

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

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Abstract :

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.

76 **Introduction**

77 Body size is a universal biological property that influences ecological processes at the
78 individual, population, and ecosystem level (1). Measuring size spectra (size-frequencies
79 plotted on a log-log scale) is therefore a useful framework through which to understand and
80 predict overexploitation (2), nutrient cycling (3), and productivity (4). Moreover,
81 understanding how body sizes are distributed in the oceans has ramifications for conservation
82 and fisheries science and is highly relevant to several of the UN Sustainable Development
83 Goals. In particular, effective biodiversity conservation (5) and 30% protection coverage by
84 2030 ('30 by 30' goal) (6) require understanding of how successful marine protected areas
85 (MPAs) are likely to be in different socio-environmental contexts (7). Within a given pelagic
86 or benthic system, size spectra typically show consistent alternations between overrepresented
87 and underrepresented sizes, resulting in regular peaks and troughs (8, 9). When slopes of size-
88 spectra are shallow and peaks are prominent, the spread between peaks is generally considered
89 to reflect predator-prey relationships, with each peak representing a different trophic group that
90 is preyed upon by the next, e.g. plankton, planktivorous fishes, piscivorous fishes (10, 11).
91 However, assessing such size-structured variation across marine habitats and regulations is
92 particularly challenging since dedicated survey methodologies with different size-selectivity
93 are used in pelagic and benthic systems. For instance, while pelagic fishes are conventionally
94 sampled through longlines and midwater trawls or acoustic techniques (12, 13), benthic fishes
95 are mainly surveyed via underwater visual census (14), or with bottom-trawls and other habitat-
96 specific gears (15), making inter-system comparisons difficult.

97

98 Stereo baited remote underwater video stations (BRUVS) represent a unifying, non-destructive
99 and fisheries independent method that can estimate relative abundance and body size across
100 virtually any marine system (16). Here, we conduct a widespread size-based assessment of
101 marine pelagic and benthic nekton fishes (>1 g), spanning 6 orders of magnitude in body size,
102 from zooplankton size-classes (~3-4 cm), to large oceanic predators (~1,000 kg, Fig. 1). We
103 combine records from multiple surveys inside and outside MPAs, resulting in 6,701 BRUVS
104 deployed in pelagic systems and 10,710 BRUVS deployed in benthic systems, corresponding
105 to 13,402 and 10,710 hours of footage respectively, across the Atlantic, Indian, and Pacific
106 oceans. This database yield length measurements for individual fish, which were converted to
107 weights using taxa-specific allometric conversion parameters (17, 18) (Fig. 2, fig. S1).

108

109 In order to better understand how MPAs may effectively protect fish size structure in the
110 context of the '30 by 30' goal, we test two competing and mutually exclusive hypotheses
111 regarding the influence of human pressures on fish size structure in pelagic and benthic
112 systems. First, we hypothesise a greater human footprint in pelagic systems compared with
113 benthic systems since the larger body size and longer life of many oceanic species renders them
114 more vulnerable to fisheries (19). Therefore, we expect that pelagic fish size structure is more
115 sensitive to protection status and human pressures than for their benthic counterparts. As an
116 alternative hypothesis, the migratory capacity of many large pelagic species and the widespread
117 activities of high-sea fishing fleets (20) result in a comparatively low human footprint and low
118 MPA effectiveness in pelagic systems, in contrast to benthic systems where local human
119 pressure has acted longer (21) and where fish size structure would therefore be more impacted,
120 and where sedentary species would benefit more from MPAs (22).

121

122

123 **Body-size structure across systems**

124 Our surveys, conducted from January 2006 to May 2020, recorded a total 823,849 individual
125 fish (pelagic: 106,424, benthic: 717,425, Fig. 2), representing 139 families and 1,460 species
126 of fishes and sharks (pelagic: 211, benthic: 1,376) and 127 species recorded in both systems),
127 weighing a combined 744 metric tonnes (pelagic: 325 Mt; benthic: 418 Mt). Our dataset lacked
128 representation from the North Pacific, and representation in the central Pacific and in most of
129 the Atlantic was limited to pelagic systems only. Size frequency distributions were generated
130 by aggregating sizes within six broad brackets of absolute latitude (Fig. 3), revealing distinct
131 patterns within each systems that were robust to an unbalanced survey design (17). Benthic
132 median sizes were generally larger than pelagic medians (range of medians; pelagic 4-134 g,
133 benthic 27-120g) due to the greater representation of smaller size classes (<30 g). Upper size-
134 classes were better represented in pelagic than in benthic size distributions (range of 95th
135 percentiles, pelagic 0.4-83.3, benthic 1.3-2.9 kg, Fig. 3A). Size spectra slopes, a measure of
136 the proportion of large to small individuals (17), were contrasted between systems by
137 regressing normalised size-frequency distributions on the \log_{10} - \log_{10} scale (Fig. 3B). Slope
138 values were consistently steeper (more negative) in benthic than in pelagic systems (table S1),
139 reflecting the greater absolute and relative number of large individuals in pelagic systems (17).

140
141 Both the spread between peaks and size spectra slope values were distinct between pelagic and
142 benthic systems across biogeographical scales, suggesting that each system supports distinct
143 food webs and energy pathways (23). The presence of prominent peaks in pelagic systems is
144 consistent with previous reports (10) and suggests that each peak reflects a trophic group
145 preyed upon by the next, with shallower slopes reflecting carnivorous feeding (11). In benthic
146 systems, peaks were less clearly defined and slopes steeper, consistent with greater levels of
147 herbivorous feeding (11) likely stemming from greater dependence on seabed algae compared
148 to in the midwater (24). Greater prevalence of carnivory in pelagic systems implies that the
149 proportion of production retained between trophic levels is higher (25), as a result of more
150 direct energy transfer than in benthic systems. Overrepresentation of intermediate size-classes
151 (30-500 g) in benthic systems is consistent with complex habitat structure in coastal ecosystems
152 such as kelp forests and coral reefs (26) providing size-selective refugia (27). Elevated benthic
153 productivity within these size classes are further promoted through system connectivity and
154 benthic-pelagic coupling (28), whereby passively drifting plankton are consumed by
155 planktivorous and piscivorous fishes near the seabed (29). Conversely, pelagic productivity
156 and energetic needs in upper trophic levels are promoted by more direct energy transfer (11)
157 and are facilitated by greater home ranges in order to forage from the top of multiple benthic
158 food-webs (30), or from more productive geographical regions such as those in temperate
159 latitudes (31). Mobile strategies in these upper trophic levels typically involve pelagic foraging
160 incursions, or are associated with fully pelagic lifestyles (32), resulting in greater prevalence
161 of upper trophic levels in pelagic systems.

162

163 **Human footprint on size structure**

164 We tested our hypotheses concerning the difference in relative sensitivity of pelagic and
165 benthic size structure by extracting three size indicators (33) from frequency size-distributions
166 of nekton fishes aggregated by survey date (17) (fig. S2), the typical body sizes (\log_{10} , kg) of
167 relatively small individuals and of relatively large individuals, as represented by the values at
168 the first and second modal frequency peaks, and the exponent b of the size spectra slope (34).
169 These three indicators capture dimensions of size structure within each system, at the scale of
170 the survey day, with the size of relatively small and large individuals representing relatively
171 lower and higher trophic levels respectively (10), and the size spectra slope theoretically
172 reflecting the steepness of the trophic pyramid (25). We then built explanatory generalised

173 least-square (GLS) models (35) to test the two competing hypotheses by identifying how
174 human pressure and protection status affected pelagic and benthic fish size indicators. In
175 addition to controlling for spatio-temporal autocorrelation and socio-environmental conditions
176 known to influence the effectiveness of spatial protection status (36) (fig. S3, table S2), our
177 models considered interactions between systems (pelagic or benthic) and protection status, as
178 represented by three different categories of spatial protection (37) (not protected, partially
179 protected, or highly protected)(17), and human pressure, as represented by travel time to human
180 markets (38) (\log_{10} minutes).

