Original Article

Trade-offs between forage fish fisheries and their predators in the California Current

Laura E. Koehn[1]*, Timothy E. Essington[1], Kristin N. Marshall[2], William J. Sydeman[3], Amber I. Szoboszlai[3], and Julie A. Thayer[3]

[1]School of Aquatic and Fishery Sciences, University of Washington, PO Box 355020, Seattle, WA 98105-5020, USA
[2]Cascade Ecology, PO Box 25104, Seattle, WA 98165, USA
[3]Farallon Institute, 101 H Street Suite Q, Petaluma, CA 94952, USA

*Corresponding author: tel: 1-206-543-4270; fax: 1-206-685-7471; e-mail: laura.koehn216@gmail.com.

Forage fish generate economic benefits through directed fisheries, but also generate benefits through their role as prey to other valued species (large piscivorous fish, seabirds, and marine mammals). Previous evaluations of the ecosystem consequences of forage fish fisheries used models with coarse taxonomic resolution of forage fish and their predators. Here, we quantify trade-offs between forage fish fisheries and predator fisheries, and between forage fish fisheries and species of conservation interest in the California Current, using a taxonomically detailed food-web model and a generalized equilibrium model. We propagated uncertainty in trade-offs to forage fish fishing based on uncertainty in food-web model parameterization and uncertainty in predator–prey functional relationships in the generalized equilibrium model. The model predicted loss in catch of some higher trophic level fisheries [mainly salmon (*Oncorhynchus* sp.) and halibut (*Paralichthys californicus*)] from fishing sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), herring (*Clupea pallasii*), or aggregated forage fish, but the lost economic revenue from predators never exceeded the economic benefit from additional forage fish catch. Predicted reductions in biomass of seabirds and marine mammals were sufficiently large that, depending on the value of these nonmarket species, consideration of nonmarket predators could tip the balance of trade-offs toward conservation of forage fish and away from harvest. This work highlights specific predators [brown pelicans (*Pelecanus occidentalis*), marbled murrelets (*Brachyramphus marmoratus*), multiple other seabirds, sea lions (*Zalophus californianus* and *Eumetopias jubatus*), baleen whales (Mysticeti)] that are potentially sensitive to specific forage fish fisheries in the California Current.

Keywords: northern anchovy, Pacific herring, Pacific sardine, seabirds, trade-offs.

Introduction

A key component of ecosystem approaches to management of natural resource systems is identifying trade-offs between conflicting demands for direct services that species provide to humans vs. indirect services those species provide through their role in ecosystems (DeFries *et al.*, 2004; Leslie and McLeod, 2007). Competing demands can exist for a large variety of species in marine ecosystems where harvested organisms have key ecosystem function through habitat structuring (such as corals, Moberg and Folke, 1999), nutrient cycling (Leslie and McLeod, 2007), and/or

trophic interactions (Pikitch *et al.*, 2014; Marshall *et al.*, 2016). These trade-offs create challenges in natural resource management because different management decisions will lead to changes in the allocation of benefits across societal objectives.

The management of forage fish species (i.e. small, mid-trophic level, pelagic species) exemplifies this challenge because forage fish both support profitable fisheries and are a main prey source for economically and culturally valuable predators. Moreover, these species can play key roles in structuring communities and interactions among species. Forage fish fisheries comprise ca. 25–30% of

global fish landings (FAO, 2015; data from 2011 to 2013) with an annual catch value of $5.6 billion USD (Pikitch *et al.*, 2014) (compared with the catch value of $87.7 billion USD for all marine fisheries, Sumaila *et al.*, 2012). Forage fish landings provide multiple benefits, including food, fishmeal for agriculture or aquaculture feed, fish oil (Alder *et al.*, 2008), and bait for fisheries (Tacon and Metian, 2009). At the same time, forage species transfer energy from plankton to upper trophic levels (Cury *et al.*, 2000) and are a food source for piscivorous fishes targeted by fisheries (Overholtz *et al.*, 2000; Butler *et al.*, 2010), possibly creating trade-offs among forage fish fisheries and other fisheries. Forage fish are also a primary food source for several protected predators such as seabirds (Furness, 2003, 2007) and marine mammals (Alder *et al.*, 2008). Fluctuations in forage fish abundance can lead to changes in predator demographic traits such as adult survival (Robinson *et al.*, 2015) or reproductive success (Tasker *et al.*, 2000; Crawford *et al.*, 2006; Cury *et al.*, 2011). Given the potentially competing roles of forage fish in directed fisheries and trophic interactions, there is a need to quantify trade-offs in the exploitation of forage species to weigh the costs of potential predator losses with the benefits from direct forage fish catch.

Trade-offs have commonly been quantified using foodweb models that simulate the likely consequences of forage fish depletion on predators (e.g. Smith *et al.*, 2011; Houle *et al.*, 2013; Kaplan *et al.*, 2013; Jacobsen *et al.*, 2015), but due to structural assumptions, existing models often have limitations for assessing trade-offs. Both the magnitude and direction of responses to depleting forage fish vary across model frameworks, each of which has distinct structural assumptions (Kaplan *et al.*, 2013; Smith *et al.*, 2015). One primary structural assumption is the level of taxonomic resolution at which forage fish and their predators are represented. Foodweb models typically have multiple predators grouped into a single functional group and are not constructed with sufficient taxonomic breadth or detail to precisely capture the sensitivity of distinct predator species to depletion of forage fish (Essington and Plagányi, 2013). Some models aggregate forage fish into a single functional group rather than representing each species distinctly (Essington and Plagányi, 2013) and, therefore, may not capture predator responses that arise through depletion of individual species (Smith *et al.*, 2011). Additionally, detailed propagation of trade-off uncertainty arising from foodweb model parameter and structural uncertainty is still uncommon (Essington and Plagányi, 2013).

The California Current along the west coast of North America is a coastal upwelling ecosystem that supports multiple fished forage fish populations, including primarily Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and Pacific herring (*Clupea pallasii*). As in other marine ecosystems (Pikitch *et al.*, 2014), forage fish in the California Current are a main prey source for culturally valued and protected seabirds and marine mammals including marbled murrelets (*Brachyramphus marmoratus*), humpback whales (*Megaptera novaeangliae*), and others (Szoboszlai *et al.*, 2015). Additionally, several economically and culturally valuable fish predators in this system depend on forage fish for a portion of their diet, including salmonids (*Oncorhynchus* sp., Brodeur *et al.*, 1987), California halibut (*Paralichthys californicus*, Wertz and Domeier, 1997), and albacore tuna (*Thunnus alalunga*, Glaser, 2009). These forage fish species have also supported profitable direct fisheries. The average annual ex-vessel revenue of the United States catch of Pacific sardine in 2004–2013 was $13.7 million, the average annual revenue of northern anchovy catch was $1 million (Pacific Fishery

Management Council [PFMC], 2014), and US revenue from herring averaged over $650,000 yearly between 2004 and 2013 (Pacific Fisheries Information Network [PacFIN], 2014).

