

ORIGINAL ARTICLE

The carrying capacity of the seas and oceans for future sustainable food production: Current scientific knowledge gaps

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Abstract

The expected increase in global food demand, as a consequence of a rising and wealthier world population, and an awareness of the limits and drawbacks of modern agriculture, has resulted in a growing attention to the potential of the seas and oceans to produce more food. The capture production of presently exploited marine fish stocks and other species has more or less reached its maximum and can only be slightly improved by better management. This leaves four alternative options open to increase marine food production: (1) manipulating the entire food web structure via removal of high trophic level species to allow an increasing exploitation of low trophic level species, (2) harvesting so far unexploited stocks, such as various fish species from the mesopelagic zone of the ocean or the larger zooplankton species from polar regions, (3) low-trophic mariculture of seaweeds and herbivorous animals, and (4) restoration of impoverished coastal ecosystems or artificially increasing productivity by ecological engineering. In this paper, we discuss these four options and pay attention to missing scientific knowledge needed to assess their sustainability. To assess sustainability, it is a prerequisite to establish robust definitions and assessments of the biological carrying capacity of the systems, but it is also necessary to evaluate broader socio-economic and governance sustainability.

KEYWORDS

ecological engineering, ecosystem manipulation, ecosystem restoration, low-trophic aquaculture, mesopelagic fisheries, zooplankton fisheries

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1 | INTRODUCTION

Global agricultural production has been increasing steadily during the last two centuries, with a strong growth spurt in the first decades after World War II (Evans, 1980; Iizumi et al., 2014). Even per capita production went up, resulting in healthier and better nourished populations (Dyson, 1994, 1999; Porkka et al., 2013), but the success has come at a cost. Growing awareness of the drawbacks of modern agriculture, such as deteriorating soils, biodiversity loss and nutrient imbalance, has stimulated the search for alternative and more sustainable approaches (e.g., van Zanten et al. (2019)). Not surprisingly attention has turned towards the oceans as well. On a global basis, only a meager 1–2% of human food and about 17% of animal protein currently come from the seas (Costello et al., 2020; Duarte et al., 2009), whereas our planet is more than 70% covered with water. High expectations were recently raised about the possibilities to increase marine yields (Costello et al., 2019; Duarte et al., 2009; Gentry et al., 2017; Jouffray et al., 2020; Marra, 2005; Pharo & Oppenheim, 2019), and the fast growth of marine aquaculture over the last decades is seen as a promising signal that such an increase can be achieved. A blue paper by the High Level Panel for a Sustainable Ocean Economy predicts more than a six-fold increase (Costello et al., 2019). The Food and Land Use coalition even claimed that the step from fishing to other forms of harvesting can increase total marine yields by orders of magnitude (Pharo & Oppenheim, 2019). However, these optimistic views have recently been challenged (Belton et al., 2020; van der Meer, 2020), and the future role of finfish marine aquaculture in global food production has been seriously questioned. van der Meer (2020), for example, states that increasing trophic efficiency at sea is not easily achievable by some forms of ‘agricultural’ practice and that the only option for improving marine food production is to harvest at lower trophic levels, either for feed or, preferably, for food. Yet, he also warns that large-scale low-trophic aquaculture of, for example, seaweed may result in serious local nutrient depletion, competition with natural phytoplankton and negative impacts on the marine ecosystem.

SAPEA (2017) identified three options to increase marine food production. The first one is improved management of presently exploited populations and better use of harvested biomass. The latter implies that fish catches are as much as possible redirected to human consumption instead of used as animal feed. At present, about one-fifth of worldwide catches are used for fishmeal and fish oil production (Costello et al., 2020) and merely used as animal feed in aquaculture and animal husbandry, so there is room for a more efficient use of fishery yields. Appropriate management for all exploited stocks might

increase worldwide yields compared to the present situation. Many exploited stocks are still unmanaged, and essential data on stock size and fishing mortality are lacking (Hilborn et al., 2020). Such management would include a reduction in fishing mortality for many stocks and a decrease in the levels of discards by fishing more selectively and avoiding bycatches. A World Bank report, using a simple bio-economic model that treats the world's fisheries as one single fishery, estimates that by proper management of fishing effort, annual harvests could increase by 13% (The World Bank, 2017). Costello et al. (2020) predict an increase of 18% if all stocks are managed at Maximum Sustainable Yield (MSY) levels. These studies did, however, not consider another possible way of increasing the catch of presently exploited populations, which is to manipulate the entire food web structure by reducing the abundance of high trophic level species. Such manipulation could potentially allow an increasing exploitation of low trophic level species.

The second option identified by SAPEA (2017) is harvesting species that are as yet not being exploited, the main candidates being mesopelagic fish species and the larger zooplankton species. Mesopelagic fish species, such as the lanternfishes (or myctophids), live in the open ocean, where during the day they occur in the twilight zone below 200 m depth, but move to shallower depth at night. Previously, it was thought that mesopelagic stocks were not very abundant (Gjørseter & Kawaguchi, 1980), and given the costly logistics, it would not pay off to exploit them. In the last decade, much higher estimates of mesopelagic fish biomass have been published (Irigoiien et al., 2014) which has aroused new interest in the possibilities of harvesting these oceanic fish populations (St John et al., 2016). Another possibility is increasing the exploitation of larger zooplankton species such as Antarctic krill *Euphasia superba* and various *Calanus* species, that occur in polar regions. Recent studies have shown their high standing stocks and the potential for an increase in harvesting is considered relevant (Atkinson et al., 2009; Nicol & Brierley, 2010).

The last option is marine aquaculture. It is important to distinguish between extensive aquaculture with no or minimal resource inputs and intensive aquaculture that entirely relies on supplementary feed. Aquaculture of low-trophic organisms such as seaweed or shellfish, belongs to the first category. Seaweeds are primary producers taking up the nutrients they require such as nitrogen and phosphorus directly from the natural ecosystem. Similarly, shellfish feed on natural phytoplankton and detritus. Intensive aquaculture of marine finfish or shrimps, on the other hand, requires supplementary feed, that is largely provided either by fishery products in the form of fishmeal and fish oil, or by terrestrial-based resources such

as soya. Fishmeal and fish oil are mainly made from small pelagic fish, such as anchovy or herring, which are edible for humans too (Ahern et al., 2021; Tacon & Metian, 2013). Finfish aquaculture based on captured fish is therefore not a very efficient way to produce human food. As most forage fish stocks are already exploited at maximum levels there is not much room for further increase either. Dependency on terrestrial-based feed basically turns finfish aquaculture into an agricultural practice, as it no longer capitalizes on marine primary production. It does not exploit the productivity of the oceans and it increases rather than releases the pressure on agricultural land. Improvements in marine finfish aquaculture as a way to efficiently exploit the richness of the seas are though possible by the use of three different types of feed. The first type consists of waste from sea food processing, which use is already rising (Arvanitoyannis & Kassaveti, 2008; Ferraro et al., 2010, 2013; Jayasinghe & Hawboldt, 2012; Jayathilakan et al., 2012; Olsen et al., 2014). The second type consists of marine species, non-edible for humans, that are not yet exploited. The third and last types are products or by-products from low-trophic aquaculture that are also non-edible for humans. Hence, the last two types are in fact part of two of the three options mentioned above, harvesting new species and low-trophic aquaculture.

A fourth opportunity to increase the food production of seas and oceans, not mentioned by SAPEA, is the use of various types of ecological engineering to restore and improve the carrying capacity of marine ecosystems. This opportunity is based on the notion that coastal urbanization and other human activities have led to a loss of productive marine habitats. Nature-inspired, engineered solutions could recover the availability of suitable habitats and shelters, reduce natural mortality and increase production, and by these means providing a range of ecosystem services such as, for example, provisioning of human food, coastal defense from erosion, carbon sequestration, and biodiversity gain (e.g., Riisager-Simonsen et al., 2022; Seaman, 2007). Such solutions can range from, e.g., the restoration of sensitive, productive habitats such as shellfish and coral reefs, seagrass and seaweed meadows, and subtidal boulders (Brears, 2020; Fitzsimons et al., 2020; Kristensen et al., 2017; Liversage, 2020; Liversage & Chapman, 2018; Patrice et al., 2015; Støttrup et al., 2014) to the deployment of purposely designed artificial reefs to create new habitats (e.g., Seaman and Sprague (1991); Bortone (2018)) and artificial sea mountains, air-lifts or other devices aimed at providing the upwelling of nutrient rich deep water to surface waters where primary production is nutrient limited (Fan et al., 2013, 2015; Kemper et al., 2022; Kirke, 2003; Okano et al., 2011; Pan et al., 2019; Suzuki & Hashimoto, 2011). The so-called 'greening of grey hard infrastructures' incorporates ecological solutions in

the design of marine infrastructures (e.g., docks, break waters, pipelines, and wind farms) to accommodate better attachment of organisms and offer shelter from predation to juvenile fish (Firth et al., 2020; Pioch & Souche, 2021).

In this paper, we explore examples of the four options outlined above: management of presently exploited fish stocks by means of manipulating food web structure, harvesting species that are not yet exploited, marine low-trophic aquaculture, and ecological engineering. Research programs on exploited fish stock management are numerous and have a long history. Recent reviews on how to improve fish stock management are available, e.g., Hilborn et al. (2020), and we will therefore not further discuss fish stock management, but with the exception of ecosystem manipulation. We will discuss the option of a shift in harvesting pressure across trophic levels, such that top predators are more intensively fished in order to increase the productivity of their prey.

New ways of food provisioning from the seas and oceans should not only be efficient in terms of exploiting primary and secondary production, but also be sustainable, by which we mean that harvesting from a system should in the long run not exceed the external supply of nutrients and that the structure and functioning of the natural ecosystem should not be fundamentally changed. One should, however, acknowledge that trade-offs exist, not only between exploitation and conservation, but also between the different types of exploitation. Large-scale seaweed culturing may, for example, come at the expense of the primary production of naturally occurring phytoplankton, with possible consequences for fishery yields and conservation values at higher trophic levels. We will therefore start with a conceptual exploration of the possible trade-off between harvesting at different trophic levels. The conceptual model that we introduce provides the basis for further and more detailed considerations on various exploitation options and the carrying capacity of the system. For all actual topics and systems addressed in this paper, a first requirement is to establish a robust definition and assessment of the biological carrying capacity of the system in order to assess the sustainability of human activities according to their impacts.

