ARTICLE

The economic tradeoffs and ecological impacts associated with a potential mesopelagic fishery in the California Current

Sally Dowd[1] | **Melissa Chapman**[1] | **Laura E. Koehn**[2] | **Porter Hoagland**[3]

[1]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, California, USA

[2]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA

[3]Marine Policy Center, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

Correspondence
Sally Dowd
Email: sallycdowd@gmail.com

Funding information
Woods Hole Oceanographic Institution, Grant/Award Number: Summer Student Fellowship, Ocean Twilight Zone project, J. Seward Johnson Fund in support of the Marine Policy Center

Handling Editor: Éva Elizabeth Plaganyi

Abstract

The ocean's mesopelagic zone (200–1000 m) remains one of the most understudied parts of the ocean despite knowledge that mesopelagic fishes are highly abundant. Apex predators from the surface waters are known to consume these fishes, constituting an important ecological interaction. Some countries have begun exploring the potential harvest of mesopelagic fishes to supply fishmeal and fish oil markets due to the high fish abundance in the mesopelagic zone compared with overfished surface waters. This study explored the economic and ecological implications of a moratorium on the harvest of mesopelagic fishes such as lanternfish off the US West Coast, one of the few areas where such resources are managed. We adapted a bioeconomic decision model to examine the tradeoffs between the values gained from a hypothetical mesopelagic fishery with the potential values lost from declines in predators of mesopelagic fishes facing a reduced prey resource. The economic rationale for a moratorium on harvesting mesopelagics was sensitive both to ecological relationships and the scale of the nonmarket values attributed to noncommercial predators. Using a California Current-based ecological simulation model, we found that most modeled predators of mesopelagic fishes increased in biomass even under high mesopelagic harvest rates, but the changes (either increases or decreases) were small, with relatively few predators responding with more than a 10% change in their biomass. While the ecological simulations implied that a commercial mesopelagic fishery might not have large biomass impacts for many species in the California Current system, there is still a need to further explore the various roles of the mesopelagic zone in the ocean.

KEYWORDS
bioeconomic model, fisheries, mesopelagic fishes, moratorium, nonmarket value, predators, *Rpath*, willingness-to-pay values

INTRODUCTION

Forage fish constitute 30% of the world's total marine fish catch (Alder et al., 2008). These small pelagic fish serve multiple purposes including direct consumption by higher trophic level fish, marine mammals, and seabirds (Pikitch et al., 2014), potential seafood for human consumption, and reduction into fishmeal and fish oil to

supply aquaculture production (Tacon & Metian, 2008) and nutraceutical markets (dietary supplements) (Pike & Jackson, 2010). Some apex marine predators, including those listed as endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN) on its Red List, rely upon forage fish as a food source (Pikitch et al., 2014). Especially in marine upwelling ecosystems, forage fish play important roles in trophic interactions as planktivores and as prey for larger predators (Cury et al., 2000). Overfishing of small pelagics in surface waters, such as anchovies, herrings, menhaden, and others, could cause a shift to the consumption of mesopelagic forage fishes by predators (Schwartzlose & Alheit, 1999). Although the ecosystem tradeoffs related to fishery harvests of pelagic forage fish have been well studied (Houle et al., 2013; Jacobsen et al., 2015; Koehn et al., 2017), less attention has been paid to the ecosystem role of mesopelagic fishes.

The mesopelagic zone is an aphotic area of the ocean, existing at depths between 200 and 1000 m. Although estimates of the global biomass of fish in this zone are uncertain, a recent acoustic study suggested that a previous approximation of 1 billion metric tons was a significant underestimate (Irigoien et al., 2014). Lanternfishes (Myctophidae) are thought to be the most abundant as they comprise 75% of the total trawl catch of mesopelagic fishes (Catul et al., 2011). It is well known that there are ecological interactions between animals that inhabit the epipelagic (0–200 m) and the mesopelagic zones. Epipelagic predators consume mesopelagic fishes by diving down hundreds of meters or when the latter migrate to shallower waters at night. Of their numerous predators, a few examples include billfish (Potier et al., 2007; Young et al., 2006), sharks (Lopez et al., 2010; Polo-Silva et al., 2013), tunas (Alverson, 1963; Bertrand et al., 2002; Potier et al., 2007), salmon (Jacobsen & Hansen, 2001; Manzer, 1968), cetaceans (Fitch & Brownell Jr, 1968; Pauly et al., 1998; West et al., 2009), and seabirds (Crawford et al., 1991; Harrison et al., 1983). Consumption by mesopelagic fishes through diel vertical migration (DVM) helps transport organic matter from the surface waters to the deep sea. Because mesopelagic fishes are a component of the ocean's biological carbon pump (Davison et al., 2013; Hidaka et al., 2001; Hudson et al., 2014; St. John et al., 2016), these organisms play a role in climate regulation.

The human exploitation of lower trophic level organisms, such as mesopelagic fishes, may impose consequences on entire ecosystems through trophic cascades. This process could alter species abundance (Trites et al., 2007), ecosystem structure (Suryan et al., 2009), and the life history strategies of organisms (Estes et al., 2011). Through wasp-waist control, a mid-trophic level species grouping, such as one composed of planktivorous fish, could influence both top-down and bottom-up processes (Cury et al., 2000; Lynam et al., 2017). Lanternfish have been shown to feed mainly on plankton (Pakhomov et al., 1996; Podrazhanskaya, 1993). In models for the eastern and western Pacific Ocean, large trophic cascades were observed from changing the abundance of epipelagic and mesopelagic fishes occupying intermediate trophic levels. Griffiths et al. (2013) suggested that the observed patterns could be a result of several wasp-waist groups.

Despite limited knowledge of the mesopelagic zone, humans have harvested its fauna in the past (Hoagland et al., 2020). In the 1980s, a Soviet fishery targeted lanternfish in the Southern Ocean, but it was discontinued once it could no longer be subsidized (Kock, 2000). Lanternfishes are not necessarily suitable for direct human consumption (Catul et al., 2011), but they can be processed into fishmeal as their balanced amino acid and protein contents are comparable with fish caught for other reduction fisheries (Seo et al., 1998). Currently, some countries are contemplating harvesting mesopelagic fishes for fishmeal production to supply expanding aquaculture operations (St. John et al., 2016; Hoagland et al., 2020). Yet, worldwide there are very limited regulations on fishing mesopelagic fauna, with the notable exceptions of quotas set by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) in the Southern Ocean and a moratorium implemented by the Pacific Fisheries Management Council (PFMC) on the harvest of certain mesopelagic fish families—such as lanternfish—in the Exclusive Economic Zone (EEZ) off the US West Coast. Until further data are collected or analyzed relating to the possible implications of a commercial mesopelagic fishery, this moratorium will continue to exist (PFMC, 2019).

This study focused on the California Current ecosystem, a region in the Pacific Ocean extending from British Columbia to Baja California Sur, for multiple reasons. First, this region hosts numerous species of conservation concern according to the IUCN Red List such as the great white shark (*Carcharodon carcharias*) and Leach's storm petrel (*Oceanodroma leucorhoa*) (IUCN, 2021) and economically important species such as coho salmon (*Oncorhynchus kisutch*) and lingcod (*Ophiodon elongatus*) that consume mesopelagic fauna. Because the California Current is relatively well studied with extensive data, there are multiple extant models including a food-web model that describes ecological relationships between species in the mesopelagic and epipelagic zone. Furthermore, the section of the California Current off the US West Coast is also one of the few areas where a restriction on harvesting mesopelagic fauna exists. It is important to explore the utility of the moratorium and

potential for this regulation to protect both the economic and ecological integrities of the ecosystem.

To determine the importance and potential impact of the PFMC moratorium, the first part of this study used a bioeconomic model for forage fish that incorporates parameters from a published California Current food-web model (Koehn et al., 2016). To explore the potential tradeoffs of a mesopelagic fishery, the hypothetical value that could be gained from the fishery was compared with the value of predators that relied on mesopelagic fish for a portion of their diet. We calculated different iterations of the model based on varying input parameters to explore the effects of parameter uncertainty on the results. Furthermore, we compared the calculated values of noncommercial predators with nonmarket values transferred from several willingness-to-pay studies. The changes in abundance of commercially and passively valued predators of mesopelagic fishes were assessed using an ecological model simulation. This is the first paper, of which we are aware, that concurrently explores the potential economic tradeoffs and ecosystem impacts associated with a mesopelagic fishery in the Pacific Ocean.

METHODS

Study overview

Within this study, we utilized two models (1) a bioeconomic model and (2) an ecological-time dynamic model, both of which used information from the Koehn et al. (2016) food-web model. We ran multiple model scenarios (Table 1) to address both the economic and ecological aspects of a potential mesopelagic fishery in the California Current and to explore uncertainty surrounding model input parameters and model assumptions. Economic scenarios 1–5 utilized the bioeconomic model introduced below. For the baseline scenario, scenario 1, we imputed original parameters to run the model. Scenarios 2–5 looked at variation in the natural mortality of mesopelagic fish or of fishing costs applied to mesopelagic fish and their commercially harvested predators. Ecological scenarios 6–8 used *Rpath*, an R-based implementation of the food-web model described below, to simulate harvesting on the mesopelagic fish group. Scenarios 6 and 7 applied different harvest rates to mesopelagic fish in the main *Rpath* model whereas scenario 8

TABLE 1 Summary of the various scenarios associated with the bioeconomic and ecological models used in this study. Through scenarios 2-5, we ran multiple iterations of the bioeconomic model using the base parameters and variations in the input parameters mentioned.

