Dividing up the pie: whales, fish, and humans as competitors

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Abstract

Similarly structured food web models of four coastal ecosystems (Northern California Current, Central Gulf of Alaska, Georges Bank, southwestern Antarctic Peninsula) were used to investigate competition among whales, fishes, pinnipeds, and humans. Two analysis strategies simulated the effects of historic baleen and odontocete whale abundances across all trophic levels: food web structure scenarios and time-dynamic scenarios. Direct competition between whales and commercial fisheries is small at current whale abundances; whales and fisheries each take similar proportions of annual pelagic fish production (4 - 7%). Scenarios show that as whale populations grow, indirect competition between whales and fish for zooplankton would more likely impact fishery production than would direct competition for fish between whales and commercial fisheries. Increased baleen whale abundance would have greater and broader indirect effects on upper trophic levels and fisheries than a similar increase in odontocete abundance. Time-dynamic scenarios, which allow for the evolution of compensatory mechanisms, showed more modest impacts than structural scenarios, which show the immediate impacts of altered energy pathways.

Structural scenarios show that in terms of energy availability, there is potential for large increases in whale abundance without major changes to existing food web structures and without substantial reduction of fishery production. For each ecosystem, a five-fold increase in baleen whale abundance could be supported with minor disruptions to existing energy flow pathways. However, such an increase would remain below historical population levels for many cetaceans. A larger expansion (20X) could be accommodated only with large reductions in energy flow to competitor groups. The scope for odontocete expansion varies between ecosystems but can be restricted because they feed at higher, less productive trophic levels.

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Key words: end-to-end model, baleen whales, odontocete whales, pinnipeds, conservation, competition, food web

1. Introduction

Whale populations worldwide were severely reduced by commercial whaling in the 19th and 20th centuries. Pre-exploitation population estimates based upon whaling logbook records indicate that current global baleen whale populations are 1/5th - 1/10th and odontocetes 1/3rd of their historical levels (Table 1). Intense campaigning by concerned individuals and organizations has drawn world attention to the perilous state of whale populations and has been the cornerstone of the conservation movement of the modern era. In the United States, whales have been protected from commercial exploitation since 1972 with enactment of the Marine Mammal Protection Act. Globally, whales have been given at least partial protection from commercial hunting by the International Whaling Commission (IWC) with the declaration of a global moratorium on commercial whaling in 1986 and the establishment of whale sanctuaries in the Indian Ocean (1979) and the Antarctic (1992). Since then, some of the great whales have been showing signs of recovery (IUCN, 2011). Indeed, humpback (*Megaptera novaeangliae*) and southern right whales (*Eubalaena australis*) have been reclassified as species of "least concern". However, other species remain endangered, e.g., blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*), western gray (*Eschrichtius robustus*), and North Atlantic right whales (*Eubalaena glacialis*).

What have been the collateral effects on ocean ecosystems of removing whales, and how will ecosystems change as whale populations recover? Whales are large, long-lived, have high metabolic rates, and as a diverse group, feed across several trophic levels. Baleen whales exert indirect bottom-up pressures on other groups by grazing and reducing the input of zooplankton production into trophic pathways supporting higher trophic levels, and odontocetes exert top-down pressures on mid-trophic levels by preying upon fish and squid. Their roles as competitors

with commercial fisheries (Trites et al., 1997), nutrient recyclers (Lavery et al., 2010; Nicol et al., 2010; Roman & McCarthy, 2010), agents of benthic community succession (Smith et al., 1989), benthic habitat engineers (Oliver & Slattery, 1985), and food web structuring agents (Essington, 2006) are all topics of current study (Bowen, 1997). Removal of baleen whales from the Antarctic ecosystem is thought to have created a "surplus" of euphausiid production and may have contributed to the expansion of penguin and pinniped populations (Laws, 1977; Balance et al., 2006; Ainley et al., 2010). Whaling in the Pacific has led to a shift in the upper trophic predator community from long-lived (sperm whales) to short-lived species (squid) and possibly increased system susceptibility to environmental variability (Essington, 2006). Recovering populations of humpback whales in the Northern California Current and the Antarctic Peninsula, through competition for food, are thought to have reduced the prevalence of seabird competitors (Ainley et al., 2010; Trivelpiece et al., 2011; Ainley & Hyrenbach, 2010). Likewise, recovering populations of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia are thought to have reduced penguin populations (Trathan et al., 2012).

Our goal was to address four questions: How important are whales as consumers at their current population levels? How much do whales compete with fisheries? What would be the effects across the food web if whale populations were to approach their estimated pre-exploitation numbers? Could the expansion of competitor groups (e.g., pinnipeds, piscivorous fishes, and commercial fisheries) limit whale recovery? In this study, food web models of four coastal ecosystems were used to reveal the possible direct and indirect effects of increased whale abundance across all trophic levels and functional groups as populations continue to recover. The ecosystems were the Northern California Current (NCC), the Central Gulf of Alaska (CGoA), Georges Bank (GB), and the southwestern Antarctic Peninsula (sWAP). To make cross-system

comparisons, models were similarly structured so that each shared common functional group definitions, with the major mammal groups (baleen whales, odontocetes, and pinnipeds) defined independently.

Food web models are used to study the effects of changes to large-scale energy flow patterns and do not address the effects that changes in demographics may have on individual populations. Yet, the production and availability of prey, as limited by these energy flow patterns, is fundamental to population growth and community composition. Two distinct model analysis strategies were employed to estimate responses to increased whale abundance. Donor-controlled, end-to-end trophic network models map the flow of energy upwards through the food web. These models are used to reveal how energy availability and potential production rates of all functional groups change over the short term following perturbations to any portion of the food web. Time-dynamic models estimate how the biomasses of individual functional groups and community compositions change over time in response to forced changes to mammal abundances. The effects of imposed changes to whale abundances were expressed as changes relative to current ecosystem states with no *a priori* attempt to define thresholds for "mild" vs. "severe" response. Both analysis techniques allowed us to address two sources of uncertainty and quantify confidence in scenario results: 1) uncertainty among physiological rate, diet, and predator-prey functional response parameters; and 2) potential compensatory changes to community composition and ecosystem-level energy transfer efficiencies over time.

2. Materials & Methods

2.1. Regional end-to-end trophic network models

This study is based upon analyses of end-to-end (E2E) trophic network models of the four coastal ecosystems identified above. E2E network models map the energy flow as biomass through the entire food web from nutrient input and primary production, across all trophic levels to fishery harvest and production export, and back through nutrient recycling. The network map is given as matrix A_{cp} describing how the consumption of each group p is partitioned among the group's bioenergetic costs (metabolism, growth), the ecological demands of higher trophic level predators and fisheries c that prey upon p, and detritus production (egestion, senescence mortality).

The basic equation for the flow of biomass through each functional group within the food web is:

Consumption = Egestion + Metabolism +[Predation + "Other" mortality + Export]

Egestion: unassimilated consumption, feces; directed to detritus pools

Metabolism: basal metabolism, specific dynamic action, and activity costs in terms of ammonium excretion (NH_4^+); directed to recycled nutrient pools

Predation: a production term; production directed to grazing or predation by other functional groups

"Other" mortality: a production term; "other" mortality is unconsumed production; principally unconsumed phytoplankton; directed to detritus pools

Export (losses): a production term; export of plankton and pelagic detritus by physical transport; export losses are handled as a reduction of group transfer efficiency (the

fraction of consumption that is passed to higher trophic level groups through grazing

or predation)

"Consumption" for phytoplankton is the uptake of new nitrate (NO_3^-) input and recycled

ammonium (NH_4^+) produced by consumer metabolism. Nitrate input was rescaled to carbon

based upon the Redfield ratio (6.625 mmole C mmole N^{-1}) and to wet weight based upon the

estimated carbon content of fish (8.8 mg wet weight mg C^{-1}) (Steele et al., 2007).

The E2E trophic network matrices for each region are provided as Supplementary Material.

The E2E network models for the Northern California Current (NCC), Central Gulf of Alaska

(CGoA), and southwestern Antarctic Peninsula (sWAP) ecosystems were derived following the

techniques of Steele and Ruzicka (2011) from solutions for biomasses, consumption rates, and

predation pressure upon each functional group calculated using ECOPATH algorithms

(Christensen & Walters, 2004). The NCC model was modified from Ruzicka et al. (2012), the

CGoA model was modified as noted in the Supplementary Material from the full Gulf of Alaska

model documented in Aydin et al. (2007), and the sWAP model was modified from Ballerini et

al. (in revision). A quantitative assessment of the Georges Bank (GB) food web is given in Steele

et al. (2007) and Collie et al. (2009). Top predators (seabirds, baleen whales, odontocetes) were

implicit in the original GB model. These components have now been explicitly defined using

information from Link et al. (2006) to provide estimates of the abundance, diets, and

consumption rates of birds and mammals on Georges Bank. (ECOPATH parameters and diet

matrices for all four regional models are provided in the Supplementary Material).

Each regional model was developed by a different team of researchers with different

emphasis of purpose but was re-structured so that each shared similar functional group

aggregations. Functional groups were aggregated using production-weighted mean values of

physiological parameters and diets and the sums of group biomasses and fishery harvests. Model currencies also differed between regional models: wet weight biomass (NCC, CGoA), nitrogen biomass (GB), and carbon biomass (sWAP). However, all analyses are expressed as comparable dimensionless metrics: relative changes in production rate (E2E network scenarios) and relative changes in biomass (time-dynamic scenarios).

2.2. Footprints: primary and secondary production required to support marine mammals

The "footprint" is a measure of the relative importance of a consumer group: the fraction of the total production of any producer group reaching the consumer via all direct and indirect pathways (details in Supplementary Material). The consumer may have a footprint upon a producer group even if it does not directly prey upon that producer group. A commonly encountered footprint in the literature is the footprint on primary producers, i.e. the primary production required (PPR) to support a consumer at a defined level of production (e.g., Christensen et al., 2005; Croll & Kudela, 2006; Essington, 2006; Pauly & Christensen, 1995). In this study we calculate the gross footprints of baleen whales, odontocetes, and pinnipeds upon primary producers, zooplankton, euphausiids, and planktivorous (forage) fishes. The gross footprint includes non-growth costs associated with production (i.e., metabolic costs and any non-predation "other" mortality). The food web for the NCC and the footprint of baleen whales on all functional groups is shown as an example in Figure 1.

2.3. Scenarios and sensitivity analyses

We investigated the impact of changing mammal grazing and predation activity within each modeled system using E2E network scenario analyses, which estimate the change in net

production rates among all functional groups following perturbations to any portion of the food web. A scenario was created by changing the relative consumption rate of baleen whales, odontocetes, or pinnipeds upon a specific producer (or producer set) at the expense of other consumer groups. This was done by changing individual elements of the trophic network matrix A_{cp}.

