Spring plankton dynamics in the Eastern Bering Sea, 1971-2050: Mechanisms of interannual variability diagnosed with a numerical model

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Key Points.

- A new model of the Bering Sea in spring replicates a wide variety of phytoplankton/grazer metrics.
- Total spring primary production is generally higher in warm years, but the relationship is indirect.
- Ice cover, mixing, and advection control distinct aspects of bloom timing and magnitude.

Abstract.

A new planktonic ecosystem model was constructed for the eastern Bering Sea based on observations from the 2007–2010 BEST/BSIERP (Bering Ecosystem Study/Bering Sea Integrated Ecosystem Research Program) field program. When run with forcing from a data-assimilative ice-ocean hindcast of 1971–2012, the model performs well against observations of spring bloom time-evolution (phytoplankton and microzooplankton biomass, growth and grazing rates, and ratios among new, regenerated, and export production). On the southern middle shelf (57°N, station M2), the model replicates the generally inverse relationship between ice-retreat timing and spring bloom timing known from observations, and the simpler direct relationship between the two that has been observed on the northern middle shelf (62°N, station M8). The relationship between simulated mean primary production and mean temperature in spring (Feb 15–Jul 15) is generally positive, although this was found to be an indirect relationship which does not continue to apply across a future projection of temperature and ice cover in the 2040s. At M2 the leading direct controls on total spring primary production are found to be advective and turbulent nutrient supply, suggesting that mesoscale, wind-driven
processes—advective transport and storminess—may be crucial to long-term trends in spring primary production in the southeastern Bering Sea, with temperature and ice cover playing only indirect roles. Sensitivity experiments suggest that direct dependence of planktonic growth and metabolic rates on temperature is less significant overall than the other drivers correlated with temperature described above.
1. Introduction

The Eastern Bering Sea (EBS) hosts extremely rich pelagic and benthic fisheries and also experiences strong interannual variation in both fisheries recruitment and the underlying physics and plankton biology [Hunt Jr et al., 2011; Coyle et al., 2011; Stabeno et al., 2012a]. This paper uses a new planktonic ecosystem model to integrate diverse observations from The Bering Sea Project (BEST/BSIERP, Bering Ecosystem Study/Bering Sea Integrated Ecosystem Research Program: Wiese et al. [2012]) and to answer the question: What controls variation in spring primary production (in both magnitude and timing) across the range of warm and cold annual conditions seen over the past 40 years? This question is part of a larger class of problems in global change biology: the response of planktonic systems to multiple drivers; in particular, the response of high-latitude marine ecosystems to changing temperature, ice-linked phenology, and other mesoscale processes when the relationships among these processes are themselves changing. We use a new future model projection of temperature and ice cover in the 2040s to sketch one possible future for the Bering Sea, and to comment on the problem of prediction under multiple, highly correlated drivers.

1.1. Interannual variation and links from climate to food webs

The EBS is a broad (> 500 km) shelf system, divided by persistent fronts into inner (< 50 m water depth), middle (50-100 m), and outer (100-200 m) domains [Coachman, 1986]. Seasonal ice cover is controlled by a balance of southward advection from Bering Strait and in situ melting and dispersion, and thus by a combination of wind forcing and temperature [Stabeno et al., 2012a]. The northern shelf (> 60°N) consistently sees
seasonal ice cover, while ice cover on the southern shelf is highly variable: at the long-term mooring site M2 (Fig. 1, Stabeno et al. [2012a]), the period of ice cover varied from several months to effectively zero among the years of the 2000s.

Hydrography and currents in the EBS respond strongly to variations in the strength and position of the Aleutian Low [Danielson et al., 2011a] and other North Pacific-scale drivers [Rodionov et al., 2007; Danielson et al., 2011b]. The warm anomaly of the early 2000s and the cold anomaly of the late 2000s (Fig. 1) have received much attention (e.g. Grebmeier et al. [2006]; Coyle et al. [2011]; Sigler et al. [2014]), largely because these anomalies left large imprints on fisheries recruitment and zooplankton composition. Large crustacean zooplankton were a much larger fraction of the late-summer mesozooplankton community on the southern shelf in cold years of the 2000s [Eisner et al., 2014]. The pattern on the northern shelf was consistent with this, but both the environmental and the biological contrast there were much smaller. A reduction in large copepod and euphausiid abundance is thought to drive both bottom-up and top-down stresses on juvenile pollock and salmon [Hunt Jr et al., 2011; Coyle et al., 2011].

Several factors could contribute to warm year/cold year variation in large zooplankton abundance at the end of the productive season: variation in total productivity of their phytoplankton and microzooplankton prey; direct temperature effects on summer growth and development and on winter metabolic losses; timing of prey availability and match/mismatch with the zooplankters’ ontogenetic cycle. Prey productivity and timing can be further broken down into its pelagic and ice-algal components [Cooper et al., 2013], and ice algae may be particularly important from a timing perspective [Durbin and Casas, 2014; Daase et al., 2013]. A follow-on model study will consider this full array of
factors linking climate to large zooplankton, whereas the present study is concerned with pelagic phytoplankton and microzooplankton production in spring (Feb-Jul), the most productive period of the year [Stabeno et al., 2012a; Sigler et al., 2014]. The model presented here was designed to answer the question: how much, and by what mechanisms, does environmental variation between cold and warm conditions affect phytoplankton and microzooplankton production and energy input into the pelagic and benthic food webs?

Fig. 1 shows the warm and cold years of the 2000s in the context of the even colder period of the early 1970s and the potentially even warmer conditions that could arrive by mid-century, according to a model hindcast/projection—described in detail below—using BESTMAS (Bering Ecosystem Study Ice-ocean Modeling and Assimilation System: Zhang et al. [2010a]). Average surface water temperature varies coherently between the northern and southern shelves (Fig. 1a) and is accompanied by variation in ice cover (Fig. 1b). Note that in the north, this is felt primarily as variation in ice-retreat timing of 1–2 mo, whereas in the south, not only is the variation in timing even greater, but the extent of maximum ice cover varies latitudinally by hundreds of km as well. Ice cover regulates pelagic production via both light penetration and stratification. Note that in ice-free areas of the EBS, thermal stratification can be intense [Stabeno et al., 2012b] but, counterintuitively, summer stratification is not well-correlated with surface temperature [Ladd and Stabeno, 2012]. Nutrient availability depends on both stratification and horizontal transport (Stabeno et al., submitted).

1.2. Multidecadal variation

It is likely that as the earth, and high latitudes in particular, continue to warm over coming decades, this set of environmental drivers will not all change in familiar propor-
tions. The multidecadal, anthropogenic shift in the thermodynamic budget of the region is a fundamentally different mechanism from the mesoscale atmospheric variability that drives interannual anomalies in temperature, ice cover, transport, and storminess, and thus we should not expect multidecadal trends in water temperature, ice cover, advective nutrient replenishment, and turbulent mixing to follow the same correlation lines as recent interannual variability. Indeed, the model projection used in this study (Fig. 2; see 2.1 below), depicts one possible future in which novel combinations of ice influence and mean temperature are commonplace by the 2040s, especially in the south.

The question then arises: as higher temperatures come to the EBS and other polar and subpolar regions, are the higher temperatures themselves likely to be the driver of crucial ecological shifts in the plankton, or important mainly as a proxy for correlated mechanisms (e.g., changes in ice-linked phenology or weather patterns)? A number of recent studies have argued for the former, drawing on the metabolic theory of ecology [Brown et al., 2004] and related empirical studies to argue that differences in the temperature dependence of photosynthesis and respiration, or the net temperature responses of phytoplankton and their grazers, will lead to a tipping point for Arctic planktonic ecosystems with 5–6°C of additional warming [Rose and Caron, 2007; Holding et al., 2013; Alcaraz et al., 2014]. A model like the one constructed and evaluated here is well suited to testing the internal consistency of this hypothesis: i.e., if the premise of differences in physiological temperature sensitivities is granted, does the conclusion of tipping-point behavior follow? (Note that this question is different from asking whether Arctic marine ecosystems are likely to show tipping-point behavior in general, a question larger than any specific mathematical model.) We will show that over the range of conditions experienced in the
EBS, and projected to be experienced there over coming decades, direct physiological responses to temperature in fact have only minor consequences compared with environmental correlates of temperature that modulate the light and nutrient environment for phytoplankton.

2. The model

2.1. Physical hindcast and forecast

The BESTMAS (Bering Ecosystem STudy ice–ocean Modeling and Assimilation System) model has been described and validated in detail by Zhang et al. [2010a] and Zhang et al. [2012]. The model domain covers the Northern Hemisphere north of 39°N, with highest horizontal resolution along the Alaskan coast and in the eastern Bering Sea. Average grid spacing in the Bering Sea is 7 km, ranging from 2 km along the Alaskan coast to 12 km along the Aleutian Chain. Twenty-six ocean grid cells across Bering Strait allow a good connection between the Bering Sea and the Arctic Ocean.

The sea ice component of BESTMAS is an 8-category thickness and enthalpy distribution (TED) sea ice model [Hibler, 1980; Zhang and Rothrock, 2001] that employs a teardrop viscous-plastic rheology [Zhang and Rothrock, 2005], a mechanical redistribution function for ice ridging [Thorndike et al., 1975; Hibler, 1980], and a line successive relaxation (LSR) dynamics model to solve the ice momentum equation [Zhang and Hibler, 1997]. The TED ice model also includes a snow thickness distribution model following Flato and Hibler [1995]. It assimilates satellite ice concentration and SST data following Lindsay and Zhang [2006]. The ocean model is based on the Parallel Ocean Program (POP) developed at Los Alamos National Laboratory [Smith et al., 1992; Dukowicz and Smith, 1994], and incorporates forcing from 8 tidal constituents. Open boundary cond-
tions at 39°N are taken from a global ice-ocean modeling and assimilation system [Zhang, 2005].

