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Bright spots and barren grounds: temperate reef states shape fish contributions to nature and people after marine heatwaves

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Abstract

Background

Climate-driven habitat reorganization is reshaping the capacity of marine ecosystems to sustain biodiversity and human well-being, with implications for SDG 14 (Life Below Water) and SDG 2 (Zero Hunger). Yet, it remains unclear to what extent post disturbance reef fish communities continue to support ecological functioning and human nutrition, particularly in temperate kelp forest ecosystems. Here, we quantify reef fish contributions to nature and people across a 600 km post-heatwave kelp forest gradient along the Pacific coast of Baja California, Mexico. Using 545 transect observations from 12 sites surveyed between 2017 and 2024, we integrated standing biomass, secondary productivity, biomass turnover, and micronutrient provisioning within a Nature for Nature and Nature for People framework.

Results

Across the 2017–2024 post-heatwave period, most reef-fish contributions remained temporally stable across regions and exploitation categories, with only limited directional changes detected among non-targeted species. Fish communities appear to have stabilized into regionally distinct configurations shaped by kelp-forest state. Reefs with persistent canopy forming kelp emerged as bright spots, supporting high contributions to both nature and people, whereas simplified reefs characterized by understory brown algae and/or urchin barrens showed more reduced contributions. Across the study period, total micronutrient supply per hectare remained temporally stable and largely tracked fish biomass, whereas nutritional quality per 100 g changed over time for zinc, vitamin A, and selenium among species not targeted by fisheries. Our analysis further indicated that fish biomass and total nutrient supply were structured mainly by spatial variation in sea surface temperature and benthic habitat composition, whereas nutrient concentrations were largely unrelated to environmental drivers.

Conclusions

Managing post-heatwave kelp forests requires moving beyond one-size-fits-all strategies, because regional reef states differ markedly in the ecological functions they support and in their contributions to people. Sustaining ocean ecosystem services requires recognizing distinct reef states, protecting ecological and social bright spots, restoring habitat complexity in simplified reefs, and managing biodiversity, fisheries, and human well-being as connected parts of the same system.

1. Background

Human activities are reshaping marine ecosystems through climate change, habitat transformation, and intensive resource use (Díaz et al., 2019; Halpern et al., 2015), to the point that the ability of degraded

ecosystems to sustain themselves and continue supporting human well-being is increasingly uncertain. This dual concern is reflected in global policy frameworks, particularly Sustainable Development Goal (SDG) 14 (Life Below Water) and SDG 2 (Zero Hunger). To address the challenge of conserving biodiversity while sustaining human well-being, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) developed the Nature Futures Framework, which distinguishes between contributions to biodiversity and ecosystem functioning (Nature for Nature; NN), human well-being (Nature for People; NP), and biocultural values (Nature as Culture) (Palacios-Abrantes et al., 2022; Pereira et al., 2020; Martin et al., 2024). Nature as Culture is a critical dimension of the framework, recognizing the relational, and identity-based connections between people and nature. While highly important, we treat it here primarily as a bridge linking ecological integrity (NN) and human well-being (NP) (Martin et al., 2016; Zhao et al., 2024). Here, we define NN as the ways ecological communities sustain ecosystem structure and functioning, and NP as the benefits arising through food provision, fisheries productivity, and human nutrition. Because both perspectives are often supported by the same ecological processes, identifying where contributions align or trade off is critical.

Harvested fish species link ecological functioning and human well-being. Beyond protein and livelihoods, fish supply bioavailable micronutrients essential for human health, including iron, zinc, calcium, vitamin A, selenium, and omega-3 fatty acids (Basurto et al., 2025; Beal & Ortenzi, 2022; Calder, 2015; Gernand, 2016; Hicks et al., 2019). These contributions are particularly important where Hidden Hunger persists. Hidden Hunger refers to the chronic deficiency of essential vitamins and micronutrients despite sufficient caloric intake (Weffort & Lamounier, 2024) and remains a major public health concern in middle-income countries such as Mexico (Cruz-Góngora et al., 2021; Herrera-González et al., 2025; Lowe, 2021). Some of these deficiencies can have serious consequences during childhood, including anemia, impaired cognitive development, and reduced growth (Benton et al., 2008; Eileen Kennedy et al., 2003). Importantly, the nutritional value of a fishery depends not only on catch volume but also on species composition. Different species carry distinct micronutrient profiles linked to their ecological traits and phylogenetic histories (Hicks et al., 2019; Lall & Kaushik, 2021; Maire et al., 2021; Waldock et al., 2025). For example, kelp rockfish (*Sebastes atrovirens*) contains substantially higher omega-3, calcium, and selenium concentrations than ocean whitefish (*Caulolatilus princeps*), despite both species occurring within the same regional reef system (Froese & Pauly, 2026). Assessing fisheries contributions to nutrition therefore requires two complementary metrics: the quantity of supply (total fish biomass or total micronutrients per area) and the quality of supply (micronutrient content of a standardized portion).

Disturbances such as marine warming can therefore alter nutritional benefits by reshaping reef habitats and redistributing fish biomass among species with different micronutrient profiles, rather than simply reducing total fish biomass across the community (Albuquerque et al., 2026; Beas-Luna et al., 2020; Castorani et al., 2018; Salland et al., 2026; Smale et al., 2019). Reef fish communities may also show compensatory responses (i.e., asynchronous population dynamics among fish species), partially maintaining productivity or nutritional provisioning despite shifts in biomass or composition (Morais et al., 2023; Robinson et al., 2022). Ecosystem change can therefore lead not only to losses but also to redistribution, buffering, or decoupling of ecological and human benefits.

Yet, ecological and nutritional dimensions of ecosystem change are typically studied in isolation, leaving it unclear how reef state, fish community structure, and the nutritional contributions these systems deliver to people are linked across a post-disturbance kelp-forest gradient. To our knowledge, no study has jointly evaluated biomass, productivity, trophic structure, and micronutrient provisioning of temperate fish communities at the regional scale required to capture these post-disturbance differences.

The Pacific coast of the Baja California peninsula provides an ideal context to address this research gap. Following the 2014–2016 marine heatwave, kelp forests in Baja California now span a mosaic of post-disturbance states across a roughly 600 km latitudinal gradient, ranging from persistent kelp canopies to transitional reefs and barren grounds where kelp recovery has been prevented by sea urchin overgrazing (Bauer et al., 2025; Filz et al., 2026). This mosaic allows us to ask whether reef fish communities along the gradientdegrade, recover, or stabilize into regionally distinct configurations after a major climatic disturbance, and how their contribution to human well-being changes accordingly. Northern reefs are now often characterized by simplified habitats with reduced kelp cover and extensive urchin barrens. Reefs in the middle region are typically dominated by subcanopy-forming kelp, whereas southern reefs retain more extensive canopy-forming kelp forests, particularly *Macrocystis pyrifera*, although with some signs of structural alteration.

Here, we draw on an eight-year monitoring dataset of 545 transect observations across 12 sites within three regions (North, Middle, South) of the Baja California Pacific coast, encompassing reef fish species from different exploitation categories, including both fisheries-targeted and non-targeted species. Our sampling design spans a broad range of the mosaic of kelp-forest states that emerged after the 2014–2016 marine heatwave. Our central question is: how do reef fish contributions to Nature for Nature (NN) and Nature for People (NP) respond to temperate reef states, and are these two dimensions coupled across regions? To address this question, we (i) quantify regional and temporal trends in standing biomass, secondary productivity, and biomass turnover; (ii) estimate the quantity and quality of micronutrient contributions by computing both the absolute supply per area (mg ha^{-1}) and the per 100 g RDI portions for six key micronutrients; (iii) identify the environmental conditions (e.g., sea surface temperature, benthic community composition, depth, chlorophyll-a) that influence these contributions; (iv) integrate ecological and people related metrics within a two-dimensional NN–NP framework adapted from Flandrin et al. (2024); and (v) evaluate the drivers of within site reorganization to identify whether ecological or fisheries related categories dominate post-heatwave reshuffling.

2. Methods

2.1 Study area and survey design

Field surveys were conducted along the Pacific coast of the Baja California peninsula, Mexico, spanning a roughly 600 km latitudinal gradient encompassing three regions (North, Middle, and South) following the monitoring design described by Filz et al. (2026) (Fig. 1A). Reef communities vary markedly along this gradient (Fig. 1B–C). Northern reefs are characterized by extensive urchin barrens interspersed with

small understory dominated brown algal assemblages and limited development of canopy forming kelps. Middle region reefs are typically structured by subcanopy kelp species, providing intermediate vertical habitat complexity. Southern reefs are dominated by extensive forests of canopy forming kelp, primarily *Macrocystis pyrifera* (Bauer et al., 2025). Surveys were conducted annually between 2017 and 2024, generating 545 transect observations across targeted and non-targeted species from 12 sites with a hierarchical sampling structure of transects nested within subsites nested within sites (Table S1).

2.2 Fish biomass, productivity, and turnover

Fish biomass was derived from underwater visual census data, including species identity, abundance, and individual body length estimated to the nearest centimeter. Individual body mass (g) was estimated from observed total length using species-specific length-to-weight relationships obtained primarily from FishBase, or from closely related taxa when parameters were unavailable. Biomass was summed across individuals, standardized to area, and converted to kilograms per hectare (kg ha^{-1}). Species were classified as targeted or non-targeted based on their exploitation status using regional literature on commonly targeted recreational species (García-Rodríguez et al., 2013; Rodríguez-Medrano, 1993; Table S2). Biomass was summarized separately for each exploitation group at the transect level and aggregated by region and year.

Fish secondary productivity was estimated using the R package rfishprod (Morais & Bellwood, 2020), which applies a temperature dependent growth framework to compute somatic production from visual census data. Growth trajectories were modeled using the von Bertalanffy growth function with species-specific growth and mortality parameters. Growth rates were scaled to local thermal conditions using sea surface temperature (SST, °C) data from the NOAA Optimum Interpolation Sea Surface Temperature dataset version 2.1 (OISST v2.1), accessed through the NOAA ERDDAP server. Daily SST data at 0.25° spatial resolution were extracted for the period 2017–2024 and matched to each transect by sampling date and nearest grid cell using nearest-neighbor searches in R (rerddap and FNN packages; R Core Team, 2023). SST values were then averaged at the transect and site levels to represent local thermal conditions. Individual production estimates were summed across species to obtain total annual productivity per hectare (kg ha^{-1} yr^{-1}), calculated separately for targeted and non-targeted assemblages. Biomass turnover was calculated as the production to biomass ratio (P/B × 100), expressed as the percentage of biomass replaced per year.

2.3 Mean assemblage body size

To support interpretation of productivity and turnover patterns, we computed biomass-weighted mean body length (cm) per transect and exploitation category as the sum of (body length × biomass) divided by total biomass across all individuals observed. This metric was modeled with the same generalized linear mixed model framework as biomass, productivity, and turnover (Section 2.6) and reported in the supplementary materials.

2.4 Nutritional contribution of reef fish

We quantified the potential nutritional contribution and nutrient density (Drewnowski, 2009) of reef fish assemblages using a standardized 100 g consumption scenario (Hamilton et al., 2024). Following the composition-based approach of Hicks et al. (2019), but applying it to local reef fish assemblages rather than fisheries landings, we treated species-specific nutrient concentrations as fixed species-level attributes that do not vary through time or space. We focused on six key micronutrients relevant to human nutrition: calcium, iron, zinc, vitamin A, selenium, and omega-3 fatty acids. Species-specific nutrient values were primarily taken from FishBase and combined according to the biomass-weighted species composition of each local fish community to estimate assemblage-level nutrient concentrations per 100 g of fish.

Reference intake values were obtained from the Dietary Reference Intakes established by the Food and Nutrition Board (Dwyer et al., 2015; Institute of Medicine, 2008) for children aged 4–8 years: Calcium, 800 mg day^{-1}; iron, 4.1 mg day^{-1}; zinc, 4.0 mg day^{-1}; vitamin A, 0.275 mg day^{-1}; selenium, 0.023 mg day^{-1}; and omega-3 fatty acids, 900 mg day^{-1}. We adopted recommended intake levels for children aged 4–8 years as a standardized nutritional benchmark for two reasons: (i) micronutrient deficiencies disproportionately affect children in Mexico, where approximately one in three to one in four children under 11 years is anemic according to ENSANUT (Cruz-Góngora et al., 2021); and (ii) the Recommended Daily Intake (RDI) for 4–8 year old children sit in the mid-range across childhood and therefore provide a conservative reference that does not maximally favor any single nutrient. RDI portions are treated here as a standardized comparative benchmark rather than as a description of actual fish-consumption patterns in Baja California.

Nutrient supply was expressed as RDI portions, defined as the fraction of the daily recommended intake supplied by 100 g of biomass-weighted reef fish biomass (RDI portions = supply_mg ÷ RDI_mg). Because per-100 g supply combines static species-level nutrient values from FishBase with the biomass-weighted composition of each local assemblage, any temporal change in per-100 g RDI portions reflects shifts in assemblage composition and relative biomass contributions among species rather than within-species changes in nutrient density. Within-species variation in nutrient density across habitats was not measured in this study. Values close to 1 indicate that a 100 g serving covers approximately the full daily requirement, whereas values around 0.33 indicate that a serving provides roughly one third of the recommended daily intake, a commonly used benchmark when evaluating the contribution of individual food types to human nutrition (Beal et al., 2024). RDI portions were computed at the transect level, separately for targeted and non-targeted assemblages. To complement the per 100 g concentration analyses, absolute nutrient supply per transect (total mg ha^{-1}) was modeled using the same statistical framework and reported in the supplementary materials.

