Estuarine, Coastal and Shelf Science 320 (2025) 109305

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

High dominance renders reef fish trophic interactions vulnerable to human pressures in oceanic islands

Iris Barroso [a,b], Mar Mourin [a], Sandra Navarro-Mayoral [a], Fernando Tuya [a], Nestor E. Bosch [a,b,*]

[a] *Grupo en Biodiversidad y Conservación, ECOAQUA, Universidad de Las Palmas de Gran Canaria, Las Palmas, 35214, Canary Islands, Spain*
[b] *Shared first authorship, Spain*

A R T I C L E I N F O

Keywords:
Trophic interactions
Feeding behaviour
Reef fishes
Ecosystem vulnerability
Human exploitation
Ecosystem stability

A B S T R A C T

Human activities alter marine ecosystems by modifying their biodiversity, often disrupting trophic interactions that determine their structure and functioning. Human influence on trophic interactions mediated by fishes have traditionally been investigated through the lens of indirect proxies, such as the biomass of trophic groups. However, fish biomass alone may not adequately capture the nuanced responses of fish to different levels of human pressures, such as changes in the nature and intensity of trophic interactions. Here, we combined visual counts and remote video surveys to assess how human pressures influence spatial patterns in reef fish biomass and feeding pressure in an oceanic island in the eastern Atlantic Ocean. The biomass and feeding pressure of reef fish assemblages strongly declined across the human pressure gradient, by two- and five-fold, respectively. These patterns were primarily driven by fishery targeted species, which comprised 87 % of fish biomass and 93 % of fish feeding pressure. Despite this marked imprint of human pressures, we found distinct responses among trophic groups. The biomass of omnivores and herbivores declined by 19- and 3-fold respectively, while feeding pressure by these groups declined by 6- and 4-fold, respectively. In contrast, the effect of human pressures on piscivores, invertivores and planktivores was weak or negligible. Importantly, some trophic groups exhibited stronger declines in fish feeding pressure than biomass, whilst others exhibited lower declines. This highlights the nuanced responses of fishes to human exploitation, with compensatory mechanisms, and calls for more detailed studies to identify how humans disrupt trophic interactions and their potential flow on effects on energy and material fluxes.

1. Introduction

Human activities can severely alter the structure and functioning of marine ecosystems. Overfishing, for instance, has caused the collapse of fish populations across the global oceans (Costello et al., 2016; Myers and Worm, 2003), particularly for targeted species that are appreciated by both professional and recreational fishers for their economic and cultural value (Eggertsen et al., 2024; Yadav et al., 2021). Fishing is essentially selective (Sampson, 2014), with different gears (e.g., hook and line, traps, seines, speargun) capturing species with specific traits (i.e., morphological, life history, behavioural and physiological) that makes them particularly vulnerable to a certain fishing modality (Barbosa et al., 2021; Mbaru et al., 2020; Trindade-Santos et al., 2020). At the population level, fisheries-induced changes in key morphological (e.g., body size structure, Bosch et al., 2021; Robinson et al., 2017) and life history traits (e.g., age at maturity, lifespan, and offspring size, Jørgensen et al., 2009; Lewin et al., 2019) can alter population dynamics (Barrowman and Myers, 1996; Barneche et al., 2018), thereby increasing their vulnerability to environmental variation (Hixon et al., 2014). At the community level, changes in trait dominance, such as declines in the trophic level of the catch (Pauly et al., 1998), can have cascading effects with often uncertain consequences for core ecological processes that mediate the flux of energy and materials within and across ecological systems (Pinnegar et al., 2000; Mumby, 2006). This duality in which traits mediate both the "response" of species to human and environmental stressors, as well as their "effect" in mediating trophic interactions, has prompted a shift in fisheries management and conservation (Barnett et al., 2019; Stuart-Smith et al., 2015) — from protecting species, populations, and communities to preserving trait configurations that promote ecosystem multifunctionality. To date,

---

* Corresponding author. Grupo en Biodiversidad y Conservación, ECOAQUA, Universidad de Las Palmas de Gran Canaria, Las Palmas, 35214, Canary Islands, Spain
E-mail address: nestor.bosch@ulpgc.es (N.E. Bosch).

https://doi.org/10.1016/j.ecss.2025.109305
Received 25 September 2024; Received in revised form 9 April 2025; Accepted 9 April 2025

however, advances in effectively implementing this framework have been hampered by the limited geographical coverage of studies that empirically quantify the nature and intensity of trophic interactions, and their flow-on effects on ecosystem functioning, in marine systems (Bellwood et al., 2019b; Brandl et al., 2019).

Trophic interactions are fundamental in ecological systems, as they mediate the transfer of energy and materials within food webs (Lindeman, 1942; Brown and Gillooly, 2003). In marine ecosystems, the impacts of fishing on trophic interactions have mostly been inferred from studies on the diversity, abundance, and biomass of species classified into predefined trophic groups, mainly based on their trophic ecology and behaviour (Morais et al., 2017; Mora et al., 2011). At biogeographical scales, this trophic group approach has been a cornerstone to identify areas that are particularly vulnerable to the effects of overexploitation — i.e., characterized by a limited number of species within each trophic group (i.e., low redundancy, Micheli and Halpern, 2005; Mouillot et al., 2014). Limited redundancy within trophic groups renders an ecosystem vulnerable to human exploitation, as the removal of one or two key species that are involved in critical trophic interactions cannot be replace by any community member (Leitão et al., 2016; Coulon et al., 2023); thereby potentially altering pathways of energy and material fluxes (i.e., ecosystem functions) (Bellwood et al., 2019b; Brandl et al., 2019). Further, the number of species within each trophic group is not the only key factor in inferring vulnerability, but also the extent to which trophic interactions are sustained by very abundant or rare species (Mouillot et al., 2013). Ecological theory predicts that dominant species contribute disproportionately to trophic interactions (i.e., mass-ratio hypothesis), but detailed empirical studies have questioned the generality of this pattern (Magneville et al., 2023; Della Marta et al., 2023). For instance, a rare reef fish species not previously observed in traditional surveys was found to account for the majority of algal biomass removal in the Great Barrier Reef (Fox and Bellwood, 2007). This and other studies exemplify the importance of direct quantification of trophic interactions, rather than relying on gradients in the distribution of richness, abundance, and biomass of species within particular trophic groups (Tebbett et al., 2021).

The advent of video methods in ecological research has greatly enhanced our ability to quantify trophic interactions in reef systems (Longo and Floeter, 2012; Mallet and Pelletier, 2014). Specifically, these methods have been used to quantify feeding rates and to understand changes in reef fish behaviour across various environmental and human pressure gradients (Della Marta et al., 2023; Longo et al., 2014; Nunes et al., 2021). While video methods can serve as a proxy for quantifying ecological processes (e.g., herbivory and predation; Bellwood et al., 2019a; Della Marta et al., 2023), challenges persist in accurately measuring parameters such as bite size or the amount of material removed (e.g., algal biomass, Tebbett et al., 2024). Feeding pressure (i.e., the intensity of feeding interactions within an ecosystem) is mostly influenced by dominant species (Tebbett et al., 2020; Ferrari et al., 2024) and modulated by a suite of environmental and biological factors, such as temperature (Nunes et al., 2021; Barneche et al., 2009; Bosch et al., 2022c), habitat composition (Canterle et al., 2020), and anthropogenic activities (Longo et al., 2014). Although previous studies have investigated human effects on reef fish feeding pressure as a proxy of trophic interactions (Ferguson et al., 2016; Della Marta et al., 2023; Longo et al., 2014), the context dependency of the contribution of different reef fish species to these processes warrants further exploration across diverse biogeographic, environmental, and socio-economic settings.

Oceanic islands are characterized by their geographic isolation from continental regions and typically exhibit low functional redundancy (Canterle et al., 2020; Floeter et al., 2008; Mendes et al., 2019). In these oceanic regions, high species dominance leads to the concentration of critical trophic interactions on a few species (Ferrari et al., 2024), increasing their vulnerability to human pressures. Specifically, the diversity of reef fishes supporting trophic interactions in the Atlantic Ocean is low compared to the species-rich regions of the Indo-Pacific, where several reef species can be involved in the same trophic interactions (Mouillot et al., 2014). Traditionally, studies have used proxies such as richness, abundance, and biomass of species within trophic groups (Williams et al., 2015; Quimbayo et al., 2017) to understand the dynamics of these systems in response to environmental and human perturbations, whilst recent studies have focused on quantifying more direct proxies, such as feeding pressure via video methods (e.g., Canterle et al., 2020; Ferrari et al., 2024). Given their intrinsic vulnerability, expanding our knowledge on reef fish contributions to critical trophic interactions and their response to varying levels of human exploitation, across distinct environmental, evolutionary and socio-economic contexts represent a critical area of research to ensure their sustainable management in an era of pervasive human-driven changes to natural ecosystems.

Here, we investigated the role of human pressures on the biomass and feeding pressure of reef fish species on an oceanic island, using a trophic group approach to indirectly infer their potential implications in rates of energy and material fluxes. Our study was conducted along the perimeter of Gran Canaria Island, a densely populated island in the subtropical eastern Atlantic Ocean with a long history of fisheries overexploitation (Couce-Montero et al., 2015; Jiménez-Alvarado et al., 2019). The low diversity of species sustaining distinct trophic interactions on this island (Bosch et al., 2021), coupled with the complex nature of the artisanal and recreational fisheries sector, which targeted multiple species through a combination of gears (Castro et al., 2019), makes this an ideal scenario to test the vulnerability of fish trophic interactions to varying levels of human exploitation. To the best of our knowledge, this is the first study to analyse human impacts through the lens of quantitative measures of trophic interactions in the region, particularly focusing on interactions with the benthos. We hypothesized that (i) reef fish biomass and feeding pressure would exhibit a marked response to human pressure gradients, (ii) human effects would be largely driven by dominant targeted species, and (iii) human pressures would differentially affect trophic groups, mediated by both changes in biomass and feeding interactions.

2. Methods

2.1. Study region and sampling design

Our study was conducted at Gran Canaria Island, a volcanic oceanic island in the subtropical northeastern Atlantic Ocean (27.9°N, 15.5°W, Fig. 1). The island forms part of the Canarian archipelago, a group of seven major islands and four islets that originated ca. 20.5 Ma through successive volcanic events (Anguita and Hernán, 2000). Their isolation from the African continent, being geologically independent and separated by depths approaching 2000 m, coupled with their age and continental shelf area, has shaped the evolution of their extant reef fish communities (Floeter et al., 2008; Ferrari et al., 2023; Tuya et al., 2021). Geophysical and environmental conditions vary strongly across the island perimeter, predominantly influenced by north-northwest swells and north-northeast trade winds, which in turn affect local nutrient levels and temperature (Barton et al., 1998; Azorin-Molina et al., 2018).

Fisheries in nearshore waters of the Canarian Archipelago are complex, comprising multiple gears and targeted species, that include both artisanal and recreational fishers (Santamaría et al., 2013). Bentho-demersal finfish species comprise ca. 50 % of the total artisanal fisheries catch (Zeller and Pauly, 2015), mainly caught through traps or pots, gillnets and longlines. Nearly 70 % of wild caught fishes comes from marine recreational fishers (Castro et al., 2019), with roughly 90,000 individuals practicing this fishing modality across the archipelago (Bilbao-Sieyro et al., 2022). Over the past 70 years, there has been a decline in the number of artisanal fishers, whilst recreational fishing has increased substantially, driven by the establishment of secondary ports or access points, technological advancements, and the growth of the

