

Deep, remote, and protected: key conditions for fish reproductive potential in marine ecosystems

Ema COICAUD-TOURNOIS

Master Biosciences, Département de Biologie, Ecole Normale Supérieure de Lyon

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Marine fish communities are increasingly threatened by the combined effects of fishing pressure and ocean warming but the last refuges of mature individuals ensuring reproduction capacity are still poorly known and understood. By imputing life-history traits for 3,220 species, we assessed the maturity structure of 32,026 fish communities surveyed globally using a generalized spatial mixed model. Our results reveal widespread immaturity in tropical pelagic ecosystems, where species face intense anthropogenic pressure. In contrast, deep and remote areas serve as thermal and remote refuges, acting as reservoirs of mature individuals, while nearshore marine protected areas promote ontogenetic diversity. These findings underscore the need to extend fully protection towards deep and remote marine areas to safeguard reproductive capacity and ensure the long-term sustainability of fish stocks.

Introduction

Defaunation, defined as the global loss of animal species and the decline in the abundance of individuals within animal populations, is one of the most alarming consequences of the Anthropocene (1). The current rate of loss of vertebrate species is up to 100 times higher than past records suggesting that life on Earth is entering its sixth mass extinction, with habitat modification and direct exploitation considered the main drivers of this process (2, 3).

Although the defaunation in the ocean is more recent than on land or in freshwater (2), it is already coined as the blue acceleration (4). The quest for new, productive and profitable fishing grounds is the main driver of this blue acceleration, especially with industrial techniques developed over the last century gradually depleting marine faunas (5). A notable feature of this wildlife overexploitation is its strong size selectivity: large-bodied individuals are consistently removed first, both within and among species (6, 7). This selective bias increases extinction risk of large species, which tend to have slower life histories and lower population densities (8, 9). Climate change further exacerbates this pattern (3), as rising temperatures disproportionately affect large-bodied organisms due to their narrower thermal tolerances and greater ecological demands (10). In marine ecosystems, ocean warming results in a reduction in oxygen availability, which compromises the metabolic performance of fish (11, 12). Thus, direct exploitation and environmental pressures act synergistically to erode populations of large marine species, particularly fish like sharks and rays, with

cascading effects on biodiversity and ecosystem functioning (13).

Indeed, large individuals are more fecund and play unique structural roles in marine ecosystems (14–17). Therefore, at the individual level, size-selective pressures can favor earlier maturation and faster growth, altering behavioral and physiological traits over time (18–20). At the population level, the loss of large individuals reduces mean body size and skews sex ratios, undermining stock renewal through diminished fecundity (21, 22). Finally, at the community level, altered size structures can trigger trophic cascades and weaken key ecological processes such as herbivory and predation (23–25). So, the selective removal of large-bodied individuals, compounded by climate change, disrupts ecosystem functioning at multiple levels.

To manage exploitation, fisheries science has long relied on life-history traits of exploited species to guide stock assessments (Jennings et al, 2001). For instance, determining the size at maturity, defined as the length at which 50% of individuals are mature (L_m), allowed us to predict reproductive outputs, long-term population dynamics, and sustainable harvest thresholds. However, a recent study challenges the robustness of such trait-based stock assessments, which have overestimated fish population status in many regions, leading to a widespread illusion of sustainability (26).

In parallel to fisheries regulations based on stock assessments, Marine Protected Areas (MPAs) have emerged as a cornerstone of conservation strategies (27). MPAs are designated zones where human activities are restricted or

prohibited to halt biodiversity loss, rebuild depleted populations, and maintain ecosystem functions (28, 29) but also contributions to people (30). Fully protected MPAs, where fishing is entirely banned, consistently support higher densities and biomass of commercially important species than adjacent exploited areas (31–33). Yet, the capacity of MPAs to act as fecundity reservoirs remains insufficiently explored (34).

Given its central role in reproductive output, *Lm* has been a cornerstone of fisheries science, but its broader application as an indicator of ecosystem health across species and human impact gradients is only beginning to be explored (35, 36). Investigating how maturity patterns respond to varying levels of exploitation, environmental pressure, and protection is thus crucial to evaluate the effectiveness of MPAs beyond fish stock recovery.

Two main hypotheses can explain how MPAs may act as fecundity reservoirs. The first and most established hypothesis suggests that MPAs act as refuges for mature and highly fecund individuals. As a result, MPAs can support large populations of mature adults and can export large numbers of larvae promoting population replenishment in fished areas (37). A complementary hypothesis proposes that, beyond preserving large individuals, MPAs may serve as ontogenetic refuges, supporting a diversity of life stages, from juveniles to adults, within a large range of habitats. By limiting mortality across the entire life cycle of many species, MPAs can act as a reservoirs of both juveniles and adults, enhancing both ecological resilience and long-term replenishment potential (e.g., (38–40)).

In light of these hypotheses, we expect that MPAs have, on average, a higher proportion of mature individuals than close but unprotected areas. We also anticipate that MPAs may have a higher diversity of body sizes than their unprotected counterparts.

Here we compiled data on 3,220 marine fish species over 32,026 global underwater surveys from two methods: Baited Remote Underwater Video Systems (BRUVS) and the Reef Life Survey (RLS) citizen science program. Both methods visually record fish identities, abundances, and body lengths. We were specifically interested in individual body length to determine what is the state of maturity in marine fish communities and its determinants? Since length-at-maturity is only available for commercial species and species of broad interest, we inferred maturity lengths for 2,875 out of the 3,220 fish species using a supervised-learning model. Rather than applying a fixed maturity threshold, we assigned a probability of being mature to each individual based on its length. This probabilistic framework allowed us to incorporate uncertainty and analyze the full distribution of maturity probabilities within each surveyed fish community. Each maturity distribution was then charac-

terized by its mean and coefficient of variation, which were used as response metrics to identify the main environmental, anthropogenic and protection drivers of immaturity in global fish communities.

