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Jellyfish diversity and distribution patterns in the tropical Southwestern Atlantic

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Abstract

Jellyfish are often the most prominent components of plankton, with severe consequences for fisheries and tourism. However, in tropical regions, there is much uncertainty about these consequences due to the lack of basic data. Our objective was to improve the knowledge about jellyfish in the Western Atlantic, with an emphasis on understanding diversity, abundance, and distribution patterns. Samples were collected at 34 stations in 1995 using a 300-μm-mesh Bongo net. The 21 species identified belonged to Hydromedusae (11), Siphonophora (nine), and Scyphomedusae (one). The overall mean density was low (5.2 ± 5.3 ind. m^{-3}). Total Hydromedusae biomass was 130.86 mg C m^{-3}, and total Siphonophora biomass was 19.04 mg C m^{-3}. *Chelophyes appendiculata* (Eschscholtz, 1829) was the most frequent species captured in the oceanic samples, and *Aglaura hemistoma* (Péron & Lesueur, 1810) was the most common in the neritic region. The latter species is sometimes characterized as a bloom associated with the most polluted and eutrophic river plumes. The main role of jellyfish species in the area is as a higher-order carnivore. A cross-shelf significant difference ($P < 0.05$) was registered, with higher species numbers in oceanic regions and higher densities and biomass in neritic regions.

Introduction

Cnidarians play an important role in the pelagic marine environment, as they prey on zooplankton, fish eggs and larvae (Lucas & Henderson 1936; Purcell 1989; Bouillon 1999), and larvae of other organisms of economic importance, such as crustaceans and mollusks (Russell 1970). As heavy consumers of zooplankton (Alldredge 1984) and as higher-order carnivores in plankton communities (Mills 2001), a disproportionate increase in jellyfish populations may harm commercial fishing (Gomez-Aguirre 1991; Boero 2009) and tourism (Mills 1995). However, these gelatinous organisms also contribute to the diet of some fish and turtles (Arai 1988, 2005; Ates 1988; Purcell & Arai 2001; James *et al.* 2006).

Jellyfish (the term here is used only in reference to pelagic members of the Phylum Cnidaria) have also been considered good indicators of abiotic factors within the water column because the distribution of some cnidarian species depends on their narrow tolerance to salinity and temperature variation (Russell 1953). Traditional methods for sampling marine plankton tend to under-sample jellyfish and, consequently, underestimate their importance in the ecosystems in which they occur (Boltovskoy 1981, 1999).

We are still far from having a sufficient inventory of many marine species across all phyla, and global species censuses are deficient for tropical systems (Mora *et al.* 2008). Our current understanding of planktonic cnidarians in tropical waters is far from acceptable due to the insufficient collections that have been made to record species diversity; such deficiencies are also notable in tropical Brazil (Morandini *et al.* 2005). Diversity is a fundamental measurement of a community and is important

for understanding basic ecology and for developing conservation strategies (Gotelli & Colwell 2001).

In spite of their vulnerability, jellyfish are now well recognized as constituting an important fraction of the biomass, especially under bloom conditions. These gelatinous blooms are considered symptoms of environmental problems, including eutrophication, and associated effects such as hypoxia, commercial over-harvesting of fish and invertebrates, habitat modification, species introductions, and global climate changes (Mills 1995; Purcell & Arai 2001).

Currently, there is increasing concern that planktonic Cnidaria are becoming more prevalent in a variety of degraded coastal areas. The vital roles that jellyfish play in the health of the oceans, their position at the core of many evolutionary debates, and their use in biotechnology have led to resurgent public consciousness and appreciation of these organisms (Haddock 2004).

The goal of this study was to contribute to a better understanding of the diversity and distribution of planktonic cnidarians in the tropical Atlantic in a region influenced by some of the most polluted estuaries along the Brazilian coast. We hypothesized that cnidarians decrease in biodiversity and increase in numbers of individuals near the most polluted and impacted estuaries over a short time frame. Furthermore, we expected that the structure and composition of the planktonic cnidarian assemblage would present cross-shelf differences.

Materials and Methods

Samples were taken at 34 stations along seven transects perpendicular to the coast off Pernambuco state (in the estuarine plumes of the main rivers in this region), between 7°33′00″–8°41′00″ S and 34º03′00″–35°00′00″ W (Fig. 1). The survey was conducted onboard the RV *Victor Hensen* between 25 February and 3 March 1995 to observe short-term temporal variation in species occurrence. During this transition period, the climate changed from the dry to the rainy season, when jellyfish blooms occur.

