MARINE CONSERVATION

Divergent responses of pelagic and benthic fish body-size structure to remoteness and protection from humans

Tom B. Letessier[1,2,3]*, David Mouillot[4], Laura Mannocci[4,1], Hanna Jabour Christ[3], Elamin Mohammed Elamin[5], Sheikheldin Mohamed Elamin[6], Alan M. Friedlander[7,8], Alex Hearn[9,10], Jean-Baptiste Juhel[11], Alf Ring Kleiven[12], Even Moland[12,13], Nicolas Mouquet[1,4], Portia Joy Nillos-Kleiven[12], Enric Sala[7], Christopher D. H. Thompson[3], Laure Velez[4], Laurent Vigliola[11], Jessica J. Meeuwig[3,14]

Animal body-size variation influences multiple processes in marine ecosystems, but habitat heterogeneity has prevented a comprehensive assessment of size across pelagic (midwater) and benthic (seabed) systems along anthropic gradients. In this work, we derive fish size indicators from 17,411 stereo baited-video deployments to test for differences between pelagic and benthic responses to remoteness from human pressures and effectiveness of marine protected areas (MPAs). From records of 823,849 individual fish, we report divergent responses between systems, with pelagic size structure more profoundly eroded near human markets than benthic size structure, signifying greater vulnerability of pelagic systems to human pressure. Effective protection of benthic size structure can be achieved through MPAs placed near markets, thereby contributing to benthic habitat restoration and the recovery of associated fishes. By contrast, recovery of the world's largest and most endangered fishes in pelagic systems requires the creation of highly protected areas in remote locations, including on the High Seas, where protection efforts lag.

Body size is a universal biological property that influences ecological processes at the individual, population, and ecosystem levels (*1*). Measuring size spectra (size frequencies plotted on a log-log scale) is therefore a useful framework through which to understand and predict overexploitation (*2*), nutrient cycling (*3*), and productivity (*4*). Moreover, understanding how body sizes are distributed in the oceans has ramifications for conservation and fisheries science and is highly relevant to several of the United Nations (UN) Sustainable Development Goals. In particular, effective biodiversity conservation (*5*) and 30% protection coverage by 2030 ("30 by 30" goal) (*6*) require understanding of how successful marine protected areas (MPAs) are likely to be in different socio-environmental contexts (*7*). Within a given pelagic or benthic system, size spectra typically show consistent alternations between overrepresented and underrepresented sizes, resulting in regular peaks and troughs (*8*, *9*). When slopes of size spectra are shallow and peaks are prominent, the spread between peaks is generally considered to reflect predator-prey relationships, with each peak representing a different trophic group that is preyed upon by the next, for example, plankton, planktivorous fishes, and piscivorous fishes (*10*, *11*). However, assessing such size-structured variation across marine habitats and regulations is particularly challenging because dedicated survey methodologies with different size selectivity are used in pelagic and benthic systems. For instance, whereas pelagic fishes are conventionally sampled through longlines and midwater trawls or acoustic techniques (*12*, *13*), benthic fishes are mainly surveyed by underwater visual census (*14*) or with bottom trawls and other habitat-specific gears (*15*), which makes intersystem comparisons difficult.

Stereo baited remote underwater video stations (BRUVS) represent a unifying, nondestructive, and fisheries independent method that can estimate relative abundance and body size across virtually any marine system (*16*). In this work, we conducted a widespread size-based assessment of marine pelagic and benthic nekton fishes (>1 g), spanning six orders of magnitude in body size, from zooplankton size classes (~3 to 4 cm) to large oceanic predators (~1000 kg; Fig. 1). We combined records from multiple surveys inside and outside MPAs, resulting in 6701 BRUVS deployed in pelagic systems and 10,710 BRUVS deployed in benthic systems, which corresponds to 13,402 10,710 hours of footage, respectively, across the Atlantic, Indian, and Pacific Oceans. This database yielded length measurements for individual fish, which were converted to weights using taxa-specific allometric conversion parameters (*17*, *18*) (Fig. 2 and fig. S1).

To better understand how MPAs may effectively protect fish size structure in the context of the "30 by 30" goal, we tested two competing and mutually exclusive hypotheses regarding the influence of human pressures on fish size structure in pelagic and benthic systems. First, we hypothesized a greater human footprint in pelagic systems compared with benthic systems because the larger body size and longer life of many oceanic species renders them more vulnerable to fisheries (*19*). Therefore, we expect that pelagic fish size structure is more sensitive to protection status and human pressures than benthic fish size structure. As an alternative hypothesis, the migratory capacity of many large pelagic species and the widespread activities of high-sea fishing fleets (*20*) result in a comparatively low human footprint and low MPA effectiveness in pelagic systems in contrast to benthic systems, where local human pressure has acted longer (*21*) and where fish size structure would therefore be more affected and sedentary species would benefit more from MPAs (*22*).

Body-size structure across systems

Our surveys, conducted from January 2006 to May 2020, recorded a total 823,849 individual fish (pelagic: 106,424, benthic: 717,425; Fig. 2), representing 139 families and 1460 species of fishes and sharks (211 pelagic, 1376 benthic, and 127 species recorded in both systems) and weighing a combined 744 metric tons (pelagic: 325 tons; benthic: 418 tons). Our dataset lacked representation from the North Pacific, and representation in the central Pacific and in most of the Atlantic was limited to pelagic systems only. Size-frequency distributions were generated by aggregating sizes within six broad brackets of absolute latitude (Fig. 3), which revealed distinct patterns within each system that were robust to an unbalanced survey design (*17*). Benthic median sizes were generally larger than pelagic medians (range of medians: pelagic 4 to 134 g, benthic 27 to 120 g) owing to the greater representation of smaller size classes (<30 g). Upper size classes were better represented in pelagic size distributions than in benthic size distributions (range of 95th percentiles, pelagic 0.4 to 83.3 kg, benthic 1.3 to 2.9 kg; Fig. 3A). Size spectra slopes, a measure of the proportion of large to small individuals (*17*), were contrasted between systems by regressing normalized size-frequency distributions on the $\log_{10}$-$\log_{10}$ scale (Fig. 3B). Slope values were consistently steeper (more negative) in benthic systems than in pelagic systems (table S1),