2.5 Environmental covariates

To account for environmental and habitat variation when modeling temporal trends in fish community attributes, we compiled five covariates that were assigned to each transect. Bottom depth (m) was recorded in situ during each visual census. Sea surface temperature (SST, °C) was derived following the procedure described in Section 2.2, using NOAA Optimum Interpolation SST v2.1 at 0.25° daily resolution

and aggregated as annual means over the calendar year in which each transect was surveyed. Surface chlorophyll *a* (mg m^{-3}) was extracted at the site location from MODIS Aqua at 4 km monthly resolution and likewise aggregated as annual means. Benthic habitat structure was summarized through a principal component analysis (PCA) on a combined matrix of algal and invertebrate functional groups. Because the two datasets are quantified in different units (algal densities in individuals m^{-2}, invertebrate frequencies as counts), values were first converted to relative abundances within each taxonomic group before being merged into a single transect by group matrix and Hellinger transformed prior to ordination. The first two principal components, explaining 33.5% and 22.2% of the total compositional variance (cumulative 55.7%), were retained as independent axes describing benthic community composition (hereafter benthic PC1 and PC2). To verify that the linear assumption underlying PCA did not impose an artificial structure on the compositional data, we additionally performed a non metric multidimensional scaling analysis (NMDS; Bray Curtis dissimilarity, k = 2; stress = 0.21) on the same matrix, and tested regional differences in community composition with PERMANOVA (999 permutations). Both ordinations recovered congruent community gradients and PERMANOVA confirmed that benthic composition differed significantly among regions ($R^2 = 0.42$, $F = 47.7$, $p < 0.001$), supporting the use of PC1 and PC2 as descriptors of habitat structure in subsequent models.

All five continuous covariates (depth, SST, chlorophyll *a*, benthic PC1, benthic PC2) were z-standardized (mean = 0, SD = 1) prior to inclusion in the mixed-effects models, to enable direct comparison of effect sizes. Multicollinearity among covariates was assessed with variance inflation factors (VIFs) corrected for the categorical interaction structure of the fixed effects; all five covariates returned adjusted VIF values below 3, indicating that the standardized effects of co-varying drivers could be interpreted as partially independent contributions.

2.6 Statistical analyses

Temporal trajectories of standing biomass, secondary productivity, biomass turnover, mean assemblage body size, per 100 g RDI portions for each of the six micronutrients, and absolute nutrient supply (total mg per transect) were analyzed within a unified generalized linear mixed model (GLMM) framework using the glmmTMB package (Brooks et al., 2017). Biomass, productivity, mean size, per 100 g RDI portions, and total mg supply were modeled as Gamma GLMMs with a log link; biomass turnover was modeled as a Gaussian GLMM on $\log(P/B + \varepsilon)$ because residual diagnostics indicated a better fit on the log-additive scale. Each model included Year, centered at the first survey year, 2017, Region (North, Middle, South), and exploitation category (targeted, non-targeted) as fixed effects, together with their two- and three-way interactions. The five environmental covariates were included as additive fixed effects. Region was included as a fixed effect to evaluate regional variation in NN and NP contributions.

To accommodate the hierarchical sampling design, we specified random intercepts for Site, Subsite nested within Site, and Year as a factor, thereby capturing year-specific anomalies not absorbed by the linear Year term. Because per 100 g RDI portions are biomass-weighted nutrient concentrations and therefore vary primarily between species rather than within subsites, the full nested random-effects structure produced singular fits in several models. We therefore used a model-specific selection

procedure that retained, for each response, the most complex random-effects structure that was non-singular and produced a positive definite Hessian (Table S3). Marginal and conditional R^2 were computed following Nakagawa and Schielzeth (2013) using the *performance* package (Lüdecke et al., 2021). Conditional R^2 was non-estimable in models with singular variance components; marginal R^2 was always reported, and Wald- and emtrends-based inference remained valid in these cases.

Overall fixed-effect significance was assessed using Type II Wald χ^2 tests with the car package (Fox & Weisberg, 2019). Region- and exploitation-category-specific temporal slopes on the link scale were estimated using *emtrends* from the *emmeans* package (Lenth et al., 2024) and back-transformed to annual percentage change as $(\exp(\beta) - 1) \times 100$, with 95% confidence intervals derived from the variance-covariance matrix of model coefficients. Slopes were considered statistically significant when their confidence intervals excluded zero ($p < 0.05$). A significant three-way Year × Region × Exploitation interaction in the absence of any significant marginal slope indicates that groups differ in their temporal patterns, although no individual slope differs significantly from zero. We retained both pieces of information, overall interaction significance and marginal slope confidence intervals, when interpreting results.

Residual diagnostics were performed for every fitted model using simulation-based scaled residuals from the DHARMa package (Hartig, 2020). Multicollinearity among continuous covariates was screened with variance inflation factors; all VIFs for the five environmental covariates were below 3, well within the conventional threshold of five. Residual diagnostic and multicollinearity summaries for all fitted models are provided in Tables S4 and S5.

2.7 Shifts in fish contributions across the NN versus NP spectrum

To evaluate trajectories of reef fish communities within the Nature Futures Framework (Pereira et al., 2020), we adapted the heuristic NN–NP framework proposed by Flandrin et al. (2024) to temperate kelp forest systems. All calculations were performed at the site by year level using transect based estimates aggregated hierarchically (transect → subsite → site, weighted by the number of contributing transects).

The NN axis was constructed from three categories: (i) functional structure, represented by biomass distribution across five major feeding groups (herbivores, planktivores, macroinvertivores, microinvertivores, piscivores); (ii) community biomass structure, summarized by the biomass-weighted mean trophic level computed across all species; and (iii) alpha diversity, captured using taxonomic and functional alpha diversity expressed as Hill numbers ($q = 0$ and $q = 1$; Chao et al., 2014) computed at the transect level using Gower distance functional matrices via the *mFD* package (Magneville et al., 2022) and aggregated to site by year by mean. The NP axis was constructed from two categories computed exclusively for fisheries-targeted species: (i) micronutrient provisioning, expressed as the per-100 g supply of the six key micronutrients; and (ii) fisheries provisioning, represented by targeted fish biomass and secondary productivity. Our approach captures the biomass-, productivity-, and nutrition-based dimensions of contributions to people that can be quantified from underwater visual census data. It

does not capture livelihood, governance, cultural, or food-sovereignty dimensions that are also central to how reef fisheries contribute to people in Baja California (Basurto et al., 2025; Narchi et al., 2025); these dimensions are discussed as a limitation in Section 4.4. All input variables were log transformed using $\log(x + 1)$ and z-standardized across all Site by Year observations. Standardized variables were averaged within their respective categories so that each category received equal weight. NN was calculated as the mean of three category level indices and NP as the mean of two category level indices. An overview of all metrics included in the NN and NP indices and their corresponding components is provided in Fig. 2.

To assess how well each composite axis summarized its underlying input variables, we computed two complementary diagnostics. First, we calculated the Pearson R^2 between each composite score (NN or NP) and each of its standardized input variables across all site-by-year observations, then averaged these R^2 values to obtain the mean per input variance shared with the composite. Second, we performed a principal component analysis on the standardized input matrix of each composite (function “prcomp”) and computed the R^2 between the composite score and the first principal component (PC1). The mean R^2 with inputs indicates how representative the composite is of its individual inputs on average, whereas the composite-to-PC1 R^2, together with the proportion of input variance captured by PC1, indicates whether the composite is aligned with the dominant axis of variation in its inputs or averages across partly orthogonal directions. Each site by year observation was assigned a position in two dimensional NN versus NP space, partitioned into four quadrants using the median NN and NP values across all observations as thresholds (Bright spots: above median in both; Dark spots: below median in both; NN only and NP only: imbalanced configurations). Pearson correlations and linear regressions of NP on NN were computed separately for each region and for the full dataset (Table S6).

To test whether reef fish contributions changed directionally over the post-heatwave period, we fitted Gaussian linear mixed-effects models to NN and NP scores (NN_score ~ Year × Region + (1 | Site); same for NP_score). Region specific temporal slopes were extracted using emtrends and considered significant when their 95% CI excluded zero. To visualize temporal trajectories within NN versus NP space, annual region-level predictions of NN and NP scores were extracted from the fitted mixed-effects models for each sampled year (2017–2024), yielding one predicted (NN, NP) coordinate per region per year. Predictions were made by averaging across the site-level random intercept, so that each predicted point represents the mean position of a typical site within a region. Consecutive yearly predictions were connected to trace the regional trajectory through NN–NP space. Predicted versus observed response plots for all fitted models are provided in Figure S1.

To identify which components of NN and NP drove site level shifts, we quantified how changes in functional structure, trophic structure, alpha diversity, micronutrient provisioning, and fisheries provisioning contributed to each consecutive site-level year-to-year shift in NN versus NP space (n = 47 shifts). Contributions were normalized within each transition so that the five categories summed to one, and uncertainty was quantified using bootstrap resampling (5,000 iterations); 95% confidence intervals were derived from the bootstrap distribution (Table S7). To evaluate whether protection regime affected reef fish position in NN versus NP space, we performed a permutational multivariate analysis of variance

(PERMANOVA) on the bivariate NN versus NP coordinates using *vegan::adonis2* (Oksanen et al., 2026) with Euclidean distances and 999 permutations. Protection status was assigned at the site level using three broad categories: unprotected sites, officially protected sites (Aguirre-Muñoz & Méndez Sánchez, 2017), and community no-take areas (Bauer et al., 2025). A map showing the site-level protection status and the spatial distribution of protected, community-managed, and unprotected sites is provided in Figure S2.

2.8 Software

All analyses were performed in R v4.3.1 (R Core Team, 2023) using *glmmTMB* v1.1.9, *emmeans* v1.10, *DHARMa*v0.4.7, *performance* v0.12, *car* v3.1, *mFD* v1.0, *vegan* v2.6, and the *tidyverse* v2.0 ecosystem. The nested treemap was created in Python using the Matplotlib library, designed and coded iteratively with Anthropic's Claude (Anthropic, 2025), and subsequently adapted in Canva (Canva, 2025).

3. Results

3.1 Biomass, productivity, and biomass turnover

Temporal trajectories of standing biomass, secondary productivity, and biomass turnover across regions and exploitation categories are shown in Fig. 3. Standing biomass remained statistically stable throughout the post-heatwave period (Year main effect: $\chi^2_1 = 0.06$, $p = 0.808$; Table S8). Biomass was, however, significantly associated with mean annual SST ($\chi^2_1 = 13.88$, $p < 0.001$) and benthic PC1 ($\chi^2_1 = 5.25$, $p = 0.022$), suggesting that fish standing stock tracks both thermal regime and benthic community structure (marginal $R^2 = 0.148$, conditional $R^2 = 0.429$). The significant Year × Region × Exploitation interaction ($\chi^2_2 = 7.18$, $p = 0.028$) indicated that biomass trajectories differed among regions and exploitation categories, but none of the six region-by-exploitation temporal slopes was significantly positive or negative (Table S9): point estimates ranged from − 10.8% yr^{-1} in non-targeted assemblages of the South (95% CI: −22.4, + 2.6) to + 11.8% yr^{-1} in non-targeted assemblages of the Middle region (95% CI: −3.4, + 29.4), and all six 95% confidence intervals encompassed zero.

Secondary productivity showed no significant three-way Year × Region × Exploitation interaction ($\chi^2_2 = 3.20$, $p = 0.202$; Table S8), so the final model retained only the lower-order two-way interactions: Year × Region ($\chi^2_2 = 11.45$, $p = 0.003$), Year × Exploitation ($\chi^2_1 = 6.88$, $p = 0.009$), and Region × Exploitation ($\chi^2_2 = 6.61$, $p = 0.037$). Productivity was additionally correlated with SST ($\chi^2_1 = 6.32$, $p = 0.012$) and benthic PC1 ($\chi^2_1 = 8.74$, $p = 0.003$) (marginal $R^2 = 0.157$, conditional $R^2 = 0.360$). Among the six region-by-exploitation temporal slopes (Table S8), only one was significantly different from zero: productivity in non-targeted southern reefs increased through time (+ 24.4% yr^{-1}, 95% CI: +10.1, + 40.6). All other combinations showed no significant change, with annual estimates between − 6.4% and + 7.7% yr^{-1}. This was the only directional temporal change detected at the assemblage level.

Biomass turnover showed the greatest difference between targeted and non-targeted species among the three response variables ($\chi^2_1 = 13.69$, $p < 0.001$; Table S8), with targeted species consistently exhibiting

higher turnover across all regions. The Year × Region × Exploitation interaction was also significant (χ^2_2 = 13.95, p < 0.001), and turnover was independently associated with bottom depth (χ^2_1 = 8.73, p = 0.003) but not with SST, chlorophyll-a, or benthic PCs (marginal R^2 = 0.066). Despite the significant three-way interaction, none of the six region-by-exploitation temporal slopes differed significantly from zero (Table S8), so these differences reflect variation in the shape and magnitude of temporal fluctuations rather than consistent directional increases or declines. The steepest non-significant trends were a decline in non-targeted fish assemblages on northern reefs (− 13.1% yr^{-1}, 95% CI: −24.6, + 0.2) and an increase in non-targeted assemblages on southern reefs (+ 11.5% yr^{-1}, 95% CI: −1.4, + 26.1).

