotian Shelf.

Statistical analysis. Within a 50 d period in a particular year, the CPR data from a region contains only a

handful of samples (mean = 5.5, range = 0–12). Furthermore, the CPR data is highly variable due to the small volume of water filtered (~3 m³, Jossi & Goulet 1993) and fine-scale patchiness in *Calanus finmarchicus* that cannot be captured by the model. For these reasons, our comparison between the model and the CPR will focus on broad patterns in the correlations, and will consider whether the model–data correlation is positive. Because of the high variability, we did not compare the model with the 50 d means used to examine the CPR patterns; instead, we paired each CPR sample with the value from the model at that point in space and time. We then examined the correlation between the CPR and the model for each CPR region (Fig. 1a) and each 50 d period. We also computed the correlation using data from all of the regions over the last 50 d.

To account for the possibility of finding significant correlations by chance, we employed a Monte Carlo procedure similar to the 'field significance' test described in Barton et al. (2003). To estimate the probability of finding *N* correlations with significance values at a particular level, we generated a random CPR time series for each region and 50 d period and computed the correlations with the model output. The random CPR series for a particular region and time period were created by selecting (with replacement) from the CPR samples from that region and time of year. We then totaled the number of correlations that were significant at the desired level. We repeated this process 10 000 times to produce a probability distribution for *N*.

RESULTS

The seasonal cycle of cooling and warming drives the climatological annual cycles of phytoplankton and zooplankton in the Gulf of Maine. All regions in the Gulf of Maine have a temperature minimum between Days 50 and 100, with the minimum occurring later in the year as one moves north and east (Fig. 2a). The western regions have a more continental climate; consequently, their winter temperatures are cooler and they warm up faster during the summer (Brown & Irish 1993).

Chlorophyll concentrations in the Gulf of Maine follow the classic spring bloom pattern. In regions away from the coast (Wilkinson Basin, Central Ledges, eastern Gulf of Maine and Great South Channel), winter chlorophyll levels are consistently below 1 mg m⁻³ throughout the winter (Fig. 2b). Beginning in mid-March (Day 75), chlorophyll values in these regions increase rapidly, peaking in late April (Day 110) at more than 2 mg m⁻³, and then decline. In

Massachusetts Bay, the most coastal region, chlorophyll values are always above 2 mg m⁻³ and reach a peak of 4.5 mg m⁻³ at the end of April (Day 120). Chlorophyll patterns in the Front Region are similar to Massachusetts Bay, although the values are consistently lower.

Based on the chlorophyll patterns, *Calanus finmarchicus* egg production should be limited over most of the Gulf of Maine until mid-March (Day 75). The rapid increase in both temperature and food after this date should support a corresponding increase in the *C. finmarchicus* population. *C. finmarchicus* abundance measured by the MARMAP survey peaked in all regions in mid-April (Day 100) (Fig. 2c), 25 d after the start of the spring bloom. According to the Ivlev function in Campbell et al. (2001), at 4°C, *C. finmarchicus* requires 56 d to develop from an egg to a C5. The discrepancy in timing suggests that the G1 peak results from eggs spawned prior to the spring bloom.

Runs of the model from the initial parameter configuration produced abundances that were much lower than the MARMAP values. To bring our model closer to the climatology, we explored a range of mortality parameters, as these relationships are less well-known than those for egg production or development. To yield a better agreement with climatological *Calanus finmarchicus* observations, we took several steps to reduce the total mortality. First, we reduced the mortality of N3, C5 and C6 to 0.026, 0.02 and 0.0001 d⁻¹, respectively. These values, and the resulting decline in mortality with stage, are consistent with other measurements from the North Atlantic (Ohman et al. 2004). We also reduced the coefficient of food-dependence, μ_{\max} , from 1 to 0.026 d⁻¹. Finally, we reduced the critical temperature, T_c , in the temperature-dependent mortality function from 8 to 6°C. Reducing T_c increased mortality in warmer waters and produced a more realistic seasonal cycle. Our exploration of the parameter space was not exhaustive, and it is possible that there are other parameter combinations that would fit the data as well or better than the values we selected.

The model captures the essential features of the *Calanus finmarchicus* population, especially in the western Gulf of Maine (Fig. 2c). After an early peak in abundance during the first month, the populations in the Front Region and Wilkinson Basin decline toward a minimum around mid-February (Day 50), and then increase rapidly through mid-May (Day 130). The modeled abundances are in line with those from MARMAP; however, there are some subtle differences between the model and observations. Although the late spring abundance peak agrees well with the data, the modeled *C. finmarchicus* populations begin increasing in mid-February, rather than remaining

low. The coastal region Massachusetts Bay begins low and increases steadily through mid-May. The Great South Channel exhibits only a slight decline in mid-March followed by a modest increase. The temporal pattern in Great South Channel is consistent with the MARMAP data, which shows little decline during the first 75 d followed by a modest increase in mid-April (Day 100).

All simulations began with a simple spatial structure, with high C5–C6 abundance over the deep basins and low abundance along the coast and over the banks (Fig. 3). As the simulations progressed, the spatial structure became more varied. The concentrations were highest in the western Gulf and Great South Channels, especially during the middle of the simulation, and overall were similar to the spatial patterns from the MARMAP survey (Meise & O’Reilly 1996).

