# Size-spectra of marine fish communities in the Anthropocene

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December 2024

Keywords: body-size; spectra; ecological assessment; marine ecosystem; fish; indicators; global warming; overfishing; conservation

Marine ecosystems are under unprecedented anthropogenic pressures, with overfishing, global warming and pollution driving significant ecological changes. Among the tools for monitoring and understanding these impacts, size spectra, a measure of the relationship between the body size of organisms and their abundance or biomass, have emerged as a robust indicator. This review synthesizes recent findings to elucidate how environmental stressors, exploitation and conservation shape the size-spectra of marine fish communities.

#### Introduction

The Anthropocene is characterized above all by a rapid increase in multiple and human-induced pressures on ecosystems and their organisms. Terrestrial ecosystems have been impacted much earlier and more intensively than their marine counterparts. In 1962, Rachel Carson denounced in her book Silent Spring (1) the serious threats posed to terrestrial ecosystems by intensive agricultural practices. More than sixty years later, land-use changes have induced the loss of 75% insect biomass (2) and at least a guarter of common bird abundance in Europe (3). For some decades, fisheries have depleted fish populations, leading to a major decline in commercial populations across all oceans (4). So marine ecosystems are no longer exception in the Anthropocene and under severe defaunation with a global decline in large marine fauna such as sharks and rays in less than half a century (5, 6). In addition to these direct impacts, global ocean warming threatens many organisms with limited thermal tolerance and that are already surviving in thermal conditions near to their maximum threshold such as warm- and cold-water corals (7, 8). Pollution also adds multiple pressures, with for instance eutrophication and microplastics (9). Together, these stressors can have interlaced and potentially synergistic effects on biodiversity and structure of ecosystems with consequences on human livelihoods and well-being (10).

To counter such threats, governments have established protected areas (PAs) for nearly 50 years (11–13), with the ambition of protecting 30% of land and sea by 2030 (14), to safeguard ecosystem integrity. Yet, these conservation efforts struggle to bend the curve of biodiversity and biomass degradation, and even more to restore ecosystems in their pre-industrialization state (15). In order to implement ef-

fective conservation solutions, we need to monitor these effects using quantitative approaches which are holistic and multiscalar across space, time, and taxa.

Size spectra are one such approach, as it examines the relationship between the size of all organisms of an ecosystem and their abundance or biomass (16). By focusing on the size of multiple species, size spectra provide a comprehensive framework for understanding energy flow and trophic interactions across different trophic levels, as shown in (Fig. 1a). The actual size spectra approach was first introduced in the seminal article of Sheldon et al., (1972) (16) where the 'Sheldon's rule' is described and suggests that the biomass of organisms is approximately constant across all logarithmic size units in marine ecosystems (Fig. 1c). Numerous empirical studies, mainly on plankton communities, have confirmed Sheldon's rule on a local as well as a global scale (17). However, notable exceptions to the uniform distribution of biomass were observed, such as higherthan-expected biomass in bacteria and lower biomass in large marine mammals (Fig. 1c), suggesting the need to integrate functional traits into size-spectra to model marine ecosystems more comprehensively (18-20).

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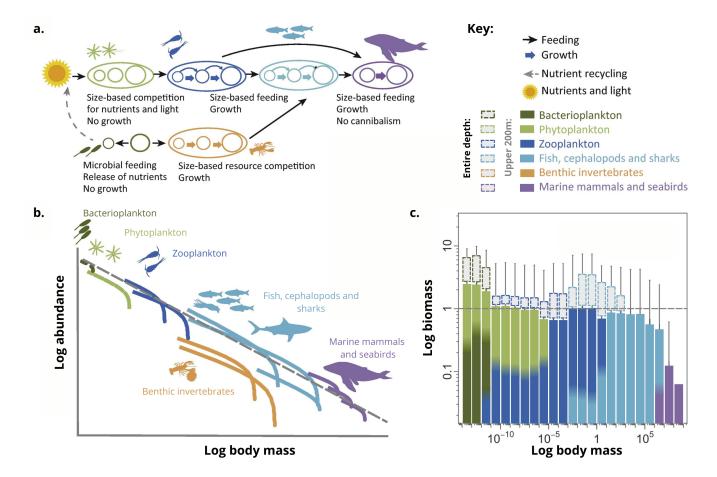


Figure 1: Body size-spectra across marine functional groups depicting the Sheldon's rule.

