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The University of Western Australia

Faculty of Science  
School of Biological Sciences

# **A trait-based approach reveals the human footprint on the functional ecology of pelagic fish assemblages**

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## **Abstract**

Impacts on biodiversity have traditionally been assessed based on the taxonomic identity of marine species. However, such assessments may not capture the roles fish perform in the maintenance of ecosystem function. The characterization of species based on life-history traits provides an alternative window into the functional ecology of fish assemblages. Human impacts on the functional ecology of pelagic fish assemblages remains a largely overlooked aspect in marine conservation. This knowledge gap is addressed by analysing a curated dataset of pelagic fishes captured on 6,145 standardized mid-water baited videos collected across 19 national jurisdictions. Trait-based metrics were assigned to each taxon to characterize aspects of the functional structure of pelagic fish assemblages. Three trait-based functional metrics, trophic level, phylogenetic diversity, and fishing vulnerability, and three conventional biodiversity metrics, abundance, taxonomic richness, and biomass, were modelled in response to environmental characteristics, seabed geomorphology, and proxies of human impacts. All three functional metrics were strongly and negatively influenced by increasing proximity to cities, in addition to environmental and geomorphological variables. Conversely, the conventional biodiversity measures were most strongly associated with chlorophyll-*a* concentration, seabed depth and sea surface temperature, with only declines in abundance associated with proximity to cities. This study suggests that human impacts on pelagic fish assemblages are detected earlier in functional metrics than conventional biodiversity measures. These results contribute to the United Nation's Sustainable Development Goal 14, Life Below Water, by documenting the human footprint on pelagic fish assemblages based on trait-based metrics and highlights the importance of ocean management strategies informed and strengthened by functional ecology.

**Keywords:** Stereo-BRUVS • Trophic Level • Phylogenetic Diversity • Fishing Vulnerability  
• Functional traits • Human impacts • Mid-water cameras

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## 1. Introduction

Seafood is of paramount importance to global food security with three billion people acquiring the majority of their protein and micronutrients from fish (FAO 2020, Vianna et al. 2020). However, fishing and climate change are transforming marine ecosystems at an unsustainable rate (Hughes et al. 2017, Palomares et al. 2020) and consequently how they function (Perry et al. 2010). Global fish catches have declined since 1996 (Pauly & Zeller 2016) as a result of technological advancements and government subsidies that allow fishing vessels to fish deeper and travel further and for longer periods (Tickler et al. 2018, Skerritt & Sumaila 2021). Key negative outcomes of fishing can include not only declines in abundance and biomass of fish but reductions in size (Froese et al. 2016). Climate change results in warming waters and decreasing oxygen concentration. Its consequent impacts include reduced fish size (Pauly 2021) and survival rate (Musa et al. 2020) due to oxygen limitation. Overall, the average maximum bodyweight of fish assemblages is expected to shrink by 14-24% due to climate-driven physiological stresses and shifts in distribution and abundance (Cheung et al. 2013, Pauly & Cheung 2018). Hypoxia and oxygen deprivation will also significantly increase mortality (Keckeis et al. 1996, Musa et al. 2020).

The effects of prolonged and widespread overfishing manifest themselves directly as fish populations decline and indirectly as functional diversity erodes (Froese & Kesner-Reyes 2002, Petrou et al. 2021). Fishing activities deplete target and non-target species throughout the world (Pauly 2019). Pelagic fish such as tunas, billfishes and sharks are heavily targeted by industrial fisheries with biomass consequently declining (Juan-Jordá et al. 2011, Dulvy et al. 2014). For example, high-value species such as the southern bluefin tuna, *Thunnus maccoyii*, is listed as Critically Endangered by the IUCN as its biomass has been reduced to 5% over three generations (Collette et al. 2011b). The global population of historically abundant oceanic whitetip shark, *Carcharhinus longimanus*, has undergone a decline of >98% and is listed as Critically Endangered (Rigby et al. 2019).

The loss of pelagic species can have several effects on function (Trenkel et al. 2015) with predator-prey interaction one of the primary components in the function of pelagic ecosystems (Pauly & Christensen 1995). Large marine predators are known as ‘ecosystem regulators’ due to their critical role in sustaining biodiversity (Ritchie & Johnson 2009) and their influence on trophic dynamics and species diversity through prey mortality and behavioural changes (Heithaus et al. 2008). The aggregation patterns of small pelagic forage species are key to

support top predators and generally, only a small number of species occupy the niche of forage species (Trenkel et al. 2015). The reduction in pelagic prey availability leads to declines in body weight and nutritional condition of predators in addition to pronounced cannibalism of young individuals (Eero et al. 2012). The foraging behaviour of pelagic species is a function of prey detection rate and the likelihood of prey capture which are both related to the functional characteristics of the prey (Lambert et al. 2019).

Human impacts are changing the composition of fish assemblages with likely impacts on function including trophic cascade effects and function extinction (MacNeil et al. 2020). Overfishing leads to a decline in the average size of fish (Cheung et al. 2013). As a result, the shrinking of fishes affect species interaction, leads to biomasses decline (Audzijonyte et al. 2013) and marine animals are required to consume more prey to achieve the same condition and growth (Queiros et al. 2019). The reduction of fish body length also leads to a positive feedback loop in trophic interactions by increasing predation mortality, prey switching and shift in distribution towards improved food supply (Audzijonyte et al. 2013) and thus, triggers indirect effects in fish assemblage structure and function of marine ecosystems (Worm et al. 2006). Overfishing can also cause a species to become functionally extinct, meaning they no longer play a significant role in the function of the ecosystem despite their ongoing presence (MacNeil et al. 2020). Even with a 'sustainable' rate of fish removal ecosystem functioning is rapidly compromised (Ripple et al. 2001, Creel et al. 2007, Ordiz et al. 2013). The loss or decline in the functional role of species are often overlooked aspects of biodiversity in conservation efforts, and yet they are essential to maintain ecosystem services (Mouillot et al. 2013b, D'Agata et al. 2014).

The function of fish in the marine ecosystem can be defined by attributes related to their fitness. Violle et al. (2007) defined functional traits as biological attributes of an individual that impact fitness indirectly through growth, reproduction, and survival. These traits provide community metrics when assessed as a function of species abundance or biomass. Trait-based metrics are also useful indicators of pelagic assemblages response to human impacts on ecosystem services (Mouillot et al. 2013b). A key functional trait is trophic level, a continuous index based on diet composition data. Trophic level has been used as a proxy for ecosystem functioning due to the predictable ratio between predator and prey size (Scharf et al. 2000). The water viscosity limits pelagic fishes body size which influences their jaw diameter and thus, prey selection and capture (Ursin 1973, Pauly & Watson 2005). High trophic level species are known as

‘ecosystem regulators’ due to their critical role in biodiversity (Ritchie & Johnson 2009) by the influence on trophic dynamics and nutrient transfer across habitat (Heithaus et al. 2008, Ferretti et al. 2010). Small pelagic “forage” species are low trophic level species whose aggregation patterns are key to support large and medium predators such as sharks, tunas, and seabirds (Pikitch et al. 2014).

Phylogenetic diversity is another relevant functional measure because it relates to extinction processes, biotic invasion and ecosystem functioning (Strecker et al. 2011, Winter et al. 2013). Phylogenetic diversity is a measure of the breadth of evolutionary history and is calculated as the mean phylogenetic distance between taxa based on cladistic information (Faith 1992). High phylogenetic diversity within an ecosystem confers a broad variety of functions in a community and is used as a complementary attribute for functional assessments (Mouchet et al. 2010, Mazel et al. 2018). Low phylogenetic diversity in assemblages can indicate low niche overlap and thus low functional redundancy (Mouchet et al. 2010).

Taxa can also be characterised by their vulnerability to fishing, a trait-based index built on a fuzzy logic expert system (Cheung et al. 2005). Fishing vulnerability is based on life-history traits that estimate the intrinsic vulnerability of marine species in response to fishing, and include maximum length, age at first maturity, growth parameter, natural mortality, longevity, geographic range, fecundity and spatial behaviour. The vulnerability index also reflects species maximum rate of population growth and density dependence i.e., when population growth rates are regulated by the density of a population (Cheung et al. 2005).

Stereo-baited remote underwater video systems (BRUVS) are a robust fishery-independent visual survey technique used to study fish assemblages (Whitmarsh et al. 2017). Stereo-BRUVS capture a wide range of taxa from herbivores to piscivores, have low inter-observer variability, provide highly accurate length measurements and create a permanent record of fish assemblages (Langlois et al. 2010). They are an effective tool to document abundance, taxonomic richness, and biomass. Stereo-BRUVS allow high levels of replication in a non-destructive setting. They provide quantitative data on cryptic species, sex, swimming speed, and foraging behaviour across a wide range of habitats (Cappo et al. 2006, Ryan et al. 2015, Barley et al. 2016, Thompson et al. 2019). Stereo-BRUVS have minimal environmental impact in contrast to fisheries-dependent methods using hooks or other fishing gears (Cappo et al. 2004, Brooks et al. 2011, Newman et al. 2011).



Curated mid-water stereo BRUVS data were analysed from 59 expeditions at 33 locations in the Indian, Pacific and Atlantic oceans and trait-based data harvested from FishBase (Froese & Pauly 2021). Combined, these data were used to document the functional ecology of pelagic fish assemblages based on trophic level, phylogenetic diversity, and vulnerability to fishing. The degree to which these functional metrics were predicted by geomorphological, environmental, and human pressure drivers were then quantified. Analogous models were generated for conventional ecological metrics of abundance, taxonomic richness, and biomass and the results contrasted with those for functional metrics. The mid-water baited videography surveys will provide evidence of the degree to which human impacts shape the function of pelagic fish assemblages, providing valuable input to ocean management strategies strengthened by functional ecology.

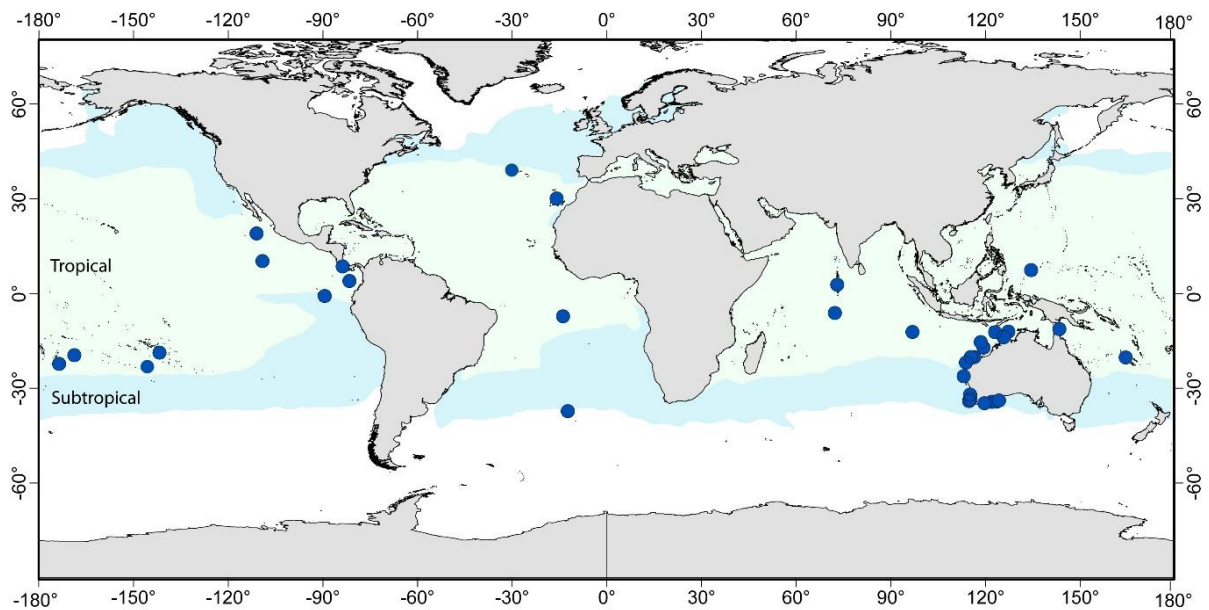
## **2. Methodology**

### *2.1 Field survey and design*

Standardized mid-water stereo-BRUVS were used to survey pelagic fish assemblages during 59 expeditions at 33 locations across the Indian, Pacific and Atlantic oceans (Fig. 1). All surveys were undertaken between 2013 and 2020, between latitudes 49.36° S and 39.72° N and longitudes 169.99° W and 167.03° E. Seabed depth ranged between 20 m and 5,740 m. Individually calibrated mid-water stereo-BRUVS were deployed in longlines of three or five rigs, separated by 200 m of line into a “string” formation with a total of 6,145 rigs deployed. Each string is the basic sampling unit and represents the average across the five or three rigs on a given string. Mid-water stereo-BRUVS were suspended at 10 m depth, for a minimum of 2 hours, and the string drifted without restrictions during daylight hours (07:00-17:00) (Bouchet et al. 2018). For each survey, a generalised random tessellation stratified (GRTS) sampling design was applied (Bouchet & Meeuwig 2015). Sampling was conducted across targeted areas that included islands, shelf breaks, seamounts and submarine canyons (Supplementary Table S1). All surveys were conducted under UWA ethics permit RA/3/100/1484, and required jurisdictional permits were obtained.

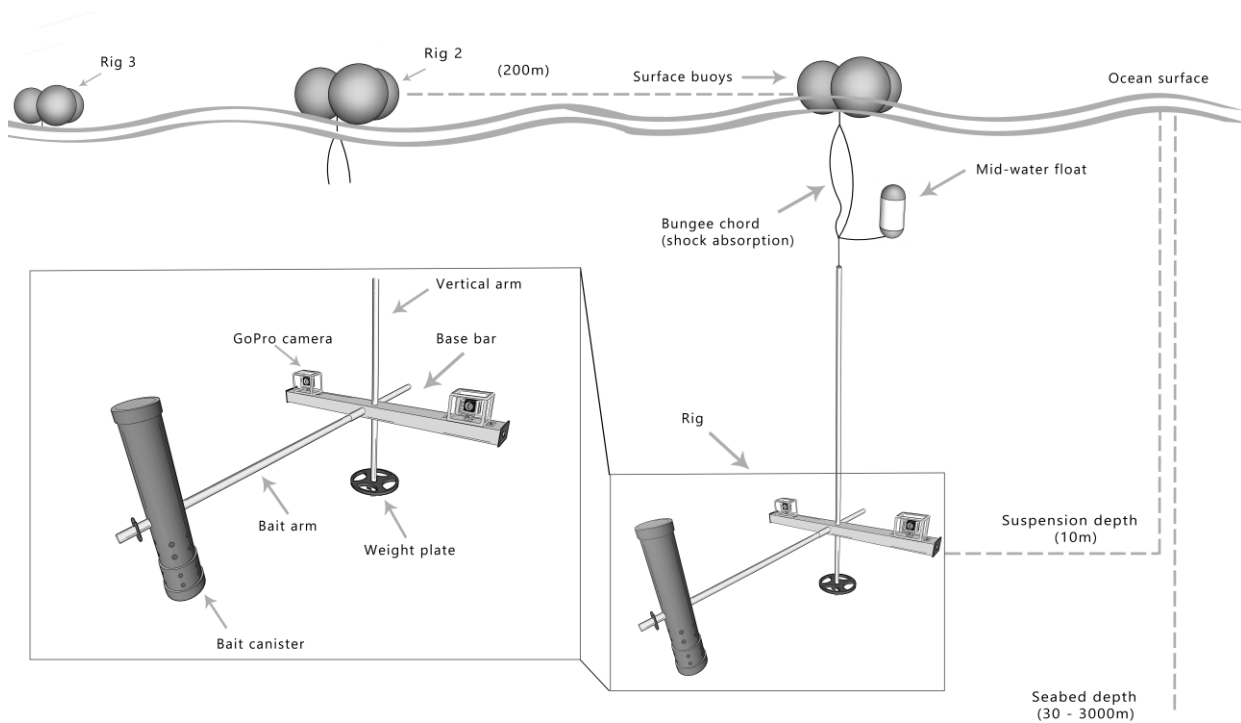
## 2.2 Mid-water stereo-BRUVS

Traditionally, stereo-BRUVS were used for demersal fishes associated with the seabed but more recently they have been adapted to survey the pelagic realm (Letessier et al. 2013, Letessier et al. 2015). Mid-water stereo-BRUVS strings cover large areas ( $\sim 3 \text{ km}^2$ ), an attribute that is particularly relevant to pelagic habitats which are characterised by patchily distributed sparse populations of wildlife (Bouchet & Meeuwig 2015, Letessier et al. 2015). Stereo-BRUVS are also less prone to biases linked to gear selectivity and the impact of targeted fishing in areas that generate greater profits (Worm et al. 2006). Alternative methods such as active acoustic biomass assessments face issues with potential vessel-avoidance biases requiring research vessels to yield minimum noise (DuFour et al. 2018) and underwater visual census despite being increasingly used are not efficient in the pelagic environment and unsafe for divers.



**Figure 1.** Locations of mid-water stereo-BRUVS, surveys from the Marine Futures Laboratory database overlaid with tropical and subtropical climatic zones (adapted from Anon., 1991).

The mid-water BRUVS consist of a 145 cm long vertical aluminium arm and a 95 cm-long horizontal aluminium base bar on which two small underwater action cameras are mounted (Fig. 2). The two cameras converge inwards at an angle of 8 degrees to generate overlap on fields of view on a bait canister suspended at the end of a 180 cm long bait arm. The bait canister contained 1 kg of pilchards (*Sardinops* spp.), dispersing a bait plume for the duration of the deployment. The video footage collected from the mid-water stereo-BRUVS was analysed with EventMeasure™ software to generate taxonomic identification, fork length measurements and relative abundance estimates (Seager 2014).