Scenario	Model	Description	Inputs	Outputs
1	Bioeconomic	Baseline calculation	Base parameters	Critical value
2	Bioeconomic	Variation in mortality of mesopelagics	Natural mortality ranging from 0.22 to 1.75 for mesopelagic fish, base parameters	Critical value
3	Bioeconomic	Variation in predator biomass	Lower and upper biomass from Koehn et al. (2016), base parameters	Critical value
4	Bioeconomic	Variation in price of commercial predators of mesopelagic fish	Lowest and highest US$/lb for commercial predators from 2007–2016, base parameters	Critical value
5	Bioeconomic	Variation in fishing costs	Fishing costs of 50:75%, 70:75%, and 70:85% of market price of predators: market price of mesopelagics, base parameters	Critical value
6	*Rpath* ecological simulation	Mesopelagic fish yearly harvest rate of 25%	*Rpath* model converted from food-web model in Koehn et al. (2016)	Biomass changes for the 92 functional groups in the food-web model
7	*Rpath* ecological simulation	Mesopelagic fish yearly harvest rate of 50%	*Rpath* model converted from food-web model in Koehn et al. (2016)	Biomass changes for the 92 functional groups in the food-web model
8	*Rpath* ecological simulation	Mesopelagic fish yearly harvest rate of 25%	Approximately 500 *Rpath* models converted from food-web models from Monte Carlo analysis in Koehn et al. (2016)	Biomass changes for the 92 functional groups in the food-web models

used ~500 *Rpath* models (variations of the initial model) to explore model uncertainty with the effects of a 25% harvest rate. The scripts and data sets used for the ecological simulations have been archived (https://doi.org/10.5281/zenodo.5806098).

California Current ecosystem model

We used an existing California Current food-web model, similar in structure to an *Ecopath* model, that examined the ecological relationships between forage fish and their predators (Koehn et al., 2016), and parameters from that model, as an input for both the economic and ecological models used in this study. Here, we summarize information on this model and include the diet matrix used in the model (Diet_CalCur_USE.csv, https://doi.org/10.5281/zenodo.5806098), but more detailed information on parameters, assumptions, and equations can be found in Koehn et al. (2016).

This food-web model was constructed following the *Ecopath* framework of Christensen and Walters (2004), assuming mass balance within the system (i.e., all biomass lost through fishing, mortality, etc. is equal to biomass produced). It is temporally static and represents a snapshot in time of the ecosystem, particularly, the average state of the system from 2000 to 2014. The spatial domain covered by the model extended from the northern end of Vancouver Island, British Columbia to Punta Eugenia in Baja California, Mexico and offshore out to the 2000-m isobath. The model was constructed with high taxonomic resolution of forage fish and their predators so that they were represented as distinct biomass pools or "functional groups." Initial parameterization for biomass, mortality, consumption, and fishery removal were compiled from published literature, fisheries stock assessments, NOAA marine mammal stock assessments, breeding abundance estimates for seabirds, and previous *Ecopath* models for the same ecosystem (Field, 2004) and for other regions with the same or similar species in comparable ecosystems (Aydin et al., 2007; Harvey et al., 2010). Please refer to appendix B in Koehn et al. (2016) for more information on specific parameters.

Diets used in Koehn et al. (2016) came from a variety of sources. The mesopelagic fish diet was taken from Field (2004) where more than 50% of their diet are euphausiids. The majority of diet information for upper trophic species came from the California Current diet database from Szoboszlai et al. (2015) although also from government documents, theses, and Field (2004) or other models (especially for a species with little information in the diet database). Generally, when multiple diet studies existed for a single species, diets were averaged but with attention to time of year, location,

sample size, and other specifics about each study. If diet studies were available for multiple regions within the larger model domain, the final diet was a weighted average, weighted by species proportional biomass in each region when known. For functional groups containing more than one species, final diets were weighted by the proportion of the biomass consisting of each species. More information on specific diet proportions, how they were calculated, and studies that contributed to the diet of each functional group can be found in appendix B in Koehn et al. (2016).

The functional group of focus for our simulations, mesopelagic fish, was one of 92 such groups included in the extant food-web model. With the exception of dragonfish (Stomiidae, mainly *Chauliodus macouni*, *Tactostoma macropus*, *Idiacanthus antrostomas*, and *Stomias atriventer*), which were omitted, the authors used the same mesopelagic species in the mesopelagic fish group as that in Field (2004). This group included myctophids, argentinids, gonostomatids, photichthyids, and bathylagids, with lanternfish occurring as the most abundant family. This model had 42 functional groups with some portion of their diets consisting of mesopelagic prey. We have listed, for predators of mesopelagic fish, the species in each functional group, the type of value associated with them, and their diet proportion of mesopelagic fish (Economic_value.xlsx, https://doi.org/10.5281/zenodo.5806098). There were 18 predator groups that held both noncommercial and commercial value, two groups with neither type of value, two groups with only commercial value, and 20 predator groups with only noncommercial value.

Bioeconomic model

We adapted a bioeconomic model developed to explore economic feasibility of a Pacific sardine fishery in the California Current (Hannesson et al., 2009) to mesopelagic fishes, using parameters from a more recently constructed food-web model (Koehn et al., 2016).

To determine the incremental portion of the mesopelagic fish stock that each predator consumes, we utilized equation (1) from Hannesson et al. (2009):

$$a_k = \frac{\left(\frac{g_k S_k d_k}{b_k}\right)}{(mS_s)} \tag{1}$$

where k represented a predator of the mesopelagic fish group, s. In the numerator, g_k was production/biomass, S_k was biomass (t/km^2), d_k was the proportion of a predator's diet that was composed of mesopelagic fish, and b_k

was the production to consumption ratio for a species. The predation mortality of mesopelagic fish per year, m, and the stock size of mesopelagic fish, S_s, made up the denominator. For this study, all the values for Equation (1) were taken from Koehn et al. (2016), with the exception of m. We calculated the predation, or natural mortality, under an assumption that the food-web model included all the predators of mesopelagic fish in the California Current ecosystem. As described in Hannesson et al. (2009), if all of the predators of the forage fish are included in the ecological model, then the per year natural mortality can be calculated based upon the principle that the a values sum to one.

A choice of whether or not it was economically beneficial to harvest the mesopelagic fish group depended on:

$$P_s > \sum_{i=1}^{N} P_i a_i b_i + v \sum_{j=1}^{M} a_j b_j \qquad (2)$$

where P_s represented the hypothetical net market price of mesopelagic fish as fishmeal, the most likely use of these organisms (here ignoring possible significant supply to the production of nutraceuticals). Note that this condition indicates whether or not it makes sense from an economic standpoint to harvest mesopelagic fish, given losses to commercially or noncommercially valuable predators; it does not indicate an optimal level of harvest from the fishery. In the absence of concrete information about harvest costs, the gross (ex-vessel) prices for mesopelagic fish and commercial predators were used. N commercial predators were indexed as i; M noncommercial predators were indexed as j. A functional group was included in the bioeconomic model if it had some portion of its diet consisting of mesopelagic fish (i.e., "predators") and was found to have either commercial or noncommercial value. P_i was the net price of predators in the market, and the a and b values were taken from Equation (1). The critical value, v, was the minimum value required to equate the price of mesopelagic fish (as landed) and the forage value of mesopelagic fish (value in the water) (the right-hand side of the equation). The value v was associated with a per unit increase in the biomass of predators that were not commercially exploited as a result of an incremental increase in mesopelagic fish as prey. This value was not an input, but rather was calculated given known values of the other parameters.

To calculate the critical value, we first calculated the predation mortality of mesopelagic fish. Assuming the food-web model included all mesopelagic fish predators, natural mortality was found to be 0.32. For model scenario 1 listed in Table 1, the baseline calculation, we calculated a critical value using this natural mortality and a price of mesopelagic fish of US$0.68/lb taken from the average fishmeal price in Peru from 2016 (Index Mundi, 2016).

As the economic model differentiated between commercial and noncommercial predators, we determined the type of value associated with each species in a functional group where species could have both market and nonmarket values. To determine whether a predator was harvested and marketed in the United States, we searched for each individual species in NOAA's database of 2016 annual commercial landings in the Pacific region by state (NOAA Fisheries, 2016). Following Hannesson et al. (2009), this study considered both nonextractive and extractive values to determine whether a species was noncommercial. Noncommercial values were derived as estimates from the literature of willingness to pay (WTP) for the existence of other relevant species. These estimates were divided by estimates of stock sizes to calculate per unit vales (WTP/lb). These estimates are taken as an admittedly rough measure of nonmarket values to compare with the critical value. Such estimates do not reflect how WTP might be influenced by changes in stock sizes of noncommercial predators. Details on determining the value of predators of mesopelagic fish and calculating gross prices for commercial predators can be found in Appendix S1: Section S1.

Analyzing uncertainty in economic model input parameters

Through scenarios 2–5 (Table 1) we examined how variations in input parameters could impact the critical value. Documented natural mortality of myctophids in various parts of the world ranges from 0.22 to 1.75. Therefore, we calculated the critical value when considering the mortality literature values of 0.70 (Gjøsæter, 1981), 0.74 (Gjøsæter, 1981), 1.21 (Sebastine et al., 2013), and 1.75 (Gjøsæter, 1973) as well as 29 estimates of natural mortality using various simulations for glacier lanternfish (*Benthosema glaciale*) (Kenchington, 2014). Additionally, we considered the lower and upper biomass estimates for each predator of mesopelagic fish in the economic model from 500 biomass values that Koehn et al. (2016) generated through Monte Carlo draws to examine parameter uncertainty. The next two critical values were calculated from the lowest and highest price per pound from NOAA's annual landings from 2007 to 2016 for commercial predators. Prices were summed from California, Oregon, Washington, and the "At-sea Process, Pacific" category and then divided by the total weight landed (in pounds [lbs]). The category "At-sea Process, Pacific" was included as the Pacific species in this category were likely to be caught as by-catch through the whiting fishery, which operates off the US West Coast (Jon McVeigh, personal communication, 2019).

The economic model was designed to include prices for forage fish and their predators that were net of fishing costs. Except for scenario 5, all other scenarios ignored the impacts of fishing costs on the market price of commercial predators as well as the hypothetical value of mesopelagic fish as fishmeal. To show the variation once net price was considered, three different fishing cost scenarios were implemented. We calculated the critical value when fishing costs encompassed 50%, 70%, and 70% of the market price of predators and 75%, 75%, and 85% of the market price of mesopelagics.