Atmospheric forcing is taken from daily NCEP/NCAR Reanalysis data (National Centers for Environmental Prediction/National Center for Atmospheric Research: Kalnay et al. [1996]). Model forcing also includes freshwater river runoff into the Bering and Arctic seas. For the Bering Sea, monthly climatological runoffs of the Anadyr, Yukon, and Kuskokwim rivers are used [Zhang et al., 2010a]. Zhang et al. [2010a] demonstrated that BESTMAS is able to capture much of the observed spatiotemporal variability of sea ice extent and thickness, the basic wind- and tide-forced features of upper ocean circulation, and seasonal and interannual variability of surface ocean temperatures at mooring site M2 (Fig. 3).

This study uses daily output from a BESTMAS hindcast 1971–2012, similar to the period analyzed by Zhang et al. [2012]. It also uses a projection of conditions 2040–2050, which was created by randomly resampling years from the hindcast and adding a linear temperature trend to the atmospheric forcing. The trend used is 8°C by 2100, close to the observed trend 1977–2012, and also close to the ensemble mean of IPCC global climate model projections for the Arctic Ocean [IPCC, 2007; Wang et al., 2012]. We will refer to this model projection as ”the 2040s” for brevity, although of course if the course of future warming differs from the mean of current models, conditions like those depicted by this model run might arise sooner or later than than 2040s. Note that this approach does not attempt to resolve future change in mesoscale atmospheric patterns or storm frequency and intensity.

2.2. Ecosystem model
The ecosystem model is a relatively simple, six-compartment nitrogen budget (Fig. 4), which tracks NO$_3$, NH$_4$, phytoplankton biomass $P$, microzooplankton biomass $Z$, and small and large detritus $D_S$, $D_L$. This model structure is a simplification of an initial model version containing two phytoplankton classes, microzooplankton, stage-resolved copepods, and euphausiids. Extensive experiments varying both the structure and parameter values in this model ($\sim 200,000$ cases) led to the conclusion that the added complexity offered no improvement in performance against the phytoplankton/microzooplankton observations shown below (Sec. 3). This finding is consistent with the more formal investigation of model complexity by Ward et al. [2013].

The ecosystem model was not run fully coupled to BESTMAS in three dimensions, but rather in ensembles of one-dimensional, flow-following water-column environments. Time series of depth-resolved temperature $T$ and vertical tracer diffusivity $\kappa$, along with photosynthetically available radiation PAR$_0$ at the water surface under ice, were extracted from BESTMAS following the trajectories of particles that track the 0–35 m depth-average currents. Particles were released Feb 15 of each model year, one per horizontal grid cell. These depth-vs.-time fields form individual, non-interacting environments in which the ecosystem model is run. Each environment spans the entire water column with time-varying bottom depth, and has 15 vertical levels with resolution concentrated at the surface. Once initialized with a profile of nitrate concentration on Feb 15, there are no exchanges through the sidewalls or bottom of each environment. This approach neglects horizontal gradients below the euphotic zone and nonlinear interactions between neighboring plankton communities, but the massive scale of the shelf system relative to typical near-surface currents [Stabeno et al., 2012b] and—crucially—the limited duration of our simulations.
(150 d) make the method appropriate, as it would not be for, say, yearlong simulations of a narrow shelf. This method offers huge gains in computational efficiency relative to a three-dimensional coupled model and therefore the opportunity to properly explore the model parameter space. The Lagrangian basis of the extracted physical forcing time series overcomes the worst of the limitations of one-dimensional Eulerian plankton models, which are in fact still widespread and useful tools (Fasham et al. [2006]; Bagniewski et al. [2011], many others).

With one exception (the IEB60 ensemble described below), each of the ensembles used in this study was constructed as the set of particle trajectories that pass within 50 km of a given station at some point within the simulation period (5). This hybrid Lagrangian/Eulerian method may appear roundabout compared with simply running a conventional, fixed-in-space, one-dimensional model at station, but it offers the crucial advantage of resolving (depth-averaged) lateral transport past each station, an ability which we will show is important to the interpretation of results at M2 (Section 3.2). Each model simulation runs Feb 15–Jul 15 of a given year, resolving the spring bloom and the transition into summer. This period was selected to match the seasonal coverage of BEST/BSIERP observations, 2007–10.

Initial profiles of nitrate are constructed as an empirical function of water-column depth $H$ alone:

$$\text{NO}_3^{\text{initial}}(z, H) = -\frac{z}{H} \text{NO}_3^{\text{bot}} + \left(1 + \frac{z}{H}\right) \text{NO}_3^{\text{surf}}$$  

(1a)
where

\[ \text{NO}_3^{\text{bot}} = (42 \text{ mmol m}^{-3}) \frac{H^2}{(116 \text{ m})^2 + H^2} \]  
(1b)

\[ \text{NO}_3^{\text{surf}} = (24 \text{ mmol m}^{-3}) \frac{H^2}{(86 \text{ m})^2 + H^2} \]  
(1c)

Values in (1b), (1c) are based on Type III fits to bottle samples within 10 m of the bottom and 2 m of the surface, respectively, from spring 2009 BEST observations [Mordy et al., 2012]. Because of the simplicity of this initial condition, interannual variation in over-winter replenishment of the nutrient pool is only partially resolved. A full treatment of this mechanism probably requires a fully coupled 3-D simulation.

The model equations are as follows:

\[ \frac{dP}{dt} = q_P \mu(E, \text{NO}_3, \text{NH}_4)P - q_Z I(P)Z - q_R m_P P - q_P m_{agg} P^2 + \text{mixing} \]  
(2)

\[ \frac{dZ}{dt} = \epsilon q_Z I(P)Z - q_Z m_Z Z^2 + \text{mixing} \]  
(3)

\[ \frac{dD_S}{dt} = (1 - \epsilon - f_{ex})q_Z I(P)Z + q_R m_P P - q_R r_{\text{remin}} D_S + \text{sinking} + \text{mixing} \]  
(4)

\[ \frac{dD_L}{dt} = q_P m_{agg} P^2 - q_R r_{\text{remin}} D_L + \text{sinking} + \text{mixing} \]  
(5)

\[ \frac{d\text{NH}_4}{dt} = -f_{\kappa} \varphi_{\text{NH}_4} \text{NH}_4 \frac{\text{N}_{\text{tot}}}{P} q_P \mu P + f_{ex} q_Z I(P)Z + q_R r_{\text{remin}}(D_S + D_L) - q_R r_{\text{nitr}} \text{NH}_4 + \text{mixing} \]  
(6)

\[ \frac{d\text{NO}_3}{dt} = -f_{\kappa} \varphi_{\text{NO}_3} \text{NO}_3 \frac{\text{N}_{\text{tot}}}{P} q_P \mu P + q_R r_{\text{nitr}} \text{NH}_4 + \text{mixing} \]  
(7)

See Table 1 for a summary of definitions and parameter values. Briefly, phytoplankton population growth is a balance among individual growth (the \( \mu \) term), microzooplankton...
grazing, mortality, and aggregation; microzooplankton population growth is a balance be-
tween prey assimilation and mortality; and the detrital pools are controlled by a balance
between these biological loss and uptake terms, remineralization, sinking, and nitrifica-
tion. The factors $q_P$, $q_Z$, $q_R$ represent the temperature dependencies of phytoplankton
metabolism, zooplankton metabolism, and respiration/bacterial metabolism respectively,
each controlled by a $Q_{10}$ factor, e.g.,

$$q_P \equiv Q_P^{T/10^\circ C}$$

where $T$ is temperature. The base model case uses a $Q_{10}$ of 2 for phytoplankton growth
and 2.8 [Hansen et al., 1997] for processes mediated by bacteria and zooplankton. The
implications of this and a spectrum of alternate choices are considered in Section 3.4
below. Note that $Q_Z$ is applied to both the growth/ingestion of the explicitly modeled
microzooplankton and also the growth/ingestion of their implicit predators, i.e. mi-
crozooplankton mortality.

### 2.3. Phytoplankton growth

Individual phytoplankton growth and nutrient uptake are considered equivalent in this
model, as in many NPZ-style models. Specific growth rate $\mu$ depends on light and nutrients
as

$$\mu = \left( \frac{\alpha E}{\sqrt{\alpha^2 E^2 + \mu_0^2}} \right) \left( \frac{N_{tot}}{k_{min} + 2 \sqrt{k_{min} N_{tot}} + N_{tot}} \right) \mu_0$$

The maximal rate $\mu_0$ was based on summer observations by Zeeman and Jensen [1990],
temperature-corrected using a $Q_{10}$ of 2 and a seasonal temperature difference of $7^\circ$C.
Nutrient limitation follows the optimal-uptake scheme of Smith et al. [2009] in which,
consistent with global observations [Collos et al., 2005], the effective half-saturation $k_{\min} + 2\sqrt{k_{\min}N_{\text{tot}}}$ increases with nutrient concentration from a minimum value $k_{\min}$, based on an optimization of intracellular resources for cell-surface uptake and internal transport. $N_{\text{tot}} = \text{NO}_3 + \varphi_{\text{NH}_4}\text{NH}_4$ is effective total nutrient concentration, where $\varphi_{\text{NH}_4}$ is a preference for $\text{NH}_4$ defined by analogy with a common formulation of grazing on multiple prey types [Gentleman et al., 2003].

