This authors' personal copy may not be publicly or systematically copied or distributed, or posted on the Open Web, except with written permission of the copyright holder(s). It may be distributed to interested individuals on request.

Vol. 710: 107–123, 2023 https://doi.org/10.3354/meps14288 MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser

Published May 4



# Warming-induced changes in reef fish community traits in the Southwestern Atlantic transition zone

Fernanda C. Silva<sup>1,\*</sup>, Sergio R. Floeter<sup>1</sup>, Martin Lindegren<sup>2</sup>, Juan P. Quimbayo<sup>3,4</sup>

<sup>1</sup>Marine Macroecology and Biogeography Lab, Universidade Federal de Santa Catarina, Florianópolis 88040-900, Brazil <sup>2</sup>Centre for Ocean Life, National Inst. of Aquatic Resources (DTU-Aqua), Technical Univ. of Denmark, Kgs Lyngby 2800, Denmark <sup>3</sup>Center for Marine Biology, University of São Paulo, São Sebastião SP 11600-000, Brazil

<sup>4</sup>Dept. of Evolution, Ecology, and Organismal Biology, The Ohio State Univ., Columbus, OH 43210, USA

ABSTRACT: Marine communities are subject to alterations in environmental conditions, due to both natural variability and climate change. For instance, a rapid increase in sea surface temperature (SST) can modify spatial distribution patterns and abundances of reef fishes and therefore alter the overall diversity, structure, and functioning of these communities. Trait-based approaches may accurately detect community responses to such environmental changes, because species traits should reflect resource and habitat requirements. Here, we investigated temporal variability in reef fish trait composition and thermal affinity and assessed whether shifts are linked to recent ocean warming. We combined species traits related to feeding, growth, and survival with abundance data on reef fish from underwater visual census at 7 islands of the Southwestern Atlantic subtropical transition zone. All islands exhibited gradual trait reorganization from fish assemblages dominated by large-size species at the beginning of the time period to small, cryptobenthic species towards the end. The temporal changes in community weighted mean traits and the community thermal index were related to SST, indicating a numerical response of species to climatic variations. Tropical species are slowly becoming more abundant over time, while temperate species are becoming less abundant, reflecting an initial change in fish composition in this transition zone. These results have ecological implications leading communities to a faster turnover, lower food-chain complexity, and higher vulnerability to change. We highlight the importance of integrating traits and abundance time series data for a holistic understanding of reef dynamics and community responses to environmental variation, including global warming.

KEY WORDS: Reef fish  $\cdot$  Fish abundance  $\cdot$  Community weighted mean  $\cdot$  Community thermal index  $\cdot$  Climate change  $\cdot$  Rocky reef  $\cdot$  Trait reorganization

- Resale or republication not permitted without written consent of the publisher

# 1. INTRODUCTION

Natural climate changes regularly occur in space and over time (Pinsky et al. 2020). However, due to increasing anthropogenic pressures involving carbon emissions and excessive resource use, human-induced changes have become more severe and frequent, threatening the health and integrity of our ecosystems (Rockström et al. 2009, IPCC 2018, Holbrook et al. 2020). Negative impacts in marine environments include a rapid increase in sea surface temperatures (SST), causing mass coral bleaching events (Sully et al. 2019) and reorganization of community structure (Stuart-Smith et al. 2017). Other negative impacts include increased metabolic stress, variation in growth and reproductive rates, and a decrease in calcification capacity in marine organisms (Harley et al. 2006, Brierley & Kingsford 2009, Barneche et al. 2018).

Reef fishes are key constituents of rocky and coral reefs, given their contribution in several ecosystem

functions (e.g. nutrient cycling and biomass production), and are an important source of food and livelihood for human societies worldwide (Moberg & Folke 1999, Villéger et al. 2017, Hicks et al. 2019). Ecology and conservation studies have focused primarily on describing patterns and changes in reef fish species richness, abundance, and biomass (Connolly et al. 2005, Floeter et al. 2007, Villéger et al. 2010). However, the use of trait-based approaches as proxies for functional structure to answer long-term and pressing ecological questions, such as how biodiversity varies along environmental gradients, or what the consequences of species loss are for ecological processes, has increased exponentially only in the last 2 decades (Mouillot et al. 2014).

Species traits can provide an essential tool to uncover and generalize biodiversity organization, allowing predictions of species and community effects on ecosystem functions and services (Mouillot et al. 2014). Moreover, trait-based ecology allows understanding of how aspects of history, ecology, and environment influence marine organisms at different spatiotemporal scales (Yeager et al. 2017). For instance, warmer seasons influence the functional composition of fish by selecting species with traits adapted for these conditions (Mouillot et al. 2013). Traits such as low generation time, rapid sexual maturity, and wide dispersal ability are correlated with warmer temperatures and tend to be more dominant under these circumstances (Pecuchet et al. 2017, McLean et al. 2018, Beukhof et al. 2019b). In this sense, temporal trait-based approaches may accurately detect how assemblages respond to environmental changes, considering that variations in species abundance promote trait turnover over time (Beukhof et al. 2019a, Pecuchet et al. 2020).

Trait-based reorganizations in communities over time have implications for the functioning of ecosystems (Pecuchet et al. 2020). For instance, studies in the Indo-Pacific showed that warmer temperatures increase macroalgae consumption by abundant herbivorous fish, affecting local productivity and nursery habitats (Bates et al. 2014, Hyndes et al. 2016, Vergés et al. 2016). However, despite the relevance of understanding how fish community traits vary over time, few studies have shown temporal variations (Anderson et al. 2020). Further, few studies have explored climate change projections and their effects on reef fish of the Atlantic Ocean (Inagaki et al. 2020). Therefore, considering the progressive increase in frequency and intensity of marine heatwaves in the Southwestern Atlantic in the last decade (Brauko et al. 2020), there is a need for characterizing community composition not only in terms of species richness and abundances, but also trait composition in response to these events.

Here, we used long-term survey data of reef fish assemblages sampled at 7 islands along an environmental transition zone in the Southwestern Atlantic to evaluate potential changes and variability in species trait composition over time using community weighted means (CWMs) and multivariate statistics. This area has been particularly impacted by global warming during the past decades and the intensification of the subtropical anticyclonic gyre, whereby the Brazil Current brings warm waters southwards (Franco et al. 2020). We also investigated potential changes in the thermal affinity dynamic using the community thermal index (CTI) and modeled the patterns and changes to assess whether they can be explained by recent warming. Since studies in the North Atlantic have shown that climatic oscillations drive modifications in functional structure (McLean et al. 2018, 2019a), we assessed whether variations in species abundance over the years can influence the trait composition in our study area. Thus, based on previous regional and global assessments of fish community responses to warming (Antão et al. 2020, McLean et al. 2021, Galvan et al. 2022), we hypothesized that tropical species are expanding their distribution range due to an increase in SST, whereas ranges of temperate species are contracting. This response was expected to occur in the present study area due to its location inside a transition zone, revealing a different pattern compared to other regions where temperate communities demonstrate wide distributional shifts (Fossheim et al. 2015). We also expected that warm-affinity traits would increase in their relative dominance in response to higher temperatures, while cold-affinity traits would decrease in dominance in the assemblages. In summary, our work aimed to investigate the temporal effects of warming on fish communities using CWM and CTI values as proxies for species range shifts in order to detect possible expansions and/or contractions in their distributions.

