



Interannual variability in the Northern California Current food web structure: Changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish

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ABSTRACT

The Northern California Current (NCC) is a seasonally productive and open ecosystem. It is home to both a diverse endemic community and to seasonally transient species. Productivity and food web structure vary seasonally, interannually, and decadal due to variability in coastal upwelling, climate-scale physical processes, and the migratory species entering the system. The composition of the pelagic community varies between years, including changes to mid-trophic level groups that represent alternate energy-transfer pathways between lower and upper trophic levels (forage fishes, euphausiids, jellyfish). Multiple data sets, including annual spring and summer mesoscale surveys of the zooplankton, pelagic fish, and seabird communities, were used to infer NCC trophic network arrangements and develop end-to-end models for each of the 2003–2007 upwelling seasons. Each model was used to quantify the interannual variability in energy-transfer efficiency from bottom to top trophic levels. When each model was driven under an identical nutrient input rate, substantial differences in the energy available to each functional group were evident. Scenario analyses were used to examine the roles of forage fishes, euphausiids, and jellyfish (small gelatinous zooplankton and large carnivorous jellyfish) as alternate energy transfer pathways. Euphausiids were the more important energy transfer pathway; a large proportion of the lower trophic production consumed was transferred to higher trophic levels. In contrast, jellyfish acted as a production loss pathway; little of the production consumed was passed upwards. Analysis of the range of ecosystem states observed interannually and understanding system sensitivity to variability among key trophic groups improves our ability to predict NCC ecosystem response to short- and long-term environmental change.

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1. Introduction

The Northern California Current (NCC) extends from roughly Vancouver Island, British Columbia in the north to Cape Mendocino, California, in the south. Seasonally, it is a highly productive upwelling ecosystem. Upwelling favorable winds predominate following the spring transition in March–April and continue through October–November (Strub et al., 1987). Lower trophic level production in the NCC is closely tied to the strength, timing, and duration of seasonal upwelling and nutrient input along the coastline (Checkley and Barth, 2009).

The NCC also lies within a zoogeographic transition zone; the pelagic community (from zooplankton to fish, birds, and mammals)

is a mix of subarctic and subtropical species (Brodeur et al., 2003; Peterson et al., 2002). During the upwelling season, it is home to a diverse pelagic fish community including both year-round resident species (anchovies, smelts, herring) and transient species migrating from the south (sardines, hake, mackerels). The composition of the pelagic community across most trophic levels varies on interannual to interdecadal time scales due to variation in local production and forcing by basin-scale physical processes (e.g., El Niño, Pacific Decadal Oscillation) and associated movement of large water masses (Emmett et al., 2006; Keister and Peterson, 2003). The structure of the NCC food web and the efficiency of energy transfer from producers to top trophic levels also varies interannually (Brodeur and Pearcy, 1992; Litz et al., 2010).

Three mid-trophic level groups are of particular importance to the structure and function of the pelagic NCC food web. (1) Forage fishes: In coastal upwelling systems, small pelagic forage fishes

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(anchovies, sardines, herring) are an important link between plankton production and upper trophic levels. They may even represent a bottleneck, limiting production at top trophic levels which become closely tied to factors that effect forage fishes (“wasp-waist” control; Bakun, 2006; Cury et al., 2000; Rice, 1995). (2) Euphausiids: In the NCC, euphausiids are dominant prey species for many of the most abundant fish species, including the most abundant piscivores (Brodeur et al., 1987; Miller et al., 2010). They represent an important alternative energy pathway for many otherwise piscivorous pelagic fishes, reducing the vulnerability of top consumers to variability in forage fish abundance. (3) Jellyfish: Large carnivorous jellyfish (scyphomedusae, hydromedusae) have high growth rates and often obtain a biomass comparable to that of forage fish during the summer season (Suchman and Brodeur, 2005). The large jellyfish also have a high degree of dietary overlap with forage fishes in the NCC (Brodeur et al., 2008; Suchman et al., 2008). Small gelatinous zooplankton (larvaceans, salps, ctenophores) also have high consumption rates but have been less well studied in the NCC. Being subject to little predation relative to other groups, the large and small jellyfish may represent a trophic “dead-end” and a loss-pathway for zooplankton production.

Our first goal was to characterize how trophic network structure within the NCC can vary between consecutive years and the effect that these differences may have on the efficiency of energy transfer through the system. Annual spring and summer mesoscale surveys of the zooplankton, pelagic fish, and seabird communities were used to infer the NCC trophic network structure for each upwelling season of years 2003–2007. End-to-end models constructed for each year were used to estimate interannual differences in the energy flow to each functional group and the energy transfer efficiency through the food web. Our second goal was to examine the roles of forage fishes, euphausiids, and jellyfish (small gelatinous zooplankton and large carnivorous jellyfish) as energy transfer pathways between plankton production and top trophic level predators. The importance of each within the system as consumers and as producers was quantified for each modeled year. Scenario analyses were used to examine system response across all trophic levels to variability in the abundance of each group.

2. Data and models

2.1. Inferred interannual food webs

The Northern California Current model domain (Fig. 1) extends from the southern Oregon border (42.00°N) to Cape Flattery, Washington (48.34°N) and cross-shelf between the 1- and 183-m isobaths (26,000 km²). We developed a series of independent, end-to-end models of energy flow through the Northern California Current ecosystem (NCC) representing five consecutive upwelling seasons: April–September, 2003–2007. Models were considered independent in that each was defined by the pelagic community observed each season and not as an evolution of the previous year’s model over time.

Satellite data, pelagic survey data, fishery data, local diet studies, marine mammal assessments, and bottom-trawl survey reports were used to infer the trophic network structure (food web) during each season. Each trophic network model was initially assembled using ECOPATH algorithms (Walters et al., 1997, Christensen and Walters, 2004) as revisions of the generalized seasonal models described in Ruzicka et al. (2007). ECOPATH models map the “top-down” consumption demand through the system from a set of ecosystem givens: functional group biomasses, physiological rates, and diet preferences. The top-down ECOPATH solutions were transformed to end-to-end models that map production-flow upwards through the food web from the input of nutrients to the

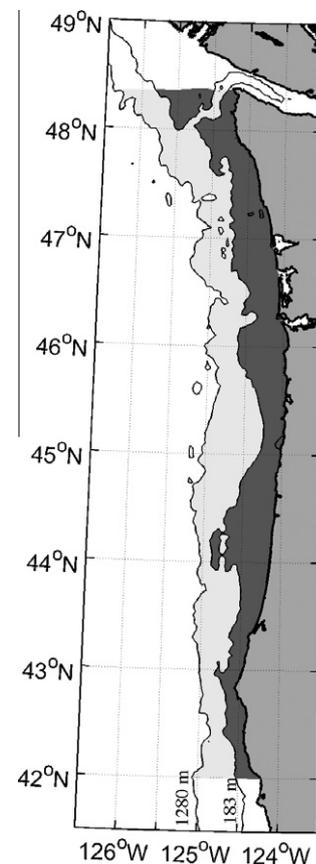


Fig. 1. The spatial domain (dark gray) of the Northern California Current food web models over the continental shelf (1–183 m isobaths) of Oregon and Washington, USA.

production of top predators and fisheries and back to recycled nutrients as described by Steele and Ruzicka (2011).

2.1.1. Model parameterization and community composition

Each fully resolved model included 77 functional groups. For the present analyses, we aggregated the balanced-system into 22 functional groups (Table A.1) using the biomass-weighted mean physiological rates (Table A.2) and mean diet (Table A.3) of the individual sub-groups. Here, we briefly summarize the data and data processing used to construct the models. Additional details for each functional group are provided in Appendix A.

Phytoplankton concentration was estimated from 8-day composite SeaWiFS Chl data (April–September) and converted to vertically-integrated biomass using standardized conversion factors. Phytoplankton biomass was divided into large (diatom; >10 μm) and small (flagellate; ≤10 μm) size-classes based upon size-fractionated chlorophyll observations across the Oregon shelf (W. Peterson, NWFSC, unpub. data).

Seasonal zooplankton, seabird, and pelagic fish surveys sponsored by the Bonneville Power Administration (BPA) provided time-series data on the spring and summer pelagic community composition over the NCC shelf and upper-slope. Regional daytime surveys sampled 9 cross-shelf transects between 44.6°N and 48.3°N during May, June, and September each year from 2003 and 2007 (Brodeur et al., 2005). Nighttime surveys sampled 2 cross-shelf transects between 46.1°N and 46.6°N approximately bi-weekly in early (May–June) and late summer (July–August) each year. Both pelagic fish surveys sampled the upper 20 m of the water column using an 18 × 30 m Nordic Rope Trawl (Emmett et al., 2006). Zooplankton abundance was estimated from samples taken at each station of the daytime survey using a 1-m diameter, 335-μm mesh ring-net

towed obliquely from 20 to 30 m to the surface (Morgan et al., 2005; Schabetsberger et al., 2003). Regional mean fish and zooplankton abundances were estimated using the method of Pennington (1996) for log-normally distributed survey data that included zero-catch stations. May and June seabird abundance and distribution was estimated from standardized visual dawn surveys conducted along each daylight transect.

Information about demersal fish biomass was acquired from a combination of coast-wide stock assessments (e.g., Kaplan and Helser, 2007) and NOAA bottom-trawl surveys (e.g., Keller et al., 2008). Marine mammal biomass was obtained from coast-wide stock assessments (Angliss and Allen, 2009; Carretta et al., 2007) and local surveys (Brown et al., 2005; Calambokidis et al., 2002; Pitcher et al., 2007; Scordino, 2006).

Model biomass units were tons wet weight per km² and rate units were per year. Because jellies have a higher water content than other groups (Shenker, 1985), their importance may be overestimated in a model expressed in wet-weight units. Therefore, the jellyfish biomass was scaled so that a unit of small gelatinous zooplankton biomass and a unit of large carnivorous jellyfish biomass had the same water content as that of the crustacean zooplankton and pelagic fishes, respectively (see Appendix A).

The physiological rate parameters used by ECOPATH are the biomass-specific production rate P/B (y^{-1}), biomass-specific consumption rate Q/B (y^{-1}), production efficiency P/Q , and assimilation efficiency AE . Physiological rate parameters (Table A.2) were taken from the literature or borrowed from other trophic models of the northeast-Pacific coastal margin (Aydin et al., 2007; Field et al., 2006; Guénette, 2005; Preikshot, 2005) (see Appendix A). Fish, large jellyfish, and seabird diet information was obtained from local NCC studies to the extent possible (Brodeur et al., 1987; Miller and Brodeur, 2007; Suchman et al., 2008; Suntsov and Brodeur, 2008; Daly et al., 2009; Miller et al., 2010). Diet sources for other NCC species were from the same sources reviewed in Dufault et al. (2009). The aggregated diet matrix is provided in Table A.3.

The models included two fisheries: commercial and recreational. Quarterly commercial fisheries data were provided by the Pacific Coast Fisheries Information Network (PacFIN; <http://pacfin.psmfc.org/>). Bi-monthly recreational fisheries data were acquired from the Pacific States Marine Recreational Fisheries Information Network (RecFIN; <http://www.recfin.org/>). Discard rates were assumed to be 10% of landings for both the commercial and recreational fisheries.

2.2. End-to-end models

We developed an end-to-end model from each balanced, steady-state ECOPATH model as described in Steele (2009) and Steele and Ruzicka (2011). The end-to-end production matrix (Table A.5) partitions the fate of biomass flowing into each functional group box between egestion losses (feces detritus), metabolic costs (ammonium production), predation by each consumer group, removal by fisheries, and unconsumed production (“surplus” production detritus). We could also account for emigration and biomass accumulation within the production matrix, but we have assumed a steady-state system with no biomass accumulation and no migration in or out of the system during the model period. Detritus and metabolism terms were calculated directly from the ECOPATH model:

$$\text{feces detritus} = 1 - AE,$$

$$\text{“surplus” production detritus} = (1 - EE) \cdot P/Q,$$

$$\text{metabolism } \text{NH}_4^+ = 1 - P/Q - \text{feces}.$$

EE is the ECOPATH ecotrophic efficiency, the fraction of a group’s production that is consumed by another group, emigrates (or immigrates) across the model domain boundary, or contributes to the growth of the group. EE is the fraction of a group’s production that does not flow to detritus as “surplus” production. Detritus and NH_4^+ production were divided between pelagic and benthic pools (Table A.4).

System production was driven by nitrate added to the system via upwelling and by nutrient recycling by consumer group metabolism and detritus remineralization by bacteria. 0.25 of the benthic detritus production was remineralized to the sub-surface NH_4^+ pool and 0.66 of the pelagic detritus production was remineralized to the surface NH_4^+ pool. Nitrate and ammonium uptake was preferentially differentiated between the two phytoplankton size classes. We assumed that nitrate was taken up mainly by the large, bloom-forming diatoms and that ammonium was taken up mainly by the smaller phytoplankton which have a higher affinity for ammonium (e.g., Wilkerson et al., 2006). 0.8 of the NO_3^- production was directed to large phytoplankton, and 0.8 of the NH_4^+ production was directed to small phytoplankton. We also allowed for the direct oxidation of ammonium to nitrate; a fraction of 0.1 of the pelagic NH_4^+ production was directed to NO_3^- . At present, the nutrient cycling parameters are working assumptions with broad uncertainty.