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

---

[1]CESAB – FRB, Montpellier, France. [2]Institute of Zoology, Zoological Society of London, Regent's Park, London, UK. [3]Marine Futures Lab, School of Biological Sciences, University of Western Australia, Perth, WA, Australia. [4]MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France. [5]Red Sea Fisheries Research Station, P.O. Box 730, Port Sudan, Red Sea State, Sudan. [6]Faculty of Marine Science and Fisheries, Red Sea State University, P.O. Box 24, Port Sudan, Red Sea State, Sudan. [7]National Geographic Society, Washington, DC 20036, USA. [8]Hawaiʻi Institute of Marine Biology, University of Hawaiʻi, Kāneʻohe, Hawaiʻi, USA. [9]Galapagos Science Center, Universidad San Francisco de Quito, Quito, Ecuador. [10]MigraMar, Olema, CA, USA. [11]ENTROPIE, Institut de Recherche pour le Développement, IRD-UR-UNC-IFREMER-CNRS, Centre IRD de Nouméa, Nouméa Cedex, New-Caledonia, France. [12]Institute of Marine Research, Nye Flødevigveien 20, 4817 His, Norway. [13]Centre for Coastal Research (CCR), Department of Natural Sciences, University of Agder, P.O. Box 422, N-4604 Kristiansand, Norway. [14]Oceans Institute, University of Western Australia, Perth, WA, Australia.
***Corresponding author. Email: tom.letessier@ioz.ac.uk**

reflecting the greater absolute and relative number of large individuals in pelagic systems (*17*).

Both the spread between peaks and size-spectra slope values were distinct between pelagic and benthic systems across biogeographical scales, which suggests that each system supports distinct food webs and energy pathways (*23*). The presence of prominent peaks in pelagic systems is consistent with previous reports (*10*) and suggests that each peak reflects a trophic group that is preyed upon by the next, with shallower slopes reflecting carnivorous feeding (*11*). In benthic systems, peaks were less clearly defined and slopes steeper, consistent with greater levels of herbivorous feeding (*11*) likely stemming from greater dependence on seabed algae compared with in the midwater (*24*). Greater prevalence of carnivory in pelagic systems implies that the proportion of production retained between trophic levels is higher (*25*) as a result of more-direct energy transfer in these systems than in benthic systems. Overrepresentation of intermediate size classes (30 to 500 g) in benthic systems is consistent with complex habitat structure in coastal ecosystems such as kelp forests and coral reefs (*26*) that provide size-selective refugia (*27*). Elevated benthic productivity within these size classes is further promoted through system connectivity and benthic-pelagic coupling (*28*), whereby passively drifting plankton are consumed by planktivorous and piscivorous fishes near the seabed (*29*). Conversely, pelagic productivity and energetic needs in upper trophic levels are promoted by more-direct energy transfer (*11*) and are facilitated by greater home ranges such that individuals in upper trophic levels can forage from the top of multiple benthic food webs (*30*) or from more productive geographical regions such as those in temperate latitudes (*31*). Mobile strategies in upper trophic levels typically involve pelagic foraging incursions or are associated with fully pelagic lifestyles (*32*), which results in a greater prevalence of upper trophic levels in pelagic systems.

Human footprint on size structure

We tested our hypotheses concerning the difference in relative sensitivity of pelagic and benthic size structure by extracting three size indicators (*33*) from frequency-size distributions of nekton fishes aggregated by survey date (*17*) (fig. S2); the typical body sizes ($\log_{10}$, kg) of relatively small individuals and of relatively large individuals, as represented by the values at the first and second modal frequency peaks; and the exponent b of the size spectra slope (*34*). These three indicators capture the main dimensions of size structure within each system, at the scale of the survey day, with the size of relatively small and large individuals representing relatively lower and higher trophic levels, respectively (*10*), and the size spectra slope theoretically reflecting the steepness of the trophic pyramid (*25*). We then built explanatory generalized least-square (GLS) models (*35*) to test the two competing hypotheses by identifying how human pressure and protection status affected pelagic and benthic fish size indicators. In addition to controlling for spatiotemporal autocorrelation and socioenvironmental conditions that are known to influence the effectiveness of spatial protection status (*36*) (fig. S3 and table S2), our models considered interactions between systems (pelagic or benthic) and protection status, as represented by three different categories of spatial protection (*37*) (not protected, partially protected, or highly protected) (*17*), and human pressure, as represented by travel time to human markets (*38*) ($\log_{10}$ minutes).

GLS models of relatively small and relatively large fishes achieved moderate explanatory power [R^2 adjusted for nonsignificant explanatory variables (adjR^2), small individuals: 0.257, large individuals: 0.343], revealing an effect of market proximity and protection status, which was consistent in direction but specific in magnitude to each system ($P < 0.05$; Fig. 4A, figs. S4

