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PRIMARY RESEARCH PAPER

Shifts in the abundance and distribution of shallow water fish fauna on the southeastern Brazilian coast: a response to climate change

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Abstract The temperature in the South Atlantic underwent an increase from 1948 to 2016, and the Brazilian coast is very likely suffering from climate change. We examined temporal shifts in the abundance of the fish fauna that inhabit shallow waters and aimed to associate these shifts with climate effects. We selected candidate species according to changes in their relative abundance over four decades (1980s, 1990s, 2000s, 2010s) in a transition area between the tropical and subtropical regions in southeastern Brazil. Forty-seven species exhibited changes in abundance during the study period. Several small pelagic/planktophagous clupeoids (*Anchoa lyolepis, Anchoa tricolor, Harengula clupeola*, and *Sardinella brasiliensis*) reacted strongly to climate change with rapid population growth, whereas others (*Anchoa marinii, Anchoviella brevirostris, Anchoviella lepidentostole*, and *Lycengraulis grossidens*) decreased in relative abundance or disappeared. Some tropical species appear to be moving to this transition zone (e.g., *Achirus lineatus, Ctenogobius boleosoma*, and *Haemulopsis corvinaeformis*) because they appeared or increased populations. Conversely, subtropical species (e.g., *Genidens barbus, Platanichthys platana, Boridia grossidens*, and *Trachinotus falcatus*) decreased populations or disappeared, probably moving southward to more favorable areas, consistent with warming. This is the first estimation of climate change impacts on the southwestern Atlantic nearshore fishes and contributes as support for management policies.

Keywords Ichthyofauna · Sandy beaches · Global warming · Temporal shifts · Tropical fishes

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Introduction

Significant changes in marine communities have been strongly associated with global warming, suggesting that marine systems are extremely vulnerable to climate change (Bernal, 1991; Holbrook et al., 1997;

Perry et al., 2005; Richardson & Poloczanska, 2008; Rutterford et al., 2015). The effects of climate change on fish communities have been documented in several areas around the world, such as the Northwest Atlantic (Murawski, 1993), the North Sea (Perry et al., 2005; Dulvy et al., 2008), Narragansett Bay (Collie et al., 2008), the Californian coast (Hsieh et al., 2008), Barents Sea (Aschan et al., 2013), and the Norwegian Skagerrak coast (Barceló et al., 2016). Such effects can be manifested as shifts in the latitudinal distributions or increases/decreases in species abundance and composition because when in situ tolerance is not possible, then species must undertake range shifts to avoid extinction (Sorte, 2013). Hiddink & Hofstede (2008) found that marine fish in the North Atlantic, a group with high potential dispersal rates in well-connected habitats, exhibited an increase in species richness with climatic warming. Last et al. (2011) recorded that more recently, there have been considerable changes in the distribution patterns of Tasmanian fishes (Australia) that corresponded to dramatic warming observed in the local marine environment. Barceló et al. (2016) noted a clear influence of ocean temperature on the region's juvenile fish community, which pointed to climate-mediated effects on the species assemblages in an important fish nursery area on the Norwegian coast. Conversely, there is little available information on the influences of climate changes on fish assemblages in the tropics or in subtropical areas (e.g., Munday et al., 2008; Sloterdijk et al., 2017).

With relatively high fish species richness and different temperatures along the coastline, which presents a large variety of ecosystems from tropical to warm-temperate realms (Diegues, 1998), the coastal ichthyofauna of Brazil is ideal for investigating temporal and spatial shifts in species composition and distribution ranges. In this study, we examined juvenile fish that occur in both oceanic and estuarine sandy beaches along the Brazilian coast in the southwestern Atlantic. Like all marine ecosystems, the Brazilian coast is highly affected by anthropogenic activity, including the intensification of fisheries exploitation, pollution, and habitat loss (Diegues, 1998; Araújo et al., 2002, 2016).

Since 1948, measurements of South Atlantic sea surface temperatures have been performed and the Tropical Southern Atlantic Index for the average temperature anomaly has been calculated (http://www.esrl.noaa.gov/psd/data/correlation/tsa.data). The sea surface temperature has warmed consistently since 1984 with anomalies oscillating between − 0.06 and 0.6°C (Fig. 1). The region is influenced by the Brazil Current, a western boundary current that transfers warm tropical water to the mid-latitudes, which showed a warming trend of 1.28 ± 0.15°C between 1900 and 2008 (Wu et al., 2012). Thus, biological responses to climate change in the region are expected to have already begun.

Changes in ocean temperatures and ocean currents that will accompany climate change will have impacts on habitat availability, trophic linkages, recruitment dynamics, connectivity between populations, and other key ecosystem processes (Najjar et al., 2010). Additionally, the response of fish populations to climate change will differ between species, depending on their adaptations to environmental conditions. For instance, the biogeographic affinity of a species may be a proxy for the expected response to a change in temperature. Populations living on the border of a distribution range are more vulnerable to changes in abiotic conditions than populations living in the center of a distribution area (Miller et al., 1991).

The following hypotheses were evaluated using a combination of historical and present-day primary data sources: (1) the shallow coastal ichthyofauna has experienced significant temporal losses or gains of some species or changes in their relative abundance since the 1980s, as evident from the distribution of some those species; and (2) tropical and subtropical species are moving southward as result of climate change to adapt to more favorable temperatures. For instance, considering that the area sampled in this study is located in the Transition Region between the Tropical (north) and Warm Temperate (south) Regions, southerly species at the northern limits of their distribution will decrease in abundance and northerly species will increase at their southern limit in the Southeast Region.