181
182 GLS models of relatively small and relatively large fishes achieved moderate explanatory
183 power ($\text{adj}R^2$, small individuals: 0.257, large individuals: 0.343) revealing an effect of market
184 proximity and protection status, which was consistent in direction but specific in magnitude to
185 each system ($P < 0.05$, Fig. 4A, fig. S4 to 5, table S3 to 4). In both systems, individuals were
186 larger if highly protected and remote from markets, consistent with our current understanding
187 regarding how vulnerability and exploitation vary with protection and accessibility (36).
188 However, relatively small and large individuals in pelagic systems were both consistently more
189 sensitive to protection status and to market remoteness, with a cumulative impact of protection
190 status and market remoteness. In benthic systems, relatively small individuals were less
191 sensitive to protection than large individuals, in keeping with expectations on how vulnerability
192 to exploitation varies with differences in life history (14, 19). Moreover, the effect of protection
193 status saturated with remoteness, with remoteness having increasingly less relative impact
194 under higher protection.

195
196 GLS models of size spectra ($\text{adj}R^2$, size spectra slope: 0.273, Fig. 4B, fig. S6, table S5) showed
197 divergent effects in each system, with size spectra slopes in pelagic systems showing a
198 pronounced and rapid steepening with market proximity under high protection, and marginal
199 effects of protection status and market proximity after that. In contrast, slopes in benthic
200 systems were marginally affected, becoming less negative (shallower) near markets,
201 independently of protection status. Without protection, steepening of pelagic slopes and
202 shallowing of benthic slopes resulted in converging size structure between systems with
203 considerable overlap in slope values in unprotected locations near markets. A sensitivity
204 analysis testing the model robustness to the unbalanced survey reported similar effects of
205 market proximity, with minor differences between models re-run with 10% of randomly
206 dropped data points (17). Greater differences were observed between model re-runs with
207 ocean-specific data dropped. Notably, the results of pelagic systems being highly responsive
208 to highly protected remote areas were conditional on the inclusion of the Indian Ocean data
209 (fig. S9). Our main findings concerning the direction of both remoteness and protection in
210 pelagic and benthic systems remained largely unchanged from those derived using the full
211 dataset.

212
213 Taken together, our models support our first hypothesis, that pelagic fish size structures are
214 more vulnerable to human pressure than their benthic counterparts. That both relatively small
215 and relatively large individuals in pelagic systems were consistently affected near markets
216 means that greater sensitivity in pelagic systems cannot be attributed solely to the greater
217 occurrence of larger (and therefore more vulnerable) individuals. In benthic systems, the
218 magnitude of protection effect declined with market distance, in contrast to a cumulative effect
219 with market distance in pelagic systems. This contrasting result means that high protection
220 status can – even near markets – mitigate human pressures in benthic systems, whereas
221 effective protection in pelagic systems requires market remoteness.

222

223 Our results suggest that size structure resilience to human pressure is lower in pelagic than in
224 benthic systems. In theory, size spectra slopes are expected to steepen with increasing human
225 exploitation as a consequence of predator depletion, leading to a commensurate decline in mean
226 trophic level (39). However, reports of human pressure responses in benthic systems are
227 conflicting, with both a steepening size spectra slope (39) and a modest increase in mean
228 trophic level reported (14, 40). This apparent conflict may stem from difficulties in
229 establishing appropriate baselines in 'pristine' benthic systems, which show wide ranging size
230 spectra slope values (39) (i.e -1.95 to -1.13) and both inverse and concave trophic pyramids
231 (14, 30). Our observations of only a marginal effect on benthic slopes are, in any case,
232 consistent with reports of a comparatively modest impact of human pressure on mean trophic
233 level, which has been corroborated from across a wide range of benthic systems, and arguably
234 by a greater range of survey methods, including underwater visual censuses, scientific trawl
235 surveys, and stock assessments (14, 40). Our confidence that human pressure results in only
236 marginally shallower benthic size spectra as a reflection of a comparatively minor change in
237 relative proportion of larger size classes is strengthened by the observed consistency of this
238 shallowing across protection status, but is in contrast with expectation from 'fishing down the
239 food web' and other predictions from size-structured biodiversity loss (41).

240
241 Our results add to a body of evidence suggesting that benthic systems are relatively resilient,
242 compared to their pelagic counterparts. The emergence of benthic resilience is not fully
243 understood and any proposed mechanism in support is speculative. However, one possible
244 explanation may be related to the emergence of alternative energy pathways when heavy
245 exploitation triggers trophic cascades (42). Prey releases are generally predicted to occur as a
246 consequence of trophic cascades under predator depletion (43). However in benthic systems
247 such as coral reefs, prey releases can be counteracted through size-based redundancy and
248 alternative feeding strategies, promoted by high species richness (14). For example, increases
249 in relative proportion of trigger fish and wrasse are observed to counteract prey-release of sea-
250 urchin, following depletion in high trophic levels (14), resulting in greater food web flexibility
251 and resilience. Benthic habitat complexity, which offers refugia for fish of intermediate sizes
252 (30-500 g), may act further to moderate top-down control (4). Conversely, pelagic systems are
253 associated with lower species richness and carnivorous feeding strategies with larger
254 movement scales (19) across a wider range of body sizes, resulting in low size-based
255 redundancy. Trophic replacements have been reported in a pelagic food web (44), in the
256 Benguela upwelling, involving a benthic species (the bearded goby *Sufflogobius bibarbatius*)
257 thriving after the depletion of sardines (*Sardinops sagax*), as a result of unique foraging
258 behaviour and physiological tolerances to anoxia. This emergence of a novel benthic-pelagic
259 association in response to external pressure suggests that lack of resilience in pelagic food webs
260 is associated with low size-based redundancy and limited alternative energy pathways.

261
262 Disentangling ecological processes from human pressures is notoriously complicated by the
263 correlated and often confounding nature of human activities. Here, potentially confounding
264 differences in exploitation histories and fisheries practices exists between pelagic and benthic
265 ecosystems. Benthic trawl fisheries were some of the first to be developed following
266 industrialisation (45), whereas pelagic fisheries developed comparatively later (21), under
267 rising profit requirements (46). As such, a loss of baseline and a preselection of particular sizes
268 likely occurred prior to our surveys (47). However, potentially confounding histories in each
269 system is unlikely to explain the distinction in size-structured characteristics, or the divergent
270 responses to human pressure. This is because human pressure near markets resulted in pelagic
271 and benthic systems that are more similar in size structure than their remote and more pristine
272 counterparts, with greater overlap in size spectra slope values and convergent size structure. If

273 the effect of market distance on size spectra or the general distinction between pelagic and
274 benthic systems were confounded by historical size preselection, we would expect to see
275 remote pelagic and benthic systems with greater overlap in size spectra value than near market,
276 as a reflection of more pristine and therefore less distinct states in those remote locations, in
277 contrast to our results. Moreover, that historical baselines in pelagic and benthic systems are
278 likely more characteristic and dissimilar to each other than their present state is consistent with
279 hypothesised preselection from historical habitat loss (45, 48): under habitat degradation
280 scenarios benthic size spectra are in fact expected to adopt characteristics more reminiscent of
281 pelagic systems, with more pronounced peaks and greater spread (4), reflecting loss in size-
282 structured refugia at intermediate sizes.

