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Mesopelagic–epipelagic fish nexus in viability and feasibility of commercial-scale mesopelagic fisheries

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Abstract

While considerable scientific uncertainties persist for mesopelagic ecosystems, the fishing industry has developed a great interest in commercial exploitation with improved technologies as part of their search for new sources of feed for fishmeal and fish oil for aquaculture, which will intensify with the planet's growing population. The multiple uncertainties surrounding the ecosystem structure and particularly the size of biomass, hinder a good understanding of the risks associated with large-scale exploitation, which is needed for a management framework for sustainable ocean uses. Despite concerns regarding irreversible losses triggered by commercial fishing, work exploring the vulnerability of mesopelagic fish to harvesting is largely missing. This study investigates the economic feasibility of mesopelagic fishing which is the primary driver for any possible future expansion. Using very limited information currently available, we conduct a high-level assessment focusing on key ecological and economic interactions and develop an initial understanding of the economic feasibility of commercial harvesting for mesopelagic fish in the coming years.

We conduct simulations using a classical bioeconomic model that captures two species groups, mesopelagic and epipelagic fish, using a wide range of price and cost parameters. We analyze different scenarios for the economic profitability of the fishery in a regional fishery management context. The results of our study highlight the importance of better understanding key biological and ecological mechanisms and parameters which can in turn help inform policies aimed at protecting the mesopelagic.

Recommendations for Resource Managers

- A high-level assessment focusing on key ecological and economic interactions suggests that commercial harvesting in the Ocean Twilight Zone with improved technologies may become economically feasible in the coming years.
- It is imperative to better understand key biological and ecological mechanisms of the mesopelagic ecosystems to facilitate the development of management institutions and proactive policies to ensure sustainability.
- The scarcity of natural science data on mesopelagic ecosystems is echoed by a paucity of information on the economic and socioecological implications of commercial-scale mesopelagic fisheries. Considering pressure for commercial exploitation to meet the world's increasing demand for fishmeal and fish oil, it is more relevant than ever to understand relevant trade-offs to inform management decision-making.

KEYWORDS

bioeconomic analysis, commercial fisheries, ecological interactions, economic feasibility, mesopelagic fish, twilight zone

1 | INTRODUCTION

Ocean waters in depths of 100–1000 m, or what is known as the “mesopelagic or twilight zone” that covers about 20% of the global ocean volume, include a large number of fish and other poorly explored marine organisms. Mesopelagic fish in these intermediate layers migrate close to the surface during the night and back down to the deep again during the daytime in what is known as the largest migration on earth (Wiebe et al., 1992). Although little knowledge is available about the biomass of mesopelagic fish, it is considered possible that their volume may exceed that of pelagic fish. Recent estimates point to mesopelagic fish biomass reaching up to 10 billion tons (or in excess of 11–15 billion tons) which are about 90% of all fish in the ocean, measured by weight (Irigoien et al., 2014; Kaartvedt et al., 2012). Even though more recent estimates bring these estimates down to 3.8–8.3 billion tons (Proud et al., 2019) or even 2.4 billion tons (Anderson et al., 2019), mesopelagic fish remain a promising resource that is largely unexploited (Grimsmo et al., 2017; Hidalgo & Browman, 2019; St. John et al., 2016).

The resource has attracted interest for exploitation from the fishing industry which is increasingly keen on finding new sources for the production of feed for farm animals, fishmeal, and fish oil for aquaculture which intensifies with the planet's growing population (FAO 2016, 2018a; Grimsmo et al., 2017; Tacon & Metian, 2015). However, the multiple uncertainties surrounding their role and value to the ocean ecosystems and ecosystem services, including climate regulation, and the lack of ability to quantify those, hinder a good understanding of the risks associated with their exploitation for feed production. The commercial potential of mesopelagic fish, therefore, remains poorly understood to date (Irigoien et al., 2014; St. John et al., 2016). The issue has attracted a lot of interest in recent years with multiple projects funding for research and initiatives across North America and Europe exploring the commercial potential of mesopelagic fish, ways for efficient and sustainable fishing along with the markets they can be directed to; examples include the OTZ[1] in the United States, several EU horizon-funded projects (the MEESO,[2] SUMMER,[3] MESOPP,[4] and PANDORA),[5] and the Norwegian Mesopelagic Initiative that brings together an international consortium of researchers (DG MARE, 2018; Roberts et al., 2020). Since 2019, the Joint Exploration of the Twilight Zone Ocean Network (JETZON) has coordinated teams of international researchers from multiple disciplines. In 2020, JETZON became one of the first 60 programs to be endorsed by the United Nations Decade of Ocean Science for Sustainable Development.

Past efforts to exploit mesopelagic fish include, among others, efforts by Iceland in the North Atlantic for the harvest of lightfish or pearlside (primarily during 2009–2010) which ceased though in 2016 due to poor catches, as well as Norwegian efforts that were largely deemed unprofitable (Marine Research Institute, 2015; Standal & Grimaldo, 2021). Furthermore, evidence from surveys in the Sea of Oman and the Arabian Sea has shown that low catch efficiency limits the economic viability for the development of a commercial fishery for mesopelagic species (FAO, 1997; Roberts et al., 2020; Valinassab et al., 2007); in spite of the fact that together with the Indian Ocean they are considered potentially among the most productive areas (Wright et al., 2020, and references therein). In addition, earlier efforts of the former Soviet Union for commercial fishing of lanternfish in the Southwest Indian Ocean and Southern Atlantic ceased in the early 1990s due to low economic viability (Kock, 2000). Ongoing efforts in India continue to explore the potential for exploitation (Remesan et al., 2016; Roberts et al., 2020). In South Africa, lanternfish caught as bycatch in the sardine fishery comprises 10% of the fishmeal produced (catches include hatchetfish as well); industrial fishing targeted specifically at lanternfish seems to have ceased in the mid-1980s due to difficulties in processing attributed to the high oil content in the fish (FAO, 1997; Roberts et al., 2020). Thus far, between 1950 and 2018, 2.68 million tonnes of landings for mesopelagic fish have been officially reported to FAO by its member countries, most of which are from British Overseas Territory in the southern Atlantic Ocean (South Georgia and Sandwich Island), followed by South Africa and Iceland (Pauly et al., 2021).

Despite progress in assessing the nutritive value of mesopelagic fish for fishmeal, some of the challenges limiting large-scale commercial exploitation persist today, with key difficulties hard to overcome pertaining to the appropriate gear for catching the target fish and avoiding bycatch (DG MARE, 2018; Olsen et al., 2020). These technical barriers result in limited efficiency and high costs of capture, beyond the processing challenges explained earlier. Ongoing work to explore and develop these fisheries is found in Norway, Pakistan, and the Bay of Biscay in the Northeast Atlantic (Olsen et al., 2020; Prellezo, 2019; Roberts et al., 2020). Despite the difficulties encountered thus far in the economic viability of commercial fisheries, ongoing developments in harvesting and processing technologies (e.g., Lamhauge et al., 2008; Underwood et al., 2021) are expected to lift these barriers and possibly render mesopelagic fisheries attractive to the industry interested in meeting the world's increasing demand for fishmeal and fish oil. In fact, in Norway, trial mesopelagic fisheries, for species such as *Maurolicus muelleri* (Mueller's pearlside) and *Benthosema glaciale* (Glacier lanternfish) have already started in 2016 (Bjordal & Thorvaldsen, 2020; Grimaldo et al., 2020). More recently the Norwegian Ministry of Trade, Industry, and Fisheries decided to transition from 1- to 10-year long permits for experimental mesopelagic fishing, in recognition of their promising potential and the need to support such investments (NFD, 2021). At the same time, the uncertainties on biological and ecological details along with the ecosystem value and role of mesopelagic fish exacerbate concerns regarding irreversible losses triggered by commercial fishing operations.