Materials and methods

Study area

The studied Brazilian coast is located in a transitional area between the tropical and the subtropical/warm temperate areas (Fig. 2). Sepetiba Bay (22°54′–

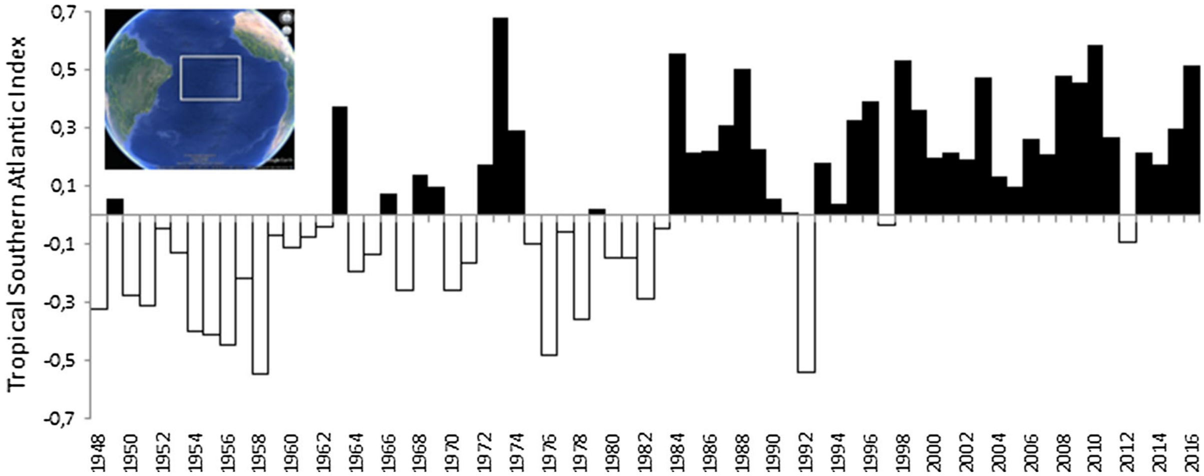

Fig. 1 Tropical South Atlantic Index—anomaly of the average of the monthly SST (sea surface temperature) from the equator 20°S and 10°E–30°W, calculated from the HadlSST and NOAA datasets for each year from 1948 to 2016. http://www.esrl.noaa.gov/psd/data/climateindices/list/

23°04′S, 43°34′–44°10′W) is a sedimentary embayment on the southeastern Brazilian coast that has a wide opening to the sea. The bay supports rich and diversified fish fauna, is used as a rearing grounds by several coastal fish species, and includes harboring mangroves, mudflats, sandy beaches, and rocky shore habitats (Araújo et al., 2002, 2016). The adjacent area has oceanic sandy beaches interspersed with rocky reefs located below low hills.

Environmental data

Averages monthly measurements of the sea surface water temperatures (30-day mean) were calculated from 1983 to 2015. Temperature data were averaged monthly within each decade—1980s, 1990s, 2000s, and 2010s—and anomalies (i.e., departures from a reference value or long-term average) were then calculated for each year with the difference between the yearly average for our 32-year average (1983–2015). The data were obtained from the United States NOAA—National Centers for Environmental Information website (https://www.ncdc.noaa.gov/cag/time-series/global/shem/ocean/all/1/1980-2017) from the location (23°20′–23°40′S, 43°35′–44°00′S) near the study area, encompassing both the estuarine and oceanic beaches. A positive anomaly of sea surface water temperature indicated that the observed temperature was warmer than the reference value, while a negative anomaly indicated that the observed temperature was colder than the reference value. We also calculated the average summer (January–February) and winter (July–August) water temperatures to avoid variation amongst the months, but only the summer information was shown because it was more critical for assessing climatic changes. A linear least-square regression line was then fitted to each time series, and an analysis of variance (ANOVA) was performed to test the significance of the models.

Fish data

Primary historical and present information on the numerical relative abundance of fish species collected in estuarine and oceanic sandy beaches with seine nets formed the basis of this study. This information was collected in Sepetiba Bay (23°S) and the adjacent area, which is influenced by the Brazil Current in the southwestern Atlantic and was grouped into four decades (1980s, 1990s, 2000s, and 2010s).

In the early eighties, a database of coastal fishes based on the beach seine sampling procedure was initiated in Southeast Brazil. Five estuarine and two adjacent oceanic sandy beaches were consistently sampled in Sepetiba Bay and the adjacent coastal area (23°S). The sampling program was standardized using beach seines with 5-mm mesh size and, measuring 12 × 2.5 m, which was seined parallel to the shoreline in waters < 1.5 m deep and then hauled directly to shore, covering an area of approximately 300 m^2.