In order to include nutrient cycling within a model based upon a wet weight currency, nutrients were expressed as live weight equivalents. Here we rescaled nitrate input into the system to wet weight using a scaling factor of 0.7 g live weight mmole NO_3^- . This scaling factor was based upon values of the Redfield ratio (6.625 mmole C mmole N^{-1}), the atomic weight of carbon (12 mg C mmole C^{-1}), and the estimated carbon content of fish on Georges Bank (8.8 mg live weight mg C^{-1} ; Steele et al., 2007).

2.3. Model analyses and metrics

2.3.1. Steady-state, interannual models

To make a broad-scale comparison of ecosystem structure between years, the steady-state, interannual models were used to estimate (1) system size in terms of production and the distribution of production across trophic levels, (2) total consumer demand upon primary producer and detritus production, and (3) the relative importance of targeted functional groups for transferring energy to higher trophic levels.

We characterized the importance of each functional group as both producer and consumer with the two non-dimensional metrics: “reach” and “footprint.” The importance of any functional group t to higher trophic levels was expressed by its “reach”: the fraction of a consumer’s production that originated with (or passed through) group t via all direct and indirect pathways. Alternatively, group t ’s trophic impact upon lower trophic levels is expressed by its “footprint”: the fraction of each producer group’s total production supporting consumer group t via all direct and indirect pathways.

Reach: For all trophic interactions between producers p and consumers c , matrix T (dimensions p by c) representing the fraction of energy passing upwards through each possible trophic linkage that originated with, or passed through, producer t may be estimated through iteration as

$$T = \theta \cdot D \quad (1)$$

Reach vector θ is the fractional contribution of group t to the diet of each consumer c . θ is initialized as $\theta = D'_p$, the transpose of row $p = t$ in diet matrix D (dimensions p by c). The diet fractions of each consumer are renormalized to sum to 1 after setting all $D_{cc} = 0$, and the energy contribution of group t to itself is defined as $\theta_t = 1$. In each subsequent iteration of Eq. (1), T represents the contribution of group t to the diet of c through direct consumption

and through indirect pathways up to length $l = \text{iteration count}$, and $\theta = (\sum T_c)$ summing across all c . We performed a maximum of $l = 1000$ iterations with the progression halted once no element of θ differed by more than 0.0001 from the previous iteration.

Footprint: The contribution of each producer p to the diet of consumer $c = t$ via each possible trophic link in the web may be represented by matrix K (dimensions p by c) and estimated through iteration as

$$K = \tau \cdot D \quad (2)$$

τ is initialized as $\tau = D'_{cc}$, the transposed vector representing the proportion of each producer p in the diet of consumer $c = t$ via direct consumption. The diet fractions of each consumer are renormalized to sum to 1 after setting all $D_{cc} = 0$, and the energy contribution of group t to itself is defined as $\tau_t = 1$. In each subsequent iteration of Eq. (2), τ represents the contribution of each p to the diet of t through direct and indirect pathways up to length $l = \text{iteration count}$: $\tau = (\sum K_p)$ summing across all p . The footprint of group t on each p is then estimated as

$$\phi = [(\sum C_{pt})\tau]/P \quad (3)$$

where $\sum C_{pt}$ (summed across all p) is the total consumption rate of t , and P is the production rate of each producer p , $P_p = B_p \cdot (P/B)_p$. We performed a maximum of $l = 1000$ iterations with the progression halted once no element of τ differed by more than 0.0001 from the previous iteration.

Footprint and reach can be defined broadly (i.e., the footprint upon all lower trophic levels) or precisely (i.e., the footprint upon one specific producer). For our general comparison of the roles of forage fishes, euphausiids, and gelatinous zooplankton, we adopted the broadest definitions possible, considering reach and footprint relative to total consumer production and total system production, respectively. The total system-wide reach metric of producer t is estimated relative to the production of each consumer P_c , where c excludes phytoplankton and detritus groups:

$$R_t = \sum (\theta_c \cdot P_c) / \sum P_c \quad (\text{summed across all } c). \quad (4)$$

The total system-wide footprint metric of consumer t is estimated relative to the total production of all groups p , where p excludes detritus groups:

$$F_t = \sum (\phi_p / P_p) \quad (\text{summed across all } p). \quad (5)$$

2.3.2. Alternate scenarios using end-to-end models

End-to-end models were used in Monte Carlo scenarios to investigate the propagation of model uncertainty through the food web and in targeted scenarios to investigate the effects of perturbations to energy flow through individual functional groups.

Uncertainty among physiological parameters, diet, and nutrient cycling terms were combined within the end-to-end production matrix. Following the general technique used for Gulf of Alaska and Bering Sea models (Aydin et al., 2007), the propagation of net uncertainty was investigated by randomly varying each term within the production matrix about the base model values. Each matrix element was varied randomly within $\pm 50\%$ from a uniform distribution, and 1000 possible food webs were drawn for each modeled year.

Alternate targeted scenarios were investigated using the 2006 end-to-end model following the methodology developed by Steele (2009). Energy flow through forage fishes, euphausiids, and jellyfish (small gelatinous zooplankton and large carnivorous jellyfish) was individually modified by reducing overall consumption by 20%. Surplus unconsumed prey production was distributed proportionally among all other consumers so that total predation pressure on each group remained unchanged. Scenarios were run on

1000 random food webs under an assumption of $\pm 50\%$ uncertainty about each trophic link.

3. Results

3.1. Interannual comparison of inferred food webs

A comparison of production among highly aggregated pelagic groups (Fig. 2a) showed phytoplankton production was high in 2007 and low in 2004 and 2005. At this scale of aggregation, there was little obvious variability among pelagic consumer groups (2005 being somewhat less productive). At higher resolution (Fig. 2b), the combined small gelatinous zooplankton and large carnivorous jellyfish group was the most productive among the carnivorous pelagic groups by a large margin.

System-level production ratios show how the relative sizes of phytoplankton, zooplankton, pelagic fish, and seabird groups compare between years (Table 1). Pelagic fishes and seabirds varied by more than a factor of 2 between years relative to the zooplankton and fish groups they prey upon. The NCC production ratios were not out of line with the same metrics calculated for other modeled regions, the coastal Gulf of Alaska (GoA) and Georges Bank (GB). Seabirds were between 2 and 4 times larger relative to pelagic fishes in the NCC than in the GoA and GB systems. The gelatinous zooplankton (small herbivorous and large carnivorous jellies) were up to four times larger relative to the total zooplankton production in the NCC than in the other systems, but it is known that the large jellyfish biomass can become very large in the coastal NCC in the summer months (Ruzicka et al., 2007).

Demand upon primary production in the pelagic and benthic subsystems was compared across years with the combined direct consumption of all groups relative to phytoplankton and benthic detritus production (Fig. 3). The greatest demand upon pelagic and benthic production was in 2004, and the lowest was in 2007. This inversely reflected the interannual pattern of phytoplankton production (Fig. 2a). A mismatch between phytoplankton and grazer demand was evident when comparing 2004 and 2005. Both were years of comparably low phytoplankton production but of very different demand on that production, with 2004 being the year with the second highest grazer production and 2005 the year of lowest grazer production.

Direct grazing pressure upon phytoplankton and meso-zooplankton production is shown in Table 2. A higher proportion of phytoplankton production was used (50–80%) than that of the meso-zooplankton (40–75%), largely because of micro-zooplankton grazing on phytoplankton. The interannual pattern between these two groups was different. The highest proportion of phytoplankton production was grazed in 2004 (Fig. 3), the year of lowest production (Fig. 2a). The highest proportion of meso-zooplankton production was eaten in 2007 (Fig. 4), the year of highest jellyfish production (Fig. 2b).

The importance of individual functional groups as energy transfer pathways may be expressed with the footprint and reach metrics (Table 3). Of the three groups of interest, the jellyfish had the largest footprint on system production, i.e., jellyfish (small gelatinous zooplankton and large carnivorous jellyfish) consumed the greater proportion of system production via combined direct and indirect pathways. However, jellyfish had the smallest reach, i.e., jellyfish contributed the least to the production of other groups. These observations showed the importance of jellyfish as both trophic dead-end and production-loss pathways (Figs. 5c and 6c). Forage fishes had a much smaller footprint but larger reach than jellyfish (Figs. 5a and 6a). Euphausiids had the largest reach-to-footprint ratio, showing that they were the more important group for transferring energy upward in the food web (Figs. 5b and 6b).

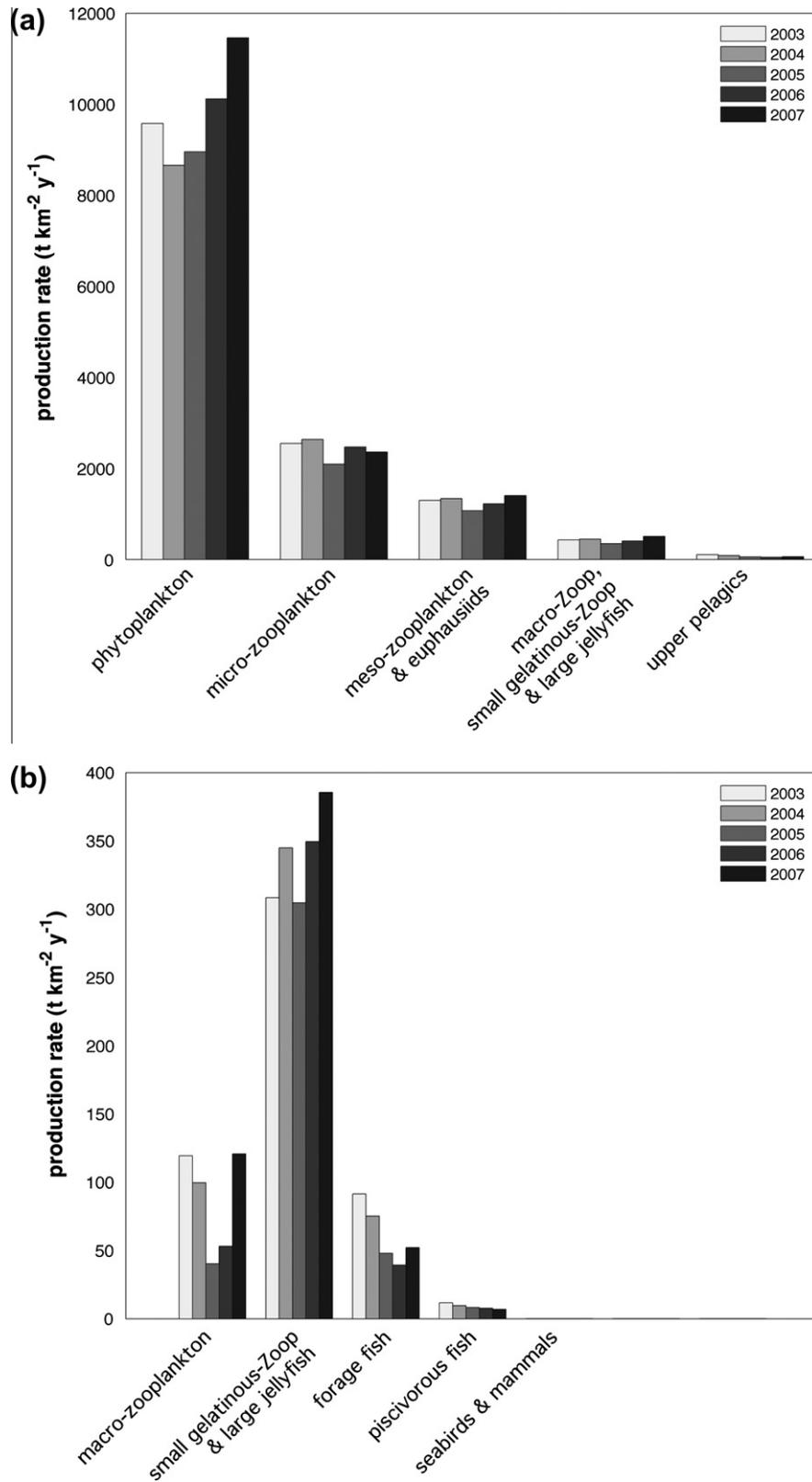


Fig. 2. Interannual comparison of production rates among pelagic functional groups as estimated by static, top-down balanced models. (a) Production rates at high level of group aggregation; (b) production rates of pelagic groups at detailed level of group resolution.

Comparison across years showed different footprint and reach patterns for each group. The jellyfish footprint was particularly large in 2004 and 2007, both years of high jellyfish production (Fig. 2b). Forage fish had a high footprint in 2003 and 2004 but

low footprint in 2005, 2006, and 2007, reflecting the interannual pattern of their own productivity (Fig. 2b) more than the productivity of their zooplankton prey (Fig. 2a). The contribution of forage fish to total system production was fairly consistent across the five

Table 1
Production rate ratios between functional groups – comparison between NCC years 2003–2007. Metrics from the coastal Gulf of Alaska (GoA) and Georges Bank (GB) are shown for comparison.