In this study, we use a foodweb model of the California Current with high taxonomic resolution of forage fish and their predators (from Koehn *et al.*, 2016) in concert with a generalized equilibrium trade-off model (Essington and Munch, 2014) to identify the potential impacts of forage fish catch on predator fisheries and predator conservation. Specifically, we broadly sought to determine whether forage fish provide greater economic benefits as prey for other valued species or through direct harvest. To that end, we asked whether predator and fishery sensitivities to forage fish catch are variable across predators/fisheries fleets and across forage fish species. Finally, we sought to determine whether predator trade-offs to fishing forage fish are robust to uncertainty in foodweb model parameterization and generalized equilibrium model functional response assumptions.

Material and methods

We used a recent foodweb model of the California Current (Koehn *et al.*, 2016) as input to a generalized equilibrium model from Essington and Munch (2014) to calculate predator responses to forage fish depletion and determine trade-offs (negative responses) and positive impacts. Briefly, the generalized equilibrium model takes information from a steady-state foodweb model (see below) to parameterize a dynamic model, so that the marginal effects of fishing forage fish can be calculated analytically and without time-intensive simulation as others have done for determining trade-offs (as in Smith *et al.*, 2011). The analytical solution first assumes the dynamic relationship that a change in abundance of a species over a change in time is a function of its abundance, growth rate, and the harvest rate it experiences. The growth rate of each species is related to prey and predator abundance. From this, we can calculate the sensitivity of equilibrium abundance to changes in catch of forage species. The advantage of the generalized linear model is that the solution is entirely analytical, allowing us to explore the sensitivity of estimated trade-offs to a wide range of alternative foodweb parameterizations.

The generalized equilibrium model of Essington and Munch (2014) presumes that each species or group in a foodweb model can be represented by the generalizable dynamic equation (as mentioned earlier):

$$\frac{dx_i}{dt} = x_i r_i(\boldsymbol{x}) - c_i \tag{1}$$

where x_i is a measure of abundance of species i (here biomass), the vector $\boldsymbol{x}$ is the biomass of all species in the model, the function $r_i(\boldsymbol{x})$ is the per capita growth rate for species i given the biomass of other species (vector $\boldsymbol{x}$), and c_i is the fisheries catch of species i. The function $r_i(\boldsymbol{x})$ includes energy loss via predation and other sources, and energy gains via consumption of prey. Given this model, the marginal change in catch of any species with a change in forage fish catch equals:

$$\frac{\partial \bar{\boldsymbol{c}}}{\partial c} = \{d(\boldsymbol{r}(\bar{\boldsymbol{x}}))[\boldsymbol{J}_r(\bar{\boldsymbol{x}})]^{-1} + d(\bar{\boldsymbol{x}})\}$$
$$\times D\big(\{d(\boldsymbol{r}(\bar{\boldsymbol{x}}))[\boldsymbol{J}_r(\bar{\boldsymbol{x}})]^{-1} + d(\bar{\boldsymbol{x}})\}\big)^{-1} \tag{2}$$

where c is catch, $(\bar{\boldsymbol{x}})$ is a vector of equilibrium biomass values, $\boldsymbol{J}_r(\bar{\boldsymbol{x}})$ is the matrix of partial derivatives of the growth rates with

respect to each state variable, and the *j*th column is a vector of changes in yield of all other groups given a change in yield of species *j*. Terms $d(r(\bar{x}))$ and $d(\bar{x})$ are matrices where vectors $r(\bar{x})$ and $\bar{x}$ are placed on the diagonal, and terms with D of a matrix are matrices with the same diagonal as the original matrix, but off-diagonal elements are set to 0. We refer to the slope of the change in catch of a predator over a change in catch of a forage fish ($\partial c_i / \partial c_j$ in (Equation 2) as S_c or the "predator catch response," and is a unitless value.

Similarly, the slope relating predator biomass for nonmarket predators (without catch) to forage fish catch is equal to:

$$\frac{\partial \bar{x}}{\partial c} = J_r(\bar{x})^{-1} D\big(d(r(\bar{x}))[J_r(\bar{x})]^{-1} + d(\bar{x})\big)\big)^{-1} \qquad (3)$$

For a change in forage fish *j*, the *j*th column of $\frac{\partial \bar{x}}{\partial c}$ is a vector of biomass changes for all other species given a change in catch of forage fish species *j*. We refer to the marginal effect on biomass to forage fish fishing as S_x or the "predator biomass response". To allow for comparisons across predators, predator biomass responses (S_x) were translated into "elasticities" (*E;* proportional change in predator biomass with a proportional change in forage catch).

The above derivations apply for any functional form for $r(x)$ (making the model generalizable), but calculating the derivatives requires that we specify a functional form. For this, we use the flexible equation used by Essington and Munch (2014). The function $r_i(x)$ is a function of the consumption of species *i* and consumption of species *i* by predators *j*:

$$r_i(x) = \text{GCE}_i \sum_j^S \frac{f(x_j, x_i)}{x_i} - \sum_j^S \frac{f(x_i, x_j)}{x_i} - M_{0,i} x_i^\gamma \qquad (4)$$

The first half of the equation represents energy gains where $f(x_i, x_j)$ represents consumption of species *j* by species *i*, and GCE_i is the gross conversion efficiency. The second half of the equation is energy losses where $f(x_i, x_j)$ is the consumption of prey *i* by species *j*. $M_{0,i}$ multiplied by the biomass of the species is the mortality of species *i* from an unspecified source and can be dictated by density dependence when γ is > 0. We define the function $f(x_i, x_j)$ as follows:

$$f(x_i, \ x_j) = \alpha_{i,j} x_i^{\theta_{i,j}} x_j^{\varepsilon_{i,j}} \qquad (5)$$

where $\alpha_{i,j}$ is the search and capture rate of predator *j* on prey *i*. The parameters θ and ε can be set to account for non-linear prey-dependence (θ) (at 1 is equal to a linear functional response) and to account for predator dependence (ε) in the functional form.

We parameterized the generalized equilibrium model using parameters from the recent foodweb model of the California Current from Koehn et al. (2016). This foodweb model has 92 functional groups and high taxonomic resolution of forage fish (10 forage fish groups) and upper trophic predators (27 fish predators, 18 seabirds, and 15 marine mammal groups). The model extends from Vancouver Island, BC to Punta Eugenia, Mexico to capture many important predator breeding sites and the full distributional range of forage fish (specifically Pacific sardine). The model represents average ecosystem conditions during 2000–2014.