(a) Structure of a marine food web emphasizing different processes across the entire body size spectrum from micro-organisms to mammals. Larger circles illustrate relative changes in size within functional groups. Black arrows illustrate the presence of feeding within and across groups but do not show the full extent of the many feeding links present in size spectrum models. Thick colored arrows represent growth in size (from Blanchard et al., 2017 (21)). (b) Emergent size-spectra estimating the relation between the abundance and the size-class for the same types of functional groups shown in (a). The relationship between size-class and abundance follows a power-law distribution, appearing linear on the logarithmic scale. The dotted line represents the generalized size-spectra across all functional groups, (from Blanchard et al., 2017 (21)). (c) Emergent size-spectra estimating the relation between the global ocean biomass and the size-class for some of the functional groups shown in (a), the dotted line underpins Sheldon's rule, which suggests that biomass is evenly distributed across body size-classes. Notable exceptions to this rule are observed for bacteria and large marine mammals (from Hatton et al., 2021 (17)).

While modeling biomass relative to size spectra captures global energy flows, modeling abundance relative to size-spectra helps to better describe the fine structure and functioning of communities (22, 23). In fact, abundance distribution within populations reveals demographic processes such as birth, mortality, and recruitment, capturing spatiotemporal dynamics. Size spectra also emphasize the ecological importance of small organisms despite their little contribution to biomass (Fig. 1b). Indeed, small cryptobenthic fish, as highlighted by Simon Brandl et al. (2019) (24), play a crucial role in marine ecosystems, acting as a persistent 'biomass conveyor belt' by supporting higher trophic

levels despite their short lifespans and rapid turnover. This makes abundance size-spectra key to understanding food web dynamics, assessing prey availability, and monitoring trophic imbalances (25). Trophic imbalances, shifts in energy flow or in functional diversity may be caused by direct or indirect effects of anthropogenic pressures and can be detected by analyzing changes in the slope of size spectra over time or across gradients.

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A steeper slope typically reflects a disproportionate higher abundance of small organisms relative to large ones, often associated with stressed ecosystems where top predators or large-bodied species are severely impacted (23). In contrast, a shallower slope may indicate a surplus of large organisms compared to small ones, potentially due to recovery or changes in the trophic structure (Fig. 2).

To shed light on the mechanisms driving changes in marine fish communities, 22 studies (17, 19, 20, 25–43) have been analyzed to investigate the effects of environmental change, overfishing and conservation on fish size spectra across the oceans (Fig. 3). The studies used a variety of methods to collect size-spectra data: invasive methods such as electrofishing, trawling, and industrial catch surveys, or noninvasive methods such as underwater visual census (UVC) and baited remote underwater video systems (BRUVS), or models of fish productivity data and species-specific information on Fishbase. Firstly, by synthesizing these results, the aim is to gain an overall understanding of how anthropogenic changes in marine ecosystems alter the demographic and trophic structure of fish communities. Secondly, it will highlight the extent to which these perturbations may have antagonistic or multiplicative interactions, depending on the system under consideration. Finally, it will be shown that protected areas are also a form of human modification of ecosystems and that, if well implemented, can be used as an effective tool to offset the effects of overexploitation.

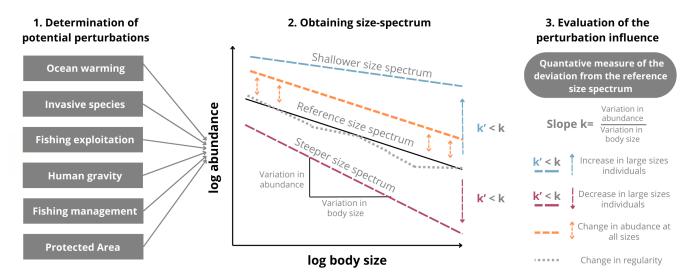


Figure 2: Assessing the influence of ecosystem perturbations on marine body size-spectra.