Production ratio	2003	2004	2005	2006	2007	GoA ^a	GB ^a
Total zooplankton/phytoplankton	0.436	0.500	0.383	0.397	0.349	0.058	0.335
Pelagic fish/total zooplankton	0.023	0.018	0.014	0.010	0.013	0.067	0.012
Seabirds/pelagic fish	1.3×10^{-4}	1.0×10^{-4}	1.6×10^{-4}	1.8×10^{-4}	2.7×10^{-4}	5.8×10^{-5}	5.8×10^{-5}
Gelatinous zooplankton/total zooplankton	0.074	0.080	0.089	0.087	0.096	0.020	0.037
Herbivorous zooplankton/total zooplankton	0.902	0.901	0.903	0.903	0.883	0.507	0.925
Forage fish/phytoplankton	0.008	0.007	0.003	0.003	0.003	–	0.002 ^b

^a Gaichas et al. (2009).

^b Link et al. (2008).

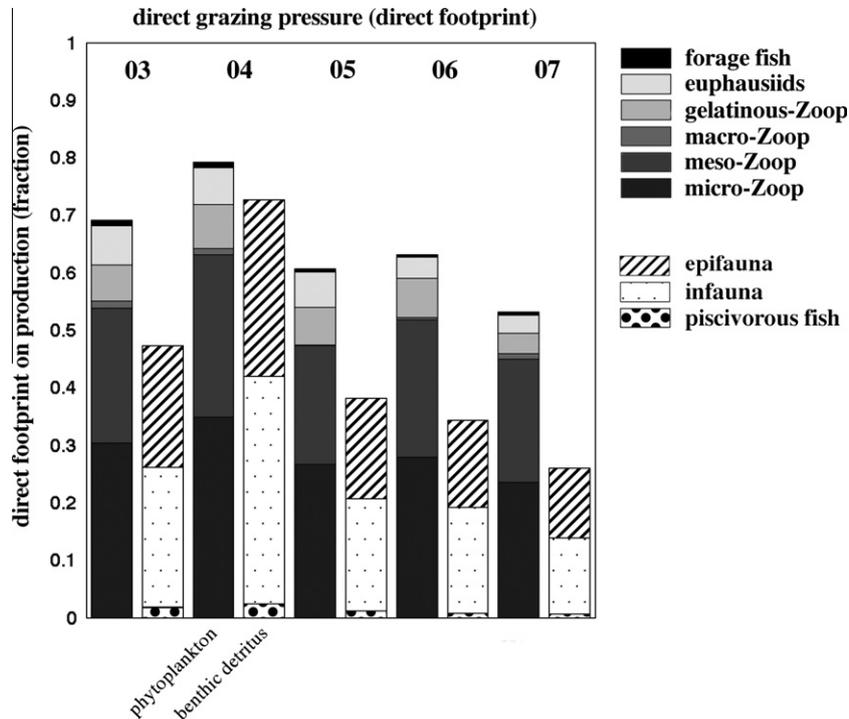


Fig. 3. Interannual variability of total direct grazing pressure upon phytoplankton production and benthic detritus production.

modeled years. The higher reach-to-footprint ratio in 2006 and 2007 implied greater predation pressure, and that small fish were a more efficient energy-transfer pathway within the system. The euphausiid footprint and reach were larger in 2003–2005 than 2006–2007. However, because euphausiid biomass was estimated by top-down demand rather than directly from observation, this interannual pattern may have been a model artifact.

A more focused investigation of the footprint upon meso-zooplankton (Table 4) and the reach to piscivorous fishes and seabirds is possible (Table 5). Euphausiids had a larger footprint on meso-zooplankton production than did forage fishes, but the gelatinous zooplankton had a much larger footprint than either the fishes or euphausiids. Dividing the jellyfish into small gelatinous zooplankton (larvaceans, salps, ctenophores) and large carnivorous jellyfish (*Chrysaora fuscescens*, *Aurelia labiata*, *Phacellophora camtschatica*, *Aequorea* spp.) size classes, the footprint of large jellyfish on meso-zooplankton was shown to be comparable to, and often exceeded, that of either the fishes or euphausiids. In 2007, large carnivorous jellyfish were particularly abundant: almost 50% of the meso-zooplankton production passed through the jellyfish. Higher in the food web, both forage fishes and euphausiids made substantial contributions to piscivorous fish and seabird production. Euphausiids contributed more to piscivorous fish

production than did forage fishes, but the small fishes contributed more to seabird production than did the euphausiids. In contrast, very little production by either the small gelatinous zooplankton or the large jellyfish ($\approx 1\%$) was transferred to piscivorous fishes or to seabirds in any year (Table 5).

Note that when jellyfish size-classes were considered separately, the small gelatinous zooplankton had a larger reach than was calculated for the aggregated jellyfish group (Table 3). This is because predation of the small jellies by the large scyphomedusae and hydromedusae jellyfish contributes to the estimate of the energy that the small jellies pass along to higher trophic levels. When the jellyfish groups are aggregated, predation of small jellies by large jellyfish is treated as a cannibalism and is excluded from the reach estimate.

3.2. End-to-end models: interannual variability in system efficiency

Monte Carlo scenarios were used to compare the interannual, steady-state models under a specific (but subjective) level of uncertainty. For all years, each Monte Carlo scenario was driven under identical nitrate input rates, and the model-estimated production rates of six important pelagic consumer groups representing low, intermediate, and upper trophic levels were compared (Fig. 7).

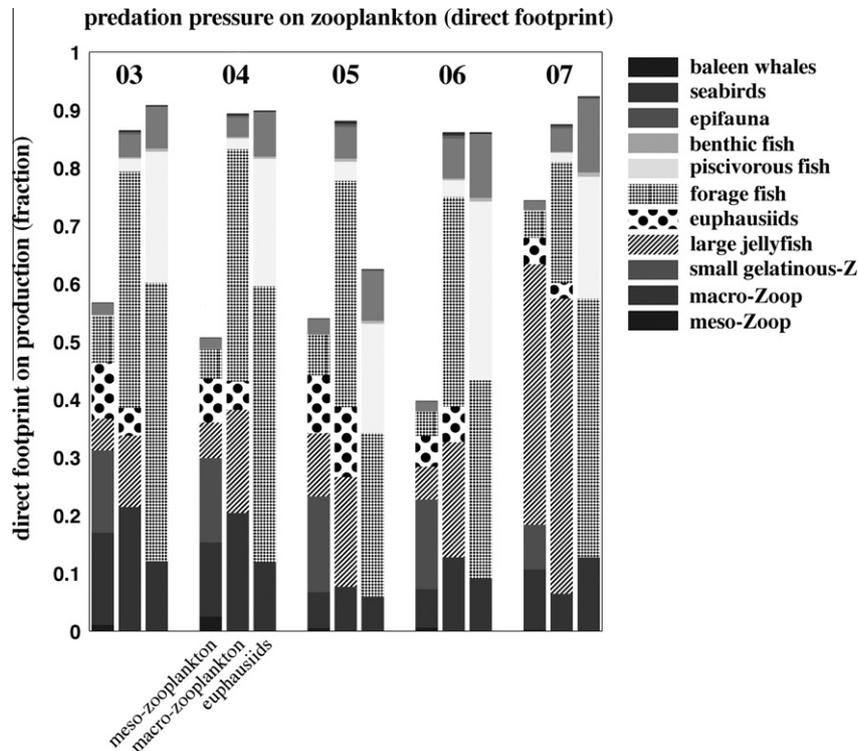


Fig. 4. Interannual variability of total direct predation pressure upon meso-zooplankton, macro-zooplankton, and euphausiid production.

Removing primary production differences between models reveals how interannual differences in food web structure affect the efficiency with which energy is transferred up the food web via all direct and indirect pathways. Large interannual differences (>100%) were evident and exceeded the defined level of model uncertainty (based upon comparison of inter-quartile ranges). More energy reached each of the meso-zooplankton, forage fishes and piscivorous pelagic fishes, and seabird groups in 2003–2004 than in 2005–2007. This division largely reflected years of high vs. low direct grazing pressure upon pelagic primary production (Fig. 3). However, patterns of interannual variability were not otherwise similar between groups, indicating structural differences across a range of trophic levels. Relative interannual differences among other groups (i.e., carnivorous mammals) were much smaller.

The propagation of parameter uncertainty also differed between groups and between years for some groups. For example, during years in which the forage fishes exerted a greater footprint upon system production (2003–2004), estimated uncertainty in fish production was also markedly greater (Fig. 7).

3.3. End-to-end models: targeted scenarios

The role of the three important mid-trophic level groups (forage fishes, jellyfish, euphausiids) as energy-transfer pathways, and the groups with which they had their strongest linkages, were investigated with targeted scenarios. A reduction of energy flow through the forage fishes reduced the productivity of upper trophic level groups that directly prey upon small fishes (piscivorous fishes, seabirds, carnivorous mammals, fishery harvest). Competitors for zooplankton production (squid, baleen whales) benefited (Fig. 8), but there was very little change at lower trophic levels.

A decrease in energy flowing through the euphausiids had a very large, negative effect on most groups, reflecting their large “reach” and importance as energy flow pathways from plankton to the upper trophic levels (Fig. 9). Unlike the forage fish and jellyfish scenarios, reduced euphausiid grazing had a strong negative

Table 2

Direct footprints (grazing pressure) on phytoplankton and meso-zooplankton production exerted by each consumer group. The direct footprint is the fraction of production consumed directly by each consumer group. (Epifauna invertebrates are deposit feeders, suspension feeders, and carnivores).

Consumer group	2003	2004	2005	2006	2007
<i>Direct footprint on phytoplankton production</i>					
Micro-zooplankton	0.3037	0.3479	0.2671	0.279	0.2352
Meso-zooplankton	0.2349	0.2828	0.205	0.2391	0.215
Macro-zooplankton	0.012	0.0106	0.0026	0.0043	0.0087
Small gelatinous-zooplankton	0.0628	0.0772	0.0643	0.068	0.0351
Large jellyfish	0	0	0	0	0
Euphausiids	0.0679	0.0639	0.0618	0.0369	0.0326
Forage and squid	0.0089	0.0088	0.0044	0.003	0.0037
Piscivorous fish	0	0	0	0	0
Benthic fish	0	0	0	0	0
Epifauna	0.0008	0.0009	0.0009	0.0007	0.0007
Baleen whales	0	0	0	0	0
Total	0.6910	0.7921	0.6061	0.6310	0.5310
<i>Direct footprint on meso-zooplankton production</i>					
Micro-zooplankton	0	0	0	0	0
Meso-zooplankton	0.0112	0.0254	0.0056	0.0063	0.003
Macro-zooplankton	0.1591	0.128	0.0621	0.0663	0.1038
Small gelatinous-zooplankton	0.1423	0.1461	0.1657	0.1552	0.0775
Large jellyfish	0.0545	0.0608	0.1084	0.0565	0.4496
Euphausiids	0.0968	0.0761	0.1003	0.0532	0.0454
Forage fish and squid	0.0809	0.0509	0.0697	0.0417	0.0469
Piscivorous fish	0.0006	0.0002	0.0003	0.0004	0.0005
Benthic fish	0.0010	0.0007	0.0008	0.0006	0.0005
Epifauna	0.0204	0.018	0.0266	0.0168	0.0161
Baleen whales	0.0000	0.0000	0.0000	0.0000	0.0000
Total	0.5668	0.5062	0.5395	0.3970	0.7433

impact on both benthic and pelagic groups. Competitors for plankton prey (micro-zooplankton, meso-zooplankton, jellies) benefited slightly. Pelagic detritus production and benthic suspension feeder

Table 3
System-level reach & footprint. Reach is the contribution of producer *t* to the productivity of all consumer groups (excluding phytoplankton and detritus) via direct and indirect pathways. Footprint is the fraction of productivity of all trophic groups (excluding detritus) that contributes to consumer *t* via direct and indirect pathways.

Group <i>t</i>		2003	2004	2005	2006	2007
Forage fish	Reach	0.0013	0.0013	0.0013	0.0008	0.0009
	Footprint	0.0404	0.0357	0.0198	0.0147	0.0182
	Reach:Footprint	0.0322	0.0364	0.0657	0.0544	0.0495
Euphausiids	Reach	0.0137	0.0116	0.0103	0.0079	0.0090
	Footprint	0.0954	0.086	0.0901	0.0537	0.0485
	Reach:Footprint	0.1436	0.1349	0.1143	0.1471	0.1856
Small gelatinous-zooplankton and large jellyfish	Reach	0.00031	0.00042	0.00025	0.00015	0.00026
	Footprint	0.1042	0.124	0.1165	0.1149	0.1541
	Reach:Footprint	0.0030	0.0034	0.0021	0.0013	0.0017
Small gelatinous-zooplankton	Reach	0.0012	0.0015	0.0018	0.0011	0.0087
	Footprint	0.0918	0.108	0.0975	0.1027	0.0543
	Reach:Footprint	0.0131	0.0139	0.0185	0.0107	0.1602
Large jellyfish	Reach	0.00004	0.00003	0.00004	0.00002	0.00004
	Footprint	0.0137	0.0175	0.0208	0.0134	0.1051
	reach:Footprint	0.0029	0.0016	0.0021	0.0014	0.0004

production also benefited slightly with the increase in pelagic detritus generated by micro-zooplankton and meso-zooplankton.

Reduced jellyfish consumption benefited the production of most other groups. As the jellyfish footprint was reduced, production otherwise lost to the system was used by other groups (Fig. 10).