In our E2E network scenarios, transfer efficiencies were held constant, implying no change to functional group physiologies (assimilation efficiencies, growth efficiencies, and weight-specific production rates) nor to predation vulnerabilities. The total consumer pressure on a given producer group was not changed; column sums within the trophic network matrix were held constant ($A_{\cdot p} = 1$). Increased consumption by one consumer (e.g., $c = odontocetes$) upon producer p was imposed by increasing the value of element A_{cp}. This was offset by reducing the other elements within column $A_{\cdot p}$, defining consumption by each competitor group in proportion to their relative importance as consumers in the original base model.

Mammal-as-consumer scenarios simulated the effects of increased baleen whale grazing on all prey groups (5X and 20X base), increased odontocete predation on all prey groups (3X base), and increased pinniped predation on all prey groups (5X base). These scaling factors were intended to represent the logbook-derived estimates of population depletion (Table 1) and the more severe genetic-based estimates of population depletion (Alter et al., 2007; Roman & Palumbi, 2003). Scenario effects were expressed as functional group production in the scenario-modified model relative to production in the original, base model: $\Delta P = P_{scenario\ model} / P_{base\ model}$. Note that changing the predation pressure on a prey group does not change that group's production but does change the fate of that production and the production rates of higher trophic level consumers.

Broad-scale sensitivity analyses (Steele & Ruzicka, 2011) were used to simulate the response of mammals to variability in the lower trophic network. Each element of the trophic network matrix A_{cp} was increased by 20% individually, and the response of each mammal group to that modification was expressed as the change in production (ΔP) relative to the base model configuration.

2.4. Parameter uncertainty

An accounting of functional group variability and the propagation of parameter uncertainty across trophic linkages was necessary to provide a confidence index about model-derived metrics and scenarios. To accomplish this, we adapted the principles of the "ECOSENSE" simplified Bayesian Synthesis methodology developed by Aydin et al. (2007) to E2E network models. The uncertainties associated with each functional group's biomass, diet, and physiology (assimilation efficiencies, growth efficiencies, and weight-specific production rates) were defined *a priori* from available observations or from a pre-established parameter "pedigree" of poorly known parameters (see Supplementary Material). A series of ECOPATH solutions were calculated from parameter sets randomly drawn via Monte Carlo sampling from each parameter's uncertainty distribution. From among potential solutions, rejection criteria were applied to enforce the thermodynamic balance of the system; predation demand could not exceed production for any group. For each region, a baseline set of valid solutions was used to generate 1000 E2E network models (Steele & Ruzicka, 2011) such that the range of model-derived metrics and scenarios expressed model-system uncertainty.

2.5. Dynamic models - system evolution over time

The donor-controlled, E2E network scenarios assume constant transfer efficiencies and do not allow changes to community composition other than the changes forced by the scenario design themselves. In order to allow for compensatory changes in community composition over time and to relax the assumption of constant transfer efficiencies, the E2E network scenarios described above were repeated using time-dynamic ECOSIM algorithms (see Christensen & Walters, 2004; Gaichas et al., 2011; Gaichas et al., 2012). Rather than redirecting trophic flows between groups as in the E2E network scenarios, we forced only the biomass for marine mammal groups and allowed changes in energy flow through the food web and all other functional group biomasses to be emergent properties of the scenario. Therefore, this analysis saw the scenarios slightly differently - how would community composition differ if whale biomass was at historical levels rather than how would energy available to individual functional groups and their resulting production rates differ?

Dynamic runs were initialized with the same mass-balanced state and parameter pedigrees as the E2E network models. For each regional model we drew 2000 random parameter sets from within the defined parameter pedigrees, retaining only models that did not lead to extinction of any functional group within a 200-year period. While the four "type-model" parameter sets defining the regional systems (see Supplementary Materials) were in equilibrium and changed little, many models within the set of Monte Carlo models allowed community composition to change over time. Investigation of unforced, non-scenario model time-series showed that most of the Monte Carlo models reached equilibrium conditions within 200 years.

Dynamic scenarios were run by increasing mammal biomasses by target scaling factors over the median non-scenario, base model time-series (baleen whales X5 and X20, odontocetes X3, pinnipeds X5). Mammal biomasses were increased to target levels over the course of 100 years

and the models run for 200 years to allow each system achieve a new steady state. Ecosystem conditions over the last 10 years were averaged to smooth any oscillations. Results were expressed as biomass in each scenario-modified model relative to biomass in each non-scenario, base model:

$$\Delta B = B_{scenario\ model} / B_{base\ model}.$$

For the time dynamic scenarios, we also considered the additional uncertainty associated with predator-prey functional responses by drawing these parameters in each run from a uniform distribution centered on the input value. Functional response parameters could vary across the full scale from hyper-stable donor-controlled dynamics to chaotic Lotka-Volterra dynamics. Drawing dynamic parameters from these relatively wide ranges reflects fairly high uncertainty in predator-prey dynamics, which are poorly known in most marine ecosystems. This in turn leads to greater proportions of randomly drawn parameter sets that did not meet thermodynamic requirements over the 200 year run; 465 viable NCC models, 419 CGoA models, 257 GB models, and 468 sWAP models were retained.

3. Results

3.1. Footprints: primary and secondary production required to support marine mammals

The footprint metric, or estimate of lower trophic level production required to support a consumer via direct and indirect trophic pathways, is an index of the consumer's importance in the system. Marine mammal footprints on planktivorous (forage) fish, squid, macro-zooplankton, and euphausiid production are given in Table 2 (see Supplementary Material for expanded results). Baleen whales exert a smaller footprint on their main prey than do the odontocetes. Baleen whales were supported by 2 - 7% of the macro-zooplankton and euphausiid production and 3 - 6% of the forage fish production in all systems while the odontocetes required 11 - 35% of the forage fish and squid production. On Georges Bank (GB), where squid are less abundant, odontocetes exerted a much larger footprint upon forage fishes than in the Central Gulf of Alaska (CGoA) and the Northern California Current (NCC). Odontocetes were not included in the southwestern Antarctic Peninsula model (sWAP) as killer whales were infrequently encountered apex predators during the GLOBEC surveys on which mammal groups were defined.

Pinnipeds were found to be less important consumers than odontocetes in the NCC and CGoA ecosystems, requiring only 6 - 9% of the forage fish and squid production. In contrast, pinnipeds were very important consumers in the sWAP ecosystem. Piscivorous Weddell (*Leptonychotes weddelli*) and planktivorous crabeater seals (*Lobodon carcinophagus*) required the support of one-third of the euphausiid production and 45% of the planktivorous fish production compared to the requirements of penguins and seabirds, 10% of the euphausiid and 14% of the planktivorous fish production. Pinnipeds are uncommon visitors to Georges Bank and were not included in the GB model.

3.2. Grazing and predation by marine mammals

Model-based estimates of the direct consumption of fish production by marine mammals and fisheries are compared in Table 3. In the CGoA, whales and pinnipeds combined took roughly the same proportion of the total pelagic fish and groundfish production as did commercial fisheries. In the NCC and GB ecosystems, fisheries took 2 - 4 times as much of the total fish production as did marine mammals. In terms of planktivorous (forage) fish production, marine mammals in the NCC and in the CGoA consumed about twice as much as was removed by the fisheries. On GB, whales and fisheries each removed similar amounts of the forage fish production.

Expressed in terms of their consumption rates relative to other pelagic consumers and fisheries, baleen whales appeared to be of relatively small importance in all four ecosystems (Fig. 2 and Supplementary Material). In the NCC and CGoA, odontocetes proved to be minor predators of forage fishes. On GB, however, odontocetes were major predators of forage fish and are of similar importance as fisheries. At higher trophic levels, fisheries were the major consumer of piscvorous fish, consuming about 80% of the production in the NCC, CGoA, and GB ecosystems. Odontocetes and pinnipeds were of less importance, consuming only about 15% of the piscivorous fish production in these three ecosystems - pinnipeds being more important in the NCC and CGoA and odontocetes being more important on GB.

3.3. E2E Network Scenarios: effects of increased mammal abundance and consumption

Estimates of global, pre-exploitation baleen whale populations indicate populations between 5 and 20 times larger than survive today (Table 1, excluding minke whales, *Balaeoptera spp.*). Using E2E trophic network models, the effect of pre-exploitation baleen whale populations on

the whole food web was simulated by increasing the allocation of all prey to baleen whales by factors of 5X and 20X and decreasing the total allocation to competitor consumers by an equal amount (Fig. 3, Table 4; see Supplementary Material for expanded results).

When baleen consumption was increased 5X, the production of mid-trophic level planktivorous (forage) fishes declined 2 - 6%, piscivorous fishes declined 7 - 24%, and top trophic level predators declined 13 - 29%. Regional differences were apparent. Fishes and pinnipeds declined the most but odontocetes the least in the CGoA. Not surprisingly, fishery production mirrored the effect on the fishes, and these were most strongly impacted in the CGoA. GB fisheries were least impacted, and this is probably due to the higher proportion of benthivorous fishes in the GB fisheries compared to the NCC and CGoA fisheries.

The estimated global pre-exploitation sperm whale (*Physeter macrocephalus*) population was about 2.5X the current population estimate (Table 1). We simulated the effect that a 3X increase in odontocete predation would have on the NCC, CGoA, and GB systems (Fig. 4, Table 4; expanded results in Supplementary Material). Because odontocetes feed at a higher trophic level than baleen whales, the effects of increased odontocete predation appeared limited to a higher and narrower trophic range than the effects of increased baleen whale grazing. The effects were greatest on GB and greater in magnitude than the effects of the similar (5X) baleen whale scenario. In the NCC and CGoA, increased odontocete predation had a much smaller effect than did increased baleen whale grazing.

Estimates of historical pinniped abundance are even less certain than estimates of historical whale abundance. To compare the ecosystem-level roles of pinnipeds and whales, we simulated the effect of a hypothetical 5X increase in pinniped abundance in the NCC, CGoA, and sWAP ecosystems (Table 4; expanded results in Supplementary Material). Increased pinniped predation

had the largest effects in the sWAP system, reflecting the already large footprints of planktivorous and piscivorous pinnipeds on euphausiid and fish production. In the NCC and the CGoA ecosystems, a 5X increase in pinniped predation generally had an equal or slightly lighter impact on fishes, seabirds, and odontocetes than the same relative increase in baleen whale grazing. Pinnipeds had a slightly greater impact on fishes, seabirds, and baleen whales in the CGoA than did a similar increase in odontocete predation (3X). In contrast, pinnipeds had a substantially larger impact on fishery yield in the NCC and CGoA than either of the whale groups.

3.4. Dynamic scenarios

Dynamic scenarios were run to investigate the effects of top-down predation feedback upon community composition. The changes in the steady-state community composition following 200 years of elevated mammal biomass are summarized in Table 5 (see also Supplementary Material). Increased mammal abundances had only very modest long-term effect on the community composition in any of the regional ecosystems.