Photosynthetically available radiation (PAR) at a given depth, $E(z)$, is attenuated from BESTMAS-derived surface PAR $E_0$ ($0.43 \cdot$ shortwave radiation) by both seawater and overlying phytoplankton:

$$E(z) = E_0 \int_0^{z_{\text{surface}}} (\text{att}_{\text{sw}} + \text{att}_P P(z)) \, dz$$

In contrast to most simple NPZ models, the initial slope of the growth-light curve $\alpha$ is not fixed but rather varies seasonally. This behavior is based on observations by Sambrotto et al. [1986], who found that $\alpha$ increased more than fourfold over 8 d in the lead-up to the spring bloom in the southeastern Bering Sea in 1981 (Fig. 6). Over these 8 d, the mixed layer shoaled from $>60$ m to $<20$ m, suggesting a release from light limitation. For simplicity we have ignored the simultaneous increase in $\mu_0$ seen in those observations; allowing seasonal increase in either of these parameters would likely produce qualitatively similar model behavior, and varying both would be redundant. Either physiological shifts or community shifts might lead to this sort of variability in $\alpha$. In general, shade-adapted phytoplankton show lower $\mu_0$ (i.e., maximum photosynthetic rate) than high-light adapted communities [Palmer et al., 2011], and both ice cover and high levels of turbulent mixing in ice-free areas in winter/early spring would lead to shade adaptation [Cianelli et al., 2004;
Palmer et al., 2011]. Note that these high-latitude observations run exactly contrary to the assumption of optimality-based models like Pahlow and Oschlies [2013] in which phytoplankton dynamically allocate their resources in order to maximize instantaneous growth rate.

In our model, \( \alpha \) changes between a winter/pre-bloom value \( \alpha_{\text{win}} \) and a spring bloom/summer value \( \alpha_{\text{sum}} \), in response to a light index \( E_{\text{eff}} \):

\[
\alpha = \alpha_{\text{win}} + \frac{1}{2}(\alpha_{\text{sum}} - \alpha_{\text{win}}) \left( 1 + \tanh \frac{E_{\text{eff}} - E_{\text{crit}}}{\Delta E} \right)
\]  

(11)

\( E_{\text{eff}} \) uses a few essential scalings to represent light conditions as experienced by phytoplankton taking into account both surface light \( E_0 \) and turbulent diffusivity \( \kappa \):

\[
E_{\text{eff}} = E_0 \exp \left( -\text{att}_{\text{sw}} \sqrt{\frac{\max \kappa}{\mu_0}} \right)
\]  

(12)

The square-root quantity is proportional to the depth over which a near-surface population is mixed in one doubling time. This formulation is inexact—appropriate as a scaling law only—but in the absence of a detailed physiological model of how the phytoplankton accomplish this change in \( \alpha \), and with the constants \( E_{\text{crit}} \) and \( \Delta E \) determined by tuning, further detail was deemed to be unwarranted. This scheme for \( \alpha \) produces rates of change in light sensitivity consistent with the observations by Sambrotto et al. [1986] (Fig. 6a; slope of model curves in spring vs. two observational values). A more specific rationale for this scheme over the alternatives is discussed in Sec. 3.1.1.

2.4. Grazing, losses, and regeneration

Phytoplankton in the model are subject to both a constant linear mortality \( m_P \) representing viral lysis and predation by mesozooplankton, and also a density-dependent loss to the fast-sinking \( D_L \) pool representing aggregation of diatom blooms. The model per-
forms distinctly better (with respect to \( f \)-ratio and \( e \)-ratio: Sec. 3.1.1) with both of these loss terms included than it does with either alone.

A generally larger loss is explicit grazing by microzooplankton \( Z \). The community grazing rate \( g \), as measured by dilution experiments [Sherr et al., 2013; Stoecker et al., 2013a] is given by

\[
gP \equiv qZI(P)Z
\]  

where \( I(P) \) is the microzooplankton ingestion rate, here assumed to follow a simple saturating response:

\[
I(P) = I_0 \frac{P}{K + P}
\]

\( I_0 \) was determined empirically (3.4 ± 1.4 d\(^{-1}\)) by taking the mean of \( gP/Z \) (see 13) over 7 dilution experiments from spring 2009 [Sherr et al., 2013] in which \( P > 400 \) mg C m\(^{-3}\), i.e., \( P >> K \), with \( K \) estimated coarsely from the laboratory experiments reviewed by Sherr and Sherr [2009] as 1 mmol N m\(^{-3}\). As did Banas et al. [2009], we credit the descriptive power of our very simple NPZ formulation (Fig. 4) largely to the availability of a local, empirical constraint on microzooplankton grazing.

Microzooplankton mortality is quadratic. This form replicates the time-evolution of mesozooplankton predation as captured by an expanded version of the model with explicit, stage-resolved, Calanus-like copepods. Other predators whose production is timed differently relative to the spring bloom would lead to mortality on microzooplankton with a different functional form.

Slow- and fast-sinking detrital pools export material from the surface layer. Estimates of overall \( e \)-ratio (vertical export as a fraction of primary production) by Cross et al. [2012] (0.29 ± 0.12 at 40 m depth for the seasonal range modeled here) were used to
constrain the choice of $D_S$ sinking rate $w_s$. The model proved to be insensitive to $D_L$ sinking rate as long as the value is on the order of 10 m d$^{-1}$ or higher. The detrital pools remineralize to NH$_4$ and NH$_4$ nitrifies back to NO$_3$ at relatively low rates compared with values commonly assumed in temperate plankton models, but similar to those used by Zhang et al. [2010b] in an Arctic model. This geographic variation is broadly consistent with the explicit temperature dependence $Q_R$ assumed here.

### 2.5. Tuning and validation experiments

Two datasets were used for tuning and validation (Fig. 3). First, we assembled a process-rich time series resolving an intense ice-edge spring bloom near 60 ° N in late April/early May 2009 from a variety of 2009 BEST/BSIERP observations (Lomas et al. [2012]; Mordy et al. [2012]; Stabeno et al. [2012b]; Stoecker et al. [2013a]; Sherr et al. [2013], R. Sambrotto, unpubl. data). Fig. 3 shows an ensemble of 98 model particle trajectories that intersect the region where the bloom peak was sampled (174–176 ° W, 59–60 ° N) on April 27, 2009 during the spring BEST/BSIERP cruise. The trajectories diverge over the following months, and so observations over a larger area (173.75–176.25 ° W, 58.5–61.25 ° N) were selected from the summer cruise to represent the fate of the sampled bloom community. Time series of BESTMAS forcing along these 98 trajectories are shown in Fig. 7 (note the temporary ice retreat in March 2009 described by Miksis-Olds et al. [2013]) and spring and summer cruise observations along with model results are shown in Fig. 8. This observational dataset ("IEB60") served as the primary standard for parameter tuning.

Second, [Sigler et al., 2014] report statistics describing bloom timing and other metrics at four long-term mooring stations along the 70 m isobath. We constructed model time
series at M2 and M8, the northernmost and southernmost of these (Figs. 3, 5) and compared them with the Sigler et al. [2014] statistics. This served as a test of the spatial and temporal portability of the model, and also a basis for tuning $E_{\text{crit}}$ and $\Delta E$.

Values for $\text{att}_{\text{sw}}$, $\alpha_{\text{min}}$, $m_p$, $m_{\text{agg}}$, $m_Z$, $w_S$, and $r_{\text{remin}}$ were determined through a series of Monte Carlo experiments in which model runs using random combinations of parameters (n $\approx$ 100,000, alongside another 100,000 exploring structural variants) were compared with a suite of biomass, rate, and ecosystem-function metrics at IEB60. Sensitivities and tradeoffs among parameters, between parameters and individual metrics, and among the metrics themselves were evaluated by regression analysis on small subsets of the best-performing model cases in each ensemble. It was determined, for example, that broad ranges of $w_S$ and $r_{\text{remin}}$ values give comparably good fits to observations, but that higher $w_S$ must be balanced by higher $r_{\text{remin}}$; the scale depth $w_S/r_{\text{remin}}$ has a log-mean value $\sim$20 m across the “nearly optimal” parameter combinations. The same analysis was used to verify the appropriateness of a priori values for $\mu_0$, $\text{att}_P$, $\text{att}_{\text{sum}}$, $I_0$, $r_{\text{nitr}}$, and biomass initial conditions. Sources for these and other parameter values are given in Table 1.

3. Results

3.1. Model validation

3.1.1. Evolution of an ice-edge spring bloom

The time course of the spring bloom at IEB60 is shown in Fig. 8, and metrics of model performance are listed in Table 2. Nitrate in the upper 35 m declined precipitously as phytoplankton biomass increased to very high levels (Fig. 8a,b). Observations of nitrate around April 27 shown great variability (0–15 mmol m$^{-3}$) but this appears to be explicable by variation in ice cover and light within this 100 km region (Fig. 7, spread in model
ensemble). Error in nitrate in July (Fig. 8a) is probably a combination of errors in vertical structure near the pycnocline—some of the high observational values represent pycnoclines shallower than 35 m, rather than cross-pycnocline fluxes—but also a failure of our model to reproduce the intermittent resupply of nitrate to the surface layer via patchy wind mixing. This may reflect the limits of our Lagrangian ensemble approach compared with a full three-dimensional biogeochemical simulation.

The model captures the timing of the spring bloom within a few days (Fig. 8b). Data in this region of the shelf from other BEST field years (Sambrotto et al., submitted) confirms the approximately 20 d spinup time of the bloom. Peak integrated biomass (measured by two independent datasets: Lomas et al. [2012], Sambrotto et al., submitted) is biased low in the model by 21% even after extensive tuning, because error in this metric is involved in a strong tradeoff with errors in e-ratio and pre-bloom biomass. Bias in summer phytoplankton biomass is smaller in absolute terms but higher in relative terms; we did not weight this time period as strongly in the parameter-tuning process.