#### 2. MATERIALS AND METHODS

#### 2.1. Study area

The temporal variation in trait composition of reef fish assemblages was assessed at 7 islands located in the subtropical-warm-temperate transition zone of



Fig. 1. Sampled islands. Numbers indicate Galé Island (1), Deserta Island (2), Arvoredo Island (3), Aranhas Island (4), Xavier Island (5), Campeche Island (6), and Moleques do Sul Island (7). The color range represents the frequency of temperature below 16°C during the austral winter along the Santa Catarina coast

the Southwestern Atlantic (Fig. 1). By applying Ward clustering to species composition and abundance (for more detail, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m710p107\_supp.pdf), the islands were divided into northern (Galé, Arvoredo, and Deserta) and southern regions (Aranhas, Xavier, Campeche, and Moleques do Sul). Three of these islands are located inside of a marine protected area (MPA), the Arvoredo Marine Biological Reserve (i.e. Arvoredo: 27° 29' S, 48° 36' W; Deserta: 27° 27' S,

48°33'W; Galé: 27°18'S, 48°41'W), and 4 are located outside the MPA: Aranhas Islands (27°48'S, 48°36'W), Molegues do Sul (27°51'S, 48°26'W), Campeche (27°42'S, 48°27'W), and Xavier Island (27°36'S, 48°23'W). Furthermore, the northern islands showed generally higher temperatures, varying from 17.3 to 28.9°C (mean summer SST), whereas the southernmost islands experienced cooler conditions, varying from 15.6 to 26.8°C (mean summer SST) (Faria-Junior & Lindner 2019). The rocky reefs in all islands were mainly covered by algal turfs, erect macroalgae, and zoanthids without clear separation of benthic habitats along the depth range gradient (Aued et al. 2018). Due to their position between subtropical and temperate biogeographical zones, all islands were exposed to the same regional variation in temperature dynamics, which plays an important role in communities due to its change in short temporal scales (Beger et al. 2014). This temperature variation supports the overlap of tropical and subtropical reef fish fauna observed in the area (Ebeling & Hixon 1991, Anderson et al. 2015).

#### 2.2. Fish sampling

Reef fish assemblages were sampled during the summer seasons through 1306 underwater visual censuses (UVCs) made while scuba diving between 2008 and 2020. In each UVC, the diver began the process at the first encounter using a tape measure and visually identified, counted, and size-estimated (total length to the nearest centimeter) all actinopterygian fish species along belt transects ( $2 \times 20$  m, 95% of them at 1.5–18 m depth interval). While unwinding the tape, the diver collected data of noncryptic species (>10 cm) in the water column and while retracting the tape, followed the same procedure for bottom-associated and cryptic species (<10 cm) (Morais et al. 2017). All the census data considered in this study are available in Quimbayo et al (2023).

### 2.3. Fish traits

In order to represent the general ecology of species, all species observed in the UVCs were classified according to 16 traits representing their morphological, physiological, or behavioral adaptations and characteristics involved in the key processes of feeding/ resource acquisition, reproduction/growth, and survival/predator-avoidance aspects (Table 1). The clas-

Table 1. Traits compiled from Quimbayo et al. (2021). All trait information was compiled through a review of published checklists, online repositories, local reports, books, and monographs. For some traits, a combination of sources was used to obtain information for all species

Class/trait	Definition and categories	Category	Levels	Reference
Feeding/resom Activity	<b>rce acquisition</b> Period of the day that species feed and breed	Categoric	Day, night, or both	Robertson & Allen (2015), Robertson & Van Tassell (2019), Froese & Pauly (2021)
Caudal fin	Shape of caudal fin	Categoric	Forked, lanceolated, pointed, rounded, or truncated	Froese & Pauly (2021)
Depth range	Difference between the maximum and minimum depth reported for the species	Numeric	1	Robertson & Allen (2015), Robertson & Van Tassell (2019), Froese & Pauly (2021)
Diet	Main items consumed	Categoric	Herbivore–detritivore (feed on epilithic algal matrix), macroalgal (macroalgae > 1 cm high or seagrass), sessile invertebrates (corals, sponges, ascidians), mobile invertebrates (crustaceans, annelids, echino- derms, mollusks), planktonic (zooplankton, coelente- rates, detrital aggregates, etc.), omnivore (animal and plant and/or detrital material) or piscivore (fishes and cephalopods)	Robertson & Allen (2015), Robertson & Van Tassell (2019), Froese & Pauly (2021)
Geographic range distribution	Estimation from the number of grid cell $(5^{\circ} \times 5^{\circ})$ where a species has been recorded	Numeric		Parravicini et al. (2014)
Level in water	Position in water column	Categoric	Bottom (staying at the bottom all the time), low (live slightly above the bottom, occasionally rest on bottom), or high (several meters above the bottom)	Robertson & Allen (2015), Robertson & Van Tassell (2019), Froese & Pauly (2021)
Mouth position	Anatomic jaw position	Categoric	Superior (lower jaw protruding upwards), terminal (upper and lower jaws equal in length), subterminal (upper jaw protruding downwards), inferior (mouth in ventral position), tubular (enlargement of mouth cavity), or elongated (long snout due to the increase in the bones premaxillary, maxillary and dental)	Froese & Pauly (2021)
Trophic level	Position in the food web based on diet compo- sition and mean trophic level of food items	Numeric		Froese & Pauly (2021)
Reproduction/ç PLD	<b>growth</b> Pelagic larval duration	Discrete	I	Luiz et al. (2013)
Maximum body size	Maximum total length of species observed in the census	Numeric	I	Robertson & Allen (2015), Robertson & Van Tassell (2019), Froese & Pauly (2021)
Spawning	Way that species deposit eggs in water	Categoric	Attach to objects, demersal (deposit directly on the substrate), live (birth without external larval stage), oral (parental care when female or male keeps the eggs in their mouth), or pelagic	Froese & Pauly (2021)
ЦS	Species temperature index: average and maximum temperature estimated from temperature reported in each island where species occur	Numeric		Quimbayo et al. (2021)

Table 1 continued on next page

Class/trait	Definition and categories	Category	Levels	Reference
<b>Survival/pred</b> Aspect ratio caudal fin	<b>lator avoidance</b> Indicative of species activity calculated from the squared height of caudal fin divided by its surface area	Numeric	1	Froese & Pauly (2021)
Body shape	Morphological specialization for swimming	Categoric	Box shaped (globular as in Diodontidae), compressed (flattened laterally), depressed (flattened dorsoventrally), eel-like (elongated, snake-like shape and locomotion), elongated (long in relation to length), or fusiform (spindle shape, most hydrodynamic form)	Froese & Pauly (2021)
Group size	Gregariousness behavior	Categoric	Solitary, pairing, small groups (3–20 individuals), medium groups (20–50 individuals) or large groups (>50 individuals)	Froese & Pauly (2021)
Mobility	Area of activity	Categoric	Sedentary, territorial, mobile, or very mobile	Froese & Pauly (2021)

Table 1 (continued)

sification and selection of traits builds on previous trait-based descriptions of marine organisms (Litchman & Klausmeier 2008, Litchman et al. 2013) adopted in recent studies on marine fish community structure and changes (e.g. Dencker et al. 2017, Pecuchet et al. 2017, Beukhof et al. 2019a,b). These traits were obtained from Quimbayo et al. (2021).

#### 2.4. Environmental data

To test relationships and the effects of warming on trait composition across years, we included 2 abiotic variables representing local- and global-scale drivers. As a local driver, we used SST of each island sampled, while El Niño/Southern Oscillation (ENSO) was used as a global driver. SST, which has the potential to impact the dynamics of communities due to direct influence on fish distribution, metabolism, and/or growth (Morais & Bellwood 2018), was compiled for winter and summer seasons. Mean SST values per summer and winter season per year were extracted from multi-scale ultra-high-resolution SST analysis (Chin et al. 2017), which presents daily SST estimated on a global 0.01° × 0.01° grid available in the NOAA repository (https://coastwatch.pfeg.noaa. gov/erddap/index.html). We obtained the Monthly Multivariate ENSO index from NOAA's Earth System Research Laboratory (esrl.noaa.gov/psd/enso/ mei) and calculated mean values per summer and winter seasons to include in the analysis. ENSO values are a combination of different variables related to sea level pressure, temperature, wind, and radiation over the Tropical Pacific basin calculated for 12 overlapping bi-monthly seasons (Wolter & Timlin 1993, Kobayashi et al. 2015).