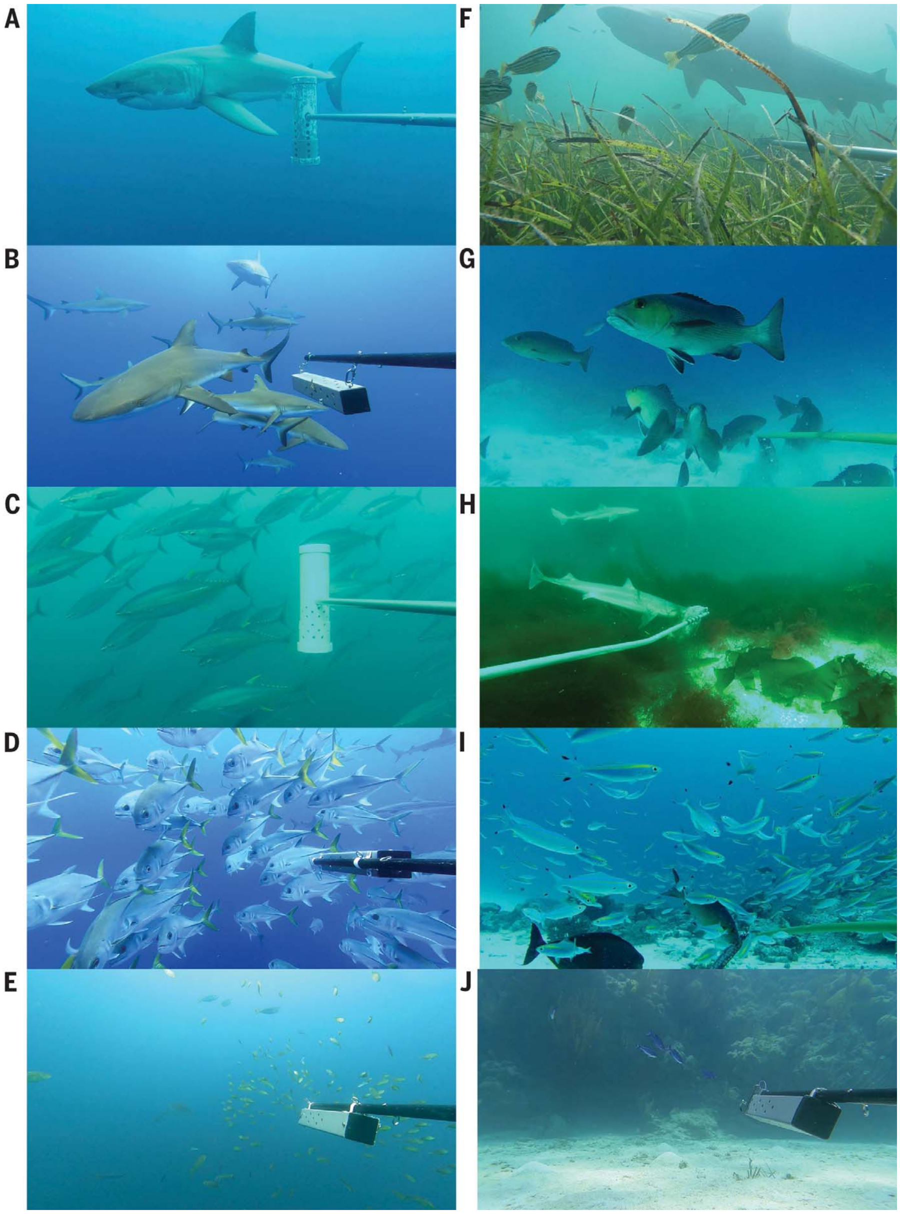

Fig. 1. Body-size variability in pelagic and benthic systems, recorded by stereo BRUVS. Pelagic systems are shown on the left and benthic systems on the right. (**A**) Great white shark (*Carcharodon carcharias*). (**B**) Grey reef shark (*Carcharhinus amblyrhynchos*). (**C**) Yellowfin tuna (*Thunnus albacares*). (**D**) Horse-eye jack (*Caranx latus*). (**E**) Juvenile jack (Carangidae sp). (**F**) Tiger shark (*Galeocerdo cuvier*). (**G**) Two-spot red snapper (*Lutjanus bohar*). (**H**) Spiny dogfish (*Squalus acanthias*). (**I**) Goldband fusilier (*Caesio chrysozona*). (**J**) Creole wrasse (*Clepticus parrae*). [Credits: Photos were taken by the authors].