Specifically, biomass, diet, consumption, production, and catch parameters from the foodweb model are fed into the growth function (Equation 4) of the generalized equilibrium model. First, GCE_i

is derived from the production to biomass (*P/B*) and consumption to biomass (*Q/B*) parameters from the foodweb model for each species/group. For $f(x_i, x_j)$ (equation 5), $\alpha_{i,j}$ is solved for based on total per capita consumption rate of predator *j* on prey *i*, the equilibrium biomass of predator and prey (x_i, x_j), and randomly assigned values for ε and θ (which we varied for each predator–prey pair, see below). Finally, the remaining mortality term from Equation (4) ($M_{0,i}$) is equal to the proportion of total mortality in a group not explicitly included via predation and fishery catch in the foodweb model.

We calculated predator responses (catch responses or biomass responses) to fishing three main forage fish from the foodweb model—Pacific sardine, northern anchovy, and Pacific herring. We also considered a second foodweb scenario where fisheries and predators can substitute freely among forage fish so that the forage fish can be considered as a single aggregate group. To do this, we combined sardine, anchovy, and herring into an aggregated forage fish group, while maintaining the same energetic and biomass properties (see Gaichas et al., 2009).

We propagated uncertainty in functional response and foodweb linkages using a randomization routine where we generated 10 000 unique permutations of the generalized equilibrium model, and calculated biomass and catch trade-offs for each. First, we incorporated uncertainty in foodweb linkages by selecting for each of the 10 000 runs, one of the 500 mass-balanced randomized foodweb parameterizations from Koehn et al. (2016) (it was not feasible to generate more than 500, because only ~1:10 000 simulated draws met the constraint of mass balance). These 500 mass-balanced model parameterizations were found by Koehn et al. (2016) using a Monte Carlo approach and assigned levels of uncertainty for each parameter based on data quality rankings (mainly based on temporal and spatial scales; see Tables 1–3 in Koehn et al. 2016 for criteria for each quality ranking and level of uncertainty). Second, to address uncertainty in functional form, we randomly varied the parameters ε (Equation 4) and γ (Equation 5) that govern the functional form in the generalized equilibrium model, but are usually not known. For each predator–prey pair, we randomly drew unique combinations of ε_{ij} and γ_i for all 10 000 permutations. Values for ε_{ij} were randomly generated from a beta distribution (constrained to be between 0 and 1). For predator–detritus and predator–import prey pairs, ε_{ij} values were set at 1 to insure consistent sources of these diet items. Values for γ were randomly drawn from a beta distribution, constrained to be between 0 and ~0.5.

Values for θ are also usually not known, and we attempted to randomly vary θ for predator–prey pairs as well, but this led to numerical instability in solutions as is common in complex models with saturating functional response relationships. Therefore, we set $\theta = 1$ for all interactions (a linear prey response), which may be realistic for fish predators (likely no satiation effect, see Essington et al., 2000), but may be less realistic for seabirds (Enstipp et al., 2007; Piatt et al., 2007; Cox et al., 2013) and marine mammals (see Mackinson et al., 2003).

In very few parameterizations (0.016%), the generalized equilibrium model predicted response magnitudes (absolute values of S_c or S_x) that exceeded 1. All of these occurred for sardine, with a total of 0.064% of all sardine predator response magnitudes exceeding 1 (0.01% of catch responses and 0.1% of biomass responses). These levels imply a >1:1 dependency of predators to prey, which we deemed biologically unlikely and instead likely arose due to numerical instabilities in the inverse matrix in

Equation (4). For this reason, we omitted slope estimates that had magnitude >1 from our analysis.

We translated predator catch responses into economic values by incorporating ex-vessel price data. Price per metric ton for predatory fish came from the PacFIN database (http://pacfin.psmfc.org/pacfin_pub/all_species_pub/woc_r307.php) for the year 2013 by dividing total revenue by catch. For functional groups with more than one species, we calculated an average price weighted by the catch of each species in the group. Prices per metric ton of sardine and anchovy were calculated as 10-year averages using information from the 2014 Coastal Pelagic Stock Assessment (PFMC, 2014) and were equal to $168 and $178, respectively, while herring price per metric ton ($580) came from a 10-year average from PacFIN (again by dividing total revenue by total catch in metric ton). We used 10-year average prices for forage fish and only single year prices for other market fish because forage fish have higher variance in biomass between years, and biomass parameters were averaged as well (see Koehn *et al.*, 2016). Ten-year averages were used instead of the full 2000–2014 (15 years) because we lacked assessment data on all forage fish species for more recent years. We used a weighted average price based on catch to generate price for the aggregated forage group.

To make economic response values easily comparable and interpretable, we calculated the change in fishery ex-vessel values from a $1 change in forage fish landings. We did this for five fishery fleets: halibut (California halibut and Pacific halibut—*Hippoglossus stenolepis*), salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*), hake (*Merluccius productus)*, groundfish (multiple species, with an average price weighted by landings), and albacore. The value lost or gained was termed the "revenue response value" and was calculated as:

$$\partial V_\mathrm{p}/\partial V_\mathrm{f} = S_\mathrm{c}\left(P_\mathrm{p}/P_\mathrm{f}\right) \tag{6}$$

where V_p is the predator fleet value, V_f is the forage fish value, S_c is the predator catch response, P_p is the price of 1 metric ton of predator catch ($USD/metric ton), and P_f is the price of 1 metric ton of forage fish catch ($USD/metric ton). This can be interpreted as the marginal effect of additional unit value of forage fish catch on value of predator catch.

For nonmarket predators (species that are not traded in markets so have no directly observable monetary value, such as seabirds and marine mammals), it is difficult to quantify trade-offs in economic terms because the price of an individual predator is not known or easily calculated, and there is no single widely agreed upon method for estimating these values (Mendelsohn and Olmstead, 2009; Hausman, 2012; Kling *et al.*, 2012). For this reason, we inverted the problem and instead determined the predator value where the conservation benefits of forage fish to a predator equals the value gained from additional forage fish catch. This method is similar to methods used by Hannesson and Herrick (2010) to calculate what the value of sardine would need to be to make sardine more valuable as forage compared with catch. We used the predator biomass response (S_x) of a nonmarket species along with the ex-vessel value of a forage fish fishery to determine the price per individual for a nonmarket predator that is necessary for conservation losses of the predator (due to decreases in prey) to exactly equal fishery benefits from increased catch:

$$\Delta c_\mathrm{f}/P_\mathrm{f} = S_\mathrm{x}/P_\mathrm{p} \tag{7}$$

where c_f is the change in forage fish catch (1 metric ton), P_f is the price of forage fish, S_x is the predator biomass response, and the unknown to be solved for is the price of the predator (P_p). We termed this price value the price equivalent point (PEP; $USD/individual), which is calculated as follows:

$$\mathrm{PEP} = P_\mathrm{f}\left(\frac{S_\mathrm{x}}{W_\mathrm{p}}\right)^{-1} \tag{8}$$

where W_p is the average individual weight of the predator in metric tons so that PEP values are in terms of price per individual predator. Therefore, species with large negative biomass responses will have lower PEP, meaning that relatively low nonmarket values are sufficient to tip the trade-off towards predator conservation, whereas species with small magnitude responses will have high PEP. We calculated PEP values for all direct predators of sardine, anchovy, or herring and that had a consistent negative response (95th percentiles of biomass responses were negative).

