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

Laura E. Koehn¹*, Timothy E. Essington¹, Kristin N. Marshall², William J. Sydeman³, Amber I. Szoboszlai³, and Julie A. Thayer³

¹School of Aquatic and Fishery Sciences, University of Washington, PO Box 355020, Seattle, WA 98105-5020, USA
²Cascade Ecology, PO Box 25104, Seattle, WA 98115, USA
³Farallon 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.

Koehn, L. E., Essington, T. E., Marshall, K. N., Sydeman, W. J., Szoboszlai, A. I., and Thayer, J. A. Trade-offs between forage fish fisheries and their predators in the California Current. – ICES Journal of Marine Science, 74: 2448–2458.

Received 10 February 2017; revised 8 April 2017; accepted 10 April 2017; advance access publication 13 May 2017.

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 pallasi), 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 pallasi). 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 (Szabo 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 her-ring 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):

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

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

$$\frac{\partial e}{\partial c} = \left\{d(r(x)) J_i(x) \right\}^{-1} \cdot D \left\{d(r(x)) J_i(x) \cdot d(x) \right\}^{-1}$$

where $c$ is catch, $(x)$ is a vector of equilibrium biomass values, $J_i(x)$ 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 $i$. Terms $d(r(x))$ and $d(x)$ are matrices where vectors $r(x)$ and $x$ 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 ($\partial c_i/\partial x_j$ in (Equation 2) as $S_i$ 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:

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

(3)

For a change in forage fish $j$, the $j$th column of $\partial x/\partial c$ 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 $S_j$, or the "predator biomass response". To allow for comparisons across predators, predator biomass responses ($S_j$) were translated into "elasticities" ($E_i$; 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 $j$ by predators $j$:

$$r_i(x) = GCE, \sum_j f(x_i, x_j) x_j - \sum_j f(x_j, x_j) M_{ij} x_j^2$$

(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 is the gross conversion efficiency. The second half of the equation is energy losses where $f(x_j, x_j)$ is the consumption of prey $i$ by species $j$. $M_{ij}$, 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 $\gamma > 0$. We define the function $f(x_i, x_j)$ as follows:

$$f(x_i, x_j) = \frac{\partial r_i}{\partial x_j} \frac{\partial r_j}{\partial x_i}$$

(5)

where $z_{ij}$ is the search and capture rate of predator $j$ on prey $i$. The parameters $\theta$ and $\eta$ can be set to account for non-linear prey-dependence ($\theta$) (at 1 is equal to a linear functional response) and to account for predator dependence ($\eta$) 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, 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), $z_{ij}$ 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 $\varepsilon$ and $\theta$ (which we varied for each predator–prey pair, see below). Finally, the remaining mortality term from Equation (4) ($M_{ij}$) 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 $\sim$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 $\varepsilon$ and $\gamma$ (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 $\varepsilon_{ij}$ and $\gamma_{ij}$ for all 10 000 permutations. Values for $\varepsilon_{ij}$ were randomly generated from a beta distribution (constrained to be between 0 and 1). For predator–detritus and predator–import prey pairs, $\varepsilon_{ij}$ values were set at 1 to insure consistent sources of these diet items. Values for $\gamma_{ij}$ were randomly drawn from a beta distribution, constrained to be between 0 and $\sim$0.5.

Values for $\theta$ are also usually not known, and we attempted to randomly vary $\theta$ 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 $S_i$ or $S_j$) 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 (Onchorhynchus tshawytscha and Onchorhynchus 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:

$$\frac{\partial V_p}{\partial V_f} = \frac{S_p}{P_p/P_f}$$

where $V_p$ is the predator fleet value, $V_f$ is the forage fish value, $S_p$ 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 be if 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:

$$\Delta c/P_f = S_p/P_p$$

where $c$ is the change in forage fish catch (1 metric ton), $P_f$ is the price of forage fish, $S_p$ 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:

$$PEP = P_f \left( \frac{S_p}{W_p} \right)^{-1}$$

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...
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 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.](image)

![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).](image)
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 $4.4e^{-5}$ 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 $14341$. 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 (Balaenoptera 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
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 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.

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).

Additionally, seabirds that consumed mostly invertebrates, other small pelagic fish [such as sand lance (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...
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 our median PEP value of ~$4,952 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 (Szabozi 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. Plaganyi 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 (Szabozi 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). 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 Szabozi 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.
Trade-offs between forage fish fisheries and predators

Acknowledgements

We thank the Pew Charitable Trusts (Ocean Science Division and the Pew Forage Fish Conservation Initiative) (L.E.K., T.E.E., W.J.S., A.I.S., J.A.T.) and National Fish and Wildlife Foundation and Marisla Foundation (J.A.T., A.I.S., and W.J.S.) for funding this research. In addition, we thank members of the Ocean Modelling Forum, namely Isaac Kaplan, Andre Pun, Phil Levin, Alec MacCall, and Tessa Francis for helpful discussion. Finally, we thank Dee Boersma, Chris Anderson, Emma Hodgson, Halley Froehlich, Pamela Moriarty, Kiva Oken, Nis Sand Jacobsen, Christine Stawitz, Margaret Siple, Elizabeth Phillips, Jennifer Lang, and Shannon Hennessey for useful comments that improved early versions of the article.