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

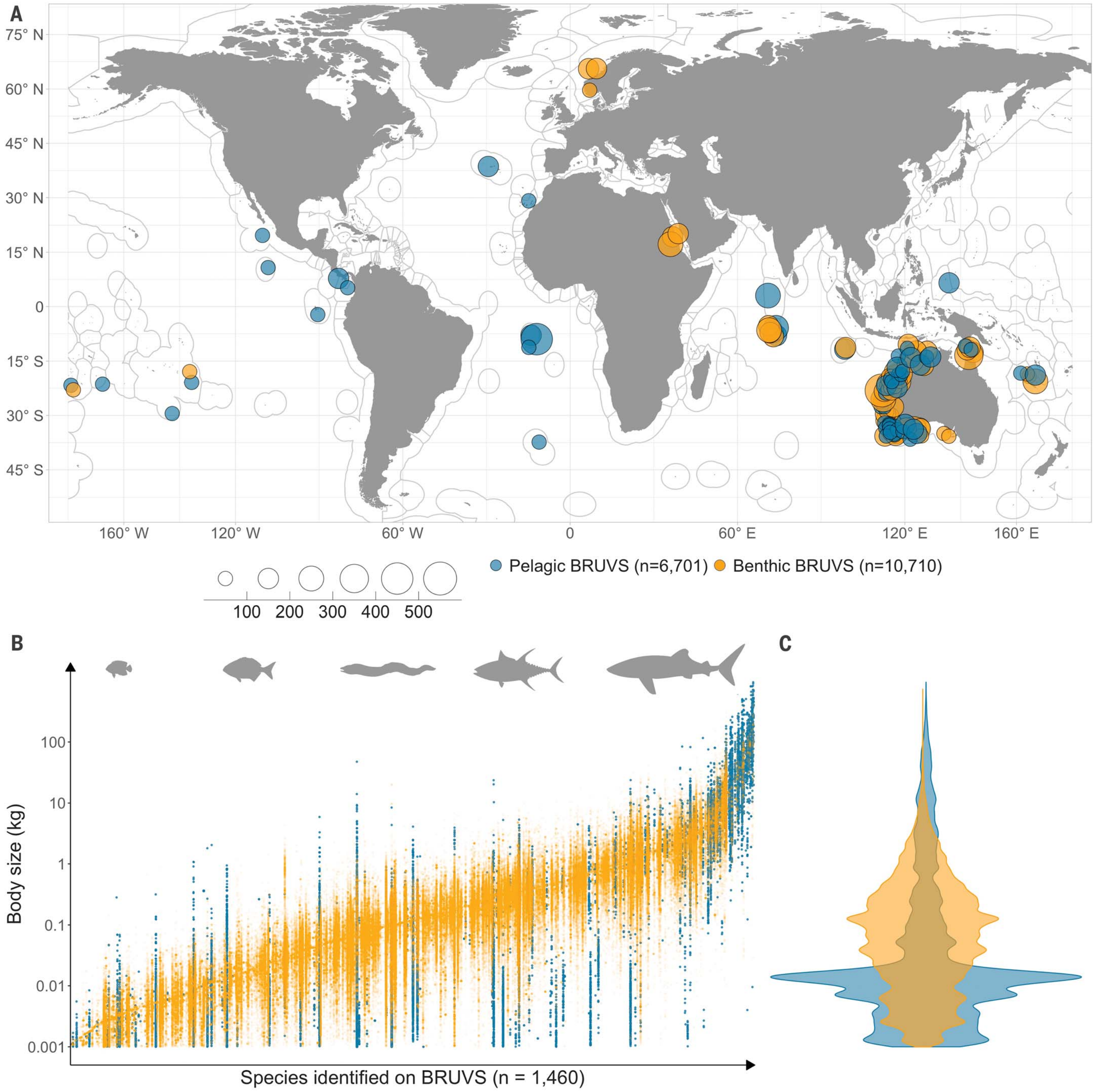

Fig. 2. Body sizes of pelagic and benthic fishes identified on BRUVS. (**A**) Survey effort of BRUVS, showing the outlines of the world's Economic Exclusive Zones in gray contours (some of which are contested). Each circle represents a single expedition, with the circle diameter being proportional to the number of BRUVS deployed. Circles are jittered to minimize overplotting. (**B**) Pelagic and benthic fish body sizes (kg, *n* = 823,849) categorized by species identity (*n* = 1460) and rank-ordered by median species body size. (**C**) Marginal density distribution plots of body sizes.

and S5, and tables S3 and S4). In both systems, individuals were larger if highly protected and remote from markets, consistent with our present understanding re-garding how vulnerability and exploitation vary with protection and accessibility (*36*). However, relatively small and large individuals in pelagic systems were both consistently more sensitive to protection status and to market remoteness, with a cumulative impact of protection status and market remoteness. In benthic systems, relatively small individuals were less sensitive to protection than large individuals, in keeping with expectations on how vulnerability to exploitation varies with differences in life history (*14*, *19*). Moreover, the effect of protection status saturated with remoteness, with remoteness having increasingly less relative impact under higher protection.

GLS models of size spectra (adjR^2, size-spectra slope: 0.273; Fig. 4B, fig. S6, and table S5) showed divergent effects in each

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

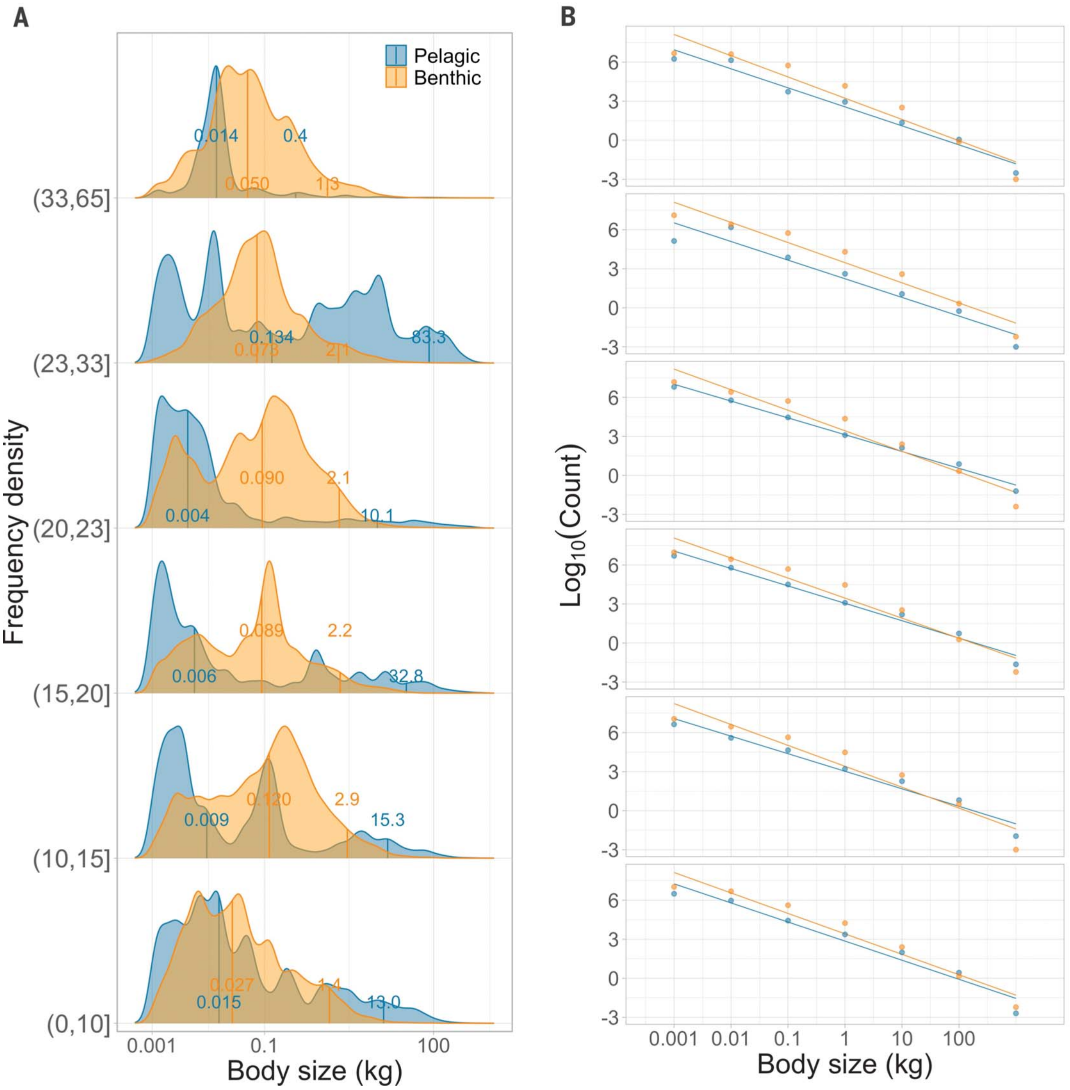

Fig. 3. Pelagic size spectra are shallower than those of their benthic counterparts across biogeographical scales. (**A**) Frequency density distribution of fish body sizes aggregated into six absolute latitude brackets (0 to 10, 10 to 15, 15 to 20, 20 to 23, 23 to 33, 33 to 65) of equal numbers of body sizes (*n* = 137,308), with vertical line and number showing median and 95th percentile values, respectively. (**B**) Abundance size spectra, normalized by dividing the frequency counts by the width of the bin, with lines representing fit of linear regressions (pelagic slope mean: −1.38, range: −1.47 to −1.29; benthic mean: −1.58, range: −1.63 to −1.54).