**Figure 2.** Schematic diagram of a suspended baited mid-water stereo-BRUVS rig. Adapted from Bouchet and Meeuwig (2015).

Fish were identified to the lowest taxonomic level possible and the maximum number of each species in one single video frame, MaxN, was recorded to conservatively estimate relative abundance (Cappo et al. 2006). Sampling by mid-water stereo-BRUVS occurred in the epipelagic zone, and while the animals detected in these relatively shallow layers do not fully capture the entire array of pelagic species, stereo-BRUVS have been reliably and consistently used to investigate pelagic fish assemblages (Bouchet & Meeuwig 2015, Letessier et al. 2019, MacNeil et al. 2020). The length measurements that are obtained from the stereo arrangement allow fish weight and thus, observed biomass to be estimated based on species-specific length-weight relationships (Froese 2006, Bouchet et al. 2018).

### *2.3 Data treatment*

The mid-water stereo-BRUVS data were used to calculate the total abundance (TA; the sum of MaxN for all species), taxonomic richness (TR; the number of taxa), and total biomass (TB; the sum of weights for all taxa) observed on each rig and averaged at the string level to maximize the independence of samples. The mean weight for each species was calculated using the length-weight relationship  $W = aL^b$  where  $a$  is a body-shape related parameter and  $b$  indicates body allometric growth (Froese & Pauly 2021). Biomass was calculated as the product of mean weight estimates and MaxN for each taxon. When length-weight relationships were not available for fork length, the fork length to total length conversion for that species was used (Supplementary Table S2; Froese & Pauly 2021). Bayesian length-weight relationships for total length were used for taxa identified only to genus or family level (Froese & Pauly 2021). Marine mammals were excluded from biomass analyses given their immense size and rarity.

### *2.4 Trait-based functional metrics*

The taxonomic identifications were used to assign taxon-specific trait-based functional metrics. These functional metrics included trophic level (TL), phylogenetic diversity (PD) and fishing vulnerability (FV) and encompass a pool of traits that can be a proxy to study the functional ecology of fish assemblages. The three functional metrics were sourced from FishBase (Froese & Pauly 2021) and applied to each taxon (Supplementary Table S2). Trophic level is a continuous variable that, for fish, generally ranges from 2.0 for herbivores to 4.7 for piscivorous predators such as sharks (Pauly & Watson 2005). Trophic level is based on diet and when not reported in the literature it was estimated based on size and trophic classes of closet relatives as reported in FishBase. Phylogenetic diversity is an indicator of biodiversity based on evolutionary history which incorporates the phylogenetic differences between species calculated by branch length estimates on the cladogram. Phylogenetic diversity ranges continuously from a low uniqueness value of 0.5 to a high uniqueness value of 2.0 (Faith 1992). In FishBase, PD is reported at the genus level with low values indicating taxa with several close sisters on the cladogram and vice versa (Faith et al. 2004). Fishing vulnerability is an index based on a fuzzy logic expert system used to estimate the intrinsic vulnerability of marine fishes to fishing exploitation (Cheung et al. 2005). This index comprises several life-history characteristics and includes maximum age, body length, age at first maturity, growth, fecundity, mortality rate, geographic ranges and aggregation strength. Fishing vulnerability ranges from 0 to 100, with species that are most vulnerable to fishing assigned values close to 100 (Cheung et

al. 2005, Jones & Cheung 2018). For taxa identified only to genus or family level, mean values for TL, PD and FV were calculated based on all species within that genus or family known to be present at that location based on FishBase records (Froese & Pauly 2021).

### *2.5 Environmental, geomorphological, and human pressure drivers*

Explanatory variables were compiled across three main categories: environmental, geomorphological and human pressure drivers (Table 1), extracted for each string. Environmental variables were (i) sea surface temperature (SST; °C) monthly data were derived from the NASA Multi-scale Ultra-high resolution data (<https://podaac.jpl.nasa.gov/MEaSURES-MUR>), given the influence of SST on the distribution of pelagic fishes (Tittensor et al. 2010); (ii) SST standard deviation (SST<sub>SD</sub>), monthly, also from the NASA Multi-scale Ultra-high resolution data (<https://podaac.jpl.nasa.gov/MEaSURES-MUR>), a proxy for thermal fronts and nutrients mixing; (iii) latitude; (iv) median chlorophyll-*a* concentration (Chl-*a*; mg·m<sup>-3</sup>) obtained from 8-day AQUA MODIS composite images (<http://www.pfeg.noaa.gov/products/EDC/>) and an indicator of primary production; and (v) distance to the Coral Triangle, a global marine biodiversity hotspot that is a proxy for patterns of diversity and endemism (Veron et al. 2009).

A set of geomorphological drivers were chosen as they are possible surrogates for nutrients and organic matter availability and included: (i) average seabed depth, the mean bathymetric value within the sample unit, string, obtained from the General Bathymetric Chart of the Oceans (GEBCO) available at [https://www.gebco.net/data\\_and\\_products/gridded\\_bathymetry\\_data](https://www.gebco.net/data_and_products/gridded_bathymetry_data); (ii) distance to the nearest coast, a measure of marine habitat extension calculated by ESRI using the Euclidean Distance Tool in ArcMap; (iii) distance to nearest seamounts, known to be highly productive hot-spots and attract predators (Morato et al. 2010); and (iv) seabed slope, which is an index for seabed morphology from flat bottom to steep rocky and used to predict species distribution and habitats (Gratwicke & Speight 2005).

Human pressure drivers were calculated based on distance and time-based proxies that are hypothesized to represent the cumulative effect of human impacts including exploitation, pollution, and industrialisation (Letessier et al. 2019). They included: (i) minimum distance to the nearest human settlement (km), referred to as distance to population, based on human settlements of any size computed with the LandScan<sup>TM</sup> 2016 database (Dobson et al. 2000); (ii) minimum distance (km) to the nearest human density centre, hereafter referred to as distance to the nearest city, based on the *World Cities* map spatial layer (ESRI<sup>TM</sup>) which includes national

capitals, provincial capitals and locally important urban centres (Maire et al. 2016); (iii) distance (km) to the nearest shipping port as reported on the *World Cities* spatial layer (ESRI™); (iv) travel time (hrs) to nearest human settlement, based on human settlements of any size computed with the LandScan™ 2016 database and; (v) travel time (hrs) to the nearest city, as reported on the *World Cities* map spatial layer (ESRI™) which includes national capitals, provincial capitals and locally important urban centres (Maire et al. 2016). Travel time is based on “cost”, or time travelling, using a cost-distance algorithm between the nearest human settlement or nearest city based on specific speeds assigned to cross each type of surface (e.g., 20 km·h<sup>-1</sup> across water bodies) as per Maire et al. (2016) calculated for the time to travel from each string to the nearest human settlement or nearest city.

The relationships among explanatory variables were tested for collinearity. Travel time to the nearest human settlement and distance to the nearest city were positively correlated ( $r$ -Pearson=0.9,  $P<0.0001$ ). Travel time to the nearest city was positively correlated with distance to port ( $r$ -Pearson=0.5,  $P<0.0001$ ) and distance to the nearest city ( $r$ -Pearson=0.9,  $P<0.0001$ ). Latitude was negatively correlated with distance to seamounts ( $r$ -Pearson=-0.45,  $P<0.0001$ ). To avoid confounding effects of collinear variables in the model, a subset of four environmental, four geomorphological and two human pressure explanatory variables were used in the analyses: (i) SST (°C), (ii) SST<sub>SD</sub>, (iii) chlorophyll-*a*, (iv) distance to the Coral Triangle, (v) seabed depth (m), (vi) distance to coast (km), (vii) distance to seamount (km), (viii) slope, (ix) distance to nearest population (km) and (x) distance to the nearest city (km).

## 2.6 Statistical analyses

The relationships between functional metrics and the environmental, geomorphological, and human pressure drivers hypothesized to influence the pelagic fish assemblages were investigated. Mean abundance, taxonomic richness, biomass and functional metrics were summed and averaged for each string since the rigs within a given string are not independent samples (Bouchet & Meeuwig 2015). Functional metrics for each taxon were weighted according to abundance and biomass to reflect their contribution to ecosystem functioning (D’Agata et al. 2016). Mean weighted values were then calculated for each string. Using trophic level (TL) weighted by abundance (TA) as an example, the weighted trophic level (TL<sub>TA</sub>) for a given string is calculated as the sum of the product of each species trophic level (TL<sub>*i*</sub>) and its abundance (A<sub>*i*</sub>) divided by the sum of abundance of all species in the string (TA), where the subscript “*i*” indicates the *i*<sup>th</sup> species (equation I). Similarly, trophic level weighted for biomass

( $TL_{TB}$ ) for each string is calculated as the sum of the product of each species trophic level ( $TL_i$ ) and its biomass ( $B_i$ ) divided by the sum of biomass of all species in the string ( $TB$ ; equation II).

$$\text{I) } TL_{TA} = \frac{\sum(TL_i \cdot A_i)}{TA} \qquad \text{II) } TL_{TB} = \frac{\sum(TL_i \cdot B_i)}{TB}$$

Linear variables were  $\log_{10}$  transformed to stabilise the variance. The analysis was conducted at the level of the survey location (Fig. 1) to assess large-scale variation. Variations in functional metrics and conventional metrics of pelagic fish assemblages were tested using one-way permutational analysis of variance (PERMANOVA) based on unrestricted permutations (Anderson 2017) with ocean basin and climatic zones as factors. This permutational approach was chosen because it is robust to heterogeneity in the data. This analysis was completed in Primer v7 with the PERMANOVA+ add-on (Clarke & Gorley 2015).

Boosted regression trees (BRTs) were used to estimate the relative influence of environment, geomorphology, and human pressure on functional metrics and conventional biodiversity measures. The models were built using the mean value of each functional or biodiversity variable for each string across all survey locations. Boosted regression trees were used to determine the relationships between functional and conventional biodiversity metrics and the hypothesised explanatory variables. This method originated from machine learning and regression techniques to improve the performance of single models by fitting and combining many models for predictions that produce a single ‘best’ model (Elith et al. 2008). Boosted regression trees can automatically cope with interaction effects between predictors, different types of explanatory variables and missing data. Data transformation or outlier removal is also not required with BRT models. The BRTs are robust to codependency across explanatory drivers and can fit complex nonlinear relationships which are often observed in ecological studies. The essential criteria used to select a good BRT model was based on the optimal combination of tree complexity, learning rate and bag fraction, which control for overfitting and stochasticity of models, with the best model minimizing the out-of-bag estimates of error rate (Leo 1996; Supplementary Table S4). In BRTs, the model considers the error in the prediction of the first fitted tree and adjusts subsequent trees accordingly in order to continually improve its accuracy. The relative importance of each driver is calculated based on the average number of times a driver is selected to split the data and then weighted by the squared improvement to the BRT model as a result of each split. The relative importance of all drivers is scaled from 0 to 100 and the most important variables are those with the highest percentage of contribution to the model. All explanatory variables were kept in the full model in order to

have a broad overview of the contribution of each variable regardless of how small the contribution was. All BRTs were built in R using the gbm package version 1.6-3.1 and the custom code available online (<http://cran.r-project.org/web/packages/gbm>). Spatial autocorrelation analysis was performed using Moran's I test for the observations of functional metrics components (Supplementary Table S4; Moran 1950).



**Table 1** - Variables used in statistical analyses to build the BRTs models.

<b>Dependent functional variables</b>	<b>Abbreviation</b>	<b>Description</b>
Trophic level	TL	Based on species diet composition, from FishBase <sup>1</sup>
Phylogenetic diversity	PD	Based on the mean phylogenetic distance clade between taxa, from FishBase <sup>1</sup> (Faith et al. 2004)
Fishing vulnerability	FV	Based on life-history traits and ecological characteristics, from FishBase <sup>1</sup> (Cheung et al. 2005)
<b>Dependent conventional variables</b>		
Abundance	TA	Obtained from mid-water BRUVS as the total number of individuals for a given taxon
Taxonomic richness	TR	Obtained from mid-water BRUVS as the total number of taxa
Biomass	TB	Calculated based on the length-weight relationship for each species from FishBase <sup>1</sup>
<b>Environmental drivers</b>		
Sea surface temperature	SST	SST of each string extracted from NASA Multi-scale Ultra-high resolution data <sup>2</sup>
Sea surface temperature SD	SST <sub>SD</sub>	SST standard deviation
Chlorophyll- <i>a</i>	Chl- <i>a</i>	Day time remote-sensed chlorophyll- <i>a</i> data (mg·m <sup>-3</sup> ) from NOAA <sup>3</sup>
Distance to Coral Triangle	Dist Coral Tri	The minimal distance of each BRUVS to the Coral Triangle
<b>Geomorphology drivers</b>		
Seabed depth	Depth	Mean depth of seafloor covered by a longline GEBCO <sup>4</sup>
Distance to coast	Dist coast	Distance to the nearest coast calculated by Esri using the Euclidean Distance Tool in ArcMap
Distance to seamount	Dist seamount	Distribution of seamounts based on 30 arc seconds bathymetry data (Yesson et al. 2011)
Slope	Slope	Bathymetric derivative generated from 3 by 3 window
<b>Human pressure drivers</b>		
Distance to the nearest population	Dist population	Nearest human settlement of any size computed with the LandScan 2016 database (Dobson et al. 2000)
Distance to the nearest city	Dist city	National and provincial capitals and locally important urban centers based on the World Cities spatial layer (ESRI)

<sup>1</sup> <https://fishbase.org><sup>2</sup> [https://podaac.jpl.nasa.gov/Multi-scale\\_Ultra-high\\_Resolution\\_MUR-SST](https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST)<sup>3</sup> <http://www.pfeg.noaa.gov/products/EDC/><sup>4</sup> [https://www.gebco.net/data\\_and\\_products/gridded\\_bathymetry\\_data](https://www.gebco.net/data_and_products/gridded_bathymetry_data)

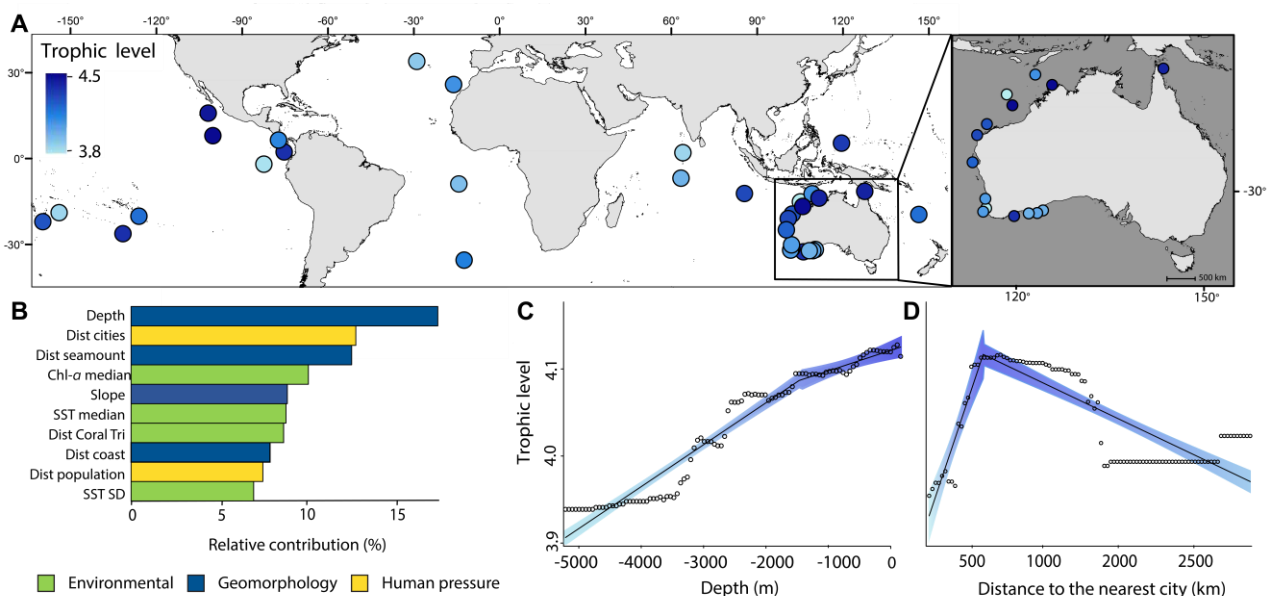
### 3. Results

The 59 surveys of baited remote underwater video systems (BRUVS) recorded 117,461 individual teleosts and chondrichthyans across the 33 survey locations. These records represent 243 species from 54 families (Supplementary Table S2). Size ranged from a 2 cm freckled driftfish (*Psenes cyanophrys*) to a 4.1 m scalloped hammerhead (*Sphyrna lewini*). Marine mammals, invertebrates and birds accounted for an additional 20 taxa with a total of 548 individuals that were excluded from this study. Relative total abundance based on MaxN averaged  $28.9$  individuals  $\pm 5.2$  SE across all locations, varying from 0.8 at Tonga and 127 at the Recherche Archipelago (West) off the south coast of Western Australia (Supplementary Fig. S1). Mean taxonomic richness across the locations was  $2.6$  species  $\pm 0.2$  SE and ranged from a low of 1 species at Tonga and to a high of 6 species in the Galapagos Islands (Supplementary Fig. S1). Total biomass across the locations was  $7,171$  kg  $\pm 1,137$  SE and ranged from 66.7 kg at Argo Terrace, offshore in the northwest of Western Australia, to 26,924 kg at Bremer Canyon in southern Western Australia (Supplementary Fig. S1). Weighted by biomass, trophic level varied between 3.8 at Geographe in the southwest of Western Australia and 4.49 at Rowley Shoals, north of Western Australia, with a mean of  $4.1 \pm 0.02$  SE across all 33 locations (Supplementary Fig. S2). Mean phylogenetic diversity across the locations was  $0.56 \pm 0.01$  SE and ranged from 0.39 at Argo Terrace to 0.81 at Selvagens Island (Supplementary Fig. S2). Fishing vulnerability ranged from a low of 30 at Argo Terrace and to a high of 78.4 at Rowley Shoals, while the mean fishing vulnerability across all locations was  $58.5 \pm 2$  SE (Supplementary Fig. S2).