Interannual variability

SST anomalies exhibited a high degree of similarity among regions (Fig. 4a). Waters were generally warmer between 1998 and 2002, with 2000 standing out as an especially warm year. The years 2004 and 2005 were much colder, nearly 5°C below average. Although there is strong agreement in the SST anomalies between regions, the anomalies often change within a year, most often between mid-March and mid-April (Days 75 to 100)

Chlorophyll variability is harder to visualize than temperature. Slight changes in the timing of the spring bloom can produce large anomalies that distract from the overall pattern. Furthermore, absolute chlorophyll values (or anomalies) have little relevance for *Calanus finmarchicus* reproduction. Egg production in *C. finmarchicus* is only limited for chlorophyll values below

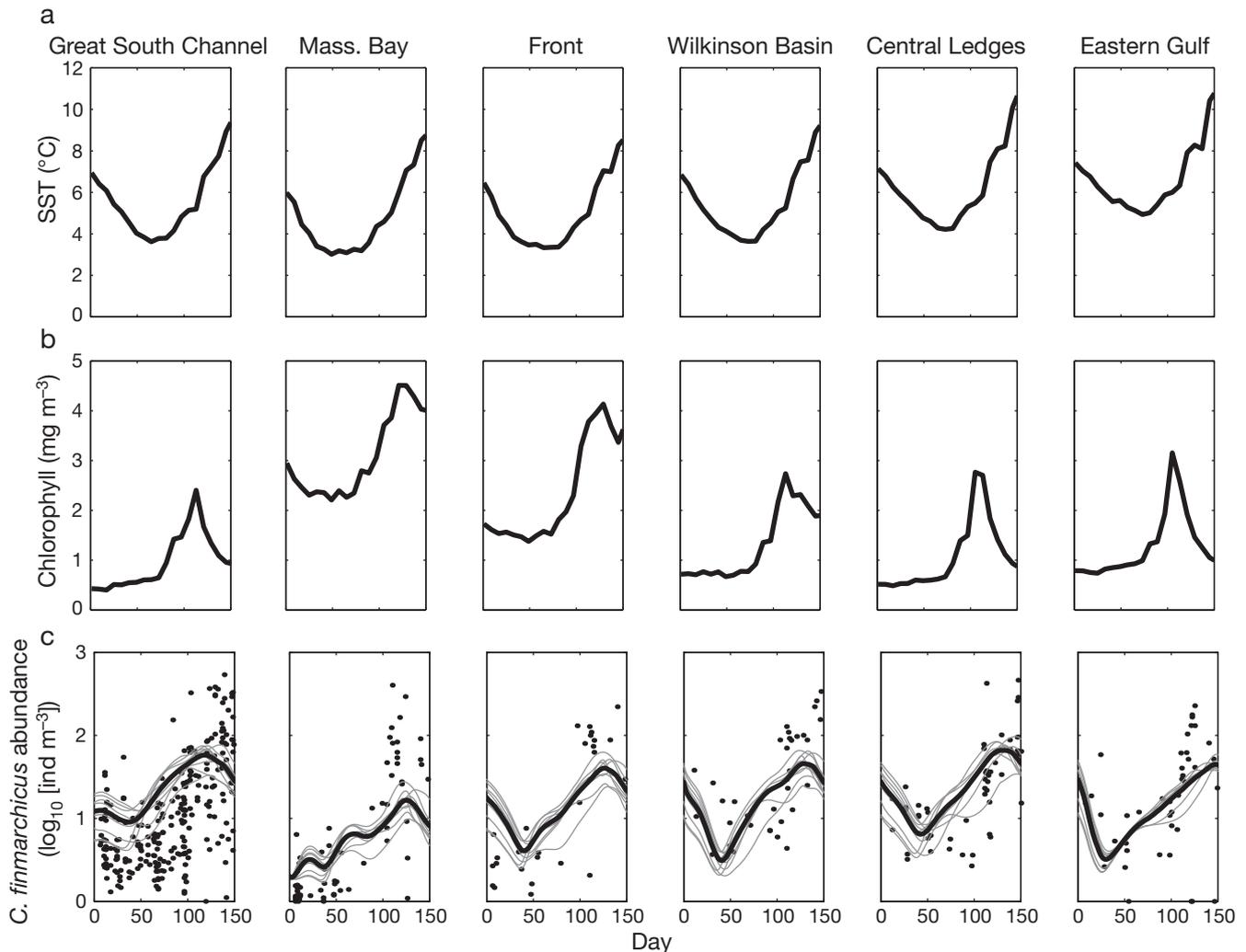


Fig. 2. *Calanus finmarchicus*. (a) Climatological annual cycles of sea surface temperature (SST) from the 5 western CPR regions and the Great South Channel, (b) chlorophyll, (c) *C. finmarchicus* abundance. The 1998–2006 runs (light lines) and the climatology (thick lines) from the model are plotted over the abundance (●) measured by the MARMAP survey

approximately 1 mg m^{-3} . Using this value as a reference highlights the impact of chlorophyll on *C. finmarchicus* egg production. The spatial coherence in the chlorophyll data is weaker than for SST; however, there is some correspondence between the regions (Fig. 4b). As in the climatologies, the 2 westernmost regions, Massachusetts Bay and the Front Region, were consistently above the 1 mg m^{-3} threshold. The 3 deep regions in the west, Wilkinson Basin, Central Ledges and Great South Channel had similar patterns. The year 1999 stood out with an early spring bloom and with little food limitation throughout the simulation period, and 2002–2005 had very low chlorophyll values during the early portion of the simulation followed by short and late spring blooms.

