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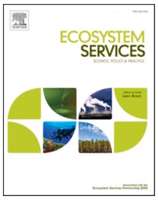

Full Length Article

Economic trade-offs of harvesting the ocean twilight zone: An ecosystem services approach

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ABSTRACT

The mesopelagic or ocean twilight zone (OTZ) in the ocean contains huge numbers of fish in a relatively pristine environment and may therefore attract interest as a commercial fishery. In this study we evaluate in economic terms, the likely trade-offs between the different services provided by the mesopelagic layer in the Bay of Biscay and the societal benefits of its commercial exploitation. Benefits arise mainly from the likely use of this group of species as raw material for producing fishmeal and fish oil. Costs are derived from the loss in climate regulating and cultural, services, but also from the loss in the provisioning service of other commercial species. To do so we compare the current non-exploited status with a situation in where mesopelagic fishes are harvested at levels capable of producing the Maximum Sustainable Yield. Results suggest that if mesopelagic fishes are harvested, a mean value of 1.2 million Euro loss in a year will be created in the Bay of Biscay, although in a range between 42 million Euro loss and 48 Euro million benefits. This uncertainty comes, mainly, from the limited existing knowledge of the mesopelagic fishes' biomass but also from the uncertainty on the biomass of the rest of the species of the studied ecosystem. The large range indicates that a better understanding of the mesopelagic ecosystem is needed, however, results also show that ecosystem services under no exploitation provided by the OTZ could be more valuable than the fishmeal and fish oil that potentially could be obtained from the fishes harvested in this sea layer.

1. Introduction

The mesopelagic or ocean twilight zone (OTZ) refers to the water masses where light intensity levels are enough to see but not enough for photosynthesis. In average, it extends from 200 to 1,000 m depth and contains a vast amount of fish biomass (Irigoien et al., 2014). Only in terms of fishes, this zone is populated by more than 30 families and 159 genera (Catul et al., 2011). Besides fish, many invertebrates such as cnidarians, crustaceans and molluscs are also part of the mesopelagic fauna. Mesopelagic organisms play a key role in marine ecosystems as they are important consumers of zooplankton and important prey for higher trophic levels (Naito et al., 2013) and represent an essential component of the biological carbon pump through the diel vertical migration (DVM) (Roberts et al., 2020). DVM is the phenomenon for which many mesopelagic fish ascend to the surface at night to feed and return to depth before dawn to avoid visual predators in accordance with the change of the sunlit depth, transferring energy and material between the surface and the deep sea (Vinogradov, 1997).

Although being one of the largest marine resources globally with 8–16 giga tonnes (Gt) of fish biomass (Irigoien et al., 2014; Proud et al., 2018), currently, only some large mesopelagic organisms are currently fished. This is the case of the *Dosidicus gigas.* Their yearly landings are close to 1 million tonnes per year in the whole Southeast Pacific, both in the high seas and in the jurisdictional waters of Peru and Chile by their own local, mostly artisanal, fleets (Arkhipkin et al., 2015; FAO, 2022). However, the rapid growth of the global population coupled with increasing demand for seafood has been placing high pressure on the aquaculture sector (FAO, 2018; Olsen et al., 2020). There is currently a

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great need for alternative marine-based resources to provide good quality balanced protein and lipids, particularly marine omega-3 (n-3) long-chain polyunsaturated fatty acids (LC-PUFAs) to sustain the aquaculture industry. Mesopelagic species have been considered as a potential source of high nutritional value proteins and PUFAs such as eicosapentaenoic acid (EPA, C20:5n3) and docosahexaenoic acid (DHA, C22:6n3) to meet aquaculture demands (Grimaldo et al., 2020; Olsen et al., 2020). Several studies have investigated the potential of mesopelagic fish biomass as a source of protein and oil for fish feed. Although the overall proximate composition (and the fish composition) has varied by haul to haul, region and season, lipid and protein constituents of mesopelagic fish were generally similar to those of other pelagic species. More recent studies showed the lipid content of *Maurolicus muelleri* and *Benthosema glaciale* (two mesopelagic fish) caught in Norwegian waters to be around 54 % and 47 %, respectively. Overall, lipid was a relatively good source of marine n-3 LC-PUFA, EPA and DHA, being in the range of 15–20 % of fatty acids. However, *B. glaciale* contains abundant amounts of wax esters that are not appreciated in fish feed industry as their utilization is limited (Olsen et al., 2020; Olsen et al., 2010). Both fish contain essential amino acid levels even higher than what required for Atlantic salmon aquaculture (Olsen et al., 2020). Nevertheless, such studies indicate that mesopelagic fish could represent a valuable source for marine protein with high nutritional value and PUFAs. Therefore, the question of a more intense commercial exploitation is open.

Currently, the possibilities for a generalized industrial fishing of the mesopelagic zone are low. The main reason is the existence of more economically profitable fisheries at least for the current fleet and based on the likely investment required on fishing nets (a smaller mesh size than those already commercially used) and the increase in operating costs (faster towing speed than when fishing, for example, small pelagic species) required to capture the mesopelagic fishes (Paoletti et al., 2021; Prellezo, 2019; Standal and Grimaldo, 2021). Current and future uncertainty – surrounding the mesopelagic biomass, habitat, distribution, trophic links, vertical transfer of material and energy, market prices of potential products and subproducts derived, and the fishing and transforming technical innovations (Hidalgo and Browman, 2019; Martin et al., 2020)– is high and a deterrent of this generalized exploitation. However, the non-generalized industrial fishing momentum may vary significantly and could be reversed with the emergence of new information and technological developments. Therefore, the overall value attached to the possibility of exploiting the mesopelagic zone may vary and it should be assessed to enhance our understanding on its real contribution to the human well-being, assessing the benefits, risks and trade-offs of the exploitation of mesopelagic resources (Ruckelshaus et al., 2015; St. John et al., 2016).

Within this context, several modelling approaches have been used in recent years assessing the economics of mesopelagic fisheries considering their potential ecological impacts. For example, Kourantidou and Jin (2022) developed a bioeconomic model where the interaction between a mesopelagic fish and other commercial species was studied, assessing the circumstances under which (fishing costs and ex-vessel prices of the prey and the predator) a mesopelagic fishery could be profitable. In addition, Dowd et al. (2022) explored the potential trade-offs of a mesopelagic fishery in the California Current, comparing the hypothetical value that could be gained from the fishery, with the potential value lost from declines in predators of mesopelagic fishes facing a reduced prey resource. Also, Johnson (2012) used an Atlantis ecosystem model in the south-eastern Tasmania to assess the ecological consequences of increasing fishing pressure on myctophids and squids, indicating that the exploitation of mesopelagic fishes may lead to increases of their competitors (i.e., other planktivorous) and declines on their predators, both demersal and pelagic.

In this study, we contribute to assessing these trade-offs for mesopelagic fisheries using the ecosystem services framework, defined as the gains acquired by societies from ecosystems (Costanza et al., 1997). Here, a distinction should be made between function and processes, and services. The first refers to a natural process that may generate services that contribute to human well-being but exists and can be measured independently of humans. They are biophysical relationships that exist regardless of human benefit. Services are the results of ecosystem functions that give benefits to human well-being, and only exist as services by reference to human users of the service (Costanza et al., 2017). In particular, we considered the cultural, provisioning and regulating services (Haines-Young and Potschin, 2018). Cultural ecosystem services (CES) are defined within a wider framework of ecosystem services as benefits that people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation and aesthetic experience (e.g. recreational fisheries, tourism). Provisioning services (PES) are the products obtained from ecosystems (e.g. fish, protein, oils, genetic resources). Finally, the regulating services (RES) refer to the benefits obtained from the regulation of ecosystem processes (e.g. climate regulation, nutrient transportation). Supporting services are also assessed in our work, but their economic evaluation is made though the provisioning and cultural services. This approach is taken to avoid double counting, which may occur when a service is valued at two different stages of the same process providing human welfare (Ojea et al., 2012). Therefore, in this work the supporting services are assessed through the impact on the abundance of other commercial (PES) or non-commercial species (CES) affected by the exploitation of the OTZ.

Under a potential mesopelagic zone exploitation scenario, the PES will start adding value in the form of direct protein, transformed or reduced products, and/or different nutraceutical or pharmaceutical compounds (Grimaldo et al., 2020). However, other services will be lost, including other PES, through the reduction of availability of other commercial species which feed from mesopelagic species (Kourantidou and Jin, 2022), CES, through the abundance loss of marine mammals, seabirds or species targeted by the recreational fisheries, which also feed on mesopelagic species (Dowd et al., 2022) and RES (climate regulation). Climate regulation is related to the link between the biological carbon pump (BCP) and atmospheric CO_2. The BCP is formed by a suite of processes exporting organic carbon (POC) from surface to deep waters. The depth at which this carbon is converted back to carbon dioxide—known as the remineralization depth—influences the rate at which it is returned to the surface ocean and, ultimately, the partitioning of carbon dioxide between the atmosphere and the ocean (Kwon et al., 2009). Therefore, it is important to assess the BCP as an ecosystem service provided by mesopelagic organisms, in particular in view of the DVM they perform (Martin et al., 2020). Each day, some of these mesopelagic fishes migrate from the depths to the shallows and back again facilitating the shuttling of carbon into the deep ocean (Buesseler et al., 2021).

Considering that mesopelagic species under no exploitation provide to society, supporting, regulating, cultural and provisioning services, trade-offs will arise if a commercial exploitation begins. In this study, we aim at explaining, quantifying, and valuing in monetary units all these services coming from the mesopelagic layer to establish the trade-offs between exploitation or not exploitation of the OTZ. Assessing the value of the ecosystem services prior to exploitation is an economically and socially more efficient way to inform a choice than having to take adaptation and mitigation measures once exploitation has begun. Herein, this is done for a specific area (Bay of Biscay in the North-East Atlantic Ocean) which was chosen due to the availability of species and ecosystem services data. However, effort was made to compute all the benefits by unit of mesopelagic fish harvested. Therefore, the methodological approach can be taken as reference or even transferred to other region considering that each area has its own characteristics in terms of ecosystem functioning, abundances, and species diversity.