Nonmarket values of noncommercial predators

Willingness-to-pay values can be compared with the critical value, or the hypothetical nonmarket value of noncommercial predators (Hannesson et al., 2009). Species-specific WTP values are often estimated through surveys of respondents about how much they would theoretically be willing to pay to ensure the existence of a species in nature through preservation or improved stock status. For the seven species in the food-web model that had documented WTP values, we transformed these estimates across their regional populations into per unit values (WTP/lb). We were able to compare the critical values generated through the base scenario and the model iterations that considered input uncertainty with the calculated WTP/lb values as these metrics had the same units and both placed a potential economic value on species in the ecological model. Note that this comparison was limited in the sense that our WTP/lb considered only one form of nonextractive value (species existence), whereas the critical value could more broadly comprise multiple nonextractive values (species existence and nonextractive economic activities) and extractive values (recreational fishing). This restriction could lead to underestimates in the noncommercial value of predators of mesopelagic fish. Additionally, the calculated WTP/lb was species-specific, yet the critical value summed the nonmarket value of all noncommercial predators. Finally, as implemented within the modeling framework, WTP/lb was kept constant; in reality, large changes in the stock sizes of a noncommercial predator might influence its WTP/lb in a nonlinear manner, due to diminishing marginal utility (leading to relatively larger gains if stock sizes were initially small or relatively smaller gains if they were initially large). Our WTP/lb was an approximation as a first step as the bioeconomic model used did not consider large changes in stock biomass. Changes to WTP/lb with stock size is a clear area for future research. The explanation

and citations for these calculations are found in Appendix S1: Section S2 and Appendix S1: Tables S1, S2.

Ecological impacts of harvesting mesopelagic fishes

To explore the ecological impacts of harvesting the mesopelagic fish group on interconnected organisms in the California Current, we converted the initial temporally static *Ecopath* framework and the 500 associated model versions developed in Koehn et al. (2016) into *Rpath* models (Lucey et al., 2020) to run dynamic simulations. The *Rpath* package incorporates the structure and methodology of *Ecopath* with *Ecosim* (EwE) software (including Polovina, 1984; Walters et al., 1997, 2000), but within R (R Core Team, 2021) and the associated linear algebra library. The equations related to the static *Ecopath* model in *Rpath* and the generation of dynamic simulations (*Ecosim*) can be found in Lucey et al. (2020). Based on a set of governing differential equations, the "Rsim" functions in *Rpath*, similar to *Ecosim*, describe the change in biomass of a functional group over time. For the dynamic simulations, for all parameters not generated from the static *Rpath* input, we used the default *Rpath* package parameterization, which mainly controls the strength of predator–prey interactions. Within this approach, the foraging arena model is used, which assumes that only a proportion of prey is vulnerable to predation at a time. In *Rpath*, the functional response (consumption by a predator on each prey at a given time) is governed by the initial diet proportion on that prey from the static model, the initial consumption rate of the predator, the biomass of each prey and the predator at a point in time relative to each initial biomass respectively, and the "vulnerability" of each prey to the predator. We utilized the default parameters for the functional responses built into *Rpath* simulations, including default parameters for vulnerability, handling time, and foraging time. Therefore, we assumed a Holling type II functional response, intermediate between bottom-up and top-down effects, and consistent time spent foraging. We also, therefore, assumed the same functional response across all predator–prey pairs. For groups such as albacore and seabirds that migrate in and out of the model domain, a percent of their diet was specified as "input consumption" so that a portion of their diet came from outside of the model system and was not explicitly modeled (species that have input consumption references are available at: Diet_CalCur_USE.csv, https://doi.org/10.5281/zenodo.5806098). Model output may be sensitive to functional response parameter uncertainty, but the overall direction of a response (decline, stable, or increase) has been shown to be relatively robust (Aydin et al., 2003), especially when

modeled fishing pressure is low to moderate (Gaichas et al., 2012; please refer to Whitehouse & Aydin, 2020 for discussion). Please refer to Lucey et al. (2020) for more information on *Rpath*, Whitehouse and Aydin (2020) and Gaichas et al. (2012) for information on the functional response in *Rpath/Ecosim* and assumptions, and Plagányi and Butterworth (2004) for a discussion on the assumptions of *Ecosim* and implications of these assumptions.

After creating a mass-balanced snapshot and establishing a base scenario from the initial model in Koehn et al. (2016), we used the "Rsim" functions to project the *Rpath* model forward in time from 2001 to 2050. Throughout the 50-year "Rsim" base scenario, the relative biomass of all functional groups was at one. We simulated the ecosystem-wide biomass impacts of harvesting mesopelagic fishes at a yearly rate of 25% and 50%. By the end of 2050, the relative end biomass for the mesopelagic fish group was reduced to 47% (loss of 53% of starting biomass) and 14% (loss of 86% of starting biomass) for the 25% and 50% harvest scenarios, respectively. We explored the relationship between the impact of both harvest rates on the end biomass of all functional groups and the proportion of mesopelagic fish in their diet (if any).

Due to uncertainty in model parameters, Koehn et al. (2016) used a Monte Carlo approach (similar to the "Ecosense" approach by Aydin et al., 2007) to generate 500 additional versions of the food-web model using the initial parameterization and estimates of uncertainty around each parameter based on data quality assessed through a data pedigree. To explore parameter uncertainty, we repeated our above process for all 500 of these models through applying a yearly 25% harvest rate on mesopelagic fish. As the mesopelagic zone is relatively inaccessible and various other factors make harvesting and processing its fauna difficult, the 25% harvest rate is more practical in approach compared with the 50% harvest rate for this simulation. We calculated quantiles of the proportional change in biomass for predators of mesopelagic fish by comparing each predator's biomass in the final month of 2050 with their initial biomass in the *Rpath* model, across the 500 models. We removed seven out of the 500 models as they produced biologically implausible biomass projections that were magnitudes of 100 times larger than projections from other models and were statistical outliers based on interquartile range values.

RESULTS

Analyzing uncertainty in economic model input parameters

For the baseline scenario, we found a critical value of US\$16.40/lb for noncommercial predators. Therefore,

considering the original parameters, noncommercial predators would need to jointly generate a value more than US\$16.40/lb per year to reverse the inequality in Equation (2) and make mesopelagic fish more valuable if left in the water as forage for their predators.

When considering uncertainty around input parameters in the bioeconomic model, the variation in natural mortality of the mesopelagic fish group led to the largest differences in the critical value (Figure 1). The lowest mortality estimate yielded a critical value ~US\$11.00/lb, the highest mortality estimate resulted in a critical value of US\$92.00/lb, and the mean critical value out of all mortality estimates was US\$57.00/lb (SD of ~US\$41.00/lb). The next four calculated critical values considered variations in the biomass and price inputs. Model iterations 6 and 7 included the lowest and highest biomass estimates from the Monte Carlo simulations in Koehn et al. (2016) for predators of mesopelagic fish, and iterations 8 and 9 considered the lowest and highest price per pound for commercial predators between 2007 and 2016 (Table 2). The mean of the critical value from these four different estimates, US\$16.25/lb (SD of 0.96), was similar to the baseline calculation of US\$16.40/lb. We calculated three more critical values after applying fishing costs to the market price of predators of mesopelagic fish and to mesopelagic fish as fishmeal through scenario 5. There was little variation when we considered net price as these model iterations had critical values ~US\$4.00/lb, US\$4.00/lb, and US\$2.00/lb.
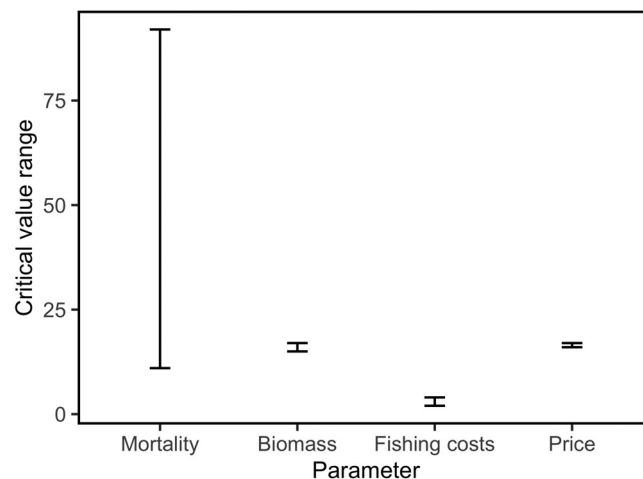

FIGURE 1 The range of critical values calculated from the bioeconomic model when testing input parameter uncertainty. Variation in the mortality of myctophids, biomass of mesopelagic fish predators, fishing costs applied to market price of mesopelagic fish and their predators, and price of commercial predators were considered

Nonmarket values of noncommercial predators

As the critical value is the hypothetical nonmarket price of all noncommercial predators and the mean WTP/lb calculated for seven predators in the *Rpath* model was greater than most of the critical values in model iterations 1–12 (Table 2), mesopelagics may be more valuable if left in the water as forage for their predators. However, the uncertainty in input parameters and WTP values as well as the large range of calculated values (Figure 2), makes it hard to draw a clear conclusion on whether mesopelagic fish would actually be less valuable as a commercial resource. Also, it is important to note that the commercial value of predators alone was not enough to reverse the inequality to potentially make mesopelagic fish more valuable as a nonharvested resource and instead the above results were generated once noncommercial value was considered as well.

The seven WTP/lb values ranged widely, with a minimum WTP/lb of US$0.07/lb and a maximum of US$254.00/lb (Appendix S1: Table S2). The mean value was ~US$36.00/lb (SD of US$74.00/lb). The baseline critical value and the average of the critical values when considering variation in biomass, price for commercial predators, and fishing costs were all lower than the mean WTP/lb calculated. Once we considered net price by applying fishing costs, the critical value was observed to be well below the mean WTP/lb. The mean ciritcal value of the mortality iterations (~US$57.00/lb) was higher than our mean WTP/lb, which would suggest that mesopelagic fish may be more valuable as a harvested resource. However, because the critical value was the sum of all nonmarket values of noncommercial predators and our mean WTP/lb was just the hypothetical average value for one of these predators, it is likely that the latter was an underestimate.

