doi:10.20944/preprints202212.0550.v1

Article

The Fall and Rise of *Diopatra* in the Brazilian Coast

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Simple Summary: Marine beach species have undergone changes in their populations over time mainly due to global climatic changes. Here we studied changes in a population of marine worm tube dwellers known as *Diopatra* in the southern Brazilian coast over 50 years. A noticeable reduction of their abundance lead to an almost local extinction of four species, followed by a small recovery of a unique species common in northern warmer waters. This reduction seems to be due to an increase in water temperature in recent years: (1) several days of warm waters ("heatwaves") in 1997/1998 and (2) a continuous increase in water temperature of around 1 °C in the last 50 years. Furthermore, a non-native species of *Diopatra*, originating from abroad, arrived recently and, according to their environmental conditions, it is likely to disperse throughout the Brazilian coast in the same habitats where the native species occur. This triggers a warning sign about the possible combination of global warming and other human mediated impact, such as species introduction and fishing bait harvesting, on the biodiversity of Brazilian sandy beaches.

Abstract: Patches of *Diopatra* species from Brazilian sandy beaches were followed for ca. 50 years. Data were accessed from papers, gray literature, images and collections to verify time changes in the South Brazilian Bight (SBB) from 1974-2021. We modeled maximum density over time at 15 beaches, observing very high densities (> 100 ind.m^{-2}) in 1974 followed by a decrease (~ 10 ind.m^{-2}) of three species of *Diopatra* until 1995 and a strong decline (1996-2002) when populations were almost regionally extinct (0-1 ind. m^{-2}). A slight recovery (3-4 ind.m^{-2}) occurred after 2006 for a single species, *D. marinae,* associated with warmer northern waters, suggesting a range shift. This pattern was associated with a) heatwaves linked to an El-Niño event (1988) and gradual SST surface warming of ca. 1 °C since 1974. The usage of *Diopatra* spp. as fishing bait could also be associated with such a reduction. After 2016, *D. neapolitana*, a likely alien species, was established in the SBB in high densities. Projections based on Species Distribution Modeling (SDM) suggest a potential of invasion in the same range of the known species of *D. cuprea* complex along the Brazilian coast despite that there are no signs of competition between both species.

Keywords: South Brazilian Bight, biogeography, heatwaves, global warming, range-shifts, alien species

1. Introduction

1.1. *A brief history of* Diopatra *on the Brazilian Coast*

Species of the genus *Diopatra* are easily noticeable, not only to trained marine biologists, but also to any person wandering sandy beaches during low tide. Of course, this is not different in the South Atlantic coast, especially the long Brazilian coast (about 7,500 km). However, the first scientific records of these worms were of new species dating from the 19th century, when four species of the genus were originally described from Brazil: *D. brasiliensis* Kinberg, 1865, *D. longicornis* Kinberg, 1865, *D. agave* Grube, 1869 and *D. variegata* Hansen, 1882. In addition to these, seven other species were reported from Brazil: *D. cuprea* (Bosc, 1802), *D. chiliensis* Quatrefages, 1865, *D. splendidissima* Kinberg, 1865, *D. viridis* Kinberg, 1865, *D. spiribranchis* Augener, 1906, *D. ornata* Moore, 1911 and *D. tridentata* Hartman, 1944.

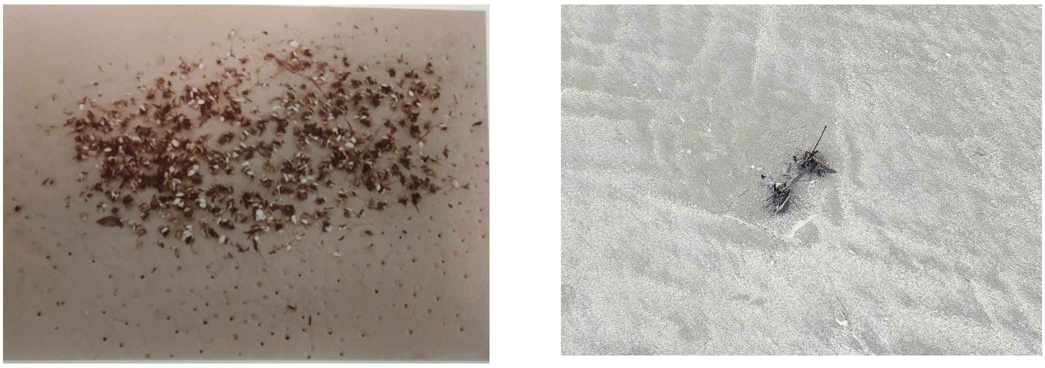
Of the species with type locality in Brazil, *D. agave* and *D. longicornis* are known only from the original description. According to Hartman [1], *D. agave* was described from a fragment, and it is almost impossible to compare it with other species. The same applies to *D. longicornis*. *Diopatra variegata* is also known only from the original description and, according to Hartman [1], this and *D. spiribranchis* are junior synonyms of *D. cuprea.* Nonato & Luna [2] argued for the validity of *D. spiribranchis*, as a possible subspecies of *D. cuprea* (peculiar to the Caribbean region), noting differences in the tube structure, in the length of the antennae and palps, and in the arrangement of the sensory buttons. *Diopatra brasiliensis* (type locality: Rio de Janeiro) was only reported later by Rullier & Amoureux [3] for the northeastern (Sergipe and Bahia) and southern coast (Rio Grande do Sul). It is a species close to *D. tridentata*, frequently reported in Brazil, suggesting the possibility of being the same species.