Five stations, located 10 miles apart, were situated within each transect. Stations were classified as neritic or oceanic according to their location over or beyond the continental shelf (200-m isobath). Of the 34 sampling stations, 14 were located in the neritic region and 20 in the oceanic region. Sampling was conducted beginning at the station closest to the coast at low tide and moving offshore. Bathymetry varied with location from a depth of 15 to 40 m at the coastal stations and from 600 to 3500 m at the oceanic sites.

Samples were collected using a 300-µm-mesh Bongo net 2 m in length and with a 60-cm mouth diameter; the net was equipped with a Hydro-Bios Flowmeter (Hydro-Bios Apparatebau GmbH, Kiel-Altenholz, Germany). The hauls were performed obliquely, reaching a maximum depth of 160 m below the surface at the oceanic stations. The duration of each haul ranged from 3 to 25 min, depending on local depth. Samples were fixed immediately in 4% formalin buffered with 0.5% sodium tetraborate (Omori & Ikeda 1984).

In the laboratory, subsamples were taken by diluting each sample in 500 ml of filtered seawater, gently homogenizing, and transferring a 12-ml aliquot to a Bogorov counting plate using a 12-ml beaker attached to a glass rod. Triplicate subsamples were analysed under a binocular
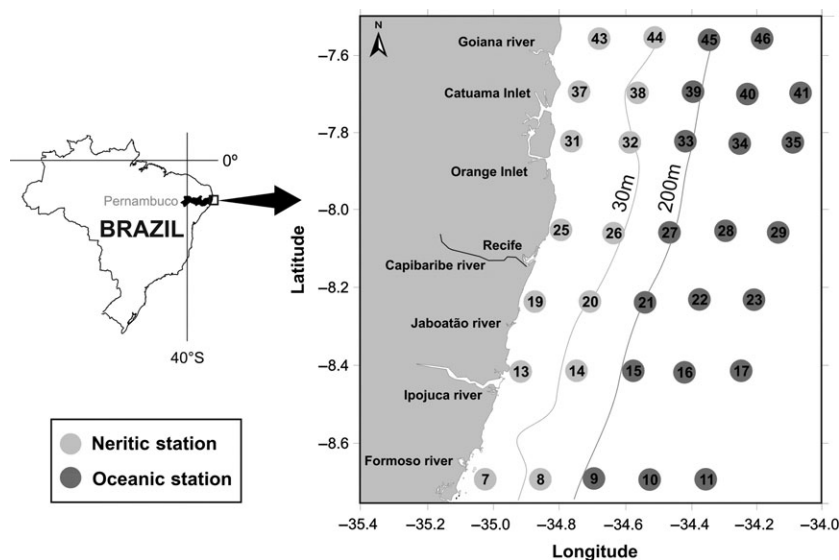
Fig. 1. Location of the study area and sampling stations in the neritic and oceanic regions off the southwestern coast of tropical Brazil.

stereomicroscope (Zeiss, Oberkochen, Germany). When a more detailed visualization of internal structures was necessary, samples were examined under a compound microscope using Rose Bengal dye. Density (ind. m^{-3}) was calculated for each species. The taxonomic diversity of medusae species was characterized using the Shannon diversity index (Shannon 1948) and the evenness calculation suggested by Pielou (1977).

Species identification and acquisition of ecological data on planktonic cnidarians was conducted with reference to standard literature (Trégouboff & Rose 1957; Kramp 1961, 1968; Navas-Pereira 1980; Boltovskoy 1999; Bouillon 1999). Salinity and temperature data from the upper 200 m were obtained at each station using a ME Meerestechnik CTD (Medeiros et al. 1999).

The biovolume was calculated for approximately 20 individuals from each taxon using the geometric formula most similar to the shape of each species. For example, the Hydromedusae and Scyphomedusae were considered spherical ($V = 4/3\pi R^3$) and the Siphonophora cylindrical ($V = \pi r^2 h$). The biovolume data were transformed to carbon biomass as described in Pugh et al. (1997) based on Larson (1986). Because cnidarians may experience shrinkage during preservation, the calculated carbon value would be slightly higher than the actual carbon content of the organism. The cnidarian specimens are currently housed in the Oceanographic Museum of the Federal University of Pernambuco, Brazil.

Abundance data were log($x + 1$)-transformed prior to multivariate analysis. Non-metric multi-dimensional scaling ordination (n-MDS) was applied to a Bray–Curtis similarity matrix to recreate the higher dimensional correlations of the cnidarian assemblage in two dimensions. In the n-MDS plot, the distance between samples is ideally equivalent to the similarity between samples. These methods were conducted using the PRIMER-6 (Plymouth, UK) software package (Clarke & Warwick 2001).

Prior to data analysis, we tested the normality of the data and homogeneity of variances using Shapiro–Wilk and Bartlett tests (Zar 1996). Because variances proved to be heterogeneous, we used Mann–Whitney U-tests (H_o: $\mu_1 = \mu_2$; $\alpha = 0.05$) to compare data from neritic and oceanic stations using STATISTICA v. 6.0 (StatSoft, Tulsa, OK, USA).