Our aim is to provide an overview of the scientific knowledge currently missing to initiate a proper assessment of the carrying capacity of the marine ecosystem for these novel activities, in terms of ecological, economic and societal impact. This overview will be used to provide the first steps towards a research agenda. What kind of research is needed to get a better view on these four future possibilities of sustainable marine food production, such that informed policy and management are possible? We acknowledge that the present situation, e.g., in terms of nutrient availability, may change due

to changing management, for example, resulting in a further decrease in riverine nutrient loads, or changing environmental conditions as a result of expected climate change. The scope of our contribution is global, but local, e.g., European examples or case studies are frequently used.

2 | CARRYING CAPACITY AND TRADE-OFFS

Ambitious plans for large-scale low-trophic aquaculture (e.g., seaweed) farms have been formulated all around the world. For the Dutch part of the North Sea, for example, the figure of 14,000 km² of sea farms has been mentioned by a governmental innovation platform (Taakgroep Innovatie Klimaataakkoord, 2019). Such plans raise the question where the limits to growth lie. When is the carrying capacity of seas, such as the North Sea, exceeded? Large-scale construction of seaweed farms can have effects on nutrient dynamics and thus indirectly on the carrying capacity for, for example, fishing in a large surrounding sea area. In order to be able to predict the consequences of new aquaculture activities, the use of mathematical models is indispensable. This section looks ahead to the type of models that are needed, but first the question is asked what the term carrying capacity actually means.

2.1 | What is carrying capacity?

For ecologists, carrying capacity is primarily the maximum number of a species that can live in a certain area. Ecological textbooks are quick to refer to the parameter K from the logistic growth model (Hartvigsen & Levin, 2001; Hixon, 2008). This model, which describes not only human population growth, but also the growth of animal populations, was already developed in the 19th century by the Belgian mathematician Verhulst and is usually represented in the form of the differential equation,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right). \quad (1)$$

Without the term in brackets, the rate at which the population size N changes (represented by dN/dt) would be proportional to the population size itself and the population would continue to grow exponentially at an instantaneous growth rate equal to r . The term in brackets inhibits this growth and equilibrium is reached when this term is equal to zero, which is the case when the population

size N is equal to the carrying capacity K . Fishery biologists often use the Schaefer model, a special version of the Verhulst model, to calculate the maximum yield of fish from a certain stock that can be harvested sustainably (see, e.g., Smith, 1994). For these applied scientists, the carrying capacity of the ecosystem is equivalent to this maximum sustainable yield (Hixon, 2008). In the Schaefer model, the harvesting is assumed to be proportional to the stock and equal to hN , where h is the instantaneous fishing mortality. The model is then written as

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - hN, \quad (2)$$

where N is often interpreted as biomass. The model can be easily rewritten in the form of the Verhulst model,

$$\frac{dN}{dt} = r_s N \left(1 - \frac{N}{K_s} \right), \quad (3)$$

where the instantaneous growth rate is equal to $r_s = r - h$ and the equilibrium is equal to $K_s = (1 - h/r)K$. At equilibrium, the catch is equal to hK_s and it is easy to deduce that maximum catch is achieved when instantaneous fishing mortality h is equal to half the instantaneous growth rate r . The population equilibrium is then equal to half of the equilibrium that would be achieved without fishing. The model predicts a quadratic relationship between fishing mortality (which can vary between 0 and r , with higher fishing mortality the population collapses) and fishing yield. These simple models illustrate that there are at least two different definitions of carrying capacity ('how many animals can live in an area' or 'how many animals can be harvested from an area'). Many more variants of carrying capacity are discussed in the scientific literature (del Monte-Luna et al., 2004; Dhondt, 1988; Hixon, 2008; McKindsey et al., 2006; McLeod, 1997; Price, 1999; Rees, 1996; Roe, 1997; Seidl & Tisdell, 1999; Wang et al., 2014; Weitzman & Filgueira, 2020), but the above distinction is the most fundamental. However, more important than the idea that there are two kinds of carrying capacity is the notion that both types of carrying capacity cannot be realized at the same time. Without stock reduction, there is no yield and in practice the size of the fish stock that generates the highest catch turns out to be significantly lower than half of the stock size that would be there without fishing. Estimates of the biomass at MSY vary between 35% and 40% of the pristine biomass (Punt et al., 2014). In a recent report, The World Bank (2017) therefore uses the Pella–Tomlinson model, which can be seen as a generalization of the Verhulst model, to describe population growth without fishing (Pella & Tomlinson, 1969),

$$\frac{dN}{dt} = rN - mN^b. \quad (4)$$

Note that this model is equal to the Verhulst model when $b=2$ and $m=r/K$. After adding a fishing term $-hN$, it can be deduced that the maximum catch is reached when

$$h = \frac{b-1}{b}r. \quad (5)$$

The stock then has a size equal to a fraction $b^{1/(1-b)}$ of the stock size without fishing. The World Bank, which used this simple model to estimate the maximum global fish catch, used a value of the exponent b approximately equal to 1.2, which means that the maximum catch is reached at 40% of the stock size without fisheries. This choice was based on the observation that many fisheries, especially those that have been intensely exploited for a long time, have shown a remarkable resilience to a persistently high fishing effort. Such observation is in accordance with a biomass growth function skewed to the left, which can be represented by the Pella-Tomlinson exponent being less than two (The World Bank, 2017). The models described here are extremely simple and, for example, do not take into account the size or age distribution of the population. However, models such as the Beverton-Holt model (Beverton & Holt, 1957), which do so and are mainly used in fisheries management in Europe, do not lead to essentially different results. These models also show that the MSY is achieved with a stock that is significantly lower than the stock that would exist without fishing.

2.2 | Seaweed and fishing

If nature conservation strives for maximum stock size and fisheries for maximum yield, the models discussed above show that both objectives cannot be achieved at the same time. Fisheries at MSY are sustainable and the survival of the species is guaranteed, but fish stocks are significantly smaller than they would have been without fisheries. Yet, to answer the question how large scale seaweed farms affect the two types of carrying capacity (maximum stock size and MSY), different models are needed, namely models that take into account energy and mass flows through the ecosystem. Fishing takes place at higher trophic levels, where little of the energy and nutrients stored by the algae are left over, and the withdrawal of fish from the ecosystem therefore has a marginal impact on the nutrient budget of the sea. The models used in fisheries biology only look at the dynamics of population numbers and do not concern themselves with nutrient fluxes, but to estimate the consequences of large-scale harvesting of primary producers such as seaweed, one cannot avoid the modeling of energy and/or nutrient flows. An attempt is made below to draw up a model that is as simple as possible, but that does meet this requirement.

In addition to the biomass density of a consumer N (e.g., mussels), the model also contains the biomass density of a producer P (e.g., seaweed or phytoplankton, which are not distinguished here). Consumers eat producers and consumption is described by a Lotka-Volterra process, i.e., the rate of consumption is proportional to the product of the producer and consumer biomass (Gurney & Nisbet, 1998). With constant producer biomass, the consumer follows the Verhulst equation. All disappearing consumer biomass is immediately converted into nutrients that are immediately absorbed by the producer. The water is continuously refreshed at a relative refreshing rate equal to q and producers flow in (with biomass density P_0) and out (with biomass density P). This leads to the following system of two differential equations:

$$\begin{aligned} \frac{dP}{dt} &= mN^2 - aNP + q(P_0 - P) \\ \frac{dN}{dt} &= aNP - mN^2. \end{aligned} \quad (6)$$

The term aNP is therefore not equal to total consumption, but only to that part that is actually converted into consumer biomass. The rest is immediately converted back into producer biomass via faeces and nutrients and therefore does not disappear from the producer compartment on a net basis. Likewise, the term mN^2 is not equal to total primary production, but only to production based on dead consumers. In equilibrium, the outflow from the system is equal to the inflow, so $q(P_0 - P) = 0$. It follows directly from this that the density of producers is equal to that of the inflowing water $P^* = P_0$. By setting the consumer equation equal to zero, the equilibrium density of consumers $N^* = aP^*/m$ follows. When harvesting is included, the equations change to

$$\begin{aligned} \frac{dP}{dt} &= mN^2 - aNP + q(P_0 - P) - bP \\ \frac{dN}{dt} &= aNP - mN^2 - hN. \end{aligned} \quad (7)$$

At equilibrium, the inflow qP_0 is equal to the outflow qP plus the harvest to producers bP and consumers hN . From this follows the system isocline (the line connecting all points where the sum of P and N does not change)

$$P = \frac{q}{q+b}P_0 - \frac{h}{q+b}N. \quad (8)$$

The consumer isocline is given by

$$P = \frac{h}{a} + \frac{m}{a}N. \quad (9)$$

The intersection of the two isoclines yields the equilibrium,

$$\begin{aligned} N^* &= \left(\frac{q}{q+b} P_0 - \frac{h}{a} \right) / \left(\frac{m}{a} + \frac{h}{q+b} \right) \\ P^* &= \left(\frac{h}{m} + \frac{q}{h} P_0 \right) / \left(\frac{a}{m} + \frac{q+b}{h} \right). \end{aligned} \quad (10)$$

It is immediately apparent from these comparisons that the consumer will not be able to maintain a viable population if the instantaneous mortality h becomes too high. Only if

$$h < \frac{aq}{q+b} P_0 \quad (11)$$

does the consumer survive. This criterion is comparable to $h < r$ from the Schaefer model. It can also be deduced that with increasing instant mortality h , the consumer density decreases monotonically, but also that this is not the case for the density of the producer. An example calculation shows that the producer density initially decreases with increasing instantaneous mortality of the consumer, but that with increasing mortality the producer density increases again (Figure 1). Because the harvest of consumers hN^* is equal to the inflow qP_0 minus the outflow $(q+b)P^*$ of producers, the harvest will therefore also be highest when the producer density is lowest. In addition, the maximum harvest of consumers will be achieved with a consumer stock that can be significantly lower than the stock without harvest. In the given example, this size is about 35% of the maximum stock size, a result that thus corresponds to the Pella–Tomlinson model with a low value for the exponent b , despite the fact that the consumer loss term ($-mN^2$) is given by a quadratic relation as in the Verhulst model. Finally, it should be noted that the harvesting of consumers hardly influences the harvesting of producers (Figure 2), while the reverse is absolutely not the case. The harvest of consumers decreases significantly when producers are also harvested. The maximum achievable yield for producers is equal to qP_0 , but the influence on the yield of consumers is already significant at a much lower yield (Figure 2).

