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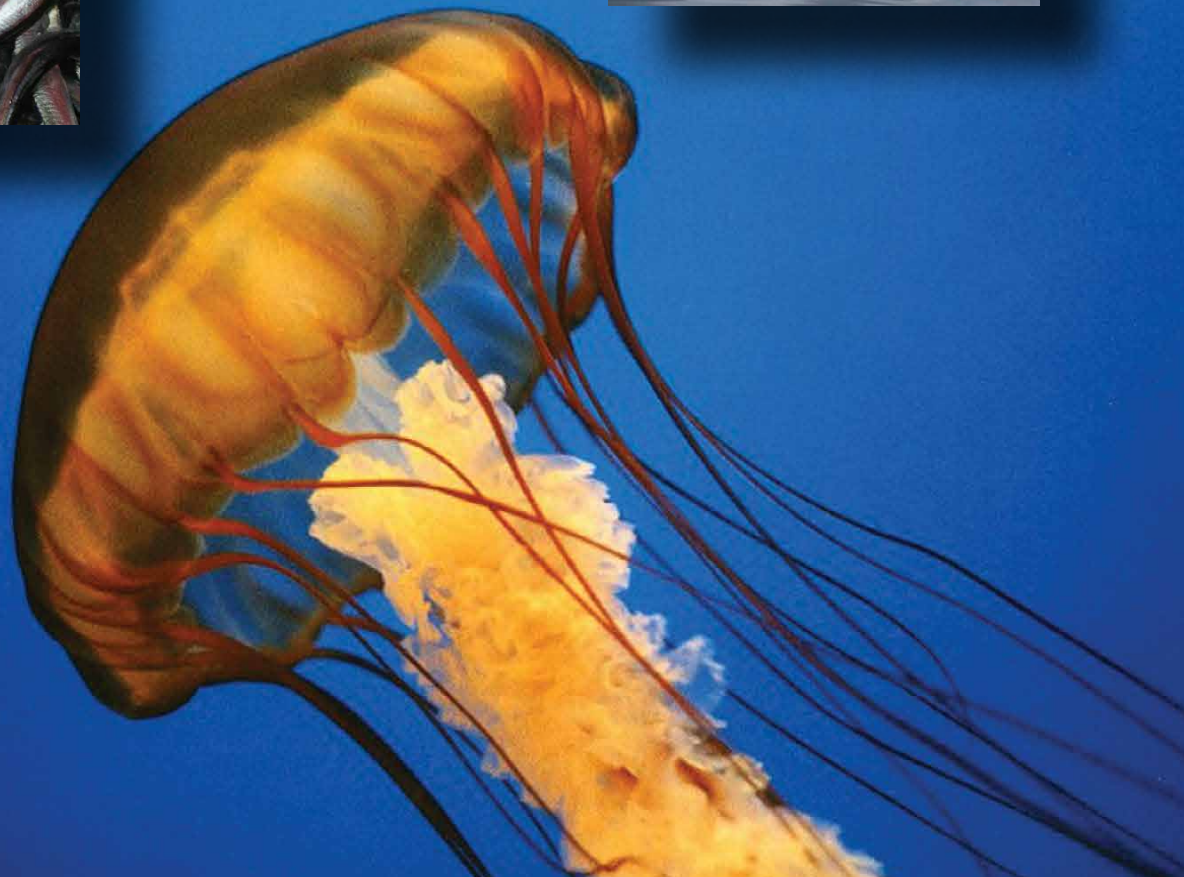
ABSTRACT. End-to-end models were constructed to examine and compare the trophic structure and energy flow in coastal shelf ecosystems of four US Global Ocean Ecosystem Dynamics (GLOBEC) study regions: the Northern California Current, the Central Gulf of Alaska, Georges Bank, and the Southwestern Antarctic Peninsula. High-quality data collected on system components and processes over the life of the program were used as input to the models. Although the US GLOBEC program was species-centric, focused on the study of a selected set of target species of ecological or economic importance, we took a broader community-level approach to describe end-to-end energy flow, from nutrient input to fishery production. We built four end-to-end models that were structured similarly in terms of functional group composition and time scale. The models were used to identify the mid-trophic level groups that place the greatest demand on lower trophic level production while providing the greatest support to higher trophic level production. In general, euphausiids and planktivorous forage fishes were the critical energy-transfer nodes; however, some differences between ecosystems are apparent. For example, squid provide an important alternative energy pathway to forage fish, moderating the effects of changes to forage fish abundance in scenario analyses in the Central Gulf of Alaska. In the Northern California Current, large scyphozoan jellyfish are important consumers of plankton production, but can divert energy from the rest of the food web when abundant.

INTRODUCTION

The broad objective of the Global Ocean Ecosystem Dynamics (GLOBEC) program was to understand the processes that control population variability. The GLOBEC approach was to study linkages between the recruitment variability of target species (e.g., calanoid copepods, euphausiids, cod, haddock, salmon) and environmental processes operating across broad temporal and spatial scales. The inability to conduct controlled experiments is a major impediment to the scientific study of the mechanics of ocean ecosystem dynamics. Ecosystem models provide the best proxy for controlled experiments (deYoung et al., 2010) and offer a way to study the integrated effects of the critical processes that occur on different scales (Fogarty and Powell, 2002).

Species-centric models have proved to be valuable tools for studying the effects of fishery management policies on individual fish stocks (Rothschild, 1986) and the effects of ocean physics on the dynamics of individual species

(e.g., Wiebe et al., 2003; Lough et al., 2005). However, understanding tropho-dynamic interactions among species has long been recognized as critical to understanding the dynamics of the ecosystem as a whole (e.g., Frank et al., 2005). Multispecies ecosystem models of increasing sophistication are being developed to meet the need for a community-level approach to management of marine resources and ecosystem services subject to fishing pressures and climatic change (Travers et al., 2007; Fogarty et al., 2013, in this issue).

Applying multispecies ecosystem models within a comparative analysis of different ecosystems provides additional insight to ecosystem structure and function. Comparative studies can serve as proxies for controlled, manipulative studies but require that each ecosystem model be similarly structured in terms of spatial and temporal scale and functional group resolution. Here, we describe the development and analysis of end-to-end ecosystem models of the trophodynamic

relationships within four US GLOBEC ecosystems. An end-to-end model describes the flow of energy (as biomass) through the ecosystem from the input of nutrients, through the production of plankton, fish, seabirds, mammals, and fisheries, to detritus and recycled nutrients. Our primary goal is to identify the main attributes that regulate each system's response to perturbations at multiple trophic levels. We use the models to estimate the relative importance of the different functional groups as energy-transfer nodes and to estimate the impact of changes at these nodes. In addition to understanding and comparing ecosystem structure and dynamics, a major goal of this study is to develop an end-to-end model platform that can be applied broadly across diverse ecosystems.

Four US GLOBEC Ecosystems

There are striking differences among the GLOBEC ecosystems in bottom depth and topography, circulation and stratification, seasonal cycles, and community composition across all trophic levels. These differences have prompted collection of different data sets and application of different food web models for each ecosystem, making direct end-to-end comparisons of energy flow patterns challenging.

