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Tropicalization of demersal megafauna in the western South Atlantic since 2013

Jose Angel Alvarez Perez [1]✉ & Rodrigo Sant'Ana [1]

Temperatures in the southwest South Atlantic Ocean have increased over recent decades due to changes in Brazil's Current dynamics affecting marine ecosystems. However, the effects of ocean warming on demersal fauna in the region are poorly understood. Here, we analyse megafauna species composition, and changes in biomass of species with warm- and cold-water affinities for 29,021 commercial demersal catches landed in the harbours of Santa Catarina state, Brazil, between 2000 and 2019. We find evidence of megafauna tropicalization in the Brazilian Meridional Margin during this period. The mean temperature of catches has increased sharply since 2013, with the averaged optimal temperature preferences of all species in commercial catches in one year increasing at a rate of 0.41 °C yr^{-1}. These changes in the mean temperature of the catch correlate well with model-based bottom water temperatures (with 0 and 1-year time-lag) and transport volumes of the Brazil Current (with 3 and 4-year time-lag).

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[1] School of Sea, Science and Technology – EMCT, University of Vale do Itajaí – UNIVALI, Itajaí, SC, Brazil. ✉email: angel.perez@univali.br

Oceans have absorbed most of the heat increase of the atmosphere since pre-industrial times gradually warming, on average, by 0.63 °C (1850–1900 period until 1986–2005[1]). Direct observations have revealed important geographic and depth variability in such change, as well as in related physical and biogeochemical transformations including sea level rise, increased frequency of storms, deceleration of thermohaline circulation, expansion of areas with well-stratified water columns, a decrease of net primary productivity, and deoxygenation[2–5]. In addition, nearly 1/3 of CO_2 added to the atmosphere by anthropogenic activities has been absorbed in the ocean surface changing seawater chemistry towards a more acidic state, which decreases carbonate availability for the development of numerous life forms[6]. Exposed to such environmental changes, marine species have shown alterations in abundance, phenology, and spatial distribution ranges (both bathymetric and geographic), modifying community species composition (beta diversity), the structure of trophic chains and the metabolic and consumption rates of their trophic levels[7–13]. Across different spatial scales, alterations in species diversity and functions are expected to disturb marine ecosystems functioning and the services they provide to society, including fisheries[14].

Poleward expanding isotherms have favoured the invasion of tropical/subtropical species to suitable habitats in higher latitudes and the retraction of the equatorward limits of temperate species distribution[9,12]. These processes have increased the diversity of pelagic and benthic fauna in subtropical regions by the addition of species with affinities for warmer waters, eventually replacing those with an affinity for cooler waters that become progressively scarce[15,16]. In such regions, where multispecies fisheries have been historically developed, reshuffling the diversity of fish and shellfish assemblages may have altered catch composition, gradually including higher and lower proportions of species with warm- and cold-water affinities, respectively. Cheung et al.[17] explored this concept by developing a metric defined as the ‘mean temperature of the catches’ (MTC), which involves averaging optimal temperature preferences of all species included in commercial catches during one year, weighed by their annual catch. In their analysis, MTC annual variation between 1970 and 2006 evidenced ocean warming signals in 52 large marine ecosystems and was shown to be related to increasing trends of regional sea surface temperatures. This global process was defined as a ‘tropicalization’ of the catch, also characterized in different regional studies[18–22].

The Southwest South Atlantic Ocean (SWAO) extending from Cabo Frio (Brazil, 22°S) to Tierra del Fuego (Argentina, 55°S), comprises one of the world’s largest marine warming hotspots, as its water temperature has increased above the global average in recent years[23,24]. In this region, satellite-derived sea surface temperatures have shown positive anomalies of 0.5–1.0 °C between 1950 and 1999, and of 0.5 °C between 2000–2016[23,25]. These anomalies have been produced by a poleward displacement of wind patterns over the South Atlantic leading to a southward expansion of the warm waters of the Brazil Current, which created, over the past decades, a warming region along its path (Fig. 1)[25–27]. Ecosystem responses to this ocean warming process in the region have been poorly studied, but Franco et al.[25] reviewed existing evidence of more frequent harmful algal blooms, events of shellfish mass mortalities, and modifications in fisheries regimes. Particularly relevant was the study by Gianelli et al.[21], which revealed an increasing trend of MTC calculated for demersal catches at the Argentinian–Uruguayan Common Fishing Zone (AUCFZ, ~34°–40°S) between 1973 and 2017. Authors detected a decreasing representation of cold-water species in the catches, a pattern significantly related to a sea surface temperature increase in the period.

The Brazilian Meridional Margin (BMM- *sensu* Alberoni et al.[28]) occupies the northern sector of SWAO (~20°S–34°S) (Fig. 1). The region is influenced by the Brazil Current that flows southwards along the shelf break and upper slope carrying Tropical Waters, South Atlantic Central Waters and, south of 28°S, deep Antarctic Intermediate Waters[29]. At ~38°S, the Brazil Current collides with subantarctic waters carried northwards by the Malvinas Current, deflecting eastwards over the South Atlantic Ocean basin. This oceanographic front, known as Brazil–Malvinas Confluence (Fig. 1), has gradually displaced poleward over the past decades (0.6–0.9° latitude per decade), as the Brazil Current expanded southwards, in association with the ocean temperature increasing trend in the region[24,26,27].

Along its path on the BMM, the Brazil Current also influences shelf waters (a) by inducing shelf break upwellings of the South Atlantic Central Waters[30,31] and (b) through lateral mixing of Tropical Waters with northward flowing coastal waters, derived from the discharge plumes of the La Plata River and the Patos/Mirim Lagoon systems, forming Subtropical Shelf Waters[32]. At the southern extreme of the BMM, this warm water mass is intersected by a wedge of cold Subantarctic Shelf Waters, derived from the Patagonian Continental Shelf, forming the Subtropical Shelf Front (Fig. 1), a shoreward continuation of Brazil–Malvinas Confluence[33]. Along the SWAO, these ocean-shelf interactions suggest that global warming-induced changes in the Brazil Current dynamics, and the resulting ocean warming process, may have extended to shelf waters altering species habitats and affecting fauna diversity[21].

Descriptions of demersal fauna geographic distribution patterns have long characterized the BMM as a transition zone between subtropical and temperate faunas[34–36] formed as a consequence of historical processes of diversification in the Western Atlantic[37] and the influence of seasonal latitudinal fluctuations of Brazil–Malvinas Confluence and the Subtropical Shelf Front[38]. These fronts affect the latitudinal and seasonal distribution of subtropical and warm-temperate species and the extent to which they seasonally overlap in the BMM[39]. The availability of this heterogeneous fauna has driven the development, since the 1960s, of large-scale multispecies demersal fisheries which economically thrived from the catch of assorted subtropical and warm-temperate teleosts, elasmobranchs, crustaceans and cephalopod species[38–43]. These species have sustained annual catches oscillating around 88,000 t between 1986 and 2004, which represented over 35% of total catches in the region, on average[41].

Based on the fact that the BMM is inserted within the Southwest South Atlantic Ocean marine warming hotspot area (Fig. 1), and the warming catch patterns revealed by Gianelli et al.[21] at the AUCFZ, we postulate that: (a) changes in the demersal community have taken place in the BMM during the past decades towards a tropicalization scenario, (b) these changes have produced detectable signals in the species composition of multispecies demersal catches and (c) they can be mostly explained by the variation of ocean temperature and the dynamics of the Brazil Current in the region. We addressed these premises by analysing the annual variation of demersal catch composition, monitored in southern Brazil between 2000 and 2019, and the effect of sea bottom temperature and transport volumes of the Brazil Current on that variation. Because these large-scale environmental changes may have a gradual and heterogeneous effect on megafauna species[13], we included time-lags (1–4 years) to allow for delayed mechanistic links between ocean warming and biological responses. The study explored two distinct analytical approaches; the analysis of annual variation of the MTC index[17], and the analysis of species composition and beta diversity applied to species recorded in the catches of the demersal fisheries[44]. In a

