Assessing drivers of tropical and subtropical marine fish collapses of Brazilian Exclusive Economic Zone

Julia Tovar Verba, Maria Grazia Pennino, Marta Coll, Priscila F.M. Lopes

PII: S0048-9697(19)34932-0
DOI: <https://doi.org/10.1016/j.scitotenv.2019.134940>
Reference: STOTEN 134940

To appear in: *Science of the Total Environment*

Received Date: 1 July 2019
Revised Date: 27 September 2019
Accepted Date: 10 October 2019

Please cite this article as: J.T. Verba, M.G. Pennino, M. Coll, P.F.M. Lopes, Assessing drivers of tropical and subtropical marine fish collapses of Brazilian Exclusive Economic Zone, *Science of the Total Environment* (2019), doi: <https://doi.org/10.1016/j.scitotenv.2019.134940>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Title page

Assessing drivers of tropical and subtropical marine fish collapses of Brazilian Exclusive Economic Zone

Running head

Tropical and subtropical fish collapse

Authors

Julia Tovar Verba^{1,2,3}, Maria Grazia Pennino^{1,4}, Marta Coll⁵, Priscila F. M. Lopes^{1,2}

¹Fishing Ecology, Management, and Economics – Ecology Department – Universidade Federal do Rio Grande do Norte, Natal, Brazil.

²Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Norte, Brazil

³Conservation Genetics Lab, Macquarie University, Australia

⁴Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Spain

⁵Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, Barcelona, Spain

juliatovarverba@gmail.com

graziapennino@yahoo.it

mcoll@icm.csic.es

priscila@cb.ufrn.br

Corresponding author

Julia Tovar Verba

Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Norte
Campus Universitário - Lagoa Nova

59078-900 - Natal, RN - Brasil

juliatovarverba@gmail.com

+55 51 98902 8138

Abstract

Overfishing is a concerning threat that can lead to the collapse of fish stocks. We assessed the combinations of factors, including biological traits, types of exploitation and responses to sea temperature and salinity changes, that drive species to collapse in the Brazilian Exclusive Economic Zone (EEZ) tropical and subtropical regions. We applied a catch-based method of stock classification and a catch time series of 61 years from 132 exploited fish species. Species were categorized as Collapsed, Overexploited, Fully Exploited or in Development, and we used a GAM analysis to understand their categorization over time. Furthermore, a Redundancy Analysis was developed to assess the species characteristics that best predicted each exploitation category. Twelve species were classified as Collapsed, 55 as Overexploited,

46 as Fully Exploited and 19 as in Development. Tropical and subtropical exploited species collapses in Brazil were best explained by a complex combination of a negative impact of warmer sea temperatures, fishery exploitation and specific life-history traits. A synergistic interaction between these factors could bring species to collapse. We hypothesize that the exploitation of species with vulnerable traits may alter how these species respond to temperature and, therefore, lead them to collapse given that intense exploitation may affect their ability to respond to temperature increases. Measures to mitigate climate change impacts should take into consideration incentives to decrease the exploitation of vulnerable species and, specifically, consider species with more sensitive biological traits. Such measures are also important to minimize the socioeconomic impacts on the people that depend on these species.

Key words

Brazil; catch data; climate change; maximum body size; overexploitation; SST

Highlights

- Overfishing and climate change are the main threats to marine communities in the Anthropocene
- Understand how a combination of fishery, climate and intrinsic traits increases the chance of a species to collapse is crucial to mitigate loss of biodiversity
- We tested which combination of these factors better explain exploitation status in 132 tropical and subtropical marine fishes in Brazil
- A combination of exploitation and smaller body size is related to collapse chance
- Already collapsed species were more vulnerable to warm sea surface temperature

1. Introduction

The Anthropocene, characterized by a wide variety of anthropic stressors, is strongly transforming the natural environments on Earth (Costello et al. 2012, Lewis and Maslin 2015). Overexploitation, species extinction, habitat degradation, pollution and climate change are putting the resilience of entire biological communities at risk, leading to dramatic changes in populations of marine and terrestrial species, including declines and collapses. The impact on the oceans is of particular concern, given that more than 38 million people, mostly in tropical low-income countries, are directly or indirectly dependent on aquatic resources (FAO, 2018). Therefore, fish population declines, evidenced by the overexploitation of more than 30% of fish stocks (FAO, 2018) and the global loss of more than 90% of large predatory fish biomass (Myers & Worm, 2003), can have a notable impact on human well-being.

The decline in marine populations is attributed to many causes, with overexploitation being an important one resulting from the fishing industry. Although industrial fisheries are largely to blame for practicing unsustainable levels, small-scale or artisanal fisheries can also reduce richness and abundance of target species (e.g. Alfaro-Shigueto et al. 2010; Goetze et al. 2011; Hawkins and Roberts 2004). In low-income tropical countries, small-scale fisheries can account for more than 50% of the total catch (Vasconcellos, Diegues, & Sales, 2007), and are generally poorly or unmanaged both in high- and low-income countries (Berkes, Mahon, McConney, Pollnac, & Pomeroy, 2001). Small-scale fisheries tend to be more restricted to coastal regions, which also happen to be more negatively impacted by cumulative anthropic activities (Jackson et al., 2001). Even selective small-scale practices, such as spearfishing, can negatively affect fish stocks, especially when targeting vulnerable species, such as groupers (Giglio, Bender, Zapelini, & Ferreira, 2017; Lindfield, McIlwain, & Harvey, 2014).

Both large- and small-scale exploitation can affect species' capacity to respond to environmental changes through several mechanisms. For example, the excessive extraction of fish can result in the removal of some population units, which reduces species' capacity to adapt to a changing environment through the "rescue effect" (Gonzalez, Lawton, Gilbert, Blackburn, & Evans-Freke, 1998; Jennings & Blanchard, 2004). The decrease in total abundance can also exclude populations from less suitable areas, leading to a distribution contraction (Blanchard et al., 2005; Ciannelli et al., 2013). Exploitation can affect species' responses to climate variability through size truncation when individuals of a specific body size are removed, due to the preference of fisheries for larger—and older—individuals (Pinsky et al. 2011). Even in moderate levels of exploitations (Berkeley, Hixon, Larson, & Love, 2004), size truncation can have several effects, such as a decrease in a population's average body size, a reduction in egg-to-recruit survival (because smaller produce less and lower quality eggs, e.g. Hislop 1988), and a loss of learning capacity due to the loss of older individuals (Planque et al., 2010). Increased mortality due to fishing can also alter growth rates and decrease maturity at age (Enberg, Jørgensen, Dunlop, Varpe, & Boukal, 2012) with the potential of affecting the speed at which species respond to a changing environment (Perry, Low, Ellis, & Reynolds, 2005).

Changes in sea temperature due to global climate change have been affecting species composition and fish production worldwide (Cheung, Watson, & Pauly, 2013; Free et al., 2019). The effect of environmental shifts, especially temperature, were detected in nearly seven out of every ten stocks analyzed by Vert-pre et al. (2013), with consequences on species occurrence or abundance due to changes in mortality rates and distributions (Blanchard et al., 2005). Nevertheless, there is still much to be learned about how, when and why a warmer sea will affect fish stocks, especially for tropical species, for which there is less information available on ecosystems, communities, populations and individuals (Cheung,

Pinnegar, Merino, Jones, & Barange, 2012; Cheung, Reygondeau, & Frölicher, 2016; Free et al., 2019). The response to changes in the environment will depend on the magnitude of climate change and the species adaptation capacity (Torda et al., 2017), which, among other factors, depends on species physiology, dispersion capacity, and genetic diversity (Post & Palkovacs, 2009). Even within the same species, the individual response can vary depending on its life stage, with some stages (e.g., eggs and larvae) being more vulnerable to temperature changes (Pörtner & Farrell, 2008). Recruits can be more severely impacted by environmental changes, and a decrease in their abundance has a large impact on a population's size (Brander, 2005; Lindegren & Checkley, 2013). On the other hand, warmer oceans can benefit fish production in some areas (Blanchard et al., 2012) or benefit some large herbivores due to effects on food web dynamics (Smith-Ramesh, Rosenblatt, & Schmitz, 2017).

It has been suggested that exploitation and climate variability interaction affects demographic dynamics and conservation of fish species (Cheung, Jones, Reygondeau, & Frölicher, 2018; Planque et al., 2010). The responses to these two factors, however, vary according to the species and region. For example, in the North Sea, changes in climate affected the primary production while fishing impacted demersal fish abundance, increasing the abundance of macro-invertebrates and unbalancing the whole food web (Heath, 2005). In the western English Channel, a long-term time series of demersal fisheries showed that small body-sized species abundance is more affected by climate, whereas larger bodied species abundance is more influenced by exploitation (Genner et al., 2010). For sardines and anchovy, climate affects long-term population variability, but fisheries can induce higher-frequency variability (Lindegren, Checkley, Rouyer, MacCall, & Stenseth, 2013). Identifying those biological traits that make species respond differently to the same climate and exploitation conditions can help predict future responses of marine communities to climate change (Sunday et al., 2015).