Results

Hydrography

Surface water temperature varied from 27.2 to 29.1 °C, with warmer waters near the coast and isotherms tending to follow the isobaths (Medeiros et al. 1999). At depths of 200 m, temperatures ranged from 14.2 to 17.8 °C. The upper mixed layer was only homogeneous in the upper 15–50 m, below which there were slight changes in temperature with depth until a well defined thermocline was reached. The upper mixed layer tended to be shallower at the shelf stations (mean 18 m) compared with oceanic stations (mean 44 m). A deep permanent thermocline was present at all oceanic stations (mean depth 120 m).

Salinity values at the surface ranged from 36.2 to 37.8, and there was an onshore–offshore gradient, with more saline conditions near the coast. At depths of 200 m, the salinity ranged from 34.5 to 36. A maximum salinity layer, one unit greater than values measured at the surface, was found overlaying the thermocline (at 30–120 m). Equatorial surface water (ESW) was the only dominant water mass (Medeiros et al. 1999) at the sampled depths (Fig. 2).

Community structure

We identified 21 cnidarian taxa (species or genera), with 11 taxa belonging to the Hydromedusae, nine Siphonophora taxa, one Scyphomedusae genus and two taxa, identified to the group level, belonging to Hydromedusae and Siphonophora (Table 1); most of these species are widely distributed in warm and temperate waters of all oceans but with strong tropical or subtropical affinity. The only scyphomedusan genus, Nausithoe sp., was found in one sample from an oceanic station.

Among cnidarians, Siphonophora was the most frequently observed group, with Chelophyes appendiculata (Eschscholtz, 1829) being present in 76% of all samples, followed by the Hydromedusae Abylopsis eschscholtzi Huxley, 1859 (49%) and Aglaura hemistoma Péron & Lesueur, 1810 (46%). Other species represented <40% of occurrences (Fig. 3).

Species diversity varied from 0.88 bits ind.$^{-1}$ (Station 19, Transect 3) to 3.18 bits ind.$^{-1}$ (Station 39, Transect 6), with a mean of 2.08 ± 0.63 bits ind.$^{-1}$. There was a general trend toward increased diversity from the neritic to the oceanic region (Fig. 3). Evenness was high with a mean value of 0.92 ± 0.11. The lowest evenness (0.44) was found at Station 19 where there was a predominance of A. hemistoma (Fig. 4).

We found 14 species or genera with higher abundances in the neritic area, whereas the other nine taxa had high densities in the oceanic area (Table 1).

The minimum density that we recorded for the cnidarian community in our samples was 1.4 ind. m^{-3}, and the maximum was 23.5 ind. m^{-3} (Fig. 5). This maximum value was due to the occurrence of A. hemistoma
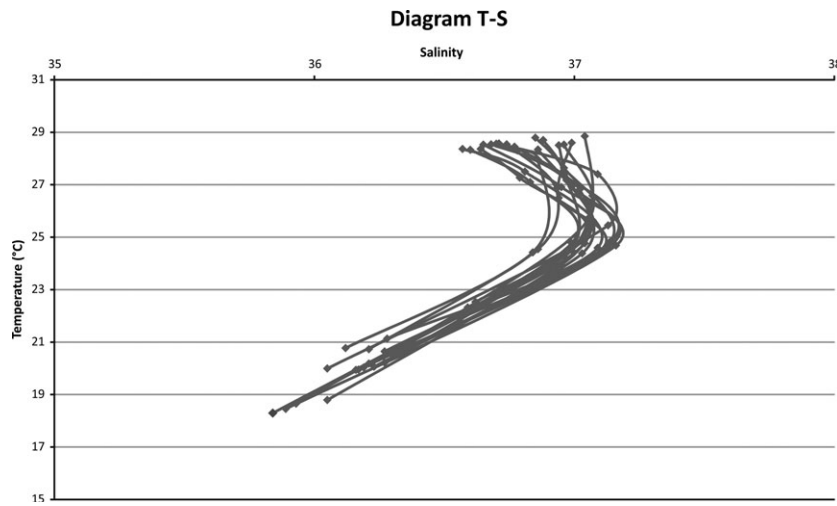
Diagram T-S

Fig. 2. Temperature and salinity diagram showing the main water masses of the studied area in southwestern, tropical Brazil.

Table 1. Mean density (ind. m^{-3}), standard deviation (SD) and frequency of occurrence (F) of planktonic cnidarian species occurring off the coast of Pernambuco state (PE). Species were classified according to Bouillon (1999).