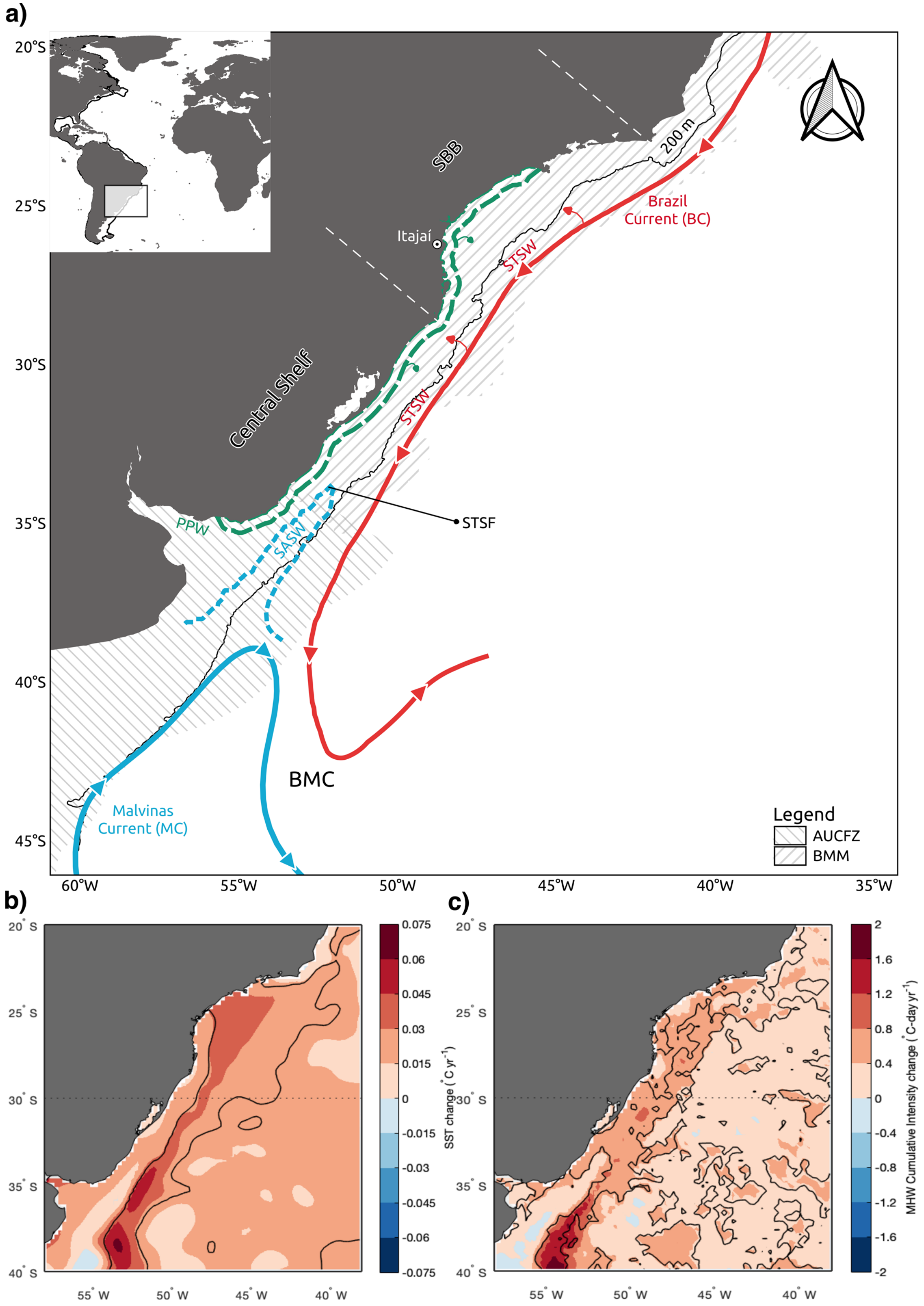


Fig. 1 The Brazilian Meridional Margin (BMM), study area and marine warming hotspot. a General map including a schematic view of main oceanographic features. **b** Linear trend of sea surface temperature (in °C year^{-1}). **c** Marine heatwave cumulative intensity (in °C-day year^{-1}) for the period 1982–2020. Solid lines encompass areas where the linear trends are statistically significant at the 99th confidence level (see the "Methods" section for more details). PPW Rio de La Plata plume waters, SASW Subantarctic Shelf Waters, STSW Subtropical Shelf Waters, STSF Subtropical Shelf Front, BMC Brazil–Malvinas Confluence, SBB South Brazil Bight, AUCFZ Argentinean and Uruguayan Common Fishing Zone.

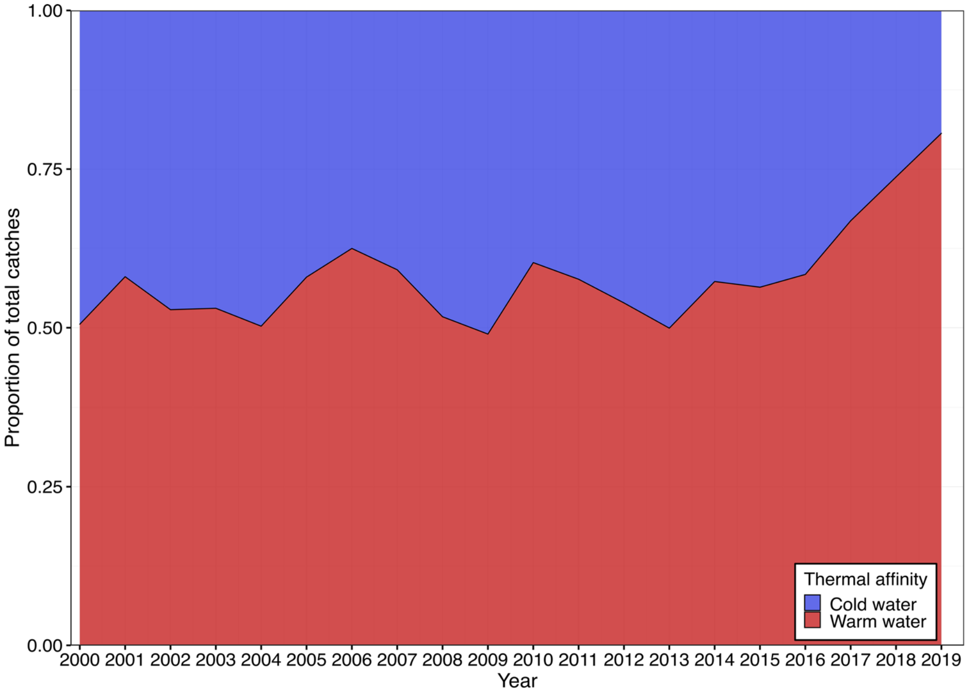


Fig. 2 Annual variation of the proportion of species with cold- and warm-water affinities in the catches of the demersal fisheries in Brazilian Meridional Margin (BMM). Catches were monitored between 2000 and 2019 in the harbours of Santa Catarina State, southern Brazil. Colours represent "warm-" (thermal preferences > 21.1 °C) and "cold-" (thermal preferences < 21.1 °C) water affinities.

previous analysis, using reconstructed regional catch data, Cheung et al.[17] obtained an oscillating pattern of MTC in the region. Conversely, a study on clupeoid fish populations in coastal areas of Rio de Janeiro State (23°S) provided robust evidence of tropical species replacing subtropical ones[45]. In the present study, we reveal signals of tropicalization of the catches during the past decades and identified patterns of abundance gains and losses of species with affinities for warm- and cold waters, respectively, throughout this process.

Results and discussion

Catches throughout the study period reached maximum levels in 2006–2012, decreasing sharply thereafter reaching low levels in 2019 (Supplementary Fig. 1). The whitemouth croaker (*Micropogonias furnieri*) and the argentine croaker (*Umbrina canosai*) were the dominant species in the catches. Jointly, they represented, on average, over 50% of the total landed biomass in the period. This biomass included other 78 species: 62 teleosts, 3 elasmobranchs, 8 crustaceans and 5 molluscs. Overall, catch composition maintained a 1.5:1 ratio of species with warm- and cold-water affinities from the beginning of the time series until 2012. After that, warm-water species abundance increased in the catches changing the resulting ratio to 4.1:1 in 2019 (Fig. 2).

