

Projecting the effects of climate-driven changes in organic matter supply on benthic food webs in the northern Bering Sea

James R. Lovvorn^{1,*}, Christopher A. North^{2,5}, Jason M. Kolts^{2,6},
Jacqueline M. Grebmeier³, Lee W. Cooper³, Xuehua Cui⁴

¹Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901, USA

²Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071, USA

³Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, Maryland 20688, USA

⁴Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA

⁵Present address: Department of Botany, University of Wyoming, Laramie, Wyoming 82071, USA

⁶Present address: Department of Biology, Metropolitan State University of Denver, Denver, Colorado 80217, USA

ABSTRACT: Climate-driven changes in seasonal sea ice are expected to affect the timing, magnitude, and fate of phytoplankton production. Production may be increased by longer ice-free periods, or decreased by reduced stratification of the water column without freshwater input from melting ice. Benthic deposit-feeders may experience changes in organic matter (OM) supply owing to altered phytoplankton production, increased zooplankton grazing, or redistribution of settling phytodetritus. Where most benthic taxa subsist on a longer-term pool of sediment OM and bacteria, communities may be partially buffered against varied inputs of phytodetritus. We used network models of benthic food webs in 3 sectors of the northern Bering Sea to simulate effects of changes in OM supply. In the models, sediment OM content, which integrates longer-term inputs of microalgae, was gradually reduced or increased over 10 yr to the lowest or highest levels observed among sampling stations. In both samples and model predictions, decreased sediment OM was linked to quite variable declines among trophic groups, with effective loss of some taxa. Increased sediment OM was coupled with moderate to dramatic increases of different taxa, sometimes with lagged peaks and declines of prey and predators. In the models, meiofauna, protists, and bacteria responded quickly, while macrofauna exhibited 2 yr delays, suggesting short-term but limited buffering by the sediment OM pool. Our results indicate that climate-related changes in phytodetrital inputs can lead to important shifts in benthic biomass, community structure, and functional diversity, with loss of various common taxa.

KEY WORDS: Benthic communities · Deposit-feeders · Food web limitation · Food web models · Network models · Phytodetritus · Sediment organic matter

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INTRODUCTION

Throughout the Arctic, climate warming and world economic forces are driving greater development of oil, gas, mineral, and fishery resources, as well as increased commercial shipping (Brigham 2011, Smith & Stephenson 2013, Christiansen et al. 2014). Strate-

gic planning to conserve representative ecosystems and related subsistence cultures requires projections of long-term changes in areas with different food web types and the predators they support (Pautzke 2005, Speer & Loughlin 2011, Reeves et al. 2012, Lovvorn et al. 2015b). In the extensive soft-bottom habitats of Arctic and subarctic continental shelves

with seasonal ice cover, the mainly deposit-feeding communities are based on phytodetritus settling from spring blooms. Thus, insights into the responses of food webs to long-term trends in phytodetrital inputs are key to considering possible trajectories of important habitats in conservation planning. In this paper, we use models of food web networks in 3 sectors of the northern Bering Sea to simulate potential effects on deposit-feeding assemblages of changes in organic matter (OM) supply over 10 yr. We then compare these simulated results to assemblages observed in the field at locations with similar levels of cumulative organic input, to assess the models' value for projecting such effects.

Decreased extent or duration of seasonal sea ice could have a range of effects on production of microalgae (ice algae and phytoplankton) that provide food for benthic communities. Extended light penetration during a longer ice-free period might increase phytoplankton production, depending on the supply of nutrients (Brown & Arrigo 2013). Alternatively, phytoplankton production and settling might decrease if lack of water-column stratification by fresh water from melting ice results in later, less intense blooms that are grazed more heavily when zooplankton are seasonally more abundant (Hunt Jr. et al. 2002, Saitoh et al. 2002; review in Lovvorn et al. 2005). Benthic communities may experience changes in OM supply owing to changes in phytoplankton production and settling, or in redistribution of settling phytodetritus by shifts in wind-driven currents (Rutgers van der Loeff et al. 2002, Lovvorn et al. 2013). Ice algae might be an important initial source of fresh OM for the benthos in early spring (review in North et al. 2014). However, ice algae typically contribute <10% of the total production of settling microalgae on Arctic shelves (Horner 1985, Gosselin et al. 1997), and in the northern Bering Sea ice algae (as do phytoplankton) apparently enter the longer-term pool of sediment OM before providing carbon to mostly bacterivorous deposit-feeders (North et al. 2014). Thus, for these benthic communities, evidence to date suggests that it is the total amount of settling microalgae, and not so much the timing, that affects the longer-term pool of sediment OM upon which most deposit-feeders (and, in turn, their predators) depend.

The term phytodetritus is often considered to include microalgae as well as bacteria and their exudates that hold clumps of settling microalgae together (Beaulieu 2002). However, here we define phytodetritus as including only living and nonliving cells, cell fragments, and lysates of 'fresh' microalgae

(produced during the current growing season) that have settled to the sea floor.

The fate of settled phytodetritus is a complex topic studied by many researchers over several decades (Beaulieu 2002). These studies have yielded varying interpretations, depending on diverse methods, the range of organizational levels considered, duration of measurements (days to months), and water depth (intertidal to abyssal) which can affect the amount and lability of deposited materials, and relative processing by microfauna versus macrofauna (Moodley et al. 2005). The importance of different pathways is therefore strongly context-dependent. Our synthesis of this information for relevance to the northern Bering Sea resulted in the following construct.

Upon settling to the sea floor, some microalgal cells are quickly ingested by macrofauna or meiofauna, or broken down and assimilated by bacteria (Witte et al. 2003, Gontikaki et al. 2011, North et al. 2014). However, within a few days, many microalgal cells and cell fragments are mixed downward into the sediments by particle diffusion and bioturbation (Blair et al. 1996, Witte et al. 2003), where they can persist during seasons of little algal production (Rudnick 1989, Hansen & Josefson 2001, Smith et al. 2012). Some authors have assumed that the fraction of settling phytodetritus that is not promptly metabolized and that becomes buried is less labile (Glud et al. 1998, Rysgaard et al. 1998). However, longer-term studies have shown the buried fraction to be in large part available to macrofauna and meiofauna, either by direct ingestion or indirectly via bacteria they consume (Rudnick 1989, Ólafsson et al. 1999, Glud et al. 2000, Hansen & Josefson 2001, Josefson et al. 2002, Witte et al. 2003, Smith et al. 2012).

The extent to which fresh phytodetritus is directly assimilated by meiofauna or macrofauna is unclear based on typical isotopic labeling experiments because label in microalgae may be assimilated by bacteria or protists before being ingested by meiofauna or macrofauna (e.g. Ólafsson et al. 1999, Franco et al. 2008, Evrard et al. 2010, Miyatake et al. 2014). For a range of deposit-feeders in the northern Bering Sea—3 bivalves (*Macoma calcarea*, *Ennucula belloti*, *Nuculana radiata*), a polychaete (*Pectinaria hyperborea*), and a brittle star (*Ophiura sarsi*)—the main fraction of biomass in their guts after the major pulse of settling microalgae from the spring bloom was diatoms. However, evidence from naturally occurring stable isotopes, and from fatty acids produced only by bacteria, dinoflagellates, or diatoms, respectively, indicated that these deposit-feeders assimilated mainly bacteria (Lovvorn et al. 2005, North et al. 2014). This

inference is consistent with experiments showing that in 3 bivalves (*Ennucula*, *Nuculana*, *Abra*), 1 gastropod (*Turritella*), 2 polychaetes (*Pectinaria*, *Polyphysia*), and 1 sipunculid (*Golfingia*), fresh diatoms passed through the gut undigested (Hansen & Josefson 2004). Thus, in soft sediments of the northern Bering Sea shelf, it appears that a substantial fraction of fresh phytodetritus is processed by bacteria or by repeated passage through the guts of deposit-feeders before being assimilated by macrofauna. Dependence of deposit-feeders on a longer-term ‘food bank’ of sediment OM, despite major seasonal pulses of fresh microalgae, has been documented in a range of environments from temperate to polar latitudes (Fleeger et al. 1989, Rudnick 1989, Franco et al. 2008, Mincks et al. 2008, Josefson et al. 2002, Byrén et al. 2006, Evrard et al. 2010, North et al. 2014). Reliance on a longer-term organic pool may partially buffer local food webs from short-term variations in either water-column production or lateral advection of settling phytodetritus (Levinton 1972). Such buffering would depend on the fraction of the sediment organic pool that is labile to bacteria, and the size of that pool relative to total bacterial demand.

Determining the fraction of bulk OM in sediments that is labile to bacteria at monthly and seasonal time scales is problematic. Pools of sediment OM can include decomposing fragments of macrofauna and meiofauna in addition to more refractory components of microalgal detritus. In a number of studies in non-littoral marine sediments, both the chemical and stable isotope composition of bulk OM have remained largely unchanged among months and seasons, despite variable pulses of settling phytodetritus that can cause shifts near the sediment surface for periods of days to weeks (Sargent et al. 1983, Rysgaard et al. 1998, Witte et al. 2003, Mincks et al. 2005, 2008, Gontikaki et al. 2011, North et al. 2014). This stability suggests relatively constant availability and utilization of different organic components at time scales of months and seasons. Most assays of the hydrolysable fraction of bulk OM in sediments (e.g. Danovaro et al. 2001) do not differentiate living and non-living protists and bacteria from other OM (Danovaro et al. 1998, Luna et al. 2002); thus, they do not specifically measure the fraction of residual phytodetritus and metazoan debris that remains labile to microbial degradation. In some areas, including the northern Bering Sea, stable isotope or fatty acid biomarkers (Mincks et al. 2008, van Oevelen et al. 2012, North et al. 2014), as well as labeled OM of differing ages (Rudnick 1989, Byrén et al. 2006), indicate that many invertebrate deposit-feeders readily assimilate

mainly older, reworked organic carbon, either directly or indirectly by ingesting bacteria. This pattern suggests that much of the older OM is quite available to macrofauna.