283

284 **Policy implications**

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

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

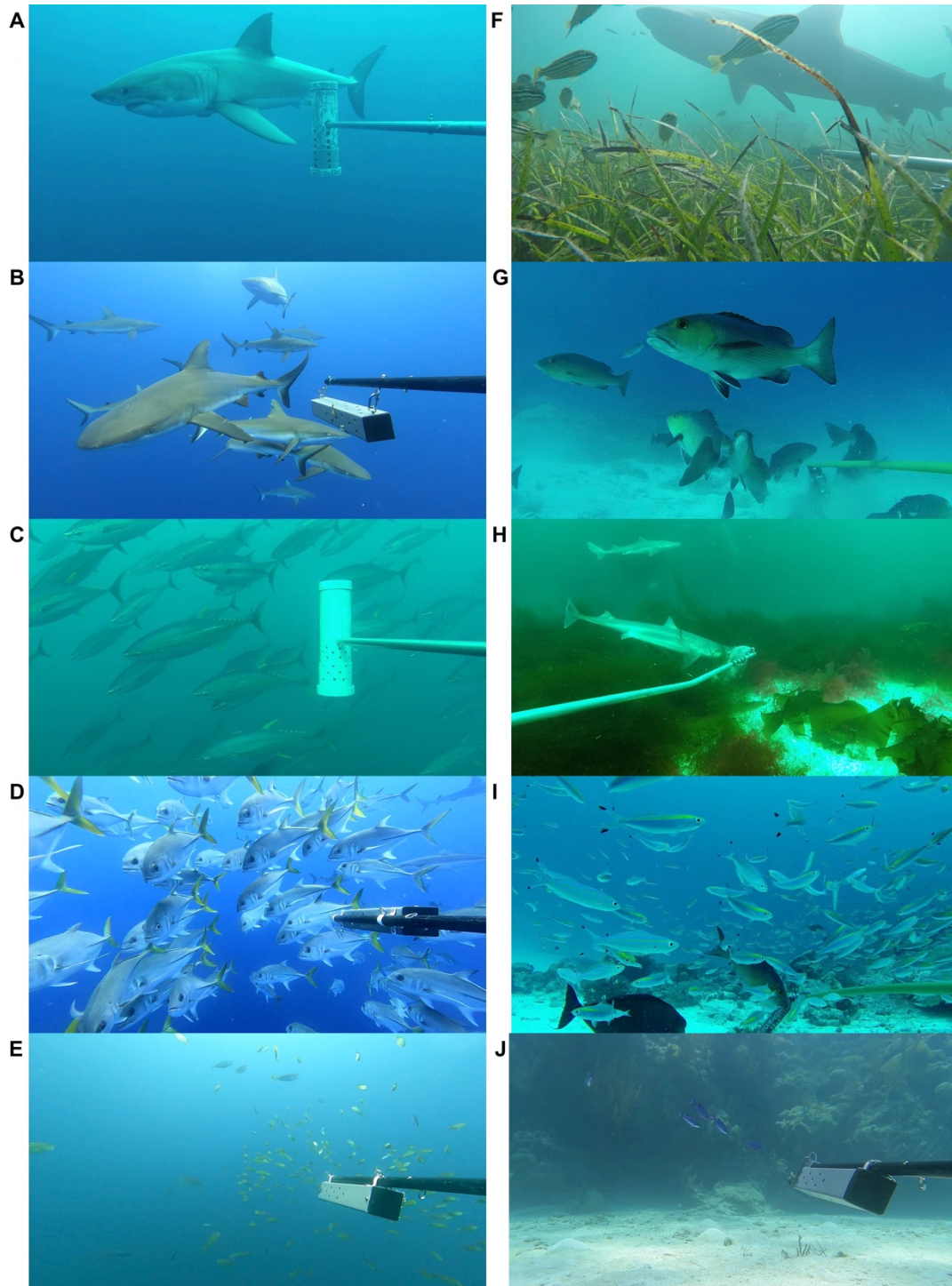
298 (ii) Pelagic vulnerability across multiple size classes reinforces the need for protection
299 to provide refugia and rebuild depleted populations. A reversal of ongoing marine
300 megafauna loss (19) is possible but require intervention efforts that include
301 implementation of highly protected MPAs in remote locations, including on the
302 High Seas, consistent with the new High Seas Treaty (50). Homogenisation of
303 pelagic and benthic size structures signals the extent of already-experienced human
304 impacts on benthic systems. For benthic systems, we confirm that protection would
305 offer greater relative benefits in accessible locations (7), which should also be
306 prioritised in order to rebuild coastal ecosystem.

307 (iii) Human impact across pelagic size-classes indicate it is not just the large predators
308 that are vulnerable but also smaller sizes, which underpin major fisheries such as
309 the anchoveta and sardines (12). Whether for single species or ‘balanced harvesting’
310 strategies that target the entire size spectra, pelagic fisheries remain attractive to the
311 commercial industry (12, 19). However, top-down control and low body-size
312 redundancy are characteristics that render pelagic ecosystems inherently dynamic
313 and vulnerable to overexploitation. We therefore caution against further expansion
314 in pelagic fisheries, many of which are already over- or fully-exploited, particularly
315 as long as pelagic megafauna and the top-down control they exert remain threatened
316 (19).

317

318 **Conclusion**

319 Our size-based assessment has enriched our understanding of ongoing marine biodiversity loss,
320 revealing divergent impacts across pelagic and benthic communities, which may – as a result
321 - converge toward a common intermediate and artificial size structure. Many processes
322 important for maintaining productivity across trophic levels are supported by size-structured
323 association within coupled benthic-pelagic systems. Convergence of pelagic and benthic
324 communities toward an artificial size structure should be of concern if this result in a
325 decoupling of pelagic and benthic ecosystem components, thereby disrupting fundamental
326 processes underpinning functionality. Alternatively, it is plausible that these processes are
327 buffered by the emergence of novel benthic-pelagic associations, thereby ensuring resilience
328 under size-structured biodiversity loss. To help address the uncertainty concerning the
329 functional consequence of size structure erosion, we recommend that future research effort
330 explores the link between size structure, ecosystem functioning, and connectivity, particularly
331 in the context of coupled benthic-pelagic systems. Such knowledge would also have
332 application within biodiversity conservation and ecosystem restoration.
333