2. Material and methods

The studied ecosystem is the Bay of Biscay. It is located in the temperate North-East Atlantic Ocean, between North-West (NW) France (offshore of Brittany) and NW Spain (Galicia) (Fig. 1). It has a long history of fishery (purse seiners, trawlers and artisanal fisheries, recreation) and tourism, but also impacted by other activities such as aquaculture, shipping, sand and gravel extraction, and more recently by wave, tide and wind power generation.

The Bay of Biscay marine ecosystem is highly diverse. A large variety of marine mammals, both boreal and temperate, have been reported in the region, including 30 species of cetaceans and seven species of seals. The Iberian Peninsula is at a strategic geographical position regarding the migratory behaviour of seabird species. As for fish, 700 described species are present. Due to environmental conditions, many species reach their southern or northern limits of distribution in the Bay of Biscay such as the albacore or the bluefin tuna which live in subtropical areas of the western Atlantic and make annual migrations to the Bay of Biscay. Most fishes are species living near the bottom of the sea (e.g. sole, dogfish or blue whiting) with limited geographical range, unless they are deep-water species. Pelagic fish such as sardine or mackerel have wide geographic distribution from Africa to Northern Europe.

2.1. Scenarios definition

We considered the existence of a benevolent social planer who aims to maximize the economic well-being. This planner has two options: to allow or not exploiting mesopelagic fishes. Under this dichotomy, the costs or benefits of exploiting the OTZ can be obtained by comparing these two options. Not fishing is named here, Business as Usual (BAU) scenario, while fishing, is named Fishing scenario. BAU implies simulating the dynamics of the ecosystem considering a harvest rate (F) for the mesopelagic fishes of nearly zero. The Fishing scenario is defined assuming a F for the mesopelagic according to the F_{MSY}, which is the fishing mortality that produces Maximum Sustainable Yield (MSY), a global standard for fishery management worldwide.

In this study, a temporal dynamic calibrated Ecosim food web model of the Bay of Biscay was used to assess the potential productivity of mesopelagic species, with a projection period starting in 2020 and ending in 2050. An extensive review of the Ecopath with Ecosim (EwE) approach (its principles, basic concepts, capabilities, and limitations), can be found in Christensen and Walters (2004) or in Heymans et al. (2016). The Bay of Biscay EwE model used here covers an area of 120,433 km^2 (of a total of 175,000 km^2 of the whole Bay of Biscay), including coastal waters up to 1,000 m in depth (Fig. 1). The Ecopath mass balance represented the 2000–2003 period (Corrales et al., 2022). In the EwE approach, the food web is modelled through functional groups, which can represent ontogenic fractions of the species (e.g. juveniles and adults), single species or groups of species that share common ecological traits (e.g. feeding habits and habitats). The Bay of Biscay EwE model includes 52 functional groups (Table 1), from primary producers to top predators and considers specific groups for the main target species, and 13 fishing fleets (Corrales et al., 2022). Based on the Ecopath model, the time dynamic module Ecosim (Walters et al., 1997) was calibrated and fitted to time series of data from 2003 to 2019 considering the effect of fishing (fishing effort and fishing mortalities), and changes in sea temperature (both Sea Surface Temperature -SST, Sea Bottom Temperature -SBT) and primary production.

One of the functional groups included in the model is the mesopelagic fishes, which is composed by seven species: *M. muelleri, B. glaciale, Lampanyctus crocodilus, Myctophum punctatum, Epigonus denticulatus, Notoscopelus kroyeri and Stomias boa*. The average total biomass fitted by the model of all these mesopelagic fish species together in the hindcast period (2003–2019) was estimated to be between 164,200 and 353,600 tonnes (t) with a model fitted value of 228,500 t (see Fig. 3 -Hindcast-).

2.1.1. Business as Usual scenario

This scenario represents the situation in where mesopelagic fishes

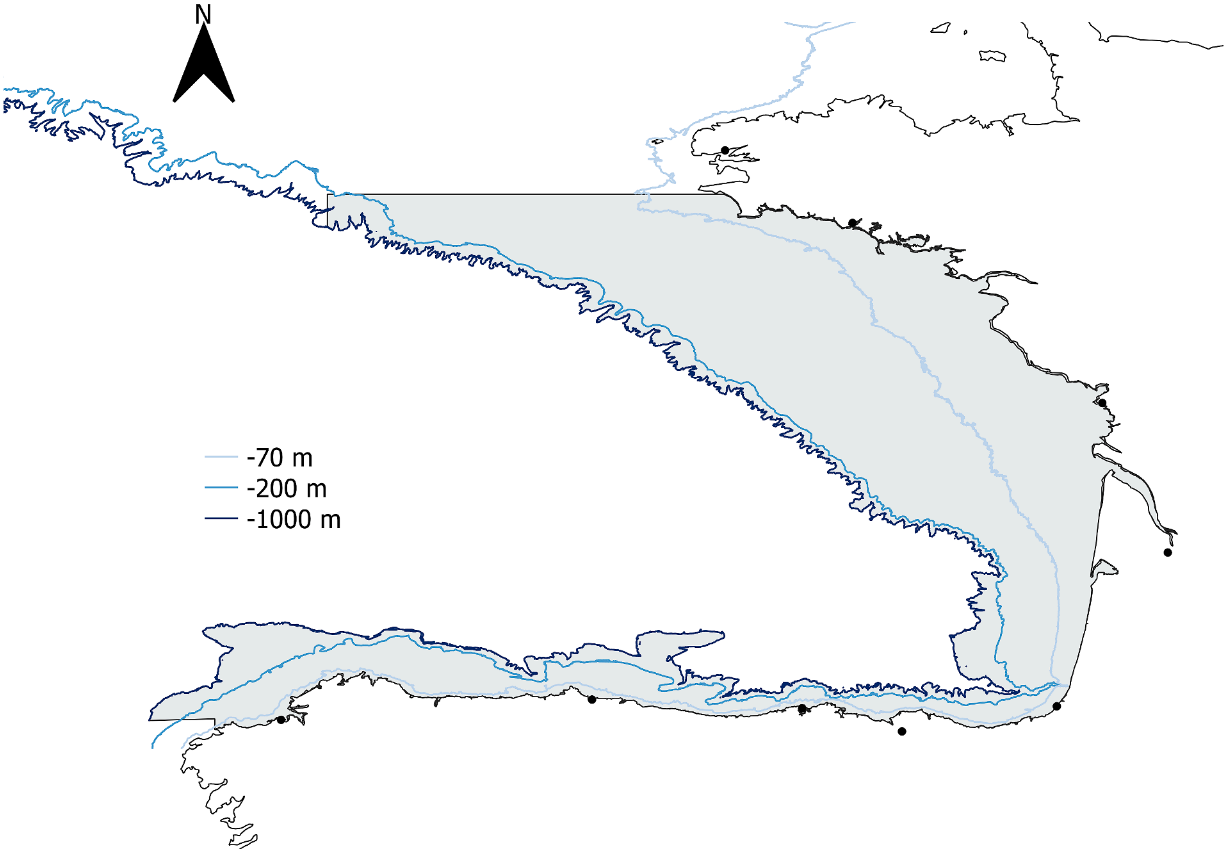

Fig. 1. Studied area. Bay of Biscay (bathymetry in metres).

Table 1

Functional groups considered in the simulation and their corresponding harvest rate (F) used to project the period 2020–2050.

Group	F	Group	F	Group	F	Group	F
Diving and persuit diverse seabirds	0.017	Sardine	0.420	Mullets	0.196	Polychaetes	0
Surface feeders seabirds	0.017	Anchovy	0.183	Large demersal fishes	0.246	Suprabenthos	0.045
Baleen whales	0	Other planktivorous fishes	0.070	Medium demersal fishes	0.196	Echinoderms	0.003
Dolphins	0.031	**Mesopelagic fishes**	**0**	Small demersal fishes	0.143	Other invertebrates	0.055
Demersal sharks	0.216	Anglerfish	0.186	Deep sea fishes	0.053	Gelatinous plankton	0
Pelagic sharks	0.091	Sea bass	0.279	Benthic cephalopods	0.192	Macrozooplankton	0
Deep sea sharks	0.101	Blue whiting	0.080	Squids	0.122	Mesozooplankton	0
Rays and skates	0.168	Large hake	0.270	Norway lobster	0.208	Microzooplankton	0
Bluefin tuna	0.033	Small hake	0.160	Pelagic crab	0.004	Benthic primary producers	0.055
Albacore	0.042	Poor cod	0.085	Zooplankton feeding shrimps	0.00003	Small phyoplankton	0
Other large Pelagic fishes	0.117	Megrim	0.151	Benthos feeders decapods	0.048	Large phytoplankton	0
Mackerel	0.199	Common sole	0.301	Detritus feeders decapods	0.0008	Detritus	0
Horse mackerel	0.140	Flatfishes	0.286	Bivalves	0.139	Discards	0

are not exploited. However, existing fishing (including bycatch) of other species groups in the food web model should be considered and projected at their F in 2019, which is the last year of the hindcast period in the model (Table 1). Environmental variables included in the model (SST, SBT- and primary production) were kept constant between 2020 and 2050 to isolate the effects of fishing mesopelagic fishes compared to not exploiting them.