#### 2.5. Data analysis

Given that sampling effort was not uniform across years and in each island (Fig. S2), sample size was standardized using a rarefaction technique (Magurran & McGill 2011). We first identified the smallest sampled area ( $120 \text{ m}^2$ ) for each island and year, and then fixed this number for all other years as the minimal sampled area, and randomly sub-sampled individual transects until the minimal sampled area was reached. This method has been used to compare fish assemblages from oceanic islands (Quimbayo et al. 2019). As multiple combinations of transects could be used to compose the minimal sampled area, samples for any given combination of year and island were bootstrapped 1000 times to produce distributions of species composition and abundance along the study area (Figs. S3–S9). In each permutation, we conducted the analysis to explore community trait variation and at the end of the bootstrap, where the mean values were used as input for the subsequent analysis.

Following bootstrapping, we conducted a multiple factor analysis (MFA) (Abdi & Valentin 2007) to identify temporal trait dynamics in the 7 islands of the transition zone. This multivariate analysis takes into account the structure of data in groups (Abdi & Valentin 2007), which in our study corresponds to 3 classes of traits (feeding/resource acquisition, reproduction/growth, and survival/predator avoidance). The data division balances the contribution of each group of traits to the total variation and allows quantifying the contribution of the most important ones. For each year, temporal trait dynamics were evaluated through CWMs (Lavorel et al. 2008), as trait values weighted by  $\log_e (x + 1)$  abundance of species to meet the assumption of equal variances in statistical analysis. Since samples were bootstrapped, we used the mean CWM values of all traits within classes obtained from reef fish composition in each island and year as input for the MFA analysis. This serves to illustrate community trait variation through time along the transitional zone but may not reflect the full range of variation in traits within individual islands. The results displaying temporal trait changes per year were summarized by assessing the loadings on the first and second dimension of the MFA. For modeling, we used only values of the first dimension since they account for the most part of the total variability. To test the sensitivity of results to the inclusion or exclusion of species targeted by local fishermen, we repeated the analysis while excluding all species classified as being under heavy fishing pressure (e.g. species targeted by multiple gear types or fishing methods across a wide range of coastline) according to Floeter et al. (2006). One mean value per region per year was used in the analysis to address potential fishing effects in large and high trophic level species over time.

To quantify warming signals, we estimated the CTI for each year based on the average thermal affinity of the community. A thermal distribution was constructed for all 147 fish species recorded, using occurrence records from available checklists of distribution (Quimbayo et al. 2021) combined with mean SST from the Bio-ORACLE data set (Assis et al. 2018). Based on the corresponding temperature reported in each locality where species were present, a temperature distribution was obtained for each

species. We used the midpoint of distribution as a measure of the central thermal tendency for each species, or thermal affinity. The midpoint was chosen to be less sensitive to the distribution across the temperature range of species (Stuart-Smith et al. 2015). The CTI was calculated from the average of thermal midpoint values for species recorded by year in each island, weighted by their log (x + 1) abundance. This measure is considered a useful proxy for detecting responses to climate change, since it reflects immediate turnover under extreme temperatures (Burrows et al. 2019). To better visualize trajectories in CTI, we compared these values with SST in both inside and outside MPA which can be grouped, respectively, into northern and southern islands. Moreover, this separation also corresponds to warmest and coldest regions and allows us to compare different community responses to temperature.

To examine potential collinearity among the predictors used in the models, we used Pearson's correlation, considering a correlation coefficient  $r < \pm 0.7$ as a cut-off value (Fig. S10), since values below this threshold are unlikely to involve multicollinearity in models (Dormann et al. 2013). We tested for the effect of SST and ENSO in summer and winter seasons, locality (i.e. the 7 islands), and survey (i.e. inside/outside MPA) on the CWM trait and CTI values per year using generalized additive models (GAMs) with Gaussian distribution. This distribution was chosen considering the nature of the data (continuous values from negative to positive sign) and that the residuals are normally distributed (Zuur et al. 2009). The degrees of freedom of the spline smoother function (s) were further constrained to 3 knots (k = 3) to allow for potential non-linearities, but also restrict flexibility and risk of overfitting. We performed a set of models testing for survey (inside or outside MPA) as specific slopes of SST and ENSO in summer and winter separately, and using islands as fixed factors to account for any geographical (i.e. latitudinal) differences between sites, not represented by variation in temperature. We then performed a model selection approach using Akaike's information criterion (AIC) (Burnham & Anderson 2002). The significance of predictors in the final model was evaluated using  $p \le 0.05$ , and to ensure model assumptions were satisfied, we verified the normal distribution of residuals (Figs. S11-S14). All statistical analysis were done in R 4.0.2 (R Core Team 2020), using the libraries 'FactoMineR' (Lê et al. 2008, Husson et al. 2013), 'mgcv' (Wood 2017), 'FD' (Laliberté et al. 2015), and 'car' (Fox & Weisberg 2019).

## 3. RESULTS

#### 3.1. Temporal patterns of trait composition

Our results showed that 30.1% of the total variability in CWM traits for the whole community weighted by abundance was explained by the first dimension (Dim 1, Fig. S15). This dimension displays a gradual temporal change in trait composition from positive to negative values from 2008 to 2020, with rather low inter-annual variability (Fig. 2a). The feeding, reproduction, and survival traits each contribute to around 30% of the explained variance, indicating that all broad trait groups have the same importance on Dim 1 (Fig. 2a). At the start of the time period, the fish assemblages are characterized by high weighted abundance of large and mobile species, as reflected by the positive loadings of these traits on Dim 1 (Fig. 2b). In the first years, the traits fusiform, mobile, pelagic spawners, large body size, forked caudal fin, and low-level water habitat dominated, hence highlighting the presence of predator species at the beginning of the time series. For instance, species belonging to highest trophic levels such as the grouper Epinephelus marginatus were frequent at the beginning of the time series, but were not represented in the last few years (Fig. S16). In contrast, the community trait composition in the latest years was primarily composed of species with traits such as elongated body, sedentary, demersal spawners, and bottom-associated, as indicated by the negative loadings. This reflects an increase in the abundance of small and cryptic species, such as Parablennius pilicornis and P. marmoreus, which have become relatively more abundant in recent years (Fig. S16). The average body size in the first years ranged from 5 to 32 cm, whereas throughout the remaining years it ranged from 1 to 26 cm. Dim 1 also shows fluctuations in the abundance of the tropical-affinity species Priacanthus arenatus and the exotic cooler-water species Chromis limbata.

The second dimension (Dim 2) accounts for 19.7% of the total variability in CWM traits weighted by abundance but does not display a clear and consistent decreasing trend across islands (Fig. 2c). Growth traits explain a large part of the CWM trait variability (37.1%), followed by survival (35.2%) and feeding traits (27.7%). This dimension mainly captures the variation in the proportion of individuals with the traits box-shaped, large body size, and rounded caudal fin in the early years (Fig. 2d). These traits refer to species such as *Stephanolepis hispidus*, which was more prevalent in early years (Fig. S16). On the other

hand, species forming large groups, having low thermal affinity (i.e. low values of CTI) and with terminal mouths were most abundant in recent years. These traits correspond to cryptic species, such as *Malacoctenus delalandii* and *Coryphopterus glaucofraenum*, which became more abundant in recent years, as well as *Chaetodipterus faber*, a species often found to form schools (Fig. S16).

The temporal trends for reef fish traits when excluding fishing target species were similar to those found when considering the entire community. The dimensions of MFA revealed a negative trend associated with the predominance of large and high trophic level traits at the beginning of the time series, while cryptobenthic traits were most abundant in the later years (Fig. S17).