Mesopelagic resources are key in the food chain of marine ecosystems; they contribute significantly to ocean uptake and carbon sequestration, therefore, playing a substantial role in climate change mitigation and driving other important biogeochemical cycles (Roberts et al., 2020). Through their predation on zooplankton, they transfer energy up the food chain and nutrients to deeper waters (Robinson et al., 2010). Mesopelagic fish such as lanternfish (Myctophidae), are also important prey for large marine mammals and commercially valuable fish such as dolphins, sharks, whales, billfish, rays, as well as tuna such as bigeye and yellowfin, and many other predators that vary geographically. Predation rates vary across these species depending on location, season, and other parameters, but generally contribute the largest proportion of prey for deeper diving, benthopelagic and pelagic-ocean species such as bigeye tuna, longnose velvet dogfish, bigeye thresher shark, respectively (Roberts et al., 2020). Results of modeling work indicate that a decline in mesopelagic fish may lead to population declines from many of their aforementioned predators (Johnson, 2012; Roberts et al., 2020; Smith et al., 2011). Despite these concerns, work exploring the vulnerability of mesopelagic fish to harvesting is largely missing, with a particularly large gap in empirical evidence. This scarcity of natural science data is echoed by a paucity of information on the economic and socioecological implications of potential fisheries.

Currently, there is no management in place to protect mesopelagic resources. Meanwhile, considering the large unexploited fish biomass in the mesopelagic zone, there is an increasing interest in the commercial exploitation of mesopelagic fish that are rich in lipids and fatty acids, for the purposes of fishmeal, oil, nutraceutical, and pharmaceutical production (Paoletti et al., 2021). Experts' concerns regarding the potential for large-scale exploitation in the absence of knowledge of the ecosystem values at stake (St. John et al., 2016), have led to some proactive management actions. For example, the United States has put a ban on any commercial fishing operations targeting mesopelagic fish in the Pacific Ocean (Pacific Fishery Management Council, 2016). However, the risk for mesopelagic resources persists considering that there is no provision for exploitation in high seas (or international waters beyond national jurisdiction) which cover around 61% of the world's oceans (O'Leary et al., 2020). Efforts to protect and improve the management and conservation of marine resources on the high seas are currently underway, such as through the negotiations for the Biodiversity Beyond National Jurisdiction agreement but with limited provision for mesopelagic fish thus far. Note though that there have been recent efforts to understand the policy dimensions related to mesopelagic fish highlighting the need to conserve them via such agreements or moratoria that may allow for an improved scientific understanding to develop (Wright et al., 2020). Meanwhile, in places where commercial fisheries are under consideration (i.e., at the stage of analysis of viability, trial, or experimental fisheries), such as in the Bay of Biscay, there is a recognition of the need for a regulatory framework that encompasses issues such as legal mesh size and the type of fleet entitled to participate (i.e., pelagic or semi-pelagic trawls) (Andrés et al., 2021).

The purpose of this study is to develop an initial assessment of the economic feasibility and potential of commercial harvesting for mesopelagic fish along with risks and opportunities from a regional fishery management perspective. We develop simulations using a simple bioeconomic model that investigates trade-offs considering interactions with commercially valuable pelagic fish. It is our hope that this exercise can help inform policies and ongoing international negotiations aimed at protecting mesopelagic resources and designing proactive actions.

2 | BIOECONOMIC ANALYSIS

2.1 | Mesopelagic fish in the marine ecosystem

The ecosystem function of mesopelagic fish in the ocean food web is a growing area of research (Anderson et al., 2019; Kelly et al., 2019). Most of the existing models focus on vertical connections and carbon fluxes and do not provide enough details on fish species interactions needed for a food web-based bioeconomic analysis (Jin et al., 2012). Notable exceptions are the food web models of the Georges Bank ecosystem (Link et al., 2008) and the California Current ecosystem (Field et al., 2006; Koehn et al., 2016). These models include a function group of mesopelagic fishes and their predators (e.g., in the California model, macrourids, mackerel, Pacific salmon, Pacific hake, sablefish, Pacific Ocean perch, several species of rockfish, shortspine thornyhead, and longspine thornyhead). The model by Koehn et al. (2016) has been used to examine the economic tradeoffs and ecological impacts associated with a potential mesopelagic fishery (Dowd et al., 2022). Because of the multitude of food web interactions, the relationship between the epipelagic and mesopelagic species is complex. The harvest of mesopelagic fish may lead to increases in the stocks of some predators (e.g., grenadiers) and decreases in others (e.g., longspine thornyhead) (Dowd et al., 2022). Indeed, the mesopelagic group is not homogeneous, and mesopelagic fishes vary in growth and reproduction (Caiger et al., 2021).

For ecosystem-based fisheries management, it is necessary to understand and predict changes in marine ecosystems. However, developing a high-resolution food web model including fishes and coupling model components across different trophic levels is a major challenge. Organisms at higher trophic levels are longer lived, with important variability in abundance and distribution, and have complex life histories. Even with powerful computers, it is necessary to simplify the problem so that parameter richness and biological relevance are balanced. Rather than model the entire ecosystem, we should focus on key target species and develop species-centric models (DeYoung et al., 2004).

Traditional bioeconomic models (Clark, 1976) typically have parsimonious functional specifications, highlighting interactions among a few species, such as the case of tuna prey on mesopelagic fishes. As a partial analysis of a large and complex ecosystem, simple bioeconomic modeling can provide useful insights, complementary to the food-web modeling approach (Dowd et al., 2022). In addition, the traditional bioeconomic modeling is the only feasible approach in data-poor regions (see, e.g., Kourantidou et al., 2022).

2.2 | The model

We consider a two-species community (Clark, 1976; Gause, 1935), assuming that both populations, the epipelagic (x_1) and the mesopelagic species (x_2), can be harvested independently.

$$\frac{dx_1}{dt} = F(x_1, x_2) - h_1(t), \tag{1}$$

$$\frac{dx_2}{dt} = G(x_1, x_2) - h_2(t), \tag{2}$$

where F and G are the growth rate of x_1 and x_2 and $h_1(t)$ and $h_2(t)$ their harvests, respectively. As in Clark (1976), we assume the growth rate for both is logistic with an additional interaction term:

$$F(x_1, x_2) = rx_1\left(1 - \frac{x_1}{K}\right) + \alpha x_1 x_2, \tag{3}$$

$$G(x_1, x_2) = sx_2\left(1 - \frac{x_2}{L}\right) + \beta x_1 x_2, \tag{4}$$

where r and s are the intrinsic growth rates of x_1 and x_2; and K and L the carrying capacities for x_1 and x_2, respectively. The α and β are coefficients of the interaction terms. The αx_1 can be interpreted as the trophic function or functional response of x_2 to the density of the x_1 and a similar interpretation follows for βx_2 (Kar & Chaudhuri, 2003).

The above system has been widely used to handle a range of possible multispecies interactions (e.g., Hannesson, 1983). We account for the interaction between stocks by evaluating the sign of α and β.

If both α and β are negative, $\alpha < 0$ and $\beta < 0$, then the two stocks are described as competing over some biological dimension such as a common food source or space. If $\alpha = \beta = 0$, then the two stocks are described as being independent. If at least one coefficient is positive meaning that at least one of the two stocks benefits, then there is a symbiotic relationship which can be one of the three: mutualism, parasitism or predation, and commensalism. If both α and β are positive, then the two stocks are described as mutualistic (benefiting each other). If α and β have opposite signs, then the relationship between stocks is a prey-predation type (or parasitic), implying that one species benefits (the predator or parasite) while the one is harmed (the prey or host). Finally, if $\alpha > 0$ and $\beta = 0$ or $\beta > 0$ and $\alpha = 0$, then the relationship between the two is described as commensalism, implying that one species benefits while the other one is not affected.