Ecological impacts of harvesting mesopelagic fishes

Overall, the majority of functional groups slightly increased over time with simulated fishing of the mesopelagic fish group. Considering the two mesopelagic fish

TABLE 2 Critical values (US$/lb), or the nonmarket value of all noncommercial predators of mesopelagic fish that we compared with willingness to pay per pound estimates, calculated to show uncertainty in model inputs

Model iteration	Mortality	Critical value (US$/lb)	Varied parameter
1	0.32	16	None
2	0.22	11	Mortality: literature values and estimates from Kenchington (2014)
3	0.62	32	Mortality: literature values and estimates from Kenchington (2014)
4	1.75	92	Mortality: literature values and estimates from Kenchington (2014)
5	1.1	92	Mortality: mean estimate from literature values only
6	0.32	17	Biomass: lowest biomass estimates from 500 food-web model versions in Koehn et al. (2016)
7	0.32	15	Biomass: highest biomass estimates from 500 food-web model versions in Koehn et al. (2016)
8	0.32	17	Price per pound: lowest US$/lb for commercial predators between 2007–2016
9	0.32	16	Price per pound: highest US$/lb for commercial predators between 2007–2016
10	0.32	4	Fishing costs: fishing costs constituting 50% of market price of predators and comprising 75% of market price of mesopelagic fish
11	0.32	4	Fishing costs: fishing costs constituting 70% of market price of predators and comprising 75% of market price of mesopelagic fish
12	0.32	2	Fishing costs: fishing costs constituting 70% of market price of predators and comprising 85% of market price of mesopelagic fish

Note: Noncommercial predators need to jointly generate a value above the critical value yearly to make mesopelagic fish more valuable left in the water as forage than harvested through a commercial fishing operation. Iteration 1 is the baseline critical value. Iterations 2–5 consider variation in the natural mortality (m) of myctophids. Iterations 6–9 included variations in price and biomass inputs for the critical value calculation. We calculated the remaining critical values by applying various fishing costs to the market price of commercial predators and the hypothetical market price of mesopelagic fish as fishmeal.
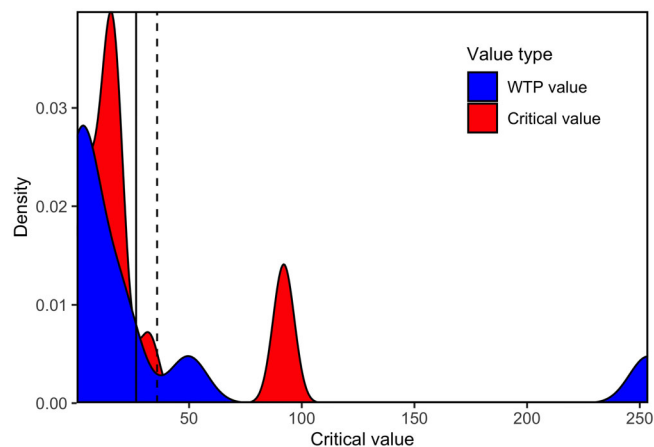
FIGURE 2 Density distribution of willingness to pay (WTP) per pound values and critical values (US$/lb). WTP/lb was calculated from WTP values found in the literature for seven species in the food-web model and the critical values are from the model iterations shown in Table 2. The dashed line represents the mean WTP/lb value, and the solid line represents the mean critical value

harvest levels, on average, 73% of all functional groups in the ecosystem exhibited an increase in biomass by the end of the 50-year simulation (Appendix S2: Table S1). For the 25% and 50% yearly harvest rates (scenarios 6 and 7), only 7 and 29 functional groups out of 92, respectively, exhibited a 10% or greater change in their biomass (increase or decrease).

The implications of fishing the mesopelagic zone were explored mainly in the context of the commercial and non-commercial predators of mesopelagic fish. For both mesopelagic fish harvest rates, 65% of commercial predators slightly increased in biomass (<10%) (Appendix S2: Figure S1a–d). Scenarios 6 and 7 resulted in only two and five commercial predator groups, respectively, to have end biomass changes of at least 10%. The longspine thornyhead (*Sebastolobus altivelis*) was the only commercial species to decrease by this magnitude.

Similar to the commercial species, ~75% of non-commercial functional groups increased at the end of scenarios 6 and 7 (Appendix S2: Figure S1a–d). Four noncommercial predator groups in scenarios 6 and 11 in scenario 7 had biomass changes equal to or greater than 10%. The groups that decreased by this magnitude included Leach's storm petrel, longspine thornyhead (which had both commercial and noncommercial value), and dolphins, which included the long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*Delphinus delphis*), and bottlenose dolphin (*Tursiops truncatus*). In total, 13 of the 15 marine mammal groups that were predators of mesopelagic fish increased under scenario 7.

Negative impacts on predator functional groups were related to their diet proportion of mesopelagic fish. We separated predators of mesopelagic fish into high and low diet proportion categories. We defined functional groups with high diet proportions as having at least 5% of their diet composed of mesopelagic fish (12 groups), whereas those with low diet proportions were defined as having less than 5% of their diet consist of mesopelagic fish (30 groups). More predators in the high diet proportion category decreased at the end of the 50-year simulations (Figure 3); while 50% of the high diet groups had a reduced end biomass, only 20% of the low diet proportion groups decreased in abundance for both scenarios 6 and 7. Leach's storm petrel, longspine thornyhead, and dolphins were the only functional groups to decrease by 10% or more, other than mesopelagic fish. These three functional groups had the largest proportions of mesopelagic fish in their diet in the *Rpath* model; Leach's storm petrel had a diet composed of nearly 30% mesopelagic fish, dolphins had 20% in their diet, and longspine thornyhead had a diet comprised of 10% mesopelagic fish (Economic_value. xlsx, https://doi.org/10.5281/zenodo.5806098). Here, 72% of functional groups with no diet dependence on mesopelagic fish (those with a 0 for the mesopelagic fish group in the diet matrix shown in Diet_CalCur_USE.csv, https://doi.org/10.5281/zenodo.5806098) increased under scenario 6, 8% decreased, and 20% did not exhibit an increase or decrease in biomass (relative biomass remained at 1). For scenario 7, 74% of functional groups with no mesopelagic fish diet dependence increased, 18% decreased, and 8% maintained a relative biomass at 1 (Appendix S2: Figure S2).

To further explore the mainly positive, but small biomass changes in functional groups that relied on mesopelagic fish, we examined the food-web dynamics more thoroughly quantitatively and qualitatively. Within the *Rpath* model, there were 42 predators of mesopelagic fish and eight prey items that mesopelagic fish relied on (Appendix S2: Figure S3a). We took predators that had at least 5% of their diet consist of mesopelagic fish and weighted their diet proportions on mesopelagic fish and mesopelagic fish prey items (such as anchovy, copepods, euphausiids and herring) based on predator biomass, in which at least one of the grouped predators had a mesopelagic prey item comprising 5% or more of their diet. We found that overall mesopelagic predators had a higher dependence on mesopelagic prey items than on mesopelagic fish (diet proportions of 0.69 vs. 0.08) (Appendix S2: Figure S3b). Mesopelagic fish decreased drastically during scenario 6 whereas weighted relative biomass for the groupings of the predators of mesopelagic fish (0.99), prey items of mesopelagic fish (1.04), and other prey of these predators (0.97) exhibited little biomass change throughout the harvest scenario (Figure 4).
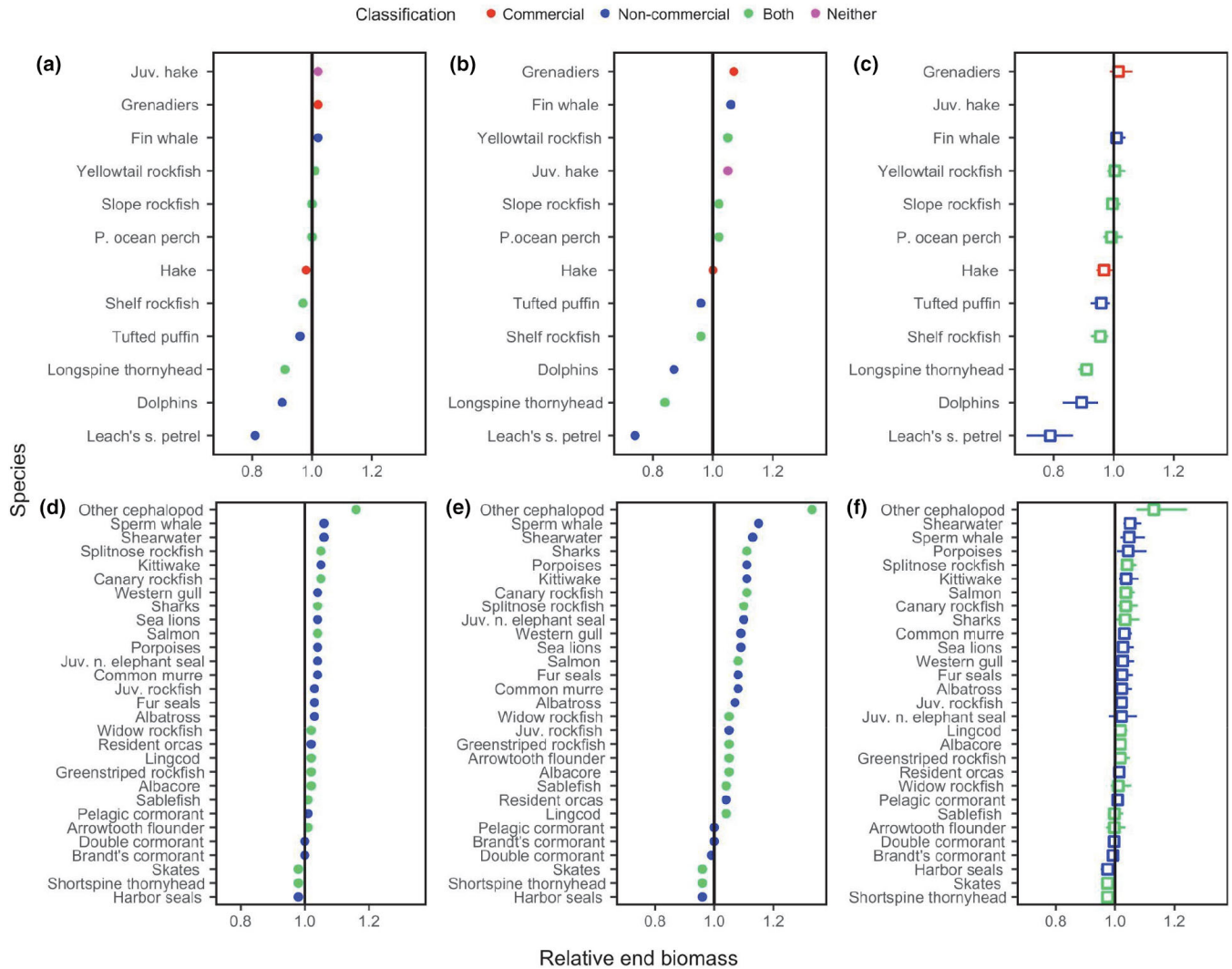
FIGURE 3 The effects of various mesopelagic harvest rates on functional groups with high diet dependence (functional groups with at least 5% of their diet consisting of mesopelagic fish) (a–c) and low diet dependence on mesopelagic fish (d–f). As the mesopelagic fish group had drastic biomass reductions, we removed it from the low diet dependence group to allow for greater readability of results for smaller biomass changes. The relative end biomass is the biomass at the end of the simulations (month 600) relative to the base scenario (base scenario end biomass is 1 for all functional groups). The results are displayed for the yearly 25% harvest rate applied to the main *Rpath* model (a, d), the yearly 50% harvest rate applied to the main *Rpath* model (b, e), and the yearly 25% harvest rate applied to ~500 different *Rpath* models to explore uncertainty in input parameters (c, f). For the last panels, the 95th percentile ranges (line) and median end biomass (square) are present. Species are distinguished by color depending on whether they held commercial or noncommercial value, both, or neither. All species shown were also included in the bioeconomic model analysis except for juvenile hake, which held neither commercial nor noncommercial value