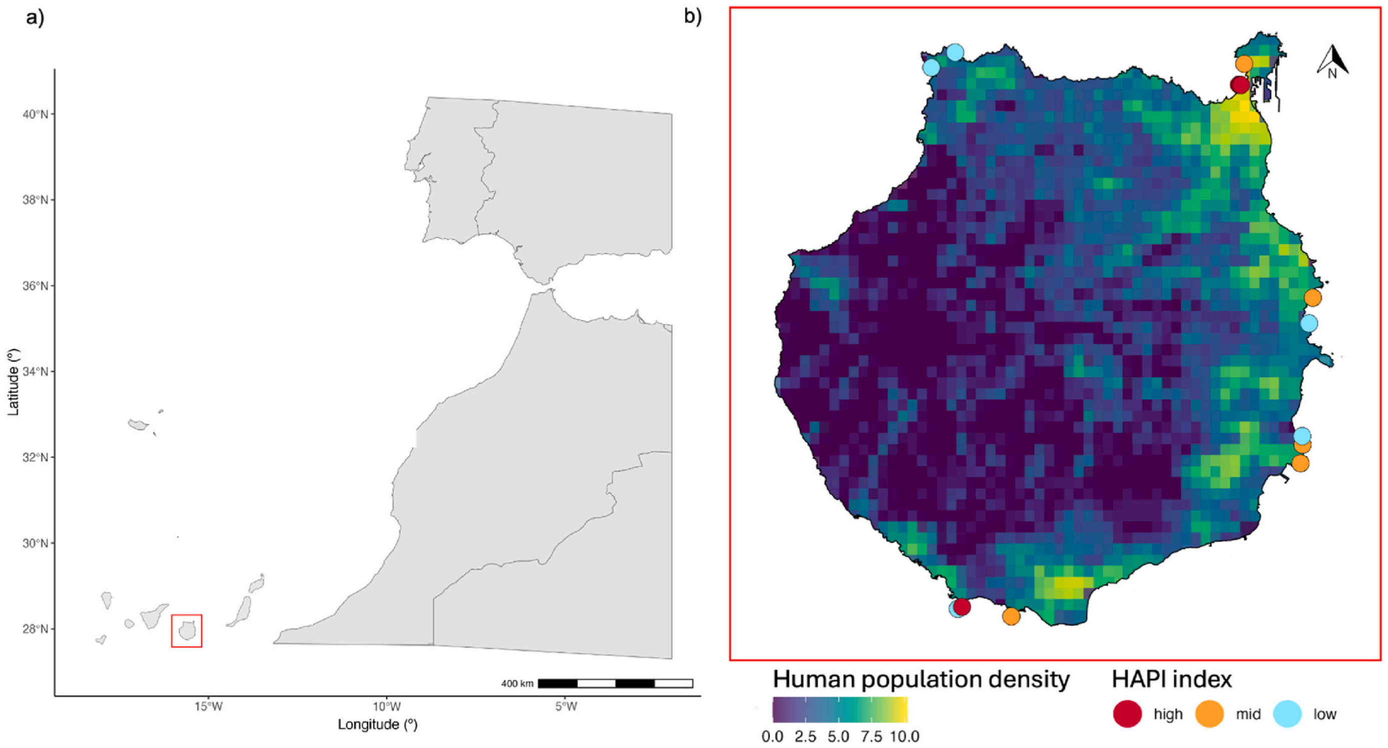


Fig. 1. Map of study sites around Gran Canaria Island (Canary Islands, NE Atlantic Ocean) with their corresponding category of human pressure (low = blue, mid = orange, high = red) based on the HAPI index. The colour palette overlaid on the island represents human population densities on a log scale, with yellow tones indicating high-density areas and dark blue indicating low-density areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tourism and leisure industry in the archipelago (Castro et al., 2019). Both sectors exert strong selection pressures in nearshore fish communities, which have profoundly altered the composition and trophic level of the catch, stock population size, and community- and species-specific size frequency distributions (Alós et al., 2014; Castro et al., 2019; Jiménez-Alvarado et al., 2019; Tuya et al., 2006a). Various fisheries management and conservation measures have been implemented to restore fish biomass in the last decades, such as minimum legal sizes, quotas per individual fisher and establishment of marine protected areas (Law 17/2003 of Fishing in the Canary Islands, of 10 April). However, considerable challenges persist, such as the increase in catch and release of undersized fish (Alós et al., 2009), variations in size-selectivity among fishing modalities (Frisch et al., 2008), and the high cost of enforcing fisheries regulations (e.g., size and catch limits), which complicates the management of the fisheries (Ahrens et al., 2020).

Our sampling design consisted of 13 sites (i.e., reefs) around the island perimeter that capture variations in human pressures, as well as geophysical and environmental drivers (Fig. 1b). Currently, there is a lack of spatiotemporal comprehensive information on the artisanal and recreational fishing effort at the scales investigated for the island, with only a few recent studies reporting fishing effort data for specific gears (e.g., traps, Cruces et al., 2024). We thus decided to use several indirect proxies of human pressures that have been previously linked to the response of fish assemblages to varying levels of human exploitation: human population density (Cinner et al., 2013), human gravity (Cinner et al., 2018; Bosch et al., 2021), and the Human Activities and Pressures Index (HAPI) (Blanfuné et al., 2017). The human population density was sourced from the LandScan 2022 population density grid, which provides highly resolved (ca. 1 km) daily average population counts derived from remote-sensing data and mapping (Sims et al., 2023). Human population values for each reef site were then extracted by summing population counts around a 5 km buffer via the "raster" R package (Hijmans, 2023). As a measure of accessibility to the reef (Cinner et al., 2018), we extracted the minimum travel distance in km to the nearest port, industrial or recreational, or boat ramp via the "sf" R package (Pebesma and Bivand, 2023). Human gravity was computed using a modification of the original proposed by Cinner et al. (2018), by dividing the human population values at each reef site by their distance to the nearest access point. Finally, we considered the HAPI index (Blanfuné et al., 2017), an aggregated metric of cumulative human pressures from both terrestrial (urban, industrial, and agricultural areas) and marine (percentage of shoreline infrastructures, as well as aquaculture facilities and discharge of waste waters) sources, which have previously been quantified for the study region at a 5 × 5 km grid resolution (Valdazo et al., 2017). We must note that the selection of 5 km buffers and grid cells to capture local human pressures was somehow arbitrary, based on the most likely distance travelled by fishers on a daily basis in the study region. We found a moderate correlation coefficient ($r > 0.5$, Figs. S1 and S2), and high variance inflation factors (VIF >5, Fig. S3) between human pressure metrics. Therefore, we retained only the HAPI index for analysis to avoid multicollinearity issues in statistical modelling (Dormann et al., 2013), given its comprehensive coverage of a broad spectrum of human pressures (Blanfuné et al., 2017). Given that our study design involves a limited number of sites (n = 12–13) covering the range of HAPI values, we decided to convert this into a categorical factor, using the "cluster" R package (Maechler et al., 2023) to find natural breaks in the data. This resulted in three levels of human pressure: low (0.0–2.1), mid (2.5–4.5), and high (5.6–5.9). All surveys were conducted between September and November 2023, at shallow (2 m–15 m, 8.0 m ± 0.5 m) reefs and during daylight hours (9 a.m.–14 p.m.), to minimize depth and within-day variability in fish assemblage structure (Azzurro et al., 2007; Bosch et al., 2023). Studied reefs were mainly dominated by algal turf (aggregations of algae less than 2 cm in height with low structural complexity that form a conglomerate of algae, detritus and cyanobacteria, Mourin et al., 2025). This pattern was consistent across the study region (Tuya and Haroun, 2006), which exhibited only sparse coverage of structurally complex brown and red foliose algae (Fig. S4). To reduce spatial dependency between survey sites, we selected those that were at least 1 km apart.

2.2. Surveys of fish biomass

We estimated the biomass of each fish individual through underwater visual census techniques (UVCs), a non-destructive method that provides information on the identity, abundance, and size of conspicuous fish species. At each site, we conducted six belt transects of 25 m length x 4 m wide (100 m^2) across two depth strata (approximately 5 m and 10 m). All sampling was conducted by the same observer, following established protocols for the study region and elsewhere (Bosch et al., 2017, 2021). Briefly, the diver identified and quantified the abundance of each species within the field of view, omitting individuals that entered from behind to reduce the likelihood of double counting. Fish size was estimated visually by placing the individuals in predefined size categories of increasing increments (2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30, 35, 40, 50, 62.5, 75 cm), following globally standardized survey protocols that minimize inaccuracies in size estimation (Edgar et al., 2004, 2020; Edgar and Stuart-Smith, 2014). The abundance of schooling fish (i.e., >20 individuals) was estimated by assessing a subset and combining it with an estimate of the overall proportion (ca. 20 % of the individuals, except for very large schools where a maximum of 20 fish is tallied). Transects were replicated at distances of, at least, 10 m to minimize the non-independence of fish counts. To obtain each fish individual biomass, we applied standard length-weight relationships recovered from a dataset of Atlantic reef fishes (Quimbayo et al., 2021).

2.3. Video surveys of feeding pressure

We quantified fish feeding pressure on the benthos via Remote Underwater Videos (RUVs), collected for 12 out of the 13 study sites. Feeding pressure was used as an indirect, quantitative, proxy of trophic interactions mediated by fishes via their feeding patterns (e.g., (Longo et al., 2014). At each site, n = 4 GoPro Hero 9 cameras (1080 p and 60 fps resolution) were haphazardly placed in the seabed, at a height of approximately 50 cm above the bottom to maximize the field of view, for quantifying interactions between fishes and the benthos. Within each site, we consistently targeted patches of the seabed dominated by algal turf, as this was the dominant benthic habitat across the study region. To standardize the sampling area, the diver first placed a 2-m transect tape perpendicular to the camera, then swam with a 1-m rope stretched out, and marked every 20 cm, towards the camera. In this way, the observation area per video sample was limited to 2 m^2, whilst the marks provided a calibration method to estimate fish sizes (Fig. S5) (Longo et al., 2014, 2019). After this procedure, the divers removed the transect and rope, and left the survey area, setting each camera recording to 15 min of video (Canterle et al., 2020).

We analysed the central 10 min of each video recording to minimize the influence of the diver's presence (Longo and Floeter, 2012, 2014). For each video sample, we identified each fish that entered the field of view, measured its size, and quantified the number of bites taken in the substratum per observation, which was defined as the time a single fish entered and left the sampling area. We considered a bite as an instance when a fish touched the benthos with its jaws open and subsequently closed its mouth (Longo and Floeter, 2012). Biomass conversion of each individual fish size was done using published length-weight relationships for the Atlantic (Quimbayo et al., 2021). When a school of fish appeared in the video, we analysed five random individuals and extrapolated by the number of fish forming the school to estimate total feeding pressure (Bosch et al., 2022c). Because identifying, sizing, and estimating the size of small-bodied individuals tend to be imprecise in RUV samples (Canterle et al., 2020; Longo and Floeter, 2012), we focused our analysis exclusively on individuals larger than 5 cm in total length. We calculated feeding pressure as the product of the number of bites taken and the biomass (kg) of each fish (Longo et al., 2014, 2015), to account for body size variations in trophic interactions (i.e., mass ratio hypothesis, Cardinale et al., 2007). In brief, we quantified fish feeding pressure, per unit of time and area (nº bites x Biomass (kg))/(2 $m^2 \times 10$ min) (Longo et al., 2014, 2015), for a total of 47 video samples (i.e., a total of 470 min of video observations).

2.4. Statistical modelling

We tested for the effect of human pressure, measured through the HAPI index (i.e., a fixed factor with three levels: low, mid, high), on the biomass and feeding pressure of reef fish assemblages using Generalized Linear Mixed Models (GLMMs). To explore how human pressures may disrupt the critical trophic pathways through which fishes transfer energy and materials in coastal food webs (Bellwood et al., 2019a; Brandl et al., 2019; Bosch et al., 2022a), we run models both at the assemblage level (i.e., values pooled for all species in a sample) and by major trophic groups: piscivores, invertivores, herbivores, planktivores, and omnivores. Then, for each group (i.e., response variable), we run three sets of models: (i) global (all species pooled, i.e., summed), (ii) targeted species by both professional and recreational fisheries, and (iii) non-targeted species. The latter served as a pseudo-control to decouple the influence of fisheries exploitation from other human-related stressors (e.g., pollution, coastal urbanization, sewage outfalls) (Bosch et al., 2021). Fishery targeted species were defined based on lists compiled from previous studies in the region (Santamaría et al., 2013; Castro et al., 2015; Jiménez-Alvarado et al., 2019), as well as the author's combined expertise. We must note that some groups had insufficient data for this partitioning, such as non-targeted piscivores for biomass models, and planktivorous fishes for feeding pressure. Site nested in sector (i.e., a factor representing each 5 × 5 km HAPI pressure grid), was included as a random effect term, to account for spatial dependency of samples taken within each site and sites within each sector. During the data exploration, three for biomass and one for feeding pressure outlying samples were detected. These resulted from the presence of (i) large schools of small pelagic, such as the bogue (*Boops boops*), and herbivorous species, such as *Sarpa salpa*, with erratic behaviour and patchy distributions, and (ii) species typically associated with sand-reef ecotones, such as the bastard grunt (*Pomadasys incisus*) and the axillary seabream (*Pagellus acarne*).