The size spectrum is an indicator of ecosystem condition. The reference size spectrum can be predicted using Sheldon's rule and compared to the empirical size spectrum. A deviation from the predicted reference size spectrum indicates if and how a perturbation is affecting the structure of a community.

## The impact of global ocean warming on fish body size spectra

## A general trend for the rise in temperature to reduce the size of individuals

Water temperature is a key factor, linked to the physiology of ectotherms such as fish, directly influencing species distribution, metabolism and growth rate (26, 27, 44, 45). The latest studies focus more on the effect of ocean warming on individual body sizes with a general trend of shrinking body size with increasing sea surface temperature (28–31). This may be explained by the fact that as temperature rises,

metabolic rates increase but less oxygen is available. Thus, warmer temperatures tend to increase respiration costs, which leaves less energy available for growth and reproduction. All in all, it affects the global ecosystem energy dynamics by lowering the energy transfer from one trophic level to another (44).

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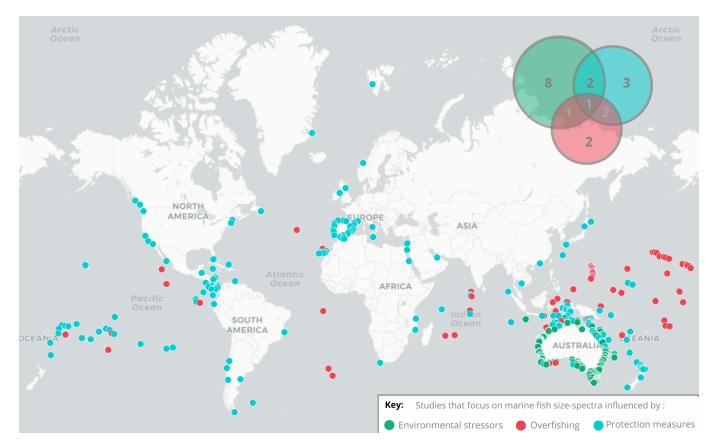


Figure 3: Geographical distribution of the studies focusing on fish size-spectra across the oceans.

This world map shows studies on the impact of anthropogenic pressures on marine fish communities, analyzed through size spectra. Each dot represents a study site, with colors indicating the factor analyzed: green for environmental stressors (e.g., warming, pollution), red for overfishing, and blue for protection measures (e.g., MPAs). The Venn diagram summarizes the distribution of studies between these three categories, showing cases where several pressures were analyzed simultaneously. The map highlights the geographical distribution of studies, with notable concentrations in regions like Australia, Southeast Asia, Europe, and Central America. It should be noted that only ten of the twenty-two studies presented gave access to coordinates of the monitored sites.

# However, the trend towards body size reduction is not homogeneous among all fish species.

Other studies suggest that certain species may not follow the general trend of shrinking body size with increasing temperature. Indeed, Kuo et al. (2022) (32) revealed significant species-specific variation in the responses of life history traits (asymptotic weight, weight at maturity, von Bertalanffy growth coefficient) to temperature increase. Audizijontyte et al. (2020) (26) even showed that large species tend to increase in body size with warmer temperature. This result contradicts experimental observations in which the greatest reductions in adult size occur in the largest species, often attributed to oxygen limitation and the general axiom that larger fish have greater metabolic activity (Pauly, 2021) (46).

Even if Audizijontyte et al. (2020) (26) did not provide a definitive explanation for this observation it could be linked

to the work of Van Rjin et al. (2017) (33). The latter concluded, firstly, that more active fish species are more likely to experience a shrinking body size in response to rising temperatures. Secondly, contrary to what is generally stated, larger fish species would not necessarily suffer greater oxygen limitation, as their gill growth rates are similar to those of their somatic tissues. This argument is in strong contradiction with Pauly's theory (46) presented earlier, although it is consistent with the observations of Audizijonytite et al. (2020) (26). Notably the effects of temperature can also vary according to the fish life stage. Early life stages, such as embryos, are generally more sensitive to changes in temperature (47).

In addition, the species-specific size-variation could be explained by the trophic and ecological role each species plays in ecosystems. Robinson Baum et al. (2016) (34) showed that carnivorous fish have a steeper size-spectra than herbivorous fish. Similarly, Coghlan et al. (2024) (31) found that different temperature-size relationships ex-

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ist between the four trophic modes of reef fish (herbivorous, planktivorous, invertivorous and piscivorous) while the trophic mode composition within communities also changes with temperature.

