

Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic

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Mesozooplankton species distribution and abundance were studied in the tropical Southwestern Atlantic, in neritic and oceanic regions off the state of Rio Grande do Norte, northeastern Brazil (3° to 6° S and 32°30' to 35°30' W). Samples were collected with a 120 µm mesh net towed horizontally at 40 stations along five transects in June 1986. A total of 151 taxa were identified. Copepoda (93 species) numerically dominated (78%) the community. The highest zooplankton abundance was recorded at a coastal station (1098 ind m⁻³), and the lowest at the station farthest offshore (82 ind m⁻³). The low abundance of zooplankton corresponded to oligotrophic water masses, and differences in abundance were locally affected by topographic upwelling. Three groups were distinguished: (i) oceanic with very low total abundance (<15 ind m⁻³), (ii) a mix of neritic and oceanic species and (iii) coastal neritic group. Species diversity was high (mean 3.14 ± 0.42 bits ind⁻¹) and increased with the ecological stability of the area. The local oceanographic conditions, with a strong connection between the oligotrophic oceanic water masses and the enriched coastal water, are of paramount importance to the local food chain and patterns of zooplankton diversity.

INTRODUCTION

The species assemblages of many habitats are under threat, and until we have a firmer idea of the diversity of a wide range of marine habitats and what controls it, we have little hope of conserving biodiversity or determining the impact of human activities such as mariculture, fishing and dumping of waste and pollution (Ormond *et al.*, 1997). Among marine habitats, the tropical pelagic Southwestern Atlantic (SWA) is poorly known particularly in relation to many holoplanktonic groups (Boltovskoy *et al.*, 2002). In this region, low diversity is expected because distributional barriers for marine plankton are few and diffuse (Angel, 1993; McGowan and Walker, 1993).

Previous investigations of the tropical SWA have been restricted to certain groups such as Copepoda (Björnberg, 1963; Araújo, 2006) and Chaetognatha (Gusmão, 1986), or to a few samples from macroscale international expeditions. Boltovskoy (Boltovskoy, 1981, 1999) published a zooplankton atlas of the SWA; however, information on the waters off northeastern Brazil remains fragmentary (Neumann-Leitão *et al.*, 1999; Cavalcanti and Larrazábal, 2004).

For pelagic plankton, circumglobal distributions are more common than endemism, and a high proportion of marine zooplankton species has already been described (Boltovskoy *et al.*, 2002). However, according to these authors, the corresponding taxonomic system is

not adequate, and biological and ecological information is extremely scarce; furthermore, large areas of the central South Atlantic have not been sampled. There is also a need to focus on tropical situations, because our knowledge of zooplankton ecology is based mainly on examples derived from temperate waters. Identification of key species and tracking changes in species composition are also important to detect the local and global changes (Fernández de Puelles *et al.*, 2003).

To make a taxonomically comprehensive assessment of the biodiversity of animal plankton throughout Northeastern Brazil, we made use of the existing data, drawn from archived zooplankton collections. In 2004, we carried out detailed studies on samples collected in 1986 by the Almirante Saldanha Oceanographic Research Vessel in neritic and oceanic regions off the state of Rio Grande do Norte. The goal was to produce accurate and complete information on zooplankton species diversity, biomass, biogeographical distribution and community structure. These samples were previously analyzed only to group level and belong to a unique plankton collection (8000 samples) held by the Department of Oceanography of the Federal University of Pernambuco in Brazil.

Taxonomic collections are important resources for studies of local biodiversity. Only with the conservation of such samples is it possible to confirm the relationship between each species and the associated environmental information. Recognizing the importance of the specimens deposited in the plankton collection, the present study recovered much valuable information on the biodiversity of the SWA, by studying these well-preserved samples.

Our results contribute to understanding the functional role of biodiversity in ocean ecosystems and to a better characterization of global-scale patterns of zooplankton biodiversity in the world ocean.