Northern California Current

The Northern California Current (NCC; Figure 1a) is a highly productive seasonal upwelling ecosystem (Huyer, 1983; Checkley and Barth, 2009). On short time scales, lower trophic level dynamics are strongly coupled to the timing, strength, and duration of upwelling (Thomas and Strub, 2001; Thomas and Brickley, 2006). On interannual to interdecadal time scales, basin-scale climate processes (e.g., El Niño-Southern

a. Northern California Current

b. Central Gulf of Alaska

c. Georges Bank

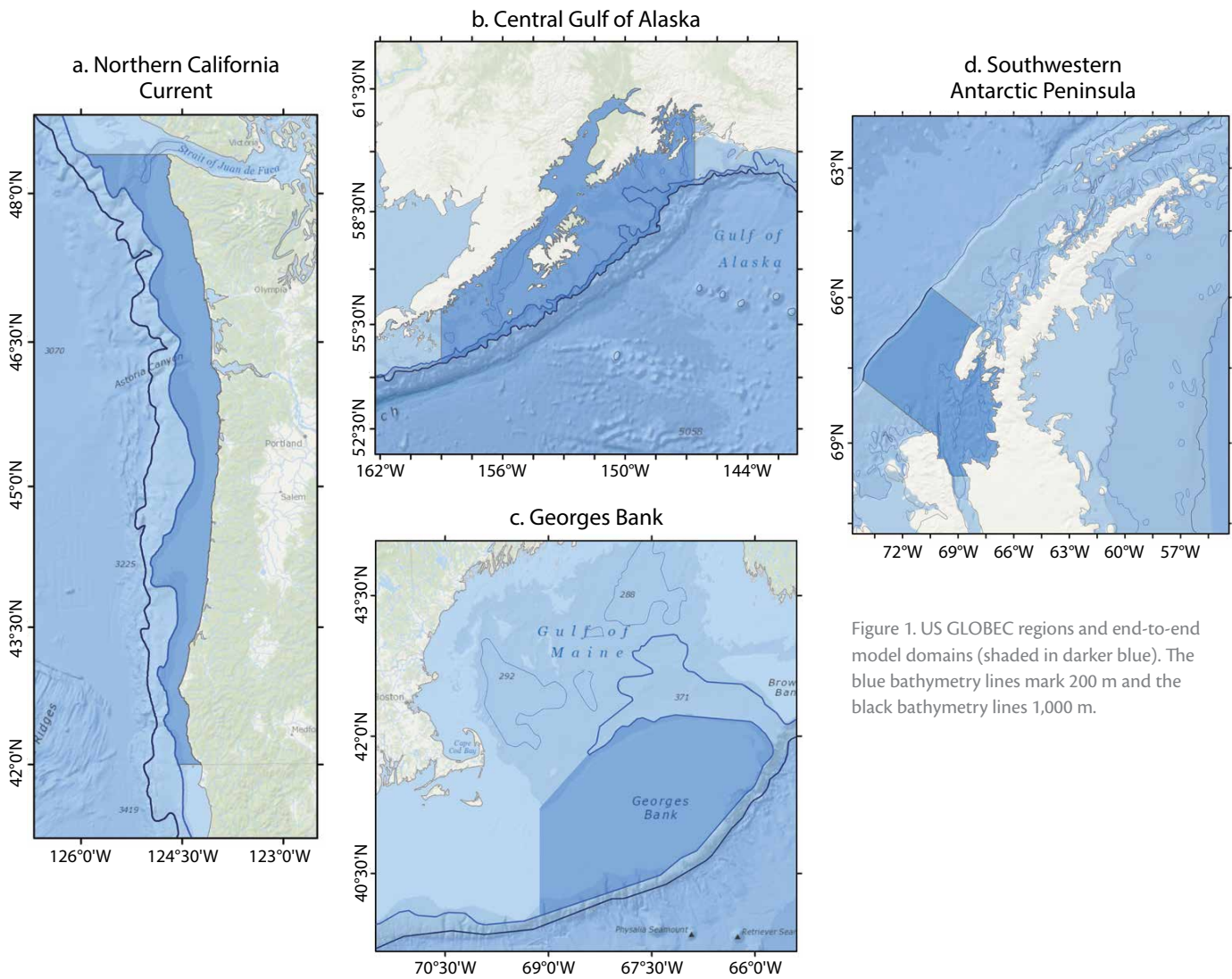d. Southwestern Antarctic Peninsula

Figure 1. US GLOBEC regions and end-to-end model domains (shaded in darker blue). The blue bathymetry lines mark 200 m and the black bathymetry lines 1,000 m.

Oscillation, Pacific Decadal Oscillation [PDO]) and interregional transport of large water masses strongly influence local ecosystem dynamics (Di Lorenzo et al., 2013, in this issue), control the composition of upwelling source waters (Huyer et al., 2002), and affect the composition of the local mesozooplankton grazer community (Batchelder et al., 2002; Keister and Peterson, 2003). These physical and lower trophic level processes directly affect the production of pelagic fishes (Brodeur and Pearcy, 1992; Ruzicka et al., 2011; Burke et al., 2013), benthic invertebrates (Barth et al., 2007), and local seabird and marine mammal populations (Ainley and Boekelheide, 1990; Keiper et al., 2005). An end-to-end

model of the NCC must incorporate both local physical processes (upwelling-driven primary production) and important nonlocal factors that affect community composition across all trophic levels.

Central Gulf of Alaska

The Central Gulf of Alaska (CGOA) system (Figure 1b) is a highly productive downwelling system (Stabeno et al., 2004). Offshore surface waters that are advected onto the shelf during downwelling events originate from the high-nutrient, low-chlorophyll (HNLC), iron-limited region of the North Pacific gyre. Mixing of HNLC waters with iron-replete shelf waters drives the production cycle (Fiechter et al., 2009). Fish and marine

mammal populations have changed dramatically over the past 40 years, with some species shifts correlating well with the 1976–1977 PDO shift (Francis et al., 1998; Anderson and Piatt, 1999). Connecting these physical and lower trophic level processes with what appear to be strong shifts among mid and upper trophic level interactions in this ecosystem (Gaichas et al., 2011) is an important challenge for end-to-end modeling.

Georges Bank

Georges Bank (GB) is a shallow bank offshore of Cape Cod (Figure 1c). It has long been the site of economically important fisheries, including cod (*Gadus morhua*), haddock

(*Melanogrammus aeglefinus*), flatfishes, Atlantic lobster (*Homarus americanus*), and scallops (*Placopecten magellanicus*). Over GB's shallow, central region, turbulent tidal mixing is sufficiently strong to keep the water column well mixed year-round. A permanent hydrographic front near the 60 m isobath separates the central bank from stratified waters on the bank's flank to the north and south (Flagg, 1987). A pronounced diatom bloom usually occurs in early spring, supporting production of the large calanoid copepod *Calanus finmarchicus*. Both the phytoplankton and zooplankton communities shift to smaller forms during the remainder of the annual cycle (Davis, 1984). Strong interactions between benthic and pelagic components at several trophic levels complicate end-to-end analysis (Steele et al., 2007).

Southwestern Antarctic Peninsula

The southwestern Antarctic Peninsula (sWAP) ecosystem supports roughly half of the total Antarctic krill (*Euphausia superba*) population (Atkinson et al., 2004) and some of the largest populations of vertebrate predators in the Southern Ocean region (Everson, 1977, 1984). Although nitrogen is not considered to be limiting, micronutrients (including iron) and sunlight are. Interannually variable seasonal sea ice cover reduces solar irradiance into the upper water column, limiting overall system production and impacting the ecology of the entire ecosystem (Longhurst, 1998; Ducklow et al., 2007). The sWAP (Figure 1d) is connected to the larger Antarctic ecosystem at several trophic levels. It is thought to be an upstream source for recruits to the krill population around South Georgia (Fach et al., 2006). Satellite tracking studies show that seabird and marine mammal predators move and forage throughout the greater Antarctic Peninsula region (Catry et al., 2004; Croxall et al., 2005; Phillips et al., 2005; Biuw et al., 2007). An end-to-end model of the sWAP ecosystem must incorporate important local physical processes and must take into account intra-regional connectivity within the greater Antarctic Peninsula–Scotia Sea ecosystem.