Mean temperature of the catches. Annual MTC oscillated around 21 °C (SD = 0.63 °C) between 2000 and 2019. Until 2013, the MTC time-series exhibited peaks (2005, 2010) and troughs (2008, 2013), but no particular trend was evidenced. After 2013, MTC increased continuously reaching maximum values in 2019 (Fig. 3). The segmented regression model defined one significant discontinuity in 2012 (95% CI: 2010–2015), which delimited an early period (2000–2012) when MTC oscillated with no significant trend (p-value = 0.789), from a late period (2013–2019) when MTC increased sharply at a 0.41 °C yr^{-1} (p-value < 0.001) (Table 1). Similar catch warming trends have been described in Large Marine Ecosystems around the globe[17] and in more limited regions including the Aegean and Ionian Seas[18,19], the Yellow and East China Seas[20] and the Bay of Biscay (Cantabrian Sea—NE Atlantic)[46]. Considering the entire time-series, the MTC increase rate in the BMM was equal to 0.57 °C. decade^{-1}, exceeding estimates for the world ocean (0.19 °C. decade^{-1}) and for non-tropical regions (0.23 °C decade^{-1})[17], as well as for the regions above, except the Aegean Sea (1.01 °C decade^{-1}) and the Ionian Sea (1.17 °C decade^{-1})[19]. During the 2013–2019 period, the decadal MTC increasing rate (4.11 °C decade^{-1}) largely exceeded any regional estimate reported, a pattern consistent with the expected ecosystem changes in a region of intense ocean temperature increase (Fig. 1)[23,24].

SBT values remained relatively stable from 2001 to 2010 but increased continuously from 2013 to 2019 (Fig. 3), as confirmed by the significant positive linear trend (0.077 °C yr^{-1}, p-value = 0.012) (Table 1). MTC variation was significantly explained by SBT with 0 and 1-year time-lag (p-value = 0.001 and p-value = 0.023, respectively) (Table 2).

These results were also consistent with global patterns[17] but particularly relevant were the trends described in the Argentinean–Uruguayan Common Fishing Zone (AUCFZ, Fig. 1), where an MTC warming trend was described from 1985 to 2017[21]. This trend was explained by sea surface temperature (SST) variation which also increased steadily since mid-1990. Authors suggested that an important 'oceanographic change has occurred in the region, which modulated the MTC index'. Because the MTC series analysed in the BMM is shorter (2000–2019) than the one analysed in the AUCFZ (1973–2017), and considered temperature at the sea bottom rather than at the surface (SST), a direct comparison between regions is not fully informative. However, the INALT20 model-derived SBT time-series, available since 1958[47] (Fig. 3), showed that positive anomalies became frequent from 1994 onwards, as observed in the AUCFZ SST time-series, indicating that such oceanographic change was noticed in both adjacent regions of the SWAO.

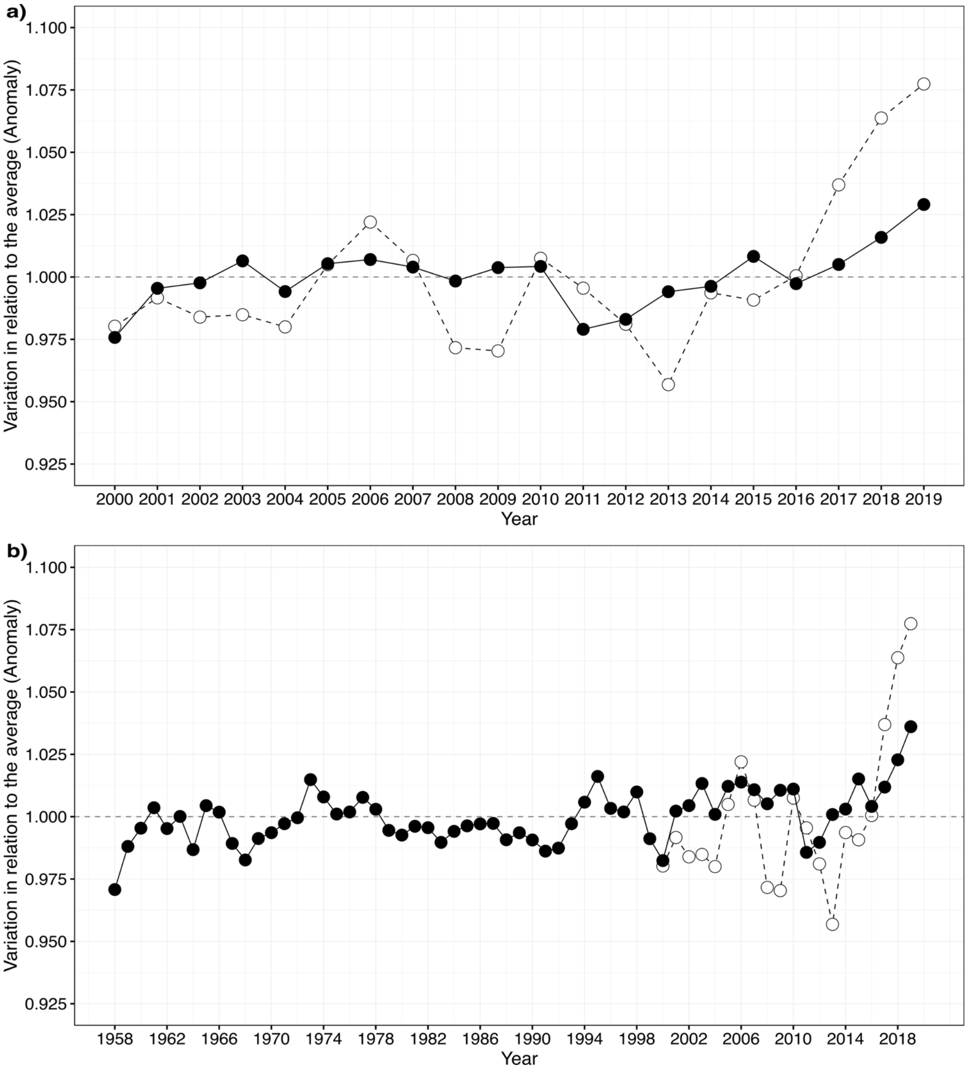


Fig. 3 Annual variation of the mean temperature of the catch (MTC) of the demersal fisheries in the Brazilian Meridional Margin (BMM). Catches were monitored between 2000 and 2019 in the harbours of Santa Catarina State, southern Brazil. MTC, white dots; sea bottom temperature (SBT), black dots. **a** 2000–2019 time-series and **b** 1958–2019 time-series.

Notwithstanding, in the BMM a noticeable steady increase of both MTC and SBT seems to take place from 2012 onwards, suggesting a more recent regional shift. If only this time period is analysed in the AUCFZ time series (Fig. 4 in ref. [21]) positive anomalies would predominate approximately from 2010 onwards and years of maximum MTC anomalies would occur after 2014, coinciding with those identified in the BMM time series. This suggests that the signal of the second MTC shift is also present in the AUCFZ. Several studies have demonstrated that an SWAO general warming process is associated with the poleward expansion of the Brazil Current and the Brazil–Malvinas Confluence[26,48]. Artana et al.[27] showed that this feature migrated southward between 1997 and 2006, oscillating widely thereafter (with southernmost positions in 1998, 2004, 2011, 2015 and 2017) and that Brazil's Current transport volumes tended to increase from 1998 to 2016. These trends are consistent with (a) periods of intensified SBT positive anomalies in the BMM time-series, and (b) the positive effect of SBT and BCt on MTC variation. BCt affected MTC with a 3-year (p-value = 0.031) and 4-year (p-value = 0.029) time-lags (Table 2). The reason for such a delayed response is uncertain, but possible explanations could be related to the complex physical interactions between the Brazil Current and the BMM shelf waters.

Gianelli et al.[21] argued that whereas many species in this dynamic transition region may be adapted to environmental oscillations, such a sustained oceanographic change would gradually provoke 'unprecedented changes in the composition and structure of ecological assemblages'. The caveat here, however, is that fishing data may affect the MTC analyses in different ways, e.g. through market-oriented behaviour of fishing fleets, which tend to establish temporal and spatial strategies in pursuit of profitable concentrations of their main fishing targets[46]. In the BMM, demersal fishing fleets explore a great variety of resources available in geographical space and different seasons in order to attain economic stability[42]. By doing so, they tend to integrate, in their catch composition, a wide spectrum of megafauna communities. However, trawl and gillnet vessels have developed a variety of *métiers*, i.e. a combination of target species, fishing area, gear, and time of the year[49,50], whose operational patterns in the BMM could partially modulate MTC variation. For instance, if fishing operations of a particular *métier* aiming at an abundant cold-water species predominated in relation to operations of other *métiers* during a year, an environment-independent MTC drop would be observed in such a year. We assessed these fishery-dependent effects in two ways. Firstly, an annual index of *métier* diversity (Dm, based on Simpson species

Table 1 Analysis of temporal trends in the mean temperature of the catch (MTC) of the demersal fisheries in the Brazilian Meridional Margin between 2000 and 2019.