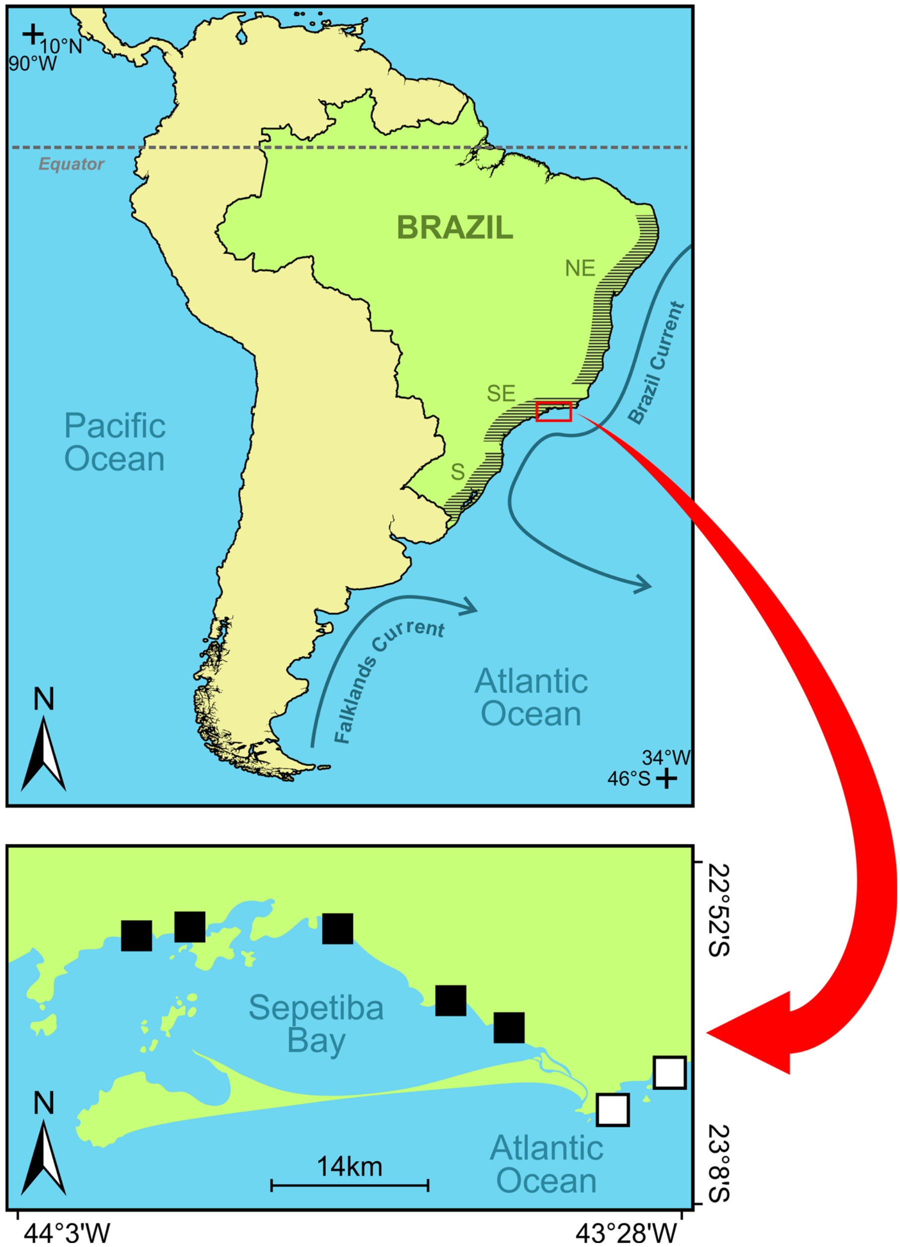

Fig. 2 The Brazilian coast, with indications of the three coastal regions (northeast, NE; southeast, SE; and south, S (above) and the sampled sites in the Sepetiba Bay and the adjacent area in the Southeast Region. Black squares, estuarine beaches; white squares, oceanic beaches

Sampling occurred during the day and at neap tides. This was the source of the historical primary database, encompassing samples collected for at least 3 years during the 1980s, 1990s, 2000s, and 2010s (present) in the Southeastern Region. In total, 1200 samples were obtained from the five estuarine beaches (95 in the eighties, 365 in the nineties, 310 in the noughties, and 430 in the twenty tens) and 166 samples were taken in the two oceanic beaches (16 in the eighties, 18 in the nineties, 48 in the noughties, and 84 in the twenty tens) (Table 1).

Sampling in the 1980s

Sampling was conducted monthly from July 1983 until June 1985 (except in January, April, July, and October 1984 and March 1985) in the five sites of Sepetiba

Table 1 Sampling program for beach seines in the estuarine sites of the Sepetiba Bay and in the adjacent oceanic beaches

Decade	Year	Estuarine sites (5 sites)			Oceanic beaches (2 sites)		
		Period	Frequency	Total	Period	Frequency	Total
1980	1983	Jul–Dec	Monthly	30	Aug–Nov	Quarterly	4
	1984	Feb–Dec	Monthly	40	Feb–Nov	Quarterly	8
	1985	Jan–Jun	Monthly	25	Feb–May	Quarterly	4
Total				95			16
1990	1993	Jul–Dec	Monthly	25			–
	1994	Jan–Sep	Monthly	30			–
	1995	Feb–Nov	Quarterly	20			–
	1996	Feb–Dec	Monthly	45			–
	1997	Jan–Dec	Monthly	45			–
	1998	Feb–Dec	Monthly[a]	90	November	One month	2
	1999	Jan–Dec	Monthly[a]	110	Jan–Dec	Monthly	16
Total				365			18
2000	2000	Jan–Dec	Monthly[b]	135	Jan–Dec	Bi-monthly	12
	2001	Jan–Nov	Monthly[b]	105	Jan–Dec	Bi-monthly	12
	2002	Aug–Dec	Bi-monthly[a]	30			–
	2003	Jan–Sep	Bi-monthly[a]	40			–
	2004				Jan–Dec	Quarterly	8
	2005				Jul–Dec	Semester	8
	2006			–	Mar–May	Quarterly	8
Total				310			48
2010	2011	Jan–Dec	Monthly[b]	180	Feb–Dec	Monthly[a]	44
	2012	Jan–Dec	Quarterly[b]	60	Jan–Dec	Quarterly[a]	16
	2013	Jun–Dec	Quarterly*	30			–
	2014	Jan–Dec	Quarterly[c]	80	Jan–Dec	Bi-monthly	12
	2015	Jan–Dec	Quarterly[c]	80	Jan–Dec	Bi-monthly	12
Total				430			84

[a]Samples in duplicate
[b]Samples in triplicates
[c]Samples in quadruplicate

Bay, and quarterly from August 1983 to May 1985 in the two adjacent oceanic sites (Table 1).

Sampling in the 1990s

The five sites in Sepetiba Bay were sampled monthly from July 1993 to September 1994 (with exception of October 1993 and February, May and July 1994), quarterly from February to November 1995, and again monthly from February 1996 to December 1999 (except in March and October 1996, May, June, September, and November 1997, January, May and September 1998, and July 1999). From February 1998 to December 1999, samples were collected in duplicates. The two adjacent oceanic beaches were sampled in November 1998, and monthly from January to December 1999 (except February, April, July, and October 1999).