METHOD

Study area

The shelf and open ocean off Northeast Brazil are largely affected by two water masses, the tropical waters (TW) and South Atlantic Central Waters (SACW) (Stramma *et al.*, 1990). A pycnocline with a stable thermocline, located between depths of 100 and 300 m, prevents mixing between the TW surface and the deeper, nutrient-rich SACW (Medeiros *et al.*, 1999). The coastal area of the state of Rio Grande do Norte has extensive beaches and high dunes. The continental shelf is 30 km wide; the continental slope begins at 80 m,

ending at depths of 1300–3600 m. Many plateau and marginal terraces are present, and sea mounts occur parallel to the continental margin, separated from the shelf by steep scarps. This irregular submarine relief is related to volcanic phenomena, which formed peaks such as Fernando de Noronha Island and Rocas Atoll (Mabesoone and Coutinho, 1970). The inner-shelf waters are dominated by the oligotrophic South Equatorial Current, and the generally low productivity is only enhanced by sporadic local upwelling events either at the shelf edge or at seamounts and islands.

Sampling and laboratory procedures

The field survey was performed in June 1986 aboard the R/V Almirante Saldanha. Zooplankton sampling was carried out at 40 stations along 5 transects perpendicular to the Rio Grande do Norte coast (lat. 3° to 6° S, long. 32°30' to 35°30' W) (Fig. 1). A standard plankton net, 2 m long, mouth diameter 30 cm and mesh size 120 µm, fitted with a flowmeter, was towed horizontally at the surface. Samples were preserved in a 4% buffered formalin–seawater solution. Biomass was estimated by the wet-weight method (Omori and Ikeda, 1984). Zooplankton species were identified using the manuals of Tregouboff and Rose (Tregouboff and Rose, 1957) and Boltvskoy (Boltvskoy, 1981, 1999), among others. Taxon abundance per cubic meter was determined from a 4 mL subsample, taken with a Stempel pipette, of the entire sample (250 mL).

The Shannon diversity index was applied to Copepoda for the estimation of community diversity (Shannon, 1948). This index is based on information theory and it is a measure of the number of different species in each sample (species richness) weighted by the abundance of individuals. Shannon's diversity index is $H = -(\sum (\rho_i \log_2 \rho_i))$, where ρ_i is the proportion of the total number of specimens i expressed as a proportion of the total number of species for all species in the sample. The product of $\rho_i \log_2 \rho_i$ for each species in the sample is summed and multiplied by -1 to give H . The species evenness index (E) is calculated as $E = H/H_{\max}$, where H_{\max} is the maximum possible value of H and is equivalent to $\log_2 S$, where S is the total number of species in the sample. Thus $E = H/\log_2 S$ (Pielou, 1977). When the base for the logarithms is 2, the model is binary and the unit of information is the bit (Legendre and Legendre, 1998).

A Mann–Whitney test was applied to assess the differences between day and night hauls. This is a non-parametric test based on ranks that compares two unpaired groups (Sokal and Rohlf, 1996).