2.1.2. Fishing scenario

Impact of fishing on other commercial and non-commercial species was simulated by selecting a positive F to the mesopelagic species group. This selection was based on a F_{MSY} estimated for all the mesopelagic species included in the model. To do it, we first estimated the natural mortality (M) for the seven mesopelagic species considered in three different ways (when it was possible):

1) Using Pauly's equation that uses W_{inf} (Pauly, 1980)

$Log_{10}M = -0.2107–0.0824 \log_{10} W_{inf} + 0.6757 \log_{10}k + 0.4687 \log_{10}T$

2) Using Pauly's equation that uses L_{inf} (Pauly, 1980):

$Log_{10}M = -0.0066–0.279 \log_{10} L_{inf} + 0.6543 \log_{10}k + 0.4634 \log_{10}T$

3) Estimations of natural mortality available in the Life-history tool of Fishbase (Froese and Pauly, 2021)

Where $W_{inf}(g)$ is the asymptotic weight, L_{inf} is the asymptotic length (cm), k is the growth parameter from the von Bertalanffy growth function (year^{-1}), and T is the mean temperature of the water (°C). W_{inf} was obtained by using the length-weight relationship using the length-weight parameters a and b (Kuriakose, 2017).

For some of these species, different population parameters (L_{inf} and K, and a and b) were available and therefore, different estimations using the same methods were possible (Table 2). In these cases, we estimated a minimum, an average and a maximum M for each method (1 to 3). When different M were available, we computed the average value obtained from the different methods (e.g. *B. glaciale*). In the cases where only one method was available, the value of M obtained from this model was used (e.g. *N. kroyeri*). In absence of the biomasses of the mesopelagic species, which would allow to consider the importance of each species within the species group by weighting the M values according to their biomasses, the M of the different species were averaged to obtain a minimum, average and maximum M for the mesopelagic fishes in the Bay of Biscay. Finally, a F_{MSY} was approached using $F_{MSY} = 0.4xM$ as in Fernandes et al. (2020).

2.1.3. Comparison between scenarios

The impact of fishing at F_{MSY} in the functioning of the ecosystem was calculated computing the difference in biomass by species group (Table 1) comparing F = 0 (BAU) and F_{MSY} (Fishing), relative to the total harvest of mesopelagic (Eq. (1)):

$$\Delta B_s = \frac{(B_{s,BAU} - B_{s,MSY})}{h_{Mesop,MSY}} \tag{1}$$

Where B is the biomass, $h_{MESOP,MSY}$ is the harvest of mesopelagics and s the species group. When in Eq. (1), $B_{S,BAU} > B_{S,MSY}$ the biomass will decrease for the species group, if a commercial exploitation of the mesopelagic zone is made. When $B_{S,BAU} < B_{S,MSY}$, the biomass will increase when exploiting the mesopelagic layer, implying that this species group competes for the same resources in the ecosystem or that are prey of mesopelagic fishes.

To obtain a single monetary value of each scenario, the surpass of gains vs losses of fishing were measured considering the average present value (APV) at time horizon 2050 (Eq. (2)) of the future value (FV) of each ecosystem service (ES) in the forecasted period (2020–2050), considering that the investment required to harvest the fish and transforming it to fishmeal or fish oil, was zero (or that it has already been done).

$$APV_{ES} = \sum_{t=2020}^{T=2050} \left[\frac{FV_{ES,t}}{(1+r)^t} \right] / (2050 - 2020) \tag{2}$$

The discount rate (r) used was 4.25 % as in Boyce (2018).

Each ES has a different FV (see sections below). However, each FV was converted to a value by tonne of mesopelagic fish. Therefore, the extrapolation to the Bay of Biscay was performed multiplying the FV by the quantity harvested of mesopelagic fish per year, and then applying equation (2) to obtain the APV of each ES for the whole area.

Table 2

Population parameters used for the calculations of the natural mortality (M) of the different mesopelagic species.

Scientific name	Growth rate	L∞	Reference	a	b	Reference
Maurolicus muelleri	0.88	5.9	Gjøsæter and Kawaguchi (1980)	0.079	3.23	Salvanes and Stockley (1996)
	1.05	4.9	Gjøsæter (1981)			
Benthosema glaciale	0.31	7.5	Gjøsæter (1981)	–	–	
	0.2	8.3	Gjøsæter (1981)			
	0.36	8.5	Halliday (1970)			
	0.45	8.6	Gjøsæter (1973)			
Lampanyctus crocodilus	–	21		0.0051	2.98	Merella et al. (1997)
Myctophum punctatum	0.32	9	Wörner (1975)	0.008	3	Pauly et al. (1998)
	0.166	10.5	Apostolidis and Stergiou (2014)			
Epigonus denticulatus	–	14.2		0.0045	3.26	Merella et al. (1997)
Notoscopelus kroyeri	0.2	14.9	Froese and Binohlan (2003)	–	–	
Stomias boa boa	–	25.9		0.005	3.36	Deval et al. (2014)

2.2. *Ecosystem services evaluation*

The ecosystem service evaluation was made following the Common International Classification of Ecosystem Services (CICES) conceptual framework (Haines-Young and Potschin, 2018). Three supporting services were evaluated, the functioning of the ecosystem, the “blue carbon” content, and the diel vertical migration of mesopelagic fish, which provide three types of final services PES, CES and RES (Fig. 2). Supporting services provide a critical role in the ecosystem, by supporting the biodiversity, carbon cycle and energy transfer. For example, mesopelagic fishes, by feeding at the surface and then moving back to the deep, play a key role in transferring energy and organic matter from productive shallow waters to the deep ocean.

These ecosystem services can be divided in different value typologies: use values, in particular consumptive values, for PES and indirect use values for RES. Also, non-use values that represent the satisfaction of certain groups in knowing that ecological structures, diversities and integrity levels can be sustained for future generations, are used for CES.

2.2.1. *Provisioning services*

Mesopelagic fishes are supporting the food chain and population dynamics of other commercial fish species (human food provisioning service). The future value of this PES ($FV_{PES(f)}$) was computed by the difference in biomass per species group of both scenarios obtained using Eq. (1) (ΔB_S), multiplied by the MSY related harvest rate of each species as reported in Table 1 (F_S) and multiplied by the ex-vessel market prices (p) obtained from the Annual Economic Report of the EU fishing Fleet (STECF, 2020) (Eq. (3)). These prices were inflated to the base year 2020 using the Harmonized Index of Consumers Prices (HCPI) (EUROSTAT, 2022) and kept constant in real terms. In other words, the prices were projected to 2050 using a fixed percentage equal to the discount rate.

$$FV_{PES(f),t} = \sum_s \Delta B_{S,t} F_S p_{S,t} \tag{3}$$

However, this is not the only provisioning service considered (Fig. 2). Except for some anecdotal examples (Hays, 2003) the mesopelagic fish species are not used as a direct source of human food (due to their low sensory quality), and have to be reduced or transformed to make their protein and fatty acid content consumable by humans (e.g. food supplements or through aquaculture). In that sense it has been proposed that mesopelagic fish could provide fishmeal (FM) and fish oil (FO) to the aquaculture sector (Olsen et al., 2020). Therefore, the harvest of mesopelagic fish under the Fishing scenario was additionally valued as a source of FM and FO. Under BAU, it was assumed that this possibility is lost and therefore, that is equal to zero.

A preliminary estimation of the FM and FO yield that could be obtained from *M. muelleri* was carried out by the authors (unpublished data). This was done analysing the basic nutritional profile (moisture, ashes, protein and fat) of seven samples of *M. muelleri* obtained in two different locations of the Bay of Biscay in two consecutive years (2019 and 2020). Results of this analysis suggested that in an ideal situation without degradation of the raw material, a yield of 250 ± 11.4 kg (mean ± s.e.m.) of FM and 19 ± 8.8 kg of FO per tonne of *M. muelleri,* could be obtained.

FM and FO were monetarized through their international prices, obtained from (IndexMundi, 2021) (for FM) and Kok et al. (2020) (for FO) (see Appendix B). Projections for the period 2020–2050 were estimated fitting and ARIMA (0,1,0) model for the logarithm of the real prices in the historical period without drift. This model selection was made based on the results provided by the forecast package for R (Hyndman and Khandakar, 2008). This package analysed different model fittings, suggesting the ARIMA (0,1,0) as the with the best fitting.

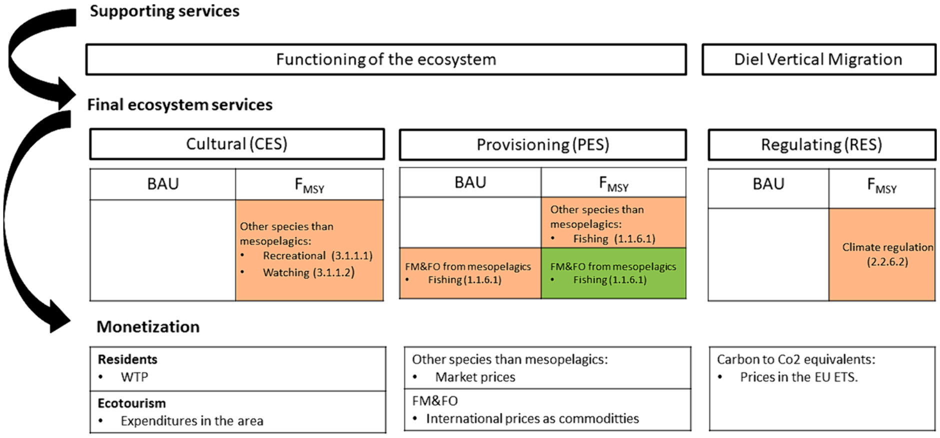

Fig. 2. Cascade model for the ecosystem services (ES) evaluation and monetization followed (under brackets the CICES codes of each ES).

The FV of this PES ($FV_{PES(FM\&FO)}$) was calculated computing the economic yield from the FM and FO perspective. That is, multiplying the quantity of FM and FO likely to be extracted from a mesopelagic fish by the FM and FO projected international prices.