Although there is no consensus (e.g. Pinsky et al. 2013; Schuetz et al. 2018), biological traits play an important role in species vulnerability to climate changes and exploitation (Cheung et al., 2018; Pörtner & Farrell, 2008). Some evidence suggests that large bodied marine fish are more likely to collapse, both because of their own life history traits and the selective harvesting to which they are exposed (Cheung et al., 2018; Dulvy, Sadovy, & Reynolds, 2003; Olden, Hogan, & Zanden, 2007). The time it takes for a species to grow is also relevant, with some evidence suggesting that slow-growth species, such as sharks, are more affected by fisheries, while fast-growth species seem to be more affected by climate (Quetglas, Rueda, Alvarez-Berastegui, Guijarro, & Massutí, 2016). Moreover, short-lived species, which tend to grow faster and are positioned at low trophic levels, are also likely to decline due to both climate and exploitation (Pikitch et al. 2018; Pinsky et al. 2011; Pinsky and Byler 2015). Other traits, such as dispersion capacity, region and distribution range affect the likelihood of species collapse due to fishing or climate variability. Among sharks and rays, more rare and specialized species living in estuarine or coastal areas are more vulnerable to climate change (Chin, Kyne, Walker, & McAuley, 2010), whereas species mobility also seems to contribute (Sunday et al., 2015).

Synergistic interactions between climate, fishing and biological traits have been identified in temperate regions (Botsford, Holland, Field, & Hastings, 2014; Lindegren et al., 2013). Here, we identify how these interactions are related to tropical and subtropical fish stock statuses, and which combinations are more likely to put species on the brink of collapse. We used 61 years of reconstructed data on the fisheries catches of 132 marine species exploited over more than 8,000 km along the Brazilian coastline. To define stock status we applied a catch-based classification method (Froese & Kesner-reyes, 2002; Kleisner, Zeller, Froese, & Pauly, 2013), which is adequate for data-poor areas like Brazil. This is the first assessment that attempts to

analyze the responses of a large set of tropical and subtropical fish facing a combination of threats, including overexploitation and climate variability.

2. Material and methods

2.1 Catch data

Brazilian Exclusive Economic Zone (EEZ) catch data for 132 studied species were extracted from the Sea Around Us website (www.seaaroundus.org) for the period 1950 to 2010 (Fig. 1). This reconstruction data is a result of a long-term project to re-estimate global catch combining reported data from FAO and estimates of other unreported sources of catch (Pauly & Zeller, 2016). The analyzed dataset includes industrial and small-scale fisheries catches expressed as wet weight equivalent of landings per year for each species. Data of discarded fish was excluded due to the lack of reliable information. Discard can have an impact on Brazilian fisheries, especially in troll fisheries – both artisanal and industrial – but the information is not available for the region.

Species were selected based on their distribution range limited within West Atlantic waters, so stock declines and collapses can be attributed mostly to Brazilian parameters (local environmental variables, exploitation and economic variables). Species were representative of 43 families, with a wide range of life history traits: maximum body size varied between 6.8 and 250 cm (average of 64.64 ± 45.87), and trophic level ranged from 2 to 4.5 (average 3.6 ± 0.58). Of 132 species, 63 were demersal, 26 pelagic and 43 reef species (*Supplementary Material Table S1*). For 110 of selected species, the exploitation is mainly by small-scale fleet, while for only 22 species the most important exploitation was the industrial fishery (*Supplementary Material Table S1*).

2.2 Ecological Traits

Four different ecological traits were selected as possible predictors of vulnerability to species

collapse: trophic level, maximum body size, resilience category and type of habitat (*Supplementary material Table S1*). All of these features, individually or aggregated, have been shown to affect the vulnerability of species to exploitation or climate change (e.g. Cheung et al. 2018; Dulvy, Sadovy, and Reynolds 2003; Olden, Hogan, and Zanden 2007; Pinsky et al. 2011; Pinsky and Byler 2015; Quetglas et al. 2016). Information on traits was extracted from the online database FishBase; all species has the necessary information on traits available (Froese & Pauly, 2017).

Trophic level represents the position that each species occupies in the food web, where higher values represent carnivorous species (Froese and Pauly, 2015). Maximum body size is the maximum size recorded for a species. The resilience index aggregates several biological features (growth parameter von Bertalanffy K, the intrinsic rate of population growth, fecundity, life span, and age of first maturity) of a species' life history and is expressed on a four categories scale that varies from high to very low resilience values (Musick, 1999). Finally, the type of habitat preferred by a fish was divided into three levels: demersal, pelagic and reefs.

2.3 External Drivers

2.3.1 Environmental Variables

As a proxy for climate variability, we used annual data of Sea Surface Temperature (SST) and Sea Surface Salinity (SSS) (*Supplementary Material Figure S2*). Data were obtained from the NEMO climatology model (<https://www.nemo-ocean.eu/>) for Brazil for the time series 1950-2010. The two variables were explored for correlation, outliers, and missing data before including them in the analyses (Zuur et al 2009). The Pearson correlation test ($r=0.8$, p -value=0.06) identified high correlation between these two variables.

2.3.2 Economic and Fishery Variables

We considered the type of fishery exploitation (industrial or small-scale) and two economic

factors (the ex-vessel price and the landed value of the species) as economic and fishery variables (*Supplementary material in Table S1*). The fishery exploitation type was computed as the proportion (from 0 to 100%) caught by small-scale fisheries for each species per year (1950-2010). The classification in small-scale or industrial fishery was provided by Sea Around Us. The ex-vessel price, the value fishers receive when they first sell the catch (in USD), was extracted from the Sea Around Us website and included the period between 1950 and 2010. This quantitative variable was available for only 56 out of the 132 species (Table 2); thus, the analyses that included price and landed value (kg of landing multiplied by ex-vessel price) as one independent variable were only performed for these species. Statistical models for species without economic information available were performed using only the other variables. For the RDA, we also used a qualitative price information variable (very low, low, medium, high, very high price categories), available from FishBase for all the species.

2.4 Stock Status Definition: Exploitation Index (EI) and Exploitation Status (ES)

Species Exploitation Status (ES) was obtained by calculating the Exploitation Index (EI) using the catch-based method of stock classification (Froese and Kesner-reyes 2002). It is important to emphasize some important caveats of catch-only methods. First, they do not include any effort data (Walsh et al., 2018). We opted for a catch-only method because effort data is not available for Brazilian fisheries, which suffer from a lack of fisheries monitoring (Ruffino, Lima, & Santana, 2016). Second, the occurrence of unusual high catch in one year (outlier) could take to a strongly classification in a collapsed stock. Aside from its limitations, this method provides an adequate indicator of stock status and is frequently the only option available for use in data-poor fisheries, such as Brazil and most developing tropical countries (Chrysafi & Kuparinen, 2015; Froese & Kesner-Reyes, 2002; Ghosh et al., 2015; Kleisner et al., 2013; Thorson et al., 2013; Tsikliras, Dinouli, Tsiros, & Tsalkou, 2015).

Firstly, the EI was defined annually based on the relationship between the catch in a given

year and the maximum catch of the historical landing data (catch of the year divided by the maximum catch). The EI ranges from 0 to 1, where values closer to 0 suggest that the species is closer to collapse, and values closer to 1 suggest that the species is at a low exploitation level. Using these values, species were classified into one of the four ES categories: values from 0 to 0.10 are Collapsed stocks, from 0.10-0.50 are Overexploited stocks, from 0.50 to 0.80 are Fully Exploited, and from 0.80-1 are Developing stocks (*Table 1*). To classify the investigated species in each category of ES, we considered the most frequent corresponding value in the last ten years of catches (time series from 2001 to 2010).

2.5 Statistical Analysis

2.5.1 Generalized Additive Models to assess External Drivers over time

Generalized Additive Models (GAMs; Hastie, T., & Tibshirani 1987) were used to test the influences of External Drivers on the species EI. In order to normalize the EI a logarithmic transformation was applied to these variables and a Gaussian distribution was used to fit it in the GAMs. Specifically, we tested the percentage of small-scale fisheries per year (considering an inverse relationship between small-scale and industrial fisheries), annual climate variability (sea surface temperature–SST and sea surface salinity–SSS) and economic factors (ex-vessel prices and landed values) on the species EI. The annual EI was used as the response variable. As explicative variables in GAMs cannot be highly correlated among them, SSS and SST (Pearson correlation, $r=0.8$, $p\text{-value}=0.06$) and ex-vessel price and landed value (Pearson correlation, $r=0.85$, $p\text{-value}=0.08$) were included in the model separately with the rest of variables.