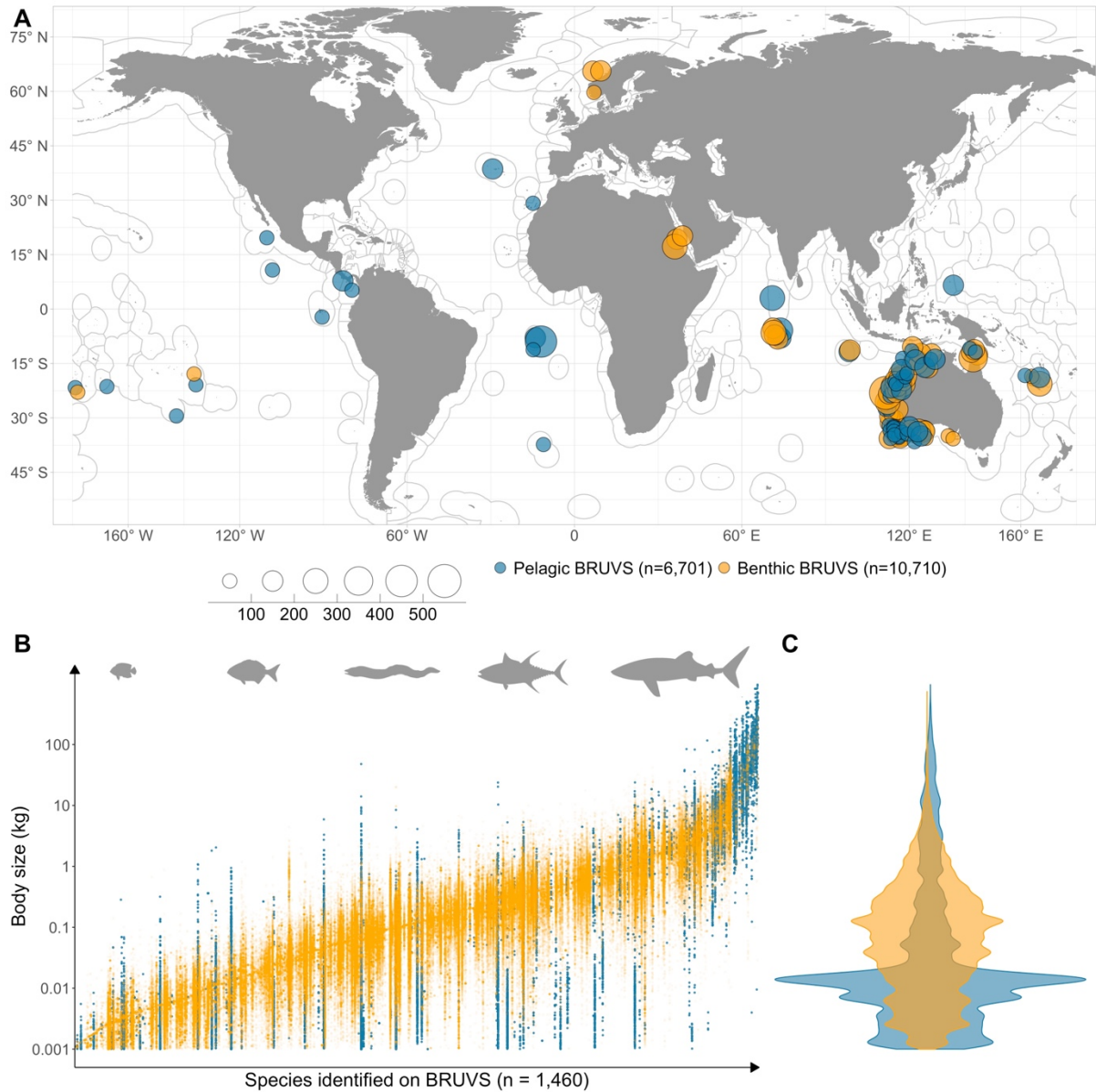


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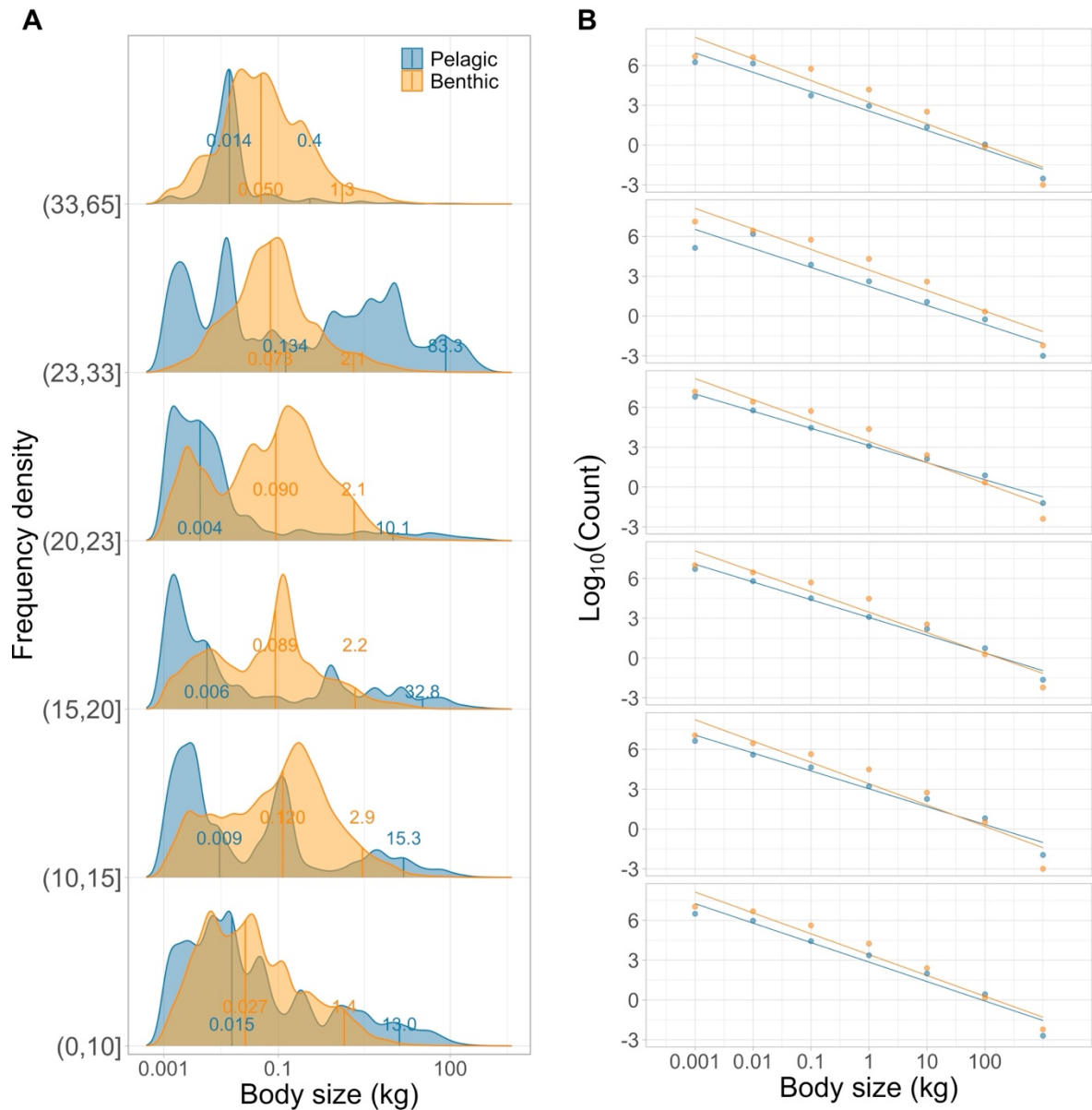
338 **Fig. 1. Body-size variability in pelagic (left panels) and benthic (right panels) systems,**339 **recorded by stereo baited remote underwater video systems (BRUVS) (A) Great white**340 **shark (*Carcharodon carcharias*). (B) Grey reef shark (*Carcharhinus amblyrhynchos*). (C)**341 **Yellowfin tuna (*Thunnus albacares*). (D) Horse-eye jack (*Caranx latus*). (E) Juvenile jack**342 **(Carangidae sp). (F) Tiger shark (*Galeocerdo cuvier*). (G) Two-spot red snapper (*Lutjanus***343 ***bohar*). (H) Spiny dogfish (*Squalus acanthias*). (I) Goldband fusilier (*Caesio chrysozona*). (J)**344 **Creole wrasse (*Clepticus parrae*)**

344



346
347

348 **Fig. 2. Body sizes of pelagic and benthic fishes identified on BRUVS.** (A) Survey effort of
 349 BRUVS, showing the outlines of the world's Economic Exclusive Zones in grey contours
 350 (some of which are contested). Each dot represents a single expedition, with the dot diameter
 351 being proportional to the number of BRUVS deployed. Dots are jittered to minimise
 352 overplotting. (B) Pelagic and benthic fish body-sizes (kg, n=823,849) categorised by species
 353 identity (n =1,460), rank-ordered by median species body size (C) Marginal density
 354 distribution plots of body-sizes.