References

Abrams, P. A., and Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology and Evolution, 15: 337–341.

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., and Pauly, D. 2008. Forage fish: from ecosystems to markets. Annual Review of Environment and Resources, 33: 153–166.

Boersma, P. D., Rebstock, G. A., and García-Borboroglu, P. 2015. Marine protection is needed for Magellanic penguins in Argentina based on long-term data. Biological Conservation, 182: 197–204.

Brodeur, R. D., Buchanan, J. C., and Emmett, R. L. 2014. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. California Cooperative Oceanic Fisheries Investigation Report, 55: 96–116.

Brodeur, R. D., Lorz, H. V., and Peary, W. G. 1987. Food habits and dietary variability of pelagic nektom on Oregon and Washington, 1979-1984. NOAA Technical Memorandum NOAA-TM-NMFS-NWFC-57. 32 pp.

Brown, G. M. 1992. Replacement Costs of Birds and Mammals. University of Washington, Seattle, WA, USA. 16 pp.

Butler, C. M., Rudershausen, P. J., and Buckel, J. A. 2010. Feeding ecology of Atlantic bluefin tuna (Thunnus thynnus) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (Brevoortia tyrannus). Fishery Bulletin USA, 108: 56–69.

Christensen, V., Steenbeek, J., and Failler, P. 2011. A combined eco-

Crawford, R. J., Furness, R. W., Mills, J. A., et al. 2003. Comparing model predictions for ecosystem-based management. Canadian Journal of Fisheries and Aquatic Sciences, 73: 666–676.

Essington, T. E. 2007. Pitfalls and guidelines for “recycling” models for ecosystem-based fisheries management: evaluating model suitability for forage fish fisheries. ICES Journal of Marine Science, 71: 118–127.

FAO. 2015. Fishery and Aquaculture Statistics. [Capture production 1950-2013] (FishStat). In FAO Fisheries and Aquaculture Department [online], Rome. [Released March 2015]. http://www.fao.org/fishery/statistics/software/fishstat

Furness, R. W. 2003. Impacts of fisheries on seabird communities. Scientia Marina, 67: 33–45.

Furness, R. W. 2007. Responses of seabirds to depletion of food fish stocks. Journal of Ornithology, 148: 247–252.

Hannesson, R., and Herrick, S. F. 2010. The value of Pacific sardine as forage fish. Marine Policy, 34: 935–942.

Hausman, J. 2012. Contingent valuation: from dubious to hopeless. Journal of Economic Perspectives, 26: 43–56.

Hill, K. T., Crane, P. R., Dorval, E., and Maciewicz, B. J. 2015. Assessment of the Pacific Sardine Resource in 2015 for USA Management in 2015–16. Pacific Fishery Management Council, Portland, Oregon. 168 pp.

Jacobsen, N. S., Essington, T. E., and Andersen, K. H. 2015. Comparing model predictions for ecosystem based management. Canadian Journal of Fisheries and Aquatic Sciences, 73: 666–676.

Kaplan, I. C., Brown, C. J., Fulton, E. A., Gray, I. A., Field, J. C., and Smith, A. D. 2013. Impacts of depleting forage species in the California Current system. Environmental Conservation, 40: 380–393.

Kling, C. L., Phaneuf, D. J., and Zhao, J. 2012. From Exxon to BP: has some number become better than no number? Journal of Economic Perspectives, 26: 3–26.

Koehn, L. E., Essington, T. E., Marshall, K. N., Kaplan, I. C., Sydeman, W. J., Szoboszai, A. L., and Thayer, J. A. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current Ecosystem. Ecological Modelling, 335: 87–100.

Leslie, H. M., and McLeod, K. L. 2007. Confronting the challenges of implementing marine ecosystem-based management. Frontiers in Ecology and the Environment, 5: 540–548.

MacCall, A. D., Sydeman, W. J., Davison, P. C., and Thayer, J. A. 2016. Recent collapse of northern anchovy biomass off California. Fisheries Research, 175: 87–94.

Mackinson, S., Blanchard, J. L., PinNEGAR, J. K., and Scott, R. 2003. Consequences of alternative functional response formulations in models exploring whale-fishery interactions. Marine Mammal Science, 19: 661–681.
Marshall, K. N., Stier, A. C., Samhouri, J. F., Kelly, R. P., and Ward, E. J. 2016. Conservation challenges of predator recovery. Conservation Letters, 9: 70–78.