Solving $F(x_1, x_2) = 0$ and $G(x_1, x_2) = 0$, we obtain the ranges of x_1 and x_2:

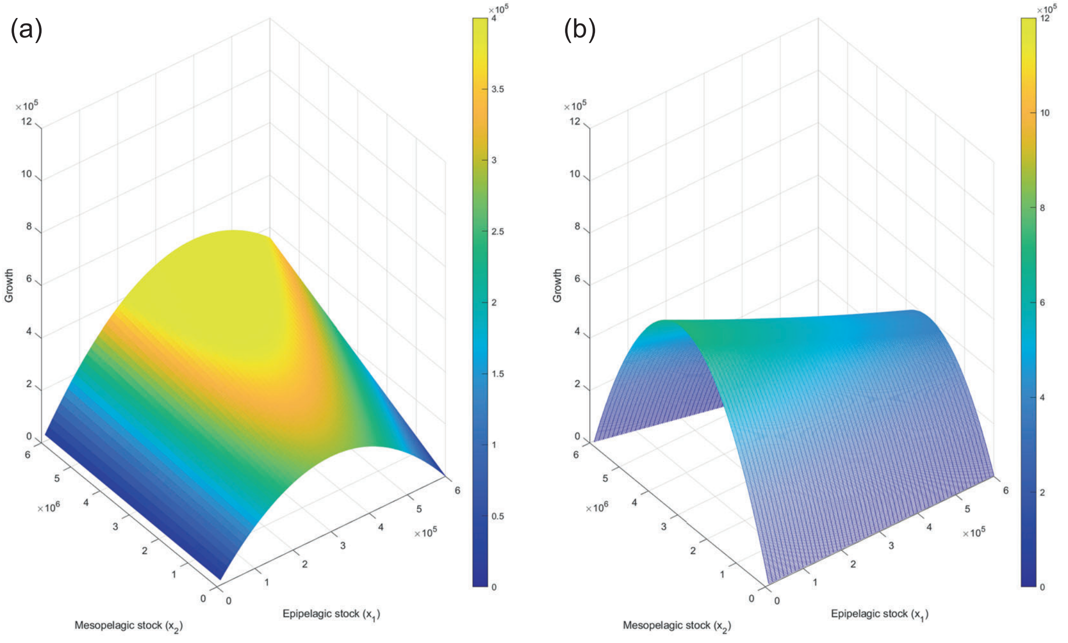

FIGURE 1 Logistic growth for a prey-predatory relationship between the (a) epipelagic (x_1) and (b) mesopelagic (x_2) stocks, where $\alpha > 0$ and $\beta < 0$.

$$0 \le x_1 \le K\left(1 + \frac{\alpha}{r}x_2\right) \quad \text{and} \quad 0 \le x_2 \le L\left(1 + \frac{\beta}{s}x_1\right). \tag{5}$$

Thus, depending on their signs and magnitudes, a and β affect the carrying capacities of K and L. Figure 1 depicts the growth under the assumption case of a prey-predatory relationship between the epipelagic and mesopelagic species ($\alpha > 0$ and $\beta < 0$), the carrying capacity and maximum sustainable yield of x_1 (x_2) rise with the population of x_2 (x_1).

For an optimal control problem with the objective function to maximize the total net revenue from harvesting two stocks:

$$\max_{h_1, h_2} \int_0^\infty \{[p_1 - c_1(x_1)]h_1(t) + [p_2 - c_2(x_2)]h_2(t)\}e^{-\delta t}dt, \tag{6}$$

subject to constraints (1) and (2), where p_i is the price fish harvested, c_i is the cost of fishing, and δ is the discount rate.

The current value Hamiltonian of this problem is $H = p_1 h_1 - c_1(x_1)h_1 + p_2 h_2 - c_2(x_2)h_2 + \lambda_1[F(x_1, x_2) - h_1] + \lambda_2[G(x_1, x_2) - h_2]$, where λ_1 and λ_2 are the costate variables for the epipelagic and mesopelagic populations, respectively. Similar to Clark (1976), application of the maximum principle yields the first-order conditions (7)–(10):

$$\frac{\partial H}{\partial h_1} = p_1 - c_1(x_1) - \lambda_1 \le 0; \ (= 0 \text{ if } h_1 > 0), \tag{7}$$

$$\frac{\partial H}{\partial h_2} = p_2 - c_2(x_2) - \lambda_2 \leq 0; \;\; (= 0 \;\text{if}\; h_2 > 0), \tag{8}$$

$$\frac{\partial H}{\partial x_1} = -c_1'(x_1)h_1 + \lambda_1 F_{x_1} + \lambda_2 G_{x_1} = \delta\lambda_1 - \dot{\lambda}_1, \tag{9}$$

$$\frac{\partial H}{\partial x_2} = -c_2'(x_2)h_2 + \lambda_1 F_{x_2} + \lambda_2 G_{x_2} = \delta\lambda_2 - \dot{\lambda}_2. \tag{10}$$

When combining the optimality conditions, at steady state ($\dot{x}_1 = \dot{x}_2 = 0$), we find that the golden rule stock and harvest for the epipelagic and the mesopelagic are defined by (11) and (12), and (1) through (4), respectively.

$$F_{x_1} - \frac{c_1'(x_1)F(x_1, x_2) - \left[p_2 - c_2(x_2)\right]G_{x_1}}{p_1 - c_1(x_1)} = \delta, \tag{11}$$

$$G_{x_2} - \frac{c_2'(x_2)G\left(x_1, x_2\right) - \left[p_1 - c_1(x_1)\right]F_{x_2}}{p_2 - c_2(x_2)} = \delta. \tag{12}$$

Clark and Munro's (1975) explanation of a single species model applies here: the rate-of-return conditions specify that the optimal stocks (x_1^*, x_2^*) are the ones at which the "own rate of return" of the stocks (LHS of Equations 11 and 12) equals the social rate of discount (RHS). The cross-dependencies of the two-species coupled dynamic system is reflected through the terms $[p_2 - c_2(x_2)]G_{x_1}$ and $[p_1 - c_1(x_1)]F_{x_2}$ which can be interpreted as the added marginal value product of the x_2 (or x_1) population due to an increase in x_1 (or x_2).

The marginal growth rates for x_1 and x_2 in (11) and (12) are from (3) and (4):

$$F_{x_1} = r - \frac{2rx_1}{K} + \alpha x_2, \tag{13}$$

$$F_{x_2} = \alpha x_1, \tag{14}$$

$$G_{x_1} = \beta x_2, \tag{15}$$

$$G_{x_2} = s - \frac{2sx_2}{L} + \beta x_1. \tag{16}$$

For the standard Schaefer harvesting function $h_i = q_i E_i x_i$ with effort E_i and catchability coefficient q_i, c_i is the unit cost of harvesting, and assuming constant costs per unit of effort, the cost functions in (11) and (12) read:

$$c_1(x_1) = \frac{c_1}{q_1 x_1} \quad \text{and} \quad c_2(x_2) = \frac{c_2}{q_2 x_2}. \tag{17}$$

The respective marginal cost functions for x_1 and x_2 read:

$$c_1'(x_1) = -\frac{c_1}{q_1 x_1^2} \quad \text{and} \quad c_2'(x_2) = -\frac{c_2}{q_2 x_2^2}. \tag{18}$$

Equations (11)–(18) with inequality constraints (5) yield an optimal equilibrium solution for $x_1 = x_1^*$ and $x_2 = x_2^*$.