## Inter-community variation in size spectra as a response to climate warming

Some studies suggest that food web structure plays a key role in how fish communities respond to warming. Heather et al. (2021) (35) and Coghlan et al. (2022) (25) have demonstrated that predator-prey dynamics and inefficient energy transfer create predictable ripples in linear abundance size spectra, highlighting the influence of trophic interactions on marine community structure. Howarth et al. (2020) (36) emphasized the importance of considering body size and functional groups to understand benthic community structuring. Heenaan et al. (2020) (48) further explained that trophic structures can vary, being topheavy (dominated by predators), bottom-heavy (dominated by primary producers and herbivores), or middle-driven (dominated by intermediate consumers), with each species abundance shaped by its surrounding energetic environment (Fig. 4).

Rapid warming is also likely to coincide with changes in productivity and in the growing seasons re-arranging community structure and body size spectra. For instance, an increase in primary production can induce more production of small body-length fish, steepening the size-spectra and leading to shift from a top-down to a more bottom-up control of ecosystems (37, 42, 48).

Fish communities can also be impacted by species redistributions which are increasingly common phenomena due to rapid warming in time (27, 49). Thus, rapid range shifts in marine species could lead to changing species interactions and can accentuate body size spectra changes through time. For example in Brodeur et al. (2019) (50), a fish gut content analysis during a 'Blob' event, which is a prolonged period of anomalously warm sea surface temperatures in the North Pacific, highlighted a switch in zooplankton community composition. The composition switched from lipid-rich taxa to less nutritious zooplankton while also showing a decrease in mean planktivorous fish size and condition, suggestive of decreased trophic efficiency. However, Buba et al. (2017) (38) study of a marine system undergoing a sharp increase in invasive fish species showed a size-spectra that remained stable overall. Predictions of species shifts are becoming increasingly important, but comparatively studies showing their impact are still limited.

Finally, some studies found that body-size shifts vary by species depending on their latitudinal range (26). However, the inconsistent results across studies suggest no clear geographical pattern but indicate that regional factors strongly

influence this relationship.

Since changes in fish body size spectra due to climate change are synergistic with those due to direct human action, studying their effects independently is a way to better understand how those pressures are interacting.

## Overfishing and protection influences on fish body size spectra

## Overfishing steepens body size spectra owing to the overdominance of small fish

Fishing is often highly selective in terms of fish body size with large fish being caught first. This manifests itself mainly in a preference for more profitable and edible fish but also meets the minimum size criteria imposed by regulations. In addition, some fish species are more prized than others because of their market value, accessibility or cultural preferences. These are known as commercial species and the market demand plays a key role in the intensity those species are exploited (51–53).

This selectivity, particularly the targeting of larger individuals, has significant ecological consequences. It steepens the size-spectra by reducing the relative abundance of large fish while comparatively increasing that of smaller ones (17). Such shifts in size distributions highlight the pervasive influence of fishing pressure on aquatic ecosystems. For instance, Carvalho et al. (2021) (19) demonstrated that fishing pressure in Indonesia was the primary driver of size-spectra slope in coral reef fish communities, with steeper slopes observed under higher pressure; a result similarly found by Robinson et al. (2017) (39) in Pacific coral reef fish communities with increasing human population density and proximity to markets, both key indicators of fishing pressure.

## More generally, human gravity is a key factor influencing fish body size-spectra

Fishing interacts with other anthropogenic factors, such as pollution and habitat destruction. To account for these multiple anthropogenic factors, the human gravity index was described in Cinner et al. (2018) (*54*) as a relevant measure of human population footprint on an ecosystem by considering both the accessibility and the density of people living nearby. Thus, a high human gravity score indicates high anthropogenic pressure and highly depleted fish biomass (*54*).

Bosch et al. (2022) (28) show that the probability of occurrence and abundance of large and legal-sized fish were

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best depicted by models that included human gravity. While there was no apparent trend for sublegal-sized fish to correlate with the index, the probability of encountering large fish and the relative abundance of legal-sized fish were negatively correlated to the human gravity index.