Biomass-weighted mean assemblage body size, modeled analogously, showed a significant Year × Region interaction (χ^2_2 = 8.41, p = 0.015). Mean size increased significantly only in non-targeted middle reefs (+ 6.8% yr^{-1}, 95% CI: +1.7, + 12.2) and remained stable in all other region by exploitation combinations (Fig. S3; Table S10). Overall, standing biomass and biomass turnover stabilized across the gradient, with one localized exception (productivity in assemblages on non-targeted southern reefs) and one subtle compensatory size shift reflected by increasing mean body size in non-targeted middle reefs.

3.2 Nutritional contributions

We modeled contributions to the recommended daily intake (%RDI) from a standardized 100 g fish serving for six key micronutrients across 545 transects using Gamma GLMMs (Table S10). Selenium contributed the largest share of daily nutritional requirements, with an average 100 g serving providing approximately 95% of a child's recommended daily intake across all observations. Omega-3 fatty acids showed the second-highest contribution (25% RDI per 100 g), followed by zinc (20%), iron (17%), vitamin A (13%), and calcium (5%). Contributions to RDI per 100 g serving differed significantly between targeted and non-targeted species, although the direction of these differences depended on the micronutrient considered (Table S11). Non-targeted species provided higher %RDI contributions for calcium (7% vs. 3% RDI per 100 g; χ^2_1 = 894.35, p < 0.001), iron (19% vs. 14%; χ^2_1 = 355.14, p < 0.001), and zinc (22% vs. 17%; χ^2_1 = 1120.61, p < 0.001). In contrast, targeted species exhibited higher contributions of selenium (106% vs. 84%; χ^2_1 = 249.75, p < 0.001) and omega-3 fatty acids (28% vs. 23%; χ^2_1 = 199.36, p < 0.001). Vitamin A contributions were similar between groups (13% vs. 13%; χ^2_1 = 0.18, p = 0.674). Region significantly affected nutrient contributions for five of the six micronutrients, and Region × Exploitation interactions were significant for all six nutrients (χ^2_2 = 11.56–102.12, all p ≤ 0.003).

Model-based temporal trajectories of %RDI contributions per 100 g are shown in Fig. 4 for each region and exploitation category. All significant temporal shifts in RDI occurred in non-targeted assemblages, while targeted species showed no significant changes over time across any of the eighteen trends tested (Table S12). Within non-targeted assemblages, zinc contributions to %RDI declined in the Middle region by 1.71% yr^{-1} (95% CI: −2.60, − 0.80) but increased slightly in both the North (+ 1.14% yr^{-1}, 95% CI: +0.20, + 2.10) and South (+ 1.13% yr^{-1}, 95% CI: +0.41, + 1.86). Vitamin A contributions increased in the North (+ 3.15% yr^{-1}, 95% CI: +0.09, + 6.32) and South (+ 2.83% yr^{-1}, 95% CI: +0.38, + 5.34), whereas selenium contributions declined only in the North (− 2.48% yr^{-1}, 95% CI: −4.62, − 0.30). Contributions to RDI for calcium, iron, and omega-3 fatty acids remained temporally stable across all regions and

exploitation categories. In contrast, the total micronutrient supply available per hectare (total mg ha^{-1}) remained temporally stable for all six micronutrients throughout the study period (Fig. S4). Exploitation category significantly predicted total nutrient supply for calcium ($\chi^2_1 = 38.99$, $p < 0.001$), iron ($\chi^2_1 = 4.89$, $p = 0.027$), omega-3 fatty acids ($\chi^2_1 = 8.37$, $p = 0.004$), selenium ($\chi^2_1 = 6.99$, $p = 0.008$), and vitamin A ($\chi^2_1 = 5.44$, $p = 0.020$), while the effect on zinc was not statistically significant ($\chi^2_1 = 3.23$, $p = 0.073$; Table S13).

3.3 Environmental drivers across community level responses

To evaluate which environmental factors structured fish community attributes, we extracted standardized effect sizes (β coefficients with 95% CI) for the five z-standardized covariates from each GLMM (Fig. 5; Table S14). Benthic community composition was summarized through a PCA on Hellinger transformed relative abundances of algal and invertebrate functional groups combined (Fig. 5A). PC1 explained 33.5% of total compositional variance and represented a canopy kelp to urchin barren gradient: negative PC1 scores were characterized by canopy kelp (loading = − 1.54) and to a lesser extent by suspension feeding invertebrates (− 0.32), while positive PC1 scores reflected reefs lacking canopy kelp and characterized by subcanopy kelp (0.88), understory brown algae (0.43), sea urchins (0.25) and herbivorous invertebrates (0.15). PC2 explained 22.2% of variance (cumulative 55.7%) and contrasted urchin barren reefs with understory browns (sea urchins 0.87, understory brown algae 0.76) against reefs dominated by subcanopy kelp with suspension feeders and other herbivorous invertebrates (subcanopy kelp − 0.80, suspension feeders − 0.45, herbivores − 0.37). A complementary NMDS on Bray Curtis dissimilarities (stress = 0.21; Fig. S5; Table S15) showed that benthic community composition differed among regions. A marginal PERMANOVA on the 258 transects that could be matched to the fish dataset confirmed that benthic composition differed strongly among regions ($R^2 = 0.31$, pseudo-$F_{5,245} = 26.91$, $p = 0.001$) with additional, weaker temporal variation among years ($R^2 = 0.05$, pseudo-$F_{7,245} = 2.75$, $p = 0.001$). β-dispersion further indicated significant differences in community dispersion across both regions (pseudo-$F_{5,252} = 42.87$, $p < 0.001$) and years (pseudo-$F_{7,250} = 3.36$, $p = 0.002$).

Across the GLMMs (Fig. 5B; Table S14), two predictors dominated the biomass and total micronutrient supply responses. Mean annual SST exerted positive effects on standing biomass ($\beta = 0.290$, $p < 0.001$), secondary productivity ($\beta = 0.134$, $p = 0.027$) and the total supply of all six micronutrients ($\beta = 0.276$ to 0.307, all $p < 0.001$). Benthic PC1 (the canopy-kelp-to-urchin-barren axis) had positive effects of similar or larger magnitude on biomass ($\beta = 0.420$, $p < 0.001$), productivity ($\beta = 0.401$, $p < 0.001$) and all six total nutrient responses ($\beta = 0.376$ to 0.436, all $p < 0.001$). Surface chlorophyll-a showed contrasting patterns between bivariate and multivariate analyses. At the transect level (n = 545 transects), chlorophyll-a was uncorrelated with reef-fish biomass (Pearson $r = 0.002$, $p = 0.957$) but strongly positively correlated with SST ($r = 0.60$, $p < 0.001$). Once SST and benthic habitat structure were included in the models, chlorophyll-a emerged as a negative predictor of biomass ($\beta = −1.161$, $p < 0.001$) and of all six total micronutrient supply models ($\beta = −0.915$ to − 1.125, all $p < 0.001$). Productivity showed only a marginal negative relationship with chlorophyll-a ($\beta = −0.512$, $p = 0.051$), and turnover was unaffected ($\beta = −0.103$,

p = 0.696). Turnover instead decreased significantly with depth (β = −0.168, p = 0.008) and did not respond to any other environmental variable. Benthic PC2 was significant only for vitamin A supply (β = 0.207, p = 0.034); all other responses were unrelated to this axis, suggesting that the second compositional axis explains little additional variation beyond PC1.

Micronutrient concentrations per 100 g of fish were largely unrelated to environmental drivers (see Supplementary Table S16). Standardized effects were typically an order of magnitude smaller than for total supply, and most predictor–nutrient combinations were non-significant. Depth was the most consistent environmental driver of micronutrient composition per 100g. Fish assemblages associated with shallower reefs tended to provide higher selenium concentrations (β = −0.045, p < 0.001), whereas assemblages associated with deeper reefs exhibited slightly higher zinc concentrations (β = 0.010, p = 0.035). Only omega-3 concentration showed significant associations with the benthic community composition axes, increasing along both benthic PC1 (β = 0.028, p = 0.010) and PC2 (β = 0.032, p = 0.002). No nutrient concentration was significantly affected by sea surface temperature or chlorophyll a. Per-100 g micronutrient concentration varied across the 18 species with ≥ 30 records (Table S17), together with their biomass-weighted occurrence across depths and benthic gradients. Calcium per 100 g ranged, e.g., from 16.9 mg in *Paralabrax nebulifer* and 17.1 mg in *Caulolatilus princeps* to 154 mg in *Oxyjulis californica*, and vitamin A from 6.4 µg in *Anisotremus davidsonii* and 7.0 µg in *Embiotoca jacksoni* to 56 µg in *Halichoeres semicinctus*. All species occurred within a relatively narrow average depth range of approximately 8–12 m (Table S17).

3.4 Shifts in fish contributions across the NN versus NP spectrum

We integrated reef fish contributions to nature and people into a two-dimensional NN–NP framework at the site by year level (n = 59 site by year observations across 12 sites; Fig. 6). Linear mixed models with a random Site intercept revealed highly significant regional differences in both NN (Region main effect: χ^2_2 = 24.95, p < 0.001) and NP scores (χ^2_2 = 13.33, p = 0.001). Southern reefs predominantly fell into the Bright quadrant (15 out of 21 site by year observations, 71%); the Middle region was distributed across all four quadrants with a Bright bias (5 out of 12, 42%); and Northern reefs were concentrated in the Dark quadrant (14 out of 26, 54%). NN and NP scores were positively correlated overall (Pearson r = 0.51, R^2 = 0.26, p < 0.001). The alignment was strongest and statistically significant in the South (r = 0.52, R^2 = 0.27, p = 0.016), weaker in the Middle (r = 0.47, p = 0.125), and absent in the North (r = 0.20, p = 0.340; Table S18).

Because linear temporal trends within regions in both NN and NP scores were not statistically supported (see test statistics below), we treat the regional structure in NN–NP space as the primary signal; the apparent movement of the three regions through NN–NP space in Fig. 6A should be read as visual reference only, not as evidence of directional trajectories. The NN axis performed reasonably well with each input variable shared on average 22% of its variance with the NN score (mean R^2 = 0.22), and the NN score aligned with the main direction of variation in its inputs (R^2 = 0.23 with the first principal component, which itself captured 36.8% of the variance). NN-axis position can therefore be read as a

meaningful gradient. The NP axis was less straightforward. Although each NP input shared a similar amount of variance with the NP score (mean $R^2 = 0.22$), the NP score was almost unrelated to the main direction of variation in its inputs ($R^2 = 0.0002$ with PC1, even though PC1 explained 55.7% of the input variance). This is because the six micronutrient variables split into two opposing groups: calcium, iron, omega-3 and selenium moved together ($r = 0.68$ to 0.99) and were strongly negatively correlated with vitamin A and zinc ($r \cong -0.68$). Averaging across all six therefore canceled much of the signal. Targeted biomass and productivity were tightly linked to each other ($r = 0.83$) but only weakly to any nutrient ($|r| \leq 0.37$), adding a second largely independent direction. The arrows represent population level predictions from linear mixed models fitted across all sampled years (2017–2024), while accounting for repeated observations within sites through a random Site intercept. Despite visible fluctuations in predicted regional positions, neither the Year main effect (NN: $\chi^2_1 = 0.29$, $p = 0.589$; NP: $\chi^2_1 < 0.01$, $p = 0.999$) nor the Year × Region interaction (NN: $\chi^2_2 = 1.47$, $p = 0.481$; NP: $\chi^2_2 = 0.006$, $p = 0.997$) was significant. Consistent with this, all six region-specific temporal slopes had 95% confidence intervals encompassing zero (NN: −0.041 to 0.025 standardized units yr^{-1}; NP: −0.003 to 0.001 standardized units yr^{-1}; Table S19). Marginal R^2 was 0.314 for NN and 0.187 for NP, indicating that most variation occurred among individual sites rather than through consistent temporal regional change.

Bootstrap decomposition of year-to-year shifts within sites (n = 47 site-year transitions, defined as pairs of consecutive sampled years at the same site; this is fewer than the 59 site-year observations available because each transition requires two consecutive years; Fig. 6B; Table S20) showed that fisheries provisioning was the largest contributor to movement within NN versus NP space (mean proportional contribution 31.8%, 95% CI: 25.1, 38.4). Smaller but still substantial contributions came from alpha diversity (18.9%, 13.7, 24.6), trophic structure (17.6%, 12.4, 23.4), and micronutrient provisioning (17.6%, 13.4, 22.2), whereas functional structure contributed least (14.2%, 10.4, 18.4). Regional patterns differed in the secondary drivers of site level shifts: alpha diversity contributed most strongly in the North (24.7%), trophic structure in the Middle (27.4%), whereas the South showed a more even contribution across NN related categories. Overall, NN related and NP related categories contributed almost equally to cumulative movement within NN versus NP space (NN total = 50.7%; NP total = 49.4%). PERMANOVA on site by year coordinates detected no significant effect of protection status (pseudo $F = 1.92$, $R^2 = 0.086$, $p = 0.144$), indicating that the management regime did not systematically alter reef fish contributions along either dimension during the study period.