At steady state, the total profit is given by:

$$\Pi\left(x_1^*, x_2^*\right) = \left[p_1 - c_1\left(x_1^*\right)\right]F\left(x_1^*, x_2^*\right) + \left[p_2 - c_2\left(x_2^*\right)\right]G\left(x_1^*, x_2^*\right). \tag{19}$$

3 | ASSUMPTIONS AND DATA

Empirical data on the price of selected mesopelagic predators are summarized in Table 1. Ex-vessel values of these predators vary greatly from above \$20,000/MT (bluefin tuna) to about \$200/MT (Pacific hake), based on NOAA fisheries data from 2000 to 2020. Also included in Table 1 are the estimated prices of mesopelagic fish in recent studies, and they range from \$250MT to \$900/MT. These estimates are typically conditioned on the price level of anchoveta and other forage fish harvested for fishmeal production.

In terms of biological interactions between epipelagic and mesopelagic species, the mesopelagic fishes vary substantially in their importance as food for different species of tuna. For deep-diving predators such as bigeye tuna, they were the most important prey in terms of weight, contributing 26% (Roberts et al., 2020). In the California Current ecosystem, there are about a dozen predators with at least 5% of their diet consisting of mesopelagic fish (Koehn et al., 2016).

TABLE 1 Price of mesopelagic predators (2000–2020) and mesopelagic fish in 2021 dollar values per metric ton (2021\$/MT).

Species	Fishing region	Average price (2021\$/MT)	Std (2021\$/MT)	Data source
Bigeye tuna	Mid-Atlantic	15,416	2654	NOAA (2022)
Bluefin tuna	New England	22,003	6708	NOAA (2022)
Yellowfin tuna	Pacific Coast	3373	2881	NOAA (2022)
Grenadiers	California	824	202	NOAA (2022)
Pacific hake	California	204	120	NOAA (2022)
Mesopelagic fish	Norway	360[a]	–	Standal & Grimaldo (2021)
Mesopelagic fish	Spain	260–500[b]	–	Prellezo (2019, 2021)
Mesopelagic fish	Denmark	350–640[b]	–	Paoletti et al. (2021)
Mesopelagic fish	Spain	243–860[b]	–	Groeneveld et al. (2021)

[a]Price used in economic assessment, assuming 1×10^5 MT of the mesopelagic catch is converted to 3×10^4 MT of fishmeal at \$1200/MT.

[b]Price range considered in economic assessment.

To assemble our baseline parameters for simulation, we expect that

$$p_1 > p_2, \quad c_1 < c_2, \quad q_1 > q_2, \quad K < L, \quad r > s. \tag{20}$$

Typically, the price of the epipelagic species will be higher than that of the mesopelagic considering that the latter is generally not destined for human consumption. Considering our knowledge of the difficulties encountered in harvesting mesopelagic fish, it is reasonable to assume that the harvesting cost for mesopelagic species will be higher compared to pelagic. Furthermore, considering the technological challenges related to suitable gear for mesopelagic harvesting, the catchability is expected to be lower for mesopelagic fish compared to epipelagic ones (DG MARE, 2018; Groeneveld et al., 2021; Olsen et al., 2020; Underwood et al., 2021). With respect to carrying capacity, given the large biomass estimates for the mesopelagic (Irigoien et al., 2014; Kaartvedt et al., 2012) we expect that their carrying capacity in any given area will far exceed that of the epipelagic fish; this is an assumption that we expect to hold at least in oceanic environments with limited certainty however for shelf areas. In addition, we expect that the intrinsic growth rate will be higher for the epipelagic compared to the mesopelagic species since the literature suggests that it is negatively related to depth (Drazen & Yeh, 2012; Watling et al., 2020). This assumption also comes with limitations, given how short-lived mesopelagic species are (which may indicate a similar or higher intrinsic growth rate), and is likely species-dependent.

For the purposes of this analysis, given all the uncertainty on mesopelagic species and limited information on commercial fishing operations, we are using a range of parameters, rather than specific estimates grounded in the literature. Our goal is to investigate the interactions between commercially valuable epipelagic and mesopelagic fish with respect to price and cost from a regional management perspective. Baseline parameters for simulations are summarized in Table 2. Those include, besides the variation in prices explained earlier, also

TABLE 2 Baseline parameters for the simulation.

Parameter	Value	Unit
K	6×10^5	MT
L	6×10^6	MT
r	1.911	time^{-1}
s	0.478	time^{-1}
α	1×10^{-7}	$(\text{MT} \times \text{time})^{-1}$
β	-2×10^{-7}	$(\text{MT} \times \text{time})^{-1}$
q_1	3.9×10^{-5}	Dimensionless
q_2	1×10^{-6}	Dimensionless
p_1	50–5000	\$/MT
p_2	$p_1/2$	\$/MT
c_1	4500–17 550	\$/fishing day
c_2	$2 \times c_1$	\$/fishing day
δ	0.03	Dimensionless

a range of harvesting costs that reflect the different possible harvesting costs of the different fleets. Epipelagic fishery parameters are from the eastern tropical Pacific yellowfin tuna fishery (Hoagland & Jin, 1997). While these parameters will undoubtedly be modified as more empirical estimates become available in the future (also considering the involvement of midwater vessels or purse seiner in mesopelagic fisheries), the current analysis will serve as an initial step towards a more complete understanding of the potential of a mesopelagic fishery. The motivation for using this simulation parameter from a tuna fishery is based on (a) the commercial value and market popularity of tuna fish and (b) evidence for ecological interactions between tuna and mesopelagic fish (see, e.g., aggregations of yellowfin and bigeye tuna that overlaps with and feed on spawning aggregations of the lanternfish *Diaphus danae* in the coral sea off of Australia (Flynn & Paxton, 2012).

4 | RESULTS

First, we examine the economic feasibility of the fishery in the presence of a prey-predatory relationship ($\alpha > 0$ and $\beta < 0$). Dark blue colors in the upper-left corner of Figure 2, where harvesting costs are high and the price is low, indicate negative profitability or that the fishery is not economically feasible. The fishery becomes feasible where profitability is positive, as shown by lighter colors in Figure 2, with the highest profitability (shown in yellow) in the lower-right corner of the figure (low harvesting costs, high price). Had the relationship between the epipelagic and mesopelagic stock been of some other type, the range of economic feasibility would be different, as shown in the Supporting Information: Appendix S1.

Next, Figure 3 shows how the size of the stock, harvest, and fishing effort for the epipelagic and mesopelagic species, respectively, within a range of harvesting costs and prices, under the prey-predatory scenario in which the stock size of mesopelagic fish is inversely related to that of the epipelagic fish as illustrated in the two subplots in the top row.

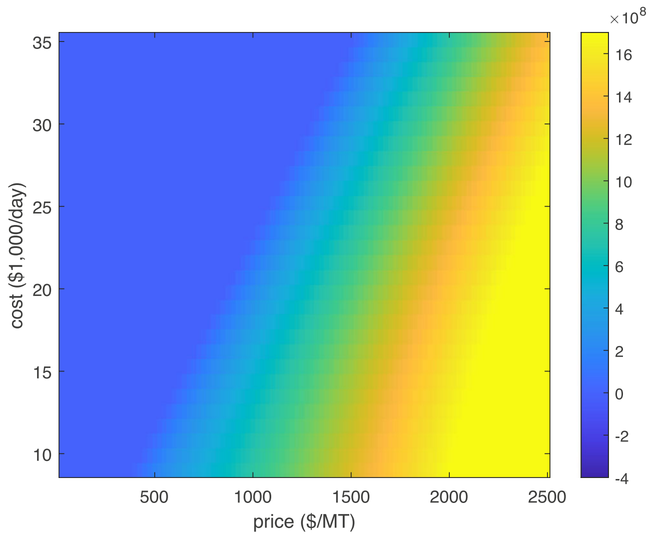

FIGURE 2 Gradient of profits indicating the economic feasibility of a fishery in the presence of a prey-predatory relationship ($\alpha > 0$ and $\beta < 0$). The fishery is economically feasible where profit is positive ($\Pi > 0$).