For predator catch responses, biomass responses, and revenue responses, we classified the direction of an individual predator's response based on the 95% quantile range (0.025–0.975 quantiles) of responses across the 10 000 bootstrapping runs. We classified a predator (or fleet) as having a "negative" response if the 95th percentiles of responses for that predator were negative. Similarly, a predator's response was "positive" if the 95th percentiles were only positive. Response 95th percentiles that span 0 could arise if there is no response (slope = 0) or if precision in the slope estimate is low. Therefore, these responses are inconsistent in direction across runs and are not classified as a negative or positive response.

All analyses were run in R version 3.1.2 (31 October 2014) (R Core Team, 2014).

Results

Predator responses were generally robust to model parameterizations. For 35–43% of predators, the majority of model runs showed a negative response (95th percentiles were negative) in response to fishing anchovy, herring, or the aggregated group. Similarly, for 30–40% of predators, 95th percentiles of responses were all positive. Only around 25% of predators had responses that varied in direction across models runs and did depend on model parameterization. In response to fishing sardine, fewer predators (57%) had responses in the same direction across the majority of runs, and 43% had ambiguous responses.

For fished predators, there was no clear pattern in catch losses or gains across predators or across forage fish species, with increases in forage fish catch (Figure 1). Positive and negative catch responses to fishing forage fish were equally common across fished predators (∼11–37% vs. ∼26–33% of predators depending on forage fish) and were similar in magnitude (average median responses of 0.0014 and −0.0012). For a given predator, many (41%) had a consistent response to fishing only one forage fish or had divergent responses to fishing one forage fish vs. another. For example, arrowtooth flounder (*Atheresthes stomias*) had a positive response to fishing anchovy, but a negative response to fishing herring. On the other hand, four predators [specifically sharks, halibut, Pacific ocean perch (*Sebastes alutus*), and splitnose
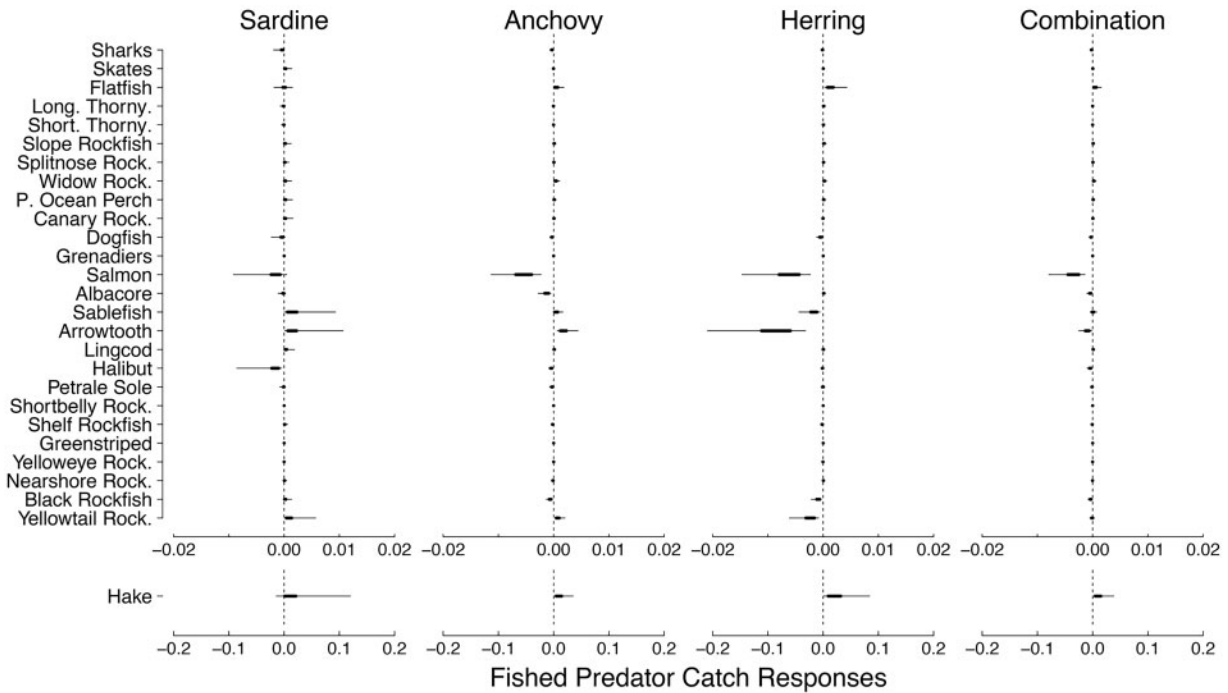
Figure 1. The effects of fishing forage fish on fished predator catches. 50th (thick line) and 95th (thin line) percentile ranges are shown for predator catch responses (the slope of the change in catch of a fished predator over a change in catch of a forage fish) in response to fishing each forage fish (sardine, anchovy, herring, and an aggregated group of sardine, anchovy, and herring) across 10 000 bootstrapping runs. Hake percentiles are wider than all other predators and are plotted on separate graphs with wider axes. A negative response means a loss in catch of the predator, while a positive response means a gain in catch.

rockfish (*Sebastes diploproa*)] had directionally the same response to fishing all three forage fish species and the aggregated group (though values are small and close to zero in response to certain forage fish). Additional predators had the same directional response to fishing two forage fish species, including large declines in salmon catch and large catch gains for hake.

Although catch of certain predator fleets declined, the revenue lost from the decline was never greater than the revenue gained from fishing forage fish (Figure 2; as represented by the 1:1 dotted line). The majority of fleets with negative responses had losses smaller than $0.10 in response to an additional $1 USD increase in catch of sardine, anchovy, herring, or the aggregated forage fish group. Only the salmon fleet had larger revenue losses, with median decreases of $0.24 and $0.16, in response to fishing anchovy and the aggregated group, respectively.

In contrast to fished predators, seabird responses were fairly consistent in direction across all seabird species, but varied in direction by forage fish species (Figure 3). In response to fishing anchovy, 61% of seabird species had declines in biomass. Alternatively, in response to fishing sardine or herring, the majority of seabirds (72 and 61%, respectively) had biomass gains. When forage fish were aggregated, most seabirds (56%) again all had a negative response to fishing forage fish.