Number of samples	39			16		23	
	Total			Neritic		Oceanic	
Species	Mean	SD	F	Mean	SD	Mean	SD
Superclass Hydrozoa							
Class Hydroidomedusae							
Bougainvillia frondosa Mayer, 1900[a]	427	222.2	0.18	56	223	91	164
Cytaeis tetrastyla Eschscholtz, 1829[a]	2230	–	0.03	139	558	0	0
Amphinema dinema (Péron & Lesueur, 1810)[a]	525	275.8	0.05	45	180	14	69
Neoturris pileata (Forsskäl, 1775)[a]	1250	975.0	0.08	217	620	12	58
Ectopleura dumortierii (van Beneden, 1844)[a]	1020	919.5	0.10	217	620	27	88
Zanclea sp.[a]	453	209.7	0.15	118	257	36	97
Clytia lomae (Torrey, 1909)[a]	997	757.6	0.15	191	531	127	407
Obelia sp.[a]	803	467.0	0.10	180	417	14	69
Solmundella bitentaculata (Quoy & Gaimard, 1833)	550	–	0.03	0	0	24	115
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)	889	555.9	0.28	56	223	387	586
Aglaura hemistoma (Péron & Lesueur, 1810)	2901	4716.9	0.46	2981	5066	197	287
Hydroidomedusae (others)	725	560.8	0.28	171	563	228	338
Class Siphonophora							
Agalma okeni Eschscholtz, 1825	433	246.6	0.21	0	0	150	252
Hippopodius hippopus (Forskäl, 1776)	220	–	0.03	0	0	10	46
Chelophyes appendiculata (Eschscholtz, 1829)	1449	2120.4	0.72	1118	1204	986	2297
Diphyes sp.	1866	1122.0	0.21	906	1248	19	92
Eudoxoides spiralis (Bigelow, 1911)	669	527.6	0.36	350	622	163	261
Lensia spp.	598	423.7	0.23	202	458	93	172
Abylopsis eschscholtzi (Huxley, 1859)	785	963.9	0.49	317	1102	428	447
Bassia bassensis (Quoy & Gaimard, 1859)	755	597.8	0.31	433	674	93	186
Enneagonum hyalinum (Quoy & Gaimard, 1827)	528	285.8	0.15	147	318	36	94
Siphonophora (others)	577	325.3	0.23	63	250	182	307
Superclass Scyphozoa							
Nausithoe sp.	460	–	0.03	0	0	20	96

[a]Species with a benthic polyp stage.

(19.8 ind. m^{-3}) at a shallow coastal station near a highly polluted urban estuary (Fig. 6). The mean density of cnidarians in all of the samples was 5.2 ± 5.3 ind. m^{-3}.

The results of the Mann–Whitney U-test indicated that there were significant differences ($P < 0.05$) in distribution between neritic and oceanic regions (Fig. 7), with a
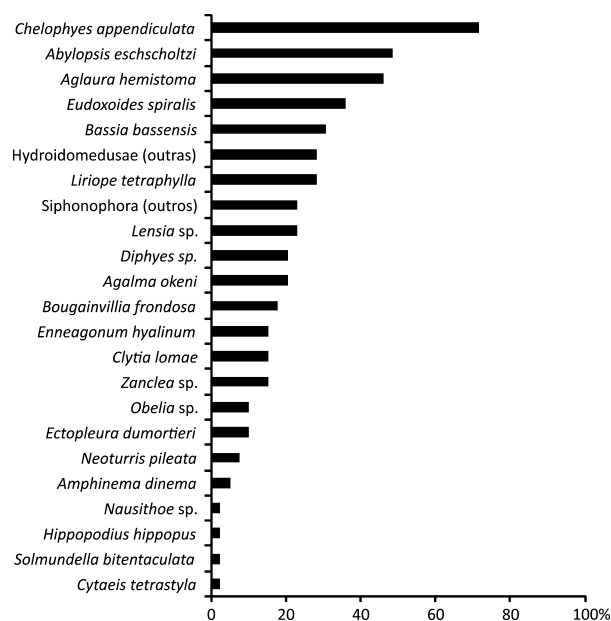
Fig. 3. Frequency of occurrence of planktonic cnidarian species in the neritic and oceanic regions off the southwestern coast of tropical Brazil.

higher species richness in the oceanic region and a higher density in the neritic region.

The total biomasses of Hydromedusae and Siphonophora were 130.86 and 19.04 mg C m^{-3}, respectively. Among the studied species, *Neoturris pileata* had the highest biomass (81.43 mg C m^{-3}), followed by *Liriope tetraphylla* (26.55 mg C m^{-3}), *Clytia lomae* (16.23 mg C m^{-3}), *C. appendiculata* (7.65 mg C m^{-3}) and *Lensia* sp. (5.68 mg C m^{-3}). The other species each had a biomass of <2 mg C m^{-3}.