For each model, we included a series of environmental and habitat covariates that have been previously shown to affect reef fish assemblage structure and feeding behaviour: depth (Fox and Bellwood, 2007; Bosch et al., 2023), sea surface temperature (Nunes et al., 2021), habitat composition (Bosch et al., 2022b; Ferrari et al., 2023), and agonistic biotic interactions (Canterle et al., 2020). Depth was obtained from *in situ* field observations using a dive computer. Temperature data for feeding pressure was obtained from HOBO TitBit loggers, which recorded data at 1-min intervals and were deployed concurrently with the video plots. For biomass data, we retrieved the average annual SST, at the study sites, from satellite observations in the MARSPEC dataset (Sbrocco and Barber, 2013). The total number of agonistic (i.e., negative) interactions per sample, defined as an instance when one fish swiftly swam towards another causing the latter to escape (Canterle et al., 2020), was quantified from the video plots. Finally, we quantified variation in the composition and structure of benthic habitats at two spatial scales: reef (i.e., site) and video plot, to use in the biomass and feeding pressure models, respectively. This data was obtained from co-located photoquadrats, taken every 2.5 m along the transect line, at approximately 50 cm above the seabed (*ca.* 30 × 30 cm area, 0.09 m^2), for biomass models; and, from n = 5 haphazardly placed PQs, of 25 × 25 cm (0.06 m^2), on the video plot area for feeding pressure models. The percent cover of benthic morpho-functional groups derived from the "Collaborative and Annotation Tools for Analysis of Marine Imagery and Video" (CATAMI) (Althaus et al., 2015) (e.g., foliose brown algae, foliose red algae, crustose coralline algae, and algal turf) and substrate types (e.g., conglomerates, gravel, sand, and bare rock) was quantified by overlaying a mesh of 5 x 5 squares of equal dimensions via the GIMP software (http://www.gimp.org.es/), and scoring the habitat located directly below each intersection ($n = 16$ points per image). To visualize and quantify variation in benthic assemblage structure, we performed a principal coordinate analysis (PCoA) on a bray-Curtis matrix summarising dissimilarity in benthic cover across samples, using the 'labdsv' (Roberts, 2023) and 'vegan' (Oksanen et al., 2022) R packages. We retained the first two PCoA axes, which cumulatively accounted for 89 % of the original variability, and then extracted the position of the samples (i.e., centroids) along these to be used as explanatory variables in the models.

All models were implemented in the 'glmmTMB' R package (Brooks et al., 2017), and were fitted using a gamma, lognormal, and Tweedie error distribution with a log-link function, depending on the underlying distributional properties of the response variables (Tables S1 and S2). To avoid multicollinearity problems in parameter estimation, we excluded predictors with a Pearson correlation >0.7, which resulted in the exclusion of depth, as it was strongly ($r = 0.7$) correlated with the HAPI index (Fig. S2). All continuous predictor variables were standardized (mean 0 and SD 1), prior to analysis, to account for differences in scaling. We used the 'DHARMA' R package (Hartig, 2020) to explore violations of model assumptions, which included QQ plots, plots of residuals *vs.* fitted values., Kolmogorov-Smirnov tests, outlier tests (Figs. S6 and S7), and Moran's I to test for spatial autocorrelation in model residuals. We performed all statistical analysis using the R software version 4.3.1.

3. Results

3.1. Island-scale patterns and drivers in fish biomass

A total of 6003 fish (from 37 species, Table S1) were censused, with five species contributing up to 50 % of the total biomass: the white seabream (*Diplodus sargus*), the common two-banded seabream (*Diplodus vulgaris*), the zebra seabream (*Diplodus cervinus*), the parrotfish *Sparisoma cretense*, and the salema (*Sarpa salpa*). Of the 37 species identified, fishery targeted species comprised up to 87 % of the total assemblage biomass (Fig. 2a), which was dominated by omnivores (46 %), mainly composed of targeted species, and herbivores (27 %) (Fig. 2b and c). Invertivores accounted for 18 % of the total biomass, represented mostly by targeted species (77 %) (Fig. 2d); piscivores comprised 5 %, of which 76 % corresponded to fishery-targeted species (Fig. 2e). The least represented group was planktivores, comprising only 3 % of the total biomass, primarily constituted by non-targeted species. Within each trophic group, biomass was strongly dominated by one or two fishery targeted species: *Diplodus sargus* (47.6 %) *and Diplodus vulgaris* (41.6 %) for omnivores, *Sparisoma cretense* (43.4 %) and *Sarpa salpa* (41.2 %) for herbivores, *Diplodus cervinus* (48.2 %) for invertivores, and *Mycteroperca fusca* (27.5 %) and *Epinephelus marginatus* (19.4 %) for piscivores.

The biomass of reef fishes strongly varied across the island perimeter, with nearly a 13-fold decrease from the highest to the lowest biomass site (30–2.3 kg 100 m^{-2}). Human pressure significantly contributed to variation in assemblage-level fish biomass patterns (Table 1), with a nearly two-fold (18.2–8.8 kg 100 m^{-2}) decrease with increasing human pressure (Fig. 3a–c). Importantly, this pattern was solely attributed to targeted species, whose biomasses decreased by 2.5-fold (17.2–7.0 kg 100 m^{-2}) from low to high human pressure sites (Fig. 3b). In contrast, the response of non-targeted fish biomass to human pressure was negligible (Fig. 3c).

The response of fish biomass to human pressure varied across fish trophic groups, a pattern influenced by their degree of human exploitation (Table 1). Omnivores and herbivores were the main trophic groups driving the observed assemblage-level response to human pressure (Table 1), with omnivores declining by 19-fold (13.0–0.7 kg 100 m^{-2}) and herbivores by three-fold (5.1–1.6 kg 100 m^{-2}) (Fig. 3e–g). For the former, fish biomass was almost entirely comprised of targeted species, so we only modelled this group; for the latter, targeted species were mostly responsible for the observed pattern with a 2.3-fold decline in biomass (3.9–1.7 kg 100 m^{-2}; Fig. 3f). In contrast, human pressure had no significant effect on non-targeted species, whose biomass varied significantly with changes in benthic habitat composition (Table 1; Fig. S4). Piscivores, comprised entirely by targeted species, also displayed a marked response to human pressure, declining by five-fold (0.5–0.1 kg 100 m^{-2}) (Fig. 3k), although there was high uncertainty in the estimates due to their relatively low biomass (5 % of the total), which resulted in non-significant effects (Table 1). However, our models did retrieve a significant effect of depth on this group. A similar response was observed for invertivorous fishes, with biomass decreasing two-fold (2.7–1.4 kg 100 m^{-2}) as human pressure increased (Fig. 3h). This decline was driven equally by both targeted and non-targeted fishes, although the high uncertainty in parameter estimates led to non-significant patterns. Finally, the biomass of small-bodied, non-targeted, planktivorous fishes did not respond significantly to human pressure, being mainly driven by depth gradients.

Overall, there was substantial variation in the variance explained by our models, from 1.0 % to 62 % explained by the fixed components for the assemblage-level models and planktivores, respectively (Table 1). Incorporating the variance explained by the random effect of site, nested in sector, generally slightly improved the goodness-of-fit of the models, for instance to 2.2 % in the targeted and 12 % in non-targeted models.

3.2. Island-scale patterns and drivers in fish feeding pressure

A total of 1956 individuals (from 19 species) were recorded biting on the benthos, with the most intense feeding interactions (i.e., bites in the substratum weighted by biomass) reported for the common two-banded seabream (*Diplodus vulgaris*), the white seabream (*Diplodus sargus*), and the parrotfish *Sparisoma cretense*, accounting for up to 85 % of the total feeding pressure (Table S2). Fish feeding pressure was strongly dominated by fishery targeted species, which accounted for up to 93 % of the total feeding pressure on the benthos (Table S2; Fig. 4a). The contribution of fish trophic groups varied, with targeted omnivores exerting the highest feeding pressure, with up to 70 % of the total feeding pressure (Fig. 4a). Herbivores were the second-ranked trophic group, contributing up to 18 %, of which 90 % corresponded to targeted species. Finally, invertivores had a relatively small contribution, 12 % of the total, of which 55 % corresponded to targeted and 45 % to non-targeted species. Within each trophic group, feeding pressure was dominated by one or two targeted species: *Diplodus vulgaris* (75 %) *and Diplodus sargus* (24.1 %) for omnivores (Fig. 4b), *Sparisoma cretense* (88.3 %) for herbivores, and *Diplodus cervinus* (37.8 %) and *Mullus surmuletus* (17.2 %) for invertivores (Fig. 4c).

Fish feeding pressure on the benthos varied markedly across the island perimeter, with nearly a 95-fold (2.84–0.03 kg m^{-2} min^{-1}) decrease from the lowest to the highest feeding pressure site. Human pressure had a pronounced effect on spatial patterns in feeding pressure, primarily driven by targeted species (Table 2). Considering all fish individuals (i.e., assemblage-level models), feeding pressure declined by five-fold (0.9–0.2 kg m^{-2} min^{-1}) from low to high human pressure areas (Fig. 5a), a pattern that was almost exclusively attributed to declines in the feeding pressure exerted by targeted fishes (0.80–0.13 kg m^{-2} min^{-1}) (Fig. 5b). In contrast, there was a negligible effect of human pressure on non-targeted species, whose spatial variation in feeding pressure was mainly attributed to habitat composition and the strength of agonistic biotic interactions.

Similarly to fish biomass, the response of fish feeding pressure to human pressure generally varied across trophic groups and the fishery status. Herbivores and omnivores exhibited the strongest response to human pressure, with up to four-fold (0.18–0.05 kg m^{-2} min^{-1}) decline in herbivores and six-fold (0.52–0.09 kg m^{-2} min^{-1}) decline in omnivores. In both groups, these patterns were almost solely driven by