4. Discussion

Eight years after the 2014–2016 marine heatwave, reef fish communities along the Pacific coast of the Baja California peninsula appear to have entered a post-disturbance phase characterized by stabilized biomass and productivity rather than by ongoing decline or recovery. Within this stabilized state, however, contributions to nature and to people respond differently to the regional reorganization of kelp forest habitats. By integrating standing biomass, secondary productivity, biomass turnover, and both quantity- and quality-based dimensions of micronutrient supply within a Nature Futures Framework (NFF) heuristic, our results show that the magnitude of reef fish contributions is largely shaped by

habitat structure and regional environmental conditions, whereas their nutritional quality is shaped by community composition. These two dimensions can shift independently, generating regionally divergent patterns of alignment and decoupling between contributions to nature and people, with direct implications for jointly pursuing SDG 14 (Life Below Water) and SDG 2 (Zero Hunger) in post-disturbance temperate ecosystems.

4.1 Reef fish communities have stabilized rather than continued to decline

Reef fish communities showed no statistically significant directional change in standing biomass, biomass turnover, or total micronutrient supply between 2017 and 2024 across regions and exploitation categories. However, because our dataset begins after the 2014–2016 marine heatwave and contains no pre-disturbance observations, we cannot directly infer resilience trajectories or quantify recovery dynamics. This suggests that either the main community changes associated with the 2014–2016 marine heatwave had already occurred before our study period, or that the reef fish contributions measured here were relatively resistant to strong directional change. Studies from California show that marine heatwaves can restructure reef fish communities, but that responses are not uniform across space, habitats, or heatwave events. Ziegler et al. (2023) found post-heatwave declines in taxonomic diversity and shifts in trophic diversity, partly buffered by marine protected areas. Schuster et al. (2026) further showed that communities recovered after the 1997–1998 El Niño, but not after the more severe 2014–2016 heatwave, highlighting that post-heatwave trajectories depend on event intensity, habitat context, and regional setting. In this context, our results suggest that Baja California reef fish communities stabilized into distinct post-heatwave configurations between 2017 and 2024, including canopy-dominated reefs in the South, subcanopy-dominated reefs in the Middle, and urchin-barren-dominated reefs in the North.

The few directional changes that did occur were limited to non-targeted species, suggesting that overall stability can still mask more subtle shifts in fish community structure. In the South, secondary productivity increased among non-targeted species, while in the Middle, non-targeted species also showed an increase in biomass-weighted mean body size. Although these trends occurred in different regions, they suggest that non-targeted species may be reorganizing through changes in size structure and production, without causing a parallel increase in standing biomass. This is ecologically plausible because somatic production increases with body size and temperature (Morais & Bellwood, 2020; Morais et al., 2020), meaning that productivity can rise even when biomass remains stable. In contrast, the consistently higher turnover of targeted species across all regions likely reflects the effects of fishing on size and age structure, as exploitation tends to favor smaller, faster-growing, and higher-mortality individuals (Barneche et al., 2018; Brandl et al., 2019). However, directional biomass change appears to have been limited to microinvertivorous and macroinvertivorous fish in the North (Filz et al., 2026), rather than reflecting a broad community-wide recovery signal.

4.2 Total micronutrient supply tracks biomass, while nutritional quality reflects community composition

The distinction between micronutrient quantity and quality further shows that reef fish contributions to people cannot be inferred from biomass alone. While total micronutrient supply showed no differences among regions and between targeted and non-targeted species within individual micronutrients (Fig. S4), per-100 g RDI contributions revealed pronounced differences in nutritional quality among fish communities and regions (Fig. 4). Before interpreting these patterns, we note that nutrient concentrations were not measured directly from local fish tissue but were imputed from species-level FishBase values. Any temporal change in per-100 g RDI portions therefore reflects compositional reweighting of the assemblage rather than within-species shifts in nutrient density, which our data cannot evaluate. Total micronutrient supply per hectare largely followed patterns in standing biomass, suggesting that the absolute amount of nutrients available per area depends mainly on the total mass of fish present. More informative is the partial decoupling between quantity and quality. While total biomass remained broadly stable, contribution to RDI per 100 g changed directionally for selenium, vitamin A, and zinc among non-targeted species, but remained stable among targeted species. This indicates that species composition can reshape human-relevant nutritional benefits even when total biomass is conserved. This interpretation is consistent with previous work showing that the nutritional value of fish depends not only on biomass, but also on species identity, body composition, and micronutrient traits, which together influence nutrient storage and transfer through food webs (Hicks et al., 2019; Maire et al., 2021; Chouvelon et al., 2022).

These compositional shifts become most relevant when viewed against dietary benchmarks. A commonly used benchmark is that one standardized serving of a single food group should provide about one third (~ 33%) of the recommended daily intake of a micronutrient to make a meaningful nutritional contribution (Beal et al., 2024). In our study, a typical 100 g portion of reef fish greatly exceeded this threshold for selenium, providing approximately 95% of the recommended daily intake throughout the post heatwave period. Marine fish species are often particularly rich in selenium, with average contributions frequently exceeding 85% of recommended daily intake values (Maire et al., 2021), highlighting the important role fisheries can play in reducing selenium deficiencies that affect up to one billion people worldwide and are projected to increase under global environmental change (Jones et al., 2017). In contrast, omega-3 fatty acids (~ 25%), zinc (~ 20%), iron (~ 17%), vitamin A (~ 13%), and calcium (~ 5%) all remained below the dietary benchmark. However, this does not imply that reef fish make only minor nutritional contributions. Broader nutrient-density assessments show that fish and seafood can provide important micronutrients relative to their caloric content, with small fish, bivalves, and crustaceans ranking among the most micronutrient-dense foods (Beal & Ortenzi, 2022).

Nutrient content is also shaped by biogeographic and food-web context. Higher omega-3 fatty acid concentrations, for example, are typically associated with pelagic energy pathways and colder thermal regimes, since these fatty acids originate from plankton and accumulate preferentially in species

adapted to low-temperature environments (Arts & Kohler, 2009; Parrish, 2013; Hicks et al., 2019). Yet this mechanism translates only weakly into local supply along Baja California, where reef fish biomass is dominated by macroinvertivores while planktivores contribute comparatively little (Filz et al., 2026). This may explain why omega-3 fatty acids did not follow the broader pattern of higher RDI portions in non-targeted species. Although micronutrient concentrations in targeted species remained stable over time, changes among non-targeted species may indicate food-web shifts that could eventually influence the nutritional contribution of fisheries (Robinson et al., 2022; Yiu et al., 2025; Willis & Sunda, 1984).

In our study region, total micronutrient supply is largely driven by biomass-dominant targeted species, such as kelp bass (*Paralabrax clathratus*) and California sheephead (*Bodianus pulcher*). These species contribute strongly to total supply because they dominate standing biomass, even though their per-100 g nutrient concentrations are relatively low. This is noteworthy because both species support economically and culturally important recreational fisheries along the Pacific coast, linking the provision of nutritional benefits to species that are also highly valued by anglers and coastal communities (Love, 2006; Braje et al., 2017). By contrast, assemblage-level per-100 g nutritional quality was influenced by a smaller set of nutrient-dense species, many of which are not directly targeted by fisheries. These included bluebanded goby (*Lythrypnus dalli*), which contributed strongly to calcium, iron, and zinc; scissortail chromis (*Chromis atrilobata*) for vitamin A; and some rockfish species (*Sebastes* spp.) for selenium and omega-3 fatty acids. Although such small, non-targeted species may not contribute directly to fisheries provisioning, their high micronutrient concentrations may still enter higher trophic levels through predator–prey pathways and thereby influence the nutritional composition of harvested reef fishes. This suggests that biodiversity can act as a reservoir of complementary micronutrients, because species with different ecological traits contribute different nutritional profiles (Bernhardt & O'Connor, 2021). Recent work shows that fish biodiversity can increase nutritional benefits through complementarity among species, allowing diverse species portfolios to provide more balanced micronutrient contributions with less biomass and greater resilience than reliance on a few nutrient-rich or biomass-dominant species alone (Heilpern et al., 2025).

4.3 Environmental drivers structure quantity, but not quality

Sea surface temperature and benthic PC1 (the canopy kelp to subcanopy kelp axis) were positively related to biomass, productivity, and absolute micronutrient supply across all eight response models (Fig. 5). The consistency with which these two variables covary across responses suggests they act not as independent drivers but as expressions of the same underlying process. The positive effect of Benthic PC1 on fish biomass, productivity and total micronutrient supply should be interpreted carefully. PC1 represents a shift from canopy kelp reefs to reefs with less canopy kelp but more subcanopy kelp, understory brown algae, sea urchins and herbivorous invertebrates. Thus, the positive effect does not mean that bare or degraded reefs support more fish. Rather, it suggests that these alternative structured habitats can still provide habitat and food resources that support fish biomass and absolute nutrient supply. Importantly, this effect appeared only for absolute quantities, such as biomass and total

micronutrients per transect. Per-100 g nutrient concentrations were largely unrelated to PC1 and most environmental drivers.

Furthermore, it is at first glance surprising that mean annual sea surface temperature emerged as a positive driver of reef fish biomass. Across productive temperate shelves, demersal fish biomass tends to be highest in cold waters, where reduced metabolic losses translate into more efficient trophic transfer through the food web (van Denderen et al., 2023). Within our study region, however, this expectation can reverse when warmer water is paired with intact habitat structure and high biological diversity (Duffy et al., 2016; Srednick & Steele, 2022). The southern reefs of the Baja California peninsula combine warmer SST, persistent canopy forming *Macrocystis pyrifera*, and higher functional alpha diversity of the reef fish community than the cooler urchin barren reefs of the North (Filz et al., 2026). This suggests that reef fish biomass in Baja California is not driven by single environmental variables in isolation, but by the combined interaction of temperature, habitat structure, and community composition. The South appears to represent a regional configuration in which relatively warm conditions coincide with the persistence of structurally complex canopy kelp habitat and comparatively high fish biomass. The positive SST effect in our models should therefore not be interpreted as evidence that warming itself benefits temperate reef fish communities.

The negative chlorophyll-a coefficient in our multivariate models should also be interpreted carefully. At the transect level chlorophyll-a was not associated with reef fish biomass (Pearson $r = 0.002$, $p = 0.957$); the negative coefficient emerged only once SST and benthic habitat structure were included in the same model, and is therefore best read as a partial-residual (suppressor-type) effect rather than as evidence that chlorophyll-a reduces fish biomass. Mechanistically, chlorophyll-a in this system likely acts as an indicator of the broader upwelling-associated environmental setting rather than as an independent driver. The southern reefs lie within the influence of the Punta Eugenia and Bahía Vizcaíno upwelling centers, which are part of the southern California Current System (Arellano & Rivas, 2019; Mauzole et al., 2020). In this region, high primary productivity, persistent canopy kelp habitat, and higher reef fish biomass co-occur, but chlorophyll-a appears to track the broader temperature and upwelling regime rather than directly structuring fish biomass. This is especially relevant along Baja California, where chlorophyll-a variability reflects not only upwelling-favorable winds, but also broader seasonal and El Niño–La Niña driven changes in oceanographic conditions (Legaard & Thomas, 2006).

4.4 Shifts in fish contributions across the NN versus NP spectrum: interpretation and study limitations

When projected into NN–NP space, reef fish communities along Baja California did not show a clear directional change over time, but instead formed a strong regional pattern. Because linear temporal trends within regions were not statistically supported, we focus our interpretation on the static spatial structure of NN–NP coordinates across regions. We suggest that the relationship between contributions to nature and to people is mainly shaped by local habitat conditions rather than by temporal dynamics. Southern reefs, where canopy kelp is still largely retained, were mostly located in the Bright quadrant and

showed a positive coupling between NN and NP. In contrast, northern reefs, dominated by urchin-barren states, were concentrated in the Dark quadrant, indicating jointly low ecological and human-benefit contributions. The Middle region occupied an intermediate position. This suggests that canopy-forming kelp links both dimensions: where kelp persists, both dimensions remain high; where it is lost, both decline together. Thus, kelp loss in this system does not create a trade off between nature and people. Instead, it might result in a fundamental ecosystem state shift in which reefs transition into barren grounds, where both dimensions are weakened. However, the mechanisms underlying change differed between the two dimensions. Fisheries provisioning was the strongest single driver of site shifts within the NP dimension, while NN-related change was spread across several ecological dimensions, including diversity, trophic structure and functional structure. This means that NP in our analysis responds strongly to changes in fishery-relevant biomass, whereas NN is less dependent on any single component.

This points to an important limitation. As Basurto et al. (2025) emphasize, fisheries contribute to people in many ways beyond biomass or catch, including livelihoods, governance, culture and social organization. Our NP score captures only part of what Baja California's reef fisheries provide, especially in cooperative systems where fishing is closely linked to community-led management and local institutions (Cabrera-Sánchez et al., 2025; Narchi et al., 2025). This also challenges the idea that NN and NP are fully separate dimensions. The IPBES framework emphasizes that culture shapes all human–nature relationships, rather than viewing benefits as flowing only from ecosystems to people (Díaz et al., 2018). Furthermore, synergies between ecosystem recovery and tackling societal challenges are increasingly recognized as a central strength of Nature-based Solutions, as the restoration and protection of marine ecosystems can simultaneously support biodiversity, climate resilience, food provisioning, and community well-being when combined with inclusive and locally driven interventions (Filz et al., 2025; Marino et al., 2025; O'Leary et al., 2023).