Lacking more definitive information, we assumed that all sediment OM derived from fresh phytodetritus becomes labile to bacteria (cf. Newell et al. 1981), and thus to bacterivorous meiofauna and macrofauna, within the span of a year. Moreover, we assumed that the fraction of older sediment OM that is labile to bacteria is adequate to allow drawdown of that older pool on a seasonal or annual basis.

MATERIALS AND METHODS

Sampling area, trophic groups, and biomasses

Data collected for models in this paper were also used in the modeling study of Lovvorn et al. (2015a). We sampled benthic organisms and sediment OM on the continental shelf of the northern Bering Sea from 18 May to 12 June 2007 from the US Coast Guard icebreaker ‘Healy’ (Fig. 1). Owing to cold temperatures in this area, fish are few and small, and snow crabs, although quite abundant, are too small to be market-

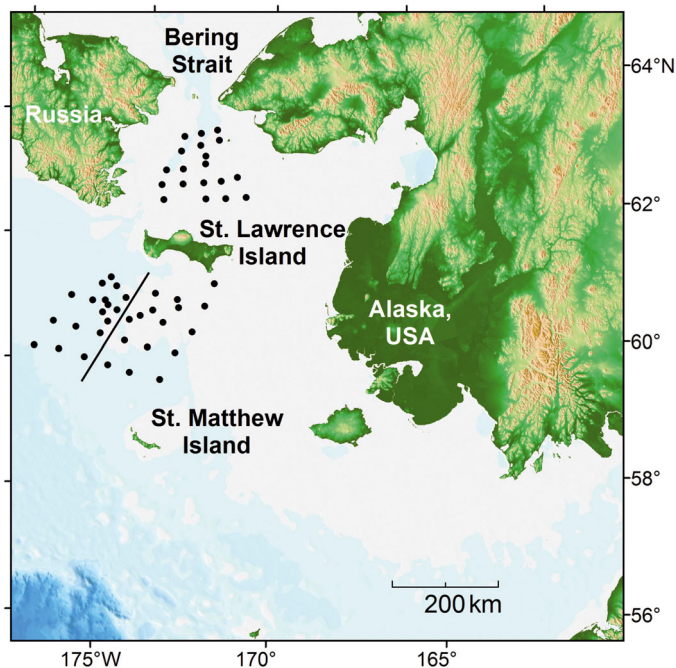


Fig. 1. Sampling stations in the northern Bering Sea in May to June 2007. Stations north of St. Lawrence Island (SLI) were in our Chirikov Basin sector, and the line south of SLI separates our East and West sectors. The shelf break at about 200 m depth is seen in the bottom left corner (reproduced from Lovvorn et al. 2015a)

able (Cui et al. 2009, Kolts et al. 2015). As a result, there are no commercial fisheries in our study region (Stram & Evans 2009).

Based on cluster analyses of epibenthic animals from trawl samples, we identified 3 primary assemblages that occurred in different sectors of the study area: the Chirikov Basin sector north of St. Lawrence Island, and the East and West sectors south of the island (Fig. 1; see Supplementary Material in Kolts et al. 2013). For most or all of the year, water temperatures near the bottom at our sampling stations are $<1^{\circ}\text{C}$ in the Chirikov, and $<0^{\circ}\text{C}$ in the southern sectors; these areas are covered by pack ice for 5 to 6 months of the year. Water depth at sampling stations ranged from 35 to 52 m in the Chirikov sector, and from 30 to 96 m in the southern 2 sectors. Infauna was sampled with a van Veen grab (4 replicates per station, 0.1 m^2 each), and organisms retained by a 1 mm sieve were preserved for later sorting in the laboratory. Epifauna was sampled with a 4 m beam trawl (1.9×1.9 cm square mesh) and sorted on the ship (Cui et al. 2009, Kolts et al. 2013).

Densities of some trophic groups were based on grab samples. These groups included Amphipoda, other small Crustacea (Isopoda, Cumacea, Tanaidacea), deposit-feeding bivalves (*Macoma* spp., *Nuculana* spp., *Ennucula tenuis*, *Yoldia* spp.), *Musculus* spp. and other bivalves, polychaete carnivores, polychaete deposit-feeders, Priapulidae, Sipuncula, and Nematoda. We classified taxa of polychaetes as carnivorous or deposit-feeding, according to published information (see Supplementary Material in Lovvorn et al. 2015a). Densities of other trophic groups were based on trawl samples. These groups included snow crabs (*Chionoecetes opilio*), Hysas crabs (*Hyas coarctatus*), hermit crabs (*Pagurus* spp.), buccinid whelks (*Neptunea* spp., *Buccinum* spp.), moon snails (*Cryptonatica clausa*, *Lunatia pallida*), sea stars (*Leptasterias* spp.), brittle stars (*Ophiura sarsi*), tunicates (Urochordata), anemones (Cnidaria), Arctic cod (*Boreogadus saida*), snailfish (Liparidae), shorthorn sculpin (*Myoxocephalus scorpius*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), and flatfish. For all sectors combined, the biomass of the flatfish group was 91% Bering flounder *Hippoglossoides robustus*, 6% Alaska plaice *Pleuronectes quadrituberculatus*, and 3% yellowfin sole *Limanda aspera*. The trophic groups of fish included in our models comprised 99% of total fish biomass (Cui 2009). To represent their functions in the benthic food web, biomasses of flatfish, Arctic cod, and snailfish were decreased to the fractions of their diets that were benthic (81.0, 53.2, and 90.8%, respectively; see Supplementary Material in Lovvorn et al.

2015a). We divided snow crabs into 2 groups depending on carapace width: either greater than or less than 20 mm (see Kolts et al. 2013). For this analysis we included only stations where both grab and trawl samples were collected. All biomasses are in terms of grams of organic carbon (conversion factors used for each taxon are in the Supplementary Material for Lovvorn et al. 2015a).

For unbiased comparisons of the responses of different trophic networks to altered conditions, each network must have a similar level of resolution for trophic groups and linkages (Pinnegar et al. 2005). A few taxa were not detected in all sectors, and made up only a trace of total biomass when they were. Therefore, these taxa were eliminated from our analyses: *Cranogon* spp., *Pandalus* spp., and other decapod shrimp; gastropods other than whelks and moon snails (mostly *Colus* spp.); sea cucumbers (Holothuroidea); and basket stars (*Gorgonocephalus caryi*). Sculpins, which were rare in the East and West sectors but had high biomass in the Chirikov sector, were retained in models for all 3 sectors. Although brittle stars were common in the East and especially the West sector, they were not found in the Chirikov and were excluded from the model for the Chirikov sector.

For macroinvertebrates and fish, the biomass (g C m^{-2}) of each trophic group was averaged across all stations in a sector (see Lovvorn et al. 2015a). We had no local measurements of the biomasses of meiofauna, protists, or bacteria, so we used values derived from an extensive review of published data for soft sediments. We measured standing stocks of chlorophyll *a* and total organic carbon in the top 1 cm of sediments at each station (Fig. 1; Grebmeier & Cooper 1995, Cooper et al. 2012); chlorophyll *a* was converted to grams of carbon of fresh microalgae by the ratio 34 g C:1 g chl *a* (details of above data and calculations are in the Supplementary Material for Lovvorn et al. 2015a). The biomass of fresh microalgae was then subtracted from total organic carbon to yield biomass of sediment OM. X-ray images of core profiles have shown these sediments to be highly bioturbated, with most infaunal organisms occurring within the top 5 cm (Grebmeier & McRoy 1989). Consequently, we multiplied our measurements of fresh microalgae and sediment OM in the top 1 cm by 5 to estimate amounts in the top 5 cm that were most available to the benthic food web.

We measured standing stocks of chlorophyll *a* in sediments when much of the ice algae and phytoplankton from the ice-edge spring bloom appeared to have settled to the bottom (Cooper et al. 2012). However, such measurements at a single time do not

integrate production over the season or entire year. On the other hand, frequent estimates of chlorophyll throughout the year via satellite measurements typically do not penetrate to the depth of the chlorophyll maximum in this region (see Lovvorn et al. 2015a). Moreover, phytodetritus settling from the water column is undoubtedly advected among areas by bed-load transport, resulting in substantially lower or higher concentrations than were produced in the overlying water column at a particular site (Lovvorn et al. 2013). Thus, we used the OM content of sediments as the best integrator of the net input of fresh microalgae over longer periods at a given sampling location.

Diets and energetics of organisms

Detailed explanation of the diets, production:biomass ratios ($P:B$), consumption:biomass ratios ($Q:B$), and assimilation efficiencies (AE) for different trophic groups used in the network models is provided in the Supplementary Material for Lovvorn et al. (2015a). In particular, we attempted to use taxon-specific energetics data for temperatures near those in our study area.

Simulated food web trajectories vs. measured extremes

We used the open-source software Ecopath with Ecosim (version 6.6, <http://www.ecopath.org>), which has been described in detail in a number of publications (Christensen & Walters 2004, Christensen et al. 2008, review in Coll et al. 2009). The Ecosim utility begins with a steady-state model balanced in Ecopath, and simulates changes in each biomass and flow over time in response to a user-defined schedule of perturbation ('forcing function' in Ecosim).

We first assessed interactions among different trophic groups in the initial balanced models in terms of Mixed Trophic Impacts. Mixed Trophic Impacts indicate the relative change in biomass of each trophic group associated with a very small relative change in biomass of each other trophic group, assuming no change in diets (Christensen et al. 2008). Mixed Trophic Impacts suggest the potential importance of interactions (both direct and indirect) among different trophic groups in a steady-state system, before the food web experiences significant perturbation.