2.3 | Model precision, realism and generality

The Schaefer model, the Pella–Tomlinson model, and the simple producer-consumer model introduced here clearly show that optimal fishing yields are achieved at fish stocks much lower than would be present without fishing, and that harvesting primary producers can have a major effect on both fisheries yields and fish stocks themselves. The

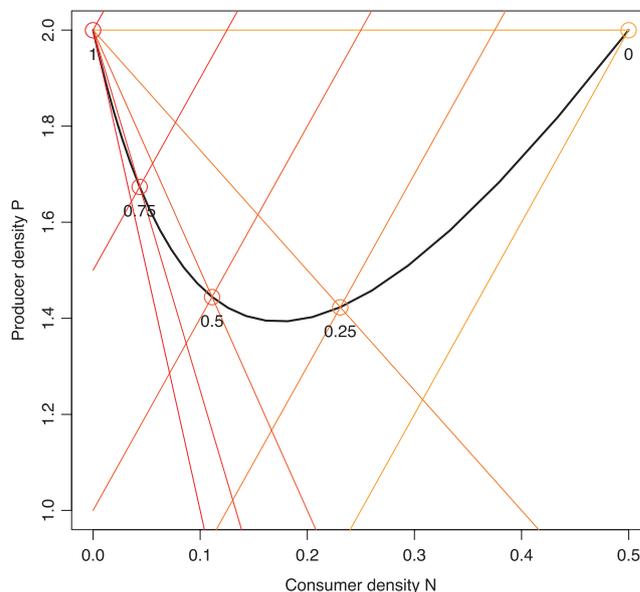


FIGURE 1 The system isocline and the consumer isocline for different values of consumer mortality h , from light ($h=0$) to dark ($h=0.8$). At the intersection of the two isoclines is the equilibrium, represented by an open circle. The black line connects the equilibria for all values of h between 0 and 1. Producers are not harvested ($b=0$). Other parameter values are $a=0.5$, $m=2$, $P_0=2$ en $q=0.1$.

results presented here are still qualitative in nature, but it should be possible to calibrate the models, i.e., estimate the parameters for a specific situation, just like the World Bank has calibrated the Pella–Tomlinson model for global fisheries. The question naturally arises how much value should be attached to the results of such extremely simple models. Although in fisheries science these simple models have proven their practical value, many scientist tend to move to much more complex models. An example of such a complex model is the so-called European Regional Seas Ecosystem Model (ERSEM), which was originally described by Baretta et al. (1995), but of which several versions are now in circulation, including those by Vichi et al. (2007) and van der Molen et al. (2018). It is usual to link this ecosystem model to the results of a complex 3-D hydrodynamic model. The ‘General Estuarine Transport Model (GETM)’ is often used for this and the combination of both models is then abbreviated as GETM-ERSEM (van der Molen et al., 2018). The 0-D ecosystem model ERSEM describes the producers, consumers and decomposers with about 20 functional groups. The model only contains herbivorous consumers and therefore excludes carnivores. Because carnivores play an important role in the marine ecosystem, calls for even more complex so-called end-to-end models are regularly heard (Bossier et al., 2020, 2021; Fulton, 2010). A fish larva of a few millimeters in size naturally behaves very differently from an adult fish with a length of many decimeters or even meters, and it is

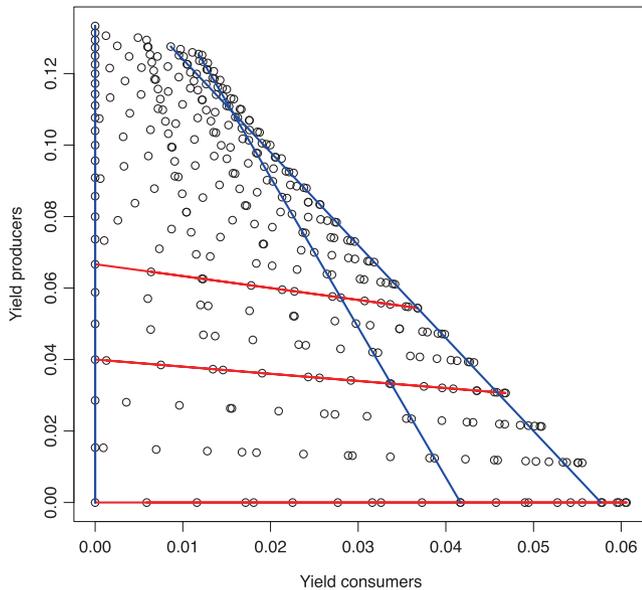


FIGURE 2 Consumer versus producer harvest. Producer mortality equal to $b=0$, $b=0.1$, and $b=0.2$ is specifically shown by blue lines (from left to right). Constant consumer mortalities shown by red lines.

therefore preferable to include the length distribution of these groups in the model structure, which naturally leads to extremely complex models with often dozens of state variables, in which all kinds of simplifications are applied to keep things manageable (Maury & Poggiale, 2013).

Levins (1966) characterizes models according to their degree of precision, realism and generality. He argues that all three criteria can never be met simultaneously, hence a model cannot be precise, realistic and general at the same time. Theoretical ecologists, including Levins himself, like to work with models that do not have to be very precise and where it is sufficient to describe the relations in general terms, for example, that the instantaneous growth rate of the producers follows a curve that changes with increasing light quantity. At low light the curve rises steeply, then the rise gradually levels off and after reaching an optimum, growth rates decreases with increasing light. Different analytical methods, including graphical ones, can then be used to qualitatively characterize the system behavior. More mathematically minded ecologists, on the other hand, like to work with precise models that are also generally valid and place less value on realism. Classic examples of this approach are the Lotka–Volterra models and the models described above, including the Verhulst and Schaefer models. Finally, more practically-oriented applied ecologists prefer to sacrifice general validity and develop models that are as realistic as possible and precise for a specific system. The GETM-ERSEM developers or the proponents of end-to-end models fall into this group.

At first sight, the more realistic models seem to be the most suitable for predicting the consequences of changing human interventions on the ecosystem. Nevertheless, there are some doubts to be raised about this. The models are so complex in terms of the number of state variables and parameters and the computation times are so long, that careful and systematic research into the consequences of uncertainty in parameter values or model structure is very difficult to perform. This type of model is certainly able to mimic the always very limited amount of ecosystem data that are available, but it is impossible to obtain any certainty whether the model can also make adequate predictions under changing circumstances. The question also remains how robust the model predictions are when slightly different choices of model structure are made. It is all the more problematic that such question is hardly answerable because the choice for a particular model structure usually takes place on an ad-hoc basis and is rarely based on a solid theoretical foundation.

The major changes that await when large scale mariculture is established ask for an adequate set of model instruments able to calculate the consequences for the carrying capacity of the ecosystem. We make a plea for the use of a diversity of model approaches, in which all ecosystem models are given a theoretical foundation that is as solid as possible. One of us (van der Meer et al., 2022) recently contributed to the further development of an ecosystem model (Kooijman, 2010; Kooijman & Nisbet, 2000; van der Meer et al., 2022) that is fully based on the Dynamic Energy Budget (DEB) theory, which is framed in a set of well-defined assumptions about the uptake, allocation, and use of energy and mass by individual organisms, and whose predictions at the individual level are consistent with a multitude of stylized facts about ecological energetics (Sousa et al., 2008, 2010). The model forms an intermediate link between the less realistic models of the producer-consumer type as introduced above and the extremely complex models such as GETM-ERSEM. In the coming years, it would be good to further develop the various model approaches alongside and with each other, and to clarify what are precisely the strengths and weaknesses of each approach. Blind faith in one type of approach should be avoided.

3 | MANIPULATE FOOD WEB STRUCTURE

According to FAO global estimates, marine capture production was substantially steady since the late 1990s and the vast majority of stocks are fully exploited or overexploited (FAO, 2020). Apart from increasing the exploitation of the few remaining underexploited stocks, or

expanding fisheries towards so far unexploited resources, as discussed in the following sections, another option would include to manipulate the entire food web structure via removal of high trophic level species, which could allow an increasing exploitation of low trophic level species. Ecological theory predicts that in ecosystems the productivity depends on the overall primary production and that energy flow to higher trophic levels diminishes with trophic efficiency at each step in the food chain. Under this assumption the total catches in a given ecosystem (C_{tot}) could be estimated with the following equation:

$$C_{\text{tot}} = \alpha P E^{L-1}, \quad (12)$$

thus being total catches a function of net primary production P , trophic efficiency E , the average trophic level of the catches L , and a scalar α that represents the availability within the local conditions and is generally set to 15–20% (Link & Watson, 2019; Stock et al., 2017).

The role of primary production as a basic limiting factor for fisheries production is widely recognised (Chassot et al., 2010; Conti & Scardi, 2010; Stock et al., 2017). However, since 1969, the idea that primary production could fully account for variation in fisheries catches across ecosystem was challenged (Ryther, 1969). Many studies have tried to address this issue testing the role played by different potential explanatory factors with the aim of understanding the ecological processes and human drivers sustaining high fisheries. Most of the studies broadly grouped ecosystems according to their location and productivity and considered both the effects of primary production and other environmental variables, as well as factors that could be manipulated by humans, such as fishing effort and the mean trophic level of the catches. Results mostly showed the relative predominance of different control in different conditions. For instance, McOwen et al. (2015) showed that bottom-up control predominates within productive, overfished regions, while top-down control plays a major role in relatively unproductive and under-exploited areas. These results were basically confirmed in further studies that pointed out the need for understanding these ecological processes for adequate management of fisheries. In particular, Ye and Carocci (2019) remarked that the factors that could be manipulated by humans to increase fisheries productivity were mainly fishing effort and the trophic level of the catches. These authors also noted that potentially the reduction in trophic level of the catches, basically described as fishing down the marine food web (FDFW) by Pauly et al. (1998), could open new fishing opportunities by releasing predator pressures on low trophic levels and consequently increasing their biomass. Whilst some studies clarified that the FDFW as shift from higher to lower

trophic level species was not the only ecological process determining the reduction of the trophic level of the catches, see for instance the concept of fishing through the marine food web (Essington et al., 2006; Sethi et al., 2010), the idea of releasing top-predator pressures on ecosystems to increase low trophic level fisheries productivity still seems a valid option to be explored.

The option of culling top predators (e.g., marine mammals) has gained traction since the late 1970s when it became apparent that many commercial fish stocks were seriously depleted by fishing and that natural predation on some target species was competing with fisheries harvesting (Boyd, 2001; Yodzis, 2001a, 2001b). All this stimulated the establishment of culling practices, in particular on marine mammals (cetaceans and pinnipeds). However, beyond the ethical and biodiversity related issues, the efficacy of such practice is debated. Indeed, the analyses conducted by Bowen and Lidgard (2013) on actual data showed that predator removal is not always effective in increasing the productivity of target prey populations. On the contrary, they may have unintended consequences for target species, other predator and prey species. Such condition is possibly determined by the complexity of food webs, where the presence of indirect effects could make the prediction of the direction and magnitude of response to culling unreliable and, in any case, affected by a large degree of uncertainty associated with the uncertainty in the parameters of multispecies models (Yodzis, 2001b). It has been claimed that large marine mammals stimulate marine primary production by replenishing nutrients in the euphotic zone (Roman & McCarthy, 2010).