Diopatra ornata was sometimes reported for Brazil, as well as *D. splendidissima*, while *D. chiliensis* is of doubtful occurrence for the Atlantic coast, being recorded only by Luederwaldt [4] in a faunistic list of species that occurred on São Sebastião Island (-23.761; -45.4121), São Paulo State. Of all the referred species, *D. cuprea* is the most mentioned in ecological and taxonomic studies. Some of them have been identified at a specific level, but with uncertainty. Lana [5], like Orensanz [6], opted to designate previous records of *D. cuprea* populations from southeastern Brazil to Argentina as *D. viridis*, rather than *D. cuprea*, until a complete revision of the genus was done. Paiva [7] analyzing specimens of *Diopatra* collected at different depths on the inner shelf of the north coast of São Paulo state, suggested the possible presence of different species or subspecies, also pointing out the possibility of being *D. cuprea* and *D. viridis.* Both species belong to the *D. cuprea* complex.

Diopatra cuprea was originally described from Charleston, South Carolina, United States. Currently, there is no type material available. It has been widely recorded in the Atlantic, Pacific and Indian Oceans: from New England (or Massachusetts) to Florida, the Gulf of Mexico, the West Indies, Panama, Venezuela, along the coast of Brazil, both sides of the African continent (Ghana, Angola, South Africa, Mozambique), and the tropical Indian Ocean, from the intertidal region to 82-m depth. Among all the species reported and considered valid only five were from intertidal areas: *D. cuprea, D. ornata, D. splendidissima, D. spiribranchis* and *D. viridis.* But, for a long time, *D. cuprea* was considered the most prevalent and dominant species in SWA (especially in South Brazilian Bight) being observed, reported and collected by several generations of marine biologists, despite the possibility of a cryptic *D. viridis* in more southern sectors (see above). In the late 1970s and 1980s there were records of patches with high densities of ~ 20-130 ind.m^2, mainly on fine sand beaches [8,9] and image records from 1974.

In the mid-1980s and 1990s, intertidal specimens started to decrease drastically with densities reduced to less than 1 ind.m^{-2} and practically disappearing on the exact same beaches where they dominated the coasts of São Paulo, Paraná and Santa Catarina States, but with patches found on the northeastern (Rio Grande do Norte State), eastern (Espírito Santo State) and southern coasts of Brazil (Rio Grande do Sul State) [10, unpublished MSc thesis]. Such disappearance was noticed and the species *D. cuprea*, was included in the

Red List of Threatened Species from Brazil [11]. Garcia [10] has noted, using allozyme data, that at least two species could be found on beaches, corroborating previous works [5,6]. Nevertheless, 10 years later, Steiner [12, unplubished thesis] carried out a detailed morphological analysis with material from intertidal and subtidal habitats, reporting nine species of *Diopatra*: the already known *D. aciculata* Knox & Cameron, 1971, *D. dexiognatha* Paxton & Bailey-Brock, 1986, *D. tridentata* Hartman, 1944 and *D. ornata* Moore, 1911 and five new species. Part of the data from this thesis was afterwards published with the aid of molecular markers reporting four new beach species, namely *D. marinae, D. victoriae, D. hannelorae* and *D. pectiniconicum*, in the South Brazilian Bight (SBB) with a complex pattern with boundaries between 22 and 28°S (a well-known biogeographic boundary for several marine species, especially coastal ones) [13]. Thus, the number of valid species re-increased from seven to 14 and in the beach/intertidal zone, from six to nine. Although all species belong to the *D. cuprea* complex, surprisingly there were no specimens of *D. cuprea* in both analyses (morphological and molecular) suggesting that *D. cuprea* is a typical case of species complex whose named references were inflated by the fact of being the genus type, a pattern well known for marine invertebrates [14]. Another result of this survey is that the almost extinct intertidal specimens were back again, but with very low densities reaching, on some beaches, up to 0.25 ind.m^{-2} (**Figure 1**). This decrease and partial recovery of patches of *Diopatra* spp. led us to determine which species overcome such long-term shifts in abundance, as well as possible causes for this pattern. Therefore, we studied material found in collections and museums of specimens from 1970-1990 to compare with more recently reported specimens.



(a) (b)

Figure 1. Patches of *Diopatra* spp. in the region of Ubatuba (São Paulo State) over time: (a) High density (1974, Praia Grande, Anchieta Island, Ubatuba) and; (b) low density (2021, Ubatumirim beach, Ubatuba).

Out of the *D. cuprea* complex, in 1998 a newcomer, *D. neapolitana*, originally described from the Mediterranean Sea, was reported for the first time in southeastern Brazil, on intertidal areas of beaches from São Sebastião Island (Ilhabela city, São Paulo State). However, the establishment of large and dense tube banks was only reported after 2016 on the southeastern Brazilian coast [15], the species identification was confirmed both by morphological and molecular analysis in a comparison with sequences from the type-locality [13,15].