We used Ecosim to track trajectories of the biomass of each trophic group during reduced or increased

supply of settling microalgae relative to the initial balanced models for each sector described by Lovvorn et al. (2015a). As explained above, we assumed that sediment OM (excluding settled fresh microalgae) was the best integrator of net microalgal deposition at a given location over a series of years. Via the Ecosim forcing function for primary production, we reduced inputs of settling microalgae over 10 yr to decrease sediment OM to the mean level for the 2 stations with lowest measurements of sediment OM in each sector. We also adjusted fresh microalgal inputs over 10 yr to increase sediment OM to the mean level for the 2 stations with highest measurements of sediment OM in each sector. The initial, low, and high values of sediment OM (g C m^{-2}) in each sector were, respectively, 10.1, 1.8, and 28.4 for Chirikov; 16.4, 6.5, and 34.7 for East; and 36.2, 17.4, and 55.0 for West. We used the extreme low and high values of sediment OM measured within each sector to restrict our simulations to values that could reasonably be observed with climatic changes in microalgal inputs.

For each trophic group in each sector, we then compared the change between its biomass in the initial balanced model and its predicted biomass after the 10 yr simulations, versus the difference between that initial biomass and the observed mean biomass for the 2 stations with lowest or highest sediment OM (i.e. modeled versus measured differences). We also compared any losses of species or trophic groups between the simulated versus observed assemblages after the same decrease or increase in sediment OM. In multiple runs of the Ecosim model, patterns of change typically stabilized within 10 yr. These comparisons indicated the ability of our Ecosim model to predict the measured response of different trophic groups associated with shifts to reasonable extremes of sediment OM. Such changes in sediment OM in turn depend on inputs of microalgae (ice algae or phytoplankton) via local production and settling, or by lateral advection of settled material.

Selection of vulnerability values (v)

In Ecosim, the vulnerability parameter v controls the rate at which production of prey becomes available to predators, depending on factors that affect the foraging success of the predators (Walters et al. 1997, Christensen et al. 2008). Limits to vulnerability may include crypsis or escape strategies of prey, prey dispersion relative to search patterns of predators, thresholds of prey density relative to profitability for predators, or other behavioral or physical factors that

affect the rate at which prey move from an invulnerable to vulnerable condition.

Vulnerabilities, with values from 0 to 1, are also thought of as spanning a gradient from entirely bottom-up ($v = 0$) to entirely top-down ($v = 1$) control, with the Ecosim default value of 0.3 representing mixed control. In other words, if predators can consume all production of a prey ($v = 1$), they control its biomass from the top down. Alternatively, if a substantial fraction of the prey's production is not accessible to predators (v closer to zero), so that prey biomass can increase in spite of predation, expansion of predator biomass in response to increased prey production is controlled from the bottom up. Choice of values for v can substantially affect the trajectories of food webs in response to perturbation, and high values of v can lead to unstable oscillations in biomass trajectories. Ecosim can search for values of v that result in best fits to time series of data (Christensen & Walters 2004); however, such fitting precludes using the same data to test the predictive capability of the model. Moreover, automated searching for values of v that yield the best fit would attribute differences between observed and predicted values to v , thereby obscuring effects of other factors that might be driving food web reorganization (see paragraph 2, p. 137 in Christensen & Walters 2004).

Our approach was to try various combinations of v for both sediment OM and the rest of the food web, with the constraint that the values used would allow sediment OM in the initial balanced model for an entire sector to reach, within 10 yr, the lowest levels measured within that sector. These simulations were done with the Ecosim forcing function (pattern of change) for primary production set to zero, so that annual inputs of fresh microalgae were gradually decreased. We reasoned that the vulnerability of sediment OM was limited by the rate at which bacteria could process that pool into bacterial biomass, and we sought values of v for sediment OM and for all higher trophic levels that would allow drawdown (within 10 yr) of the organic carbon pool to the lowest level measured in the field. The lowest level was the mean of sediment OM (excluding fresh microalgae) for the 2 stations with lowest values for a given sector. Higher values of v generally resulted in longer drawdown times, but patterns of relative biomass among trophic groups typically stabilized within 10 yr. Results of different combinations of v were compared in terms of the sums of squared differences between biomasses of all trophic groups at the modeled endpoints versus measured values at the stations with lowest sediment OM. Based on these

explorations, in subsequent modeling we used $v = 0.3$ for sediment OM and $v = 0.5$ for the rest of the food web for both decreases and increases of sediment OM. As food web structure was similar among sectors, we assumed that these same vulnerability parameters applied to all sectors, and that differences among sectors in the fit between simulated and observed biomasses resulted from other factors.

RESULTS

Initial balanced model and Mixed Trophic Impacts

The initial balanced model for the West sector (Fig. 2) was similar to models for the other 2 sectors (see Lovvorn et al. 2015a). The brittle star *Ophiura sarsi*, which had appreciable biomass (g C m^{-2}) in the East and especially West sectors, was absent in samples from the Chirikov Basin. Based on our stable isotope, fatty acid, and gut content assays for dominant bivalves, polychaetes, and the brittle star, most carbon from settling microalgae passes through the longer-term sediment OM pool and bacteria before being assimilated by deposit-feeders (Fig. 2; North et al. 2014).

Mixed Trophic Impacts indicate the relative change in biomass of each trophic group associated with a very small relative change in biomass of each other trophic group. These values include both direct and indirect interactions between each group in a steady-state system. In initial balanced models, patterns in the West (Fig. 3) were generally similar to those in the other sectors, except in the Chirikov where there were major negative impacts of shorthorn sculpins (which had appreciable biomass only in the Chirikov) on snow crabs <20 mm and *Hyas* crabs, and of flatfish on Nemertean worms. Partitioning the matrix between major trophic categories (Fig. 3) indicated that slight changes in the 'small food web' (fresh microalgae, sediment OM, bacteria, Protista, meiofauna) had relatively small proportional effects on higher trophic levels, with most strong interactions within the small food web itself. Among carnivores, most strong impacts were negative and involved carnivores competing for prey or preying on each other, except for positive impacts where a carnivore benefited from eating another carnivore but not vice versa. Carnivores had mostly negative impacts on deposit-feeders, and deposit-feeders had mostly positive but sometimes negative impacts on predators (as when clam deposit-feeders replaced amphipods, which were the preferred prey of several fish species).

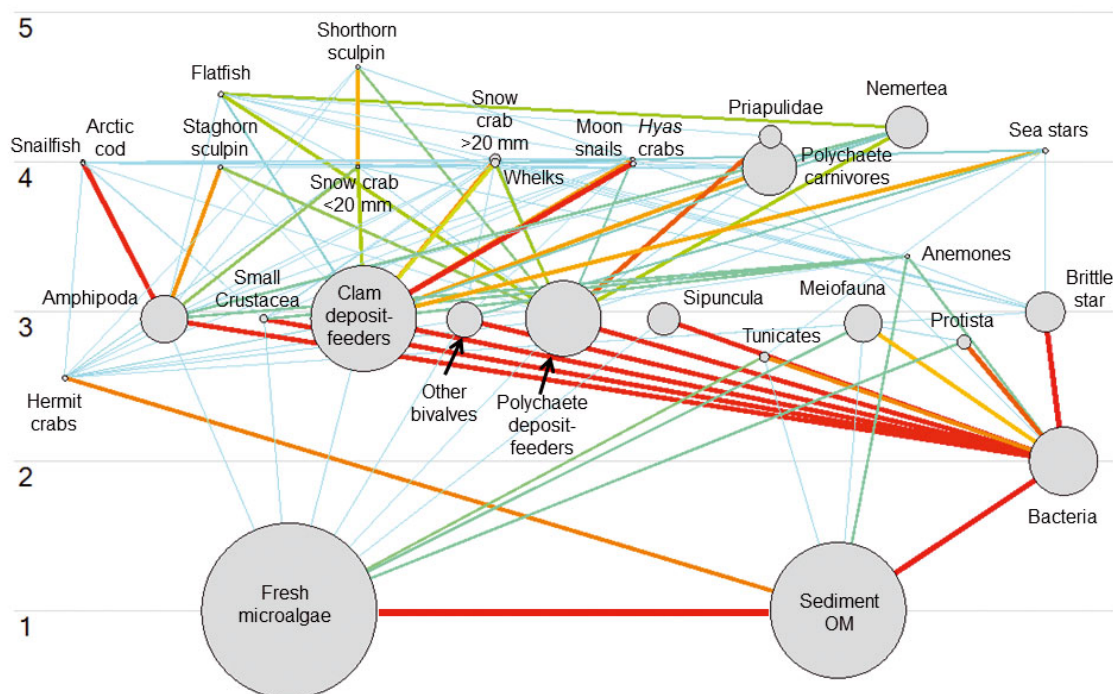


Fig. 2. Diagram of trophic levels, relative biomasses (g organic C), and relative carbon flows of different trophic groups in the benthic food web of the West sector of the northern Bering Sea (Fig. 1). Sizes of circles are in correct rank order of biomasses, but for display purposes are not in exact quantitative proportions. Magnitudes of carbon flows are scaled by line thickness and by color from light blue to red. Linkages between groups in the East and Chirikov sectors were very similar to those in the West sector shown here, although the biomasses and magnitudes of flows differed (biomass data for all sectors, and a diagram for the Chirikov sector, are in Lovvorn et al. 2015a). OM: organic matter

Predicted vs. observed biomasses and loss of trophic groups

There were some substantial differences in biomass between the initial balanced model for each sector and either simulated or measured values for individual trophic groups at stations with extreme values of sediment OM. In the Chirikov, the model accurately predicted the major decrease in polychaete detritivores, and declines in Sipuncula, Nemertea, tunicates, anemones, and *Musculus* and other bivalves (Fig. 4). However, the model substantially overestimated the declines in Amphipoda, clam deposit-feeders, and polychaete carnivores. We did not attempt to balance the measured biomasses at the extreme stations because there were no direct measurements of meiofaunal, protist, or bacterial biomasses, and balanced models would be modified to fit those estimated values. Despite lack of biomass measurements for meiofauna or bacteria at the extreme stations, simulations predicted a slight decrease in standing stocks of these groups relative to the initial network. In the East sector, the model failed to predict the higher biomass of clam deposit-feeders and of *Musculus* and other bivalves, or the minor decrease in

both carnivorous and deposit-feeding polychaetes, that were observed at the 2 stations with lowest sediment OM (Fig. 4). In the West, the main change was in clam deposit-feeders; the magnitude of decrease predicted by the model was far less than the observed difference. Overall, prediction of the direction and magnitude of change in biomass of different trophic groups was much better for the 82% decrease of sediment OM in the Chirikov than for the 60 and 52% reductions of sediment OM in the East and West, respectively. When measured changes were fewer and smaller, as in the East and West, the models predicted fewer and minimal changes.