system, with size spectra slopes in pelagic systems showing a pronounced and rapid steepening with market proximity under high protection and marginal effects of protection status and market proximity after that. By contrast, slopes in benthic systems were marginally affected, becoming less negative (shallower) near markets, independently of protection status. Without protection, steepening of pelagic slopes and shallowing of benthic slopes resulted in converging size structure between systems with considerable overlap in slope values near markets in unprotected locations. A sensitivity analysis testing the model robustness to the unbalanced survey reported similar effects of market proximity, with minor differences between models rerun with 10% of randomly dropped data points (*17*). Greater differences were observed between model reruns with ocean-specific data dropped. Notably, the results that showed that pelagic systems were highly responsive to highly protected remote areas were conditional on the inclusion of the Indian Ocean data (fig. S9). Our main findings concerning the direction of both remoteness and protection in pelagic and benthic systems remained largely unchanged from those derived using the full dataset.

Taken together, our models support our first hypothesis, that pelagic fish size structures are more vulnerable to human pressure than their benthic counterparts. That both relatively small and relatively large individuals in pelagic systems were consistently affected near markets means that greater sensitivity in pelagic systems cannot be attributed solely to the greater occurrence of larger (and therefore more vulnerable) individuals. In benthic systems, the magnitude of protection effect declined with market distance, in contrast to a cumulative effect with market distance in pelagic systems. This contrasting result means that high protection status can, even near markets, mitigate human pressures in benthic systems, whereas effective protection in pelagic systems requires market remoteness.

Our results suggest that size-structure resilience to human pressure is lower in pelagic systems than in benthic systems. In theory, size spectra slopes are expected to steepen with increasing human exploitation as a consequence of predator depletion, leading to a commensurate decline in mean trophic level (*39*). However, reports of human pressure responses in benthic systems are conflicting, with both a steepening size spectra slope (*39*) and a modest increase in mean trophic level reported (*14*, *40*). This apparent conflict may stem from difficulties in establishing appropriate baselines in "pristine" benthic systems, which show wide-ranging size spectra slope values (*39*) (i.e, −1.95 to −1.13) and both inverse and concave trophic pyramids (*14*, *30*). Our observations of only a marginal effect on benthic slopes are, in any case, consistent with reports of a comparatively modest impact of human pressure on mean trophic level, which has been corroborated from across a wide range of benthic systems and arguably by a

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

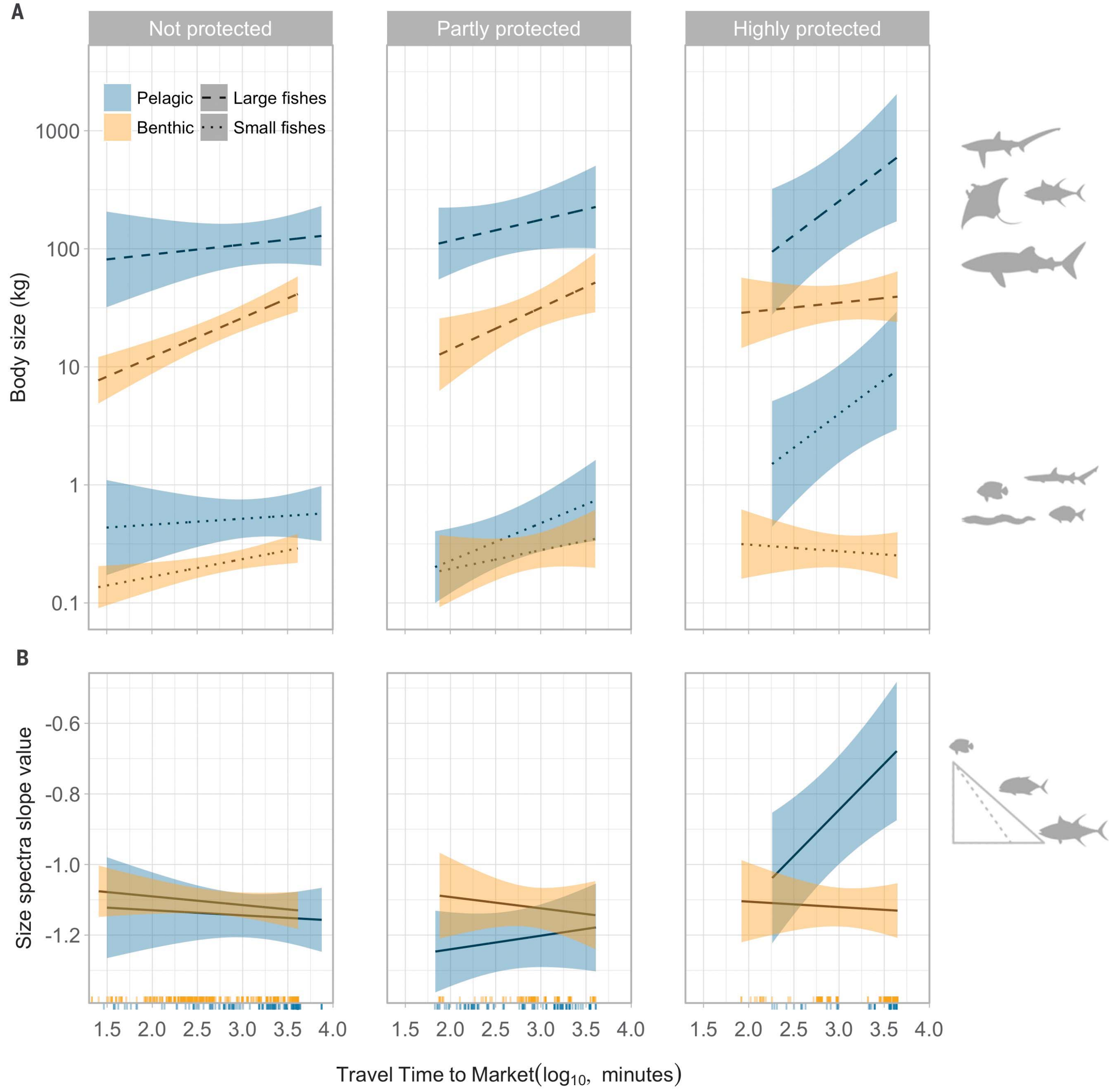

Fig. 4. Human influences on fish body-size structure in pelagic and benthic systems. Marginal plots of the influence of increased travel time to market ($\log_{10}$, min) on fish size indicators under different levels of protection status (not protected, partly protected, and highly protected). (**A**) Mean body size of relatively small and relatively large fishes ($\log_{10}$, kg). (**B**) Slopes of fish size spectra. Lines indicate predictions from GLS models, and shaded areas indicate 95% confidence intervals.

greater range of survey methods, including underwater visual censuses, scientific trawl surveys, and stock assessments (*14*, *40*). Our confidence that human pressure results in only marginally shallower benthic size spectra as a reflection of a comparatively minor change in relative proportion of larger size classes is strengthened by the observed consistency of this shallowing across protection status but is in contrast with expectation from "fishing down the food web" and other predictions from size-structured biodiversity loss (*41*).