2.2.2. Cultural services

In addition to supporting the food chain and population dynamics of commercial species, mesopelagic fishes are also supporting the food chain and population dynamics of non-commercial species, such as marine mammals or seabirds (Olafsdottir et al., 2016). Therefore, a similar procedure as in the case of commercial species was followed, assessing the changes in the functioning of the ecosystem by the difference in biomass (of the non-commercial species) from fishing and not fishing mesopelagic fishes as calculated using Eq. (1). The difficulty is that CES cannot be reflected by a market price and therefore, alternative approaches (revealed preference and stated preference methods) are needed to determine their monetary value.

The Willingness to Pay (WTP) by household was used as a proxy of the value that people are willing to pay for the preservation of the biodiversity and/or a particular species for future generations. In the absence of a WTP value for all the functional groups and/or individual species included in the model (Table 1, presents 52 functional groups with 340 individual species), we opted for the benefit transfer of the estimated function used to conduct a WTP assessment developed in Amuakwa-Mensah et al. (2018). This function provides a meta-analysis regression to identify explanatory variables for the variation in WTP for threatened and endangered group of species. The groups considered were fishes, birds, invertebrates and marine mammals, where the threat and charisma have a positive effect on the WTP. The function adapted for the Bay of Biscay expressing the annual payment to a trust fund of a visitor for specific species groups, takes the following form:

$$\begin{aligned} LnWTP(2015\$) = 4.19 + 1.106 Endangered{*}LowCharisma \\ +0.709 Endangered{*}HighCharisma \\ +0.658 Threatened{*}HighCharisma - 0.904 Resident \\ -0.786 Fish - 0.285 Mammal - 0.765 Invertebrate \end{aligned} \tag{4}$$

This function was used categorizing as threatened or endangered all the individual species included in the functional groups considered in the EwE model (Table 1) according to the OSPAR Commission (Ospar, 2022). If they are not considered as threatened or endangered, these factors in Eq. (4) take the zero value. The same procedure was also followed for high or low charisma. The complete matrix of factors considered for applying Eq. (4) for each functional group is presented in Table A.1.

For the evaluation, visitors' perception was split between the entire population (19.3 million in 2020) and the tourist (88 million in 2019[1]) in the Bay of Biscay regions (in France and Spain). The reason for doing was to better identify peoples' purpose when visiting this area. Coastal tourism usually represents the 75 % of the total tourism (Fernández-Macho et al., 2015) being the visit to a natural space the main motivation for most of the tourists (70 %), according to the survey developed in Spain by Frechilla and Guzmán (2021). These authors state that tourists allocate 24 % of their time to visit the natural space (followed by other activities as visiting friends, do sport, be relax in the nature, among others), and they pay most of the total budget (30 %) to be used in those activities related to a guide visit to the natural space. Therefore, in this work we modified the WTP coefficient by 75 %*30 %.

It was further considered that 54 % of the residents are willing to pay a positive amount (individuals with WTP $\neq 0$ Euro). This percentage was obtained from the meta-analysis performed by Richardson and Loomis (2009). Therefore, the number of residents of the Bay of Biscay area was multiplied by this percentage. In addition, following White et al. (1997), we further assumed that the observed mean WTP does not increase with the number of species being conserved. Therefore, responders seem to be able to pay a specific amount of money (as a symbolic) rather than assuming an additive value. Thus, we considered the broader framework of the groups categorized following OSPAR Commission, getting a WTP for the overall group which provides lower values than those that can be obtained if valuing each species in isolation. Finally, and considering that there could be an increase of biomass for some species because they occupy a similar niche as the mesopelagic fishes (Shannon et al., 2003), these values were truncated to zero, given that it was considered that households will not receive a payment for increases in biomass. These prices were inflated to the base year 2020 using the same procedure as in the market prices for commercial species.

The CES future evaluation of fishing mesopelagic fishes was obtained multiplying the WTP of residents (Eq. (5.1)) and tourists (Eq. (5.2)), by the difference in biomass from fishing and not fishing mesopelagic fishes as calculated using Eq. (1).

$$FV_{CES(resi),t} = \begin{cases} \sum_{s} \Delta B_{S,t} WTP(resi)_{S,t} & if \Delta B_{S,t} > 0 \\ 0 & if \Delta B_{S,t} \leq 0 \end{cases} \tag{5.1}$$

$$FV_{CES(tour),t} = \begin{cases} \sum_{s} \Delta B_{S,t} WTP(tour)_{S,t} & if \Delta B_{S,t} > 0 \\ 0 & if \Delta B_{S,t} \leq 0 \end{cases} \tag{5.2}$$

2.2.3. Regulating services

The ocean carbon flux can be divided in two different main processes. The first one, named the solubility pump, is based on that dissolved inorganic carbon (DIC), delivers cold, dense, DIC-rich waters to depth mostly at high latitudes. The second mechanism known as the BCP is formed by a suite of processes exporting particulate organic carbon (POC) from surface to deep waters. In these last processes, the biological gravitational pump (BGP) which stands for the settling of a subset of the particle assemblage, is of major importance but not the only mechanism that contributes to the BCP. Other article-injection pumps (PIPs) are defined as physically or biologically inject particles to depth (Boyd et al., 2019).

Among these pumps, the DVM (Vinogradov, 1997) is relevant in our estimates, because is particularly unique compared to other fishes. Regarding how many fishes perform this DVM in our estimations we took the value estimated for the North east Atlantic by Klevjer et al. (2016) of 38 % of these organisms performing the daily excursions. By feeding in the epipelagic zone at nigh migrating mesopelagic fishes contribute to increased vertical carbon flux, fixation, storage and/or sequestration depending on the deepness of this vertical migration (Martin et al., 2020). This is because the carbon ingested as food in the epipelagic is rapidly transported by swimming to mesopelagic depths. Here, parts of this carbon are respired as CO_2 (DIC), excreted as dissolved organic carbon (DOC), defecated as sinking POC and consumed by stationary mesopelagic, migrating abyssal piscivores or by diving epipelagic species such as tuna and sea mammals. DVM is considered a carbon sequestration mechanism of high strength (the rate of particle 'export' from the euphotic zone, the surface mixed layer, or across an arbitrary horizon) and of high efficiency (the time that exported carbon is kept out from the atmosphere) and therefore, relevant to climate regulation (Hudson et al., 2014).

There are no specific studies on the role of the mesopelagic fishes in the Bay of Biscay on carbon transport. Therefore, more general studies were used. These studies (Davison et al., 2013; Langbehn et al., 2019) show that respiration flux is the most important mechanism of this physical pump (DVM) with 14.5 ± 10.9 mg carbon per gram of carbon of migrating organisms per day ($mgCgC^{-1}d^{-1}$). Egestion (2.61 ± 0.7 $mgCgC^{-1}d^{-1}$) and excretion is suggested to only make up a minor proportion of the total flux (0.88 ± 0.14 $mgCgC^{-1}d^{-1}$), although all these values are subject to high regional and species variability.

Each mesopelagic fish "blue carbon" content is, on average, 15 % of carbon relative to its whole-body wet weight (Bar-On et al., 2018). We,

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[1] For the number of tourists, year 2020 was not used due to the COVID-19 travelling restrictions.

therefore, further took into account that by fishing mesopelagic this carbon is extracted.

The monetization of this carbon transport and content was made by transforming the carbon transport into CO_2 equivalents using the molecular weight of carbon and using exchange prices of the existing CO_2 trade schemes. The European Union (EU) Emission Trading System (ETS) was used as the exchange price reference in this work. The price per tonne of CO_2 equivalents in October 2021 was set at 60 Euro t^{-1}_{CO2} and projected at a growth rate of 4.25 %. The future evaluation of the RES was calculated multiplying the CO_2 extracted (blue carbon) and not transported (DVM) per tonne of mesopelagic fish by the projected CO_2 prices.

3. Results

3.1. Ecosystem services in the Bay of Biscay

Based on the results of the EwE under no exploitation of the mesopelagic fishes, the total commercial value (PES) of the mean projected landings for the period 2020–2050, would be 1.436 billion Euro y^{-1}, being other invertebrates (11 %), hake (9 %), benthos feeders decapods (8 %) and sole (7 %) the major contributors.

Results for CES suggest that WTP for threatened marine mammals (baleen whales and dolphins), is significantly higher than for other fish groups. Residents' WTP average estimation reached 39 and 21 Euro per resident or tourist, for whales and dolphins, respectively. They were very closely followed by the WTP for birds reaching 27 Euro y^{-1} per resident and tourist. For the overall group consisting on 26 fish species where six are considered to be high charismatic and additionally four other species as threated, the WTP obtained was 12 Euro y^{-1}. Similar WTP was obtained for the fourth group of species, consisting on 19 species as benthic cephalopods, squids, Norway lobster, pelagic crab, bivalves, echinoderms, gelatinous plankton, mesozooplankton, among others.

Considering the estimation of the mean biomass for the period 2020–2050, the total CES value was obtained to be 2.1 billion Euro y^{-1}, of which mammals and birds represent 37 % and 28 % of the total value, respectively.

Results for RES are based on the projection of ETS prices which suggests a prices of 87 Euro t^{-1}_{CO2} in 2030 and 201 Euro t^{-1}_{CO2} in 2050. Considering the different methodological assumptions, the carbon that can be transported and sequestered by the DVM of mesopelagic fishes, ranges between 0.43 and 4.77 tonnes of CO_2 equivalents by tonne of mesopelagic fish biomass. This provides a maximum total CO_2 sequestered estimation in the Bay of Biscay through the DVM that can be situated between 70,271 and 784,000 tonnes of CO_2 equivalents, with a mean value (considering the mean values reported for respiration, egestion and excretion and the mean value of mesopelagic biomass calculated by the model) of 468,000 tonnes of CO_2. With all these data the future value of RES of the DVM of mesopelagic fishes was estimated to be in the range of 4.5 to 51 million Euro y^{-1}, with a mean value of 30.5 million Euro y^{-1}.