As for decreased sediment OM, changes predicted by the model for increased sediment OM were for the same groups and generally of the same relative magnitude as measured at extreme stations, but the absolute magnitudes of change often did not agree (Fig. 5). In the Chirikov, the model overestimated the positive responses of clam deposit-feeders, polychaete carnivores, and *Musculus* and other bivalves, while underestimating the major observed increase in polychaete detritivores. The model predicted a substantial increase in Amphipoda, whereas a slight decline was measured in the field. In the East, with a

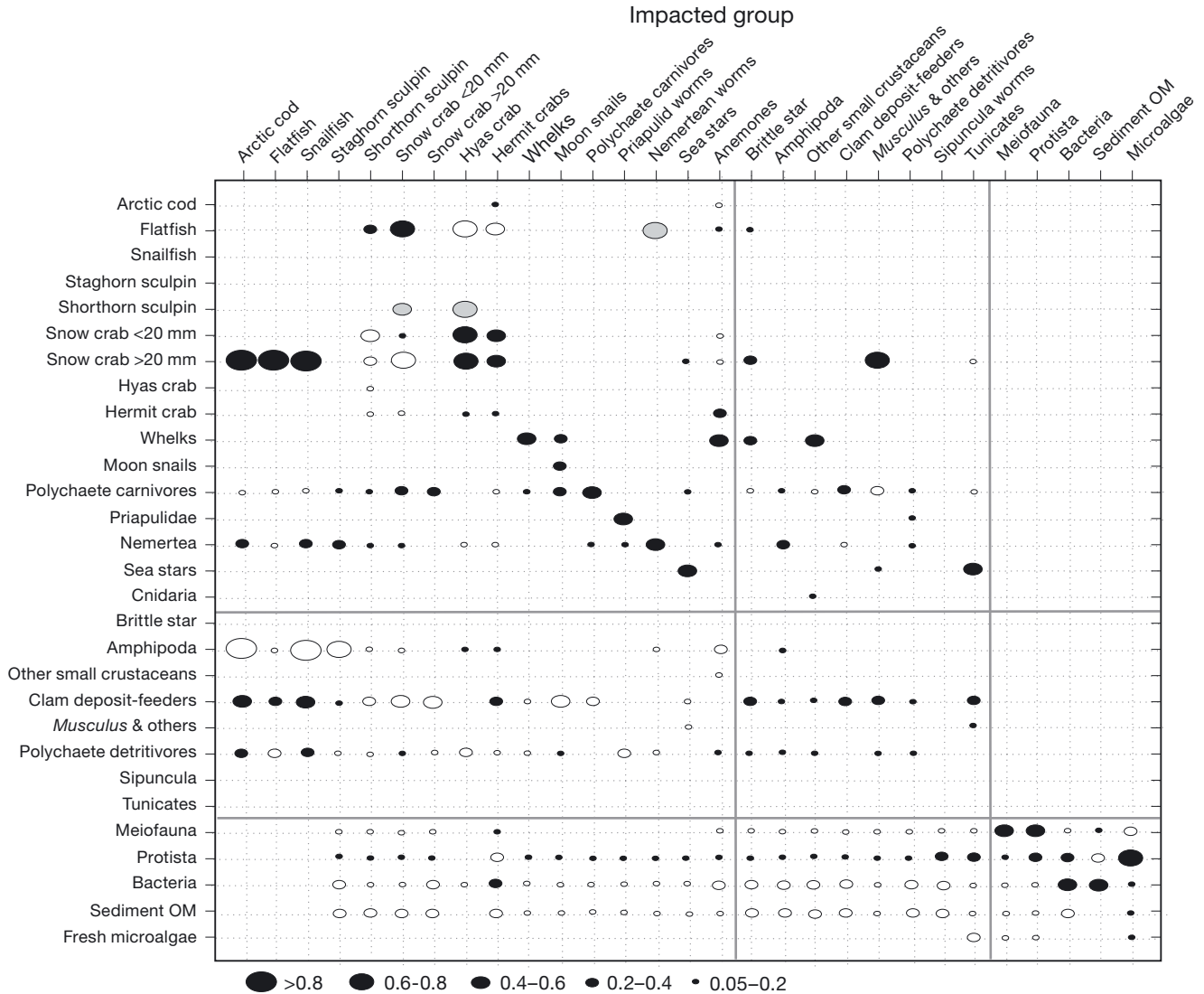


Fig. 3. Mixed Trophic Impacts—the relative (fractional) change in biomass of each trophic group associated with a very small relative change in biomass of each other trophic group—in the initial balanced model for the West sector (Fig. 2). Solid symbols denote negative impacts, open symbols positive impacts, and several gray symbols represent important negative impacts that occurred only in the Chirikov sector. OM: organic matter. The entire matrix is partitioned by gray lines into general categories of mostly carnivores, deposit-feeders, and the ‘small food web’ (microalgae, sediment OM, bacteria, Protista, and meiofauna)

much lower increase in sediment OM (111 vs. 181% in the Chirikov), there were almost no predicted or observed changes in biomass of different trophic groups; only slight increases were seen in clam deposit-feeders and in *Musculus* and other bivalves. In the West, also with a much smaller increase in sediment OM (52%), there was almost no change predicted or observed in any trophic group except clam deposit-feeders. Although the model did predict this increase in clam deposit-feeders, it greatly underestimated the measured increase at the 2 stations with highest sediment OM (Fig. 5).

We compared trophic groups lost from the food web during simulated or measured decreases in sed-

iment OM from levels in the initial model to the mean for the 2 stations with lowest values in each sector (Table 1). Loss of groups generally is not evident based on biomass changes in Fig. 4 because the biomass of lost groups was relatively quite small initially. Of 24 trophic groups in the initial balanced model for which we had field samples, the model did not predict loss of any group that was not also missing from the observed (field) samples. In each sector, as many as 10 trophic groups were missing from the 2 stations with lowest sediment OM. In the Chirikov sector, the model predicted loss of 6 groups that were also missing from the low station samples, and the other predicted losses were 2 groups that were still

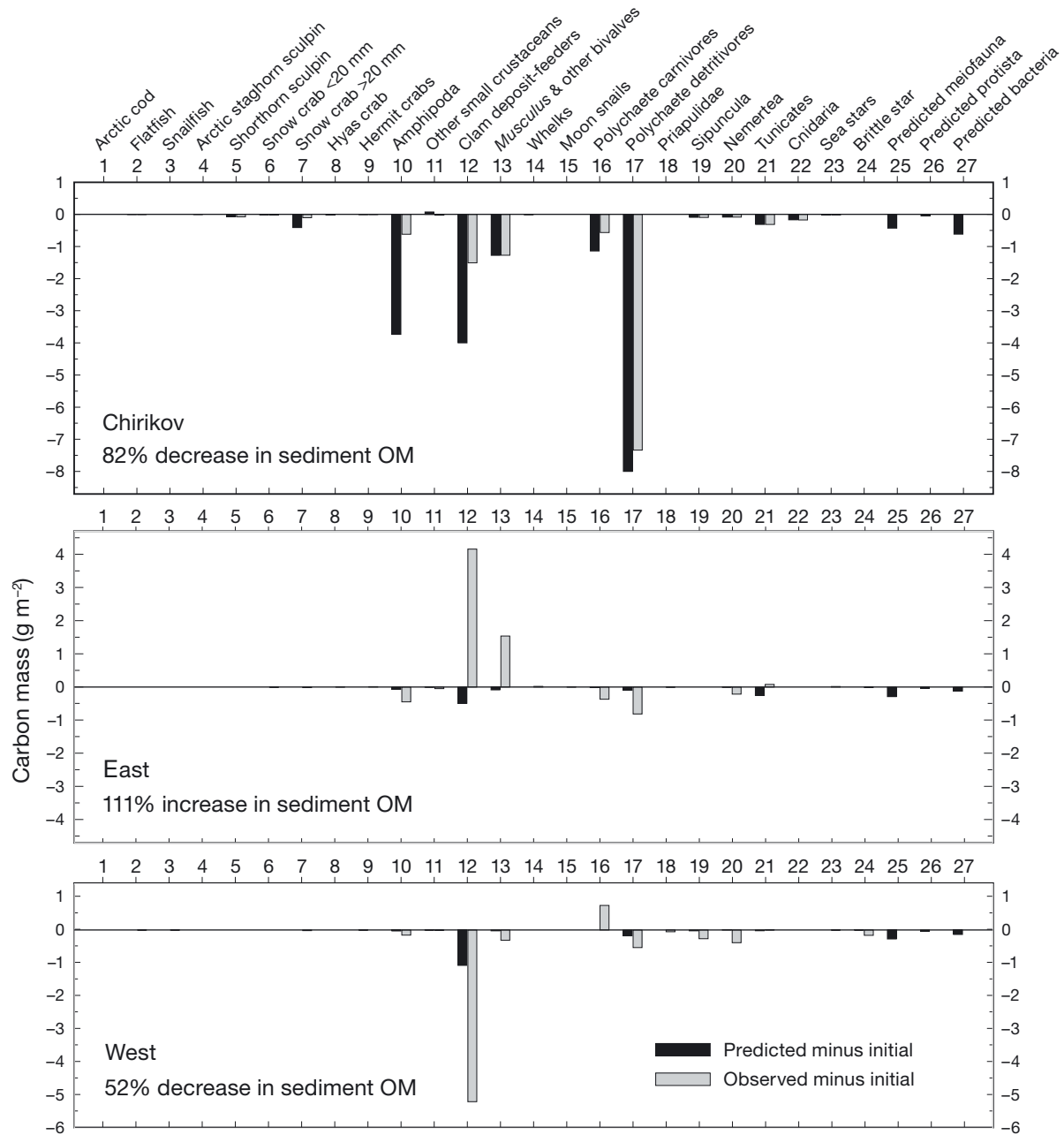


Fig. 4. Difference in biomass (g C m^{-2}) for different trophic groups between the initial balanced model for each sector (Fig. 1) and biomasses predicted by Ecosim (predicted minus initial) after reduction of sediment organic matter (OM, excluding fresh microalgae) to the mean level measured at the 2 stations with lowest sediment OM, and differences between the initial balanced model and measured biomasses at those 2 stations (observed minus initial). Percentage reduction of sediment OM for each sector is indicated. There were no direct biomass measurements for meiofauna, Protista, or bacteria for the initial model or for the 2 stations with lowest sediment OM