CPR data is most often used to quantify variability over interannual to interdecadal scales, often over large spatial scales (e.g. MERCINA 2001, Beaugrand 2004). When parsed to finer temporal and spatial scales, the data becomes noisy and data gaps begin to appear (Fig. 4c); nevertheless, some patterns are discernible. *Calanus finmarchicus* abundance was lower during the early years (1998–2001) and higher in the remaining years. The shift between 2001 and 2002 has been attributed to a broader reorganization of the Gulf of Maine zooplankton community associated with

increased freshwater input and fall phytoplankton during the 1990s (Pershing et al. 2005, Greene & Pershing 2007). Within this interdecadal pattern were several notable years: 1999 began with a strong negative anomaly in all regions, but returned to normal or nearly normal conditions by the last third of the period; 2000 and 2002 started high and then decreased; and 2006 began near the climatology, increased, and then returned to average conditions.

The full version of the model, with initial conditions from the CPR and interannually varying chlorophyll and temperature, exhibits considerable interannual and seasonal variability (Fig. 4d). Some years, such as 2000 and 2006, show consistently negative or positive anomalies throughout the year. In other years, such as 1999 and 2005, the anomalies switch sign in the middle of the year. Many of the patterns in the model output are also visible in the CPR. For example, 1999 begins with a low anomaly and then becomes average or positive in the middle of the simulation, while 2002 begins with a positive anomaly that fades. As in the CPR, anomalies in the model tend to span adjacent regions.

There are some fundamental challenges with interpreting a comparison between the CPR data and model output. CPR data is highly variable in space and time, reflecting fine-scale physical and biological pro-