The blue carbon content of mesopelagic was estimated at 0.55 tonnes of CO_2 equivalents by tonne of mesopelagic fish. This provides a CO_2 budget that can be situated between 96,000 and 174,000 tonnes of CO_2 equivalents, with a mean value of 136,000 tonnes of CO_2 equivalents. With all these data the future value of RES of the blue carbon content of mesopelagic fishes was estimated to be in the range of 6 to 11 million Euro y^{-1}, with a mean value of 8.5 million Euro y^{-1}.

3.2. Defining the F_{MSY} harvest rate for mesopelagic fishes

Results for the MSY approximation of the F used to simulate the exploitation of mesopelagic species are presented in Table 3.

Table 3
Average, minimum mean and maximum natural mortality (M) and fishing mortality compatible with the Maximum Sustainable Yield (F_{MSY}) for the most common mesopelagic fishes in the Bay of Biscay.

Statistic	M	F_{MSY}
min	0.684	0.274
mean	0.792	0.317
max	0.924	0.370

The range of F to be used in the simulation of the Fishing scenario was obtained to be between 0.27 and 0.37 with a mean value of 0.31. For simplicity in the exposition, we wanted to use a single F_{MSY} value (the mean) and not the whole range. However, we wanted to test if using only the mean was adequate from the diversity of the ecosystem point of view. For doing so, a Shannon diversity index (H) was calculated for all these harvest rates to obtain a proxy of the average diversity of each F. We tested if the ecosystem diversity at each MSY option (0.27 to 0.37) was statistically different from the one obtained under the BAU scenario ($F \approx 0$) using a Hutcheson *t*-test, which allows to compare two samples when no replicated data exists. The Shannon biodiversity index (H) values obtained within the F_{MSY} range were statistically similar ($p > 0.05$), although all harvest rates within this range showed significant differences ($p < 0.05$) when compared to the BAU scenario (Table 4).

Therefore, the comparison between BAU and Fishing scenario was obtained to be adequate, in the sense that the two scenarios were presenting different diversity index values. Furthermore, given that there were not significant differences among the F_{MSY} rates within the range (0.27–0.37), the use of the mean value ($F = 0.31$) to illustrate the Fishing scenario was also found to be representative of this scenario.

Using this F_{MSY} harvest rate, results suggest that in the Bay of Biscay the quantity of mesopelagic fishes that could be extracted is between 52,000 and 95,000 tonnes per year (ty^{-1}) (with a mean of 62,700 ty^{-1}) leaving a remaining biomass for mesopelagics between 149,000 and 305,000 ty^{-1} (see Fig. 3 -Forecast-).

3.3. Effects of fishing mesopelagic fishes in the Bay of Biscay

Fig. 4 presents the changes in biomass from BAU to Fishing scenario on other species than mesopelagic species of harvesting one tonne of mesopelagic fishes (Eq. (1)). It is presented, representing the average of the forecast period (per year) tonnes lost by species group per tonne of harvested mesopelagic fishes.

According to the model results, the main species negatively affected (their biomass will be reduced) would be important predators of mesopelagic fishes such as bluefin tuna (*Thunnus thynnus*), albacore (*T. alalunga*) and marine mammals such as dolphins.

However, the model also predicts that there will be other species or group of species positively impacted (their biomass will be increased): Groups that have similar diets as mesopelagic fishes (e.g. shrimps and anchovy), that face a reduced competition for feeding, and groups that are the main prey of mesopelagic fishes (e.g. macrozooplankton).

The biomass changes from BAU to Fishing scenarios presented in Fig. 4 were economically evaluated through the PES and CES they are providing following the methodologies previously explained. The result of these valuations is presented in Fig. 5.

Table 4
Shannon index (H) and Hutcheson test (*t*-test) for the BAU ($F = 0$), and Fishing (F_{MSY}) scenarios uncertainty estimation.

Scenario	BAU	F_{MSY_LO}	F_{MSY_mean}	F_{MSY_up}
H	4.536592	4.524399	4.519071	4.514179
t-test (vs BAU)		Hutcheson t-statistic: 5.3465 Df: 57,903,925 p-value: 8.969e-08*	Hutcheson t-statistic: 7.6876 Df: 57,901,290 p-value: 1.499e-14*	Hutcheson t-statistic: 9.8401 Df: 57,898,957 p-value: < 2.2e-16*

[*] Alternative hypothesis: true difference in H' is not equal to 0.

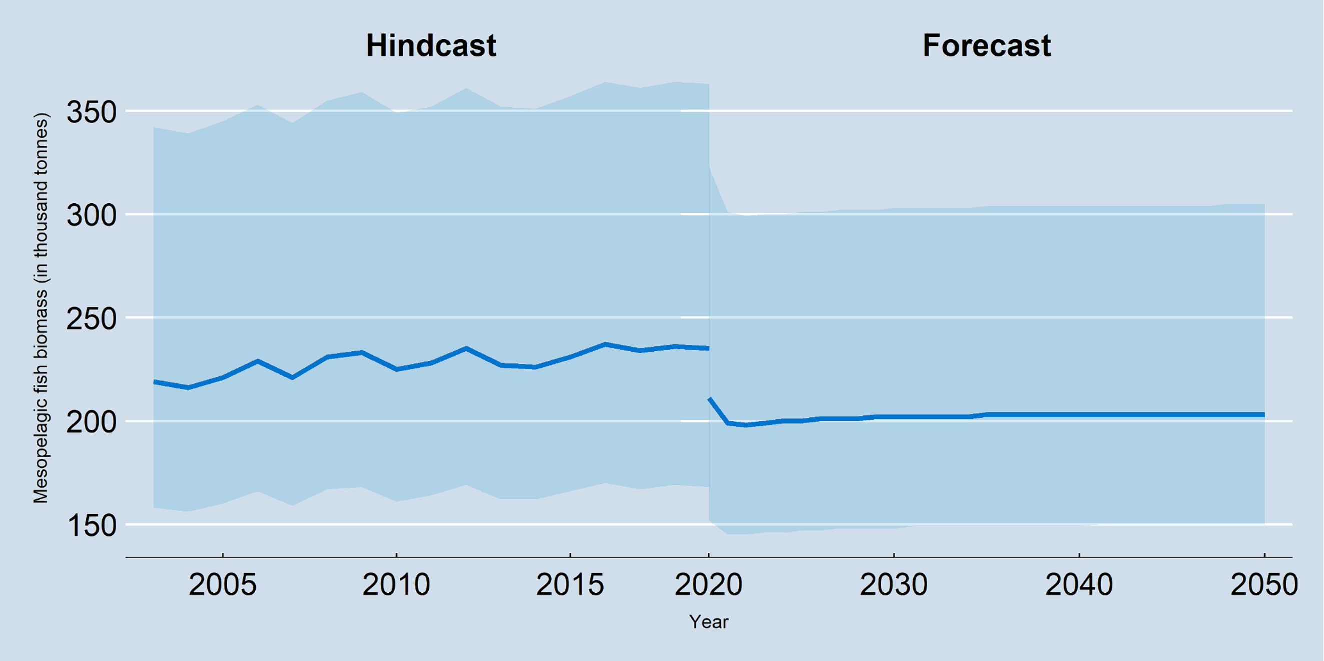

Fig. 3. Evolution of the mesopelagic species biomass fitted by the Ecosim food web model in the observed (hindcast) and projected under exploitation (forecast) periods. The shaded area represents the 95% confident interval of the fitted values. The gap between the blue line in the year 2020 represents the mesopelagic fishes harvest (from zero at the end of year 2019 to F_{MSY} at the beginning of year 2020).

Fig. 5 points out some important results. CES loss for some species can be high if mesopelagic species are caught. This is the case for dolphins for which the model suggests that between 57 and 65 Euro would be lost for each tonne of mesopelagic fish harvested. In the case of whales, up to 20 Euro $t_{meso}^{-1}y^{-1}$ loss is predicted by the model. The overall result for CES is a loss that ranges between 57 and 103 Euro $t_{meso}^{-1}y^{-1}$. The model fitted value would be 67 Euro $t_{meso}^{-1}y^{-1}$. Extrapolated to the whole Bay of Biscay area, the CES economic value (APV) will decrease 4.1 million Euro y^{-1}.

The biggest loss in the APV from BAU to Fishing scenario considering the PES, comes from large tunas and squids (Fig. 5). Albacore (15 Euro t_{meso}^{-1} y^{-1} lost) and squids (12 Euro t_{meso}^{-1} y^{-1} lost) are representative of this impact. The model is also suggesting that the loss on other commercial species such as mackerel can be high (2.8–22 Euro $t_{meso}^{-1}y^{-1}$). Considering all the species, the loss in the APV in the PES was estimated to be between −394 to 342 Euro $t_{meso}^{-1}y^{-1}$, with a model fitted value of 38 Euro $t_{meso}^{-1}y^{-1}$ lost. Extrapolated to the whole Bay of Biscay area, the PES economic value (APV) will decrease by 0.2 % (2.7 million Euro y^{-1}). However, PES should also consider the FM and FO that could be obtained from reducing mesopelagic fishes. Results are provided in Fig. 6.

The APV of FO, ranges between 5 and 55 Euro $t_{meso}^{-1}y^{-1}$ with a mean value of 17 Euro $t_{meso}^{-1}y^{-1}$. FM can be valued at 63 to 486 Euro $t_{meso}^{-1}y^{-1}$ with the mean value at 192 Euro $t_{meso}^{-1}y^{-1}$. Extrapolated to the whole Bay of Biscay area, the PES economic value (APV) of fishing mesopelagic for producing FM and FO would be 13 million Euro y^{-1}.