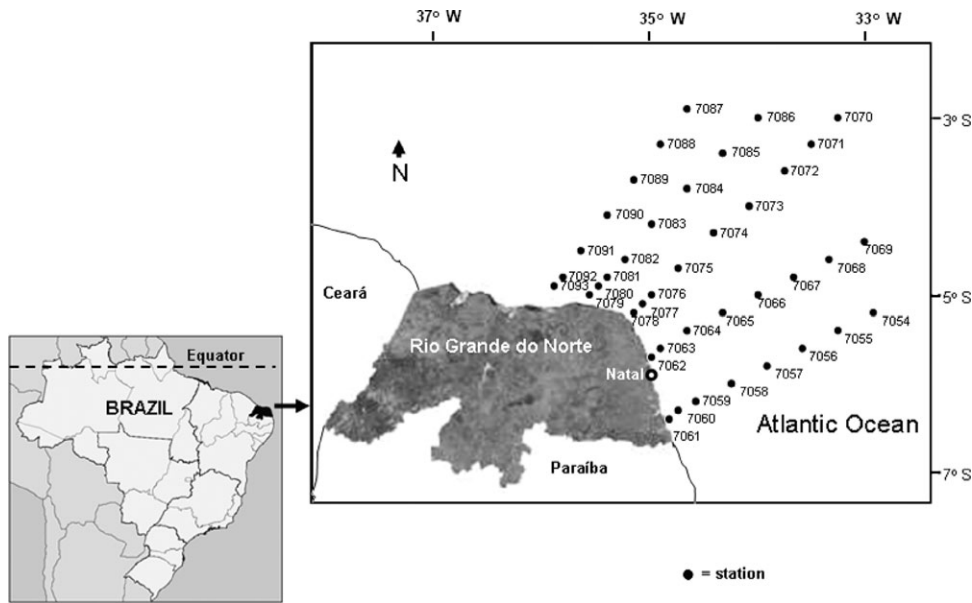


Fig. 1. Area and sampling stations off northeastern Brazil.

Multivariate procedures included: (i) classification (cluster analysis) on the sample-copepod species data matrix using the Bray–Curtis index and the weighted pair group method-arithmetical averages (WPGMA) link method for the dendrograms (Legendre and Legendre, 1998). A cophenetic value matrix was applied to measure the extent to which the clustering result corresponds to the original resemblance matrix, thus testing the goodness of fit of the cluster analysis to the data (Rohlf and Fisher, 1968). (ii) A principal coordinate analysis (PCA) was used to assess sample similarities. The computation was based on a matrix of distances (Bray–Curtis) between the objects after having been double-centered, and then factored, and a plot was constructed, showing the objects in two-dimensional space.

RESULTS

Altogether, 151 taxa were identified (Tables I and II). Holoplankton dominated with 80% of taxa. The relative importance of different taxa varied among stations, although copepods were by far the most important group in terms of species richness and numerical abundance. In general, copepods dominated at 80% of the stations, with >60% relative abundance, except at stations 7085 (37%), 7086 (31%), 7061 (58%) and 7069 (49%). There were 93 species of Copepoda (Table II); the most abundant species in decreasing order of numerical abundance were: *Calocalanus pavo*, *Undinula*

vulgaris, *Oncaea venusta*, *Oithona plumifera* and *Corycaeus (Onychocorycaeus) latus*. Copepodites were also abundant. Nearly 83% of the copepods were oceanic, 6% neritic, 8% oceanic and neritic and 2% neritic and estuarine (Table II).

Other major holoplanktonic groups were Chaetognatha and Appendicularians, comprising 13% of the total population. The young stages of nine species of Chaetognatha were recorded (Table I) and accounted for nearly 21% of relative abundance at ocean station 7070. The most common species were *Sagitta enflata* and *S. serratodentata*, with 88 and 85% frequency of occurrences, respectively. Appendicularians were frequent (~95%) and attained high relative numerical abundance at stations 7069 (36%) and 7068 (22%).

Meroplankton abundance fluctuated spatially. The group consisted of larval gastropods and bivalves dominating at coastal stations and fish larvae offshore.

Among the taxa with the widest spatial distribution were the Copepoda (*C. parvo*, *U. vulgaris*, *O. plumifera*, *O. venusta*, *Macrosetella gracilis*, *Microsetella rosea* and *C. speciosus*), Chaetognatha (*S. enflata* and *S. serratodentata*) and the Larvacea (*Oikopleura* spp.).

Zooplankton diversity was generally high (>3.0 bits ind^{-1}). The lowest value was found at station 7074 (2.27 bits ind^{-1}), mainly due to the high numerical abundance of copepodites, mostly of *Undinula vulgaris*. The highest diversity was recorded at the southern coastal station 7061 (3.82 bits ind^{-1}) (Fig. 2). Evenness was high at all stations, with values above 0.6 (Fig. 2).