Ojeda et al. (2022) take this further with the concept of reciprocal contributions, where people are understood as active parts of nature and contributions move in both directions through feedback that sustain biocultural continuity. Seen from this perspective, treating nature and people as two separate axes is useful analytically, but conceptually limited. The decoupling of NN and NP scores in the North should therefore not be read as evidence that NN and NP are generally independent, but rather as a sign of ecological simplification. In a reciprocal framing, the loss of canopy kelp weakens the feedback between kelp, herbivores, predatory fish and fishing communities that have historically developed together (Gonzales-Aragon et al., 2026). Our results may also have implications for nutritional pathways and micronutrient provisioning across the food web. Because our nutrient values were derived from species-level estimates rather than direct tissue measurements (see Section 4.2), the analysis reflects compositional shifts in nutrient provisioning driven by changes in species identity and biomass structure. We therefore cannot determine whether habitat-specific within-species variation in nutrient density (Robinson et al., 2022; Willis & Sunda, 1984), also occurs across Baja California kelp forest habitats. Nevertheless, species composition and biomass are known to strongly shape reef fish

nutritional contributions (Hicks et al., 2019; Maire et al., 2021), suggesting that the patterns identified here likely capture ecologically meaningful differences in nutrient provisioning among reef states.

4.5 Management implications

Because the same algal habitat structure that supports ecological functioning also underpins nutritional benefits (Pfister et al., 2019; Srednick, 2025), benefits to people cannot be managed separately from ecosystem structure and function. Our findings align with calls to move beyond purely human-centered valuations of nature, recognizing that maintaining kelp forests is both ecologically necessary and part of a broader responsibility toward nonhuman ecosystems (Piccolo et al., 2022). However, such coupled benefits are likely to depend on the protection of both the ecological processes that maintain kelp forests and the social-management conditions that make protection effective. In our models, protection status did not have a significant positive effect on NN–NP coordinates, which may reflect that the 2014–2016 marine heatwave overrode local protection effects, as shown in other temperate kelp systems (Smith et al., 2023; Kumagai et al., 2024). On the other hand, the community-managed areas and biosphere reserves in our study are relatively young and some are only partially protected, so positive effects may be weak or not yet detectable. Positive effects of protection have nevertheless been shown elsewhere, with MPAs buffering trophic diversity and accelerating post-heatwave fish-community recovery (Ziegler et al., 2023), no-take areas amplifying kelp-restoration benefits (Hopf et al., 2022), and joint Nature for Nature and Nature for People benefits emerging most clearly in old, fully protected areas (Flandrin et al., 2026).

The key issue is therefore not protection designation alone, but the quality, legitimacy, and enforcement of governance (Ulate et al., 2018). On the Pacific coast of Mexico, such outcomes have been linked to cooperative design principles - small management scales, clear territorial boundaries, transparent governance, and internal enforcement (McCay et al., 2014). Bauer et al. (2025a) showed that community-led marine reserves along Pacific Baja California maintained higher densities and biomass of spiny lobster, California sheephead, and horn shark than federally managed MPAs across the heatwave and its aftermath, and the southern region, where cooperative management is most strongly institutionalized, also retained kelp canopy while the northern region lost roughly 95% of canopy cover by 2023. Our null protection effect should therefore not be read as evidence that protection is irrelevant in Baja California, but as evidence that the binary protection variable used here captures formal designation imperfectly: it does not distinguish reserve age, enforcement strength, restoration potential, or whether protection is embedded in community-led and cooperative governance. Looking ahead, protection will need to become more preventive and adaptive in the context of rapid environmental change, where humans are transforming ecosystems at an unprecedented pace, often before their functioning and recovery dynamics are fully understood (Filz, 2026). Under strong climatic forcing, the capacity of protected areas to deliver ecological and social benefits may therefore depend less on designation alone than on timely action and locally embedded governance.

5. Conclusion

This study provides one of the first quantitative assessments of how reef fish communities simultaneously support nature and people in a temperate kelp forest system after a major climatic disturbance. By integrating ecological functioning, fisheries productivity, and micronutrient provisioning within a NN–NP framework, we show that, over the eight years following the 2014–2016 marine heatwave, these functions did not continue to decline. We found no statistically significant directional change between 2017 and 2024, with only a few shifts among non-targeted metrics, indicating that post-heatwave reef fish contributions were characterized primarily by regional stability rather than continued decline or recovery. Reefs with persistent canopy forming kelp supported high contributions to both nature and people, whereas simplified urchin barren reefs showed weaker and more decoupled support for ecological functioning and human wellbeing. At the same time, total micronutrient supply remained broadly stable, while changes in species composition altered nutritional quality on the reef.

The strong regional separation among temperate reef states suggests that these ecosystems cannot be managed through a single strategy. Reefs with persistent canopy and subcanopy kelp should be prioritized as ecological and social bright spots that sustain both ecosystem functioning and nutritional provisioning under climate change, whereas barren grounds require strategies aimed at restoring trophic interactions and rebuilding habitat structure. Effective governance and community led stewardship may be as important as formal protection itself if we want to shape more desirable futures for temperate reefs. More broadly, our findings highlight that biodiversity, ecosystem functioning, fisheries productivity, and human wellbeing cannot be treated as isolated dimensions, but should be understood as interconnected parts of the same system. In this sense, integrated contribution frameworks can help link SDG 14 and SDG 2 while supporting a broader perspective in which people are understood as part of nature.

6. Declarations

6.1 Ethics approval and consent to participate

This study used non-invasive underwater visual census data and did not involve animal capture, animal handling, experimental manipulation, or human participants. Therefore, ethics approval and consent to participate were not required. Clinical trial number: not applicable.

6.2 Consent for publication

Not applicable.

6.3 Availability of data and materials

The R codes generated during the current study are available in the Zenodo repository (https://doi.org/10.5281/zenodo.20480695). The raw datasets analyzed during the current study are

available from the corresponding author on reasonable request.

6.4 Competing interests

The authors declare that they have no competing interests.

6.5 Funding

The authors received no specific funding for this work.

6.6 Authors' contributions

PF conceived the study, performed the statistical analyses, prepared the figures, and wrote the first draft of the manuscript. PF, NL, EM, and GS developed the analytical framework. PF, RB, JL, and LM carried out field data collection and data curation. EM, NL, GS, RB, and LM contributed to the interpretation of the results and manuscript development. All authors reviewed, edited, and approved the final manuscript.

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7. References

1. Aguirre-Muñoz A, Méndez Sánchez F. La nueva reserva de la biosfera Islas del Pacífico de la Península de Baja California establece un hito en la conservación: todas las islas de México están protegidas. Fremontia. 2017;45:27–31.
2. Albuquerque FC, Longo GO, Waechter LS, Bender M, França FM. Fish loss in tropical coastal ecosystems can jeopardise nutrient supply to traditional fishing communities: A case study from Northeast Brazil. People Nat. 2026. doi:10.1002/pan3.70285.
3. Anthropic. (2025). *Claude* [Large language model]. https://www.anthropic.com
4. Arellano B, Rivas D. Coastal upwelling will intensify along the Baja California coast under climate change by mid-21st century: insights from a GCM-nested physical-NPZD coupled numerical ocean model. J Mar Syst. 2019;199:103207. doi:10.1016/j.jmarsys.2019.103207.

5. Arts MT, Kohler CC. Health and condition in fish: the influence of lipids on membrane competency and immune response. In: Kainz M, Brett MT, Arts MT, editors. Lipids in aquatic ecosystems. New York: Springer; 2009. doi:10.1007/978-0-387-89366-2_10.
6. Barneche DR, Robertson DR, White CR, Marshall DJ. Fish reproductive-energy output increases disproportionately with body size. Science. 2018;360(6389):642–645. doi:10.1126/science.aao6868.
7. Basurto X, Gutierrez NL, Franz N, et al. Illuminating the multidimensional contributions of small-scale fisheries. Nature. 2025;637(8047):875–884. doi:10.1038/s41586-024-08448-z.
8. Bauer J, Beas-Luna R, Malpica-Cruz L, et al. Community-led management maintains higher predator biomass supporting kelp forests persistence in Baja California. Sci Rep. 2025;15(1):23253. doi:10.1038/s41598-025-86140-6.
9. Bauer J, Lorda J, Beas-Luna R, et al. Extreme marine heatwaves drive divergent kelp forest trajectories and alternative stable states. Front Mar Sci. 2025;12. doi:10.3389/fmars.2025.1691156.
10. Beal T, Manohar S, Miachon L, Fanzo J. Nutrient-dense foods and diverse diets are important for ensuring adequate nutrition across the life course. Proc Natl Acad Sci USA. 2024;121(50):e2319007121. doi:10.1073/pnas.2319007121.
11. Beal T, Ortenzi F. Priority micronutrient density in foods. Front Nutr. 2022;9:806566. doi:10.3389/fnut.2022.806566.
12. Beas-Luna R, Micheli F, Woodson CB, Carr M, Malone D, Torre J, Boch C, Caselle JE, Edwards M, Freiwald J, Hamilton SL, Hernandez A, Konar B, Kroeker KJ, Lorda J, Montaño-Moctezuma G, Torres-Moye G. Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes. Glob Change Biol. 2020;26:6457–6473.
13. Benton D, ILSI Europe a.i.s.b.l. Micronutrient status, cognition and behavioral problems in childhood. Eur J Nutr. 2008;47(3):38–50. doi:10.1007/s00394-008-3004-9.
14. Bernhardt JR, O'Connor MI. Aquatic biodiversity enhances multiple nutritional benefits to humans. Proc Natl Acad Sci USA. 2021;118(15):e1917487118. doi:10.1073/pnas.1917487118.
15. Braje TJ, Erlandson JM, Rick TC, Dayton PK. Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. Sci Adv. 2017;3:e1601759. doi:10.1126/sciadv.1601759.
16. Brandl SJ, Tornabene L, Goatley CHR, et al. Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. Science. 2019;364(6446):1189–1192. doi:10.1126/science.aav3384.
17. Brooks ME, Kristensen K, van Benthem KJ, et al. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 2017;9(2):378–400. doi:10.32614/RJ-2017-066.
18. Cabrera-Sánchez CT, Montaño-Moctezuma G, Coronado E, Delgado-Ramírez CE, Garza-Lagler MC. Analysis of value chain of the artisanal sea urchin fishery of Baja California, México. Mar Policy. 2025;172:106509. doi:10.1016/j.marpol.2024.106509.

19. Calder PC. Marine omega-3 fatty acids and inflammatory processes: effects, mechanisms and clinical relevance. Biochim Biophys Acta Mol Cell Biol Lipids. 2015;1851(4):469–484. doi:10.1016/j.bbalip.2014.08.010.
20. Canva. (2025). *Canva* [Graphic design software]. https://www.canva.com
21. Castorani MCN, Reed DC, Miller RJ. Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. Ecology. 2018;99:2442–2454. doi:10.1002/ecy.2485.
22. Chao A, Chiu CH, Jost L. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu Rev Ecol Evol Syst. 2014;45:297–324. doi:10.1146/annurev-ecolsys-120213-091540.
23. Chouvelon T, Gilbert L, Caurant F, et al. Nutritional grouping of marine forage species reveals contrasted exposure of high trophic levels to essential micro-nutrients. Oikos. 2022;2022(7):e08844. doi:10.1111/oik.08844.
24. Cruz-Góngora V, Martinez-Tapia B, Shamah-Levy T, Villalpando S. Nutritional status of iron, vitamin B12, vitamin A and anemia in Mexican children: results from the Ensanut 2018-19. Salud Publica Mex. 2021;63(3):359–370.
25. van Denderen D, Maureaud AA, Andersen KH, et al. Demersal fish biomass declines with temperature across productive shelf seas. Glob Ecol Biogeogr. 2023;32(10):1846–1857. doi:10.1111/geb.13732.
26. Díaz S, Pascual U, Stenseke M, et al. Assessing nature's contributions to people. Science. 2018;359(6373):270–272. doi:10.1126/science.aap8826.
27. Díaz S, Settele J, Brondízio ES, et al. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science. 2019;366(6471):eaax3100. doi:10.1126/science.aax3100.
28. Drewnowski A. Defining nutrient density: development and validation of the Nutrient Rich Foods Index. J Am Coll Nutr. 2009;28(4):421S-426S. doi:10.1080/07315724.2009.10718106.
29. Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ. Biodiversity enhances reef fish biomass and resistance to climate change. Proc Natl Acad Sci USA. 2016;113(22):6230–6235. doi:10.1073/pnas.1524465113.
30. Dwyer JT, Melanson KJ, Sriprachy-anunt U, Cross P, Wilson M. Table 15. Dietary reference intakes (DRIs): recommended intakes for individuals, vitamins. Food and Nutrition Board, Institute of Medicine, The National Academies. MDText.com; 2015. https://www.ncbi.nlm.nih.gov/books/NBK278991/table/diet-treatment-obes.table15die/. Accessed 21 May 2026.
31. Filz P, Beas-Luna R, Rindi L, Lorda J, Freiwald J, Malpica-Cruz L. Coastal resilience could be enhanced by co-interventions and synergistic Nature-based Solutions. Nature-Based Solutions. 2025;8:100244. doi:10.1016/j.nbsj.2025.100244.
32. Filz P, Beas-Luna R, Loiseau N, Lorda J, Freiwald J, Bauer J, Malpica-Cruz L. Diversity persists while function shifts: post-heatwave reorganization of reef fish communities in Baja California. PeerJ.