#### 3.1 Drivers of fish functional structure

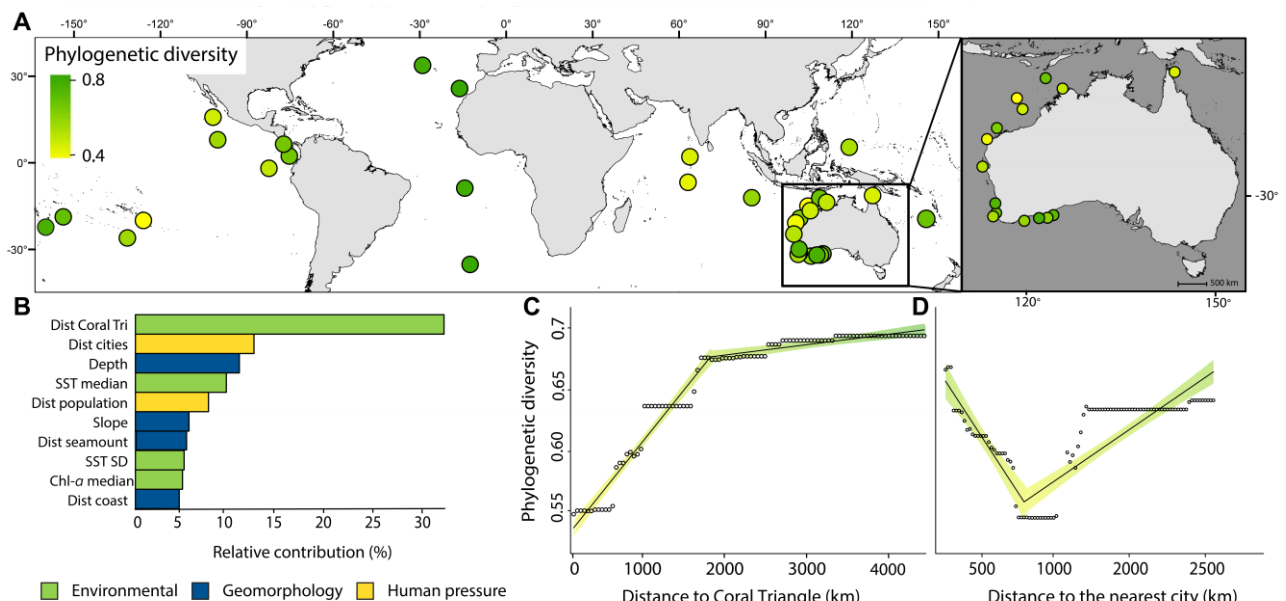
Boosted regression tree (BRT) models based on ten explanatory variables (environmental, geomorphological, and human pressure drivers, Table 1) explained 55%, 57% and 66% of the variance in TL, PD and FV, respectively. Seabed depth and distance to cities were the two metrics that best predicted TL (30%) and FV (35%). Phylogenetic diversity was best predicted by distance to Coral Triangle and distance to cities (46%).

The distribution of trophic level weighted by biomass ( $TL_{TB}$ ; Fig. 3A) was primarily explained by geomorphology. Seabed depth accounted for 17% of the variation in  $TL_{TB}$  and was higher in shallow waters and decreased with depth (Fig. 3B, 3C). The second most important explanatory variable for  $TL_{TB}$  was the distance to the nearest city, accounting for 13% of the variation in  $TL_{TB}$ . The  $TL_{TB}$  was lowest in survey locations near cities and increased sharply to a peak at approximately 650 km from the nearest city, and then decreased in areas further from city centres (Fig. 3D). The  $TL_{TB}$  did not vary by ocean basin ( $p=0.92$ ) or climatic zone ( $p=0.44$ ). Trophic level weighted by abundance was also best explained by seabed depth (15%) and the distance to cities (13%; Supplementary Table S3).



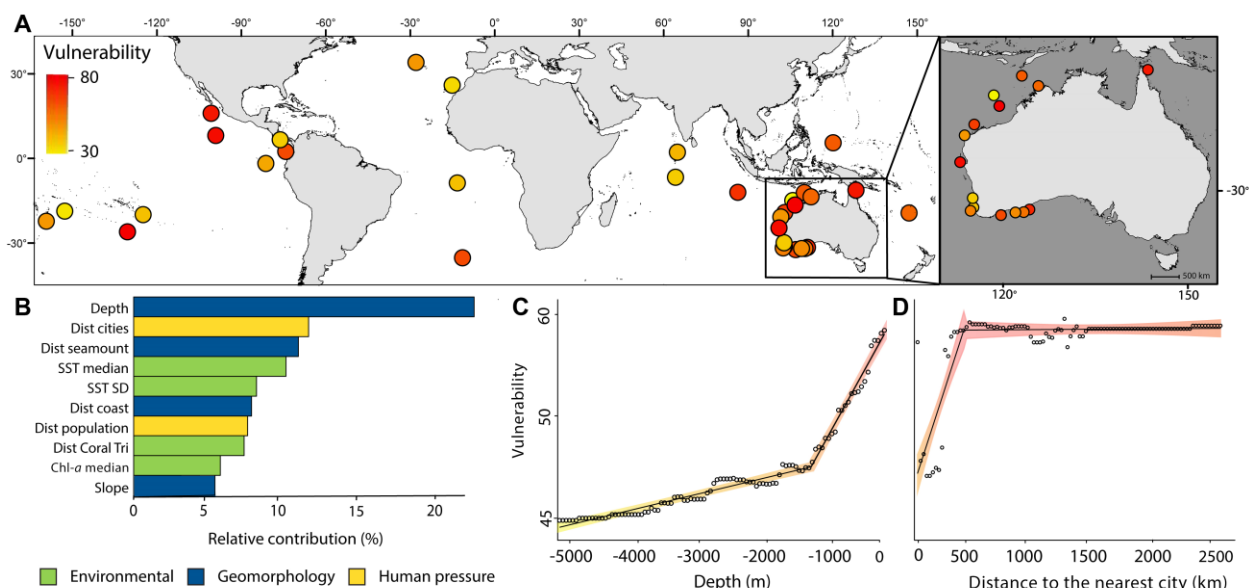
**Figure 3.** Drivers and patterns of trophic level weighted by biomass ( $TL_{TB}$ ). (A) Spatial variation of observed  $TL_{TB}$  across survey locations. (B) Relative contribution of main drivers explaining variations in  $TL_{TB}$ , as were generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for seabed depth (depth; C) and distance to nearest city (dist cities; D). The comparative values for (A) can be found in Supplementary Figure S2. Dist seamount, distance to the nearest seamount; Chl- $a$ , chlorophyll- $a$ ; SST, sea surface temperature; dist CoralTri, distance to the Coral Triangle; dist coast, distance to the nearest coast; dist population, distance to the nearest population; SST<sub>SD</sub>, sea surface temperature standard deviation.

The phylogenetic diversity weighted by biomass ( $PD_{TB}$ ) across locations (Fig. 4A) was explained by environmental and human pressure drivers. Distance to the Coral Triangle explained 33% of the variation, while the distance to the nearest city explained a further 13% of the variation (Fig. 4B). Lower  $PD_{TB}$  was observed in waters nearest the Coral Triangle and increased with increasing distance from the Coral Triangle (Fig. 4C). The  $PD_{TB}$  was high at locations near cities, decreasing to a breakpoint at approximately 800 km from the nearest city, and then increasing steadily to similar levels as near cities at distances of approximately 1,500 km (Fig. 4D). The variation of  $PD_{TB}$  across ocean basins and climatic zones was significant ( $p=0.002$  and  $p=0.001$ ). The pairwise test showed no interaction between oceans and climate, with  $PD_{TB}$  significantly higher in the Atlantic Ocean compared to the Indian Ocean ( $p=0.001$ ) and also significantly higher in the temperate climate zone (Supplementary Table S5). Phylogenetic diversity weighted by abundance also suggested that the distance to the Coral Triangle (15%) and the distance to cities (15%) were the two most associated metrics, explaining 30% of the variation (Supplementary Table S3).



**Figure 4.** Drivers and patterns of phylogenetic diversity weighted by biomass ( $PD_{TB}$ ). (A) Spatial variation of  $PD_{TB}$  across survey locations. (B) Relative contribution of the main drivers explaining the variations in  $PD_{TB}$ , as generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for distance to the Coral Triangle (dist CoralTri; C) and the distance to the nearest city (dist cities; D). The comparative values for (A) can be found in Supplementary Figure S2. Depth, seabed depth; SST, sea surface temperature; dist population, distance to the nearest population; dist seamount, distance to nearest seamount;  $SST_{SD}$ , sea surface temperature standard deviation; chl- $\alpha$ , chlorophyll- $\alpha$ ; dist coast, distance to the nearest coast.

The fishing vulnerability weighted by biomass ( $FV_{TB}$ ; Fig. 5A), was primarily explained by geomorphology and human pressure drivers. Seabed depth accounted for 23% of the variation and distance to the nearest city explained an additional 12% (Fig. 5B). Species more vulnerable to exploitation were observed in shallower waters and  $FV_{TB}$  decreased with increasing water depth at the survey locations (Fig. 5C). The  $FV_{TB}$  was lower near cities and increased sharply to a peak at approximately 550 km from the nearest city, after which it remained high in more distant waters (Fig. 5D). There was no variation in  $FV_{TB}$  across ocean basins ( $p=0.4$ ) and climatic zone ( $p=0.9$ ). Fishing vulnerability weighted by abundance was also best explained by seabed depth (21%) and the distance to cities (14%), with an increased effect demonstrated by the mean SST (15%; Supplementary Table S3).



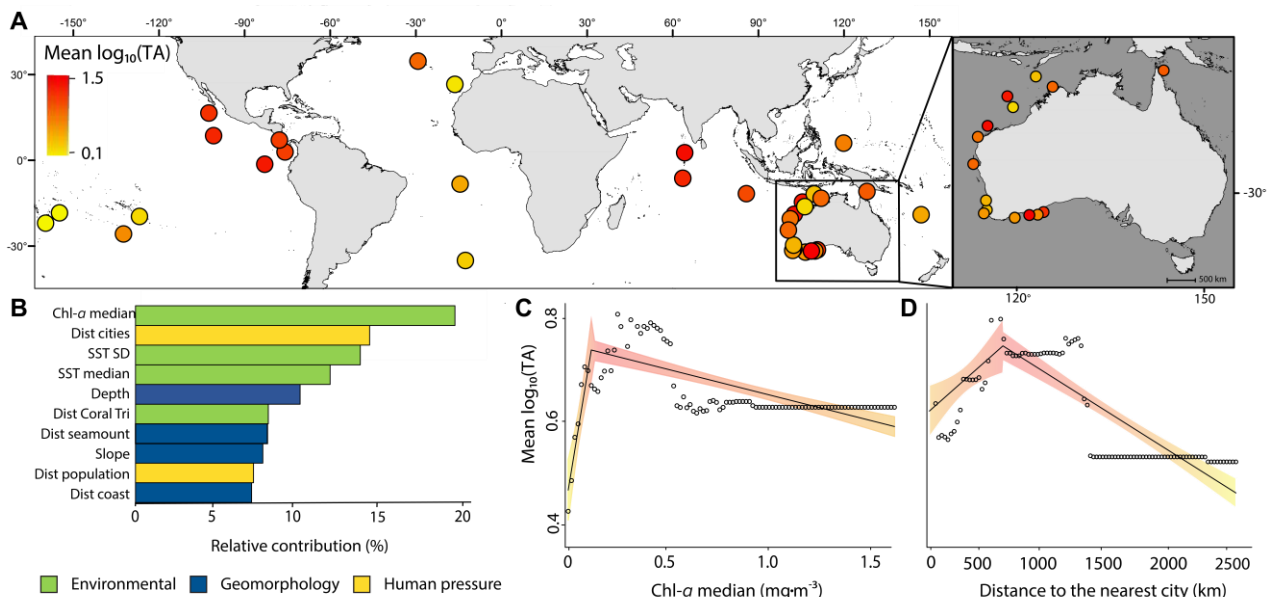
**Figure 5.** Drivers and patterns of fishing vulnerability weighted by biomass ( $FV_{TB}$ ). (A) Spatial variation of  $FV_{TB}$  across survey locations. (B) Relative contribution of main drivers explaining variations in  $FV_{TB}$ , as generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for distance to seabed depth at survey location (depth; C) and the distance to nearest city (dist cities; D). The comparative values for (A) can be found in Supplementary Figure S2. Dist seamount, distance to the nearest seamount; SST, sea surface temperature;  $SST_{SD}$ , sea surface temperature standard deviation; dist coast, distance to the nearest coast; dist population, distance to the nearest population; Dist CoralTri, distance to the Coral Triangle; chl-*a*, chlorophyll-*a*.

### 3.2 Drivers of fish species biodiversity

The BRT based on the ten explanatory variables (environmental, geomorphological and human pressure drivers, Table 1) explained 59%, 66% and 68% of the variance in total abundance, taxonomic richness and total biomass respectively. Total abundance was the only conventional

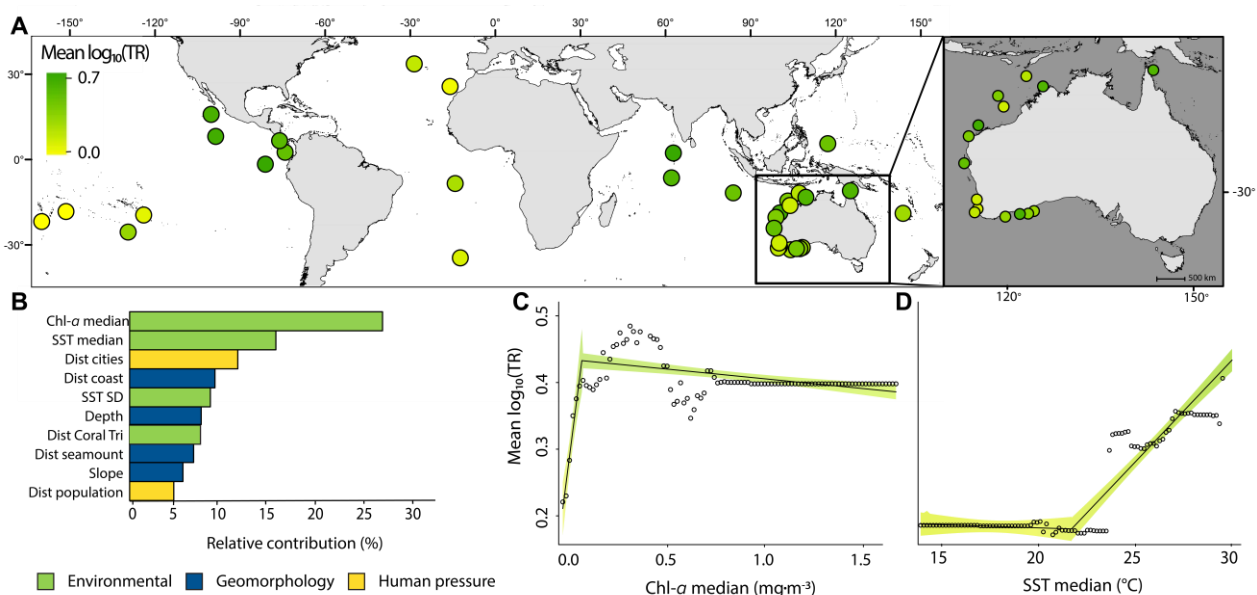
metric that showed a human footprint in addition to the influence of natural conditions. The relative contribution of the explanatory variables showed that environmental drivers, chlorophyll-*a* and sea surface temperature (SST) explained the majority of variation across taxonomic richness and total biomass.

The range of total abundance distribution (TA; Fig. 6A) was explained by environmental and human pressure drivers. Chlorophyll-*a* (Chl-*a*) explained 18% of the variation, with an additional 13% explained by the distance to the nearest city (Fig. 6B). The lowest TA was found at very low Chl-*a* concentrations and sharply increased to a peak TA in relatively low Chl-*a* concentrations ( $0.29 \text{ mg}\cdot\text{m}^{-3}$ ; Fig. 6C). Total abundance thereafter decreased in waters with high Chl-*a* concentrations. Similarly, TA was lower in waters closest to the nearest city, increased to a high TA at approximately 700 km from the nearest city, and then decreased with increasing distance from cities (Fig. 6D). The variation of TA across the ocean basins was significant, TA in the Western Pacific Ocean was significantly lower than in the Eastern Pacific and Indian oceans ( $p=0.039$  and  $p=0.38$ ; Supplementary Table S5). There was no variation in TA across climate zones ( $p=0.078$ ).