Table I: List of zooplankton taxa and species off northeastern Brazil, June 1986 (Copepoda not included)

Radiolaria	Cirripedia (nauplius and cypris)
Spumellaria (others)	Stomatopoda (larvae Erichthus and Alima)
<i>Dictyocoryne profunda</i> Ehrenberg, 1872	Euphausiacea
<i>Rhopalastrum malleus</i> Haeckel, 1887	<i>Stylocheiron</i> sp.
Foraminifera	<i>Euphasia</i> sp. (adults and furcilia, calyptopis)
<i>Globigerinoides ruber</i> (d'Orbigny, 1839)	Cumacea
<i>G. trilobus</i> (Reuss, 1850)	Decapoda
<i>G. sacculifer</i> (Brady, 1879)	<i>Lucifer typus</i> H. Milne-Edwards, 1837
<i>Globigerinoides</i> sp.	<i>Lucifer faxoni</i> Borradaile, 1915
<i>Globorotalia menardii</i> (Jones & Brady, 1865)	<i>Lucifer</i> (protozoaeae)
<i>Orbulina universa</i> d'Orbigny, 1839	Penaeidae (Larvae)
<i>Tetomphalus bulloides</i> d'Orbigny, 1826	Paguridae larvae (<i>Parapagurus</i> sp.)
<i>Bolivina</i> sp.	Carideae (larvae)
<i>Triloculina</i> sp.	Brachyura (zoeae and megalopa)
<i>Planispirillina</i> sp.	Palinuridae (phyllosoma)
Cnidaria	Porcellanidae (larvae)
Hydrozoa	Mysidacea
<i>Zanclaea costata</i> Gegenbaur, 1856	Isopoda
<i>Liriope tetraphylla</i> (Chamisso & Eysenhardt, 1821)	Epicaridea (larvae)
<i>Aglaura hemistoma</i> Péron & Lesueur, 1809	Amphipoda
<i>Solmundella bitentaculata</i> Quoy & Gaimard, 1833	Gammaridea
Siphonophora	Hyperidae
<i>Agalma okeni</i> Eschscholtz, 1825	Bryozoa (cyphonauta of <i>Membranipora</i> sp.)
<i>Lensia</i> sp.	Chaetognatha
<i>Eudoxoides spiralis</i> (Bigelow, 1911)	<i>Sagitta enflata</i> Grassi, 1881
<i>Abylopsis eschscholtzi</i> (Huxley, 1859)	<i>S. hispida</i> Conant, 1895
<i>Bassia bassensis</i> (Quoy & Gaimard, 1834)	<i>S. hexaptera</i> d'Orbigny, 1834
Scyphomedusae	<i>S. serratodentata</i> Krohn, 1853
<i>Nausithoe punctata</i> K��lliker, 1853	<i>S. bipunctata</i> Quoy & Gaimard, 1827
<i>Aurelia aurita</i> Linnaeus, 1758	<i>S. helenae</i> Ritter-zahony, 1911
Nematoda	<i>P. draco</i> (Krohn, 1853)
Mollusca	<i>K. subtilis</i> (Grassi, 1881)
<i>Limacina inflata</i> (d'Orbigny, 1836)	<i>K. pacifica</i> (Ainda, 1897)
<i>Cresceis acicula</i> (Rang, 1828)	Echinodermata
<i>Cavolinia longirostris</i> (de Blainville, 1821)	Pluteus, bipinnaria, brachiolaria
Gastropoda other (veliger/adult)	Enteropneusta (tornaria)
Bivalvia (veliger/juvenile)	Larvacea
Cephalopoda (paralarvae)	<i>Oikopleura dioica</i> Fol, 1872
Polychaeta	<i>O. longicauda</i> (Vogt, 1854)
<i>Maupasias coeca</i> Viguer, 1886	<i>Oikopleura</i> sp.
Alciopidae (larvae)	<i>Fritillaria</i> sp.
<i>Tomopteris</i> sp.	Thaliacea
<i>Sagittella kowalevskii</i> N. Wagner, 1872	<i>Thalia democratica</i> (Forsk��l, 1775)
Polychaeta other larvae (different stages)	<i>Doliolum</i> sp.
Crustacea	Ascidacea (larva)
Cladocera	Cephalochordata
<i>Penilia avirostris</i> Dana, 1849	Amphioxus (<i>Branchiostoma lanceolatum</i>)
<i>Evadne tergestina</i> (Claus, 1862)	Vertebrata
Ostracoda	Pisces (larvae)
<i>Euconchoecia chierchiae</i> Muller, 1890	Pisces (egg)

In general, mesozooplankton biomass decreased from nearshore to offshore stations. Biomass varied from 14.35 mg m⁻³ (7086: offshore station of transect 4) to 155.11 mg m⁻³ (7061: nearshore station of transect 1) (Fig. 3). The overall mean was 63.97 ± 33.49 mg m⁻³.