The MDS analysis indicated two principal groups (Fig. 8): (i) coastal stations (P1), with the highest total density, and (ii) a mix of other neritic and oceanic stations.

Discussion

The study area is influenced by the SEC, which dominates the top 200 m close to the Brazilian shelf (Medeiros *et al.* 1999). The plankton community was characteristic of the SEC water mass and included representatives from all major groups of planktonic Cnidaria, with Hydromedusae being the most frequent and abundant. In studies of mesozooplankton in the Rio Grande do Norte neritic and oceanic areas (Northeastern Brazil), Neumann-Leitão *et al.* (2008) noted the presence of 11 cnidarian species, most of which were also observed in this study. Our biodiversity results are similar to those of Segura-Puertas *et al.* (2010), who studied a shelf area in the Mexican

tropical Pacific where the climate is warm and the coastal area is influenced by runoff from large rivers.

The present study revealed clear differences between neritic and oceanic assemblages, most likely due to substrate requirements for polyps, estuarine inputs, and westward surface currents. These westward currents, forced by trade winds, push water against the Brazilian coast, which concentrates plankton in neritic waters due to downwelling and coastal accumulation (Peterson & Stramma 1991). The aggregation of zooplankton can also be explained by accumulation in turbulent areas (*e.g.* frontal zones) because these organisms cannot swim against strong downwelling currents (Genin *et al.* 2005). The latitudinal range of species distribution is generally acknowledged to be limited by temperature tolerance (Briggs 2007). This temperature effect may also explain longitudinal ranges. Higher temperatures and greater diversity occur on the western rims of the Atlantic and Pacific, primarily due to eastern boundary upwelling and coastal accumulation caused by the trade winds.

Species richness was highest in the more oceanic waters. We found a maximum of 10 species at one station. With the exception of the transect near the most polluted urban estuary (Jaboatão River), all transects showed an increase in cnidarian diversity with distance from the coast. However, the species richness might be underestimated because larger and sparser species of planktonic Cnidaria, primarily the siphonophores (see Pugh 1999) and large medusae (Suchman & Brodeur 2005), are poorly sampled by plankton nets. For example, we failed to sample any specimens of the common large siphonophore *Physalia physalis* (Linnaeus, 1758), also known as the Portuguese man o'war, which are the only pleustonic siphonophore and are a common nuisance along the entire Brazilian coast (Migotto *et al.* 2002; Bardi & Marques 2007; Haddad Jr *et al.* 2010).

Previous studies on zooplankton off Pernambuco (Paranaguá 1966) identified two other rare Hydromedusae species in coastal areas that were not found in the present study, *Blackfordia virginica* Mayer, 1910 and *Ostrumovia inkermanica* Hadzi, 1928, now *Moerisia inkermanica* Paltschikowa-Ostroumova, 1925. Both species are considered invasive and may have been introduced to Brazilian waters by ship ballast water (Nogueira Jr & Oliveira 2006). Haydar (2012) examined disjunction distributions by investigating the scale of cryptogenesis in the North Atlantic Ocean. He found that Hydrozoa had the highest relative number of disjoint species. This distribution could be explained by historical, undocumented rafting but is more likely the result of dispersal by ships, which travel relatively fast, are independent of currents, and provide greater surface area. For example, *B. virginica* was introduced by ship hull fouling. The *B. virginica*
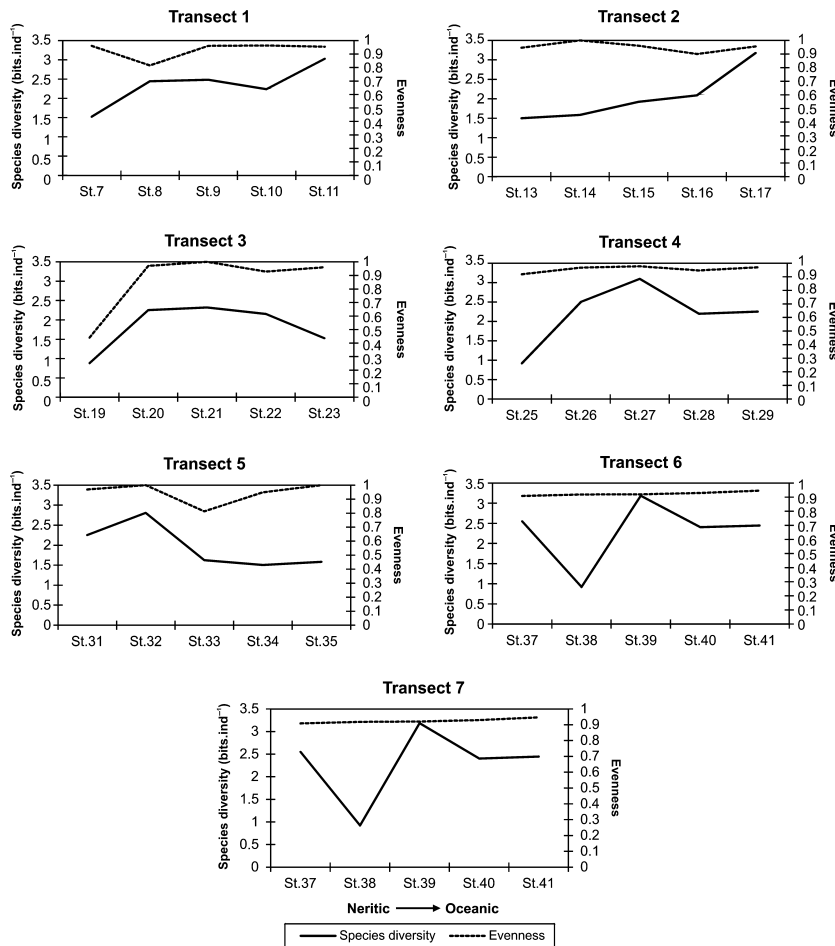
Fig. 4. Diversity and evenness of planktonic cnidarian species occurring in neritic and oceanic regions off the southwestern coast of tropical Brazil.