GAMs are often used for their ability to deal with non-linear and non-monotonic relationships between response variables and explanatory variables (Hastie and Tibshirani 1987; Wood 2006). Separated GAMs for each of the 132 species were fitted using a Gaussian

distribution.

Models by species were run for each of the possible combinations of terms. Variables were selected with forward and backward stepwise procedures based on three different criteria including Akaike Information Criterion (AIC), Un-Biased Risk Estimator (UBRE) and deviance explained (D^2). The best (and most parsimonious) model was ultimately chosen based on the compromise between low AIC and UBRE values, high D^2 values, and significant predictors. GAMs were performed using the “*mgcv*” package (Wood, 2011) of the R software (Team, 2015).

2.5.2 Redundancy Analysis to identify Ecological Traits and External Drives related to EI

A Redundancy Analysis (RDA) was applied to explore links between the species' ES and intrinsic characteristics of the species (ecological traits) and external parameters. Specifically, the ecological traits used were trophic level, maximum body size, resilience category (very low, low, medium, high) and the type of habitat (demersal, pelagic, reef), whereas the external traits were the percentage of catch by small-scale fisheries (considering total catch) and the ex-vessel price (very low, low, medium, high, very high).

In particular the response variable $y=(y_1, \dots y_n)$ was the EI matrix of the entire time-series (1950-2010) by species, while the set of explanatory variables $x=(x_1, \dots x_n)$ was represented by a mean of the ecological and external factors by species.

In RDA it is possible to assess the influence of each co-variables (partial RDA), which allows testing the effect of a particular explanatory variable after removing the variation explained by the co-variables. This technique was used to verify how much of the total variation of the EI was explained by the different variables. The significance of each RDA model was tested using Monte Carlo permutation tests (Manly, 1991) to retain the ten variables that best explained the variation in EI. For this purpose, the “*vegan*” package (Oksanen et al., 2011) of

the R software was used.

3. Results

3.1 Exploitation Status

Of the 132 species analyzed, 12 species were classified as Collapsed, 55 as Overexploited, 46 as Fully Exploited and 19 as in Development (*Table 2*). External and intrinsic variables tested affected species in each category differently (more details below).

3.2 Explaining the Exploitation Index and Status – External Drivers

3.2.1 Collapsed species

The collapsed species models (GAMs) explained between 14% and 78% of the EI variation (deviance D^2) (*Table 2*, *Supplementary Material Figure S3a*). The Ground croaker *Bairdiella ronchus* was the only species without a significant predictor. EI of seven species (Argentine menhaden *Brevoortia pectinata*, White sea catfish *Genidens barbus*, Argentine hake *Merluccius hubbsi*, Black drum *Pogonias cromis*, Wreckfish *Polyprion americanus*, Sandperch *Pseudoperca numida*, Lookdown *Selene vomer*) had a mostly negative relationship with the SST or SSS; *i.e.*, these species were captured less under conditions of higher temperatures or salinity (*Fig. 2a*).

For five species the proportion of exploitation by small-scale fisheries was a significant predictor. For two species (Argentine hake *Merluccius hubbsi* and Narrownose Smoothhound *Mustelus schmitti*), the relationship was positive, meaning that when the species were more exploited by small-scale fishery, the EI was closer to 1 (less collapsed); whereas for three other species (White sea catfish *Genidens barbus*, Namorado sandperch *Pseudoperca numida*, Brazilian guitarfish *Rhinobatos horkelii*) the relationship was negative, higher levels of exploitation by small-scale fisheries meant lower EI (*Fig. 2b*). Two species had their exploitation affected by the ex-vessel price in opposite ways: the Narrownose

Smoothhound *Mustelus schmitti* was negatively related to it, whereas the Argentine menhaden *Brevoortia pectinata* was positively related to ex-vessel price (Fig. 2c).

3.2.2 Overexploited species

The GAM models explained between 11% and 88% of the EI variability for 34 species (Table 2). In only six of the 55 species (Madamango sea catfish *Cathorops spixii*, Spotfin butterflyfish *Chaetodon ocellatus*, Bluelip parrotfish *Cryptotomus roseus*, Cottonwick grunt *Haemulon melanurum*, Sailor's grunt *Haemulon parra*, Cubera snapper *Lutjanus cyanopterus*), the variables used in the model could not significantly explain the EI variability (Table 2, Supplementary material Figure S3b). Out of the 42 species affected by the climatic variables, 34 showed a positive relationship, meaning that when either SST or SSS was higher, the EI was higher, meaning that the catch was higher and the risk of collapsing was lower (Fig. 2a). Conversely, for seven species (Softhead sea catfish *Amphiarus rugispinis*, Black margate *Anisotremus surinamensis*, Pluma porgy *Calamus pennatula*, Southern king weakfish *Macrodon atricauda*, Lebranche mullet *Mugil liza*, Smalleye croaker *Nebris microps*, Permit *Trachinotus falcatus*), data suggested that higher temperatures were associated with a lower Exploitation Index, indicating a higher risk of collapse (Fig. 2a). Climatic variables were not relevant in seven species (Western Atlantic seabream *Archosargus rhomboidalis*, Barred grunt *Conodon nobilis*, Red grouper *Epinephelus morio*, Tomtate grunt *Haemulon aurolineatum*, Bigtooth corvina *Isopisthus parvipinnis*, Argentine goatfish *Mullus argentinae*, Atlantic moonfish *Selene setapinnis*).

3.2.3 Fully Exploited species

The GAM models were significant for 44 of the 47 species with a Fully Exploited status, which explained between 14% and 69% of the EI variation (Table 2, Supplementary material Figure S3c). Whereas one species (Vaillant's anchovy *Anchoviella vaillanti*) showed a mostly negative relationship between salinity and the EI, the other 39 showed a positive relationship:

with higher temperatures or salinity, their risk of collapse decreased (*Fig. 2a*). For eight of these species (Coco sea catfish *Bagre bagre*, Dog snapper *Lutjanus jocu*, Southern red snapper *Lutjanus purpureus*, Silk snapper *Lutjanus vivanus*, Southern kingcroaker *Menticirrhus americanus*, Whitemouth croaker *Micropogonias furnieri*, Atlantic thread herring *Opisthonema oglinum*, Parona leatherjacket *Parona signata*), price was also important: in years when these species were more expensive, the EI was lower (*Fig. 2c*). For five species, the type of fishery was important: for three of them (Acoupa weakfish *Cynoscion acoupa*, King weakfish *Macrodon ancylodon*, Castin leatherjacket *Oligoplites saliens*) when the proportion of fish caught by small-scale fisheries was higher, the species EI were lower, whereas for two (Green weakfish *Cynoscion virescens*, Sand tilefish *Malacanthus plumieri*), the EI were higher (*Fig. 2b*).

3.2.4 Developing species

The GAM models explained between 15% and 52% of the developing status variation of species, except for one species (Lane snapper *Lutjanus synagris*) (*Table 2, Supplementary material Figure S3d*). Seventeen species were positively affected by SST or SSS, meaning that when temperature or salinity was higher, so was the EI, whereas the risk of collapse was smaller (*Fig. 2a*). One species (Irish mojarra *Diapterus auratus*) was negatively affected by small-scale fisheries (*Fig. 2b*). Three species (Ladyfish *Elops saurus*, French angelfish *Pomacanthus paru*, Vermilion snapper *Rhomboplites aurorubens*) EI presented negative relationship with their prices (*Fig. 2c*).

3.3 Biological and fishery effects on Exploitation Index (RDA)

The full RDA model (all factors together, Fig. 3) explained 61% of the species ES (i.e. constrained variance) ($t=1.50$, $df=6$, $p\text{-value} < 0.001$). Particularly, the main fishing fleet used to exploit species was the principal factor (34% conditioned variance of the partial RDA; Monte Carlo: $F = 3.08$, $p\text{-value} < 0.001$), followed by price (12% conditioned variance of the partial RDA; Monte Carlo: $F = 2.12$, $p\text{-value} < 0.001$), resilience (10% conditioned variance of the partial RDA; Monte Carlo: $F = 1.58$, $p\text{-value} < 0.001$) and maximum body size (10% conditioned variance of the partial RDA; Monte Carlo: $F = 2.47$, $p\text{-value} < 0.001$). Habitat and trophic level were the less relevant variables (8% and 6% conditioned variance of the partial RDAs; Monte Carlo: $F = 2.11$, $p\text{-value} < 0.001$ and Monte Carlo: $F = 1.95$, $p\text{-value} < 0.001$ respectively). Fully Exploited and in Development species were more affected by type of fishery and price, with a negative relationship, meaning that when species were more exploited by Small-Scale fisheries and presented a higher price, they were in a worst situation. These variables were not important to explain the EI variation for Overexploited and Collapsed species. Maximum size had some effect in Overexploited and Collapsed species, meaning that species with larger body sizes are in a better situation than smaller ones. Resilience was important to explain ES for the four categories, meaning that higher Resilience values were related with higher EI, then, a better situation.