present in field samples but were indeed rare. Field samples in the Chirikov were missing 3 groups that were not predicted to be lost, 1 of which (snow crabs <20 mm) was quite abundant at a number of other stations in the sector (Kolts et al. 2015). In the East, the model predicted loss of 5 groups; these groups were also missing from the low station samples along with 5 others. For the West sector, the model and observations agreed on 5 of 6 groups missing from the

station samples. In all but 1 case (brittle star in the East), groups predicted to be lost from each sector were missing from samples at the low stations in at least 1 of the other sectors.

Results of the above analyses indicate that the model was usually good at identifying the trophic groups that would be lost, those that would show substantial increase or decrease, and the direction and relative magnitude of change. However, in sev-

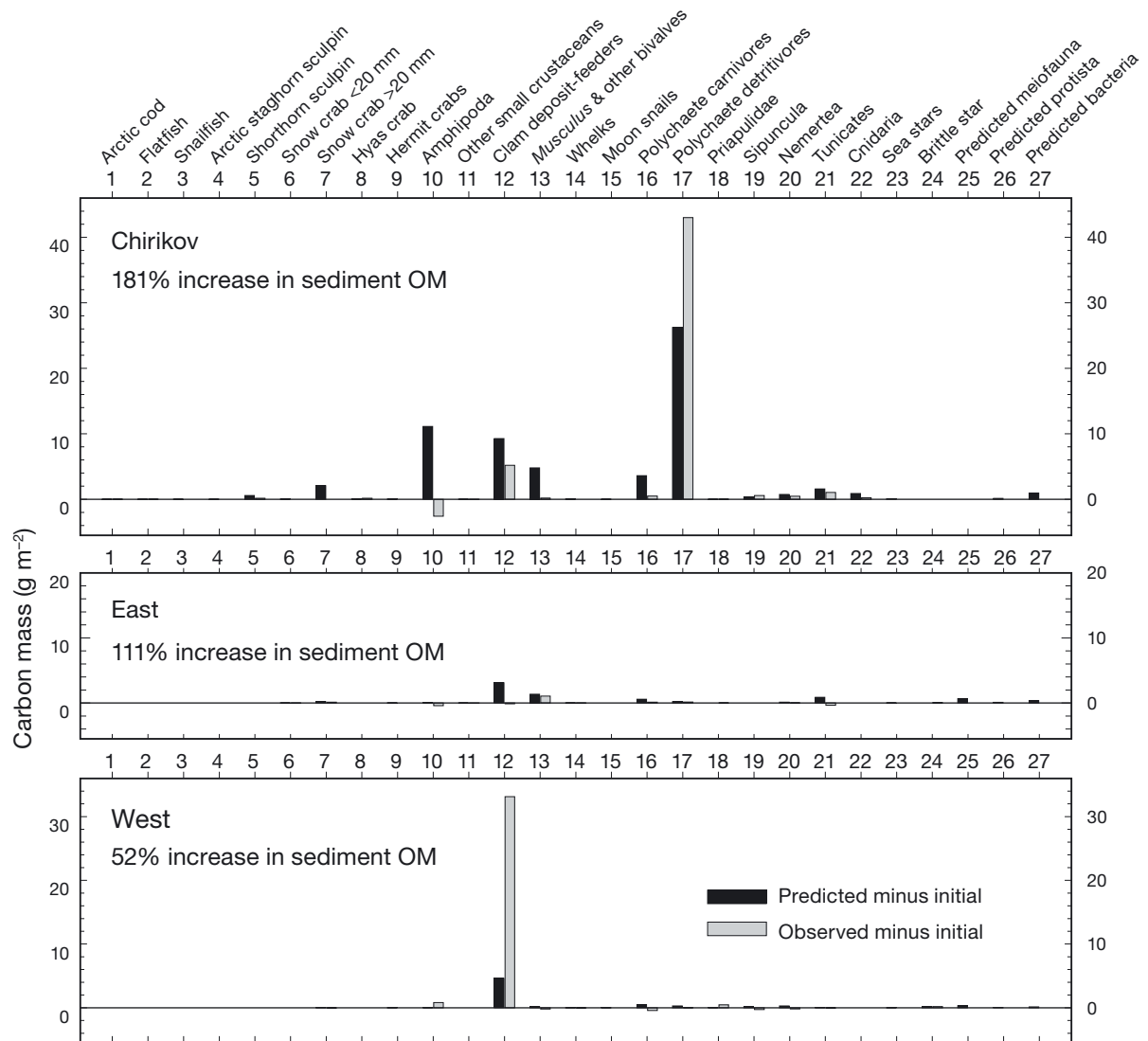


Fig. 5. Difference in biomass (g C m^{-2}) for different trophic groups between the initial balanced model for each sector (Fig. 1) and biomasses predicted by Ecosim (predicted minus initial) after increase of sediment organic matter (OM, excluding fresh microalgae) to the mean level measured at the 2 stations with highest sediment OM, and differences between the initial balanced model and measured biomasses at those 2 stations (observed minus initial). Percentage increase of sediment OM for each sector is indicated. There were no direct biomass measurements for meiofauna, Protista, or bacteria for the initial model or for the 2 stations with highest sediment OM

eral cases the model substantially overestimated or underestimated the absolute magnitude of change.

Simulated trajectories for 10 yr declines in organic inputs

We tracked relative changes in biomass of each trophic group over 10 yr in response to decrease or increase of settling microalgae. In Ecosim, levels of settling microalgae in the initial balanced models for each sector were gradually reduced or increased so that sediment OM at the end of 10 yr was the same as

the mean for the 2 stations with the lowest or 2 stations with the highest values measured in each sector in mid-May to early June 2007.

Sediment organic content (g C m^{-2} , excluding fresh microalgae) in the initial balanced models was 10.095 in the Chirikov, 16.442 in the East, and 36.205 in the West sectors. Reducing sediment OM to the mean of the 2 stations in each sector with lowest measured values required decreases of 82% (to 1.7904) in the Chirikov, 60% (to 6.4960) in the East, and 52% (to 17.445) in the West (Fig. 6). In Ecosim, long-term forcing functions for primary production of 1.07, 0.472, and 0.565, respectively, were needed to

Table 1. Trophic groups (or species) lost from the initial balanced model for each sector after simulated reduction of sediment organic matter (OM, excluding fresh microalgae) to the mean level measured at the 2 stations with lowest sediment OM in each sector, compared to groups observed to be absent from field samples at those 2 stations. Reduction of sediment OM was 82% for Chirikov, 60% for East, and 52% for West sectors. Trophic groups were predicted to be lost or observed to be absent if their density was $\leq 0.0005 \text{ g C m}^{-2}$. The brittle star *Ophiura sarsi* was not found in the Chirikov Basin and was excluded from the model for that sector

Predicted to be lost after reducing OM	Observed to be absent at reduced OM
Chirikov Arctic cod, snailfish, Arctic staghorn sculpin, snow crab >20 mm, Priapulidae, Nemertea, anemones, tunicates	Arctic cod, flatfish, snailfish, shorthorn sculpin, snow crab <20 mm, Priapulidae, Nemertea, anemones, Sipuncula, tunicates
East Arctic cod, snailfish, Arctic staghorn sculpin, shorthorn sculpin, Sipuncula	Arctic cod, flatfish, snailfish, Arctic staghorn sculpin, shorthorn sculpin, snow crab <20 mm, Priapulidae, Sipuncula, anemones, brittle star
West Arctic cod, Arctic staghorn sculpin, shorthorn sculpin, snow crab <20 mm, <i>Hyas</i> crab	Arctic cod, Arctic staghorn sculpin, shorthorn sculpin, snow crab <20 mm, <i>Hyas</i> crab, anemones

achieve these declines over 10 yr. At the end of 10 yr, simulated levels of microalgae (g C m^{-2}), either settling or retained after lateral transport, had reached lows of 5% (7.5), 46% (80.4), and 56% (111.9) of levels in the initial balanced models for these sectors (147, 176, and 201, respectively).