2026. In press.
33. Filz P. Bumblebees should make us humble beings. Nat Rev Biodivers. 2026. doi:10.1038/s44358-026-00165-x.
34. Filz, P. (2026). Bright spots and barren grounds: temperate reef states shape fish contributions to nature and people after marine heatwaves. Zenodo. https://doi.org/10.5281/zenodo.20480695
35. Flandrin U, Mouillot D, Albouy C, et al. Fish communities can simultaneously contribute to nature and people across the world's tropical reefs. One Earth. 2024;7(10):1772–1785. doi:10.1016/j.oneear.2024.09.011.
36. Flandrin U, Mouquet N, Loiseau N, et al. Marine protected areas marginally offset anthropogenic declines in tropical reef fish contributions to nature and people. Nat Ecol Evol. 2026;10(4):733–750. doi:10.1038/s41559-026-03008-2.
37. Fox J, Weisberg S. An R Companion to Applied Regression. 3rd ed. Thousand Oaks (CA): Sage; 2019.
38. Froese R, Pauly D. FishBase. World Wide Web electronic publication. 2026. .
39. García Rodríguez E, Sosa Nishizaki O, Guerrero Ávila C, Rodríguez Medrano MC, Mejía Mercado BE, Domínguez Reza RH. Guía para la identificación de las especies capturadas en la pesca deportiva de Baja California, México. Informe Técnico. Ensenada: Centro de Investigación Científica y de Educación Superior de Ensenada; 2013.
40. Gernand AD, Schulze KJ, Stewart CP, West KP, Christian P. Micronutrient deficiencies in pregnancy worldwide: health effects and prevention. Nat Rev Endocrinol. 2016;12(5):274–289. doi:10.1038/nrendo.2016.37.
41. Gonzalez-Aragon D, Flores C, Torres FI, Broitman BR. Tracing the kelp highway hypothesis in South America: poleward shifts in kelp past distribution and archaeological evidence of human use. Front Ecol Evol. 2026;13. doi:10.3389/fevo.2025.1720175.
42. Halpern BS, Frazier M, Potapenko J, et al. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nat Commun. 2015;6(1):7615. doi:10.1038/ncomms8615.
43. Hamilton M, Maire E, Monteil C, Vane V, Graham NAJ, Brun V, et al. Drivers of nutrient intakes from fisheries in French Polynesia. Ecosyst People. 2024;20(1):2351385. doi:10.1080/26395916.2024.2351385.
44. Hartig F. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.2.0. 2020. http://florianhartig.github.io/DHARMa/. Accessed 21 May 2026.
45. Heilpern SA, Simon FW, Sethi SA, Fiorella KJ, Flecker AS, Gomes C, McIntyre PB. Leveraging biodiversity to maximize nutrition and resilience of global fisheries. Nat Sustain. 2025;8:753–762. doi:10.1038/s41893-025-01577-x.
46. Herrera-González A, Gutierrez-Gómez YY, Moreno-García CF, Aceves-Martins M. Obesity and its association with micronutrient deficiency among Mexican children and adolescents: a systematic review and meta-analysis. Nutr Rev. 2025;nuaf148. doi:10.1093/nutrit/nuaf148.

47. Hicks CC, Cohen PJ, Graham NAJ, et al. Harnessing global fisheries to tackle micronutrient deficiencies. Nature. 2019;574(7776):95–98. doi:10.1038/s41586-019-1592-6.
48. Hopf JK, Caselle JE, White JW. No-take marine protected areas enhance the benefits of kelp-forest restoration for fish but not fisheries. Ecol Lett. 2022;25(7):1665–1675. doi:10.1111/ele.14023.
49. Institute of Medicine (US) Committee on Nutrition Standards for National School Lunch and Breakfast Programs; Stallings VA, Taylor CL, editors. Nutrition Standards and Meal Requirements for National School Lunch and Breakfast Programs: Phase I. Proposed Approach for Recommending Revisions. Appendix K, Dietary Reference Intakes for Individuals Ages 4 Through 18 Years, Including Those Who Are Pregnant or Lactating. Washington (DC): National Academies Press; 2008. Available from: https://www.ncbi.nlm.nih.gov/books/NBK214999/. Accessed 29 May 2026.
50. Jones GD, Droz B, Greve P, Gottschalk P, Poffet D, McGrath SP, Seneviratne SI, Smith P, Winkel LHE. Selenium deficiency risk predicted to increase under future climate change. Proc Natl Acad Sci U S A. 2017;114(11):2848–2853. doi:10.1073/pnas.1611576114.
51. Kennedy G, Nantel G, Shetty P. The scourge of "hidden hunger": global dimensions of micronutrient deficiencies. Food, Nutrition and Agriculture. FAO; 2003.
52. Kumagai JA, Goodman MC, Villaseñor-Derbez JC, Caselle JE, Claisse JT, Crowder LB, Estes JA, Stier AC, White JW. Marine protected areas that preserve trophic cascades promote resilience of kelp forests to marine heatwaves. Glob Change Biol. 2024. doi:10.1111/gcb.17620.
53. Lall SP, Kaushik SJ. Nutrition and metabolism of minerals in fish. Animals. 2021;11(9):2711. doi:10.3390/ani11092711.
54. Legaard KR, Thomas AC. Spatial patterns in seasonal and interannual variability of chlorophyll and sea surface temperature in the California Current. J Geophys Res Oceans. 2006;111. doi:10.1029/2005JC003282.
55. Lenth RV. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.10.0. 2024. https://CRAN.R-project.org/package=emmeans.
56. Love MS. Subsistence, commercial, and recreational fisheries. In: Allen LG, Pondella DJ, Horn MH, editors. The ecology of marine fishes: California and adjacent waters. Berkeley: University of California Press; 2006. p. 567–594.
57. Lowe NM. The global challenge of hidden hunger: perspectives from the field. Proc Nutr Soc. 2021;80(3):283–289. doi:10.1017/S0029665121000902.
58. Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw. 2021;6(60):3139. doi:10.21105/joss.03139.
59. Magneville C, Loiseau N, Albouy C, et al. mFD: an R package to compute and illustrate the multiple facets of functional diversity. Ecography. 2022;2022(1):e05904. doi:10.1111/ecog.05904.
60. Maire E, Graham NAJ, MacNeil MA, et al. Micronutrient supply from global marine fisheries under climate change and overfishing. Curr Biol. 2021;31(18):4132–4138.e3. doi:10.1016/j.cub.2021.06.067.

61. Marino M, Baptist MJ, Alkharoubi AIK, et al. Nature-based Solutions as building blocks for coastal flood risk reduction: a model-based ecosystem service assessment. Sci Rep. 2025;15:12070. doi:10.1038/s41598-025-95230-4.
62. Martin A, Gomez-Baggethun E, Quaas M, Rozzi R, Tauro A, Faith DP, Kumar R, O'Farrell P, Pascual U. Plural values of nature help to understand contested pathways to sustainability. One Earth. 2024;7:806–819. doi:10.1016/j.oneear.2024.04.003.
63. Martin CL, Momtaz S, Gaston T, Moltschaniwskyj NA. A systematic quantitative review of coastal and marine cultural ecosystem services: current status and future research. Mar Policy. 2016;74:25–32. doi:10.1016/j.marpol.2016.09.004.
64. Mauzole Y, Torres H, Fu LL. Patterns and dynamics of SST fronts in the California Current System. J Geophys Res Oceans. 2020;125. doi:10.1029/2019JC015499.
65. McCay BJ, Micheli F, Ponce-Díaz G, et al. Cooperatives, concessions, and co-management on the Pacific coast of Mexico. Mar Policy. 2014;44:49–59. doi:10.1016/j.marpol.2013.08.001.
66. Morais RA, Bellwood DR. Principles for estimating fish productivity on coral reefs. Coral Reefs. 2020;39(5):1221–1231. doi:10.1007/s00338-020-01969-9.
67. Morais RA, Depczynski M, Fulton C, et al. Severe coral loss shifts energetic dynamics on a coral reef. Funct Ecol. 2020;34(7):1507–1518. doi:10.1111/1365-2435.13568.
68. Morais RA, Smallhorn-West P, Connolly SR, et al. Sustained productivity and the persistence of coral reef fisheries. Nat Sustain. 2023;6:1199–1209. doi:10.1038/s41893-023-01137-1.
69. Nakagawa S, Schielzeth H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol. 2013;4(2):133–142. doi:10.1111/j.2041-210x.2012.00261.x.
70. Narchi NE, Zepeda-Domínguez JA, Malpica-Cruz L. History and ethnography of the popular gastronomic culture leading to the BajaMed movement in Baja California, Mexico. Discov Food. 2025;5(1):163. doi:10.1007/s44187-025-00443-1.
71. Ojeda J, Salomon AK, Rowe JK, Ban NC. Reciprocal contributions between people and nature: a conceptual intervention. BioScience. 2022;72(10):952–962. doi:10.1093/biosci/biac053.
72. Oksanen J, Simpson GL, Blanchet FG, et al. vegan: community ecology package. R package version 2.7-3. 2026. https://cran.r-project.org/web/packages/vegan/index.html. Accessed 21 May 2026.
73. O'Leary BC, Fonseca C, Cornet CC, et al. Embracing Nature-based Solutions to promote resilient marine and coastal ecosystems. Nat Based Solut. 2023;3:100044. doi:10.1016/j.nbsj.2022.100044.
74. Palacios-Abrantes J, Badhe R, Bamford A, Cheung WWL, Foden W, Frazão Santos C, Grey KA, Kühn N, Maciejewski K, McGhie H, et al. Managing biodiversity in the Anthropocene: discussing the Nature Futures Framework as a tool for adaptive decision-making for nature under climate change. Sustain Sci. 2022. doi:10.1007/s11625-022-01200-4.
75. Parrish CC. Lipids in marine ecosystems. Int Sch Res Notices. 2013;2013(1):604045. doi:10.5402/2013/604045.

76. Pereira LM, Davies KK, den Belder E, et al. Developing multiscale and integrative nature-people scenarios using the Nature Futures Framework. People Nat. 2020;2(4):1172–1195. doi:10.1002/pan3.10146.
77. Pfister CA, Altabet MA, Weigel BL. Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. Ecology. 2019;100(10). doi:10.1002/ecy.2798.
78. Piccolo JJ, Taylor B, Washington H, et al. "Nature's contributions to people" and peoples' moral obligations to nature. Biol Conserv. 2022;270:109572. doi:10.1016/j.biocon.2022.109572.
79. R Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2023. https://www.R-project.org/. Accessed 21 May 2026.
80. Robinson JPW, Maire E, Bodin N, et al. Climate-induced increases in micronutrient availability for coral reef fisheries. One Earth. 2022;5(1):98–108. doi:10.1016/j.oneear.2021.12.005.
81. Rodríguez-Medrano MC. Descripción y análisis biológico de la pesca deportiva en Bahía de Todos Santos, Ensenada, B.C. [Master's thesis]. Ensenada (Baja California, Mexico): Centro de Investigación Científica y de Educación Superior de Ensenada; 1993. 88 p.
82. Salland N, Wilding CM, Galobart C, et al. Temporal shifts in kelp forest structure and distribution largely reflect recent ocean warming trends. Ecography. 2026;e08280. doi:10.1002/ecog.08280.
83. Schuster J, Kushner D, Bates A. Rapid fish community response to two severe marine heat events in the Pacific. Mar Ecol Prog Ser. 2026;780:1–19. doi:10.3354/meps15065.
84. Smale DA, Wernberg T, Oliver ECJ, et al. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change. 2019;9(4):306–312. doi:10.1038/s41558-019-0412-1.
85. Smith JG, Free CM, Lopazanski C, et al. A marine protected area network does not confer community structure resilience to a marine heatwave across coastal ecosystems. Glob Change Biol. 2023;29(19):5634–5651. doi:10.1111/gcb.16862.
86. Srednick GS, Steele MA. Macroalgal physical structure predicts variation in some attributes of temperate fish assemblages better than macroalgal species composition. Mar Biol. 2022;169:147. doi:10.1007/s00227-022-04135-7.
87. Srednick G, Swearer SE. Habitat attributes mediate top-down and bottom-up drivers of community development in temperate and tropical algae. Ecosphere. 2025;16(8). doi:10.1002/ecs2.70345.
88. Ulate K, Alcoverro T, Arthur R, Aburto-Oropeza O, Sánchez C, Huato-Soberanis L. Conventional MPAs are not as effective as community co-managed areas in conserving top-down control in the Gulf of California. Biol Conserv. 2018;228:100–109. doi:10.1016/j.biocon.2018.09.033.
89. Waldock C, Maire E, Albouy C, et al. Micronutrient levels of global tropical reef fish communities differ from fisheries capture. People Nat. 2025;7(1):32–51. doi:10.1002/pan3.10736.
90. Weffort VRS, Lamounier JA. Hidden hunger – a narrative review. J Pediatr (Rio J). 2024;100(Suppl 1):S10–S17. doi:10.1016/j.jped.2023.08.009.