An example of the potential of such ecosystem manipulation through harvesting is given by Szuwalski et al. (2017) who made an assessment of the very high catches in the East China Sea, i.e., one of the most productive ecosystems in the world. According to the authors the reported catches can be approximated using an ecosystem model that allows for trophic cascades, that is the depletion of predators and consequent increases in production of their prey. This would be the world's largest known example of marine ecosystem 'engineering'. However, whilst ecological theory can justify such intense catches in the area, associated ecological costs must be considered. Indeed, Andersen and Gislason (2017) remarked that the simulated high fishing pressure (up to 95% of the standing stocks are estimated to be caught every year) makes individual fish populations highly susceptible to crashes. Thus, the high catches obtained in the East China Sea and similar heavily exploited systems 'come at the price of an ecosystem that is not only impoverished in terms of biodiversity (e.g., loss of top predators) but is also increasingly fragile. It is therefore questionable whether the high production can be sustained' (Andersen & Gislason, 2017).

Hence, the idea of ecosystem manipulation raises concerns about possible shifts in ecosystem structure (e.g., jellyfish outbreaks), and about possible negative effects on components with conservation value, like top predators that could present high vulnerability to fishing effects due to their inherent life history traits, along with the need for addressing the overall profitability of fisheries in the long run.

In this light, exploiting fisheries resources under a multispecies pretty good yield approach (see Rindorf et al. (2017)) would represent a viable option to reduce at least parts of these concerns, and possibly ensure a high multispecies productivity, as also proposed by Worm et al. (2009). Still the limits to the appropriation of primary production by fishing are to be considered as an ecological boundary. In this regards, a range of indexes has been proposed to address whether or not fisheries in marine ecosystems is causing ecosystem overfishing (Link & Watson, 2019). Such tools could allow embedding considerations on the physical and biological conditions of the ecosystem into the tactical fisheries management that is still predominantly single-species oriented (Skern-Mauritzen et al., 2016).

However, the capability to understand the drivers and limits to fisheries productivity across ecosystems is still limited and its thorough understanding could guide setting options for enhancing seafood production while preventing the compromising of both ecosystem structure and functioning, and biodiversity. In this context, it emerged that better addressing ecosystem-level variations in the energy flows in and between the pelagic and benthic domains can be necessary (Stock et al., 2017). Such an approach could also allow for a better distinction of exploitation of the two domains, as well as to highlight where highest potential for further increase in seafood production might still be present in different ecosystems. For instance, enhancing seafood production from the benthic system could be a potential approach, but disturbing the seafloor through industrial bottom trawl fisheries and harvesting benthic species, could have negative direct and indirect impact on exploited stocks and overall productivity by affecting for example, C-fluxes and NPP (Sala et al., 2021; Stock et al., 2017). Marine sediments are the largest pool of organic carbon on the planet (Sala et al., 2021). Based on satellite information, Sala et al. (2021) have estimated that 1.3% of the global ocean is trawled each year. Trawling induces increased carbon metabolism in the sediment which is estimated to be equivalent to 15–20% of the atmospheric CO₂ absorbed by the ocean each year, which is comparable to carbon loss in terrestrial soils caused by farming (Sala et al., 2021). The increase in CO₂ in the water column and sediment pore waters may have complex and hardly predictable effects

on biodiversity, marine carbon cycling, and primary productivity (Sala et al., 2021).

Overexploitation of benthic communities could have also direct and indirect impact on ocean productivity. Benthic species provide important marine ecosystem functions (such as bioturbation, nutrient regeneration). Deposit-feeders, for instance, improve mineralization of organic matter through bioturbation, feeding, and ventilation activities promoting nutrient fluxes between water and sediment, favouring the oxygenation of the sediment, and enhancing organic matter mineralization and recycling of nutrients (Heilskov & Holmer, 2001). Moreover, benthic primary production has an important effect in the global ocean production. Krause-Jensen and Duarte (2016) have suggested that macroalgae, the dominant primary producers in the coastal zone, could represent an important source of the carbon sequestered in marine sediments and the deep ocean. Macrophytes were recently estimated to provide 1.5 Pg C per year, or about 3% of global net primary production NPP (Krause-Jensen & Duarte, 2016). In food web models, it is therefore important to consider direct (reduction of benthic species) and indirect effect (loss of key functions) on benthic ecosystems and test, for instance, sensitivity of models to inclusion of benthic NPP scenarios as suggested by Stock et al. (2017).

4 | SUSTAINABLE EXPLOITATION OF THE MESOPELAGIC ZONE

Due to the global food demand and questions on how much food, we can expect the ocean to sustainably produce (Branch et al., 2010; Costello et al., 2020; Garcia & Rosenberg, 2010; van der Meer, 2020). There is an increasing interest in the potential for exploitation and harvesting of marine mesopelagic resources for use in production of fishmeal, oil, nutraceuticals as sources for dietary supplements, and in relation to bio-prospecting and production of pharmaceuticals (Grimaldo et al., 2018, 2020; Hidalgo & Browman, 2019; Paoletti et al., 2021; Standal & Grimaldo, 2021; Wright et al., 2020). Proposals are emerging for fishery (Grimaldo et al., 2020; Paoletti et al., 2021), but despite increasing research in the field, the scientific understanding of the mesopelagic zone and communities is extremely limited and there are considerable gaps in our scientific knowledge of the biological and biogeochemical importance, dynamics and processes of the mesopelagic system (Glover et al., 2018; Hidalgo & Browman, 2019; St John et al., 2016; Sutton et al., 2020; Wright et al., 2020). A comprehensive investigation of the potential target and by-catch stocks, food web interactions, and effects on biodiversity is necessary to assess whether such exploitation is at all ecologically precautionary and sustainable, also

in the long-term (Branch et al., 2010; Gascuel et al., 2016; Glover et al., 2018; Hall, 1999; Hidalgo & Browman, 2019; Hilborn et al., 2015; Paoletti et al., 2021; Proud et al., 2018; St John et al., 2016).

4.1 | Biomass estimates and biological sustainability of potential exploitation of single target stocks

The mesopelagic zone hosts significant fish stock biomass. Some of the most abundant families are the Myctophidae and Sternoptychidae (Catul et al., 2011; Davison et al., 2015; Grimaldo et al., 2020; Irigoien et al., 2014; Valinassab et al., 2007). The myctophid family consists of several hundred species of small (less than 20 cm) fish, which are widely distributed; and species of the two families have very high abundances in the global oceans (Catul et al., 2011; Davison et al., 2015). Preliminary investigations suggest that there may be an economic viable potential for capture fishery exploitation of a few of these species, specifically the Myctophid *Benthoosema glaciale* (Glacier lanternfish) and the Sternoptychid *Maurolicus muelleri* (Mueller's pearlside; FAO, 1997, 2001, 2014; Gjørseter & Kawaguchi, 1980; Grimaldo et al., 2020; Paoletti et al., 2021; St John et al., 2016; Valinassab et al., 2007). Both species are small (50–80 mm) and perform extensive diel vertical migration between the mesopelagic and epipelagic zone (Dypvik et al., 2012; Grimaldo et al., 2020; Hudson et al., 2014; Ishihara & Kubota, 1997; Paoletti et al., 2021; Staby & Aksnes, 2011; Sutton et al., 2008). The pearlside is a short lived species (4–5 years), but only a small fraction of the population reaches the age of 3 years (Gjørseter, 1981), and in some areas only age 0 and 1 are observed. However, even though abundant, the genetic composition, stock identities, and stock delineations of these species and families as transboundary resources are unknown, as well as the full stock spatio-temporal distribution and horizontal migration patterns, which is a prerequisite to estimate stock specific MSY reference levels.

Global estimates along the continental slopes of mesopelagic fish biomass have so far varied considerably from very high values around 10–20 billion tonnes to relatively low estimates of 1–2 billion tonnes based on acoustic surveys and food web models (Anderson et al., 2005, 2019; Gjørseter & Kawaguchi, 1980; Hidalgo & Browman, 2019; Irigoien et al., 2014; Jennings & Collingridge, 2015; Proud et al., 2017, 2019; Sigurdsson et al., 2002; Sobradillo et al., 2019; Standal & Grimaldo, 2021) introducing significant scientific uncertainty about the actual abundance and available biomass for potential harvesting. In addition, the abundance estimates have shown high spatial and temporal variability (Anderson et al., 2005; Grimaldo et al., 2020;

Proud et al., 2019; Standal & Grimaldo, 2021). Extensive spatio-temporal variability in size structure and production of mesopelagic fish have been observed in global scale transects (Fock & Czudaj, 2019) inducing high variability in biomass estimates which are dependent on the size structure. Furthermore, catch rates have varied significantly between years in recent experimental fisheries conducted so far under an ongoing EU H2020 research project (www.meeso.org; Standal and Grimaldo (2021)). Plankton nets and midwater trawls are, despite their small mesh size, very selective. Because of the different catchability they do not sample the whole mesopelagic community, i.e., not all species and size groups are caught in surveys and experimental fisheries (Bjordal & Thorvaldsen, 2020; Grimaldo et al., 2020; Kaartvedt et al., 2008, 2012; Standal & Grimaldo, 2021). Hydroacoustic survey abundance estimates may also be biased because of extensive vertical migration, high variability in acoustic target strength and less robust Target-Strength-Fish-Length-relationships, as well as acoustic resonance problems (Grimaldo et al., 2020; Standal & Grimaldo, 2021). All this introduces high uncertainty in abundance estimates of available mesopelagic fish biomasses for potential commercial exploitation.

Assessment of mesopelagic fish abundance has so far been based on acoustic research survey estimates and food web models, while a few have used environmental variables as predictors of biomass (Anderson et al., 2005, 2019; Blanluet et al., 2019; Davison et al., 2015; Gjørseter & Kawaguchi, 1980; Grimaldo et al., 2020; Hidalgo & Browman, 2019; Irigoien et al., 2014; Jennings & Collingridge, 2015; Khodabandeloo et al., 2021; Proud et al., 2017, 2019; Sigurdsson et al., 2002; Sobradillo et al., 2019; Standal & Grimaldo, 2021), but they have not distinguished and divided between different species and stocks. It has even been very difficult to distinguish between different trophic levels (e.g., planktivorous and piscivorous fish) in the mesopelagic survey abundance estimates. One attempt has been made to estimate spawning stock biomass of an important myctophid fish in the China Sea from daily egg and larvae production (Sassa, 2019). Accordingly, abundance estimates and Total Allowable Catch (TAC) settings are in general not available for individual stocks for the relevant mesopelagic fish species (Standal & Grimaldo, 2021), upon which MSY and Precautionary Approach (PA) reference levels and associated harvest control rules and management plans need to be estimated and established for potential biological sustainable exploitation of the different fish stocks, according to the United Nations Convention of the Law of the Sea UNCLOS (Standal & Grimaldo, 2021; UN, 1982), see also below under the Governance section.