Analyzing uncertainty around *Rpath* model input parameters

There was relatively small variance between the end biomass of all functional groups across the multiple "Rsim" models after the most realistically possible fishing scenario was implemented (a yearly 25% harvest rate on mesopelagic fish). We found that 45% of all functional groups showed a clear increase in their median biomass across model runs and only 10% showed a clear decrease

(95% biomass percentile range did not cross the 1:1 ratio of start to end biomass; Figure 3; Appendix S2: Figure S2). We were uncertain of an increase or decrease for 46% of all functional groups, as the 95th percentile biomass ranges for these predators crossed the base scenario relative biomass of 1. The mean relative biomass range between the lower (2.5%) and upper (97.5%) quantiles across groups was 5% for scenario 8. This value implies that, on average, there was only a 5% variation in relative end biomass in 95% of the data for all functional
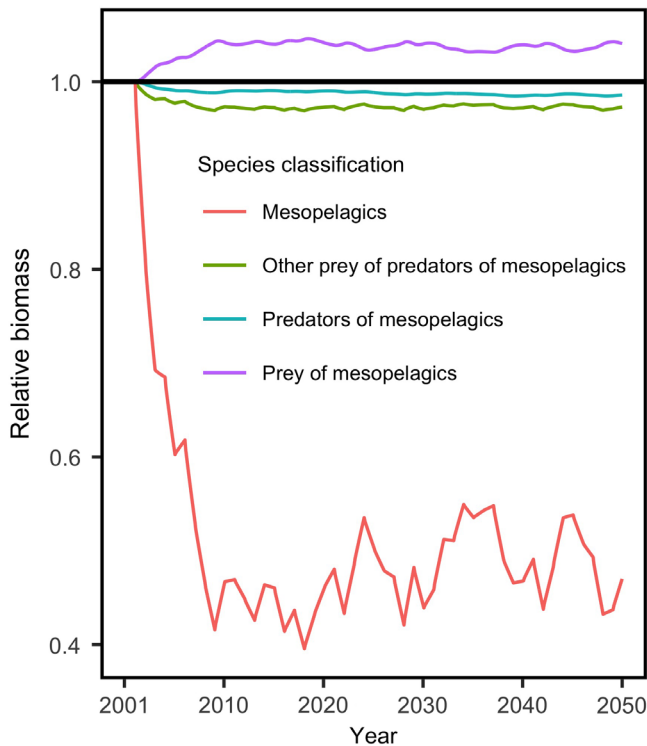
FIGURE 4 A projection of weighted relative biomass of various species groupings from applying a yearly 25% harvest rate on mesopelagic fish for 50 years. Species classifications include "Mesopelagics," "Predators of mesopelagics" (functional groups that had at least 5% of their diet that consisted of mesopelagic fish), "Other prey of predators of mesopelagics" and "Prey of mesopelagics" (nonmesopelagic prey items and mesopelagic prey items that at least one of these predators relied on for at least 5% of their diet). Lines for relative biomass were weighted based on the contribution of a functional group's original biomass to the total biomass of their species classification. Projections above the solid black line represent an increase and projections below represent a decrease in original functional group biomass

groups in the food-web model. The maximum range in biomass values across model runs was 23.44% for mesopelagic fish and the minimum was 0.46% for the transient orcas group.

DISCUSSION

To examine the importance of the PFMC moratorium on mesopelagic fishes, this study considered the economic value and ecology associated with predators of mesopelagic fishes off the US West Coast. We highlighted the large variation and uncertainty attached to species existence values by comparing our calculated critical values from the bioeconomic model to ranges of WTP per pound for select predators. Model iterations that considered net price revealed that the steep costs of harvesting

mesopelagic fauna would lower the nonmarket critical value, suggesting that mesopelagic fishes could be more valuable as forage for their predators. However, with simulated fishing on mesopelagics, at the end of both 50-year harvest scenarios, most functional groups in the California Current showed a slight increase in biomass (mean increase of 4% and 9% for scenarios 6 and 7). When the mesopelagic fish stock was fished at a yearly 25% and 50% harvest rate, only 4% of functional groups decreased by more than 10% in abundance. This effect was related to diet on mesopelagics; species with higher mesopelagic diet proportions were more likely to decrease in abundance (Appendix S2: Figure S4). The different structure and assumptions behind the economic and ecological models were responsible for the apparent contradictions in results among these approaches and presented a range of possible outcomes given parameter uncertainty.

There were a few key differences between the static, bioeconomic model and the dynamic "Rsim" approach. The package *Rpath* allows for both bottom-up and top-down forcing, whereas Hannesson et al. (2009) designed a model that incorporated only bottom-up processes and ignored the interactions between fishing and forage fish abundance and productivity (Essington & Munch, 2014). This bioeconomic model assumed only linear relationships between functional groups (Kaplan et al., 2013) and that an increase in the target forage fish (in this case mesopelagic fish) would have a positive effect on its predators. The simplest explanation is that if there was a reduction in the harvest of mesopelagic fish there would be increased prey availability for their predators. Although the bioeconomic model had extensive food-web complexity and was designed to examine tradeoffs in an ecosystem, the "Rsim" scenarios incorporated the interactions mentioned above (bottom-up and top-down) that the bioeconomic approach ignored.

This modeling framework provided an approach to begin to understand the tradeoffs arising among ecologically linked species in the California Current system. It is important to note, however, that large changes in the stock sizes of any of the linked species might result in changes in prices or in nonmarket values. For the commercial species, we adopted the usual assumption that yields from these fisheries would be small enough that they would not affect prices in the larger markets. For nonmarket species, we adopted a similar assumption, but we added the caveat that understanding changes in WTP for nonmarket species in relation to stock size (e.g., economic scope sensitivity; please refer to Lopes and Kipperberg (2020) for a recent review) may not be well constrained in most cases. Further modeling assumptions (e.g., diminishing marginal utility with increases in stock sizes) or empirical data that relate

changes in WTP to stock sizes may be needed to implement the modeling framework in practice.

In this study, we presented two models with uncertainty in model parameters that varied assumptions to provide a range of possible outcomes for the ecosystem. For ecosystem-based fisheries management purposes, using multiple model approaches in lieu of a single model can help to address structural uncertainties that cause variability in results. There is then a need to generalize or average the results from these multiple models to form a holistic fisheries management approach that acknowledges model uncertainty (Ianelli et al., 2016; Kaplan et al., 2019). The models presented in this study may have led to underestimates or overestimates for various responses, but it is possible that together they span the range of realistic scenarios.

For the bioeconomic model analysis, we considered passive values associated with nonmarket predators, although the WTP approaches used to generate these values can sometimes be problematic. As Hannesson et al. (2009) acknowledges, survey participants never actually pay these values, stretching the credibility of these estimates. Our calculated WTP/lb for seven species in the food-web model ranged widely, from US$0.07/lb to US$254/lb. These hypothetical species existence values make it difficult to draw a clear conclusion on the practicality of a moratorium and are only part of the value that can be attributed to noncommercial predators. In the future, nonextractive economic activities such as ecotourism and extractive activities such as recreational fishing need to be considered to place a value on noncommercial predators. Within California alone, there are nine established shark ecotourism operators (Gallagher & Hammerschlag, 2011) that focus on either white, blue, or mako sharks—organisms that have been included in the food-web model used. While economic analyses of shark tourism operators off the US West Coast were not used here, at a dive site in the Maldives (Indian Ocean), a single gray reef shark was estimated to generate US$33,500 in shark-watching revenue from divers each year (Anderson & Ahmed, 1993). Additionally, saltwater recreational fishing generates large expenditures in the United States that are useful for income and employment purposes (Steinback et al., 2004).