Period	MTC range (°C)	MTC.yr^{-1} (°C)	*p*-value	R^2
2000–2019	20.07–22.60	0.057	0.016**	0.281
2000–2012	20.36–21.44	0.007	0.789	0.007
2013–2019	20.07–22.60	0.411	<0.001***	0.945
Period	**SBT range (°C)**	**SBT.yr^{-1} (°C)**	***p*-value**	**R^2**
2000–2019	14.97–15.79	0.013	0.058	0.185
2000–2012	14.97–15.45	−0.001	0.931	0.001
2013–2019	15.25–15.79	0.077	0.012*	0.750
Period	**BCt range (Sv)**	**BCt.yr^{-1} (Sv)**	***p*-value**	**R^2**
2000–2017	−30.10 to −19.06	−0.323	0.014*	0.273
2000–2012	−26.34 to −19.06	−0.221	0.240	0.123
2013–2017	−30.10 to −22.96	−0.728	0.504	0.160
Period	**Dm range**	**Dm. yr^{-1}**	***p*-value**	**R^2**
2000–2019	0.70–0.84	−0.002	0.077	0.164
2000–2012	0.78–0.83	<−0.001	0.927	0.001
2013–2019	0.70–0.84	0.010	0.371	0.162

Other variables included were: sea bottom temperature (SBT), transport volumes of the Brazil Current (BCt, negative values indicate north–south transport) and the index of *métier* diversity (Dm). Ranges and slopes of fitted linear models are indicated (MTC.yr^{-1}, SBT.yr^{-1}, BCt.yr^{-1} and Dm.yr^{-1}) for the entire time series (2000–2019) and for two consecutive periods discriminated by the segmented regression analysis. Significant code for reference: (*) *p*-value < 0.05; (**) *p*-value < 0.01; (***) *p*-value < 0.001. R^2 values computed for each test are informed.

Table 2 Results for linear models fitted between the mean temperature of the catch (MTC—response variable) and the explanatory variables: sea bottom temperature (SBT), annual transport volumes of the Brazil Current (BCt) and index of *métier* diversity (Dm) with and without time-lags (years).

Variable	Time lag (yr)	Slope	SE	*p*-value	R^2
SBT	0	2.356	0.583	0.001**	0.476
	1	2.119	0.848	0.023*	0.269
	2	1.449	1.057	0.189	0.105
	3	0.514	1.157	0.663	0.013
	4	0.791	1.175	0.512	0.031
BCt	0	−0.007	0.033	0.842	0.002
	1	0.026	0.043	0.558	0.022
	2	0.062	0.052	0.253	0.081
	3	0.114	0.048	0.031*	0.273
	4	0.124	0.051	0.029*	0.296
Dm	0	−0.948	4.218	0.825	0.003
	1	2.417	4.570	0.604	0.016
	2	3.624	4.695	0.451	0.036
	3	−2.622	4.895	0.600	0.019
	4	−14.113	3.696	0.002**	0.510

R^2 values computed for each model are informed. Significant code for reference: (*) *p*-value < 0.05; (**) *p*-value < 0.01.

diversity index) was computed and used to express the effect of dominance (low Dm values) vs. evenness (high Dm values) of *métiers* in the catches. Annual *Dm* did not exhibit any particular trend along the analysed time-series (p-value > 0.08, Table 1) and affected negatively MTC with a 4-year time-lag (p-value = 0.002, Table 2). This approach was first proposed by Gianelli et al.[21], who found similar results in the AUCFZ, i.e. the effect of fishing *métiers* on MTC time-series was either non-significant or in an opposed direction to that exerted by the ocean temperature. Secondly, we submitted the MTC time-series to a species sensitivity analysis, showing that the accentuated positive trend of MTC, observed between 2013 and 2019, remained unchanged no matter which species we removed from the analysis (Table 3). Between 2000 and 2012, when no particular trend was evidenced in the MTC time series (Table 1), the estimated slope of the linear model increased, becoming significantly positive, when the codling *Urophycis mystacea* was excluded from the time-series (Table 3). This is an abundant slope species (mean thermal preference = 16 °C) whose catches remained above average between 2007 and 2013 (Supplementary Fig. 3), mostly through the activity of a double-rig trawl *métier* which included slope species in the period (DR_1, Supplementary Table 3).

In the AUCFZ, the exclusion of the most abundant argentine hake (*Merluccius hubsi*; cold-water affinity) and the whitemouth croaker (*Micropogonias furnieri*; warm-water affinity) from the catch time-series changed considerably MTC variation[21]. Important catch reductions of the former have been attributed to overfishing, which has also a potential for modulating MTC time-series. This can be the case of several cold- and warm-water species that largely contributed to BMM demersal catches during the studied period, whose exploitation regimes were categorized as unsustainable[51]. In this region, for instance, important abundance declines of the cold-water argentine croaker (*Umbrina canosai*, from 2010 onwards) and the monkfish (*Lophius gastrophysus*, from 2000 onwards) in the BMM (Cardoso et al., unpublished results) could modulate MTC leading towards a catch warming scenario. However, at least in the latter species, biomass levels have remained extremely low after 2010, a period when the fishing effort was maintained below critical levels, suggesting that factors other than fishing pressure (i.e. ocean warming) could be driving temporal patterns of the species abundance. In any case, as pointed out in other MTC study regions[19,20], overfishing effects on MTC seems hardly dissociable from, for instance, poleward retractions of cold-water species and, in fact, may have a synergistic effect.

Catch composition analysis. Changes in species abundances in the catches of the demersal fisheries in the BMM evidence strong contrasts between the early (2000–02) and late (2017–19) periods of the time-series. These periods were aggregated into two largely dissimilar year-groups by the multiple regression tree-principal coordinate analysis (Fig. 4), which discriminated an initial scenario (Group I), when annual catches were characterized by 15 main species, most of them with cold-water affinity (species on quadrants 1 and 2 in Fig. 4b), from a late scenario (Group IV) defined by scores attributed by eight species mostly with warm-water affinity (species in quadrant 3, Fig. 4b). Such a contrast was also corroborated by (a) the elevated contributions of these year-groups to the estimated total beta diversity, statistically significant in 2000 (14.2%), 2001 (10.8%), 2002 (9.2%) and 2019 (10.1%) (Supplementary Fig. 4), and (b) the Temporal Beta Diversity indices (TBI) comparing years within Groups I and IV, which resulted in significant losses in species abundance (Fig. 5). It is important to note that mean biomass gains and losses were significant between these groups (second largest among the periods compared), and dominated by warm- and cold-water species, respectively (Fig. 6, Supplementary Table 2). The argentine croaker (*Umbrina canosai*) concentrated 15.4% of cold-water species biomass losses in the catches, along with the argentine hake (*Merluccius hubbsiI*), the argentine stiletto shrimp (*Artemesia longinaris*), the monkfish (*Lophyus gastrophysus*) and

Table 3 Sensitivity analysis of temporal trends estimated for a mean temperature of the catch (MTC) of the demersal fisheries in the Brazilian Meridional Margin between 2000 and 2019.

Species	Thermal affinity	Temperature preference (°C)	Slope	*p*-value	Slope change (%)
2000–2012			0.007	0.789	
Urophycis mystacea	Cold	16.0	0.068	0.012*	870.3
Cynoscion guatucupa	Warm	23.5	0.013	0.634	80.4
Merluccius hubbsi	Cold	12.6	0.012	0.638	68.3
Cynoscion jamaicensis	Warm	23.2	0.011	0.684	54.1
Octopus americanus	Warm	26.0	0.010	0.690	48.3
Nemadactylus bergi	Cold	14.1	0.009	0.723	31.0
Paralonchurus brasiliensis	Warm	22.1	0.008	0.745	20.3
Percophis brasiliensis	Cold	18.0	0.008	0.749	18.9
Penaeus paulensis	Cold	15.0	0.008	0.756	15.2
Doryteuthis pleii	Warm	21.1	0.008	0.764	12.0
Porichthys porosissimus	Cold	18.1	0.008	0.768	9.0
Carcharias taurus	Cold	15.3	0.008	0.770	8.2
Polymixia lowei	Cold	18.5	0.007	0.772	7.0
Cynoscion acoupa	Cold	20.8	0.007	0.805	−5.6
Zenopsis conchifer	Cold	12.8	0.006	0.803	−7.7
Doryteuthis sanpaulensis	Cold	16.0	0.006	0.810	−11.1
Conger orbignianus	Cold	11.2	0.006	0.813	−12.7
Paralichthys patagonicus	Warm	23.0	0.006	0.821	−14.8
Genypterus brasiliensis	Cold	13.5	0.006	0.814	−15.1
Penaeus brasiliensis	Warm	27.0	0.006	0.829	−19.3
Balistes capriscus	Warm	22.9	0.005	0.854	−30.0
Xiphopenaeus kroyeri	Warm	26.0	0.003	0.919	−64.3
Illex argentinus	Cold	10.0	0.002	0.942	−71.5
Umbrina canosai	Cold	19.0	−0.006	0.855	−181.3
Pleoticus muelleri	Cold	14.0	−0.006	0.805	−186.8
Lophius gastrophysus	Cold	12.6	−0.007	0.823	−195.2
Artemesia longinaris	Cold	16.0	−0.010	0.645	−248.3
Micropogonias furnieri	Warm	21.9	−0.034	0.214	−591.8
2013–2019			0.411	<0.001***	
Cynoscion guatucupa	Warm	23.5	0.445	0.0005***	8.2
Umbrina canosai	Cold	19.0	0.432	0.0003***	5.1
Merluccius hubbsi	Cold	12.6	0.366	0.0010**	−11.0
Artemesia longinaris	Cold	16.0	0.357	0.0002***	−13.2
Urophycis mystacea	Cold	16.0	0.341	0.0035**	−17.0