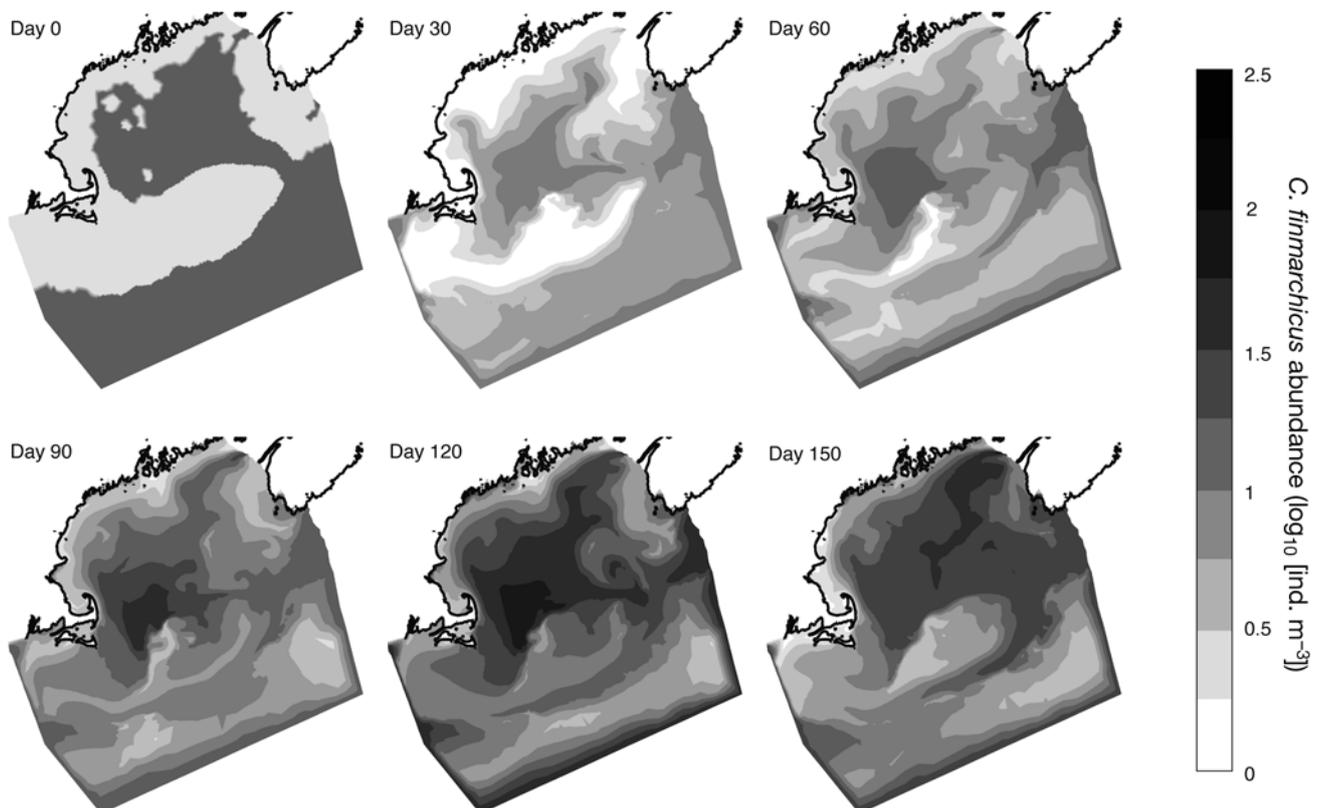


Fig. 3. *Calanus finmarchicus*. Spatial distribution of stage C5–C6 *C. finmarchicus* from the model using climatological inputs

cesses that are not represented in our model. This variability is enhanced by the small volume of water represented by each sample and the small number of samples. Thus, we expect a considerable amount of variability in the CPR data that the model will be unable to explain. Despite these considerations, the model was positively correlated with the CPR in all regions and time periods (Fig. 5). At the beginning of the simulation, the correlations in the Central Ledges, Wilkinson Basin and Front Region are especially strong. The strong correlations at the start of the simulation are unsurprising, as the model is initialized based on the mean of the CPR data over this period. As

the simulation progresses, the correlations weaken but remain positive. Between Days 50 and 100, only the Central Ledges and Massachusetts Bay correlations are significant. During the last third of the simulation, only the Eastern Gulf region is significantly correlated with the CPR, although the correlation with the Front Region is strong. The significant correlation with the eastern Gulf of Maine at the end of the simulation is surprising. Because this region is near the boundary, variability in the modeled *Calanus finmarchicus* time series is due almost exclusively to the influence of the satellite data. The strength of this correlation strongly suggests that the model's use of satellite data captures