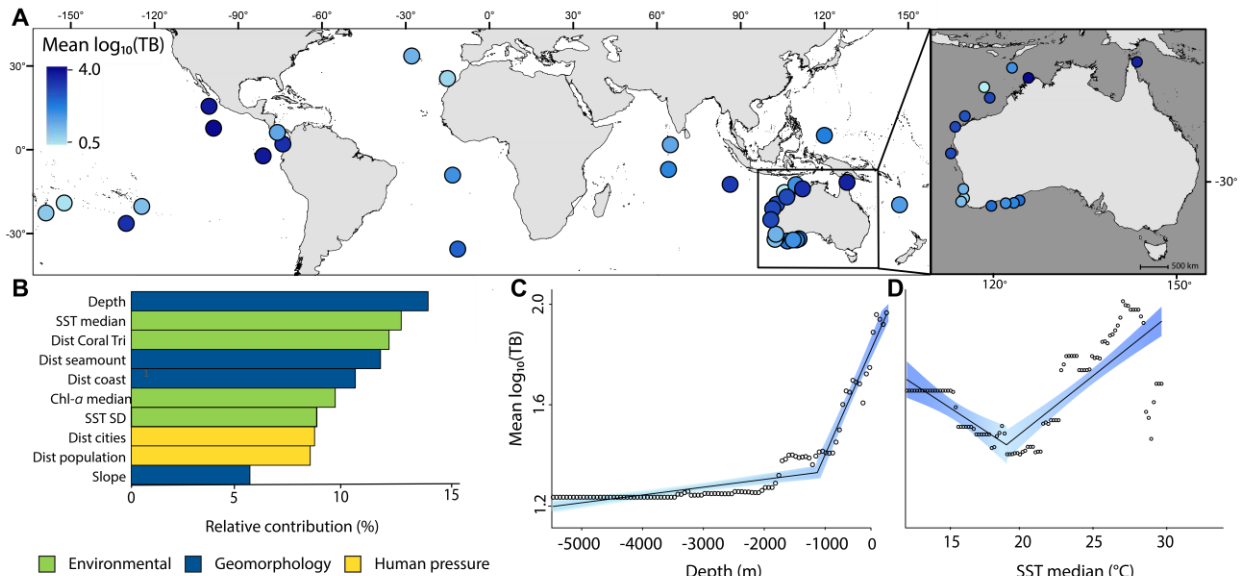
**Figure 6.** Drivers and patterns of mean  $\log_{10}$  total abundance (TA). (A) Spatial variation of mean TA across survey locations. (B) Relative contribution of main drivers explaining variations in TA as generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for chlorophyll-*a* (Chl-*a*) concentrations (C) and distance to nearest city (dist cities; D). The comparative values for (A) can be found in Supplementary Figure S1. SST<sub>SD</sub>, sea surface temperature standard deviation; SST, sea surface temperature; depth, seabed depth; dist CoralTri, distance to the Coral Triangle; dist seamount, distance to nearest seamount; dist population, distance to the nearest population; dist coast, distance to the nearest coast.

Taxonomic richness across locations (Fig. 7A) was primarily explained by environmental drivers (41%). Chlorophyll-*a* accounted for 26% and mean SST for a further 15% of the variation (Fig. 7B). The lowest TR was observed at very low Chl-*a* concentrations and sharply increased to reach peak TR in relatively low Chl-*a* concentrations ( $0.34 \text{ mg}\cdot\text{m}^{-3}$ ; Fig. 7C). Thereafter, taxonomic richness slightly decreased from a peak in waters with higher Chl-*a* concentration. High TR was found at high SST and steadily decreased as SST dropped to about  $23^\circ\text{C}$  and remained low in cooler waters (Fig. 7D). Taxonomic richness was significantly higher in the Eastern Pacific Ocean than in the Western Pacific Ocean ( $p=0.03$ ; Supplementary Table S5). Taxonomic richness was also significantly higher in tropical waters ( $p=0.06$ ; Supplementary Table S5).



**Figure 7.** Drivers and patterns of mean  $\log_{10}$  taxonomic richness (TR). (A) Spatial variation of TR across survey locations. (B) Relative contribution of main drivers explaining variations in TR, as generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for chlorophyll-*a* (Chl-*a*) concentration (C) and sea surface temperature (SST; D). The comparative values for (A) can be found in Supplementary Figure S1. Dist cities, distance to the nearest city; dist coast, distance to the nearest coast;  $\text{SST}_{\text{SD}}$ , sea surface temperature standard deviation; depth, seabed depth; dist CoralTri, distance to the Coral Triangle; dist seamount, distance to nearest seamount; dist population, distance to the nearest population.

The distribution of total biomass (TB; Fig.8A) was primarily explained by geomorphology. Seabed depth accounted for 13% of the variation and TB was higher in shallow waters and decreased with increasing water depth at the survey locations (Fig. 8B; 8C). The second most important explanatory variation was sea surface temperature (SST) accounting for 13% of the variation. Total biomass was high at locations with low SST, decreasing to a breakpoint at approximately 19° C and then increasing steadily with increasing SST (Fig. 8D). Total biomass did not vary by ocean basin ( $p=0.08$ ) and climatic zone ( $p=0.07$ ).



**Figure 8.** Drivers and patterns of mean  $\log_{10}$  total biomass (TB). (A) Spatial variation of TB across survey locations. (B) Relative contribution of main drivers explaining variations in TB, as generated from 100 iterations of BRTs. Partial dependence plot (lines), observed values (dots), and 95% confidence intervals for distance to seabed depth (depth; C) and sea surface temperature (SST; D). The comparative values for (A) can be found in Supplementary Figure S1. Dist CoralTri, distance to the Coral Triangle; dist seamount, distance to nearest seamount; dist coast, distance to the nearest coast; chl- $\alpha$ , chlorophyll- $\alpha$ ; SST<sub>SD</sub>, sea surface temperature standard deviation; dist cities, distance to the nearest city; dist population, distance to the nearest population.



## 4. Discussion

Studies of marine biodiversity are often based on conventional metrics such as abundance, richness and biomass with metrics based on functional ecology less of a focus. The characterization of pelagic fish assemblages by functional traits shows that there is a strong human footprint on functional ecology against a background of natural environmental and geomorphological conditions. The human footprint is also more apparent in functional metrics such as trophic level, phylogenetic diversity and fishing vulnerability than in the conventional taxonomic richness and biomass counterparts. This human footprint on the ecological function of marine systems is consistent with the results of D'Agata et al. (2014) and Cinner et al. (2020) in reef fish assemblages.

### *4.1 Human impacts on the function of pelagic fish assemblages*

Trophic level generally declines with increased fishing effort (Pauly et al. 2000). This pattern has largely been inferred from fisheries catch data (Pauly & Zeller 2016). The patterns observed from the fisheries-independent BRUVS-derived data are consistent with fisheries catch data results, showing that trophic level declines with increasing proximity to cities. A fundamental aspect of the maintenance of healthy pelagic ecosystems is selective harvests and moderate fishing of resilient species for human consumption (Pauly et al. 2016). Kolding et al. (2016) explored fishing pressure at the ecosystem level and found exploitation to be highly unbalanced and overly concentrated on low abundance, less fecund, high trophic level species, a pattern these results also confirm. The consequences of harvests that disproportionately exploit non-resilient high trophic level animals include trophic cascades, change in biomass distribution and increased biomass flow (Pauly et al. 1998, Gascuel 2005). Trophic cascades mediated by consumer-prey interactions can lead to a loss of functional biodiversity (Pace et al. 1999). Specifically, declines in the mean trophic level reduce “compensatory” effects of functionally redundant species at high trophic levels due to its variability and complexity (Otto et al. 2008). Moreover, the decline of high trophic level species increases biomass flow because lower trophic level species have quicker metabolism (Rigler 1975). Faster biomass transfer passes through trophic classes while slow flows accumulate biomass at each trophic class. Gascuel (2005) found that assemblages characterized by fast biomass transfers such as those with fewer species at high trophic levels are more sensitive to fishing pressure. As such, the knock-on effects of human-driven reductions of trophic level in pelagic fish assemblages are complex, with potentially significant consequences that to some degree are still unknown.

The resilience of pelagic fish assemblages is also a function of their phylogenetic diversity. Human-driven loss of phylogenetic diversity has been observed on reef fish assemblages (D'Agata et al. 2014). However, this pattern is not observed here in the pelagic assemblages. Rather, phylogenetic diversity seems to be high at locations near cities, rapidly decreasing to an inflection point at approximately 800 km distance from the nearest city, and then increasing steadily to a level similar to that near cities. This pattern indicates that independent of the distance to the Coral Triangle, a hotspot of taxonomic diversity (Veron et al. 2009) but low phylogenetic diversity (Mouillot et al 2014), exist areas near humans that remain characterized by taxa with high phylogenetic diversity. This pattern may have emerged because coastal fishing initially targets abundant pelagic taxa with low phylogenetic diversity such as herrings and mackerels (Tacon & Metian 2009), with taxa of high phylogenetic diversity remaining. The rapid decline in phylogenetic diversity to 800 km suggests either a natural paucity of high phylogenetic diverse taxa or a change in fisheries target species at these distances. Phylogenetic diversity then increases substantially with distance to cities, controlling for natural variables. It is possible that fishing pressure at these locations targets low phylogenetically diverse taxa, such as small forage species, or that open oceans naturally sustain phylogenetic diverse assemblages (Holland et al. 2021). The BRUVS-derived data also show the Coral Triangle to have high abundances of low phylogenetic diverse species. This result is consistent with Mouillot et al. (2014) who showed that functionally unique species tend to be rare in high biodiversity tropical biotas such as the Coral Triangle. Phylogenetically diverse assemblages are of important conservation value because distantly related individuals likely result in low niche overlap (Faith 1992). As a result, high phylogenetic diversity at locations near cities and further away from the Coral Triangle may be an indicator of resilience.

The third trait-based metric, fishing vulnerability, shows the degree to which marine fishes may be affected by exploitation as a consequence of their life history and ecological characteristics (Cheung et al. 2005). Overexploitation has led to a decline in the average intrinsic vulnerability of taxa in global catches (Cheung et al. 2007). The BRUVS-derived results are consistent with this pattern, showing fish assemblages characterized by resilient, low vulnerability taxa at locations near cities. This result indicates that highly vulnerable species are the first to be removed from the assemblage with proximity to humans. Assemblages composed of fishes with high vulnerability are also more susceptible to rapid biomass declines. Morato et al. (2006) used a time-series simulation of fish assemblages to demonstrate that those assemblages with a higher intrinsic vulnerability had larger biomass declines than those characterized by low

fishing vulnerability species. Top predator species are some of the most intrinsically vulnerable species and highly susceptible to rapid biomass declines. Therefore, the disproportionate impact on large-bodied, slow-growing species is two-fold, due to their high intrinsic vulnerability and the targeted removal associated with their higher value and catchability (Jennings et al. 2001, Collette et al. 2011a). The BRUVS-derived data show that seabed depth is also a major driver of fishing vulnerability which decreases with increasing water depth at survey locations. This result is consistent with global analyses that showed more vulnerable species in shallower waters (Morato et al. 2006) compared to less vulnerable, small-pelagic species that inhabit the surface waters of deep continental shelves (Pikitch et al. 2014).

#### *4.2 Conventional biodiversity metrics overview*

Traditionally, the human impacts on fish assemblages have been explored with abundance, richness and biomass, based on taxonomic identifications (Myers & Worm 2003, Tickler et al. 2018, Palomares et al. 2020). The BRUVS-derived data show a human footprint on the abundance of pelagic fish as abundance declined with proximity to cities. The human-driven declines in the abundance of pelagic taxa are consistent with Letessier et al. (2019) and Juhel et al. (2019) who saw similar patterns in pelagic predators and reef sharks respectively. However, previous studies have shown that human pressure such as fishing can lead to an increase in the abundance of prey species following reductions in predator numbers, also known as mesopredator release (Palacios & McCormick 2021).

The taxonomic richness of pelagic fish assemblages is primarily explained by environmental and geomorphological factors with human impact less of an influence. That taxonomic richness is less sensitive to proxies of human impact likely reflects the ability of species to persist at low numbers once they are no longer fished or targeted. Taxonomic richness would not likely indicate the impact of fishing pressure as fishers tend to shift in target species once the original target becomes unprofitable due to a decline in abundance or biomass (Pauly et al. 2000). It is notable that in the marine protected area literature, diversity is often similarly less responsive to protection than, for instance, abundance and biomass (McCook et al. 2010, Halpern et al. 2019). The results of high taxonomic richness at locations with high chlorophyll-*a* concentration and high sea surface temperature are analogous to patterns observed in demersal fish species (Leathwick et al. 2006). Worm et al. (2003) showed sea surface temperature to be a proxy for latitudinal gradients of pelagic marine biodiversity.

The lack of a strong human footprint on biomass was inconsistent with patterns in fisheries catch that showed declines (Pauly and Zeller 2016). This difference is likely due to the availability of catch data dating back to 1950 compared to the current study which was not sampled over time. Although declines of exploited marine fishes have been observed on a global scale (Palomares et al. 2020), the biomass of prey fishes such as small pelagic species has increased over the last 100 years in certain locations likely due to predation release (Christensen et al. 2014). The BRUVS results show pelagic fish biomass decreases with increasing water depth at survey locations. This pattern is consistent with Letessier et al. (2016) who showed that oceanic atolls and seamounts are hotspots for pelagic biomass at epipelagic (200 m) and mesopelagic (100 – 1,000 m) depths. In addition, strong relationships are observed between schooling pelagic fish biomasses and warmer waters, a pattern these results also confirm (Lindegren et al. 2013). Furthermore, sea surface temperature has been used as a predictor of pelagic fish biomasses in fisheries management decisions (Tommasi et al. 2017).

#### *4.3 Influence of climatic zones and ocean basins on pelagic fish assemblages*

Climatic zones and ocean basins are integral to understanding the ecology of fish assemblages due to large temperature variations and biogeographical isolation (Palomares et al. 2020). The effect of both climatic zones and ocean basins on pelagic fish assemblages is evident in phylogenetic diversity and taxonomic richness but not the other metrics. Total abundance on the other hand only showed effects of ocean basins. The warm waters and stable climatic regimes characteristic of the tropics are hypothesized to have high diversity and high phylogenetic niche conservatism (Brown 2014). Phylogenetic niche conservatism refers to the tendency of species to retain their familial traits (Losos 2008). The results from the BRUVS-derived data are consistent with these patterns and shows tropical waters to be characterized by lower phylogenetic diversity and high taxonomic richness. Historical patterns of phylogeny have shown that Atlantic fish lineages were subjected to earlier evolutionary isolation whilst the Indian Ocean has an evolutionary history of connectivity, consistent with the BRUVS results (Cowman & Bellwood 2013). Climatically more stable areas, such as the tropics, harbour many species which enable speciation and promote genetic diversity (Pellissier et al. 2014), a pattern these results confirm. Taxonomic richness is also found to be significantly greater in the Eastern Pacific compared to the Western Pacific Ocean. However, Tittensor et al. (2010) showed coastal taxa to have peaks of diversity in the Western Pacific Ocean. Total abundance does not vary across climatic zone but is significantly higher in the Eastern Pacific Ocean compared to the Western Pacific Ocean. Previous studies of pelagic predator species

however have shown lower abundance in the Eastern Pacific and an increase north and south of the Central Pacific (Worm et al. 2005). This difference possibly suggests that the abundance pattern of top predators is distinct from the total abundance of pelagic fish assemblages.

#### *4.4 Functional metrics vs. conventional metrics*

The expansion beyond conventional metrics in biodiversity assessments is advantageous as functional metrics are more sensitive to human impact than conventional metrics. An exclusive focus on conventional attributes such as taxonomic richness, abundance and biomass may provide an incomplete view of biodiversity (Villéger et al. 2010). The BRUVS-derived data show strong evidence that functional attributes are more sensitive to human drivers than their conventional counterparts. This contrast suggests that indices based only on taxonomical identity risk overlooking the loss or diminishment of functional roles in the ecosystem. Taxonomic richness of fish assemblages is an indicator of high functional diversity and elevated levels of redundancy (Tilman et al. 1997). High levels of taxonomic richness contribute to long-term ecosystem functioning in unstable environments and are a sign of intact and resilient ecosystems (Yachi & Loreau 1999). However, despite an actual increase in taxonomic richness more recent studies have shown that species replacements tend to occur between functionally redundant species (Villéger et al. 2010). Furthermore, functions supported by rare species, those with distinct combinations of traits represented by only a few species, exhibit low redundancy even in taxonomically diverse locations such as the Coral Triangle (Mouillot et al. 2013a). This suggests that function may be affected more rapidly by human impacts while influencing or changing taxonomic richness would require entire populations to be eroded before it shows signs of disturbance.

#### *4.5 Mid-water stereo-BRUVS to assess functional ecology*

Mid-water stereo-BRUVS are a useful tool to examine the functional ecology of pelagic fish assemblages. Prior to this study, they have been largely used to document taxonomic richness, abundance and biomass, both spatially (Letessier et al. 2015, Bouchet et al. 2020) and temporally (Forrest et al. 2021). Previous studies on the functional ecology of fish assemblages were based on diver operated underwater video transects (Mouillot et al. 2013a), which are not efficient in the pelagic environment, and trawl surveys intended for fisheries stock assessments (Carrington et al. 2021), which favours highly productive fishing areas. A limitation of mid-water stereo-BRUVS, however, is the difficulties associated with readily identifying morphologically similar species such as members of the clupeids and decapterids that use

camouflage adaptations including transparency, mirrors and counter-illumination (Johnsen 2014). Species identification is also difficult for juveniles. These are common challenges across various visual survey techniques of fish assemblages, although they can be more problematic for pelagic species. In this functional analysis, the challenge of taxonomic identification to species level is likely less of a barrier, as confamilials and congeners are generally more similar to each other in functional attributes and, in the case of small juveniles, the weighting by biomass reduces their influence on the results. There are generic challenges for stereo-BRUVS including variability in underwater visibility and the extent of bait plumes. Nevertheless, the stereo-BRUVS-derived data show that functional metrics can be generated by combining key assemblage attributes such as abundance and biomass with trait-based metrics to further our understanding of pelagic assemblages.