4. Discussion

Most studies that address the vulnerability of marine fish stocks rely on “data-rich” fisheries, using quantitative methods such as stock assessment models (Fernandes et al., 2017). However, in tropical developing countries such as Brazil, fisheries tend to be poorly documented and inadequately managed due to a lack of research funding and official

statistics for stock monitoring and analyses (Honey, Moxley, & Fujita, 2010), compromising comprehensive assessments. For example, there is no effort data for the analyzed area. Therefore, to measure the state of fish stocks, it is essential to adapt or develop flexible and reliable alternative analytical tools that can perform well with limited available information (Fonseca, Pennino, de Nóbrega, Oliveira, & de Figueiredo Mendes, 2017; Rufener, Kinas, Nóbrega, & Lins Oliveira, 2017).

The collapse of marine fishes is a result of a myriad of factors and cannot be assessed in a univariate approach. Our results provide evidence that tropical and subtropical exploited species collapse in Brazil is best explained by a complex combination of a negative impact of climate, fishery exploitation type (industrial fisheries versus small-scale fisheries) and specific ecological traits – here, smaller body size. These factors have been shown to explain fish population fluctuation in other contexts, including sardine, salmon, cod and herring, mostly from temperate regions (Botsford et al., 2014; Cheung et al., 2018; Lindegren et al., 2013; Rouyer et al., 2011). Our study suggests that a synergistic interaction among these factors can lead species to collapse in a tropical context as well, which can be especially exacerbated by the fishery type and a negative effect of temperature increase.

Temperature and salinity affect different species in opposite ways: whereas some apparently flourish in higher temperatures and/or salinity concentrations, as demonstrated by higher catches, others struggle under these same conditions, showing decreased catches. Even within the same species, stocks located in different environmental conditions can present antagonistic effects to changes in temperature (Ottersen et al., 2013). Tropical species are frequently considered to have a lower capacity to adapt to warmer temperatures because they evolved in stable environments (Stillman, 2003; Tewksbury, Huey, & Deutsch, 2008). In this study, however, results showed that more than 70% of tropical and subtropical species seemed to benefit from warmer temperatures at first glance. Each species presents an optimal

thermal window in which its fitness is higher, and its physiological functions performances are maintained (Ern et al., 2016). Small increases in temperature, within a species thermal tolerance, can increase its metabolic rate and, then, be positive for species production (Thresher et al., 2007).

Yet, when only the collapsed species are considered, we found that almost 60% of them presented a negative relationship with higher temperatures or salinity. Intrinsic traits can explain how species respond to variability in the environment. This depends on species' thermal tolerance, physiology and behavior (Pörtner, 2006). Temperature affects marine organisms' metabolic rates by influencing water oxygen availability (Holt and Jorgensen 2015). When an increase in temperature is higher than the species thermal tolerance, the effect on physiological performance will be negative. Warmer temperatures are known to increase growth rate in early stages, which can reduce pelagic larval duration and, then, affect larval dispersion (O'Connor et al., 2007), decrease body size in late stages due to limitations in oxygen acquisition by gills (Pauly and Cheung 2018; Atkinson 1994), reduce reproduction (Miller et al., 2015), and cause a general decrease in aerobic performance (Pörtner and Knust 2007).

We found that, among already overexploited species, smaller body size species are more at risk than larger ones. This result suggests that overexploited smaller species have a higher chance of collapsing in our study area. In fact, fast-growth and small-sized species can be more vulnerable to climate variability, making them more likely to collapse, when exploited (Pinsky and Byler 2015). Small species with short generation times and early maturation can respond more quickly to climate variability (Botsford et al., 2014). One mechanism that may be at work is the negative effect of temperature on recruitment, which is particularly crucial for population maintenance of small species with short generation times (Checkley et al. 2009; Hamdoun and Epel 2007; Van Der Lee, Koops, and Shuter 2016; Pinsky et al. 2013).

Three major hypotheses could explain this pattern: (i) species negatively affected by warmer temperatures are more likely to collapse due to intrinsic traits, (ii) exploitation is focused on more sensitive species, and/or (iii) after a certain level of exploitation, species start to respond negatively to warmer temperatures.

The exploitation regime is also an important aspect to be considered to avoid collapse. In this study, the type of fishery was an important factor in explaining EI variation for species in better status (Fully Exploited and in Development), therefore reinforcing the hegemonic paradigm that attests that small-scale fisheries can be less impactful to marine fish populations than industrial fisheries. We found that some stocks classified as in Development or Fully Exploited had lower chances of becoming Overexploited or Collapsed when harvested by small-scale fisheries, while others had a higher chance of collapse when exploited by small-scale. However, it is important to emphasize that most species currently performing better are not exploited by industrial fisheries. However, when looking only at collapsed species, 50% were industrial targets. This combination of large effort and vulnerable species can explain why the Brazilian coast is one of the most vulnerable areas for commercial harvesting (Di Minin et al., 2019).

Moreover, climate adds new threats to the system. We found that collapsed species are vulnerable to warmer sea temperatures. One possible explanation is that these species have already reached a level of exploitation that makes them respond negatively to warmer temperatures, thus increasing their vulnerability. It is known that industrial fisheries can have a degrading effect on fish stocks (Free et al., 2019), especially when the gear used has a low selective capacity for species or size, by overexploiting small-bodied species or juveniles. Also, it is known that the recruitment and biomass of exploited stocks in temperate climates (Northern Atlantic) respond to warmer temperatures (Ottersen et al., 2013), although the mechanisms behind this observation are complex – some stocks presented a positive

relationship, while others showed a negative relationship. The effect of temperature on the recruitment of herrings, for example, seems to be related to stock location, in which cold water stocks being positively affected by warmer waters (Ottersen et al., 2013). Most of the species considered here, even the overexploited ones, tend to respond positively to warmer temperatures. However, the impact of fisheries on collapsed species may have led them to respond negatively to warmer temperatures, thus increasing their vulnerability further.

The collapse of tropical and subtropical fishes is shown here to be a consequence of a combination of a biological trait (body size), and a negative response to warmer sea temperatures. Thus, marine fish species collapse in Brazil could be produced due to: (i) exploitation focus on more vulnerable species; (ii) a decrease in population size, age truncation and other population structure changes due to overexploitation (not measured here); and (iii) in turn, a higher sensitivity to warmer temperature. Therefore, besides analyzing the synergetic effect of exploitation and climate sensitivity, it is necessary to include specific vulnerable traits. A deeper understanding of which traits and how these traits can affect the relationship of tropical and subtropical species to climate and exploitation is crucial, especially when considering that climate change may be the main factor leading species to extinction in the future (Thomas et al., 2004).

Saving species from the brink of extinction is one of the most vital challenges of modern civilizations. Our results bring important information to understand the collapse of tropical and subtropical marine fish species, but strategies to reverse population declines should be thought in different scales of decision-making. To start, tropical developing countries could consider adopting broader governance systems within fisheries, especially regarding species with vulnerable traits. It is also urgent to apply measures to mitigate climate change to prevent the loss of more species, especially because the economic impacts of the effects of climate change on fisheries are difficult to predict (Sumaila, Cheung, Lam, Pauly, & Herrick,

2011). Our results can contribute to designing better strategies, and provide examples of how to mitigate climate variability effects through management and regulations of marine organisms (e.g. Le Bris et al. 2018; Gattuso et al. 2018; Kritzer et al. 2019).

Acknowledgements

This work was possible thanks to the Sea Around Us effort to reconstruct catch data. JTV was funded by CAPES with a PhD scholarship. PFML thanks CNPq for a productivity grant. We also thank the Graduate Program in Ecology at UFRN for the infrastructural support. This study was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Finance Code 001.