Data limited stock assessment methods and associated estimation of stock specific MSY reference levels are not

adequately investigated, conditioned and implemented for mesopelagic fish stocks. However, extensive research is ongoing for implementing length based stock assessment methods (Kokkalis et al., 2017; Mildenerger et al., 2017, 2020) for *B. glaciale* and *M. muelleri* in the North Atlantic (e.g., EU H2020 Research Projects, www.meeso.org), also aiming at estimating the required data on population specific individual growth, stock production and natural mortality parameters. Data limited production models using catch data cannot be used as such data are not available because there is no ongoing fishery (Mildenerger et al., 2020). The same EU projects also use broader ecosystem and trophodynamic models aiming at assessing the mesopelagic fish stock biomasses, but also these approaches are not stock specific and still rather uncertain.

Integrating broader ecosystem effects, ecosystem resilience, and environmental impact assessments of potential fishery is necessary. Ecologically sustainable harvesting of mesopelagic resources does not only need to involve sustainability criteria according to stock specific MSY and PA reference levels (UNCLOS, 1982, and several later conventions). It very much also needs to consider ecosystem based criteria and indicators involving food web interactions, ecosystem dependencies and functioning, trophic links and the role in vertical transport of energy (carbon) in the sea, and not least in relation to sustain marine biodiversity. Though the fishery would focus on some of the most abundant mesopelagic fish species as *B. glaciales* and *M. muelleri*, and stock assessment would be provided for stocks under these species enabling setting quotas following the MSY and PA principles, such a fishery will likely not be sustainable according to broader ecosystem impacts of the fishery as highlighted below.

4.2 | Wider ecosystem effects

The mesopelagic layers represent high biodiversity and consist of aggregations of several species from different taxa. Exploitation will for sure involve mixed fishery and will need very large fishing gears with small trawl mesh sizes. The selectivity of such trawls will be poor, and extensive by-catch of many species can be expected, many of which will likely be highly vulnerable, with negative effects on biodiversity. To develop very large, small meshed trawls that only target the target stocks (to guarantee sustainable fishing, and also to secure that the catch will provide high-quality oils and proteins) and release the by-catch of unwanted species and size groups, involves very extensive challenges (Grimaldo et al., 2020). Such fishing gears and methods have not been developed yet. There will inevitably be broader and wider ecosystem effects from mesopelagic fishery on by-catch species and

stocks including their biological interactions with other trophic levels, and so far no specific by-catch rules are elaborated and implemented (Gilman et al., 2014; Standal & Grimaldo, 2021).

The mesopelagic community provides several essential ecosystem services, and plays, with its extensive biomass and production, a critical role in marine food webs and in the global carbon circle. Because of the daily vertical migration of mesopelagic fishes through the water column, with upward migration during dusk into the epipelagic zone to feed and downward migration during dawn, and the high significance of their biomass in the oceans, they are a critical component of the global carbon exchange between the epipelagic and mesopelagic food webs (Anderson et al., 2019; Costello & Breyer, 2017; Davison et al., 2013; Gartner, 1993; Hays, 2003; Hudson et al., 2014; Irigoien et al., 2014; Ishihara & Kubota, 1997; Proud et al., 2017, 2018; Robinson et al., 2010; Sutton et al., 2008). Such massive diel vertical migration transfers material, e.g., carbon, and energy by active transport between the productive surface waters and the deep, less productive water layers (Costello & Breyer, 2017; Davison et al., 2013; Dypvik et al., 2012; Irigoien et al., 2014; Klevjer et al., 2016; Trueman et al., 2014; Willis & Pearcy, 1982).

Mesopelagic fishes are intensively involved in transporting and mediating carbon from the epipelagic layers of the ocean to be sequestered in deep ocean sea floors and water layers (Davison et al., 2013; Hudson et al., 2014) by grazing on primary consumers also having extensive diel vertical migration, and being important prey for many predatory and higher trophic level fish species also of commercial fishery importance (Catul et al., 2011; Choy et al., 2013, 2016, 2017; Davison et al., 2013; Hernández-León et al., 2020; Standal & Grimaldo, 2021). This energy transport has been called the “carbon pump” (Jin et al., 2020; Luo et al., 2020). The links to lower trophic levels of mesopelagic fish are considerably better known than the predation on mesopelagic fish and their role as key prey, see Hidalgo and Browman (2019) reviewing this in papers of a special issue in ICES Journal of Marine Science. Furthermore, there are also extensive gaps in our knowledge on the important role that the mesopelagic communities and fish seems to play in climate regulation in relation to the carbon pump (Costello & Breyer, 2017; Grimaldo et al., 2020; Hidalgo & Browman, 2019; Wright et al., 2020; Yool et al., 2013).

How vulnerable and resilient the marine ecosystems are to harvesting of the mesopelagic community and organisms in relation to carbon transport and sequestering as well as the ecosystem role of the mesopelagic organisms and community in the marine ecosystems are currently intensively investigated, but results are so far inconclusive. Because of the ecosystem functions,

ecosystem services and biological interactions of the mesopelagic fish, potential exploitation and mismanagement could very likely have significant wider ecosystem impacts and consequences involving long recovery periods (Proud et al., 2019; Standal & Grimaldo, 2021; Wright et al., 2020), such as a reduction of the resilience of mesopelagic communities and marine ecosystems, and change of carrying capacities. Summing up, the risk for disruption of critical life-support systems necessitates strong application of the PA (UN, 1982) on a wider ecosystem level and early action to ensure effective management (Proud et al., 2019; Standal & Grimaldo, 2021; Wright et al., 2020). Furthermore, it is critical to have additional knowledge and understanding of the spatio-temporal variability and uncertainty in estimation of the mesopelagic biomass to assess the degree to which it is possible to exploit it sustainably (Grimaldo et al., 2020; Hidalgo & Browman, 2019; Proud et al., 2019; Standal & Grimaldo, 2021; Thorhaug et al., 2020).

5 | HARVESTING LARGER ZOOPLANKTON SPECIES

Recently zooplankton fishing attained much attention in fisheries management and ecology, but the topic is not completely new. The idea of exploiting zooplankton was already put forward in the 19th century by Herdman (1891) and later reiterated by Clarke George (1939), Graham (1941) and Hardy (1941). They pointed to the opportunity of considering copepods and other crustacean zooplankton as potential food sources and also mentioned the need to overcome technical constraints for efficient exploitation. In 1978, Omori (1978) reported that about 20 zooplankton species belonging to crustaceans (copepods, mysids, euphausiids, sergestids) and cnidarians (Scyphomedusae) were actively exploited worldwide, with associated landings of about 210 thousand tonnes.

Zooplankton fisheries have not shown strong increases in landings over the last decades. However, given the presence of species with high density and standing stock biomass, the option of substantially increasing their exploitation to sustain worldwide seafood production could be considered. These species include, in particular, the Antarctic krill *Euphausia superba*, belonging to the euphausiids and exploited in the Southern Ocean, and the copepod *Calanus finmarchicus*, which is exploited in the North Atlantic. *E. superba* is spread around Antarctica and represents a typical prey for whales and penguins; its biomass, in the Southern Ocean, reaches about 200–379 million tonnes (Atkinson et al., 2009; Nicol & Brierley, 2010).

The commercial fishery for Antarctic krill was initiated in 1961/62 by two research vessels from the USSR and developed into a multi-vessel multi-nation fishery in the early to mid-1970s. Krill fisheries faced two major drops in 1984 and 1992–1993 due to environmental and political issues (CCAMLR Secretariat, 2022c). Since then landings kept increasing and were from 2010 onwards largely driven by catches from Norway, in particular in the Atlantic-Antarctic Area 48. Krill is currently exploited by fleets belonging to a few countries (Norway, China, Republic of Korea, Chile, Ukraine) with total landings of about 400 thousand tonnes (CCAMLR Secretariat, 2022b, 2022c). Vessels may use a continuous fishing system which transports krill from the codend of the net to the vessel while the vessel is trawling. Pumps may also be used to clear nets hauled alongside the vessels.

In Antarctica, the exploitation of *E. superba* is regulated by the Commission for the Conservation of Antarctic Marine Living Resources CCAMLR, which sets precautionary catch and trigger limits that are currently around 9% (i.e., about 5.6 million tonnes per year) and 1% (i.e., 620 thousand tonnes per year) of species' local biomass in Area 48, which was estimated at 60.3 million tonnes during the CCAMLR-2000 Survey (CCAMLR Secretariat, 2018). Conservation measures adopted by CCAMLR address the wider environmental considerations on a spatial basis, providing a spatial repartition of precautionary limits across management areas (CCAMLR Secretariat, 2022a). Despite the relatively low (yet increasing) values of landings, recent concerns have been raised regarding the indirect effects of krill exploitation on some vulnerable species, such as penguins, also in relation to climate change. Watters et al. (2020) identified a mismatch between quota limitation and spatio-temporal effort distribution resulting in a negative prognosis for krill predators like penguins. Using multi-decadal monitoring data and modeling, they showed that expected penguin performance was reduced when local harvest rates were high; an effect comparable in magnitude to the effect of poor environmental conditions. Similar results were obtained by Krüger et al. (2021), who reported that catches in combination with climate change (warm winters and low sea ice associated with negative Southern Annular Mode values) increased the probability of negative population growth rates, implying a decrease in population size of two Antarctic penguin species in the following year. Additional evidence of a reduction in krill CPUE and a higher spatial concentration of fishing (Santa Cruz et al., 2022) further supports the need for improving fisheries management and considering more refined spatial scales. Such a management approach should be informed by better science and understanding of

krill ecology (e.g., behaviour, movement and relation with oceanographic conditions) and the role of krill as prey of the most vulnerable species (Prado-Cabrero & Nolan, 2021; Trathan et al., 2022).

Another major concern on krill exploitation emerged recently in relation to the lack of understanding of the possible impact of krill fishing on nutrient dynamics and the carbon sink, given the important role of krill in biogeochemical cycles. Indeed, as pointed out by Cavan et al. (2019), its large body size, high biomass and swarming ability, coupled with physiological traits such as large faecal pellets and excretion into nutrient-limited waters, means that *E. superba* has a prominent role in the cycling of carbon, iron and ammonium in the Southern Ocean. However, the exact role of krill in the biogeochemical cycles is still largely unknown and there is a need to improve Antarctic krill biomass estimates and to determine residence depths and migration patterns, both in adults and larvae. Such knowledge, along with an enhancement of application of food-web models where low trophic level groups are better represented, could shed more light on the possible impacts of harvesting and support better fisheries management (Cavan et al., 2019).