91. Willis JN, Sunda WG. Relative contributions of food and water in the accumulation of zinc by two species of marine fish. Mar Biol. 1984;80(3):273–279. doi:10.1007/BF00392822.
92. Yiu DS, Elliott Smith EA, Farrell SP, Rasher DB. Kelp forest loss and emergence of turf algae reshapes energy flow to predators in a rapidly warming ecosystem. Sci Adv. 2025;11(23):eadw7396. doi:10.1126/sciadv.adw7396.
93. Ziegler SL, Johnson JM, Brooks RO, et al. Marine protected areas, marine heatwaves, and the resilience of nearshore fish communities. Sci Rep. 2023;13(1):1405. doi:10.1038/s41598-023-28507-1.
94. Zhao Y, Han Z, Zhang C, Wang Y, Zhong J, Gao M. Coastal cultural ecosystem services: a bridge between the natural ecosystem and social ecosystem for sustainable development. Land. 2024;13(9):1352. doi:10.3390/land13091352.

Figures

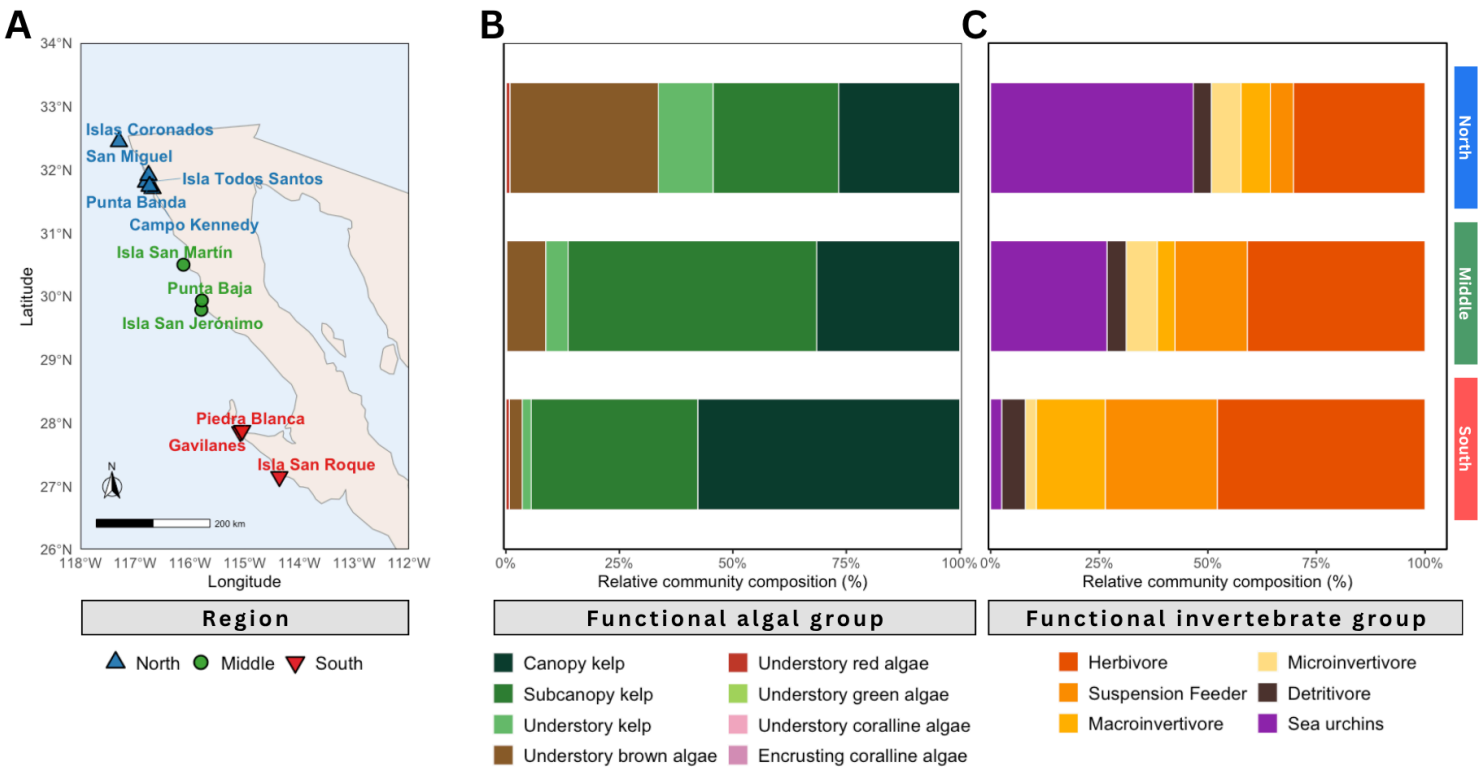


Figure 1

Study area and functional composition of benthic communities along Baja California.
(A) Map of the Pacific coast of the Baja California peninsula, Mexico, showing the ~600 km latitudinal extent of the survey region and the distribution of monitoring sites grouped into three regions (North, Middle, South). Regions are distinguished by color and symbols. North sites are dominated by understory brown algae, Middle sites by subcanopy kelp, and South sites by canopy-forming kelp. **(B–C)** Mean relative functional composition of benthic communities across the three regions. Horizontal

stacked bars show the proportional contribution of (B) algal and **(C)** invertebrate functional groups, averaged across years (2017–2024). Values were converted to relative abundance within each taxonomic group before averaging. Colors indicate functional groups.

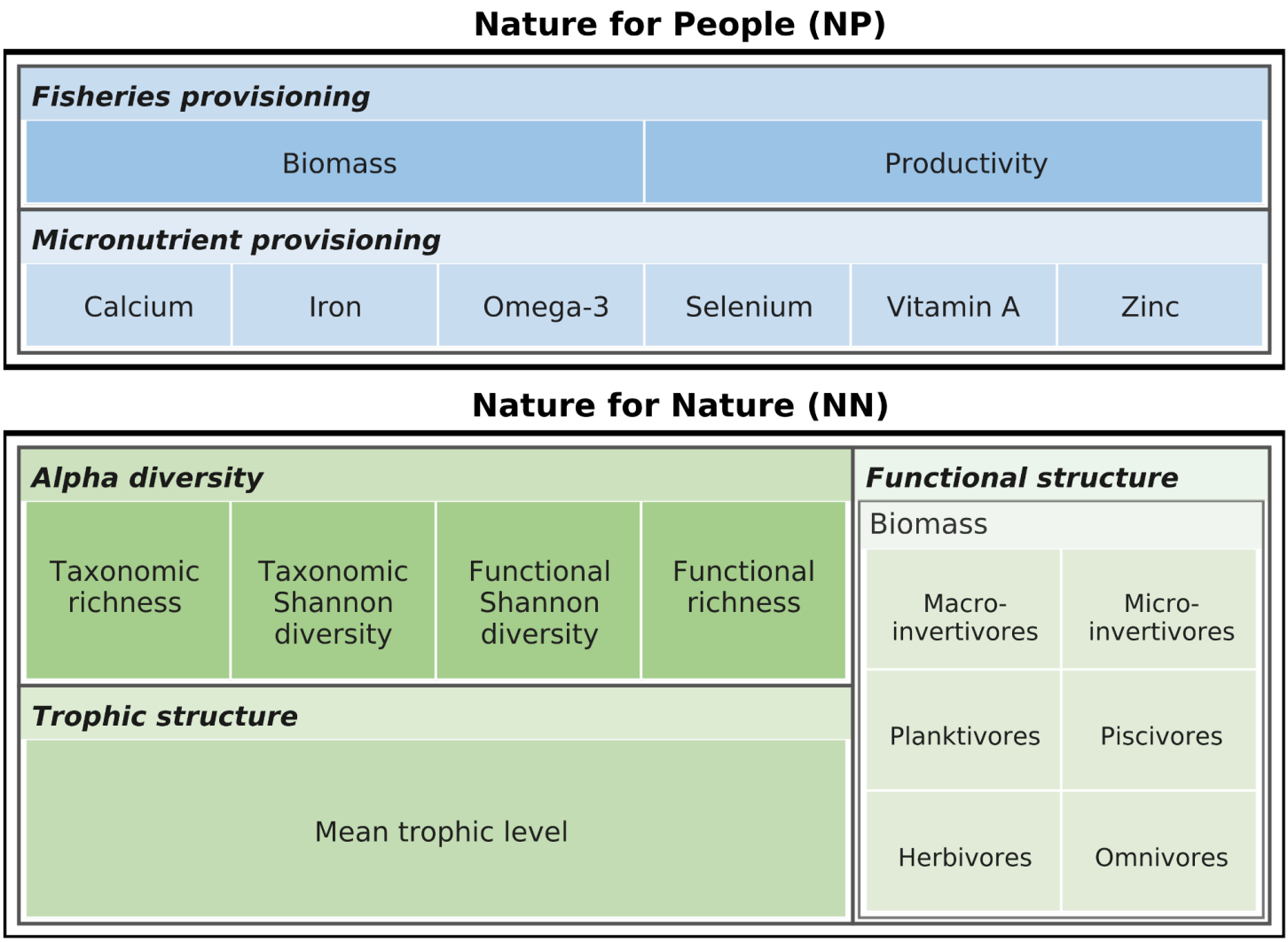


Figure 2

Components of the Nature for Nature (NN) and Nature for People (NP) indices. The treemap illustrates the hierarchical structure of all metrics used to construct the NN and NP composite indices. Metrics were grouped into alpha diversity, trophic structure, and functional structure (NN), and fisheries provisioning and micronutrient provisioning (NP), following the conceptual framework of Flandrin et al. (2024). All variables were log1p-transformed and z-standardized prior to index calculation.

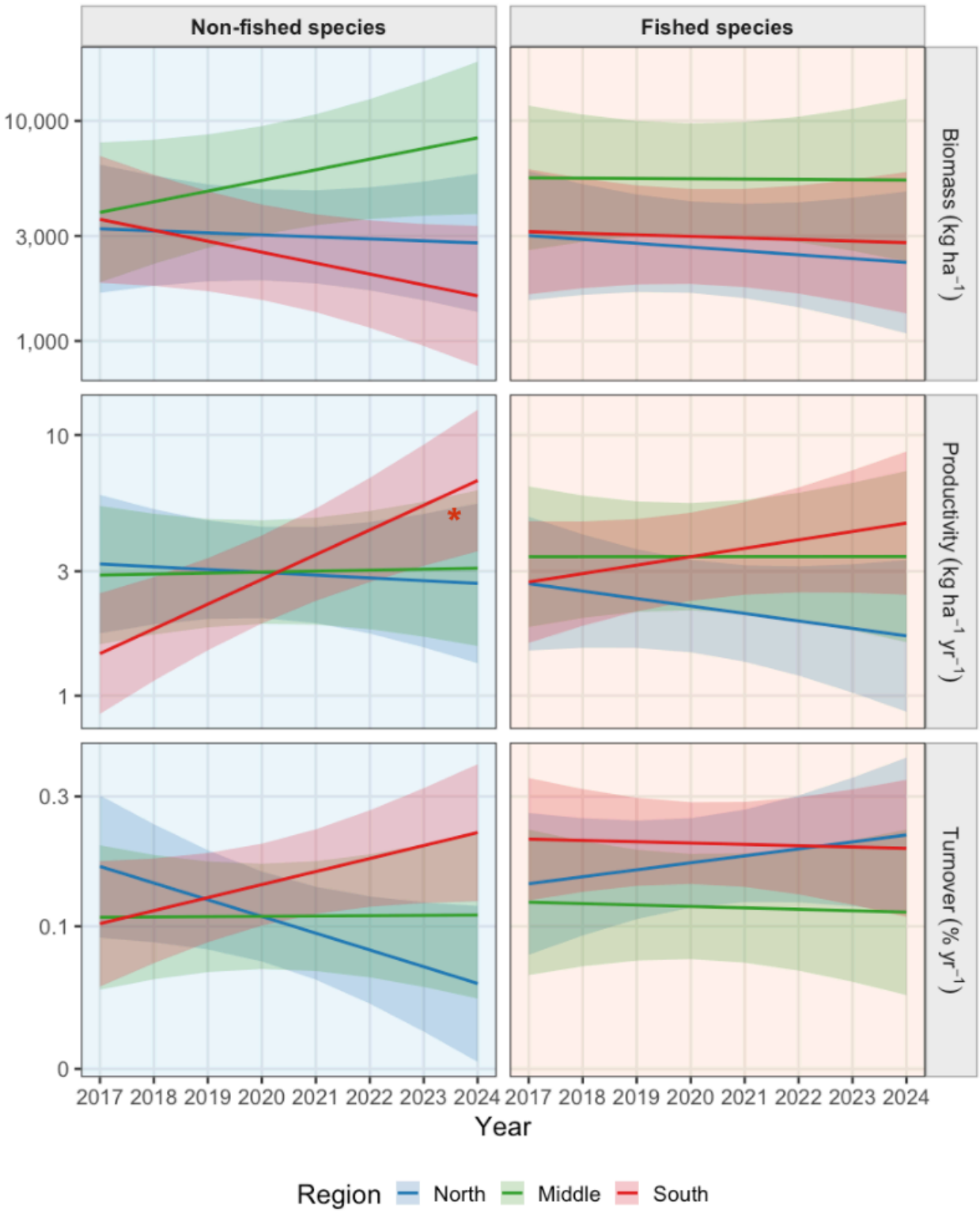


Figure 3

Temporal trajectories of reef fish biomass, secondary productivity, and biomass turnover across regions and exploitation categories following kelp forest reorganization.