References

- Alfaro-Shigueto, J., Mangel, J. C., Pajuelo, M., Dutton, P. H., Seminoff, J. A., & Godley, B. J. (2010). Where small can have a large impact: Structure and characterization of small-scale fisheries in Peru. *Fisheries Research*, 106(1), 8–17. <https://doi.org/10.1016/j.fishres.2010.06.004>
- Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29(8), 23–32.
- Berkes, F., Mahon, R., McConney, P., Pollnac, R., & Pomeroy, R. (2001). *Managing Small-scale Fisheries*.
- Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., ... Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2979–2989. <https://doi.org/10.1098/rstb.2012.0231>
- Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., & O'Brien, C. M. (2005). Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(9), 2001–2009. <https://doi.org/10.1139/f05-109>
- Botsford, L. W., Holland, M. D., Field, J. C., & Hastings, A. (2014). Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science*, 71, 2158–2170.
- Brander, K. M. (2005). Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science*, 62(3), 339–343. <https://doi.org/10.1016/j.icesjms.2004.07.029>
- Checkley, D. M., Alheit, J., Oozeki, Y., & Roy, C. (2009). Climate change and small pelagic fish. In *Climate Change and Small Pelagic Fish*. <https://doi.org/10.1017/CBO9780511596681>
- Cheung, W. W. L., Jones, M. C., Reygondeau, G., & Frölicher, T. L. (2018). Opportunities for climate-risk reduction through effective fisheries management. *Global Change Biology*, 24(11), 5149–5163. <https://doi.org/10.1111/gcb.14390>
- Cheung, W. W. L., Pinnegar, J., Merino, G., Jones, M. C., & Barange, M. (2012). Review of climate change impacts on marine fisheries in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22(3), 368–388. <https://doi.org/10.1002/aqc.2248>
- Cheung, W. W. L., Reygondeau, G., & Frölicher, T. L. (2016). Large benefits to marine fisheries of meeting the 1.5°C global warming target. *Science*, 354(6319), 1591–1594. <https://doi.org/10.1126/science.aag2331>
- Cheung, W. W. L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, 497(7449), 365–368. <https://doi.org/10.1038/nature12156>
- Chin, A., Kyne, P. M., Walker, T. I., & McAuley, R. B. (2010). An integrated risk assessment for climate change: Analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology*, 16(7), 1936–1953. <https://doi.org/10.1111/j.1365-2486.2009.02128.x>
- Chrysafi, A., & Kuparinen, A. (2015). Assessing abundance of populations with limited data: Lessons learned from data-poor fisheries stock assessment. *Environmental Reviews*, 24, 1–14. <https://doi.org/10.1139/er-2015-0044>
- Ciannelli, L., Fisher, J. A. D., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., & Bailey, K. M. (2013). Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: A review. *Marine Ecology Progress Series*,

- 480, 227–243. <https://doi.org/10.3354/meps10067>
- Costello, C., Ovando, D., Hilborn, R., Gaines, S. D., Deschenes, O., & Lester, S. E. (2012). Status and solutions for the world's unassessed fisheries. *Science*, 338(6106), 517–520. <https://doi.org/10.1126/science.1223389>
- Di Minin, E., Brooks, T. M., Toivonen, T., Butchart, S. H. M., Heikinheimo, V., Watson, J. E. M., ... Moilanen, A. (2019). Identifying global centers of unsustainable commercial harvesting of species. *Science Advances*, 5(4), eaau2879. <https://doi.org/10.1126/sciadv.aau2879>
- Dulvy, N. K., Sadovy, Y., & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries*, 4(1), 25–64. <https://doi.org/10.1046/j.1467-2979.2003.00105.x>
- Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., & Boukal, D. S. (2012). *Fishing-induced evolution of growth : concepts , mechanisms and the empirical evidence*. (ii), 1–25. <https://doi.org/10.1111/j.1439-0485.2011.00460.x>
- Ern, R., Norin, T., Gamperl, A. K., & Esbaugh, A. J. (2016). Oxygen dependence of upper thermal limits in fishes. *Journal of Experimental Biology*, 219(21), 3376–3383.
- FAO. (2016). The State of World Fisheries and Aquaculture. In *Contributing to food security and nutrition for all*. <https://doi.org/10.5860/CHOICE.50-5350>
- Fernandes, P. G., Ralph, G. M., Nieto, A., García Criado, M., Vasilakopoulos, P., Maravelias, C. D., ... Carpenter, K. E. (2017). Coherent assessments of Europe's marine fishes show regional divergence and megafauna loss. *Nature Ecology & Evolution*, 1(7), 0170. <https://doi.org/10.1038/s41559-017-0170>
- Fonseca, V. P., Pennino, M. G., de Nóbrega, M. F., Oliveira, J. E. L., & de Figueiredo Mendes, L. (2017). Identifying fish diversity hot-spots in data-poor situations. *Marine Environmental Research*, 129(June 2017), 365–373. <https://doi.org/10.1016/j.marenvres.2017.06.017>
- Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 983(March), 979–983. <https://doi.org/10.1126/science.aau1758>
- Froese, R., & Kesner-reyes, K. (2002). Impact of Fishing on the Abundance of Marine Species. In *ICES Council Meeting Report*.
- Froese, R., & Pauly, D. (2017). Fish Base. World Wide Web eletronic publication.
- Gattuso, J.-P., Magnan, A. K., Bopp, L., Cheung, W. W. L., Duarte, C. M., Hinkel, J., ... Rau, G. H. (2018). Ocean Solutions to Address Climate Change and Its Effects on Marine Ecosystems. *Frontiers in Marine Science*, 5(October). <https://doi.org/10.3389/fmars.2018.00337>
- Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., ... Hawkins, S. J. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, 16(2), 517–527. <https://doi.org/10.1111/j.1365-2486.2009.02027.x>
- Ghosh, S., Muktha, M., Rao, M. V. H., Behera, P. R., Regional, V., & Fisheries, I. M. (2015). *Assessment of stock status of the exploited fishery resources in northern Bay of Bengal using landed catch data*. 62(4), 23–30. <https://doi.org/10.1136/sbmj.b5274>
- Giglio, V. J., Bender, M. G., Zapelini, C., & Ferreira, C. E. L. (2017). The end of the line? Rapid depletion of a large-sized grouper through spearfishing in a subtropical marginal reef. *Perspectives in Ecology and Conservation*, 15(2), 115–118. <https://doi.org/10.1016/j.pecon.2017.03.006>
- Goetze, J. S., Langlois, T. J., Egli, D. P., & Harvey, E. S. (2011). Evidence of artisanal fishing impacts and depth refuge in assemblages of Fijian reef fish. *Coral Reefs*, 30(2), 507–517. <https://doi.org/10.1007/s00338-011-0732-8>

- Gonzalez, A., Lawton, J. H., Gilbert, F. S., Blackburn, T. M., & Evans-Freke, I. (1998). Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281(5385), 2045–2047. <https://doi.org/10.1126/science.281.5385.2045>
- Hamdoun, A., & Epel, D. (2007). Embryo stability and vulnerability in an always changing world. *Proceedings of the National Academy of Sciences*, 104(6), 1745–1750. <https://doi.org/10.1073/pnas.0610108104>
- Hastie, T., & Tibshirani, R. (1987). Generalized additive models: some applications. *Journal of the American Statistical Association*, 82(398), 371–386.
- Hawkins, J. P., & Roberts, C. M. (2004). Effects of Artisanal Fishing on Caribbean Coral Reefs. *Conservation Biology*, 18(1), 215–226. <https://doi.org/10.1111/j.1523-1739.2004.00328.x>
- Heath, M. R. (2005). Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*, 62(5), 847–868. <https://doi.org/10.1016/j.icesjms.2005.01.023>
- Hislop, J. R. G. (1988). The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. *Journal of Fish Biology*, 32(6), 923–930. <https://doi.org/10.1111/j.1095-8649.1988.tb05435.x>
- Holt, R. E., & Jørgensen, C. (2015). Climate change in fish: effects of respiratory constraints on optimal life history and behaviour. *Biology letters*, 11(2), 20141032.
- Honey, K. T., Moxley, J. H., & Fujita, R. M. (2010). From Rags to Fishes: Data-Poor Methods for Fishery Managers In: Managing Data-Poor Fisheries Workshop: Case Studies, Models and Solutions. *California Sea Grant College Program*. ISBN:978-1-888691-23-8, 1(978), 159–184.
- Jackson, J. B. C., Michael X. Kirby, Berger, W. H., Karen A. Bjorndal, Louis W. Botsford, Bruce J. Bourque, ... Warne. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, 293(5530), 629–637. <https://doi.org/10.1126/science.1059199>
- Jennings, S., & Blanchard, J. L. (2004). Fish abundance with no fishing: Predictions based on macroecological theory. *Journal of Animal Ecology*, 73(4), 632–642. <https://doi.org/10.1111/j.0021-8790.2004.00839.x>
- Kleisner, K., Zeller, D., Froese, R., & Pauly, D. (2013). Using global catch data for inferences on the world's marine fisheries. *Fish and Fisheries*, 14(3), 293–311. <https://doi.org/10.1111/j.1467-2979.2012.00469.x>
- Kritzer, J. P., Costello, C., Mangin, T., & Smith, S. L. (2019). Responsive harvest control rules provide inherent resilience to adverse effects of climate change and scientific uncertainty. *ICES Journal of Marine Science*. <https://doi.org/10.1093/icesjms/fsz027>
- Le Bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., ... Pershing, A. J. (2018). Climate vulnerability and resilience in the most valuable North American fishery. *Proceedings of the National Academy of Sciences*, (21), 201711122. <https://doi.org/10.1073/pnas.1711122115>
- Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, 519(7542), 171–180. <https://doi.org/10.1038/nature14258>
- Lindegren, M., & Checkley, D. M. (2013). Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(2), 245–252. <https://doi.org/10.1139/cjfas-2012-0211>
- Lindegren, M., Checkley, D. M., Rouyer, T. A., MacCall, A. D., & Stenseth, N. C. (2013). Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *PNAS*, 110(33), 13672–13677. <https://doi.org/10.1073/pnas.1305733110>