Cautions and concerns about the exploitation of larger zooplankton species emerge also in relation to the copepod *C. finmarchus*, which is exploited in the Northern Ocean. This species plays a key role in the energy transfer from primary producers to higher trophic levels such as herring, capelin, and cod larvae (Skjoldal, 2005). Its seasonal and vertical distribution is influenced by climate-driven changes in the physical and biological oceanographic features, with major implications for the flow of energy and nutrients (Kvile et al., 2022). Estimated production equals 190–290 million tonnes per year and the species has a standing stock biomass of about 30 million tonnes. *C. finmarchus* is also considered an indicator of climate change; a decrease in abundance over the last few decades in the North Sea affected total forage fish biomass and fisheries yield (Clausen et al., 2018). Catch quota are now set under the Norwegian Management plans that account to 254 thousand tonnes, of which 3 thousand tonnes can be caught in shallow water. In the Norwegian waters, copepod fishery started around 1960 and kept an experimental stage till at least the mid 1970s, with about 20 to 50 tonnes per year of catches (Wiborg, 1976). Current landings are, still, rather limited as compared to quota and reached 352 tonnes in 2019. Recent studies have addressed some aspects of the possible ecosystem effects of *C. finmarchus* exploitation indicating that the current quota should be sustainable. Yet, they also identified the need for further scientific data, on, for example, food

web links and fishing impact on larvae, fish eggs and by-catch species. Such data would reduce uncertainty in model-based assessments (Hansen et al., 2021).

Overall, what emerges is that despite all studies conducted so far on the sustainability of zooplankton harvesting as source of sustainable seafood, many gaps of knowledge have not been filled in. Indeed, a range of questions need to be addressed by experiments and modelling in order to ascertain direct and indirect effects of zooplankton fishing, not just on the exploited zooplankton stocks, but also on other commercial and vulnerable or sensitive species, for example, those feeding on zooplankton. Possible adverse effects on all stages (eggs, various larval stages, juveniles, adults) should be studied, which requires a more accurate understanding of the species' ecology. Ecosystem effects—including those on biogeochemical cycles—should also be considered. Such studies would help in setting quota, which are now merely determined by applying a precautionary principle, and providing more accurate spatial management rules. Given the current concern on climate change effects, particularly at high latitudes, any prediction or assessment would also need to incorporate the new climatic scenarios.

In addition to the issue of the sustainability of expanding zooplankton fisheries, another associated scientific question needs to be addressed. To what extent can zooplankton catches really enhance seafood production, if the catch is only used as feed for aquaculture production? To answer this question, the efficiency of energy transfer in natural marine ecosystems (e.g., considering the exploitation of predators of zooplankton as sources of protein) should be compared with the efficiency in aquaculture systems.

At present, both Antarctic krill and *C. finmarchus* have a further recognized value for human consumption and in aquaculture, being used in the form of feed additive, given they accumulate oils rich in eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), see, for instance, the review of Eysteinnsson et al. (2018) on *C. finmarchus*. Recently, the added value of such foods for the production of nutraceuticals for human diet has been challenged by Prado-Cabrero and Nolan (2021) for two reasons. First, enhanced consumption of EPA and DHA would significantly benefit only specific groups and not the general human population. Second, the removal of key players in the food web could affect bio-geochemical fluxes and possibly climate regulation (Prado-Cabrero & Nolan, 2021). Accordingly, the authors suggest the use of other sources of EPA and DHA to supply nutraceuticals for human consumption. Such concerns need to be alleviated and informed by science prior to a full, if any, development of zooplankton fisheries.

6 | EXTENSIVE LOW-TROPHIC AQUACULTURE

Extensive or non-fed marine aquaculture uses no or minimal resource inputs and differs from intensive aquaculture that entirely relies on supplementary feed. Aquaculture of low-trophic organisms, such as macro-algae (seaweed) or bivalves, is usually extensive. Macro-algae are primary producers and they take up the nutrients they require such as nitrogen and phosphorus directly from the natural ecosystem. Bivalves are mainly herbivorous and detritivorous, and they feed prominently on natural phytoplankton and detritus. The terms extensive and low-trophic should not be confused, and the culture of low-trophic micro-algae in land-based fertilized basins or the culture of herbivore finfish fed with agricultural products can be considered as a form of intensive aquaculture, which does not depend upon the natural primary productivity of the sea. Low-trophic organisms can also be used in a multi-trophic aquaculture setting where they may utilize the waste from the high-trophic finfish. The obvious advantage of human consumption of extensive low-trophic aquaculture products compared to captured or cultured carnivore finfish is because ‘the inherent inefficiency of trophic transfers through food webs means that the higher the trophic level of animal eaten by humans, the more ecosystem energy is embodied in its production’ (Cottrell et al., 2021).

6.1 | Seaweed

Aquaculture at the lowest trophic level, i.e., the primary producers, is dominated by the cultivation of brown and red seaweeds in Asia. The most important species for human food usage are *Saccharina japonica*, *Undaria pinnatifida*, *Pyropia* spp., and *Sargassum fusiforme* (Buschmann et al., 2017). In 2019 global seaweed cultivation reached 34.7 million tonnes, from which 34.5 million tonnes were produced in Asia (Cai et al., 2021; FAO, 2021). Wild collection was only 1.1 million tonnes worldwide. Most seaweed production in Eastern Asia is consumed directly as human food, in other regions seaweed consumption is low (Cai et al., 2021). Comparing these figures with, for example, the production of terrestrial cereals, which is about 3 billion tonnes (<https://www.fao.org/faostat/en/#data/QCL>; <https://ourworldindata.org/agricultural-production>), shows that presently seaweeds produce only a minor fraction of the global supply of biomass used by humans (Buschmann et al., 2017). Although off-shore cultivated seaweeds could potentially provide a sustainable alternative source of biomass for food and feed, that can release the pressure on arable land and fresh water resources, several basic questions have to be answered

(Buschmann et al., 2017); first of all, the question on the nutritional value, digestibility, and bio-availability of seaweed compounds for humans, livestock, poultry, and fish (Buschmann et al., 2017; Saleh, 2020; Wells et al., 2017). Wells et al. (2017) emphasized that collaborative approaches between among others phycologists and nutritional and medical groups are required to study how algal nutritional and functional constituents interact in human metabolism. The same probably holds to answer the question to what extent seaweed components can be used as feed in fish farming. The second question asks what the carrying capacity of the natural marine system is for seaweed production and how it interacts with other forms of aquaculture, fisheries and other components of the marine foodweb, as was already pointed out in Section 2.

Assessing the carrying capacity of a coastal ecosystem for seaweed production requires at least a coupled biogeochemistry-hydrodynamics model in which a seaweed growth model is incorporated. The earliest seaweed growth models did not consider nutrient availability (Duarte & Ferreira, 1997; Seip, 1980), but more recent work included nutrient availability as a steering variable (Aveytua-Alcazar et al., 2008; Broch & Slagstad, 2012; de Guimaraens et al., 2005; Duarte et al., 2003; Lavaud et al., 2020; Ren et al., 2014; Shi et al., 2011; Zhang et al., 2016). Several studies combined the seaweed growth model with a coupled biogeochemistry-hydrodynamics model in order to arrive at predictions of potential production. Predictions ranged from about 200 g DW m⁻² year⁻¹ for the Oosterschelde (The Netherlands) to 300–500 g DW m⁻² year⁻¹ for Sungo Bay, China (Duarte et al., 2003; Shi et al., 2011). These figures are much lower than the predictions for the Norwegian coast, which ranged from 2250 to 3000 g DW m⁻² year⁻¹ (Broch et al., 2019). These latter production figures are much higher than net primary production estimates for the natural phytoplankton in the same area, which are around 70 g DW m⁻² year⁻¹ (Hansen & Samuelsen, 2009). Lehahn et al. (2016) estimated the global potential of offshore seaweed farming and arrived at a biomass production of 10¹¹ dry weight tonnes per year over a surface area of about 10⁸ km², which is equivalent to 1000 g DW m⁻² year⁻¹. In a recent review on seaweed production, Buschmann et al. (2017) warned that ‘great caution should be exercised as some results might be rather unrealistic and what was perceived as high potential may not become a practical reality’.

6.2 | Bivalves and other herbivores

For understanding the carrying capacity of the ecosystem (in terms of MSY) for extensive aquaculture of organisms occurring one step higher in the trophic chain, i.e.,

herbivores or detritivores, similar models as discussed above are required, see, for example, Nunes et al. (2003). The culture of filter-feeding bivalves is well developed in coastal areas and worldwide about 15 million tonnes are produced each year, mainly clams, cockles, oysters, scallops, and mussels (Wijsman et al., 2019). China is by far the largest producer of cultured bivalves. Wild fishery of bivalves produces much less, about 1.6 million tonnes in 2018 (FAO, 2020) with a more or less steady production over the last decade (FAO, 2020). Production carrying capacity was reached or even exceeded in several inshore areas (Smaal & van Duren, 2019). The possibility of offshore culture is now explored in many areas around the world, e.g., the U.S. east coast, Tasmania, Great Britain, and Belgium (Mizuta et al., 2019; Villalba et al., 2022).

Deposit-feeding species may be of potential interest in aquaculture, although the production is still low compared to other low-trophic species such as molluscs and seaweeds. Many species of large holothurians, or sea cucumbers, have been overexploited in more than 70% of regions across the world (Félix et al., 2021; Gonzalez-Wanguemert et al., 2018; Wolkenhauer et al., 2010), and, for example, the Japanese spiky sea cucumber *Apostichopus japonicus* is classified as an endangered species by the IUCN (Mercier & Hamel, 2013). The decline of holothurians could have indirect cascading ecological consequences (Purcell et al., 2016; Wolkenhauer et al., 2010), including reduction of nutrient recycling, of biodiversity of associated symbionts, and of the transfer of organic matter from detritus to higher trophic levels (Purcell et al., 2016). Due to decreasing wild stocks and the growing demand for sea cucumbers, aquaculture of these organisms has emerged in the 1980s and developed since. Sea cucumber aquaculture represents a production of 178 thousand tonnes per year worldwide, with two main species farmed, *A. japonicus* and *Holothuria scabra* (FAO, 2018).