355

356

357 **Fig. 3. Pelagic size spectra are shallower than their benthic counterparts across**

358 **biogeographical scales. (A)** Frequency density distribution of body sizes aggregated into six

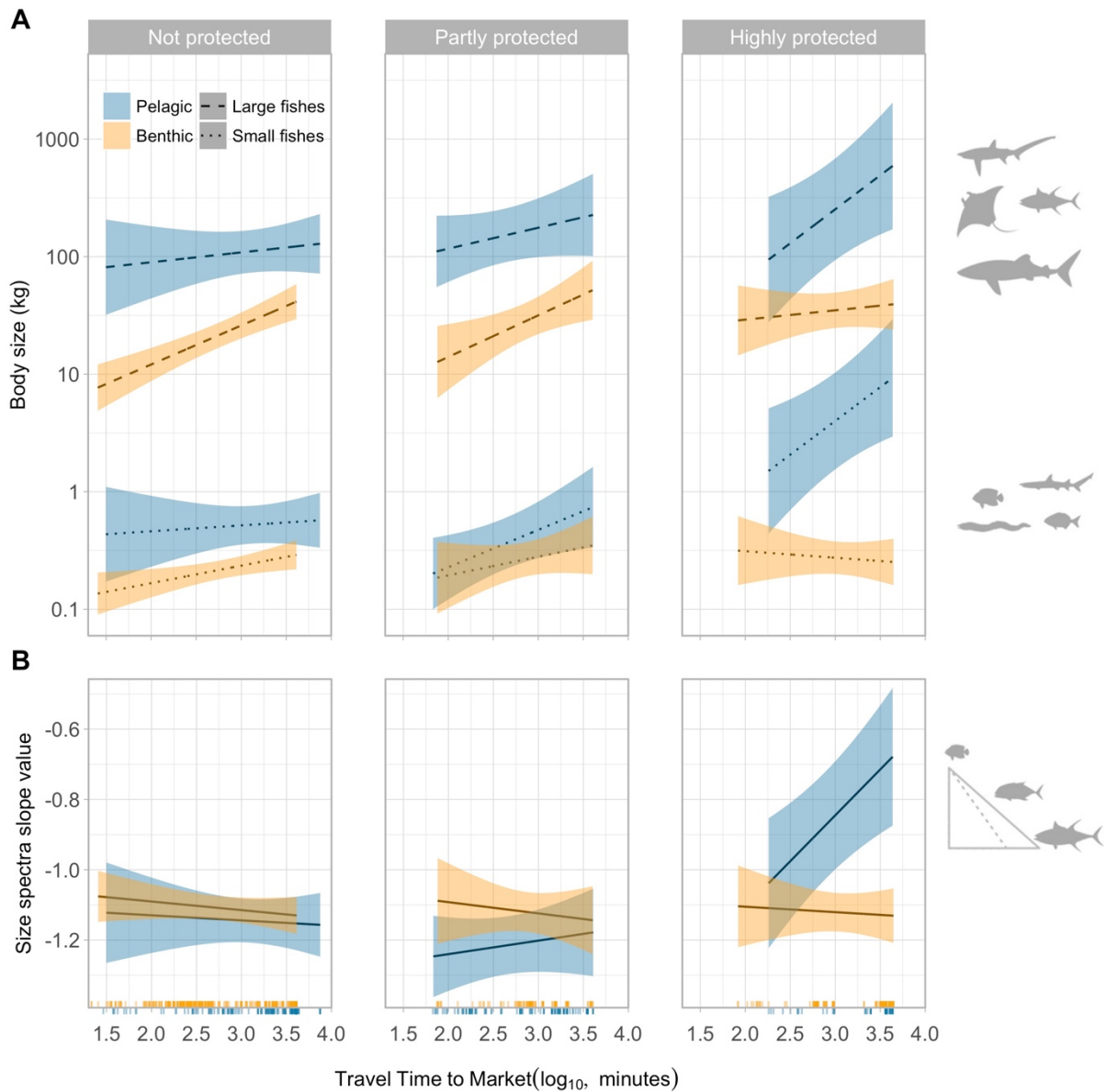
359 absolute latitude brackets (0-10, 10-15, 15-20, 20-23, 23-33, 33-65) of equal numbers of body

360 sizes ($n = 137,308$), with vertical line and number showing median and 95th percentile values.

361 **(B)** Abundance size spectra, normalised by dividing the frequency counts by the width of the

362 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).



363
 364 **Fig. 4. Human influences on fish body-size structure in pelagic and benthic systems.**
 365 Marginal plots of the influence of increased travel time to market (\log_{10} , minutes) on fish size
 366 indicators under different levels of protection status (not protected, partly protected, and highly
 367 protected). **(A)** Mean body size of relatively small and relatively large fishes (\log_{10} kg). **(B)**
 368 Slopes of fish size spectra. Lines indicate predictions from generalised least-square models,
 369 and shaded areas indicate 95% confidence intervals.
 370

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400

401 **Data availability statement**

402 Data from New Caledonia, Tonga and French Polynesia will be made available upon
403 acceptance on Zenodo at <https://doi.org/10.5281/zenodo.7793637> for seabed BRUVS and at
404 <https://doi.org/10.5281/zenodo.7793697> for midwater BRUVS. The remaining data from the
405 other 77 locations and reproducible code for this analysis will be made available upon
406 acceptance at <https://github.com/LauraMannocci/sizespectra> and can be found on the FishBase
407 BRUVS portal (www.fishbase.org).

408

409 **Permits**

410 All research activities were conducted under national authority permit issued by: Ascension
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432 **Author contributions**

433 Conceptualisation: TBL, DM, LVi, and JJM.

434 Data curation: TBL, JJM, HJC, LM

435 Formal analysis: TBL, DM, LM

436 Funding acquisition: JJM, ES, TBL, LVi, DM, NM, EM

437 Visualisation: TBL

438 Writing – original draft: TBL, DM, LM

439 Writing – review & editing: DM, LM, HJC, EME, SME, AMF, AH, JBJ, ARK, EM, NM,

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441

442 **Competing interests**

443 The authors declare no competing interests

444

445

446 **Supplementary Materials**

447

448 Materials and Methods

449

450 Result in context

451

452 Figs. S1 to S9

453 Tables S1 and S5

454 References (51-79)

455 **Material and Methods**

456 ***Fish survey***

457 We assessed size structure of fish assemblages in pelagic and benthic systems by collating data
458 from new and existing baited videographic surveys, deployed in the midwater and on the
459 seabed, respectively. The surveys were conducted from January 2006 to May 2020, with
460 varying geographical representation of tropical, subtropical, temperate, and subarctic regions,
461 in the Indian, Pacific and Atlantic Ocean, ranging from 64° N to 40° S. The surveys used
462 standardised stereo baited remote underwater video systems (BRUVS, n = 17,411, Fig. 2A),
463 described below, deployed in the midwater (n = 6,701) and on the seabed (n = 10,710), from
464 147 expeditions (66 in the midwater, 81 on the seabed) nested within 80 locations (39 in the
465 midwater, 50 in the seabed, 9 in both).

467 Considerable efforts have already established the strengths and characteristics of BRUVS in
468 accurately survey fish assemblages, and they have repeatedly been shown to be robust in time
469 and space to detect changes in marine ecosystems (51, 52). In brief, stereo-BRUVS provide a
470 video record of fish species relative abundance and their size which are generated through fully
471 standardised deployments and video-processing (53). A permanent video record ensures that
472 species identifications can be retrospectively validated or revised as a function of new
473 information (e.g., independent ground-truthing) or in the case of taxonomic revisions. As is the
474 case for every survey method, BRUVS do not capture the entire species pool equally (54).
475 Notably, the use of bait means BRUVS are considered particularly effective at surveying
476 predatory fishes and sharks at the top end of the trophic/size spectrum (55). While BRUVS are
477 particularly suited at sampling carnivores, they also quantify herbivores and omnivores (56)
478 and we would therefore expect to quantify these taxa in a size class if present. Here, these
479 particular BRUVS consisted of a central bar with two fixed, underwater cameras (either GoPros
480 Hero versions 2 to 7 or - prior to 2012 - Sony HDR-CR2 version or similar), calibrated in
481 stereo. From the central bar a bait-pole was fixed, from which a bait container (either a meshbag
482 or perforated cylinder) loaded with approximately 1 kg of fresh or defrosted mashed fish,
483 typically a small pelagic species like herring (*Sardinops* spp) or small tuna (e.g., *Katsuwonus*
484 spp). The central bar was then customised for deployment using rigs tailored for either
485 midwater or seabed deployments. In midwater deployments, for surveying of pelagic systems,
486 the central bar was suspended at ten meters from a surface float, and counter-balanced with a
487 ballast held underneath, typically a 1-2 kg metal piece. These midwater units were then either
488 moored on the seabed, using a separate mooring line (n = 300) or – more frequently - deployed
489 as a freely drifting string of five (57) (n = 6,400), with 200 meters of surface line separating
490 each unit. The string was left to soak, record and drift for at least two hours. Two strings were
491 typically deployed as a pair, separated by approximately 500 meters, one pair in the morning
492 and one in the afternoon. The daily survey regimes varied, usually as a consequence of vessel
493 and crew capacity but ranged between 5 and 30 BRUVS (median 10) per day. In seabed
494 deployments, for surveying of benthic systems, the central bar was either encased within a steel
495 frame or supported on a tripod, which was lowered to- and recovered from the seabed using a
496 tether line and surface float. These units were left to record on the seabed for one hour. The
497 number of seabed deployments ranged between 1 and 69 per day (median 13). All deployments
498 occurred between 08:00 and 17:30 local time.