- Lindfield, S. J., McIlwain, J. L., & Harvey, E. S. (2014). Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. *PLoS ONE*, 9(3), 1–12. <https://doi.org/10.1371/journal.pone.0092628>
- Miller, G. M., Kroon, F. J., Metcalfe, S., & Munday, P. L. (2015). Temperature is the evil twin: effects of increased temperature and ocean acidification on reproduction in a reef fish. *Ecological Applications*, 25(3), 603–620.
- Musick, J. A. (1999). Criteria to Define Extinction Risk in Marine Fishes. *Fisheries*, 24(6), 6–13. [https://doi.org/10.1577/1548-8446\(1999\)024<0006](https://doi.org/10.1577/1548-8446(1999)024<0006)
- Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of large predatory fish communities. *Nature*, 423(May), 280–283. <https://doi.org/10.1038/nature01610>
- O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, 104(4), 1266–1271.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ..., & Wagner, H. (2011). *vegan: Community ecology package* (pp. 117–118). pp. 117–118.
- Olden, J. D., Hogan, Z. S., & Zanden, M. J. Vander. (2007). Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, 16(6), 694–701. <https://doi.org/10.1111/j.1466-8238.2007.00337.x>
- Ottersen, G., Stige, L. C., Durant, J. M., Chan, K. S., Rouyer, T. A., Drinkwater, K. F., & Stenseth, N. C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: Effects of spawning stock and temperature. *Marine Ecology Progress Series*, 480(Hjort 1914), 205–225. <https://doi.org/10.3354/meps10249>
- Pauly, D., & Zeller, D. (2016). Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications*, 7(10244), 1–9. <https://doi.org/10.1038/ncomms10244>
- Pauly, D., & Cheung, W. W. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global change biology*, 24(1), e15–e26.
- Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate Change and Distribution in Marine Fishes. *Science*, 308(June), 1912–1924. Retrieved from http://johnreynolds.org/wp-content/uploads/2012/07/perry_et_al-_science_05.pdf
- Pikitch, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T. E., ... Steneck, R. S. (2018). The strong connection between forage fish and their predators: A response to Hilborn et al. (2017). *Fisheries Research*, 198(August), 220–223. <https://doi.org/10.1016/j.fishres.2017.07.022>
- Pinsky, M. L., & Byler, D. (2015). Fishing, fast growth and climate variability increase the risk of collapse. *Proceedings of the Royal Society B: Biological Sciences*, 282(1813), 1–9. <https://doi.org/10.1098/rspb.2015.1053>
- Pinsky, M. L., Jensen, O. P., Ricard, D., & Palumbi, S. R. (2011). Unexpected patterns of fisheries collapse in the world's oceans. *Proceedings of the National Academy of Sciences*, 108(20), 8317–8322. <https://doi.org/10.1073/pnas.1015313108>
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, 341(6151), 1239–1242. <https://doi.org/10.1126/science.1239352>
- Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., & Kifani, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79(3–4), 403–417. <https://doi.org/10.1016/j.jmarsys.2008.12.018>

- Pörtner, H. O. (2006). Climate-dependent evolution of Antarctic ectotherms: An integrative analysis. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 53(8–10), 1071–1104. <https://doi.org/10.1016/j.dsr2.2006.02.015>
- Pörtner, H. O., & Farrell, A. P. (2008). Ecology: Physiology and climate change. *Science*, 322(5902), 690–692. <https://doi.org/10.1126/science.1163156>
- Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *science*, 315(5808), 95–97.
- Post, D. M., & Palkovacs, E. P. (2009). Eco-evolutionary feedbacks in community and ecosystem ecology: Interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1523), 1629–1640. <https://doi.org/10.1098/rstb.2009.0012>
- Quetglas, A., Rueda, L., Alvarez-Berastegui, D., Guijarro, B., & Massutí, E. (2016). Contrasting responses to harvesting and environmental drivers of fast and slow life history species. *PLoS ONE*, 11(2), 1–15. <https://doi.org/10.1371/journal.pone.0148770>
- Rouyer, T., Ottersen, G., Durant, J. M., Hidalgo, M., Hjermann, D., Persson, J., ... Stenseth, N. C. (2011). Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology*, 17(10), 3046–3057. <https://doi.org/10.1111/j.1365-2486.2011.02443.x>
- Rufener, M. C., Kinas, P. G., Nóbrega, M. F., & Lins Oliveira, J. E. (2017). Bayesian spatial predictive models for data-poor fisheries. *Ecological Modelling*, 348(March), 125–134. <https://doi.org/10.1016/j.ecolmodel.2017.01.022>
- Ruffino, M. L., Lima, L. H., & S'antana, R. (2016). *Situação e tendências da pesca marítima no Brasil e o papel dos subsídios*. WWF.
- Schuetz, J. G., Mills, K. E., Allyn, A. J., Stamieszkin, K., Bris, A. Le, & Pershing, A. J. (2018). Complex patterns of temperature sensitivity, not ecological traits, dictate diverse species responses to climate change. *Ecography*. <https://doi.org/10.1111/ecog.03823>
- Smith-Ramesh, L. M., Rosenblatt, A. E., & Schmitz, O. J. (2017). Multivariate Climate Change Can Favor Large Herbivore Body Size in Food Webs. *The American Naturalist*, 191(3), 000–000. <https://doi.org/10.1086/695768>
- Stillman, J. H. (2003). Acclimation capacity underlies susceptibility to climate change. *Science*, 301(5629), 65. <https://doi.org/10.1126/science.1083073>
- Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., & Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1(9), 449–456. <https://doi.org/10.1038/nclimate1301>
- Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., ... Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18(9), 944–953. <https://doi.org/10.1111/ele.12474>
- Team, R. C. (2015). *R: A language and environment for statistical computing*. Retrieved from <https://www.r-project.org/>
- Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Putting the Heat on Tropical Animals. *Science*, 320(4), 1296–1297. <https://doi.org/10.1126/science.1084296>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- Thorson, J. T., Minto, C., Minto-Vera, C. V., Kleisner, K. M., Longo, C., & Jacobson, L. (2013). A new role for effort dynamics in the theory of harvested populations and data-poor stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(12), 1829–1844. <https://doi.org/10.1139/cjfas-2013-0280>
- Thresher, R. E., Koslow, J. A., Morison, A. K., & Smith, D. C. (2007). Depth-mediated

- reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences*, 104(18), 7461-7465.
- Torda, G., Donelson, J. M., Aranda, M., Barshis, D. J., Bay, L., Berumen, M. L., ... Munday, P. L. (2017). Rapid adaptive responses to climate change in corals. *Nature Climate Change*, 7(9), 627–636. <https://doi.org/10.1038/nclimate3374>
- Tsikliras, A. C., Dinouli, A., Tsiros, V. Z., & Tsalkou, E. (2015). The Mediterranean and Black Sea fisheries at risk from overexploitation. *PLoS ONE*, 10(3), 1–19. <https://doi.org/10.1371/journal.pone.0121188>
- Van Der Lee, A. S., Koops, M. A., & Shuter, B. (2016). Are small fishes more sensitive to habitat loss? A generic size-based model 1. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(4), 716–726. <https://doi.org/10.1139/cjfas-2015-0026>
- Vasconcellos, M., Diegues, A. C. S. A. C. A., & Sales, R. R. D. R. (2007). Limites e possibilidades na gestão da pesca artesanal costeira. *Nas Redes Da Pesca Artesanal*, pp. 2–70. Retrieved from <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Limites+e+possibilidades+na+gestão+da+pesca+artesanal+costeira#0>
- Vert-pre, K. A., Amoroso, R. O., Jensen, O. P., & Hilborn, R. (2013). Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences*, 110(5), 1779–1784. <https://doi.org/10.1073/pnas.1214879110>
- Walsh, J. C., Minto, C., Jardim, E., Anderson, S. C., Dickey-collas, M., Kleisner, K. M., ... Cooper, A. B. (2018). Trade-offs for data-limited fisheries when using harvest strategies based on catch- only models. *Fish and Fisheries*, 19, 1130–1146. <https://doi.org/10.1111/faf.12316>
- Wood, S. N. (2006). *Generalized additive models: an introduction with R*. Chapman and Hall/CRC.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(1), 3–36. <https://doi.org/https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (E. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, Ed.). New York: Spring Science and Business Media.