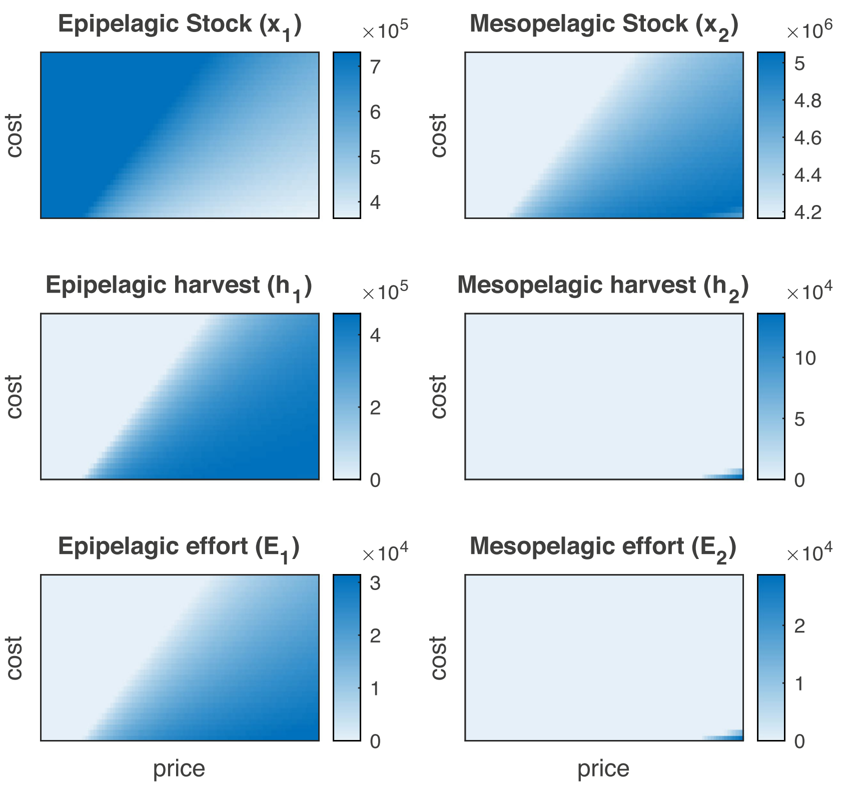

FIGURE 3 Stock, harvest, and fishing effort for the epipelagic (left column) and mesopelagic (right column) species, assuming a prey-predatory relationship ($\alpha > 0$ and $\beta < 0$), under varying harvesting costs and prices.

As shown in the left panel of Figure 3, as price increases and costs diminish the size of the epipelagic stock declines, driven by increased fishing effort and harvest. Although with a much smaller range of variation, the mesopelagic stock remains low at low price levels and starts increasing with an increase in price and declines gradually as costs start to increase. Notice though that for a very high price and very low costs, the size of the stock declines, which is driven by high fishing effort and harvest as shown in the lower-right corner of the left middle and lower panel, respectively. Significant harvest for mesopelagic fish is almost nonexistent until prices climb very high and on the condition that costs remain very low.

Figures 4 and 5 illustrate how the stocks, harvest, and effort levels of the epipelagic and mesopelagic species evolve with varying prices and costs of the mesopelagic fishery, respectively. In this case, we have the price for mesopelagic fish ranging from \$25/MT up to \$2500/MT for a fixed cost of \$9000/day (Figure 4), and the harvesting costs in the range of \$9000/day to \$35,100/day for the mesopelagic operation holding the price at \$2500/MT. The impact of predation of the epipelagic upon the mesopelagic can be seen clearly in Figure 4. One can also see from Figure 4 that, for the given simulation parameters, harvest for the mesopelagic becomes feasible for a price above \$2000/MT (\$2/kg), implying that a high price is necessary for the mesopelagic fishery to operate. Similarly, as shown in Figure 5, harvest for the mesopelagic ceases with a small increase in costs or shortly after costs exceed \$10,000/day.

Considering the ecological uncertainty present in the relationship between epipelagic and mesopelagic fish, we further vary the interaction coefficients α and β. As shown in Figure 6, the

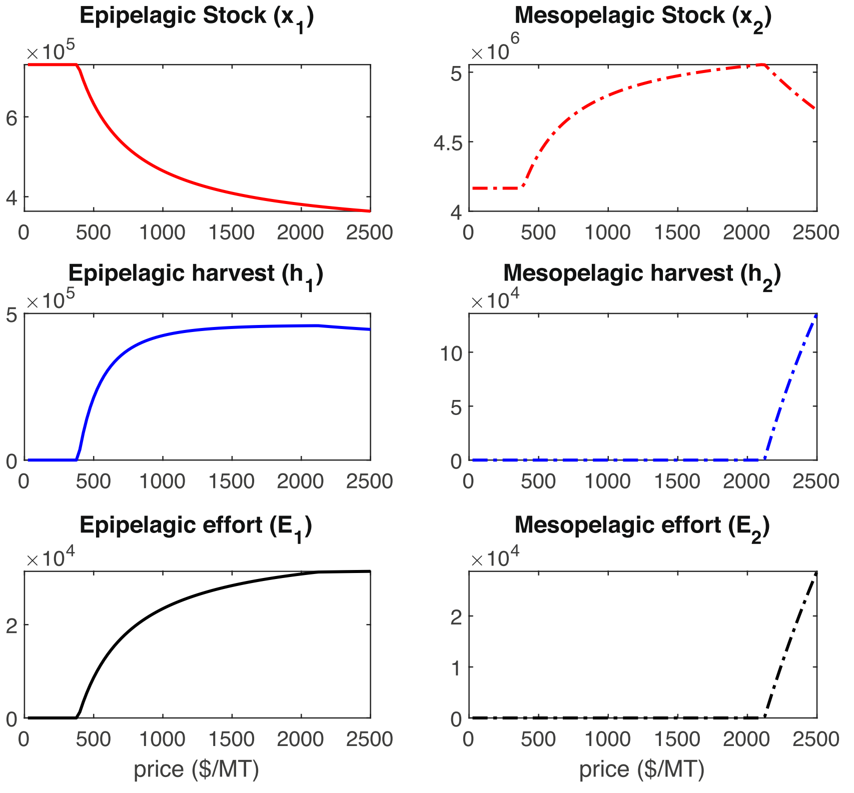

FIGURE 4 Sensitivity analysis with respect to price for the stock, harvest, and effort levels of epipelagic (left column) and mesopelagic (right column) species, assuming a prey-predatory relationship ($\alpha > 0$ and $\beta < 0$) and a price structure for the mesopelagic of $p_2 = p_1/2$. All horizontal axes depict p_2. Harvesting costs for the mesopelagic species are $9000/fishing day.

sign and the magnitude of the ecological interaction can affect profitability significantly in a complex way. Generally, higher profitability is associated with a mutualistic relationship ($\alpha > 0$ and $\beta > 0$, upper-right section), and a negative-profit region is in the lower-left section with $\alpha < 0$ and $\beta < 0$ (the two species are competing). The results highlight the need for ecological research to reduce uncertainties associated with marine food webs.