Note that the model value for light attenuation by phytoplankton $\text{at}_{P}$ was chosen based on a detailed, unpublished calculation of 1% light level at spring 2009 BEST stations in relation to chlorophyll concentration (E. Cokelet, pers. comm.). The value used for $\text{at}_{sw}$ is an ad hoc downward adjustment of the estimate from that analysis (from approx. 0.1 m$^{-1}$ to 0.05 m$^{-1}$). This adjustment proved to be necessary to capture the magnitude of the IEB60 bloom without distortions in other metrics. We speculate that this artificial reduction in light attenuation compensates for bias in the vertical structure of turbulent mixing either in BESTMAS or in our one-dimensional reimplementation. At IEB60, our ad hoc adjustment in $\text{at}_{sw}$ is equivalent to a change of 0.15 d$^{-1}$ in mean growth rate over
the euphotic zone, enough to cause a twofold change in biomass accumulation over 5 d. It would only take a bias of 4 m in the depth over which euphotic-zone phytoplankton are mixed in the model—a bias smaller than our vertical resolution—to have a comparable effect on growth rate. These extreme sensitivities suggest that beyond a factor of two or so, it would be unwarranted to place special emphasis on any model’s skill at reproducing absolute chlorophyll concentration in this region, compared with other timing or functional metrics.

The model reproduces observed rates and rate ratios at IEB60 well. Four independent observational estimates of phytoplankton community growth rate, from microzooplankton dilution experiments and $^{14}$C, $^{13}$C, and $^{15}$N uptake experiments, are shown in (Fig. 8c). We converted primary production estimates to specific growth rate estimates, rather than vice versa, because specific growth rate is the component of primary production independent from biomass accumulation (Fig. 8b). The model ensemble-average time series of $\mu$ (Fig. 8c) matches the observations as well as well the four observational time series match each other, following the dilution experiment data (red) most closely. In spring (but not in summer), the model ensemble actually replicates the severalfold near-instantaneous variance of the observations, suggesting that this variance could be the result of physically forced, $< 100$ km-scale variation in bloom evolution.

The ratio of new, nitrate-driven to total primary production ($f$) was estimated from the ratio of NO$_3$ to NH$_4$ uptake (Fig. 8d; Sambrotto et al., submitted). The $f$-ratio decreased from $\sim 1$ at the height of the bloom to $\sim 0.3$ in July (Fig. 8d), and the model—despite inclusion of only one phytoplankton compartment—replicated this shift. On a methodological level, this suggests that when clear empirical guidance from rate
experiments is available, an NPZ model does not necessarily need two or more explicit $P$ compartments to capture the transition from a diatom-like, rapidly growing bloom community to a small-cell-like, summer recycling community (Moran et al. [2012], Eisner et al., submitted). The mean $e$-ratio for the spring-summer analysis period is also shown in Fig. 8d, as estimated by Cross et al. [2012] for the middle–outer shelf as a whole and for the model at IEB60, where the modeled value falls within the range of empirical uncertainty.

Finally, the model also captures microzooplankton biomass and grazing rate during the bloom (Fig. 8e,f). Summer observations of microzooplankton biomass [Stoecker et al., 2013b] were not sufficiently resolved in the vertical to estimate in situ integrated biomass with confidence, and thus are not included. Only one of the July dilution experiments described by Stoecker et al. [2013a] fell within the narrow matchup region for the IEB60 ensemble and so the absolute in situ grazing rate is not as well constrained in summer, but the ratio $g/\mu$ for the ensemble in July is consistent with the observed ratio of rates for broader spatial averages in the Stoecker et al. [2013a] dataset (Fig. 8c,e).

Over the course of these observations at IEB60, the $>5 \mu m$ fraction of phytoplankton biomass changes significantly, from $\sim 0.5$ before the bloom to $\sim 1$ during the bloom to $\sim 0.2$ in July (not shown). This dataset is thus a complex test of a simple, 1-P NPZ model like ours, although it is parameterized to allow two modes of time variation in community functional responses (nutrient half-saturation and growth-light initial slope: see above) which can be taken in part to represent species composition shifts. As mentioned above, we ran extensive Monte Carlo experiments in a version of the model with a second phytoplankton compartment which was allowed its own nutrient and light responses, a distinct
mortality rate, and a distinct susceptibility to microzooplankton grazing. We did not find any parameterization among these 2-P model cases that noticeably outperformed the 1-P model version described here. Replicating the time evolution of the > 5μm biomass fraction proved to be a major constraint on parameter combinations, but a constraint that was only weakly related to other skill criteria. This might indicate that a single microzooplankton compartment is insufficient to resolve the grazers’ own seasonal community shift, or perhaps that the small-phytoplankton community in winter cannot be naturally conflated with that in summer.

At the same time, our Monte Carlo experiments clearly indicated that seasonal variation in α as described above was essential to reproducing the magnitude of ice-edge spring blooms while avoiding spurious late winter blooms. (Note that likely bias in the model light field is in the wrong direction to resolve the issue [Ladd and Bond, 2002], and that the earliest spring 2009 biomass and rate observations (Fig. 8 below) are difficult to reconcile with any top-down explanation.) In other words, plasticity in phytoplankton community responses appears to be essential to spring dynamics in this system; but modeling this plasticity as a competition between exactly two size classes of phytoplankton with fixed responses appears to be, at best, a roundabout approach.

3.1.2. Patterns of bloom timing

The diversity of simultaneous BEST/BSIERP observations allows us to verify the consistency of stocks, rates, and functional relationships during the IEB60 bloom event to a degree seldom possible with field data. A separate question, however, is whether the model, tuned to the IEB60 dataset, is able to capture the diversity of spring bloom time histories across subregions and across years in the EBS. Fig. 9a shows the relationship
between ice-retreat timing $t_{\text{ice}}$ (the date on which ice cover drops below 10 %) and bloom timing $t_{\text{bloom}}$ (the date of maximum integrated biomass) for all hindcast years at M2 and M8. The results replicate the essential pattern described by Hunt Jr et al. [2002, 2011] and more recently quantified by Brown and Arrigo [2013] and Sigler et al. [2014] using satellite and moored observations respectively. At M8, $t_{\text{ice}}$ and $t_{\text{bloom}}$ are close and well-correlated, indicating an ice-retreat-triggered bloom in all years. At M2, the same association is seen in some years, but when $t_{\text{ice}}$ is earlier than yearday 80, the spring bloom is delayed until May or early June. The model replicates this qualitative pattern (after tuning of $E_{\text{crit}}$ and $\Delta E$, but not other parameters, against the M2 data shown here). Year-by-year comparisons between observed and predicted $t_{\text{bloom}}$ are quite good at M8 (Fig. 9b), with a Willmott skill score of 0.86, where 1 represents a perfect model and 0 a model that performs no better than the mean of the observations [Willmott, 1981]. At M2 (Fig. 9c), skill is significant (0.68) but errors of up to a month occur in some years. Comparisons of modeled and observed $t_{\text{bloom}}$ at PROBES Station 12 (Fig. 3 in Sambrotto et al. [1986]) are also shown in Fig. 9c to extend the record.

Brown and Arrigo [2013] also report satellite-based $t_{\text{bloom}}$ at M2 for nine ice-free years that overlap with the Sigler et al. [2014] moored observations. Remarkably, these two observational time series disagree with each other to the same extent as the model disagrees with either of them. Root-mean-square differences between model and mooring, model and satellite, and mooring and satellite are 16, 19, and 21 d respectively (n=9). Differences among the means are smaller (5, 1, and 4 d for the same three comparisons). This suggests that the date of maximum chlorophyll is an inherently noisy or ill-defined metric and that apparent signals with variance less than two weeks or so may not be significant.
3.2. Drivers of interannual variability

Full time series of modeled near-surface temperature, ice cover, and integrated phytoplankton and microzooplankton biomass at M8 and M2 are shown in Figs. 10 and 11. Hindcast years have been re-sorted by mean temperature to better show relationships. A few patterns are evident by inspection: at M8, warm conditions are associated with earlier ice retreat, the timing of the spring bloom and ice retreat are closely associated, and microzooplankton biomass follows phytoplankton biomass, although somewhat integrated and smoothed. At M2, spring bloom timing follows ice-retreat timing in the minority of years when ice is present, but does not show a monotonic relationship with mean temperature overall. Modeled phytoplankton blooms at M2 are intermittent, with multiple peaks in most years, as seen in moored fluorometer observations there [Stabeno et al., 2012a]. This intermittency is likely to contribute to the noisiness of the date of maximum chlorophyll as a timing metric.

There are a large number of confounded correlations among variables in these results, which complicate their mechanistic interpretation. In this section, we use a systematic correlation analysis and some ancillary model experiments to determine which relationships between environmental conditions and phytoplankton responses are actually causal in our modeled northern and southern EBS.

Modeled primary production is positively correlated with temperature at both M2 and M8 (Table 3, Fig. 12). This result is consistent with the empirical conclusion by Liu [2014] and others that primary production is higher overall in warm years. Either direct effects or indirect correlates of temperature could be responsible, however. By ”direct effects” we mean the appearances of temperature within the ecosystem model equations: these include
direct physiological effects (like the $Q_{10}$ dependence of phytoplankton maximum growth rate) and community-metabolism effects (like the imposed difference in $Q_{10}$ responses for phytoplankton and zooplankton). We will return to these community dynamics in more detail later, but for now the crucial result is that modeled primary production changes only marginally when we turn off all these direct temperature effects entirely. Fig. 13 shows a comparison between mean Feb 15–Jul 15 integrated primary production at M2 and M8 in the model base case and in a variant in which we set $Q_P = Q_Z = Q_R = 1$, so that all biological rates maintain their 0°C base value across all conditions. Results at M8 are essentially indistinguishable, and at M2 show a simple, close-to-linear bias. As one would expect, results from an intermediate case in which $Q_P = Q_Z = Q_R = 2$ (the $Q_P$ base value) fall in between the case shown in Fig. 13 and the 1:1 line.