The potential for invasion of *D. neapolitana* has already been observed in the Pacific and Eastern Atlantic and recent reports for Brazil have raised the alarm for the potential invasion of other regions along the Brazilian coast. *Diopatra neapolitana*, well known throughout Mediterranean and French/Spanish Atlantic coasts, is generally considered a sister taxa of *D. aciculata* (Knox & Lowry, 1971) [16]. Despite the high morphological similarities of both species, Paxton [17] maintained both species as valid. Recently, an integrative taxonomic study found some evidence to delimit both species but the authors argue that species are on the gray zone of speciation due to the difficulty of finding conclusive molecular and morphological differences [18]. Thus, in this paper we considered them as a single ecological unit in order to model their distribution and invasion potential on the Brazilian coast.

1.2. *Diopatra as an economic resource*

Although the use of *Diopatra* spp as bait is reported for many areas around the world [19,20,21], few publications have been done in South America, and as pointed out by Cole [22], researchers from South American countries report no evidence that polychaetes are commonly used as bait. Only two references were found in small regions of the southern coast of Brazil: in RS State where the fish were captured by sportfishermen using hook-and-line of different sizes and employing different bait including *Diopatra* spp and some species of mollusks and crustaceans (Lewis & Fontoura 2004) and in SC State where the authors report that the replacement of hook-and-line by nets resulted in the loss of importance of *Diopatra* as bait [23]. Nevertheless, there is no quantitative data about the amount of specimens collected or the impact on local populational biology of *Diopatra* in the Brazilian Coast.

Considering the complex pattern of distribution of the *Diopatra cuprea* complex and the newcomer, *D. neapolitana*, herein we evaluate: (1) temporal density shifts of *Diopatra* sp. (group *cuprea*) in SBB sandy beaches over the past 41 years; (2) which species of *Diopatra* were responsible for such shifts; i.e., is the same species recovering or has this species been replaced over time? (3) the invasive potential of an exotic species, *D. neapolitana*, recently found in the Brazilian coast through species distribution modeling.

2. Materials and Methods

2.1. *Density estimation in* Diopatra *spp. (complex* cuprea*)*

Population densities were obtained from publications, grey literature, photographic records, and personal/expert observations. Even though *Diopatra* spp. from *D. cuprea* complex were distributed throughout the Brazilian coast from the extreme south (32°S) [13] to the northern Amazonian coast (1°S) [24], populational information was restricted to the Southeastern Brazilian Bight (SBB, Figure 1). SBB is an area of biogeographical concern because it is a transitional zone where several closely-related intertidal polychaete species have distribution overlap, including *Diopatra* [25,13].

Density data from beaches of SBB, especially in São Paulo State, were estimated or measured whenever past and present density records were available. Four beaches in this region were sampled more than once over 20-40 years. Nevertheless, data were grouped by localities (**Figure 2, Table S1**), sometimes with estimates from different beaches since information of maximum density shifts over time did not vary within localities.

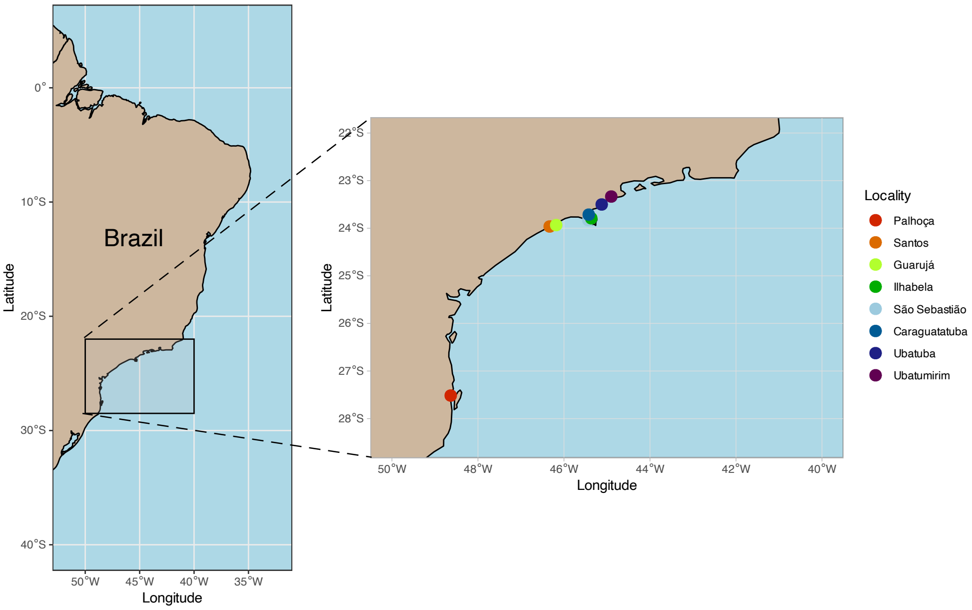


Figure 2. Brazilian Coast and Southern Brazilian Bight with localities from where density estimations were obtained.

As the size of *Diopatra* patches depends on the sediment type and beach conditions (tidal range, slope, etc.) population densities were estimated only for the main area of occurrence on the intertidal region. Two measurements were obtained, mean density in the occurrence area and maximum density, both per square meter. Maximum densities were measured on a square meter scale and not extrapolated from lower measured scales, since many patches were smaller than 1 m^{-2}. Since there is a dependence in time-series data, we fitted a local polynomial regression with the best span parameter selected by a Generalized Cross-Validation using the “fANCOVA” package [26].

2.2. Surface Sea-Water Temperature (SST)

Historical data of Surface Sea-Water Temperature (SST) were obtained from NOAA (NOAA NCDC ERSST version5) [27] through R package “rerddap”[28]. From this data we extracted mean annual temperatures, mean of the warmest and coldest months and thermal anomalies from 1970 to 2021 along the Brazilian coast. Intensity of El Niño events were accessed through the Multivariate and El Niño/Southern Oscillation (ENSO) Index (MEI v.2), obtained from the NOAA Physical Sciences Laboratory [29].