Method




Global fish survey

Species-specific lengths were obtained from two major global databases of standardized fish surveys. The Reef Life Survey (RLS) citizen science program estimates individual fish total length from benthic underwater visual censuses conducted by divers (41). The second consists of data from Baited Remote Underwater Video Systems (BRUVS) compiled by the Marine Futures Lab. BRUVS use stereo video footage to estimate fork length from photogrammetric analysis of fish within 7 meters of the cameras, not occluded by habitat or other individuals, and viewed at suitable angles (42). BRUVS surveys are further divided in two categories: pelagic BRUVS, deployed in the water column and targeting midwater species, and benthic BRUVS, placed near the seafloor and sampling demersal and reef-associated fish communities. These methods not only provide fish body size data, but also generate abundance estimates per species (Table1).

The full dataset combines over 18 million fish measurements collected from 12,066 sites for 3,200 fish species. As some sites have been surveyed more than once, the total number of surveyed communities is 32,036. RLS surveys dominate the dataset in terms of contribution to individual measurements (80%) and species covered (2,719), with an average of 59 individuals measured per site. Pelagic BRUVS contributed fewer measurements (2%) with only 566 species. In contrast, benthic BRUVS accounted for 18.1% of total measurements and had the highest proportion of sites inside MPAs (22.9%). Overall, 48% of the sites in the dataset were located within some form of protection making the design an ideal case study to assess MPA effect.

Table 1: Summary of survey methods and data collected across three visual monitoring methods:

pelagic BRUVS, benthic BRUVS, and Reef Life Survey (RLS). The table shows the number of species considered, the proportion of sites surveyed, the total number of individual measurements, the average number of individuals measured per survey, and the percentage of surveyed sites located within protected areas.

Summary of Survey Methods and Data Collected						
Method		Species considered	Sites surveyed	Measurements taken	Mean individuals measured per survey	Sites protected (%)
Total		3222	12066	1862668	46.6	48%
Pelagic BRUVS		566	20.5%	2%	6.9	10.1%
Benthic BRUVS		2046	50.4%	18.1%	36.5	22.9%
RLS		2719	29%	79.9%	59.0	15%

Imputation of length at maturity for over 2,800 species

Among the 3,220 fish species recorded in the combined RLS and MFL databases, only 345 had documented length-at-maturity (L_m) values in FishBase (43). Since L_m correlates strongly with other life-history traits such as maximum length (L_{max}), growth rate, and trophic level (44, 45), we inferred L_m for the remaining 2,875 species using a trait-based Random Forest model. This method was chosen for its strong predictive ability and capacity to handle complex, mixed-type data (46). We also carefully checked that the 345 species with known L_m represent a wide range of fish families, to support the reliability of our predictions of the remaining data-deficient species.

We first imputed missing values for a set of key ecological, physiological, and taxonomic traits (70% completeness) using the MissForest algorithm, a non-parametric method that can use mixed data types and capture interactions between traits (47). To incorporate phylogenetic signals while imputing traits (48), we used a Multiple Correspondence Analysis (MCA) based on five categorical taxonomic ranks (class, order, family, genus, species). Although there are only five input variables, MCA generates orthogonal dimensions that capture combinations of levels across taxonomic ranks. We retained the ten most informative dimensions, which collectively explained most of the taxonomic structure and improved trait imputations (Figure1.a) (49). Here, taxonomic hierarchy was used as a proxy for phylogenetic relatedness, as closely related fish species tend to share life-history and functional traits (50–52).

transformed to improve prediction stability. Miss Forest performance was assessed via masking-based cross-validation, using R^2 for continuous traits and classification accuracy for categorical ones (Figure1.b). Once the imputation of the trait matrix was complete, we applied a Recursive Feature Elimination (RFE) procedure on a preliminary Random Forest model using the 345 species with known L_m values as the training set. This iterative process identified the most predictive subset of traits by ranking their importance on the predictive power and progressively removed the least informative traits to prevent overfitting. We trained the final Random Forest model with a five-fold cross-validation procedure to ensure accurate generalization to unseen species by minimizing overfitting.

Defining community’s maturity under a probabilistic approach

For many species, multiple values of length at maturity are reported in FishBase suggesting uncertainty that needs to be considered. To summarize this variability, we computed the mean ($L_{m_{mean}}$) of the minimum and maximum reported values for each species. The Random Forest model described earlier was trained to predict $L_{m_{mean}}$ for species lacking observed data, and final estimates were averaged across the five cross-validation folds. Based on the confidence intervals around these predictions, we defined a plausible maturity range: $L_{m_{min}}$ as the predicted mean minus the lower confidence bound, and $L_{m_{max}}$ as the mean plus the upper bound.

Prior to modeling, skewed continuous traits were log-

Rather than applying a fixed maturity threshold, we used

a Bayesian generative model to assign a probability of maturity to each individual knowing its body length. This model assumes that if an individual's total length is below $L_{m_{min}}$ its probability of being mature increases proportionally with length, up to a maximum of 10%. Conversely, if the individual is longer than $L_{m_{max}}$, the probability exceeds 90% and continues increasing asymptotically towards 100%. Within the $L_{m_{min}}$ and $L_{m_{max}}$ interval, the transition from immaturity to maturity is modeled using a logistic function, describing a gradual increase in maturity probability (Figure2.a). This model can thus capture the expected ontogenetic pattern in fish populations and is consistent with the maturity models used in fisheries science (53).

This probabilistic approach allowed us to compute maturity distributions across surveyed sites, considering only sites with more than five individuals measured. We summarized each distribution using its mean probability of maturity (mean p_{mat}) and its coefficient of variation (CV), which reflects maturity disparity and contributes to resilience since communities with both juvenile and mature individuals are more likely to resist threats like fishing or heatwaves (54, 55). Finally, these community-level metrics (e.g. mean p_{mat} and CV) were then spatially mapped (1° grid) using the *sf* R package to explore global patterns in maturity structure (Figure2.c).

