



Modeling spatial patterns of limits to production of deposit-feeders and ectothermic predators in the northern Bering Sea



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ABSTRACT

Network models can help generate testable predictions and more accurate projections of food web responses to environmental change. Such models depend on predator–prey interactions throughout the network. When a predator currently consumes all of its prey's production, the prey's biomass may change substantially with loss of the predator or invasion by others. Conversely, if production of deposit-feeding prey is limited by organic matter inputs, system response may be predictable from models of primary production. For sea floor communities of shallow Arctic seas, increased temperature could lead to invasion or loss of predators, while reduced sea ice or change in wind-driven currents could alter organic matter inputs. Based on field data and models for three different sectors of the northern Bering Sea, we found a number of cases where all of a prey's production was consumed but the taxa involved varied among sectors. These differences appeared not to result from numerical responses of predators to abundance of preferred prey. Rather, they appeared driven by stochastic variations in relative biomass among taxa, due largely to abiotic conditions that affect colonization and early post-larval survival. Oscillatory tendencies of top-down versus bottom-up interactions may augment these variations. Required inputs of settling microalgae exceeded existing estimates of annual primary production by 50%; thus, assessing limits to bottom-up control depends on better corrections of satellite estimates to account for production throughout the water column. Our results suggest that in this Arctic system, stochastic abiotic conditions outweigh deterministic species interactions in food web responses to a varying environment.

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1. Introduction

In large marine ecosystems, models of food web interactions are central to making testable predictions and more accurate projections of species and community responses to environmental change (Woodward et al., 2010). In some cases, climate-change effects on the abundances and distributions of different species may be modeled successfully based on thermal tolerances of

individual taxa (Beaugrand et al., 2014). However, in other cases, unequal thermal influence on the energetics of prey versus predators, or indirect effects such as threshold prey switching by one predator that abruptly impacts the prey of others, can either reduce or amplify the individual responses of component species (Kirby and Beaugrand, 2009; Dell et al., 2014). Understanding existing controls on biomass and energy flows, and the probable lability of those controls to environmental changes, is important to assessing the vulnerability and likely trajectory of food webs experiencing climate changes or direct human impacts (Baird, 2012; Niiranen et al., 2013).

Network models of oceanic food webs have often focused on processes in the water column, where most biomass and energy flows of economic interest to humans occurred (Heymans et al.,

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2004; Field et al., 2006; Aydin et al., 2007). However, on Arctic continental shelves with seasonal ice cover, various factors shift biomass and dominant energy flows to benthic systems (Grebmeier et al., 2006; Whitehouse et al., 2014). Annual primary production is concentrated during the brief bloom at the receding ice edge, the biomass of grazing zooplankton is low at the end of winter, and water columns are shallow; thus, a high fraction of fresh bloom material settles to the sea floor for consumption by benthic organisms (Lovvorn et al., 2005). As a result, many endothermic top predators such as sea ducks, walrus (*Odobenus rosmarus*), bearded seals (*Erignathus barbatus*), and gray whales (*Eschrichtius robustus*) feed almost entirely on sea floor invertebrates (Lowry et al., 1980; Coyle et al., 2007; Sheffield and Grebmeier, 2009; Lovvorn et al., 2014).

The extensive soft-bottom habitats of Arctic shelves support a large biomass of mainly deposit-feeding invertebrates (Grebmeier et al., 2006), whose response to climate shifts can depend on trophic interactions. One possible change is in organic matter supply. Such change could result from altered sea ice patterns which affect the timing, duration, or magnitude of microalgal blooms (ice algae and phytoplankton), or from shifts in wind-driven currents that redistribute settled bloom material (Cooper et al., 2012; Brown and Arrigo, 2013; Lovvorn et al., 2013b). Another expected change is increased water temperature, which could alter the species composition, abundance, or metabolic demands of predators or prey. If control is currently bottom-up, decreased inputs of microalgae settling from the water column might reduce deposit-feeder biomass. If control is top-down, invasion or altered biomass of predators might also affect the abundance of deposit-feeders. However, there can be a complex pattern of top-down and bottom-up regulation throughout a food web (Baird and Ulanowicz, 1989; Bănarău et al., 2010). In such cases, changes in food web structure owing to climatic or direct human effects will hinge on a mixture of shifts in trophic control (Essington and Hansson, 2004). Indeed, in empirically-parameterized models of real systems, the patterning of top-down and bottom-up interactions throughout a web can be critical to its overall stability (Neutel and Thorne, 2014).