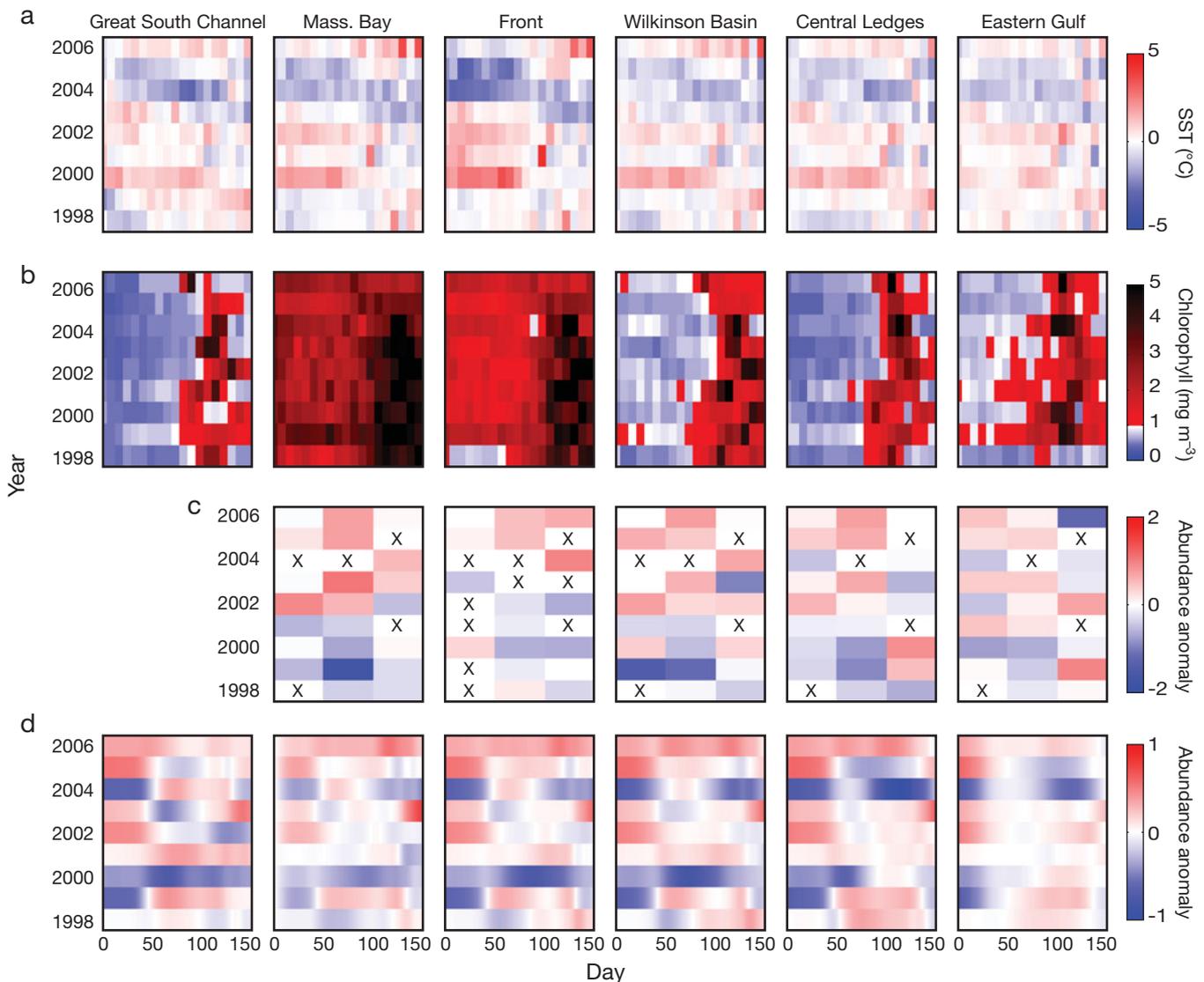


Fig. 4. *Calanus finmarchicus*. Interannual variability in (a) SST, (b) chlorophyll, (c) *C. finmarchicus* abundance anomaly from the CPR, and (d) *C. finmarchicus* from the model. SST is represented as the difference between the measured value and the climatological values in Fig. 2a. Chlorophyll is displayed in absolute units, with values likely to cause food-limited reproduction in *C. finmarchicus*, shown in shades of blue and white. *C. finmarchicus* abundance anomalies from the CPR are relative to the 1998–2006 mean for each period. X: No data for that period. Anomalies from the model are relative to the climatologies in Fig. 2c

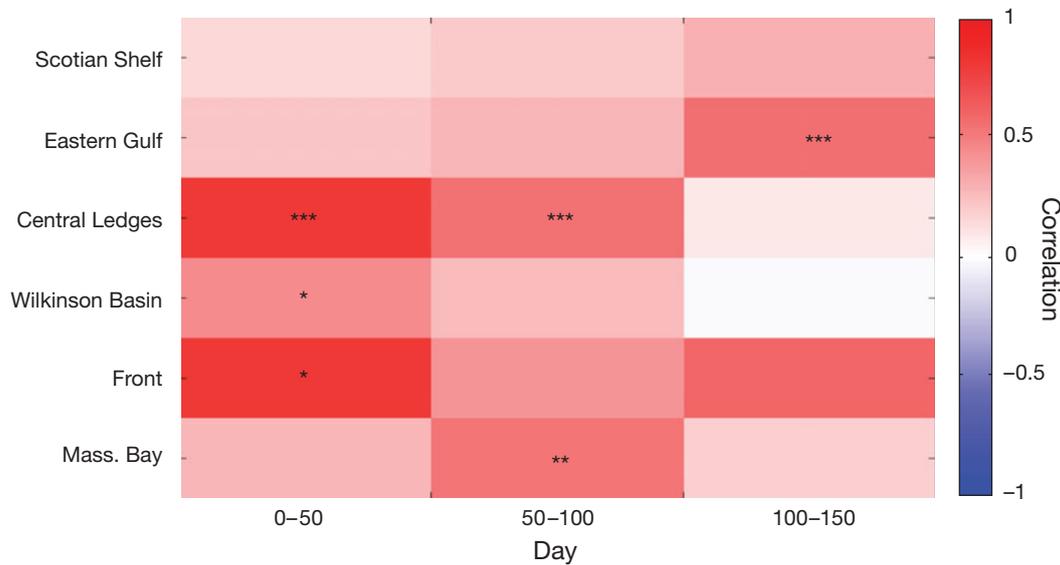


Fig. 5. *Calanus finmarchicus*. Correlation between the CPR and model abundances for the *C. finmarchicus* model. *, **, ***: correlations significant at the 90, 95 and 99% levels, respectively

real variability in *C. finmarchicus* population dynamics. The field significance tests indicate that the number of significant correlations is unlikely to arise by chance (Table 3). Furthermore, the probability of finding 17 positive correlations by chance is only 1 in 1000. Considering all of the regions together, the model is significantly correlated with the CPR ($r = 0.42$, $p < 0.01$) over the last 50 d of the simulations. If the Scotian Shelf and eastern Gulf of Maine regions are excluded, the correlation is weaker but still significant ($r = 0.33$, $p < 0.01$). The consistent correlations between the CPR and the model suggest that the model is capturing a significant portion of the interannual signal in the CPR data. However, there is a large amount of fine-scale variability in the CPR data that is outside the scope of the model.

Evaluating model inputs

One advantage of using a model is that it is possible to conduct controlled experiments that are not possible in nature. For example, we conducted 3 additional runs of our model to evaluate the relative importance of variability in SST, chlorophyll and initial conditions in driving interannual variability in *Calanus finmarchicus*. In each run, 2 of the 3 inputs (initial conditions, SST or chlorophyll) were replaced with their climatologies. This leaves an interannual signal from only a single factor. Allowing only initial conditions to vary from year to year reveals the persistence of anomalies and the influence of the boundary conditions (Fig. 6a). In the eastern Gulf of Maine, near the open boundary, the anomalies fade after 50 d. The initial anomalies last

longer in the western regions where the influence of the boundary conditions is weaker. In these regions, the anomalies fade substantially around Day 50 when the modeled abundance is at its minimum (e.g. Fig. 2c). As the G1 cohort builds, the anomalies reemerge.