As model parameters are uncertain, it is important to analyze the variation around the critical value produced by the bioeconomic model approach by discussing the assumptions behind the baseline calculation. We calculated the natural mortality of the mesopelagic fish group by assuming that all their predators were included in the food-web model, exploring the uncertainty around this assumption through various model iterations. Because our calculated critical values that consider variation in

mortality ranged from ∼US$11.00/lb to US$92.00/lb, it suggests that our baseline mortality of 0.32 and critical value of US$16.40/lb may both be too low. More research is needed for an accurate estimate of natural mortality of mesopelagic fishes in the California Current as the nonmarket value, or the value needed to equate the price and forage value of mesopelagic fish, can significantly change once variations in mortality are considered.

When we included hypothetical net price in calculations and applied higher fishing costs to the harvest of mesopelagic fishes, compared with their predators, the critical value of noncommercial predators lowered drastically (average of ∼US$3.00/lb) in reference to the baseline critical value. Compared with the surface waters, the mesopelagic zone is more difficult to access, probably resulting in higher fishing costs for multiple reasons. The harvest of mesopelagic fishes involves steep costs of search, deployment of nets in deep waters, and onboard processing. Additionally, mesopelagic fishes can exhibit effective trawl-avoidance behavior (Kaartvedt et al., 2012), potentially making them difficult to catch. Considering increased operating expenses, Prellezo (2019) found that the potential profit margin for a hypothetical mesopelagic fishery in the Bay of Biscay was marginal. Once we considered hypothetical fishing costs, the resulting low critical value implied that a moratorium on the harvest of mesopelagic fishes might be justifiable from an economics perspective. This being said, before supporting or opposing a moratorium on mesopelagic fishing, aspects of this potential fishery such as operating costs and economic profitability need to be evaluated, as done in Prellezo (2019) and Paoletti et al. (2021).

Due to the high operating costs associated with a mesopelagic fishery, we focused on the impacts on predator biomass after applying a yearly 25% and 50% harvest rate on mesopelagic fishes for 50 years. Most mesopelagic fish predators exhibited positive, but small changes in their biomass, with few functional groups increasing or decreasing by more than 10% of their original biomass. Although an economic analysis was not performed, the longspine thornyhead, the only commercial predator of mesopelagic fish that decreased by this magnitude, was priced at only US$0.53/lb in 2016. No predators that yielded the highest economic value (at least US$1.00/lb in 2016) decreased by 10% or more. Other studies based on ecosystem models have observed similar effects of harvesting mesopelagic fishes. Smith et al. (2011) found that reducing mesopelagic fishes to 60% of their original biomass caused no functional groups to change in abundance by more than 40% in an EwE Northern California Current model from Field (2004). Choy et al. (2016) documented results similar to our study; most apex predators in a Central North Pacific EwE model barely changed in

biomass when the mesopelagic fish group, composed of mostly lanternfish, were harvested. Their work found that the strongest connections between lower trophic levels and apex predators were through crustaceans and mollusks, and that other functional groups encompassed inefficient energy flow pathways.

A reason for the minimal and mostly positive impact of mesopelagic fish depletion on functional group biomass in the California Current could be a result of diet composition and trophic pathways such as those documented by Choy et al. (2016). Kaplan et al. (2013) showed that harvesting euphausiids and forage fish compared with mesopelagic fish, had the most drastic ecosystemwide impacts for the California Current. In our simulations, euphausiids and forage fish increased, likely due to the high diet dependence of mesopelagic fish on euphausiids and the reduced interspecific competition for forage fishes that prey on euphausiids. As reported in Surma et al. (2018), we believe that the increases in these groups due to reduced predation and competition, could be responsible for the minimal change in biomass for certain functional groups as mesopelagic fish were harvested. Weighted biomass diet proportions revealed that predators of mesopelagic fish relied more on mesopelagic fish prey items (e.g., euphausiids) than mesopelagic fish themselves. Although the food-web energy flow pathways in this ecosystem are complex (Appendix S2: Figure S3a), together these results suggest that diet dependence can partially explain the observed increases of many functional groups.

While our study suggests that the ecological implications of harvesting mesopelagic fishes in the California Current may not be that large, this result might not apply to other ecosystems or if a higher diet dependence on mesopelagic fishes comes to light in the California Current system. For example, in contrast with the California Current, mesopelagic fishes are an important food source for predators in certain parts of the Southern Ocean (McCormack et al., 2020; Saunders et al., 2019), forming energy pathways through mid-trophic levels as shown through an EwE study (McCormack et al., 2021). Also, it is important to note that various factors could influence our results, and there is less information known about the consumption of mesopelagic fishes by apex pelagic predators compared with other prey due to the difficulties of studying this zone (Naito et al., 2013). As much of the mesopelagic zone is oceanic (Sutton et al., 2017) and deeper than surface waters, this area is less accessible for predators and the scientists studying them. For instance, a predator's stomach may already be empty upon returning from foraging offshore on mesopelagic fauna (Cherel et al., 2008), which can limit the diet data that scientists collect. Additionally, proportions of forage fish in diets can vary over time and space (Brodeur et al., 2014; Thayer & Sydeman, 2007) and certain methods for diet studies may produce more errors than others (Baker et al., 2014). Finally, because the Koehn et al. (2016) model was focused on high taxonomic resolution of forage fish (such as anchovy, sardine, and herring, but not mesopelagic fish) and their predators, this model may more accurately capture those energy flow pathways than the ones involving mesopelagic fish.

As we manipulated a food-web model with *Rpath* that was not calibrated with historical reference data, we addressed uncertainty through using multiple model runs. A model can be fitted using time series data on the relevant functional groups in *Ecosim* to allow a user to assess the accuracy of their model (Heymans et al., 2016). To evaluate the integrity of our original simulation without fitting the *Rpath* model to time series data, we explored the results from approximately 500 "Rsim" scenarios based on 500 different food-web models. The 95th percentile ranges of the end biomass did not capture substantially large variation between models for most functional groups. On average, for the 10 groups that had the widest 95% quartile range, there was only a 13% range in relative biomass across models. Although this analysis, for the most part, did not expose large output discrepancies between models, the results of this study should not be used as a foundation for management for the harvest of mesopelagic fishes. Because the exact ecological implications of fishing the mesopelagic zone are unknown, the simulations described here can better serve as a framework to guide future research on mesopelagic fauna. However, because there was little variation in results across the 500 model runs that address parameter uncertainty, the general patterns of response for predator biomass may generally hold even with further research. Additionally, because *Rpath* is an open-source package with reproducible commands, the methods used in this study can serve as a baseline for future studies.

There is a lack of research on the ecological, physical, and biogeochemical properties of the mesopelagic zone (Martin et al., 2020), and there is a pressing need to gather more information to understand the ecosystem services of mesopelagic fauna. This study is the first to examine some of the economic tradeoffs and ecological implications of a potential mesopelagic fishery through the lens of predators of mesopelagic fish. Mesopelagic fishes serve roles outside the consumption by predators or for human use because they comprise an element of the biological carbon pump, which is essential for climate regulation. Estimates of the percentage of total carbon transport by mesopelagic fishes from surface waters, or fish-mediated transport, ranges from less than 10% in the California Current to more than 40% in the North Pacific Subtropical Gyre (Davison

et al., 2013). Furthermore, this study did not consider the interactions between climate change and fishing. Climate change can influence the biomass of mesopelagic fishes through reducing oxygen availability. Mesopelagic fishes have declined in oxygen minimum zones in the California Current when there has been low oxygen availability, possibly due to increased exposure to predators in a shifted hypoxic boundary layer (Koslow et al., 2011). Before developing a commercial mesopelagic harvest operation, it is necessary to understand not only the impacts of harvesting mesopelagic fishes on their predators, but also the intersection between harvesting mesopelagic fishes and climate change, as well as the role of these fauna in climate regulation.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data used in this study were sourced from Koehn et al. (2016), and we modified code originating from Lucey et al. (2020). Novel code and the original and modified datasets have been archived through Zenodo (Dowd et al., 2021, https://doi.org/10.5281/zenodo.5806098).

REFERENCES

Alder, J., B. Campbell, V. Karpouzi, K. Kaschner, and D. Pauly. 2008. "Forage Fish: From Ecosystems to Markets." *Annual Review of Environment and Resources* 33: 153–66.

Alverson, F. G. 1963. "The Food of Yellowfin and Skipjack Tunas in the Eastern Tropical Pacific Ocean." *Inter-American Tropical Tuna Commission Bulletin* 7(5): 293–396.

Anderson, R. C., and H. Ahmed. 1993. *The Shark Fisheries of the Maldives*. Rome and Male: FAO and Ministry of Fisheries.

Aydin, K. Y., G. A. McFarlane, J. R. King, and B. A. Megrey. 2003. "The BASS/MODEL Report on Trophic Models of the Subarctic Pacific Basin Ecosystems." *PICES Scientific Reports* 25: 93.

Aydin, K. Y., S. K. Gaichas, I. Ortiz, D. H. Kinzey, and N. Friday. 2007. *A Comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems through Food Web Modeling*. Seattle, WA: Alaska Fisheries Science Center, NOAA.

Baker, R., A. Buckland, and M. Sheaves. 2014. "Fish Gut Content Analysis: Robust Measures of Diet Composition." *Fish and Fisheries* 15(1): 170–7.

Bertrand, A., F. X. Bard, and E. Josse. 2002. "Tuna Food Habits Related to the Micronekton Distribution in French Polynesia." *Marine Biology* 140(5): 1023–37.

Brodeur, R. D., J. C. Buchanan, and R. L. Emmett. 2014. "Pelagic and Demersal Fish Predators on Juvenile and Adult Forage Fishes in the Northern California Current: Spatial and Temporal Variations." *CalCOFI Reports* 55: 96–117.

Catul, V., M. Gauns, and P. K. Karuppasamy. 2011. "A Review on Mesopelagic Fishes Belonging to Family Myctophidae." *Reviews in Fish Biology and Fisheries* 21(3): 339–54.

Cherel, Y., S. Ducatez, C. Fontaine, P. Richard, and C. Guinet. 2008. "Stable Isotopes Reveal the Trophic Position and Mesopelagic Fish Diet of Female Southern Elephant Seals Breeding on the Kerguelen Islands." *Marine Ecology Progress Series* 370: 239–47.