Moreover, Letessier et al. (2024) (40) studied whether there was a differential effect of human gravity (approximated as "distance to the market") on the size-spectra between pelagic and benthic systems. They made two contradictory hypotheses. The first one is that there is a larger human footprint in pelagic systems due to increased vulnerability of large and long-lived species. The second one is that there is a smaller human footprint in pelagic systems due to the migratory capacity of species and the extent of offshore fisheries. By studying 17,411 baited stereo video (BRUVS) deployments in the Atlantic, Indian and Pacific oceans, covering both pelagic and benthic systems, they found that pelagic size structures are more sensitive to human pressure than their benthic counterparts, confirming only the first hypothesis made. Also, both small and large pelagic individuals are affected by a high gravity index, indicating a sensitivity that is not limited to large individuals. Finally, human pressure leads to a convergence in size structure between pelagic and benthic systems, in contrast to those in remote and more pristine areas.

## A systemic body size spectra response to protection measures

Not only the study by Letessier et al (2024) (40) showed a systemic size spectra response to human gravity, but also a systemic response to protection measures in interaction with gravity. Indeed, they reveal that the protection effect drops with decreasing human gravity in benthic systems, while it is cumulative with increasing human gravity in pelagic systems. Thus, high protection can mitigate human pressure in benthic systems, even in areas with a high gravity index. In contrast, effective protection of pelagic systems requires focusing on areas with lower gravity index. All in all, it shows that the resilience of fish body size structure to human pressure is lower in pelagic ecosystems compared to benthic ones, highlighting also the significant role of habitat structure in shaping community size-spectra.

Carvalho et al. (2021) (19) specifically examined how habitat complexity, linked to coral cover, influences fish size spectra in coral reefs. They found that habitat complexity significantly affects herbivores, leading to shallower size spectrum slopes. This suggests that complex habitats reduce the impact of fishing by providing refugia that modify predator-prey interactions and competition, allowing larger individuals to survive.

## A species-specific response to protection measures

The study by Sanchez et al. (2024) (41) explored the response to protection using underwater sightings data of tropical reef fish from the Reef Life Survey, a global scale citizen science program. The analysis focused on 658 fish species and 57 marine protected areas (MPAs) spread across the Indo-Pacific and Atlantic oceans. The study revealed that half of species show an increase of at least 16% in their occurrence, 35% in their abundance and 22% in their biomass in highly protected areas compared to fished areas. The variations in species responses to protection were linked to ecological traits such as vulnerability to fishing, trophic level and maximum body length. Though, the study highlights that rarity modulates species responses to protection. Rare species, particularly small herbivores and large top predators, show the greatest increases in abundance and biomass in highly protected MPAs.

In summary, even if the study was not specifically focused on the size-spectra, it suggests that protection can have a positive effect on fish body size, particularly for rare species, those occupying higher trophic levels and which are large and therefore suffer from heavy fishing pressure. The conclusion that the benefits of protection are uneven across species, depending on their body size and ecological traits, has also been reached by a number of studies at varying scales (7, 28, 55–57). Yet, the study of Sanchez et al. (2024) (41) suggests that marine protected areas deeply modify body size spectra by favoring the largest and rarest fish, while most small bodied-fish species benefit less from protection resulting in a size-spectra flattening.

# The anthropogenic influences on size-spectra have ecological consequences

#### Multiple pressures alter fish life history traits

Temperature is a major environmental factor influencing species life history traits (44). As show before, warmer waters, induced by climate change, exert selective pressure on fish populations, leading to adaptation such as a modification of maximum body size, acceleration of metabolic rate, increased thermal tolerance, or accommodation such as migration towards thermal refuges (26, 33, 49).

Selective fishing also exerts evolutionary pressure on fish populations. Removing larger specimens disproportionately reduces reproductive output due to the hyperallometry of reproductive potential, whereby larger females

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contribute exponentially more to the number and quality of offspring compared to smaller ones (58–60). By targeting these larger individuals, fisheries not only lower the average individual fitness of populations but also disrupt recruitment dynamics, leading to long-term reductions in population resilience and potential recovery.