4. Discussion

Our goal was to characterize how the trophic network structure of the Northern California Current upwelling ecosystem varies over a specific interannual period. We also wanted to see how this structural variability could affect the efficiency of energy transfer through the system and the production of individual functional groups. To do this, we used observations of the pelagic community composition made during mesoscale surveys of pelagic fishes, seabirds, and zooplankton and knowledge of diet compositions to infer the trophic network structure (food webs) during five consecutive upwelling seasons, 2003–2007. Analysis of static models allowed comparison of the cumulative energy transfer between functional groups via all direct and indirect trophic pathways. Targeted scenario analyses were used to examine how system efficiency can be affected by the variability of three specific functional groups: forage fishes, euphausiids, and jellyfish.

4.1. Interannual variability and Northern California Current dynamics

Interannual variability in food web structure across all trophic levels was revealed by differences among the annual end-to-end models in the efficiency that energy reaches different functional groups. Each of these models was driven by identical nutrient input rates (Fig. 7). Among most of the six pelagic consumer groups used as indicators, these interannual differences were large (>100%) and exceeded the defined level of model uncertainty ($\pm 50\%$).

What drives the dynamics of the Northern California Current (NCC) ecosystem? Certainly, the seasonally high productivity of the system is due to the input of nutrients via coastal upwelling, and the strength and timing of upwelling is in turn controlled by local winds (Huyer, 1983). However, the observed interannual differences in community composition across trophic levels point to more complex dynamics than direct dependence on upwelling. Upwelling systems worldwide appear to share a common structure, at least within the pelagic environment (Fr on et al., 2009). They have high species diversity among the lower and upper trophic levels, but little diversity at mid-trophic levels. Pelagic

mid-trophic levels are dominated by forage fishes, usually a single sardine and anchovy species that alter their relative dominance over annual-to-decadal periods. In such an energy transfer bottleneck situation, the dynamics of a single (or a very few) species could control the dynamics of the entire system (Rice, 1995). This has been termed a “wasp-waist” control mechanism in analogy with bottom-up and top-down control mechanisms (Bakun, 2006; Cury et al., 2000, 2002).

In the conceptual wasp-waist framework, forage fishes exert top-down control on zooplankton production and bottom-up control on upper-trophic levels (piscivorous fish, seabirds, mammals). Because of their short life cycles and irregular recruitment strength, forage fish populations are particularly variable over time, driving fluctuations across trophic levels within wasp-waist systems (Bakun, 2006). Variability may be further enhanced by unstable feedback loops. During times of high abundance, forage fish species may suppress the growth of their own predators by preying upon the early life-history stages of piscivorous fishes (Bakun, 2006).

The NCC upwelling system does not appear to be structured or to behave as a wasp-waist system, however. There are important, alternative energy transfer pathways between plankton and higher trophic levels that do not include the forage fishes, and the recruitment dynamics of several of the most important pelagic fishes are regulated outside of the NCC region.

On a system-level scale, analysis of inferred food webs suggests that euphausiids were a more important energy transfer pathway than forage fishes, having both a larger footprint on production and contributing more to consumer production (larger reach; Fig. 5). In a combined analysis of stomach content and tissue isotopic enrichment, Miller et al. (2010) noted a high level of omnivory among most pelagic fishes in the NCC, largely due to the prevalence of euphausiids as prey. Others have noted the importance of euphausiids in the diets of planktivorous and piscivorous NCC fishes since the 1980s (Brodeur et al., 1987; Brodeur and Pearcy, 1992; Emmett and Krutzikowsky, 2008; Robinson, 2000; Tanasichuk, 2002). A high level of system omnivory would bypass the forage fish bottleneck and dampen wasp-waist control (Miller et al., 2010).

Patterns of forage fish and piscivorous fish abundance over the past decade do not support the idea of bottom-up control of piscivore production by forage fish (Emmett, 2006). The major teleost piscivores in the NCC system (Pacific hake, Pacific mackerel, jack mackerel) are highly mobile seasonal residents. Adults spawn in the Southern California Current and migrate north into the NCC in

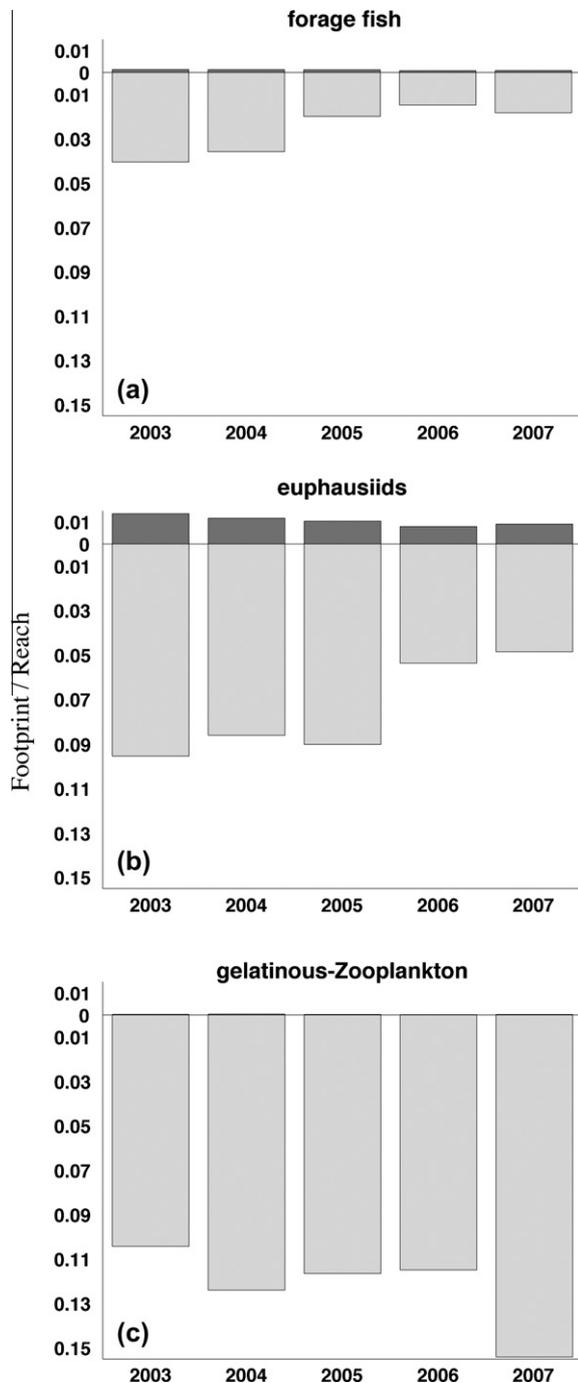


Fig. 5. Interannual comparison of total footprint (gray) and reach (black) for forage fishes (a), euphausiids (b), and gelatinous-zooplankton (small herbivorous jellies and large carnivorous jellyfish) (c). Y-axis represents the fraction of total system production (for footprint) or consumer production (for reach).

the spring and summer to feed (Dorn, 1995). Trophic interactions affecting early life-history survival and piscivorous fish recruitment is de-coupled from the NCC in space, though adult feeding success of migrants within the NCC may still affect egg production rates within southern spawning areas. Large annual changes in piscivore abundance within the NCC appear to be related to ocean climate conditions. During warm ocean years, northward migration begins earlier, occurs faster, and ranges further north (Dorn, 1995; Pearcy and Schoener, 1987; Ware and McFarlane, 1995), and warm winter conditions allow year-round residence and spawning in the NCC (Benson et al., 2002; Phillips et al., 2007).

Similarly, direct top-down control of zooplankton by grazers (planktivorous fishes and others) seems unlikely. Across all model years, the direct grazing footprint on meso-zooplankton is between 0.40 and 0.74 (Table 2). In other words, $\approx 25\text{--}60\%$ of zooplankton production is not consumed and is not available to the pelagic food web but is lost from the system as detritus or exported via Ekman transport to the open ocean (Keister et al., 2009). Of the groups that directly consume meso-zooplankton production, forage fish are much less important than jellies (Table 2 and Fig. 4). Physics probably plays a larger bottom-up role than top-down feedback links in controlling meso-zooplankton production. Region-scale climate processes (El Niño, Pacific Decadal Oscillation) and the associated movements of large water masses have definite effects on the composition (Keister and Peterson, 2003; Peterson and Keister, 2003; Peterson et al., 2002) and production of the copepod community (Ruzicka et al., 2011).

System dynamics may change over long periods with the expansion and contraction of the range of migratory species. During a warm ocean climate, migrants (hake, jack mackerel, Pacific mackerel, sardine) dominate the system, and the factors that control migration processes and recruitment dynamics in the Southern California Current are important in shaping the NCC system. During an extended warm ocean climate, migrant species extend their breeding into the NCC and may begin to complete their entire life-cycles within the system. This may be beginning today. Observations of hake and sardine juveniles since 2003 show expansion of spawning into the NCC during recent warm ocean years (Emmett et al., 2005; Phillips et al., 2007). As planktivorous forage fish begin to consume the early life-history stages of piscivorous fishes, local recruitment dynamics may become important, establishing the wasp-waist feedback links between forage fish and their predators proposed by Bakun (2006). During a cold ocean phase, as between the late 1940s and late 1970s (Mantua et al., 1997), local conditions and ecosystem dynamics may again be more important as migratory species are less abundant. In the late 1970s, locally produced planktivores (anchovy, eulachon, market squid) made up a large proportion of the pelagic fish community. In contrast, the post-1970s community has been dominated by migratory jack mackerel, Pacific mackerel, and sardine, with greater hake abundance (Emmett and Brodeur, 2000).

4.2. The role of three target groups (forage fish, euphausiids, jellyfish)

Targeted scenarios showed that variability in forage fish production had an especially strong effect on seabirds and carnivorous mammals (Fig. 8). For these top trophic level groups, forage fishes were an energy bottleneck and exhibited the potential to exert bottom-up control. Our analysis of the reach metric showed that nearly 70% of seabird production was supported by forage fish (Table 5). In different coastal ecosystems around the world, the availability of forage fishes has been correlated with the production of seabirds (Crawford and Jahncke, 1999; Jahncke et al., 2004; Suryan et al., 2002), and depletion of forage fish has significant effects on seabird populations (Cury et al., 2011). Lower-trophic level variability has been shown to affect seabird survival within the California Current (Hodder and Graybill, 1985; Parrish et al., 2007; Pearcy and Schoener, 1987), but there are not yet any comprehensive studies that link the availability of forage fish with seabird survival and reproductive success within the NCC.

Because euphausiids were so important for energy transfer through the system (Figs. 5b and 6b), the factors that affected euphausiid production could be expected to exert strong effects throughout the entire system. However, there is no strong evidence indicating close dependence between euphausiid production and ocean conditions (Tanasichuk, 2002). Euphausiid egg production in the NCC has shown a loose correspondence with lower

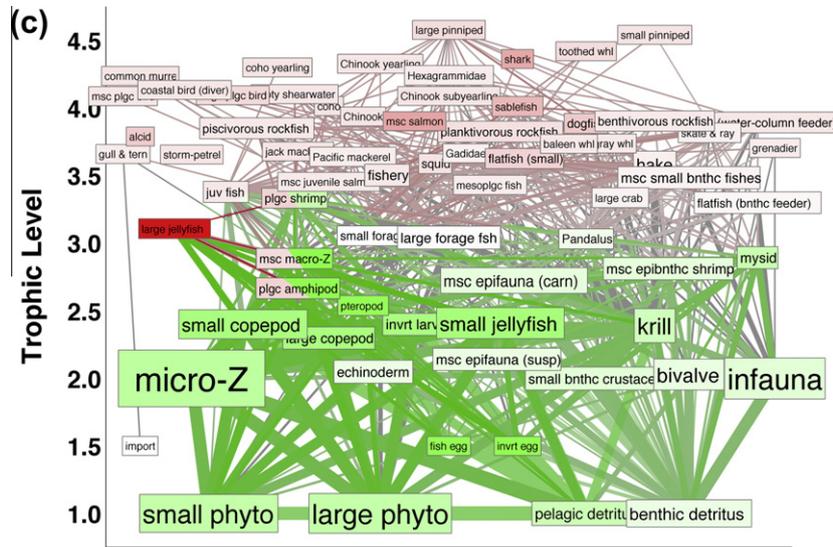


Fig. 6 (continued)

Table 4

Focused investigation of the footprints of three target groups: forage fishes, euphausiids, and gelatinous zooplankton (further divided between small gelatinous zooplankton and large jellyfish). Shown is the footprint upon meso-zooplankton production: the fraction of meso-zooplankton production that contributes to consumer group *t* via direct and indirect pathways.

Consumer group <i>t</i>	2003	2004	2005	2006	2007
<i>Footprint on meso-zooplankton production</i>					
Small pelagic fish	0.0765	0.0515	0.0413	0.0284	0.0323
euphausiids	0.0992	0.0781	0.1032	0.0546	0.0465
Small gelatinous-zooplankton and large jellyfish	0.2059	0.2176	0.2845	0.219	0.6104
Small gelatinous-zooplankton	0.1423	0.1461	0.1657	0.1552	0.0775
Large jellyfish	0.0629	0.0706	0.1168	0.0631	0.4862

Table 5

Focused investigation of the reach of three target groups: forage fishes, euphausiids, and gelatinous zooplankton (further divided in small gelatinous zooplankton and large jellyfish). Shown is the reach to piscivorous fishes and seabirds: the contribution of producer group *t* to piscivorous fish and seabirds via direct and indirect pathways.