Generalized linear mixed-model predictions (lines ± 95 % confidence intervals) for standing biomass (top row), secondary productivity (middle row), and biomass turnover (bottom row) from 2017 to 2024 across

the North (blue), Middle (green), and South (red) regions of the Baja California peninsula. Left panels show non-targeted species; right panels show targeted species. Shaded ribbons represent 95 % confidence intervals from the fitted mixed-effects models. Region × exploitation combinations with a statistically significant temporal slope (95 % CI excluding zero) are marked with an asterisk; all other combinations showed no significant directional change.

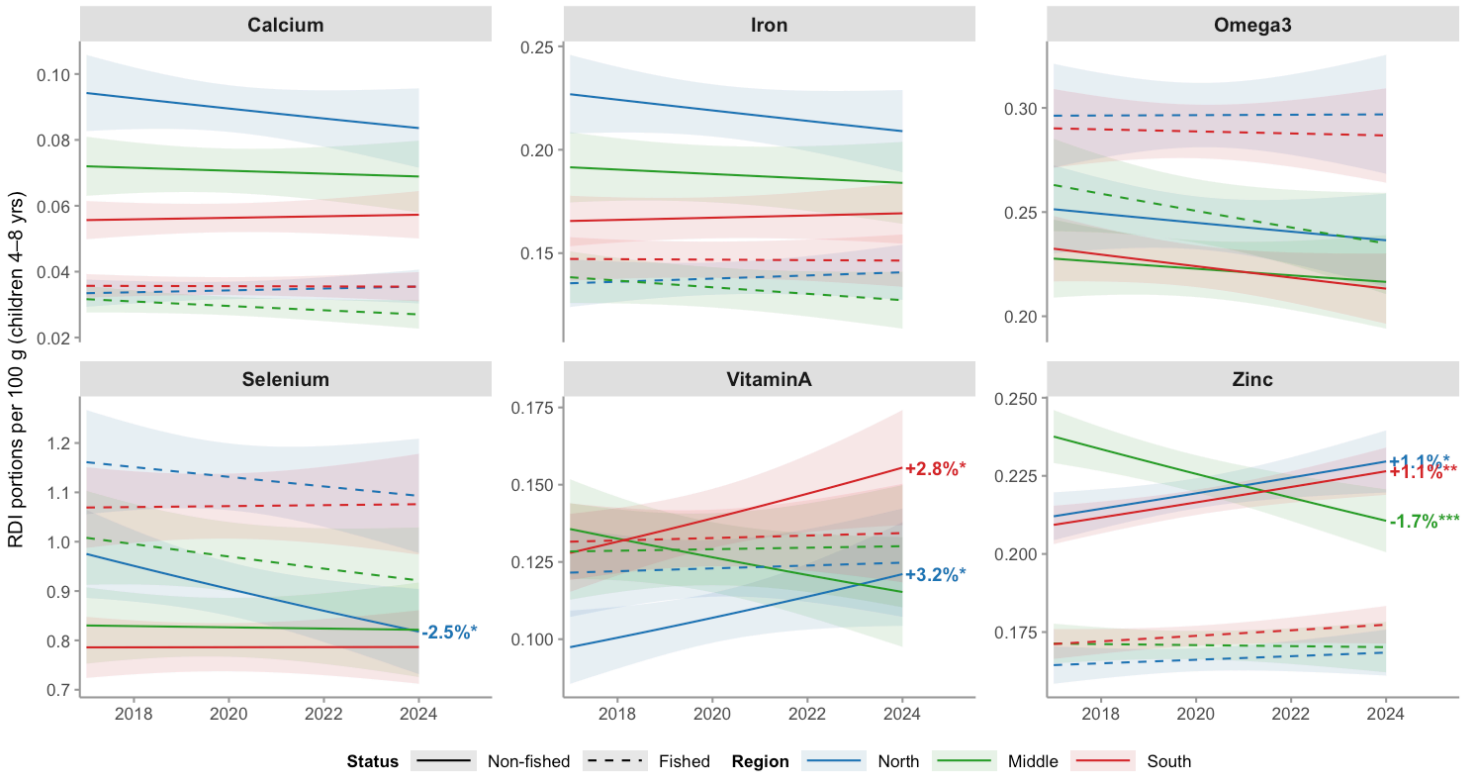


Figure 4

Temporal trends in micronutrient contributions per 100 g of reef fish biomass.

Recommended daily intake (RDI) portions provided by a standardized 100 g serving of biomass-weighted reef fish biomass for children aged 4–8 years from 2017 to 2024. A value of 1.0 indicates that a single 100 g serving supplies the full daily requirement of that micronutrient. Panels show calcium, iron, omega-3 fatty acids, selenium, vitamin A, and zinc. Colors indicate regions along the Baja California peninsula: North, Middle, and South. Solid lines represent non-targeted species and dashed lines represent targeted species. Shaded bands indicate 95 % confidence intervals around temporal trends. Annual percentage change is reported only for statistically significant slopes (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

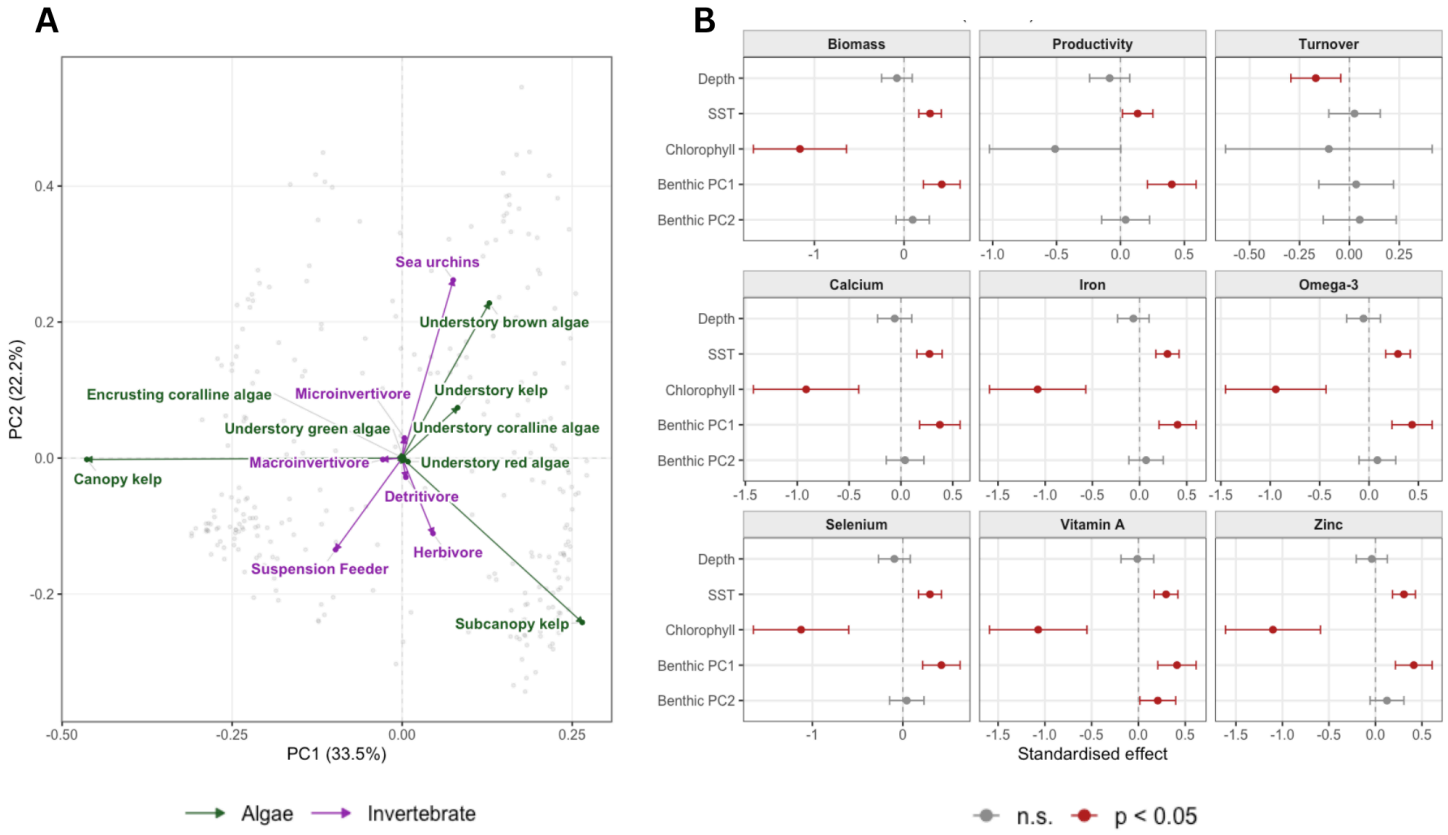


Figure 5

Benthic community structure and environmental drivers of fish community metrics.

(A) Principal component analysis (PCA) of combined algal and invertebrate functional group composition across transects. Points represent individual transects. Arrows indicate the functional groups with the strongest loadings on the first two principal components, which explained 33.5 % and 22.2 % of the total compositional variance, respectively. Green vectors represent algal groups and purple vectors represent invertebrate groups. **(B)** Standardized effect sizes (± 95 % CI) of environmental predictors on fish community responses, derived from generalized linear mixed-effects models. Responses are standing biomass, secondary productivity, biomass turnover, and total supply of each of the six micronutrients. Red points indicate significant effects ($p < 0.05$), whereas gray points indicate non-significant effects.

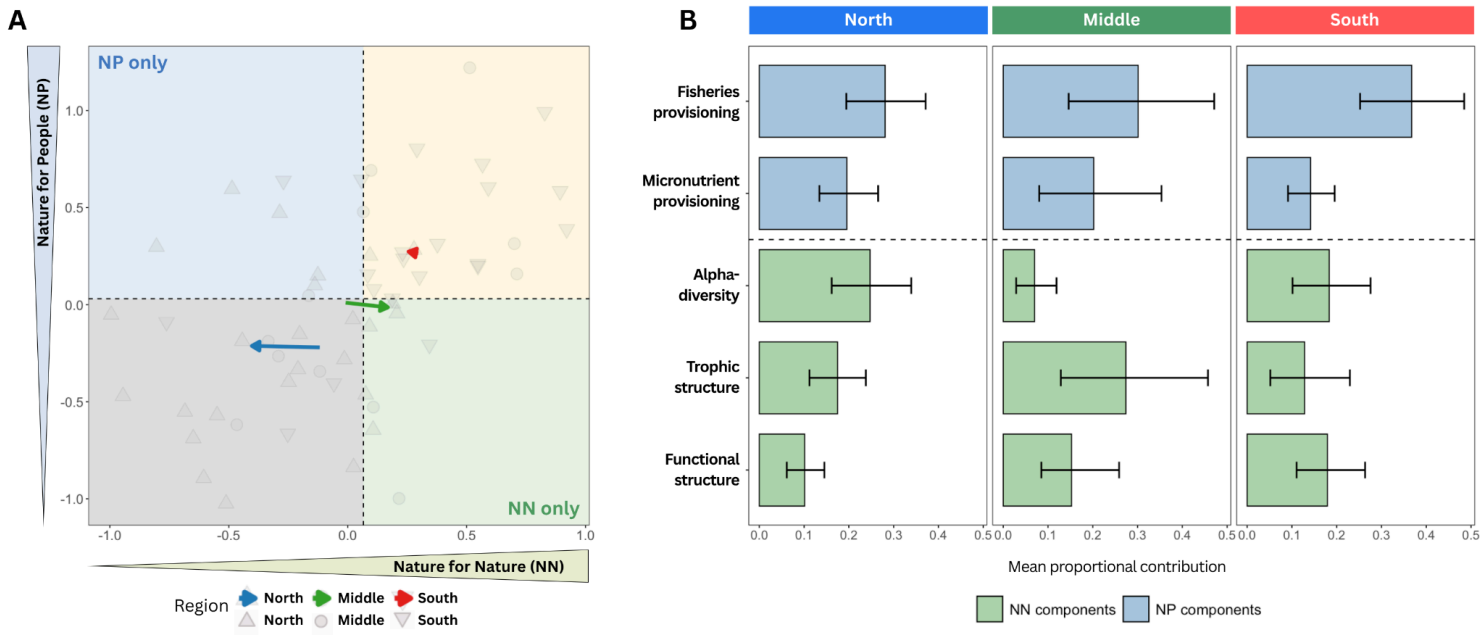


Figure 6

Reef fish contributions to Nature for Nature (NN) and Nature for People (NP) across post-heatwave kelp forest states.
(A) Site-by-year observations in NN–NP space, shown as gray semi-transparent symbols, with dashed lines indicating median NN and NP values. These medians define bright spots (high NN and high NP), dark spots (low NN and low NP), NN-only and NP-only configurations. Colored arrows show model-predicted regional trajectories from 2017 to 2024 based on Gaussian linear mixed-effects models with Site as a random intercept. Arrows illustrate net temporal shifts only, as neither Year nor Year × Region effects were significant. **(B)** Bootstrap decomposition of year-to-year within-site shifts in NN–NP space. Bars show mean proportional contributions ± 95% confidence intervals for NN components (green: functional structure, trophic structure, alpha diversity) and NP components (blue: micronutrient and fisheries provisioning) across regions.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- FilzSupplementaryFigures.docx
- FilzSupplementaryTables.docx