The species listed are those that, when excluded from the analysis, changed the slope of the fitted linear model by more than 5% (positive or negative). Thermal affinities are included: warm > 21.11 °C; cold < 21.11 °C. Significant code for reference: (*) *p*-value < 0.05; (**) *p*-value < 0.01; (***) *p*-value < 0.001.

others (Supplementary Table 2, Supplementary Fig. 3). The whitemouth croaker (*Micropogonias furnieri*) concentrated 25.6% of warm-water species biomass gains in the catches, followed by the grey triggerfish (*Balistes capriscus*) and the spotted pink shrimp (*Penaeus brasiliensis*) (Supplementary Table 2, Supplementary Fig. 2). Jointly, these biomass gains and losses contributed to a warming of the catches between the two extreme periods, and supported the process of tropicalization, as revealed by the MTC analysis.

Catch composition analysis also suggested that the important changes in the demersal assemblages, as proposed by Gianelli et al.[21], may have taken place in the BMM between 2003 and 2012. Unlike in the MTC analysis, however, a more precise shift period was not evident. The progression of years in the 2-D ordination plot (Fig. 4) suggested a temporal modification in catch composition from the initial scenario (Group I), when cold-water species were abundant in the catches (species on quadrants 1 and 2 in Fig. 4b), to two intermediate scenarios (Groups II and III) when these species were gradually less abundant and substituted by other cold-water species (on quadrant 4 in Fig. 4b). TBIs calculated between years within Groups I and II produced three significant comparisons, two indicating losses (2000/2003, 2000/2006) and one indicating gains (2000/2007) (Fig. 5). There were important mean biomass gains between these two periods (Fig. 6), concentrated in the warm-water whitemouth croaker (*M. furnieri*, 39.0%) and striped weakfish (*Cynoscion guatucupa*, 10.3%), and the cold-water argentine croaker (14.9%) and codling (13.1%) (Supplementary Table 2). Biomass changes were limited between years within Groups II and III. Cold-water species, chiefly the codling (*U. mystacea*) and the argentine croaker (*U. canosai*), dominated both gains and losses of biomass, respectively (Fig. 6, Supplementary Table 2), but TBI comparisons indicated that these were not significant changes (Fig. 5). The last transition in the catch composition (Groups III and IV) was marked by great biomass losses mostly of cold-water species (Fig. 6), including the codling (*U. mystacea*, 16.3%), Argentine croaker (*M. furnieri*, 15.3%), the Argentine stiletto shrimp (*A. longinaris*, 9.7%), the Argentine hake (*M. hubbsi*, 6.9%), the monkfish (*L. gastrophysus*, 2.4%) and others (Supplementary Table 2). TBI comparisons also indicated species losses, but they were significant only in relation to the year 2019 (Fig. 5).

Interpreting such changes in demersal catch composition, in light of the warming trend in the SWAO, required prior consideration of the physical processes associated with known patterns of the spatial distribution of fish and shellfish populations[46]. In the BMM, demersal fauna diversity tends to change from typically subtropical in the South Brazil Bight (23°S–28°S) to a mixed subtropical/warm-temperate towards the 'central shelf' subregion (south of 28°S, Fig. 1), which comprises the continental shelf area off southern Brazil, Uruguay and

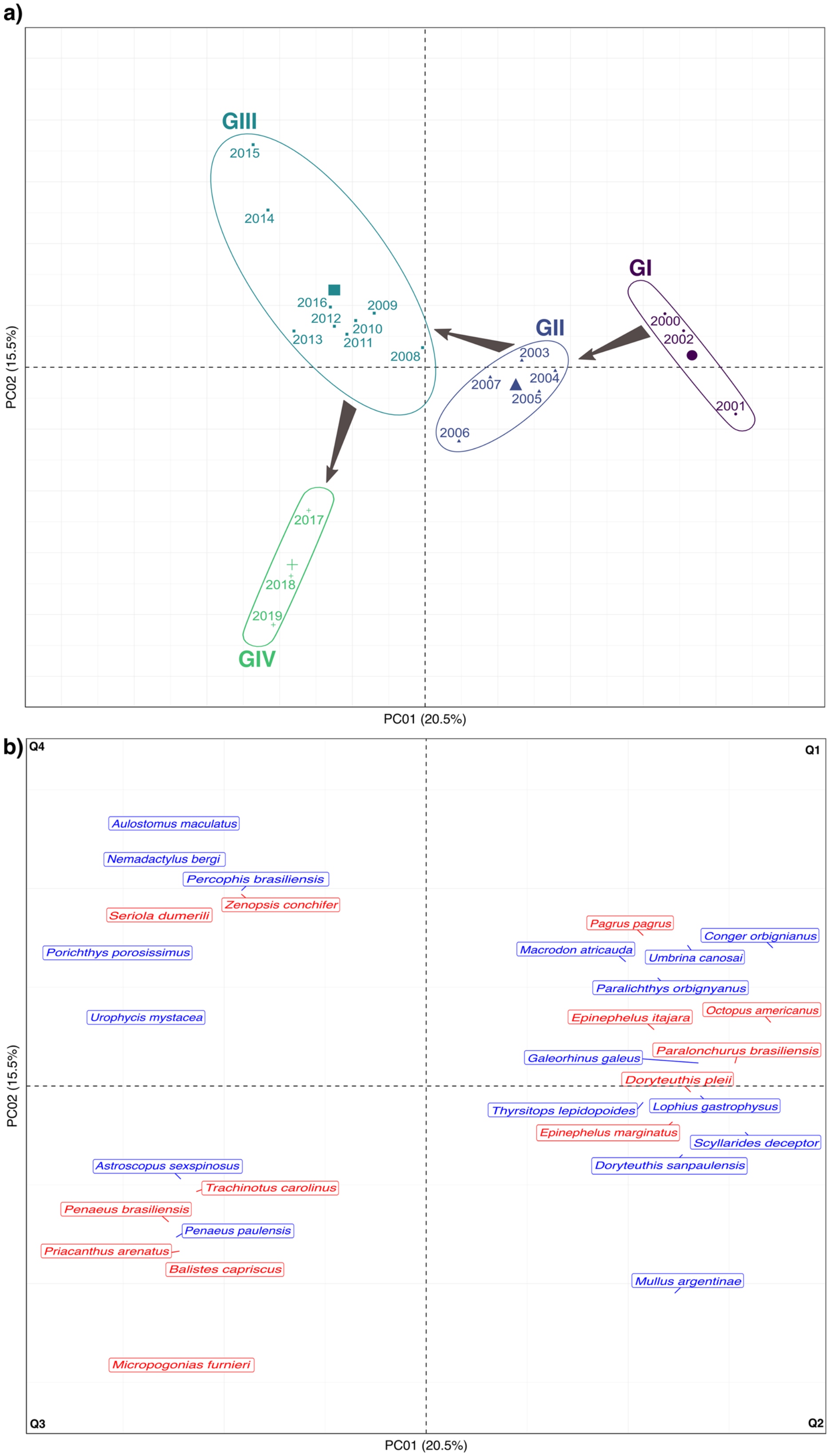
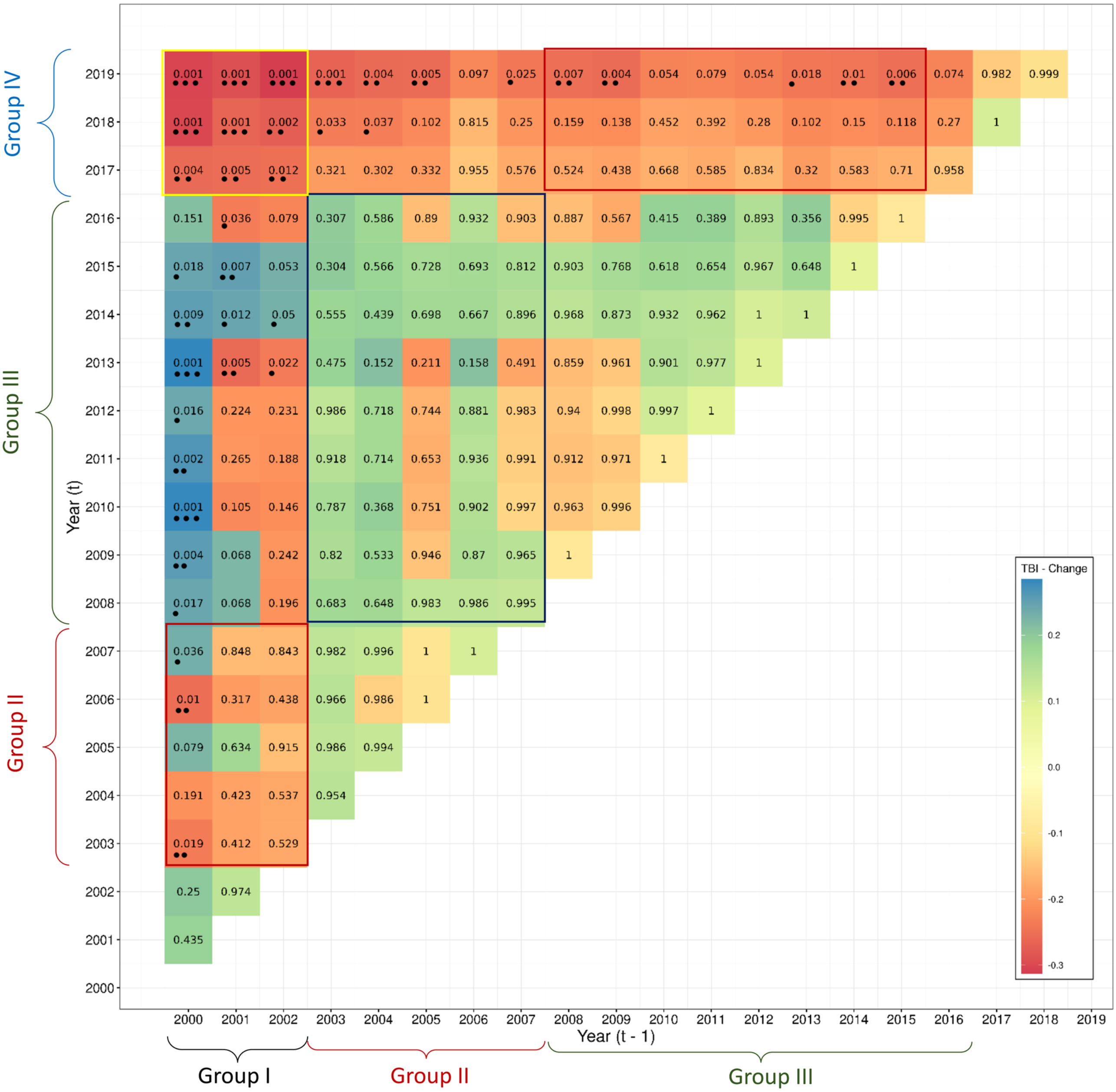