Choy, C. A., C. C. C. Wabnitz, M. Weijerman, P. A. Woodworth-Jefcoats, and J. J. Polovina. 2016. "Finding the Way to the Top: How the Composition of Oceanic Mid-Trophic Micronekton Groups Determines Apex Predator Biomass in the Central North Pacific." *Marine Ecology Progress Series* 549: 9–25.

Christensen, V., and C. J. Walters. 2004. "Ecopath with Ecosim: Methods, Capabilities and Limitations." *Ecological Modelling* 172(2–4): 109–39.

Crawford, R. J. M., P. G. Ryan, and A. J. Williams. 1991. "Seabird Consumption and Production in the Benguela and Western Agulhas Ecosystems." *South African Journal of Marine Science* 11(1): 357–75.

Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quinones, L. J. Shannon, and H. M. Verheye. 2000. "Small Pelagics in Upwelling Systems: Patterns of Interaction and Structural Changes in 'Wasp-Waist' Ecosystems." *ICES Journal of Marine Science* 57(3): 603–18.

Davison, P. C., D. M. Checkley, Jr., J. A. Koslow, and J. Barlow. 2013. "Carbon Export Mediated by Mesopelagic Fishes in the Northeast Pacific Ocean." *Progress in Oceanography* 116: 14–30.

Dowd, S., M. Chapman, and L. Koehn. 2021. "Exploration of Ecological Implications of a Mesopelagic Fishery (v.1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.5806098

Essington, T. E., and S. B. Munch. 2014. "Trade-Offs between Supportive and Provisioning Ecosystem Services of Forage Species in Marine Food Webs." *Ecological Applications* 24(6): 1543–57.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, and J. B. C. Jackson. 2011. "Trophic Downgrading of Planet Earth." *Science* 333(6040): 301–6.

Field, J. 2004. "Application of Ecosystem-Based Fishery Management Approaches in the Northern California Current." Ph.D.

dissertation, School of Aquatic and Fishery Sciences, University of Washington, Seattle.

Fitch, J. E., and R. L. Brownell Jr. 1968. "Fish Otoliths in Cetacean Stomachs and their Importance in Interpreting Feeding Habits." *Journal of the Fisheries Board of Canada* 25(12): 2561–74.

Gaichas, S. K., G. Odell, K. Y. Aydin, and R. C. Francis. 2012. "Beyond the Defaults: Functional Response Parameter Space and Ecosystem-Level Fishing Thresholds in Dynamic Food Web Model Simulations." *Canadian Journal of Fisheries and Aquatic Sciences* 69(12): 2077–94.

Gallagher, A. J., and N. Hammerschlag. 2011. "Global Shark Currency: The Distribution, Frequency, and Economic Value of Shark Ecotourism." *Current Issues in Tourism* 14(8): 797–812.

Gjøsæter, J. 1973. "Age, Growth, and Mortality of the Myctophid Fish, Benthosema Glaciale (Reinhardt), from Western Norway." *Sarsia* 52(1): 1–14.

Gjøsæter, J. 1981. "Growth, Production and Reproduction of the Myctophid Fish Benthosema Glaciale from Western Norway and Adjacent Seas." *Fiskeridiretoratets Skrifter, Serie Havundersøkelser* 17: 79-108.

Griffiths, S. P., R. J. Olson, and G. M. Watters. 2013. "Complex Wasp-Waist Regulation of Pelagic Ecosystems in the Pacific Ocean." *Reviews in Fish Biology and Fisheries* 23(4): 459–75.

Hannesson, R., S. Herrick, and J. Field. 2009. "Ecological and Economic Considerations in the Conservation and Management of the Pacific Sardine (Sardinops Sagax)." *Canadian Journal of Fisheries and Aquatic Sciences* 66(5): 859–68.

Harrison, C. S., T. S. Hida, and M. P. Seki. 1983. "Hawaiian Seabird Feeding Ecology." *Wildlife Monographs* 85: 3–71.

Harvey, C. J., K. K. Bartz, J. R. Davies, T. B. Francis, T. P. Good, A. D. Guerry, B. Hanson, K. K. Holsman, J. J. J. Miller & M. L. Plummer. 2010. "A Mass-Balance Model for Evaluating Food Web Structure and Community-Scale Indicators in the Central Basin of Puget Sound." Seattle, WA: Northwest Fisheries Science Center, NOAA.

Heymans, J. J., M. Coll, J. S. Link, S. Mackinson, J. Steenbeek, C. Walters, and V. Christensen. 2016. "Best Practice in Ecopath with Ecosim Food-Web Models for Ecosystem-Based Management." *Ecological Modelling* 331: 173–84.

Hidaka, K., K. Kawaguchi, M. Murakami, and M. Takahashi. 2001. "Downward Transport of Organic Carbon by Diel Migratory Micronekton in the Western Equatorial Pacific: Its Quantitative and Qualitative Importance." *Deep Sea Research Part I: Oceanographic Research Papers* 48(8): 1923–39.

Hoagland, P., D. Jin, M. Holland, K. Kostel, E. Taylor, N. Renier, and M. Holmes. 2020. *Value beyond View: Illuminating the Human Benefits of the Ocean Twilight Zone*. Woods Hole, MA: Ocean Twilight Zone Program, Woods Hole Oceanographic Institution.

Houle, J. E., K. H. Andersen, K. D. Farnsworth, and D. G. Reid. 2013. "Emerging Asymmetric Interactions between Forage and Predator Fisheries Impose Management Trade-Offs." *Journal of Fish Biology* 83(4): 890–904.

Hudson, J. M., D. K. Steinberg, T. T. Sutton, J. E. Graves, and R. J. Latour. 2014. "Myctophid Feeding Ecology and Carbon Transport along the Northern Mid- Atlantic Ridge." *Deep Sea Research Part I: Oceanographic Research Papers* 93: 104–16.

Ianelli, J., K. K. Holsman, A. E. Punt, and K. Aydin. 2016. "Multi-Model Inference for Incorporating Trophic and Climate Uncertainty into Stock Assessments." *Deep Sea Research Part II: Topical Studies in Oceanography* 134: 379–89.

Index Mundi. 2016. "Fishmeal Monthly Price- US Dollars Per Metric Ton." https://www.indexmundi.com/commodities/?commodity=fish-meal.

Irigoien, X., T. A. Klevjer, A. Røstad, U. Martinez, G. Boyra, J. L. Acuña, A. Bode, et al. 2014. "Large Mesopelagic Fishes Biomass and Trophic Efficiency in the Open Ocean." *Nature Communications* 5(1): 3271. https://doi.org/10.1038/ncomms4271

IUCN. 2021. "The IUCN Red List of Threatened Species." https://www.iucnredlist.org.

Jacobsen, J., and L. P. Hansen. 2001. "Feeding Habits of Wild and Escaped Farmed Atlantic Salmon, Salmo Salar L., in the Northeast Atlantic." *ICES Journal of Marine Science* 58(4): 916–33. https://doi.org/10.1006/jmsc.2001.1084

Jacobsen, N. S., T. E. Essington, and K. H. Andersen. 2015. "Comparing Model Predictions for Ecosystem-Based Management." *Canadian Journal of Fisheries and Aquatic Sciences* 73(4): 666–76. https://doi.org/10.1139/cjfas-2014-0561

Kaartvedt, S., A. Staby, and D. Aksnes. 2012. "Efficient Trawl Avoidance by Mesopelagic Fishes Causes Large Underestimation of their Biomass." *Marine Ecology Progress Series* 456: 1–6. https://doi.org/10.3354/meps09785

Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. M. Smith. 2013. "Impacts of Depleting Forage Species in the California Current." *Environmental Conservation* 40(4): 380–93.

Kaplan, I. C., T. B. Francis, A. E. Punt, L. E. Koehn, E. Curchitser, F. Hurtado-Ferro, K. F. Johnson, S. E. Lluch-Cota, W. J. Sydeman, and T. E. Essington. 2019. "A Multi-Model Approach to Understanding the Role of Pacific Sardine in the California Current Food Web." *Marine Ecology Progress Series* 617: 307–21.

Kenchington, T. J. 2014. "Natural Mortality Estimators for Information-Limited Fisheries." *Fish and Fisheries* 15(4): 533–62. https://doi.org/10.1111/faf.12027

Kock, K.-H. 2000. *Understanding CCAMLR's Approach to Management*. Hobart: CCAMLR.

Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 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. https://doi.org/10.1016/j.ecolmodel.2016.05.010

Koehn, L. E., T. E. Essington, K. N. Marshall, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 2017. "Trade-Offs between Forage Fish Fisheries and their Predators in the California Current." *ICES Journal of Marine Science* 74(9): 2448–58. https://doi.org/10.1093/icesjms/fsx072

Koslow, J., R. Goericke, A. Lara-Lopez, and W. Watson. 2011. "Impact of Declining Intermediate-Water Oxygen on Deepwater Fishes in the California Current." *Marine Ecology Progress Series* 436: 207–18. https://doi.org/10.3354/meps09270

Lopes, A. F., and G. Kipperberg. 2020. "Diagnosing Insensitivity to Scope in Contingent Valuation." *Environmental and Resource Economics* 77(1): 191–216.

Lopez, S., R. Meléndez, and P. Barría. 2010. "Preliminary Diet Analysis of the Blue Shark Prionace Glauca in the Eastern South Pacific." *Revista de Biología Marina y Oceanografia* 45: 745–9. https://doi.org/10.4067/S0718-19572010000400017

Lucey, S. M., S. K. Gaichas, and K. Y. Aydin. 2020. "Conducting Reproducible Ecosystem Modeling Using the Open Source Mass Balance Model Rpath." *Ecological Modelling* 427: 109057. https://doi.org/10.1016/j.ecolmodel.2020.109057

Lynam, C. P., M. Llope, C. Möllmann, P. Helaouët, G. A. Bayliss-Brown, and N. C. Stenseth. 2017. "Interaction between Top-Down and Bottom-Up Control in Marine Food Webs." *Proceedings of the National Academy of Sciences of the United States of America* 114(8): 1952–7. https://doi.org/10.1073/pnas.1621037114

Manzer, J. I. 1968. "Food of Pacific Salmon and Steelhead Trout in the Northeast Pacific Ocean." *Journal of the Fisheries Board of Canada* 25(5): 1085–9.