MODELS AND METHODS
Building the Food Web Models

The basic information needed to build a food web model consists of: (1) diet information for each functional group, which defines the topology of the food web network, and (2) terms for biomasses and physiological rates, which define the rate of energy flow through each trophic linkage. Except for GB, the models were initially constructed as Ecopath food web models (Christensen and Walters, 2004; http://www.ecopath.org). Ecopath models infer the strength of individual trophic linkages from the energy demand of consumers upon their prey. The logic behind this "top-down" approach is that data availability and quality are typically better for upper trophic level consumers and fisheries than for low and mid-trophic level groups. It is then mathematically simple to transform a top-down linear expression of predation pressure (Ecopath) into a bottom-up map of energy flow from lower trophic level producers to upper trophic level consumers (Steele, 2009). With the inclusion of external nutrient fluxes as input for uptake by phytoplankton, nutrient recycling via bacterial metabolism of detritus and consumer metabolism, and an accounting for production losses from the system via physical export, an end-to-end ecosystem model may be constructed (Steele and Ruzicka, 2011). From diverse model origins, all four ecosystems were described within similar end-to-end model frameworks.

For a comparative ecosystem study, care must be taken to (1) define functional groups similarly across models, (2) define model domains on similar temporal and spatial scales as appropriate to the data, (3) be aware of connectivity to neighboring systems, and (4) account for uncertainty and variability among parameters. Figure 2 shows the food webs of each US GLOBEC region; Table 1 provides the details about the underlying data sets used to build each model. The full parameter sets defining each model are available in the supplementary material for Ruzicka et al. (2013).

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Metrics and Scenarios

Basic metrics are extracted from observations of each ecosystem and from food web models to describe the overall size of each system in terms of energy flow, the relative importance of each functional group as an energy transfer pathway, and the efficiency of energy transfer through the food web network. These parameters are highly integrated descriptions of the food web at a single point in time (see Box 1).

Two types of model scenarios are used to compare responses of the four US GLOBEC ecosystems to postulated food web changes. Structural scenarios show the immediate effects of perturbations to any portion of the food web (Steele, 2009; Steele and Ruzicka, 2011). A structural scenario is constructed by changing the relative consumption rate of one or more consumer group(s) upon any specified prey group. In the scenarios presented here, the imposed change comes at the direct expense of (or benefit to) any consumer group competing for the same prey. The total consumer pressure on a given prey group was not changed and transfer efficiencies were held constant, implying no changes to group physiologies (assimilation efficiencies, growth efficiencies, and weight-specific production rates) nor to predation vulnerabilities. The impacts of a structural scenario are evaluated as the change in the amount of energy flowing along each trophic pathway and the change in the production rate of each group in the food web, integrating both direct and indirect effects of the scenario. Here, we show three examples of scenarios to compare the effects of:
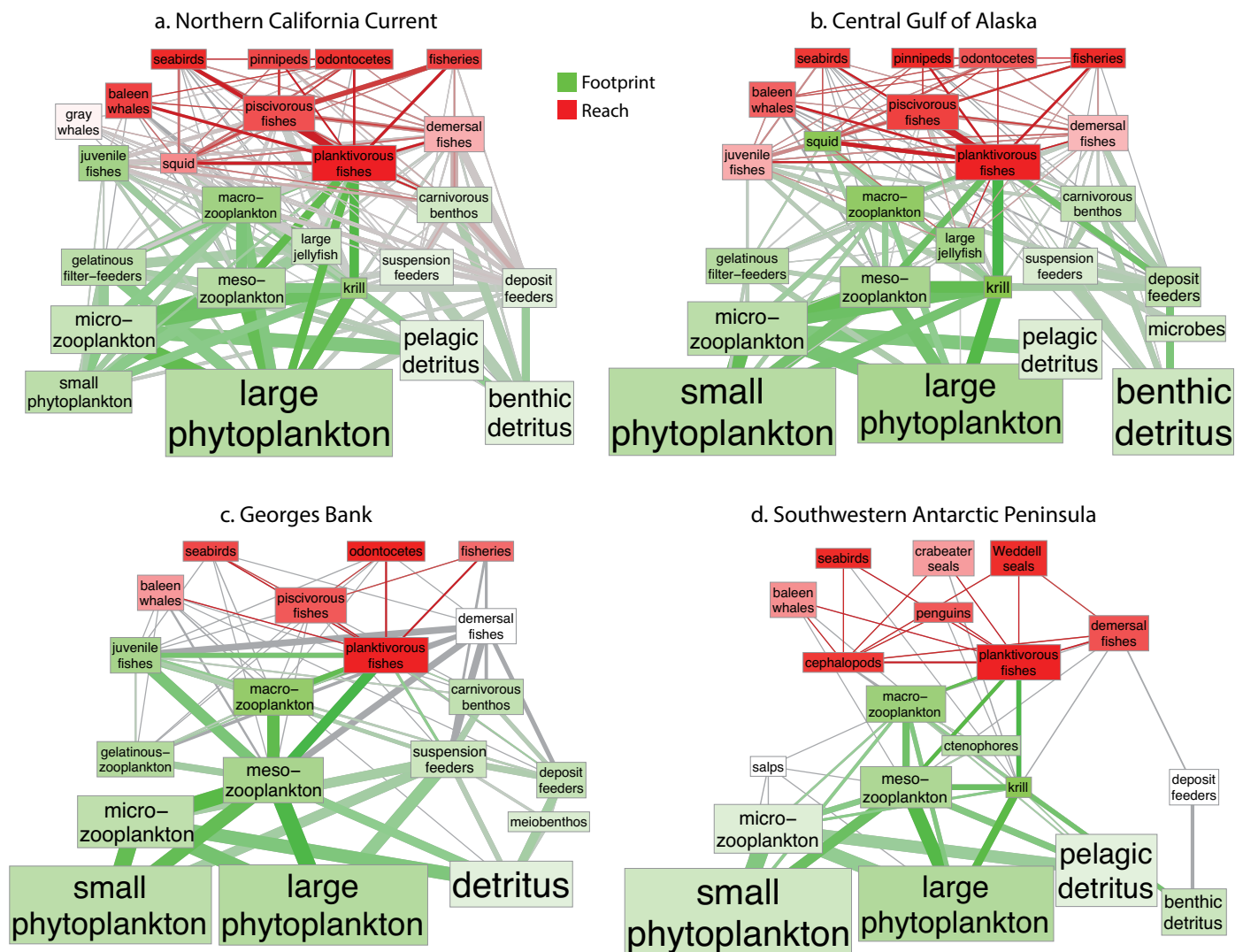

Figure 2. Food webs for each US GLOBEC region. Color shows the footprint and reach of the planktivorous fishes (forage fishes). Footprint (green) is the fraction of each group's production consumed by the planktivorous fishes. Reach (red) is the fraction of each consumer's production that has originated with the planktivorous forage fishes via all direct and indirect pathways.

Table 1. Background information about each food web model. See primary references for more complete information.