In the NCC and CGoA, baleen whales had more broadly distributed effects across multiple community groups than did either odontocetes or pinnipeds. However, even a twenty-fold increase in baleen whale abundance lead to reductions of only a few percent (<6%) in the biomasses of pelagic fishes and top predators (seabirds, odontocetes, pinnipeds, and fisheries). A three-fold increase in odontocete abundance led to very slight long-term reductions (1-2%) in pinniped biomass in the NCC and squid biomass in the CGoA. On GB, the effects of increased baleen and odontocete whale abundances were even smaller than in the other ecosystems. In the sWAP ecosystem, baleen whales had almost no detectable impact, but pinnipeds had large and

broadly distributed effects - though still modest ($< 5\%$). Increased pinniped abundances in the

NCC and CGoA ecosystems led to reductions on the order of 1-3% among pelagic fishes and

fishery harvests. Mammals had no detectable long-term on effect zooplankton groups in any of

the ecosystems.

Consideration of parameter uncertainty allowed for the inclusion of Monte Carlo models that

showed larger changes in community composition over time before reaching steady-state

conditions than did any of the forced scenario changes to mammal biomass. The largest changes

to the non-scenario, base models were observed among the top trophic levels of the NCC. Over

the 200-year run of the NCC models, seabirds increased by a factor of 2.5 on average,

odontocetes by 2.4, and pinnipeds by 5.7. In the CGoA, seabirds increased by a factor of 1.6,

odontocetes by 2.1, but pinnipeds increased by only a factor of 1.1. In the sWAP, seabirds and

penguins increased by factors of 1.5 and piscivorous pinnipeds (Weddell seals) increased by a

factor of 1.8. In contrast, baleen and odontocete whale biomasses among the non-scenario GB

models remained constant. Plankton and fish biomasses also changed over time, but by a much

smaller amount than top trophic levels and not in a consistently positive or negative pattern

(expanded results in Supplementary Material).

3.5. Sensitivity analyses of baleen and odontocete whales

The sensitivities of baleen whales, odontocetes, and pinnipeds to changes in individual

trophic linkages were systematically analyzed for all four ecosystems (Fig. 5, expanded results in

Supplementary Material).

Baleen whales benefited most from increased energy flow along the trophic pathways

through their main prey groups: the planktivorous (forage) fish → baleen pathway (NCC,

CGoA), the phytoplankton → euphausiid → baleen pathway (NCC, CGoA, sWAP), or the phytoplankton → meso-zooplankton → baleen pathway on GB (where euphausiids are less important components of the zooplankton). Baleen whales were disadvantaged by competitive energy flows: euphausiids → planktivorous fish and planktivorous fish → piscivorous fish. In the sWAP, the effect of increased competition for euphausiids by planktivorous fish was particularly harmful to baleen whales, the effect being larger than the primary 20% modification to the network structure (-62%). A 20% increase in the fishery removals had very negative small impact on baleen whale production (<1%) in the NCC and CGoA ecosystems. GB fisheries had a moderately larger effect on baleen whales; increased harvest of demersal fishes reduced production by 8%. Baleen whales were relatively insensitive to changes in pinniped populations. A 20% increase in pinniped abundance lead to <1% decline in baleen whale production in any of the three systems having large pinniped communities (NCC, CGoA, sWAP).

Odontocetes benefited from increased energy flow via their main prey groups, planktivorous fish and cephalopods. Cephalopods were more influential in the CGoA while planktivorous fish were more important in the NCC and GB. Odontocetes suffered with increased competition for these resources with effects that were often magnified across the food web, exceeding the primary 20% modification to the network structure. Odontocetes were more sensitive to changes in fishery removals than were the baleen whales, especially on GB (Fig. 5). A 20% increase in removals of planktivorous fish reduced odontocete production on GB by 15%, and increased harvest of demersal fishes reduced production by almost 40%. In the NCC, a 20% increase in the harvest of piscivorous fishes reduced odontocete production by 12%. Odontecetes in the CGoA were less sensitive to changes in fishery harvest. Changes in the NCC and CGoA pinniped populations had relatively little effect on odontocetes.

4. Discussion

Commercial whaling through the 19th and 20th centuries reduced whale populations to small fractions of their pre-exploitation numbers (Table 1). To avert extinctions of whole species and to allow recovery of individual populations, the International Whaling Commission (IWC) prohibited commercial whaling of gray whales (1946), right whales (1949), humpback and blue whales (1965), southern fin whales (1976), and declared a global blanket moratorium on commercial whaling in 1986. A 2008 review of whale status reveals that some of the great whales are showing signs of recovery, while other populations remain near extinction (IUCN, 2011).

The dramatic reduction of global whale populations has been implicated to have had numerous direct and indirect effects upon ecosystem structure, function, and productivity (Estes et al., 2006; Emslie & Patterson, 2007; Ainley et al., 2010). To understand those possible effects more fully, our modeling study aimed to address four questions about the consequences of past whale removal and potential whale recovery: How important are whales as consumers in the ecosystems of the Northern California Current (NCC), the Central Gulf of Alaska (CGoA), Georges Bank (GB), and the southwestern Antarctic Peninsula (sWAP) ecosystems? Are whales important competitors for fishery resources? What would be the effects across the food web if whales were to increase to their estimated pre-exploitation numbers? Does the expansion of competitor groups and altered ecosystem structure limit whale recovery (Leaper & Miller, 2011)? Because the exploitation of whales preceded thorough scientific observation and documentation we do not have baseline before-and-after information by which to gauge ecosystem changes. Multi-species modeling studies are an appropriate, and often the only means, to reveal how perturbations propagate through the food web via direct and indirect pathways

(Yodzis, 2001). Our approach has been to use trophic network analyses to estimate the potential and most likely ecosystem-level effects of changes to marine mammal abundance.

4.1. Are whales important consumers today?

The primary production required (PPR) to support whale production has been used to illustrate the relative importance of whales as consumers in various ecosystems (Trites et al., 1997; Croll & Kudela, 2006; Essington, 2006; Morissette et al., 2012). At current population levels, we have estimated that baleen whales require approximately 2 – 4% and odontocetes require 8 – 11% of the primary production in the coastal NCC, CGoA, GB, and sWAP ecosystems (Table 2). Fisheries in these coastal ecosystems are supported by a much higher percentage of phytoplankton production, 20 – 32%. In comparison, commercial fisheries worldwide have been estimated to be supported by 8% of the total global primary production (Pauly & Christensen, 1995).

The precise definition and calculation of PPR vary between studies and comparisons must be made with caution. With this in mind, our values are similar to Morissette et al.'s (2012) recent estimates from four temperate coastal systems that marine mammals as a group require 2 – 10% of the net primary production. Essington (2006) made similar estimates for the North Pacific; baleen whales are supported by 4% of the net primary production (or 6% at pre-exploitation population numbers) and sperm whales are supported by 7% of the net primary production (10% pre-exploitation). Our estimates are lower than Trites et al.'s (1997) estimate that baleen and odontocete whales over the whole of the Pacific basin require 15 – 22% of the net primary production, and they are lower than Croll and Kudela's (2006) estimate that whales in the North Pacific are supported by 26% of the net primary production.

The PPR and footprint metrics do not convey information about competition between groups. Model scenarios in which the abundance, vital rates, or diets of individual functional groups are altered provide much more detailed information about trophic interactions throughout the food web. Given their current low contribution to the total predation pressure upon zooplankton and planktivorous (forage) fish (Fig. 2), baleen whales should have much potential for expansion before their impact upon the rest of the food web would become evident. End-to-end network scenarios in all four modeled ecosystems showed that a five-fold increase in baleen whale abundance reduced the production of competing planktivores (macro-zooplankton, euphausiids, carnivorous jellies, squid, forage fish) by less than 10% (Fig. 3, Table 4; expanded results in Supplementary Material). From the whales' perspective, the model analyses show that baleen whales are very sensitive to competition for zooplankton and forage fish prey. Episodic reports of emaciated individuals (e.g., Mate, 2001; Moore et al., 2001) indicate that food shortages may be occurring in recent, real world environments.

Because odontocetes feed upon higher, less productive trophic levels than do baleen whales, we might expect that their potential for expansion is more limited. This appears to be the case on Georges Bank where odontocete consumption already accounts for a high proportion of fish production and predation pressure (Table 3; Fig. 2). Only a small increase in odontocete consumption on GB - about a factor of 3 - would be possible even with the elimination of all competition for fish. Seabirds, in particular, would be the most severely impacted group on GB as they are in closest competition with odontocetes for small pelagic fishes (Table 4). In the NCC and CGoA ecosystems, however, odontocetes are not currently as important as predators as they are on GB (Fig. 2), and these systems appear able to accommodate larger population without large reductions in competition by seabirds, pinnipeds, or humans (Table 4).

4.2. Do whales compete with humans for fishery resources?

International whale conservation and management policy has recently been challenged by the "whales-eat-fish" argument that whales consume large quantities of fish and that the active management (culling) of whale populations is a responsible strategy for assuring food security among coastal nations (IWC, 2006). In the coastal ecosystems considered here, we have asked how whales and fisheries compare in terms of the amount of fish production consumed, and what changes to ecosystem structure and fishery yield may be expected in an era of expanding whale populations.

In the CGoA, baleen and odontocete whales take only slightly less of the total pelagic and groundfish production as do fisheries (Table 3). In the NCC, where there is a large Pacific hake fishery (*Merluccius productus*), whales take only $1/4^{th}$ as much of the total fish production as do fisheries. With the inclusion of pinniped consumption, which is slightly less than that of the whales in both of these Pacific ecosystems, the combined marine mammal consumption of fish is roughly equal to that taken by fisheries in the CGoA and about half that taken by fisheries in the NCC. Over the whole of the Pacific basin, Trites et al. (1997) estimated that mammals consume three times as much biomass (fish and invertebrates) as is taken by commercial fisheries. However, they show that most of the prey caught by mammals, deep-sea squids and small deep-sea fishes, are not types targeted by humans.

We have estimated that whales consume about 4% of the total fish production on GB, or about $1/4^{th}$ as much fish as is taken by commercial fisheries (Table 3). Our estimates of the importance of whales as consumers on GB are lower than two previous studies. Bax (1991) has estimated that fisheries and whales each take about 10% of the fish production on GB. Overholtz

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et al. (1991) have estimated that whales and seals together consume 17% of the fish production along the northeast US coast.