Modeling and explaining fish communities' maturity

To assess the effects of environmental and anthropogenic pressures on fish community maturity and to test MPA effectiveness, we compiled a broad set of global covariates. Climatic contexts were characterized using sea surface temperature (mean, min, max) and chlorophyll-a concentration extracted via the *geoenrich* R package from Copernicus data, using a 7-day temporal and 1 km² spatial buffer around each survey. Sampling depth was also included from survey metadata. Anthropogenic pressure was captured through several proxies: distance to the nearest seaport (Global Fishing Watch), local GDP (56), and human gravity, an index of population density and accessibility (57). For assessing protection level, we classified MPAs into three protection statuses based on the Protected Seas database, that compiles spatial and regulatory information on MPAs. Thus, an area was considered 'highly' protected if all forms of fishing are prohibited, 'moderately' protected if some forms of fishing (e.g., recreational) is allowed under restrictions, and 'lightly' protected if fishing was generally permitted but with some regulatory limits.

Those listed covariates were included as fixed effects in the mixed-effects spatial models implemented via the

spaMM package in R to predict the maturity structure of fish communities. The response variables were the mean and CV of the maturity probabilities at the fish community level, both derived from the trait-based imputation framework described previously. To account for potential non-independence among observations due to shared methodology or spatial clustering, we included the following random effects: data source (i.e., BRUVS benthic/pelagic and RLS), sampling date, and biogeographic province. The model can be written as follows:

$$Y_i = \beta_0 + \beta_1 \cdot \text{ProtectionStatus}_i + \beta_2 \cdot \text{GDP}_i + \beta_3 \cdot \text{Gravity}_i + \beta_4 \cdot \text{DistanceToPort}_i + \beta_5 \cdot \text{Depth}_i + \beta_6 \cdot \text{SST}_i + \beta_7 \cdot \text{Chlorophyll}_i + u_{\text{Source}[i]} + u_{\text{SurveyDate}[i]} + u_{\text{Province}[i]} + \varepsilon_i$$

Where Y_i is either the mean or CV of fish maturity probability for sample i , β are fixed-effects coefficients, u are random intercepts for the respective grouping levels, and ε_i is the residual error.

This hierarchical spatial modeling approach is well suited to ecological datasets, which are often characterized by nested structure, non-independence, and spatial autocorrelation, as close observations are likely to be more similar in terms of covariates and ecological characteristics than distant ones (58). By explicitly modeling these dependencies, the approach provides more reliable estimates of the effects of protection and environmental gradients on the structure of fish communities' maturity.

Results

Accurate predictions of length-at-maturity for over 2,800 fish species

The Random Forest model predicting the log-transformed mean length at maturity ($\log_L_{m_{mean}}$) for fish species lacking empirical data achieved high accuracy, with an R^2 of approximately 0.9 between observed and predicted values using a cross-validation procedure (Figure 1.b). Prediction performance was consistent across major fish classes, including both Elasmobranchii ($R^2=0.84$) and Teleostei ($R^2=0.80$). The most influential predictor was the log-transformed maximum length (\log_L_{Max}), followed by a marginal contribution of vulnerability to fishing, the first two taxonomic dimensions derived from Multiple Correspondence Analysis, trophic level (Troph), and the growth coefficient (\log_K) (Figure 1.d). This strong predictive performance supports the use of trait-based imputation to estimate maturity lengths for data-deficient species in global-scale analyses.

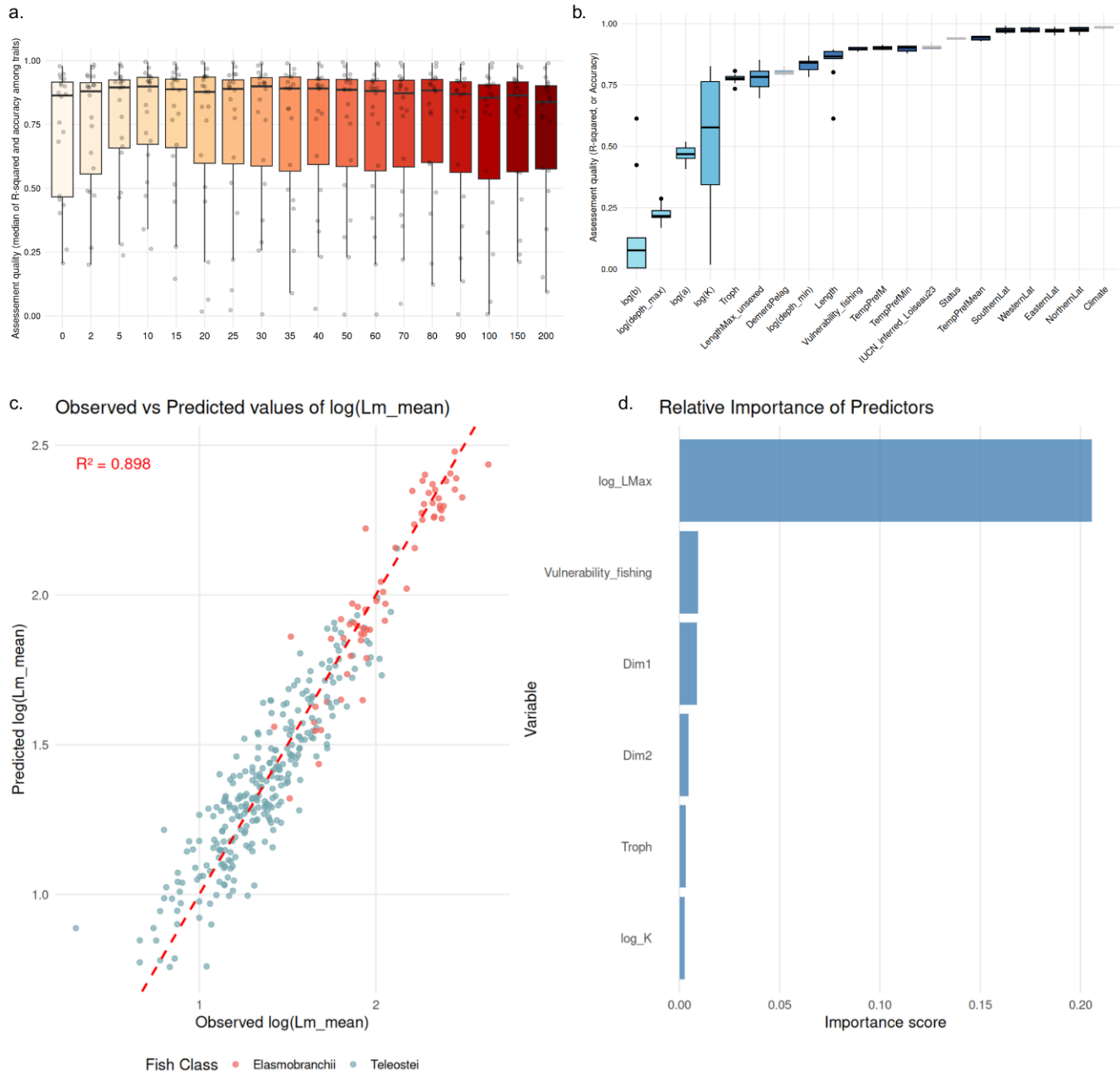


Figure 1: Prediction of fish length at maturity using a Random Forest model and a cross-validation procedure.

