

Energy-based ecosystem modelling illuminates the ecological role of Northeast Pacific herring

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ABSTRACT: The ecological importance of Pacific herring (*Clupea pallasii*) in the Northeast Pacific was re-evaluated by accounting for its high average energy content. An existing mass-balanced Ecopath food web model focusing on northern British Columbia waters was converted into a set of energy-balanced models using published energy content values for all functional groups. Ecosystem size spectrum slopes, proportions of herring in predator diets, and proportions of several large ecological categories in total ecosystem biomass and energy pools were compared across all models. Trophic effects of depleted whale population recovery were reassessed using Ecosim runs in the mass- and energy-balanced models. Balancing the high-energy model required a noticeable but non-significant increase in size spectrum slope relative to the original mass-balanced model. This may reflect energy content overestimates for large organisms, but more likely points to underestimated energy content, and possibly biomass, of planktonic groups. Forage fish and other pelagic organisms also accounted for higher proportions of the total ecosystem pool in the energy-balanced models. The reassessed trophic effects of whale population recovery were noticeably stronger for some active endothermic predators (small odontocetes and piscivorous seabirds) than suggested by published mass-balanced model results. However, most energy-balanced model outputs agreed qualitatively with those of the mass-balanced parent model. These findings suggest a potential for improved analysis of ecosystem structure and function, and forage fish trophodynamics, when prey group energy content is accounted for in ecosystem models.

KEY WORDS: Ecosystem modelling · Energy content · Northeast Pacific · Pacific herring · *Clupea pallasii* · Forage fish · Trophodynamics

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INTRODUCTION

Energy content distribution among marine prey species is highly non-uniform, with forage fish values typically exceeding those for other fish and invertebrates in both the North Atlantic (Spitz et al. 2010) and North Pacific (Anthony et al. 2000, Vollenweider et al. 2011). Spitz & Jouma'a (2013) placed Northeast Atlantic forage fish in the upper two of 3 prey quality categories (low, moderate and high) based on energy content. Marine mammal energetic demands increase with their metabolic cost of living (Spitz et al. 2012), inducing highly active predators such as porpoises

(Wisniewska et al. 2016), as well as some humpback whale populations (Moran et al. in press, Straley et al. in press), to feed largely on energy-rich forage fish. Many seabirds also preferentially target such high-energy prey to meet the steep metabolic demands of thermoregulation, flight and reproduction (e.g. Litzow et al. 2004). A preference for energy-rich prey (spawning Pacific salmon *Oncorhynchus* spp.) individuals has also been observed in a terrestrial omnivore (brown bear *Ursus arctos*) when hunting in easily accessible environments (Gende et al. 2004).

Energy content differences among prey species and the naturally fluctuating availability of high-

energy prey may, according to the 'junk food hypothesis' (Alverson 1992, Anderson & Piatt 1999, Österblom et al. 2008), profoundly impact marine predator health at both individual and population levels. Observations supporting this claim include a marked decline in Steller sea lion *Eumetopias jubatus* abundance in western Alaska since the 1970s (Rosen & Trites 2000, Trites & Donnelly 2003), a concurrent drop in breeding success at pigeon guillemot *Cephus columba* and black guillemot *C. grylle* colonies in the western Gulf of Alaska (Litzow et al. 2002) and western Beaufort Sea (Divoky et al. 2015), respectively, and mass starvation of California sea lion *Zalophus californianus* pups in the southern California Current since 2004 (McClatchie et al. 2016a, Banuet-Martínez et al. 2017). In these and other similar cases, predator populations appear to have been adversely affected by reduced availability of energy-rich forage fish caused by oceanographic fluctuations or regime shifts (Anderson & Piatt 1999, Österblom et al. 2008, McClatchie et al. 2016b). There are also at least 4 known, persistent shifts in dominance of marine ecosystems (Bering Sea, Gulf of Alaska, North Sea and Benguela Current) from lipid- and energy-rich forage fish to lipid- and energy-poor fish species. In all 4 cases, endothermic predator (marine mammal and/or seabird) population declines were associated with reduced availability of energy-rich prey (Litzow et al. 2006, Roux et al. 2013). In two of these ecosystems (Bering Sea and Benguela Current), forage fish declines were followed by increased jellyfish abundance (Brodeur et al. 2002, Brotz et al. 2012), suggesting even stronger shifts in food web structure. Reduced breeding success and abundance of blue-footed boobies *Sula nebouxi* in the Galápagos Islands, an equatorial upwelling system, has been linked to a decline in energy-rich Pacific sardine *Sardinops sagax* and a lack of alternative high-energy prey (Anchundia et al. 2014). This indicates a widespread reliance of endothermic marine predators on high-energy prey from arctic to equatorial waters.

Recent revisions to the oscillating control hypothesis on recruitment dynamics of Bering Sea walleye pollock *Gadus chalcogrammus* (Hunt et al. 2011), along with investigations in a British Columbia (BC) fjord ecosystem (Tommasi et al. 2013), have highlighted the importance of trophic control mechanisms in the NE Pacific. These mechanisms, originating in algal bloom phenology, trigger seasonal and interannual shifts in zooplankton community dominance between energy-rich and energy-poor species (Hunt et al. 2011, Tommasi et al. 2013). In turn, altered timing of such shifts affects juvenile fish

energy content and recruitment directly, via temporal and spatial mismatches with energy-rich zooplankton blooms, and indirectly, via resultant prey switching by omnivorous larger fish (Cooney et al. 2001, Heintz et al. 2013, Siddon et al. 2013). In the California Current, the 2015–2016 intrusion of a large, anomalously warm water mass and associated energy-poor zooplankton appears to have adversely affected many species at higher trophic levels (Di Lorenzo & Mantua 2016, McClatchie et al. 2016b). Increased abundance of energy-poor subtropical copepods (e.g. *Paracalanus parvus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis*) and a simultaneous decline in energy-rich subarctic species (e.g. *Calanus marshallae*, *Pseudocalanus minimus*, *Acartia longiremis*) off northern BC from 1990 to 2006 may also have affected fish nutrition (Cummins & Haigh 2010), and will likely be strengthened by future climate change. These studies underscore the importance of ecosystem control mechanisms acting through reduced availability of high-energy prey and spanning at least 3 trophic levels, with potentially noticeable repercussions for entire food webs, including predators and fisheries.

Pacific herring *Clupea pallasii* is a relatively large, long-lived forage fish inhabiting coastal waters from Korea to California (Hay et al. 2008). Throughout its range, this species forms a conduit for energy flow from zooplankton to higher predators (Schweigert et al. 2010, Pikitch et al. 2012a,b, Brodeur et al. 2014, Kumar et al. 2016), particularly during the spawning season (Willson & Womble 2006). Predators reliant on Pacific herring include charismatic and protected marine mammals (Womble & Sigler 2006, Moran et al. in press) and seabirds (Bishop et al. 2015, Sydesman et al. 2017), as well as numerous commercial fish (Brodeur et al. 2014, Osgood et al. 2016). Furthermore, the trophic role of Pacific herring is likely substantially enhanced by its high annual average energy content. Among NE Pacific coastal fish (Anthony et al. 2000, Vollenweider et al. 2011), adult herring is only exceeded in this respect by eulachon *Thaleichthys pacificus*, a depleted smelt species subject to bycatch in the shrimp trawl fishery (Moody & Pitcher 2010). Energy content values for 2 smaller local forage fish, Pacific sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus*, overlap with those of Pacific herring but are typically lower (Anthony et al. 2000, Vollenweider et al. 2011). Values reported for adult Pacific herring (Vollenweider et al. 2011) consistently place these fish among high-quality prey *sensu* Spitz & Jouma'a (2013). When energy content is accounted for, Pacific herring are

among the most important prey of Steller sea lions in SE Alaska (Vollenweider et al. 2006, Womble & Sigler 2006) and humpback whales *Megaptera novaeangliae* in Prince William Sound and Lynn Canal (Moran et al. in press). Furthermore, Alaskan humpback whales feed most heavily on adult herring when its energy content reaches its annual peak of $\sim 10 \text{ kJ g}^{-1}$ (Moran et al. in press), while Steller sea lion distribution in SE Alaska is correlated with both local herring biomass (Womble & Sigler 2006) and aggregation persistence (Gende & Sigler 2006, Sigler et al. 2017).