Producer group <i>t</i>	2003	2004	2005	2006	2007
<i>Reach to piscivorous fish production</i>					
Forage fish	0.3228	0.3515	0.2374	0.2037	0.2454
Euphausiids	0.6141	0.6317	0.5859	0.6442	0.5392
Small gelatinous-zooplankton and large jellyfish	0.0061	0.0104	0.0146	0.0049	0.0093
small gelatinous-zooplankton	0.0053	0.0099	0.0084	0.0042	0.0066
Large jellyfish	0.0010	0.0007	0.0079	0.0008	0.0034
<i>Reach to seabird production</i>					
Forage fish	0.7057	0.6671	0.6706	0.6973	0.6787
Euphausiids	0.4157	0.4174	0.4233	0.4209	0.4066
Small gelatinous-zooplankton and large jellyfish	0.0051	0.014	0.0086	0.0053	0.0049
Small gelatinous-zooplankton	0.0051	0.014	0.0086	0.0053	0.0049
Large jellyfish	0.0003	0.0003	0.0004	0.0003	0.0003

sub-surface ammonium production (Fig. 10). We have assumed that jellyfish excretion contributes equally to the surface and sub-surface ammonium pools. The weak, positive increase in pelagic ammonium production was the result of the enhanced production (and metabolism) of other pelagic groups.

Because jellyfish consumption is restricted to lower trophic levels, the impact of variation in jelly consumption is distributed broadly higher in the food web (Fig. 10). From an energy-transfer point of view, jellyfish variability had more a web scaling effect and less a community restructuring effect. However, the large carnivorous jellyfish are important consumers of eggs, larvae, and early juvenile stages of euphausiids and fish (Suchman et al.,

2008), and thus have a direct impact on the recruitment dynamics of these groups. In at least one other upwelling system, the Benguela Current off Namibia, jellyfish have displaced the once abundant planktivores (sardines and anchovies) causing major ecosystem changes (Lynam et al., 2006; Utne-Palm et al., 2010).

As shown by Shannon et al. (2009) using simulations of mass-balance models (ECOPATH with ECOSIM) for upwelling (Benguela and Humboldt Currents) and non-upwelling (South Catalan and Adriatic Sea in the Mediterranean) systems, many ecosystems would show a proliferation of gelatinous zooplankton following the collapse of pelagic fish stocks, and conversely, a dramatic decline in jellyfish following closure of the fisheries. As jellyfish

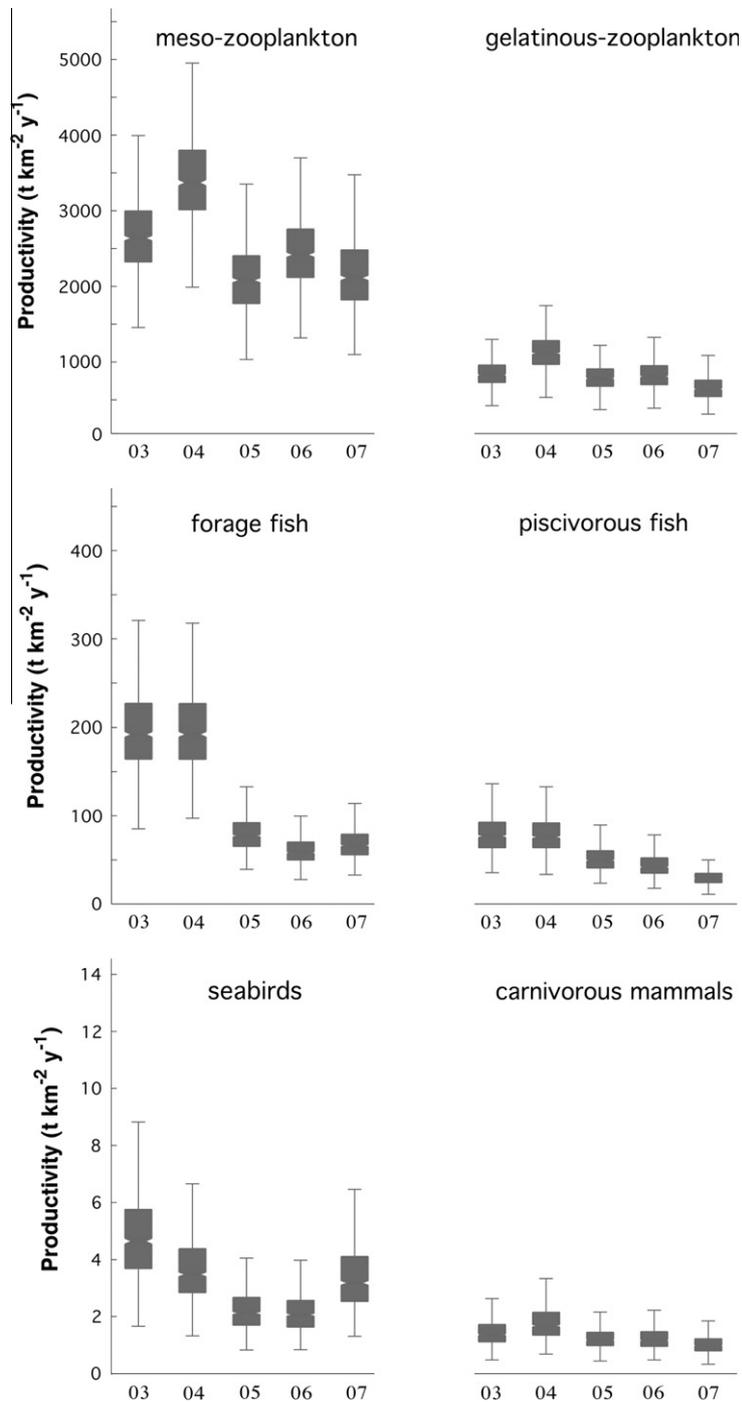


Fig. 7. Interannual comparison of energy flow through five inferred food web models for years 2003–2007. Differences in production rates when models were driven under identical nutrient input rates reveal differences in system energy transfer efficiency. The six indicator groups represent low, mid, and upper trophic levels within the pelagic ecosystem. Inter-quartile range box plots represent the distribution of 1000 randomly drawn models where each term of the bottom-up production index was allowed to vary within $\pm 50\%$ from each year's base model. (box = first – third quartile, waist = median, whiskers cover 1.5 above and below inter-quartile range).

populations continue to rise globally (Richardson et al., 2009), this important trophic group needs to be better represented in most ecosystem models (Pauly et al., 2009).

4.3. Comments on modeling technique

Our analysis shows that interannual variability in community composition and trophic network structure affects the efficiency of energy transfer through the system and the production rates of different functional groups (e.g., Fig. 7). This general conclusion

is consistent with the modeling effort of Field et al. (2006). Performance of their dynamic NCC ECOSIM model, measured against stock assessment and fishery yield time-series, improved when parameters were fit to climate condition indices correlated with variability in predation pressure. However, neither our model analysis nor Field et al.'s incorporate migration and recruitment dynamics.

Since the 1980s, the pelagic fish community has been dominated by species that spawn in the south and migrate into the NCC as adults. To fully capture the processes underlying the variability of

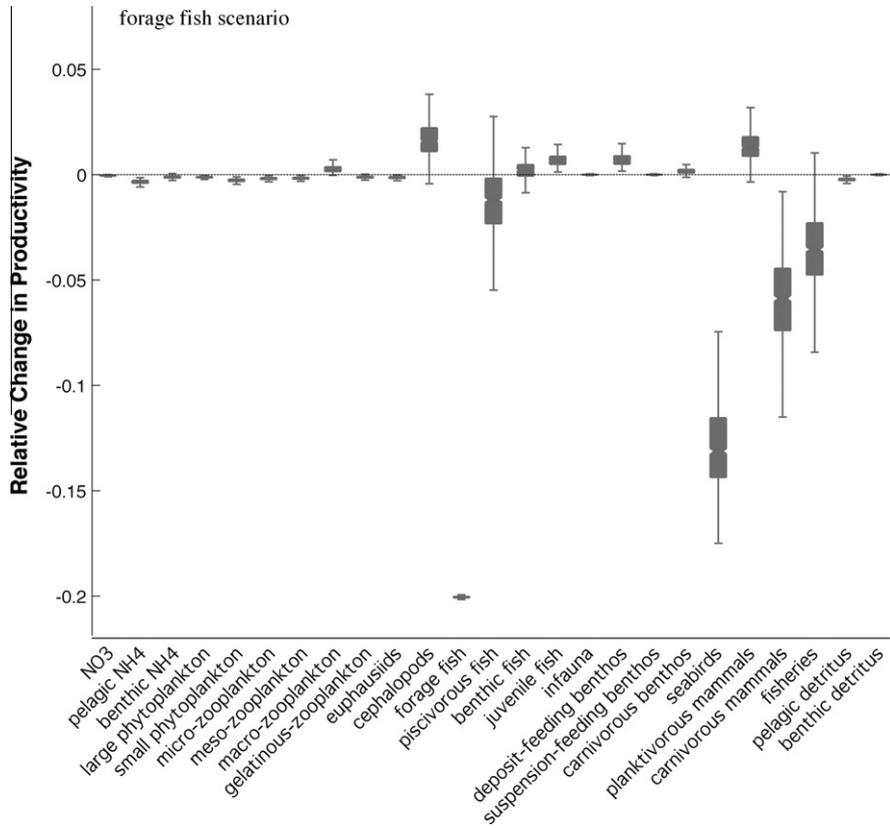


Fig. 8. System response to a 20% reduction in consumption by forage fishes. $Relative\ change\ in\ productivity = (scenario\ model - base\ model) / base\ model$.

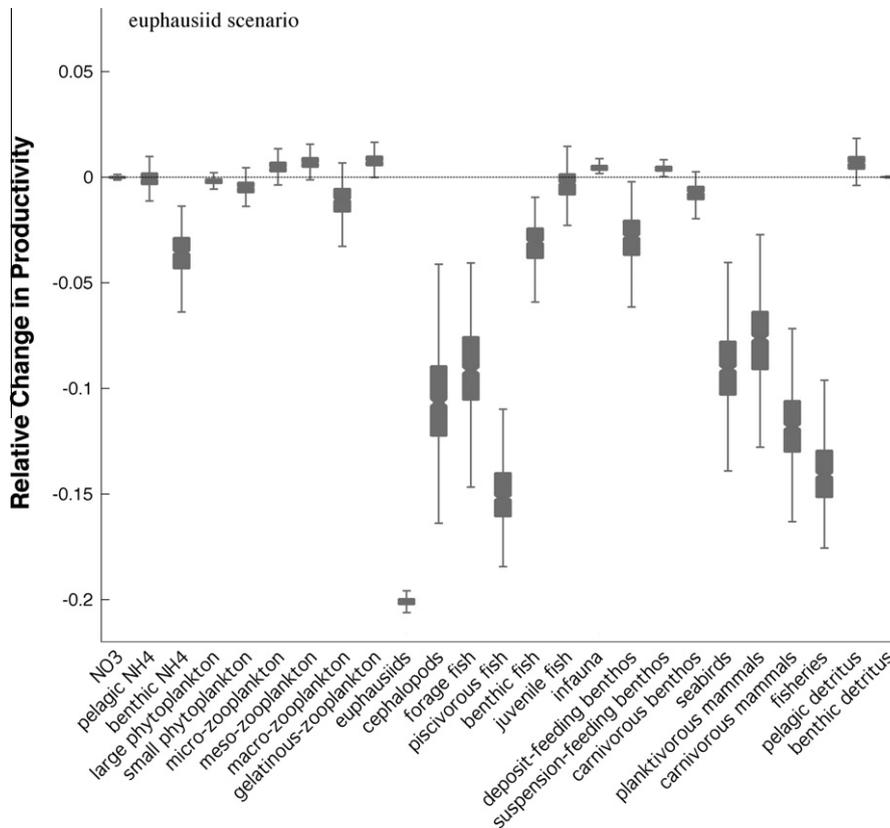


Fig. 9. System response to a 20% reduction in consumption by euphausiids. $Relative\ change\ in\ productivity = (scenario\ model - base\ model) / base\ model$.

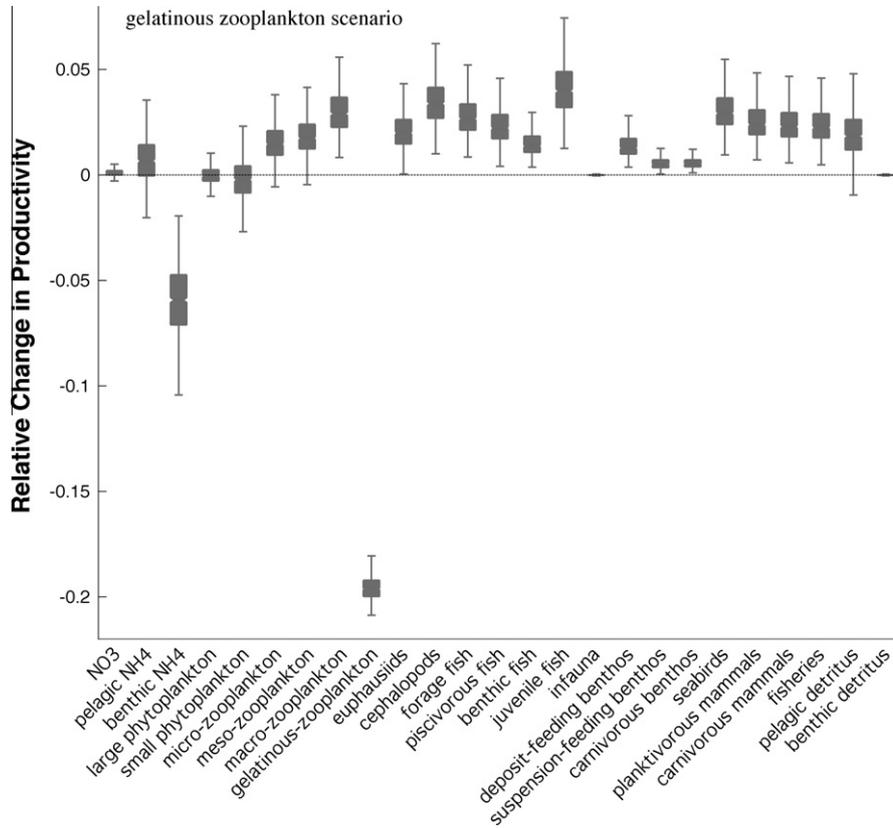


Fig. 10. System response to a 20% reduction in consumption by gelatinous-zooplankton (small gelatinous zooplankton and large jellyfish, predominately *Chrysaora fuscescens*). Relative change in productivity = (scenario model – base model)/base model.