#### 3.2. Temporal patterns of the CTI

We observed an increase in abundance of warmaffinity species over time reflected by the higher CTI values (Fig. 3), whilst some tropical species also showed increasing trends in abundance (Fig. S18). The trend is even more pronounced for southern islands, revealing a spatial response of fish assemblages in terms of thermal affinity. This trend was related to the corresponding shifts in environmental temperature for both outside the MPA (southern) and inside the MPA (northern) islands and broadly followed patterns in SSTs of the Southwestern Atlantic transition zone. Particularly for islands outside the MPA, the observed CTI values were slightly below the SST, compared to islands inside the MPA. The CTI trends of the community without the fishing target species were also similar to the trends observed for the whole fish community (Fig. S19).

# 3.3. Environmental effects on CWM and CTI dynamics

The overall trait dynamic represented by Dim 1 of the MFA for the whole community was negatively related to summer SST without specific slopes (inside/outside MPA) in the model (p = 0.012, Fig. 4). The final GAM selected by AIC explained 35% of the total variance (Table 2). Furthermore, the islands (i.e. fixed factor) inside the MPA (Arvoredo, Deserta, and Galé; Table 3) had significantly higher intercepts. This result indicates differences between regions not only in terms of taxonomic composition, as previously mentioned, but also in terms of trait composition. In



Fig. 2. Temporal variation in the reef fish traits (community weighted mean, CWM) weighted by abundances in several islands of Santa Catarina, Brazil, arranged by latitudinal gradient (Galé, Deserta, Arvoredo, Aranhas, Xavier, Campeche, and Moleques) obtained from multiple factor analysis (MFA). After bootstrapping, mean CWM values were used as input to conduct the MFA resulting in a single value per island per year. Time-series of (a) Dimension (Dim) 1 and (c) Dim 2 of CWM trait variability and the contribution of each group of traits to the overall dynamic. CWM trait loadings displayed for (b) Dim 1 and (d) Dim 2. The classes of traits on the top right of panels a and c are represented by colors: gray (feeding), violet (growth), and green (survival) and show the contribution of each group to the total variation. Horizontal red dashed line highlights 30%. The vertical black dotted line separates loading values higher and lower than 0.5. Trait loadings >0.5 were considered as the most important for the temporal trends. The circled numbers in the key correspond to the island numbers in Fig. 1. PLD: pelagic larval duration; CTI: community thermal index; HM: macroalgal feeder; HD: herbivore-detritivore; IS: sessile invertebrate; IM: mobile benthic invertebrate; FC: planktivore; OM: omnivore





Year

Fig. 3. Sea surface temperature (SST) in the (a) northern and (b) southern region of the Santa Catarina transition zone from 2008 to 2020, and associated community thermal index (CTI) trends for reef fishes weighted by abundance. Northern and southern regions are equivalent to inside and outside of the marine protected area (MPA), respectively. CTI represents the mean of the species temperature index for all species recorded in a survey weighed by their abundances and is presented here as the mean across all surveys in each year. 'Summer SST' represents the mean SST in summer on each survey date

terms of CTI, the final GAM explained 68% of the variability (Table 2), where the increasing trend in CTI over time was positively related to winter SST (Fig. 5a) but showed a significant slope only inside the MPA (northern islands, p < 0.01). Furthermore, the model demonstrated a significant effect of island, where those inside the MPA (Arvoredo, Deserta, and Galé) showed higher intercepts, indicating a higher mean CTI compared to islands outside the MPA (southern islands; Table 3). These results were not obtained while analyzing islands separately in regressions (Table S1).

The trait dynamic for the community after removing fisheries target species was also negatively related to summer SST (p < 0.01, Table 3). However, the CTI model showed a positive relation to summer SST only on islands outside the MPA (p =0.01 for Aranhas, Xavier, Campeche, and Moleques do Sul, Fig. 5b). We did not observe any effect of ENSO for any model.

## 4. **DISCUSSION**

Our study is the first assessment in the Southwestern Atlantic transition zone that investigated the temporal variation in trait composition of reef fish assem-



Fig. 4. Generalized additive model smooth plot showing the partial effects of summer SST on the community weighted mean (CWM) dynamic for the whole community. Trends for data excluding fishing target species were the same; data not shown. The gray band indicates the 95% confidence interval, and the dots represent the partial residuals of the model

Table 2. Model selection using Akaike's information criterion (AIC) of generalized additive models for community weighted mean (CWM) traits and community thermal index (CTI) values considering the whole community data set and when excluding fishing target species. The islands were considered as a fixed factor and the survey (inside/outside marine protected area) as specific slopes (smooth term in the model) for sea surface temperature (SST) and El Niño/ Southern Oscillation (ENSO) values for winter and summer seasons. Results are presented for the best models in Table 3. All combinations tested with their corresponding degrees of freedom (df) and adjusted coefficient of determination  $(r^2 adj)$  are shown

Response variable	AIC	df	r² adj
Model			3
CWM traits (whole community)			
s(summer SST) + Survey + Island	132 59	Q	0.35
s(summer SST) + Survey + Island	134.37	10	0.33
s(summer ENSO) + Survey + Island	134.37	0	0.33
s(winter ENSO) + Survey + Island	130.81	10	0.24
s(winter SST) + Survey + Island	140.38	0	0.21
s(summer ENSO, by = Survey) + Island	140.30	9	0.13
s(winter ENSO, by = Survey) + Island	140.75	10	0.23
s(winter SST, by = Survey) + Island	142.35	10	0.10
CWM traits (without fishing target species)			
s(summer SST) + Survey + Island	129.73	9	0.41
s(summer SST, by = Survey) + Island	130.99	10	0.40
s(summer ENSO) + Survey + Island	136.93	9	0.28
s(winter ENSO) + Survey + Island	137.98	10	0.24
s(winter SST) + Survey + Island	138.89	9	0.23
s(summer ENSO, by = Survey) + Island	139.45	9	0.28
s(winter ENSO, by = Survey) + Island	140.15	10	0.23
s(winter SST, by = Survey) + Island	141.32	10	0.21
CTI (whole community)			
s(winter SST, by = Survey) + Island	6.19	10	0.68
s(summer SST) + Survey + Island	7.29	11	0.67
s(summer SST, by = Survey) + Island	7.72	10	0.68
s(winter SST) + Survey + Island	11.77	9	0.62
s(summer ENSO) + Survey + Island	12.30	10	0.61
s(summer ENSO, by = Survey) + Island	13.27	9	0.63
s(winter ENSO) + Survey + Island	14.98	9	0.59
s(winter ENSO, by = Survey) + Island	15.45	11	0.60
CTI (without fishing target species)			
s(summer SST, by = Survey) + Island	2.10	11	0.74
s(summer SST) + Survey + Island	2.27	10	0.74
s(winter SST, by = Survey) + Island	2.85	10	0.73
s(summer ENSO, by = Survey) + Island	6.65	10	0.71
s(winter SST) + Survey + Island	7.04	9	0.70
s(summer ENSO) + Survey + Island	8.95	9	0.68
s(winter ENSO, by = Survey) + Island	9.26	11	0.69
s(winter ENSO) + Survey + Island	9.31	9	0.68

blages. Our results showed that all islands broadly followed the same general pattern of change over time. The trait composition changed substantially, reflecting variations in species abundances. Additionally, we found signs of warmer thermal affinity in response to rising temperatures, supporting our hypothesis that tropical species are expanding their range distribution in response to an increase in SST. These patterns reveal a new perspective for temporal changes in the Southwestern Atlantic transition zone, since previous studies did not find any relationship between global predictors (e.g. El Niño and La Niña) and species-specific data (Anderson et al. 2020).