In the Chirikov sector, much greater reductions (82%) in sediment OM to the lowest measured levels ($1.7904 \text{ g C m}^{-2}$) resulted in a dramatic decline of meiofauna, a decrease of almost 60% in bacteria, and a fluctuating but eventual 80% decline in Protista (Fig. 6, bottom panel). Among deposit-feeders, tunicates were lost within 3 yr, while most other taxa declined steadily toward loss after a delay of 1 to 2 yr. In our model, tunicates were eaten mainly by sea stars (Table 2), which remained stable for 2 to 3 yr before declining more gradually than other predators (Fig. 6, middle panel). After initial declines, clam deposit-feeders stabilized at about 60% of initial biomass after 4 yr. In contrast, other small crustaceans (Isopoda, Cumacea, Tanaidae) declined through the third year and then increased dramatically to 4 times their initial biomass. These small (non-amphipod) crustaceans were eaten mostly by whelks (Table 2), which after

2 yr declined rapidly to near zero at the point where small crustaceans increased with very little predation. Carnivorous worms, echinoderms, and anemones (Fig. 6, middle panel) all decreased steadily to low levels after a delay of 2 yr; sea stars, with their diverse diet, declined more slowly. Crabs and carnivorous gastropods also showed a 2 yr delay before declining dramatically; however, whelks and snow crabs <20 mm virtually disappeared, while snow crabs >20 mm and *Hyas* crabs recovered moderately toward the end of the decade (planktonic snow crab larvae often settle in areas with few adults, and then migrate ontogenetically to areas more favorable to adults; Kolts et al. 2015). Moon snails, after an initial large decline, increased to above original levels as competing predators on their main prey of clam deposit-feeders decreased to low levels. Fish, like most other predators and scavengers, showed little change for 2 yr. Beyond that initial period, when sediment OM had declined to below 70% of its original value, Arctic cod and both sculpin

species declined dramatically to near zero, flatfish by 65%, and snailfish by 50%.

In the East and West sectors, sediment OM (g C m^{-2}) decreased by only 60% (to 6.4960) and 52% (to 17.445) compared to 82% (to 1.7904) in the Chirikov (Fig. 6). Most components of the small food web (Fig. 6, bottom panels) declined immediately to relatively stable but slowly decreasing levels after 4 yr. However, in the East and West sectors, with much lower percentage decrease in sediment OM, bacteria showed little long-term change. Relative to the Chirikov, where meiofauna were essentially lost, meiofauna decreased by only 61 to 63% in the East and West. Despite major declines in tunicates that also occurred in the Chirikov, deposit-feeding Sipuncula, clams, and *Musculus* and other bivalves decreased by only 25 to 50%, while polychaete detritivores and amphipods were mostly unchanged in the southern sectors. Other small crustaceans, which in our model consumed mainly fresh microalgae and were eaten in small amounts by a range of predators but mainly by whelks (Table 2), actually increased by over 50% in the West sector. In stark contrast to the Chirikov, sea stars and carnivorous worms (polychaete

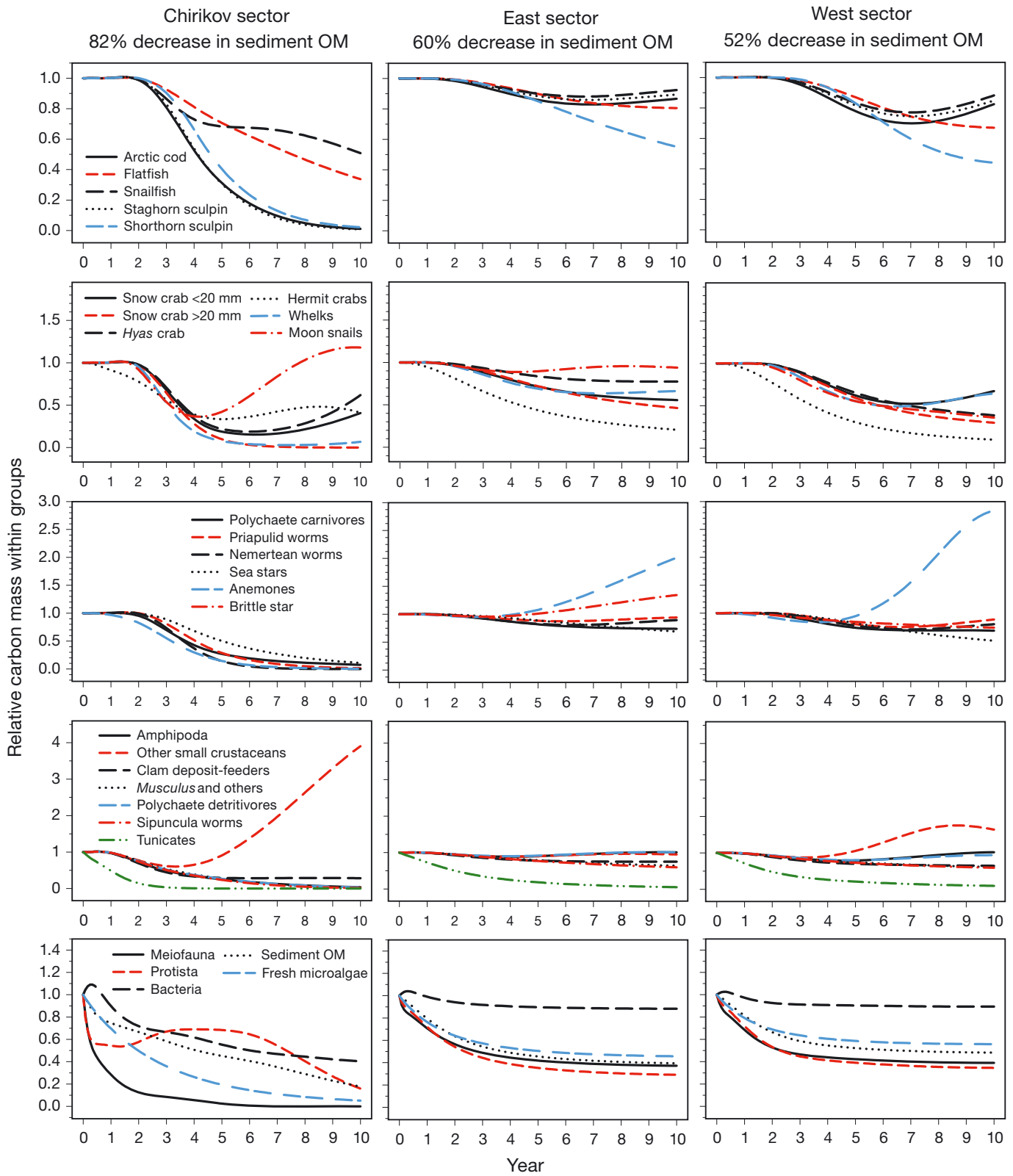


Fig. 6. Simulated relative change in biomass (g C m^{-2}) within each trophic group over 10 yr for decrease in sediment organic matter (OM, excluding fresh microalgae) from the initial balanced model to the mean level for the 2 stations with lowest sediment OM in each sector in late May 2007

Table 2. Consumption estimates (mg C m⁻²) for each trophic group from the initial balanced model for the West sector. tr: consumption <0.01. Numbering for predators is the same as for prey

Prey	Predator													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Arctic cod	-	-	-	-	-	-	tr	tr	-	-	-	-	-	-
2. Flatfish	-	-	-	-	-	-	0.04	tr	-	-	-	-	-	-
3. Snailfish	-	-	-	-	-	-	0.01	tr	-	-	-	-	-	-
4. Staghorn sculpin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. Shorthorn sculpin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6. Snow crab <20 mm	-	0.31	-	-	tr	0.05	tr	tr	-	-	-	-	-	-
7. Snow crab >20 mm	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Hyas crab	-	-	-	-	tr	0.01	tr	tr	-	-	-	-	-	-
9. Hermit crabs	0.03	-	-	-	tr	0.11	0.04	tr	-	-	-	-	-	-
10. Amphipoda	1.14	0.47	3.76	tr	tr	0.29	2.97	0.01	1.89	-	-	-	-	-
11. Other small crustaceans	tr	-	0.01	-	-	-	0.14	tr	-	-	-	-	-	17.69
12. Clam deposit-feeders	-	1.27	-	tr	-	0.40	68.79	0.30	2.49	-	-	-	-	127.80
13. <i>Musculus</i> and others	-	-	-	-	-	-	2.51	0.01	-	-	-	-	-	-
14. Whelks	-	-	-	-	-	-	-	-	-	-	-	-	-	6.23
15. Moon snails	-	-	-	-	-	-	0.06	tr	-	-	-	-	-	3.99
16. Polychaete carnivores	0.07	-	0.16	tr	-	-	6.74	0.03	-	-	-	-	-	-
17. Polychaete detritivores	-	3.98	0.01	tr	tr	0.09	18.75	0.08	1.38	-	-	-	-	87.69
18. Priapulidae	-	0.20	-	-	-	-	-	-	-	-	-	-	-	-
19. Sipuncula	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20. Nemertea	-	3.58	-	-	-	-	-	-	-	-	-	-	-	-
21. Tunicates	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22. Anemones	-	-	-	-	-	-	-	-	0.28	-	-	-	-	0.50
23. Sea stars	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24. Brittle star	-	0.37	-	-	-	0.05	3.13	0.01	0.32	-	-	-	-	5.23
25. Meiofauna	-	-	-	-	-	-	-	-	0.18	-	-	-	-	-
26. Protista	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27. Bacteria	-	-	-	-	-	-	-	-	-	3087.5	89.49	58885	1274.4	-
28. Fresh microalgae	-	-	-	-	-	-	-	-	-	162.50	4.71	3099.2	67.07	-
29. Sediment OM	-	-	-	-	-	-	-	-	16.53	-	-	-	-	-
Sum	1.25	10.18	3.94	tr	tr	0.99	103.21	0.45	23.08	3250.0	94.20	61984	1341.5	249.12
Prey	Predator													
	15	16	17	18	19	20	21	22	23	24	25	26	27	
1. Arctic cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2. Flatfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Snailfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4. Staghorn sculpin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. Shorthorn sculpin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6. Snow crab <20 mm	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7. Snow crab >20 mm	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Hyas crab	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9. Hermit crabs	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10. Amphipods	-	200.96	-	-	-	430.00	-	0.97	-	-	-	-	-	-
11. Other small crustaceans	-	-	-	-	-	-	-	0.97	-	-	-	-	-	-
12. Clam deposit-feeders	77.33	2612.5	-	-	-	322.50	-	0.97	4.71	-	-	-	-	-
13. <i>Musculus</i> and others	-	-	-	-	-	-	-	-	1.24	-	-	-	-	-
14. Whelks	-	-	-	-	-	-	-	-	0.94	-	-	-	-	-
15. Moon snails	3.22	-	-	-	-	-	-	-	-	-	-	-	-	-
16. Polychaete carnivores	-	401.93	-	62.69	-	322.50	-	-	-	-	-	-	-	-
17. Polychaete detritivores	-	401.93	-	501.48	-	860.00	-	-	0.27	-	-	-	-	-
18. Priapulidae	-	-	-	62.69	-	-	-	-	-	-	-	-	-	-
19. Sipuncula	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20. Nemertea	-	-	-	-	-	215.00	-	-	-	-	-	-	-	-
21. Tunicates	-	-	-	-	-	-	-	-	0.15	-	-	-	-	-
22. Anemones	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23. Sea stars	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-
24. Brittle star	-	-	-	-	-	-	-	-	0.06	-	-	-	-	-
25. Meiofauna	-	-	-	-	-	-	-	-	-	-	-	2280.0	-	-
26. Protista	-	-	-	-	-	-	-	-	-	-	-	1596.0	-	-
27. Bacteria	-	401.93	10619	-	1182.1	-	354.60	0.97	-	1245.5	13680	264000	-	-
28. Fresh microalgae	-	-	558.89	-	62.22	-	126.64	-	-	-	4560.0	66000	-	-
29. Sediment OM	-	-	-	-	-	-	25.33	0.97	-	-	684.00	-	623000	-
Sum	80.55	4019.2	11179	626.85	1244.3	2150.0	506.57	4.85	7.38	1245.5	22800	330000	623000	-