Our results add to a body of evidence that suggests that benthic systems are relatively resilient compared with their pelagic counterparts. The emergence of benthic resilience is not fully understood, and any proposed mechanism in support is speculative. However, one possible explanation may be related to the emergence of alternative energy pathways when heavy exploitation triggers trophic cascades (*42*). Prey releases are generally predicted to occur as a consequence of trophic cascades under predator depletion (*43*). However, in benthic systems such as coral reefs, prey releases can be counteracted through size-based redundancy and feeding flexibility, which exist

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

as a result of high species richness (*14*). For example, increases in the relative proportion of trigger fish and wrasse are observed to counteract prey release of sea urchin, after depletion in high trophic levels (*14*), which results in greater food web flexibility and resilience. Benthic habitat complexity, which offers refugia for fish of intermediate sizes (30 to 500 g), may act further to moderate top-down control (*4*). Conversely, pelagic systems are associated with lower species richness and carnivorous feeding strategies with larger movement scales (*19*) across a wider range of body sizes, which results in low size-based redundancy. Trophic replacements have been reported in a pelagic food web (*44*): In the Benguela upwelling, a benthic species (the bearded goby *Sufflogobius bibarbatus*) was discovered to thrive after the depletion of sardines (*Sardinops sagax*) as a result of distinctive foraging behavior and physiological adaptations to anoxia. This replacement, which involved the emergence of a previously unknown benthic-pelagic association in response to external pressure, suggests that lack of resilience in pelagic food webs is associated with low size-based redundancy and limited alternative energy pathways.

Disentangling ecological processes from human pressures is notoriously complicated by the correlated and often confounding nature of human activities. In this work, potentially confounding differences in exploitation histories and fisheries practices exists between pelagic and benthic ecosystems. Benthic trawl fisheries were some of the first to be developed after industrialization (*45*), whereas pelagic fisheries developed comparatively later (*21*), under rising profit requirements (*46*). As such, a loss of baseline and a preselection of particular sizes likely occurred before our surveys (*47*). However, potentially confounding histories in each system is unlikely to explain the distinction in size-structured characteristics or the divergent responses to human pressure. This is because human pressure near markets resulted in pelagic and benthic systems that are more similar in size structure than their remote and more pristine counterparts, with greater overlap in size spectra slope values and convergent size structure. If the effect of market distance on size spectra or the general distinction between pelagic and benthic systems were confounded by historical size preselection, we would expect to see remote pelagic and benthic systems with greater overlap in size spectra value than those near market, as a reflection of more pristine and therefore less distinct states in those remote locations, in contrast to our results. Moreover, that historical baselines in pelagic and benthic systems are likely more characteristic and dissimilar to each other than they are in their present state is consistent with hypothesized preselection from historical habitat loss (*45*, *48*): Under habitat degradation scenarios, benthic size spectra are in fact expected to adopt characteristics more reminiscent of those of pelagic systems, with more pronounced peaks and greater spread (*4*), which reflects loss in size-structured refugia at intermediate sizes.

Policy implications

International policy, including the Kunming-Montreal Global Biodiversity Framework (GBF) COP15 declaration of 30% of the ocean to be protected by 2030 (*6*), requires that extensive areas of the oceans are set aside for protection in order to enhance biodiversity, ecosystem function, and ecological integrity and connectivity. To meet multiple GBF targets and address several of the UN Sustainable Development Goals, our analysis addressed two questions that are critical to the implementation of MPAs, related to ecological indicators and MPA placement, and one question concerning sustainable fisheries practices more broadly.

1) Particular characteristics of pelagic systems result in size structure that is highly sensitive to human pressure and render size indicators a powerful guide for priority placements of spatial protection, monitoring, and ecosystem-based management. In benthic systems, size indicators are comparatively less sensitive, so decisions should be informed through other indicators such as biomass (*7*) or functional diversity (*49*).

2) Pelagic vulnerability across multiple size classes reinforces the need for protection to provide refugia and rebuild depleted populations. A reversal of ongoing marine megafauna loss (*19*) is possible but requires intervention efforts that include implementation of highly protected MPAs in remote locations, including on the High Seas, consistent with the new High Seas Treaty (*50*). Homogenization of pelagic and benthic size structures signals the extent of already-experienced human impacts on benthic systems. For benthic systems, we confirm that protection would offer greater relative benefits in accessible locations (*7*), which should also be prioritized in order to rebuild coastal habitats and ecosystems.

3) Human impact across pelagic size classes indicates that it is not just the large predators that are vulnerable but also smaller-sized species, which underpin major fisheries, such as the anchoveta and sardines (*12*). Whether for single species or "balanced harvesting" strategies that target the entire size spectra, pelagic fisheries remain attractive to the commercial industry (*12*, *19*). However, top-down control and low body-size redundancy are characteristics that render pelagic ecosystems inherently dynamic and vulnerable to overexploitation. We therefore caution against further expansion in pelagic fisheries, many of which are already overexploited or fully exploited, particularly as long as pelagic megafauna and the top-down control they exert remain threatened (*19*).