We also perform additional sensitivity analyses on the predator's price and the relative price structure. Specifically, we first extend the predator price p_1 to $20,000/MT and change the relative price structure to $p_2 = p_1/10$ from $p_2 = p_1/2$ (Table 2), so that the price of the epipelagic is now in the range of $200–$2000/MT. As shown in Figure 7 when the price of the mesopelagic p_2, is lowered relative to the price of the epipelagic p_1, then there is no mesopelagic harvest. This is an intuitive result considering that mesopelagic fish serve as prey to support the highly valued epipelagic fish.

We then change the relative price structure to $p_2 = p_1/1.5$, so that the price of the mesopelagic is only 50% lower than the price of the epipelagic (recall that the baseline is $p_2 = p_1/2$ as shown in Table 2). The price of the epipelagic is also extended in this case as well and as previously continues to be in the range of $200–$2000/MT. As shown in Figure 8, only when the price of the mesopelagic p_2 is higher relative to p_1, does mesopelagic harvest become feasible? However, in this case, p_2 is significantly higher than all those used in the various

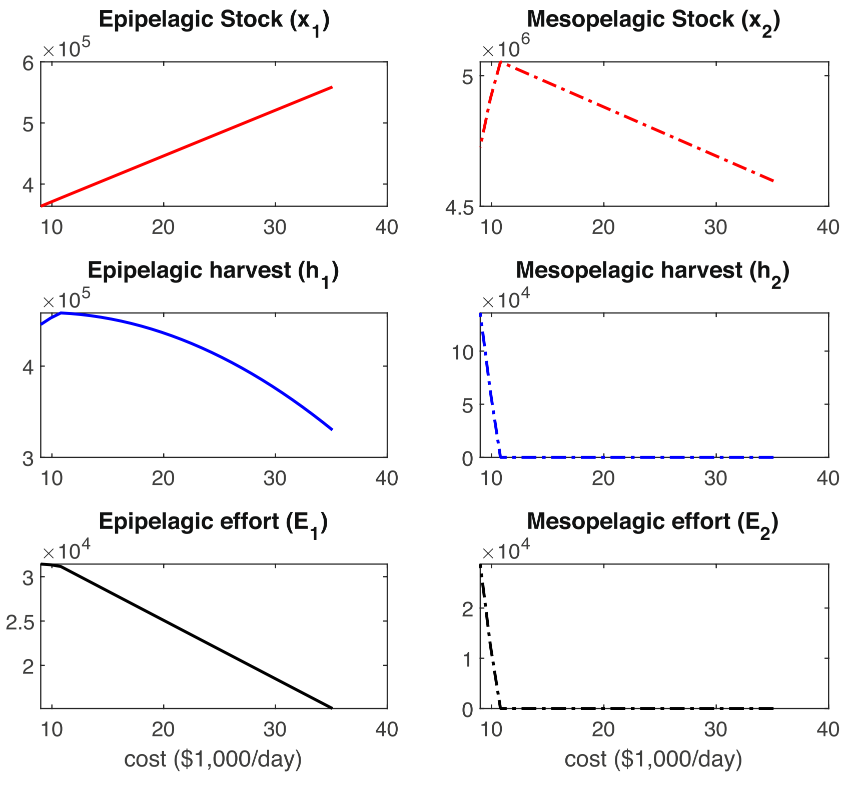

FIGURE 5 Sensitivity analysis with respect to harvesting costs for stock, harvest and effort levels of epipelagic (left column) and mesopelagic (right column), assuming a prey-predatory relationship ($\alpha > 0$ and $\beta < 0$) and a cost structure for the mesopelagic of $c_2 = 2 \times c_1$. All horizontal axes depict c_2. The price for the mesopelagic species is $2500/MT.

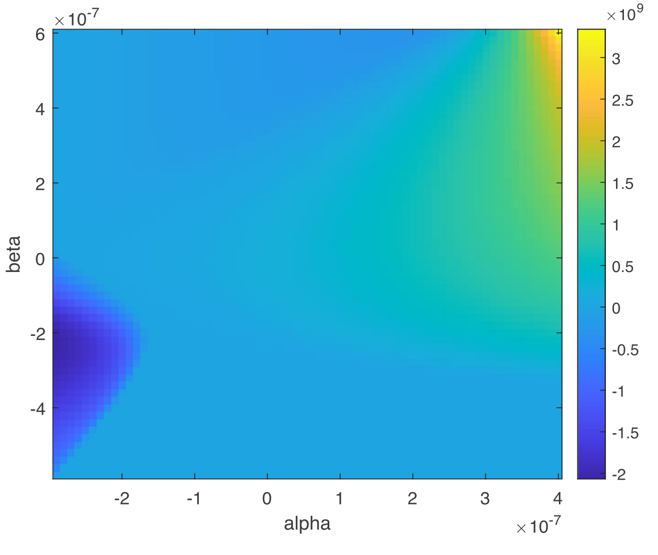

FIGURE 6 Gradient of profits from a sensitivity analysis with respect to the ecological interaction coefficients between the epipelagic and mesopelagic fish stocks (α and β). The price assumed for the mesopelagic fish is $500/MT ($1000/MT for the epipelagic) and the harvesting cost assumed is $9000/day ($4500/day for the epipelagic).

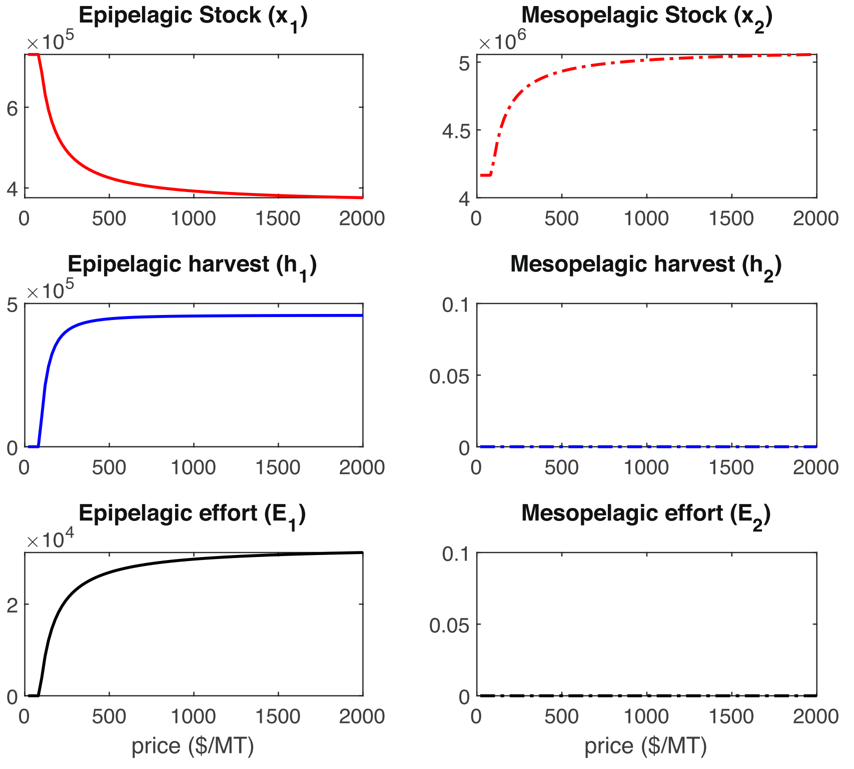

FIGURE 7 Sensitivity analysis with respect to price for the stock, harvest, and effort levels of epipelagic (left column) and mesopelagic (right column) species, assuming a price for epipelagic fish that reaches up to $20,000/MT and a price structure for the mesopelagic of $p_2 = p_1/10$. All horizontal axes depict p_2. Prey-predatory relationship with $\alpha > 0$ and $\beta < 0$. Harvesting cost assumed is $9000/day.

economic assessments cited in Table 1, implying that such prices are unrealistic at present. This sensitivity analysis with respect to the relative price structure and the extended price range for the predator, therefore, provides additional evidence that mesopelagic fishing is not really economically feasible in most cases, given the current price level of fishmeal from existing sources.