carnivores, Priapulids, Nemertea) declined only slightly, with brittle stars increasing by 30% in the East and anemones by 2 times in the East and 2.8 times in the West. Brittle stars consumed mostly bacteria, whereas anemones consumed diverse prey, but both were eaten mainly by whelks and large hermit crabs (Table 2). Crabs and predatory gastropods all declined by 20 to 70% (hermit crabs by 80 to 90%) in the East and West sectors, although moon snails remained stable in the East (Fig. 6). After a delay of 2 to 3 yr, fish initially declined but later recovered to 80 to 90% of original biomass, except for flatfish, which decreased by 40% in the West, and shorthorn sculpins, which declined in both sectors by 45 to 60%.

Simulated trajectories for 10 yr increases in organic inputs

Increasing sediment OM (g C m^{-2}) to the mean for the 2 stations in each sector with highest measured values required increases of 181% (to 28.400) in the Chirikov, 111% (to 34.723) in the East, and 52% (to 54.950) in the West (Fig. 7). In Ecosim, the long-term forcing functions for primary production needed to reach these values in 10 yr were 4.02, 2.45, and 1.59, respectively. At the end of 10 yr, the simulated level of microalgae (g C m^{-2}) either settling or accumulated by lateral transport had reached a high of +172% (399.5) in the Chirikov, +91% (336.3) in the East, and +40% (280.7) in the West relative to values in the initial balanced models.

In general, the lower the initial sediment organic content and the greater the absolute and percentage increase over 10 yr, the greater and more variable the increase among trophic groups. When original levels of sediment OM were high and the increase relatively low as in the West, most groups in the small food web increased but the change in bacteria was minimal. Meiofaunal response was especially variable, increasing by 6 times in the Chirikov and decreasing by 20% in the East. This variability in meiofauna, which in our model were eaten mainly by other meiofauna, appeared to result mainly from varying increases in their main foods of Protista and especially of bacteria (Table 2), which increased greatly in the Chirikov but not in the other sectors (Fig. 7).

Among deposit-feeders in all sectors, tunicates, which experienced very little predation and consumed about 70% bacteria, 25% fresh microalgae, and 5% sediment OM, showed the greatest relative increases. In the Chirikov, initial major increases of

all deposit-feeders resulted in major increases of their predators that subsequently drove the biomasses of clams and especially other small crustaceans back down, although deposit-feeding clams stabilized at about 2.8 times their original level. Deposit-feeding worms (polychaetes, Sipuncula) and amphipods achieved and maintained levels of 4 to 5 times their original values. Also in the Chirikov, carnivorous worms (polychaetes, Priapulidae, Nemertea) and anemones showed very large, rapid increases, Nemertea by up to 10-fold, before stabilizing under increased predation. Sea stars increased steadily to 5 times their initial biomass. Crabs and carnivorous gastropods, after increasing rapidly in response to major initial increases in their prey, subsequently decreased dramatically as their prey declined and their own fish predators responded to their initial large increases. At the end of 10 yr in the Chirikov, the biomass of all fish groups except flatfish had reached asymptotes as levels of their prey stabilized (Fig. 7). Except for substantial increases in shorthorn sculpins and snow crabs >20 mm in the East, and moderate declines of anemones in the East and West, relative changes in biomass of various predators were quite low in the southern sectors compared to those in the Chirikov Basin.

DISCUSSION

The initial mean value of sediment OM (g C m^{-2}) in the Chirikov sector (10.0954) was substantially lower than in the East (16.442) or West (36.205), and percentage reductions to the lowest observed values were also much greater in the Chirikov (82% to 1.7904) than in the East (60% to 6.4960) or West (52% to 17.445). Hydrographic differences among sectors, and resulting spatial variations in bottom temperatures, dispersal, and recruitment (e.g. Kolts et al. 2015), undoubtedly modify purely trophic effects on benthic communities. Nevertheless, these observed decreases of OM inputs were enough to cause quite different trajectories among trophic groups over 10 yr, with appreciable loss of trophic diversity and function.

In contrast, increases in sediment OM (g C m^{-2}) of 111% (to 34.723) and 52% (to 54.950) in areas with higher sediment organic content initially (as in the East and West sectors, respectively) led to moderate and predictable increases in most taxa, although some groups, such as anemones and small non-amphipod crustaceans decreased. When original sediment OM was lower and percentage increase in organic inputs higher as in the Chirikov (181% to

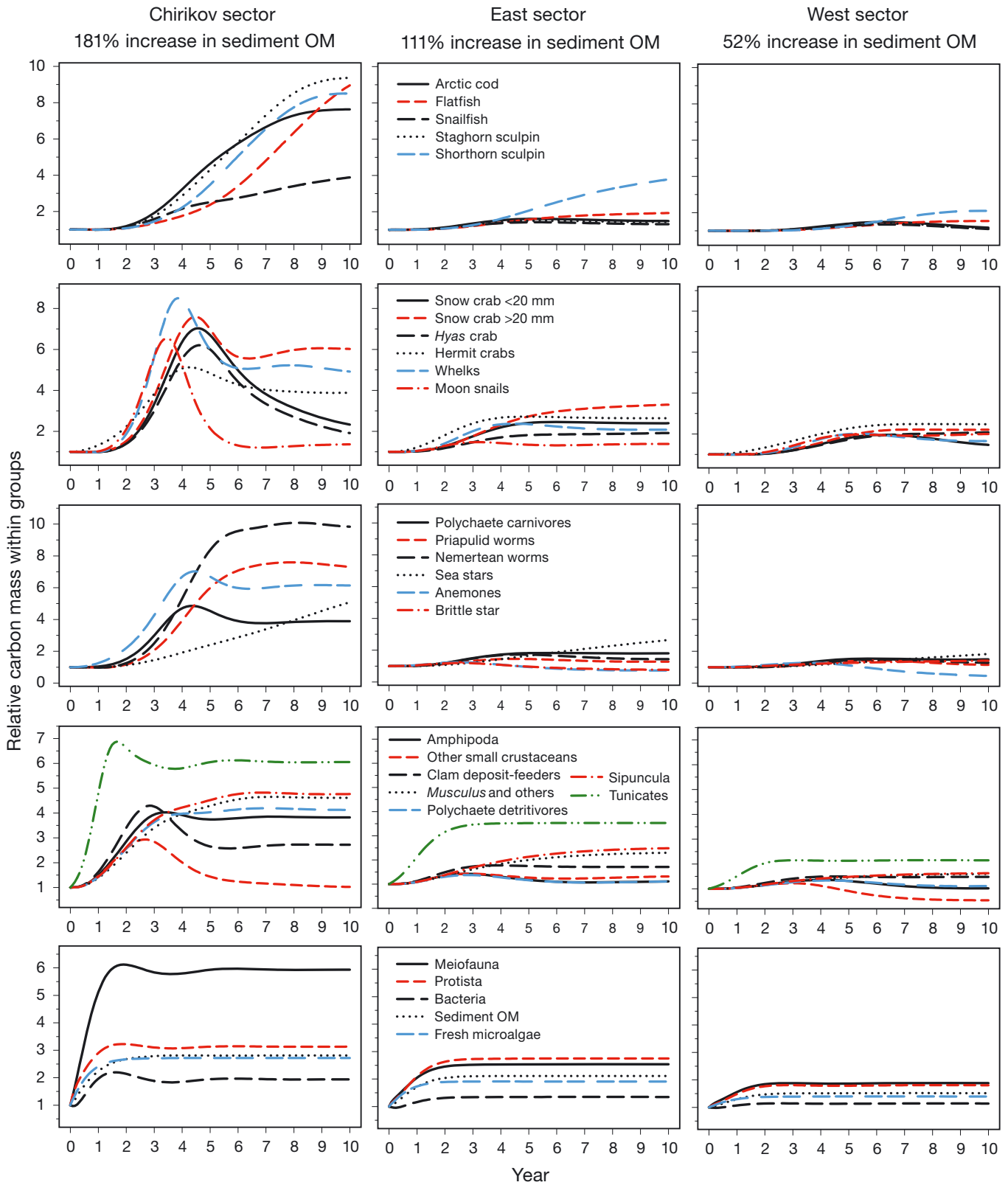


Fig. 7. Simulated relative change in biomass (g C m^{-2}) within each trophic group over 10 yr for increase in sediment organic matter (OM, excluding fresh microalgae) from the initial balanced model to the mean level for the 2 stations with highest sediment OM in each sector in late May 2007

28.400), responses of all trophic groups from bacteria to fish could be radical and often highly unstable. Thus, when projecting effects of altered organic inputs due to shifts in ice patterns or lateral advection, it appears that both initial conditions and the relative magnitude of OM change can have important effects on resulting benthic food web structure.