2.3. Species Distribution Modeling (SDM)

Regarding the taxonomic status of *D. neapolitana* and *D. aciculata,* there is strong evidence that both species are distinct based on both morphological and molecular data [18,13]. Thus, we decided to combine worldwide distribution of both species in order to obtain their occurrences for modeling. Data from a total of 593 occurrences obtained from GBIF and two more references from our collected material of Rio de Janeiro State. Data were filtered, leaving only data with lat/long and thinned to a 5-km distance to avoid oversampling in close areas. Thus, the remaining 290 occurrences were used for modeling. Environmental data were obtained through “sdmpredictors” package (Bosch &

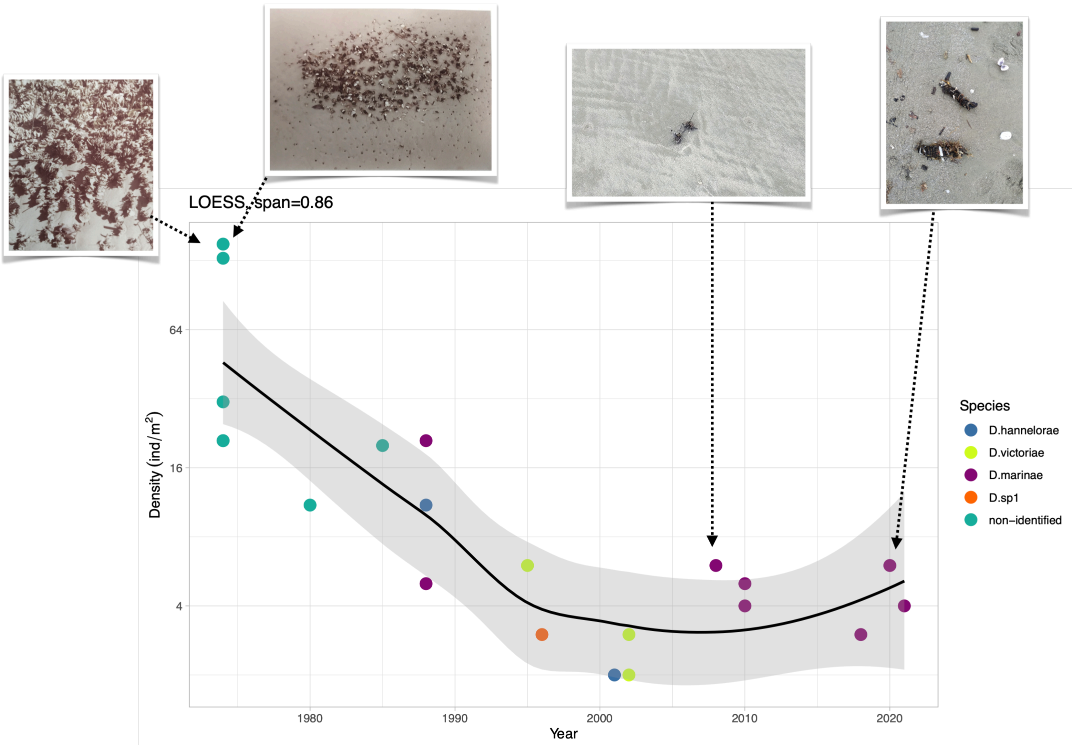
Fernandez, 2021) from Bio-Oracle [31], for marine data, and WorldClim [32] for terrestrial data of 5 arcmin.

Modeling was performed using biomod2 package [33] using 70% of the data for calibration and 30% for evaluation, in four runs. Since we have only presence data, pseudo-absences (=background) data was generated 10 times. The number of pseudo-absences (PAs) are like the number of presence data as suggested by [34,35]. Performance of the combination of models, runs and PAs were assessed by True Skill Statistics (TSS) with values higher than 0.7 selected for building an ensemble model. This being the combination of several algorithms: General Linear Model (GLM), General Additive Model (GAM), Boosted Regression Trees (GBM), Random Forest (RF), Multiple Adaptative Regression Splines (MARS), Flexible Discriminant Analysis (FDA) and Maximum Entropy (MaxEnt). Despite the worldwide modeling, forecast of habitat suitability was projected only for the area of interest, the Brazilian coast.

3. Results

3.1. Diopatra *spp. fall and rise over time*

A total of 28 density estimates were obtained from 15 beaches over 37 years (1974-2021) in the Southeastern Brazilian Coast (22-28°S), four of which were sampled more than once in this period. Since maximum density was strongly correlated with mean density (r=0.88) analysis were performed only for the former. Densities were very high (>100 ind.m^{-2}) in 1974 followed by a decrease (~10 ind.m^{-2}) until 1995. After that, there was a sharp decline (1996-2002) when populations were almost regionally extinct (0-1 ind.m^{-2}) and the species (named as *D. cuprea*) was included in the Red List of Threatened Species of Brazil [11]. However, this reduction was followed by a slight recovery (2008-2021) with maximum patches of 3-4 ind.m^{-2}. The local polynomial regression (LOESS) model fitted to the data showed that there were strong long-term population changes (**Figure 3**).



doi:10.20944/preprints202212.0550.v1

Figure 3. Density variation of *Diopatra cuprea* complex species over time (1974-2021) from beaches of the South Brazilian Bight (22-28ºS). Species not identified or reported as *Diopatra cuprea* are plotted as nonidentified (green).