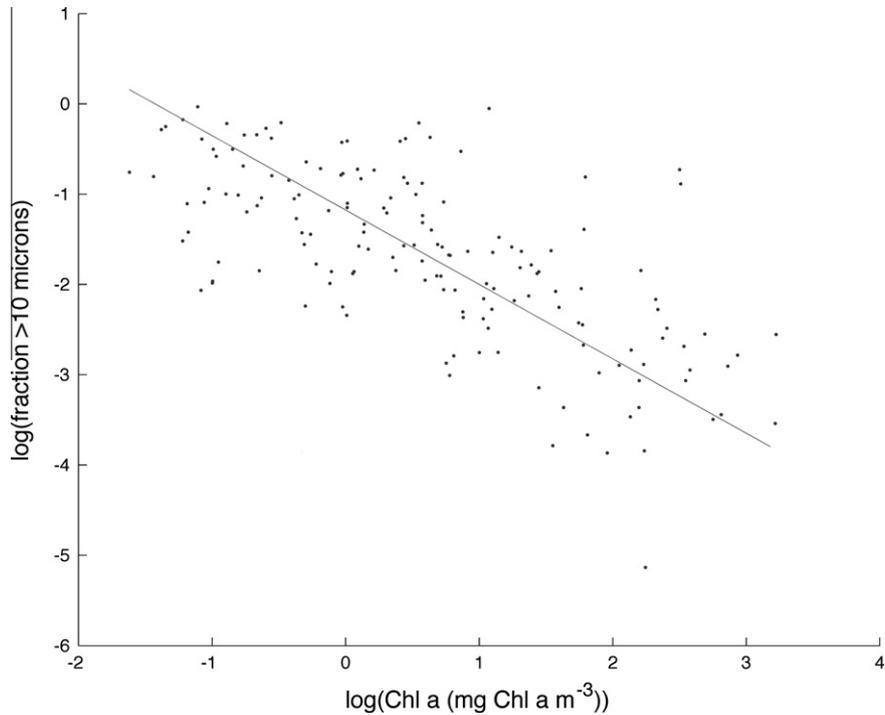


Fig. A.1. Relation between the fraction of small phytoplankton ($\leq 10 \mu\text{m}$) and total Chl *a* in surface samples collected bi-weekly from 1997 to 2005 at stations 5 and 10 miles off the central Oregon coast ($R^2 = 0.47$).

the NCC system, an ecosystem model needs to encompass a coast-wide domain. It must couple the demographic (recruitment) dynamics of these species in the south with the trophic dynamics of the adults in the north. It must also incorporate the factors that drive seasonal migration and spawning-range expansion or contraction. The “Atlantis” modeling effort is laying the groundwork to do this within the California Current (Brand et al., 2007; Horne et al., 2010). Driven by a coupled hydrographic-plankton production model and fishing pressure time-series, the Atlantis models reproduce the time-series of commercially important demersal species but do not yet capture the observed interannual variability of the more mobile pelagic groups (Horne et al., 2010).

To side-step the limitations of our current poor understanding of migration and recruitment complexities, our compromise has been to construct a series of independent snapshots of food web structure inferred from available survey data. This provides valuable information about system function and variability while minimizing the number of assumptions required in complex model systems. Scenario analyses of these end-to-end models reveal system sensitivity to variability in the abundance or physiological rates of specific functional groups. The propagation of parameter uncertainty across trophic linkages can also be assessed to provide an accurate measure of confidence in model-derived metrics and scenarios. In the analyses presented here, we have defined a uniform level of uncertainty about each trophic linkage, but future analyses can account for the uncertainty and variability associated with specific biomass, diet, and physiological rate parameters.

5. Conclusion

Our interannual comparison of Northern California Current food webs revealed substantial interannual differences in energy flow pathways across all trophic levels, even under a high level of diet and parameter uncertainty. We investigated the importance of variability in three mid-trophic level groups in terms of their “footprint” on the total system production and their “reach” supporting upper

trophic level production. Jellyfish, both small gelatinous zooplankton and large carnivorous jellyfish, have a large footprint but transfer very little energy upwards in the food web. Having high reach-to-footprint ratios, forage fishes and euphausiids are shown to be effective links between plankton production and top trophic level predators. Through alternate scenario investigations of end-to-end models, the effect of variability within each of these groups throughout the food web can readily be seen. Variability in jelly and euphausiid production (and consumption) had large but broadly distributed effects throughout the system, while the effect of a variable forage fish community was more narrowly focused upon piscivorous seabirds and mammals.

Acknowledgements

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Appendix A

Tables A.1–A.5 provide details on model group aggregation, ECOPATH parameterization, and end-to-end model parameterization.

A.1. Phytoplankton

SeaWiFS satellite Chl *a* data was available as regional median chlorophyll concentrations ($\text{mg Chl } a \text{ m}^{-3}$) and converted into large and small phytoplankton size-class wet weight biomass (mt km^{-2}). For temporal averaging of 8-day composites, mean chlorophyll

Table A.1
Functional group definitions and aggregation (see Appendix A for more detail).

Code	Aggregated group	Fully resolved model
4	Large phytoplankton	>10 μm (large chain and centric diatoms)
5	Small phytoplankton	$\leq 10 \mu\text{m}$ (cyanobacteria, dinoflagellates, small diatoms)
6	Micro-zooplankton	Micro-zooplankton
7	Meso-zooplankton	Large copepods, small copepods, invertebrate larvae, pteropods, invertebrate eggs
8	Macro-zooplankton	Pelagic amphipods, pelagic shrimp, other macro-zooplankton, fish eggs
9	Gelatinous-zooplankton	Asmall jellies (larvaceans, salps, ctenophores, misc. small medusae), large jellyfish (<i>Chrysaora fuscescens</i> , <i>Aurelia labiata</i> , <i>Phacellophora camtschatica</i> , <i>Aequorea</i> spp., <i>Cyanea capillata</i>)
10	Euphausiids	<i>E. pacifica</i> and <i>T. spinifera</i> (adult and juveniles)
11	Cephalopods	Cephalopods
12	Forage fish	Smelt (whitebait, eulachon), shad, sardine, herring, anchovy, saury, juvenile salmon, mesopelagic fish, planktivorous rockfish
13	Piscivorous fish	Hake, salmon, sharks, jack mackerel, Pacific mackerel, dogfish, sablefish, lingcod and greenling, piscivorous rockfish, flatfishes (Pacific halibut, arrowtooth flounder, petrale sole),
14	Benthic fish	Skates and rays, benthivorous rockfish, Gadidae, flatfishes (English sole, Dover sole, rex sole, misc. small flatfish), grenadier, misc. small benthic fishes
15	Juvenile fish	Juveniles of all fish groups
16	Infauna	Infauna
17	Deposit feeding benthos	<i>Pandalus</i> spp., other epibenthic shrimp (Caridea), mysids, echinoderms (urchins, brittle stars, sea cucumbers), benthic amphipods, isopods, cumaceans
18	Suspension-feeding benthos	Bivalves, misc. epifauna suspension feeders
19	Carnivorous epifauna	Dungeness crab, Tanner crab, misc. epifauna carnivores (small crabs, isopods, misc. gastropods, starfish)
20	Seabirds	Sooty shearwaters (<i>Uria aalge</i>), common murre (<i>Puffinus griseus</i>), gulls and terns, alcids, large pelagic seabirds, other pelagic seabirds, coastal seabirds (divers), storm-petrels
21	Baleen whales	Gray whales, other baleen whales
22	Carnivorous mammals	Pinnipeds, porpoises and dolphins, odontocetes
23	Fisheries	Commercial fisheries, recreational fisheries
24	Pelagic detritus	Pelagic detritus
25	Benthic detritus	Fishery offal, benthic detritus

Table A.2

ECOPATH parameterization of the 2006 aggregated mode. P/B = weight-specific production rate, P/Q = production efficiency, AE = assimilation efficiency, EE = ecotrophic efficiency.

Code	Functional group	Biomass (t km ⁻²)	P/B (y ⁻¹)	P/Q	AE	Fishery (+discards) (t km ⁻² y ⁻¹)	EE
4	Large phytoplankton	37.24	180.00	1.00	1.00	0.000	0.63
5	Small phytoplankton	34.14	100.00	1.00	1.00	0.000	0.63
6	Micro-zooplankton	67.67	36.50	0.35	0.80	0.000	0.85
7	Meso-zooplankton	32.12	32.84	0.25	0.80	0.000	0.39
8	Macro-zooplankton	7.65	6.93	0.25	0.80	0.000	0.89
9	Gelatinous-zooplankton	23.30	15.00	0.25	0.80	0.000	0.06
10	Euphausiids	27.00	6.11	0.25	0.80	0.000	0.86
11	Cephalopods	1.84	3.20	0.30	0.80	0.001	0.85
12	Forage fish	13.48	1.89	0.21	0.80	0.708	0.86
13	Piscivorous fish	25.82	0.30	0.10	0.80	4.567	0.94
14	Benthic fish	17.59	0.30	0.11	0.80	0.125	0.89
15	Juvenile fish	3.98	2.00	0.25	0.80	0.000	0.85
16	Infauna	40.00	3.50	0.20	0.80	0.000	0.94
17	Deposit-feeders	28.87	3.66	0.21	0.80	0.110	0.85
18	Suspension-feeders	28.39	1.30	0.20	0.80	0.027	0.85
19	Carnivorous epifauna	12.92	2.76	0.20	0.80	0.052	0.86
20	Seabirds	0.06	0.12	0.00	0.80	0.000	0.24
21	Baleen whales	0.23	0.04	0.00	0.80	0.000	0.00
22	Carnivorous mammals	0.16	0.07	0.00	0.80	0.000	0.00
23	Fisheries	5.59	0.98	0.98	0.98	0.000	1.00
24	Pelagic detritus	10.00	773.53	1.00	1.00	0.000	0.57
25	Benthic detritus	15.00	254.58	1.00	1.00	0.000	0.25

Table A.3

Diet matrix D_{pc} of the 2006 aggregated model (trace fraction, TR < 0.0005).

Code	Producer p	Consumer c																	
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
4	Large phyto	0.265	0.409	0.175	0.326	0.378	0	0.195	0	0	0.062	0	0.017	0.012	0	0	0	0	0
5	Small phyto	0.135	0.208	0.089	0.166	0.193	0	0.007	0	0	0.007	0	0.008	0.006	0	0	0	0	0
6	Micro-zooplankton	0	0.369	0.151	0.234	0.300	0	0	0	0	0	0	0.026	0	0	0	0	0	0
7	Meso-zooplankton	0	0.013	0.425	0.160	0.085	0.185	0.155	0.002	0.019	0.686	0	0.042	0.002	0	0.005	0.002	0	0
8	Macro-zooplankton	0	0	0.042	0.008	0.005	0.247	0.146	0.022	0.012	0.124	0	0.009	0	0	0.061	0.115	0	0
9	Gelatinous-zooplankton	0	0	0.005	0.013	0	0	0.005	0.003	0.001	0.010	0	0	0	0	0	0	0	0
10	Euphausiids	0	0	0.095	0	0	0.461	0.419	0.510	0.024	0.055	0	0.046	0.001	0.002	0.021	0.133	0	0
11	Cephalopods	0	0	0	0	0	0.001	0.004	0.039	0.007	0	0	0	0.001	0.162	0.006	0.047	TR	
12	Forage fish	0	0	0	0	0	0.060	0.014	0.195	0.017	0	0	0	0.002	0.695	0.028	0.247	0.127	
13	Piscivorous fish	0	0	0	0	0	0	0	0.026	0.002	0	0	0	0.001	0.008	0.002	0.446	0.817	
14	Benthic fish	0	0	0	0	0	0	0.003	0.058	0.019	0	0	0	0.002	0.033	0	0.168	0.022	
15	Juvenile fish	0	0	0	0	0	0.012	0.025	0.032	0.016	0.021	0	0.001	0	0.004	0	0.009	0.001	0
16	Infauna	0	0	0	0	0	0	0	0.006	0.310	0.007	0	0.141	0	0.314	0	0.025	0	0
17	Deposit-feeder	0	0	0.010	0	0	0.034	0.011	0.059	0.225	0.007	0	0.103	0.008	0.188	TR	0.652	0.023	0.020
18	Suspension-feeder	0	0	0	0	0	0	0	0.006	0.010	0	0	0.016	0	0.148	0.001	0.008	0	0.005
19	Carniv. epifauna	0	0	0	0	0	0	0.016	0.035	0.325	0.021	0	0.018	0.008	0.033	0.001	0.020	0.069	0.009
20	Seabirds	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0
21	Baleen whales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	Carnivorous maml	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	Fisheries	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	Pelagic detritus	0.600	0.001	0.007	0.094	0	0	0	0	0	0	0	0	0.042	0	0	0	0	0
25	Benthic detritus	0	0	0	0	0.039	0	0	0.007	0.014	0	1	0.599	0.896	0.304	0.013	0	0	0

concentrations were used. Division into large (>10 μm) and small ($\leq 10 \mu\text{m}$) size-classes was accomplished using an observation-based algorithm from size-fractionated Chl a surface samples collected bi-weekly from 1997 to 2005 at stations 5 and 10 miles off the central Oregon coast (Fig. A.1; W. Peterson, NWFSC, unpub. data):

$$\text{small phytoplankton fraction} = 0.30821 \cdot [\text{Chl } a \text{ (mg m}^{-3}\text{)}]^{-0.82351}.$$

Conversion from chlorophyll concentrations to carbon concentrations were made using standardized conversion factors for large phytoplankton (C:Chl $a = 25 \text{ mg C mg Chl } a^{-1}$) and small phytoplankton (C:Chl $a = 25 \text{ mg C mg Chl } a^{-1}$) (S. Strom and D. Gifford,

Table A.4

Detritus and excretion fates assumed for each functional group.