5 | DISCUSSION

The increasing demand for seafood globally along with the growth in the aquaculture sector, which supplies more than half of consumers' seafood, has for many years put pressure on wild capture fisheries for the production of fishmeal (FAO, 2018a, 2018b, 2020) and is now expanding to other potential sources of fishmeal such as mesopelagic fish. Although other feed sources such as plant crops are also available and suitable, farmed fish (especially higher-value piscivorous fish such as salmon or striped bass), require a high level of dietary protein which is easier to obtain from fishmeal. While the aquaculture industry has been stigmatized for contributing to the depletion of wild-caught fish stocks along with criticism for reducing fisheries supplying forage fish that are fished to maximum capacity, demand for fishmeal

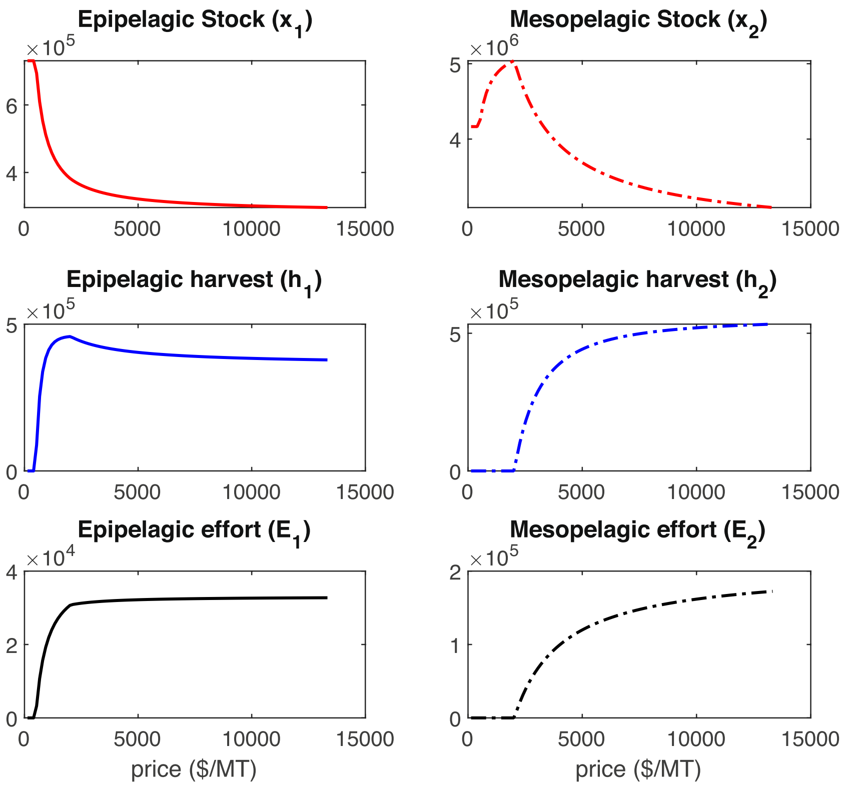

FIGURE 8 Sensitivity analysis with respect to price for the stock, harvest, and effort levels of epipelagic (left column) and mesopelagic (right column) species, assuming a price for epipelagic fish that reaches up to $20,000/MT and a price structure for the mesopelagic of $p_2 = p_1/1.5$. All horizontal axes depict p_2. Prey-predatory relationship with $\alpha > 0$ and $\beta < 0$. Harvesting cost assumed is $9000/day.

continues to steadily increase. This has led to increased industry interest to understand whether mesopelagic fish can make a viable source of fishmeal.

In fact, arguments over making the harvest of mesopelagic fish viable include the urgent need for fatty acids to cover the demand for fishmeal, considering the rich-lipid content of several mesopelagic fish (Olsen et al., 2020). Increasing the nutritional value of feeds for highly-valued farmed species such as salmon is at the epicenter of the industry's interest (Olsen et al., 2020). However, the limited understanding of key ecological dimensions of the mesopelagic hinders a good understanding of the effects of such an endeavor on the health of the marine ecosystem as a whole (e.g., from effects to commercially valuable predators of mesopelagic fish to disruptions to ecosystem services such as carbon sequestration). In the presence of multiple uncertainties, questions about the sustainability of harvest become even more challenging.

Despite evidence for the nutritional value of mesopelagic fish (Olsen et al., 2020), which may have the potential to contribute to food and feed security (Alvheim et al., 2020; Nordhagen et al., 2020; Wiech et al., 2020), evidence that fishing for this resource can be done sustainably and efficiently remains limited to date. Neither their large abundance nor the technological capacity to harvest them, alone, can support the reasoning behind commercial harvest operations (Radchenko, 1991).

Our results, from this attempt to examine the economic feasibility of a potential mesopelagic fishery, are subject to the persisting ecological and market uncertainties (i.e., including the choices of a predator, relative price and cost structure, and types of fleets involved) and are generally in line with experiences of commercial harvesting operations so far. For example, the Icelandic fishery for Mueller's pearlside or bristle-mouth fish, *M. muelleri* only lasted for a few years, from late 2008 to 2016, with the interest shifting back to capelin once the prices of the capelin increased again (Groeneveld et al., 2021; Fishsource, nd). The fact that the catch (quality of fish) deteriorates quickly, as experience in Icelandic and Norwegian experimental fisheries for Maurolicus has shown, limits fishing operators to only short seasonal trips (maximum 3–5 days from catch to landing) provided that the processing happens onshore (see also Paoletti et al., 2021). The potential for onboard processing or preservation, albeit difficulties associated with both freezing (due to high-fat content) and ensiling (which reduces nutrient quality), presents a significant advantage since it allows for longer trips. However, space availability on board vessels is an important cost consideration especially if it comes at the cost of other fisheries, with new vessels designed to serve the needs of these fisheries being particularly risky in the presence of so much uncertainty.

Most importantly, given that these are not seasonal fisheries, there are opportunity costs involved, especially for large trawlers; for example, fishing operators would have to give up some other target fishery to get involved in the mesopelagic fishery. In a country like Iceland where there are plenty of opportunities for other lucrative target fish, such opportunity costs from engagement in mesopelagic fisheries are expected to be high. Similar attempts, for seasonal small-scale mesopelagic fisheries, have been assessed for pelagic trawlers in Ireland (active in January–April and September–December 2014–2018) and otter trawls in the Basque country (active in April–September 2018). High initial investment costs,[6] high operational costs (such as from higher fuel costs due to smaller mesh size required) along with uncertain revenues from highly variable catches[7] and limited duration of trips to ensure that the catch does not deteriorate,[8] all create skepticism to industry players on the economic viability of the fishery (Groeneveld et al., 2021).