	NCC	CGOA	GB	sWAP
PRIMARY REFERENCES	Ruzicka et al. (2007, 2012)	Aydin et al. (2007) Gaichas et al. (2009, 2010)	Steele et al. (2007) Gifford et al. (2009) Collie et al. (2009)	Ballerini et al. (2013)
DOMAIN	Shelf (0–200 m)	Shelf & slope (50–1,000 m)	Bank crest & slope	Deep shelf
	26,000 km²	170,000 km²	42,000 km²	84,000 km²
SEASON	Spring-summer: annualized	Spring-summer: annualized	Annual	Winter data: annualized
PERIOD	1999–2011	1990–1993	1993–2002	2001–2002
FUNCTIONAL GROUPS	77	133	19	24
PRIMARY DATA SOURCES — Phytoplankton	SeaWiFS: http://www.science.oregonstate.edu/ocean.productivity/standard.product.php	GLOBEC: Suzanne Strom, Western Washington University, *pers. comm.* (2013) Literature	O'Reilly et al. (1987)	Model estimate, SeaWiFS
Zooplankton, pelagic fishes	Various field surveys: Batchelder et al. (2002) Brodeur et al. (2005) Morgan et al. (2005) Emmett et al. (2006) Ainley et al. (2009)	NOAA Fisheries Oceanography Coordinated Investigations (FOCI)	GLOBEC broadscale survey: See Wiebe et al. (2003) Literature cited in Steele et al. (2007)	GLOBEC: Ashjian et al. (2004, 2008) Marrari et al. (2011) Daly (2004) Scolardi (2004) Pakhomov et al. (2006) Donnelly and Torres (2008)
Demersal fishes	Stock assessments: Kaplan and Helser (2007) NOAA: Keller et al. (2008)	Stock assessments NOAA: Britt and Martin (2001)	NOAA: Azarovitz (1981) NEFC (1988) Smith (2004)	Donnelly et al. (2004)
Benthic invertebrates	Literature	Literature	Literature cited in Steele et al. (2007)	Smith et al. (2006)
Seabirds	NOAA: Recent work of Jeanette E. Zamon, NOAA Oregon/Washington Fish & Wildlife Services	US Fish & Wildlife Service	Link et al. (2006)	Ribic et al. (2011) Ainley (2002)
Marine mammals	Angliss and Allen (2009) Carretta et al. (2007) Brown et al. (2005) Calambokidis et al. (2002) Pitcher et al. (2007) Scordino (2006)	National Marine Mammal Laboratory (NMML)	Link et al. (2006)	GLOBEC: Erickson and Hanson (1990) Chapman et al. (2004) Thiele et al. (2004) Branch (2006, 2007) Ribic et al. (2008) Literature
Fisheries	PacFIN: http://pacfin.psmfc.org RecFIN: http://www.recfin.org	NOAA	NOAA	
Diet	See Dufault et al. (2009)	NOAA Resource Ecology & Ecosystem Management (REEM) diet database	Literature cited in Steele et al. (2007)	Literature

NCC = Northern California Current. CGOA = Central Gulf of Alaska. GB = Georges Bank. sWAP = Southwestern Antarctic Peninsula

BOX 1. FOOD WEB METRICS

ECOSYSTEM SIZE: The relative size of an ecosystem in terms of the production rates of major functional groups.

FOOTPRINT: The relative importance of a group as a consumer expressed as the energy demand of the consumer upon one or more producers. A consumer may have a footprint upon a producer even if it does not directly prey upon that producer. A commonly encountered footprint in the literature is the "primary production required" (PPR) to support a fishery or consumer group of particular interest.

REACH: The relative importance of a group as a producer expressed as the fraction of the group's production that reaches one or more consumer groups via all direct and indirect food web pathways.

FOOD WEB EFFICIENCY: How efficiently energy is transferred through a food web, considering all alternate energy pathways and physiological losses at each link in the web. Food web efficiency, expressed as the realized production rate of each functional group per unit of primary production, is insensitive to differences in overall ecosystem size.

(1) doubling forage fish abundance, (2) doubling gelatinous zooplankton abundance, and (3) a fivefold increase in baleen whale abundance in each of the four ecosystems.

While static structural scenarios show the immediate consequences of ecosystem perturbations throughout the food web, dynamic scenarios that allow for the evolution of compensatory changes in community composition over time are needed to estimate long-term ecosystem changes. For example, the structural forage fish doubling scenario described above was repeated using time-dynamic Ecosim algorithms (Christensen and Walters, 2004; Gaichas et al., 2011). Dynamic runs were initialized using the same conditions as the structural scenarios. Base models, without forcing forage fish biomasses, were run for 200 years to allow ecosystems to

achieve steady-state conditions. Scenario models were then run by doubling the final base model forage fish biomasses gradually over 100 years and then run at the target biomass for the remainder of a 200-year run. The effects of the forced forage fish biomass on other groups in the food web were expressed as ratios of final biomasses in the scenario model to final biomasses in the base model (using the means of the last 10 years as "final" biomasses).

Both structural and time-dynamic scenarios account for the propagation of model observed variability and parameter uncertainty through the food web. We adapted the principles of the "ECOSENSE" simplified Bayesian Synthesis methodology (Aydin et al., 2007) to end-to-end models. A series of potential models were randomly generated via Monte Carlo sampling from

each model parameter's uncertainty distribution (established a priori; see supplementary material for Ruzicka et al., 2013). Parameter-set rejection criteria were applied to consider only potential models that maintained the thermodynamic balance of the system (i.e., predation demand could not exceed the production rate for any group). Scenarios were run across all of the potential models generated for each ecosystem, and the distribution of scenario results provided a confidence index about predicted model responses. For the time-dynamic scenarios, we also considered the uncertainty associated with predator–prey functional responses. Potential functional response parameters were sampled across the full range from stable donor-controlled (linear) dynamics to chaotic Lotka-Volterra dynamics. This wide range reflects the high uncertainty in predator-prey dynamics, which are poorly known in most marine ecosystems.

RESULTS
Food Web Metrics
Ecosystem Size and Production (Table 2)
Phytoplankton production sets the overall energy scale of each system. The Northern California Current upwelling system is the most productive and the polar southwestern Antarctic Peninsula system is the least productive, at half the size of the NCC. Systems differ in terms of which functional group classes are most productive—highlighting differences in their energy flow patterns. The NCC is twice as productive as both the Central Gulf of Alaska and Georges Bank in terms of total fish production, but the NCC, CGOA, and GB are of similar size in terms of energy flow to top predators: seabirds, marine mammals, and fisheries.

Footprint and Reach (Table 3, Figure 3)

Euphausiids stand out as the most important group in terms of transferring energy from plankton to top trophic levels in the NCC, CGOA, and sWAP ecosystems. Euphausiids exert the largest footprint on system production and have the greatest reach, transferring the greatest amount of energy to higher consumer groups. On GB where euphausiids are a minor component of the community, mesozooplankton are most important.

Planktivorous forage fishes are also an important link between plankton production and top predators in shelf ecosystems (e.g., Cury et al., 2002). Processes that affect forage fish can exert a strong regulating influence on upper trophic levels. Forage fish have relatively large footprints in all four ecosystems (1–2% of total system production), and their large reach shows them to be an important prey group in the NCC and the CGOA (Figure 2). On Georges Bank, however, demersal fishes are the more important fish group in terms energy transfer up the food web.

In the NCC, gelatinous zooplankton have a particularly large footprint on system production—much larger than in the other systems. Large scyphozoan jellyfish such as the sea nettle (*Chrysaora fuscecens*) can attain very high densities during late summer months (Suchman et al., 2012). They also have an apparently large reach, though much of it can be attributed to predation among the different classes of gelatinous zooplankton (e.g., larger jellyfish preying upon salps and larvaceans). If large jellyfish are considered separately, their footprint is almost 4% of total system production while their contribution back to the system represents only 0.05% of total consumer production in the system. In this system, jellyfish might be considered a trophic dead end: they consume much more in comparison to what they return to the ecosystem.

Table 2. Model-derived mean annual production rates (t C km^{-2} yr^{-1}).