Therefore, NE Pacific ecosystem models may need to more explicitly account for prey energy content to fully represent the trophic roles of Pacific herring and other forage fish. Given the recent poor status of many herring stocks in BC (DFO 2015) and Alaska (NMFS 2014), ongoing recovery of whale populations feeding on herring and other forage fish (Surma & Pitcher 2015), the current importance of herring as prey to BC coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon (Osgood et al. 2016, Kumar et al. 2016), and increasing calls for precautionary, ecosystem-based forage fish management worldwide (Pikitch et al. 2012a,b), there is a clear need to re-examine the importance of energy-rich forage fish, especially herring, in NE Pacific food webs.

Ecosystem models can be constructed using several different currencies or types of units, including biomass, number of individuals or nutrient mass (Plagányi 2007). However, energy remains a rarely used model currency, even though ecosystem structure and function are fundamentally based on thermodynamic processes, i.e. highly inefficient energy transfer to higher trophic levels (Pauly & Christensen 1995). Plagányi & Butterworth (2004) noted the lack of representation of energy content differences among prey and their effects on predators as a major shortcoming of Ecopath with Ecosim (EwE) (Christensen & Walters 2004), one of the most prevalent ecosystem modelling frameworks (Coll et al. 2015). While EwE includes energy as a model currency option (Christensen & Walters 2004) the latter remains rarely used, and was only introduced to Ecosim (dynamic food web simulation) in EwE 6.

Size spectra (i.e. distributions of log-transformed biomass or abundance versus log-transformed individual size) are often used to characterize and predict ecosystem structure and status (Blanchard et al. 2017). A biomass size spectrum slope of zero is nearly universal across marine, freshwater and even terrestrial ecosystems (Blanchard et al. 2017), although minor deviations from this pattern have been occasionally

observed (e.g. Jennings & Mackinson 2003). Based on the first and second laws of thermodynamics and the correlations between size, metabolic rate and trophic level in consumers (Blanchard et al. 2017), biomass and energy size spectrum slopes (i.e. distributions of biomass and energy versus size) should be similar for the same state of a marine ecosystem.

The aim of this paper is to investigate the influence of energy content on the trophic role of forage fish, particularly herring, off northern BC and SE Alaska, and to test the viability and utility of energy-based ecosystem models for the examination of similar questions in the future. The present study endeavours to bridge the ecosystem and bioenergetic modelling approaches to yield an integrated view of NE Pacific ecosystems grounded in the laws of thermodynamics and basic ecological theory. To this end, it employs published energy content data to convert a mass-balanced NE Pacific ecosystem model to a set of energy-balanced models. The present study then compares the role of herring and other forage fish in predator diets, gross ecosystem structure, and the effects of increased herring consumption by recovering whale populations across mass-balanced and energy-balanced models. These analyses are informed by the hypotheses that elevated energy content raises the importance of prey such as herring to at least some predators and that biomass and energy dynamics similarly represent thermodynamically determined ecosystem structure. Hence, increased herring consumption by whales can be hypothesized to affect mass and energy balance for other herring predators, with particularly strong energetic effects on active, endothermic groups such as small marine mammals and seabirds.

METHODS

Model structure and parameters

A mass-balanced Ecopath food web model of northern BC and southern SE Alaska (Kumar et al. 2016; most recent model version) was used to generate a set of energy-balanced models. All models contain 80 functional groups spanning the size spectrum from phytoplankton to whales (Table S1 in the Supplement at www.int-res.com/articles/suppl/m588p147_supp.pdf). These include 4 local herring stocks (Haida Gwaii, Haida Gwaii Area 2 West, Prince Rupert District and Central Coast), each split into 3 age classes (0–1, 1–3 and 3+ yr) in the multi-stanza approach (Kumar et al. 2016). Two other large forage fish, eulachon and Pacific saury *Cololabis saira*, are also repre-

sented separately, while smaller energy-rich schooling fish (resident smelts, capelin, and sandlance and occasionally present Pacific sardine) form a single 'forage fish' group. All models also include 4 primary producer groups and one detritus group.

Functional group biomass densities (B , t km⁻²) from the mass-balanced model (Table S1) were converted to energy densities (E , J m⁻²) for the energy-balanced models using published higher and lower energy content (e_i , kJ g⁻¹) values (Table S2). Wherever possible (i.e. for most groups), these were based on bomb calorimetry (or extrapolations from proximate composition) of whole specimens from the Gulf of Alaska Large Marine Ecosystem (containing the study area) or neighbouring NE Pacific Large Marine Ecosystems (Bering Sea–Aleutian Islands, and California Current). When e_i values were unavailable for local species (e.g. Pacific dogfish *Squalus suckleyi* and spotted ratfish *Hydrolagus colliei*), values for the most closely related species represented in the literature (e.g. the Atlantic *Squalus acanthias* and *Chimaera monstrosa*) or widely distributed higher taxa (e.g. Decapoda) were used. Annual averages were employed to account for seasonal changes in energy content (e.g. Vollenweider et al. 2011). Pairs of mean e_i values were utilized where higher and lower values were derived from separate sources (e.g. for chinook salmon). Elsewhere (e.g. for coho salmon), standard deviations or interquartile ranges from a single source were employed to set higher and lower values. For 9 functional groups, only one e_i value was found in the literature. In the absence of published data, e_i values for detritus and 'import' (food consumed outside model area) were set to biomass-weighted averages of all other group e_i values and average e_i values for all prey of a given predator weighted by their proportional contributions to the predator diet, respectively.

Densities (t km⁻²) of biomass, landings and discards for all functional groups in the mass-balanced model were multiplied by the higher and lower e_i values (kJ g⁻¹), yielding 2 sets of energy pool sizes (Tables S3 & S4) and landing and discard matrices (J m⁻²). Biomass accumulation and net migration were zero across all models. Original production per biomass (P/B , yr⁻¹) or total mortality (Z , yr⁻¹) values were retained as input for all groups, as the definition of these equivalent parameters (Christensen & Walters 2004) is independent of model currency. Consumption per biomass (Q/B , yr⁻¹) values from the mass-balanced model were used to calculate new diet compositions and Q/B for all consumers to account for differences in e_i among functional groups com-

prising consumer diets and avoid errors derived from transferring biomass-based parameters from the original model.