found by us to be blooming in the last 2 years in the northern part of the studied area (unpublished data) may have been introduced by similar means. Studies carried out on specimens collected in the Northeastern Brazil at various times between 1987 and 2000, led Freire *et al.* (2013) to hypothesize that *B. virginica* has long inhabited estuaries in the area while going unnoticed.

Most of the Hydromedusae found here are epi- or mesopelagic, coastal and exhibit a widespread distribution in the Atlantic and Indo-Pacific (Vannucci 1963; Ramirez & Zamponi 1981; Bouillon 1999; Migotto *et al.* 2002). Only *Bougainvillia frondosa* has a distribution restricted to the Atlantic (Bouillon 1999). *Bougainvillia frondosa* is most likely a coastal species found in continental shelf regions and is very rare in plankton hauls (Vannucci 1963). Its occurrence at oceanic stations in this study is due to the narrow continental shelf off Pernambuco, which allows the intrusion of oceanic waters and *vice versa*. According to Bouillon (1999), this species is mero-planktonic and neritic, occurring in the southwestern and northern regions of the Atlantic. In Brazil, *B. frondosa* has been reported in the southern, southeastern, and

northeastern coastal regions (Moreira 1973; Goy 1979; Navas-Pereira 1981; Migotto *et al.* 2002).

Another species with rare distribution in our study was *Solmundella bitentaculata*, with a unique occurrence in one oceanic sample. However, this species is widely distributed in all oceans and in the Mediterranean, from the surface to the bathypelagic zone, and is particularly common in the southern hemisphere, with greatest abundance between 100–500 m (Vannucci 1957, 1963; Bouillon 1999).