Fig. 4 Similarities of annual catch composition of the demersal fisheries in the Brazilian Meridional Margin (BMM). Catches were monitored between 2000 and 2019 in the harbours of Santa Catarina State, southern Brazil. Principal Coordinate Analysis ordination diagram representing **a** the spatial distribution of years included in the time-series and **b** of the species present in the catch according to scores of the first two extracted axes. Encircled years are groups discriminated by the Multiple Regression Tree procedure. Species in red and blue are those with warm- and cold-water affinities, respectively. Arrows indicate time progression between year groups.



Year (t)	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
2019	0.001 ●●●	0.001 ●●●	0.001 ●●●	0.001 ●●●	0.004 ●●	0.005 ●●	0.097	0.025 ●	0.007 ●●	0.004 ●●	0.054	0.079	0.054	0.018 ●	0.01 ●●	0.006 ●●	0.074	0.982	0.999	
2018	0.001 ●●●	0.001 ●●●	0.002 ●●	0.033 ●	0.037 ●	0.102	0.815	0.25	0.159	0.138	0.452	0.392	0.28	0.102	0.15	0.118	0.27	1		
2017	0.004 ●●	0.005 ●●	0.012 ●●	0.321	0.302	0.332	0.955	0.576	0.524	0.438	0.668	0.585	0.834	0.32	0.583	0.71	0.958			
2016	0.151	0.036 ●	0.079	0.307	0.586	0.89	0.932	0.903	0.887	0.567	0.415	0.389	0.893	0.356	0.995	1				
2015	0.018 ●	0.007 ●●	0.053	0.304	0.566	0.728	0.693	0.812	0.903	0.768	0.618	0.654	0.967	0.648	1					
2014	0.009 ●●	0.012 ●	0.05 ●	0.555	0.439	0.698	0.667	0.896	0.968	0.873	0.932	0.962	1	1						
2013	0.001 ●●●	0.005 ●●	0.022 ●	0.475	0.152	0.211	0.158	0.491	0.859	0.961	0.901	0.977	1							
2012	0.016 ●	0.224	0.231	0.986	0.718	0.744	0.881	0.983	0.94	0.998	0.997	1								
2011	0.002 ●●	0.265	0.188	0.918	0.714	0.653	0.936	0.991	0.912	0.971	1									
2010	0.001 ●●●	0.105	0.146	0.787	0.368	0.751	0.902	0.997	0.963	0.996										
2009	0.004 ●●	0.068	0.242	0.82	0.533	0.946	0.87	0.965	1											
2008	0.017 ●	0.068	0.196	0.683	0.648	0.983	0.986	0.995												
2007	0.036 ●	0.848	0.843	0.982	0.996	1	1													
2006	0.01 ●●	0.317	0.438	0.966	0.986	1														
2005	0.079	0.634	0.915	0.986	0.994															
2004	0.191	0.423	0.537	0.954																
2003	0.019 ●●	0.412	0.529																	
2002	0.25	0.974																		
2001	0.435																			
2000																				

Fig. 5 Changes in catch composition of the demersal fisheries in the Brazilian Meridional Margin (BMM). Catches were monitored between 2000 and 2019 at the harbours of Santa Catarina State, southern Brazil. The heat map presents Temporal Beta Diversity Indices (TBI) computed between all possible pairs of years within the time series considered (Biomass gains—TBI > 0, Biomass losses—TBI < 0). Boxes enclose comparisons between years included in the four groups discriminated by the multiple regression trees and principal coordinate analysis.

northern Argentina[33]. In this subregion, off southern Brazil, Martins and Haimovici[39] described four teleost fish demersal assemblages formed by species with similar temperature affinities, whose latitudinal and bathymetric distribution are associated with seasonal interactions of coastal, subantarctic and subtropical shelf water masses. A 'cold shelf assemblage' was shown to expand over mid-shelf bottoms during the austral winter, as driven by the increased influence of subantarctic shelf waters and the northward displacement of Subtropical Shelf Front. This assemblage contained some abundant cold-water species present in the demersal catches, including the argentine croaker (*U. canosai*) and the argentine hake (*M. hubbsi*), which have accounted for important biomass losses (>20%) in the BMM. In addition, a 'coastal' and a 'warm shelf' assemblages were shown to expand southwards over the shelf during the austral summer. These assemblages contained fish species with warm-water affinity, including the whitemouth croaker (*M. furnieri*), which alone accounted for 25% of biomass gains in demersal catches. In an ocean warming scenario, induced by the southward displacement of the Brazil Current and its influence over the shelf, a southward retraction of the 'cold water shelf' assemblage and expansion of the 'coastal' and 'warm water shelf' assemblages would be expected, justifying the observed *MTC* trends and temporal patterns of species abundance in the BMM demersal catches.