When only SST is allowed to vary, the model produces strong anomalies (Fig. 6b). Because each year begins the same, there are no anomalies at the beginning of the simulations. Anomalies begin to appear around Day 50, just as those from the initial conditions (Fig. 6a) fade. Cold conditions, such as those in 2004, tend to produce negative anomalies due to delayed development. However, the competing influences of temperature on development and mortality make the impact of warm conditions less clear. For example, in 2000, waters throughout the Gulf of Maine were very warm early in the year (Fig. 4a); warm enough at the beginning of the simulation for temperature-dependent mortality to become significant, producing strong negative abundance anomalies. Years such as 2006

Table 3. Results of the field significance tests of the correlations in Fig. 5. Using the Monte Carlo procedure described in the text, we computed the probability of finding N or more correlations that are significant at the 99, 95, and 90% level, where N is the number found in the present study. We also computed the probability of finding N or more positive correlations

Correlations	Number	Probability
$p < 0.01$	3	0.0001
$p < 0.05$	4	0.0086
$p < 0.10$	6	0.0057
$r > 0$	17	0.001

that were warm, but not extremely warm, had positive *Calanus finmarchicus* anomalies.

The effect of variability in chlorophyll on the model was much weaker than temperature (Fig. 6c). Although the variability is lower than for the other experiments, the chlorophyll run provides some insight into the influence of variability phytoplankton abundance on *Calanus finmarchicus*. Specifically, the pattern of anomalies in Fig. 6c is more similar to the chlorophyll values in late winter, suggesting that phytoplankton dynamics during the late winter have a stronger influence on the *C. finmarchicus* population than variability in the spring bloom. For example, positive anomalies in the chlorophyll-only run appear in 1999, 2001, 2004 and 2006. Each of these years had chlorophyll values near 1 mg m⁻³ in the winter. Years

with low chlorophyll in winter, for example, 2002 and 2003, have negative anomalies in the model.

If the anomalies from the 3 runs described above are combined (Fig. 6d), the result is nearly identical to the anomalies from the full model run (Fig. 4d). This demonstrates that the model's reaction term is nearly linear, with the only nonlinearity coming from the density-dependence in the mortality function.

DISCUSSION

The main goal of our project is to develop a system to estimate *Calanus finmarchicus* abundance using readily available data, notably, SST and chlorophyll from satellites. The model as currently configured is posi-