Figures and Tables

Figure 1: a and b) Map showing Brazilian Exclusive Economic Zone along a more than 8,000 km of coastline; c) Temporal catch (in tons) of 132 analyzed species, separated by habitat (demersal, pelagic or reef).

Table 1: Definition of the Exploitation Status of a stock using the catch-based method. This method is based on the relationship between the catches (C_Y) of a given year (Y_C) and the year ($Y_{C_{max}}$) of historical maximum catch (C_{max}).

Exploitation Status	Criterion applied
Collapsed	$Y_C > Y_{C_{max}}$ and $C_Y \leq 0.1 C_{max}$
Overexploited	$Y_C > Y_{C_{max}}$ and $0.1 C_{max} < C_Y \leq 0.5 C_{max}$
Fully exploited	$C_Y > 0.5 C_{max}$
Developing	$Y_C < Y_{C_{max}}$ and $0.1 C_{max} < C_Y < 0.5 C_{max}$

Figure 2: Relationship between temporal Exploitation Index and a) Sea Surface Temperature (SST) or Sea Surface Salinity (SSS), b) Small-scale fishery and c) ex-vessel price, based on Generalized Additive Model results. Colors show current Exploitation Status. Negative values imply that the Exploitation Index was negatively related to the variable, positive values imply that the relationship was positive, and neutral means that the variable was not selected as an important predictor for the species' Exploitation Index variability.

Table 2: Summary of the main results of the multi-step analytical approach. Results of the GAMs refer to the final selected model for each species, based on the compromise between low AIC and UBRE values, high D2 values, and significant predictors. Ex-vessel price and landed value were only available for the species indicated by asterisks. In order to summarize the overall trends of the explicative variable seen all the GAMs fitted, we reported in Table 2 these trends as (+) if the functional curve of the GAM was mainly with an increasing trend and (-) if was mainly a decreasing pattern.

Species	Family	Exploitation status	GAMs significant predictors	GAMs D ² explained (%)
<i>Amphiarius rugispinis</i>	Ariidae	Collapsed	SST (-)	18
<i>Anchoa januaria</i>	Engraulidae	Fully exploited	SST (+)	15
<i>Anchoa spinifer</i> *	Engraulidae	Collapsed	SSS (+) and Price (-)	45
<i>Anchovia clupeioides</i>	Engraulidae	Developing	SST (+)	15
<i>Anchoviella lepidentostole</i>	Engraulidae	Developing	No significance	
<i>Anchoviella vaillanti</i>	Engraulidae	Fully exploited	SSS (-)	14
<i>Anisotremus surinamensis</i>	Haemulidae	Collapsed	SSS (-)	26
<i>Anisotremus virginicus</i>	Haemulidae	Fully exploited	SST (+)	38
<i>Archosargus rhomboidalis</i> *	Sparidae	Fully exploited	Price (-)	15
<i>Aspistor luniscutis</i>	Ariidae	Overexploited	SST (+)	37
<i>Aspistor quadriscutis</i> *	Ariidae	Fully exploited	SST (+)	42
<i>Astroscopus sexspinosus</i>	Uranoscopidae	Overexploited	SSS (+)	20
<i>Bagre bagre</i> *	Ariidae	Fully exploited	Price (-)	32
<i>Bairdiella ronchus</i> *	Scianidae	Fully exploited	No significance	
<i>Batrachoides surinamensis</i>	Batrachoididae	Fully exploited	SST (+)	45
<i>Brevoortia pectinata</i> *	Clupeidae	Collapsed	SST (-) and Price (+)	42
<i>Calamus pennatula</i>	Sparidae	Collapsed	SSS (-) and Artisanal fishery (-)	88
<i>Carangoides bartholomaei</i>	Carangidae	Developing	SST (+)	16
<i>Cathorops spixii</i>	Ariidae	Overexploited	No significance	
<i>Caulolatilus chrysops</i>	Malacanthidae	Developing	SST (+)	29
<i>Centropomus ensiferus</i>	Centropomidae	Overexploited	SSS (+)	13
<i>Centropomus parallelus</i>	Centropomidae	Fully exploited	SST (+)	15
<i>Centropomus pectinatus</i>	Centropomidae	Overexploited	SSS(+)	13
<i>Centropomus undecimalis</i> *	Centropomidae	Developing	SST (+)	15
<i>Cephalopholis fulva</i> *	Serranidae	Developing	SST (+)	22
<i>Cetengraulis edentulus</i> *	Engraulidae	Overexploited	SSS (+)	21
<i>Chaetodipterus faber</i>	Ephippidae	Developing	SST (+)	23
<i>Chaetodon ocellatus</i>	Chaetodontidae	Overexploited	No significance	
<i>Conodon nobilis</i> *	Haemulidae	Overexploited	Artisanal fishery (+)	48
<i>Cryptotomus roseus</i>	Scaridae	Overexploited	No significance	
<i>Ctenosciaena gracilicirrhus</i> *	Scianidae	Fully exploited	SST (+)	15
<i>Cynoscion acoupa</i> *	Scianidae	Developing	SST (+) and	69

			Artisanal fishery (-)	
<i>Cynoscion guatucupa</i>	Scianidae	Fully exploited	SST (+)	30
<i>Cynoscion jamaicensis</i>	Scianidae	Fully exploited	SST (+)	36
<i>Cynoscion leiarchus</i>	Scianidae	Overexploited	SSS (+) and Artisanal fishery (+)	49
<i>Cynoscion microlepidotus</i>	Scianidae	Fully exploited	SST (+)	39
<i>Cynoscion virescens</i>	Scianidae	Fully exploited	SST (+) and Artisanal fishery (+)	53
<i>Dasyatis americana</i>	Dasyatidae	Overexploited	SST (+)	31
<i>Dasyatis guttata</i> *	Dasyatidae	Overexploited	SST (+)	31
<i>Diapterus auratus</i>	Gerreidae	Developing	Artisanal fishery (-)	34
<i>Diapterus rhombeus</i> *	Gerreidae	Overexploited	SST (+) and Price (-)	27
<i>Elops saurus</i> *	Elopidae	Developing	SST (+) and Price (-)	48
<i>Epinephelus itajara</i> *	Serranidae	Overexploited	SST (+)	22
<i>Epinephelus morio</i> *	Serranidae	Collapsed	Artisanal fishery (-)	47
<i>Eugerres brasiliensis</i>	Gerreidae	Developing	SST (+)	44
<i>Genidens barbatus</i>	Ariidae	Collapsed	SST (-) and Artisanal fishery (-)	46
<i>Genyatremus luteus</i> *	Haemulidae	Overexploited	SSS (+) and Price (+)	32
<i>Genypterus brasiliensis</i>	Ophidiidae	Fully exploited	SST (+)	14
<i>Gobioides broussonnetii</i>	Gobiidae	Fully exploited	SST (+)	17
<i>Gobionellus oceanicus</i>	Gobiidae	Overexploited	SST (+)	28
<i>Haemulon aurolineatum</i>	Haemulidae	Overexploited	Artisanal fishery (-)	40
<i>Haemulon chrysargyreum</i>	Haemulidae	Fully exploited	SST (+)	20
<i>Haemulon flavolineatum</i>	Haemulidae	Fully exploited	SST (+)	23
<i>Haemulon melanurum</i>	Haemulidae	Overexploited	No significance	
<i>Haemulon parra</i>	Haemulidae	Overexploited	No significance	
<i>Haemulon plumieri</i>	Haemulidae	Developing	SST (+)	33
<i>Haemulon squamipinna</i>	Haemulidae	Developing	SST (+)	52
<i>Harengula clupeola</i> *	Clupeidae	Overexploited	SST (+)	22
<i>Harengula jaguana</i> *	Clupeidae	Overexploited	SST (+)	12
<i>Hexanematichthys herzbergii</i>	Ariidae	Fully exploited	SST (+)	39
<i>Hyporhamphus unifasciatus</i>	Hemiramphidae	Overexploited	SST (+) and Artisanal fishery (-)	51