The trait changes observed during the 13 yr period indicate recent, largescale reorganizations of fish assemblages in this area in response to ocean warming. The traits showing the largest changes were the same for all islands and reflect a general decrease in larger-sized predator species (e.g. groupers) and an increase in smaller, bottom-dwelling species (i.e. cryptobenthic fish), even after removing the fishing target species from the data set. Changes in the trait composition can be related to a shift in the dominance of different lifehistory strategies (Pecuchet et al. 2017, Beukhof et al. 2019b), notably a general increase in species with rapid growth and short generation time, which favor a faster population increase in response to temperature variations (McLean et al. 2018, Brandl et al. 2020). The increase in smaller and opportunistic species in the communities over time would lead to faster turnover by introducing novel trophic interactions and modifying mortality and competition rates (Cantor et al. 2018). Body size is considered one of the most influential traits in behavior and demographic characteristics (such as diet, dispersal, metabolic rate, and mortality rates; Luiz et al. 2013, Barneche et al. 2019), consequently influencing nutrient transport, trophic regulation, and community composition (Tavares et al. 2019). In this sense, food webs can be affected by species

variations reducing their stability and robustness due to the depletion of large and highly connected species (Navia et al. 2016). In healthy and protected ecosystems, the high energy transfer efficiency is maintained in part by a high production of lower trophic levels which is converted into production at the upper trophic levels reflected by their higher abundance and biomass (Seguin et al. 2023). Conversely, fish communities in the Southwestern Atlantic could

represent the complexity of the Table 3. Effects of islands and abiotic predictors on the community weighted mean (CWM) values and community thermal index (CTI) for the whole community and the community without fishing target species based on generalized additive models with Gaussian distribution selected by Akaike's information criterion. The islands were considered as a fixed factor and the surveys (inside/outside marine protected area, MPA) as specific slopes for sea surface temperature (SST) and El Niño/Southern Osof results in relation to the null hypothesis. Significant values (p < 0.05) are highlighted in **bold**; (estimated degrees of freedom) and df ns: nonsignificant in the model Edf ( for each parametric coefficient. smooth term in the model. The p-value represents the significance Standard error (SE) was estimated cillation (ENSO) values.

				Vhole con	nmunity —	H ک				M	- Withon	ut fishinç	J target speci	es		
imate SE	SE C	M	$\frac{1}{t}$	р	Estimate	SE	t	d	Estimate	SE SE	M t	р	Estimate	SE CI	t	d
2.21 0.9	0.0	06	-2.43	0.02	24.64	0.16	148.74	<0.01	-2.43	0.87	-2.79	< 0.01	24.72	0.15	160.58	< 0.01
0.67 0.	0	39	1.69	0.10	0.89	0.17	5.02	<0.01	0.81	0.37	2.13	0.04	0.81	0.16	4.91	< 0.01
0.30 1	-	.57	0.19	0.84	-0.06	0.31	-0.19	0.84	0.25	1.51	0.16	0.86	-0.59	0.26	-2.20	0.03
1.19 0	0	.42	2.83	< 0.01	0.97	0.18	5.34	<0.01	1.26	0.40	3.01	< 0.01	0.95	0.17	5.64	< 0.01
0.26 0	0	.45	0.57	0.56	1.01	0.18	5.42	<0.01	0.21	0.43	0.50	0.61	0.93	0.17	5.36	< 0.01
1.78 1	1	.60	1.11	0.27	-0.06	0.28	-0.21	0.82	1.87	0.54	1.21	0.23	0.15	0.29	0.51	0.61
0.11 1	1	.07	1.03	0.30	0.48	0.19	2.49	0.01	1.43	1.03	1.39	0.17	0.47	0.18	2.59	0.01
Edf		df	F	d	Edf	df	F	d	Edf	df	F	đ	Edf	df	F	d
1		1	7.18	0.01	ns				1	1	8.85	< 0.01	Inside MP/	4		
													1.73 Outside MP	1.92 A	1.32	0.23
													1	1	6.28	0.01
ns					Inside MPA				ns				ns			
					1	1	8.42	< 0.01								
				Ū	Outside MP	A										
					1	1	1.84	0.18								
ns					su				ns				ns			
ns					ns				su				su			
	1															

be experiencing a higher turnover associated with the positive temperature response of small and lower trophic level species with fast growth, suggesting disruption of the ideal trophic structure. Thus, it is important to recognize the implications of trait reorganization on the structure and functioning of ecosystems, since these temporal changes could result in higher community variability and vulnerability to environmental changes.

A pronounced decline in the values of CWM was revealed for all islands. Although our results demonstrated changes in reef fish abundances, with an overall increase in cryptic species, this does not necessarily reflect a decrease in the abundance of large-sized species (Fig. S18). Furthermore, many large-sized and high trophic level species could be growing and increasing in total length over years, especially in the northern islands (Arvoredo, Galé, and Deserta located within the Arvoredo MPA). Effective MPAs promote larger species and optimize marine biodiversity conservation (Edgar et al. 2014). Therefore, the large individuals present in early 2008 could still be present and growing in size and biomass in later years, even if the actual abundances are unchanged, as shown in another study at the same MPA (Anderson et al. 2020). Taken together, our results indicate that the temporal trait changes observed across the transition zone are primarily due to numerical responses of species abundance to warming, while potential changes in fishing pressure may have played a minor, or more local, role on the overall trait dynamic. This can be supported by the same trends found in the analysis excluding fishing target species from the data set. Nevertheless, we stress the need for further studies investigating the unique and cumulative impact of fishing and other anthropogenic stressors, including



Fig. 5. Generalized additive model smooth plots showing the partial effects of sea surface temperature (SST) on the community thermal index (CTI) dynamic for (a) the whole community and (b) the community after removing fishing target species in islands inside and outside of the marine protected area (MPA) of the Southwestern Atlantic transition zone. For CTI models, results (specific slope) were significant inside the MPA when the whole community was analyzed and outside the MPA when excluding fishing target species (represented by asterisks, \*). Gray bands indicate 95% confidence intervals, and the dots represent the partial residuals of the models

climate change and habitat loss on the trait composition of reef fish communities worldwide (Pecuchet et al. 2020, Pinsky et al. 2020).

The abundance-driven changes in traits observed in our study underpin community reorganization with increasing temperatures. This change was also evident in trends of CTI weighted by abundances using the whole data set and filtering fishing target species, which showed reef fish assemblages to be responsive to temperature. For islands located in both the northern and southern part of this transition zone, CTI followed the increasing trends of SST, suggesting CTI to be a good indicator of community changes associated with temperature variations (Day et al. 2018). Underlying the changes in CTI is an increase in abundance of tropical species over time, while temperate species were becoming less abundant (Fig. S11). This is in line with findings from previous studies in transition zones (Vergés et al. 2014, Horta e Costa et al. 2014), albeit to a lesser extent. For instance, in the tropical-temperate reefs of Australia, the range extension of tropical herbivorous fishes (tropicalization) shifts the community to an alternate kelp-free state, threatening the stability of these ecosystems (Vergés et al. 2016). We could not assume the same response for the Southwestern Atlantic reefs, since the benthic structure is mainly composed of turf algae (Aued et al. 2018), which does not support the same functional richness as other marine regions where corals are dominant (Mouillot et al. 2014). On the other hand, we may foresee a potential increase in the demographic connectivity of tropical species in future years due to their ability to acclimate to ocean warming (Lima et al. 2021). As an example, observations of tropical parrotfishes such as Sparisoma spp. and Scarus trispinosus have become more frequent in Santa Catarina over the last 3 yr (S. R. Floeter pers. obs.). In the future, this increase in abundance may trigger a gradual process of tropicalization. Interestingly, our results indicate that the fish communities have more tropical affinity than expected, because the maximum values of CTI are close to the maximum SST values, especially in the northern islands. Therefore, the species composition in this area is mostly constituted of species with tropical affinity. However, species inhabiting transition zones are less tropical and more temperate due to the wider thermal tolerance allowing them to withstand temperatures higher than their optimal (Rummer & Munday 2017). This may imply that the communities in our study area have lower thermal vulnerability and are potentially more resilient to climate disturbances because of their wide thermal tolerance. Considering that the CTI values were below SST outside the MPA (southern islands), we could expect a negative impact of extreme minimum temperatures, due to the inability of the fish to maintain homeostasis during colder periods (Feary et al. 2014).