New diet composition matrices for the energy-balanced models were obtained by calculating the proportion of each functional group i in the diet of each consumer j (DC_{ij}) as:

$$DC_{ij} = \frac{Q_{ij} \cdot e_i}{\sum_{i=1}^n Q_{ij} \cdot e_i} \quad (1)$$

where $Q_{ij} = B_j(Q/B)_j DC_{ij(\text{mass})}$ (t km⁻²) is the consumption of group i by consumer j , B_j (t km⁻²) is the biomass density of consumer j , $(Q/B)_j$ (yr⁻¹) is the consumption per biomass of consumer j , and n is the number of groups i in the diet of consumer j . $DC_{ij(\text{mass})}$ is the proportion of group i in the diet of consumer j in the original mass-balanced model. This calculation is based on the observation that many predators preferentially target energy-rich prey (Österblom et al. 2008, Litzow et al. 2004).

New Q/B values accounting for energy content differences were calculated as:

$$\left(\frac{Q}{B}\right)_j = \left(\frac{Q}{B}\right)_{\text{mass}} \cdot \frac{\left(\frac{\sum_{i=1}^n (e_i \cdot DC_{ij})}{\sum_{i=1}^n DC_{ij}}\right)}{e_j} \quad (2)$$

where $(Q/B)_{\text{mass}}$ is the original Q/B from the mass-balanced model, DC_{ij} is the new proportion of group i in the diet of consumer j and e_j is the energy content of j . The numerator of the scaling term on the right side of the equation represents the average energy content of the biomass intake of consumer j consisting of n functional groups, weighted by the proportions DC_{ij} of each group i in the diet of j ($\sum_{i=1}^n DC_{ij} = 1$).

The new models (hereafter high-energy and low-energy) based on high and low e_i sets were balanced using the standard Ecopath approach (Christensen & Walters 2004), yielding the parameters shown in Tables S3 & S4. Selected predator diet compositions from the mass-balanced, high-energy and low-energy models appear in Tables S5–S10. In addition, a separate set of models was constructed based on independent random resampling of integers, with replacement, from uniform distributions bounded by the higher and lower e_i values for all functional groups (Table S11). This resampling yielded 5 energy-balanced 'randomization' models whose parameters appear in Tables S12–S16, while ratios of balanced to input group energy pool sizes appear in Table S17. These models were parameterized and balanced using the same methods described above for the high-energy and low-energy models.

Model analyses and simulations

Based on their e_i values, all fish and invertebrate functional groups were placed in one of the 3 prey quality categories (low $<4 \text{ kJ g}^{-1}$, moderate $4\text{--}6 \text{ kJ g}^{-1}$, high $>6 \text{ kJ g}^{-1}$) established by Spitz & Jouma'a (2013). The relative contribution of each category to total ecosystem biomass was calculated by dividing the total biomass of all groups in each category by that of all groups in the mass-balanced model.

In order to compare the size spectra suggested for northern BC by the mass- and energy-balanced models, log-transformed biomass and energy densities from all Ecopath models were tested for correlation with log-transformed average individual mass (kg) for each functional group. Where correlations were significant ($p < 0.05$), ANCOVA was used to test for differences among spectrum slopes and for departures from a slope of zero, the value expected based on its regular presence in models and empirical observations of marine ecosystems (Blanchard et al. 2017). In the absence of any evidence to the contrary, we hypothesized that energy and biomass spectrum slopes would not differ significantly from each other or from zero.

In order to further compare the ecosystem structures indicated by the mass- and energy-balanced models, the proportional contributions of 7 large functional categories (producers, benthos, zooplankton, forage fish, other fish, mammals and others) to the total ecosystem biomass or energy pools were compared across all models by dividing the total biomass or energy densities of the groups comprising each category (Table S1) by the ecosystem totals summed over all model groups. The forage fish category included herring, eulachon and Pacific saury.

In order to compare the functioning of dynamic simulations in the mass- and energy-balanced models, we reassessed the effects of depleted whale population recovery on the local food web (Surma & Pitcher 2015) using the same Ecosim scenario in all models. Predicted recovery of humpback, blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*) and sperm (*Physeter macrocephalus*) whale populations was simulated by time series forcing of biomass and energy densities in the mass- and energy-balanced models, respectively. These time series were derived from the species-specific surplus production models presented in Surma & Pitcher (2015) and based on whaling catch data (Nichol & Heise 1992), but reflected improved local whale abundance estimates which have been incorporated into the mass-balanced model (Kumar et al. 2016).

Whale biomass density (t.km^{-2}) time series values were separately converted to energy densities (J m^{-2}) using the e_i values applied in each energy-balanced model. Ecosim runs lasted the 500 simulation years required for full recovery of all whale populations, whereupon percentage changes in other functional group biomass and energy densities in response to whale recovery were compared across all models. The goal of this analysis was to investigate the effects of prey energy content differences on simulated whale recovery impacts on prey (particularly herring), other predators and the food web at large. We examined effects on all herring stocks together as well on each separately.

RESULTS

Based on both sets of energy content (e_i) values (lower and higher), low-quality prey groups comprised most ($>50\%$) of the total ecosystem biomass, followed by moderate- ($<20\%$) and high- quality ($<10\%$) prey (Fig. 1).

The contributions of herring (summed over all stocks and age classes) to 8 marine mammal, seabird and commercial fish diets were $\sim 20\text{--}110\%$ higher in the high- and low-energy models than in the mass-balanced model (Fig. 2A). In the randomization models, these proportions consistently exceeded those in the mass-balanced model and exhibited a wider range than among the high- and low-energy models (Fig. 2B). While in the mass-balanced model no predator diet included $\geq 20\%$ herring, 8 predators exceeded this threshold in at least one energy-balanced model. The greatest increases in the con-

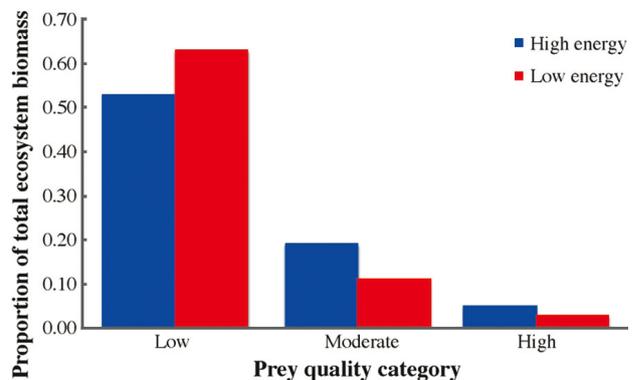


Fig. 1. Distribution of fish and invertebrate biomass in the ecosystem across 3 prey quality categories, based on high and low estimates of functional group energy content (kJ g^{-1}). Prey quality categories were as follows: low: $<4 \text{ kJ g}^{-1}$; moderate: $4\text{--}6 \text{ kJ g}^{-1}$; and high: $>6 \text{ kJ g}^{-1}$ (established by Spitz & Jouma'a 2013)