Sampling in the 2000s

Monthly sampling was conducted with three replicates at five sites in Sepetiba Bay from January to December 2000 (except in April, August, and November 2000) and from January to November 2001 (except in March, May, August, and October 2001). Bi-monthly samplings with two replicates were conducted in the 5 estuarine sites from August 2002 to September 2003. At the two oceanic beaches, bi-monthly sampling occurred between January and December in 2000 and 2001, quarterly between January and December 2004, in each semester with two replicates (July and

December) in 2005, and bi-monthly with two replicates between March and May 2006.

Sampling in the 2010s

Samplings with three replicates were performed monthly at the five estuarine sites, between January and December 2011 and quarterly between January and December 2012. Duplicate samplings were performed at the estuarine sites quarterly between June and December 2013, and quarterly samplings with four replicates were performed between January and December in 2014 and 2015. The two oceanic beaches were sampled monthly with two replicates between February and December 2011, and quarterly between January and December 2012. Bi-monthly samplings were conducted in each oceanic beach between January and December in 2014 and 2015. During these four periods, some samples were not conducted due to technical constraints or poor weather conditions.

Analysis

Data sources, as listed above, were used to compile a list of Brazilian fish species that occurred in sandy beaches and that were exhibiting temporal shifts in their distribution and relative abundance. For the primary data collected in Sepetiba Bay and adjacent areas, we grouped the samples into the four decades and averaged the relative abundance of each species across the decades (in Supplementary Material—Tables S1–S3). Fish that did not inhabit sandy beaches, such as coral fishes and rocky reefs fishes were not considered in this study. The selected species were those that represented the majority of the numerical abundance and biomass of the total fish samples and that occurred in more than 1% of the samples in the survey.

The biogeographic affinities (tropical/northern and subtropical/southern) of each species were derived from the available literature (Froese & Pauly, 2017) and the scientific knowledge of regional researchers. In the Atlantic South American coast, tropical fishes are those considered to be northerly taxa (equator and low latitudes) which can extend southward to the Transition Region (latitude 22–28°S), although some may still occur farther south, either in low numbers or as vagrants. Subtropical fishes are those that tend to be abundant from the Transition Region to as far south as the Argentinean coast.

Temporal trends among the four decades (fixed factors, 1980s, 1990s, 2000s, 2010s) in species richness and in the abundance of candidate species (those that contributed more than 1% of the frequency of occurrence in each habitat (estuaries or oceanic beaches) were compared using a non-parametric Kruskal–Wallis test, followed by a multi-comparison median test. This procedure was conducted to test the first hypothesis of losses/gains of some fish species in the Transition Region. The abundance data (number of individuals per sample) were previously log transformed ($x + 1$) for fish numerical relative abundance. Relationships between species richness and temperature were explored using a single linear regression model and correlation analysis.

By combining the available data, we reconstructed change profiles for candidate species at each of the time intervals and assigned them to one of the four main qualitative categories/statuses of distributional change as defined in Table 2 (increasing/decreasing abundance; and appeared/disappeared in SE). This was conducted to test the second hypothesis that some fish species are moving towards more favorable temperatures. We considered appeared/disappeared those species that were not recorded in the two first/two last decades, respectively. When a species was rare (< 0.1 individuals per sample or $< 0.1\%$ frequency of occurrence) in all four decades, it was not used to establish a trend, which was defined when a species was present (0.1–5.0 individuals per samples) or abundant (> 5.0 individuals per sample) in at least one decade.

Results

Sea surface water temperatures in Atlantic waters have increased significantly since 1980 in the Southern Hemisphere, specifically in the area of Sepetiba Bay by 0.06°C y^{-1} during the summer ($F = 21.9$, $P = 0.0004$) and by 0.06°C y^{-1} during the winter $F = 82.2$, $P = 0.00001$). In the Sepetiba Bay area, there was an increase in the average summer water temperature between 1983 and 2015 from 26 to 26.9°C and in the positive anomalies (Fig. 3).

The number of species per sample and the total number of recorded species increased over time and

Table 2 Classification of distributional changes in the Brazilian coastal fish species in each of the different categories based on the observed abundance changes for the Southeast Region

Category	Definition	Number of species
1. Appeared in 2000-15 (previously rare species or not listed)	Not listed or very rare in the past, now residing or settling.	13
2. Increasing relative abundance—favored by CC	Residents exhibiting increased abundance (mainly south); previously rare or not represented	8
3. Disappeared in 2000–2015 (Species lost?)	Registered in the past but very rare or absent in recent records	10
4. Decreasing the relative abundance—prejudiced by CC	Declines relative abundance over the period	16

CC climate change

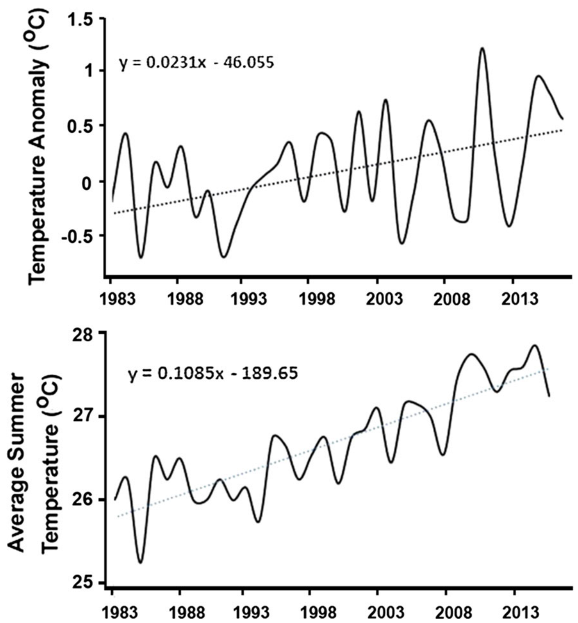

Fig. 3 The standardized anomalies (above) and average summer temperature (below) spanning from 1983 to 2015 in the area near Sepetiba Bay (23.2°S, 43.0°W) in Southeast Brazil. Data are from the NOAA database at https://www.ncdc.noaa.gov/cag/time-series/global/shem/ocean/all/1/1980-2017