Our results suggest that warmer temperatures can profoundly alter trait composition in reef fish communities. Warmer SSTs in the summers were related to an increase in cryptobenthic fish traits, such as elongated body, demersal spawning, and a bottomdwelling habitat association. These findings agree with previous studies showing fish trait changes with increasing temperatures (McLean et al. 2018, 2019b, Beukhof et al. 2019a). Temperature-driven changes in fish populations may occur through a range of physiological and/or behavioral responses (avoiding unsuitable habitats), changes in the balance between mortality, growth, and reproduction during thermal stress, and changes in productivity and/or trophic interactions (Rijnsdorp et al. 2009). During summer, the SST in the Southwestern Atlantic shelf is generally warmer near the coast due to seasonal stratification, averaging 25.5°C, while the winter average SST is lower (18.2°C; this study, see Section 2.1) and vertically more homogeneous as a consequence of weak currents (Matano et al. 2010). Thus, the mechanism behind our observed pattern could be explained by the metabolic theory, which states that warm waters accelerate growth and reproduction of short-lived small species, whereas cold waters favor the dominance of large and slow-growing species (Pecuchet et al. 2017, Beukhof et al. 2019b).

The increase in the thermal average of communities driven by warming, as illustrated by higher CTIs, suggests a strong indication of the sensitivity of ocean communities in response to climate changes (Burrows et al. 2019). CTI for the whole community inside the MPA shows a positive response to winter SST, reflecting the tolerance and maintenance of species to higher temperatures reached in winter (±20°C). In other words, maximum winter temperatures are within the range of temperatures encountered in summer, which are tolerated by the community. When fishing target species are removed from the data set, summer SST becomes the driver of CTI, and the trend remains positive. This highlights that species other than fishing targets are responding to the increase in temperature. However, our sampled area is located in a transition zone and is affected by southern winds during winter, which transport nutrients and contribute to decrease sea temperatures (Lopes et al. 2006, Bordin et al. 2019). This suggests that in the southern hemisphere, the impact of warming in fish communities could be less intense due to the buffering action of cold-water currents (Inagaki et al. 2020). Studies using mark-recapture techniques could be helpful to verify whether tropical species can tolerate winter conditions and remain in the region over consecutive summer seasons, which would confirm a tropicalization trend. Additionally, temperature also plays an important role in the vertical structure and distribution of marine organisms through stratification (Rijnsdorp et al. 2009). Comparing aspects of physiology such as the optimum temperature for aerobic performance among fish populations also provides a tool to test whether species are adapting to their thermal environment (Rummer & Munday 2017). In this sense, further studies examining temporal trends of ecological traits could be improved by taking into account the effects of water column stratification on the depth distribution of fish species, in addition to horizontal changes in distributions (range expansion) and physiological tolerance to warming. Considering the unknown effects of the increased frequency of marine heatwaves in the Southwestern Atlantic (Rodrigues et al. 2019, Brauko et al. 2020), more integrative studies are needed to identify reorganizing patterns in fish community structure and their links to environmental changes.

Overall, out results have important implications, demonstrating that communities respond to environmental changes altering species abundances and reorganizing trait composition according to external factors. This study presents new evidence about the increase in frequency of warm-affinity species in response to temperature, although less intense than the tropicalization processes observed in other marine provinces located at the same latitude and in the northern hemisphere (Vergés et al. 2014, 2019). Therefore, tropicalization should be evaluated not only considering shifts in abundance of species, but also variations in terms of species traits, which can present a different response to the environmental temperature.

#### 5. CAVEATS

Although Aranhas and Moleques islands have few years of data, the inclusion of these southernmost islands increases sample size and variability and highlights the differences between regions. Furthermore, our standardization method based on resampling the minimal sampled area, which is equivalent to a sample-based rarefaction procedure for species richness (Gotelli & Colwell 2001), was fully developed to cope with such limitations while incorporating most of the data set rather than excluding UVCs and/or islands. Although we did not specifically account for the potential effects of MPA performance in our study, it has been shown to play a role in determining species and trait composition (Hackradt et al. 2014, Karlovic et al. 2021). However, since we obtained similar results for both inside and outside MPAs when repeating all analyses while excluding fishing target species, we deem these effects to be of less direct importance. This implies that the observed trait responses likely result primarily from variations in SST rather than other factors, including fishing. Nevertheless, we stress the need for information and data regarding MPA enforcement and performance

to assess potential fishing impacts on fish community composition in the area. Lastly, habitat quality/composition would also play an important role filtering species and trait dominance in the system (Aued et al. 2018). Regardless of lack of data, we acknowledge that species pool metrics may be influenced by habitat, and further studies including this variable would certainly be useful in understanding trait dynamics over time. Thus, despite the limitations due to the lack of fishing effort data, MPA performance, and quality composition to include in the present analysis, we have provided interesting results and insights for the ecology of reef fish in the Southwestern Atlantic. Our findings open an avenue for further studies to investigate potential impacts of these aspects on trait composition of reef fish communities.

#### 6. CONCLUSIONS

The gradual trait reorganization observed in the Southwestern Atlantic subtropical-warm-temperate transition zone has potential implications for reef ecosystem functioning. Trophic dynamics, for instance, could be affected if the abundance of smaller and r-selected species (see definition in McLean et al. 2018) changes over time, leading to variations in prey consumption of large piscivorous species (McLean et al. 2019a). The assemblage, which was composed of large fish at the beginning of the time series, became dominated by small cryptobenthic species in recent years. These can produce large amounts of consumable biomass and larvae that dominate the near-reef ichthyoplankton (Brandl et al. 2019). This shift may directly impact the energy transfer in reef habitats and can provide insights for future studies on the underlying mechanisms of reef ecosystem functioning and its changes in space and time. Overall, the trait reorganization can lead to changes in the food web structure, ecosystem functioning, and community vulnerability. Notably, the increase in smaller, opportunistic species may lead to faster turnover, lower food-chain complexity, and higher vulnerability to change.

Our study shows the influence of warming on community trait structure, indicating possible responses of reef fish assemblages to ongoing climate changes. Considering the progressive increase in SST (Frölicher et al. 2018) and marine heatwaves (Brauko et al. 2020), and that some responses to disturbances are only detected by a functional-trait view (Mouillot et al. 2013), our approach could help to reach a holistic understanding of reef fish dynamics under environmental variations in the Southwestern Atlantic. Acknowledgements. The time-series data were collected thanks to the field support of ICMBio and the Marine Macroecology and Biogeography Laboratory (LBMM) staff and students over time and to the following projects and their funding sources: Projeto Ilhas do Sul (CNPq 475367/ 2006-5 - PI: S.R.F.), SISBIOTA-Mar (CNPg 563276/2010-0; FAPESC 6308/2011-8 - PI: S.R.F.), Projeto MAArE - Monitoramento Ambiental do Arvoredo e Entorno (PI: B.S.). F.C.S. acknowledges her CAPES scholarship. F.C.S., M.L. and S.R.F. are supported by the Mission Atlantic project (European Union's Horizon 2020 Research and Innovation Program under Grant Agreement N° 862428). S.R.F is supported by a CNPg research productivity grant (307340/ 2019-8). J.P.Q. received a post-doctoral fellowship from FAPESP (2018/21380-0 and 2021/09279-4). We also thank 2 anonymous reviewers for their constructive comments, as well as Neil Maginnis for additional input and assistance regarding use of grammar and language.