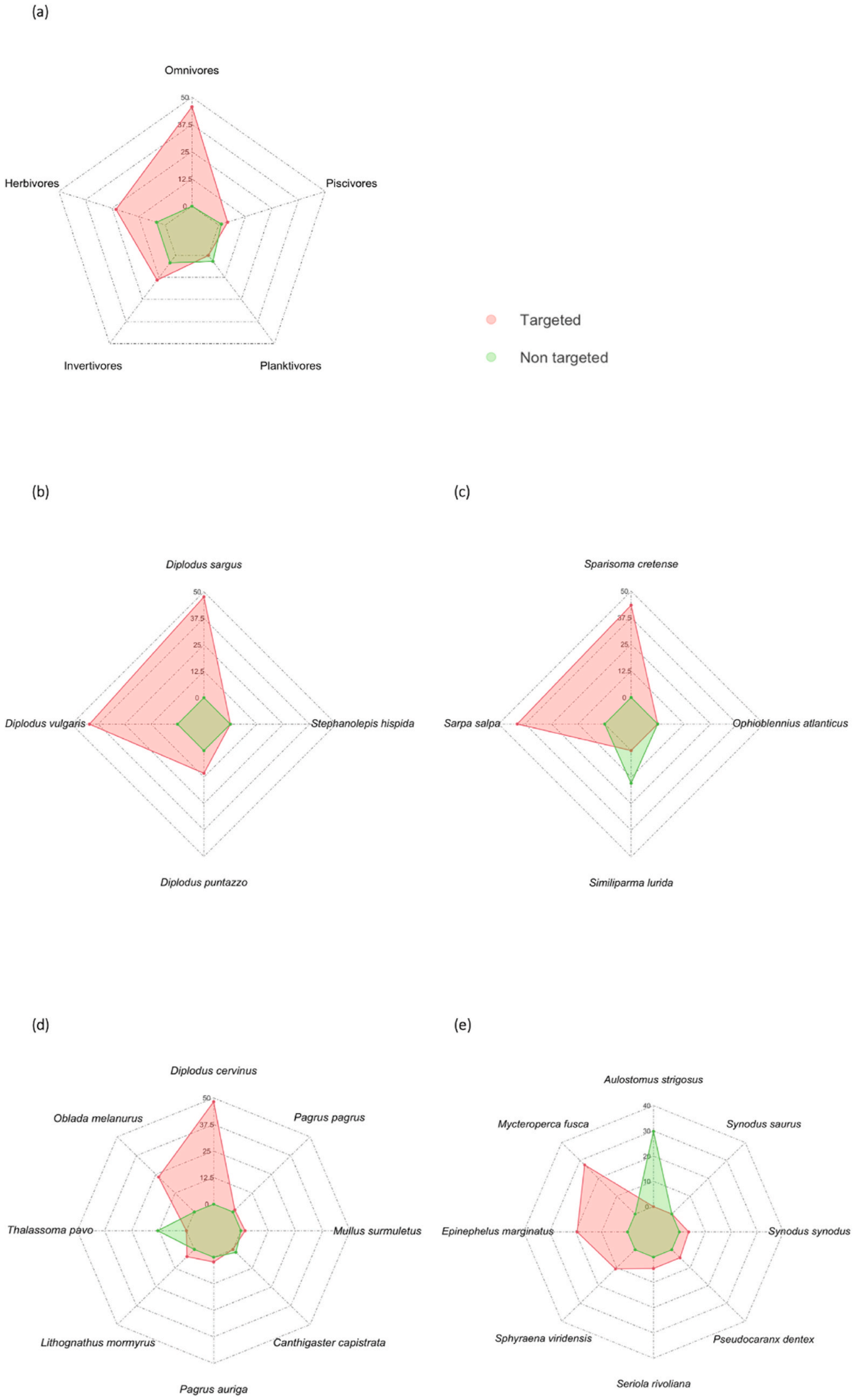
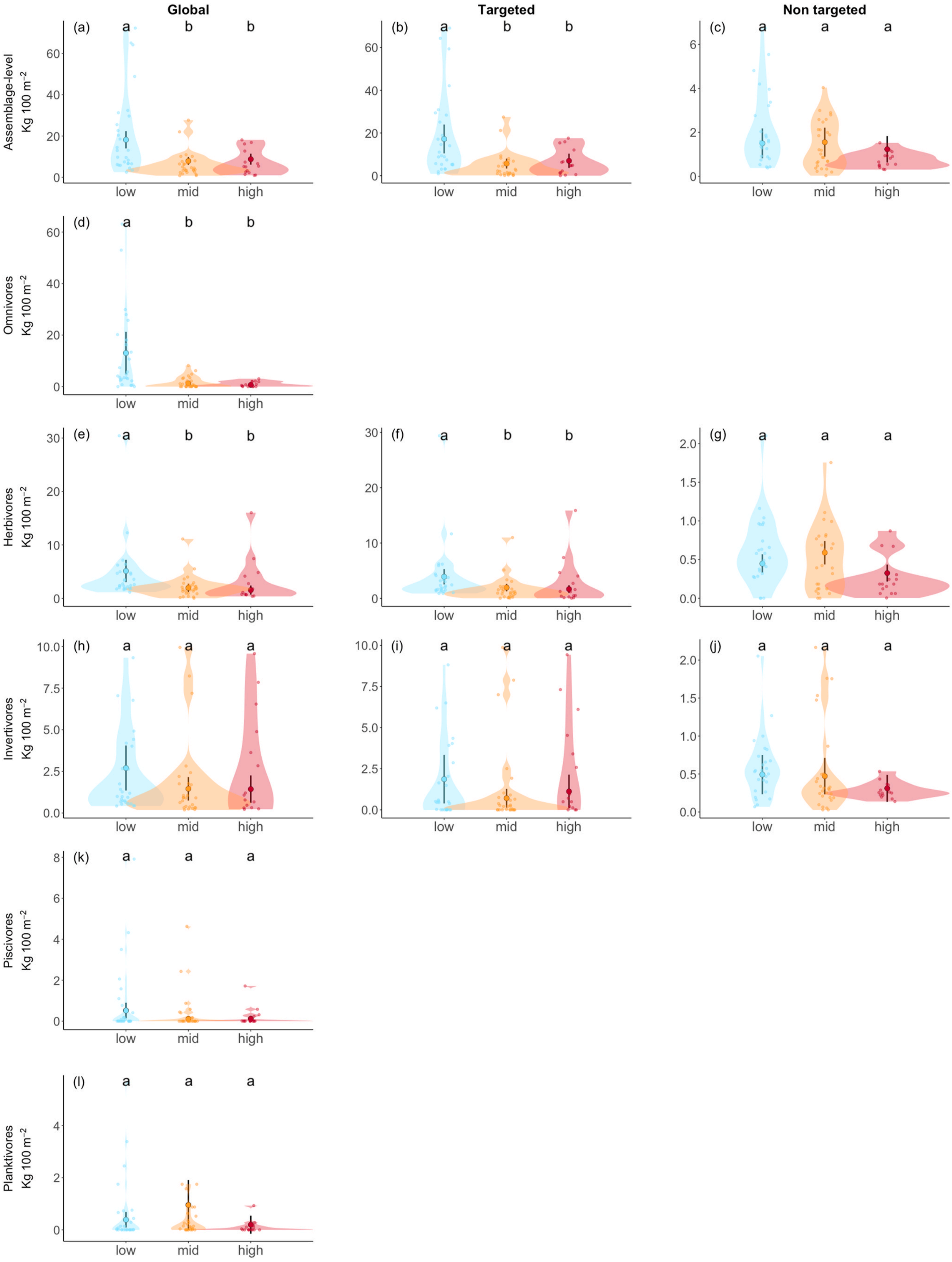


Fig. 2. (a) Radar plot illustrating the percent contribution of each fish trophic group, according to its fishery status (red = targeted; green = non-targeted), to total assemblage biomass. (b–e) Percent contribution of fish species, according to its fishery status (red = targeted; green = non-targeted), to total biomass within each trophic group: (b) omnivores, (c) herbivores, (d) invertivores, and (e) piscivores. Note, planktivores were not represented as they only comprised a single non-targeted species (*Chromis limbata*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summary of GLMM results testing for the effect of human pressure, habitat composition, sea surface temperature, and depth on the biomass of reef fish assemblages. Predictor effect (estimate ± SE), z-statistic, p-value, and R2 (marginal and conditional) are reported for model comparisons. For categorical factors, i.e., HAPI, "high human pressure" level is used as the reference value.

Response variable	Predictor	Estimate ± SE	Z statistic	p value	R marginal	R Conditional
	(Intercept)	2.14 ± 0.25	8.59	**<0.001**		
	HAPI_Categorylow	0.73 ± 0.29	2.52	**0.012**		
	HAPI_Categorymid	−0.10 ± 0.28	−0.37	0.714		
	Habitat_PCoA1	0.01 ± 0.11	0.13	0.897		
	SST	0.19 ± 0.12	1.51	0.130		
Assemblage-level	Depth	0.07 ± 0.09	0.74	0.460	1.0 %	–
	(Intercept)	1.87 ± 0.36	5.16	**<0.001**		
	HAPI_Categorylow	0.90 ± 0.41	2.22	**0.026**		
	HAPI_Categorymid	−0.20 ± 0.40	−0.51	0.611		
	Habitat_PCoA1	0.05 ± 0.16	0.33	0.741		
	SST	0.22 ± 0.18	1.21	0.224		
Targeted	Depth	0.07 ± 0.11	0.61	0.539	1.4 %	2.2 %
	(Intercept)	0.16 ± 0.29	0.56	0.577		
	HAPI_Categorylow	0.20 ± 0.36	0.55	0.582		
	HAPI_Categorymid	0.23 ± 0.34	0.69	0.491		
	Habitat_PCoA1	−0.06 ± 0.10	−0.55	0.582		
	SST	−0.20 ± 0.15	−1.33	0.184		
Non targeted	Depth	−0.03 ± 0.10	−0.32	0.752	3.7 %	12 %
	(Intercept)	−0.44 ± 0.60	−0.73	0.466		
	HAPI_Categorylow	3.00 ± 0.75	4.02	**<0.001**		
	HAPI_Categorymid	0.65 ± 0.72	0.89	0.371		
	Habitat_PCoA1	0.08 ± 0.21	0.41	0.683		
	SST	0.40 ± 0.26	1.52	0.129		
Omnivores	Depth	−0.17 ± 0.21	−0.80	0.421	54.2 %	–
	(Intercept)	0.34 ± 0.50	0.69	0.493		
	HAPI_Categorylow	1.19 ± 0.60	1.99	**0.046**		
	HAPI_Categorymid	0.24 ± 0.59	0.40	0.690		
	Habitat_PCoA1	−0.23 ± 0.14	−1.68	0.092		
	SST	0.08 ± 0.26	0.30	0.763		
Herbivores	Depth	−0.01 ± 0.14	−0.09	0.927	27.5 %	–
	(Intercept)	0.50 ± 0.32	1.60	0.110		
	HAPI_Categorylow	0.85 ± 0.38	2.23	**0.026**		
	HAPI_Categorymid	0.15 ± 0.33	0.47	0.641		
	Habitat_PCoA1	0.06 ± 0.10	0.55	0.583		
	SST	0.06 ± 0.13	0.48	0.628		
Herbivores targeted	Depth	−0.13 ± 0.10	−1.33	0.183	3.2 %	–
	(Intercept)	−1.13 ± 0.28	−3.95	**<0.001**		
	HAPI_Categorylow	0.32 ± 0.36	0.88	0.379		
	HAPI_Categorymid	0.59 ± 0.32	1.88	0.060		
	Habitat_PCoA1	0.30 ± 0.13	2.33	**0.019**		
	SST	−0.17 ± 0.12	−1.44	0.151		
Herbivores non-targeted targeted	Depth	−0.12 ± 0.11	−1.04	0.298	39.5 %	–
	(Intercept)	0.36 ± 0.41	0.87	0.384		
	HAPI_Categorylow	0.63 ± 0.55	1.14	0.253		
	HAPI_Categorymid	0.01 ± 0.49	0.03	0.977		
	Habitat_PCoA1	−0.24 ± 0.17	−1.43	0.154		
	SST	0.25 ± 0.20	1.21	0.225		
Invertivores	Depth	0.13 ± 0.16	0.82	0.414	14.7 %	–
	(Intercept)	0.10 ± 0.64	0.15	0.877		
	HAPI_Categorylow	0.51 ± 0.84	0.61	0.543		
	HAPI_Categorymid	−0.46 ± 0.78	−0.58	0.559		
	Habitat_PCoA1	−0.28 ± 0.25	−1.12	0.264		
	SST	0.52 ± 0.34	1.53	0.127		
Invertivores targeted	Depth	0.30 ± 0.26	1.15	0.251	28.2 %	–
	(Intercept)	−1.19 ± 0.35	−3.39	**<0.001**		
	HAPI_Categorylow	0.46 ± 0.46	0.99	0.320		
	HAPI_Categorymid	0.42 ± 0.40	1.04	0.299		
	Habitat_PCoA1	−0.12 ± 0.10	−1.22	0.222		
	SST	−0.06 ± 0.18	−0.34	0.733		
Invertivores non-targeted	Depth	−0.16 ± 0.08	−1.95	0.051	14.2 %	–
	(Intercept)	−2.36 ± 1.02	−2.32	**0.020**		
	HAPI_Categorylow	1.46 ± 1.18	1.23	0.217		
	HAPI_Categorymid	−0.05 ± 1.18	−0.05	0.963		
	Habitat_PCoA1	−0.33 ± 0.34	−0.96	0.335		
	SST	0.65 ± 0.52	1.24	0.214		
Piscivores targeted	Depth	1.05 ± 0.35	2.99	**0.003**	50.9 %	–
	(Intercept)	−2.90 ± 1.71	−1.70	0.090		
	HAPI_Categorylow	0.68 ± 1.91	0.35	0.723		
	HAPI_Categorymid	1.58 ± 1.91	0.83	0.408		
	Habitat_PCoA1	−0.44 ± 0.40	−1.10	0.272		
	SST	−0.67 ± 0.78	−0.86	0.392		
Planktivores	Depth	1.06 ± 0.29	3.71	**<0.001**	62.2 %	–



(caption on next page)

Fig. 3. Fish biomass response to varying levels of fisheries exploitation (low = blue, mid = orange, and high = red) for assemblage-level data (a–c) and each trophic group: omnivores (d), herbivores (e–g), invertivores (h–j), piscivores (k), and planktivores (l). For each trophic group (i.e., response variable) (left column), models were partitioned for fishery targeted (middle column) and non-targeted (right column) species. Larger dots are model-averaged predictions from GLMs, and whiskers are SE around the predicted mean. Violin plots and smaller dots are included within each panel to depict the distribution of replicate-level values. Significant patterns are denoted with a letter (e.g. a or b) marking significant differences between levels of fisheries explotation within each panel. We note omnivores were exclusively conformed of targeted species, and for simplicity were included in the global panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