The overall PES value considering what is lost from the commercial value of other species than mesopelagic and what can be obtained from FM and FO, gives a positive economic value of 10.7 million Euro y^{-1}.

Finally, RES was also monetarized using the ETS projected prices (Fig. 7).

The RES from the DVM was economically valued (APV) between 28 and 312 Euro $t_{meso}^{-1}y^{-1}$, with a mean value of 86 Euro $t_{meso}^{-1}y^{-1}$. The blue carbon adds another 36 Euro $t_{meso}^{-1}y^{-1}$ to this loss.

Extrapolating it to the Bay of Biscay area, this service APV loss can be between 4 and 22 million Euro y^{-1}, with a mean value of 7.6 million Euro y^{-1}.

3.4. *Trade-offs of fishing mesopelagic species*

To contrast the provisioning value if mesopelagic fishes were harvested (FM and FO provisioned) with the current services that society is receiving from the mesopelagic fishes in the Bay of Biscay, a trade off analysis was done. It is presented by taking advantage of the monetization of the ecosystem services developed as way to assess these trade-offs using the same unit (2020 Euro), as the cost (negative) or gain (positive) in the APV in the forecast period of moving from BAU (not fishing) to Fishing (at F_{MSY}) scenarios (Fig. 8).

Fishing mesopelagic fishes will create a mean cost to the society of 19 Euro $t_{meso}^{-1}y^{-1}$, although there could be a benefit (up to 762 Euro $t_{meso}^{-1}y^{-1}$,) or even a higher cost (678 Euro $t_{meso}^{-1}y^{-1}$). If we extrapolate it to the overall Bay of Biscay the estimate of the APV ranges between 48 million Euro y^{-1} benefit to a 42 million Euro y^{-1} loss, with a mean APV of 1.2 million Euro y^{-1} loss.

4. Discussion and conclusions

Uncertainty dominates the estimates of what society is obtaining and of what can be obtained from the mesopelagic layer and represented here as the wide range of the estimates for each ES. As pointed out by Martin et al. (2020), more research is needed to make a more informed choice. However, it should be noted that as reflected in our work these wide ranges do not only arise from the limited existing knowledge of the mesopelagic fishes' biomass but also from the uncertainty on the biomass of the rest of the species of the studied ecosystem. The current limited scientific knowledge of OTZ is reflected in the lower degree of public awareness of this sea layer. Therefore, it becomes complex to infer the social benefits of protecting the OTZ, or the other way around, the social costs of exploiting it. As some of these uncertainties will be resolved (or at least reduced) with the existing and new research projects, social WTP for the OTZ protection estimations will be required, even acknowledging the unfamiliar characteristic that it has to the society in general as, for example, in Aanesen et al. (2015) for cold-water-corals.

In this work, an economic evaluation is performed to obtain the

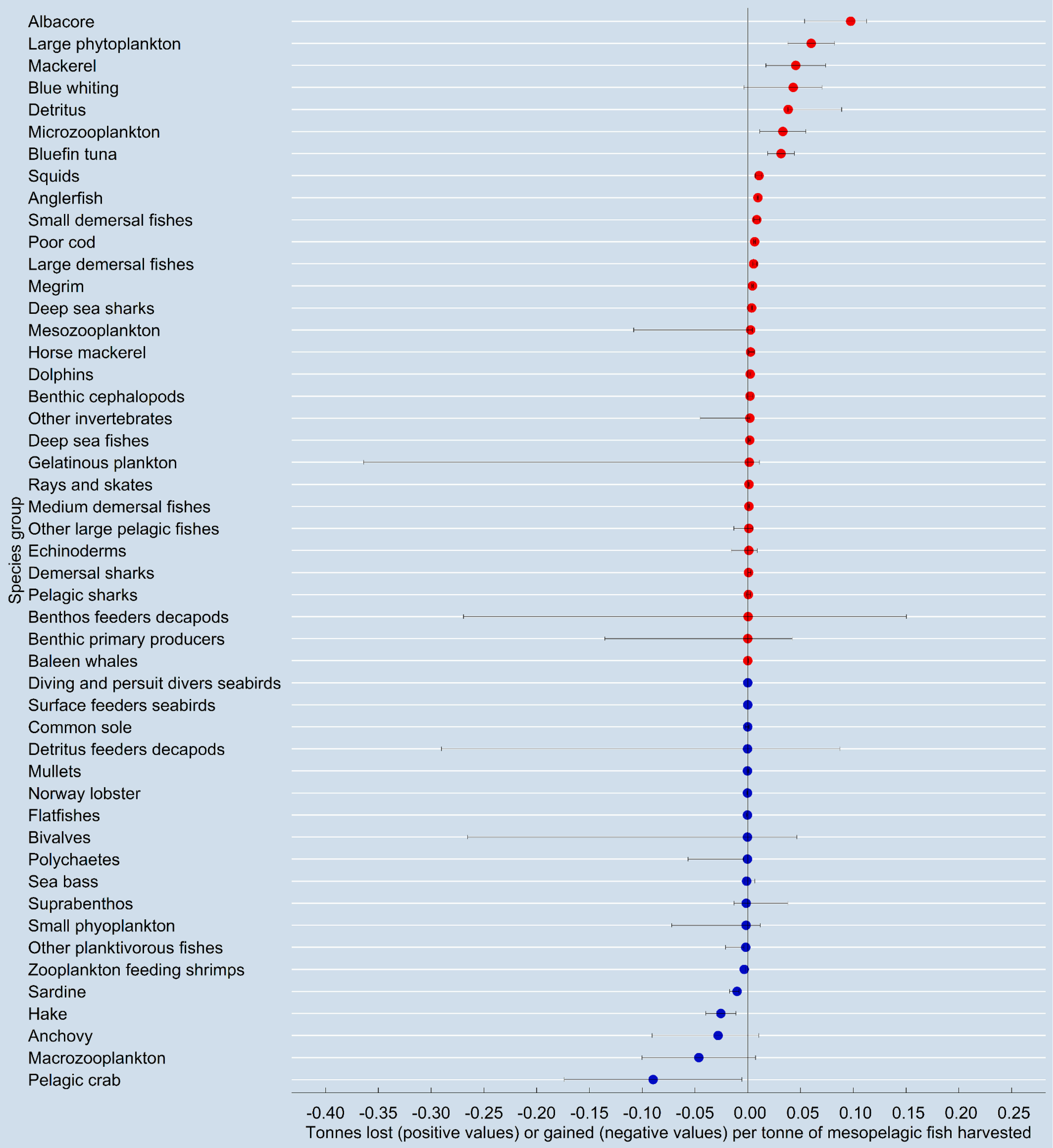

Fig. 4. Average change in biomass of the forecasted period (2020–2050) (t y^{-1}) from BAU to Fishing scenario by tonne (t) of mesopelagic fish harvested per year (y). Dots represent the model fitted values while error bars are constructed using 95% confident interval of the mean. Positive values imply tonnes lost (red dots) and negative values tonnes gained (blue dots).

needed information to consider trade-offs of exploiting the OTZ. Our results show that we still can't be sure whether there is a net gain or loss if the decision of fishing the OTZ is taken, but that trade-offs will arise among different ES. A key message is that trade-offs arise even considering the exploitation of the mesopelagic fish at sustainable rates. This is because F_{MSY} is limiting the sustainability concept to an individual stock level, or as in this case, to a group of mesopelagic species and not considering climate or other ecosystem functioning derived services. The argumentation followed here is not essentially different to any other fish stock. Foragers, or any other similar trophic level fish, would also present these trade-offs, although the magnitude could be different from those obtained for the mesopelagic species. For example, the vertical migration is not fully exclusive of the mesopelagic fishes (e.g. the whale pump (Roman and McCarthy, 2010) and all fishes contribute to the

Fig. 5. Changes in the average present value (Euro y^{-1}) from BAU to Fishing scenario by tonne of mesopelagic fish harvested of the forecasted period (2020–2050). Dots represent the model fitted values while error bars are constructed using 95% confident interval of the mean. Positive values imply Euro lost (red dots) and negative values Euro gained (blue dots).

biological pump through faecal pellets (Saba and Steinberg, 2012). Market prices also differ, because in many cases these species can be valued for direct human consumption (e.g. anchovies). However, those currently exploited fish stocks have constructed different social and economic structures around them, including fishing companies, transforming industries and cultural values, that should be taken into account when analysed (Konar et al., 2019).