The implication is that direct effects of temperature play only a small role in determining which model years have higher primary production than others. Results for $t_{bloom}$ (not shown) are noisier but likewise indicate no overall causal role on the interannual scale we are considering. Among the correlates of temperature, then, which are most directly responsible for interannual variation in bloom timing and mean spring primary production (hereafter PP) in the north and the south?

1. $t_{bloom}$ at M8: Mean spring fractional ice cover $\overline{ice}$, mean PAR at the water surface (under-ice when ice is present) $\overline{E_0}$, and the mean of the composite light index defined above $\overline{E_{eff}}$ are all well-correlated with $t_{bloom}$ (Fig. 12, Table 3) and with each other (Table 4). The most straightforward interpretation is that ice cover controls light availability and thereby the timing of the bloom.
2. *t* _bloom_ at M2: In the south, however, neither surface light availability (*ice, E_0*) nor turbulent mixing (*κ*, the 0–35 m, Apr 1—Jul 15 turbulent diffusivity) is well-correlated with *t* _bloom_ by itself, but the composite light index *E_{eff}*, which combines these surface and subsurface effects on light availability, is a moderately good predictor (*r*^2 = 0.52: Table 3). This is consistent with the classic picture (see Sec. 3.1.2) in which ice retreat controls bloom timing at M2 in some years while early spring storms delay the bloom in others.

3. *PP* at M8: Primary production in the north is correlated with the same factors as *t* _bloom_, and inversely with *t* _bloom_, implying that interannual variation in *PP* mainly reflects the position of the bloom within the Feb 15–Jul 15 analysis window (see Fig. 10).

4. *PP* at M2: Here the correlation with *t* _bloom_ is weakly positive, indicating different dynamics. *PP* is correlated with *ice* and *E_0* overall (Fig. 12) but these relationships fail to explain twofold variation in *PP* among ice-free years. The best correlate of *PP* at M2 is mean temperature, but this is necessarily an indirect relationship, as discussed above. The next best correlate is mean along-shelf transport *u_rot*, calculated as from the net motion Feb 15–Jul 15 of particle trajectories that intersect M2 (see Fig. 5). The component of net displacement oriented 120° was taken as along-shelf transport. (In our Lagrangian model setup, this metric indicates the water depth of the starting positions of each year’s ensemble of one-dimensional cases, and thus the nitrate initial condition (Eq. (1)); since we are analyzing results as Eulerian time series extracted from the Lagrangian ensemble (Fig. 5), *u_rot* can also be interpreted in a conventional way as the strength of advection of deep-water nutrients past the station.) The residuals between *PP* and *u_rot* at M2 (not shown) are in turn correlated with *κ*. This correlation is positive, suggesting the effect of turbulence on nutrient supply, not light limitation as above. Consistent
with this interpretation, the slope between interannual variations in $PP$ and $NO_3^{initial}$, relative to their 1971–2012 means, is steeper than 1:1 (Fig. 14), whereas ancillary model experiments in which we manipulated $NO_3^{initial}$ directly (varying the leading coefficients in (1c) and (1b) by $\pm 30\%$) show an almost exactly 1:1 relationship (Fig. 14). This suggests that multiple mechanisms of interannual variation in nutrient supply—one lateral, one vertical—are at work simultaneously at M2, both of them correlated with seasonal-mean temperature.

### 3.3. Implications for future change

The importance of distinguishing causal from merely correlated environmental drivers becomes clear when we switch our focus to longer-term change in the model. Fig. 15 shows $t_{bloom}$ and $PP$ at M2 in relation to a subset of the drivers shown in Fig. 12. Here, the 1971–1976 cold period is distinguished from the generally warmer period that followed (1977–2012; see Fig. 1) and from the 2040s projection discussed above. The relationships that we identified above as causal remain consistent across the full model run, whereas relationships that we identified as indirect do not (most dramatically, compare Figs. 15a and 15b). In this model run, the mean difference in bloom timing between warm and cold years described by the original Oscillating Control Hypothesis [Hunt Jr et al., 2002]—later blooms in warmer years—appears to be contingent on a particular decadal-scale regime, and does not continue to hold farther into either the past or the future. (Predictions based on ice cover rather than temperature are more consistent: not shown).

Likewise, 2040s $PP$ in this model projection falls well below an extrapolation based on regression to temperature across the model hindcast years. Relationships with $E_{eff}$ and $\pi$...
suggest why: these proximate controls on light and nutrient limitation are similar across
the model hindcast and projection, even as seasonal-mean temperature changes by > 2°C.
This result is as likely to be a methodological artifact as a proper prediction, since the
model projection used here is driven by a trend in the regional thermodynamics but not
trends in the mesoscale dynamics that control seasonal flushing and storm mixing. Given
the diagnosis of environmental drivers based on the model hindcast, there is no reason to
think that we can extrapolate future change in $t_{\text{bloom}}$ or $\overline{P}$ in the southern, increasingly
ice-free EBS from gross measures of surface temperature and ice cover (Fig. 2). This
cautionary result appears to be true for either statistical or dynamical extrapolations.

3.4. Trophic coupling in spring

Some researchers have suggested that in high-latitude systems, the degree of coupling
between primary and secondary zooplankton production is highly temperature-dependent
and that this dependence is a major factor in structuring those ecosystems. Rose and
Caron [2007], for example, suggest that microzooplankton grazing is limited by low tem-
peratures to the point that it cannot keep up with phytoplankton growth at near-freezing
temperatures, and that this partial decoupling is a major driver of the intense algal blooms
often seen at high-latitudes. Our model—or rather, the measured community growth and
grazing rates at $\sim 0^\circ\text{C}$ that the model is based on [Sherr et al., 2013]—is inconsistent
with this hypothesized mechanism, and thus consistent with Sherr and Sherr [2009] and
Franzè and Lavrentyev [2014]. When we compare time histories of microzooplankton and
phytoplankton biomass at M2 and M8 (Fig. 16a), we do see a greater time lag between
the phytoplankton and their grazers at the colder site (phase-space trajectories more el-
liptical at M8, more linear at M2). Superficially this seems to corroborate the Rose and
Caron [2007] hypothesis of a greater decoupling in colder conditions, but when we turn off direct temperature effects in the model \( Q_P = Q_Z = Q_R = 1 \), the pattern persists almost unchanged (Fig. 16a, dashed vs. solid lines). The relative phasing of phytoplankton and microzooplankton at these model stations must be controlled not by the metabolic mechanisms Rose and Caron [2007] proposed, but rather by other aspects of the environment, perhaps the suddenness of ice-retreat-regulated spring blooms relative to those in ice-free conditions. Furthermore, in the seasonal average, the model shows very little variation in the relationship between phytoplankton and microzooplankton production (Fig. 16b): the latter is a near-constant fraction of the former. Microzooplankton appear to be tightly coupled to their prey even at the lowest temperatures observed in this system.

Other studies have suggested that the different temperature responses in autotrophs and heterotrophs will drive a restructuring of high-latitude ecosystems as those systems continue to warm. Many studies have found temperature sensitivity in zooplankton and marine bacteria to be higher than than of phytoplankton [Pomeroy and Wiebe, 2001; Vaquer-Sunyer et al., 2010; Chen et al., 2012], although the effective \( Q_{10} \) values of these sensitivities are highly variable and the commonly assumed difference between heterotroph and autotroph responses is not universally observed [Robinson and Williams, 1993]. (Some of the variability in these past results may arise from inappropriateness of the \( Q_{10} \) functional form as opposed to a linear [Montagnes et al., 2003] or Arrhenius-type response [Brown et al., 2004]; we have kept our analysis in terms of \( Q_{10} \) because of its familiarity.)

The metabolic theory of ecology is also generally taken to predict a difference in temperature sensitivity between photosynthesis and respiration [Brown et al., 2004; López-Urrutia et al., 2006], and this hypothesis has motivated experimental studies [Holding et al., 2013]
and empirical and theoretical arguments that with ~ 5°C of warming, polar ecosystems
pass a tipping point where respiration exceeds photosynthesis and carbon flows change
fundamentally. A model like ours cannot test the ultimate validity of this “metabolic
tipping point” hypothesis (i.e., whether the premise of a sensitivity difference is correct,
or whether the conclusion of a tipping point accurately predicts the future) but the model
does provide a framework in which we can impose the premise and test whether the
conclusion follows, in EBS-like conditions.

Fig. 17 shows results of two final ensembles of model cases in which the model was forced
by spring 2009 conditions at M8 (a relatively cold year and location) and spring 2004
conditions at M2 (relatively warm conditions) under an array of combinations of $Q_P$ and
$Q_Z = Q_R$. A range of estimates of these parameters from the literature (converted where
necessary from activation energies over -2–8°C) are shown for comparison. As expected,
as one moves from the balanced-response end of the parameter space ($Q_P \approx Q_Z$) to the
high-$Q_Z$ end, export ratio decreases (Fig. 17b,d), suggesting a shift toward a recycling
community fueled increasingly by regenerated nutrients. Primary production does not
collapse under this increased grazing pressure but rather increases at both stations with
increasing $Q_Z$, indicating that gains due to increased nutrient retention outweigh the direct
losses to grazing. It is important to note the modest scale of the response of ecosystem
function to $Q_P, Q_Z$: at M2 in 2004, for example, primary production only varies 6% over
the entire parameter range.