Though whales currently consume less of the total fish production than do commercial fisheries in the NCC, CGoA, and GB ecosystems, direct competition between humans and whales may be less important than indirect interactions or "food web" competition (Trites et al., 1997; Gerber et al., 2009). In each ecosystem model, fish were a smaller component of the baleen whale diet than were zooplankton and euphausiids. Yet, changes to baleen whale abundance had as great or greater impact on fish and fisheries than similar changes to odontocetes (Table 4) - even though odontocetes were almost exclusively piscivorous and were supported by greater "footprint" upon plankton and fish production than were baleen whales (Table 2). For example, in the E2E network scenarios, a five-fold increase in baleen whale abundance led to a 30% reduction in fishery removals in the CGoA. A three-fold increase in odontocete abundance reduced fishery removals in the CGoA by less than 10%.

The E2E network scenarios are designed to show the immediate effects of modified energy flow pathways. Time-dynamic scenarios allow for the evolution of compensatory responses over time. These include changes to community composition and allow for reduced senescence mortality to support increased predation mortality. Thus, the long-term effects seen in the time-dynamic scenarios are smaller than the effects seen in the E2E network scenarios (Tables 4 and 5). The time-dynamic scenarios still indicate that fishery harvests would decrease with increased competition from baleen whales and odontocetes, but only by 5% or less (Table 5). In comparison, Morissette et al. (2012) ran time-dynamic mammal eradication scenarios for four temperate coastal systems using ECOSIM (Christensen & Walters, 2004). Their general finding was that elimination of all marine mammals would result in an increase of the biomass of

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commercially important species by less than 20%. These extreme culling scenarios show stronger effects than our whale-recovery scenarios, but both sets suggest that culling whales for the sake of fisheries management would yield small results.

4.3. Whales as ecosystem structuring agents

Whales have important community structuring roles beyond their importance as consumers (Trites et al., 1999; Essington, 2006; Willis, 2007). Could removal of whales have restructured ocean ecosystems by allowing the expansion of competitor groups, and could this limit whale recovery? The role of whales as food web structuring agents has best been studied in Antarctic waters. Laws (1977) estimated that the hunting of baleen whales in the Antarctic made 150 million t y^{-1} of "surplus" krill production otherwise consumed by whales available to other groups. He hypothesized that this led directly to observed growth among penguins and remaining marine mammal populations. Similarly, the more recent decline of penguin populations has been attributed to increased competition for krill from recovering whale and pinniped populations in the Southern Ocean (Trivelpiece et al., 2011; Trathan et al., 2012). In the central California Current ecosystem, periods of reduced seabird production have been attributed in part to episodes of increased local competition from recovering humpback whale populations (Ainley & Hyrenbach, 2010).

Our model analyses show that baleen whales were most sensitive to the availability of euphausiids (or meso-zooplankton production on GB) and planktivorous (forage) fishes (Fig. 5). This is a reflection of the importance of euphausiids and forage fish as major links between plankton production and upper trophic levels in coastal ecosystems (e.g., Cury et al., 2002) and shows the two most critical nodes in the trophic network through which baleen whales are likely

to limit or be limited by competing consumers. Regional differences in sensitivity to variability in energy flow through euphausiids or forage fishes reflect differences in model diets. Feeding at different trophic levels, euphausiids and fish, may provide baleen whales some resilience to variability in food web structure and opportunity for population expansion. Sensitivity analyses showed baleen whales to be insensitive to modest (20%) increases in fishery removals.

At the level of functional group aggregation used in this study, we could not consider how abundance changes among species of baleen whales may have affected one another. Laws (1977) proposed that minke whales in the Antarctic may have increased as a result of the decimation of the larger species. However, more recent genetic analysis indicating large pre- and post-exploitation minke whale populations in Antarctic waters does not support the idea that minke whales have been limited by competition with larger baleen whales for krill (Ballance et al., 2006; Ruegg et al., 2010). (Nor does it support the hypothesis that large minke numbers may be inhibiting recovery of large baleen whales today.)

Odontocete whales were most strongly affected by competition for their immediate prey (fishes and squid). Regional differences in sensitivity to variability in energy flow through forage fishes or squid again reflect differences in model diets. Most of this competition was from fisheries or from other fish (Fig. 5). Odontocete whales were particularly sensitive to competition with fisheries in the GB and NCC ecosystems. The high proportion of squid in the CGoA odontocete diet reduced direct competition between whales and commercial fisheries. It is interesting that odontocetes were insensitive to competition with pinnipeds in the NCC and CGoA given that pinnpeds are also piscivores and that their numbers have generally been increasing following years of hunting and culling (IUCN, 2011). Structural scenarios indicate that a five-fold increase in pinniped abundance would reduce odontocete production in the NCC

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and CGoA by only 15% (Table 4). An examination of their diets (diet matrices in Supplementary Material) show how odontocetes and pinnipeds target different fish and squid groups as prey, thus reducing competition. Changes to the lower food web had lesser, indirect effects on odontocetes.

Using time-dynamic ECOSIM scenarios, Trites et al. (1999) and Essington (2006) inferred the evolution of the Bering Sea and North Pacific ecosystems through time following imposed changes to mammal and fishery harvest rates to a final end-state (assumed approximate the pre-exploitation state). Trites et al. concluded that the heavy exploitation and loss of whale biomass in the Bering Sea may have contributed to, but could not explain large-scale shifts in ecosystem structure observed since the 1950s. Essington concluded that while the removal of whales from the oceanic North Pacific did not lead to broad-scale restructuring of energy flow patterns, a more subtle change in the composition of the top predator community from odontocetes to squid may have occurred. Essington further speculated that a change in top predators from long-lived (whales) to short-lived groups (squid) could lead to more rapid response times and greater ecosystem susceptibility to environmental variability.

Though we did not consider non-trophic processes, whales may also affect the physical environment and chemical cycling. For example, re-suspension of shelf sediments by feeding gray whales may be substantial. Changes in gray whale feeding intensity may have strong effects on nutrient cycling, the composition of the benthic community, and increase exposure of benthic invertebrates to predation by seabirds (Alter et al., 2007) and fishes. In the Southern Ocean, where trace nutrients are limiting, removal of whales may have attenuated an important iron-delivery pathway to oceanic waters and reduced ecosystem productivity (Lavery et al., 2010; Nicol et al., 2010; Smetacek, 2008).

4.4. Pinnipeds

The static E2E network scenarios indicate that expanding pinniped populations would have very large, negative impacts upon NCC and the CGoA fisheries. The disproportionately large impact of seals and sea lions on fisheries compared to the impact of expanding whale populations may be attributed to a diet richer in fish than in cephalopods. Odontocete diets, while rich in fish, include more cephalopods, especially in the CGoA. Pinnipeds also forage in the benthic environment, bringing them in closer direct competition with humans for crab and groundfish than are the whales.

The time-dynamic scenarios, which allowed for compensatory changes in community composition and relaxed the assumption of constant transfer efficiencies, indicate much less severe impacts upon fisheries by pinnipeds. However, parameter uncertainty allowed for the Monte Carlo selection of base models (i.e., models run without forcing mammal biomass) that showed large increases over time among seabird and mammal populations before reaching equilibrium conditions. The most extreme change among all four ecosystems was for the NCC pinnipeds, which on average increased by nearly six-fold over a 200-year period. Fisheries harvest in these long-period scenarios decreased by 7%.

Could the hypothetical five-fold expansion of pinniped biomass used as our target scenario actually be realized? While NCC and CGoA pinniped populations are below estimated historical levels, this scenario may exceed historical levels in both systems. In the NCC, California sea lions (*Zalophus californicus*) and harbor seals (*Phoca vitulina*) represent half of the total pinniped biomass and may already be near their carrying capacities (Carretta et al., 2009). The

eastern Steller sea lion population (*Eumetopias jubatus*), the largest single contributor to the overall pinniped biomass in both the NCC and the CGoA, has been growing steadily since the 1970s (Allen & Angliss, 2011). The sustainable carrying capacity of the west coast ecosystem is unknown, but the eastern Steller sea lion population appears to have recovered to levels observed in the early 20th century (Pitcher et al., 2007). On the other hand, northern fur seals (*Callorhinus ursinus*), an important pinniped group in the CGoA, have been reduced to 1/3rd the number observed in the 1950s and are not showing strong signs of recovery (Allen & Angliss, 2011). The models do not resolve individual pinniped groups so they cannot be used to explain why some populations are expanding and others are not. Energy resource competition between pinniped species may be one reason.

In the sWAP ecosystem, a hypothetical five-fold increase in pinniped abundance led to decreases in seabirds, penguins, and baleen whales in both the E2E network scenarios and time-dynamic scenarios. These effects were greater than any of the other mammal scenarios run in the other regions. The magnitude of the effect may be attributed to the fact that pinnipeds were already important consumers in the sWAP ecosystem before the increased biomass scenario was run. The broad distribution of their impact may be attributed to the fact that the planktivorous seal group, represented by crabeater seals (*Lobodon carcinophagus*), feed directly upon euphausiids - the main energy transfer pathway from phytoplakton to most upper trophic levels. Antarctic fur seals also eat euphausiids but were not explicitly included with the planktivorous pinnipeds in the current sWAP model. Fur seals are most abundant in the northern Antarctic Peninsula and the sub-Antarctic islands. They have largely recovered to their pre-exploitation numbers, but we can speculate on the possible expansion of the number of fur seals foraging in the south with the retreat of sea-ice in a warming world. An expansion of fur seal abundance in

the sWAP ecosystem could have a similar effect on the whole food web as the simulated expansion of crabeater seals conducted here. However, we do not estimate the carrying capacity the sWAP ecosystem, and the ultimate number of planktivorous seals supported may be limited by direct competition between crabeater seals and fur seals.

4.5. Comments on modeling technique and uncertainty

The donor-controlled, E2E network scenarios show the immediate effects of imposed changes to the food web structure upon individual functional groups under the assumption that food resources are limiting (Steele, 2009; Steele & Ruzicka, 2011). These static scenarios do not estimate ecosystem evolution over time but define alternate system states (trophic network matrix A_{cp}) directly. We were not forced to assume the accuracy of explicitly defined predator-prey relationships nor of implicit recruitment processes within the model, but we did have to define *a priori* how competitors could respond to targeted changes to the consumption rate of a particular functional group. As the simplest assumption, an imposed change to the consumption rate of a group was offset by an opposite change among all its competitors in proportion to their relative importance as consumers in the initial model.

Time-dynamic scenarios allow for the evolution of compensatory responses over time. These include changes to community composition and allow for reduced senescence mortality to support increased predation mortality. The dynamic model scenarios produced qualitatively similar, though smaller, changes to the ecosystem as did the E2E network scenarios. As we did not see large changes to community composition or system biomass, transfer efficiencies must have increased and less "surplus" production was lost to the detritus. In neither model system did

the imposed scenarios change the topology of the system - existing links were strengthened or attenuated but neither created nor destroyed.