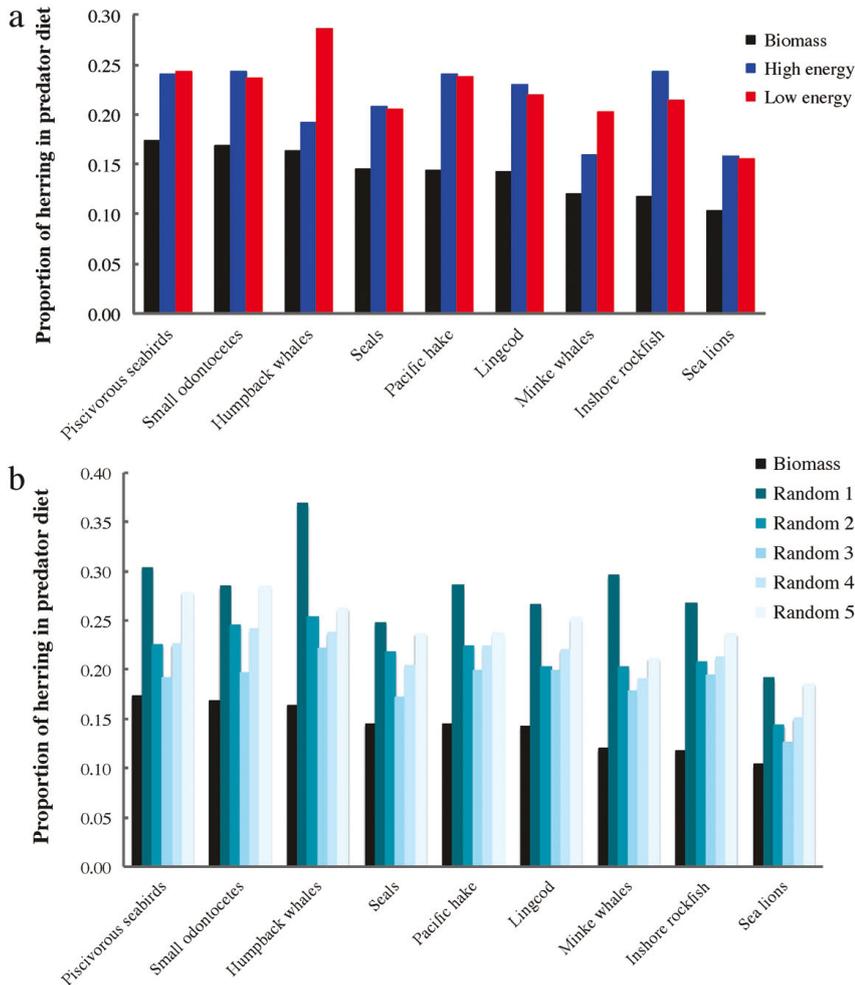


Fig. 2. Proportion of herring in the diet of various predators in the mass-balanced model versus (a) high-energy and low-energy models and (b) randomized energy-balanced models. These proportions are in terms of biomass in the mass-balanced model and in terms of energy in the energy-balanced models

tribution of herring relative to the mass-balanced model occurred in humpback whale, Pacific hake *Merluccius productus*, lingcod *Ophiodon elongatus* and inshore rockfish *Sebastes* spp. diets.

Significant correlations (Spearman's rank correlation, $p < 0.0001$) between $\log(\text{individual mass, kg})$ and $\log(\text{biomass or energy density, t km}^{-2} \text{ or J m}^{-2})$ were detected for all models (Table S18). All spectrum slopes (Fig. 3) differed significantly from the expected value of zero (ANCOVA; $df = 8$, $F = 3.06$, $p = 0.022$) but did not differ among models (ANCOVA; $df = 7$, $F = 0.13$, $p = 0.996$). Balancing the high-energy model required a noticeable but non-significant increase in size spectrum slope relative to the original mass-balanced model (Fig. 3A). This change resulted from the strong (over 10-fold) increases in energy densities for 10 functional groups (primarily at mid-to-low trophic levels) necessary for energy balance (Fig. 4A).

The total ecosystem energy pool in the high-energy model therefore became over 3-fold larger than its low-energy counterpart. Balancing the low-energy and randomization models required much smaller increases in energy densities (Fig. 4B, Table S17) and no noticeable changes in spectrum slope (Fig. 3), although energy densities had to increase over 10-fold for 5 groups occupying low trophic levels in the low-energy model. No increases of this magnitude were necessary in any randomization model (Table S17), and differences in spectrum slope among these models were negligible (Fig. 3B). Among functional groups with biomasses derived from stock assessments, only Pacific Ocean perch *Sebastes alutus*, a benthopelagic rockfish surveyed exclusively in a small region south of the model area, required energy density to increase over 2-fold in the low-energy model (Fig. 4B). The total herring energy density increased only modestly across the energy-balanced models (by 36% in the high-energy model, 32% in the low-energy model and 28–11% in the randomization models).

Conversion of biomass to energy densities for all energy-based models predicted reduced proportions of benthos and producers, an increased proportion of fish and a nearly constant zooplankton proportion in the total ecosystem biomass and energy pools (Fig. 5).

However, upon achieving energy balance, the proportional reduction in benthos and producers was reversed in some models, the increase in fish persisted only for forage fish, and the proportion of zooplankton increased strongly in all but the high-energy model (Fig. 6). These changes resulted from the increases in several group pool sizes at mid-to-low trophic levels (Fig. 4, Table S17).

In the Ecosim whale recovery scenario, a slight majority (~53%) of functional groups (with all herring stocks and age classes considered together) showed changes of $\geq 5\%$ to their biomass or energy densities (Figs. 7 & 8, Fig. S1). A larger majority (~64%) of these groups (including herring) demonstrated such changes in both the biomass- and energy-balanced

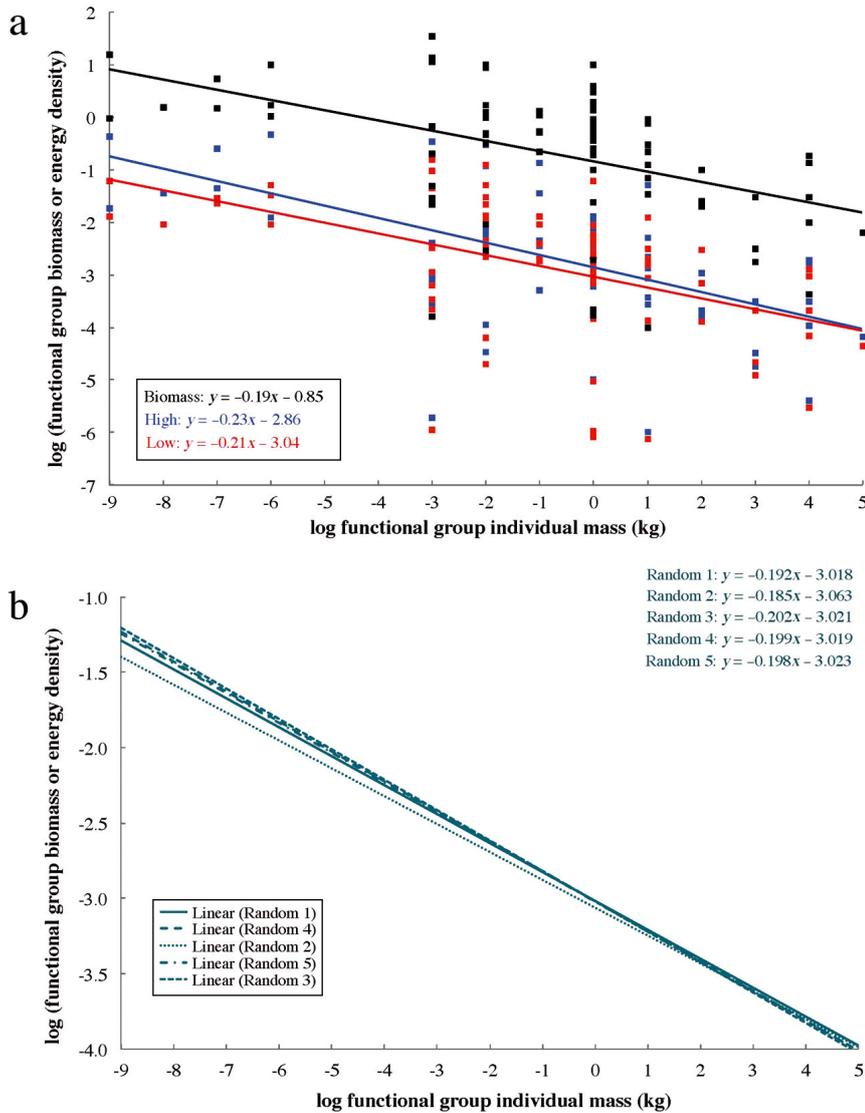


Fig. 3. Biomass- and energy-based size spectra of (a) the mass-balanced (black), high-energy (blue) and low-energy (red) models and (b) the randomized energy-balanced models (data points omitted for clarity). The dependent variable is log biomass density for the mass-balanced model and log energy density for the energy-balanced models