499
500 After recovery, the video footage was downloaded and analysed following a set protocol using
501 EventMeasure (<http://seagis.com>), by research technicians or postgraduate students trained in
502 fish taxonomy and video analysis. The protocol consisted of identifying all fish observed on
503 footage to the nearest taxonomic resolution, and recording their relative abundance as MaxN,

504 the maximum number of individuals on a single frame for a given species. Although we
505 expected midwater and seabed BRUVS to sample the pelagic and benthic fish size-distribution
506 equally, small fish in benthic systems (3-4 cm) are typically cryptic (58) and may be harder to
507 spot on the portion of the seabed footage comprising benthic habitat, than against a uniformly
508 coloured background in the midwater. Lengths measurement (fork length; midwater $n =$
509 $27,697$, seabed $n = 297,651$) were recorded at the time of MaxN. Although efforts were made
510 to measure each individual fish, this was not always possible, either because of time constraints
511 (e.g., for very high MaxN values $\sim >300$) or because the fishes were located too far from the
512 rigs for accurate stereo measurements (nominally >7 m). Individual fish not measured at the
513 time of MaxN were allocated a value in a hierarchical manner, based on availability, starting
514 with species average either from the BRUVS in question (or string, in the case of midwater
515 BRUVS), from the expedition or, from across all expeditions. All individual fork lengths (cm)
516 were converted to body mass (kg) using published Bayesian species-specific parameters (log
517 a vs b) for allometric length-weight conversion from FishBase (18) (www.fishbase.org, fig.
518 S1). For individuals not identified to species, lengths were converted to weight (kg) by
519 allocating average a and b conversion parameters for the genus, family or assemblage.
520 Conversions were made using the R package rfishbase (59). We applied a lower cut-off point
521 of 1 g (~ 3 -4 cm, $n=56,393$) since these small individuals were probably not comparatively
522 sampled in pelagic and benthic systems, nor are the stereo measurements and allometric
523 conversions associated with those sizes particularly reliable. This restricted all further analysis
524 to nekton fish size classes (>1 g, ~ 3 -4 cm, $n=823,849$).

525

526 *Survey design*

527 Surveys prior to 2012 ($n \sim 4,000$) were limited to seabed BRUVS within Western Australia.
528 Surveys outside of Western Australia, and in the midwater occurred from 2012 onwards. The
529 spatial design between locations varied as a function of expedition-specific differences in
530 survey vessels type (which included small skiffs, tugboats, private yachts, fishery and
531 oceanography research vessels) and in research objectives, but was broadly aimed to cover a
532 diverse range of pelagic and benthic systems in oceanic and coastal regions. For locations with
533 recurring expeditions, subsequent expeditions either aimed for partial replacement of
534 previously surveyed locations or replication of a fixed survey design.

535

536 Habitats targeted included shallow and deep seamounts, abyssal plains, continental shelves and
537 slopes, temperate and coral reefs, and submerged banks and shoals. Midwater BRUVS
538 deployments covered a range of seabed depth from shallow to abyssal (mean depth (m), range:
539 $642 [2-5725]$). Seabed BRUVS deployments were primarily in shallow water (mean depth (m),
540 range: $28.3 [2-468]$). The survey spanned a gradient of human pressures from near coastal hubs
541 and cities to remote locations such as the Galapagos (Ecuador), Cocos Island (Costa Rica), the
542 Chagos Archipelago (UK), the Chesterfields Islands (France), the Ascension (UK), the
543 Selvagens (Portugal) and Gough Island (UK), in the Atlantic, Indian, and Pacific Oceans, and
544 in marginal and often heavily exploited seas such as the Red Sea, Norwegian Sea, North Sea,
545 and Coral Sea.

546

547 *Contrasting size structure across pelagic and benthic systems*

548

549 Analysis of body-size frequency distributions and size spectra are highly sensitive to the spatio-
550 temporal and taxonomic scale across which sizes are aggregated (60). Our analysis was
551 therefore hierarchical, at two levels, to capture different ecological processes that may be
552 occurring at either biogeographical scales or at the scale of the survey day. First, we assessed
553 high-level generalities and differences between pelagic and benthic systems at biogeographical

554 scales, by grouping body sizes into six absolute latitude brackets (0-10, 10-15, 15-20, 20-23,
555 23-33, 33-65), each containing an equal number of body-size records ($n = 137,308$, Fig. 3A).

556

557 For each of the resulting six body-size frequency distributions, we estimated and visualised the
558 normalised slope of the pelagic and benthic abundance size spectra. Although some of the
559 guiding principles had been identified earlier, the concept of the size spectra stems from work
560 originally pioneered by Sheldon *et al* (61) and their conjecture that ‘the total mass within log
561 spaced size bins was constant over the size range from bacteria to whales’. We estimated the
562 size spectra slope from a linear regression of frequency distribution of pelagic or benthic sizes
563 on a \log_{10} - \log_{10} scale, within each latitudinal bracket (Fig. 3B). Within each bracket, we fitted
564 linear regression models of \log_{10} counts (n) of either pelagic or benthic sizes as a function of
565 counts within \log_{10} unit bins. We normalised the abundance (count) by dividing the count
566 within each bin by the actual width of the bin. This normalisation procedure is customary (62)
567 in order to account for different bin width and has the effect of reducing the linear regression
568 coefficient of the size-spectrum by 1, thus making the estimates directly comparable to the
569 exponent b derived from a power law using a Maximum Likelihood Estimate (34) (MLE).
570 Given the unequal number of midwater and seabed BRUVS deployed within each absolute
571 latitudinal bracket, we use these regressions only for purposes of comparing the slope between
572 pelagic and benthic size spectra, not the y-axis intercept value, which would vary depending
573 on the number BRUVS deployed.

574

575 ***Deriving size indicators of size structure***

576 Fishing is a highly size-selective activity and typically targets large individuals first which are
577 more economically attractive (33). Size indicators are therefore commonly used to assess
578 ecosystem responses to environmental change and to human activities, as part of ecosystem-
579 based management. Next, in order to assess the local-scale impact of human pressures on size
580 structure, we therefore developed three size indicators of pelagic and benthic fish assemblages
581 (fig. S2). Individual frequency distributions were generated by aggregating sizes using the date
582 of the BRUVS deployments as a grouping term ($n = 1,470$), resulting in a median number of
583 10 midwater BRUVS and 13 seabed BRUVS being aggregated, per date of survey. This
584 approach ensured strengthening the existing signal-to-noise ratio, by reducing variability in our
585 indicators, whilst retaining sensitivity to local environmental and human drivers.