	NCC	CGOA	GB	sWAP
Phytoplankton	439.58 [a]	300.00	344 [b]	190.88
Zooplankton	139.79 [a]	85.53	136 [b]	50.29
Fish	10.77 [a]	5.53	4 [b]	0.41
Benthic invertebrates	28.71 [a]	14.47	39 [b]	0.88
Seabirds	0.0022 [a]	0.0036	0.0010 [c]	0.0003
Marine mammals	0.0088 [a]	0.0064	0.0054 [c]	0.0025
Fisheries	0.58 [a]	0.32	0.54	–

[a] Annualized from an upwelling season model (Ruzicka et al., 2012); local production scaled based on observation that 75% of annual primary production occurs in upwelling season; migratory species scaled based on fraction of annual residence
[b] From Collie et al. (2009), their Table 2
[c] From Link et al. (2006), their Appendix A
NCC = Northern California Current. CGOA = Central Gulf of Alaska.
GB = Georges Bank. sWAP = Southwestern Antarctic Peninsula

Table 3. Ecosystem-scale Footprint and Reach metrics of mid-trophic level groups.
Footprint = percentage of total system production supporting each consumer group.
Reach = percentage of total system consumer production that passes through each mid-trophic level group.
(Flows to and from detritus groups excluded.) (See Figure 3).

	NCC Footprint	NCC Reach	CGOA Footprint	CGOA Reach	GB Footprint	GB Reach	sWAP Footprint	sWAP Reach
Macro-zooplankton	3.58	0.49	0.71	0.11	2.57	0.44	2.00	0.23
Euphausiids	7.72	1.28	8.12	1.48	–	–	3.28	0.53
Gelatinous zooplankton	5.89	0.64	0.48	0.07	0.34	0.05	0.14	0.02
Cephalopods	0.29	0.01	0.43	0.03	–	–	0.17	0.00
Forage fishes	1.73	0.16	1.96	0.18	1.06	0.03	1.17	0.05
Demersal fishes	0.20	0.02	0.13	0.02	0.54	0.09	0.07	0.00
Benthic invertebrates*	1.01	1.34	2.06	3.44	6.23	0.94	0.00	0.03

*Reach in excess of footprint represents detritus feeding and recycling of "lost production" back into the food web
NCC = Northern California Current. CGOA = Central Gulf of Alaska. GB = Georges Bank. sWAP = Southwestern Antarctic Peninsula

Food Web Efficiency (Figure 4)

The NCC and the CGOA are significant producers of forage fishes, producing almost twice the biomass of small planktivorous fish per unit of phytoplankton production than the GB and sWAP ecosystems. The NCC is also a large producer of "piscivorous" fishes, such as Pacific hake (*Merluccius productus*), that have mixed diets of fish and euphausiids (Miller et al., 2010). Omnivory across trophic levels may contribute to the higher efficiency of fishery production in the NCC. On Georges Bank,

more of the energy in the system supports the production of demersal fishes, for example, cod (*G. morhua*) and haddock (*M. aeglefinus*), than production of pelagic fishes.

Structural Scenarios

Forage Fishes (Small Pelagic Planktivores)

In the Northern California Current model, doubling consumption by forage fishes (sardine, anchovy, herring, smelts) directly benefitted groups that prey directly upon forage fish: seabirds, baleen

and odontocete whales, and pinnipeds (Figure 5a). Seabirds in particular benefited, and competitor groups (piscivorous fishes, demersal fishes, squid) were negatively impacted. While piscivorous fishes (dominated by Pacific hake) should be expected to benefit directly from increased forage fish abundance, there is a high degree of omnivory in the NCC where piscivorous fish also prey heavily upon euphausiids (Miller et al., 2010). This scenario indicates that any benefit to Pacific hake from increased forage fish abundance may be more than offset by
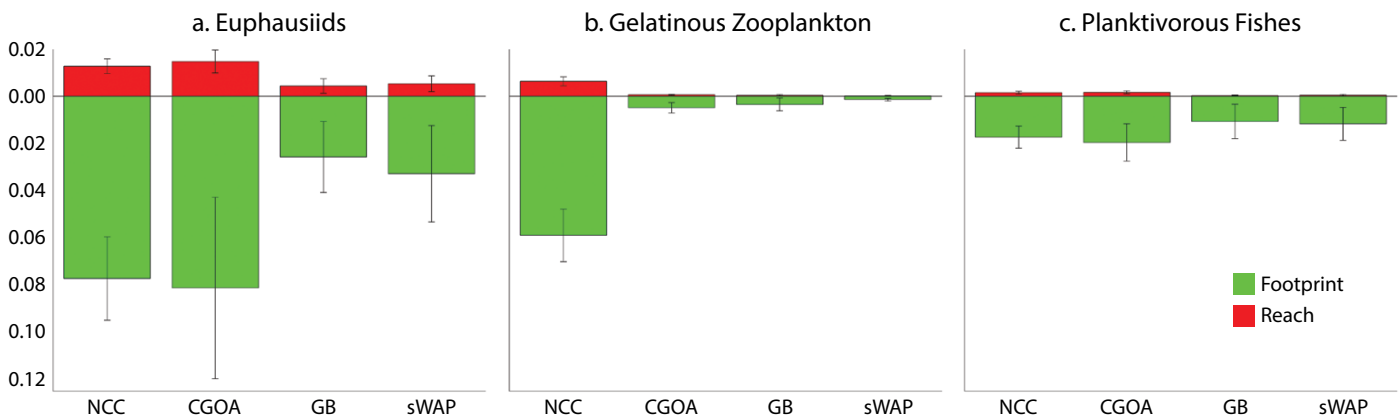

Figure 3. Footprint and reach metrics for three functional groups: (a) euphausiids (macrozooplankton on Georges Bank), (b) gelatinous zooplankton, and (c) planktivorous fish (forage fish). Green bars are the footprints, the fraction of total system production consumed by the group of interest. Red bars are the reach, the fraction of total system consumer production that is produced by (or passes through) the group of interest. (See Table 3.) NCC = Northern California Current. CGOA = Central Gulf of Alaska. GB = Georges Bank. sWAP = Southwestern Antarctic Peninsula.
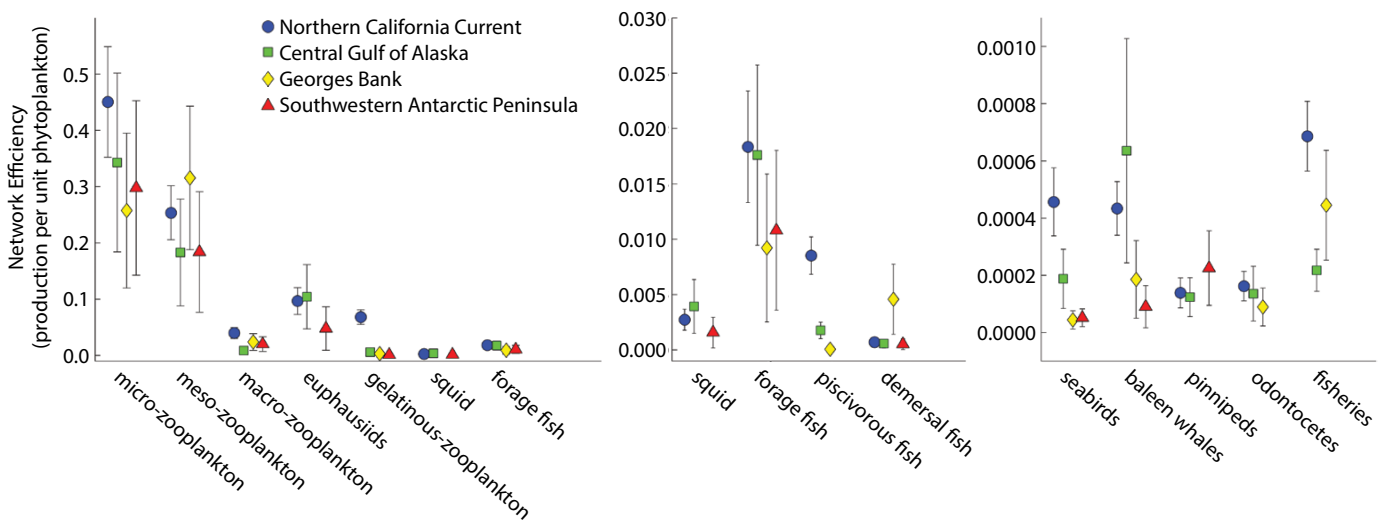

Figure 4. Network (food web) efficiency for the production of specific functional groups. Values represent the amount of each group produced per unit of phytoplankton production. Note the large changes of scale between lower trophic level (left), mid-trophic level (center), and top trophic level groups (right). (Production supported by nutrient and detritus recycling is not included.)

increased competition for euphausiids.