models, but only ~44% showed changes of $\geq 5\%$ across all energy-balanced models. For slightly less than half (~47%) of groups with changes of $\geq 5\%$, including 3 whale prey groups (herring, large squid and planktivorous rockfish), 95% confidence intervals around the mean changes across all energy-balanced models overlapped with mass-balanced model outputs. These confidence intervals overlapped with zero for only 3 groups. The sign of the whale recovery response differed between mass- and energy-balanced models for 5 groups, including 2 important herring predators (small odontocetes and piscivorous seabirds). In all models, as in Surma &

Pitcher (2015), increased whale predation substantially impacted herring as well as piscivorous and planktivorous rockfish (*Sebastes* and *Sebastolobus* spp.). Herring responses to whale recovery varied considerably but were consistently and strongly negative across all stocks (Fig. S2).

In all models, the decrease in herring due to increased humpback and fin whale predation precipitated noticeable declines in minke whales (*Balaenoptera acutorostrata*), inshore rockfish, coho salmon and lingcod. It also had cascading positive effects on amphipods and macrozooplankton, resulting in small gelatinous zooplankton and euphausiid declines due to increased predation. This trophic cascade was somewhat damped in the energy-balanced models. Increasing whale predation also contributed to the euphausiid decline, as did the release of forage fish from herring competition. The latter precipitated an increase in seals and their main predators (transient orcas), leading to a gray whale decline and exacerbating the effects of the herring decrease on minke whales. The decrease in euphausiids combined with increased whale predation to adversely impact Pacific hake, walleye pollock and Pacific saury (this last effect was absent in some energy-balanced models). The coho salmon decline adversely affected apex predators (resident orcas, salmon and blue sharks), releasing seabirds from shark predation pressure. Finally, increased predation from recovering sperm whales

precipitated substantial declines in planktivorous and piscivorous rockfish, dogfish, sablefish and large demersal sharks, leading to mesopredator release for small demersal elasmobranchs, ratfish, arrowtooth flounder, octopus and seals.

DISCUSSION

The findings of the present study highlight the importance of energy-rich prey at low and intermediate trophic levels in supporting the entire food web. The rescaled diet composition matrices used in the

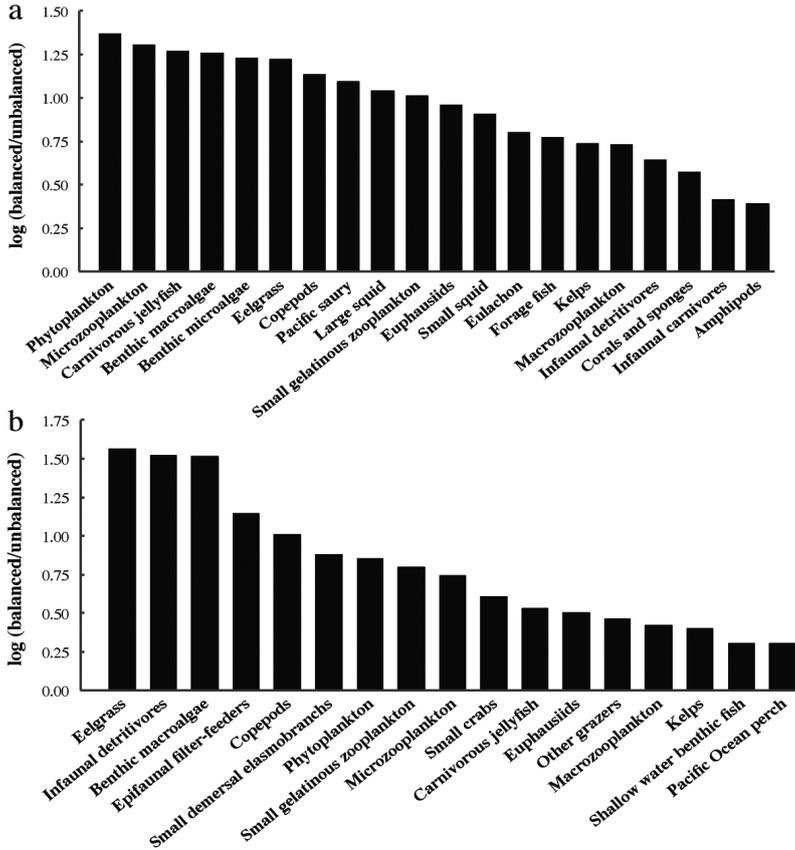


Fig. 4. Ratios (log scale) of functional group energy pool sizes before and after energy balance in (a) the high-energy model and (b) the low-energy model. Only groups increasing by a factor of ≥ 2 are shown

While low-quality prey (*sensu* Spitz & Jouma'a 2013) dominate the total ecosystem biomass (Fig. 1), high-quality prey (e.g. adult herring) may be more important to many predators than prey biomasses would suggest (Fig. 2). Furthermore, recent attempts to characterize interannual food web dynamics in 2 Northwest Pacific epipelagic communities indicate that food web structure, complexity and, ultimately, overall productivity (including fisheries yield) depend strongly on the changing identity of dominant mid-size nektonic consumers (Naydenko & Khoruzhiy 2017). These findings indicate that while the integrity of such communities may be robust to various climatic regime scenarios, their overall productivity is likely enhanced when high-energy forage fish species dominate.

The size spectrum slope seen across all models (~ -0.20) differs slightly but signifi-

energy-balanced models suggest that, as hypothesized above, biomass-based diet compositions may underestimate the importance of Pacific herring as prey to many seabirds, mammals and fish (Fig. 2). When energy content differences between functional groups are accounted for, herring emerges as an important item in the diets of small odontocetes (dolphins and porpoises), humpback and minke whales, seals and sea lions, piscivorous seabirds (including many cormorants, alcids and gulls), inshore rockfish, lingcod and Pacific hake. This is so despite the greater biomass and energy densities of the aggregated forage fish group across all models. These findings are in agreement with those of Vollenweider et al. (2006) on the enhanced dietary importance of herring to Steller sea lions in SE Alaska when prey energy content is considered.