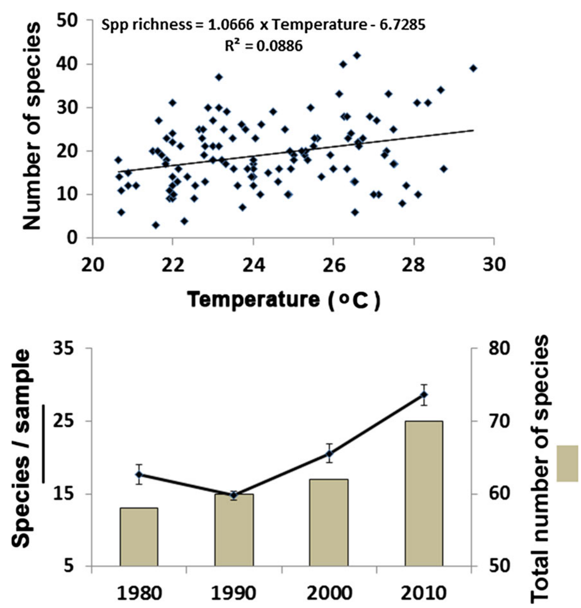

Fig. 4 Relationships between the number of species and temperature (above), temporal changes in the mean number of species per sample (± SD), and in the total number of species (below) in Sepetiba Bay and the adjacent area in Southeast Brazil

had exhibited a positive relationship with the temperature (Fig. 4). Additionally, the species richness was positively related to temperature in the estuarine habitats ($F_{1,\ 118} = 11.5$, $P = 0.001$; $r = 0.31$) and in the oceanic beaches ($F_{1,\ 66} = 4.9$, $P = 0.03$; $r = 0.26$). The number of individuals also had a significant positive relationship with temperature in the estuarine habitats ($F_{1,\ 118} = 4.12$, $P = 0.04$, $r = 0.18$) but not in the oceanic beaches ($F_{1,\ 66} = 2.49$, $P = 0.12$, $r = 0.19$).

Changes in individual fish species over time

In total, we recorded 135 marine species that were candidate species for detecting changes in relative abundance over the studied period in our primary information from Southeast Brazil (Supplementary Material—Table S1). Nearly 35% of these species changed distribution patterns across the four decades, which may be associated with climate change on the Brazilian coast (Supplementary Material—Tables S2–S3). A large number of species were too rare (44 species in estuarine habitat and 13 in oceanic beaches) to depict a trend or have no clear trend (37 species in estuarine habitats and 36 in oceanic beaches) (Tables S2–S3 in the Supplementary Material). Forty-seven species have undergone important compositional shifts over the time periods considered (i.e., 1980s, 1990s, 2000s, and 2010s) leading to overall changes in relative abundance (Table 2, Supplementary Material—Tables S2–S3). Of the primary data for 135 species, 16 declined in relative abundance over the study period, with 14 in the estuarine beaches (Supplementary Material—Fig. S1) and three in the oceanic beaches (Supplementary Material—Fig. S2), with one species declining in both. In addition, ten species disappeared from the records during the last two decades (Table 2). However, another eight species increased in relative abundance (Table 2), with seven in the estuarine beaches (Supplementary Material—Fig. S3) and three in the oceanic beaches (Supplementary Material—Fig. S4), with two species increasing in both the estuarine and oceanic beaches. Another 13 species recently (2000s–2010s) appeared in the records.

An estimation for detecting the “status” of the principal species, which had trends of increasing/decreasing and appearing/disappearing in the Southeast Region, is shown in Tables S2 and S3 in the Supplementary Material. Such estimations are a baseline for comparisons and tests to assess climate changes and their effects on ichthyofauna. Changes in each of these categories are described further below.

Species that have disappeared recently in the SE Region

At least three anchovies—*Anchoa marinii* Hildebrand, 1943, *Anchoviella brevirostris* (Günther, 1868) and *Anchoviella lepidentostole* (Fowler, 1911), one catfish—*Genidens barbus* (Lacepède, 1803), one clupeid—*Platanichthys platana* (Regan, 1917), and two grunts—*Boridia grossidens* Cuvier, 1830 and *Pomadasys ramosus* (Poey, 1860) ‘went missing’ from the estuarine beaches on the southeastern Brazilian coast in the present (2000s–2010s) records (Table 3). *Boridia grossidens. G. barbus* and *P. platana* also disappeared from the records from the oceanic beaches in the two latest periods.

Species that appeared recently in the SE Region

A total of 13 ‘previously unlisted’ species have appeared in the recent surveys (two latter decades, 2000s and 2010s) for sandy beaches located in the southeastern Brazil (Table 3). They included one clupeid—*Brevoortia aurea* (Spix & Agassiz, 1829) and two flatfishes—*Achirus lineatus* (Linnaeus, 1758) and *Symphurus tessellatus* (Quoy & Gaimard, 1824) that were unlisted and appeared in estuarine beaches; one engraulid—*Anchoa lyolepis* (Evermann & Marsh, 1900), one carangid—*Caranx latus* Agassiz, 1831 and one ladyfish—*Elops saurus* Linnaeus, 1766 that appeared in the oceanic beaches; and a grunt—*Haemulopsis corvinaeformis* (Steindachner, 1868) that appeared in both habitats and became abundant in the oceanic beaches.