This is known as the Allee effect. Since fishing often targets the same areas, individuals that reach maturity at a smaller size or have faster growth rates are favoured in these particular areas, so fisheries-induced evolutionary changes are rapid and can alter the size structure of populations in the long term (19, 61).

However, MPAs could provide a form of mitigation for the Allee effect by providing refugia for rare top predators and large-bodied individuals, the latter contributing disproportionally to the amount of offsprings produced in a given population (41, 54, 58). Indeed, MPAs can create breeding hotspots where mature individuals can easily mate, ensuring the persistence of populations (62).

So, fish body size spectra are intrinsically linked to reproductive potential.

### **Modifications of interspecific interactions**

Ecosystem disturbances lead not only to changes in the life histories of species, but also to changes in interspecific interactions. A trophic cascade explains the effect of overfishing in exacerbating a steeper size-spectra. Indeed, reductions in the abundance of larger species, often occupying higher trophic levels, have knock-on effects at lower levels, leading to increases in the abundance of smaller species of lower trophic levels (20, 63) (Fig. 4). For example, the reduction in sharks can lead to an increase in mesopredators, which in turn can exert greater pressure on their prevs. The result is a shift from a top-heavy to a middle-driven trophic pyramid (64). On the contrary, the implementation of MPAs tends to have the opposite effect, with small and medium-sized fish species of medium trophic level benefiting less from the protection than larger individuals (41). The establishment of MPAs therefore makes it possible to restore a top-heavy structure in one part of the ecosystem without necessarily reducing the abundance of smaller species outside the MPAs, as the latter flourish not inside but near the MPAs. Therefore MPAs create spill-over benefits of large and often commercial species (65). So, source-sink dynamics between ecosystems can promote a diversity of size-spectra shapes across the ocean and human uses.

#### Alteration of ecosystems functioning

Maintaining a top-heavy trophic structure in the ecosystem helps to keep it productive and highly diverse. Large fish often play an important role in nutrient cycling, bioturbation and the regulation of diseased populations. Their reduction can therefore affect the overall functioning of ecosystems, leading to changes in the composition of benthic communities, a decrease in primary productivity and in overall biomass (6, 28, 39, 43, 66). In addition, a size-spectra dominated by small fish can make the ecosystem more vulnerable to disturbances and environmental changes. Indeed, large and rare fish often have a greater adaptive capacity, so their depletion can make ecosystems less resilient to climate change (39, 67).

Finally, in lightly exploited marine ecosystems, biomass production is generally positively correlated to primary productivity (66). However, this relationship is reversed in heavily exploited systems, where productivity declines more slowly than biomass and can therefore mask an environmental perturbation. Morais et al. (2020) (43) coined the phenomenon of 'buffer productivity' and highlighted the importance of monitoring fish size-spectra in order to better detect potential impacts of overexploitation on ecosystems.

# Conclusions: adapting protection to the socio-ecological context

This review highlights the critical need to adapt conservation measures to the dual pressures of anthropogenic activities and climate change, particularly their synergistic impacts on marine fish size spectra. Size-spectra provides a powerful, integrative tool for understanding community responses to these pressures, offering insights into trophic, energy, and biodiversity shifts across ecosystems. By focusing on organism body size rather than species identity or biomass, size-spectra enable the detection of structural changes within communities that are often overlooked by traditional taxonomic approaches. For instance, steepening size-spectra slopes may provide early-warning signals of stress increases on large-bodied individuals under overfishing, warming, or bottom-up shift in ecosystem control.

However, the utility of size-spectra is not without limitations. Their broad focus on size can mask species-specific variations in response to environmental changes, such as those observed with rising temperatures. Studies have shown that warming does not uniformly reduce body size; certain species may increase in size due to regional or ecological factors, while others experience sharp declines (26, 32). These variations underline the importance of

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complementing size-spectra analyses with functional and taxonomic data to capture the full complexity of community responses. Additionally, size-spectra may struggle to fully account for rapid changes in species distributions and interactions, such as those driven by marine heatwaves or invasive species (38, 50). Size-spectra also ignore species-specific vulnerabilities or roles in ecosystems by providing synthetic measures like slope. Such indicators could be completed by others like the number of species on the IUCN Red List or species functional distinctiveness (68).