#### LITERATURE CITED

- Abdi H, Valentin D (2007) Multiple factor analysis (MFA). In: Salkind NJ (ed) Encyclopedia of measurement and statistics. SAGE Publications, Thousand Oaks, CA, p 1–14
- Anderson AB, Carvalho-Filho A, Morais RA, Nunes LT, Quimbayo JP, Floeter SR (2015) Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records. Check List 11:1688
- Anderson AB, Joyeux JC, Floeter SR (2020) Spatiotemporal variations in density and biomass of rocky reef fish in a biogeographic climatic transition zone: trends over 9 years, inside and outside the only nearshore no-take marine-protected area on the southern Brazilian coast. J Fish Biol 97:845–859
- Antão LH, Bates AE, Blowes SA, Waldock C and others (2020) Temperature-related biodiversity change across temperate marine and terrestrial systems. Nat Ecol Evol 4:927–933
- Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O (2018) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Glob Ecol Biogeogr 27:277–284
- Aued AW, Smith F, Quimbayo JP, Cândido DV and others (2018) Large-scale patterns of benthic marine communities in the Brazilian province. PLOS ONE 13:e0198452
- Barneche DR, Robertson DR, White CR, Marshall DJ (2018) Fish reproductive-energy output increases disproportionately with body size. Science 360:642–645
- Barneche DR, Rezende EL, Parravicini V, Maire E and others (2019) Body size, reef area and temperature predict global reef-fish species richness across spatial scales. Glob Ecol Biogeogr 28:315–327
- Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ (2014) Resilience and signatures of tropicalization in protected reef fish communities. Nat Clim Change 4:62–67
- Beger M, Sommer B, Harrison PL, Smith SDA, Pandolfi JM (2014) Conserving potential coral reef refuges at high latitudes. Divers Distrib 20:245–257
- Beukhof E, Dencker TS, Pecuchet L, Lindegren M (2019a) Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Mar Ecol Prog Ser 610:205–222

- Beukhof E, Frelat R, Pecuchet L, Maureaud A and others (2019b) Marine fish traits follow fast-slow continuum across oceans. Sci Rep 9:17878
- Bordin LH, Machado EC, Carvalho M, Freire AS, Fonseca ALDO (2019) Nutrient and carbon dynamics under the water mass seasonality on the continental shelf at the South Brazil Bight. J Mar Syst 189:22–35
- Brandl SJ, Tornabene L, Goatley CHR, Casey JM and others (2019) Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. Science 364:1189–1192
- Brandl SJ, Johansen JL, Casey JM, Tornabene L, Morais RA, Burt JA (2020) Extreme environmental conditions reduce coral reef fish biodiversity and productivity. Nat Commun 11:3832
- Brauko KM, Cabral A, Costa NV, Hayden J and others (2020) Marine heatwaves, sewage and eutrophication combine to trigger deoxygenation and biodiversity loss: a SW Atlantic case study. Front Mar Sci 7:590258
- Brierley AS, Kingsford MJ (2009) Impacts of climate change on marine organisms and ecosystems. Curr Biol 19: R602–R614
  - Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY
- Burrows MT, Bates AE, Costello MJ, Edwards M and others (2019) Ocean community warming responses explained by thermal affinities and temperature gradients. Nat Clim Change 9:959–963
  - Cantor M, Longo GO, Fontoura L, Quimbayo JP, Floeter SR, Bender MG (2018) Interaction networks in tropical reefs.
    In: Dáttilo W, Rico-Gray V (eds) Ecological networks in the Tropics: an integrative overview of species interactions from some of the most species-rich habitats on Earth. Springer, Cham, p 141–154
- Chin TM, Vazquez-Cuervo J, Armstrong EM (2017) A multiscale high-resolution analysis of global sea surface temperature. Remote Sens Environ 200:154–169
- Connolly SR, Hughes TP, Bellwood DR, Karlson RH (2005) Community structure of corals and reef fishes at multiple scales. Science 309:1363–1365
- Day PB, Stuart-Smith RD, Edgar GJ, Bates AE (2018) Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation. Divers Distrib 24:1036–1046
- Dencker TS, Pecuchet L, Beukhof E, Richardson K, Payne MR, Lindegren M (2017) Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: causes and consequences. PLOS ONE 12:e0189731
- Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46
  - Ebeling AW, Hixon MA (1991) Tropical and temperate reef fishes: comparison of community structures. In: PF Sale (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, p 509–563
- Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–220
- Faria-Junior E, Lindner A (2019) An underwater temperature dataset from coastal islands in Santa Catarina, southern Brazil: high accuracy data from different

122

depths. SEANOE. https://www.seanoe.org/data/00510/ 62120/

- Feary DA, Pratchett MSJ, Emslie M, Fowler AM and others (2014) Latitudinal shifts in coral reef fishes: Why some species do and others do not shift. Fish Fish 15:593-615
- Floeter SR, Halpern BS, Ferreira CEL (2006) Effects of fishing and protection on Brazilian reef fishes. Biol Conserv 128:391–402
- Floeter SR, Krohling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environ Biol Fishes 78:147–160
- Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Change 5:673–677
- Fox J, Weisberg S (2019) An R companion to applied regression, 3<sup>rd</sup> edn. Sage, Thousand Oaks, CA
- Franco BC, Defeo O, Piola AR, Barreiro M and others (2020) Climate change impacts on the atmospheric circulation, ocean, and fisheries in the southwest South Atlantic Ocean: a review. Clim Change 162:2359–2377
- Froese R, Pauly D (2021) FishBase. www.fishbase.org (accessed on 13 August 2021)
- Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560:360–364
- Galvan DE, Bovcon ND, Cochia PD, González RA and others (2022) Changes in the specific and biogeographic composition of coastal fish assemblages in Patagonia, driven by climate change, fishing, and invasion by alien species. In: Helbling EW, Narvarte MA, González RA, Villafañe VE (eds) Global change in Atlantic coastal Patagonian ecosystems – a journey through time. Springer, Cham, p 205–231
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391
- Hackradt CW, García-Charton JA, Harmelin-Vivien M, Pérez-Ruzafa A and others (2014) Response of rocky reef top predators (Serranidae: Epinephelinae) in and around marine protected areas in the Western Mediterranean Sea. PLOS ONE 9:e98206
- Harley CDG, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241
- Hicks CC, Cohen PJ, Graham NAJ, Nash KL and others (2019) Harnessing global fisheries to tackle micronutrient deficiencies. Nature 574:95–98
- Holbrook NJ, Sen Gupta A, Oliver ECJ, Hobday AJ and others (2020) Keeping pace with marine heatwaves. Nat Rev Earth Environ 1:482–493
- Horta e Costa B, Assis JM, Franco G, Erzini K, Henriques M, Gonçalves EJ, Caselle JE (2014) Tropicalization of fish assemblages in temperate biogeographic transition zones. Mar Ecol Prog Ser 504:241–252
  - Husson F, Josse J, Le S, Mazet J (2013) FactoMineR: multivariate exploratory data analysis and data mining with R. R package version 1(1.29). https://cran.r-project.org/ web/packages/FactoMineR/index.html
- Hyndes GA, Heck KL Jr, Vergés A, Harvey ES and others (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. BioScience 66: 938–948
- Inagaki KY, Pennino MG, Floeter SR, Hay ME, Longo GO (2020) Trophic interactions will expand geographically