Species with decreased populations

Fourteen species decreased in relative abundances in estuarine beaches, among them two gerreids—*Eucinostomus argenteus* Baird & Girard, 1855, and *Eucinostomus melanopterus* (Bleeker, 1863), two flatfishes—*Achirus declivis* Chabanaud, 1940, and *Symphurus plagusia* (Bloch & Schneider, 1801), two mugilids—*Mugil curema* Valenciennes, 1836, and *Mugil gaimardianus* Desmarest, 1831, and two carangids—*Oligoplites saurus* (Bloch & Schneider, 1801), and *Trachinotus falcatus* (Linnaeus, 1758) (Table 3, Supplementary Material—Fig. S1). Only three species decreased in relative abundances in oceanic beaches: the sciaenid *Umbrina coroides* Cuvier, 1830, the carangid *T. falcatus,* and the barbu *Polydactylus virginicus* (Linnaeus, 1758) (Supplementary Material—Fig. S2).

Species with increased populations

Eight species exhibited an increase in relative abundance in the transitional Southeast Region (Table 3), four of them were the clupeoids *A. lyolepis, Anchoa tricolor* (Spix & Agassiz, 1829), *Harengula clupeola* (Cuvier, 1829) and *Sardinella brasiliensis* (Steindachner, 1879). The gobiid *Ctenogobius boleosoma* (Jordan & Gilbert, 1882) also increased in abundances

Table 3 Species that have undergone recent increases/decreases in abundance (% of numerical relative abundance) or that appeared/disappeared from the records over four decades in Southeast Brazil

Species	Periods				Kruskal–Wallis test	
	1980s (1)	1990s (2)	2000s (3)	2010s (4)	*H*	Differences
Estuarine habitat						
Status: increasing						
Anchoa lyolepis	Ra	Pr	Ra	Pr	45.7**	4 > 1, 2, 3
Anchoa tricolor	Ab	Ab	Ab	Ab	105.3**	4 > 2, 3
Centropomus undecimalis	Nr	Ra	Ra	Pr	7.97*	4 > 1, 2, 3
Ctenogobius boleosoma	Ra	Pr	Pr	Pr	7.53*	4 > 1, 2, 3
Harengula clupeola	Ab	Ab	Ab	Ab	36.58**	4 > 1, 2, 3
Menticirrhus littoralis	Ra	Ra	Ra	Pr	71.85**	4 > 1, 2, 3
Sardinella brasiliensis	Pr	Nr	Pr	Ab	11.31**	3, 4 > 2, 1
Status: decreasing						
Achirus declivis	Pr	Ra	Ra	Nr	37.54**	1 > 2, 3, 4
Bathygobius soporator	Pr	Ra	Ra	Ra	21.26**	1 > 2, 3, 4
Cathorops spixii	Pr	Ra	Ra	Ra	93.63**	1 > 2, 3, 4
Chilomycterus spinosus	Pr	Ra	Ra	Ra	71.57	1 > 2, 3, 4
Eucinostomus argenteus	Ab	Ab	Ab	Ab	26.69**	1, 2, 3 > 4
Eucinostomus melanopterus	Pr	Pr	Pr	Pr	24.44**	1, 3 > 4
Lycengraulis grossidens	Pr	Nr	Ra	Nr	59.17**	1 > 2, 3, 4
Menticirrhus americanus	Pr	Ra	Ra	Ra	13.11**	1, 2 > 3, 4
Mugil curema	Pr	Ra	Ra	Ra	60.9**	1 > 2, 3, 4
Mugil gaimardianus	Pr	Nr	Nr	Ra	105.59**	1 > 2, 3, 4
Oligoplites saurus	Pr	Pr	Pr	Pr	19,04**	3 > 4
Sphoeroides testudineus	Pr	Pr	Pr	Ra	70.97**	1 > 2, 3, 4
Symphurus plagusia	Pr	Ra	Ra	Nr	49.07**	1 > 2, 3, 4
Trachinotus falcatus	Ab	Pr	Pr	Pr	36.77**	1 > 4
Status: appeared						
Achirus lineatus	Nr	Nr	Ra	Pr	66.27**	4 > 1, 2, 3
Brevoortia aurea	Nr	Nr	Ra	Pr	8,86*	4 > 3, 2, 1
Ctenosciaena gracilicirrhus	Nr	Nr	Nr	Ra	ns	
Haemulopsis corvinaeformis	Nr	Nr	Ra	Pr	33.06**	4 > 3, 2, 1
Lagocephalus lagocephalus	Nr	Nr	Ra	Ra	ns	
Strongylura marina	Nr	Nr	Ra	Ra	15.17**	4 > 1, 2, 3
Symphurus tessellatus	Nr	Nr	Ra	Ra	15.17**	4 > 1, 2, 3
Status: disappeared						
Anchoa marinii	Pr	Pr	Nr	Nr	12.21**	1 > 2, 3, 4
Anchoviella brevirostris	Pr	Pr	Nr	Nr	49.45**	1, 2 > 3, 4
Anchoviella lepidentostole	Ab	Pr	Nr	Nr	52.36**	1, 2 > 3, 4
Boridia grossidens	Pr	Nr	Nr	Nr	11.65**	1 > 2, 3, 4
Genidens barbus	Ab	Nr	Nr	Nr	46.90**	1 > 2, 3, 4
Gymnothorax ocellatus	Ra	Ra	Nr	Nr	12.05**	1 > 2, 3, 4
Hippocampus reidi	Ra	Ra	Nr	Nr	ns	–
Platanichthys platana	Pr	Pr	Nr	Nr	27.04**	1, 2 > 3, 4
Pomadasys ramosus	Ra	Ra	Nr	Nr	ns	–