Buffering by the sediment OM pool

A number of authors have concluded that deposit-feeders often depend strongly on a longer-term 'food bank' of sediment OM, despite major seasonal pulses of fresh microalgae (Fleeger et al. 1989, Rudnick 1989, Josefson et al. 2002, Byrén et al. 2006, Franco et al. 2008, Mincks et al. 2008, Evrard et al. 2010, North et al. 2014). Levinton (1972) suggested that in such cases, deposit-feeders can be buffered from seasonal and annual variations in settling phytodetritus. We simulated effects of declining microalgal inputs starting with the mean sediment OM pool measured for each sector. During gradual decreases in microalgal inputs, biomass responses of almost all macrofaunal groups did not occur for 2 to 3 yr, despite very rapid response among heterotrophic components of the 'small food web' (meiofauna, Protista, and bacteria; Fig. 6). In fact, in our initial steady-state networks, although Mixed Trophic Impacts within the small food web were often quite strong, interactions of small food web components with deposit-feeders and other higher organisms were less striking (Fig. 3). The very small perturbations used in calculating Mixed Trophic Impacts were apparently inadequate to overcome buffering of macrofauna from changes in the small food web.

However, after 2 yr in the simulations when sediment OM fell below 70% of initial values, effects on higher trophic levels slowly to rapidly accelerated, depending on initial OM values and the rate of decrease of organic inputs (Fig. 6). In a number of cases there were severe biomass declines, sometimes leading to effective loss of trophic groups (Table 1). For a few groups in some sectors (small non-amphipod crustaceans, moon snails, anemones, brittle stars), declines of important predators or competitors allowed those trophic groups to increase substantially despite lower total carbon supply to the food web.

We predicted that taxa with higher fractions of fresh microalgae (in addition to sediment OM or bacteria) in their diets would be most vulnerable to (least buffered from) declines in phytodetritus inputs. Based on diet fractions drawn from the literature, the

tunicates, meiofauna, and Protista were in this category (Table 2). Tunicates indeed decreased to a greater extent than other benthic deposit-feeders, as did meiofauna and Protista by the end of 10 yr (Fig. 6). All these groups responded immediately to declines in fresh microalgal inputs, whereas groups more dependent on sediment OM or bacteria generally did not respond for 2 to 3 yr. These results suggest that the pool of sediment OM can buffer much of the deposit-feeding community from gradual declines in fresh microalgal inputs for 2 to 3 yr, but after that the biomasses of a number of trophic groups can decrease rapidly and their trajectories can diverge dramatically.

Alteration of food web structure

We were interested in whether decreases or increases of microalgal inputs over the reasonable ranges we studied might alter food web structure in ways that could hinder short-term recovery if original inputs were restored. Local loss of species is an important criterion of persistent ecological effects, as recovery of the food web upon restoration of initial inputs would not be the same without lost trophic groups. Even if a trophic group persists at much lower relative biomass, increases in its predators or competitors might hinder that group's recovery, as apparently occurred with depleted cod after fishing closures in the Northwest Atlantic (Frank et al. 2011).

Simulated losses of diverse fish and invertebrate taxa were often consistent with those observed in field samples (Table 1). Fish, which already had very low biomass at these low temperatures (Cui et al. 2009), were particularly susceptible to declines in their prey caused by decreased microalgal inputs. Relative changes in biomass of almost all predators were greatest in the Chirikov sector for either decrease or increase in sediment OM (Figs. 6 & 7). Measured levels of sediment OM at different stations spanned a much greater range relative to the initial mean in the Chirikov than in the other sectors, suggesting more extreme patchiness of phytodetrital scouring and accumulation. Depending on the dispersal and colonization capabilities of various taxa, and the spatial extent of microalgal deficits (distance from sources of recruits in less affected areas), these losses of trophic groups could result in substantial alteration of community structure despite later restoration of original microalgal inputs.

Losses of entire trophic groups suggest that from a spatial or metacommunity perspective, what is more

important to resilience of food webs is not local redundancy of functions that can mitigate species loss, but rather larger-scale redundancy of patch types that can serve as refugia and sources of recruits after local extirpation (so-called 'rescue effects'; Gravel et al. 2011, Bellmore et al. 2015). Most contemporary network models that assume homogeneity of both biomasses and trophic interactions over large areas do not consider this potentially fundamental mechanism of food web resilience to perturbation. Development of modeling approaches that integrate internally homogeneous food web networks with meta-community processes among spatially distributed patches are an important challenge for the future.

Increased microalgal inputs resulted in no complete losses of trophic groups. Nevertheless, increase in microalgae appeared capable of inducing dramatic and unstable effects among a broader complement of groups than did microalgal declines. In the Chirikov sector, immediate increase of bacteria in response to increased sediment OM promoted rapid increase in deposit-feeders (Fig. 7). However, this initial surge in deposit-feeders was followed by an increase in their invertebrate predators, which caused deposit-feeder biomass to stabilize or decline. Increased availability of all prey types allowed fish predators to maintain or increase their biomass, resulting in important declines in some predatory invertebrates that fish either preyed upon or competed with. Thus, increase in microalgal inputs, although resulting in no complete loss of trophic groups, may cause substantial changes in biomass structure among groups.

Implications for endothermic predators

A number of endothermic predators that feed mainly on benthic organisms, such as sea ducks (Mergini), bearded seals *Erignathus barbatus*, walrus *Odobenus rosmarus*, and in certain areas gray whales *Eschrichtius robustus*, are common in our study area. Our models did not consider effects of food web changes on these endothermic predators, or the impacts of such predators on the food web. Relative to invertebrates and fish, these predators have very high per capita energy demands, and some (especially eiders and walrus) often feed in large groups. However, because their high energy requirements demand high intake rates, and their mobility allows them to seek the high prey densities they need, their annual trophic impacts and role in food webs are typically limited to relatively small portions of total habitat (Nelson et al. 1987, Jay et al.

2014, Lovvorn et al. 2014). As a result, the roles of these predators in food webs may not be well represented when averaged over large areas, as they are in most network models for large marine ecosystems (Ciannelli et al. 2004, Whitehouse et al. 2014). Trophic impacts that depend on thresholds of prey density that allow profitable foraging (e.g. Lovvorn et al. 2009, 2015b) may further modify the trajectory of benthic communities during increases or decreases of OM inputs. Such thresholds and their spatially explicit context must be characterized and integrated with network models before the food web relations of these endothermic predators can be properly modeled and understood.

Improving model predictions

Our comparisons of simulated and observed community structure revealed agreement in most patterns but also important discrepancies. Some differences might have resulted from physically driven factors such as larval dispersal and settlement, which were not considered in our trophic models (Ólafsson et al. 1994, Palmer et al. 1996). However, even if most measured variations in community structure did result from trophic effects, we do not know the schedule of microalgal inputs at each sampling station in years leading up to 2007. The longer-term chronology of inputs might have had important influence on the relationship between sediment OM and food web structure observed in that given year. Better time series of data to guide the schedule of perturbations in the models would provide better tests of their predictive accuracy.

Regarding shifts in temperature that might accompany changes in sea ice or wind-driven currents, we minimized this issue by modeling effects of changes in phytodetrital inputs over ranges that occurred in the same sectors in the same year. For mobile epibenthic predators such as crabs and fish, their recruitment, consumption rates, and movements can be greatly affected by shifts in temperature likely to occur in this area in the future (Mueter & Litzow 2008, Wang et al. 2012, Kolts et al. 2015, review in the Supplementary Material for Lovvorn et al. 2015a). In particular, a temperature increase to 2°C or higher would allow invasion by a number of predatory fish that could strongly impact benthic community structure (Quijón & Snelgrove 2005, Mueter & Litzow 2008, Hollowed et al. 2009).

However, for bacteria and deposit-feeders of polar regions, experiments and field studies have often

indicated that rates of metabolism and assimilation respond mainly to seasonal pulses of food availability, with relatively little effect of temperature variations within ranges normally experienced (Arnosti et al. 1998, Ahn et al. 2003, Sejr & Christensen 2007, Carroll et al. 2009). Differing responses to temperature among taxa might nevertheless amplify trophic effects, and introduce important nonlinearities to model predictions (Kirby & Beaugrand 2009). For deposit-feeders, relevant measurements will be challenging, as respiration by heterotrophic bacteria on which they feed in complex sediments is difficult to separate from respiration of the deposit-feeders themselves. Nevertheless, suitable experiments on joint responses to food and temperature by local taxa, coupled with field samples in areas with similar organic inputs but different temperature regimes, would allow more reliable predictions of climate-driven changes. Such models are essential to moving beyond predictions based solely on temperature tolerances of individual species, to more realistic consideration of species interactions in spatially heterogeneous environments (Christensen et al. 2014, Fisher et al. 2014, Gilbert et al. 2014).

Our modeling was hindered by lack of measurements in our study area of the biomass or production rates of meiofauna, protists, or bacteria. In a range of environments, studies based on stable isotopes, fatty acid biomarkers, and other tracers have indicated trophic reliance by deposit-feeders on heterotrophic microbes (Fleeger et al. 1989, Rudnick 1989, Josefson et al. 2002, Byrén et al. 2006, Franco et al. 2008, Mincks et al. 2008, Evrard et al. 2010, McTigue & Dunton 2014, North et al. 2014). Nevertheless, as yet there have been no critical tests of the adequacy of heterotrophic microbial production to meet the energy demands of the entire deposit-feeding community. Bacterial production and assimilation of phytodetritus, as well as consumption and assimilation rates of deposit-feeders and their predators, must be measured or estimated accurately at the very low bottom temperatures in this polar region. Model explorations such as those described here help place the need for such empirical studies in the context of ecosystem impacts of expected climatic changes.

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