Biomass losses were commonly greater in magnitude than any biomass gains across nonmarket predators (seabirds and mammals) in response to fishing forage fish (Figure 3). For example, 89% nonmarket predators with negative responses to fishing anchovy had losses greater in magnitude than gains for predators with positive responses (considering median values). Similarly, in
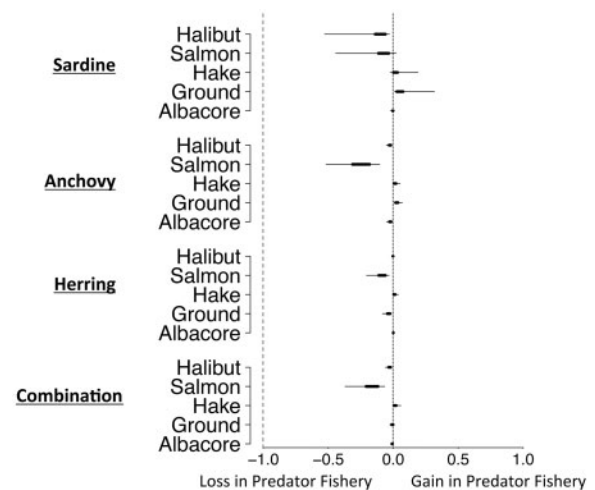

Figure 2. The effects of fishing forage fish on predator fleet revenue. 50th (thick black line) and 95th (thin black line) percentile ranges are shown for predator fleet revenue responses (halibut, salmon, hake, groundfish, and albacore) given a $1 increase in forage fish catch (sardine, anchovy, herring, or combined group of sardine, anchovy, and herring). Values left of 0 (dotted, black line) indicate loss in catch to a predatory fishery, while values left of −$1 (dotted, gray line) indicate where losses in predator catch value exceeds the gain in forage fish value. Losses to predator fleets never exceeded gain from increased forage fish catch ($1).
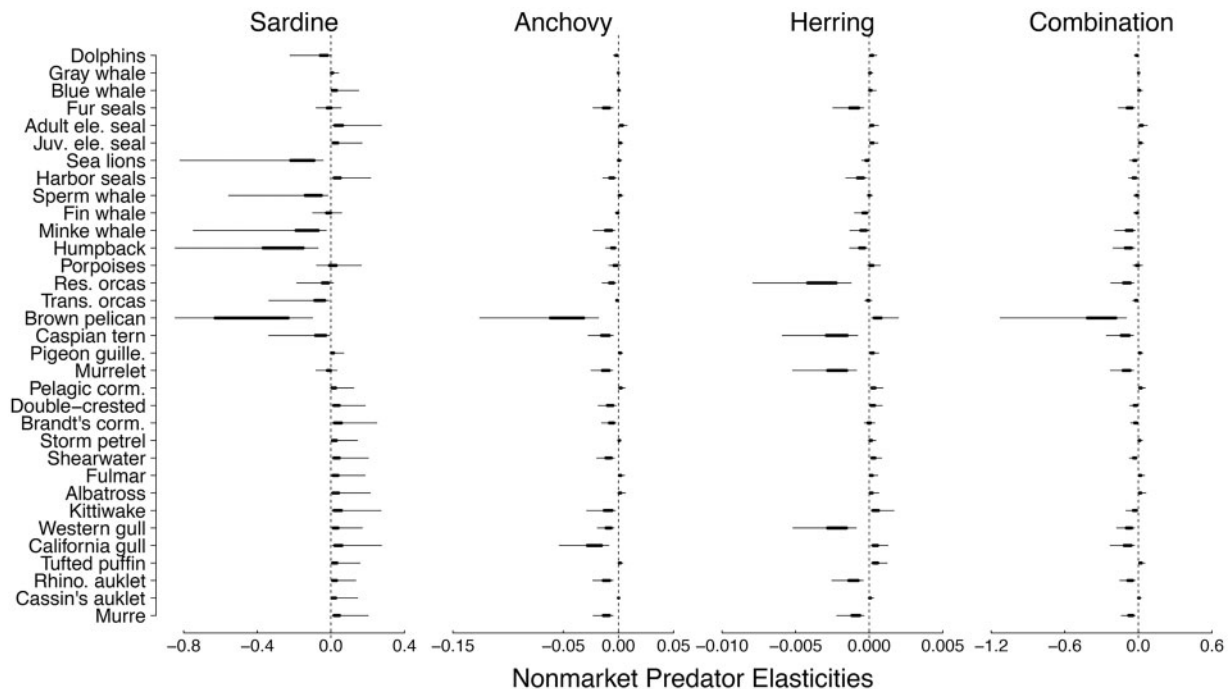
Figure 3. The effects of fishing forage fish on nonmarket predator (seabirds and marine mammals) biomass. 50th (thick black line) and 95th (thin black line) percentile ranges are shown for elasticities—proportional change in predator biomass with a proportional change in forage catch—in response to fishing sardine, anchovy, and herring separately and fishing an aggregated forage fish group (sardine, anchovy, and herring). Note the change in scale between the forage fish species/groups. Biomass losses for specific predators were commonly larger than biomass gains for other predators.

response to fishing sardine, herring, or the aggregated group, 73–100% of predators with negative responses had median losses greater than gains for other predators. Median losses ranged from −0.0002 to −0.37 compared with median positive responses of $4.4\mathrm{e}^{-5}$ to 0.036 (all proportional changes in biomass with a proportional gain in forage fish catch). At the same time, positive and negative biomass responses were as common across nonmarket predators (∼30–52% positive, ∼21–55% negative). Amongst the losses, brown pelican (*Pelecanus occidentalis*) had the largest losses (in response to fishing sardine, anchovy, and the aggregated group), and mammals tended to have large losses in response to fishing sardine.

The PEPs—the nonmarket value at which predator loss equals value gained in forage fish catch—were commonly smaller for seabirds than mammals (Figure 4). Shearwaters (*Puffinus* spp.) had the lowest PEP values, with a median value of $91 in response to fishing anchovy. In other words, if the nonmarket value exceeded $91 per individual shearwater, then the lost value of shearwaters would exceed the economic benefits of an additional metric ton of anchovy catch. Other seabirds also had low PEP values, likely from relatively large negative biomass responses, with median values ranging from $100 to $14 341. PEP values for mammals were commonly larger, ranging from a median of $600 for sea lions (*Eumetopias jubatus* and *Zalophus californianus*) (in response to sardine) to above $13 000 000 for a minke whale (*Balanoptera acutorostrata*, in response to herring). However, fur seals (*Callorhinus ursinus*) and harbour seals (*Phoca vitulina*) had lower values than a few individual seabirds in response to fishing anchovy and/or herring, and sea lions had the lowest PEP value of all predators in response to fishing sardine.