To more directly address the hypothesis of a polar-ecosystems tipping point at 5°C
of warming, we ran an additional set of cases which duplicate the hindcasts shown in
Fig. 17a–d but with 5°C added uniformly (i.e., rate constants increased by $Q_P^{5/10}, Q_R^{5/10}$,
Percent changes in the six metrics are shown in Fig. 17e–h. Results are consistent in direction with the sensitivity experiment in Fig. 17a–d: increasing grazing rate relative to maximum phytoplankton growth rate decreases export and increases mean primary production, to a modest degree. None of the results here could be described as the passing of a tipping point in plankton productivity.

4. Discussion

4.1. Implications for higher trophic levels

As discussed above, large interannual variation in the recruitment of pollock, salmon, and other pelagics have been linked to the relative abundance of lipid-rich zooplankton taxa in the EBS (Hunt Jr et al. [2011]; Coyle et al. [2011]. It remains an open question how exactly temperature, ice cover, and primary production magnitude and phenology combine to influence large zooplankton production, but this model study serves to narrow the likely hypotheses. In short, it appears much more likely that climate change shapes mesozooplankton production and composition through the timing of prey availability (both phytoplankton and microzooplankton) than through the overall magnitude of prey production. Over recent decades (1979–2012), our model suggests that total spring/early summer primary production has generally been higher in warmer years, consistent with the productivity model by Liu et al. (submitted) but contrary to the observed variation in large zooplankton [Eisner et al., 2014]. At the same time, the timing of the spring pelagic phytoplankton/microzooplankton bloom varies by a month or more between cold and warm years, in the model as in long-term observations (Fig. 9), which is more than enough to have major interactions with copepod life histories [Varpe et al., 2007; Ji et al., 2010; Mackas et al., 2012]. A number of recent studies [Søreide et al., 2010; Wassmann...
and Reigstad, 2011; Daase et al., 2013] have suggested that this type of climate-linked phenological change could have critical impacts on the future recruitment success of large arctic/subarctic copepod taxa like Calanus, in which life history and reproductive strategy are closely tied to the spring bloom. Our model does not include in-ice algal production, which may be critical to large copepods in this system [Durbin and Casas, 2014] as in others [Daase et al., 2013]. If ice algal prey are available in Feb–Mar in cold years but not warm years in the southern EBS, this would further amplify the modeled interannual timing pattern (Fig. 9, 12a), and work against the variation in total production (Fig. 12g).

4.2. Implications for the metabolic tipping-point hypothesis

We have argued that variation in spring bloom magnitude is modest on the interannual scale compared with phenological and other environmental variation. It is, of course, still possible that on a longer timescale, the planktonic ecosystem could prove to have a sigmoidal response to temperature [Holding et al., 2013], with the multidecadal warming trend leading to only small effects in the short term but driving the system past a tipping point at some point in the future. As discussed above, metabolic theory and recent observational and experimental studies have proposed exactly this. Our model strongly suggests that even if we grant the central premise—that respiration has a steeper temperature dependence than photosynthesis—the consequences may not be what the metabolic tipping-point hypothesis suggests (Fig. 17). Even large variations in the temperature sensitivities of phytoplankton, zooplankton, and bacterial respiration drive only modest overall effects on primary and export production, and increasing zooplankton/bacterial rates actually increase total primary production in this model, rather than reducing it.
For differences between phytoplankton and zooplankton $Q_{10}$ values in the vicinity of the median prediction found in the literature (model base case; annotations, Fig. 17b), we find that 5°C of warming is accompanied by a 20–30% increase in primary production.

Why would this model result be so different from, say, mesocosm studies of this topic such as Holding et al. [2013]? We speculate that the issue is the complexity of the biogeochemical role played by microzooplankton in a dynamic system where total primary production is controlled more by the physics of nutrient supply, as described above, than by grazing losses. It is true that the intense spring blooms seen in the northern EBS appear to involve a transient escape from grazer control (Fig. 16a), but on longer and broader scales, it appears that nutrient regeneration by microzooplankton is actually essential to sustaining the bloom after nitrate is exhausted.

Even in several-month averages, $e$-ratio and $f$-ratio are highly imbalanced in this system (Fig. 8), despite the close coupling of phytoplankton and their primary grazers (Fig. 16). The nutrient budget of this wide shelf system takes a full seasonal cycle or more to close (Mordy et al., submitted), and this may well be true for the primary production budget. We tentatively conclude that this ability to "evade gravity" for months at a time—nutrients ascend the water column and the trophic ladder and do not come down—is responsible for the result in which combinations of $Q_{10}$ values that correspond to dramatic tipping points in other analyses produce nothing of the kind in modeled spring dynamics here. The lag time between peak rates of primary productivity and export appears to be similar in high-latitude [Green and Sambrotto, 2006] and tropical [Sambrotto, 2001] systems, suggesting that the insensitivity of phytoplankton–microzooplankton interactions
to temperature that we observe in the EBS may be a quite general pattern. This is a hypothesis that requires empirical, rather than numerical, exploration.

5. Summary and conclusion

A new planktonic ecosystem model was constructed for the EBS based on diverse observations from the BEST/BSIERP field program: nitrate concentration, phytoplankton and microzooplankton biomass, community growth and grazing rates from dilution experiments, primary production rates from three other independent methods, and $f$-ratio from stable-isotope NO$_3$ and NH$_4$ uptake experiments. When run coupled to a data-assimilative ice-ocean hindcast of 1971–2012, the model performs well against in situ observations of spring bloom time-evolution and multi-year statistics of bloom timing, across a gradient of ice influence.

Capturing 1) the intensity of spring biomass accumulation at the northern IEB60 site in April-May and 2) the rapidity of the bloom’s onset there while also capturing 3) the observed lack of a bloom at IEB60 during the partial ice retreat in March and 4) the delay of the spring bloom until May or June in ice-free conditions at M2 proved to be a major constraint on the model parameterization, especially given the additional constraints of 5) significant export out of the euphotic zone during spring and 6) significant microzooplankton grazing during the IEB60 bloom maximum (see Sec. 3.1.1). To our knowledge no other NPZ model has been shown to pass this precise of a multivariate test of bloom magnitude, timing, and internal dynamics at specific Bering Sea stations (or indeed to have been tested against such a dataset). We have included a detailed set of metrics for the IEB60 testbed (Table 2) to encourage other modeling efforts to consider this mech-
anistically detailed benchmark along with spatially comprehensive but mechanistically ambiguous variables like chlorophyll.

This study examined only one projection of future climate, not an ensemble, and by a method that does not resolve indirect effects of global climate on the mesoscale atmospheric patterns that drive interannual variation in mixing and advection in the EBS. It captures, rather, the gross effect of the regional thermodynamic trend (imposed via a middle-of-the-road estimate of 8°C of air temperature increase by 2100) on surface water temperature and ice cover. Even as temperature in the southern EBS moves outside the range of historically observed conditions (Fig. 2), the model projection does not find these novel combinations of temperature and ice cover, in themselves, to drive total spring primary production or spring bloom timing outside their historical ranges (Fig. 15). This negative result required us to consider in detail whether temperature and ice cover, the most obvious indices of climate impacts on subarctic seas, are the right indices, or merely correlated historically with the right indices.

On the northern middle shelf, we found that ice cover straightforwardly controls spring bloom timing in the model; that bloom timing controls interannual variation in spring primary production; and that temperature and ice cover are correlated similarly across interannual and interdecadal scales (Fig. 2). Thus it is not particularly important—in a strictly predictive sense, on the northern shelf in particular—whether the individual sensitivities of phytoplankton to temperature, light, mixing, and so on are accurate or not in the model. In contrast, the dependencies proved to be more subtle on the southern middle shelf. The model hindcast suggests that bloom timing at M2 is controlled by surface (ice cover) and subsurface (turbulent mixing) effects on light availability in combination, as
in the Oscillating Control Hypothesis [Hunt Jr et al., 2011]. It suggests that total spring primary production at M2 is controlled not by bloom timing as at M8 but by nutrient supply, with both advective transport and turbulent mixing contributing to interannual variation. (These patterns are summarized in Fig. 18.) Crucially, both advection and wind mixing are processes that our future projection does not resolve trends in, and that global-scale climate models are not likely to predict accurately because of scale and their resolution of shelf processes.

These results are motivation for extremely careful spatial downscaling of climate projections in the Eastern Bering Sea, with particular attention to flushing, retention, and vertical mixing on the shelf. Advances in this area are very likely necessary even to determine whether total middle-shelf primary production in a warmer world is likely to be higher or lower than the present era. Accurate prediction of future trends in bloom timing is likely to also require advances in our conceptual and numerical models of plasticity in phytoplankton community light response, which turned out in this study to be both crucial and poorly constrained by available data. Our solution—allowing $\alpha$ to vary as a function of a synthetic parameter that involves both surface light and subsurface mixing—is just one possibility among many. More generally, our numerical experiments regarding community metabolism suggest that similar issues may well arise across many other high-latitude systems, with direct effects of temperature on the plankton—although easier to conceptualize than plasticity in functional responses or regional shelf dynamics—proving to play a smaller role in future change than temperature’s indirect, imperfect correlates.