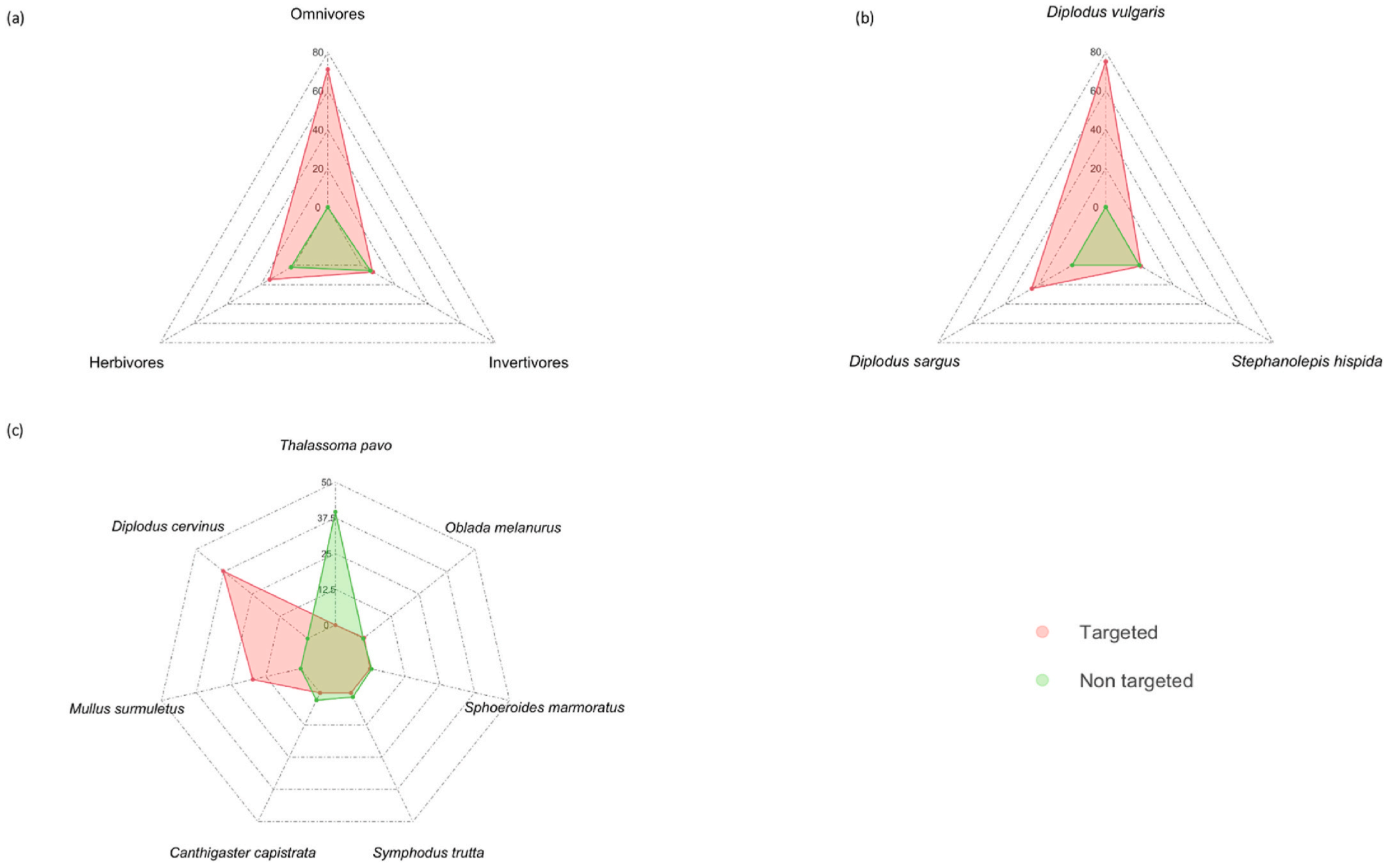


Fig. 4. (a) Radar plot illustrating the percent contribution of each fish trophic group, according to its fishery status (red = targeted; green = non-targeted), to total assemblage feeding pressure. (b–c) Percent contribution of fish species, according to its fishery status (red = targeted; green = non-targeted), to total feeding pressure within each trophic group: (b) omnivores, and (c) invertivores. Note, herbivores were not represented, as the trophic group comprised only one targeted species, *Sparisoma cretense* (88.3 % of the herbivore feeding pressure), and one non-targeted species, *Similiparma lurida* (11.7 %). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

targeted species (Table 2), with feeding pressure by targeted herbivorous fishes declining up to three-fold (0.17–0.05 kg m^{-2} min^{-1}) with increasing human pressure, whilst non-targeted species displayed non-significant patterns. For omnivores, we observed high variability in feeding pressure at the video plot scale, which resulted in high uncertainty in parameter estimates and hence non-significant patterns ($p = 0.07$). In contrast to these groups, feeding pressure by invertivorous fishes displayed non-significant associations with human pressure, being majorly driven by the strength of agonistic biotic interactions in non-targeted fishes.

Considering only the fixed effects, the amount of explained variance varied from 30 % for invertivores, to 54 % for the model on non-targeted invertivores (Table 2). Incorporating the variance explained by the random effect of site slightly improved the goodness-of-fit of the models, for instance to 59 % in assemblage-level models.

4. Discussion

Our study revealed a profound imprint of human activities on trophic interactions mediated by reef fishes in an oceanic island in the eastern Atlantic Ocean. Despite we used a compound metric of human pressures not directly related to fishing pressure, the HAPI index (Blanfuné et al., 2017), the contrasting response of targeted *vs.* non-targeted species points towards community-wide impacts of extractive fishing activities at an island scale, beyond a mere and direct alteration of biomass patterns. Prior studies in the region have extensively reported the depletion of fish abundances and biomasses among specific targeted species and trophic groups due to a long-history of overexploitation by both recreational and professional fisheries (Tuya et al., 2006b; Castro et al., 2019; Jiménez-Alvarado et al., 2020). However, our study is the first to provide a quantitative comparison of the concomitant response of fish biomass and feeding pressure to varying levels of human exploitation.

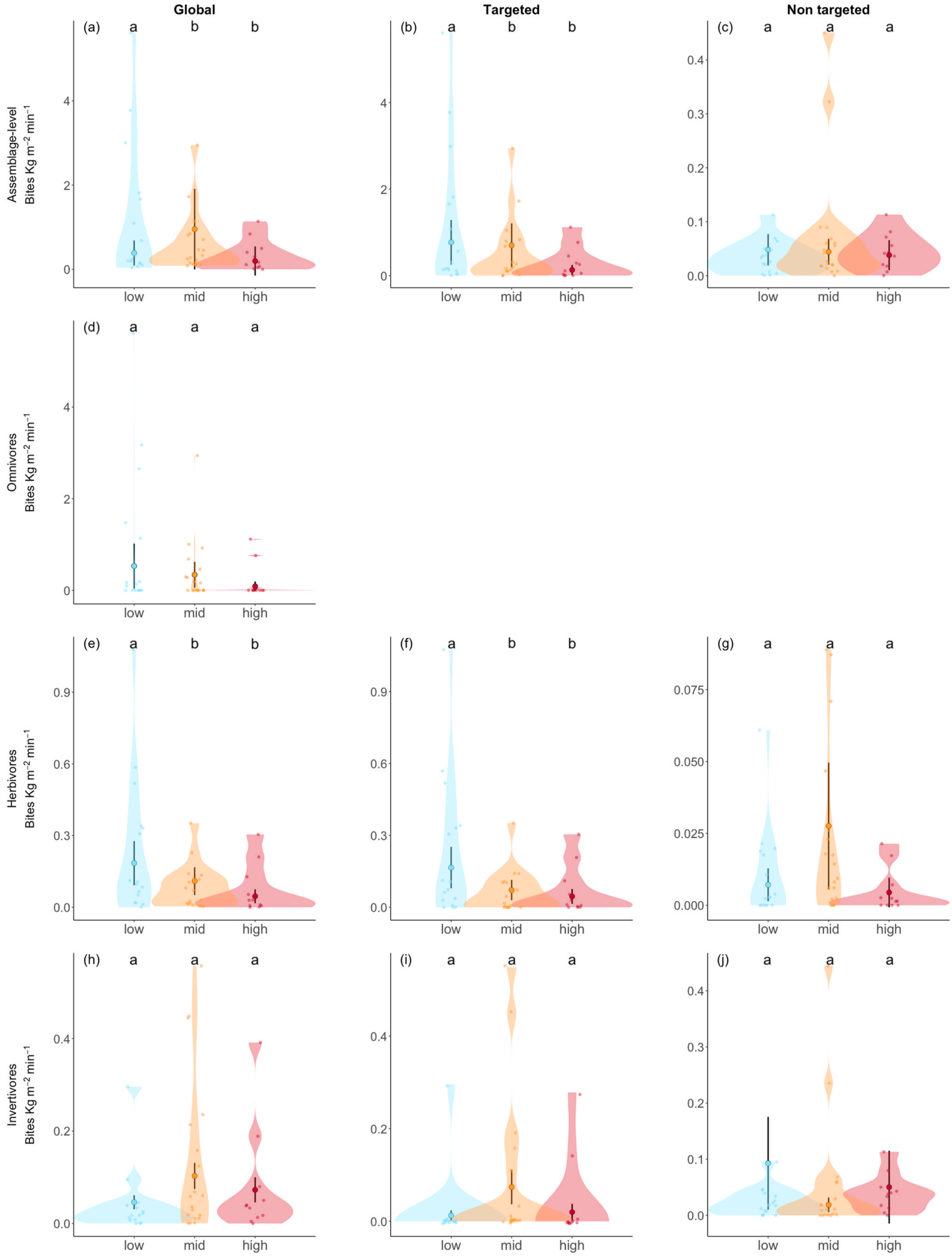
We documented a two-fold declined in fish biomass under high levels of human pressure, whilst feeding pressure declined five-fold. The stronger decline in feeding pressure has important implications for management strategies aimed at preserving trophic interactions (Bellwood et al., 2019b; Canterle et al., 2020), as it may indicate hidden impacts of fishing on behaviour or competitive interactions that impair

Table 2
Summary of GLMM results testing for the effect of human pressure level, habitat composition, temperature, and negative biotic interactions on the feeding pressure of reef fish assemblages. Predictor effect (estimate ± SE), z-statistic, and p-value are reported for model comparisons. For categorical factors, i.e., HAPI, "high human pressure" level is used as the reference value.

Response variable	Predictor	Estimate ± SE	Z statistic	p value	R Marginal	R Conditional
	(Intercept)	−1.86 ± 0.66	−2.80	**0.005**		
	Temp_mean	−0.16 ± 0.30	−0.54	0.589		
	Habitat_PCoA1	−0.51 ± 0.21	−2.45	**0.014**		
	HAPI_Categorylow	1.68 ± 0.73	2.30	**0.022**		
	HAPI_Categorymid	1.45 ± 0.86	1.68	0.094		
Assemblage-level	negative.interaction	0.17 ± 0.19	0.90	0.370	32.9 %	59.0 %
	(Intercept)	−2.18 ± 0.83	−2.62	**0.009**		
	Temp_mean	−0.10 ± 0.34	−0.29	0.773		
	Habitat_PCoA1	−0.68 ± 0.24	−2.84	**0.004**		
	HAPI_Categorylow	1.77 ± 0.90	1.97	**0.048**		
	HAPI_Categorymid	1.67 ± 0.96	1.74	0.082		
Targeted	negative.interaction	−0.11 ± 0.26	−0.44	0.661	47.3 %	–
	(Intercept)	−3.51 ± 0.68	−5.14	**<0.001**		
	Temp_mean	−0.30 ± 0.27	−1.11	0.266		
	Habitat_PCoA1	0.02 ± 0.17	0.09	0.925		
	HAPI_Categorylow	0.24 ± 0.82	0.28	0.776		
	HAPI_Categorymid	0.15 ± 0.79	0.19	0.848		
Non targeted	negative.interaction	0.47 ± 0.12	3.77	**<0.001**	31.4 %	–
	(Intercept)	−2.43 ± 1.00	−2.42	**0.015**		
	Temp_mean	−0.25 ± 0.38	−0.65	0.514		
	Habitat_PCoA1	−0.80 ± 0.39	−2.06	**0.040**		
	HAPI_Categorylow	1.79 ± 1.00	1.80	0.072		
	HAPI_Categorymid	1.35 ± 1.07	1.26	0.206		
Omnivores	negative.interaction	0.01 ± 0.39	0.04	0.971	34.5 %	–
	(Intercept)	−3.11 ± 0.55	−5.67	**<0.001**		
	Temp_mean	−0.14 ± 0.24	−0.59	0.553		
	Habitat_PCoA1	−0.32 ± 0.21	−1.50	0.134		
	HAPI_Categorylow	1.39 ± 0.62	2.22	**0.026**		
	HAPI_Categorymid	0.86 ± 0.69	1.25	0.212		
Herbivores	negative.interaction	−0.33 ± 0.25	−1.31	0.190	40.6 %	–
	(Intercept)	−3.11 ± 0.58	−5.32	**<0.001**		
	Temp_mean	−0.19 ± 0.27	−0.71	0.478		
	Habitat_PCoA1	−0.23 ± 0.26	−0.88	0.379		
	HAPI_Categorylow	1.29 ± 0.63	2.05	**0.041**		
	HAPI_Categorymid	0.46 ± 0.78	0.59	0.554		
Herbivores targeted	negative.interaction	−0.55 ± 0.39	−1.40	0.162	45.0 %	–
	(Intercept)	−5.79 ± 0.98	−5.94	**<0.001**		
	Temp_mean	0.55 ± 0.47	1.18	0.239		
	Habitat_PCoA1	0.00 ± 0.23	0.01	0.988		
	HAPI_Categorylow	0.47 ± 1.18	0.40	0.691		
	HAPI_Categorymid	1.82 ± 1.12	1.63	0.104		
Herbivores non-targeted	negative.interaction	0.18 ± 0.25	0.70	0.484	53.9 %	–
	(Intercept)	−2.62 ± 0.37	−7.01	**<0.001**		
	Temp_mean	−0.31 ± 0.22	−1.45	0.146		
	Habitat_PCoA1	−0.15 ± 0.20	−0.76	0.446		
	HAPI_Categorylow	−0.46 ± 0.51	−0.91	0.364		
	HAPI_Categorymid	0.35 ± 0.47	0.74	0.462		
Invertivores	negative.interaction	0.43 ± 0.19	2.25	**0.025**	29.7 %	–
	(Intercept)	−3.92 ± 0.90	−4.35	**<0.001**		
	Temp_mean	−0.86 ± 0.58	−1.49	0.137		
	Habitat_PCoA1	−0.91 ± 0.56	−1.61	0.107		
	HAPI_Categorylow	−0.47 ± 1.16	−0.41	0.685		
	HAPI_Categorymid	1.32 ± 1.01	1.30	0.193		
Invertivores targeted	negative.interaction	0.37 ± 0.50	0.74	0.459	44.1 %	–
	(Intercept)	−3.81 ± 1.18	−3.22	**0.001**		
	Temp_mean	−0.59 ± 0.30	−1.95	0.051		
	Habitat_PCoA1	−0.05 ± 0.20	−0.24	0.810		
	HAPI_Categorylow	0.61 ± 1.40	0.44	0.662		
	HAPI_Categorymid	−0.98 ± 1.39	−0.71	0.481		
Invertivores non-targeted	negative.interaction	0.49 ± 0.14	3.62	**<0.001**	54.4 %	–