Code	Functional group	Feces fate		"Surplus" production		NH ₄ ⁺ excretion	
		Pelagic	Benthic	Pelagic	Benthic	Surface	Sub-surface
4	Large phyto	0	0	0	1	1	0
5	Small phyto	0	0	1	0	1	0
6	Micro-zooplankton	1	0	1	0	1	0
7	Meso-zooplankton	0	1	0	1	1	0
8	Macro-zooplankton	0	1	0	1	0.5	0.5
9	Gelatinous-zooplankton	0	1	0	1	0.5	0.5
10	Euphausiids	0	1	0	1	0.5	0.5
11	Cephalopods	0	1	0	1	0.8	0.2
12	Forage fish	0	1	0	1	0.9	0.1
13	Piscivorous fish	0	1	0	1	0.75	0.25
14	Benthic fish	0	1	0	1	0.5	0.5
15	Juvenile fish	0	1	0	1	1	0
16	Infauna	0	1	0	1	0	1
17	Deposit-feeders	0	1	0	1	0	1
18	Suspension-feeders	0	1	0	1	0	1
19	Carniv. epifauna	0	1	0	1	0	1
20	Seabirds	0	1	0	1	1	0
21	Baleen whales	0	1	0	1	1	0
22	Carnivorous maml	0	1	0	1	1	0
23	Fisheries	0	0	0	1	1	0
24	Pelagic detritus	0	0	0	1	0	1
25	Benthic detritus	0	1	0	0	0	0

pers. comm.). Conversions from carbon to dry weight (DWT) and wet weight (WWT) concentrations were based on Strickland (1966):

$$C : DWT = 0.5 \text{ mg C mg DWT}^{-1}$$

$$DWT : WWT = 0.2 \text{ mg DWT mg algal WWT}^{-1}.$$

The vertically integrated phytoplankton biomass (biomass per km²) was estimated based upon an assumed euphotic zone depth that varied sinusoidally from 25 m (summer) to 50 m (winter).

P/B values were derived as the mean April–September ratio of production rates and biomasses mean across years 1998–2007. The production rates used were the Eppley version of the Vertically Generalized Production Model (M. Behrenfeld, Oregon State University) (<http://www.science.oregonstate.edu/ocean.productivity/standard.product.php>).

A.2. Zooplankton

Meso-zooplankton include copepods, pteropods, invertebrate eggs, invertebrate larvae. Macro-zooplankton include pelagic amphipods, pelagic shrimp, cheatognaths, ichthyoplankton, pelagic polychaetes, ostracods, cladocerans, megalopae, and fish eggs. Abundance of most functional groups was estimated from samples taken at each station of the Bonneville Power Administration-sponsored daytime survey (BPA survey) using a 1-m diameter, 335- μ m mesh ring-net towed obliquely from 20 to 30 m to the surface (Morgan et al., 2005; Schabetsberger et al., 2003). Pelagic amphipod, megalopus, and fish egg abundances were estimated from 0.6-m, 335- μ m mesh bongo net samples from the same BPA survey stations, towed under the same protocols as the ring net (Morgan et al., 2005). Pelagic shrimp biomass was estimated by the model based on predator demand.

Vertically integrated zooplankton abundance was estimated using assumed, species-specific depth ranges, generally 60 m for meso-zooplankton and 100 m for macro-zooplankton. All abun-

dances, except eggs and pelagic shrimp, were scaled $\times 2$ as an assumed net efficiency correction factor. Abundance was converted to wet weight biomass density using individual species and development stage size estimates from the literature or unpublished measurements (W. Peterson, NWFSC).

P/B values for meso- and macro-zooplankton were estimated from Hirst et al. (2003), adjusted for mean functional group size and a temperature of 10 °C by assuming $Q_{10} = 2$. *P/Q* was assumed as 0.25 (0.1–0.4 for zooplankton; Parsons et al., 1984).

A.3. Gelatinous zooplankton

Gelatinous zooplankton includes small jellies (larvaceans, salps, ctenophores, misc. small medusae), and large jellyfish (*C. fuscescens*, *A. labiata*, *P. camtschatica*, *Aequorea* spp., *Cyanea capillata*).

Small jelly abundance was estimated from the BPA survey 1-m ring net. Vertically integrated abundance was estimated assuming small jellies were distributed through the upper 50 m. Abundance was converted to wet weight biomass density using individual species size estimates from the literature. Wet weight biomass (WWT) was scaled by 0.21 so that a unit of small jelly biomass had approximately the same water content as that of zooplankton: DWT:WWT of zooplankton = 0.19 (Omori, 1969) and DWT:WWT of small jellies = 0.04 (ctenophores; Hoeger, 1983).

Large jellyfish abundance estimates were obtained from the BPA survey Nordic Rope Trawl. Jellyfish abundance was scaled to account for the effective mouth area of the trawl used during the BPA survey. The effective mouth area is a function of the mean jellyfish diameter and net mesh size: 123 m² for larger jellyfish (*C. fuscescens*, *A. labiata*, *P. camtschatica*, *C. capillata*), 86 m² for smaller jellyfish (*Aequorea* spp.) (Suchman and Brodeur, 2005). The mouth area of the Nordic Rope Trawl (30 \times 18 m) was 540 m²; we scaled estimated area-swept abundance by factors of 4.4 and 6.3 for large and small jellyfish, respectively. Remotely Operated Vehicle observations over the Oregon shelf showed that *C. fuscescens* extend throughout the water-column with peak abundance at or just below the depth sampled by the BPA trawl surveys (C. Suchman, pers. comm.). To conservatively account for jellyfish below the trawl sampling depth, we further scaled jellyfish abundance upward by a factor of 1.5. Wet weights of individual jellies were estimated from

Table A.5
End-to-end production matrix of the 2006 aggregated model (trace fraction, TR < 0.0005). End-to-end production matrix ($E2E_{pc}$).

Code	Consumer <i>c</i>	Producer <i>p</i>																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	NO ₃ ⁻	0	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Surface NH ₄ ⁺	0	0	0	0	0	0.450	0.545	0.275	0.275	0.275	0.400	0.533	0.526	0.344	0.550	0	0
3	Sub-surface NH ₄ ⁺	0	0	0	0	0	0	0	0.275	0.275	0.275	0.100	0.059	0.175	0.344	0	0.600	0.585
4	Large phyto	0.800	0.180	0.200	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Small phyto	0.200	0.720	0.800	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Micro-zooplankton	0	0	0	0.279	0.279	0	0	0	0	0	0	0	0	0	0	0	0
7	Meso-zooplankton	0	0	0	0.242	0.242	0.207	0	0	0	0	0	0	0	0	0	0	0
8	Macro-zooplankton	0	0	0	0.004	0.004	0.004	0.017	0	0.001	0.024	0	0	0	0	0	0	0.003
9	Gelatinous-zooplankton	0	0	0	0.068	0.068	0.046	0.054	0.050	0	0	0	0	0	0	0	0	0
10	Euphausiids	0	0	0	0.037	0.037	0.028	0.014	0.016	0	0	0	0	0	0	0	0	0
11	Cephalopods	0	0	0	0	0	0	0.001	0.023	0	0.014	0	0.010	0	0	0.007	0	0.001
12	Forage fish	0	0	0	0.003	TR	0	0.004	0.073	TR	0.067	0.023	0	0	0.006	0.082	0	0.002
13	Piscivorous fish	0	0	0	0	0	0	0	0.009	TR	0.067	0.171	0.139	0	0.106	0.089	0.001	0.011
14	Benthic fish	0	0	0	0	0	0	TR	0.003	0	0.002	0.018	0.007	0.002	0	0.025	0.022	0.023
15	Juvenile fish	0	0	0	TR	TR	0	0.005	0.019	TR	0.003	0	0	0	0	TR	TR	0
16	Infauna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Deposit-feeders	0	0	0	0.001	0.001	0	0.005	0.022	0	0.035	0	0	0	0	0.018	0.101	0
18	Suspension-feeders	0	0	0	TR	TR	0.001	TR	0	0	TR	0	0	0	0	0	0	0.003
19	Carniv. epifauna	0	0	0	0	0	0	0	0	0	0.001	0.009	0.003	0.002	0.007	0.024	0.080	0.068
20	Seabirds	0	0	0	0	0	0	0	0.001	0	TR	0.035	0.024	TR	0.003	0	0	0
21	Baleen whales	0	0	0	0	0	0	0	0.001	0	TR	0.001	0.001	0	0	0.001	TR	0.003
22	Carnivorous maml	0	0	0	0	0	0	0	0	0	0	0.006	0.005	0.015	0.009	TR	0	TR
23	Fisheries	0	0	0	0	0	0	0	0	0	0	0.006	0.058	0.003	0	0	TR	0
24	Pelagic detritus	0	0	0	0	0.367	0.264	0	0	0	0	0	0	0	0	0	0	0
25	Benthic detritus	0	0	0	0.364	0	0	0.355	0.235	0.449	0.237	0.238	0.214	0.221	0.178	0.205	0.195	0.300

Code	Consumer <i>c</i>	Producer <i>p</i>							
		18	19	20	21	22	23	24	25
1	NO ₃ ⁻	0	0	0	0	0	0	0	0
2	Surface NH ₄ ⁺	0	0	0.798	0.795	0.795	0	0.667	0
3	Sub-surface NH ₄ ⁺	0.600	0.600	0	0	0	0	0	0.250
4	Large phyto	0	0	0	0	0	0	0	0
5	Small phyto	0	0	0	0	0	0	0	0
6	Micro-zooplankton	0	0	0	0	0	0	0.183	0
7	Meso-zooplankton	0	0	0	0	0	0	TR	0
8	Macro-zooplankton	0	0	0	0	0	0	TR	0
9	Gelatinous-zooplankton	0	0	0	0	0	0	0.006	0
10	Euphausiids	0	0	0	0	0	0	0	0.005
11	Cephalopods	0	0	0	0	0	0	0	0
12	Forage fish	0	0.010	0	0	0	0	0	0
13	Piscivorous fish	0.003	0.017	0	0	0	0	0	TR
14	Benthic fish	0.003	0.091	0	0	0	0	0	TR
15	Juvenile fish	0	0.004	0	0	0	0	0	0
16	Infauna	0	0	0	0	0	0	0	0.138
17	Deposit-feeder	0.042	0.050	0	0	0	0	0	0.059
18	Suspension-feeder	0	0.008	0	0	0	0	TR	0.033
19	Carniv. epifauna	0.143	0	0	0	0	0	0	0.011
20	Seabirds	0	0	0	0	0	0	0	0
21	Baleen whales	TR	TR	0	0	0	0	0	0
22	Carnivorous maml	0	0.001	0	0	0	0	0	0
23	Fisheries	TR	0	0	0	0	0	0	0
24	Pelagic detritus	0	0	0	0	0	0	0	0
25	Benthic detritus	0.209	0.219	0.202	0.205	0.205	0.019	0.145	0.505

bell diameters using Shenker's relation for *C. fuscescens* (Shenker, 1985), $WWT \text{ (mg)} = 0.06844 \cdot BD \text{ (mm)}^{2.9702}$. The same relation was used for all species. Wet weight biomass (WWT) was further scaled by 0.13 so that a unit of large jellyfish biomass had approximately the same water content as that of fish: $DWT:WWT \text{ of fish} = 0.3$ and $DWT:WWT \text{ of large jellyfish} = 0.04$ (derived from tables in Shenker, 1985). P/B values for small jellies were estimated from Hirst et al. (2003). P/B for large jellyfish was estimated as described in Ruzicka et al. (2007). P/Q for all small jellies and large jellyfish were assumed as 0.25 (Parsons et al., 1984).