Data from older surveys (1970-1990) are mainly based on images or density estimates in the field, referring mainly to *D. cuprea* or only to the generic level and with rare vouchers. Thus, we are not sure to be working with the same species, considering the taxonomic knowledge update for the region that does not consider *D. cuprea* as an inhabitant of the Brazilian coast. Nevertheless, we were able to retrieve some vouchers from the same beaches and surveys in museum collections and identified them at specific level. According to this analysis, the oldest samples (1988) from Lázaro Beach (Ubatuba) -higher densities=10 ind.m^{-2} - were identified as *D. hannelorae* Steiner & Amaral, 2021. In the period of lowest densities, (1996-2002) the rare specimens found were *D. hannelorae* and *D victoriae*. Those found on the recent slight recovery (2010-2021) from the beaches of Santos, Guarujá and Ubatuba were identified only as *D. marinae* Steiner & Amaral, 2021. A collection voucher from Santos in 1958, not included in the plot since there is no quantitative density information, was also an individual of *D. hannelorae*. Nevertheless, anecdotal information obtained from older observations indicated that high-density patches were common in the region.

Thus, it seems what was considered the sign of populational recovery of a threatened species was due to species replacement, at least in this region. The surveyed region (SE Brazil) is the one where more species of *Diopatra* were found [13] The distribution range of the species, showing an overlap of at least four species in the South Brazilian Bight, does not mean that they are still sympatric in their distribution since they were sampled at different periods, except for those collected recently (all reported as *D. marinae*).

The observed pattern of strong decline (~1996-2002) and recovery (after 2010) of *Diopatra* seems to be associated with the variation in surface sea-water temperature (SST) in the region reflected in temperature anomalies (**Figure 4** and **Figure 5**).

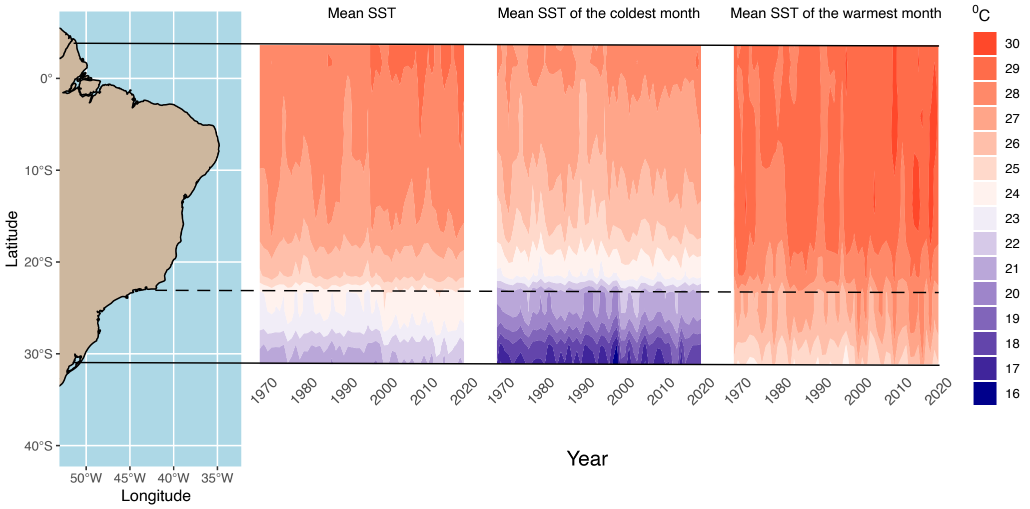


Figure 4. SST (Sea-Surface Temperature) variation over time (1970 – 2020) on the Brazilian Coast. South Brazilian Bight is shown below shaded line.