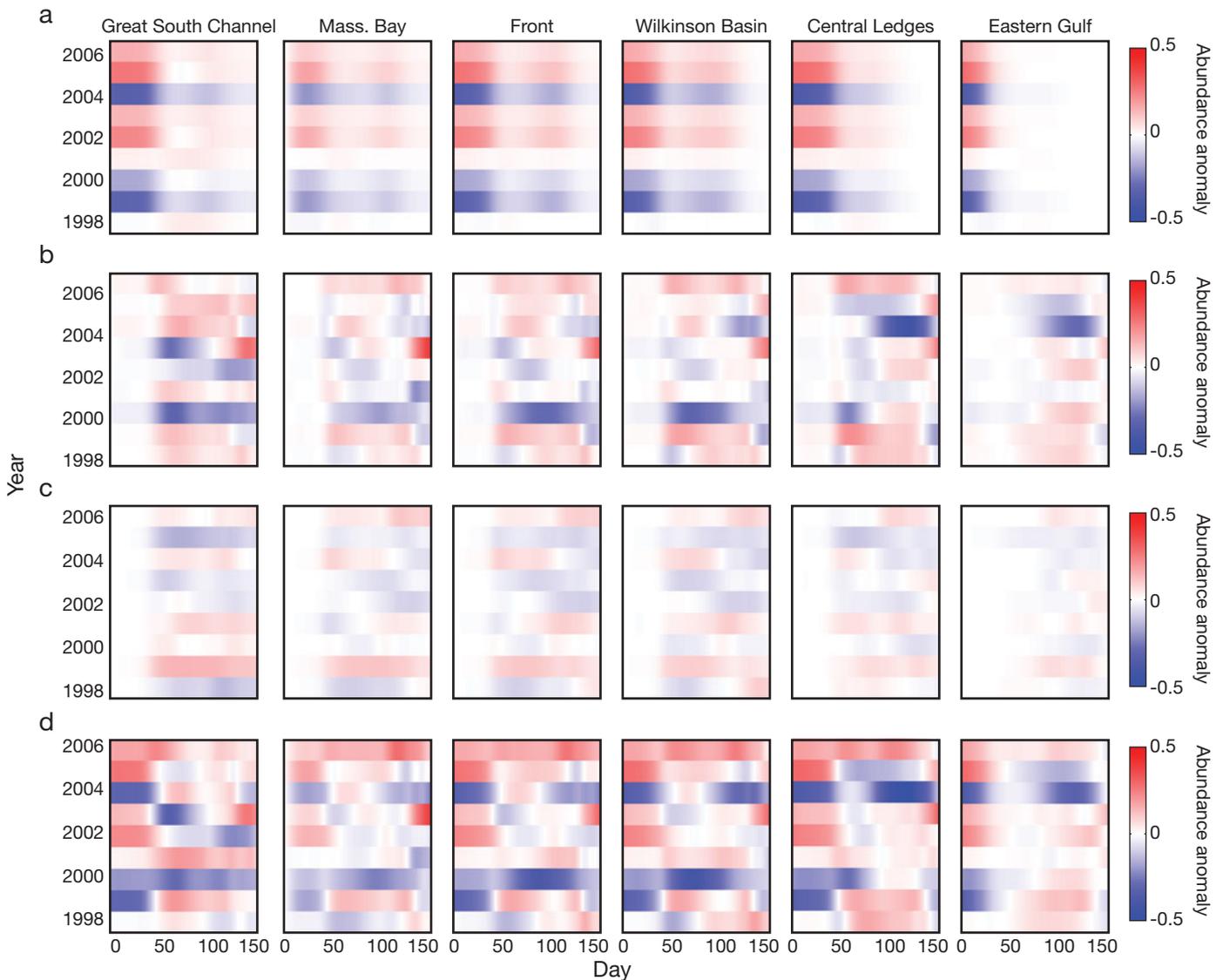


Fig. 6. *Calanus finmarchicus*. Abundance anomalies (relative to 1998–2006 average) from model simulations with interannual (a) initial conditions, (b) SST and (c) chlorophyll. (d) Sum of the anomalies in (a–c)

tively correlated with the CPR data, suggesting that the model captures a portion of the dynamics driving interannual variability in *C. finmarchicus*. Here, we will consider in more detail how the model can be used to understand interannual variability in *C. finmarchicus* and how the model could be improved to realize our stated goal of near real-time estimates of this population.

Interannual variability in *Calanus finmarchicus*

Numerous studies have documented interannual variability in *Calanus finmarchicus* populations across the North Atlantic (reviewed in Pershing et al. 2004). The mechanisms that may drive interannual changes in zooplankton can be grouped into hypotheses about production (reproduction, growth or mortality) or supply. For example, the decline of *C. finmarchicus* in the North Sea has been attributed to reduced production in warmer waters (Beaugrand 2004), in contrast with the hypothesis of Heath et al. (1999) that the decline is due to reduced supply from the North Atlantic. In the Gulf of Maine, MERCINA (2004) proposed that the supply of *C. finmarchicus* from the Scotian Shelf is a main driver of interannual variability; however, changes in reproduction can overcome the supply signal. By decomposing the modeled *C. finmarchicus* anomalies into anomalies from initial conditions, temperature and chlorophyll, we can evaluate the relative importance of these factors, and the scales over which they apply, to *C. finmarchicus* in the Gulf of Maine.

Compared with other copepods, *Calanus finmarchicus* has a long life span, and variability in its abundance in a small region should be more sensitive to changes in supply than to changes in growth rate or mortality (Aksnes & Blindheim 1996). The issue is the scale, both in time and space, over which this supply-side hypothesis applies. While we did not directly manipulate the abundances along the boundary, changes in the initial conditions, by virtue of being independent of population dynamics in the domain, should have a similar effect to changes in boundary conditions (Fig. 6a). Changes in population dynamics require a generation to appear as a change in C5–C6 abundance. Thus, anomalies in initial conditions or the abundance along the boundary should persist for several weeks in winter, less in the warmer waters of spring and summer. An anomaly from the western Scotian Shelf will reach the Central Ledges in 50 d and will reach the Great South Channel in 90 d (Lynch et al. 1998). Therefore, the effect of boundary conditions will be strongest in the eastern and central Gulf of Maine and will be strongest during late winter, when *C. finmarchicus* generation times are longest. Thus,

our model supports the assertion that variability in the abundance of *C. finmarchicus* on the Scotian Shelf, or the rate at which *C. finmarchicus* is transported into the Gulf of Maine, is a significant source of variability in *C. finmarchicus* abundance in the Gulf of Maine (MERCINA 2004).

The production hypothesis proposes that changes in *Calanus finmarchicus* are related to changes in population dynamics within the region. The strong anomalies in the SST-only simulations (Fig. 6b) suggest that the production hypothesis also applies in the Gulf of Maine. In addition to being a source of interannual variability in *C. finmarchicus*, temperature likely plays a role in creating the strong G1 pulse in the spring. Individuals spawned in the spring will experience warmer conditions and faster growth rates, allowing them to catch up to individuals spawned in earlier, colder conditions. This helps create the rapid increase in late stage *C. finmarchicus* that defines the G1 pulse. Even if egg production were constant, our model would still produce a well-defined G1 in the spring. Conversely, cooling conditions, such as those in the fall, would tend to smear out any cohort structure.