(a) Evaluation of the optimal number of phylogenetic dimensions to include in the MissForest imputation process. The quality of assessment (median R^2 or accuracy across traits) is displayed for an increasing number of phylogenetic dimensions in the MissForest model. (b) Assessment of the MissForest imputation model performance for each trait. Each boxplot summarizes the model's performance in predicting a trait across multiple iterations of cross-validation. (c) Model performance on the test set, showing the predicted vs. observed log-transformed Lmmean values. The model has a prediction accuracy of $R^2=0.897$. Each species is colored by its taxonomic class: blue for Teleostei and pink for Elasmobranchii (sharks and rays). (d) Importance of the predictive variables selected through the Recursive Feature Elimination (RFE) procedure. Variable importance is based on the contribution to the Random Forest model.

Fish communities' maturity across the oceans

To analyze fish communities' maturity based on individual body size, we used the species-specific logistic function describing the probability that a fish is mature given its body length. Figure2.a illustrates this maturity curve for an example species. The curve shows a sigmoidal transition from low to high maturity probability, with the steepest change occurring between $L_{m_min}=30\text{cm}$ and $L_{m_max}=40\text{cm}$. This function reflects the expected ontogenetic trend in fish populations, where individuals gradually mature as they grow, and serves as a conceptual baseline to interpret community-level maturity structure.

Based on the distributions of maturity probability within surveyed sites, we identified three archetypal community-level patterns (Figure2.b): predominantly "Immature" communities (Community 1), "Intermediate" communities (Community 2), and predominantly "Mature" communities (Community 3). Immature communities are characterized by low maturity probabilities, with individual densities concentrated below 0.1, indicative of communities composed mostly of immature fish. Intermediate communities exhibit broader or bimodal distributions, often with densities peaking near both 0 and 1, suggesting transitional states or high diversity of habitats hosting different life stages. Mature communities show a narrow distribution with a sharp peak near 1.0, reflecting assemblages mostly composed of mature individuals.

Figure2.c shows the global distribution of these maturity structures. Each dot represents a site, with the color indicating mean maturity probability and dot size reflecting the inverse of the CV, with larger dots indicating more homogeneous communities. Out of the 32,026 communities analyzed, 2,859 were classified as immature, 18,352 as intermediate, 6,773 as mature, and 4092 as uncertain. Globally, the mean maturity probability across all sites was 0.57 ($sd = 0.31$), with a negative skewness (-0.21), suggesting a prevalence of communities with low maturity levels. The average CV of maturity within sites was 0.84 ($sd = 0.64$), indicating substantial within-site variability maturity disparity.

The global mapping of fish maturity distribution revealed some clear spatial patterns (Figure2.c). Communities in remote or highly protected areas, such as in the Central Pacific or the Southern Ocean, tended to display high average probabilities of maturity (e.g., mean $p_mat > 0.7$) and low within-community heterogeneity (inverse of $CV > 5.0 \times 10^{-16}$). This latter result suggests that remote areas host more stable and mature fish communities. In contrast, regions under intense anthropogenic pressures, such as coastal zones of Southeast Asia, the Mediterranean, parts of the Indian Ocean, and the eastern seaboard of North America, were characterized by lower mean maturity probabilities (mean $p_mat < 0.5$) and higher heterogeneity within communities ($CV < 5.0 \times 10^{-16}$), that could be indicative of fishing pressure

or other environmental stressors.

These global trends were further supported by latitudinal and ecosystem-specific analyses (Figure3). Mean maturity probabilities were significantly higher in temperate zones (mean $\pm sd = 0.75 \pm 0.15$) compared to tropical (mean $\pm sd = 0.55 \pm 0.20$) and subtropical areas, for both benthic and pelagic systems ($****p < 0.0001$, Figure3.a). Conversely, the CV in maturity probabilities was markedly higher in tropical communities (often $CV > 2.5$), indicating greater within-community variability in these regions, while temperate communities tended to be more homogeneous ($CV < 1.5$) (Figure3.b).

Immaturity hotspots and spatial aggregation of maturity

Cumulative distribution curves of mature individuals (Figure3.c) further revealed ecosystem-specific contrasts. In tropical pelagic systems, maturity was highly aggregated spatially: 80% of mature individuals were concentrated in only 30% of the sites and have the lowest mean probability maturity (mean $\pm sd = 0.38 \pm 0.33$). By comparison, benthic systems exhibited a more even spatial distribution, with 50% of sites containing 80% of mature individuals. This suggests that maturity is more spatially widespread in benthic systems, whereas in tropical pelagic ecosystems, mature individuals are over-aggregated in fewer, isolated sites, revealing a fragmented maturity pattern. These results highlight the existence of a pervasive immaturity across tropical pelagic areas whereas temperate areas and benthic systems support more mature fish communities.