Zooplankton abundance ranged between 74 ind m⁻³ (Station 7070) and 2537 ind m⁻³ (Station 7074) near Rocas Atoll. The mean abundance was 426 ± 428 ind m⁻³ (Fig. 4). Peaks in copepod abundance were

related to topographic upwelling mainly close to the shelf break.

There was no clear pattern of mesozooplankton vertical migration, since no significant differences ($P > 0.05$) in diversity or abundance were observed between day and night hauls. Therefore, the absence of samples from deepest waters makes it difficult to ascertain the complete pattern of zooplankton vertical distribution in these oligotrophic waters.

Table II: List of species of Copepoda off northeastern Brazil, June 1986

<i>Mesocalanus tenuicornis</i> (Dana, 1849) ^O	<i>Candacia longimana</i> Claus, 1863 ^O
<i>Nannocalanus minor</i> (Claus, 1863) ^O	<i>C. pachydactyla</i> (Dana, 1848) ^O
<i>Neocalanus gracilis</i> Dana, 1849 ^O	<i>C. curta</i> (Dana, 1849) ^O
<i>N. robustior</i> (Giesbrecht, 1888) ^O	<i>C. elongata</i> (Boeck, 1873) ^O
<i>Undinula vulgaris</i> (Dana, 1849) ^N	<i>C. varicans</i> (Giesbrecht, 1892) ^O
<i>Pareucalanus sewelli</i> (Fleminger, 1973) ^O	<i>Paracandacia simplex</i> (Giesbrecht, 1889) ^O
<i>Subeucalanus pileatus</i> (Giesbrecht, 1888) ^O	<i>P. bispinosa</i> (Claus, 1863) ^O
<i>Eucalanus hyalinus</i> Claus, 1866 ^O	<i>Pontella atlantica</i> (Milne-Edwards, 1840) ^O
<i>Rhincalanus cornutus</i> (Dana, 1849) ^O	<i>Labidocera acutifrons</i> (Dana, 1849) ^O
<i>Paracalanus aculeatus</i> Giesbrecht, 1888 ^O	<i>L. fluviatilis</i> F. Dahl, 1894 ^N
<i>P. quasimodo</i> Bowman, 1971 ^N	<i>L. nerii</i> (Kroyer, 1849) ^O
<i>P. indicus</i> Wolfenden, 1905 ^N	<i>Pontellina plumata</i> (Dana, 1849) ^O
<i>Acrocalanus longicornis</i> Giesbrecht, 1888 ^O	<i>P. perspicax</i> (Dana, 1849) ^O
<i>Calocalanus pavo</i> (Dana, 1849) ^O	<i>P. regalis</i> (Dana, 1849) ^O
<i>C. pavoninus</i> Farran, 1936 ^O	<i>Calanopia americana</i> F. Dahl, 1894 ^N
<i>Mecynocera clausi</i> Thompson, 1888 ^O	<i>Acartia</i> (<i>Odontacartia</i>) <i>lilljeborgi</i> Giesbrecht, 1889 ^{N,E}
<i>Clausocalanus furcatus</i> (Brady, 1883) ^O	<i>Acartia</i> (<i>Acartia</i>) <i>danae</i> Giesbrecht, 1889 ^O
<i>Aetideus giesbrechti</i> (Cleve, 1904) ^O	<i>A. (Acartia) negligens</i> Dana, 1849 ^O
<i>Euchirella amoena</i> Giesbrecht, 1888 ^O	<i>Oithona atlantica</i> Farran, 1908 ^O