Furthermore, it remains unclear how economically competitive they can be compared to other fish traditionally used for fishmeal and/or fish oil such as herring, blue whiting, and menhaden, even if the use of those is controversial and the fishing unsustainable (e.g., see the loss of Marine Stewardship Council certification of Atlanto-Scandian herring and blue whiting and recent discontinuation of use by an aquaculture feed company in Holland (2020). Note, however, that interactions with epipelagic fisheries may vary across space—for example, in an ecosystem with limited ecological interactions (the independent case in our model, $\alpha = \beta = 0$), such as that of the Gulf of Oman where a commercial fishery for the myctophid *Benthosema pterotum* would focus on densities in the rather monospecific layer of 130–200 m, direct effects to mesopelagic fish stocks (x_2) are expected to be minimal (FAO, 1997; Valinassab et al., 2007) With further removal of a considerable portion of myctophids in the case of the Gulf of Oman, while competitor species (e.g., salps and carnivorous crustaceans) and those preying on myctophids (e.g., cetacean species) would likely be affected, other highly valued species such as tunas, mackerels, and billfishes (x_1) would likely not, considering the small role myctophids play in their diet.

Despite the general sentiment and evidence of limited possibilities for an economically feasible commercial mesopelagic fishery, there is evidence that does not exclude the possibility of positive net revenues (Groeneveld et al., 2021) and ongoing work to improve catchability (e.g., through artificial lights) through better identification of species that can ensure cost-effective fishing operations, holds promise (Underwood et al., 2021). Such advances in trawl selectivity for mesopelagic fish that offer the possibility of releasing unwanted species also contribute to ensuring a high-quality production of oil and proteins (Underwood et al., 2021), considering also that not all mesopelagic fish caught, have the same nutrient composition which implies that they require different processing methods. In addition, recent preliminary evidence on the viability of a commercial fishery for *M. muelleri* in the Bay of Biscay shows that while it may not be profitable for trawlers used in the deep-sea fleet to pursue a commercial mesopelagic fishery, it is highly likely that it is profitable for the cod fleet (otter trawlers) which has relatively lower opportunity costs compared to other fleets (Andrés et al., 2021). Furthermore, the cod fleet's technical capacity (considering fishing gear, storage capacity, and possibly onboard processing) along with its financial capacity make it a more suitable candidate compared to other fleets (Andrés et al., 2021).

Similarly, evidence from the intentions, willingness, and expectations of the Danish pelagic sector suggest a potentially economically viable mesopelagic fishery (Paoletti et al., 2021). Specifically, Paoletti et al. (2021) suggest that a new mesopelagic fishery can be realized either through investments in new vessels or through switching from the least profitable current fisheries to a new mesopelagic fishery by expanding the capacity of the Danish large vessel pelagic fleet. Both prices and harvesting costs support such a scenario: prices (in 2019–2020) for *Maurolicus* (in the range of 3.5 and 4.5 NOK or 0.30–0.40 €/kg or converted to USD $0.40–0.50/kg) exceed those of other fisheries such as blue whiting that are also used for fishmeal and fish oil production; costs for a potential mesopelagic fishery resemble those of the blue whiting fishery (among the current large pelagic vessel fisheries), considering that it is also a small meshed deep-sea trawl fishery[9] (Paoletti et al., 2021). Meanwhile, the Danish pelagic sector (Danish Pelagic Producers Organization), expects that revenues may be similar to those in the herring fishery.

The key determinants of economic feasibility and profitability, in absence of consideration of ecological interactions, seem to lie in the fleet type, the vessel's storage capacity, the speed at which fishing succeeds in filling the vessel's storage, and the distance between fishing areas and landing harbors that determines the trade-off in quality that in turn define prices (Groeneveld et al., 2021; Paoletti et al., 2021). Despite any new investments that might be required in gear, storage facilities, and even new vessels,[10] the Danish pelagic industry (and likely others) sees a possible opportunity to enter the fishery to establish historical fishing rights that will be an asset in the future when quotas are allocated and management comes into place (Paoletti et al., 2021).

6 | CONCLUSION

Using a simple bioeconomic model that focuses on the interaction between a mesopelagic fish population and a commercially valuable epipelagic fish population indicates that it is not possible to reject the possibility of large-scale commercial-scale fishing of mesopelagic fish being feasible in terms of economic profitability, as the demand for fishmeal grows and as technological change leads to cost reductions in deep-ocean fishing and subsequent processing. The utility of these kinds of simple bioeconomic models is not their ability to provide precise quantitative assessments but rather to explain the trade-offs, as we have done in this exercise given the considerable uncertainty on many of the model parameters. These models are of course subject to improvements as more knowledge informs these parameters, so that the trade-offs can be seen as more realistic, that is, in terms of magnitudes of harvest for an economically feasible and sustainable fishery. Already, since several decades ago, it has become clear that understanding the dynamics of mesopelagic fish populations to provide input for management is very complex and thus far no single answer prevails on means of estimating optimal yields. Considering for example the annual variability of biomass data along with the short lifespan of some of these species along with their patchy density distribution, it becomes clear that measures such as the maximum sustainable yield will likely be inadequate (FAO, 1997).

The bioeconomic exercise presented here can be seen as an initial step that provides insights into trade-offs and the economic potential in a regional management context, while more ecological knowledge is acquired and ecosystem models are being developed. The approach in this paper is the first example of an effort to quantify the trade-offs embedded in harvesting mesopelagic fish, considering ecological interactions with other commercially valuable fish. For the purposes of better understanding, the socioecological dynamics considering the complex food-web interactions within the mesopelagic and epipelagic zones, an ecosystem type of model would be necessary. As more biological and ecological uncertainties are resolved, it will become feasible to build such ecosystem models and reassess the feasibility and potential for sustainable outcomes for such a fishery. Ecosystem models accommodate a broader set of ecological interactions that affect fish stocks but given that they typically have less resolution on specific population dynamics, they could be used in parallel with the type of models described in the study (Howell et al., 2021).

Our work highlights persisting knowledge gaps along with the need for more future research that aims at understanding the trade-offs between conservation and commercial exploitation of mesopelagic fish. Advancing our understanding of these trade-offs is key within a short-term horizon to inform policies and management as well as precautionary approaches if deemed necessary to avoid irreversible ecological losses.

AUTHOR CONTRIBUTIONS

Melina Kourantidou: Conceptualization (equal); formal analysis (equal); methodology (equal); supervision (supporting); writing–original draft (lead); writing–review and editing (equal). **Di Jin**: Conceptualization (equal); formal analysis (equal); methodology (equal); supervision (lead); writing–original draft (supporting); writing–review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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ENDNOTES

[1] OTZ, Ocean Twilight Zone.

[2] MEESO, Ecologically and Economically Sustainable Mesopelagic Fisheries.

[3] SUMMER, SUstainable Management of MEsopelagic Resources.

[4] Mesopelagic Southern Ocean Prey and Predators.

[5] PAradigm for New Dynamic Ocean Resource Assessments and exploitation.

[6] Estimated at ~324,000 USD for Basque otter trawlers, 92% of which is for the purchase of nets with small mesh size that is required for mesopelagic fish and 8% for suction pump (Groeneveld et al., 2021).

[7] Estimated at 18–720 ton per trip for Basque otter trawlers or 0–40 ton/h (Groeneveld et al., 2021).

[8] 18 h steaming; 50 h fishing for Basque otter trawlers (Groeneveld et al., 2021).

[9] The small-meshed trawl gears filtering large quantities of water through fine mesh sizes and the heavy weight of the gear imply high fuel consumption and extensive engine power.

[10] Additional requirements may include development of new (a) trawling methods that allow for both deep fishing (day fishing) and shallow fishing (night fishing) according to the vertical distribution patterns of mesopelagic species (Grimaldo et al., 2020), (b) herding mechanisms to improve the catch rates and to reduce by-catches, (c) more energy and cost efficient trawling methods in relation to drag resistance of the small meshed fishing gears—see more details in Paoletti et al., (2021).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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