Other taxa, such as *Zanclea* sp. and *Obelia* sp., are considered cosmopolitan in their distribution (Bouillon 1999). According to Vannucci (1963), medusae of the genus *Obelia* may be considered indicators of coastal water quality. The species of this genus are eurythermic and euryhaline, preferring high temperature and low salinity, although they can tolerate higher salinity and cooler waters. These medusae are found throughout the year but tend to be more abundant during the summer; this distribution pattern is similar to that noted here. *Obelia* have a marked preference for surface waters, and the occurrence of the *Obelia bidentata* Clark 1875 in
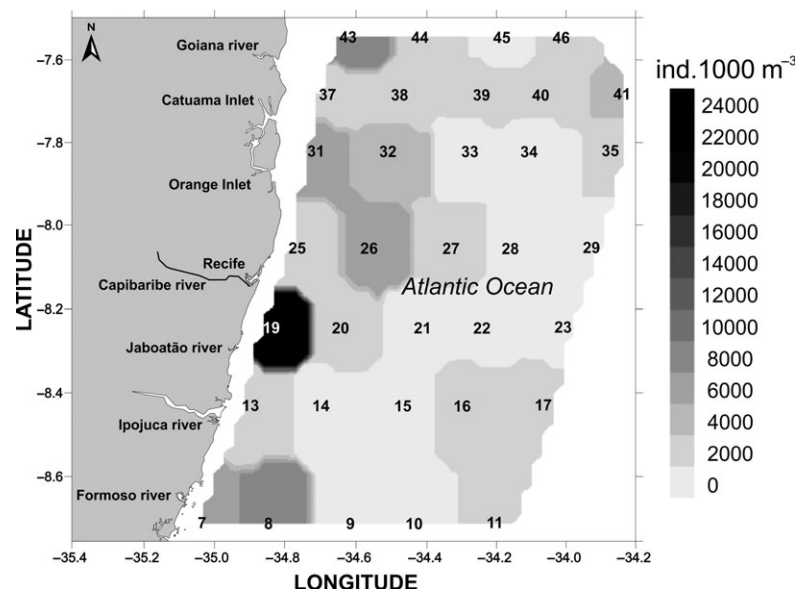
Fig. 5. Density of planktonic cnidarian species occurring at all stations of the neritic and oceanic regions off the southwestern coast of tropical Brazil.
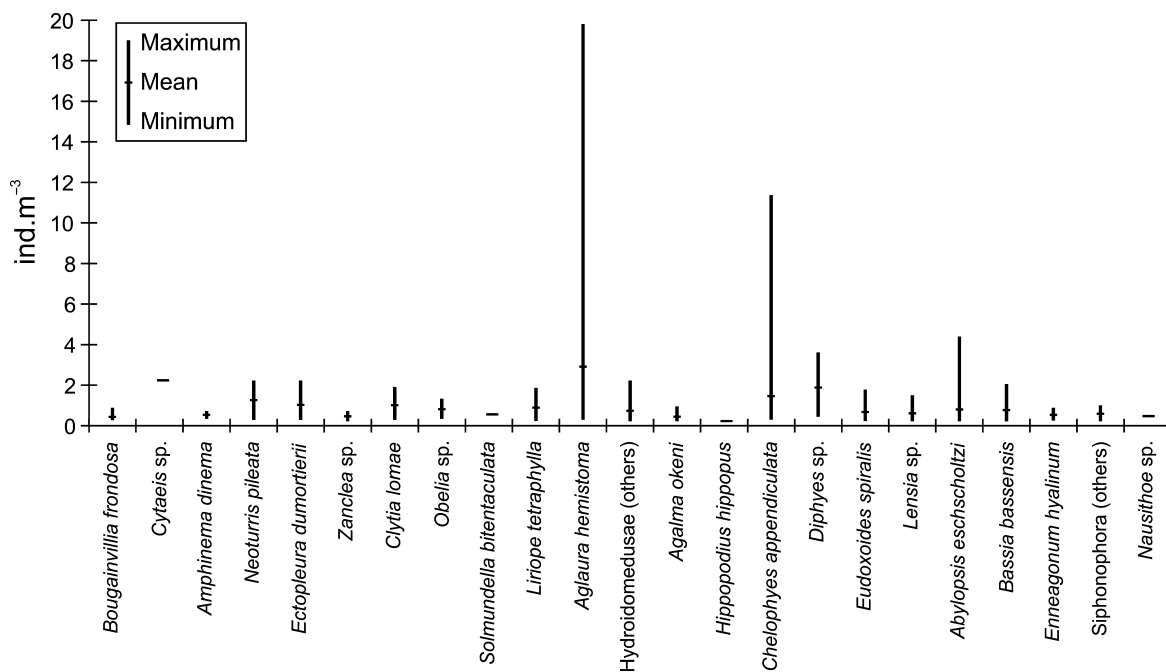

Fig. 6. Mean, minimum, and maximum density of planktonic cnidarian species occurring in the neritic and oceanic regions off the southwestern coast of tropical Brazil.

coastal waters off Pernambuco was cited by Calder & Mayal (1998).

Within the Siphonophora, we identified seven species, with two other taxa identified to genera (*Diphyes* sp. and *Lensia* spp.), which could represent more than two species. For example, there are 13 *Lensia* sp. that occur in Brazilian waters (Migotto *et al.* 2002). In general, the majority of the siphonophoran species found in our study

are known to inhabit the temperate and warm regions of the Atlantic, Indian, and Pacific Oceans (Pugh 1999) and have a wide distribution in the epipelagic zone of neritic and oceanic provinces (Alvariño 1981). However, most siphonophoran species are truly oceanic and rarely appear inshore (Pugh 1999). In Brazilian waters, these species all occur in most regions (Alvariño 1971; Pugh 1999; Migotto *et al.* 2002).
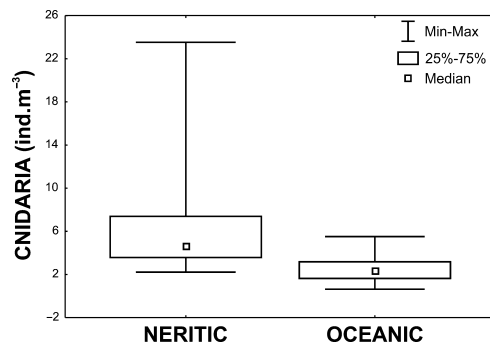
Fig. 7. Combined mean density and standard deviation of cnidarian species from all of the neritic and oceanic regions off the southwestern coast of tropical Brazil.