<i>E. rostrata</i> (Claus, 1866) ^O	<i>O. nana</i> Giesbrecht, 1892 ^{N,E}
<i>Gaetanus minor</i> Farran, 1905 ^O	<i>O. robusta</i> Giesbrecht, 1891 ^{O,N}
<i>Euchaeta marina</i> (Prestandrea, 1833) ^O	<i>O. plumifera</i> Baird, 1843 ^{O,N}
<i>E. media</i> Giesbrecht, 1888 ^O	<i>O. setigera</i> (Dana, 1849) ^{O,N}
<i>E. pubera</i> Sars, 1907 ^O	<i>Oithona</i> sp.
<i>Paraeuchaeta sarsi</i> (Farran, 1908) ^O	<i>Oncaea media</i> Giesbrecht, 1891 ^O
<i>Phaenna spinifera</i> Claus, 1863 ^O	<i>O. venusta</i> Philippi, 1843 ^{O,N}
<i>Scolecithrix bradyi</i> Giesbrecht, 1888 ^O	<i>Lubbockia aculeata</i> Giesbrecht, 1891 ^O
<i>S. danae</i> (Lubbock, 1856) ^O	<i>Sapphirina auronitens-sinuicauda</i> Brady, 1863 ^O
<i>Scottocalanus securifrons</i> (T. Scott, 1894) ^O	<i>S. nigromaculata</i> Claus, 1863 ^O
<i>Haloptilus acutifrons</i> (Giesbrecht, 1892) ^O	<i>S. angusta</i> Dana, 1849 ^O
<i>H. spiniceps</i> (Giesbrecht, 1892) ^O	<i>Copilia mirabilis</i> Dana, 1849 ^O
<i>Temora stylifera</i> (Dana, 1849) ^{O,N}	<i>C. quadrata</i> Dana, 1849 ^O
<i>Pleuromamma abdominalis</i> (Lubbock, 1856) ^O	<i>C. lata</i> Giesbrecht, 1891 ^O
<i>P. gracilis</i> Claus, 1863 ^O	<i>Corycaeus</i> (<i>Corycaeus</i>) <i>speciosus</i> Dana, 1849 ^O
<i>P. piseki</i> Farran, 1929 ^O	<i>C. (Onychocorycaeus) giesbrechti</i> F. Dahl, 1894 ^O
<i>P. quadrangulata</i> (F. Dahl, 1893) ^O	<i>C. (Onychocorycaeus) latus</i> Dana, 1849 ^O
<i>P. xiphias</i> (Giesbrecht, 1889) ^O	<i>Corycaeus</i> sp.
<i>Centropages violaceus</i> (Claus, 1863) ^O	<i>Farranula gracilis</i> (Dana, 1849) ^O
<i>C. gracilis</i> (Dana, 1849) ^{O,N}	<i>Microsetella rosea</i> (Dana, 1847) ^O
<i>C. furcatus</i> (Dana, 1849) ^{O,N}	<i>M. norvegica</i> (Boeck, 1864) ^{O,N}
<i>Heterorhabdus papilliger</i> (Claus, 1863) ^O	<i>Miracia efferata</i> Dana, 1849 ^O
<i>H. spinifrons</i> (Claus, 1863) ^O	<i>Macrosetella gracilis</i> (Dana, 1847) ^O
<i>Lucicutia flavicornis</i> (Claus, 1863) ^O	<i>Clytemnestra scutellata</i> Dana, 1847 ^O
<i>L. gemina</i> Farran, 1926 ^O	<i>C. rostrata</i> (Brady, 1883) ^O
<i>L. longicornis</i> (Giesbrecht, 1889) ^O	<i>Pachos tuberosum</i> (Giesbrecht, 1891) ^O
<i>L. wolfendeni</i> Sewell, 1932 ^O	<i>Hemicyclops thalassius</i> Vervoort & Ramirez, 1966 ^N
<i>Metridia princeps</i> Giesbrecht, 1889 ^O	

O, oceanic; N, neritic; E, estuarine (according to Björnberg, 1963, 1981; Bradford-Grieve *et al.*, 1999).