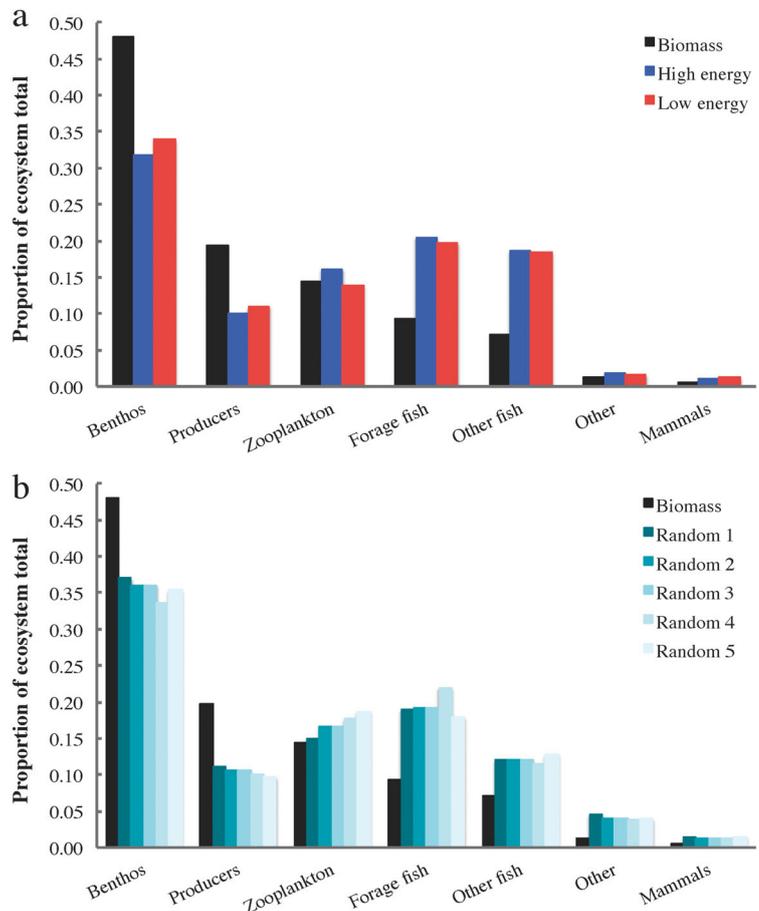


Fig. 5. Proportion of several large ecological categories in the total ecosystem biomass and energy pools (energy models not balanced), comparing (a) the high- and low-energy models and (b) the randomization models to the mass-balanced model

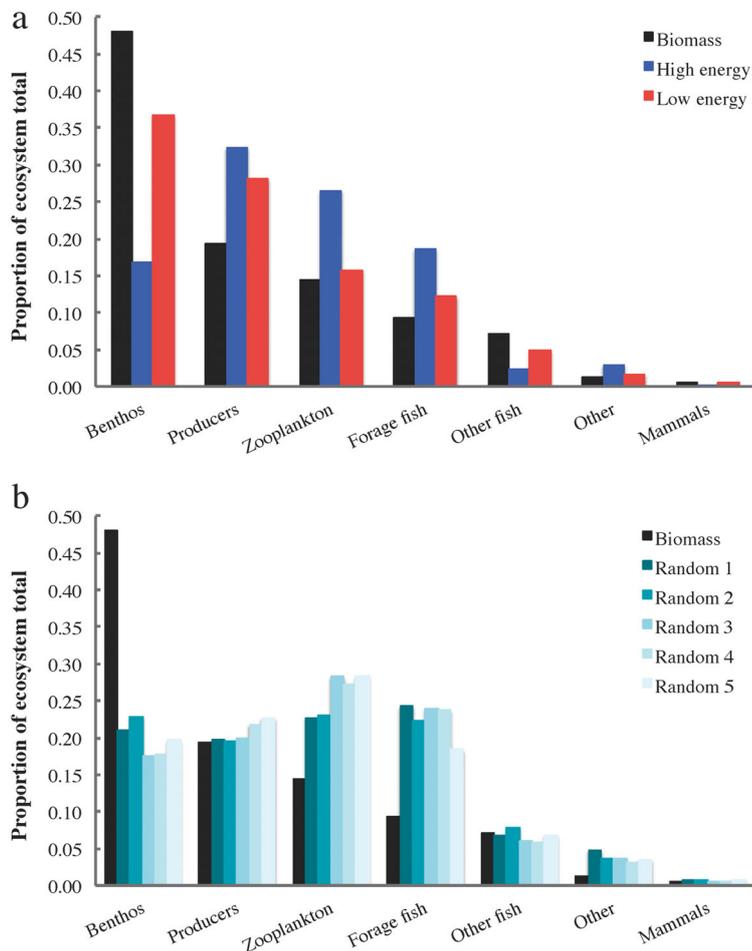


Fig. 6. Proportion of several large ecological categories in the total ecosystem biomass and energy pools (energy models balanced), comparing (a) the high- and low-energy models and (b) the randomization models to the mass-balanced model

cantly from the zero value predicted by an empirical relationship nearly universal across diverse ecosystems (Blanchard et al. 2017). However, the slope found in the present study is nearly identical to that reported from the North Sea by Jennings & Mackinson (2003), although the latter was based on sampling of size classes from zooplankton to medium-sized fish only. This deviation from the expected zero slope may result from increasing predator–prey mass ratio with individual mass (e.g. baleen whales versus zooplankton) or from underestimation of abundance in the largest size classes. The size spectrum slope of the high-energy model is noticeably but not significantly steeper than in other models (Fig. 3A), reflecting increases in some functional group energy densities required for energy balance (Fig. 4A). The shallower spectrum slopes of the low-energy (Fig. 3A) and randomization (Fig. 3B) models likely

derive from the reduced energetic demands of top predators (particularly marine mammals) compared to the high-energy model due to lower e_i values (Tables S2 & S11). Nevertheless, the lack of significant differences in spectrum slope across all models supports our hypothesis that energy and biomass follow the same general distribution pattern across size classes based on fundamental trophodynamic principles.

The energy density increases needed for energy balance, especially in the high-energy model with its noticeably steeper size spectrum slope (Fig. 3), may reflect underestimates in published e_i and/or biomass density values for these groups (e.g. forage fish, euphausiids, copepods, phytoplankton). This is particularly likely given that planktonic group e_i values are often based on data for several constituent species only (e.g. Whyte 1987, Harvey et al. 2012) or for large, diverse taxonomic groups (Cauffopé & Heymans 2005). For phytoplankton (Whyte 1987), such values could only be found for North Atlantic species. Furthermore, prey e_i varies on seasonal and interannual scales as well as through ontogeny (e.g. Vollenweider et al. 2011, Siddon et al. 2013). Some juvenile planktivorous fish (e.g. Bering Sea walleye pollock) respond with decreased energy content to climatically driven seasonal and interannual shifts in zooplankton community composition towards energy-poor species (Hunt et al. 2011, Heintz et al. 2013, Siddon et al. 2013). Furthermore, biomass densities of many planktonic and forage fish groups in the original model (Kumar et al. 2016) were not based on systematic surveys but rather on extrapolations from incomplete field data (e.g. phytoplankton) or Ecopath mass-balance equation solutions (e.g. Pacific saury). Finally, e_i overestimates for upper-level predators (mammals and sharks) may cause Ecopath to impose excessively high demands on prey energy pools, necessitating increases in energy densities to maintain energy balance, and predator energetic demands vary with age and breeding status. Energy density increases in the low-energy model may be considered approximately realistic once likely errors in biomass and e_i estimates are accounted for. This is not true, however, of the high-energy model, whose total ecosystem energy pool size exceeds that of its low-energy counterpart 3-fold. Outputs of the low-