An important species found in this study was *Chelophyes appendiculata*, which was observed in all oceanic samples. According to Kirkpatrick & Pugh (1984), this species is most likely the most common siphonophore in the warmer waters of the world's oceans. Of the Scyphomedusae, we found *Nausithoe* sp. in one oceanic sample. Three species from this group have been found in the South Atlantic (Mianzan & Cornelius 1999). It is possible that the species in our sample was *Nausithoe punctata* Kölliker, 1853. Marques *et al.* (2003) studied the distribution of medusae from a geographical and historical perspective and emphasized the lack of knowledge in some areas also covered by our study. For example, the northeastern region of Brazil is among the most poorly studied with respect to planktonic Cnidaria.

The generally low density of Cnidaria in our samples was related to the oligotrophic nature of the study area (Medeiros *et al.* 1999) and to the collection methods we used, which were selected with the major goal of sam

pling the entire zooplankton community at a given location. In general, there were higher cnidarian densities in the northern sector of the study area, suggesting more favorable conditions for this group in that region. The northern sector of Pernambuco is also characterized by the presence of high densities of microzooplankton (Neumann-Leitão *et al.* 1999) in response to the highly productive estuarine system of Santa Cruz Channel (Neumann-Leitão *et al.* 2001; Melo Junior *et al.* 2007). Some studies have demonstrated that microzooplankton may be the major food source for small planktonic cnidarian (Colin *et al.* 2005; Sabatés *et al.* 2010), and the high densities of microzooplankton observed in the northern sector of Pernambuco area can support high populations of planktonic cnidarian species. Previous studies in this area also demonstrated high abundances of Hydroidomedusae and Siphonophorae (Porto Neto *et al.* 1999; Neumann-Leitão *et al.* 2001). Some variations in density could also be related to wind effects; however, additional data are needed to confirm this relationship.

Communities of planktonic cnidarians are frequently dominated by a few highly adaptable species (Gili *et al.* 1988). This was most likely the case for the coastal station near the polluted Jaboatão River, where the small hydromedusa *A. hemistoma* showed a maximum density of 19.8 ind. m^{-3}. This cosmopolitan species was the most important of all species in the nearshore area. Its high abundance in this area could be characterized as a bloom. Although present at the highest density, *A. hemistoma* exhibited a small form with a smaller contribution to the total biomass. Thus, it is important to consider the bigger forms of jellyfish in trophic studies.

Recent studies have shown that the increasing anthropogenic influence on the oceans has begun to cause real
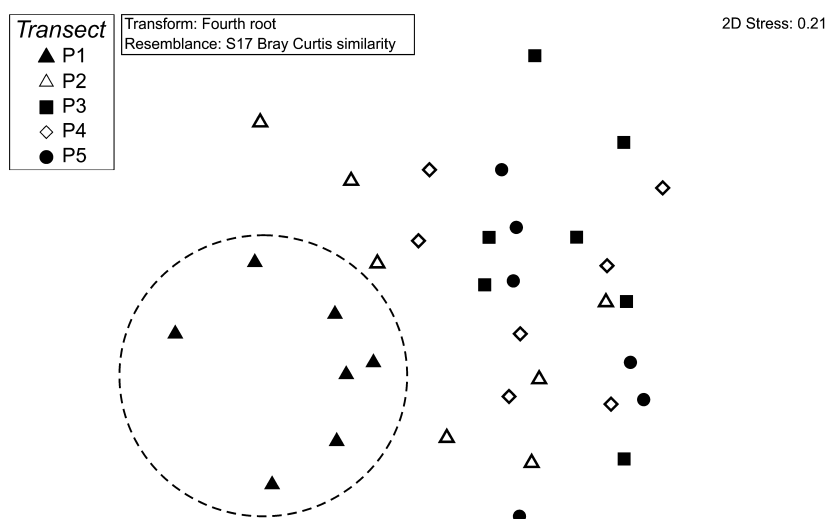
Fig. 8. Multi-dimensional scaling (MDS) of planktonic cnidarian community samples from the neritic and oceanic regions off the southwestern coast of tropical Brazil.

change. There is evidence that in some regions jellyfish blooms are occurring in response to some of the cumulative effects of these impacts (Mills 2001), thereby reducing biodiversity (Benović *et al.* 2002). The high density of *A. hemistoma* associated with the polluted and eutrophic plumes of rivers is one example of such a bloom.

Most species observed in this study had a wide geographical distribution, and there was a high degree of similarity between the planktonic cnidarians of the Northern and Southern Atlantic; the South Atlantic also shares many species with the Indo-Pacific.

Acknowledgements

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