We have also shown that areas with a limited human footprint can act as refuges for large individuals. Therefore there is a need to maintain and reinforce existing MPAs or create new ones in order to maintain the reference sizespectrum in marine communities by limiting the impact of fishing on the largest individuals (28). However, the observed differences in how pelagic and benthic fish communities respond to human pressures (40) highlight the need for tailored conservation strategies. Pelagic systems, which are particularly sensitive to warming and trophic disruptions, benefit most from highly protected MPAs in remote areas with low human gravity, including the high seas, to restore fish populations and maintain ecosystem functioning. Conversely the protection of benthic systems could be prioritized in areas with higher human gravity to restore coastal fish communities and their contributions to local people (66, 69). Thus, the conservation efforts should prioritize habitat restoration, such as the protection of Posidonia seagrass beds or coral reefs, which is critical for sustaining biodiversity and productivity (19, 28, 70-72).

To address these challenges, MPAs also must be integrated into broader networks connected by ecological corridors. These corridors facilitate species migrations and predator-prey interactions, preventing the imbalances often observed in isolated MPAs (73). This is particularly important as warming accelerates species redistributions and alters trophic structures. However, implementing such measures may face socio-economic challenges, particularly for fisheries, which are already suffering as overfishing and size reductions impact both biodiversity and food security (74). Transitioning towards a balanced economy that integrates sustainable fishing and eco-tourism could provide a viable path to achieving long-term environmental and human well-being.

In conclusion, size-spectra are invaluable for understanding the evolution of fish communities under changing conditions, but future research should use size-spectra alongside complementary approaches to address their limitations. Conservation strategies must be adaptive, integrative, and socio-ecologically informed to ensure that marine ecosystems remain functional and resilient in the face of global changes of the Anthropocene.

#### **ACKNOWLEDGMENTS**

I would like to thank my internship supervisors David Mouillot, for giving me the opportunity to work on this fascinating subject and for the time and invaluable advice he has given me. I would also like to thank my academic tutor, Marc Coudel, for his for his pedagogical and methodological support.

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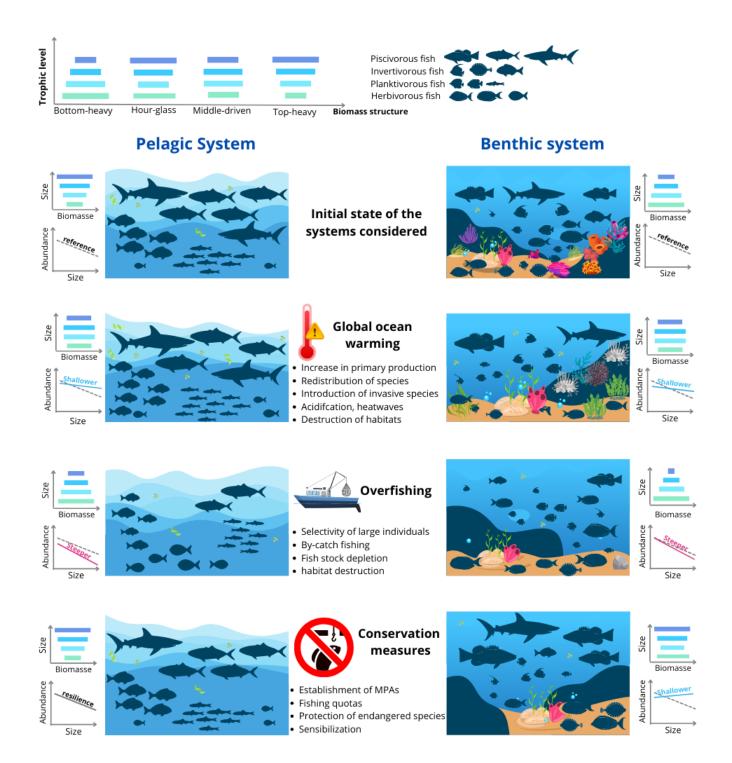


Figure 4: Comparison of global warming impacts, overfishing and conservation measures on pelagic and benthic marine ecosystems.

The figure summarises the effects of global warming and overfishing on the trophic structure and size-spectra of pelagic and benthic marine ecosystems, as well as the effectiveness of conservation measures to restore and maintain these ecosystems.

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