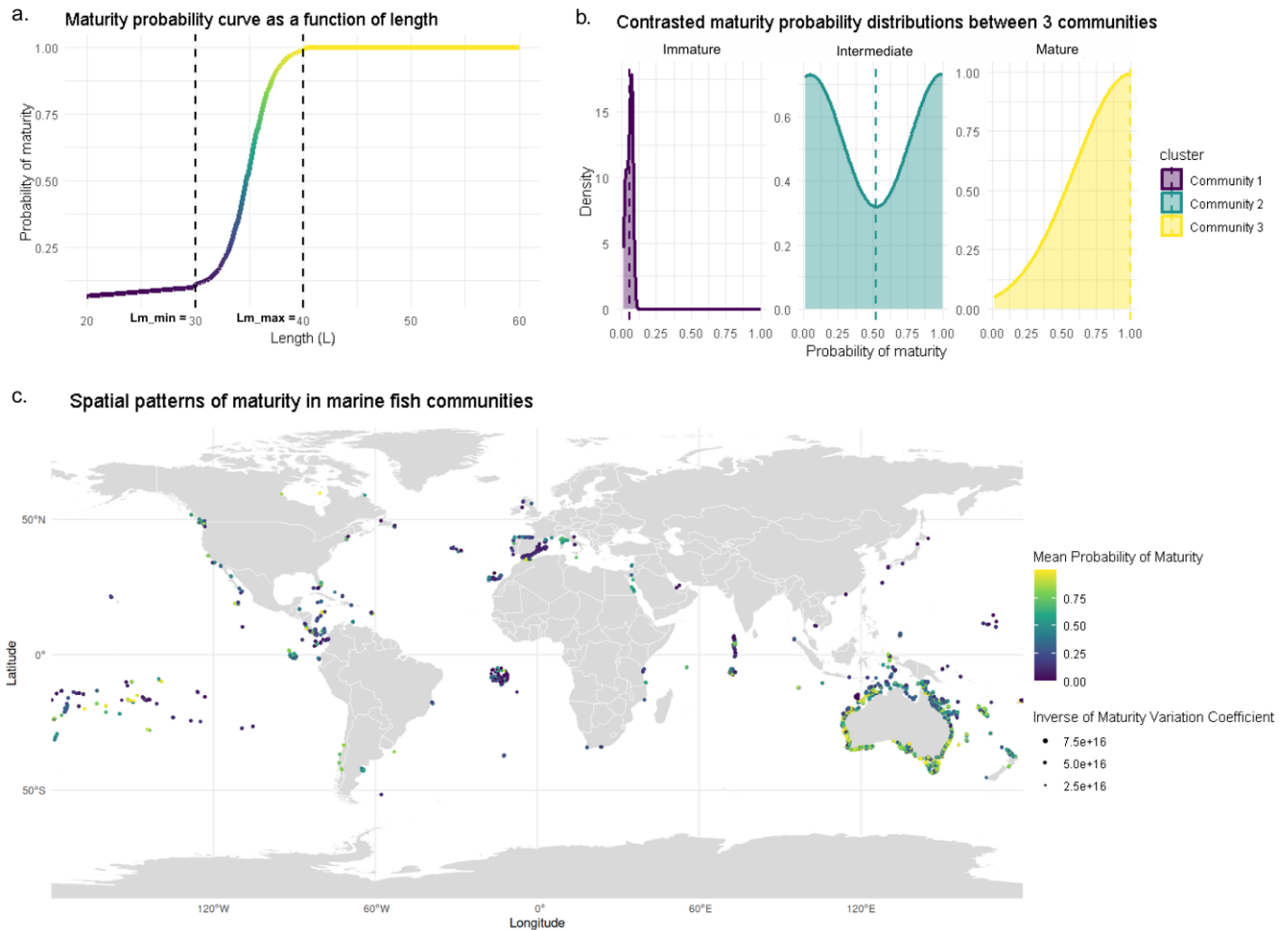


Figure 2: Patterns of maturity probability in marine fish communities.

(a) Example of the maturity probability curve as a function of individual fish length. The curve increases sharply between L_{mmin} and L_{mmax} (dashed lines), defining the transition from immature to mature stages. (b) Distributions of maturity probabilities for three representative communities, highlighting distinct maturity structures: predominantly immature (Community 1), bimodal (Community 2), and predominantly mature (Community 3). The mean probability of maturity is indicated with a dashed line on each distribution. (c) Global spatial distribution of the mean maturity probability across surveyed sites. Color intensity represents the average maturity probability within each community, while dot size reflects the relative variation in the maturity probabilities: larger dots correspond to a greater homogeneity and smaller dots indicate more heterogeneous maturity distributions.