## **5. Conclusion**

Research and conservation efforts need to focus on changes in the functional ecology of pelagic fish assemblages in addition to changes in metrics such as abundance, richness, biomass and catches (McCook et al. 2010, Pauly & Zeller 2016). The comparison of both, as undertaken here, indicates that changes in function in response to human impacts are more sensitive than changes in taxonomic richness and biomass. The effects of human activities on the function of fish assemblages may not be captured by ecological assessments without the consideration of trait-based metrics of biodiversity. The evidence that fish assemblages characterized by low fishing vulnerability and low trophic levels are most proximate to cities reflects their resilience and shows that human pressure is causing declines in highly vulnerable and high trophic level species. Consequently, the ecological functions that large-bodied fishes support may be eroding. Ecosystem functional maintenance entails a wide breadth and redundancy of function and this study demonstrates that this extends from reef to pelagic species (Tilman et al. 1997, D'Agata et al. 2016). This study builds on earlier functional studies based on fisheries data (Pauly et al. 1998), effectively using mid-water stereo-BRUVS to illustrate the expected patterns in response to human impact. The true impact of humans on fish assemblages is likely to be greater given the cumulative impacts and the change of pace in human activities (Halpern et al. 2019). Ultimately, understanding the human impact on functional ecology will also contribute to the achievement of the United Nation's Sustainable Development Goal 14, Life Below Water, as we hopefully advance towards an ecologically sustainable ocean management framework.

## 6. References

- Anderson MJ (2017) Permutational multivariate analysis of variance (PERMANOVA). Wiley Statsref: Statistics Reference Online: 1-15
- Audzijonyte A, Kuparinen A, Gorton R, Fulton EA (2013) Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biology Letters* 9:20121103
- Barley SC, Mehta RS, Meeuwig JJ, Meekan MG (2016) To knot or not? Novel feeding behaviours in moray eels. *Marine Biodiversity* 46:703-705
- Bouchet P, Meeuwig J (2015) Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves. *Ecosphere* 6:1-29
- Bouchet P, Meeuwig J, Huvneers C, Langlois T, Letessier T, Lowry M, Rees M, Santana-Garcon J, Scott M, Taylor M (2018) Marine Sampling Field Manual for Pelagic Stereo BRUVS (Baited Remote Underwater Videos). In *Field Manuals for Marine Sampling to Monitor Australian Waters*, Przeslawski R, Foster S (Eds). National Environmental Science Programme (NESP). 105-132 pp.
- Bouchet PJ, Letessier TB, Caley MJ, Nichol SL, Hemmi JM, Meeuwig JJ (2020) Submerged carbonate banks aggregate pelagic megafauna in offshore tropical Australia. *Frontiers in Marine Science* 7:530
- Brooks EJ, Sloman KA, Sims DW, Danylchuk AJ (2011) Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research* 13:231-243
- Brown JH (2014) Why are there so many species in the tropics? *Journal of Biogeography* 41:8-22
- Cappo M, Harvey E, Shortis M Counting and measuring fish with baited video techniques-an overview. *Proc Australian Society for Fish Biology Workshop Proceedings*. Australian Society for Fish Biology Tasmania
- Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology* 302:123-152
- Carrington VG, Papa Y, Beese CM, Hall J, Covain R, Horn P, Ladds MA, Rogers A (2021) How functionally diverse are fish in the deep? A comparison of fish communities in deep and shallow-water systems. *Diversity and Distributions* 00:1-16
- Cheung WW, Pitcher TJ, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* 124:97-111
- Cheung WW, Sarmiento JL, Dunne J, Frölicher TL, Lam VW, Palomares MD, Watson R, Pauly D (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* 3:254-258
- Cheung WW, Watson R, Morato T, Pitcher TJ, Pauly D (2007) Intrinsic vulnerability in the global fish catch. *Marine Ecology Progress Series* 333:1-12
- Christensen V, Coll M, Piroddi C, Steenbeek J, Buszowski J, Pauly D (2014) A century of fish biomass decline in the ocean. *Marine Ecology Progress Series* 512:155-166
- Cinner JE, Zamborain-Mason J, Gurney GG, Graham NA, MacNeil MA, Hoey AS, Mora C, Villéger S, Maire E, McClanahan TR (2020) Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* 368:307-311
- Clarke K, Gorley R (2015) Getting started with PRIMER v7. PRIMER-E: Plymouth, Plymouth Marine Laboratory 20

- Collette B, Carpenter K, Polidoro B, Juan-Jordá M, Boustany A, Die DJ, Elfes C, Fox W, Graves J, Harrison L (2011a) High value and long life—double jeopardy for tunas and billfishes. *Science* 333:291-292
- Collette B, Chang S, Di Natale A, Fox W, Juan Jorda M, Miyabe N, Nelson R, Uozumi Y, Wang S (2011b) *Thunnus maccoyii*. The IUCN Red List of Threatened Species 2011. <http://dx.doi.org/10.2305/IUCN.UK.2011-2.RLTS.T21858A9328286.en>
- Cowman PF, Bellwood DR (2013) The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *Journal of Biogeography* 40:209-224
- Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315:960-960
- D'Agata S, Mouillot D, Kulbicki M, Andréfouët S, Bellwood DR, Cinner JE, Cowman PF, Kronen M, Pinca S, Vigliola L (2014) Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology* 24:555-560
- D'Agata S, Mouillot D, Wantiez L, Friedlander AM, Kulbicki M, Vigliola L (2016) Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications* 7:1-10
- Dobson JE, Bright EA, Coleman PR, Durfee RC, Worley BA (2000) LandScan: a global population database for estimating populations at risk. *Photogrammetric engineering and remote sensing* 66:849-857
- DuFour MR, Mayer CM, Qian SS, Vandergoot CS, Kraus RT, Kocovsky PM, Warner DM (2018) Inferred fish behavior its implications for hydroacoustic surveys in nearshore habitats. *Fisheries research* 199:63-75
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP (2014) Extinction risk and conservation of the world's sharks and rays. *elife* 3:e00590-e00590
- Eero M, Vinther M, Haslob H, Huwer B, Casini M, Storr-Paulsen M, Köster FW (2012) Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Conservation Letters* 5:486-492
- Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802-813
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biological conservation* 61:1-10
- Faith DP, Reid C, Hunter J (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology* 18:255-261
- FAO (2020) The State of World Fisheries and Aquaculture 2020. Sustainability in action, Rome
- Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13:1055-1071
- Forrest J, Bouchet P, Barley S, McLennan A, Meeuwig JJ (2021) True blue: Temporal and spatial stability of pelagic wildlife at a submarine canyon. *Ecosphere* 12:e03423
- Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22:241-253
- Froese R, Kesner-Reyes K (2002) Impact of fishing on the abundance of marine species. [ICES Council Meeting Report, International Council for the Exploration of the Sea (ICES), Copenhagen, Denmark, 2002]
- Froese R, Pauly D (2021) FishBase. World Wide Web electronic publication, [www.fishbase.org](http://www.fishbase.org).
- Froese R, Winker H, Gascuel D, Sumaila UR, Pauly D (2016) Minimizing the impact of fishing. *Fish and Fisheries* 17:785-802



- Gascuel D (2005) The trophic-level based model: a theoretical approach of fishing effects on marine ecosystems. *Ecological Modelling* 189:315-332
- Gratwicke B, Speight M (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66:650-667
- Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. *Scientific reports* 9:1-8
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* 23:202-210
- Holland MM, Everett JD, Cox MJ, Doblin MA, Suthers IM (2021) Pelagic forage fish distribution in a dynamic shelf ecosystem—Thermal demands and zooplankton prey distribution. *Estuarine, Coastal and Shelf Science* 249:107074
- Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373-377
- Jennings S, Kaiser M, Reynolds JD (2001) *Marine fisheries ecology*. John Wiley & Sons, 417 pp.
- Johnsen S (2014) Hide and seek in the open sea: pelagic camouflage and visual countermeasures. *Annual Review of Marine Science* 6:369-392
- Jones MC, Cheung WW (2018) Using fuzzy logic to determine the vulnerability of marine species to climate change. *Global Change Biology* 24:e719-e731
- Juan-Jordá MJ, Mosqueira I, Cooper AB, Freire J, Dulvy NK (2011) Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences* 108:20650-20655
- Juhel J-B, Vigliola L, Wantiez L, Letessier TB, Meeuwig JJ, Mouillot D (2019) Isolation and no-entry marine reserves mitigate anthropogenic impacts on grey reef shark behavior. *Scientific reports* 9:1-11
- Keckeis H, Bauer-Nemeschkal E, Kamler E (1996) Effects of reduced oxygen level on the mortality and hatching rate of *Chondrostoma nasus* embryos. *Journal of Fish Biology* 49:430-440
- Kolding J, Bundy A, van Zwieten PA, Plank MJ (2016) Fisheries, the inverted food pyramid. *ICES Journal of Marine Science* 73:1697-1713
- Lambert C, Authier M, Doray M, Dorémus G, Spitz J, Ridoux V (2019) Hide and seek in the Bay of Biscay—a functional investigation of marine megafauna and small pelagic fish interactions. *ICES Journal of Marine Science* 76:113-123
- Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. *Aquatic Biology* 9:155-168
- Leathwick J, Elith J, Francis M, Hastie T, Taylor P (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series* 321:267-281
- Leo B (1996) *Bagging Predictors in Machine Learning*. 123-140 pp.
- Letessier TB, Cox MJ, Meeuwig JJ, Boersch-Supan PH, Brierley AS (2016) Enhanced pelagic biomass around coral atolls. *Marine Ecology Progress Series* 546:271-276
- Letessier TB, Juhel J-B, Vigliola L, Meeuwig JJ (2015) Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *Journal of Experimental Marine Biology and Ecology* 466:120-126
- Letessier TB, Meeuwig JJ, Gollock M, Groves L, Bouchet PJ, Chapuis L, Vianna GM, Kemp K, Koldewey HJ (2013) Assessing pelagic fish populations: The application of

- demersal video techniques to the mid-water environment. *Methods in Oceanography* 8:41-55
- Letessier TB, Mouillot D, Bouchet PJ, Vigliola L, Fernandes MC, Thompson C, Boussarie G, Turner J, Juhel J-B, Maire E (2019) Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. *PLoS Biology* 17:e3000366
- Lindgren M, Checkley DM, Rouyer T, MacCall AD, Stenseth NC (2013) Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proceedings of the National Academy of Sciences* 110:13672-13677
- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11:995-1003
- MacNeil MA, Chapman DD, Heupel M, Simpfendorfer CA, Heithaus M, Meekan M, Harvey E, Goetze J, Kiszka J, Bond ME (2020) Global status and conservation potential of reef sharks. *Nature* 583:801–806
- Maire E, Cinner J, Velez L, Huchery C, Mora C, Dagata S, Vigliola L, Wantiez L, Kulbicki M, Mouillot D (2016) How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters* 19:351-360
- Mazel F, Pennell MW, Cadotte MW, Diaz S, Dalla Riva GV, Grenyer R, Leprieur F, Mooers AO, Mouillot D, Tucker CM (2018) Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications* 9:1-9
- McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B (2010) Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences* 107:18278-18285
- Moran PA (1950) Notes on continuous stochastic phenomena. *Biometrika* 37:17-23
- Morato T, Cheung WW, Pitcher TJ (2006) Vulnerability of seamount fish to fishing: fuzzy analysis of life-history attributes. *Journal of Fish Biology* 68:209-221
- Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences* 107:9707-9711
- Mouchet MA, Villéger S, Mason NW, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24:867-876
- Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N (2013a) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology* 11:e1001569
- Mouillot D, Graham NA, Villéger S, Mason NW, Bellwood DR (2013b) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28:167-177
- Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-González JE, Bender M, Chabanet P, Floeter SR, Friedlander A, Vigliola L (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences* 111:13757-13762
- Musa SM, Ripley DM, Moritz T, Shiels HA (2020) Ocean warming and hypoxia affect embryonic growth, fitness, and survival of small-spotted catsharks, *Scyliorhinus canicula*. *Journal of Fish Biology*
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280-283

- Newman SJ, Skepper CL, Mitsopoulos GE, Wakefield CB, Meeuwig JJ, Harvey ES (2011) Assessment of the potential impacts of trap usage and ghost fishing on the Northern Demersal Scalefish Fishery. *Reviews in Fisheries Science* 19:74-84
- Ordiz A, Bischof R, Swenson JE (2013) Saving large carnivores, but losing the apex predator? *Biological Conservation* 168:128-133
- Otto SB, Berlow EL, Rank NE, Smiley J, Brose U (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology* 89:134-144
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14:483-488
- Palacios MdM, McCormick MI (2021) Positive indirect effects of top-predators on the behaviour and survival of juvenile fishes. *Oikos* 130:219-230
- Palomares M, Froese R, Derrick B, Meeuwig J, Noël S-L, Tsui G, Woroniak J, Zeller D, Pauly D (2020) Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins. *Estuarine, Coastal and Shelf Science* 243:1-10
- Pauly D (2019) *Vanishing fish: shifting baselines and the future of global fisheries*. Greystone Books Ltd
- Pauly D (2021) The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances* 7:eabc6050
- Pauly D, Cheung WW (2018) Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global change biology* 24:e15-e26
- Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374:255-257
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860-863
- Pauly D, Froese R, Holt SJ (2016) Balanced harvesting: the institutional incompatibilities. *Marine Policy* 69:121-123
- Pauly D, Froese R, Palomares ML (2000) Fishing down aquatic food webs: Industrial fishing over the past half-century has noticeably depleted the topmost links in aquatic food chains. *American Scientist* 88:46-51
- Pauly D, Watson R (2005) Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360:415-423
- Pauly D, Zeller D (2016) Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications* 7:10244
- Pellissier L, Leprieur F, Parravicini V, Cowman PF, Kulbicki M, Litsios G, Olsen SM, Wisz MS, Bellwood DR, Mouillot D (2014) Quaternary coral reef refugia preserved fish diversity. *Science* 344:1016-1019
- Perry RI, Cury P, Brander K, Jennings S, Möllmann C, Planque B (2010) Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *Journal of Marine Systems* 79:427-435
- Petrou EL, Fuentes-Pardo AP, Rogers LA, Orobko M, Tarpey C, Jiménez-Hidalgo I, Moss ML, Yang D, Pitcher TJ, Sandell T (2021) Functional genetic diversity in an exploited marine species and its relevance to fisheries management. *Proceedings of the Royal Society B* 288:20202398
- Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* 15:43-64

- Queiros Q, Fromentin J-M, Gasset E, Dutto G, Huiban C, Metral L, Leclerc L, Schull Q, McKenzie DJ, Saraux C (2019) Food in the sea: size also matters for pelagic fish. *Frontiers in Marine Science* 6:385
- Rigby C, Barreto R, Carlson J, Fernando D, Fordham S, Francis M, Herman K, Jabado R, Liu K, Marshall A (2019) *Carcharhinus longimanus*. The IUCN Red List of Threatened Species:2019-2013
- Rigler F (1975) The concept of energy flow and nutrient flow between trophic levels. In: van Dobben W.H. L-MRH (ed) *Unifying Concepts in Ecology*. Springer, Dordrecht. 15-16 pp. [https://doi.org/10.1007/978-94-010-1954-5\\_2](https://doi.org/10.1007/978-94-010-1954-5_2)
- Ripple WJ, Larsen EJ, Renkin RA, Smith DW (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227-234
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12:982-998
- Ryan LA, Meeuwig JJ, Hemmi JM, Collin SP, Hart NS (2015) It is not just size that matters: shark cruising speeds are species-specific. *Marine Biology* 162:1307-1318
- Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208:229-248
- Seager J (2014) SeaGIS. Accessed November, 14. <http://www.seagis.com.au>
- Skerritt DJ, Sumaila UR (2021) Broadening the global debate on harmful fisheries subsidies through the use of subsidy intensity metrics. *Marine Policy* 128:104507
- Strecker AL, Olden JD, Whittier JB, Paukert CP (2011) Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecological Applications* 21:3002-3013
- Tacon AG, Metian M (2009) Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. *Ambio* 38:294-302
- Thompson CD, Bouchet PJ, Meeuwig JJ (2019) First underwater sighting of Shepherd's beaked whale (*Tasmacetus shepherdi*). *Marine Biodiversity Records* 12:6
- Tickler D, Meeuwig JJ, Palomares M-L, Pauly D, Zeller D (2018) Far from home: Distance patterns of global fishing fleets. *Science advances* 4:ear3279
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300-1302
- Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098-1101
- Tommasi D, Stock CA, Pegion K, Vecchi GA, Methot RD, Alexander MA, Checkley Jr DM (2017) Improved management of small pelagic fisheries through seasonal climate prediction. *Ecological Applications* 27:378-388
- Trenkel VM, Hintzen NT, Farnsworth KD, Olesen C, Reid D, Rindorf A, Shephard S, Dickey-Collas M (2015) Identifying marine pelagic ecosystem management objectives and indicators. *Marine Policy* 55:23-32
- Ursin E (1973) On the prey size preferences of cod and dab. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser N.S.* 7, 85-98
- Veron JE, Devantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, Peterson N (2009) Delineating the coral triangle. *Galaxea, Journal of Coral Reef Studies* 11:91-100
- Vianna GM, Zeller D, Pauly D (2020) Fisheries and Policy Implications for Human Nutrition. *Current Environmental Health Reports* 7:1-9

- Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20:1512-1522
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116:882-892
- Whitmarsh SK, Fairweather PG, Huveneers C (2017) What is Big BRUVver up to? Methods and uses of baited underwater video. *Reviews in Fish Biology and Fisheries* 27:53-73
- Winter M, Devictor V, Schweiger O (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution* 28:199-204
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JB, Lotze HK, Micheli F, Palumbi SR (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787-790
- Worm B, Lotze HK, Myers RA (2003) Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences* 100:9884-9888
- Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. *Science* 309:1365-1369
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences* 96:1463-1468
- Yesson C, Clark MR, Taylor ML, Rogers AD (2011) The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers* 58:442-453