<i>Hyporthodus niveatus</i> *	Serranidae	Fully exploited	SST (+)	37
<i>Isopisthus parvipinnis</i>	Scianidae	Overexploited	Artisanal fishery (-)	50
<i>Larimus breviceps</i>	Scianidae	Collapsed	SST (+)	27
<i>Lile piquitinga</i>	Clupeidae	Developing	SST (+)	38
<i>Lophius gastrophysus</i> *	Lophiidae	Overexploited	SST (+)	11
<i>Lopholatilus villarii</i>	Malacanthidae	Overexploited	SST (+) and Artisanal fishery (-)	57
<i>Lutjanus alexandrei</i>	Lutjanidae	Fully exploited	SST (+)	29
<i>Lutjanus analis</i> *	Lutjanidae	Fully exploited	SST (+)	33
<i>Lutjanus cyanopterus</i>	Lutjanidae	Collapsed	No significance	
<i>Lutjanus jocu</i> *	Lutjanidae	Fully exploited	SST (+) and Price (-)	55
<i>Lutjanus purpureus</i> *	Lutjanidae	Fully exploited	SST (+) and Price (-)	59
<i>Lutjanus synagris</i> *	Lutjanidae	Developing	No significance	
<i>Lutjanus vivanus</i> *	Lutjanidae	Fully exploited	SST (+) and Price (-)	25
<i>Lycengraulis grossidens</i>	Engraulidae	Fully exploited	SST (+)	20
<i>Macrodon ancylodon</i> *	Scianidae	Fully exploited	SST (+) and Artisanal fishery (-)	33
<i>Macrodon atricauda</i>	Scianidae	Collapsed	SST (-)	32
<i>Malacanthus plumieri</i>	Malacanthidae	Fully exploited	SST (+) and Artisanal fishery (+)	27
<i>Menticirrhus americanus</i> *	Scianidae	Fully exploited	SST (+) and Price (-)	33
<i>Merluccius hubbsi</i> *	Merluccidae	Collapsed	SST (-) and Artisanal fishery (+)	42
<i>Micropogonias furnieri</i> *	Scianidae	Fully exploited	SSS (-) and Price (-)	23
<i>Mugil gaimardianus</i>	Mugilidae	Overexploited	SST (+)	14
<i>Mugil incilis</i>	Mugilidae	Developing	SST (+)	37
<i>Mugil liza</i> *	Mugilidae	Collapsed	SST (-) and Artisanal fishery (-)	46
<i>Mugil trichodon</i>	Mugilidae	Fully exploited	SST (+)	14
<i>Mullus argentinae</i> *	Mullidae	Fully exploited	Artisanal fishery (-) and Price (-)	68
<i>Mustelus schmitti</i> *	Triakidae	Collapsed	SST (+), Price (-) and Artisanal fishery (+)	75
<i>Mycteroperca bonaci</i> *	Serranidae	Overexploited	SST (+) and Artisanal fishery (-)	45

<i>Myrichthys breviceps</i>	Ophichthidae	Fully exploited	No significance	
<i>Nebris microps</i> *	Scianidae	Collapsed	SST (-) and Price (-)	23
<i>Notarius grandicassis</i> *	Ariidae	Overexploited	SST (+) and Price (-)	30
<i>Ocyurus chrysurus</i> *	Lutjanidae	Developing	SST (+)	19
<i>Odontesthes argentinensis</i>	Atherinopsidae	Collapsed	SST (+)	22
<i>Odontoscion dentex</i>	Scianidae	Fully exploited	No significance	
<i>Oligoplites palometa</i>	Carangidae	Fully exploited	SST (+)	29
<i>Oligoplites saliens</i>	Carangidae	Fully exploited	Artisanal fishery (-)	36
<i>Opisthonema oglinum</i> *	Clupeidae	Fully exploited	SST (+) and Price (-)	43
<i>Orthoprists ruber</i>	Haemulidae	Fully exploited	SST (+)	24
<i>Paralichthys orbignyanus</i>	Paralichthyidae	Fully exploited	SST (+)	34
<i>Paralonchurus brasiliensis</i> *	Scianidae	Overexploited	SST (+), Price (-) and Artisanal fishery (-)	38
<i>Parona signata</i> *	Carangidae	Fully exploited	SSS (+) and Price (-)	53
<i>Peprilus paru</i> *	Stomateidae	Overexploited	SSS (+) and Artisanal fishery (+)	70
<i>Percophis brasiliensis</i> *	Percophidae	Fully exploited	SST (+) and Price (-)	35
<i>Pogonias cromis</i> *	Scianidae	Overexploited	SSS (-)	23
<i>Polydactylus virginicus</i>	Polynemidae	Overexploited	SST (+)	32
<i>Polyprion americanus</i> *	Polyprionidae	Collapsed	SST (-)	22
<i>Pomacanthus paru</i>	Pomacanthidae	Developing	SST (+) and Price (-)	47
<i>Prionotus punctatus</i>	Triglidae	Developing	SST (+)	18
<i>Pseudopercis numida</i>	Pinguipedidae	Collapsed	SSS (-) and Artisanal fishery (-)	78
<i>Pseudupeneus maculatus</i>	Mullidae	Developing	SST (+)	18
<i>Pterengraulis atherinoides</i>	Engraulidae	Overexploited	SST (+)	23
<i>Rhinobatos horkelii</i>	Rhinobatidae	Collapsed	SST (+) and Artisanal fishery (-)	48
<i>Rhizoprionodon lalandii</i>	Carcharhinidae	Fully exploited	SST (+)	41
<i>Rhizoprionodon porosus</i>	Carcharhinidae	Fully exploited	SST (+)	40
<i>Rhomboplites aurorubens</i> *	Lutjanidae	Developing	SST (+) and Price (-)	28
<i>Sardinella brasiliensis</i> *	Clupeidae	Overexploited	SST (+)	27
<i>Sciades couma</i> *	Ariidae	Fully exploited	SST (+)	15

<i>Sciades herzbergii</i>	Ariidae	Overexploited	SST (+) and Artisanal fishery (+)	30
<i>Sciades parkeri</i> *	Ariidae	Fully exploited	SST (+)	25
<i>Sciades proops</i> *	Ariidae	Fully exploited	SST (+)	20
<i>Scomberomorus brasiliensis</i> *	Scombridae	Fully exploited	SST (+)	23
<i>Scorpaena plumieri</i>	Scorpaenidae	Developing	SST (+)	18
<i>Selene setapinnis</i> *	Carangidae	Overexploited	Artisanal fishery (+) and Price (+)	52
<i>Selene vomer</i> *	Carangidae	Collapsed	SSS (-)	14
<i>Sparisoma axillare</i>	Scaridae	Fully exploited	SST (+)	23
<i>Sphyaena tome</i>	Sphyaenidae	Overexploited	SST (+)	33
<i>Stellifer brasiliensis</i>	Scianidae	Developing	SST (+)	36
<i>Trachinotus carolinus</i> *	Carangidae	Fully exploited	SSS (+) and Artisanal fishery (-)	88
<i>Trachinotus falcatus</i>	Carangidae	Overexploited	SSS (-)	15
<i>Trachurus lathami</i>	Carangidae	Overexploited	SST (+)	24
<i>Umbrina canosai</i> *	Scianidae	Fully exploited	SST (+)	38
<i>Urophycis brasiliensis</i> *	Phycidae	Fully exploited	SST (+)	28

Figure 3: Two-dimensional RDA plot of the Exploitation Status groups for the 132 Brazilian species studied.

Conflict of Interest Statement

This work entitled “*Assessing drivers of tropical and subtropical marine fishes collapse of Brazilian Exclusive Economic Zone*”, by Verba (corresponding author), Pennino, Coll and Lopes, implies no competing interests, it conforms to the legal requirements of the country in which it was carried out, and to accepted international ethical standards.

The authors

Highlights

- Overfishing and climate change are the main threats to marine communities in the Anthropocene
- Understand how a combination of fishery, climate and intrinsic traits increases the chance of a species to collapse is crucial to mitigate loss of biodiversity
- We tested which combination of these factors better explain exploitation status in 132 tropical and subtropical marine fishes in Brazil
- A combination of exploitation and smaller body size is related to collapse chance
- Already collapsed species were more vulnerable to warm sea surface temperature