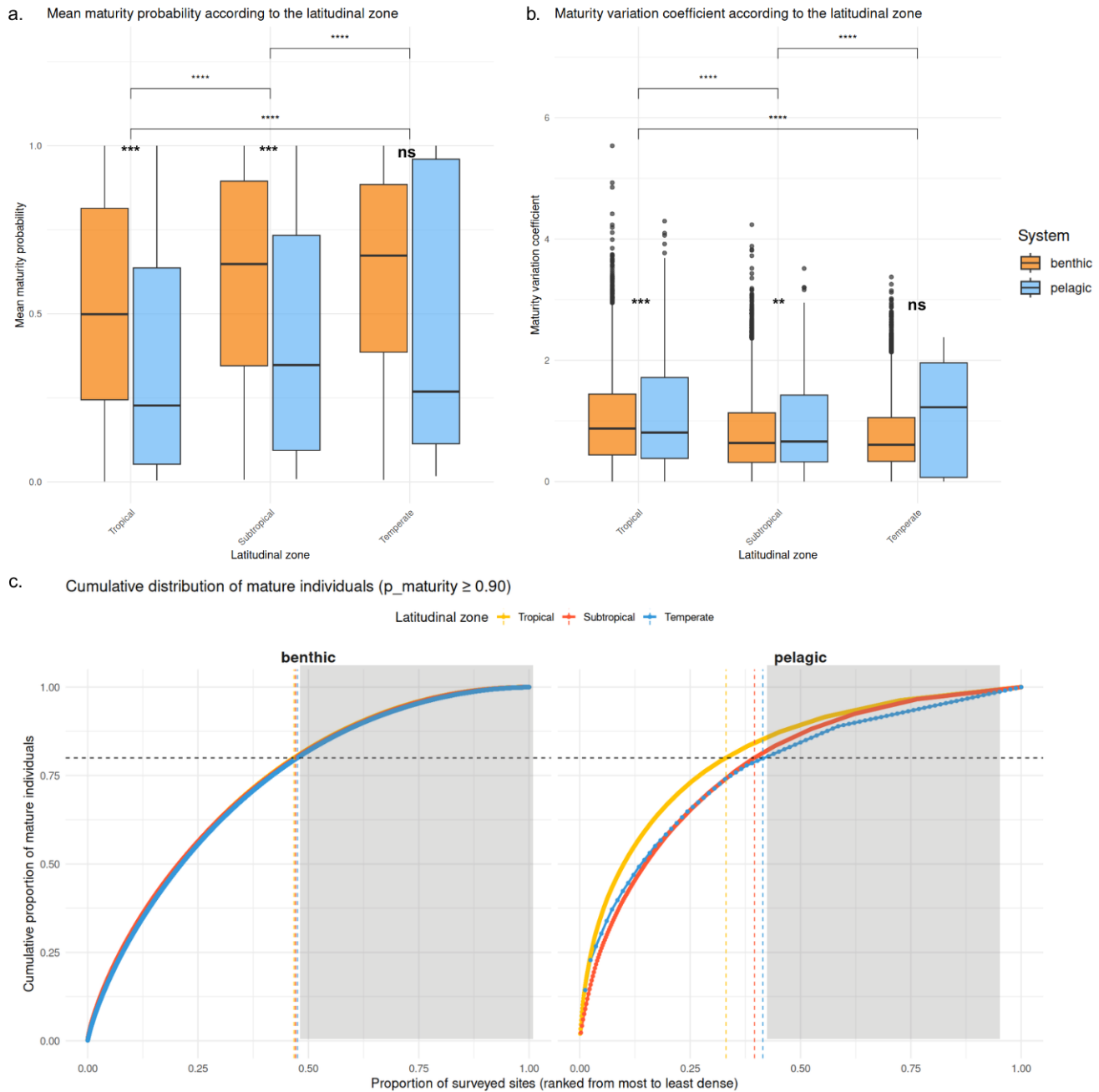


Figure 3: Comparison of fish maturity cumulative curves across latitudinal zones and systems (benthic vs. pelagic)

(a) Mean maturity probability by latitudinal zone (Tropical, Subtropical, Temperate) for benthic (orange) and pelagic (blue) systems. Statistical significance between groups is indicated as follow; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$; ns = not significant). **(b)** Maturity variation across latitudinal zones and systems, with the same color coding and significance annotations as panel (a). **(c)** Cumulative distribution curves of mature individuals ($p_{\text{mat}} \geq 0.90$) by latitudinal zone and system. Each curve represents the cumulative proportion of mature individuals as a function of the proportion of cumulated surveyed sites, ranked from most to least dense. Dashed vertical lines indicate the proportion of sites required to reach 80% of cumulated mature individuals. The shaded area highlights the section where the cumulative maturity exceeds 80% whatever the latitudinal zone considers. Tropical, Subtropical, and Temperate zones are color-coded in yellow, orange, and blue, respectively.

Deep and remote habitats host more mature individuals

The spatial mixed models revealed distinct marginal effects of environmental, anthropogenic, and MPA on fish community maturity, assessed through both the mean probability of maturity and CV. Environmental and anthropogenic predictors had contrasting effects on these two maturity metrics. High chlorophyll-a concentration and sea surface temperature (SST) negatively affected mean maturity and had no significant effect on CV (Figure 4). In contrast, depth and distance to nearest seaport showed positive associations with mean maturity probability, while they had negative associations with CV, indicating that fish communities in deeper and more remote areas were on average more mature and exhibited less variability in maturity (type 3 communities). Human gravity showed negative associations mean maturity and positive association with CV, suggesting that areas under easier access may sustain less mature but mixed communities with a broad range of maturity stages. GDP showed no significant effect on either metrics.

Marine protection enhances ontogenetic diversity

Regarding protection status, highly and unprotected areas exhibited significantly higher mean maturity probabilities compared to low protection levels ($p < 0.001$). However, for CV, both low and high protection levels showed significantly higher values compared to unprotected areas ($p < 0.001$), suggesting that protection may enhance the diversity of maturity stages within communities.

Discussion

Trait-based inference of maturity length is supported by life-history theory

The high predictive performance of the Random Forest model demonstrates the reliability of trait-based approaches for estimating length at maturity (L_m) in data-deficient fish species. The importance of the predictors such as maximum length (L_{max}), growth rate (K), and trophic level is consistent with life-history theory, which posits strong correlations between L_m and those traits (59), especially with L_{max} which emerges as the strongest predictor, reflecting allometric and demographic constraints whereby larger species generally grow slower and mature later. This result is expected under the growth-maturation trade-off, since investment in somatic growth delays reproduction. It was firstly described by Beverton and Holt (1959) and reaffirmed by recent meta-analyses (60). However, alternative hypotheses (45) suggest that maturation may also be trig-

gered by environmental signals rather than being strictly limited by growth rate.

Furthermore, the predictive power of 'vulnerability to fishing' for L_m may reflect multiple underlying mechanisms. First, vulnerability to fishing likely acts as a proxy for body size, since large-bodied species are disproportionately targeted by fisheries due to their commercial value and catchability (13). Secondly, vulnerability to fishing may also capture anthropogenic evolutionary pressures. There is growing evidence that species more exposed to fishing tend to evolve towards earlier maturation as a compensatory response to elevated mortality risks (61). In this sense, vulnerability acts not only as a short-term forcing factor but also as a long-term evolutionary constraint, highlighting the extent to which humans can impact species' life-history strategies (62).

The model's generalization across major fish clades from Teleostei to Elasmobranchii suggests that most traits are evolutionarily conserved. Thus, the taxonomic structure introduced via the two first dimensions of the Multiple Correspondence Analysis also contribute to predict L_m, suggesting that taxonomic relatedness is a good proxy for shared evolutionary history (48, 50, 63). Despite these strengths, some limitations remain. First, the model assumes that the observed trait correlations are stable across ecological contexts, potentially overlooking plasticity or local adaptations. Second, while Random Forests are powerful for prediction, they offer limited interpretability and may underperform for extrapolating beyond the trait space of observed species. Importantly, using imputed trait values can propagate uncertainty and bias if not rigorously evaluated (64, 65). Although importance scores and cross-validations were used to assess our model's accuracy, formal multiple imputation frameworks with uncertainty propagation would strengthen confidence in the downstream ecological inferences.