feeding activities (Wilson et al., 2008). Further, we observed varying responses to human pressure among different fish trophic groups, with targeted herbivorous and omnivorous fish displaying the strongest responses to human pressures, while the response of invertivores, piscivores and planktivores was highly stochastic. Importantly, the response of fish omnivores and herbivores was almost solely attributed to targeted species, which markedly dominated spatial patterns in fish biomass and feeding pressure irrespective of the level of human pressure. Given the importance of omnivores and herbivores in mediating energy flow to higher trophic levels, our study points towards the development of management strategies both at local and regional scales, which consider the complex relationships between fish biomass and trophic interactions (Bellwood et al., 2019b; Tebbett et al., 2020).

The contrasting response of target and non-target fish species to human pressure suggested fishing as the primary anthropogenic factor influencing spatial patterns in fish biomass and feeding pressure. Furthermore, although the HAPI index is not a direct proxy for fishing pressure, numerous studies have used human population density as an



(caption on next page)

Fig. 5. Fish feeding pressure response to varying levels of fisheries exploitation (low = blue, mid = orange, and high = red) for assemblage-level data (a–c) and each trophic groups: omnivores (d), herbivores (e–g), and invertivores (h–j). For each trophic group (i.e., response variable) (left column), models were partitioned for fishery targeted (middle column) and non-targeted (right column) species. Larger dots are model-averaged predictions from GLMs, and whiskers are SE around the predicted mean. Violin plots and smaller dots are included within each panel to depict the distribution of replicate-level values. Significant patterns are denoted with a letter (e.g. a or b) marking significant differences between levels of fisheries explotation within each panel. We note omnivores were exclusively conformed of targeted species, and for simplicity were included in the global panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

indirect proxy, demonstrating a decrease in fish biomass in more populated areas (Cinner et al., 2013; Mora et al., 2011; Bosch et al., 2021). The decrease in fish biomass was mostly attributed to targeted omnivores and herbivores, while there was substantial heterogeneity in the response of the other trophic groups. The composition of these trophic groups primary consists of targeted species, such as *Sparisoma cretense* and those of the genus *Diplodus* ssp., that are of particular interest due to their economic and cultural value on the islands (Tuya et al., 2006a; Espino et al., 2015; Jiménez-Alvarado et al., 2019, 2020; Gonzalez et al., 2020). High selective pressures from both recreational and professional fishers have thus likely underscored their marked biomass reduction in the region (Jiménez-Alvarado et al., 2020; Castro et al., 2015), as reported elsewhere (e.g., Mumby, 2006; Valles and Oxenford, 2014; Bellwood et al., 2012).

In parallel, fish biomass reductions in response to a long history of human exploitation are often accompanied by substantial reductions in fish feeding pressure, a pattern also reported from other oceanic islands regions (Ferrari et al., 2024; Robinson et al., 2020). The impact of fishing on feeding pressure is also evident in studies of marine protected areas. For instance, Ferguson et al. (2016) and Della Marta et al. (2023) observed an increase in biomass and feeding pressure of the species *Girella tricuspidata* in regions protected from fishing. Interestingly, in the case of omnivores, we observed a significantly more pronounced decrease in fish biomass than feeding pressure along the human pressure gradient, which may point towards compensatory behavioural mechanism (Tebbett et al., 2020). The major contribution of omnivores and herbivores to reef fish-benthos interactions (i.e., feeding pressure) aligns with research conducted in other regions of the Atlantic Ocean, including oceanic islands (Canterle et al., 2020; Ferrari et al., 2024). This contrasts with well recognised patterns in tropical regions, which have highlighted herbivores as the primary contributors to feeding pressure on the benthos (Bellwood et al., 2019a; Cook et al., 2024). This emphasizes the context dependency of the identity and intensity of trophic interactions, and the need to empirically quantify this in response to a range of environmental and human perturbations (Brandl et al., 2019; Tebbett et al., 2020).

Contrary to expectations, we found no significant effect of human pressure on the biomass of piscivores and invertivores, despite their intrinsic higher vulnerability (e.g., slow-growth and late maturity, Reynolds et al., 2005) to fishing pressure (Froese, 2004; Jiménez-Alvarado et al., 2019). The sparse presence of piscivores in the area suggests that this trophic group has historically been subjected to overexploitation, reducing its abundance and biomass to near collapse (e.g., groupers, Couce-Montero et al., 2015; Jiménez-Alvarado et al., 2019; Tuya et al., 2006b). This finding aligns with other studies attributing the decline in piscivorous fish biomass to human activities (Jennings and Polunin, 1997; Valdivia et al., 2017). Furthermore, we showed a significant relationship between their biomass and increasing depth, suggesting greater abundance and size at depths where most fishing activities are limited (Bosch et al., 2023; Jiménez-Alvarado et al., 2020). In the case of invertivores, the lack of response to the human pressure gradient in both biomass and feeding pressure could be further attributed to certain species exhibiting erratic behaviour and irregular distributions, as they typically inhabit sand-reef ecotones for feeding (e.g., *Mullus surmuletus*, Labropoulou et al., 1997). Additionally, many targeted species primarily feed on larger mobile invertebrates, such as sea urchins (Clemente et al., 2010; Sangil et al., 2012), which are rare in exposed turf seascapes, possibly due to a lack of refuges against predators. In contrast, small-bodied non-targeted species, like *Thalassoma pavo,* are abundant and feed on small epifauna that proliferate within turf seascapes (Fraser et al., 2020, 2021). The removal of targeted species could reduce resource competition and increase space availability, favouring non-targeted invertivorous fish (Wilson et al., 2008).

Our results provide compelling evidence of the imprints of human pressures on trophic interactions mediated by reef fishes, evidenced by the response of fish biomass and feeding pressure to the HAPI index. However, the lack of spatiotemporally resolved data on fishing effort (e.g., capture per m^{-2}), from both the recreational and artisanal sectors, at fine spatial scales, limit our ability to attribute a cause-effect relationship between fishing and the ecological metrics investigated here. Furthermore, to mechanistically link realised ecosystem functions with trophic interactions inferred from feeding pressure patterns, future studies should employ more detailed analysis, e.g., by linking changes in key traits of herbivores with rates of macroalgal removal and sediment reworking. The reliance on trophic group classifications can result in weak correlations with actual functions, as some species might differ in behavioural or morphological traits that are often poorly defined (Bellwood et al., 2019b; Tebbett et al., 2020). Finally, given the vulnerability of overpopulated oceanic islands with a long history of human exploitation, it remains essential to derive adequate proxies of fishing pressure across spatiotemporal comprehensive scales to guide management and conservation actions that aim to preserve ecosystem multifunctionality.

5. Conclusions

Our study underscores the significant imprint of human pressures on trophic interactions mediated by reef fishes. The observed decline in feeding pressure, generally surpassing that of biomass, suggests that fishing activities may exert additional, hidden, negative effects on these interactions beyond what biomass variation can reveal. This highlights the inadequacy of relying solely on biomass proxies to quantify trophic interactions, necessitating the acquisition of more comprehensive data. Moreover, our findings reveal varying impacts across trophic groups, with significant declines in feeding pressure among omnivores and herbivores. Given that these groups play a pivotal role in transferring energy and materials from primary producers to upper trophic levels, there is an urgent need for fostering their sustainable management and conservation within these oceanic island ecosystems. Moreover, the concentration of trophic interactions among a limited number of species (low redundancy) in oceanic islands, that are highly targeted by fishers, heighten the vulnerability of these ecosystems to intense human pressures. Our study points to the critical importance of identifying and understanding which species within trophic groups drive core trophic interactions in oceanic island systems, highlighting the need for implementing species-specific management strategies. These strategies are crucial for protecting these species from the potential detrimental effects of human activities and ensuring the resilience of these vulnerable systems.

CRediT authorship contribution statement

Iris Barroso: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Mar Mourin:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Sandra Navarro-Mayoral:** Writing – review & editing, Investigation. **Fernando**

Tuya: Writing – review & editing, Investigation, Funding acquisition. **Nestor E. Bosch:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The author's declare no conflict of interest.

Acknowledgements

N.E.B was supported by the Spanish Minister of Science and Innovation through the Juan de La Cierva-Formación postdoctoral fellows (JDC2022-048733-I), funded by MCIN/AEI/10.13039/501100011033 and the EU "Next Generation EU" program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109305.

Data availability

All data and R code used for this article will be published in the author's personal Figshare repository upon acceptance. It will also be provided to reviewers upon request.

References

Ahrens, R.N., Allen, M.S., Walters, C., Arlinghaus, R., 2020. Saving large fish through harvest slots outperforms the classical minimum-length limit when the aim is to achieve multiple harvest and catch-related fisheries objectives. Fish Fish. 21 (3), 483–510. https://doi.org/10.1111/faf.12442.

Alós, J., Palmer, M., Grau, A.M., 2009. Mortality of *Diplodus annularis* and *Lithognathus mormyrus* released by recreational anglers: implications for recreational fisheries management. Fish. Manag. Ecol. 16 (4), 298–305. https://doi.org/10.1111/j.1365-2400.2009.00675.x.

Alós, J., Palmer, M., Catalan, I.A., Alonso-Fernández, A., Basterretxea, G., Jordi, A., et al., 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Mar. Ecol. Prog. Ser. 503, 219–233. https://doi.org/10.3354/meps10745.

Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H., Gowlett-Holmes, K., 2015. A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: the CATAMI classification scheme. PLoS One 10 (10), 1–18. https://doi.org/10.1371/journal.pone.0141039.

Anguita, F., Hernán, F., 2000. The Canary Islands origin: a unifying model. J. Volcanol. Geoth. Res. 103 (1–4), 1–26. https://doi.org/10.1016/S0377-0273(00)00195-5.

Azorin-Molina, C., Menendez, M., McVicar, T.R., Acevedo, A., Vicente-Serrano, S.M., Cuevas, E., et al., 2018. Wind speed variability over the Canary Islands, 1948–2014: focusing on trend differences at the land–ocean interface and below–above the trade-wind inversion layer. Clim. Dyn. 50, 4061–4081. https://doi.org/10.1007/s00382-017-3861-0.

Azzurro, E., Pais, A., Consoli, P., Andaloro, F., 2007. Evaluating day–night changes in shallow Mediterranean rocky reef fish assemblages by visual census. Marine Biology 151 (6), 2245–2253. https://doi.org/10.1007/s00227-007-0661-9.

Barbosa, M.C., Luiz, O.J., Cordeiro, C.A., Giglio, V.J., Ferreira, C.E., 2021. Fish and spearfisher traits contributing to catch composition. Fish. Res. 241, 105988. https://doi.org/10.1016/j.fishres.2021.105988.

Barneche, D.R., Floeter, S.R., Ceccarelli, D.M., Frensel, D.D.M.B., Dinslaken, D.F., Mário, H.F.S., Ferreira, C.E., 2009. Feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae). Marine Biology 156, 289–299. https://doi.org/10.1007/s00227-008-1083-z.