586

587 Next, for each date-aggregated individual frequency distribution, we generated two indicators
588 of representative sizes by extracting the value of the first and second mode, when two modes
589 were significantly detected ($p < 0.05$; $n = 919$). These modal values were chosen to represent
590 the size of relatively small fish and relatively large fishes, respectively. We opted for modal
591 values due to the multimodal nature of the frequency distributions, which would render
592 measures such as the median or mean value (63) unrepresentative of common values, since
593 median or means would typically belong to a size class that was underrepresented e.g located
594 in the trough between two modes. Modal significance testing and extractions were done using
595 the function `modetest()`, and `locmodes()` in base R.

596

597 Finally, for individual size distributions that included a minimum of 20 individuals ($n = 1,041$)
598 we estimated the slope of the size spectra. We opted for the Maximum Likelihood Estimate
599 (MLE) of the power law exponent b of the size spectra slope, using code provided in (34). The
600 MLE approach directly estimates the coefficient b using classical likelihood methods, which
601 finds the value that maximizes the likelihood function for – in this case – the individual body
602 size data defined by the probability density function

603

604

$$f(x) = \frac{(b + 1)x^b}{x_{\max}^{b+1} - x_{\min}^{b+1}}$$

605

606 where x is the body size, b is the scaling exponent, and the distribution is bounded by the
607 possible sizes (x_{\min} and x_{\max}). We opted for the MLE approach for slope estimates at the scale
608 of the survey day, in contrast to regressing the count within bin (e.g. the log-linear method)
609 used at the biogeographical scales. Other alternative approaches for estimating the slopes were
610 considered during analysis (34), although the MLE approach produces values that were most
611 consistent and coherent values across the greater variability of frequency distributions
612 encountered at the scale of the survey day. All size indicators were truncated to three standard
613 deviations from the mean, to remove outliers (< 2% of records, for each indicator).

614

615 *Assessing size structure under human pressures*

616 Our objectives were to identify how size structures in pelagic and benthic systems would be
617 affected along a human pressure gradient under different levels of protection status. Our
618 analysis relies on an extensive body of literature documenting mechanisms by which pelagic
619 and benthic ecosystems are shaped through bio-geophysical processes and human activities.
620 These processes were captured by a suite of 25 socioeconomic (human), environmental, and
621 geomorphic variables, which we considered as potential explanatory variables in our
622 explanatory models of size indicators (table S2). All explanatory variables were extracted at
623 the latitude and longitude coordinates of the individual midwater or seabed BRUVS
624 deployment, and then averaged at the level of the survey date, to yield values corresponding
625 with the resolution and location of the size indicator records. In addition to these numerical
626 variables, we also considered two categorical variables, namely protection status (see below)
627 and system habitat (pelagic or benthic).

628

629 A considerable body of literature has already established the power in using metrics of human
630 accessibility- whether measured by travel-time to nearest market, distance to nearest population
631 or human ‘gravity’- in capturing the comprehensive nature of human pressures on benthic
632 systems (16, 38). Notably, conservation gain from protection status has been shown to be
633 highly contingent upon human accessibility (7). Here, although we anticipated human
634 accessibility to be the most generalisable indicator of human pressure on local size structure,
635 the inclusion of pelagic systems within our modelling framework, for which accessibility
636 indicator are less established than for benthic systems (although see (64)), meant that we
637 initially considered a broad range of human activity indicators, prior to model selection. We
638 developed metrics of human accessibility which included travelling time to market (min), and
639 linear distance to nearest population (38), linear distance to cities, and distance to nearest port
640 (m, <https://globalfishingwatch.org/>). Human variables related to governance included the
641 following national level variables: government effectiveness (World Governance Indicators,
642 WGI, https://papers.ssrn.com/sol3/papers.cfm?abstract_id=1682130) (65), number of year of
643 conflict (UCDP/PRIO Armed Conflict Dataset version 19.1), rule of law (WGI), absence of
644 violence (WGI), voice and accountability (WGI), control of corruption (WGI), Human
645 development index (<https://hdr.undp.org/>), number of active NGO, marine ecosystem
646 dependency (66). Fisheries activities specifically was considered by including an estimate of
647 total reconstructed catch (67) (<https://www.seaaroundus.org/>), total fishing effort from
648 automated identification systems (20) (<https://globalfishingwatch.org/>). Protection status was
649 classified as a three-level categorical term, determined using the World Database of Protected
650 Areas(68). Sites were classed as ‘highly protected’ if geographically situated inside a no-take
651 marine protected area (MPA) or inside an MPA with a no-take section (IUCN category I-II),

652 ‘partly protected’ if inside an MPA with some fishing allowed or of unknown status (IUCN
653 category III-VI), ‘not protected’ if open to fishing. For each site, we used the protection status
654 two years prior to the date of survey, to ensure sufficient time had passed for the protection
655 status to take effect. As a result of this classification scheme, each protection status category
656 contained a balanced number of records (between one quarter or one third of records), and each
657 system and protection status combination contained a range of variate values with substantial
658 overlap (fig. S3).

659

660 Environmental variables included the following variables: primary productivity, chlorophyll-a
661 concentration, sea surface temperature, weekly median and standard deviation
662 (<https://oceancolor.gsfc.nasa.gov/atbd/sst/>)

663

664 Geomorphic variables included the following variables: seabed depth (30 arcsecond,
665 https://www.gebco.net/data_and_products/gridded_bathymetry_data/), seabed slope
666 (computed using QGIS tools and GEBCO layer), distance to seamount (69) (m, computed
667 using QGIS and predictions of seamount locations), distance to coast (computed using QGIS
668 and coast lines from GADM 3.6), distance to coral reef (computed using QGIS tools,
669 <https://data.unep-wcmc.org/datasets/1>).

670

671

672 ***Explanatory modelling***

673 Prior to model fitting, the full suite of candidate explanatory variables was tested for
674 correlation: whenever a pair of variables were found to be correlated one of the variables was
675 discarded (Pearson’s correlation values >0.7 , table S2). To disentangle the interactions between
676 system (pelagic vs benthic), protection status, and human pressures on the three size indicators,
677 we build explanatory generalised least-square models (GLS) using the R nlme package (70).
678 These models controlled for background variability in socio-environmental and geomorphic
679 conditions which varied between midwater and seabed BRUVS deployments across our
680 survey, whilst accounting for spatial and temporal autocorrelation in the model residuals.

681

682 The fully saturated models, where system and protection status were interaction terms of all
683 socioeconomic variables, and system was an interaction term of all remaining variables (either
684 untransformed or using the \log_{10} value, table S2), took the following form, for each size
685 indicator:

686

687 Size indicator \sim System * protection status * (Travel time to market + Distance to port) +
688 System * (Seabed depth + Seabed slope + Distance to Seamount + Distance to Coral Reef +
689 Distance to Coast + Year of Survey + poly(Sea surface temperature median, 2) +
690 poly(Chlorophyll-a, 2))

691

692 The saturated models were further simplified using a variance inflation factor approach to
693 identify and remove residual collinear variables, in which variables yielding $VIF > 10$ were
694 removed. Different correlation structures were tested and compared using their Akaike
695 Information Criteria (AIC) values. The rational quadratic correlation structure (‘corRatio’)
696 yielded the lowest AIC value, for all size indicators. The VIF-simplified models and correlation
697 structure were further simplified using stepwise model selection, using the AIC, and the
698 *stepAIC* function in the ‘MASS’ package (71). Simplified models were further evaluated by
699 deriving the adjusted R^2 value, using the *model_performance* function in the ‘performance’
700 package (72), and through visual inspections of model prediction vs residuals plots, and
701 semivariograms. We tested for spatial autocorrelation in the model residuals using a Moran’s

702 index I. Standardized effect sizes of each explanatory variables and their interactions were
703 extracted and visualised with the function *plot_model* using the ‘sjPlot’, ‘sjlabelled’, and
704 ‘sjmisc’ packages (fig. S4 to 6, table S3 to 5).