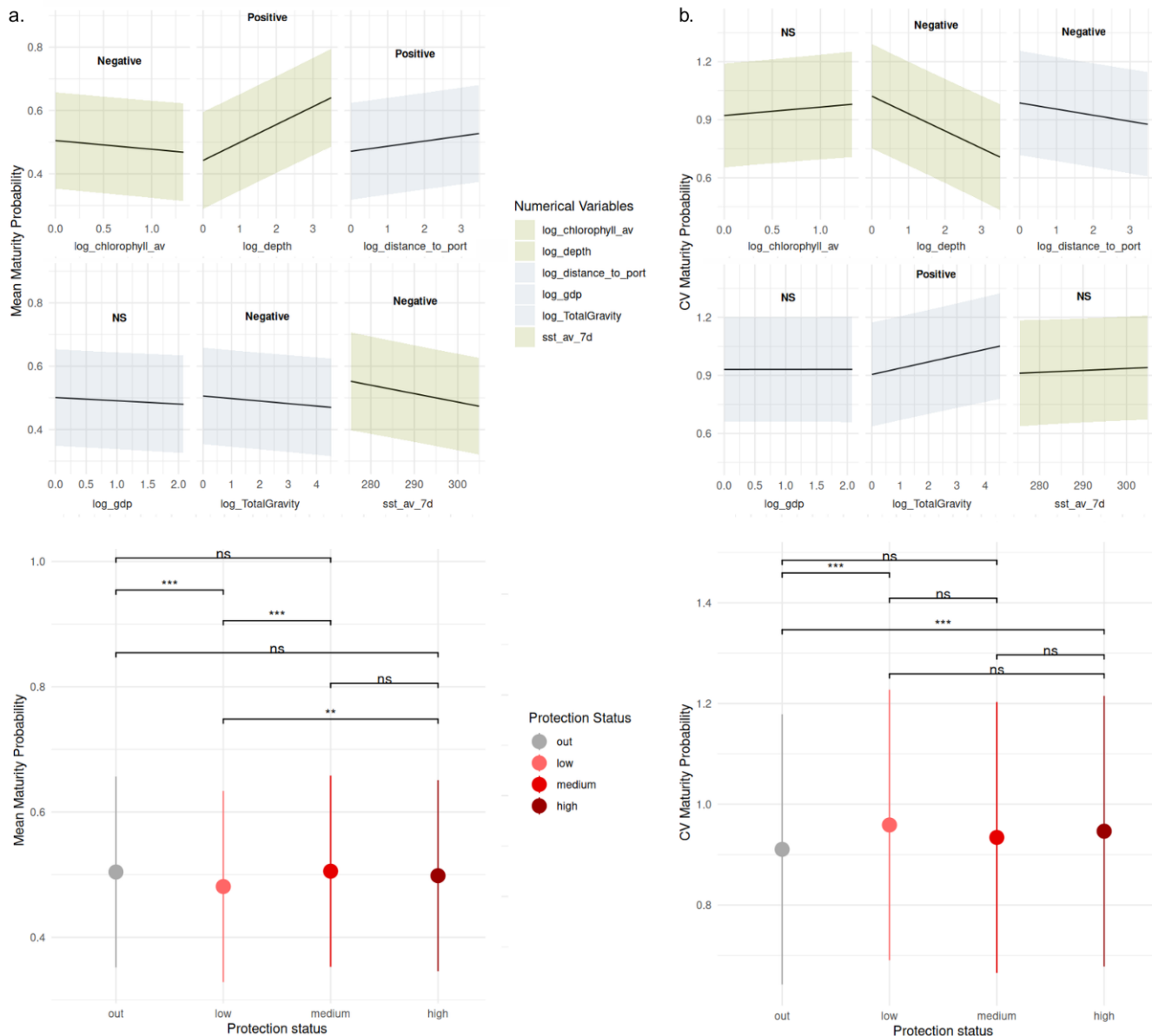


Figure 4: Effects of environmental, anthropogenic, and protection variables on fish communities' maturity.

Top panels show the partial effects of continuous predictors on two maturity metrics: maturity probability and (right) and the coefficient of variation (CV) (left), based on a spatial mixed model. Shaded areas represent 95% confidence intervals. Significant effects are labeled as 'Positive', 'Negative', or 'NS' (not significant). Bottom panels show the estimated effects of protection status (unprotected, low, medium, high) on both maturity metrics. Dots represent predicted values from the model, with vertical lines indicating standard deviations. Significance levels from pairwise comparisons are indicated: ***p < 0.001, **p < 0.01, *p < 0.05, and "ns" for non-significant differences. Protection status is based on spatial and regulatory information from the Protected Seas database.

The heterogeneous distribution of fish maturity structure across the oceans

The analysis of maturity structure distribution across the oceans reveals ecological, anthropogenic and latitudinal gradients. Tropical remote reefs tend to host communities with low mean maturity, but more heterogeneous communities made of juveniles and adults, while more temperate regions display higher maturity levels and more homogeneous communities. These patterns reflect strong biogeographic structuring in fish traits and community composition along latitudinal gradients.

Tropical ecosystems support high species richness and complex trophic webs dominated by specialists, which may increase competition and limit resource access for individuals to reach maturity (66). In contrast, temperate communities are composed of fewer but more generalist species with broader niches and more efficient resource use, allowing for greater development of mature individuals, survival of juveniles and more homogeneous communities (67).

Additionally, we observed systematic differences between pelagic and benthic systems. Tropical benthic systems, especially coral reefs, offer more habitat complexity and support a wider range of life stages with shallower size-spectra (68). This complexity translates into our results with a high heterogeneity associated with potentially greater ontogenetic diversity in this system whereas pelagic fish communities generally exhibit lower heterogeneity. Indeed, pelagic systems have lower trophic complexity and present steeper size spectra reflecting the prevalence of larger-bodied top predators in the open ocean (69). However, surprisingly, our results reveal lower maturity probabilities in pelagic than benthic communities. Based on theoretical expectations (70, 71), pelagic systems are characterized by more direct energy transfers between trophic levels, a higher prevalence of carnivory, supporting greater biomass at upper trophic levels. In such contexts, mature individuals, particularly large-bodied predators, are expected to dominate in pelagic systems whereas benthic systems favor intermediate-sized individuals and may offer refuges that may buffer predation pressure for immature individuals.