In the Central Gulf of Alaska, forage fish abundance (walleye pollock, herring, capelin, eulachon, sandlance, myctophids) could only be increased by about 60% (Figure 5b). Prey resources were insufficient to support more planktivores without restructuring trophic relationships within the food web or increasing food web efficiency. In contrast to the NCC, most top predators suffered in this scenario: only pinnipeds benefited. Why this would be so may be explained by the response of squid, which are a more important energy transfer node in the CGOA model (see Table 3). Increased competition with planktivorous fishes reduces realized squid production and the efficiency of energy transfer to seabird and mammal predators.

On Georges Bank, doubling forage fish abundance (Atlantic herring) had a smaller effect than in the NCC or the CGOA (Figure 5c). Odontocetes benefited directly from increased prey abundance while baleen whales and demersal fishes suffered from increased competition with forage fish for zooplankton.

In the southwestern Antarctic Peninsula area, the planktivorous fishes (nototheniids, myctophids) could only increase by about 60% without restructuring trophic relationships or increasing food web efficiency (Figure 5d). No group benefited substantially. The sWAP groups most impacted were those that prey heavily upon euphausiids: penguins, crabeater seals (*Lobodon carcinophagus*), squid, and baleen whales.

Gelatinous Zooplankton (Larvaceans, Salps, Ctenophores, Large Scyphozoans)

In the NCC, all groups were impacted negatively by doubling gelatinous zooplankton abundance (Figure 6a). As

the footprint and reach metrics show (Table 3), gelatinous zooplankton consume much of the total system production but pass relatively little upward in the NCC food web. The impact of gelatinous zooplankton was much stronger here than in the other US GLOBEC ecosystems. In the CGOA, except for an increase in demersal fish production, increased gelatinous zooplankton abundance had very little effect (Figure 6b). Smaller forms (salps, larvaceans, ctenophores) are a large component of sablefish (*Anoplopoma fimbria*) diet; increased sablefish grazing upon gelatinous zooplankton is responsible for the overall increase in CGOA demersal fish production. On GB, the most heavily impacted groups suffered 8% reductions in production (Figure 6c). In the sWAP, the most heavily impacted groups (pelagic fishes and squid, and the pinnipeds that prey upon them) suffered only
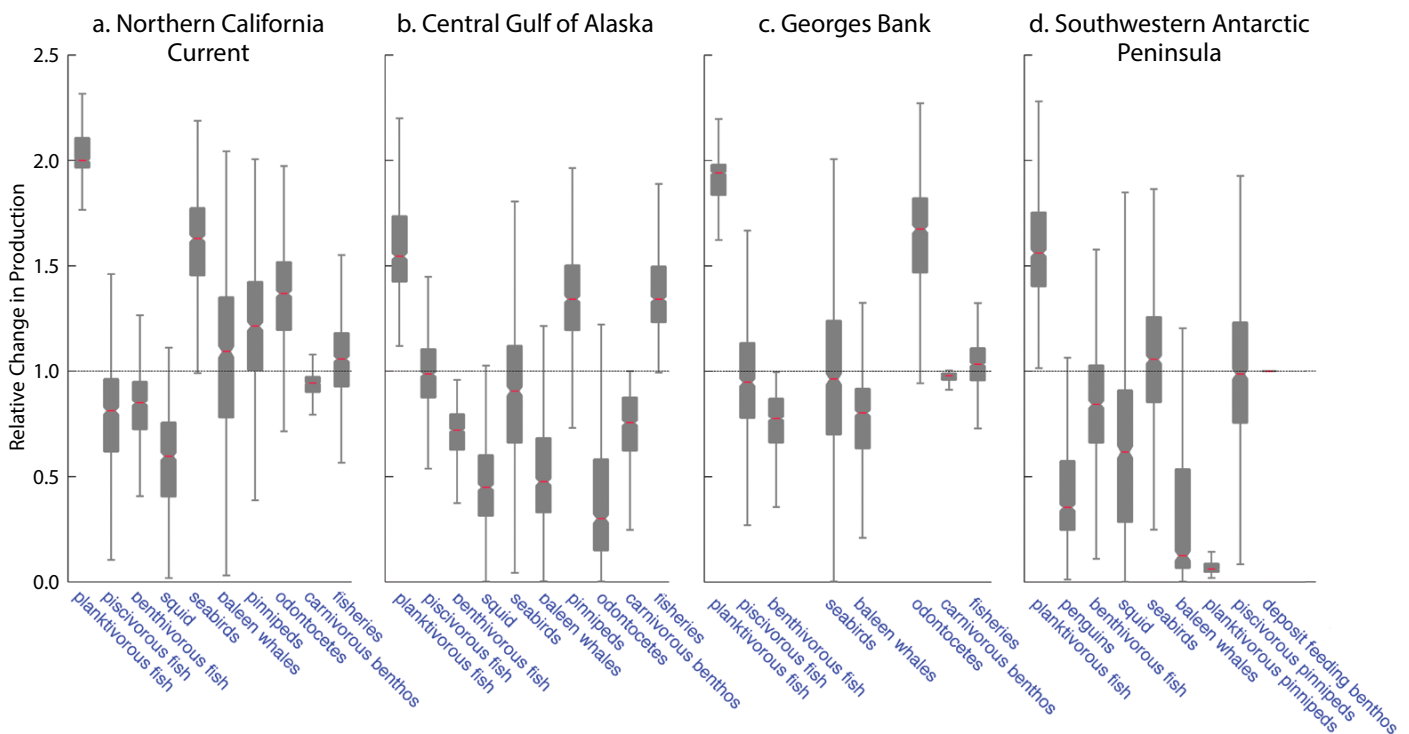

Figure 5. Structural scenario showing effects of doubling the abundance of planktivorous fishes (forage fishes) in each US GLOBEC system. Scenario effects are expressed as functional group production in the scenario-modified model relative to production in the original base model: $\Delta P = P_{scenario\ model} / P_{base\ model}$.

4% reductions in production.

A potential future sWAP scenario may be considered in which warming temperature, decreasing sea ice, and a shift in the phytoplankton community toward smaller cells favors salp production over krill (Loeb et al., 1997; Ducklow et al., 2007). Redirection of phytoplankton production away from krill by 50% and toward salps would lead to reductions in the production of intermediate and top trophic levels of 20–30% (Figure 6d). Such a salp-dominated system would not support the seabird and mammal populations we observe today (Ballerini et al., 2013).

Baleen Whales

In all four ecosystems, a fivefold increase in baleen whale abundance had much smaller effects than did doubling of forage fish abundance or gelatinous zooplankton abundance (Figure 7a–d). Piscivorous fishes in the CGOA have diets richer in small pelagic fishes than they do in the NCC or GB, and piscivores in the CGOA were more heavily impacted by direct competition with baleen whales than in the other regions. Increased baleen whale abundance had a smaller impact in the sWAP ecosystem than in the other ecosystems. Seabirds, penguins, and pinnipeds were the most heavily impacted sWAP groups, with all exhibiting a small decline in production rate.