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Table 1. Free parameters of the ecosystem model. μM N $\equiv$ mmol nitrogen m$^{-3}$. All rates are reported at 0 °C. Parameter values calculated from local data are in bold.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton</td>
<td>$\mu_0$</td>
<td>1.2</td>
<td>d$^{-1}$</td>
<td>summer data [Zeeman and Jensen, 1990], temperature-corrected</td>
</tr>
<tr>
<td></td>
<td>$\alpha_{\text{sw}}$</td>
<td>0.05</td>
<td>m$^{-1}$</td>
<td></td>
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<tr>
<td></td>
<td>$\alpha_{\text{Ph}}$</td>
<td>0.006</td>
<td>m$^{-1}$ μM N$^{-1}$</td>
<td>1% light level and chl concentration, spring 2009 ice-free stations (E. Cokelet, pers. comm.)</td>
</tr>
<tr>
<td></td>
<td>$\alpha_{\text{win}}$</td>
<td>0.01 (W m$^{-2}$)$^{-1}$ d$^{-1}$</td>
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</tr>
<tr>
<td></td>
<td>$\alpha_{\text{sum}}$</td>
<td>0.16 (W m$^{-2}$)$^{-1}$ d$^{-1}$</td>
<td>Sambrotto et al. [1986], bloom maximum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$E_{\text{crit}}$</td>
<td>30</td>
<td>W m$^{-2}$</td>
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<tr>
<td></td>
<td>$\Delta E$</td>
<td>5</td>
<td>W m$^{-2}$</td>
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<td></td>
<td>$k_{\text{min}}$</td>
<td>0.16</td>
<td>μM N</td>
<td>Collos et al. [2005]</td>
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<td></td>
<td>$\varphi_{\text{NH}_4}$</td>
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<tr>
<td></td>
<td>Chlorophyll:N ratio</td>
<td>9</td>
<td>mol : mol</td>
<td>spring 2009 observations (Sambrotto et al., submitted)</td>
</tr>
<tr>
<td></td>
<td>Phytoplankton mortality</td>
<td>$m_{\text{P}}$</td>
<td>0.03</td>
<td>d$^{-1}$</td>
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<tr>
<td></td>
<td>Phytoplankton loss via aggregation</td>
<td>$m_{\text{agg}}$</td>
<td>0.009 (μM N)$^{-1}$ d$^{-1}$</td>
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<tr>
<td>Zooplankton</td>
<td>Max microzooplankton ingestion rate</td>
<td>$I_0$</td>
<td>3.4</td>
<td>d$^{-1}$</td>
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<td>Grazing half-saturation</td>
<td>$K$</td>
<td>1</td>
<td>μM N</td>
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<td>Microzooplankton growth efficiency</td>
<td>$\epsilon$</td>
<td>0.3</td>
<td></td>
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<td></td>
<td>Fraction of grazing excreted to NH$_4$</td>
<td>$f_{\text{ex}}$</td>
<td>0.35</td>
<td></td>
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<tr>
<td></td>
<td>Microzooplankton mortality</td>
<td>$m_{\text{Z}}$</td>
<td>1.5</td>
<td>d$^{-1}$</td>
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<td>Regeneration and export</td>
<td>Small detritus sinking rate</td>
<td>$w_S$</td>
<td>3</td>
<td>m d$^{-1}$</td>
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<td></td>
<td>Large detritus sinking rate</td>
<td>$w_L$</td>
<td>100</td>
<td>m d$^{-1}$</td>
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<td></td>
<td>Detrital remineralization rate</td>
<td>$r_{\text{remin}}$</td>
<td>0.05</td>
<td>d$^{-1}$</td>
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<td>Nitrification rate</td>
<td>$r_{\text{nitr}}$</td>
<td>0.03</td>
<td>d$^{-1}$</td>
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<td>Temperature dependence</td>
<td>$Q_{\text{10}}$ for phytoplankton</td>
<td>$Q_{\text{P}}$</td>
<td>2</td>
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<td></td>
<td>$Q_{\text{10}}$ for zooplankton</td>
<td>$Q_{\text{Z}}$</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$Q_{\text{10}}$ for bacterial respiration</td>
<td>$Q_R$</td>
<td>2.8</td>
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<td>Initial conditions</td>
<td>Integrated phytoplankton</td>
<td>$P$</td>
<td>6</td>
<td>μM N · m</td>
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<td></td>
<td>Integrated microzooplankton</td>
<td>$Z$</td>
<td>0.4</td>
<td>μM N · m</td>
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<tr>
<td></td>
<td>Small detritus</td>
<td>$D_S$</td>
<td>0</td>
<td></td>
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<tr>
<td></td>
<td>Large detritus</td>
<td>$D_L$</td>
<td>0</td>
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<tr>
<td></td>
<td>Nitrate</td>
<td>NO$_3$</td>
<td>eq. (1)</td>
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<td></td>
<td>Ammonium</td>
<td>NH$_4$</td>
<td>0</td>
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</table>
Table 2. Detailed metrics of model performance at IEB60, spring–summer 2009. Sources: Mordy et al. [2012]; Lomas et al. [2012]; Cross et al. [2012]; Sherr et al. [2013]; Stoecker et al. [2013a], Sambrotto et al., submitted.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Time period</th>
<th>Obs. value</th>
<th>Model value</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO₃, 0–35 m (µM N)</td>
<td>Apr 10–11 (pre-bloom)</td>
<td>16.5</td>
<td>17.4</td>
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<tr>
<td></td>
<td>Apr 26–30 (early bloom)</td>
<td>7.7</td>
<td>15.0</td>
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<tr>
<td></td>
<td>May 6–7 (late bloom)</td>
<td>1.9</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Jun 26–Jul 6 (summer)</td>
<td>4.3</td>
<td>0</td>
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<tr>
<td>Integrated phytoplankton (g C m⁻²)</td>
<td>Apr 10–11</td>
<td>0.86</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Apr 26–30</td>
<td>34</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>May 6–7</td>
<td>47</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Jun 26–Jul 6</td>
<td>2.0</td>
<td>11</td>
</tr>
<tr>
<td>Integrated microzooplankton (g C m⁻²)</td>
<td>Apr 10–11</td>
<td>0.0028</td>
<td>0.0055</td>
</tr>
<tr>
<td></td>
<td>Apr 26–30</td>
<td>0.066</td>
<td>0.016</td>
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<tr>
<td></td>
<td>May 6–7</td>
<td>0.18</td>
<td>0.11</td>
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<td>Phytoplankton specific growth rate (d⁻¹)</td>
<td>Apr 10–11</td>
<td>0.091</td>
<td>0.024</td>
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<tr>
<td></td>
<td>Apr 26–30</td>
<td>0.38</td>
<td>0.41</td>
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<tr>
<td></td>
<td>May 6–7</td>
<td>0.19</td>
<td>0.24</td>
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<td></td>
<td>Jun 26–Jul 6</td>
<td>0.22</td>
<td>0.21</td>
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<tr>
<td>Specific grazing rate (d⁻¹)</td>
<td>Apr 10–11</td>
<td>0</td>
<td>0.0076</td>
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<tr>
<td></td>
<td>Apr 26–30</td>
<td>0.15</td>
<td>0.019</td>
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<td></td>
<td>May 6–7</td>
<td>0.17</td>
<td>0.12</td>
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<td></td>
<td>Jun 26–Jul 6</td>
<td>0.24</td>
<td>0.17</td>
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<tr>
<td>f-ratio</td>
<td>Apr 26–30</td>
<td>0.94</td>
<td>0.99</td>
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<td></td>
<td>May 6–7</td>
<td>0.71</td>
<td>0.50</td>
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<tr>
<td></td>
<td>Jun 26–Jul 6</td>
<td>0.31</td>
<td>0.46</td>
</tr>
<tr>
<td>e-ratio</td>
<td>Feb 15–Jul 15</td>
<td>~0.29</td>
<td>0.26</td>
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</table>
**Table 3.** Coefficients of determination $r^2$ between forcing and phytoplankton-response variables across model hindcast years, 1971–2012. Only correlations significant at the 0.1% confidence level are shown. Forcing variables included are 0–35 m mean temperature $T_{35}$ ($^\circ$C), mean fractional ice cover $\overline{\text{ice}}$, date of ice retreat $t_{\text{ice}}$ (yearday), mean PAR at the water surface $E_0$ (W m$^{-2}$), mean light index $E_{\text{eff}}$ (W m$^{-2}$; see eq. (12)), mean 0–35 m turbulent diffusivity $\overline{\kappa}$ (m$^2$ s$^{-1}$), and mean along-shelf transport $\overline{u_{\text{rot}}}$ (km d$^{-1}$). Response variables are date of spring bloom maximum $t_{\text{bloom}}$ and mean integrated primary production $\overline{PP}$ (g C m$^{-2}$ d$^{-1}$). All means are taken over the entire simulation period, Feb 15–Jul 15, except $\overline{\kappa}$, which is taken Apr 1–Jul 15.

<table>
<thead>
<tr>
<th>$t_{\text{bloom}}$, M8 (North)</th>
<th>$T_{35}$</th>
<th>$\overline{\text{ice}}$</th>
<th>$t_{\text{ice}}$</th>
<th>$E_0$</th>
<th>$E_{\text{eff}}$</th>
<th>$\overline{\kappa}$</th>
<th>$\overline{u_{\text{rot}}}$</th>
</tr>
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<tbody>
<tr>
<td>$\overline{PP}$, M8 (North)</td>
<td>0.82</td>
<td>0.88</td>
<td>0.83</td>
<td>0.90</td>
<td>0.79</td>
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<tr>
<td>$t_{\text{bloom}}$, M2 (South)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.30</td>
<td>0.52</td>
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<tr>
<td>$\overline{PP}$, M2 (South)</td>
<td>0.64</td>
<td>0.53</td>
<td>0.48</td>
<td>0.47</td>
<td>0.46</td>
<td>0.54</td>
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**Table 4.** Coefficients of determination $r^2$ among forcing variables across model hindcast years, 1971–2012. Only correlations significant at the 0.1% confidence level are shown. Variables are defined as in Table 3.