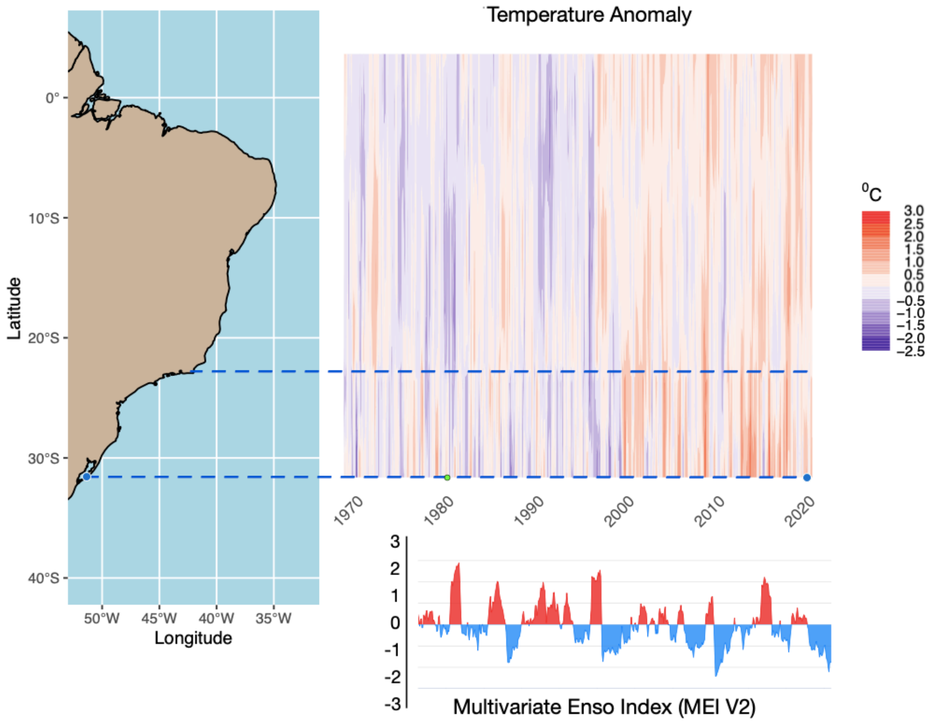


Figure 5. Temperature anomaly variation in time (1970 – 2020) and Multivariate Enso Index 1979-2022) along the Brazilian coast. South Brazilian Bight is shown between shaded lines. MEI values in red indicated El Niño events, and blue values, La Niña.

The disappearance of the endemic *D. victoriae* as well as of the colder/southern *D. hannelorae* in the same region, could be due to the ca. 1 °C mean monthly increase in the last 50 years, suggesting a warm limit of more than 27 °C. In fact, in the SBB (ca. 12-22°S) where the species is rare, mean temperature of warmer months (MTWM), higher than 28 °C, occurred only after 2000 (**Figure 4** and **Figure S1**)

The mean annual temperature increased in the SBB from 22 °C to 23 °C before 2000 (23 °C in 1970) to 23 to 24 °C after 2000 (24 °C in 2021) (**Figure 4**). The SBB warming, especially after 2000, gave rise to peaks of temperature anomalies (monthly mean) of ca. 1.8 °C in contrast to ca. 1 °C before (**Figure 5**) with a significant ($p < 0.005$) increase in mean anomaly of 0.53 °C between 1970-2000 and 2000-2021 intervals. Thus, southward seawater warming in recent years would allow *D. marinae*, typical from northern warmer waters **(Figures S1, S2**) and with a southern limit in SBB, to expand its range to be the dominant intertidal species in more recent years, even though still in lower densities.

3.2. *The newcomer* D. neapolitana

Despite the restricted area of occurrence of *D. neapolitana* (=*D. aciculata*) on the South-eastern Brazilian coast, its higher densities in some beaches (Araça Bay, São Sebastião, São Paulo State), Engenhoca Beach (Governador Island, Rio de Janeiro State) and Japonês Island (Cabo Frio, Rio de Janeiro State) with around 20 ind.m^{-2} (**Figure 6**) in the same region where *D. cuprea* complex once dominated triggered the alarm for its potential invasion on the Brazilian coast.

Figure 6. Tubes of *Diopatra neapolitana* in Engenhoca Beach (Governador Island, Rio de Janeiro State, 2017).

Since intertidal animal distribution and tolerance depends on both water- and air conditions, we modeled the suitability of *D. neapolitana* (=*D. aciculata*) habitat for both marine and terrestrial environmental drivers. After removing collinear and correlated factors, we modeled with just four drivers: sea-surface temperature range, mean salinity and maximum air-temperature and precipitation of the wettest month. TSS values (threshold of 0.7), all algorithms (GLM, GAM, GBM, MARS, RF, FDA and Maxent) were included for at least one run and PA. The final ensemble model with the four environmental variables, salinity, maximum air temperature (MAT), precipitation of the wettest month (PWM) and range of surface sea-water temperature (rSST) were very informative, with high evaluations (TSS = 0.941, **Figure S3**). Importance of each variable was rather different among them with salinity being the most important (median >0.75) while all others with lower medians (<0.20) but with some higher values for specific models and runs (**Figure S4**).

Ensemble results projecting the habitat suitability of the species are shown in **Figure 7**. While the current distribution, which is in the short latitudinal range of 22.8 to 27.7^{o}S, the habitat suitability for the establishment of the species is much higher, ranging from 9 to almost 30^{o}S. This suggests that, in relation to current conditions mainly of salinity and temperature (air and water), the species could increase its distribution, especially northward, wherever sandy beaches and tidal flats occur. The range is the same of intertidal species of *D. cuprea* complex, except for the Amazon River mouth (around 0-1 ^{o}S) where patches of *D. cuprea* were reported [24], but it seems to be not a suitable habitat for *D. neapolitana*, mainly due to lower salinity (**Figure S3)**. Likewise, the medium suitability areas within high suitability areas between 10^{o}S and 21^{o}S, for instance are located close to two river mouths (Doce and São Francisco rivers). Despite its worldwide distribution, *D. neapolitana* presented low tolerance to lower salinities (<21 PSU) in lab experiments [36]. Our modeling based on actual occurrences, indicated a higher probability in salinities greater than 34 PSU, which in association with lower levels of precipitation (<250mm in the wettest month) suggest a strong limitation to areas of brackish waters.

Despite being a tube dweller, and thus not likely to be strongly affected by temperature variation [37], mainly air temperature, a short range between 22 °C and 33 °C was predicted for its distribution.