Barneche, D.R., Robertson, D.R., White, C.R., Marshall, D.J., 2018. Fish reproductive-energy output increases disproportionately with body size. Science 360 (6389), 642–645. https://doi.org/10.1126/science.aao686.

Barnett, L.A., Jacobsen, N.S., Thorson, J.T., Cope, J.M., 2019. Realizing the potential of trait-based approaches to advance fisheries science. Fish Fish. 20 (5), 1034–1050. https://doi.org/10.1111/faf.12395.

Barrowman, N.J., Myers, R.A., 1996. Is fish recruitment related to spawner abundance. Fish. Bull. 94, 707–724. https://doi.org/10.1126/science.aao6868.

Barton, E.D., Arıstegui, J., Tett, P., Cantón, M., Garcıa-Braun, J., Hernández-León, S., et al., 1998. The transition zone of the Canary Current upwelling region. Prog. Oceanogr. 41 (4), 455–504. https://doi.org/10.1016/S0079-6611(98)00023-8.

Bellwood, D.R., Hoey, A.S., Hughes, T.P., 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc. Biol. Sci. 279 (1733), 1621–1629. https://doi.org/10.1098/rspb.2011.1906.

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., et al., 2019a. Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol. Conserv. 236, 604–615. https://doi.org/10.1016/j.biocon.2019.05.056.

Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., 2019b. The meaning of the term 'function'in ecology: a coral reef perspective. Funct. Ecol. 33 (6), 948–961. https://doi.org/10.1111/1365-2435.13265.

Bilbao-Sieyro, A., Pérez-González, Y., Martín-Sosa, P., Castro-Hernández, J.J., Jiménez-Alvarado, D., Pascual-Fernández, J.J., 2022. Marine recreational fisheries in the canary islands: state of knowledge, preliminary results. Biology and Life Sciences Forum 13 (1), 7. https://doi.org/10.3390/blsf2022013007.

Blanfuné, A., Thibaut, T., Boudouresque, C.F., Mačić, V., Markovic, L., Palomba, L., et al., 2017. The CARLIT method for the assessment of the ecological quality of European Mediterranean waters: relevance, robustness and possible improvements. Ecol. Indic. 72, 249–259. https://doi.org/10.1016/j.ecolind.2016.07.049.

Bosch, N.E., Espino, F., Tuya, F., Haroun, R., Bramanti, L., Otero-Ferrer, F., 2023. Black coral forests enhance taxonomic and functional distinctiveness of mesophotic fishes in an oceanic island: implications for biodiversity conservation. Sci. Rep. 13 (1), 4963. https://doi.org/10.1038/s41598-023-32138-x.

Bosch, N.E., Gonçalves, J.M., Tuya, F., Erzini, K., 2017. Marinas as habitats for nearshore fish assemblages: comparative analysis of underwater visual census, baited cameras and fish traps. Sci. Mar. 81 (2), 159–169.

Bosch, N.E., Monk, J., Goetze, J., Wilson, S., Babcock, R.C., Barrett, N., et al., 2022a. Effects of human footprint and biophysical factors on the body-size structure of fished marine species. Conserv. Biol. 36 (2), e13807. https://doi.org/10.1111/cobi.13807.

Bosch, N.E., Pessarrodona, A., Filbee-Dexter, K., Tuya, F., Mulders, Y., Bell, S., et al., 2022b. Habitat configurations shape the trophic and energetic dynamics of reef fishes in a tropical–temperate transition zone: implications under a warming future. Oecologia 200 (3), 455–470. https://doi.org/10.1007/s00442-022-05278-6.

Bosch, N.E., McLean, M., Zarco-Perello, S., Bennett, S., Stuart-Smith, R.D., Vergés, A., et al., 2022c. Persistent thermally driven shift in the functional trait structure of herbivorous fishes: evidence of top-down control on the rebound potential of temperate seaweed forests? Glob. Change Biol. 28 (7), 2296–2311. https://doi.org/10.1111/gcb.16070.

Bosch, N.E., Wernberg, T., Langlois, T.J., Smale, D.A., Moore, P.J., Franco, J.N., et al., 2021. Niche and neutral assembly mechanisms contribute to latitudinal diversity gradients in reef fishes. J. Biogeogr. 48 (11), 2683–2698. https://doi.org/10.1111/jbi.14237.

Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., Duffy, J.E., 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Front. Ecol. Environ. 17 (8), 445–454. https://doi.org/10.1002/fee.2088.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal 9 (2), 378–400. https://doi.org/10.3929/ethz-b-000240890.

Brown, J.H., Gillooly, J.F., 2003. Ecological food webs: high– quality data facilitate theoretical unification. Proc. Natl. Acad. Sci. 100 (4), 1467–1468. https://doi.org/10.1073/pnas.0630310100.

Canterle, A.M., Nunes, L.T., Fontoura, L., Maia, H.A., Floeter, S.R., 2020. Reef microhabitats mediate fish feeding intensity and agonistic interactions at príncipe island biosphere reserve, tropical eastern atlantic. Mar. Ecol. 41 (5), e12609. https://doi.org/10.1111/maec.12609.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., et al., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the national academy of sciences 104 (46), 18123–18128. https://doi.org/10.1073/pnas.0709069104.

Castro, J.J., Divovich, E., de Molina Acevedo, A.D., Barrera-Luján, A., Riera, R., 2019. Reconstruction of marine small-scale fisheries captures in the canary islands (NE Atlantic Ocean) from 1950 to 2010. Sci. Mar. 83 (1), 7–17.

Castro, J.J., Divovich, E., Delgado de Molina, A., Barrera-Luján, A., 2015. Over-looked and Under-reported: a Catch Reconstruction of Marine Fisheries in the Canary Islands, Spain, 1950–2010. Fisheries Centre. The University of British Columbia. *Working Paper Series*. http://hdl.handle.net/10553/107044.

Cinner, J.E., Graham, N.A., Huchery, C., MacNeil, M.A., 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. Conserv. Biol. 27 (3), 453–458. https://doi.org/10.1111/j.1523-1739.2012.01933.x.

Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., et al., 2018. Gravity of human impacts mediates coral reef conservation gains. Proc. Natl. Acad. Sci. 115 (27), E6116–E6125. https://doi.org/10.1073/pnas.1708001115.

Clemente, S., Hernández, J.C., Rodríguez, A., Brito, A., 2010. Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. Mar. Ecol. Prog. Ser. 413, 55–67. https://doi.org/10.3354/meps08700.

Cook, D.T., Schmitt, R.J., Holbrook, S.J., Moeller, H.V., 2024. Modeling the effects of selectively fishing key functional groups of herbivores on coral resilience. Ecosphere 15 (1), e4749. https://doi.org/10.1002/ecs2.4749.

Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., et al., 2016. Global fishery prospects under contrasting management regimes. Proceedings of the national academy of sciences 113 (18), 5125–5129. https://doi.org/10.1073/pnas.1520420113.

Couce-Montero, L., Christensen, V., Castro, J.J., 2015. Effects of small-scale and recreational fisheries on the Gran Canaria ecosystem. Ecol. Model. 312, 61–76. https://doi.org/10.1016/j.ecolmodel.2015.05.021.

Coulon, N., Lindegren, M., Goberville, E., Toussaint, A., Receveur, A., Auber, A., 2023. Threatened fish species in the Northeast Atlantic are functionally rare. Global Ecol. Biogeogr. 32 (10), 1827–1845. https://doi.org/10.1111/geb.13731.

Cruces, L., Rodríguez, M., Monterroso, Ó., Álvarez, O., Pérez, Ó., Riera, R., 2024. Spatial and temporal variability of the two main caught species of an artisanal trap fishery in an oceanic island. Aquat. Conserv. Mar. Freshw. Ecosyst. 34 (3), e4090. https://doi.org/10.1002/aqc.4090.

Della Marta, I.R., Vergés, A., Powell, S., Smith, S.M., Poore, A.G., 2023. Marine protected areas are linked to higher predation rates by fish in shallow urbanised reefs, but only in no-take reserves. Mar. Ecol. Prog. Ser. 721, 135–150. https://doi.org/10.3354/meps14421.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Edgar, G.J., Barrett, N.S., Morton, A.J., 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. J. Exp. Mar. Biol. Ecol. 308 (2), 269–290. https://doi.org/10.1016/j.jembe.2004.03.004.

Edgar, G.J., Stuart-Smith, R.D., 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. Sci. Data 1 (1), 1–8.

Edgar, G.J., Cooper, A.T., Baker, S.C., Barker, W., Barrett, N.S., Becerro, M., et al., 2020. Reef life survey: establishing the ecological basis for conservation of shallow marine life. Biol. Conserv. 252, 108855.

Eggertsen, L., Luza, A.L., Cordeiro, C.A., Dambros, C., Ferreira, C.E., Floeter, S.R., et al., 2024. Complexities of reef fisheries in Brazil: a retrospective and functional approach. Rev. Fish Biol. Fish. 34, 511–538. https://doi.org/10.1007/s11160-023-09826-y.

Espino, F., González, J.A., Haroun, R., Tuya, F., 2015. Abundance and biomass of the parrotfish *Sparisoma cretense*in seagrass meadows: temporal and spatial differences between seagrass interiors and seagrass adjacent to reefs. Environ. Biol. Fish. 98, 121–133. https://doi.org/10.1007/s10641-014-0241-z.

Ferguson, A.M., Harvey, E.S., Knott, N.A., 2016. Herbivore abundance, site fidelity and grazing rates on temperate reefs inside and outside marine reserves. J. Exp. Mar. Biol. Ecol. 478, 96–105. https://doi.org/10.1016/j.jembe.2016.02.008.

Ferrari, D.S., Floeter, S.R., Leprieur, F., Quimbayo, J.P., 2023. A trait-based approach to marine island biogeography. J. Biogeogr. 50 (3), 528–538. https://doi.org/10.1111/jbi.14549.

Ferrari, D.S., Nunes, L.T., Mendes, T.C., Ferreira, C.E., Floeter, S.R., 2024. Hyperdominance and habitat composition drive reef fish foraging at Atlantic oceanic islands. Mar. Ecol. Prog. Ser. 726, 1–15. https://doi.org/10.3354/meps14483.

Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., et al., 2008. Atlantic reef fish biogeography and evolution. J. Biogeogr. 35 (1), 22–47. https://doi.org/10.1111/j.1365-2699.2007.01790.x.

Fox, R.J., Bellwood, D.R., 2007. Quantifying herbivory across a coral reef depth gradient. Mar. Ecol. Prog. Ser. 339, 49–59. https://doi.org/10.3354/meps339049.

Fraser, K.M., Lefcheck, J.S., Ling, S.D., Mellin, C., Stuart-Smith, R.D., Edgar, G.J., 2020. Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. Proceedings of the Royal Society B 287 (1941), 20201798. https://doi.org/10.1098/rspb.2020.1798.

Fraser, K.M., Stuart-Smith, R.D., Ling, S.D., Edgar, G.J., 2021. High biomass and productivity of epifaunal invertebrates living amongst dead coral. Marine Biology 168 (7), 102. https://doi.org/10.1007/s00227-021-03911-1.

Frisch, A., Baker, R., Hobbs, J.-P., Nankervis, L., 2008. A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: implications for management of multi-sector coral reef fisheries. Coral Reefs 27 (1), 85–95. https://doi.org/10.1007/s00338-007-0293-z.

Froese, R., 2004. Keep it simple: three indicators to deal with overfishing. Fish Fish. 5, 86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x.

Gonzalez, J.A., González-Lorenzo, G., Tejera, G., Arenas-Ruiz, R., Pajuelo, J.G., Lorenzo, J.M., 2020. Artisanal fisheries in the Canary Islands (eastern-central Atlantic): description, analysis of their economic contribution, current threats, and strategic actions for sustainable development. Acta Ichthyol. Piscatoria 50 (3), 269–289. http://hdl.handle.net/10553/74506.

Hartig, F., 2020. DHARMa: residual diagnostics for hierarchical (multi–level/mixed) regression models. R package version 0.3.3.0.

Hijmans, R., 2023. Raster: geographic data analysis and modeling. R package version 3, 6–26. https://CRAN.R-project.org/package=raster.

Hixon, M.A., Johnson, D.W., Sogard, S.M., 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 71 (8), 2171–2185. https://doi.org/10.1093/icesjms/fst200.

Jennings, S., Polunin, N.V.C., 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16, 71–82. https://doi.org/10.1007/s003380050061.

Jiménez-Alvarado, D., Guerra-Marrero, A., Sarmiento-Lezcano, A., Meyers, E.K., Castro, J.J., 2020. First assessment of the spearfishing impact in the Canary Islands. Regional studies in marine science 38, 101385. https://doi.org/10.1016/j.rsma.2020.101385.