Dynamic Scenarios

The effects of increased forage fish abundance are evaluated as the relative change in biomasses in the non-altered base runs and the perturbed scenario runs. Figure 8 shows biomass time series for two of the most affected groups, seabirds and odontocete whales. There are some notable differences between the immediate effects of the forage fish perturbation shown by the structural scenario and the long-term effects shown by the dynamic scenario. These are especially evident among the upper trophic levels. For example, odontocetes in the CGOA are strongly and negatively impacted over the short term due to competition between forage fish and the main prey of odontocetes in the CGOA model, squid. Over the long term, squid and odontocete populations adjust to higher forage fish abundance and are much less strongly impacted.

DISCUSSION

The simple comparative analysis presented here has focused on differences in the trophic network structure. Comparison of group footprint and reach metrics (Figure 3, Table 3) show euphausiids and forage fish to be important nodes for the transfer of energy to higher trophic levels in most ecosystems. Scenario analyses show that variability in forage fish abundance has large effects in all four ecosystems. However, some
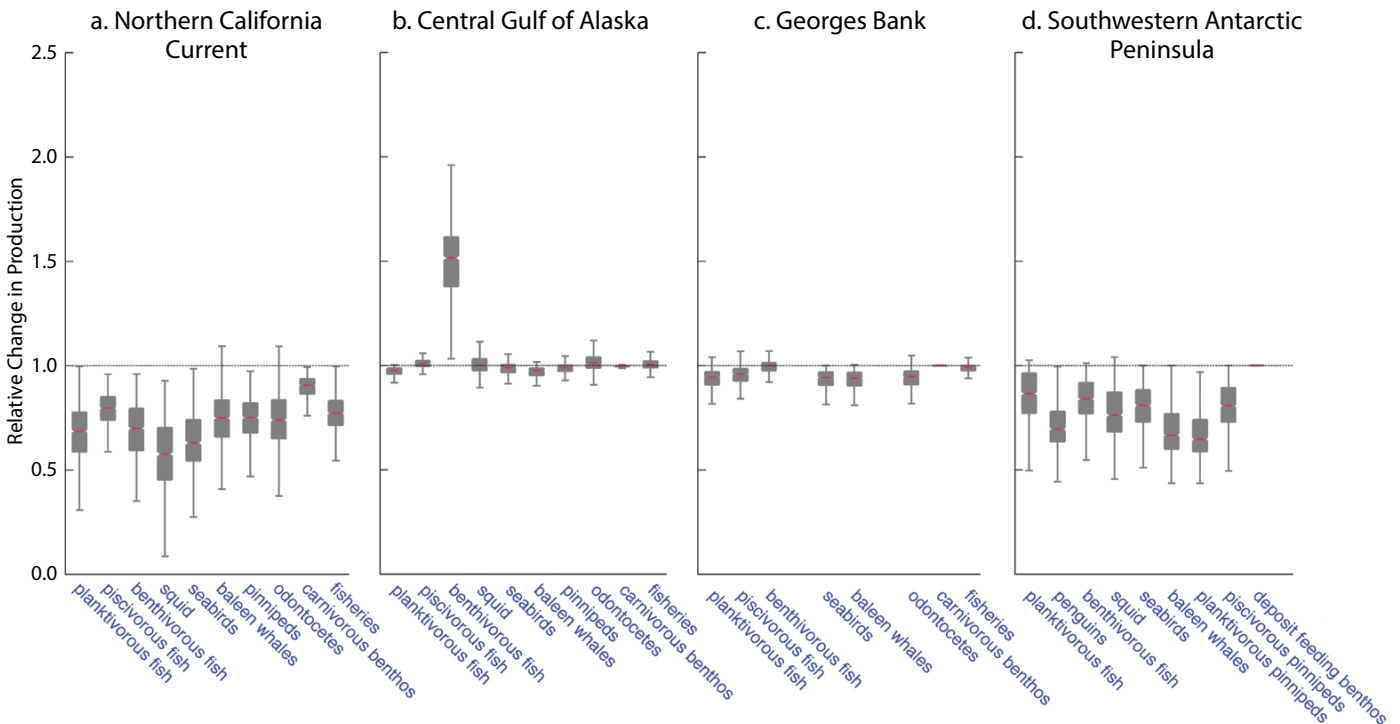

Figure 6. Structural scenario showing effects of doubling the abundance of gelatinous zooplankton in each US GLOBEC system. The Southwestern Antarctic Peninsula scenario shows the effect of a 50% transfer of phytoplankton production from euphausiids toward salps.

differences between ecosystems are apparent. On Georges Bank, demersal fishes are the most important fish group in terms energy transfer up the food web. Along the Central Gulf of Alaska, squid constitute an important energy transfer node, more so than in the other ecosystems, as evidenced by the comparatively small impact of a doubling of forage fish abundance in the CGOA dynamic scenario. In the Northern California Current, large scyphozoan jellyfish are important consumers of plankton production but provide little support to higher trophic level production.

The development of ecosystem-level models requires consideration of three conceptual design elements: (1) model structure, (2) functional relations among ecosystem components, and (3) choice of parameter values. Model structure includes both the resolution—the complexity or "size"—of the model in terms of components and the relevant biological and physical processes. Biological processes of particular concern include those that define nutrient recycling rates (e.g., detritus and bacterial dynamics), define connectivity with neighboring ecosystems at upper trophic levels (migration), and contribute to population size and structure and community composition (recruitment dynamics). Physical processes that must be considered are the local processes that drive nutrient input and support primary production (e.g., vertical mixing and upwelling) and the regional-scale processes that regulate lower trophic level connectivity with neighboring ecosystems ("horizontal advection bottom-up forcing"; Di Lorenzo et al., 2013, in this issue). Food web models that incorporate basic physical processes are still in their relative infancy. Examples include the Atlantis class of models currently under development (Horne et al., 2010; Fulton et al., 2011); these "virtual world" models combine food web, oceanographic, biogeochemical, and economic submodels.

End-to-end ecosystem models are at the high end of the scale of model complexity in terms of the number of parameters that must be defined. Biomass, diet, physiological rates, fishery harvest and discard, and functional response relationships must be defined for each group. Some parameters are well known, some are interpolated to maintain internal consistency, and some are informed assumptions. Each parameter value has associated uncertainty and natural variability in time and across space. In order to quantify confidence in model-derived metrics and scenarios, the propagation of uncertainty and variability through the system must be accounted for, as we have done here through Monte Carlo analysis.