Polychaetes are also potential candidates for aquaculture. Cultured polychaetes have the potential for diversification of aquaculture, either as the main crop species or produced in integrated systems with other species (Albrektsen et al., 2022; Pombo et al., 2020). Polychaetes have been suggested as good candidates in Integrated Multi-Trophic Aquaculture systems (Fang et al., 2017; Galasso et al., 2020; Tsutsumi et al., 2005). The high level of polyunsaturated fatty acids measured in several polychaete species (Brown et al., 2011; Nederlof et al., 2019) makes it interesting to explore the feasibility of using polychaetes to convert waste from fish farms into alternative sources for fish diets and thus reduce pressure on wild fish stocks for animal feed. Polychaetes are already used together with shrimps in a multi-trophic aquaculture setting (Jerónimo et al., 2021).

7 | ECOLOGICAL ENGINEERING AND RESTORATION

To halt and reverse the degradation of ecosystems worldwide, the United Nations declared the period 2021–2030 as the UN Decade on Ecosystem Restoration (UN, 2020). Ecological engineering, which is an interdisciplinary approach integrating human, engineering, and natural sciences, can be used not just to actively restore disturbed ecosystems but also to develop new sustainable ecosystems that can provide a variety of ecosystem services (Mitsch & Jørgensen, 1989; Pioch & Souche, 2021). The notion of ecological engineering includes a technical design that is enriched with some ecological features (e.g., rough surfaces, holes, etc.) that can contribute to increased and faster colonization by benthic organisms, as well as provide suitable shelter for fish and other organisms, without increasing the costs of construction (Mitsch & Jørgensen, 1989; Pioch & Souche, 2021). It is also a main component of the more recent concept of Nature Based Solutions defined as ecologically sustainable options for protecting, restoring and improving coastal ecosystems (Eggermont et al., 2015; Seddon et al., 2021). By mimicking features of the natural habitat, ecological engineering can lead to an increase of carrying capacity and productivity of the marine ecosystem.

Originating in Japan in the middle of the 17th century, the use of marine ecological engineering solutions has strongly increased around the world since the second half of last century, often in connection with aquaculture. Apart from the aim to increase food production, marine ecological engineering has addressed a range of other societal challenges, such as climate change mitigation, economic and social development, improvement of coastal risk management and resilience, and mitigation of environmental degradation and biodiversity loss (Seddon et al., 2021). The interventions are diverse and of different level of complexity and range from, e.g., the protection and restoration of productive habitats such as seagrass and seaweed meadows, boulder fields, coral reefs, and shellfish beds (Bacci et al., 2019; Bayraktarov et al., 2016; Boström-Einarsson et al., 2020; Brears, 2020; Carranza & Zu Ermgassen, 2020; Fitzsimons et al., 2019; Liversage, 2020), the provisioning of new habitats for shellfish and other marine organisms (e.g., Seaman and Sprague (1991)), the greening of grey infrastructures by incorporating habitat features (Morris et al., 2018; Pioch & Souche, 2021; Strain et al., 2018) to even the creation of artificial deep water upwelling in waters where primary production is nutrient limited (Okano et al., 2011; Suzuki & Hashimoto, 2011).

Seagrass and seaweed meadows, boulder fields, coral reefs, and shellfish beds are essential habitats characterized

by great spatial heterogeneity, supporting high biodiversity and productivity and acting as nursery areas and foraging grounds for a variety of marine organisms. In addition to increased food provision, their restoration can provide further benefits such as carbon sequestration. For example, two hectares of restored seagrass meadow in Dale Bay (Pembrokeshire, UK) has been trapping up half a ton of carbon dioxide per hectare each year, and became a nursery area supporting around 160,000 fish and 200 million invertebrates (Brears, 2020). Similarly, the restoration of the Laeso Trindel cavernous boulder reef (Kattegat Sea, Denmark) which had been destroyed by boulder extraction for land constructions, led to a re-colonization of the reef region with macroalgae, provided improved habitat for large fish predators and for recruitment of wrasses, and resulted in an increased abundance of cod and saithe by a factor of 3–6 (Støttrup et al., 2014).

Artificial reefs, designed to provide additional substrates for settlement, shelter, and food for target species and hence increasing reproduction and reducing natural mortality, are widely constructed worldwide (e.g., Bortone, 2018; Bortone et al., 2011; Seaman & Sprague, 1991). Restored oyster reefs along the U.S. mid Atlantic coast supported a production from 15 to 50 oysters/m², in line with the oyster restoration success metrics previously established, with the stone reefs providing four times more oysters than reefs built using a shell-substrate base. These reefs increased the harvest of blue crab (*Callinectes sapidus*) by more than 150% (Fitzsimons et al., 2019).

Natural upwelling zones near islands, cliffs, underwater sea mountains and drop offs are known as rich fishing grounds, and one of the most advanced types of interventions is the creation of artificial upwelling in deeper areas with flat bottoms and strong water currents, where stratification often impedes vertical mixing. Artificial upwelling has been induced in Japan since the 1990s through the deployment of wall- or cone-shaped, high-profile artificial reefs, called 'artificial sea mountains'. The idea was to push nutrient-rich bottom water up to the euphotic zone, thus promoting the productivity of phytoplankton and through the food chain that of mesopelagic fish (Okano et al., 2011; Suzuki & Hashimoto, 2011). Nutrient and chlorophyll concentrations in the euphotic zone close to the sea mountain increased up to four and three times, respectively, and zooplankton abundance increased along the whole water column. Composition, density and biomass of the benthic community close to the artificial sea mounts also increased up to around three to four times. The overall yearly fish catch recorded at a fishing ground enriched with an artificial sea mountain was six times that obtained previous to the reef deployment (Suzuki & Hashimoto, 2011). An experimental application of an

air-lift system causing artificial upwelling in Chinese coastal waters doubled the weight growth of brown kelp (Fan et al., 2020).

Finally, the 'greening of grey hard infrastructures' (Firth et al., 2020) has to be considered, which means inclusion of specific features to the design of marine infrastructures to enhance attachment of sessile organisms and offer shelter from predation to juvenile fish, thus supporting biodiversity and productivity while complying with all engineering requirements (Pioch & Souche, 2021). This approach has been successfully tested in different countries, i.e., Australia, England, Italy, United States, Israel and France (Dafforn et al., 2015; La Marca et al., 2014; O'Shaughnessy et al., 2021; Pioch et al., 2011; Pioch & Léocadie, 2017). As an example, the use of eco-blocks to construct a breakwater in the new Haifa harbour, led to significantly higher species richness and biodiversity of both invertebrates and fish, as well as to a lower dominance of invasive species (Pioch & Souche, 2021). Scaling up such greening could consistently increase the carrying capacity of the marine ecosystem. Effects are expected to be more consistent in coastal areas, which commonly constitute spawning and nursery grounds for a large variety of organisms.

The above examples demonstrate the feasibility of active interventions as an additional or alternative approach to passive restoration focused on removing environmental stressors. Benefits can, however, significantly differ among areas depending upon local conditions. For example, shellfish reef restoration can fail when nutrient supply is not sufficient to support increased biomass of filter feeders. Although ecological engineering has been implemented worldwide at many places, long data series on technical performance as well as on the response of the physical, biological and social system, are scarce. Similarly, the success in terms of pre-established targets has only been evaluated in a few cases, e.g., seagrass and shellfish restoration (Fitzsimons et al., 2019; Thorhaug et al., 2020). It is difficult to assess whether an ecological engineering project has succeeded, when key performance indicators or associated thresholds are lacking. Whereas the impact on sessile organisms may be relatively easily assessed using, for example, the habitat suitability index (Theuerkauf & Lipcius, 2016), and where nearby natural rocky bottoms may provide targets, it is much more challenging to evaluate the impact on mobile macrofauna, especially for applications implemented at local scale, due to the continuous exchanges of biomass with the surrounding environment. Indirect indicators, e.g., body growth rates, are often employed in this case (Fabi et al., 2006; Ito, 2011; Polovina, 1991; Scarcella et al., 2011), but more work is needed on developing appropriate and feasible indicators.

8 | ECONOMIC AND SOCIETAL SUSTAINABILITY

Any intervention in the marine ecosystem will, next to the ecological sustainability, also raise issues of economic and societal sustainability. Be it the exploitation of new marine food resources or interventions such as ecological engineering or other manipulations of the food web structure, socioeconomic viability as well as an efficient governance system are fundamental prerequisites for the sustainable exploitation of marine resources (Hicks et al., 2016; Hidalgo & Browman, 2019; Holling, 2001; Paoletti et al., 2021; Wright et al., 2020). In addition to this, especially relating to the governance aspects of the management of the marine resources, spatial and temporal factors, as well as the cumulative effects of these interventions should be taken into consideration (van den Burg et al., 2020; van Hoof et al., 2020). Even though some of the interventions in the marine ecosystem may only be implemented on a local and national scale, the ecosystem effects in time and place may be of a much larger cross boundary/cross border scale. Accordingly, it will be necessary to take a broader governance perspective across national, international and supranational institutions. This will result in a multi-level governance approach across these institutional levels in which the traditional formal rules of governing are challenged resulting in the co-existence of steering mechanisms; laws, international protocols and directives co-exist next to soft law, procedural regulation, covenants, and best practices (van Hoof & van Tatenhove, 2009).

The existing (international) governance and legal frameworks, as well as their institutional set-up, are currently considered inadequate to ensure effective management (e.g., Standal & Grimaldo, 2021; Wright et al., 2020). Whereas in the EU at national level and EU level, there is quite an extensive governance framework relating to exploitation of fish (Common Fisheries Policy), the environmental status of the marine ecosystem (Marine Strategy Framework Directive), the protection of birds and habitats (Bird and Habitat directives and Natura 2000) and the principles of Marine Spatial Planning (Marine Spatial Planning Directive; van Hoof et al., 2011; van Hoof & van Tatenhove, 2009), at the international level the management framework is less firm (Berkes, 2010; Berkes et al., 2006; Wilcox & Bergseth, 2021).

For example, for the exploitation of meso-pelagic stocks a major concern is the insufficient national and international obligations concerning environmental impact assessment and limited implementation of ecosystem-based management approaches in current fisheries management that will be essential for managing potential exploitation of mesopelagic resources as detailed in

the paragraph below and in the Appendix S1 (Standal & Grimaldo, 2021; Wright et al., 2020). If at all there is a biomass that could sustainably be exploited in an ecological and economic sense according to the sustainability criteria and indicators outlined below, proper determination of harvesting options is needed in order to sustainably manage and govern the exploitation. In order to arrive at such a robust governance system, both at the national and international scale, the key interactions of the ecological, economic, social, and governance systems involved need to be understood (Garcia & Rosenberg, 2010; Hicks et al., 2016; Holling, 2001; Paoletti et al., 2021; Standal & Grimaldo, 2021; Wright et al., 2020). In the Appendix S1, we discuss in more detail the challenges and prerequisites in fishing and conservation methods for economic sustainable mesopelagic exploitation.