In both the E2E network models and the time-dynamic models, we incorporated the propagation of parameter uncertainty and variability through the trophic network to estimate uncertainty about each model-derived metric and scenario. The uncertainty ranges presented should not be given the same weight of meaning as a formal statistical analysis of independent observations - but rather interpreted as the uncertainty within the set of implicit assumptions of the fundamental modeling technique (E2E network structure vs. time-dynamic scenario). These assumptions define the relative importance of production driven ("bottom-up") vs. consumer driven ("top-down") controls on ecosystem behavior. The uncertainty ranges were also defined by the rejection criteria used to distinguish viable from non-viable food webs. In the donor-controlled, E2E network scenarios we considered a model viable as long as the predation pressure was less than the production rate of every functional group. Valid arguments could be made for other criteria, e.g., to allow for emigration and immigration, to allow the extinction of some groups, or to require the biomass growth of some groups.

Finally, model-based investigation of the impact of current and expanded whale populations on ecosystem structure and energy flow patterns and of factors limiting population growth must consider the limitations of our models and of trophic models in general. Is model resolution sufficient to reveal important processes? These ecosystem-scale food web models represent large-scale spatial averages of energy flow. If direct competition for prey is more important at the mesoscale than at the regional scale or if local interference competition is important, then these models provide lower bound estimates of competition and the consequences of whale expansion. Indeed, as an example, the decrease of penguins on South Georgia has been attributed

to increased numbers of fur seals feeding on the same prey in the same local foraging areas (Trathan et al., 2012). Aggregation of species and species life-history stages into less resolved functional groups may also mask important subtleties of resource partitioning. Other processes, not generally considered in energy flow models, but known to be important include recruitment dynamics and demographic limitations (difficulty finding a mate).

5. Conclusions

I) The main conclusion from this modeling study is that the estimates of historical populations fit well with the estimates of potential population increase for both baleen and odontocete whales. A five-fold increase in baleen whale abundance would have only a small impact on other plankton consumers. In the E2E network scenarios, a twenty-fold increase would be possible energetically but would require significantly decreased production by the competitors of baleen whales. The scope for odontocete expansion varied between ecosystems but could be restricted (as on Georges Bank) because they feed at higher, less productive trophic levels than baleen whales.

II) The dominant prey of baleen whales - meso-zooplankton, macro-zooplankton, and euphausiids - are the main energy source for all higher trophic level pelagic production. In the E2E network scenarios, changes in baleen whale abundance have much greater and broader indirect effects on upper trophic levels and fisheries than changes in odontocete abundance have upon their direct competitors (Table 4). Pinnipeds appeared to be in closer competition with fisheries in the NCC and CGoA but showed less influence on the rest of the food web than the whales. In the sWAP where pinnipeds, whales, and birds are all competing for euphausiid prey, changes in pinniped abundance had a large, negative effect on birds and

whales. Time-dynamic scenarios (Table 5) did not show as large tradeoffs because they allowed for the development of compensatory mechanisms over time (e.g., increased transfer efficiency).

III) We did not see strong evidence for competition between whales and commercial fisheries. Neither a five-fold increase in baleen whale abundance nor a three-fold increase in odontocete abundance would have a substantial negative effect on fishery yield, as shown in both the network and time-dynamic scenarios. This agreed with the general conclusion drawn from the Morissette et al. (2012) model study: the culling or eradication of whales would not lead to meaningful increases among commercially important fish species.

IV) These results, showing the potential for large increases in marine mammal abundance, raise the question of why baleen whales have not regained higher population levels following the protections for individual species and the blanket, global whaling moratorium in 1986. Besides food limitations, whales face many lethal dangers including pollution, fishery mortality, and illegal hunting. Demographic limitations are likely to be important for the most severely decimated populations. Will recovery occur over longer time scales? Critical ecosystem functions may have been lost or attenuated as a result of dramatically reduced whale populations (e.g. Willis, 2007; Nicol et al., 2010). Alternatively, recovery may depend on how well whales compete with groups that have expanded in the absence of large whale populations. Our model analyses do not suggest any obviously empty niche waiting to be filled by whales. Comparison of ecosystem structure pre- and post-exploitation is not a simple task. The accurate reconstruction of pre-exploitation food webs requires the use of scientific observation, oral history, and archeological information (Pitcher, 2004). This type of information is largely unavailable for these ecosystems where commercial whaling has

preceded scientific observation and that have been largely inaccessible to pre-industrial societies. Thus, model scenario analysis based on existing knowledge of food web structure remains one of our best tools for exploring the limits to and impacts of expanding whale populations.

References

Ainley, D.G., Ballard, G., Blight, L.K., Ackley, S., Emslie, S.D., Lescroël, A., Olmastroni, S., Townsend, S.E., Tynan, C.T., Wilson, P., & Woehler, E., 2010. Impacts of cetaceans on the structure of southern ocean food webs. *Marine Mammal Science*, 26, 482-489.

Ainley, D.G., & Hyrenbach, K.D., 2010. Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). *Progress in Oceanography*, 84, 242-254.

Allen, B.M., & Angliss, R.P., 2011. Alaska Marine Mammal Stock Assessments, 2010. *NOAA Technical Memorandum NMFS- AFSC-223*, 292 pp.

Alter, S.E., Rynes, E., & Palumbi, S.R., 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proceeding of the National Academy of Sciences*, pnas.0706056104, 6 pp.

Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., & Friday, N., 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. *NOAA Technical Memorandum NMFS-AFSC-178*, 298 pp.

Ballance, L. Pitman, R.L., Hewitt, R.P., Siniff, D.B., Trivelpiece, W.Z., Clapham, P.J., & Brownell, R.L.Jr., 2006. The removal of large whales from the Southern Ocean: evidence for long-term ecosystem effects? In J.A. Estes, D.P. DeMaster, D.F. Doak, T.M. Williams, & R.L. Brownell Jr., *Whales, whaling, and ocean ecosystems*. University of California Press, Berkeley, CA, pp. 215-230.

Ballerini, T., Hofmann, E.E., Ainley, D.G., Daly, K., Marrari, M., Ribic, C.A., Smith, W.O., Steele, J.H. (in revision). Productivity and linkages of the food web of the southern region of the Western Antarctic Peninsula continental shelf. *Progress in Oceanography*.

Bax, N.J., 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Marine Science Symposia*, 193, 217-224.

Bowen, W.D., 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, 158, 267-274.

Carretta, J.V., Forney, K.A., Lowry, M.S., Barlow, J., Baker, J., Johnston, D., Hanson, B., Brownell Jr., R.L.J., Robbins, J., Mattila, D.K., Ralls, K., Muto, M.M., Lynch, D., & Carswell, L., 2009. U.S. Pacific marine mammal stock assessments: 2009. *NOAA Technical Memorandum NMFS-SWFSC-453*, 336 pp.

Christensen, V., & Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172, 109-139.

Christensen, V., Walters, C.J., & Pauly, D., 2005. Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver, Canada, 154 pp.

Collie, J.S., Gifford, D.J., & Steele, J.H., 2009. End-to-end foodweb control of fish production on Georges Bank. *ICES Journal of Marine Science*, 66, 2223-2232.

Croll, D.A., & Kudela, R., 2006. Ecosystem impact of the decline of large whales in the North Pacific. In J.A. Estes, D.P. DeMaster, D.F. Doak, T.M. Williams, & R.L. Brownell Jr., *Whales, whaling, and ocean ecosystems*. University of California Press, Berkeley, CA, pp. 202-214.

Cury, P., Shannon, L., & Shin, Y.-J., 2002. The functioning of marine ecosystems. In: Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem. Reykjavik, FAO Fisheries Report, 22 pp.

Emslie, S.D., & Patterson, W.P., 2007. Abrupt recent shift in δ13C and δ15N values in Adélie penguin eggshell in Antarctica. *Proceeding of the National Academy of Sciences*, 104, 11666-11669.

Essington, T.E., 2006. Pelagic ecosystem response to a century of commercial fishing and whaling. In J.A. Estes, D.P. DeMaster, D.F. Doak, T.M. Williams, & R.L. Brownell Jr., *Whales, whaling, and ocean ecosystems*. University of California Press, Berkeley, CA, pp. 38-49.

Estes, J.A, Demaster, D.P., Doak, D.F., Williams, T.E., & Brownell, R.L.Jr. (eds.). 2006. Whales, whaling and ocean ecosystems. University of California Press, Berkeley, CA.

Gaichas, S.K., Aydin, K.Y., & Francis, R.C., 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling, *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1553-1578.

Gaichas S.K., Odell, G.M., Aydin, K.Y., & Francis, R.C., 2012. Beyond the defaults: functional response parameter space and ecosystem-level fishing thresholds in dynamic food web model simulations. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 2077-2094.

Gerber, L.R., Morisette, L., Kaschner, K., & Pauly, D., 2009. Should whales be culled to increase fishery yield? *Science*, 323, 880-881.

Hutchings, J.A., & Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk, *Bioscience*, 54, 297-309.

IUCN, 2011. International Union for Conservation of Nature and Natural Resources Red List of
Threatened Species. Version 2011.2. <www.iucnredlist.org> Accessed 20 February 2012.

IWC, 2006. St. Kitts and Nevis Declaration. 2006 Annual Meeting of the International Whaling
Commission, IWC/58/16-Agenda Item 19, Document id: 58-16, Rev 6/20/2006.

Kareiva, P., Yuan-Farrell, C., & O'Conner, C., 2006. Whales are big and it matters. In J.A. Estes,
D.P. DeMaster, D.F. Doak, T.M. Williams, & R.L. Brownell Jr., *Whales, whaling, and ocean
ecosystems*. University of California Press, Berkeley, CA, pp. 379-387.

Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J.G., &
Smetacek, V., 2010. Iron defecation by sperm whales stimulates carbon export in the
Southern Ocean. *Proceedings of Royal Society B*, doi: 10.1098/rspb.2010.0863, 1-5.

Laws, R.M., 1977. Seals and whales of the Southern Ocean. *Philosophical Transactions of the
Royal Society of London. Series B*, 279, 81-96.

Link, J.S., Griswold, C.A., Methratta, E.T., & Gunnard, J., 2006. Documentation for the Energy
Modeling and Analysis eXercise (EMAX). *NOAA Northeast Fisheries Science Center
Reference Document 06-15*, 166 pp.

Mate, B., 2001. Movements of blue whales in the eastern north Pacific. *AGU Ocean Sciences
Meeting*. Honolulu, HI, 11-15 February 2002.

Moore, S.E., Urban, R.J., Perryman, W.L., Gulland, F., Perez-Cortes, M.H., Wade, P.R., Rojas-
Bracho, L., & Rowles, T., 2001. Are gray whales hitting "K" hard? *Marine Mammal Science*,
17, 954-958.

Morissette, L., Christensen, V., & Pauly, D., 2012. Marine mammal impacts in exploited
ecosystems: would large scale culling benefit fisheries? *PLoS ONE*, 7, e43966.

doi:10.1371/journal.pone.0043966.

Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K.M., & van der Merwe, P., 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish and Fisheries*, 11, 203-209.

Oliver, J.S., & Slattery, P.N., 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology*, 66, 1965-1975.

Overholtz, W.J., Murawski, S.A., & Foster, K.L., 1991. Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA. *ICES Marine Science Symposia*, 193, 198-208.

Pauly, D., & Christensen, V., 1995. Primary production required to sustain global fisheries. *Nature*, 374, 255-257.

Pitcher, K.W., Olesiuk, P.F., Brown, R.F., Lowry, M.S., Jeffries, S.J., Sease, J.L., Perryman, W.L., Stinchcomb, C.E., & Lowry, L.F., 2007. Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. *Fishery Bulletin*, 107, 102-115.

Pitcher, T.J., 2004. Back to the Future: advances in methodology for modelling and evaluating past ecosystems as future policy goals. *Fisheries Centre Research Reports*, 12, 158 pp.

Roman, J., & McCarthy, J.J., 2010. The whale pump: marine mammals enhance primary production in a coastal basin. *PLoS ONE*, 5, 1-8.

Roman, J., & Palumbi, S.R., 2003. Whales before whaling in the North Atlantic. *Science*, 301, 508-510.

Ruegg, K.C., Anderson, E.C., Baker, C.S., Vant, M., Jackson, J.A., & Palumbi, S.R., 2010. Are Antarctic minke whales unusually abundant because of 20th century whaling? *Molecular Ecology*, 19, 281-291.

Ruzicka, J.J., Brodeur, R.D., Emmett, R.L., Steele, J.H., Zamon, J.H., Morgan, C.A., Thomas, A.C., & Wainwright, T.W., 2012. Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and an End-to-End model to investigate system response to alternate forcing scenarios. *Progress in Oceanography*, 102: 19-41.

Smetacek, V., 2008. Are declining Antarctic krill stocks a result of global warming or the decimation of the whales? In Duarte, C. (Ed.), *The impact of global warming on polar ecosystems*. Fundacion BBVA, Spain, 46-83.

Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A., & Deming, J.W., 1989. Vent fauna on whale remains. *Nature*, 341, 27-28.

Steele, J., Collie, J., Bisagni, J., Fogarty, M., Gifford, D., Link, J., Sieracki, M., Sullivan, B., Beet, A., Mountain, D., Durbin, E., Palka, D., & Stockhausen, W., 2007. Balancing end-to-end budgets of the Georges Bank ecosystem. *Progress in Oceanography*, 74, 423-448.

Steele, J., & Ruzicka, J.J., 2011. Constructing end-to-end models using ECOPATH data. *Journal of Marine Systems*, 87, 227-238.

Steele, J.H., 2009. Assessment of some linear food web methods. *Journal of Marine Systems*, 76, 186–194.

Trathan P.N., Ratcliffe N., & Masden E.A., 2012. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. *Ecography*, 35, 1-11.

Trites, A.W., Christensen, V., & Pauly, D., 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science*, 22, 173–187.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M., & Pauly, D., 1999. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. *Fisheries Centre Research Reports*, 7, 106 pp.

Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., & Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceeding of the National Academy of Sciences*, 108, 7625-7628.

Willis, J., 2007. Could whales have maintained a high abundance of krill? *Evolutionary Ecology Research*, 9, 651–662.

Yodzis, P., 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution*, 16, 78-84.

Figure Captions

Figure 1. The main energy flow pathways in the Northern California Current, from primary producers to top predators and fisheries. Box height is proportional to production rate, and linkage thickness is proportional to energy flow rate. The intensity of green shading is proportional to the footprint of baleen whales on each functional group via direct and indirect pathways.

Figure 2. Major pelagic predators on euphausiids (or macro-zooplankton for Georges Bank) and pelagic fishes as fractions of total predation and fishery removal. Empty wedges represent non-pelagic predation. (Expanded results given in Supplementary Material Tables A19 - A20.)

Figure 3. End-to-end network structure scenario showing effects of increasing baleen whale abundance and grazing by a factor of 5. (Complete scenario results are given in Table 4 and in the Supplementary Material.)

Figure 4. End-to-end network structure scenario showing effects of increasing odontocete abundance and predation by a factor of 3. (Complete scenario results are given in Table 4 and in the Supplementary Material.)

Figure 5. Sensitivity analyses showing trophic linkages having the strongest impact upon marine mammals. Producers are listed across the top. Consumers are listed down the side. Dot size shows effect of 20% alterations to individual trophic linkages upon marine mammal productivity. Green dots show positive impacts. Red dots show negative impacts. Strong color

represents a net impact that exceeds the 20% primary alteration. (Sensitivity analysis results

summarized in Supplementary Material Tables A29 - A31).

Table 1. Population estimates of the great whales, pre-exploitation and most recent current estimates.

species	region	Population pre-exploitation		Population current		Depletion level (relative to historic)	IUCN Red List (a) population status	trend
BALEEN WHALES								
blue whale	GLOBAL	280,000	a	17,500	a	6%	endangered	increasing
fin whale	GLOBAL	548,000	b	47,300	b	9%	endangered	?
sei whale	GLOBAL	256,000	b	54,000	b	21%	endangered	?
humpback whale	GLOBAL	115,000	b	21,570	b	19%	least concern	increasing
right whale	GLOBAL	100,000	b	3,000	b	3%	endangered (Northern hemisphere)	?
							least concern (Southern hemisphere)	increasing
gray whale	NE Pacific	37,364	b	19,126	c	51%	least concern (NE Pacific)	stable
							critically endangered (NW Pacific)	--
minke whale	GLOBAL	490,000	b	505,000	b	103%	least concern (common minke)	stable
							data deficient (Antarctic minke)	?
bowhead whale	GLOBAL	> 39,000	a	> 10,000	a	25%	least concern	increasing
Bryde's whale	GLOBAL	?	a	?	a	?	data deficient	?
ODONTOCETES								
sperm whale	GLOBAL	1,100,000	b	452,000	b	41%	vulnerable	?
killer whale	GLOBAL	?		50,000	a	?	data deficient	?
beaked whales	GLOBAL	?	a	?	a	?	data deficient	?

[a] (IUCN, 2011)
[b] (Kareiva et al., 2006)
[c] (Allen & Angliss, 2011)

Table 2. Percentage of production required to support marine mammals, seabirds, and fisheries (the "footprint"). Values are gross footprints and include the non-growth costs associated with prey group production (i.e., metabolic costs and any "other" non-predation mortality). Values in parentheses are ± 1 standard deviation of 1000 random, thermodynamically balanced models. (See Table A17 in the Supplementary Material for expanded detail)

	planktivorous fish	cephalopods	macro-zooplankton	euphausiids	phytoplankton (diatoms)
Northern California Current					
baleen whales	**5.0%** (4.0)	**2.8%** (2.9)	**3.1%** (1.8)	**2.7%** (1.2)	**2.4%** (1.3)
odontocetes	**22.8%** (8.4)	**32.8%** (11.4)	**14.7%** (4.5)	**14.4%** (3.7)	**11.1%** (2.8)
pinnipeds	**7.0%** (2.9)	**5.9%** (2.9)	**4.5%** (1.9)	**6.2%** (2.6)	**3.9%** (1.5)
seabirds	**11.8%** (6.6)	**19.0%** (12.2)	**6.8%** (3.2)	**5.6%** (2.2)	**4.6%** (1.8)
fisheries	**37.2%** (8.4)	**26.6%** (10.5)	**22.3%** (5.5)	**34.0%** (4.5)	**19.8%** (3.2)
Central Gulf of Alaska					
baleen whales	**5.4%** (4.6)	**2.9%** (2.5)	**6.6%** (5.0)	**5.2%** (3.2)	**3.9%** (2.3)
odontocetes	**11.2%** (5.6)	**21.4%** (11.6)	**14.0%** (6.9)	**10.2%** (4.7)	**7.9%** (3.6)
pinnipeds	**8.5%** (3.9)	**6.5%** (3.7)	**6.0%** (3.1)	**6.5%** (3.1)	**4.6%** (2.2)
seabirds	**4.5%** (2.8)	**6.1%** (5.0)	**5.0%** (3.0)	**4.2%** (2.1)	**3.2%** (1.6)
fisheries	**52.3%** (7.3)	**48.8%** (7.8)	**44.9%** (4.4)	**44.1%** (4.4)	**31.9%** (3.7)
Georges Bank					
baleen whales	**5.6%** (7.6)	--	**4.3%** (5.7)	--	**1.7%** (2.2)
odontocetes	**34.8%** (19.2)	--	**15.7%** (12.0)	--	**7.6%** (5.6)
pinnipeds	--	--	--	--	--
seabirds	**5.6%** (7.6)	--	**4.3%** (5.7)	--	**1.7%** (2.2)
fisheries	**57.8%** (9.9)	--	**47.7%** (6.9)	--	**28.4%** (4.3)
southwestern Antarctic Peninsula					
baleen whales	**3.2%** (5.9)	**2.6%** (5.0)	**2.0%** (3.7)	**3.1%** (3.5)	**1.7%** (2.3)
odontocetes	--	--	--	--	--
plank pinniped	**4.0%** (3.9)	**5.5%** (4.7)	**2.7%** (2.5)	**5.7%** (4.2)	**2.7%** (2.1)
pisc pinniped	**41.5%** (13.9)	**41.7%** (14.9)	**29.9%** (11.8)	**27.0%** (8.8)	**19.5%** (6.7)
penguins	**9.8%** (9.0)	**19.6%** (14.1)	**7.7%** (6.6)	**7.7%** (5.8)	**5.2%** (4.1)
seabirds	**3.9%** (8.2)	**3.4%** (6.9)	**2.8%** (5.9)	**2.5%** (5.1)	**1.8%** (3.6)

Table 3. Percentage of fish production directly consumed by mammals or removed by fishery harvest. Values are based on total fish production and exclude the costs of metabolism. Fishery harvest includes yield and discards. Values in parentheses are ± 1 standard deviation of 1000 random, thermodynamically balanced models. (See Table A18 in the Supplementary Material for expanded detail)