Conclusions

Our size-based assessment has enriched our understanding of ongoing marine biodiversity loss, revealing divergent impacts across pelagic and benthic communities, which may, as a result, converge toward a common intermediate and artificial size structure. Many processes that are important for maintaining productivity across trophic levels are supported by size-structured association within coupled benthic-pelagic systems. Convergence of pelagic and benthic communities toward an artificial size structure should be of concern if this results in a decoupling of pelagic and benthic ecosystem components, thereby disrupting fundamental processes that underpin functionality. Alternatively, it is plausible that these processes are buffered by the emergence of previously unknown benthic-pelagic associations, thereby ensuring resilience under size-structured biodiversity loss. To help address the uncertainty concerning the functional consequence of size structure erosion, we recommend that future research efforts explore the link between size structure, ecosystem functioning, and connectivity, particularly in the context of coupled benthic-pelagic systems. Such knowledge would also have application within biodiversity conservation and ecosystem restoration.

REFERENCES AND NOTES

1. R. H. Peters, *The Ecological Implications of Body Size*, Cambridge Studies in Ecology (Cambridge Univ. Press, 1983).
2. C. F. Clements, M. A. McCarthy, J. L. Blanchard, *Nat. Commun.* **10**, 1681 (2019).
3. P. Le Mézo, J. Guiet, K. Scherrer, D. Bianchi, E. Galbraith, *Biogeosciences* **19**, 2537–2555 (2022).
4. A. Rogers, J. L. Blanchard, P. J. Mumby, *J. Appl. Ecol.* **55**, 1041–1049 (2018).
5. E. Sala *et al.*, *Nature* **592**, 397–402 (2021).
6. Convention on Biological Diversity, *Conference of the Parties to the Convention on Biological Diversity (CBD/COP/15/Part-II/L.1)* (United Nations Environment Programme, 2022).
7. J. E. Cinner *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **115**, E6116–E6125 (2018).
8. P. M. Yurista *et al.*, *Can. J. Fish. Aquat. Sci.* **71**, 1324–1333 (2014).
9. F. J. Heather, R. D. Stuart-Smith, J. L. Blanchard, K. M. Fraser, G. J. Edgar, *Ecol. Lett.* **24**, 2146–2154 (2021).
10. A. G. Rossberg, U. Gaedke, P. Kratina, *Nat. Commun.* **10**, 4396 (2019).
11. J. P. W. Robinson, J. K. Baum, *Can. J. Fish. Aquat. Sci.* **73**, 496–505 (2016).
12. M. A. Peck *et al.*, *Prog. Oceanogr.* **191**, 102494 (2021).
13. S. Medoff, J. Lynham, J. Raynor, *Science* **378**, 313–316 (2022).
14. N. A. J. Graham *et al.*, *Curr. Biol.* **27**, 231–236 (2017).
15. M. McLean *et al.*, *Glob. Change Biol.* **25**, 3972–3984 (2019).
16. N. E. Bosch *et al.*, *Conserv. Biol.* **36**, e13807 (2022).
17. See supplementary materials and methods.
18. R. Froese, P. Pauly, FishBase (2022); https://www.fishbase.org.
19. N. Pacoureau *et al.*, *Nature* **589**, 567–571 (2021).
20. D. A. Kroodsma *et al.*, *Science* **359**, 904–908 (2018).
21. D. Tickler, J. J. Meeuwig, M.-L. Palomares, D. Pauly, D. Zeller, *Sci. Adv.* **4**, eaar3279 (2018).
22. M. Di Lorenzo *et al.*, *Nat. Commun.* **13**, 4381 (2022).
23. J. L. Blanchard, R. F. Heneghan, J. D. Everett, R. Trebilco, A. J. Richardson, *Trends Ecol. Evol.* **32**, 174–186 (2017).
24. C. M. Duarte *et al.*, *Glob. Ecol. Biogeogr.* **31**, 1422–1439 (2022).
25. R. Trebilco, J. K. Baum, A. K. Salomon, N. K. Dulvy, *Trends Ecol. Evol.* **28**, 423–431 (2013).

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024

26. K. L. Nash, N. A. J. Graham, S. K. Wilson, D. R. Bellwood, *Ecosystems* **16**, 478–490 (2013).
27. A. Rogers, J. L. Blanchard, P. J. Mumby, *Curr. Biol.* **24**, 1000–1005 (2014).
28. J. L. Blanchard *et al.*, *J. Anim. Ecol.* **78**, 270–280 (2009).
29. R. A. Morais, D. R. Bellwood, *Curr. Biol.* **29**, 1521–1527.e6 (2019).
30. J. Mourier *et al.*, *Curr. Biol.* **26**, 2011–2016 (2016).
31. C. S. Bird *et al.*, *Nat. Ecol. Evol.* **2**, 299–305 (2018).
32. P. D. van Denderen, M. Lindegren, B. R. MacKenzie, R. A. Watson, K. H. Andersen, *Nat. Ecol. Evol.* **2**, 65–70 (2018).
33. Y.-J. Shin, M.-J. Rochet, S. Jennings, J. G. Field, H. Gislason, *ICES J. Mar. Sci.* **62**, 384–396 (2005).
34. A. M. Edwards, J. P. W. Robinson, M. J. Plank, J. K. Baum, J. L. Blanchard, *Methods Ecol. Evol.* **8**, 57–67 (2017).
35. A. C. AitkenIV, *Proc. R. Soc. Edinb.* **55**, 42–48 (1936).
36. G. J. Edgar *et al.*, *Nature* **506**, 216–220 (2014).
37. K. Grorud-Colvert *et al.*, *Science* **373**, eabf0861 (2021).
38. E. Maire *et al.*, *Ecol. Lett.* **19**, 351–360 (2016).
39. J. P. W. Robinson *et al.*, *Glob. Change Biol.* **23**, 1009–1022 (2017).
40. T. A. Branch *et al.*, *Nature* **468**, 431–435 (2010).
41. D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., *Science* **279**, 860–863 (1998).
42. W. J. Ripple *et al.*, *Trends Ecol. Evol.* **31**, 842–849 (2016).
43. T. Fung, K. D. Farnsworth, D. G. Reid, A. G. Rossberg, *Nat. Commun.* **6**, 6657 (2015).
44. A. C. Utne-Palm *et al.*, *Science* **329**, 333–336 (2010).
45. C. Roberts, *The Unnatural History of the Sea: The Past and Future of Humanity and Fishing* (Gaia, 2007).
46. S. A. Sethi, T. A. Branch, R. Watson, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 12163–12167 (2010).
47. D. Pauly, *Trends Ecol. Evol.* **10**, 430 (1995).
48. N. A. J. Graham *et al.*, *Conserv. Biol.* **21**, 1291–1300 (2007).
49. A. Dalongeville *et al.*, *J. Appl. Ecol.* **59**, 2803–2813 (2022).
50. United Nations General Assembly, "Draft agreement under the United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction" (United Nations, 2023).
51. L. Vigliola, G. Mou Tham, J.-B. Juhel, BRUVS_Seabed_APEX. Zenodo (2024); https://doi.org/10.5281/zenodo.7793637.
52. L. Vigliola, G. Boussarie, T. Letessier, J. Meeuwig, BRUVS_Midwater_APEX. Zenodo (2024); https://doi.org/10.5281/zenodo.7793697.