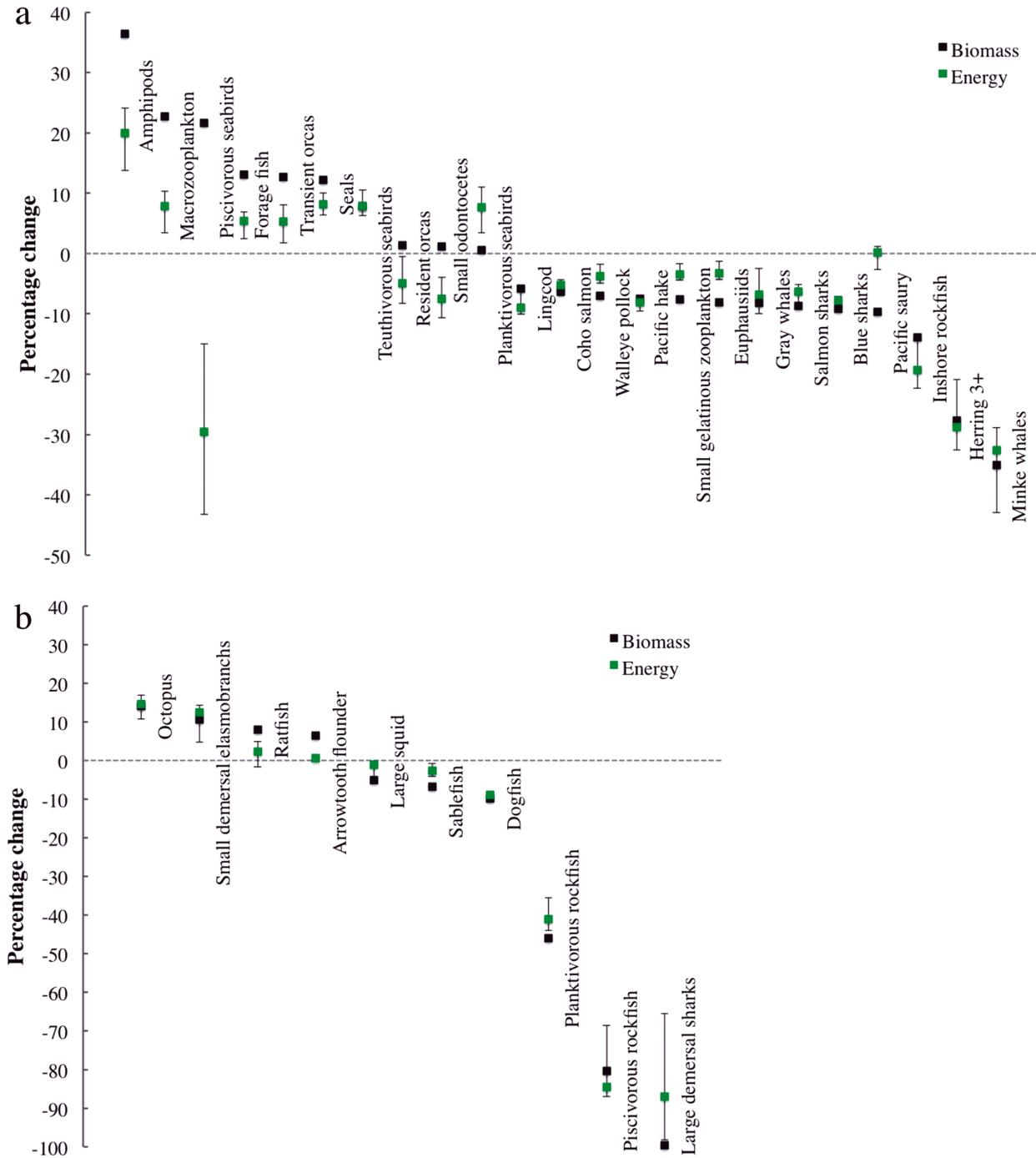


Fig. 7. Percentage change to functional group biomass and energy densities in response to simulated recovery of (a) baleen whales and (b) sperm whales. Error bars indicate 95 % confidence intervals around mean changes (green squares) across all energy-balanced models

energy model are therefore more trustworthy than those of its high-energy sibling. Randomization model outputs inspire still greater confidence, as it is doubtful whether consistent patterns in e_i (high or low) can persist in a real food web for any meaningful length of time.

The proportional contributions of several large functional categories to total ecosystem energy pools (Fig. 5), even considering adjustments necessary for energy balance (Fig. 6), suggest that the mass-balanced model may underestimate the importance of forage fish (e.g. herring), zooplankton and perhaps

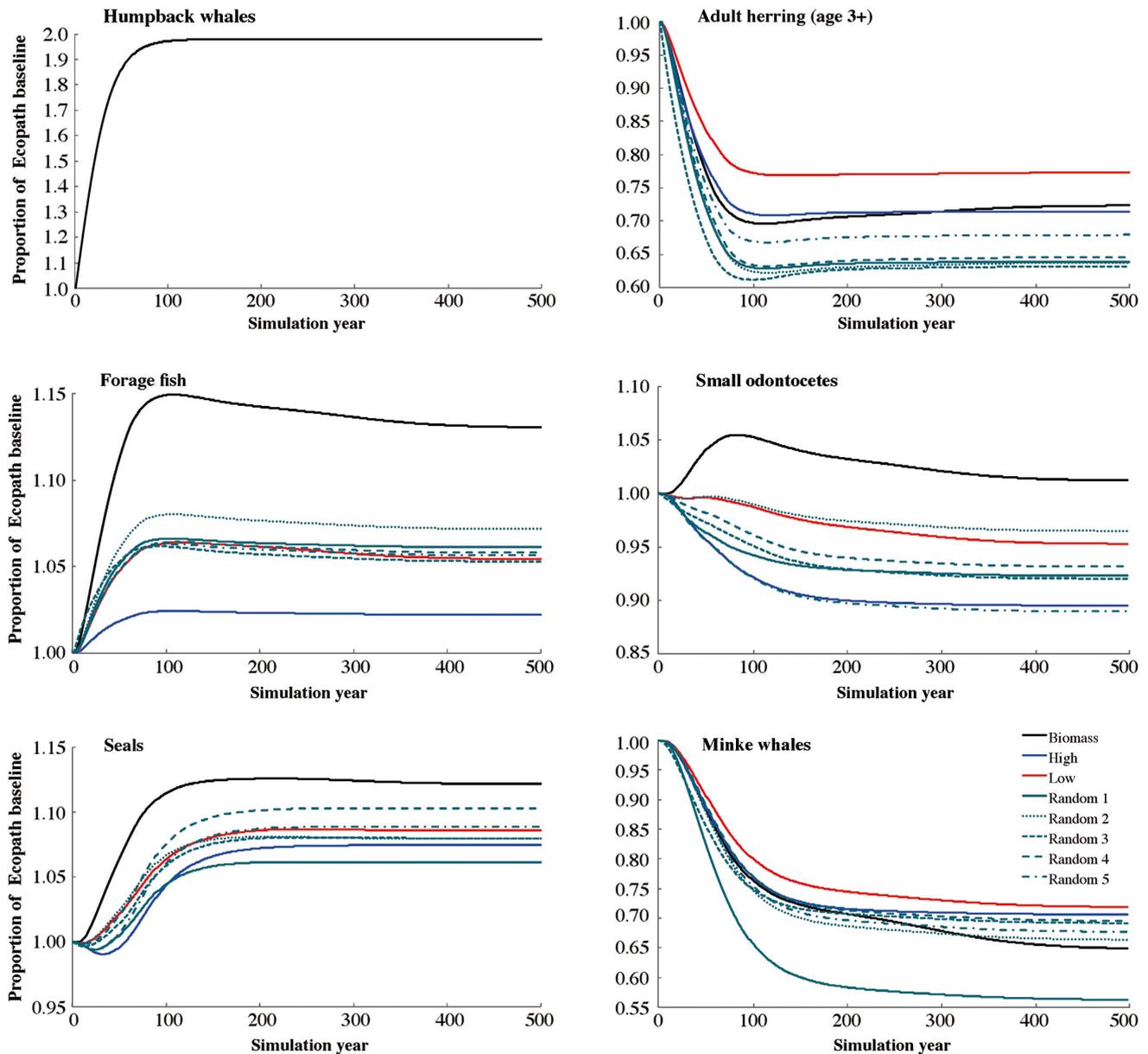


Fig. 8. Selected functional group trends relative to Ecopath baseline biomass densities (mass-balanced model, black) and energy densities (energy-balanced models, colour). The humpback whale trend (upper left) is an identical driver across all models, while other group trends are variable responses

producers, and overestimate that of benthos, in ecosystem structure. These results indicate that the pelagic realm may retain a greater proportion of the total ecosystem pool for energy than for biomass, a conclusion supported by the findings of Litzow et al. (2006).