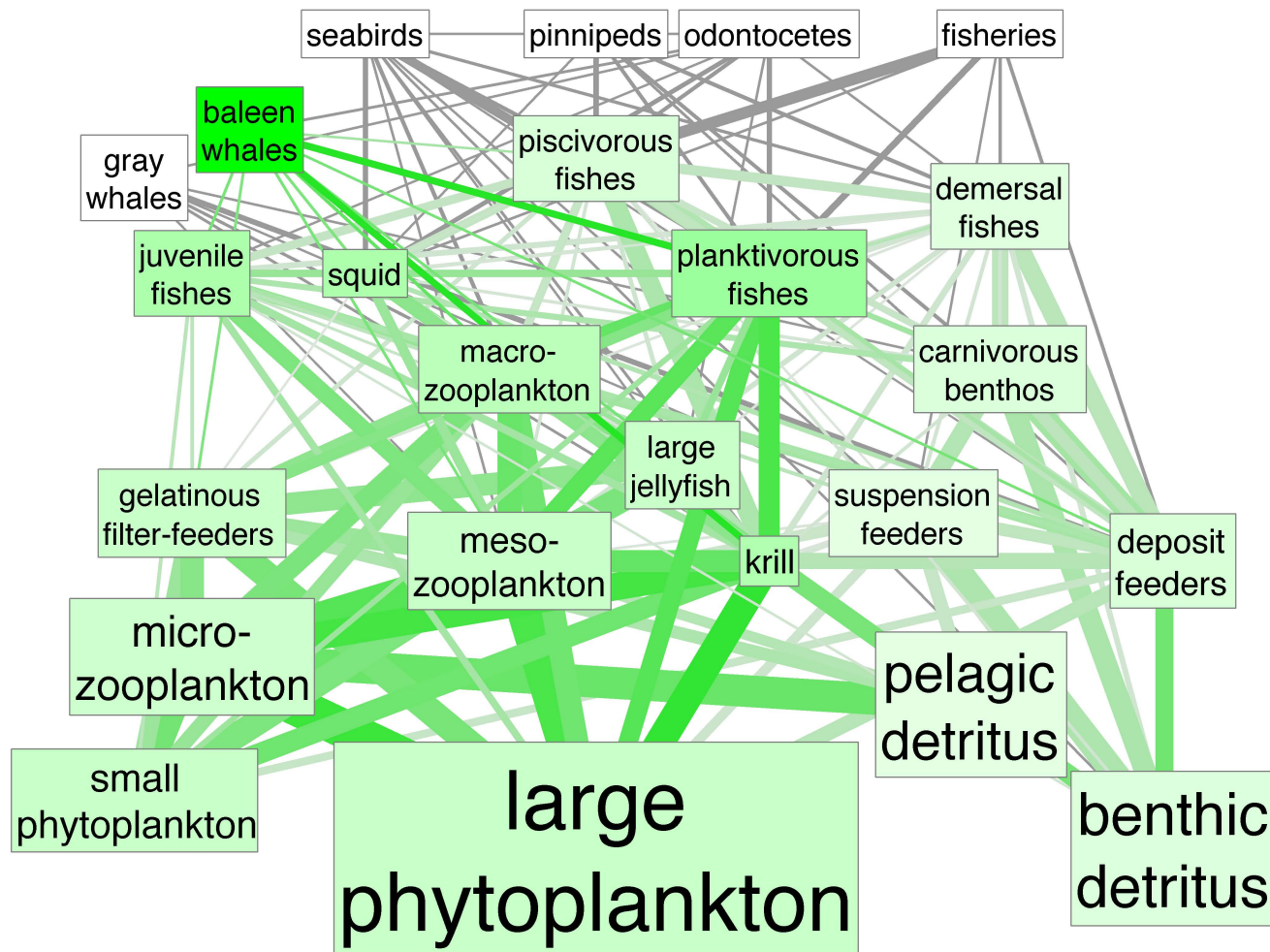|	planktivorous fish	ALL fish
Northern California Current		
baleen whales	**3.8%** (2.8)	**2.5%** (1.7)
odontocetes	**2.0%** (1.2)	**2.1%** (0.9)
pinnipeds	**1.2%** (1.0)	**3.6%** (1.7)
fisheries	**3.5%** (1.1)	**20.2%** (4.9)
Central Gulf of Alaska		
baleen whales	**4.0%** (3.8)	**3.6%** (3.3)
odontocetes	**0.8%** (1.1)	**1.0%** (1.1)
pinnipeds	**3.1%** (1.9)	**3.0%** (1.6)
fisheries	**4.6%** (1.3)	**6.1%** (1.4)
Georges Bank		
baleen whales	**1.1%** (2.8)	**0.6%** (1.4)
odontocetes	**5.8%** (7.0)	**2.9%** (2.7)
fisheries	**6.2%** (6.5)	**14.3%** (9.1)
Antarctic Peninsula		
baleen whales	**0.8%** (1.4)	**0.7%** (1.3)
plankt. pinnipeds	**0.6%** (0.7)	**0.6%** (0.6)
pisc. pinnipeds	**0.9%** (1.1)	**1.2%** (1.3)
penguins	**0.6%** (0.5)	**0.5%** (0.5)
seabirds	**0.1%** (0.1)	**0.1%** (0.1)

Table 4. Response of upper trophic level pelagic groups in each ecosystem to alternate increased mammal abundance in end-to-end network models. Scenario effects are expressed as group production in the scenario-modified model relative to the base model: $\Delta P = P_{scenario\ model} / P_{base\ model}$. Values in parentheses are ± 1 standard deviation of 1000 random, thermodynamically balanced models. Baleen whales include gray whales in the NCC and CGoA. sWAP seabirds exclude penguins. sWAP pinniped scenarios pool planktivores (crabeater seals) and piscivores (Weddell seals) but all responses shown here are for piscivorous pinnipeds only (See Tables A21 - A24 in the Supplementary Material for expanded scenario results)
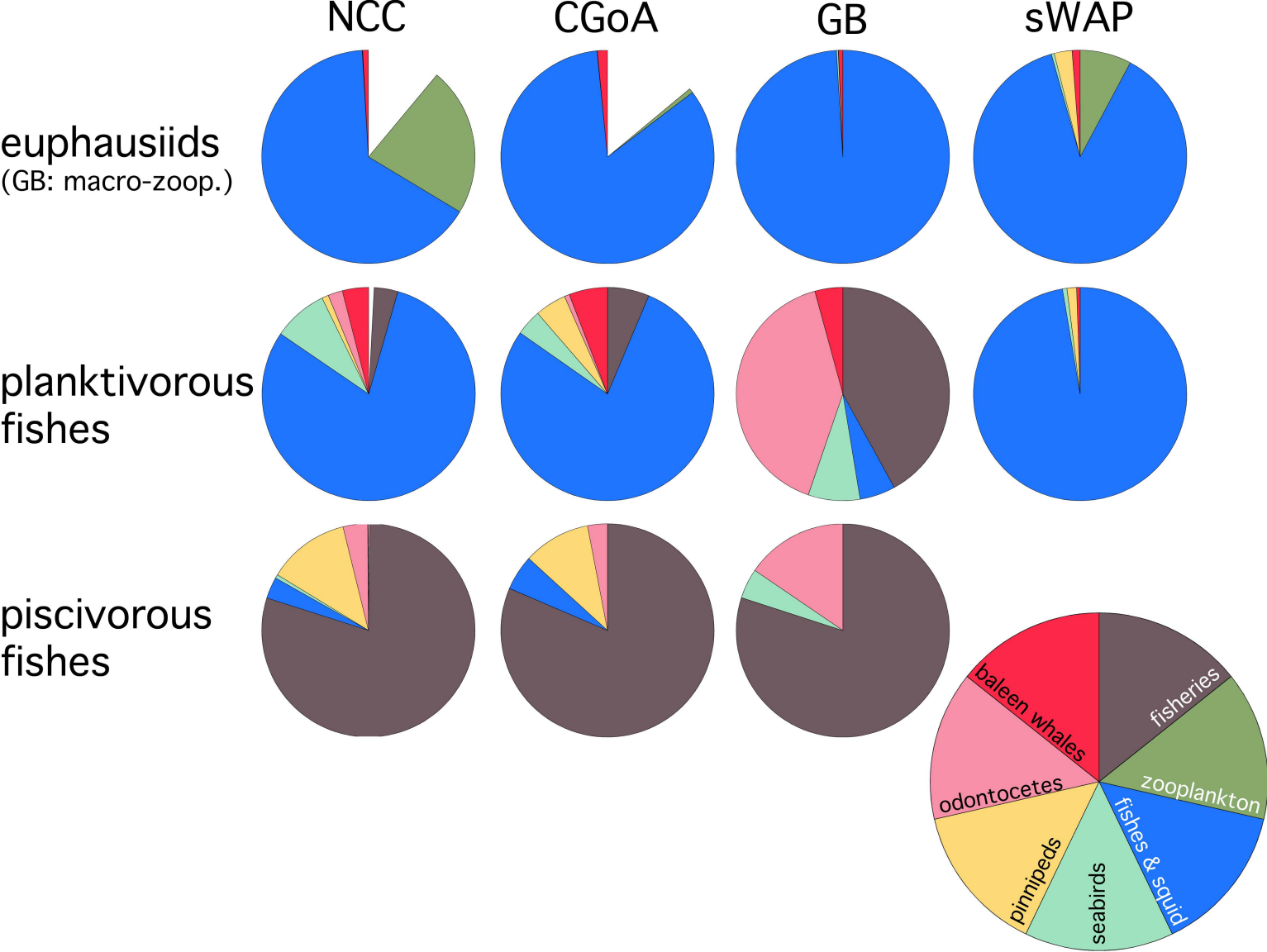
Baleen whales 5X	NCC	CGoA	GB	sWAP
planktivorous fish	**0.98** (0.01)	**0.94** (0.04)	**0.98** (0.02)	**0.98** (0.02)
piscivorous fish	**0.92** (0.04)	**0.76** (0.14)	**0.91** (0.10)	--
seabirds	**0.77** (0.17)	**0.77** (0.16)	**0.85** (0.16)	**0.87** (0.15)
baleen whales	**4.96** (0.13)	**4.92** (0.14)	**4.93** (0.30)	**4.97** (0.20)
odontocetes	**0.80** (0.13)	**0.86** (0.11)	**0.77** (0.25)	--
pinnipeds	**0.84** (0.12)	**0.71** (0.21)	--	**0.86** (0.15)
fisheries	**0.87** (0.06)	**0.71** (0.20)	**0.95** (0.06)	--

Baleen whales 20X	NCC	CGoA	GB	sWAP
planktivorous fish	**0.92** (0.05)	**0.72** (0.18)	**0.90** (0.09)	**0.91** (0.09)
piscivorous fish	**0.69** (0.13)	**0.36** (0.19)	**0.76** (0.17)	--
seabirds	**0.34** (0.24)	**0.37** (0.22)	**0.62** (0.25)	**0.61** (0.24)
baleen whales	**17.18** (3.02)	**17.23** (2.60)	**18.63** (2.63)	**18.89** (2.70)
odontocetes	**0.39** (0.20)	**0.56** (0.20)	**0.47** (0.33)	--
pinnipeds	**0.52** (0.19)	**0.27** (0.25)	--	**0.58** (0.25)
fisheries	**0.58** (0.13)	**0.25** (0.23)	**0.87** (0.09)	--