Deviations from this general pattern, however, were also characterized partially because targeted species may display different levels of adaptation and respond differently to a warming environment[13]. For instance, the whitemouth croaker (*M. furnieri*) contributed significantly to warm-water species biomass gains in the period, but also to biomass losses. The

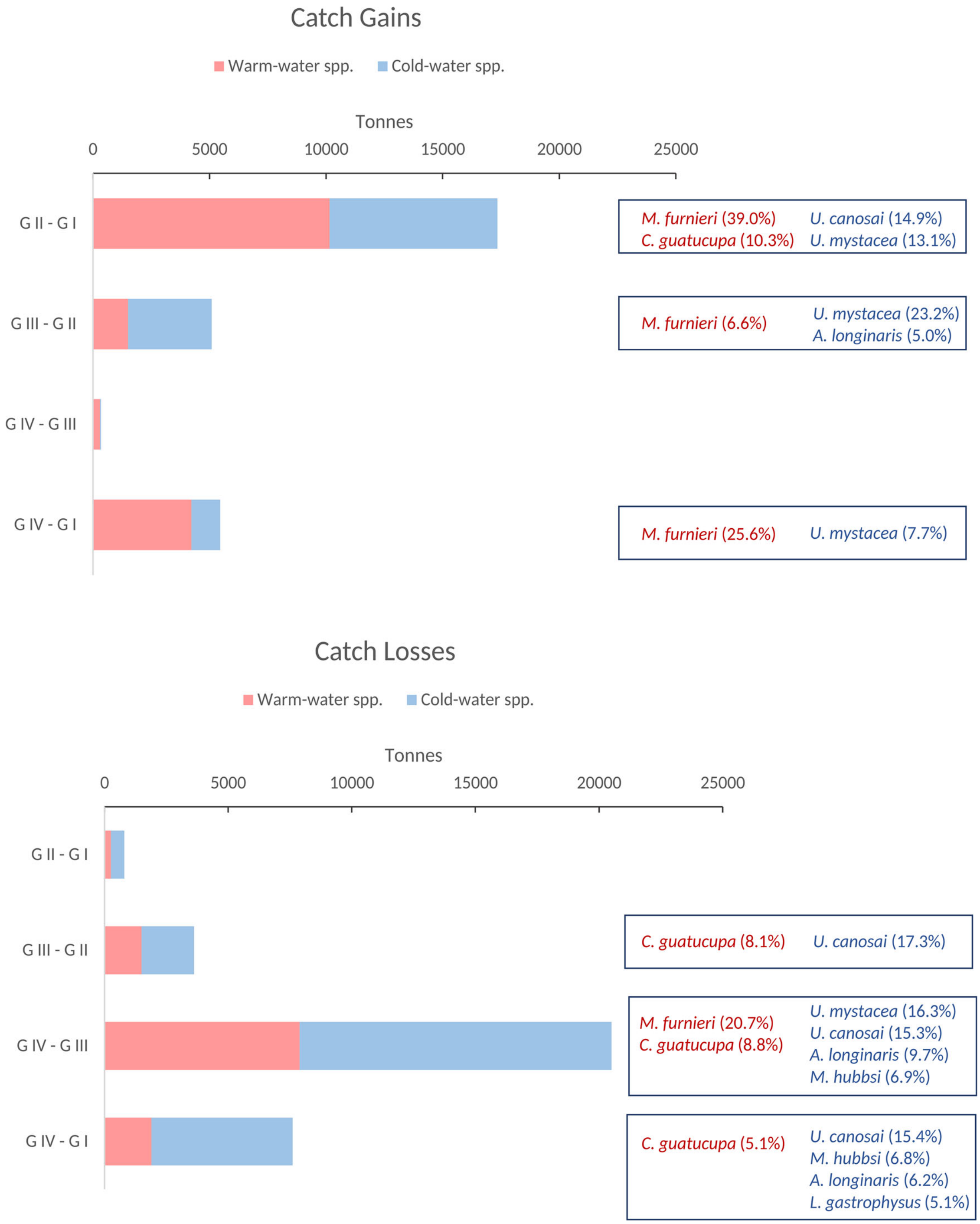


Fig. 6 Biomass gains and Losses in the catches of demersal species in the Brazilian Meridional Margin (BMM). Catches were monitored between 2000 and 2019 in the harbours of Santa Catarina State, southern Brazil. Bars indicate mean biomass gains and losses (in tonnes) between periods 2000–02/2003–07 (GII–GI), 2003–07/2008–16 (GIII–GII), 2006–16/2017–19 (GIV–GIII) and 2000–02/2017–19 (GIV–GI). Bar colours indicate mean gains and losses of species with “warm-water” (thermal preferences > 21.1 °C) and “cold-water” (thermal preferences < 21.1 °C) affinities. Species that concentrated the majority of mean biomass changes (in %) during each transition are indicated next to the bars. Species name colours also indicate their thermal preference.

species exhibits a complex stock structure that includes three spatially delimited stocks: one occupying the South Brazil Bight (‘Southeastern Brazil Stock’) and two extending over the central shelf off southern Brazil (‘Southern Brazilian Stock’) and at the AUCFZ (‘common Argentinean—Uruguayan stock’)[52]. Despite its warm-water affinity, the species exhibits a wide thermal tolerance, making it plausible that these stocks display some level of adaptation to local conditions and respond differently to the ocean warming process they have been exposed to in the SWAO. In addition, the La Plata River and the Patos/Mirim Lagoon systems are important nursery grounds for this species that may also respond to other climate-change-related effects such as freshwater discharge variability in these systems[21]. In that sense, the general tropicalization scenario characterized in the BMM demersal catches may be affected in different ways by multiple specific population processes operating at smaller spatial scales.

An additional source of error may derive from thermal preferences being attributed to demersal species from sea surface temperature distribution[17]. How much this affected MTC temporal trends in the BMM is uncertain but it was likely dampened by (a) the large proportion of catches originating from species in shallow shelf areas where temperatures are more homogeneous throughout the water column and (b) a positive correlation between SST and SBT values derived from the INALT20 model ($r = 0.84$) suggesting that, regionally, MTC calculated with surface temperatures should still be related to thermal changes on the seafloor. Finally, annual MTC may also be modulated by spatial factors (e.g. latitude, depth) and trophic levels[22,46]. Addressing these components is critical for a more comprehensive analysis of temperature-related community changes in the BMM.

Notwithstanding such limitations, historical catch data has proven to be an effective proxy for global climate effects on marine ecosystems regionally, with the advantage of further signalling future changes in the economic performance of current fishing regimes. How will the demersal fishing industry adapt to changes in the availability of traditional and non-traditional targets in the BMM? Which *métiers* will no longer be viable and which ones may emerge to explore expanding stocks of subtropical species? What adaptive measures can be incorporated into fishing management regimes (both national and transnational) to attain ecological and economic objectives in the coming decades? These are critical questions that could influence industry adaptive strategies and guide management measures over the next decades in the BMM, but whose answers will require extended analyses, with a database expanded to include spatial components and fisheries economic descriptors.

As a preliminary approach, however, we may infer that most *métiers* have included cold-water species among their most frequent targets (Supplementary Table 3) and will potentially face the need to adapt their fishing strategies. Particularly relevant seems the future performance of double-rig trawlers (*métier* DR_1) that have largely dominated the demersal fishing activity in the study period (Supplementary Table 1). Their operations, however, have long been driven by a generalist fishing behaviour and will likely be adaptable to new opportunities, as seen in the past[49]. Gillnet fishing (*métier* GN_1) was the second most active demersal fishing activity heavily focused on the whitemouth croaker (Supplementary Table 3). Whereas this may appear as a winner species under an ocean warming scenario, it is uncertain how long could it sustain fishing pressures increased by the effect of the progressively scarce cold-water target-species (e.g. *métier* GN_2 and others)[53]. Trawling for the warm-water sea-bob shrimp (*Xyphopenaeus kroyeri - métier* DR_2) can be an opportunity for trawlers in the future, especially those targeting cold-water shrimps (*A. longinaris* and *Pleoticus muelleri*—DR_3) (Supplementary Table 3). Such a perspective, however, will likely be limited by the increased competition with artisanal fisheries that have long exploited this coastal species in the BMM[54]. Finally, the likely decline of the argentine croaker in the catches may threaten the future viability of trawl (*métiers* PT_2, ST_2, ST_3) and gillnet (*métier* GN_2) operations that currently concentrate in the central shelf region. These catches have been mostly sustained by a population that migrates between the northern Patagonian shelf and southern Brazil[55] suggesting that, in the future, these *métiers* could only be viable south of Brazilian waters. These are some possible scenarios that indicate how demersal fisheries can be reshuffled at the BMM, calling for adaptive management that will require rigorous assessments of sustainable catches of subtropical species, and include actions that redistribute effort in areas that take into account species with changing distribution patterns, including transboundary stock management[56].