Jiménez-Alvarado, D., Sarmiento-Lezcano, A., Guerra-Marrero, A., Tuya, F., Santana Del Pino, Á., Sealey, M.J., Castro, J.J., 2019. Historical photographs of captures of recreational Fishers indicate overexploitation of nearshore resources at an oceanic island. J. Fish. Biol. 94 (6), 857–864. https://doi.org/10.1111/jfb.13969.

Jørgensen, C., Ernande, B., Fiksen, Ø., 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. Evolutionary Applications 2 (3), 356–370. https://doi.org/10.1111/j.1752-4571.2009.00075.x.

Labropoulou, M., Machias, A., Tsimenides, N., Eleftheriou, A., 1997. Feeding habits and ontogenetic diet shift of the striped red mullet, *Mullus surmuletus* Linnaeus, 1758. Fish. Res. 31 (3), 257–267. https://doi.org/10.1016/S0165-7836(97)00017-9.

Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., et al., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proc. Biol. Sci. 283 (1828), 20160084. https://doi.org/10.1098/rspb.2016.0084.

Lewin, W.C., Weltersbach, M.S., Ferter, K., Hyder, K., Mugerza, E., Prellezo, R., et al., 2019. Potential environmental impacts of recreational fishing on marine fish stocks and ecosystems. Reviews in Fisheries Science & Aquaculture 27 (3), 287–330. https://doi.org/10.1080/23308249.2019.1586829.

Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23 (4), 399–417. https://doi.org/10.2307/1930126.

Longo, G.O., Floeter, S.R., 2012. Comparison of remote video and diver's direct observations to quantify reef fishes feeding on benthos in coral and rocky reefs. J. Fish. Biol. 81 (5), 1773–1780. https://doi.org/10.1111/j.1095-8649.2012.03441.x.

Longo, G.O., Ferreira, C.E.L., Floeter, S.R., 2014. Herbivory drives large-scale spatial variation in reef fish trophic interactions. Ecol. Evol. 4 (23), 4553–4566. https://doi.org/10.1002/ece3.1310.

Longo, G.O., Hay, M.E., Ferreira, C.E., Floeter, S.R., 2019. Trophic interactions across 61 degrees of latitude in the western atlantic. Global Ecol. Biogeogr. 28 (2), 107–117. https://doi.org/10.1111/geb.12806.

Longo, G.O., Morais, R.A., Martins, C.D.L., Mendes, T.C., Aued, A.W., Cândido, D.V., et al., 2015. Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: rocas Atoll, NE Brazil. PLoS One 10 (6), e0127176. https://doi.org/10.1371/journal.pone.0127176.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2023. Cluster: cluster analysis basics and extensions. R package version 2 (1.6).

Magneville, C., Leréec Le Bricquir, M.L., Dailianis, T., Skouradakis, G., Claverie, T., Villéger, S., 2023. Long-duration remote underwater videos reveal that grazing by fishes is highly variable through time and dominated by non-indigenous species. Remote Sensing in Ecology and Conservation 9 (3), 311–322. https://doi.org/10.1002/rse2.311.

Mallet, D., Pelletier, D., 2014. Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). Fish. Res. 154, 44–62. https://doi.org/10.1016/j.fishres.2014.01.019.

Mbaru, E.K., Graham, N.A., McClanahan, T.R., Cinner, J.E., 2020. Functional traits illuminate the selective impacts of different fishing gears on coral reefs. J. Appl. Ecol. 57 (2), 241–252. https://doi.org/10.1111/1365-2664.13547.

Mendes, T.C., Quimbayo, J.P., Bouth, H.F., Silva, L.P., Ferreira, C.E., 2019. The omnivorous triggerfish Melichthys Niger is a functional herbivore on an isolated Atlantic oceanic island. J. Fish. Biol. 95 (3), 812–819. https://doi.org/10.1111/jfb.14075.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8 (4), 391–400. https://doi.org/10.1111/j.1461-0248.2005.00731.x.

Mora, C., Aburto-Oropeza, O., Ayala Bocos, A., Ayotte, P.M., Banks, S., Bauman, A.G., et al., 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biol. 9 (4), e1000606. https://doi.org/10.1371/journal.pbio.1000606.

Morais, R.A., Ferreira, C.E.L., Floeter, S.R., 2017. Spatial patterns of fish standing biomass across Brazilian reefs. J. Fish. Biol. 91 (6), 1642–1667. https://doi.org/10.1111/jfb.13482.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., et al., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. 111 (38), 13757–13762. https://doi.org/10.1073/pnas.1317625111.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., et al., 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol. 11 (5), e1001569. https://doi.org/10.1371/journal.pbio.1001569.

Mourin, M., Barroso, I., Pessarrodona, A., Navarro-Mayoral, S., Tuya, F., Bosch, N.E., 2025. Local human pressures modulate turf sediment loads in a warm-temperate oceanic island. Mar. Environ. Res. 205, 107030. https://doi.org/10.1016/j.marenvres.2025.107030.

Mumby, P.J., 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol. Appl. 16 (2), 747–769. https://doi.org/10.1890/1051-0761(2006)016[0747:TIOEGS]2.0.CO;2.

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423 (6937), 280–283. https://doi.org/10.1038/nature01610.

Nunes, L.T., Barneche, D.R., Lastrucci, N.S., Fraga, A.A., Nunes, J.A., Ferreira, C.E., Floeter, S.R., 2021. Predicting the effects of body size, temperature and diet on animal feeding rates. Funct. Ecol. 35 (10), 2229–2240. https://doi.org/10.1111/1365-2435.13872.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Cáceres, M., Durand, S., et al., 2022. *Vegan: Community Ecology Package* (Version 2.6-4). CRAN [R package]. https://CRAN.R-project.org/package=vegan.

Parliament of the Canary Islands, 2003. Law 17/2003, of April 10, on fishing in the canary islands. Official Bulletin of the Canary Islands (74). https://www.boe.es/eli/es-cn/l/2003/04/10/17/con. (Accessed 17 April 2003).

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, Jr F., 1998. Fishing down marine food webs. Science 279 (5352), 860–863. https://doi.org/10.1126/science.279.5352.860.

Pebesma, E., Bivand, R., 2023. Spatial Data Science: with Applications in R. Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., et al., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27 (2), 179–200. https://doi.org/10.1017/S0376892900000205.

Quimbayo, J.P., Mendes, T.C., Kulbicki, M., Floeter, S.R., Zapata, F.A., 2017. Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific. Environ. Biol. Fish. 100, 149–162. https://doi.org/10.1007/s10641-016-0557-y.

Quimbayo, J.P., Silva, F.C.D., Mendes, T.C., Ferrari, D.S., Danielski, S.L., Bender, M.G., et al., 2021. Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. Ecology. https://doi.org/10.1002/ecy.3298.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. Proc. Biol. Sci. 272 (1579), 2337–2344. https://doi.org/10.1098/rspb.2005.3281.

Roberts, D.W., 2023. Labdsv: ordination and multivariate analysis for ecology. R package version 2. https://CRAN.R-project.org/package=labdsv.

Robinson, J.P., Williams, I.D., Edwards, A.M., McPherson, J., Yeager, L., Vigliola, L., et al., 2017. Fishing degrades size structure of coral reef fish communities. Glob. Change Biol. 23 (3), 1009–1022. https://doi.org/10.1111/gcb.13482.

Robinson, J.P., McDevitt-Irwin, J.M., Dajka, J.C., Hadj-Hammou, J., Howlett, S., Graba-Landry, A., et al., 2020. Habitat and fishing control grazing potential on coral reefs. Funct. Ecol. 34 (1), 240–251. https://doi.org/10.1111/1365-2435.13457.

Sampson, D.B., 2014. Fishery selection and its relevance to stock assessment and fishery management. Fish. Res. 158, 5–14. https://doi.org/10.1016/j.fishres.2013.10.004.

Sangil, C., Clemente, S., Martín-García, L., Hernández, J.C., 2012. No-take areas as an effective tool to restore urchin barrens on subtropical rocky reefs. Estuar. Coast Shelf Sci. 112, 207–215. https://doi.org/10.1016/j.ecss.2012.07.025.

Santamaría, M., Jiménez, S., Gonzáles, J., 2013. Artisanal Fisheries in the Canary Islands: Tenerife. GEPETO.

Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: ocean climate layers for marine spatial ecology: ecological Archives E094–086. Ecology 94 (4), 979. https://doi.org/10.1890/12-1358.1.

Sims, K., Reith, A., Bright, E., Kaufman, J., Pyle, J., Epting, J., Gonzales, J., Adams, D., Powell, E., Urban, M., Rose, A., 2023. LandScan Global 2022. Oak Ridge National Laboratory. https://doi.org/10.48690/1529167 [Data set].

Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J., Bates, A.E., 2015. Thermal biases and vulnerability to warming in the world's marine fauna. Nature 528 (7580), 88–92. https://doi.org/10.1038/nature16144.

Tebbett, S.B., Bennett, S., Bellwood, D.R., 2024. A functional perspective on the meaning of the term 'herbivore': patterns versus processes in coral reef fishes. Coral Reefs 43 (2), 219–232. https://doi.org/10.1007/s00338-023-02378-4.

Tebbett, S.B., Morais, R.A., Goatley, C.H., Bellwood, D.R., 2021. Collapsing ecosystem functions on an inshore coral reef. J. Environ. Manag. 289, 112471. https://doi.org/10.1016/j.jenvman.2021.112471.

Tebbett, S.B., Hoey, A.S., Depczynski, M., Wismer, S., Bellwood, D.R., 2020. Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. Coral Reefs 39 (1), 203–214. https://doi.org/10.1007/s00338-019-01874-w.

Trindade-Santos, I., Moyes, F., Magurran, A.E., 2020. Global change in the functional diversity of marine fisheries exploitation over the past 65 years. Proceedings of the Royal Society B 287 (1933), 20200889. https://doi.org/10.1098/rspb.2020.0889.

Tuya, F., Haroun, R.J., 2006. Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multi-scaled approach. Mar. Ecol. Prog. Ser. 311, 15–28. https://doi.org/10.3354/meps311015.

Tuya, F., Ortega-Borges, L., Sanchez-Jerez, P., Haroun, R.J., 2006a. Effect of fishing pressure on the spatio-temporal variability of the parrotfish, Sparisoma cretense (Pisces: scaridae), across the Canarian Archipelago (eastern Atlantic). Fish. Res. 77 (1), 24–33. https://doi.org/10.1016/j.fishres.2005.07.017.

Tuya, F., Sanchez-Jerez, P., Haroun, R.J., 2006b. Populations of inshore serranids across the Canarian Archipelago: relationships with human pressure and implications for conservation. Biol. Conserv. 128 (1), 13–24. https://doi.org/10.1016/j.biocon.2005.09.012.

Tuya, F., Aguilar, R., Espino, F., Bosch, N.E., Meyers, E.K., Jiménez-Alvarado, D., et al., 2021. Differences in the occurrence and abundance of batoids across an oceanic archipelago using complementary data sources: implications for conservation. Ecol. Evol. 11 (23), 16704–16715. https://doi.org/10.1002/ece3.8290.

Valdazo, J., Viera-Rodríguez, M.A., Espino, F., Haroun, R., Tuya, F., 2017. Massive decline of cystoseira abies-marina forests in gran Canaria island (canary islands, eastern atlantic). Sci. Mar. 81 (4), 499–507. https://doi.org/10.3989/scimar.04655.23a.

Valdivia, A., Cox, C.E., Bruno, J.F., 2017. Predatory fish depletion and recovery potential on Caribbean reefs. Sci. Adv. 3 (3), e1601303. https://doi.org/10.1126/sciadv.1601303.

Valles, H., Oxenford, H.A., 2014. Parrotfish size: a simple yet useful alternative indicator of fishing effects on Caribbean reefs? PLoS One 9 (1), e86291. https://doi.org/10.1371/journal.pone.0086291.

Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O., Brainard, R.E., 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. PLoS One 10 (4), e0120516. https://doi.org/10.1371/journal.pone.0120516.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., et al., 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob. Change Biol. 14 (12), 2796–2809. https://doi.org/10.1111/j.1365-2486.2008.01696.x.

Yadav, S., Fisam, A., Dacks, R., Madin, J.S., Mawyer, A., 2021. Shifting fish consumption preferences can impact coral reef resilience in the Maldives: a case study. Mar. Pol. 134, 104773. https://doi.org/10.1016/j.marpol.2021.104773.

Zeller and Pauly, 2015. Online publication. Reconstructing Marine Fisheries Catch Data. Catch Reconstruction: Concepts, Methods and Data Sources. University of British Columbia. Sea Around Us. www.seaaroundus.org.