The direction of response to fishing forage fish was partly explained by the importance of forage fish in predator diets (Figure 5). This was most pronounced for seabirds, where negative responses to forage fish fishing were associated with higher proportions of diet consisting of forage fish. For example, among the species that declined from anchovy fishing, the median proportion of diet consisting of anchovy was 0.14 (range of 0.077–0.64). In contrast, seabirds that had either no consistent response or positive responses had diet proportions ranging from 0 to 0.7%. We observed similar patterns for marine mammal and fish predators, although there was a wider range of diet proportions among predators whose responses did not differ from 0 or were positive. Also, two mammal groups [transient and resident killer whales (*Orcinus orca*)] had negative responses to fishing a forage fish, but did not consume that forage fish (though do rely on other prey like salmon that had negative responses).

Discussion

We estimated changes in predator catch or biomass in response to fishing forage fish in the California Current using a method that is generalizable, analytical, integrates over all energy flow pathways of a foodweb, and explicitly accounts for parameter uncertainty. Overall, we did not find evidence that forage fish are more valuable when left in the water to feed piscivorous fish, which are, in turn, subjected to directed fisheries. However, the nonmarket value related to the conservation of many seabirds and some marine mammals may tip trade-off scales towards certain forage fish species being more valuable left in the ocean. We found losses of predator fishery catches were variable across predators and forage fish fisheries, though there were specific predator
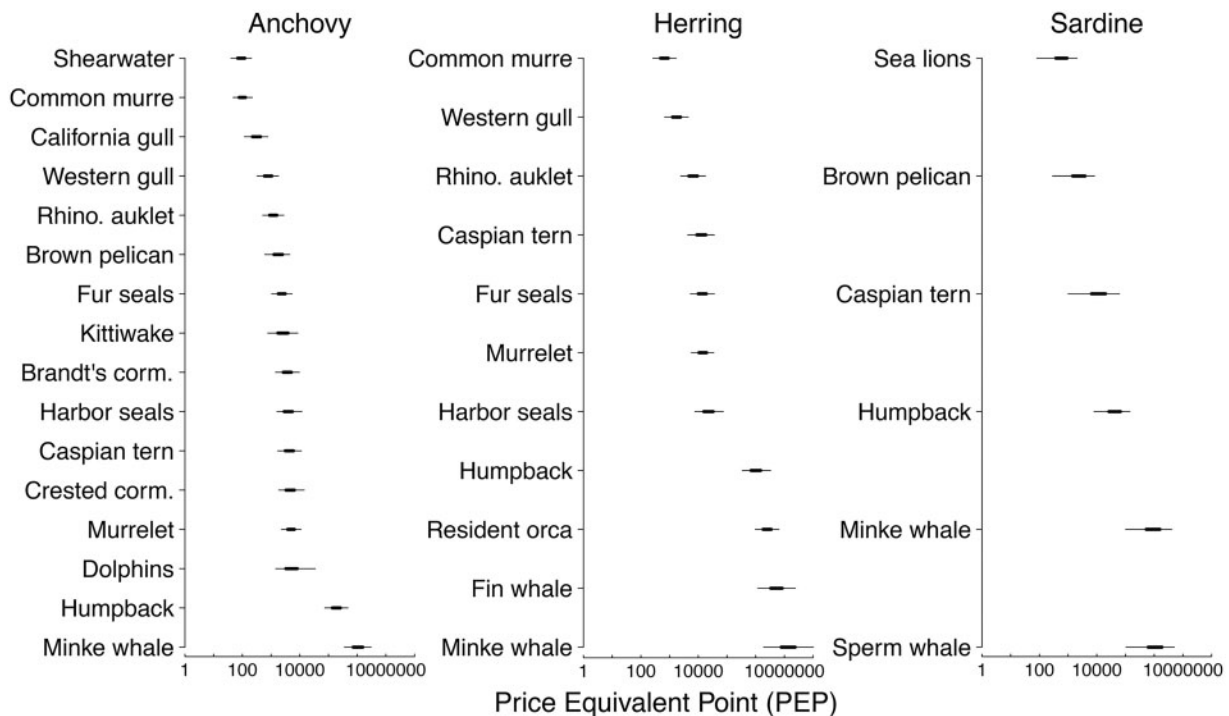
Figure 4. PEPs that a nonmarket predator would need to cost to equal the revenue value gained from an additional 1 metric ton of sardine, anchovy, or herring catch. 50th (thick lines) and 95th (thin lines) percentiles are shown. PEP values are only listed for nonmarket predators that consume the forage fish in consideration and had negative responses (all negative 95th percentile range). Values are generally smaller for seabirds than marine mammals (but see sardine).

fisheries (specifically salmon and halibut) with losses in response to fishing all or most forage fish. For unfished predators, biomass losses were larger than gains across seabirds and marine mammals, creating notable trade-offs between fisheries and conservation objectives.

Though fishing forage fish led to net economic gains for fisheries (due to the additional forage fish catch), the distribution of those gains among stakeholders was not equal, creating economic trade-offs among fisheries. Specifically, large catch losses for salmon and halibut in response to fishing forage fish led to economic losses for the salmon fleet and the halibut fishery. Fishing salmon is additionally already restricted and lowered due to ESA listings (PFMC, 2016). Fishing anchovy, in particular, had the largest negative impact on salmon, and salmon likely have a large impact on anchovy mortality (Koehn *et al.*, 2016), so future modelling effort could further explore trade-offs between these two specific fisheries. Additionally, the magnitudes of trade-offs could change over time with any changes in market prices of species or changes in the dependence of a predator on a forage fish (Hannesson and Herrick, 2010). Certain changes could result in a switch to where forage fish are more valuable as prey than as direct catch, such as increases in predator prices and/or decreases in forage fish price.

Our results suggest that seabirds in this system likely have simpler energy flow pathways connecting them to forage fish than do piscivorous fish, making seabirds potentially higher priority for future management considerations of specific forage fish fisheries. The directions of seabird responses to forage fisheries were generally predictable based on diets, with negative responses commonly associated with feeding on a forage fish species.