705
706 Marginal relationships between travel time to market and size indicator in the six alternative
707 interaction term categories combination (System: pelagic or benthic; protection status: not
708 protected, partly protected, or highly protected) were evaluated using the *ggpredict* function
709 from the ‘ggeffects’ package (73). Usually, marginal relationships between a response variable
710 and an explanatory variable of interest are evaluated by generating model predictions across
711 the range of the explanatory variable of interest, whilst holding the remaining variables fixed
712 at the mean values. However, since the range of travel time to market sampled within each
713 categorical combination differed, this approach could lead to extrapolation and illegitimate
714 predictions beyond this range. Furthermore, using a global mean value may give an unrealistic
715 picture because of the different variable values within each system. To avoid extrapolation and
716 unrealistic predictions, we imposed three restrictions: 1) Marginal predictions were produced
717 only for the range of travel time to market encountered within each categorical combination,
718 meaning that the range of predictions varied between combinations. 2) We held remaining
719 variables at the mean values of either pelagic or benthic records for predictions in their
720 corresponding system (fig. S4). 3) We avoided combinatorial extrapolation by not
721 extrapolating marginal predictions into new combinations of variables, e.g. instances where
722 distance to port is high but travel time to market is low do not exist in reality (since every
723 market is by requirement also a port), so distance to port was by necessity held at the most
724 common value sampled within each category combination ($1.2 = \log_{10}15$, km).

725 726 *Sensitivity analyses*

727 All locations were not equally sampled by both midwater and seabed BRUVS, and some
728 locations were disproportionately surveyed. To ensure the robustness of our analysis to
729 unbalanced survey design and uneven effort we performed three sensitivity analyses. First, we
730 conducted the biogeographical analysis but this time aggregating the sizes within six
731 longitudinal brackets instead of absolute latitude (fig. S7). Second, we reran the GLS models
732 on 10 data subsets, after randomly removing 10% of the size indicators records (fig. S8). Third,
733 we reran the GLS models on 3 data subsets, by dropping all records from either the Atlantic,
734 Indian and Pacific oceans (fig. S9).

735
736 Our sensitivity analysis revealed that differences between pelagic and benthic size structure
737 across latitude were also congruent with differences across longitude (fig. S7). Moreover, GLS
738 models produced through the sensitivity analysis on subset datasets reported similar effects of
739 market proximity (fig. S8). Although we observed some minor to moderate differences in
740 model reruns with different ocean dropped (fig. S9) our main findings concerning the direction
741 of both remoteness and protection status in pelagic and benthic systems remained largely
742 unchanged. Taken together, these results suggest that our analysis was not overtly influenced
743 by unbalanced survey-design and uneven effort. Moreover, this suggests that our conclusions
744 concerning distinctness between pelagic and benthic size structures, relative influences of
745 market proximity, and effect of protection status across different systems are robust.
746 Geographical expansion in unsampled and unbalanced regions remains a priority in our
747 ongoing investigations. Nevertheless, we find it improbable that our conclusion concerning
748 pelagic and benthic response to human pressure and protection status will change with further
749 geographic coverage, as the inclusion of heavily fished areas (e.g., in the North Pacific and
750 Atlantic) will likely make these patterns more pronounced (10, 27). Moreover, our conclusion
751 that pelagic systems invariably contain the largest and smallest individuals, while being

752 species-poor, in contrast to benthic systems that contain an overrepresentation of medium
753 sized-individuals, though species-rich – appear robust.

754

755 **Results in context**

756 Through use of stereo-BRUVS and size indicators, we have conducted a fish size assessment
757 across marine habitats, and revealed fundamental differences in vulnerability of pelagic and
758 benthic systems, with implication for effective conservation strategies. We find that pelagic
759 size structures are only effectively protected inside highly protected MPAs if they are remote
760 from markets. More generally, pelagic size spectra are very rapidly eroded under increasing
761 human pressures, in contrast to benthic size spectra, which show resilience.

762

763 The value of the global abundance size spectra slope was originally hypothesised to be equal
764 to a b exponent of -2 (61). This value was recently confirmed empirically for the global ocean,
765 yielding a b exponent estimate of -2.04 (74). At smaller spatial scales, empirical size spectra
766 slopes typically deviate from this theoretical expectation. This in part due to variability inherent
767 in ecological systems but also because slope estimates are sensitive to taxonomic and spatio-
768 temporal resolutions, and to methodological differences (23). Here, the greater spread of
769 pelagic size spectra slopes compared with the benthic values (standard error, pelagic: 0.16,
770 benthic: 0.09) at the scale of the survey day probably reflects the greater patchiness of pelagic
771 ecosystems (75). However, this variability further means that the averages of our slope
772 estimates at the scale of the survey day (fig. S3) are not directly comparable between pelagic
773 and benthic systems, and that the comparison is better done at biogeographical scales, showing
774 consistently shallower size spectra in pelagic systems than in benthic counterparts (fig. S2 and
775 S8, table S1).

776

777 Elevated size-selectivity of most pelagic fishing gear means few applications of size spectra
778 analysis to pelagic fish assemblages exist in marine systems, with most existing pelagic
779 examples stemming from freshwater lakes (8, 10), making it difficult to find independent
780 validation of our slope values. In benthic systems however, fish size spectra analysis is
781 commonly applied to size structure. Our benthic slope estimates at biogeographical scales
782 (mean: -1.58, range: -1.63 to -1.54, Fig. 3, table S1) are shallower than previous estimates at
783 similar scales (76) (-1.88 ± 0.06). Consistently, our benthic size indicators MLE slope estimates
784 (mean -1.11, range: -2.28 to -0.13, fig. S2) are also shallower than those previously reported
785 (39) (-1.95 to -1.13). This contrast is consistent with expectation from BRUVS size-selectivity,
786 compared with size-selectivity of underwater visual census (UVC), from which these previous
787 slope estimates are derived. Although UVC typically under-sample larger size classes due to
788 predators such as sharks avoiding divers (77), BRUVS are baited precisely in order to attract
789 predators from across a greater catchment. We would therefore expect larger size-classes to be
790 relatively overrepresented in BRUVS compared to other survey methods, leading to shallower
791 slope estimates, in line with our findings. We note that inverted trophic pyramids with very
792 shallow slopes have been reported from UVC in both tropical and temperate systems [-0.49 to
793 -0.45 ± 0.13 to 0.14 (30); -0.55 ± 0.3 (78); we subtracted 1 from the unnormalized slope values
794 reported by (30) and (78) to make them directly comparable]. Such slope values are consistent
795 with ecological theory only in the presence of strong trophic subsidies from adjacent systems,
796 which act to support overrepresentation of larger size-classes. Our near-global survey reported
797 several instances of such abundant levels of sharks (e.g. $\text{Max}N > 30$), but only near remote
798 oceanic islands, on seamounts or on submerged reefs, where localised nutrient and energy
799 subsidies in the absence of human pressure can occur e.g. (79). Our maximum slope value of -
800 0.13 and our slope estimate of ~ -0.7 derived from the GLS model in remote and protected

801 locations are therefore consistent with values reported elsewhere, under comparable conditions,
802 using UVC. Finally, we note that although BRUVS probably resulted in overrepresentation in
803 larger size classes compared with other survey methods, our size spectra showed truncation at
804 larger size classes for the linear regression fit (fig. S2B), as is commonly observed in empirical
805 spectra (23).

806

807 MPAs can be more effective in countries under efficient management regimes (36). However,
808 our investigation did not detect any evidence of government effectiveness influence on neither
809 pelagic nor benthic size indicators, and the term was discarded due to high Variance Inflation
810 Factor (IF>10) in our GLS. Further inspection did not reveal any indication that size spectra in
811 effectively managed countries were less impacted, with shallower size spectra slopes. This
812 absence of a clear signal may be related to two possible factors (i) overall low variability of
813 benthic size-indicators resulting in low power to detect effect of government effectiveness, and
814 (ii) high sensitivity of pelagic size-indicators meaning that government effectiveness has little
815 to no influence near markets where pelagic size structure has already been impacted.

816

817

818

819

820

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