In any ecosystem services assessment, once the important final services have been agreed or identified, the discussions about sustainability and appropriate management strategies would have to be focused on the underlying ecosystem structures and processes, and functional characteristics that give rise to them. Thus, the final services, as those assessed here, are seen as the entry-points for these kinds of discussion, and it was felt that broad labels like ‘nutrient cycling’ or ‘primary’ production’ are

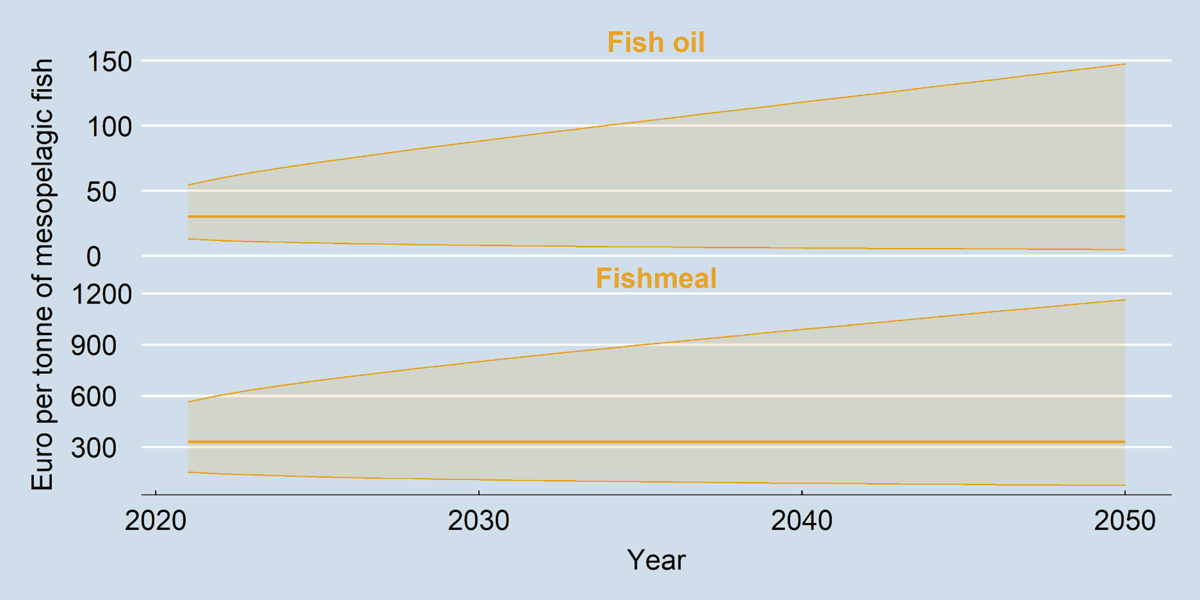

Fig. 6. Expected economic yield in fish oil (FO) and fishmeal (FM) per tonne of mesopelagic fish. The shaded area represents the 95% confident interval of the mean.

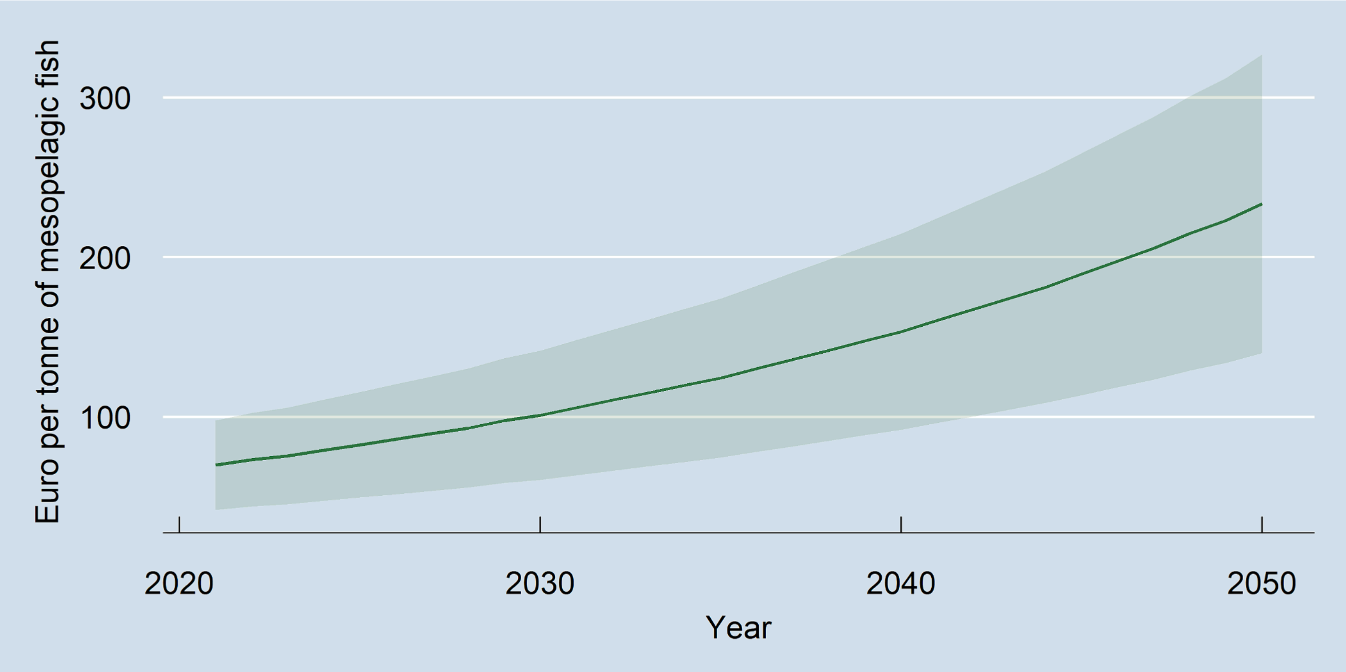

Fig. 7. Euro per tonne of mesopelagic fish, regarding the sequestration of CO_2. The shaded area represents the 95% confident interval of the mean.

not particularly helpful in this respect; for most final services there are probably multiple structures, processes, and functions that 'support' them. Nevertheless, a description and analysis of these processes and functions is necessary therefore, we have opted to start the exploration via the functioning of the ecosystem with a single model. Functioning is an underlying concept here, because due to their morphology, deep habitat and low sensorial qualities, mesopelagic fishes are unlikely to be directly valued by the society, unless we explain and evaluate what they are currently giving to us. Nevertheless, additional ecosystem models would be required to capture all the support and therefore, the final services provided by the mesopelagic fishes.

Acknowledging this limitation, our results in terms of the main species affected, are in line with the literature (Olafsdottir et al., 2016; Shannon et al., 2003) and the value of the mesopelagic biomass obtained using this model is in the range of the acoustic biomass estimation for *M. muelleri*, the dominant species in the area, that has been estimated between 70,000 and 160,000 tonnes in the Eastern part of the Bay of Biscay (Sobradillo et al., 2019). Furthermore, the relative changes in biomass (increases and decreases due to the exploitation the mesopelagic species) are also predicted by Dowd et al. (2022). In addition, we had not considered the impact of ocean warming and this may limit our results as, currently, climate change is already impacting the region and is expected that these impacts would be amplified for some species (Chust et al., 2022).

We further conclude the importance of considering the functioning at different values beyond the provisioning of other species. Cultural

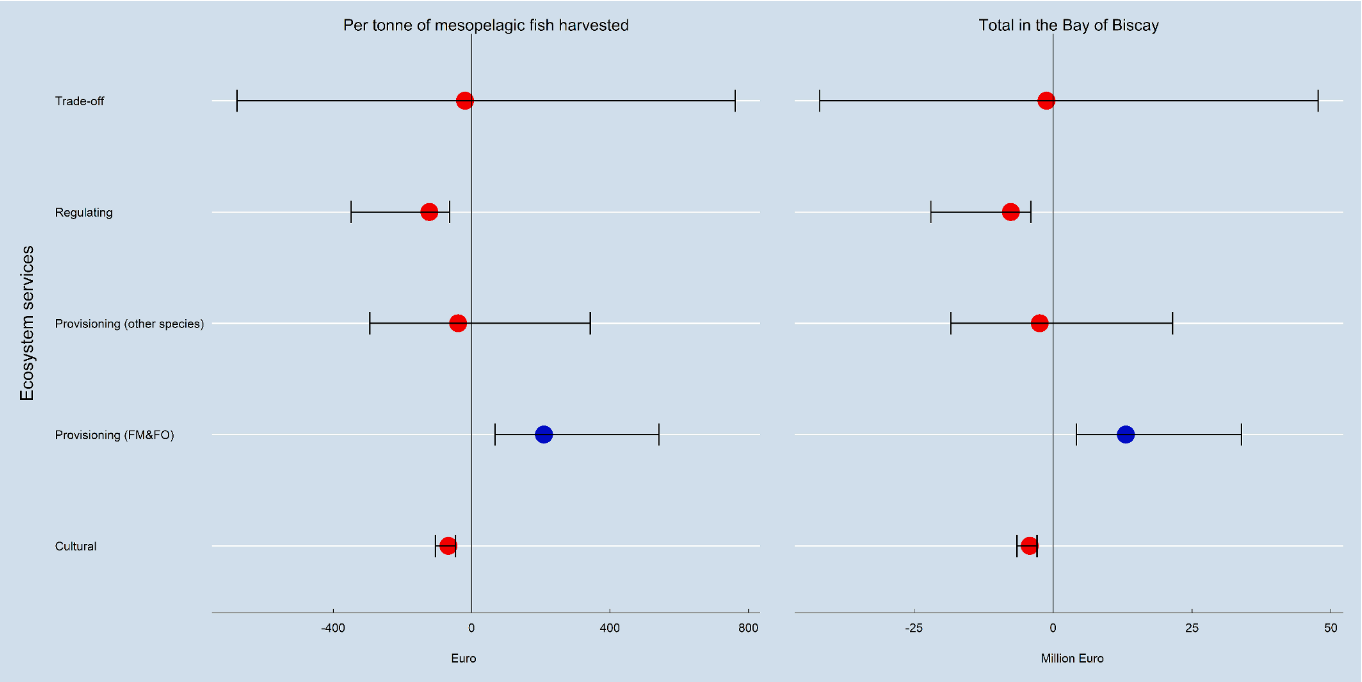

Fig. 8. Trade-off and Ecosystem Services gain or loss when exploiting mesopelagic fishes at F_{MSY} in Euro per tonne of mesopelagic fish harvested (left) and extrapolated for the Bay of Biscay (right). The values are calculated as the average present value of the period 2020–2050, considering a discount rate of 4.25%. A negative value (red dot) implies a service currently provided by the ecosystem and therefore, a mean loss if mesopelagic fishes are exploited. A positive value (blue dot) implies a mean gain when mesopelagic fishes are harvested.

services, including the ecotourism, contribute to our wellbeing, and in some cases (and for some species) beyond the commercial one. In here at least two limitations should be acknowledged. First, the use of a meta-analysis to infer the WTP per household and per species group. On this side a specific set of experiments/surveys should be performed in the studied area to obtain a more area specific WTP estimations. Second, the limitation of relating WTP to the stock size (Lopes and Kipperberg, 2020) although we also note that the WTP values for the different species are in the same range with those estimated in the literature (Lew and Larson, 2014; Ojea and Loureiro, 2010; Wallmo and Lew, 2012). Furthermore, the CES economic valuation made here does not completely capture the full spectrum of the social values of the ecosystem services (Scholte et al., 2015). Finally, there could be other supporting services such as habitat maintenance or genetic diversity that have not been assessed.