but be less intense as oceans warm. Glob Change Biol 26:6805–6812

- IPCC (2018) Summary for policymakers. In: Global Warming of 1.5°C. Intergovernmental Panel on Climate Change, Geneva, p 7–22
- Karlovic TC, Gomes RR, Paiva PC, Babcock EA, Dias JF (2021) Functionality and effectiveness of marine protected areas in southeastern Brazilian waters for demersal elasmobranchs. Front Mar Sci 8:694846
- Kobayashi S, Ota Y, Harada Y, Ebita A and others (2015) The JRA-55 reanalysis: general specifications and basic characteristics. J Meteorol Soc Jpn 93:5–48
  - Laliberté E, Legendre P, Shipley B (2015) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. 1–28. https://cran.r-project.org/web/packages/FD/index. html
  - Lavorel S, Grigulis K, McIntyre S, Williams NSG and others (2008) Assessing functional diversity in the field – Methodology matters! Funct Ecol 22:134–147
- Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18
- Lima LS, Gherardi DFM, Pezzi LP, dos Passos LG, Endo CAK, Quimbayo JP (2021) Potential changes in the connectivity of marine protected areas driven by extreme ocean warming. Sci Rep 11:10339
- Litchman E, Klausmeier CA (2008) Trait-based community ecology of phytoplankton. Annu Rev Ecol Evol Syst 39: 615–639
- Litchman E, Ohman MD, Kiørboe T (2013) Trait-based approaches to zooplankton communities. J Plankton Res 35:473–484
- Lopes RM, Katsuragawa M, Dias JF, Montú MA, Muelbert JH, Gorri C, Brandini FP (2006) Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. Sci Mar 70:189–202
- Luiz OJ, Allen AP, Robertson DR, Floeter SR and others (2013) Adult and larval traits as determinants of geographic range size among tropical reef fishes. Proc Natl Acad Sci USA 110:16498–16502
- Magurran AE, McGill BJ (eds) (2011) Biological diversity. Frontiers in measurement and assessment. Oxford University Press, Oxford
- Matano RP, Palma ED, Piola AR (2010) The influence of the Brazil and Malvinas Currents on the Southwestern Atlantic Shelf circulation. Ocean Sci 6:983–995
- McLean M, Mouillot D, Lindegren M, Engelhard G and others (2018) A climate-driven functional inversion of connected marine ecosystems. Curr Biol 28:3654–3660.e3
- McLean MJ, Mouillot D, Goascoz N, Schlaich I, Auber A (2019a) Functional reorganization of marine fish nurseries under climate warming. Glob Change Biol 25: 660–674
- McLean M, Mouillot D, Lindegren M, Villéger S, Engelhard G, Murgier J, Auber A (2019b) Fish communities diverge in species but converge in traits over three decades of warming. Glob Change Biol 25:3972–3984
- McLean M, Mouillot D, Maureaud AA, Hattab T and others (2021) Disentangling tropicalization and deborealization in marine ecosystems under climate change. Curr Biol 31:4817–4823.e5
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233
- Morais RA, Bellwood DR (2018) Global drivers of reef fish growth. Fish Fish 19:874–889

- Morais RA, Ferreira CEL, Floeter SR (2017) Spatial patterns of fish standing biomass across Brazilian reefs, Southwestern Atlantic. J Fish Biol 91:1642–1667
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28: 167–177
- Mouillot D, Villéger S, Parravicini V, Kulbicki M and others (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci USA 111:13757–13762
- Navia AF, Cruz-Escalona VH, Giraldo A, Barausse A (2016) The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management. Ecol Model 328:23–33
- Parravicini V, Villéger S, McClanahan TR, Arias-González JE and others (2014) Global mismatch between species richness and vulnerability of reef fish assemblages. Ecol Lett 17:1101–1110
- Pecuchet L, Lindegren M, Hidalgo M, Delgado M and others (2017) From traits to life-history strategies: deconstructing fish community composition across European seas. Glob Ecol Biogeogr 26:812–822
- Pecuchet L, Lindegren M, Kortsch S, Całkiewicz J and others (2020) Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography 43:197–208
- Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species ranges: scaling from organisms to communities. Annu Rev Mar Sci 12:153–179
- Quimbayo JP, Dias MS, Kulbicki M, Mendes TC and others (2019) Determinants of reef fish assemblages in tropical oceanic islands. Ecography 42:77–87
- Quimbayo JP, Silva FC, Mendes TC, Ferrari DS and others (2021) Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. Ecology 102:e03298
  - Quimbayo JP, Nunes LT, Silva FC, Anderson AB and others (2023) TimeFISH: long-term assessment of reef fish assemblages in a transition zone in the Southwestern Atlantic. Ecology 104:e3966
  - R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570–1583
  - Robertson DR, Allen GR (2015) Shore fishes of the Tropical Eastern Pacific: online information system. Version 2.0. https://biogeodb.stri.si.edu/sftep/en/pages (accessed 13 March 2020)
  - Robertson DR, Van Tassell J (2019) Shorefishes of the Greater Caribbean: online information system. Version 2.0. https://biogeodb.stri.si.edu/caribbean/en/pages (accessed 13 March 2020)
- Rockström J, Steffen W, Noone K, Persson Å and others (2009) A safe operation space for humanity. Nature 461: 472–475

Editorial responsibility: Simon Pittman, Oxford, UK Reviewed by: M. P. Rincón-Díaz, C. P. Lavin

- Rodrigues RR, Taschetto AS, Sen Gupta A, Foltz GR (2019) Common cause for severe droughts in South America and marine heatwaves in the South Atlantic. Nat Geosci 12:620–626
- Rummer JL, Munday PL (2017) Climate change and the evolution of reef fishes: past and future. Fish Fish 18:22–39
- Seguin R, Mouillot D, Cinner JE, Stuart Smith RD and others (2023) Towards process-oriented management of tropical reefs in the anthropocene. Nat Sustain 6:148–157
- Stuart-Smith RD, Edgar GJ, Barrett NS, Kininmonth SJ, Bates AE (2015) Thermal biases and vulnerability to warming in the world's marine fauna. Nature 528:88–92
- Stuart-Smith RD, Edgar GJ, Bates AE (2017) Thermal limits to the geographic distributions of shallow-water marine species. Nat Ecol Evol 1:1846–1852
- Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. Nat Commun 10:1264
- Tavares DC, Moura JF, Acevedo-trejos E (2019) Traits shared by marine megafauna and their relationships with ecosystem functions and services. Front Mar Sci 6:262
- Vergés A, Steinberg PD, Hay ME, Poore AGB and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281:20140846
- Vergés A, Doropoulos C, Malcolm HA, Skye M and others (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proc Natl Acad Sci USA 113: 13791–13796
- Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, Steinberg PD (2019) Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Funct Ecol 33: 1000–1013
- Villéger S, Ramos Miranda J, Flores Hernández D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522
- Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ (2017) Functional ecology of fish: current approaches and future challenges. Aquat Sci 79:783–801
  - Wolter K, Timlin MS (1993) Monitoring ENSO in COADS with a seasonally adjusted principal component index. In: Proceedings of the 17th Annual Climate Diagnostics Workshop. NOAA/NMC/CAC, NSSL, Oklahoma Clim Survey, CIMMS and the School of Meteor, Univ of Oklahoma, Norman, OK, p 52–57
  - Wood SN (2017) Generalized additive models: an introduction with R, 2<sup>nd</sup> edn. CRC Press, Boca Raton, FL
  - <sup>K</sup>Yeager LA, Deith MCM, McPherson JM, Williams ID, Baum JK, Belmaker J (2017) Scale dependence of environmental controls on the functional diversity of coral reef fish communities. Glob Ecol Biogeogr 26:1177–1189
  - Zuur AF, Ieno EN, Walker NJ, Savaliev AA, Smith GH (2009) Mixed effects models and extensions in ecology with R. Springer Science and Business Media, New York, NY

Submitted: November 2, 2022

Accepted: March 14, 2023

Proofs received from author(s): April 12, 2023