As for the operations in international waters, the UN Straddling Fish Stocks Agreement (UNFSA; UN, 1995), the UN Food and Agriculture Organization (FAO) Code of Conduct for Responsible Fishery (FAO, 2015), and the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (UN, 2009) cover to a large extent both the geographical areas and transboundary (fish) resources. However, focus has mainly been on sustainable exploitation of single stocks according to the MSY and PA principles (Standal & Grimaldo, 2021; Wright et al., 2020).

In order to improve management of resource exploitation, increased cooperation between states through the UNCLOS Regional Fisheries Management Organizations (RFMO's) with a central role of implementing regulations in international waters, is called for (Wright et al., 2020). In addition, moving from a single stock approach to an ecosystem based approach to sustainable harvesting, including broader ecosystem indicators and broader ecosystem impacts of fishing including biodiversity and large fish indicators (Crespo et al., 2019; Gascuel et al., 2016; Gilman et al., 2014) as well as benthic impacts (Bastardie et al., 2020) and by-catches will be required.

Similar to UNCLOS, the Convention on Biological Diversity (CBD; <https://www.cbd.int/>) and the UN Sustainability Goal 14 (SDG14; <https://sdgs.un.org/goals/goal14>) call for all fish stocks to be sustainably harvested and managed by 2020, applying an ecosystem based approach and developing science based management plans (UN CBD; UN SDG14; Wright et al. (2020)). However, again implementation of this in a broader context than single stock management has not been very efficient (Standal & Grimaldo, 2021; Wright et al., 2020).

Wright et al. (2020) and Fischer (2022) propose different modifications and a range of options to strengthening the institutional set-up, including the development of appropriate governance systems and management measures prior to the authorization or expansion of mesopelagic

fishery, including the further expansion of the UNCLOS and CBD. Among others, it covers application of the UNFSA and United Nations General Assembly (UNGA) resolutions and enhancing the capacity and effectiveness of RFMO's (Crespo et al., 2019; Fischer, 2022) to implement effective management measures.

Pivotal in the development and expansion of the governance system is addressing the issues of transparency, responsibility, and participation (van Hoof, 2010). Following Johnson et al. (2019), under the circumstances of nested governance in the international arena, with national international and supra-national institutions (van Hoof, 2015; van Hoof & van Tatenhove, 2009), the situation requires agreement on overarching principles by regional management bodies. For example, in the northeast Atlantic, OSPAR and NEAFC have signed a formal memorandum of understanding and implemented a Collective Arrangement. This represents an ongoing trust-building exercise recognizing aspects of common purpose and respecting specific legal mandates (Johnson et al., 2019).

Concerning the economic viability of (new) activities such as a new fishery or harvesting zooplankton, the viability and economic sustainability of the potential fishery plays an important role (Grimaldo et al., 2020; Malvarosa et al., 2019; Paoletti et al., 2021; Prellezo, 2019; Valinassab et al., 2007). For the exploitation of mesopelagic species, initial studies have shown that, compared to current large scale pelagic fisheries (Paoletti et al., 2021), there are still gaps and uncertainties in central parameters determining the economic sustainability such as catch rates, fishing costs, price dynamics according to oil content and contaminants, of potential commercial fishery of mesopelagic resources like myctophids and small squids (Grimaldo et al., 2020; Paoletti et al., 2021; Prellezo, 2019).

The economic viability of any activity is determined by the scale of availability of the resource, availability in minimum needed densities for successful harvesting, but also on quality and prices of the resources, their durability in processing, as well as on the costs compared to other alternative activities and potential switching possibilities, cf. (Grimaldo et al., 2020; Paoletti et al., 2021; Prellezo, 2019). In the case of the development of an entire new activity, this may also require investments in the development of appropriate harvesting, processing, and marketing instruments. Hence, if at all from an ecological perspective this harvesting can be implemented sustainably, the economics of the undertaking and the societal acceptance are equally important to develop these types of marine food production.

The social acceptance of (new) food production initiatives at sea will depend on the biological and ecosystem sustainability herein, but also on the economic, social, governance, and biological trade-offs and risks involved

in exploitation and management (Hicks et al., 2016; Holling, 2001; Malvarosa et al., 2019; Mullon et al., 2009; Nielsen et al., 2018; Ostrom, 2009; Paoletti et al., 2021; Soma et al., 2018; Wright et al., 2020). In addition, for example, when manipulating the food web, as in the case of targeted fisheries on predators in order to reduce predator pressures on lower trophic levels and consequently increasing their biomass, ethical concerns will determine a potential social license to operate (Cullen-Knox et al., 2017). Similar considerations can be expected in the case of ecological engineering, especially when used not to restore disturbed ecosystems, but actively create new ecosystems that can provide a variety of ecosystem services.

9 | CONCLUSION AND PERSPECTIVE

Our analysis pointed to many uncertainties for all four options to increase food production from the sea. It is therefore a big question whether they will be able to fill in the gaps in future needed global food supply. Manipulation of food web structure remains a risky exercise, because the required understanding of complex foodweb interactions is still limited. With respect to the exploitation of new resources, we pointed to extensive uncertainties and deficiencies in actual knowledge on (a) biomass estimates of potential resources, (b) stock identity and population dynamic parameters and vital rates, (c) robust stock assessments to assess biological sustainable biomass available on single stock basis to be harvested according to MSY, (d) biological food web interactions and importance in ecosystem functioning and services including biodiversity, ecosystem stability and evaluation of resilience of the marine ecosystem to potential exploitation, and (e) the role of the stocks in sequestration of greenhouse gasses. The potential for large-scale mariculture in offshore areas in relation to the carrying capacity is still largely unknown, both for seaweeds and low-trophic animals. Experiments on, for example, potential growth rates of seaweed have been performed at small-scales, but to predict the consequences of upscaling requires the use of mathematical ecosystem models that keep track of nutrient, mass, and energy budgets. Few of these models are already available, but they should be validated with appropriate data from large-scale pilots. We made a plea for using different model approaches. When low-trophic products, whether obtained from extensive aquaculture or from fisheries of new resources, are used for feed in finfish aquaculture, such practice should always be compared with the option of keeping the energy and protein in

TABLE 1 Main scientific knowledge gaps for the four topics discussed: ecosystem manipulation, harvesting so-far unexploited resources, low-trophic aquaculture and ecological engineering and restoration.

Ecosystem manipulation	<p>What multi-species models should be used to optimize total fishing yield?</p> <p>For what systems should a benthic compartment be included in the multi-species modelling?</p> <p>What level of ecosystem manipulation could be ecologically and ethically acceptable in relation to sensitive species and biodiversity conservation?</p> <p>How to ensure preventing regime shifts and secure ecosystem resilience while enhancing productivity through ecosystem manipulation?</p>
Mesopelagic zone	<p>What role do the mesopelagics have in the carbon sequestering in the sea on regional and global scale?</p> <p>What is the stock specific and wider ecosystem carrying capacity and sustainability for potential exploitation and what are the risks in harvesting mesopelagic resources?</p> <p>What knowledge basis and sustainability evaluations are necessary before starting potential exploitation of mesopelagic resources?</p> <p>What is the efficiency in exploiting mesopelagic fish in relation to use for feed in finfish aquaculture compared to keeping the energy and protein in the sea for natural food for natural predators and then sustainably harvest the predators, especially in context of mesopelagic fish may not be used for direct consumption because of contaminants?</p> <p>What are the technical challenges in developing a potential efficient mesopelagic fishery (both sea based and land based challenges, such as effective by-catch reduction and efficient storage and processing methods according to fast deterioration after harvest)?</p> <p>What are the stock identities, delineations, spatio-temporal distribution patterns and migrations of key potential mesopelagic resources?</p>
Larger zooplankton	<p>What are the direct and indirect effects of harvesting on the exploited zooplankton stocks, other commercial species, and vulnerable species (in particular predators)?</p> <p>What are the effects at ecosystem level, including biogeochemical cycles and resilience to climate change?</p> <p>What technical and management solutions are needed to reach sustainable fishing of zooplankton species and is this goal achievable?</p> <p>Is farming species based on zooplankton feed ecologically efficient and desirable?</p>
Low trophic mariculture	<p>What is the carrying capacity of ecosystems for large-scale culturing of seaweed and shellfish?</p> <p>What are the trade-offs between the various types of low-trophic aquaculture?</p> <p>What is the impact of large scale low-trophic aquaculture on natural NPP, fisheries and biodiversity?</p> <p>What are the nutritional value, digestibility and bio-availability of seaweed compounds for humans and animals?</p> <p>What are potential species for low-trophic aquaculture?</p>
Ecological engineering and restoration	<p>What are environmental, economic, and social key indicators to evaluate the success of a specific ecological engineering solution or restoration project?</p> <p>How can the possible contribution of greening of grey hard infrastructures to the increase of the ocean's carrying capacity be assessed?</p> <p>How can the technical performance of ecological engineering solutions and the ability to adapt to changing environmental conditions be optimized?</p> <p>What are adaptive, integrated management strategies to maintain benefits and avoid negative impacts of ecological engineering solutions in the long run?</p>
Economic and societal sustainability	<p>What efficient governance systems and legal frameworks, as well as their institutional set-up, are fundamental prerequisites for potential exploitation of new marine resources and establishing systems for that?</p> <p>What are the gaps and uncertainties in central parameters determining the economic sustainability and social acceptance of potential exploitation?</p>

the sea for natural food for natural predators and then sustainably harvest these predators. Finally, ecological engineering seems a promising avenue for many local situations, but what the potential contribution is to

global food production is still unknown and needs to be quantified.

For all four options, it is also a question whether there are adequately economic incentives for potential

exploitation. The economic sustainability of the fishery for so far unexploited resources, for example, is very much dependent on relatively high densities of the stocks, stable high catch rates, effective and selective fishing methods to avoid by-catch, as well as adequately high oil content and prices. Finally, effective governance systems and management measures need to be developed and implemented before new exploitation methods should be initiated. It should be noted, that the demand for yield and exploited biomass will likely be lower for production of high value products like pharmaceuticals and nutraceuticals compared to the demand for harvested biomass used for human food or for feed in intensive marine finfish aquaculture. Accordingly, the scaling and efficiency in the use as nutrition for humans is important when considering the sustainability of new harvesting and aquaculture approaches. The main scientific knowledge gaps concerning the topics discussed are summarized in Table 1.

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CONFLICT OF INTEREST STATEMENT

The authors have stated explicitly that there are no conflicts of interest in connection with this article.

DATA AVAILABILITY STATEMENT

No original data have been used in this paper.

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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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