It can be further argued that the analysis is limited to the current existing options of transforming the mesopelagic fishes into FM and FO, while there could be other valuable compounds e.g. those with pharmaceutical and nutraceutical relevance, that could enter the options portfolio, increasing the value of potential exploitation. This implies that the evaluation of the trade-offs can change over time. However, these compounds are still to be discovered and therefore, no studies are available, yet. Another caveat is the future projection of the FM and FO prices. Our results suggest that prices will evolve as a random walk without drift for both FM and FO, which simply states that the further we go in the future the less we will know about prices. However, we note that our approach is consistent with the literature. The exclusion of a drift is consistent with the projections made by the OECD/FAO (2018) that predicted that real prices would continue to fall but by only just under 0.5 % p.a. for FM and 0.7 % p.a. for FO. They are also compatible with the sustainability scenario in Kreiss et al. (2020) where prices for these two products are forecasted to be relatively stable, but highly variable under other, more extreme scenarios. In our work uncertainty in the projection is rather related to the past variability of prices due to effect of El Niño years in the anchoveta production. In addition, it should be noted how sensitive are the results to these prices and the expected evolution of them. An increase in the future mean prices of FM and FO of 9 % from those used here would change the results presented in Fig. 8 from net loss in mean to zero. Everything above this 9 % will create a net social gain of exploiting mesopelagic resources.

The importance of considering the carbon sequestration ecosystem service from a monetary perspective is for example explained in Canu et al. (2015), in where using a conservative estimate of the social cost of carbon (SCC), they valued this service for the Mediterranean Sea at 127–1,722 million Euro y^{-1}. However, new theories suggest a reduction in carbon pump transfer efficiency associated with anthropogenic warming (Boscolo-Galazzo et al., 2021), and that this will imply a total reduction in the carbon sequestration. Therefore, the physical carbon sequestration estimated here can be considered as an upper limit. However, the monetization of the service is, on the contrary, conservative. If SCC would be used instead of ETS, the value of the regulatory service will be increased by a factor of three to five. ETSs differ substantially from the social cost of it (Nordhaus, 2017) being the former (much) lower, due to many factors such as firms not being constrained to emission caps, under-assessment of climate derived risks and budgets or simply due to political or social (lobbies) pressures or desires. The SCC prescribes an emissions trajectory and time path for carbon prices tied to each other by a presumed relationship between quantity and price. SCC includes costs such as climate damages, catastrophic risks and co-pollutant impacts, given a time horizon and it is highly sensitive to the discount rate used in the calculation. The mean projected carbon values for ETS are within the range of what the literature suggests (close to the 90 Euro t_{CO2}^{-1} for 2030 predicted by Reuters (2021) and 201 Euro t_{CO2}^{-1} for 2050).

Additionally, there are other regulating services currently provided by the mesopelagic layer and not considered here. The mortality flux of these fishes can be of high relevance (Hidaka et al., 2001), given that if they are fished we are not allowing fishes to naturally die (Mariani et al., 2020). Overall, this service requires further exploration as uncertainties about the mechanisms between BCP and carbon cycle are resolved

(Monteiro et al., 2021).

At the management level, future steps will require managing fisheries under ecosystem-based fisheries management or if resilience and diversity of oceans are fully embodied, under the wider concept of ecosystem-based management (Curtin and Prellezo, 2010). There is a clear interrelationship among this work and the United Nations (UN) Sustainable Development Goals. While the UN stresses that each goal needs to be achieved so that no one is left behind, we have shown, that this is not likely to happen by exploitation of the OTZ. The impact in the biomass of other commercial species is obtained to be low as in Dowd et al. (2022) and potentially five times lower than what can be obtained from reducing mesopelagic fishes to FM and FO. However, it is not only the exploited system what matters here. Current services are high enough to keep them untouched and they split outside the system at a planetary level (e.g. climate regulation), requiring a balanced policy action. Therefore, the policy recommendation obtained from this work is not to start a generalized fishing on these resources, but to continue exploring the functioning and the role of the OTZ in the ecosystem, the contribution to the carbon sequestration of this sea layer, and at the same time, explore the different products that can be obtained upon exploitation. A future definition of a sustainable harvest rate for mesopelagic species should go beyond the scope of the single stock (e.g. single stock MSY approach) and consider all the services this sea layer offers. Our challenge is not only to find the best policy today for the future, but to select a prudent strategy and to adjust it over time. This would require a precautionary approach as the one supported by The Pacific Fishery Management Council which prohibits the development of new directed fisheries on forage species, until the potential impact of the new fishery is scientifically assessed (Hidalgo and Browman, 2019). Our work, we think, is just a step forward in this direction.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Matrix for application of the WTP to produce the cultural values of all the species groups

Table A1

Matrix for application of the WTP estimation (Eq. (1) in the main text) to produce the cultural values of all the functional groups.

Group of species	Endangered	Low Charismatic	High Charismatic	Threated	Fish	Mammal	Invertebrate
Diving and persuit divers seabirds	0	1	0	1	0	0	0
Surface feeders seabirds	0	1	0	0	0	0	0
Baleen whales	0	0	1	1	0	1	0
Dolphins	0	0	1	0	0	1	0
Demersal sharks	0	1	0	1	1	0	0
Pelagic sharks	0	1	0	1	1	0	0
Deep sea sharks	0	1	0	1	1	0	0
Rays and skates	0	1	0	1	1	0	0
Bluefin tuna	0	0	1	0	1	0	0
Albacore	0	0	1	0	1	0	0
Other large pelagic fishes	0	0	1	0	1	0	0
Mackerel	0	0	1	0	1	0	0
Horse mackerel	0	0	1	0	1	0	0
Sardine	0	0	1	0	1	0	0
Anchovy	0	0	1	0	1	0	0
Other planktivorous fishes	0	1	0	1	1	0	0
Mesopelagic fishes	0	1	0	0	1	0	0
Anglerfish	0	1	0	0	1	0	0
Sea bass	0	1	0	0	1	0	0
Blue whiting	0	1	0	0	1	0	0
Hake	0	1	0	0	1	0	0
Poor cod	0	1	0	0	1	0	0
Megrim	0	1	0	0	1	0	0
Common sole	0	1	0	0	1	0	0
Flatfishes	0	1	0	0	1	0	0
Mullets	0	1	0	0	1	0	0
Large demersal fishes	0	1	0	0	1	0	0
Medium demersal fishes	0	1	0	0	1	0	0
Small demersal fishes	0	1	0	0	1	0	0
Deep sea fishes	0	1	0	0	1	0	0
Benthic cephalopods	0	1	0	0	0	0	1
Squids	0	1	0	0	0	0	1
Norway lobster	0	1	0	0	0	0	1
Pelagic crab	0	1	0	0	0	0	1
Zooplankton feeding shrimps	0	1	0	0	0	0	1
Benthos feeders decapods	0	1	0	0	0	0	1
Detritus feeders decapods	0	1	0	0	0	0	1
Bivalves	0	1	0	0	0	0	1
Polychaetes	0	1	0	0	0	0	1
Suprabenthos	0	1	0	0	0	0	1

(*continued on next page*)

Table A1 (*continued*)

Group of species	Endangered	Low Charismatic	High Charismatic	Threated	Fish	Mammal	Invertebrate
Echinoderms	0	1	0	0	0	0	1
Other invertebrates	0	1	0	0	0	0	1
Gelatinous plankton	0	1	0	0	0	0	1
Macrozooplankton	0	1	0	0	0	0	1
Mesozooplankton	0	1	0	0	0	0	1
Microzooplankton	0	1	0	0	0	0	1
Benthic primary producers	0	1	0	0	0	0	1
Small phyoplankton	0	1	0	0	0	0	1
Large phytoplankton	0	1	0	0	0	0	1
Detritus	0	1	0	0	0	0	1
Discards	0	1	0	0	0	0	1

Source: Authors made based on Ospar (2022).

Appendix B. Prices of fishmeal (FM) and fish oil (FO) used as base for the estimations

Table B1

Prices of Fishmeal (FM) and Fish oil (FO) in nominal and real (2020 year) terms used as the base of the estimations of future prices of FM and FO.

	Nominal in €/tonne		Real in €/tonne base 2020 (HCPI)	
Year	FM	FO	FM	FO
2001	529	384	1,002	727
2002	576	460	1,054	842
2003	539	473	954	836
2004	534	492	913	842
2005	560	527	926	872
2006	667	589	1,068	942
2007	730	617	1,129	954
2008	771	772	1,154	1,156
2009	849	808	1,229	1,169
2010	1,019	877	1,426	1,227
2011	1,068	826	1,445	1,117
2012	1,241	1,179	1,623	1,542
2013	1,216	1,372	1,538	1,735
2014	1,260	1,471	1,541	1,799
2015	1,507	1,734	1,783	2,050
2016	1,441	1,640	1,648	1,875
2017	1,309	1,468	1,447	1,624
2018	1,312	1,453	1,403	1,554
2019	1,295	1,461	1,339	1,511
2020	1,310	1,540	1,310	1,540

Source: (IndexMundi, 2021) (for FM) and Kok et al. (2020) (for FO). HCPI from Eurostat.

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