Each of these three conceptual levels of ecosystem model design presents its own set of inherent unknowns and technical problems. Taken together, they present a
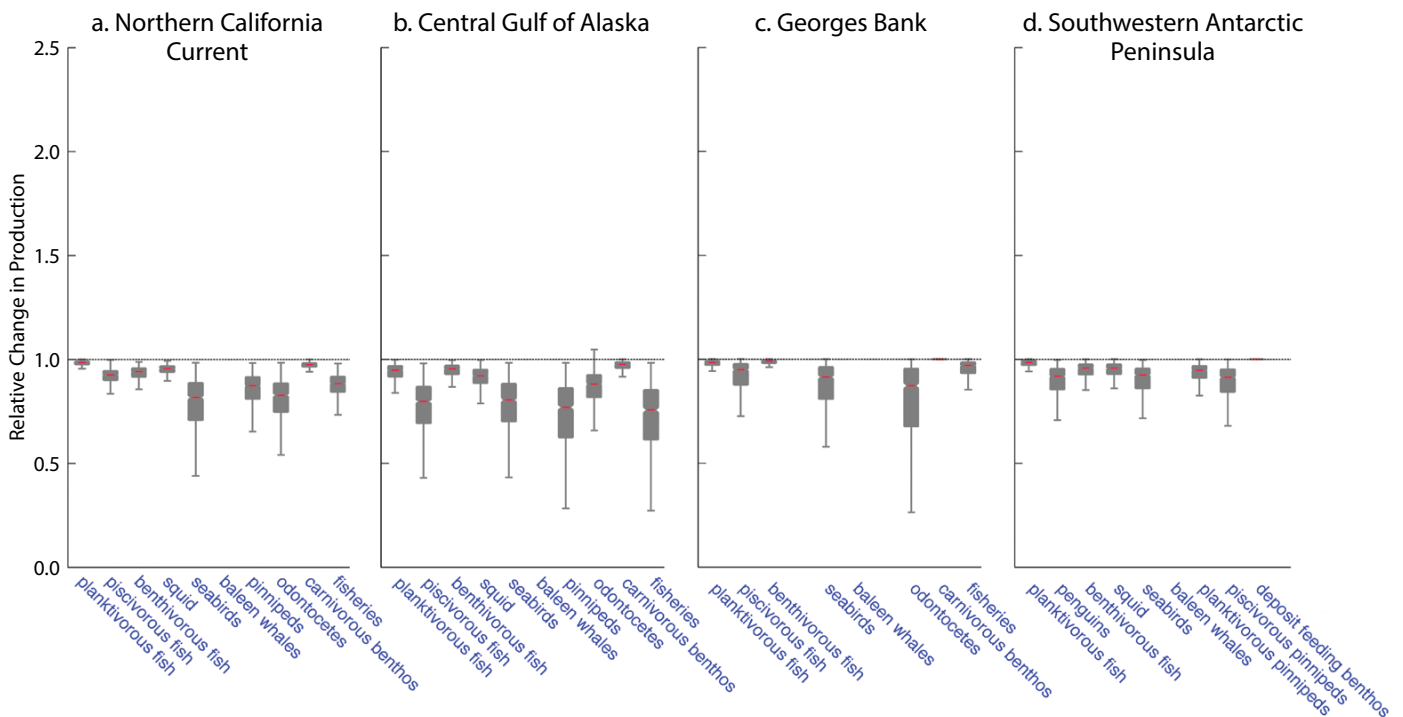

Figure 7. Structural scenario showing effects of a fivefold increase in the abundance of baleen whales in each US GLOBEC system.

daunting task to the modeler. We chose to develop models of "intermediate complexity" (Hannah et al., 2009)—a loosely defined level of structural complexity between that of four-component NPZD (nutrient-phytoplankton-zooplankton-detritus) plankton models and virtual world simulations with dozens to hundreds of components. Model components may be defined in terms of function and diet (Garrison and Link, 2000) rather than taxonomy. This is a practical way to compact the food web to a manageable size, and, more importantly, it allows different ecosystems to be compared within a standardized framework. Intermediate complexity end-to-end models offer tractability in terms of parameterization and demand for computing resources. The intermediate approach allows us to consider uncertainty and complexity at a feasible scale so that multiple hypotheses regarding ecosystem behavior under perturbation (climate change, natural resource extraction) can be considered

without imposing strong assumptions that could lead to misguided conclusions.

Gaichas et al. (2009) have identified additional challenges that must be addressed for meaningful comparative studies using food web models. Models used in comparative studies are likely built under different standards of precision and data quality and are likely to use different assumptions where data are missing. Interpretation of ecosystem differences must consider differences in the time period. Comparison of models representing different time periods may change our view of differences in large-scale patterns. Comparison of network metrics derived from models with different levels of group aggregation is difficult and may be counterproductive. The standard food web network metrics produced by popular modeling platforms (e.g., connectance, omnivory, trophic linkage density) are highly correlated with the number of model groups. Finally, differences in spatial domain become important

when the arbitrary definition of a model's boundary affects the relative importance of different habitats contained within that boundary. Arbitrary habitat differences may affect the relative importance of individual groups or of large-scale processes that differ between habitats, including the relative importance of pelagic vs. benthic processes.

CONCLUSION

Multi-species, end-to-end ecosystem models are useful tools for understanding the processes that drive ecosystem variability. They are also tools for assessing the health of an ecosystem as an ecological unit (Integrated Ecosystem Assessment) and are necessary for testing the impacts of alternate management policies across entire marine communities (ecosystem-based management; Levin et al., 2009; Fogarty et al., 2013, in this issue). With the combined efforts of integrated data collection programs like GLOBEC and
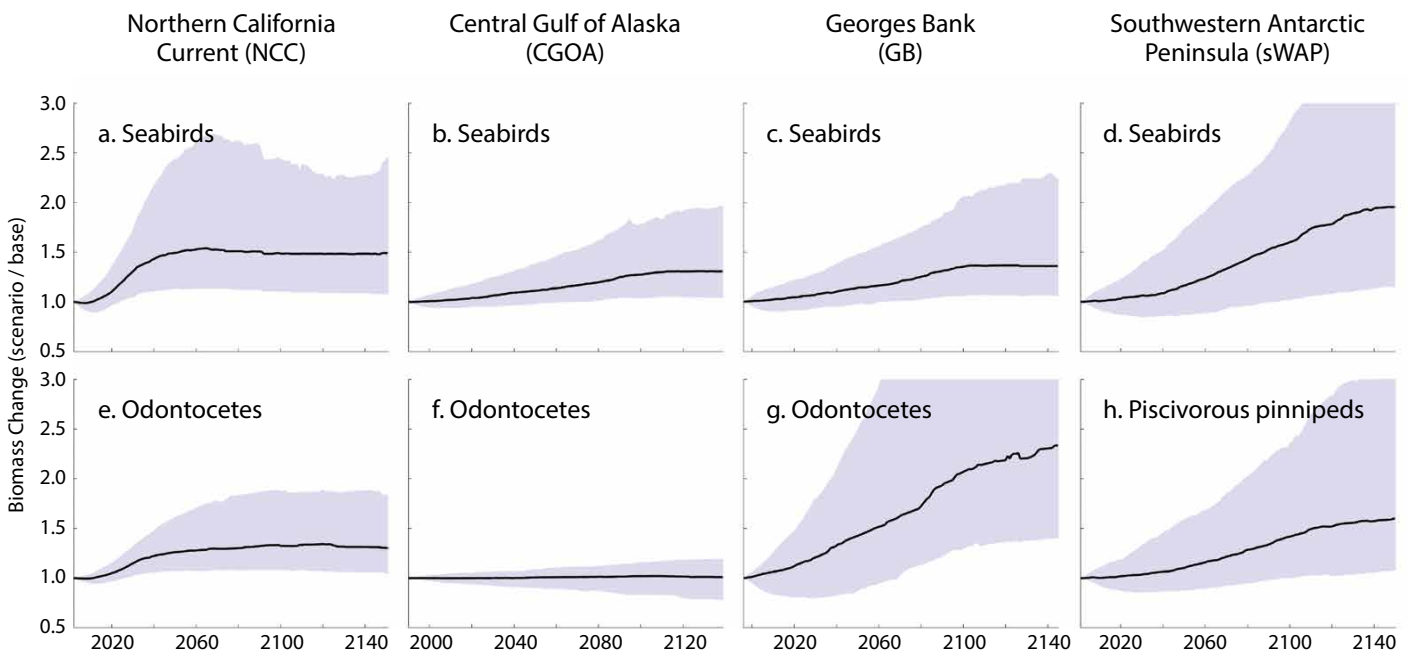

Figure 8. Dynamic scenario showing the evolution of the seabirds and odontocete biomasses over time following a doubling of planktivorous (forage) fish abundance in each US GLOBEC system. Plots show the change in biomass of the perturbed, scenario model relative to the unchanged, base model ($\Delta B = B_{scenario\ model} / B_{base\ model}$). Shaded areas cover the 25th through 75th percentiles of scenarios run on randomly drawn models: 465 NCC models, 419 CGOA models, 257 GB models, and 468 sWAP models.

comparative modeling activities such as those presented here, more detailed models of specific processes may be developed to improve understanding of ecosystem structure, mechanics, and response to environmental variability and anthropogenic perturbation.

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