<table>
<thead>
<tr>
<th>M8 (North)</th>
<th>$\overline{\text{ice}}$</th>
<th>$t_{\text{ice}}$</th>
<th>$E_0$</th>
<th>$E_{\text{eff}}$</th>
<th>$\overline{\kappa}$</th>
<th>$\overline{u_{\text{rot}}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_{35}$</td>
<td>0.81</td>
<td>0.83</td>
<td>0.80</td>
<td>0.61</td>
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<td>0.34</td>
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<tr>
<td>$\overline{\text{ice}}$</td>
<td>0.87</td>
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<td>$t_{\text{ice}}$</td>
<td>0.93</td>
<td>0.75</td>
<td>—</td>
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<tr>
<td>$E_0$</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.86</td>
<td>—</td>
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</tr>
<tr>
<td>$E_{\text{eff}}$</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>$\overline{\kappa}$</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.34</td>
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</table>

<table>
<thead>
<tr>
<th>M2 (South)</th>
<th>$T_{35}$</th>
<th>$\overline{\text{ice}}$</th>
<th>$t_{\text{ice}}$</th>
<th>$E_0$</th>
<th>$E_{\text{eff}}$</th>
<th>$\overline{\kappa}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_{35}$</td>
<td>0.73</td>
<td>0.67</td>
<td>0.65</td>
<td>—</td>
<td>0.68</td>
<td>0.28</td>
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<tr>
<td>$\overline{\text{ice}}$</td>
<td>0.80</td>
<td>0.95</td>
<td>—</td>
<td>0.47</td>
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<tr>
<td>$t_{\text{ice}}$</td>
<td>0.73</td>
<td>—</td>
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<td>0.52</td>
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<tr>
<td>$E_0$</td>
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<td>—</td>
<td>0.25</td>
<td>0.32</td>
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<tr>
<td>$E_{\text{eff}}$</td>
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<td>0.34</td>
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</table>
Table 4. Coefficients of determination $r^2$ among forcing variables across model hindcast years, 1971–2012. Only correlations significant at the 0.1% confidence level are shown. Variables are defined as in Table 3.

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td>$T_{35}$ (North)</td>
<td>0.73</td>
<td>0.67</td>
<td>0.65</td>
<td>0.68</td>
<td>0.28</td>
<td></td>
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<tr>
<td>$T_{35}$ (South)</td>
<td>0.73</td>
<td>0.52</td>
<td>0.47</td>
<td>0.55</td>
<td>0.28</td>
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<td>$E_0$</td>
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<tr>
<td>$E_{eff}$</td>
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</table>

Figure 1. (a) Annual-mean temperature averaged over 0–35 m water depth on the EBS middle–outer shelf, from the BESTMAS model. Averages are shown for the northern ($> 60^\circ$N: dashed) and southern ($< 60^\circ$N: solid) shelves. (b) Annual-maximum ice cover and date of ice retreat (the last date on which ice cover > 10%) averaged over four contrasting sets of years (a), colored dots, also from BESTMAS.
Figure 2. Relationship between ice cover and temperature, averaged Feb 15–Jul 15 for the northern and southern middle–outer shelf separately, for each of the BEST-MAS model years shown in Fig. 1. Regression lines are shown for four subsets (north/south, hindcast/future).
Figure 3. Study area and sites of model-data comparisons. Long-term mooring sites M2 and M8 [Stabeno et al., 2012a], along with PROBES Station 12 [Sambratto et al., 1986], are marked with 50-km-radius circles, the area over which model time series were extracted from particle-path ensembles. The bounds for CTD matchups with the "IEB60" model experiment (see text) are marked by light and dark green rectangles for spring and summer 2009, with individual CTD stations marked by small circles. The 50, 100, 150, and 200 m isobaths are also shown.
Figure 4. Structure of the ecosystem model. Solid arrows denote growth and dotted arrows denote regeneration pathways.

Figure 5. Example of an ensemble of surface-layer particle trajectories used as the environment for a seasonal model run. (a) Blue lines indicate particles passing within 50 km of mooring station M2 (red circle) at some point within the Feb 15-Jul 15 model run in 2002 (an example year). (b) The same particle paths, plotted as latitude vs. time; each continuous line represents a distinct ecosystem model run. The segments of these trajectories < 50 km from M2 are shown in red. Final model time series at M2 were constructed by averaging across the highlighted segments.
Figure 6. (a) Modeled time histories of $\alpha$ according to Eq. (11) for each hindcast year at mooring M2. Black dots show the two values measured at PROBES Station 12 (see Fig. 3) in 1981 [Sambrotto et al., 1986], Fig. 14 in that study). The rate of increase between these two values is consistent with the range of rates of increase that arise in the model. (b) Black dots give daily values of the surface light-limitation coefficient $\alpha_{E_0} (\mu_0^2 + \alpha^2 E_0^2)^{-1}$ (see (9)) as a function of surface PAR $E_0$, across all hindcast years at M2. The upper and lower bounds on this functional response, corresponding to $\alpha = \alpha_{\text{sum}}$ and $\alpha = \alpha_{\text{win}}$, respectively, are shown as red and blue lines. Scatter in the functional response arises from the dependence of $\alpha$ on turbulent mixing in addition to $E_0$. 
Figure 7. Forcing time series for the IEB60 ensemble (see Figs. 3, 8) extracted from BESTMAS.
Figure 8. Time history of an ice-edge bloom in spring 2009 from observations and the model. Individual model cases—responses to the 98 individual forcing trajectories in the IEB60 ensemble (Figs. 3, 7)—are shown as gray lines, and the ensemble mean as a black line. Solid circles denote standing-stock measurements (nitrate and phytoplankton: green; microzooplankton: red) while open circles denote rate measurements (microzooplankton dilution experiments: red; $^{14}$C, $^{13}$C, $^{15}$N uptake experiments: blue, green). Red bars in (c), (e) denote areal means from Stoecker et al. [2013a] (north/mid-north, middle/outer, in that study) over the duration of the summer 2009 cruise. An empirical estimate of mean export ratio ± 1 std dev (red) is shown along with the model value in (d) (inset). Data sources are discussed in the text.
Figure 9. (a) Relationship between spring bloom timing and ice-retreat timing at M2 and M8 from observations (Sigler et al. [2014]; open circles) and the model (solid dots). Years with no ice at M2 or ice retreat earlier than Feb 15 (the start of the NPZ simulation period) are plotted at Feb 15, rather than omitted. (b),(c) Date of the spring bloom maximum (as in (a),(b)) over time. Model time series are shown as lines, observations as open circles. Black line/crosses in (c) show M2 results; for Probes Station 2, compare red circles (obs.) with red crosses (model).
Figure 10. Model time series of (c,d) vertically-integrated phytoplankton and microzooplankton biomass at M8 in relation to (a,b) temperature and fractional ice cover, for every year in the model hindcast and future projection. Years have been sorted by mean surface temperature within the hindcast and projection periods, in order to show patterns more clearly; individual years are labeled at top and bottom, color-coded and staggered by decade.
Figure 11. Time series for all years in the model hindcast and projection, as in Fig. 10, for station M2.
Figure 12. Relationships between six environmental forcing metrics and two metrics of the phytoplankton response, at M2 (orange) and M8 (blue). Each symbol represents one model hindcast year, averaged Feb 15–Jul 15 except as otherwise noted. Cf. Table 3.

Figure 13. Comparison between mean primary production in the model base case and an alternate parameterization with direct effects of temperature omitted ($Q_r = Q_x = Q_N = 1$), across hindcast years.
Figure 14. (blue) Relationship between initial NO$_3$ concentration (vertical mean and mean across ensemble members) and Feb 15–Jul 15 mean primary production across model hindcast years at M2. (red) Comparison between model base case (mean of hindcast years/blue symbols) and two alternate model cases in which initial NO$_3$ was adjusted upward and downward by 30%. Values are shown as percent change relative to model base-case mean.

Figure 15. Modeled mean primary production and date of spring bloom in relation to selected environmental metrics at M2, for the 1971–76 cold period (green, open triangles), 1979–2012 period (orange circles), and 2040s projection (black, solid triangles). Orange and green symbols together correspond to the orange symbols in Fig. 12.
Figure 16. (a) Relative phasing of modeled phytoplankton and microzooplankton biomass, over the course of each hindcast spring at M2 (orange/yellow) and M8 (blue). Solid lines show the model base case, dashed lines the alternate $Q_P = Q_Z = Q_R = 1$ parameterization with direct effects of temperature omitted. Time from Feb 15–Jul 15 runs generally counter-clockwise along these phase-space trajectories. (b) Relationship between primary and microzooplankton production across hindcast and projected future years at M2 and M8.
Figure 17. (a)–(d) Primary production and export ratio as functions of imposed $Q_{10}$ values for phytoplankton and zooplankton, averaged Apr 10–Jul 15, for 2009 at M8 (relatively cold conditions) and 2004 at M2 (warm conditions). The model base case is marked with a +. Literature estimates of $Q_p$ and $Q_z$ are indicated at the margins of (d); one outlier ($Q_z=6.2$, the "Arctic" case reported by Vaquer-Sunyer et al. [2010]) is off the scale. Note the narrow range on the color scales. (e)–(h) As in (a)–(d), but showing relative change in each metric between the case shown in (a)–(d) and a version in which temperature was uniformly raised 5°C.
Figure 18. Summary of causal pathways from climate-linked environmental drivers to primary production magnitude and timing, for the northern middle shelf (M8) and southern middle shelf (M2), as diagnosed from the model hindcast (Figs. 12–14. This summary applies to interannual-scale variation in spring/early summer processes in particular.

---

- **temperature**
- **ice cover**
- **transport**

- **maximum growth rate**
- **community metabolism**
- **turbulent mixing (stratification)**
- **surface PAR**
- **pre-bloom NO3**
- **light limitation**
- **nutrient limitation**

- **spring bloom timing**
- **total spring primary production**

---

- **dotted line**: minor contributor to interannual variation
- **red line**: major contributor at M2 (south)
- **blue line**: major contributor at M8 (north)