Martin, A., P. Boyd, K. Buesseler, I. Cetinic, H. Claustre, S. Giering, S. Henson, et al. 2020. "The Oceans' Twilight Zone Must Be Studied Now, before It Is Too Late." *Nature* 580(7801): 26–8.

McCormack, S. A., J. Melbourne-Thomas, R. Trebilco, J. L. Blanchard, and A. Constable. 2020. "Alternative Energy Pathways in Southern Ocean Food Webs: Insights from a Balanced Model of Prydz Bay, Antarctica." *Deep Sea Research Part II: Topical Studies in Oceanography* 174: 104613. https://doi.org/10.1016/j.dsr2.2019.07.001

McCormack, S. A., J. Melbourne-Thomas, R. Trebilco, J. L. Blanchard, B. Raymond, and A. Constable. 2021. "Decades of Dietary Data Demonstrate Regional Food Web Structures in the Southern Ocean." *Ecology and Evolution* 11(1): 227–41. https://doi.org/10.1002/ece3.7017

Naito, Y., D. P. Costa, T. Adachi, P. W. Robinson, M. Fowler, and A. Takahashi. 2013. "Unravelling the Mysteries of a Mesopelagic Diet: A Large Apex Predator Specializes on Small Prey." *Functional Ecology* 27(3): 710–7. https://doi.org/10.1111/1365-2435.12083

NOAA Fisheries. 2016. "Commercial Fisheries Statistics." https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-Landings/Index.

Pakhomov, E., R. Perissinotto, and C. McQuaid. 1996. "Prey Composition and Daily Rations of Myctophid Fishes in the Southern Ocean." *Marine Ecology Progress Series* 134: 1–14. https://doi.org/10.3354/meps134001

Paoletti, S., J. R. Nielsen, C. R. Sparrevohn, F. Bastardie, and B. M. J. Vastenhoud. 2021. "Potential for Mesopelagic Fishery Compared to Economy and Fisheries Dynamics in Current Large Scale Danish Pelagic Fishery." *Frontiers in Marine Science* 2021: 1145.

Pauly, D., A. W. Trites, E. Capuli, and V. Christensen. 1998. "Diet Composition and Trophic Levels of Marine Mammals." *ICES Journal of Marine Science* 55(3): 467–81. https://doi.org/10.1006/jmsc.1997.0280

PFMC. 2019. *Coastal Pelagic Species Fishery Management Plan as Amended through Amendment 17*. Portland, OR: Pacific Fisheries Management Council.

Pike, I. H., and A. Jackson. 2010. "Fish Oil: Production and Use Now and in the Future." *Lipid Technology* 22(3): 59–61. https://doi.org/10.1002/lite.201000003

Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, et al. 2014. "The Global Contribution of Forage Fish to Marine Fisheries and Ecosystems." *Fish and Fisheries* 15(1): 43–64. https://doi.org/10.1111/faf.12004

Plagányi, É. E., and D. S. Butterworth. 2004. "A Critical Look at the Potential of Ecopath with Ecosim to Assist in Practical Fisheries Management." *African Journal of Marine Science* 26: 261–87.

Podrazhanskaya, S. G. 1993. "Feeding Habits of Mesopelagic Species of Fish and Estimation of Plankton Graze in the Northwest Atlantic." *NAFO Scientific Council Studies* 19(1993): 79–85.

Polo-Silva, C., S. D. Newsome, F. Galván-Magaña, M. Grijalba-Bendeck, and A. Sanjuan-Muñoz. 2013. "Trophic Shift in the Diet of the Pelagic Thresher Shark Based on Stomach Contents and Stable Isotope Analyses." *Marine Biology Research* 9(10): 958–71. https://doi.org/10.1080/17451000.2013.793802

Polovina, J. J. 1984. "Model of a Coral Reef Ecosystem." *Coral Reefs* 3(1): 1–11.

Potier, M., F. Marsac, Y. Cherel, V. Lucas, R. Sabatié, O. Maury, and F. Ménard. 2007. "Forage Fauna in the Diet of Three Large Pelagic Fishes (Lancetfish, Swordfish and Yellowfin Tuna) in the Western Equatorial Indian Ocean." *Fisheries Research* 83(1): 60–72. https://doi.org/10.1016/j.fishres.2006.08.020

Prellezo, R. 2019. "Exploring the Economic Viability of a Mesopelagic Fishery in the Bay of Biscay." *ICES Journal of Marine Science* 76(3): 771–9. https://doi.org/10.1093/icesjms/fsy001

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Saunders, R. A., S. L. Hill, G. A. Tarling, and E. J. Murphy. 2019. "Myctophid Fish (Family Myctophidae) Are Central Consumers in the Food Web of the Scotia Sea (Southern Ocean)." *Frontiers in Marine Science* 6: 1021. https://doi.org/10.3389/fmars.2019.00530

Schwartzlose, R. A., and J. Alheit. 1999. "Worldwide Large-Scale Fluctuations of Sardine and Anchovy Populations." *African Journal of Marine Science* 21: 289–347.

Sebastine, M., K. K. Bineesh, E. M. Abdussamad, and N. G. K. Pillai. 2013. "Myctophid Fishery along the Kerala Coast with Emphasis on Population Characteristics and Biology of the Headlight Fish, Diaphus Watasei." *Indian Journal of Fisheries* 60(4): 7–11.

Seo, H.-S., Y. Endo, M. Moku, K. Muramoto, K. Fujimoto, and K. Kawaguchi. 1998. "Amino Acid Composition of Proteins in Myctophid Fishes in the Subarctic and Tropical Pacific Ocean." *Fisheries Science* 64(4): 652–3.

Smith, A. D. M., C. J. Brown, C. M. Bulman, E. A. Fulton, P. Johnson, I. C. Kaplan, H. Lozano-Montes, et al. 2011. "Impacts of Fishing Low-Trophic Level Species on Marine Ecosystems." *Science* 333(6046): 1147–50. https://doi.org/10.1126/science.1209395

St. John, M. A., A. Borja, G. Chust, M. Heath, I. Grigorov, P. Mariani, A. P. Martin, and R. S. Santos. 2016. "A Dark Hole in our Understanding of Marine Ecosystems and their Services: Perspectives from the Mesopelagic Community." *Frontiers in Marine Science* 3: 31. https://doi.org/10.3389/fmars.2016.00031

Steinback, S. R., B. Gentner, and J. Castle. 2004. *The Economic Importance of Marine Angler Expenditures in the United States.* Seattle, WA: National Marine Fisheries Service, NOAA.

Surma, S., T. J. Pitcher, R. Kumar, D. Varkey, E. A. Pakhomov, and M. E. Lam. 2018. "Herring Supports Northeast Pacific Predators and Fisheries: Insights from Ecosystem Modelling and Management Strategy Evaluation." *PLoS One* 13(7): e0196307.

Suryan, R. M., V. S. Saba, B. P. Wallace, S. A. Hatch, M. Frederiksen, and S. Wanless. 2009. "Environmental Forcing on Life History Strategies: Evidence for Multi-Trophic Level Responses at Ocean Basin Scales." *Progress in Oceanography* 81(1): 214–22. https://doi.org/10.1016/j.pocean.2009.04.012

Sutton, T. T., M. R. Clark, D. C. Dunn, P. N. Halpin, A. D. Rogers, J. Guinotte, S. J. Bograd, et al. 2017. "A Global Biogeographic Classification of the Mesopelagic Zone." *Deep Sea Research Part I: Oceanographic Research Papers* 126(August): 85–102. https://doi.org/10.1016/j.dsr.2017.05.006

Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. "Forage Species in Predator Diets: Synthesis of Data from the California Current." *Ecological Informatics* 29(September): 45–56. https://doi.org/10.1016/j.ecoinf.2015.07.003

Tacon, A. G. J., and M. Metian. 2008. "Global Overview on the Use of Fishmeal and Fish Oil in Industrially Compounded Aquafeeds: Trends and Future Prospects." *Aquaculture* 285(1): 146–58. https://doi.org/10.1016/j.aquaculture.2008.08.015

Thayer, J., and W. Sydeman. 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(January): 253–65. https://doi.org/10.3354/meps329253

Trites, A. W., A. J. Miller, H. D. G. Maschner, M. A. Alexander, S. J. Bograd, J. A. Calder, A. Capotondi, et al. 2007. "Bottom-up Forcing and the Decline of Steller Sea Lions (Eumetopias Jubatus) in Alaska: Assessing the Ocean Climate Hypothesis." *Fisheries Oceanography* 16(1): 46–67.

Walters, C., V. Christensen, and D. Pauly. 1997. "Structuring Dynamic Models of Exploited Ecosystems from Trophic Mass-Balance Assessments." *Reviews in Fish Biology and Fisheries* 7(2): 139–72. https://doi.org/10.1023/A:1018479526149

Walters, C., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. "Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II." *Ecosystems* 3(1): 70–83. https://doi.org/10.1007/s100210000011

West, K. L., W. A. Walker, R. W. Baird, W. White, G. Levine, E. Brown, and D. Schofield. 2009. "Diet of Pygmy Sperm Whales (*Kogia breviceps*) in the Hawaiian Archipelago." *Marine Mammal Science* 25(4): 931–43. https://doi.org/10.1111/j.1748-7692.2009.00295.x

Whitehouse, G. A., and K. Y. Aydin. 2020. "Assessing the Sensitivity of Three Alaska Marine Food Webs to Perturbations: An Example of Ecosim Simulations Using Rpath." *Ecological Modelling* 429: 109074.

Young, J., M. Lansdell, S. Riddoch, and A. Revill. 2006. "Feeding Ecology of Broadbill Swordfish, Xiphias Gladius, off Eastern Australia in Relation to Physical and Environmental Variables." *Bulletin of Marine Science* 79(3): 17.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.