Odontocetes 3X	NCC	CGoA	GB	sWAP
planktivorous fish	**1.00** (0.00)	**0.99** (0.01)	**1.00** (0.00)	--
piscivorous fish	**0.98** (0.01)	**0.96** (0.03)	**0.80** (0.17)	--
seabirds	**0.90** (0.06)	**0.92** (0.08)	**0.71** (0.22)	--
baleen whales	**0.96** (0.03)	**0.99** (0.01)	**0.94** (0.09)	--
odontocetes	**2.99** (0.09)	**2.93** (0.33)	**2.65** (0.53)	--
pinnipeds	**0.91** (0.04)	**0.92** (0.08)	--	--
fisheries	**0.91** (0.04)	**0.93** (0.06)	**0.87** (0.08)	--

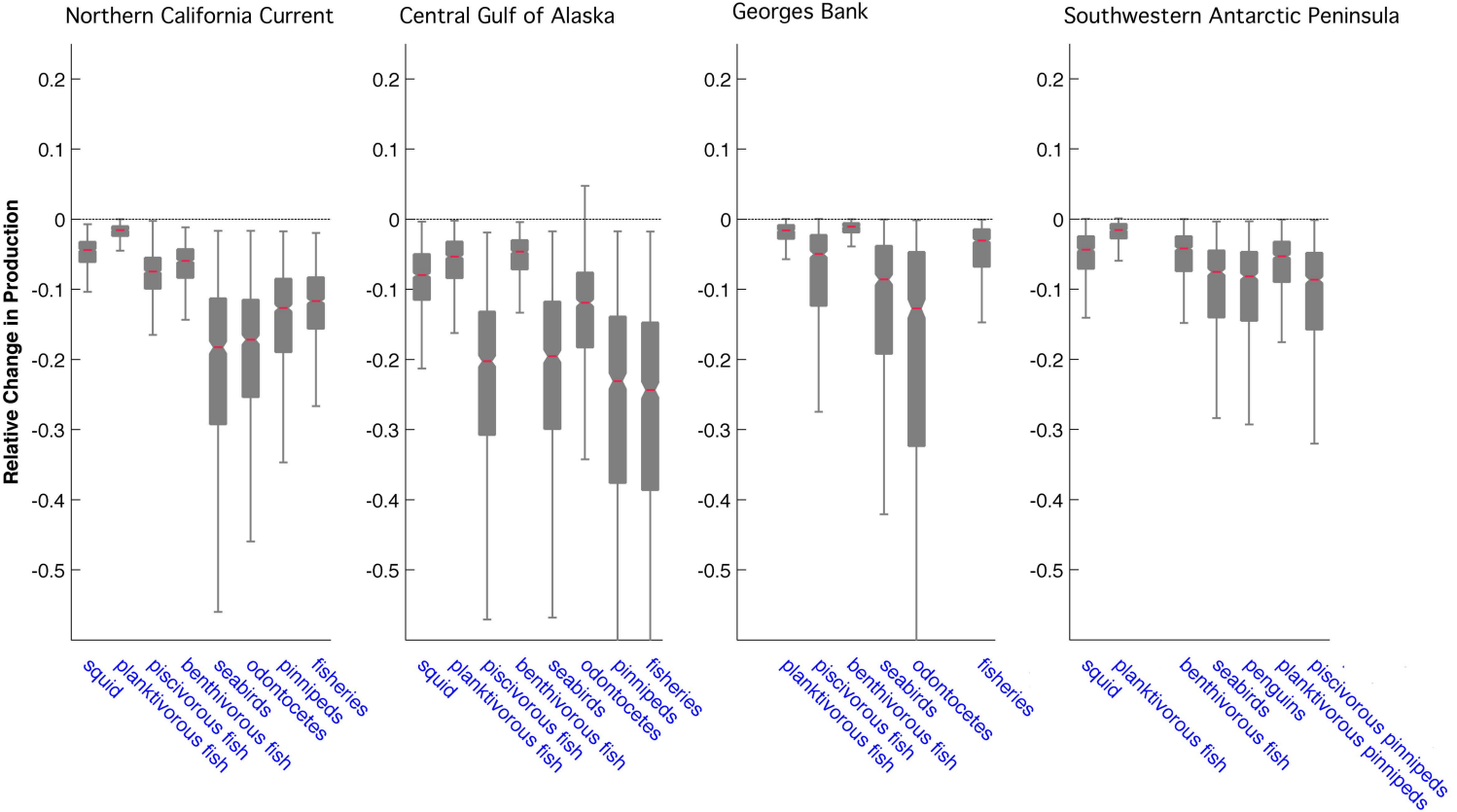| Pinnipeds 5X	NCC	CGoA	GB	sWAP
planktivorous fish	**1.00** (0.00)	**1.00** (0.00)	--	**0.95** (0.04)
piscivorous fish	**0.99** (0.01)	**0.87** (0.07)	--	--
seabirds	**0.93** (0.06)	**0.88** (0.08)	--	**0.57** (0.19)
baleen whales	**0.97** (0.04)	**0.95** (0.05)	--	**0.80** (0.19)
odontocetes	**0.87** (0.07)	**0.86** (0.10)	--	--
pinnipeds	**4.92** (0.31)	**4.89** (0.25)	--	**3.43** (0.91)
fisheries	**0.55** (0.24)	**0.69** (0.13)	--	--

Table 5. Time-dynamic model response of upper trophic pelagic groups to alternate mammal abundance scenarios. Scenario effects are expressed as biomass in the modified model relative to the base model after 200 years: $\Delta B = B_{scenario\ model} / B_{base\ model}$. Values in parentheses are the 1st and 3rd quartiles of 465 random NCC models, 419 CGoA models, 257 GB models, and 468 sWAP models. Baleen whales include gray whales in the NCC and CGoA. sWAP seabirds exclude penguins. sWAP pinniped scenarios pool planktivores (crabeater seals) and piscivores (Weddell seals) but responses shown are for piscivores only. (See Tables A25 - A28 in the Supplementary Material for base model time-series changes and expanded scenario results)

Baleen whales 5X	NCC	CGoA	GB	sWAP
planktivorous fish	**0.99** (0.93, 1.00)	**0.99** (0.92, 1.00)	**1.00** (0.99, 1.00)	**1.00** (0.99, 1.00)
piscivorous fish	**1.00** (0.97, 1.00)	**0.99** (0.94, 1.00)	**1.00** (0.99, 1.00)	--
seabirds	**0.98** (0.92, 1.00)	**0.98** (0.90, 1.00)	**1.00** (0.98, 1.00)	**1.00** (0.97, 1.00)
baleen whales	**4.98** (3.18, 6.99)	**4.94** (2.96, 7.40)	**4.99** (3.34, 8.13)	**4.97** (2.20, 8.52)
odontocetes	**0.99** (0.95, 1.00)	**1.00** (0.97, 1.01)	**1.00** (0.97, 1.00)	--
pinnipeds	**0.99** (0.97, 1.00)	**0.98** (0.88, 1.00)	--	**1.00** (0.97, 1.00)
fisheries	**0.99** (0.97, 1.00)	**0.98** (0.93, 1.00)	**1.00** (1.00, 1.00)	--

Baleen whales 20X	NCC	CGoA	GB	sWAP
planktivorous fish	**0.98** (0.78, 1.00)	**0.98** (0.75, 1.00)	**1.00** (0.97, 1.00)	**1.00** (0.97, 1.00)
piscivorous fish	**0.99** (0.92, 1.00)	**0.96** (0.83, 1.00)	**1.00** (0.98, 1.00)	--
seabirds	**0.96** (0.76, 0.99)	**0.94** (0.74, 1.00)	**0.99** (0.95, 1.00)	**0.99** (0.91, 1.00)
baleen whales	**19.9** (12.7, 27.9)	**19.7** (11.8, 29.6)	**20.0** (13.4, 32.6)	**19.9** (8.79, 34.1)
odontocetes	**0.97** (0.84, 1.00)	**1.00** (0.90, 1.03)	**0.99** (0.93, 1.00)	--
pinnipeds	**0.99** (0.92, 1.00)	**0.95** (0.70, 1.00)	--	**0.99** (0.92, 1.00)
fisheries	**0.99** (0.91, 1.00)	**0.96** (0.80, 1.00)	**1.00** (0.98, 1.00)	--

Odontocetes 3X	NCC	CGoA	GB	sWAP
planktivorous fish	**1.00** (0.99, 1.01)	**1.00** (1.00, 1.01)	**1.00** (0.96, 1.00)	--
piscivorous fish	**1.00** (0.98, 1.00)	**1.00** (0.98, 1.00)	**1.00** (0.95, 1.00)	--
seabirds	**1.00** (0.96, 1.01)	**1.00** (0.99, 1.01)	**1.00** (0.98, 1.00)	--
baleen whales	**1.00** (0.99, 1.01)	**1.00** (0.98, 1.00)	**1.00** (1.00, 1.00)	--
odontocetes	**2.95** (1.56, 4.94)	**3.02** (1.37, 7.44)	**2.99** (1.31, 7.18)	--
pinnipeds	**0.98** (0.84, 1.00)	**1.00** (0.98, 1.00)	--	--
fisheries	**1.00** (0.99, 1.00)	**1.00** (0.98, 1.00)	**1.00** (0.99, 1.00)	--

Pinnipeds 5X	NCC	CGoA	GB	sWAP
planktivorous fish	**1.00** (1.00, 1.02)	**1.00** (0.96, 1.00)	--	**1.00** (0.98, 1.06)
piscivorous fish	**0.99** (0.91, 1.00)	**0.97** (0.91, 1.00)	--	--
seabirds	**1.00** (0.99, 1.01)	**1.00** (0.98, 1.01)	--	**0.97** (0.86, 1.00)
baleen whales	**1.00** (1.00, 1.02)	**1.00** (1.00, 1.00)	--	**0.99** (0.87, 1.00)
odontocetes	**1.01** (1.00, 1.13)	**1.00** (0.97, 1.00)	--	--
pinnipeds	**4.86** (1.67, 20.4)	**4.93** (2.64, 7.48)	--	**5.12** (2.39, 9.83)
fisheries	**0.99** (0.95, 1.00)	**0.98** (0.95, 1.00)	--	--

	NCC	CGoA	GB	sWAP
euphausiids (GB: macro-zoop.)				
planktivorous fishes				
piscivorous fishes				

baleen whales

fisheries

zooplankton

odontocetes

fishes & squid

pinnipeds

seabirds

| | Northern California Current | Central Gulf of Alaska | Georges Bank | Southwestern Antarctic Peninsula |

Northern California Current | Central Gulf of Alaska | Georges Bank

y-axis: Relative Change in Production

Categories: squid, planktivorous fish, piscivorous fish, benthivorous fish, seabirds, baleen whales, pinnipeds, fisheries