Ecosim simulation results from energy-balanced models (Figs. 7 & 8) suggest that herring declines could impact active, endothermic predators (small odontocetes and seabirds) more strongly than mass-balanced models predict. This inference agrees with

the findings of Spitz et al. (2012) and Wisniewska et al. (2016) on the high metabolic demands of small odontocetes and their resulting preferences for high-energy prey. It also accords well with the findings of Litzow et al. (2004) on similar energetic drivers of seabird ecology, as well as with our original hypothesis. However, this picture may be complicated by the fact that while many active, endothermic marine predators preferentially target energy-rich prey (Litzow et al. 2004, Spitz et al. 2012, Wisniewska et al. 2016), such predators (e.g. small penguins) may

supplement their high-energy diets with low-energy taxa (e.g. scyphozoan jellyfish and ctenophores) even when higher-energy prey are available (Thiebot et al. 2017). Furthermore, while herring is the most energy-rich prey for NE Pacific seabirds (Vermeer & Devito 1986), negative correlations between seabird breeding success and the proportion of herring in diet have been observed at colonies in the California Current (Gladics et al. 2015) and at Triangle Island off NW Vancouver Island, BC (Hedd et al. 2006). These correlations may derive from a more offshore distribution of herring relative to smelts and sandlance (Gladics et al. 2015), reducing herring provisioning rates for nestlings (Hedd et al. 2006), or to the incompatibility of large herring with the small gapes of young chicks (Hedd et al. 2006). Spatial mismatch may likewise explain negative correlations between black rockfish (*S. melanops*) growth increments and herring abundance in the California and Alaska Coastal Currents (von Biela et al. 2016). Nevertheless, such correlations are far from universal (e.g. they do not occur at the Seabird Rocks colony off SW Vancouver Island; Bertram et al. 2002), and are unlikely to hold for seabird colonies across the entire study area. This is not at all surprising as depth, local density and persistence of prey patches also noticeably influence seabird and marine mammal foraging strategies (Sigler et al. 2017, Sydeman et al. 2017, Benoit-Bird et al. 2013). Unfortunately, such fine-scale factors are presently quite difficult to represent even in spatially explicit ecosystem models.

While NE Pacific pinniped populations have also repeatedly suffered from reduced availability of high-energy forage fish (Trites & Donnelly 2003, McClatchie et al. 2016a), deleterious effects of herring decline on seals (Figs. 7 & 8) or sea lions were not observed here. This may be due to highly diverse pinniped diets (Tables S5–S10) in our study area (Gregar 2004, Vollenweider et al. 2006), which include high proportions of small but energy-rich forage fish (capelin, smelts and sandlance) released by whale recovery from competition with herring (Figs. 7 & 8). The relatively high energy content of all forage fish, combined with dynamic Ecosim diet compositions (the Ecopath diet composition matrix serves as a simulation starting point only), also explains the agreement across all models in the Ecosim responses of most herring predators to whale recovery (Figs. 7 & 8). This pattern accords with our hypothesis that as conserved quantities, mass and energy should similarly represent underlying ecosystem dynamics and thus frequently predict at least qualitatively similar scenario outcomes.

The present study reinforces the importance of herring as a notable node in NE Pacific food webs and a vital prey species for numerous predators, particularly many small endotherms, as well as the more general importance of forage fish as an energy conduit linking zooplankton to higher predators. The findings presented above indicate that demand of these predators for herring and other energy-rich forage fish should be included in a comprehensive view of pelagic ecology and a precautionary, ecosystem-based approach to forage fisheries management (Pikitch et al. 2012a,b). Furthermore, given the demonstrated potential for climatically driven seasonal and interannual shifts in energy-rich zooplankton abundance to reduce NE Pacific fish energy content and recruitment (Cummins & Haigh 2010, Hunt et al. 2011, Heintz et al. 2013, Siddon et al. 2013), these concerns gain additional urgency from global climate change and recent oceanographic anomalies (Di Lorenzo & Mantua 2016, McClatchie et al. 2016b).

The set of energy-balanced EwE models presented in this study is a proof of concept, and the underlying parameterization framework requires further research and development to resolve several issues. Firstly, energy content of fish such as herring varies widely on seasonal and interannual scales (Vollenweider et al. 2011). Representing such changes and their consequences in ecosystem models would necessitate intensive and frequent field sampling and laboratory analyses, posing a serious challenge to all but the most developed ecosystem monitoring programs. In many cases, replacement of bomb calorimetry with rapid assays of lipid levels, combined with empirical relationships between lipid and energy content, would be required to streamline monitoring efforts, particularly as these techniques yield equivalent results (Vollenweider et al. 2011). This could create an iterative feedback loop between monitoring and modeling, improving the quality of both. Secondly, current energy-balanced models cannot distinguish between effects of changes in biomass and energy content, both of which affect a single parameter (energy density). This issue could perhaps be resolved by introducing energy content into EwE as an independent input parameter and automating the calculation of energy densities, as well as energy-based Q/B and diet compositions, within the program. This would allow monitoring-derived prey energy content and biomass time series to be simultaneously entered into Ecosim and jointly affect predator energy density. Thirdly, the current models also cannot distinguish between climatically driven (e.g. Siddon et al. 2013) and density-dependent (e.g. Casini et al. 2006)

energy content changes. An Ecosim setting forcing energy content to decrease as biomass increases could simulate density-dependent energy content trends. Fourthly, techniques for rescaling Ecopath assimilation efficiencies and Ecosim predator–prey interaction parameters based on prey energy content have yet to be researched and developed. Finally, the current energy-balanced models were based on an existing mass-balanced model, in a sense predetermining their food web structure and functional group assortment. While this need not apply to all future energy-balanced models, structural differences between representations of the same ecosystem in alternative currencies would impair the comparability of their outputs.

Nevertheless, the results of the present study indicate that energy-balanced models, particularly those based on randomized energy content values, both validate and complement the original mass-balanced model. The similarity of spectrum slopes and most Ecosim scenario results based on mass and energy balance generally supports the qualitative predictions of the original model. However, the noticeable differences between mass- and energy-balanced models in predator diet compositions, proportional representation of pelagic and benthic groups, and some Ecosim scenario outputs suggest that energy-balanced models could help examine uncertainty in mass-balanced model predictions and account for elements of ecosystem structure and function implicit in the latter. In accounting for prey energy content differences, and explicitly representing the thermodynamic basis of trophic interactions and ecosystem structure, an expanded and improved energy-balance approach could enhance both the realism and predictive capacity of food web models.

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