Additionally, seabirds that consumed mostly invertebrates, other small pelagic fish [such as sandlance (*Ammodytes hexapterus*), juvenile rockfish (*Sebastes*), smelt (*Osmeridae*), etc.], or had substantially larger diets of other forage fish considered, had positive responses. In contrast, though many fish predators with diets on a forage fish showed negative responses, others showed positive or inconsistent responses, implying that the relationship between diet and fish response direction is less consistent. There are multiple energy-flow pathways connecting fish predators to forage fish because piscivorous fish in this system have relatively generalist diets, feed at multiple trophic levels, and consume both forage fish and forage fish prey (Miller *et al.*, 2010; Koehn *et al.*, 2016). Conversely, many seabirds tend to have more specialized diets (Koehn *et al.*, 2016), creating primarily direct energy-flow pathways between seabirds and forage fish. This is corroborated by other modelling studies for this system that have shown that piscivorous fish that consume forage fish (particularly hake) do not necessarily benefit from increased forage fish abundance, likely due to competition with forage fish (see Ruzicka *et al.*, 2013). The stronger relationship between seabird diet and response direction created many strong, clear trade-offs for seabirds in response to fishing anchovy and clear gains in response to fishing herring and sardine, compared with fish predators.

Alternative forage fish harvest strategies, compared with constant fishing rates, could be considered to reduce indirect impacts of fishing on predators listed under the US Endangered Species Act (ESA). Many seabirds and marine mammals that we identified to be negatively impacted by forage fish fishing are currently ESA-listed including marbled murrelets (*B. marmoratus*), humpback whales (*M. novaeangliae*), resident killer whales, Steller sea
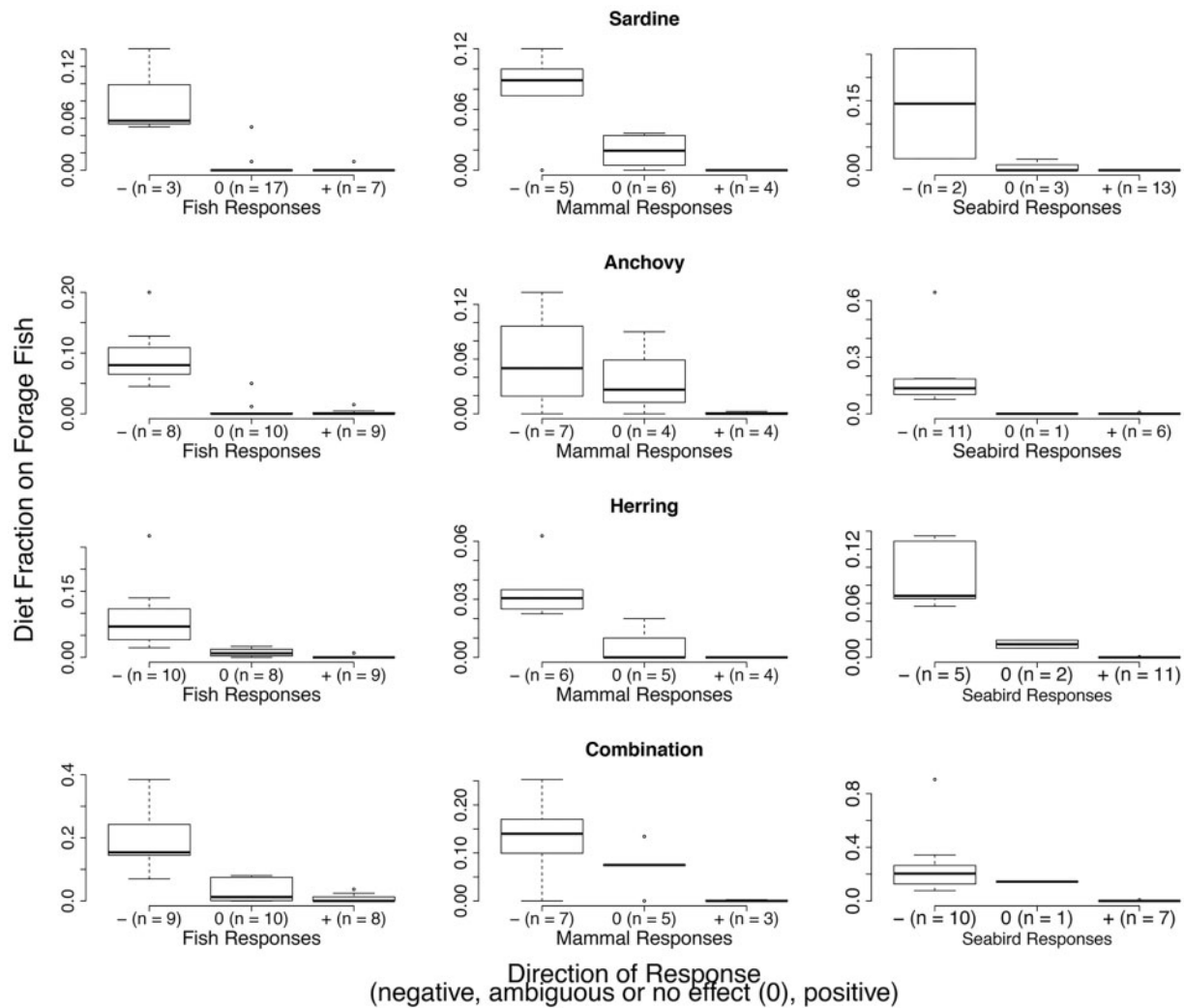
Figure 5. Boxplots for different predator groups (fish, mammals, and seabirds) based on responses to fishing sardine, anchovy, herring, or an aggregate forage fish group ("combination" = sardine, anchovy, and herring). Predators were broken up into response groups: consistent negative responses ("–," negative 95th percentile), no effect or ambiguous responses (inconsistent, "0," 95th percentile spans zero), and consistent positive response ("+," positive 95th percentile). Negative responses were commonly associated with a wide range of non-zero diet fractions, while positive responses were almost always associated with low or zero diet on forage fish.

lions (*E. jubatus*), and grey whales (*Eschrichtius robustus*). Previously listed brown pelicans also had large negative responses to fishing sardine, anchovy, and the aggregated forage fish group in our model. Alternative management strategies to reduce impacts could include spatial or temporal restrictions on fishing to conserve prey for central place foragers (seabirds and some marine mammals) during critical feeding periods (Boersma *et al.*, 2015). However, our model is on a coast-wide scale, and it is unclear if fishing is localized near predators. Future modelling efforts could focus the spatial resolution and test the need and effectiveness of these strategies for minimizing indirect effects of fishing on listed predators.

Declines in nonmarket predators in general, along with their potential value, could make conservation of these species an important consideration with future forage fish management decisions. Specifically, seabird conservation may be of needed consideration with the allocation of anchovy catch, due to the

negative impacts for multiple seabird species, including murres (*Uria aalge*), marbled murrelets, and brown pelicans, with anchovy fishing. Additionally, seabirds are particularly sensitive to localized prey depletion, due to small body size, correspondingly high metabolic rates, and diet specializations related to limited foraging ambits in time and space (Furness and Tasker, 2000). Models also predicted large losses for certain mammals (e.g. sea lions) in response to fishing sardine. Though sardine are managed with a cut-off rule (PFMC, 2014), which theoretically maintains prey biomass for predators at low sardine abundance, anchovy fisheries lack such a control rule, and anchovy abundance in 2011 was at ~1% of historical peak abundance (MacCall *et al.*, 2016). Anchovy was previously managed with a cut-off rule in order to account for the needs of predators (see PFMC, 1990), but this was not maintained when management of anchovy and other forage was combined into the Coastal Pelagic Species fisheries management plan (see PFMC, 2014). Our predicted losses for seabirds

along with the recent decline in anchovy (as well as sardine, Hill *et al.*, 2015) in this ecosystem, emphasizes the need to explore ecosystem-based harvest rules for multiple forage fish.