Table 3 continued

Species	Periods				Kruskal–Wallis test	
	1980s (1)	1990s (2)	2000s (3)	2010s (4)	*H*	Differences
Oceanic beaches						
Status: increasing						
Atherinella brasiliensis	Pr	Ab	Pr	Ab	30.2**	4 > 1, 2, 3
Harengula clupeola	Pr	Pr	Pr	Ab	9.4*	4 > 1, 2, 3
Sardinella brasiliensis	Pr	Nr	Pr	Ab	8.0*	4 > 1, 2, 3
Status: decreasing						
Polydactylus virginicus	Pr	Pr	Pr	Ra	7.6*	1, 2, 3 > 4
Trachinotus falcatus	Ab	Pr	Pr	Pr	17.56**	1 > 4
Umbrina coroides	Ab	Pr	Pr	Pr	17.07**	1 > 2, 3
Status: appeared						
Anchoa lyolepis	Nr	Nr	Pr	Ab	11.01*	4 ≫ 3>1, 2
Caranx latus	Nr	Nr	Pr	Pr	ns	4, 3 > 1, 2
Chilomycterus spinosus	Nr	Nr	Ra	Ra	ns	4, 3 > 1, 2
Ctenosciaena gracilicirrhus	Nr	Nr	Nr	Pr	ns	
Dactyloscopus crossotus	Nr	Nr	Ra	Ra	ns	4, 3 > 1, 2
Elops saurus	Nr	Nr	Pr	Ra	ns	4, 3 > 1, 2
Haemulopsis corvinaeformis	Nr	Nr	Ra	Ab	16.77**	4 > 3 > 2, 1
Pogonias cromis	Nr	Nr	Nr	Pr	ns	
Lagocephalus lagocephalus	Nr	Nr	Ra	Ra	ns	
Status: disappeared						
Boridia grossidens	Pr	Nr	Nr	Nr	9,79*	1 > 2, 3, 4
Genidens barbus	Ra	Nr	Nr	Nr	9,73*	1 > 2, 3, 4
Platanichthys platana	Pr	Nr	Nr	Nr	9,79*	1 > 2, 3, 4
Selene setapinnis	Pr	Nr	Nr	Nr	9.70	1 > 2, 3, 4

Not recorded (Nr), species not in the records; rare (Ra), < 0.1 individuals per sample; present (Pr), 0.1 to 5; abundant (Ab), > 5

ns, non-significant

$*P < 0.05$; $**P < 0.01$

in estuarine beaches in Southeast Brazil (Table 3, Supplementary Material—Fig. S3). The clupeids *H. clupeola* and *S. brasiliensis* and the atherinid *Atherinella brasiliensis* (Quoy & Gaimard, 1825) also increased in relative abundance in the oceanic beaches (Supplementary Material—Fig. S4).

Discussion

The data synthesized in this study strongly supported changes in ichthyofaunal relative abundance over the span of nearly four decades ('1980s' to '2010s'). Forty-seven fish species changed in relative abundance with some of them indicating a changing environment. We tested whether species boundaries have also been displaced by warming temperatures by examining those species from our data set with a southern or a northern range limit in the Southeast Brazilian region. Changes include species currently present that were once considered rare or unrecorded in the region; others primarily confined to tropical areas in Northeast Brazil (tropical species) that have become resident or occur frequently farther south in the Southeast such as *Achirus lineatus, Ctenogobius boleosoma*, and *Haemulopsis corvinaeformis*.

Additionally, we detected species that now are likely moving southward (subtropical species), and decreasing/disappearing from the Southeast Region such as *Genidens barbus, Platanichthys platana, Boridia grossidens*, and *Trachinotus falcatus*. This may imply that the Southeast Region is becoming too warm for these species. Because of increases in water temperature, fish from the Brazilian coast may be moving to avoid the warmer water. This provides further evidence of climate-induced change (see also Root et al., 2003; Rijnsdorp et al., 2009; Hofstede et al., 2010; Last et al., 2011) and confirms the second hypothesis that some species are moving southward as result of climate change to adapt to more favorable temperatures.

Climate change is highly likely to cause the Brazil Current flow to strengthen and extend southward, resulting in warming of the Brazilian coast. An estimated increase in the southwestern Atlantic sea surface temperatures over the past 45 years, which resulted in changes to the Brazil Current (De Ruijter, 1982; Beal et al., 2011). The sea surface temperatures increased 1.93 ± 0.28°C between 1950 and 2008 (Wu et al., 2012), and a southward advance by the Brazil Current is expected, although no information on its extent is available. Especially following 1980, there has been a clear trend of increases in water temperature. Moreover, the enhanced warming of the Brazil Current may be partly induced by the poleward axial shift of these western boundary currents (Wu et al., 2012).

Some small pelagic/planktophagous clupeoids (*Anchoa lyolepis, Anchoa tricolor, Harengula clupeola*, and *Sardinella brasiliensis*) seemed to react strongly and quickly to climate change because of their fast population growth over the studied period, suggesting that they may be taking advantage of climate change to increase their populations. Others clupeoids (*Anchoa marinii, Anchoviella brevirostris, Anchoviella lepidentostole*, and *Lycengraulis grossidens*) decreased or disappeared from the records, which suggests that they suffered some disadvantage with climate changes or non-climate-related anthropogenic activities, such as overfishing, pollution, or habitat losses. In general, planktonic fishes are projected to show the greatest shifts in abundance/distribution because of the higher rate of predicted change in ocean conditions in the surface water layer and the higher mobility rates of these species (Murawski, 1993). Pelagic/planktophagous species differ from demersal/benthophagous species in their responses to warming because the former can more easily follow changes in water masses than the latter, which have more geographically fixed habitat requirements (Genner et al., 2004). Clupeiformes are likely to be one of the most sensitive groups of fishes to climate change, since the plankton is very sensitive to increases in temperature. Increases in water temperature have a direct effect on phytoplankton and zooplankton population growth rates, affecting fish survival rates and abundance/distribution ranges (Hays et al., 2005; Henson et al., 2017). Anchovy and sardine populations vary primarily in response to climate. Anchovies are more closely associated with land, including coasts, capes, orographic features, and rivers, all of which are geographically fixed, whereas sardines rely more on open-ocean processes, away from land (Checkley et al., 2017). Hence, anchovies have different constraints than sardines in their ability to respond to latitudinal shifts in water properties (such as warming) and hydrology. The difference in trends for Clupeiformes observed in this study confirms the first hypothesis that significant temporal losses or gains of some species, or changes in their relative abundance since the eighties, are occurring and illustrates the importance of performing further analyses on this subject. Until recently, no clear explanations for this observation were available, and it was merely predicted that climate change was among the causal factors of the different trends. Further studies are necessary to clarify the causes of such changes.