ACKNOWLEDGMENTS

This work and associated analyses were only made possible through the dedicated video-processing efforts from numerous colleagues, technicians, and students. In particular, we thank P. Bouchet, T. Langlois for Global Archive, S. Weber, A. López, G. Kendrick, J. Clough, N. Casajus, J. Monk, D. Tickler, and G. Boussarie. We are also grateful for the assistance of the master and crew of the numerous vessels from which the field work was conducted. T.B.L. acknowledges OKEANOS, Department of Oceanography and Fisheries, University of the Azores, for hosting him and thus facilitating collegial discussions around the analysis. Other aspects of this work also benefited from discussions with experts and colleagues at the Institute of Marine and Antarctic Studies, University of Tasmania, and at the Australian Antarctic Program. **Funding:** This work was funded by the Australian Institute of Marine Science; PTT Exploration and Production PLC; Australian Academy of Science; Chevron; Darwin Initiative (grant no. DPLUS063); European Union's BEST initiative (grant no. 1599); Fisheries Research and Development Corporation; Ian Potter Foundation; Jock Clough Foundation; MERL; National Geographic - Pristine Seas; Natural Heritage Trust; National Environmental Research Program (UK); National Environmental Science Program (AUS); Pilbara Marine Conservation Partnership (AUS); Rottnest Island Authority; TeachGreen; Totale (Fr); Vermilion Oil and Gas Australia; Waitt Institute; WA Marine Science Institute; Woodside Energy; Galapagos Conservation Trust; Galapagos Science Center; MigraMar (EC); European Union, MARHAB (grant no. 101135307); Norwegian Agency for Development Cooperation (NORAD); Norwegian Embassy in Khartoum (SD) through UNIDO (SAP ID 130130); Norway county municipality of Trøndelag; municipalities of Hitra, Frøya, and Tvedestrand; French Oceanographic fleet through Pristine and Apex campaigns; and the IMR Coastal Ecosystems Programme. T.B.L. was funded by the synthesis center CESAB of the French Foundation for Research on Biodiversity (FRB), the Mediterranean Centre for Environment and Biodiversity Laboratory of Excellence (CeMEB LabEx) (https://www.labex-cemeb.org), and the Bertarelli Foundation. **Permits:** All research activities were conducted under national authority permits issued by Ascension Island Government (ERP-2017-08); Australian Commonwealth Government [PKNP_2016_1, PA2018-00091-1 (variation PA2018-00091-3), PA2018-00091-2 (variation PA2018-00091-4),CMR-16-000426, CMR-18-000550, CMR-17-000526, PA2018-00036-1, PA2018-00079-1, CMR-17-000526, CMR-17-000526]; Australian Government Great Barrier Reef Marine Park Authority G17/39150.1, DBCA 01-000049-8; Delegation regionale à la recherche et à la technologie - Haut-commissariat de la Republique en Polynesie Francaise, 05/08/2014; Department of Parks and Wildlife 01-000049-7; Directorate of Fisheries 23/4532; Foreign and Commonwealth Office, British Indian Ocean Territory Directorate; France's Ministry of Ecological Transition, Le Haut commissariat de la république en Polynésie Française; Galapagos National Park Directorate, El rol de los islotes oceánicos para la protección de especies marinas migratorias; Government of French Polynesia Declaration 01/03/2013; Government of New Caledonia Convention 120325; Marine Fisheries Administration, Port Sudan, Red Sea State; Ministerio de Medio Ambiente y Desarrollo Sostenible, Ministry of Fisheries, Marine Resources and Agriculture; Environment Protection Agency Permit for route through MPA work; Ministry of Foreign Affairs of the Kingdom of Tonga; Niue Department of Fisheries, Agriculture and Forestry; Regional Government of the Azores; Palau National Government; Sistema Nacional de Áreas de Conservación (SINAC); Ministerio de Medio Ambiente y Energía; Serviço do Parque Natural da Madeira; Norwegian Directorate of Fisheries; Southern and Northern Province of New Caledonia; Tristan da Cunha Government. **Author contributions:** Authors 4 to 17 appear in alphabetical order and contributed equally to this work. Conceptualization: T.B.L., D.M., L.Vi., and J.J.M.; Data curation: T.B.L., J.J.M., H.J.C., L.M.; Formal analysis: T.B.L., D.M., L.M.; Funding acquisition: J.J.M., E.S., T.B.L., L.Vi., D.M., N.M., E.M.; Visualization: T.B.L.; Writing – original draft: T.B.L., D.M., L.M.; Writing – review and editing: D.M., L.M., H.J.C., E.M.E., S.M.E., A.M.F., A.H., J.-B.J., A.R.K., E.M., N.M., P.J.N.-K., E.S., C.D.H.T., L.Ve., J.J.M. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Data from New Caledonia, Tonga, and French Polynesia for seabed BRUVS (*51*) and for midwater BRUVS (*52*) are available at Zenodo. The remaining data from the other 77 locations and reproducible code for this analysis are available at https://github.com/LauraMannocci/sizespectra and can be found on the FishBase BRUVS portal (www.fishbase.org). **License information:** Copyright © 2024 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. https://www.science.org/about/science-licenses-journal-article-reuse

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adi7562
Materials and Methods
Supplementary Text
Figs. S1 to S9
Tables S1 to S5
References (*53*–*80*)
MDAR Reproducibility Checklist

Submitted 16 May 2023; accepted 24 January 2024
10.1126/science.adi7562

Downloaded from https://www.science.org at bibCNRS INSB on February 29, 2024