## 7. Supplementary material

**Table S1.** Study locations by country, ocean basin, climatic zone, number of rigs and number of strings deployed.

Location	Country	Ocean basin	Climatic zone	Rigs	Strings
Argo-Terrace	Australia	Indian Ocean	Tropical	240	48
Ascension Island	United Kingdom	Atlantic Ocean	Tropical	655	128
Azores	Portugal	Atlantic Ocean	Temperate	155	31
Ashmore Reef	Australia	Indian Ocean	Tropical	200	40
Bremer Canyon	Australia	Indian Ocean	Temperate	200	40
British Indian Ocean Territory	United Kingdom	Indian Ocean	Tropical	546	109
Clipperton Island	France	Eastern Pacific Ocean	Tropical	51	17
Cocos (Keeling) Island	Australia	Indian Ocean	Tropical	110	22
Far North Queensland	Australia	Western Pacific Ocean	Tropical	164	33
French Polynesia	French Polynesia	Western Pacific Ocean	Tropical	50	8
Galapagos	Ecuador	Eastern Pacific Ocean	Tropical	150	49
Geographe Bay	Australia	Indian Ocean	Temperate	350	45
Gracetown	Australia	Indian Ocean	Temperate	300	58

<b>Location</b>	<b>Country</b>	<b>Ocean basin</b>	<b>Climatic zone</b>	<b>Rigs</b>	<b>Strings</b>
Long Reef	Australia	Indian Ocean	Tropical	200	39
Maldives	Maldives	Indian Ocean	Tropical	205	39
Malpelo	Colombia	Eastern Pacific Ocean	Tropical	85	16
Montebellos	Australia	Indian Ocean	Tropical	200	40
New Caledonia	New Caledonia	Indian Ocean	Tropical	160	30
Ningaloo	Australia	Indian Ocean	Tropical	280	56
Niue	Niue	Western Pacific Ocean	Tropical	160	12
Osa Peninsula	Costa Rica	Eastern Pacific Ocean	Tropical	169	34
Palau	Republic of Palau	Western Pacific Ocean	Tropical	147	29
Perth Canyon	Australia	Indian Ocean	Temperate	419	77
Rapa	Rapa Iti	Western Pacific Ocean	Temperate	53	15
Recherche Archipelago - East	Australia	Indian Ocean	Temperate	110	22
Recherche Archipelago - Middle	Australia	Indian Ocean	Temperate	110	22
Recherche Archipelago - West	Australia	Indian Ocean	Temperate	110	22
Revillagigedo	Mexico	Atlantic Ocean	Tropical	75	25
Rowley Shoals	Australia	Indian Ocean	Tropical	55	10

<b>Location</b>	<b>Country</b>	<b>Ocean basin</b>	<b>Climatic zone</b>	<b>Rigs</b>	<b>Strings</b>
Selvagens Island	Portugal	Atlantic Ocean	Temperate	57	12
Shark Bay	Australia	Indian Ocean	Temperate	342	65
Tonga	Tonga	Western Pacific Ocean	Tropical	36	12
Tristan da Cunha	United Kingdom	Atlantic Ocean	Temperate	81	25



**Table S2.** Taxonomic information including family name, scientific name, common name and fork length (FL)  $\pm$  standard error (SE) in cm obtained from mid-water stereo-BRUVS. For individuals only identified to family level, the scientific name assigned was “Family name sp.” and a generic common name for this entry was also given e.g., cardinalfish. Total length (ToL), fork length relationships, length-weight coefficient, taxon's trophic level (TL), phylogenetic diversity (PD) and fishing vulnerability (FV) were obtained from FishBase. ‘-’ indicates that no information was available.

Family	Scientific name	Common name	FL $\pm$ SE	ToL:FL	a	b	TL	PD	FV
Acanthuridae	<i>Acanthurus</i> sp.	surgeonfish	42 $\pm$ 0	1.06500	0.03300	2.920	2.9	26.5	0.5
Acanthuridae	<i>Acanthurus xanthopterus</i>	yellowfin surgeonfish	39 $\pm$ 1.4	1.12000	0.03300	2.920	2.9	37	0.5
Acanthuridae	<i>Naso hexacanthus</i>	sleek unicornfish	57 $\pm$ 3.0	1.05606	0.02017	2.956	3.06	41	0.5
Acanthuridae	<i>Naso</i> sp.	unicornfish	66 $\pm$ 0	1.07361	0.02017	2.956	3.06	41	0.5
Acanthuridae	<i>Naso tonganus</i>	bulbnose unicornfish	56 $\pm$ 0	1.01617	0.02577	2.967	2	51	0.5
Acanthuridae	<i>Prionurus laticlavus</i>	razor surgeonfish	33 $\pm$ 4.7	1.05800	0.01995	3.010	2.7	1.058	2.7
Alopiidae	<i>Alopias pelagicus</i>	pelagic thresher	27 $\pm$ 0	2.00000	0.00911	3.080	4.5	73	0.75
Apogonidae	<i>Apogon</i> sp.	Apogon cardinalfish	4 $\pm$ 0	1.10900	0.01380	3.080	3.6	10.6	0.5
Apogonidae	Apogonidae sp.	cardinalfish	7 $\pm$ 0.5	1.00000	0.01380	3.080	3.61	11	0.5156
Apogonidae	<i>Ostorhinchus holotaenia</i>	copperstriped cardinalfish	7 $\pm$ 0	1.05935	0.01380	3.080	3.52	10	0.5
Apogonidae	<i>Pristiapogon abrogramma</i>	Lateralstripe cardinalfish	3 $\pm$ 0	1.08200	0.00646	3.190	3.5	1.082	3.5
Apogonidae	<i>Pristiapogon exostigma</i>	narrowstripe cardinalfish	3 $\pm$ 0	1.05300	0.01635	3.039	3.7	12	0.5312
Apogonidae	<i>Pristiapogon</i> sp.	cardinalfish	3 $\pm$ 0	1.05300	0.01635	3.039	3.7	12	0.5312
Aracanidae	<i>Anoplocapros amygdaloides</i>	western smooth boxfish	28 $\pm$ 0	1.00000	0.01995	3.010	3.4	16	0.6252
Aulostomidae	<i>Aulostomus chinensis</i>	Chinese trumpetfish	16 $\pm$ 0.4	1.00000	0.00021	3.514	4.2	34	0.75
Balistidae	<i>Abalistes stellatus</i>	starry triggerfish	38 $\pm$ 0	1.04992	0.02570	2.940	3.4	44	0.62
Balistidae	<i>Balistes capriscus</i>	grey triggerfish	30 $\pm$ 0.3	1.06274	0.01930	2.896	3.76	32	0.5078
Balistidae	<i>Balistes polylepis</i>	finescale triggerfish	35 $\pm$ 2.8	1.07600	0.04200	2.701	3.3	1.076	3.3
Balistidae	Balistidae sp.	triggerfishes	2 $\pm$ 0.1	1.05633	0.01930	2.896	3.38	32	0.625
Balistidae	<i>Canthidermis maculata</i>	rough triggerfish	31 $\pm$ 1.6	1.00000	0.02570	2.940	3.5	41	0.625
Balistidae	<i>Melichthys niger</i>	black triggerfish	18 $\pm$ 0.7	1.00000	0.02570	2.940	2.4	44	0.625
Balistidae	<i>Pseudobalistes fuscus</i>	yellow-spotted triggerfish	29 $\pm$ 1.5	1.00000	0.07255	2.760	4	41	0.625
Balistidae	<i>Pseudobalistes naufragium</i>	stone triggerfish	5 $\pm$ 1.1	1.00000	0.02570	2.940	3.4	59	0.625
Belonidae	<i>Ablennes hians</i>	flat needlefish	61 $\pm$ 5.0	1.03306	0.00036	3.322	4.5	40	1

Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Blenniidae	<i>Aspidontus dussumieri</i>	lance blenny	4±7	1.00000	0.00550	3.050	2	23	0.625
Blenniidae	<i>Aspidontus</i> sp.	cleanerfish	4±0	1.00000	0.01438	3.014	2.87	22.47	0.625
Blenniidae	<i>Aspidontus taeniatus</i>	false cleanerfish	4±0.1	1.00000	0.00550	3.050	3.8	22	0.625
Blenniidae	<i>Aspidontus tractus</i>	aspidotus blennie	5±0.1	1.00000	0.00537	3.050	2.9	1	2.9
Blenniidae	Blenniidae sp.	blennies	8±0	1.01291	0.01438	3.014	2.3	18.06	0.54
Blenniidae	<i>Plagiotremus</i> sp.	combtooth blenny	4±0	1.00000	0.00468	3.000	3.8	24	0.5005
Blenniidae	<i>Plagiotremus tapeinosoma</i>	piano fangblenny	3±0.3	1.02669	0.00566	2.908	3.8	24	0.5005
Caesionidae	<i>Caesio teres</i>	yellow and blueback fusilier	25±0	1.14479	0.01795	3.045	3.4	28	0.502
Caesionidae	<i>Pterocaesio</i> sp.	fusilier	20±0	1.09300	0.00948	3.229	3.4	18	0.5002
Caesionidae	<i>Pterocaesio tile</i>	dark-banded fusilier	21±0	1.12571	0.00948	3.229	3.33	24	0.5002
Caproidae	<i>Capros aper</i>	boarfish	3±9	1.00000	0.01905	2.830	3.1	51	1
Carangidae	<i>Alectis ciliaris</i>	African pompano	5±0	1.12370	0.07860	2.579	3.71	69	0.625
Carangidae	<i>Alepes apercna</i>	smallmouth scad	9±1.0	1.14155	0.01349	2.960	3.5	24	0.5312
Carangidae	<i>Alepes</i> sp.	Alepes scad	31±0	1.12994	0.01740	3.113	3.6	29.5	0.5312
Carangidae	<i>Alepes vari</i>	herring scad	12±0.6	1.14155	0.01349	2.960	3.7	35	0.5312
Carangidae	<i>Atule mate</i>	yellowtail scad	13±0.4	1.06952	0.01660	2.949	4.2	19	1
Carangidae	Carangidae sp.	jacks	4±0.1	1.15056	0.02570	2.937	3.79	49.4	0.613
Carangidae	<i>Carangoides armatus</i>	longfin trevally	4±0.5	1.21655	0.01145	3.126	4.2	35	0.5
Carangidae	<i>Carangoides ferdau</i>	blue trevally	9±0.9	1.20048	0.03160	2.910	4.3	44	0.5
Carangidae	<i>Carangoides gymnostethus</i>	bludger	94±7.7	1.09649	0.04631	2.746	4.1	47	0.5
Carangidae	<i>Carangoides orthogrammus</i>	island trevally	21±0	1.11359	0.02230	2.980	4.5	40	0.5
Carangidae	<i>Carangoides</i> sp.	fat jack	4±0.1	1.13494	0.02940	2.932	4.3	46.4	0.5
Carangidae	<i>Caranx caballus</i>	green jack	30±2.1	1.13516	0.02875	2.955	4.05	34	0.5
Carangidae	<i>Caranx crysos</i>	blue runner	38±6.4	1.16064	0.02987	2.951	3.88	34	0.5
Carangidae	<i>Caranx hippos</i>	crevalle jack	20±6.7	1.13300	0.05170	2.734	3.83	41	0.5
Carangidae	<i>Caranx ignobilis</i>	giant trevally	94±8.7	1.07066	0.03530	3.050	4.2	82	0.5
Carangidae	<i>Caranx melampygus</i>	bluefin trevally	62±9.2	1.08400	0.02350	2.920	4.5	56	0.5
Carangidae	<i>Caranx sexfasciatus</i>	bigeye trevally	5±0.1	1.08460	0.05010	2.710	4.5	45	0.5
Carangidae	<i>Caranx</i> sp.	Caranx trevally	4±0.1	1.15056	0.02567	2.937	3.84	37.88	0.567

Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Carangidae	<i>Decapterus macarellus</i>	mackerel scad	12±0.6	1.10497	0.00783	3.140	4	20	0.0501
Carangidae	<i>Decapterus muroadsi</i>	amberstripe scad	9±3.4	1.07400	0.01094	3.000	3.4	41	0.501
Carangidae	<i>Decapterus</i> sp.	Decapterus scad	9±0.1	1.08082	0.00890	3.139	4	20	0.0501
Carangidae	<i>Echeneis naucrates</i>	live sharksucker	74±0.1	1.00000	0.00075	3.358	3.7	54	0.7539
Carangidae	<i>Elagatis bipinnulata</i>	rainbow runner	70±1.7	1.29870	0.01000	2.850	4.3	51	1
Carangidae	<i>Gnathanodon speciosus</i>	golden trevally	5±0.8	1.21655	0.01992	2.995	4.3	38	1
Carangidae	<i>Megalaspis cordyla</i>	torpedo scad	10±0.9	1.11359	0.03200	2.582	3.9	29	1
Carangidae	<i>Naucrates ductor</i>	pilotfish	12±0.6	1.06952	0.01470	3.040	3.4	24	1
Carangidae	<i>Parastromateus niger</i>	black pomfret	45±0	1.12108	0.03220	3.010	2.9	30	1
Carangidae	<i>Pseudocaranx dentex</i>	white trevally	7±0.7	1.20919	0.02710	2.886	3.9	74	0.5625
Carangidae	<i>Pseudocaranx</i> sp.	Pseudocaranx trevally	25±6.8	1.20919	0.01413	2.960	3.9	74	0.5625
Carangidae	<i>Scomberoides lysan</i>	doublespotted queenfish	22±0	1.20773	0.04910	2.640	4	40	0.5625
Carangidae	<i>Scomberoides</i> sp.	queenfish	52±0	1.14566	0.01847	2.826	4.28	42.04	0.562
Carangidae	<i>Scomberoides tol</i>	needlescaled queenfish	37±0	1.09905	0.01642	2.767	4.31	35	0.5625
Carangidae	<i>Selar boops</i>	oxeye scad	7±0.9	1.12740	0.01622	3.030	3.5	14	0.75
Carangidae	<i>Selar crumenophthalmus</i>	bigeye scad	14±0.4	1.12994	0.00400	3.259	3.8	39	0.75
Carangidae	<i>Selar</i> sp.	Selar scad	44±0	1.13340	0.01124	3.151	3.57	19.765	0.75
Carangidae	<i>Selene peruviana</i>	Peruvian moonfish	2±2.4	1.13400	0.02100	2.749	4.3	29	0.5039
Carangidae	<i>Seriola dumerili</i>	greater amberjack	16±0.7	1.13636	0.04230	2.747	4.5	54	0.502
Carangidae	<i>Seriola hippos</i>	samson fish	67±8.8	1.12740	0.01370	3.000	4.6	71	0.502
Carangidae	<i>Seriola lalandi</i>	yellowtail amberjack	60±2.6	1.11607	0.04320	2.850	4.2	69	0.502
Carangidae	<i>Seriola rivoliana</i>	longfin yellowtail	34±3.3	1.10742	0.03590	2.801	4.5	76	0.502
Carangidae	<i>Seriola</i> sp.	amberjack	5±1.3	1.11457	0.02580	2.913	4.35	72.5	0.502
Carangidae	<i>Seriolina nigrofasciata</i>	blackbanded trevally	7±1.2	1.11359	0.02580	2.913	4.2	38	1
Carangidae	<i>Trachurus novaezelandiae</i>	yellowtail horse mackerel	16±0.7	0.86300	0.04780	2.770	3.2	38	0.5001
Carangidae	<i>Trachurus</i> sp.	horse mackerel	9±0.5	1.11744	0.01239	2.945	3.56	40.16	0.5
Carangidae	<i>Trachurus trachurus</i>	Atlantic horse mackerel	13±0	1.07914	0.00832	2.960	3.78	53	0.5001
Carcharhinidae	Carcharhinidae sp.	requiem sharks	11±8.2	1.21582	0.00427	3.100	4.31	73.76	0.5
Carcharhinidae	<i>Carcharhinus albimarginatus</i>	silvertip shark	12±2.8	1.23762	0.00427	3.100	4.2	76	0.5

Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Carcharhinidae	<i>Carcharhinus altimus</i>	bignose shark	18±0	1.20627	0.00100	3.461	4.5	76	0.5
Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	blacktail reef shark	11±2.7	1.17647	0.00227	3.373	4.1	85	0.5
Carcharhinidae	<i>Carcharhinus amboinensis</i>	pigeye shark	18±6.8	1.19048	0.00479	3.100	4.3	74	0.5
Carcharhinidae	<i>Carcharhinus brachyurus</i>	copper shark	19±3.9	1.22100	0.01040	2.900	4.5	87	0.5
Carcharhinidae	<i>Carcharhinus brevipinna</i>	spinner shark	15±7.8	1.20192	0.00429	3.020	4.2	62	0.5
Carcharhinidae	<i>Carcharhinus falciformis</i>	silky shark	14±2.0	1.21507	0.01540	2.922	4.5	79	0.5
Carcharhinidae	<i>Carcharhinus galapagensis</i>	Galapagos shark	13±4.1	1.23732	0.00427	3.100	4.29	84	0.5
Carcharhinidae	<i>Carcharhinus leucas</i>	bull shark	19±11	1.22956	0.01750	2.840	4.33	88	0.5
Carcharhinidae	<i>Carcharhinus limbatus</i>	blacktip shark	11±2.7	1.16009	0.01242	2.850	4.4	55	0.5
Carcharhinidae	<i>Carcharhinus longimanus</i>	oceanic whitetip shark	18±17	1.21655	0.02540	2.691	4.2	79	0.5
Carcharhinidae	<i>Carcharhinus obscurus</i>	dusky shark	21±2.5	1.19760	0.03240	2.786	4.3	88	0.5
Carcharhinidae	<i>Carcharhinus plumbeus</i>	sandbar shark	13±1.6	1.22249	0.01090	3.012	4.5	88	0.5
Carcharhinidae	<i>Carcharhinus sorrah</i>	spot-tail shark	86±4.3	1.19617	0.00072	3.656	4.2	51	0.5
Carcharhinidae	<i>Carcharhinus</i> sp.	requiem shark	14±3.9	1.21788	0.00427	3.100	4.31	73.76	0.5
Carcharhinidae	<i>Carcharhinus tilstoni</i>	Australian blacktip shark	10±2.5	1.21882	0.00878	3.299	4.37	70	0.5
Carcharhinidae	<i>Galeocerdo cuvier</i>	tiger shark	25±8.8	1.14155	0.00253	3.260	4.3	64	1
Carcharhinidae	<i>Negaprion acutidens</i>	sicklefin lemonshark	20±0.5	1.12740	0.00841	3.000	4.1	81	0.75
Carcharhinidae	<i>Prionace glauca</i>	blue shark	16±4.9	1.21655	0.00318	3.131	4.4	77	1
Carcharhinidae	<i>Rhizoprionodon acutus</i>	milk shark	68±2.0	1.22249	0.00790	2.987	4.3	61	0.5078
Centriscidae	<i>Macroramphosus scolopax</i>	longspine snipefish	6±0.3	1.00000	0.00400	3.150	3.5	27	0.7502
Centrolophidae	<i>Centrolophus niger</i>	black ruff	22±2.7	1.07643	0.00240	3.346	3.9	85	1
Centrolophidae	<i>Schedophilus ovalis</i>	Imperial blackfish	39±0	1.09200	0.00220	3.460	3.5	60	0.5039
Centrolophidae	<i>Schedophilus</i> sp.	warehou	43±0	1.09200	0.00891	3.090	3.8	60	0.5039
Centrolophidae	<i>Schedophilus velaini</i>	violet warhou	61±3.1	1.07562	0.01562	3.078	4.15	61	0.5039
Centrolophidae	<i>Serirolella</i> sp.	medusa fish	51±0	0.00000	0.01930	3.000	4.35	72.5	0.502
Chaetodontidae	<i>Heniochus</i> sp.	bannerfish	3±0	1.00000	0.01928	3.193	4.3	16.44	0.504
Chanidae	<i>Chanos chanos</i>	milkfish	91±5.8	1.19000	0.09050	2.520	2.4	76	1.5
Clupeidae	Clupeidae sp.	herrings	12±1.0	1.00000	0.01820	3.131	3.13	15.8	0.5
Clupeidae	<i>Sardinella</i> sp.	sardine	6±0.7	1.15607	0.01290	2.870	2.76	15.8	0.5

Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Coryphaenidae	<i>Coryphaena equiselis</i>	pompano dolphinfish	34±2.7	1.17647	0.01000	2.840	4.5	39	1
Coryphaenidae	<i>Coryphaena hippurus</i>	common dolphinfish	74±1.9	1.21507	0.02020	2.799	4.4	40	1
Dasyatidae	<i>Bathytoshia brevicaudata</i>	short-tail stingray	12±0	1.00000	0.03320	2.940	3.9	87	0.625
Dasyatidae	Dasyatidae sp.	whiptail stingray	85±0	1.00000	0.01290	3.031	3.7	80	0.625
Dasyatidae	<i>Dasyatis pastinaca</i>	common stingray	90±0	1.00000	0.04190	3.317	4.1	79	0.5002
Dasyatidae	<i>Pteroplatytrygon violacea</i>	pelagic stingray	80±0	1.00000	0.02190	3.006	4.4	1	4.4
Diodontidae	<i>Diodon hystrix</i>	spot-fin porcupinefish	60±0	1.00000	0.02360	3.124	3.64	48	0.5313
Echeneidae	Echeneidae sp.	remoras	13±0	1.01252	0.00075	3.358	3.42	41.26	0.64
Echeneidae	<i>Echeneis naucrates</i>	live sharksucker	74±0.1	1.00000	0.00075	3.358	3.7	54	0.7539
Echeneidae	<i>Remora australis</i>	whalesucker	52±0	1.03199	0.00275	3.150	3.5	45	0.5352
Echeneidae	<i>Remora remora</i>	shark sucker	15±1.1	1.05708	0.00080	3.358	3.5	48	0.5352
Echeneidae	<i>Remora</i> sp.	remora	9±1.8	1.00000	0.00080	3.358	3.5	48	0.5352
Engraulidae	<i>Engraulidae</i> sp	anchovies	3±0.1	1.10800	0.00550	3.170	4.3	13	0.5
Exocoetidae	<i>Cheilopogon</i> sp	Cheilopogon flyingfish	35±1.2	1.13931	0.00427	3.120	3.6275	19.04	0.5
Exocoetidae	<i>Cheilopogon suttoni</i>	Sutton's flyingfish	19±0	1.13931	0.00427	3.120	3.94	20	0.5
Exocoetidae	Exocoetidae sp.	flyingfish	24±1.4	1.16686	0.00430	2.878	3.75	16	0.5
Fistulariidae	<i>Fistularia commersonii</i>	bluespotted cornetfish	15±0.4	1.00000	0.01180	2.727	4.3	68	0.625
Fistulariidae	<i>Fistularia petimba</i>	red cornetfish	13±1.3	1.00000	0.00030	3.158	4.3	71	0.625
Fistulariidae	<i>Fistularia</i> sp.	Fistularia cornetfish	14±0.2	1.00000	0.00030	3.182	4.3	69.5	0.625
Fistulariidae	Fistulariidae sp.	cornetfish	17±0.1	1.19167	0.00029	3.182	4.3	63.94	0.625
Gerreidae	<i>Gerres</i> sp.	silver-biddy	20±0	1.14500	0.01200	3.232	3.2	26	0.5
Istiophoridae	<i>Istiompax indica</i>	black marlin	18±9.6	1.12740	0.00653	2.960	4.5	78	1.0005
Istiophoridae	Istiophoridae sp.	billfishes	18±8.8	1.12621	0.00710	2.989	4.48	62.66	0.792
Istiophoridae	<i>Istiophorus platypterus</i>	Indo-Pacific sailfish	19±9.4	1.16550	0.00238	3.000	4.5	68	0.7505
Istiophoridae	<i>Kajikia albida</i>	Atlantic white marlin	21±0	1.16400	0.00463	3.000	4.5	43	0.7505
Istiophoridae	<i>Kajikia audax</i>	striped marlin	17±18	1.08342	0.01300	2.810	4.5	43	0.7505
Istiophoridae	<i>Makaira nigricans</i>	blue marlin	21±7.6	1.09012	0.00700	2.960	4.5	52	0.7505
Kyphosidae	<i>Kyphosus ocyurus</i>	bluestriped chub	41±0.8	1.17371	0.01778	3.010	3.5	47	0.5
Kyphosidae	<i>Kyphosus sydneyanus</i>	silver drummer	47±0	1.05820	0.02260	3.055	2	59	0.5

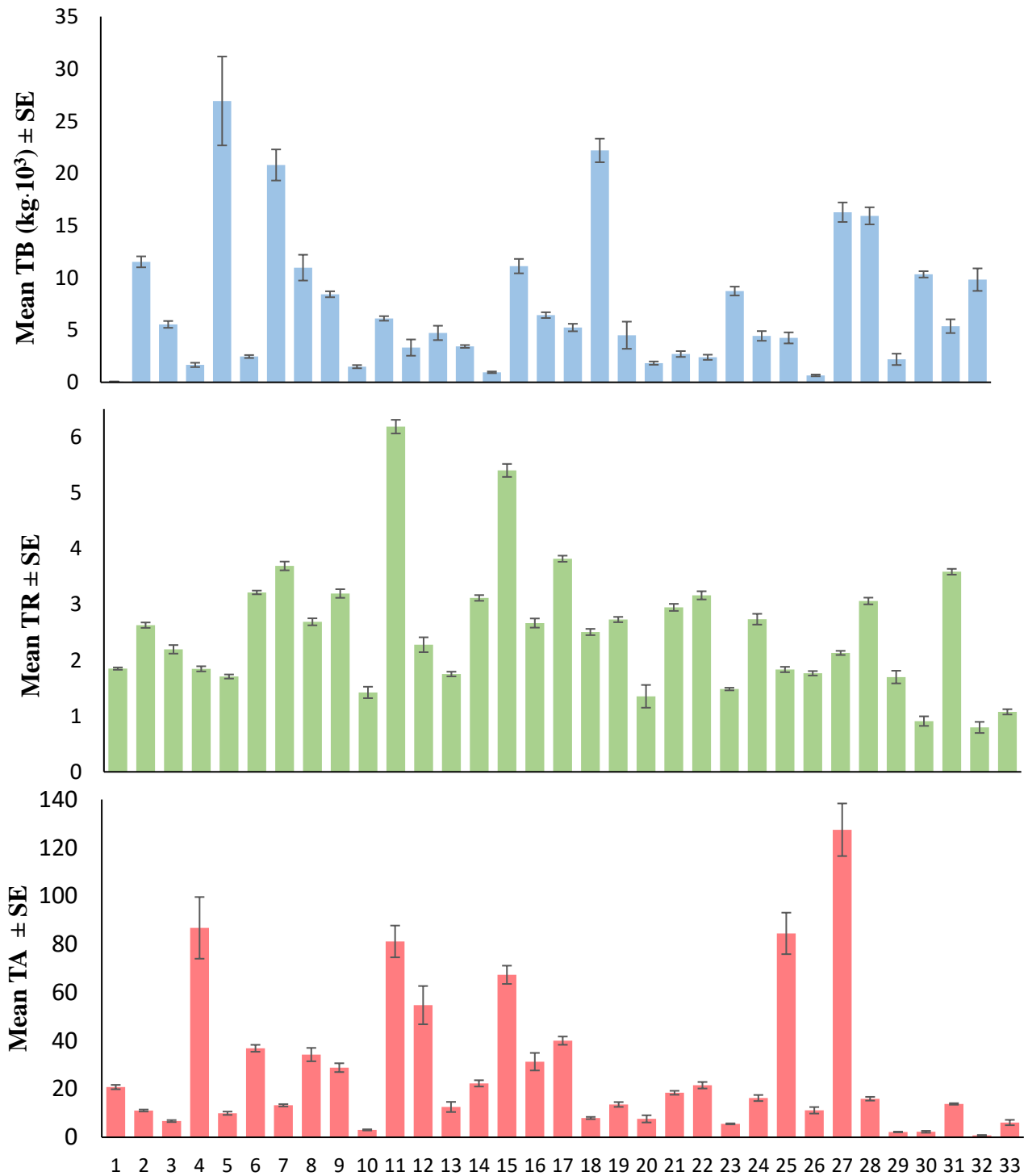
Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Kyphosidae	<i>Kyphosus vaigiensis</i>	brassy chub	41±0	1.07100	0.01998	3.037	2	0	2
Kyphosidae	<i>Neotypus obliquus</i>	footballer sweep	15±0	1.08108	0.02291	2.990	3.5	27	1
Kyphosidae	<i>Scorpius aequipinnis</i>	sea sweep	36±0	1.12486	0.01445	3.000	3.3	48	0.5312
Labridae	<i>Choerodon rubescens</i>	baldchin groper	29±0	1.00000	0.01698	3.030	3.6	65	0.5
Labridae	<i>Coris auricularis</i>	western king wrasse	33±1.5	1.00000	0.01000	3.060	3.5	50	0.5
Labridae	Labridae sp.	wrasses	20±0	1.00877	0.01869	2.966	3.48	29.25	0.541
Labridae	<i>Labroides dimidiatus</i>	bluestreak cleaner wrasse	5±0.4	1.00000	0.00585	3.231	3.5	24	0.5312
Labridae	<i>Notolabrus parilus</i>	brownspeckled wrasse	34±0	1.00000	0.01000	3.050	3.6	52	0.5078
Labridae	<i>Ophthalmolepis lineolata</i>	southern maori wrasse	26±0	1.00000	0.00447	3.140	3.5	36	1
Lamnidae	<i>Carcharodon carcharias</i>	white pointer	31±28	1.05932	0.00758	3.085	4.5	86	1.0313
Lamnidae	<i>Isurus oxyrinchus</i>	shortfin mako	15±9.3	1.07643	0.01670	2.847	4.5	83	0.7813
Lamnidae	<i>Lamna nasus</i>	porbeagle	95±0	1.12613	0.02860	2.924	4.47	86	0.7813
Lobotidae	<i>Lobotes surinamensis</i>	tripletail	80±0	1.00000	0.02399	3.000	4	35	0.02399
Lutjanidae	<i>Aprion virescens</i>	green jobfish	63±6.6	1.17723	0.01570	3.041	4.13	61	1
Lutjanidae	<i>Lutjanus argentiventris</i>	yellow snapper	47±0	1.04300	0.01770	2.960	4	1.043	4
Lutjanidae	<i>Lutjanus bengalensis</i>	bengal snapper	20±0	1.05396	0.03502	3.000	3.78	27	0.5
Lutjanidae	<i>Lutjanus bohar</i>	two-spot red snapper	11±0	1.05448	0.01491	3.071	3.94	69	0.5
Lutjanidae	<i>Lutjanus jordani</i>	Jordan's snapper	54±3.0	1.05000	0.01479	2.970	4.5	39	0.5
Lutjanidae	<i>Lutjanus novemfasciatus</i>	Pacific dog snapper	76±21.	-	0.01700	2.930	-	-	-
Macroramphosidae	<i>Notopogon lilliei</i>	crested bellowfish	3±0	1.01576	0.01479	2.940	3.4	33	0.5315
Molidae	<i>Masturus lanceolatus</i>	sharptail mola	12±32	1.00000	0.06610	2.910	3.8	70	1.0312
Molidae	<i>Mola alexandrini</i>	southern ocean sunfish	19±31	1.00000	0.02455	3.010	3.8	81	0.6262
Molidae	<i>Mola mola</i>	ocean sunfish	11±15	1.00000	0.04540	3.050	3.3	67	0.6562
Molidae	Mola sp.	sunfish	15±0	1.00000	0.04540	3.050	3.55	74	0.6412
Monacanthidae	<i>Aluterus monoceros</i>	unicorn leatherjacket filefish	22±1.3	1.03413	0.02220	2.860	3.8	48	0.5625
Monacanthidae	<i>Aluterus scriptus</i>	scribbled leatherjacket filefish	11±1.0	1.00000	0.82300	1.814	2.8	68	0.5625
Monacanthidae	<i>Aluterus</i> sp.	leatherjacket filefish	4±0.8	1.00000	0.02140	2.910	3.3	58	0.5625
Monacanthidae	<i>Cantherhines dumerilii</i>	whitespotted filefish	24±0	1.00000	0.02455	2.920	3.1	36	0.5002
Monacanthidae	<i>Cantherhines fronticinctus</i>	spectacled filefish	5±0.1	1.00000	0.01445	3.076	3.5	33	0.5002

Family	Scientific name	Common name	FL±SE	ToL:FL	a	b	TL	PD	FV
Monacanthidae	<i>Cantherhines macrocerus</i>	American whitespotted filefish	4±0.5	1.00000	0.01445	3.076	2.9	46	0.5002
Monacanthidae	<i>Cantherhines</i> sp.	spotted filefish	17±0	1.00000	0.02089	2.930	3.1	38	0.5002
Monacanthidae	<i>Eubalichthys caeruleoguttatus</i>	blue-spotted leatherjacket	4±0.2	1.05820	0.02089	2.930	4.3	36	0.5156
Monacanthidae	<i>Eubalichthys</i> sp.	filefish	2±0.1	1.05820	0.02089	2.930	4.3	36	0.5156
Monacanthidae	<i>Monacanthidae</i> sp.	leatherjackets	4±0.1	1.00000	0.01440	3.076	3.78	49.14	0.618
Monacanthidae	<i>Nelusetta ayraud</i>	ocean leatherjacket	13±0.2	1.00000	0.01930	2.808	3.7	56	1
Monacanthidae	<i>Pervagor aspricaudus</i>	orangetail filefish	8±0.3	1.00000	0.02089	2.930	2.9	20	0.5039
Monacanthidae	<i>Pseudalutarius nasicornis</i>	rhinoceros leatherjacket	4±0	1.00000	0.00695	3.262	3.32	29	1
Monacanthidae	<i>Rudarius excelsus</i>	diamond leatherjacket	1±0	1.00000	0.02089	2.930	3	10	0.625
Mullidae	Mullidae sp.	goatfish	23±0	1.00000	0.01148	3.080	3.425	36	0.5
Mullidae	<i>Mulloidichthys flavolineatus</i>	yellowstripe goatfish	4±0	1.09300	0.02600	3.210	3.8	1	3.8
Mullidae	<i>Mulloidichthys</i> sp.	goatfishes	4±0	1.09300	0.02600	3.210	3.7	31	3.8
Mullidae	<i>Parupeneus barberinus</i>	cash-and-dot goatfish	36±0	1.12995	0.01409	3.100	3.35	40	0.5
Mullidae	<i>Parupeneus macronemus</i>	long-barbel goatfish	5±0.2	1.12995	0.03975	3.048	3.5	32	0.5
Mobulidae	<i>Mobula birostris</i>	giant mobula	22±5.9	1.00000	0.01640	3.000	3.5	78	0.5005
Mobulidae	<i>Mobula japonica</i>	spinetail mobula	25±39	1.00000	0.01000	3.040	3.41	55	0.502
Mobulidae	<i>Mobula</i> sp.	mobula ray	13±4.8	1.00000	0.00630	3.000	3.43	62.66	0.501
Myliobatidae	<i>Myliobatidae</i> sp.	eagle rays	13±0	-	0.00630	3.000	3.2	75	0.5078
Myliobatidae	<i>Rhinoptera steindachneri</i>	Pacific cownose ray	10±11	1.00000	0.01148	2.980	3.6	46	0.5039
Nematistiidae	<i>Nematistius pectoralis</i>	roosterfish	10±16	1.17786	0.01072	3.020	4.5	90	1.5
Nomeidae	<i>Cubiceps</i> sp.	Cubicep driftfish	8±0.7	1.11300	0.00389	3.040	3.6	11	0.501
Nomeidae	Nomeidae sp.	driftfishes	5±0.9	1.11300	0.00389	3.040	3.52	15	0.51615
Nomeidae	<i>Psenes cyanophrys</i>	freckled driftfish	3±0.1	1.19501	0.01995	3.010	3.44	19	0.5313
Nomeidae	<i>Psenes</i> sp.	Psenes driftfish	2±5	1.14334	0.02000	3.010	3.52	15	0.51615
Pomacanthidae	<i>Holacanthus passer</i>	king angelfish	22±0	-	0.02710	3.084	2.6	1	2.6
Pomacentridae	<i>Chromis klunzingeri</i>	black-headed puller	7±0	1.13800	0.01820	3.000	2.7	15	0.5
Pomacentridae	<i>Pomacentrus caeruleus</i>	caerulean damsel	8±0	1.05664	0.03672	2.995	2.7	21	0.5
Priacanthidae	<i>Heteropriacanthus cruentatus</i>	glasseye	9±0	1.00000	0.02157	2.912	4.3	29	1
Priacanthidae	<i>Priacanthus blochii</i>	Paeony bulleye	5±0	1.00000	0.02212	2.913	3.99	23	0.5002