Although biomasses may vary over the course of a study period, network models often assume that the biomasses of each compartment are the same at the beginning and end of the period over which the biomasses are averaged (e.g., over a particular season or entire year) (Christensen and Walters, 2004; Fath et al., 2007). Either top-down or bottom-up control can occur with unchanged biomasses – the difference in control depends on the potential fate of production. Assuming no net export, human harvest, or change in biomass over the study period, ecotrophic efficiency (EE , values from 0 to 1) represents the fraction of production that is directly consumed as opposed to flowing to detritus. If the EE of the prey has a value near 1, the predator is consuming all production of its prey over the period of mass balance. Under these conditions, future biomass accumulation over time by either predator or prey will be limited unless the predator's diet shifts, additional factors (e.g., migration of predators or prey, impacts of higher predators) change the predator's relative biomass and resulting consumption, or altered production of the prey's food changes the production of prey. If the EE of the prey is appreciably less than 1 under steady state, and there are no non-predatory limits on the growth, reproduction, or survival of the prey, uncropped production could allow increase in prey biomass over time regardless of predation by this predator.

Benthic food webs on shallow Arctic shelves ultimately depend on primary production settling from the water column. However, despite the great importance of this variable, annual microalgal production in this region has been difficult to quantify. On the

Bering Sea shelf, depth profiles and depth-integrated concentrations of chlorophyll vary greatly in space and time (Rho and Whitley, 2007; Mordy et al., 2012). Thus, direct field measurements of primary production are specific to locations and periods of particular oceanographic cruises (Cooper et al., 2002; Lomas et al., 2012). Satellite images of chlorophyll concentrations near the water surface are available over large areas at regular intervals throughout the year (Brown and Arrigo, 2013). However, in highly productive waters, such sensors often penetrate to depths of only 5–6 m (maximum euphotic depth = 4.6, Morel and Berthon, 1989), whereas chlorophyll maxima during the spring on Arctic shelves are commonly at depths of 20–40 m (Cooper et al., 2012). As a result, satellite measurements can substantially underestimate total water-column production. Correction factors to extrapolate near-surface satellite data to depths of greater production (Frolov et al., 2012) have not been developed for shallow Arctic shelves with seasonal ice cover. Until such capabilities are developed, minimum annual inputs of primary production to benthic food webs might be estimated more comprehensively by modeling total trophic demand. At the least, such trophic estimates would indicate the likely error in using either satellite production estimates, or direct production measurements at limited places and times, to calculate annual inputs.

In mid-May to early June 2007, we measured the abundance and biomass of benthic macroinvertebrates and their ectothermic predators in the northern Bering Sea. Principal component analyses distinguished three assemblage types of invertebrate epibenthic predators in different geographic areas: East and West sectors south of St. Lawrence Island, and the Chirikov sector north of the island (Kolts et al., 2013a, Fig. 1). All three sectors experienced bottom temperatures below $-1\text{ }^{\circ}\text{C}$ for most or all of the year, and cover by pack ice for 5–6 mo per year. This region exhibits large spatial differences in sediment chlorophyll, grain size, and organic content (Grebmeier and Cooper, 1995; Grebmeier et al., 2006), and showed major shifts in the species, abundance, and dispersion of dominant deposit-feeders over four decades (Lovvorn et al., 2009,

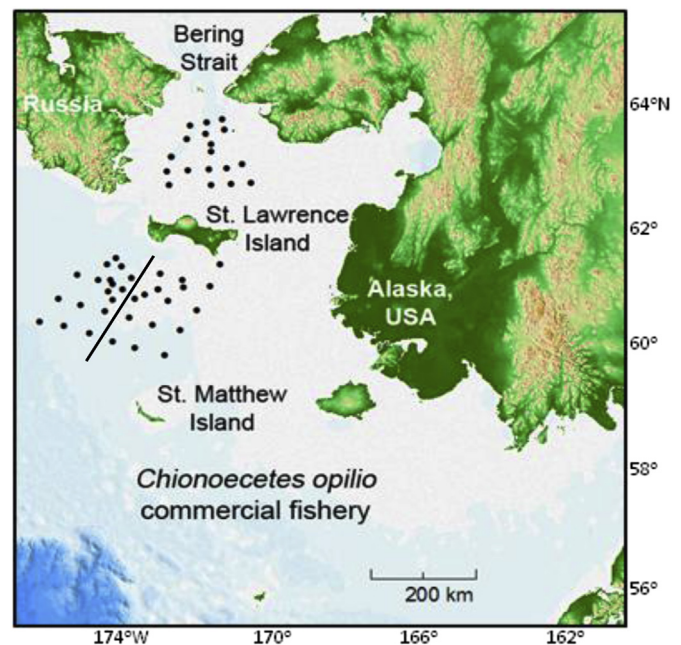


Fig. 1. Sampling stations in the northern Bering Sea in May–June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors. The shelf break at about 200 m depth is seen at bottom left.

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