The two mojarras *E. argenteus* and *E. melanopterus* and two mullets (*M. curema* and *M. gaimardianus*) that are abundant in tropical estuarine beaches seem to be decreasing in abundance in Southeast Brazil. Moreover, increases in abundance of the silverside *A. brasiliensis* in oceanic beaches also suggest different responses of these widely distributed species. Such varied responses among species have important potential consequences for trophic dynamics and fishery yields of the ecosystem and further studies on this subject are urgently needed.

Other non-climatic influencing factors (e.g., fisheries, habitat degradation, and pollution) could also contribute to changes in fish relative abundance, although the magnitude of their effects is a challenge for further studies. Fishing pressure could not be included in our analyses because reliable fishing effort data on a comparable spatial and temporal scale does not exist for Southeast Brazil. Further temperature rises are likely to have profound impacts on commercial fisheries through species-specific responses, which are likely to vary according to rates of population turnover (Rijnsdorp et al., 2009; Savo et al., 2017). Fish species with more rapid generational turnover may show the most rapid demographic responses to temperature changes, resulting in stronger distributional responses to warming.

Sardinella brasiliensis is one of the most important fishery resources in Brazil that experienced considerable population decreases in the eighties as result of overfishing (Cergole, 1995; Jablonski, 2007). This species is recovering after the implementation of fishing regulations and protection efforts, and the recent substantial population increases seem to be associated, at least in part, with those protection measures. By 1980, *S. brasiliensis* populations had been seriously depleted off the Southeast Brazilian coast, and a total ban on their capture was implemented in 1990, because large catches were fished in excess of the maximum sustainable levels (Cergole, 1995; Jablonski, 2007).

In the available literature, we also examined information on species moving beyond their distribution ranges towards higher latitudes. The gobies *Ctenogobius stigmaticus* (Poey, 1860) and *Evorthodus lyricus* (Girard, 1858) that were recorded in southeastern coast up to 23°S expanded their distribution range, being recorded in southern Brazil at 32°S (Burns et al., 2010; Cheffe et al., 2010). Four Elopomorpha—*Elops smithi* McBride, Rocha, Ruiz-Carus & Bowen, 2010, *E. saurus, Albula vulpes* (Linnaeus, 1758) and *Albula nemoptera* (Fowler, 1911), which occur in northeast and southeast coasts, were recorded in the south of Brazil (32°C) (McBride et al., 2010; Lucena & Neto, 2012) and even farther down along the north coast of Argentina (35°S) (Milessi et al., 2012). The silverside *Atherinella blackburni* (Schultz, 1949) and the herring *Lile piquitinga* (Schreiner & Miranda Ribeiro, 1903), common in northeastern Brazil, expanded their distribution range to southeastern Brazil (21–23°S) (Mattox et al., 2008; Di Dario et al., 2011). The Perciformes *Eucinostomus melanopterus* (Solari et al., 2010), *Epinephelus marginatus* (Lowe, 1834) (Rico & Acha, 2003), *Stellifer rastrifer* (Jordan, 1889) (Segura et al., 2009), *Rachycentron canadum* (Linnaeus, 1766) (Milessi et al., 2012), *Uraspis secunda* (Poey, 1860) (Loebmann & Vieira, 2005), *Caulolatilus chrysops* (Valenciennes, 1833) (Milessi et al., 2012), and the Tetraodontiformes *Aluterus scriptus* (Osbeck, 1765) (Izzo et al., 2010) expanded their range of distribution expanded to the Uruguayan/north Argentinian coast (34–35°S).

In this study, we have shown examples of climate-related impacts on a wide variety of fishes on the Brazilian coast, with 47 species, including several planktophagous Clupeiformes, displaying recently altered relative abundance. Species with shifting distributions, such as the Clupeiformes, have more accelerated life cycles and smaller body sizes than non-shifting species (Perry et al., 2005). However, many other species have not undergone any clear distributional shifts, despite noticeable shifts in other co-occurring species. Consequently, gains and losses of species are predicted along the Brazilian coast. According to Cheung et al. (2012), such changes in species assemblages may have considerable ecological and socio-economic implications through shifts in fishing grounds and unexpected trophic effects. Additionally, the Brazilian Southeast Region is expected to experience a 'tropicalization' of the marine community in the future, with increasing dominance of warm-water species. Improvement to models of changes in species range will require greater realism in the representation of dispersal (Travis et al., 2013). A multitude of ecological and evolutionary processes will likely lead to complex dispersal responses to climate change.

Changes in the abundance and distribution of fish species may indicate the impacts of warming temperatures, but further studies are needed to clarify these effects. We aimed to compare species and species-groups that have different ecological characteristics and are therefore likely to differ in their responses to climate change. The classification of species based on biogeographic affinity, habitat occupancy and fish guilds may be an important starting point. We confirmed that the response of pelagic species is stronger than that of demersal species, and this concurs with a number of studies regarding changes in fish assemblages (Genner et al., 2004; Rijnsdorp et al., 2009; Checkley et al., 2017). Climate change and the responses of affected fish populations are complex and multifaceted issues. This study is a first estimation of climate change impacts on the southwestern Atlantic nearshore fish communities and contributes as support for improving management policies in the area. The hypotheses proposed here are by no means complete and should be regarded as a first step in contributing to this important issue of climate change in the south-western Atlantic.

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