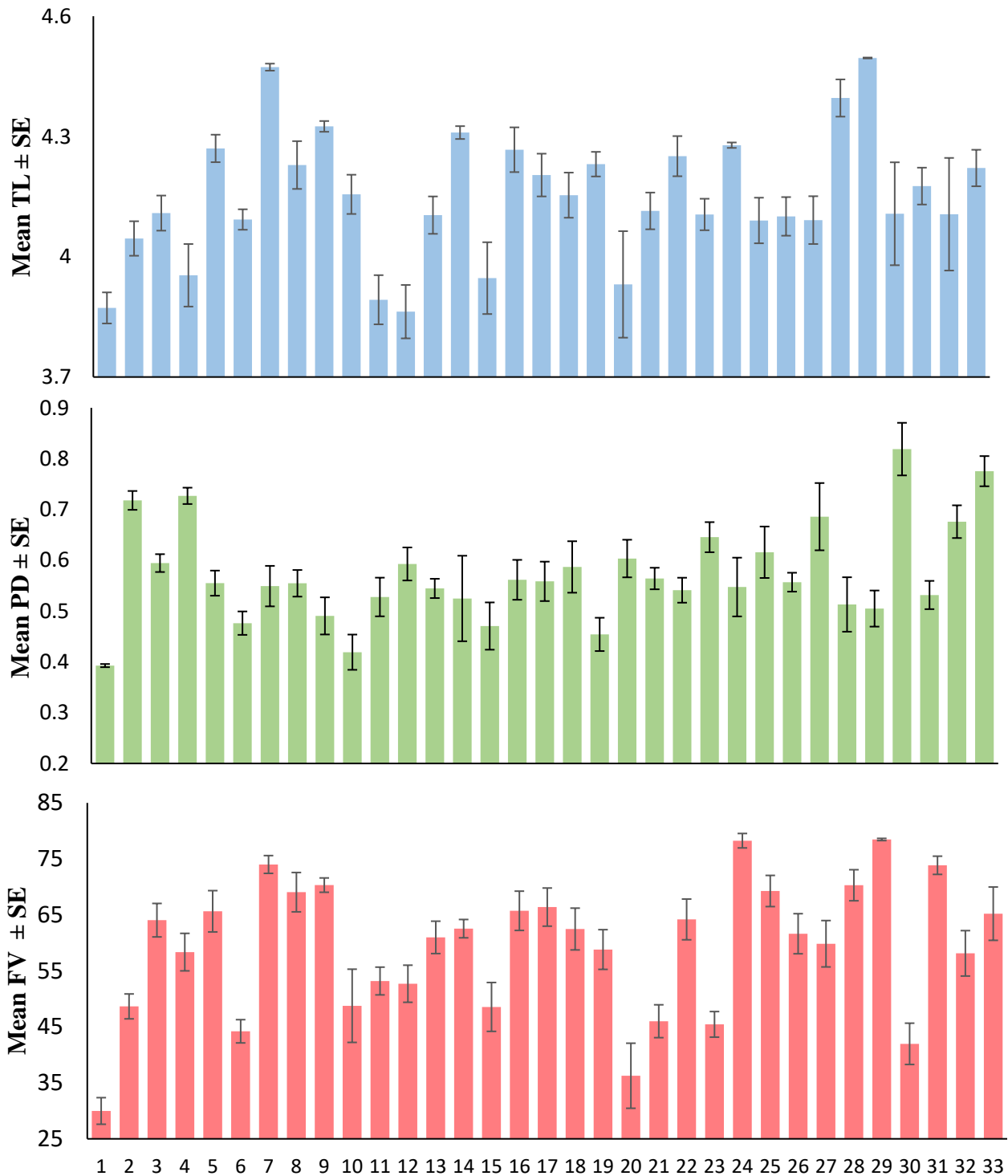
<b>Family</b>	<b>Scientific name</b>	<b>Common name</b>	<b>FL±SE</b>	<b>ToL:FL</b>	<b>a</b>	<b>b</b>	<b>TL</b>	<b>PD</b>	<b>FV</b>
Priacanthidae	<i>Priacanthus</i> sp.	bigeye	3±4	1.02926	0.02212	2.913	3.98	22.48	0.5
Rachycentridae	<i>Rachycentron canadum</i>	cobia	93±2.4	1.12108	0.00153	3.428	4	44	1.5
Rhincodontidae	<i>Rhincodon typus</i>	whaleshark	26±0	1.01010	0.00425	3.000	3.6	87	1.5
Scombridae	<i>Acanthocybium solandri</i>	wahoo	12±3.0	1.05263	0.00160	3.275	4.3	46	1
Scombridae	<i>Auxis</i> sp.	bullet tuna	31±2.3	1.04200	0.00760	3.249	4.4	27	0.5625
Scombridae	<i>Euthynnus affinis</i>	kawakawa	45±7.4	1.06838	0.02860	2.858	4.3	37	0.625
Scombridae	<i>Euthynnus lineatus</i>	black skipjack	54±7.3	1.06600	0.01000	3.050	4.3	44	0.625
Scombridae	<i>Euthynnus</i> sp.	tunny	60±8.0	1.06806	0.03346	2.884	4.3	46.08	0.625
Scombridae	<i>Grammatorcynus bicarinatus</i>	shark mackerel	40±0	1.09363	0.01705	3.006	4.3	54	0.75
Scombridae	<i>Grammatorcynus bilineatus</i>	double-lined mackerel	46±0	1.09363	0.01705	3.006	4.3	49	0.75
Scombridae	<i>Grammatorcynus</i> sp.	mackerel	75±3.6	1.05152	0.00450	3.000	4.3	49	0.75
Scombridae	<i>Gymnosarda unicolor</i>	dogtooth tuna	16±1.5	1.09833	0.02570	2.933	4.3	73	1
Scombridae	<i>Katsuwonus pelamis</i>	skipjack tuna	60±3.2	1.00000	0.00654	3.293	4.4	38	1
Scombridae	<i>Sarda</i> sp.	bonito	34±4.8	1.09363	0.01388	2.936	4.36	44.17	0.531
Scombridae	<i>Scomber australasicus</i>	blue mackerel	33±0.6	1.08200	0.00500	3.247	4.2	43	0.5625
Scombridae	<i>Scomber japonicus</i>	chub mackerel	31±3.9	1.01000	0.00452	3.351	3.4	34	0.5625
Scombridae	<i>Scomberomorus commerson</i>	Spanish mackerel	10±2.4	1.06045	0.01600	2.802	4.5	52	0.5
Scombridae	<i>Scomberomorus munroi</i>	Australian spotted mackerel	60±0	1.14054	0.00646	2.920	4.3	36	0.5
Scombridae	<i>Scomberomorus sierra</i>	Pacific sierra	70±5.6	1.14054	0.01440	2.730	4.5	39	0.5
Scombridae	<i>Scomberomorus</i> sp.	Spanish mackerels	94±1.8	1.14054	0.01291	2.947	4.36	46	0.5
Scombridae	Scombridae sp.	mackerels	49±8.0	1.09363	0.01710	3.006	3.79	49.53	0.617
Scombridae	<i>Thunnus alalunga</i>	albacore	32±4.0	1.08878	0.01698	2.990	4.22	71	0.5039
Scombridae	<i>Thunnus albacares</i>	yellowfin tuna	97±4.2	1.10742	0.05200	2.798	4.4	51	0.5039
Scombridae	<i>Thunnus maccoyii</i>	southern bluefin tuna	60±2.4	1.07991	0.01670	3.060	3.9	67	0.5039
Scombridae	<i>Thunnus obesus</i>	bigeye tuna	50±3.4	1.09529	0.01190	3.090	4.5	56	0.5039
Scombridae	<i>Thunnus orientalis</i>	Pacific bluefin tuna	35±0	1.07819	0.02320	2.927	4.25	76	0.5039
Scombridae	<i>Thunnus</i> sp.	Thunnus tuna	50±3.0	1.08814	0.01020	3.080	4.255	61.33	0.504
Scombridae	<i>Thunnus tonggol</i>	longtail tuna	60±9.4	1.08789	0.02320	2.927	4.26	47	0.5039
Serranidae	<i>Paranthias colonus</i>	Pacific creole-fish	25±0.6	1.19000	0.01480	2.863	3.8	1.195	3.8



<b>Family</b>	<b>Scientific name</b>	<b>Common name</b>	<b>FL±SE</b>	<b>ToL:FL</b>	<b>a</b>	<b>b</b>	<b>TL</b>	<b>PD</b>	<b>FV</b>
Sparidae	<i>Pagrus auratus</i>	pink snapper	37±6.6	1.14943	0.04470	2.793	3.6	69	0.5156
Sphyraenidae	<i>Sphyraena barracuda</i>	great barracuda	84±3.0	1.12867	0.00380	3.086	4.5	79	0.5
Sphyraenidae	<i>Sphyraena jello</i>	pickhandle barracuda	10±0	1.11152	0.01400	2.810	4.4	75	0.5
Sphyraenidae	<i>Sphyraena qenie</i>	blackfin barracuda	90±12	1.11200	0.00930	2.900	4.5	76	0.5
Sphyraenidae	<i>Sphyraena</i> sp.	barracuda	84±19	1.12867	0.00190	3.160	4.46	76.66	0.5
Sphyrnidae	<i>Sphyrna lewini</i>	scalloped hammerhead	15±7.6	1.28866	0.01100	2.790	4.1	81	0.5029
Sphyrnidae	<i>Sphyrna mokarran</i>	great hammerhead	19±8.0	1.33333	0.00191	3.160	4.3	86	0.5029
Sphyrnidae	<i>Sphyrna zygaena</i>	smooth hammerhead	23±26	1.25000	0.00851	2.840	4.32	85	0.5029
Syngnathidae	<i>Syngnathidae</i> sp.	pipefish	6±0.2	1.00503	0.02320	2.927	3.44	10	0.75
Tetraodontidae	<i>Arothron firmamentum</i>	starry toado	38±1	1.28500	0.03388	2.870	3.4	36	0.5
Tetraodontidae	<i>Lagocephalus lagocephalus</i>	oceanic puffer	50±0	1.03842	0.00660	3.302	3.7	44	0.5005
Tetraodontidae	<i>Lagocephalus sceleratus</i>	silver-cheeked toadfish	66±0	1.02564	0.01940	2.904	3.7	71	0.5005
Tetraodontidae	<i>Lagocephalus</i> sp.	puffer	40±0	1.03203	0.01413	2.860	3.7	57.5	0.5005
Tetraodontidae	<i>Sphoeroides annulatus</i>	bullseye puffer	28±0.3	-	0.01800	3.050	3.1	1	3.1
Tetraodontidae	<i>Tetraodontidae</i> sp.	puffers	3±0	1.00000	0.02510	2.880	3.7	57.5	0.5005
Zanclidae	<i>Zanclus cornutus</i>	moorish idol	7±0	-	0.01470	3.370	2.5	-	2.5

































**Figure S1.** Mean values with standard errors (SE) for total biomass (TB; kg·10<sup>3</sup>), taxonomic richness (TR) and total abundance (TA) by location where (1) Argo-Terrace, (2) Ascension, (3) Ashmore Reef, (4) Azores, (5) Bremer, (6) British Indian Ocean Territory, (7) Clipperton, (8) Cocos, (9) Far North Queensland, (10) French Polynesia, (11) Galapagos, (12) Geographe, (13) Gracetown, (14) Long Reef, (15) Maldives, (16) Malpelo, (17) Montebellos, (18) New Caledonia, (19) Ningaloo, (20) Niue, (21) Osa Peninsula, (22) Palau, (23) Perth Canyon, (24) Rapa, (25), Recherche East, (26) Recherche Middle, (27) Recherche West, (28) Revillagigedo, (29) Rowley Shoals, (30) Selvagen, (31) Shark Bay, (32) Tonga, (33) Tristan da Cunha.



**Figure S2.** Mean values with standard errors (SE) for trophic level (TL), phylogenetic diversity (PD) and fishing vulnerability (FV) by locations where (1) Argo-Terrace, (2) Ascension, (3) Ashmore Reef, (4) Azores, (5) Bremer, (6) British Indian Ocean Territory, (7) Clipperton, (8) Cocos, (9) Far North Queensland, (10) French Polynesia, (11) Galapagos, (12) Geographe, (13) Gracetown, (14) Long Reef, (15) Maldives, (16) Malpelo, (17) Montebellos, (18) New Caledonia, (19) Ningaloo, (20) Niue, (21) Osa Peninsula, (22) Palau, (23) Perth Canyon, (24) Rapa, (25), Recherche East, (26) Recherche Middle, (27) Recherche West, (28) Revillagigedo, (29) Rowley Shoals, (30) Selvagen, (31) Shark Bay, (32) Tonga, (33) Tristan da Cunha.

**Table S3.** Relative contribution of each BRT explanatory variable for trophic level, phylogenetic diversity and fishing vulnerability weighted by abundance and the category to which the variable is assigned: geomorphology (blue), environmental (green) and human pressure (yellow).

	<b>Driver</b>	<b>Relative contribution (%)</b>	<b>Category</b>	
<b>Trophic level</b>	Depth	15.0	Geomorphology	
	Dist cities	13.2	Human pressure	
	SST SD	12.6	Environmental	
	Chl- <i>a</i> median	10.3	Environmental	
	Dist Coral Tri	10.3	Environmental	
	Dist seamount	9.7	Geomorphology	
	Slope	8.5	Geomorphology	
	Dist coast	7.9	Geomorphology	
	SST median	7.8	Environmental	
	Dist population	4.8	Human pressure	
<b>Phylogenetic diversity</b>	Dist cities	15.7	Human pressure	
	Dist Coral Tri	15.5	Environmental	
	Depth	13.5	Geomorphology	
	SST SD	10.9	Environmental	
	SST median	10.4	Environmental	
	Slope	8.1	Geomorphology	
	Dist seamount	7.2	Geomorphology	
	Dist population	6.7	Human pressure	
	Dist coast	6.4	Geomorphology	
	Chl- <i>a</i> median	5.6	Environmental	
<b>Fishing vulnerability</b>	Depth	21.6	Geomorphology	
	SST median	15.3	Environmental	
	Dist cities	14.3	Human pressure	
	SST SD	8.7	Environmental	
	Dist seamount	7.9	Geomorphology	
	Chl- <i>a</i> median	7.1	Environmental	
	Dist Coral Tri	6.9	Environmental	
	Dist coast	6.7	Geomorphology	
	Slope	5.9	Geomorphology	
	Dist population	5.6	Human pressure	

**Table S4.** BRT parameters chosen to fit the models on specific attributes. Spatial autocorrelation is reported by Moran’s I for the raw data. An index of 1 indicates high positive autocorrelation; 0 no autocorrelation; –1 high negative autocorrelation.

Model features	Trophic level weighted by biomass	Phylogenetic diversity weighted by biomass	Fishing vulnerability weighted by biomass
Tree complexity*	5	5	5
Number of Trees*	50	50	50
Learning Rate*	0.01	0.01	0.01
Bag Fraction*	0.5	0.5	0.5
Max Trees*	10,000	10,000	10,000
Spatial autocorrelation in observations	0.14	0.12	0.24

\* Same parameters were set to calculate functional metrics weighted by abundance and conventional biodiversity metrics.

**Table S5.** Permutational multivariate analysis (PERMANOVA) of significant variations showing  $\log_{10}$  taxonomic richness across climatic zones and ocean basins,  $\log_{10}$  abundance across ocean basin and  $\log_{10}$  phylogenetic diversity across climatic zone and ocean basins. No other effects were significant.

<b><math>\log_{10}</math> taxonomic richness</b>						
Source	d.f.	SS	MS	PseudoF	P(perm)	Unique perms
Climatic zones	1	0.090	0.090	5.987	0.026	995
Ocean basin	3	0.167	0.055	3.702	0.023	999
Residuals	28	0.421	0.015			
Total	32	0.742				
<b><math>\log_{10}</math> abundance</b>						
Source	d.f.	SS	MS	PseudoF	P(perm)	Unique perms
Ocean basin	3	0.904	0.301	3.286	0.039	999
Residuals	29	2.661	0.091			
Total	32	3.565				
<b><math>\log_{10}</math> phylogenetic diversity</b>						
Source	d.f.	SS	MS	PseudoF	P(perm)	Unique perms
Climatic zones	1	0.025	0.025	15.179	0.001	996
Ocean basin	3	0.032	0.010	6.470	0.002	999
Residuals	28	0.047	0.001			
Total	32	0.113				