This ecological divergence raises the question of how ecosystems respond to pressures, setting the context for understanding patterns of exploitation and conservation. Indeed, body size diversity contributes to buffer climate warming and fishing effects, so is a key aspect of marine ecosystem resilience (55). Under this hypothesis benthic fish communities appear less vulnerable to global change than their pelagic counterparts.

Exploitation and environmental pressures alter fish maturity structure

The maturity structure of fish communities is strongly shaped by the contrasting exploitation regimes across ecosystems and latitudes. Benthic and pelagic systems are targeted by different fishing sectors: benthic reef fishes are mainly exploited by artisanal and small-scale fisheries in coastal and tropical areas, whereas pelagic species tend to be targeted by industrial and large-scale offshore fleets. These differences result in distinct spatial patterns of exploitation and pressure.

Latitudinal gradients further modulate these dynamics. Tropical systems, especially near densely populated coastlines, are under intense and chronic fishing pressure. Our data show that in tropical pelagic systems there is a spatial over-aggregation of maturity in a few key locations, potentially acting as the last strongholds of highly mature communities and as refuges of reproduction potential. In contrast, benthic systems display a more even spatial distribution pointing to more diffuse and potentially resilient maturity structures.

These patterns are reinforced by our spatial mixed model analysis which confirms that maturity probabilities decrease in high gravity coastal areas near human infrastructure such as seaport, where exploitation pressure is highest. These areas show clear signs of truncated size and age structures, a common consequence of selective harvesting that disproportionately removes large, fecund individuals and alters ontogenetic trajectories (68).

In addition to anthropogenic pressure, climatic conditions exert a strong influence on community maturity structure. Our spatial mixed models show that maturity probabilities decline in warmer environments. This result is consistent with known physiological and metabolic constraints: higher temperatures and lower oxygen availability can reduce energy available for reproduction, leading to smaller body size and earlier maturation (19, 72, 73).

So, this temperature–size relationship remains debated, with some studies highlighting variability across taxa and systems (35, 36). A more broadly accepted response to warming is the spatial reorganization of fish communities, with range shifts toward higher latitudes or deeper waters (74, 75).

Remoteness, depth, and MPAs as refuges for ontogenetic diversity

Considering increasing human-induced and environmental pressures on fish maturity structures, identifying and preserving the last refuges of maturity and body size diversity becomes essential to support sustainable fish populations. Contrary to expectations, our models did not show a sig-

nificant increase in mean maturity probability within MPAs when compared to fished areas. Low and medium protection levels show lower mean maturity values than full protection level and no protection, suggesting that partial protection is quite ineffective to maintain large fish and reproductive potential.

However, MPAs host fish communities with significantly higher within-site heterogeneity in maturity structure. This suggests that MPAs may not consistently enhance overall maturity levels but rather provide shelter for individuals across a broader range of life stages, supporting a higher ontogenetic diversity (Di-Lorenzo et al, 2020). MPAs, by buffering juvenile and subadult stages, may thus maintain reproductive potential even when environmental or anthropogenic conditions change rapidly (55). This finding resonates with ecological theory, where systems that include a wider range of developmental stages are often more resilient to disturbances (76, 77).

Yet, many MPAs remain located in shallow, coastal, and accessible zones therefore often under higher pressure (78). Their effectiveness in these contexts remains questionable (57). The findings of Letessier et al. (2024) suggest that protection can remain effective for benthic ecosystems, whose structural complexity allows some resilience even under high anthropogenic pressure. In contrast, for pelagic systems, protection near densely populated areas often proves insufficient. This contrast in protection effectiveness reinforces the need to extend conservation efforts beyond coastal zones and cover the high sea.

Our results further highlight the importance of deep and remote areas as critical refuges for mature individuals and body size diversity. These areas remain less exposed to fishing and harbor more intact size and age structures. This bathymetric stratification was highlighted by Frank et al, (2018), who demonstrated that fishing pressure can drive an ‘ontogenetic-like deepening’, where larger, older individuals find refuge in deeper waters to escape exploitation. As fishing fleets expand into deeper and more remote waters in the ongoing blue acceleration (4), the refugia role of these habitats is increasingly at risk (78). Anticipating this trend is crucial: protecting mesophotic and bathyal zones can safeguard large, late-maturing individuals essential for population recovery. Studies stress the need for vertically structured and connected MPAs to act as effective ontogenetic refuges, especially for pelagic and migratory species facing both fishing and climate pressures (12, 79–81).

Conclusion

Trait-based models provide a promising avenue for filling life-history data gaps, especially when grounded in evolutionary theory and ecological context. Yet, transparency

and reproducibility in imputation quality are critical to ensure these predictions remain biologically meaningful and suitable for further studies.

By using a probabilistic approach to estimate the distribution of size at maturity, we were able to capture the inherent plasticity of this trait and reduced biases from fixed-threshold approaches. Moreover, the analysis of fish maturity structure on a global ocean scale reveals that remote and deep habitats consistently support more mature fish communities. These systems likely act as natural refuges, where limited human access buffers large and slow-growing individuals from harvesting.

However, isolation alone is not sufficient to guarantee protection. Deep and remote habitats are increasingly targeted by expanding fisheries, facilitated by technological advances. Without regulatory frameworks, their refuge role for large pelagic species may erode over time.

In contrast, MPAs offer a managed form of refuge. While only fully protected “no-take” zones consistently support high maturity, even moderately protected areas can help preserve ontogenetic diversity and foster resilient communities. These protections likely reduce fishing pressure on larger individuals, promoting the rebuilding of natural age and size distributions. Yet, the effectiveness of MPA depends on ecological design and governance quality.

Together, these findings support the complementarity between passive refuges provided by remoteness and depth, and active management through MPAs. Combining both strategies may be key to preserving ontogenetic diversity and ensuring the sustainability of exploited fish communities.

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