Methods

Catch composition, thermal preferences and oceanographic data. Analysed data included catches reported in the harbours of Santa Catarina state (Itajaí and Navegantes) from 2000 to 2019. These harbours have historically concentrated approximately 25% of total catches reported in the region[57] and a significant part of the demersal fishing fleet that operates widely on the BMM (Fig. 1), from 21°S to the southern border of the Brazilian Economic Exclusive Zone (34°S), and from the coastal areas down to 500 m depths. Landed catches were monitored by the University of 'Vale do Itajaí' along a sequence of scientific projects and contracts developed to meet governmental demands for oceanic and deep fisheries development and management and in support of the licencing processes of the offshore oil and gas exploration activities. Monitored demersal catches have been dominated by sciaenid fish (e.g. the whitemouth croaker (*M. furnieri*), the argentine croaker (*U. canosai*), the striped weakfish (*C. guatucupa*), the southern king weakfish (*Macrodon atricauda*) and the shrimps *X. kroyeri* (Atlantic sea-bob shrimp), *A. longinaris* (argentine stiletto shrimp), *Penaeus paulensis* (São Paulo pink shrimp) and *Penaeus brasiliensis* (spotted pink shrimp). Demersal fishing expanded to the upper slope from 2001 onwards adding some new fishing resources, e.g. the codling *U. mystacea* and the monkfish *L. gastrophysus*[43].

We analysed landings of 29,021 fishing trips conducted by double-rig trawlers (56.4%), pair trawlers (6.9%), stern trawlers (5.7%) and gillnet vessels (31.0%) (Supplementary Table 1). The number of fishing trips recorded each year varied between 561 and 2,036, and total catches varied between 11,000 and 53,000 t yr^{-1} during the studied period (2000–2019) (Supplementary Fig. 1). Reported catches contained records of 133 fish and shellfish categories. These were defined by single species or groups of species (e.g. rays, *Squalus* spp.). Only single species categories were included in the analysis, which resulted in a total of 78 species jointly representing 81.3% of total reported biomass. A temperature preference was assigned to each of the considered species, as obtained from global compilations made available by Cheung et al.[17] and in FishBase[58]. In both compilations, thermal preferences derive from considerations about the species distribution ranges and sea surface temperature maps (e.g. ref. [17], Supplementary material). An overall mean temperature preference value was calculated for all 78 species combined (21.1 °C) and used to assign warm- or cold-water affinities for species whose thermal preferences were above or below this value, respectively. The mean temperature of the catch—MTC was estimated for each year (y) of the time series, as proposed by Cheung et al.[17]:

$$\mathrm{MTC}_y = \frac{\sum_i^n T_i C_{i,y}}{\sum_i^n C_{i,y}} \tag{1}$$

where n is the total number of species recorded in one year, T_i is the temperature preference of the ith species and $C_{i,y}$ is the recorded catch of the ith species in the yth year. The composition of demersal catches and MTC time-series are publicly available at Perez and Sant'Ana[59].

Sea bottom temperature (SBT) was considered a predictor of MTC variation during the study period. SBT was derived from estimates provided by the high-resolution ocean general circulation model INALT20[47] for the study period (2000–2019), and was calculated by averaging the temperatures over 0.25° × 0.25° grid cells of the BMM and a water column up to 50 m above the seafloor. Additionally, MTC was confronted to annual volume transports of the Brazil Current (BCt) near the Brazil–Malvinas confluence (in Sverdrups, Sv) as estimated between 2000–2017 by Artana et al.[27] using high-resolution (1/12°) global Mercator Ocean reanalysis (GLORYS12) from Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu/). All BCt values are negative, as they represent north–south transport[27]. Annual values of both variables were normalized by their mean value over the time series and expressed as anomalies. In Fig. 1, daily gridded sea surface temperature (SST) data were obtained from the National Oceanic and Atmospheric Administration Optimum Interpolation Sea Surface Temperature (OISST) V2.0 with a horizontal resolution of 1/4° for the period 1982–2020[60]. The Mann and Kendall test was used to determine where the trends were statically significant at the 99th confidence interval.

In addition, we tested the effect of fishers' behaviour over catch composition, which could introduce environment-independent signals in the MTC (e.g. driven by market oscillations and other factors). For that purpose, individual fishing trips within the database were firstly classified by *métiers* (i.e. combination of target species, gear, and time of the year) using the K-means clustering algorithm[61]. Within the years of the time-series, catches of each *métier* were summed and used to calculate an annual index of *métier* diversity (Dm) using the Simpson diversity index formulation[21]:

$$Dm_y = 1 - \sum_{m=1}^{M} \left(\frac{C_{m,y}}{C_y} \right)^2 \tag{2}$$

where m is the fishing *métier* and M is the total number of *métiers* defined in the time-series.

Temporal trends of MTC, SBT, BCt and Dm were explored by fitting linear models to their variation through time. A segmented regression model was also adjusted to MTC time series in order to detect potential trend shifts through time and their association with SBT, BCt and Dm variation. Estimated MTC trends were tested for the influence of individual species in the catch data (species sensitivity analysis). This procedure intended to verify whether catch variation of the most abundant species could modulate MTC variation, significantly masking the combined effect of the wider group of species present in the catches. In this analysis, the linear models fitted to MTC along time were adjusted to scenarios where the species were iteratively excluded one-by-one. In each scenario, the estimated slope of the regression was compared to the slope obtained with all species included and verified whether the original trend was maintained or significantly changed. The effect of the environmental predictors *SBT*, BCt and Dm, over MTC variation was tested by fitting linear models that included a time-lag structure of 0–4 years, intended to verify any delayed responses of MTC to SBT, BCt and Dm variation.

Catch composition analysis. The patterns of change in the abundance of species present in the BMM demersal catches along the 19-year time-series were explored using ordination methods and estimates of beta diversity. Initially, a multiple regression tree procedure was applied to Hellinger-transformed annual species catches (abundance data) using the *mvpart* fuction of R package mvpart[62]. The size of the tree (i.e. number of splits) was selected after calculating the cross-validation error and deciding between the best-fitted and more parsimonious models[44]. A principal coordinate analysis was applied to the Hellinger distances to ordinate years in the 2-D (Euclidean) space and explore patterns of similarity/dissimilarity among years and among groups of years as previously defined by the MRT analysis[44].

The total non-directional beta diversity (BD_{total}) was estimated by computing the total sum of squares (SS_{total}) of the years vs. species matrix and the total variance by dividing SS_{total} by $n-1$. BD_{total} was further partitioned into relative contributions of years (here named YCBD)[63]. YCBD estimates were tested for significance by 999 random independent permutations of the columns of years *vs.* species matrix, using the *beta.div* function of R package adespatia'[64]. This analysis was used to identify year(s) when the catch composition was particularly altered. Temporal changes in catch composition were investigated by computing temporal beta diversity indices (TBI), using the TBI function of R package adespatial[64]. This procedure involved computing Percentage Difference dissimilarity indices between years (two-by-two) and partitioning these dissimilarities into gains ($1 > \text{TBI} > 0$) and losses ($0 > \text{TBI} > -1$)[65]. The computed difference between gains and losses was tested using a paired *t*-test. Patterns of gains and losses between time periods (e.g. groups of similar years as defined by the ordination methods) were investigated by analysing catch variation of individual species and thermal preferences.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The time series (2000–2019) of catch composition and mean catch temperature for demersal species in the Brazilian Meridional Margin that support the findings of this study are available in Pangea Data Publisher for Earth & Environmental Science with the identifier https://doi.org/10.1594/PANGAEA.946292 [59].

Code availability

The figures and data analyses presented in this manuscript were conducted using R 4.2.0, along with the following R packages: mvpart [62], adespatial [64]. Custom code for the analyses can be accessed here: https://github.com/rodrigosantana/DemersalTropicalizationBMM. All other code used to make figures is available upon request by contacting the corresponding author.

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Author contributions

J.A.A.P. and R.S. contributed equally to the conception of this study and interpretation of the results. J.A.A.P. led the writing and preparation of the submitted manuscript. R.S. led quantitative data processing and analysis.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Jose Angel Alvarez Perez.

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