A.4. Euphausiids

The euphausiid group contains adult and juvenile *E. pacifica* and *Thysanoessa spinifera*. There are currently no reliable estimates of euphausiid biomass within the Northern California Current region; biomass was estimated by the model based on predator demand. P/B values were from Tanasichuk (1998a, 1998b). P/Q was assumed as 0.25 (Parsons et al., 1984).

A.5. Cephalopods

Cephalopod biomass was estimated by the model based on predator demand. P/B was borrowed from Aydin et al.'s (2007) Gulf of Alaska model. P/Q was assumed as 0.3.

A.6. Fishes

Four types of biomass information were required for each fish group: inter-annual biomass density, relative seasonal change of biomass density, spatial distribution north-to-south and across depth strata, and the relative contribution of individual species to total functional group biomass. This information was acquired from a combination of three sources: stock assessments (e.g., Gertseva and Schirripa, 2008; Hill et al., 2009; Kaplan and Helser, 2007), NOAA bottom-trawl survey reports (e.g., Weinberg et al., 2002; Keller et al., 2008), and Bonneville Power Administration (BPA) pelagic survey data. Stock assessments provided the definitive inter-annual estimates of coast-wide biomass for individual species but little information about spatial distribution. NOAA bottom-trawl surveys provided coast-wide biomass estimates for (primarily) groundfish species and large-scale spatial distribution data that was used to extrapolate the NCC contribution to coast-wide stock assessments. The BPA daytime pelagic survey provided adult salmon, juvenile salmon, and shark biomass estimates and information about the latitudinal distribution of other pelagic species. The BPA nighttime pelagic survey provided inter-annual biomass estimates of forage fishes and some pelagic piscivores (Pacific mackerel, jack mackerel). Abundance data from the pelagic surveys were converted to wet weight biomasses using species-specific length-weight relationships.

Two classes of scaling factors were used to account for each data source's efficiency for sampling different species and to account for individual species-components of functional groups for which there were no reliable biomass density estimates. For assessment-derived estimates, sampling efficiency was defined as 1. For NOAA bottom-trawl surveys, we adopted a working assumption that semi-pelagic species and flatfish species should be scaled by $\times 2$ to account for individuals swimming within the water-column above the bottom-trawl or individuals escaping beneath the bottom-trawl. For BPA pelagic surveys, sampling efficiency was estimated against available coast-wide stock assessments (sardine, Pacific mackerel) after extrapolation of the fraction of coast-wide abundance within the NCC. For non-assessed species, bottom-trawl survey reports provided an index of the relative contribution of the individual species to total functional group biomass. For

species lacking reliable biomass density estimates, a working assumption of their relative abundance within a functional group was employed.

A.7. Forage fishes

The forage fishes are the small, schooling pelagic fishes (smelts, shad, sardine, herring, anchovy, saury). In the analyses presented here, we aggregate all the small planktivorous fish together: forage fishes, juvenile salmon, planktivorous rockfish (widow, darkblotched, Pacific ocean perch, blue, pygmy, rosy, shortbelly, redstripe, stripetail, Puget Sound, splitnose, sharpchin, bank, greenstriped, harlequin, aurora, yellowmouth), and mesopelagic fish. The abundance and length distribution of the forage fishes was obtained from the BPA nighttime survey. Juvenile salmon information was obtained from the BPA daytime survey. We applied a scaling factor ($\times 15$) to each forage fish species caught during the BPA nighttime survey based upon a comparison between survey-based sardine biomass estimates and the assessed sardine biomass (Hill et al., 2009) under the assumption that 40% of the assessed biomass was within the NCC domain during the summer. We applied a scaling factor ($\times 8$) to each juvenile salmon species caught during the BPA daytime survey (see adult salmon details). Planktivorous rockfish biomass was estimated from stock assessments for widow rockfish (He et al., 2007), darkblotched rockfish (Hamel, 2008), and Pacific ocean perch (Hamel, 2007) and scaled by $\times 1.25$ to account for un-assessed species. Mesopelagic fish biomass was estimated by the model based on predator demand. P/B was borrowed from Pauly and Christensen's (1996) Strait of Georgia Model "small pelagics". P/Q was assumed as 0.25 as in other eastern Pacific coast models ($P/Q = 0.2\text{--}0.3$; Field, 2004; Guénette, 2005; Preikshot, 2005; Aydin et al., 2007).

A.8. Piscivorous fishes

The piscivorous fishes are salmon, sharks, hake, jack mackerel, Pacific mackerel, dogfish, sablefish, hexagrammidae (lingcod, greenling), piscivorous rockfish (yellowtail, canary, chilipepper, bocaccio, yelloweye, black, blackgill), and some flatfish (Pacific halibut, arrowtooth flounder, petrale sole). Adult salmon biomasses were estimated from the BPA daytime survey, and scaled $\times 8$ based upon a comparison between survey biomass estimates and the estimated coho terminal run sizes and ocean fishery take. Shark biomass was obtained from the BPA daytime survey; no scalers were applied. Hake biomass was obtained from the assessed coast-wide biomass (Helser et al., 2009), and the fraction within the NCC domain was estimated based on the spatial distribution observed during the 2005 Pacific hake integrated acoustic and trawl survey (Fleischer et al., 2008) and the distribution observed during the NOAA bottom-trawl surveys. Jack mackerel and Pacific mackerel biomasses were obtained from the BPA nighttime surveys. Jack mackerel biomass was scaled $\times 40$ based on comparison with the coast-wide stock assessment (Dorval et al., 2008). Pacific mackerel was scaled $\times 9$. Piscivorous rockfish biomass was estimated from stock assessments for yellowtail rockfish (Wallace and Lai, 2005), canary rockfish (Stewart, 2007a), chilipepper rockfish (Field, 2007), bocaccio (MacCall, 2008), yelloweye rockfish (Wallace et al., 2006), and black rockfish (Sampson, 2008; Wallace et al., 2008), and no additional scaling factor was applied. Spiny dogfish biomass was obtained from the NOAA bottom-trawl surveys and scaled by $\times 1.25$ for a rough accounting of individuals swimming within the water-column. Sablefish biomass was extrapolated from the west-coast stock assessment (Schirripa, 2008). Lingcod biomass was extrapolated from the coast-wide assessment (Jagiello and Wallace, 2005). Greenling biomass was extrapolated from the assessment of the Oregon stock (Cope and

MacCall, 2005) and the assumption that greenling were evenly distributed within the NCC. Piscivorous flatfish biomasses were extrapolated from stock assessments of arrowtooth flounder (Kaplan and Helser, 2007) and petrale sole (Lai et al., 2006) and scaled $\times 1.4$ to account for Pacific halibut.

P/B values were taken from literature sources representing a combination of experimentally measured rates and mortality rates provided in stock assessments: salmon (Rand and Stewart, 1998), sharks (PFMC, 2003), hake (Helser et al., 2009), jack mackerel (MacCall and Stauffer, 1983), Pacific mackerel (Parrish and MacCall, 1978; Hill and Crone, 2005), dogfish (Field, 2004), sablefish (Schirripa, 2008), Hexagrammidae (Cope and MacCall, 2005; Jagielo and Wallace, 2005), piscivorous rockfish (rockfish assessments cited above), piscivorous flatfish (Lai et al., 2006; Kaplan and Helser, 2007; Clark and Hare, 2009). P/Q values were held within a conservatively narrow range (0.1–0.2) and were taken from literature estimates for individual groups or were assumed identical to similarly-sized groups.

A.9. Benthic fishes

The benthic fishes are the skates and rays, benthivorous rockfish (longspine thornyhead, shortspine thornyhead, China, copper, quillback, tiger, rosethorn, shortraker, roughey, redbanded, silvergray, and the sculpin cabezon), Gadidae (cod, haddock, pollock), benthivorous flatfishes (English sole, Dover sole, rex sole), misc. small flatfishes (sanddabs, starry flounder, slender sole), grenadier, and miscellaneous small benthic fishes. Skate and ray biomass was extrapolated from the coast-wide longnose skate stock assessment (Gertseva and Schirripa, 2008) and scaled by a factor of 1.38 to account for other species. Benthivorous rockfish biomass was extrapolated from stock assessments for longspine thornyhead (Fay, 2005) and shortspine thornyhead (Hamel, 2005) and scaled $\times 2$ to account for other species. Gadid biomass was estimated by the model. Benthivorous flatfish biomass was extrapolated from the stock assessments of English sole (Stewart, 2007b) and Dover sole (Sampson, 2005) and scaled $\times 1.3$ to account for rex sole. The miscellaneous small flatfish biomass was estimated from the sanddab biomass reported in NOAA bottom-trawl survey reports and scaled $\times 1.3$ to account for other small flatfish species and again $\times 2$ to account for individuals escaping beneath the bottom-trawl. Grenadier biomass was obtained from the NOAA bottom-trawl survey reports. The biomass of the miscellaneous small benthic fishes was estimated by the model. P/B values for individual groups were taken from mortality rates provided in stock assessments and from other coastal north-east Pacific food web models. P/Q values for all groups were held within a conservatively narrow range (0.1–0.2).

A.10. Juvenile fishes

Juvenile fish biomass was estimated by the model based on predator demand. P/B was borrowed from Pauly and Christensen's (1996), Straight of Georgia Model "small pelagics". P/Q was assumed as 0.25.

A.11. Benthic invertebrates

Benthic invertebrates were parameterized as in Ruzicka et al. (2007) with a few modifications. Biomasses of most benthic invertebrate groups were estimated by the model based upon predator demand. Biomasses of Dungeness crab and Tanner crab were obtained from the NOAA bottom-trawl survey reports and scaled by $\times 1.75$ during model balancing.

A.12. Seabirds

The aggregated seabird group includes eight functional groups: sooty shearwaters, common murre, gulls and terns, alcids, large pelagic seabirds, small pelagic seabirds, coastal seabirds (divers), and storm-petrels. June seabird abundance and distribution was estimated from standardized visual dawn surveys conducted along each transect of the BPA survey (J. Zamon, NWFSC, unpub. data). BPA survey-based abundance estimates were adjusted to account for birds ashore in rookeries or on nests, birds foraging near the coastline inshore of survey efforts, the efficiency of survey technique. Appropriate scaling factors for individual functional groups were determined by comparing the BPA survey abundance estimates to breeding colony censuses (Speich and Wahl, 1989; Naughton et al., 2007) and the 1989/1990 synoptic survey of seabirds and mammals within the NCC (Briggs et al., 1992). Most species that do not nest locally have marine distributions and do not concentrate foraging along the coastline. These groups (shearwaters albatross, jaegers, fulmars, phalaropes) were not obviously under-estimated by the BPA survey and no scaling factor was applied to these groups. Some locally nesting groups (common murre, gulls and terns, murrelets) were not obviously underestimated by the BPA survey relative to breeding colony census estimates, and no scaling factor was applied to these groups. Other locally nesting groups (auklets, pigeon guillemots, puffins, storm-petrels) were one-third to one-half that of breeding colony census estimates and were scaled by a factor of $\times 2$ to account for seabirds inshore of the BPA survey effort, or offshore of the survey effort in the case of storm-petrels. Coastal diver (cormorants) abundance estimated by the BPA survey was about half that indicated from the breeding colony census. Cormorants are tightly associated with the coastline but forage both at sea and within bays, estuaries, lakes, and rivers (Ainley and Boekelheide, 1990; Marshall et al., 2003; Naughton et al., 2007). No scaling factor was applied to the BPA coastal diver estimate on the assumption that the fraction of the population inshore of the survey effort was approximately equal to the fraction of foraging done within bays, estuaries, and freshwater.

P/B and Q/B values were borrowed from Aydin et al.'s (2007) Gulf of Alaska model, and these were based upon estimated mortality rates (Furness and Monaghan, 1987; Schreiber and Burger, 2002) and daily energy requirements (Hunt Jr. et al., 2000).

A.13. Marine mammals

Planktivorous mammals: Planktivorous mammals include gray whales and baleen whales (minke, humpback, fin whale, blue). Coast-wide baleen whale abundance was obtained from stock assessments (Carretta et al., 2009). Summer resident gray whale abundance was assumed to be 250 (Calambokidis et al., 2009). Distribution data to estimate the proportion of each population within the NCC model domain were based on the sighting maps in Carretta et al. (2009).

Carnivorous mammals: Carnivorous mammals are the pinnipeds (California sea lion, steller sea lion, harbor seals, northern elephant seal), porpoises and dolphins (harbor porpoise, Pacific white-sided dolphin, northern right whale dolphin, killer whale), and odontocetes (sperm whale, pilot whale). Pinniped abundance data was obtained from a combination of coast-wide stock assessments (Angliss and Allen, 2009; Carretta et al., 2009; Allen and Angliss, 2011) and local surveys (Harvey et al., 1990; Brown, 1997; Jeffries et al., 2003; Brown et al., 2005; Scordino, 2006; Pitcher et al., 2007). Distribution data to estimate the proportion of each pinniped population within the NCC model domain were based on the sighting maps in the stock assessments, and the local surveys. Porpoises, dolphin, and odontocete abundance was obtained from

coast-wide stock assessments (Carretta et al., 2009). Distribution data to estimate the proportion of each population within the NCC model domain were based on the sighting maps in Carretta et al. (2009).

For all mammals, abundance converted to biomass based on mean size estimates (Trites and Pauly, 1998). P/B and Q/B values were borrowed from Field's Northern California Current model (Field, 2004).

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