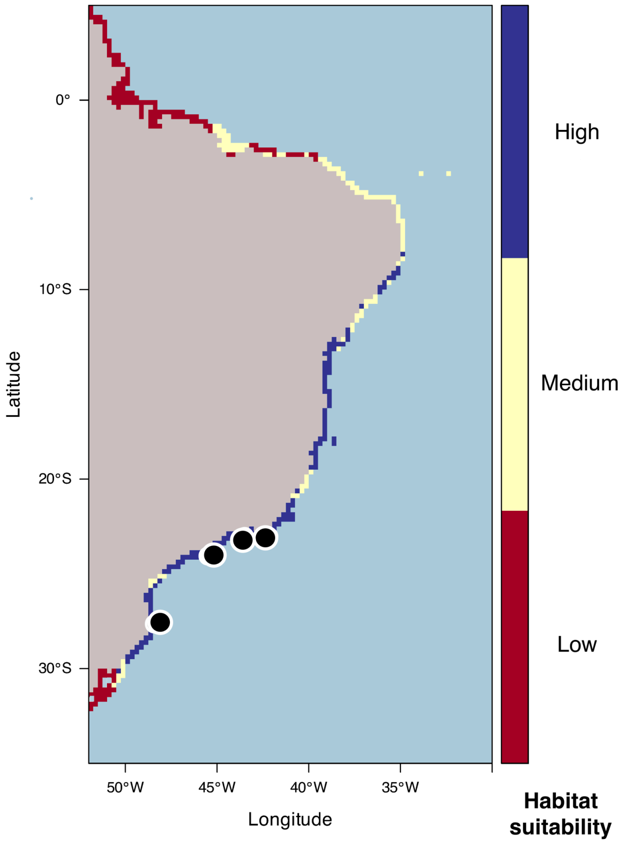


Figure 7. Ensemble model (TSS weighted mean) of current habitat suitability for *D. neapolitana*/*D. aciculata* along the Brazilian coast. Current occurrences are shown as blackspots.

Thus, besides environmental constraints, *D. neapolitana* has potential to expand its current distribution to the same geographical range inhabiting the same beaches of the native species of the *D. cuprea* complex.

4. Discussion

4.1. Diopatra *spp. density variation over time in SBB and the role of climatic change*

Data on thermal requirements of *Diopatra* species are difficult to obtain since many of them were based on *D. cuprea* and other species of the genus that seem to belong to species complexes and not a unique evolutionary unit. Thus, observed patterns are generally not species-specific requirements. Experiments performed with *D. cuprea* from the type locality, in North Carolina (the "real" *D. cuprea*), showed a wide range of thermal tolerance surviving in warm waters up to 42.5 °C and, for specimens from the Gulf of Mexico, 40.1 °C during summer [21,38]. However, for field data of another species, *D. biscayensis* from Biscay Bay (western European coast) in similar latitudes and thermal conditions, the tolerance limits ranged from 16 °C to 24 °C [39]. In the South Brazilian Bight (SBB), where expansion *of D. marinae* seems to have occurred, lower monthly-mean SST temperatures varied from 19.5 °C to 27.8 °C (08/2000 and 02/2019 respectively) with a range shift from 19.5 °C to 26.9 °C in the period of 1970-2000 to 20.1 °C to 27.8 °C in 2001-2021, suggesting a thermal lower tolerance of this species around 20 °C. Mean SST of the coldest month being always greater than 20 °C after 2000 in the northern part of the SBB (**Figure 4**), being a clear sign of warming in the last 20 years. Conversely, the warming of coastal waters after 2000 was likely to be responsible for the retraction of *D. hannelorae* to southern areas, disappearing from the SBB as well as the apparent extinction of *D. victoriae*, endemic from this region.

Shifts in the range of distribution of the *Diopatra* species were already recorded for the northeastern Atlantic coast (European beaches) with range shifts of *D. biscayensis* and *D. neapolitana* related to an increase in SST (surface sea-water temperatures and anomalies) over time [39,40]. However, this process was related to expansion in the time scale of decades in a gradual process of tropicalization. While, in the SBB, the unusual and acute disappearance of all species, except for *D. marinae,* from the SSB was before the main gradual global warming, more intense in the last decades (2000-2020). Marine heatwaves, i.e. a wave of extreme and prolonged continuous warming for several days or even months [41] are likely to have sudden devastating impact in coastal environments such as coral bleaching and high mortality/local extinction of marine species [41,42]. Heatwaves were associated with a retreat in the distribution of the lugworm *Arenicola marina,* a species with similar habitats of *Diopatra*, forecasting its complete disappearance in Mediterranean in the future [43]. Intense and frequent heatwaves were associated with an El Niño—Southern Oscillation (ENSO) event in 1997/1998 [42], one of the three most intense ENSO events since MEI started to be measured (**Figure 4**). This event affected all oceans but, particularly in SWA, the South Brazilian Bight [44]. It could be responsible for the above cited sudden fall of *Diopatra* species densities in the SBB followed by the maintenance of only a single species, the warmer water associated *D. marinae* typical from the eastern and northern coasts of Brazil owing to the gradual SST increase after 2000. *Diopatra marinae* already occurred in the SBB in the past. Its maintenance as the single species after 1998 events (heatwaves) and the fact that SST warming is a long-term process that would be causing its spatial expansion, as suggested by molecular analysis in the area [13], made us hypothesize that it is expanding its distribution, a historical process in course that was enhanced more recently. This SST driven range-shift could indicate a process of tropicalization and deborealization [45] with a warm-water species expansion and cold-water species retreat of the intertidal species from the *D. cuprea* complex in SBB. Range shifts of marine species, besides appearing to be less "dangerous" at first sight than the impact of introduced species, are likely to affect biological systems at the community level with similar magnitude as those from introduced ones [46].