Many of the PEP values calculated for seabirds, and some marine mammals, are within an order of magnitude of other attempts to quantify nonmarket values, though we do not claim to know the value of these predators. The replacement costs for murre losses following the Exxon Valdez oil spill were estimated at $274 per murre (ca. $466 today) (Brown, 1992) vs. our median estimates of $100 and $656 for fishing anchovy or herring, respectively. For another species, marbled murrelet, $4 908 883 was spent on the recovery of this federally listed species in 2014 (US Fish and Wildlife, 2014). Considering the size of the US murrelet population (∼16 700 breeders, Miller *et al.*, 2012) and a ten-year life span, this would likely equate to near our median PEP value of ∼$4952 per bird in response to anchovy fishing. For marine mammals, most PEP values were larger than seabird values (especially for whales) which is expected because many marine mammals are less dependent on forage fish and consume larger fish as well (Szoboszlai *et al.*, 2015; Koehn *et al.*, 2016). However, sea lion PEP value in response to fishing sardine was substantially lower than estimated by Brown (1992). The study by Brown (1992) also put marine mammals prices in the tens of thousands, similar to some of our other estimated mammal prices.

Comparing results between scenarios—forage fish individually or in an aggregated group—reveals the benefit of a taxonomically resolved model for identifying specific predator sensitivities. Many seabirds had biomass losses with increasing anchovy catch, but gains with increases in sardine and herring catch (though there were exceptions). When the forage fish were aggregated and predators were assumed to switch freely between forage fish groups, many seabirds again had losses. Therefore, aggregation in this case exaggerated the losses of seabirds, making them appear negatively impacted by the depletion of any forage fish. Alternatively, there were a few mammals and fish predators with negative responses to fishing individual forage fish, but no response to fishing the aggregated forage fish group, showing that aggregation can also mask sensitivities.

The connection between predator diets and predator response directions reveals potential use of empirical diet information as indication of forage fish importance. This result supports the use of predator diet as a metric of predator dependency on forage fish to evaluate the importance of individual forage fish (e.g. Plagányi and Essington, 2014) or to predict the impacts of forage fish fisheries on predators (e.g. Pikitch *et al.*, 2012). Therefore, empirical information could potentially be used in substitution of an ecosystem model for managers to identify sensitive predators to forage fish fishing. However, forage fish in predator diet can vary spatially and temporally (Thayer and Sydeman, 2007; Brodeur *et al.*, 2014). Many seabirds in the model have zero sardine in their diet and, thereby, positive responses to fishing sardine. But most seabird diet data came from the 1970s to 1980s (Szoboszlai *et al.*, 2015) when sardine were not abundant. It is unclear if the absence of sardine in seabird diet is only a reflection of diet data temporal scale, or if seabirds do not consume sardine, possibly due to the offshore distribution of sardine (Zwolinski *et al.*, 2012). Also, diets used in the foodweb model were often averaged over time possibly dampening interannual prey importance (Koehn *et al.*, 2016). Therefore, to use diet information directly as an indicator of forage fish fishing impacts, data may need to be temporally and spatially complete.

The method we used for estimating trade-offs from fishing forage fish is based only on energy flow within a foodweb, and this and other model assumptions may impact results. First, due to instability in responses, we assumed a linear relationship between forage fish availability and predator feeding response in the generalized equilibrium model, which may be appropriate for fish (see Essington *et al.*, 2000), but less so for seabirds (Piatt *et al.*, 2007). Saturation in the functional response may reduce the magnitude of impacts (Abrams and Ginzburg, 2000), and prey-switching in the response (e.g. Holling type III functional response) may do the same (see Mackinson *et al.*, 2003). Additionally, size/age structure representation is limited. The few existing "juvenile" compartments in the model were not linked to the corresponding adult compartments (Koehn *et al.*, 2016). This could decrease bottom–up effects of removing forage fish and reduce trade-offs of forage fish fishing if juveniles of predator fish compete with, or are consumed by, forage fish (as in Houle *et al.*, 2013, Jacobsen *et al.*, 2015). Alternatively, this could increase bottom–up effects and trade-offs if there is higher predation on juveniles of predator fish after the removal of forage fish (because juvenile salmon, rockfish, and hake are alternative forage prey for many predators, see Szoboszlai *et al.*, 2015). Finally, the foodweb model only looks at average abundance and interactions at an ecosystem scale and doesn't capture ecological effects of localized depletion, which may be especially impactful on central-place foragers (Furness and Tasker, 2000). Therefore, our analysis points to species and fisheries catch that are generally likely to decline with increases in forage fish catch, but the magnitude of trade-offs may be variable.

Our economic analyses only considered ex-vessel prices, but a full cost-benefit analysis of fishing a forage fish would include all sources of revenue and costs for the entire production process from supplier to consumer. For forage fish, downstream benefits along the supply chain after ex-vessel revenue include revenue from reduction factories, fish oil factories, agriculture, aquaculture, and direct consumers (see Shepherd and Jackson, 2013). Therefore, the value of fishing forage fish could be substantially greater than the value represented by ex-vessel price. However, the total values of predators may be greater as well. Predator fish also have downstream benefits or supply chains, through processors, distributors, and consumers (see Christensen *et al.*, 2011). Nonmarket predators can have additional benefits other than existence value, including ecotourism revenue (whale watching, bird watching, etc.). Because of these additional economic benefits not considered, any potential trade-offs discussed here are only at the scale of fishers and only one part of the economic environment and cost-benefit analysis.

Our trade-off results can help direct management and conservation or focus future modelling efforts. Though response magnitudes may be over- or underestimated, future modelling efforts for all forage fish could further explore specific, individual effects of fishing revealed by our analysis. This includes the predicted economic trade-offs for salmon and halibut fisheries with forage fish fishing as well as the negative impacts across multiple seabirds with increases in anchovy catch and mammals with sardine catch. It is time and data intensive to develop models of high taxonomic resolution and run trade-off analyses for multiple species and over multiple model parameterizations. However, these efforts can save time and money in the long term by prioritizing future research and management actions, in the face of uncertainty, to the species and fisheries most impacted.

Acknowledgements

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Handling editor: Emory Anderson