Although changes in chlorophyll, especially early in the year, can have an effect on *Calanus finmarchicus*, the overall effect of chlorophyll is weak. According to the Ivlev function, *C. finmarchicus* egg production will only be limited if chlorophyll is lower than roughly 1 mg m^{-3} . Even over the deep basins in winter, the satellite chlorophyll values are close to this level. Thus, changes in chlorophyll will have a small effect on the *C. finmarchicus* population in the model. One major caveat to this assertion is the quality of the satellite chlorophyll data in the Gulf of Maine. Comparisons between *in situ* chlorophyll measurements and satellite estimates suggest that the satellites overestimate chlorophyll low levels (below $\sim 2 \text{ mg m}^{-3}$), and underestimate higher values (S. Bailey and J. Werdell pers. comm., based on Gulf of Maine data from Balch et al. 2008). If the winter chlorophyll values are really lower than the satellite estimates, we would expect changes in chlorophyll to have a larger impact on *C. finmarchicus* than Fig. 6 suggests.

Towards real-time *Calanus finmarchicus* estimates

Our model provides a good, if perhaps imperfect, representation of *Calanus finmarchicus* abundance. With the current configuration (climatological circulation, low resolution initial conditions), the model is most accurate in the western Gulf of Maine at regional scales and at time scales of several weeks. At these scales, the model can be used to explain specific events in the CPR record such as the recovery in 1999

described in MERCINA (2004). In order to use our model to support management decisions, it is important to understand the weaknesses of the model and how it might be improved.

The largest source of model uncertainty is mortality. To achieve a better agreement with the MARMAP data, we had to adjust the parameters in the Speirs et al. (2006) formulation to reduce mortality levels. There are several likely explanations for why the initial configuration of the model would need to be adjusted to apply to the Gulf of Maine. For example, the stage-based mortalities from Eiane et al. (2002) were measured in a Norwegian fjord during the summer. It is likely that the predator populations in their study differ from those in the Gulf of Maine during the spring. Similarly, the Speirs et al. (2006) study was dominated by data from the deep portions of the North Atlantic, which is different in many ways from the shelf environment in the Gulf of Maine.

Even though we were able to adjust the Speirs et al. (2006) formulation to better represent the Gulf of Maine, there is still the larger question of how mortality should be parameterized. There is very little information on the distribution of *Calanus finmarchicus* predators such as chaetognaths, small fish and gelatinous predators. Assuming that the predators are tracking *C. finmarchicus*, either through their own population dynamics or through active foraging, we would expect mortality to increase in proportion to *C. finmarchicus* abundance. The Speirs et al. (2006) temperature-dependent mortality formulation approximates this summer increase in predation, although by using temperature and, to a lesser degree, *C. finmarchicus* abundance as a proxy for predator abundance. In most years, the temperature-dependent mortality only becomes a major factor during the last 1 to 2 wk of the simulation. However, the temperature in the Gulf of Maine does not peak until 2 mo later, rising on average another 6.7°C at the surface, 2°C when integrated over the top 50 m. This relatively small change in temperature would cause computed mortality to increase by a factor of 4.6. While mortality rates will increase in the summer (due to predation from fish and invertebrates), the nearly 5-fold increase in mortality is likely unrealistic. Thus, while using temperature as a proxy for mortality seems reasonable, additional work is needed to adapt the Speirs et al. (2006) formulation for the Gulf of Maine.

The present study suggests several improvements that could be made to the model to provide better information on *Calanus finmarchicus*, and thus, on the distribution of *C. finmarchicus* predators such as right whales. The most obvious improvement is to move from climatological flow fields to high frequency nowcasts or forecasts from an operational circulation model (e.g. Xue et al. 2005). From the point of view of provid-

ing information relevant to right whale movements, including diapause dynamics would provide the biggest improvement in the model. This would allow the model to simulate an entire year and would provide information on feeding conditions in the late summer habitats of the Bay of Fundy and Roseway Basin (Kenney et al. 2001). There is nothing in our model formulation that would prevent including any of these dynamics, and all would likely be a significant improvement on the current model.

The biggest limitation to using our model in real-time is uncertainty in the initial and boundary conditions. Initial conditions from the CPR were a major source of interannual variability in the present study. Variability along the boundary could be addressed in a similar fashion using data from a high frequency time series on the Scotian Shelf such as Fisheries and Oceans Canada's Atlantic Zone Monitoring Program (AZMP) station southeast of Halifax, Nova Scotia (Pepin et al. 2005). Additional observations within the model domain and within the simulation period could be assimilated into the model (e.g. Natvik & Evensen 2003). A major limitation to incorporating observations into our model is the time, often several months, required to process zooplankton samples. Incorporating electronic instruments such as a video plankton recorder (Davis et al. 1996) or optical plankton counter (Herman 1988) into ongoing surveys or time series would provide more timely information. However, even if real-time estimates of initial or boundary conditions are not available, our model still provides realistic information on *Calanus finmarchicus* abundance. For example, the anomalies during the latter half of our simulations, especially in the western regions, were more strongly influenced by the satellite data than the initial or boundary conditions (Fig. 6).

CONCLUSIONS

A model is a formal, quantitative representation of the processes that the modeler hypothesizes are important. In this vein, our model expresses the relationship between chlorophyll and temperature as measured by satellites, circulation and *Calanus finmarchicus* population dynamics in the Gulf of Maine. Our model provides realistic estimates of interannual variability in *C. finmarchicus* and allows us to quantify the relative impact of different processes that lead to variability in this population.

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