Range shifts of intertidal species distribution seem to be a complex process, with a combination of gradual long-term changes punctuated by shifts caused by extreme events such as heatwaves [47]. Furthermore, other human impacts, like collecting specimens for fishing bait, are likely to affect population density and do interact with climate change, especially in areas in the range limit of the species. Nevertheless, as quantitative data about the amount of worms harvested and the impact of such activities on population resilience are not yet available, we cannot assess the actual impact of such activities on the fall and rise of *D. cuprea* complex in the region.

4.2. What about the newcomer?

There is still some uncertainty about the worldwide distribution of *D. neapolitana* [18,21] considering a more restricted Mediterranean, Atlantic Iberian and French coast distribution with all other occurrences (e.g. Southeastern Atlantic, Pacific and Indian Oceans) as being from related similar species [48]. But, recent surveys validated some of this doubtful records that show a wider distribution to the species [15,49]. Data on genetic distance indicate that the species in the Brazilian Coast is the same evolutionary unit than those from Mediterranean Sea [13] and western European coast [15]. Likewise, reproductive patterns, with a typical sequential protandric hermaphroditism [15,48], were also similar in populations from both sides of the Atlantic, despite some subtle morphological differences that could indicate populational variation.

Thus, it seems that *D. neapolitana* is an alien species that spreads out owing to a wide range of environmental conditions. Furthermore, the species shows some plasticity regarding its reproductive cycle, with a single annual spawning in temperate regions and a continuous cycle in tropical ones [50], with reproductive plasticity being a precondition for the success of marine invasive species providing competitive advantages over native species [51].

Diopatra neapolitana and *D. marinae* are sympatric in southern Brazil they are seldom syntopic (coexisting in only one or two beaches), probably because *D. neapolitana* appears to occupy lower-energy, muddier habitats than *D. cuprea* [21]. Thus, negative interactions between them seem not to be an issue, and competition for resources in soft sediments, mainly intertidal tube dwellers, is not common [52]. Nevertheless, projections of habitat suitability for *D. neapolitana* are rather similar, except for the estuarine and brackish waters in the eastern and northern Brazilian coast. But considering the struggle for survival in sandy beaches with all human-mediated impacts in such an environment (e.g. nourishment, fishing bait, trampling, cleaning, [53]) we cannot disregard the new risk for the native species coming from a closer related congeneric species.

5. Conclusion

Despite taxonomic problems regarding correct identification of old records of *Diopatra* in the South Brazilian Bight, global warming and heatwaves are likely to be involved in the fall and rise of species of *Diopatra* from the complex *cuprea* over the last 50 years through retraction, extinction, and expansion of ranges of different species of the group. Also, an exotic species, *D. neapolitana*, just arrived and seems to have a potential for dispersing to the same beaches that native species inhabit. Human impact is also likely to act on populational changes, even though its relative role is still to be evaluated.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Density variability of *Diopatra* spp. (complex *cuprea*) on SBB beaches. Both published and unpublished data (grey literature and personal observations) are provided (For details see M&M text). Figure S1: Species of *Diopatra* referred to the Brazilian Coast. Pattern of geographic distribution and variation over time time (1974-2021). Figure S2: Mean SST (Mean) and Mean SST of the warmest month (MWMT) of the years 1970 and 2021. Figure S3: Spatial variation of selected variables: SST range and Salinity (sea-water), Maximum Air Temperature and Precipitation (air), Marine data were obtained from Bio-Oracle [31], and terrestrial/air from WorldClim [32]. Figure S4: Relative importance of each environmental variable from ensemble models.

Author Contributions: Conceptualization, P.C.P., M.A.V.P., A.C.Z.A., T.M.S. and V.C.S.; methodology, P.C.P., V.C.S.; software, P.C.P.; validation, M.A.V.P., A.C.Z.A., T.M.S. and V.C.S.; formal analysis, P.C.P., A.C.Z.A., T.M.S., M.A.V.P. and V.C.S.; investigation, P.C.P., M.A.V.P., A.C.Z.A., T.M.S. and V.C.S.; resources, A.C.Z.M., M.A.V.P. and P.C.P.; data curation, A.C.Z.A., T.M.S. and M.A.V.P.; writing—original draft preparation, P.C.P. and M.A.V.P.; writing—review and editing, P.C.P., M.A.V.P., A.C.Z.A., T.M.S. and V.C.S.; visualization, P.C.P.; supervision, A.C.Z.M.; project administration, A.C.Z.M. and P.C.P.; funding acquisition, A.C.Z. and P.C.P.. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, grant number 2018/10313-0), FAPERJ (Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro, grant number E-E26/202607/2019) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, grants number 306788/2021-7, 428447/2018-0 and 301551/2019-7).

Institutional Review Board Statement:

Not applicable

Informed Consent Statement:

Not applicable

Data Availability Statement:

Not applicable

Acknowledgments: Specimens of *Diopatra* examined were loaned by Marcelo V. Fukuda (MZUSP), Joana Zanol (MN-RJ), Tatiana M. Steiner (MDBio) and Monica A. V. Petti (ColBIO). We also thank Dr Natalia Venturini (Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay) for her valuable comments. Jim Hesson copyedited the manuscript (https://www.AcademicEnglish-Solutions.com).

Conflicts of Interest:

The authors declare no conflict of interest.

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