Mendelsohn, R., and Olmstead, S. 2009. The economic valuation of environmental amenities and disamenities: methods and applications. Annual Review of Environment and Resources, 34: 325–347.

Miller, S. L., Raphael, M. G., Falxa, G. A., Strong, C., Baldwin, J., Bloxton, T., Galleher, B. M., et al. 2012. Recent population decline of the marble murrelet in the Pacific Northwest. The Condor, 114: 771–781.

Miller, T. W., Brodeur, R. D., Raul, G., and Omori, K. 2010. Prey dominance shapes trophic structure of the Northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series, 420: 15–26.

Moberg, F., and Folke, C. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics, 29: 215–233.

Overholtz, W. J., Link, J. S., and Suslowicz, L. E. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science, 57: 1147–1159.

Pacific Fisheries Information Network (PacFIN) report 307, retrieval dated January 2014, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org).

Pacific Fishery Management Council (PFMC). 1990. Sixth Amendment to the Northern Anchovy Fishery Management Plan. PFMC, Portland, Oregon. 70 pp.

Pacific Fishery Management Council (PFMC). 2014. Status of the Pacific Coast Coastal Pelagic Species Fishery and Recommended Acceptable Biological Catches: Stock Assessment and Fishery Evaluation. PFMC, Portland, Oregon. 94 pp.

Pacific Fishery Management Council (PFMC). 2016. Pacific Coast Salmon Fishery Management Plan for Commercial and Recreational Salmon Fisheries off the Coasts of Washington, Oregon, and California as Amended through Amendment 19. PFMC, Portland, Oregon. 91 pp.

Platt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., van Pelt, T. L., Drew, G. S., and Kettle, A. B. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. Marine Ecology Progress Series, 352: 221–234.

Plüschke, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., Heppell, S. S., et al. 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean Program, Washington, DC. 108 pp.

Plüschke, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., et al. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, 15: 43–64.

Plagányi, É. E., and Essington, T. E. 2014. When the SURFs up, forage fish are key. Fisheries Research, 159: 68–74.

R Core Team. 2014: R: The R project for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Robinson, W. M., Butterworth, D. S., and Plagányi, É. E. 2015. Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. ICES Journal of Marine Science, 72: 1822–1833.

Ruzicka, J. J., Steele, J. H., Gaichas, S. K., Bailerini, T., Gifford, D. J., Brodeur, R. D., and Hofmann, E. E. 2013. Analysis of energy flow in US GLOBEC ecosystems using end-to-end models. Oceanography, 26: 82–97.

Shepherd, C. J., and Jackson, A. J. 2013. Global fishmeal and fish-oil supply: inputs, outputs and markets. Journal of Fish Biology, 83: 1046–1066.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., et al. 2011. Impacts of fishing low–trophic level species on marine ecosystems. Science, 333: 1147–1150.

Smith, M. D., Fulton, E. A., Day, R. W., Shannon, L. J., and Shin, Y.-J. 2015. Ecosystem modelling in the southern Benguela: comparisons of Atlantis, Ecopath with Ecosim, and OSMOSE under fishing scenarios. African Journal of Marine Science, 37: 65–78.

Sumaila, U. R., Cheung, W., Dyck, A., Gueye, K., Huang, L., Lam, V., Pauly, D., et al. 2012. Benefits of rebuilding global marine fisheries outweigh costs. PloS One, 7: e40542.

Szabo, A. I., Thayer, J. A., Wood, S. A., Sydeman, W. J., and Koehn, L. E. 2015. Forage species in predator diets: Synthesis of data from the California Current. Marine Informatics, 29: 45–56.

Tacon, A. G. J., and Metian, M. 2009. Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. AMBIO: A Journal of the Human Environment, 38: 294–302.

Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Monteverchi, W. A., and Blaber, S. J. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science, 57: 531–547.

Thayer, J. A., and Sydeman, W. J. 2007. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, Cerorhinca monocerata, in an upwelling system. Marine Ecology Progress Series, 329: 253–265.

US Fish and Wildlife 2009. Endangered and threatened wildlife and plants: removal of the Brown Pelican (Pelecanus occidentalis) from the Federal List of Endangered and Threatened Wildlife. Federal Register, 74: 59444–59472.

US Fish and Wildlife. 2014. Federal and State Endangered and Threatened Species Expenditures: Fiscal Year 2014. Department of the Interior, US Fish and Wildlife Service. Washington, DC. 415 PP.

Wertz, S. P., and Domeier, M. L. 1997. Relative importance of prey items to California halibut. California Fish and Game, 83: 21–29.

Zwolinski, J. P., Demer, D. A., Byers, K. A., Cutter, G. R., Renfree, J. S., Sessions, T. S., and Macewicz, B. J. 2012. Distributions and abundances of Pacific sardine (Sardinops sagax) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic-trawl surveys. Fishery Bulletin US, 110: 110–122.

Handling editor: Emory Anderson