The PCA revealed four groups in the bi-dimensional space (Fig. 5): (i) comprising most offshore samples, dominated by oceanic indicators; (ii) grouped the Northern offshore stations on the South Equatorial Under Current retroflexion; (iii) containing the oceanic samples affected by some neritic influence, because of the narrow shelf; (iv) comprising most coastal stations with higher abundances; (v) comprising neritic, shelf break and oceanic samples, with a mixture of oceanic and neritic communities (based on copepods as indicators; Table II). Homogeneity of the samples was high, caused by the narrow continental shelf that allows

nearshore incursion of oceanic species and vice versa. Station 7072 did not group and had the highest copepodite abundance (576 ind m⁻²), whereas Station 7081 also was alone and had a high abundance of *Oikopleura dioica* and *O. venusta*.

The species cluster analysis indicated three principal groups (Fig. 6): 1) Comprised of oceanic species with lowest abundance (<15 ind m⁻³); 2) a mix of neritic and oceanic species, with higher total abundance (>100 until ~1300 ind m⁻³); 3) Coastal neritic group, with mean abundance (~50–200 ind m⁻³). Smaller groups 4) and 5) were comprised of very rare oceanic species.

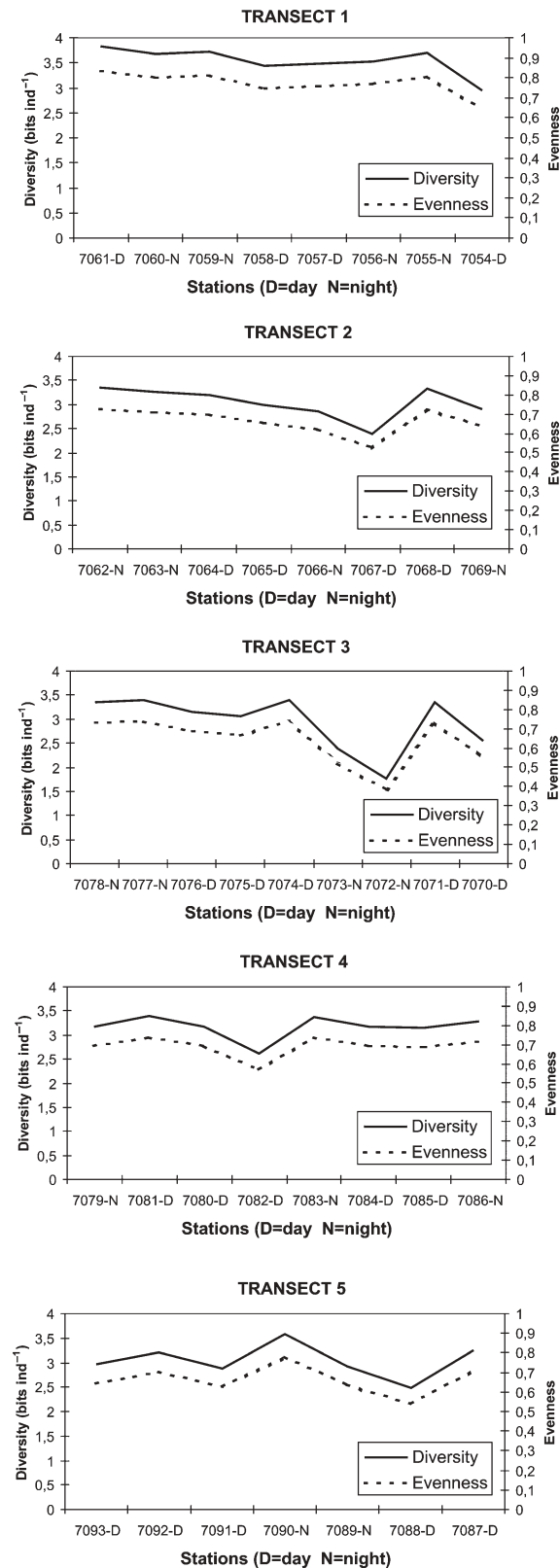


Fig. 2. Mesozooplankton species diversity and evenness off northeastern Brazil, June 1986.

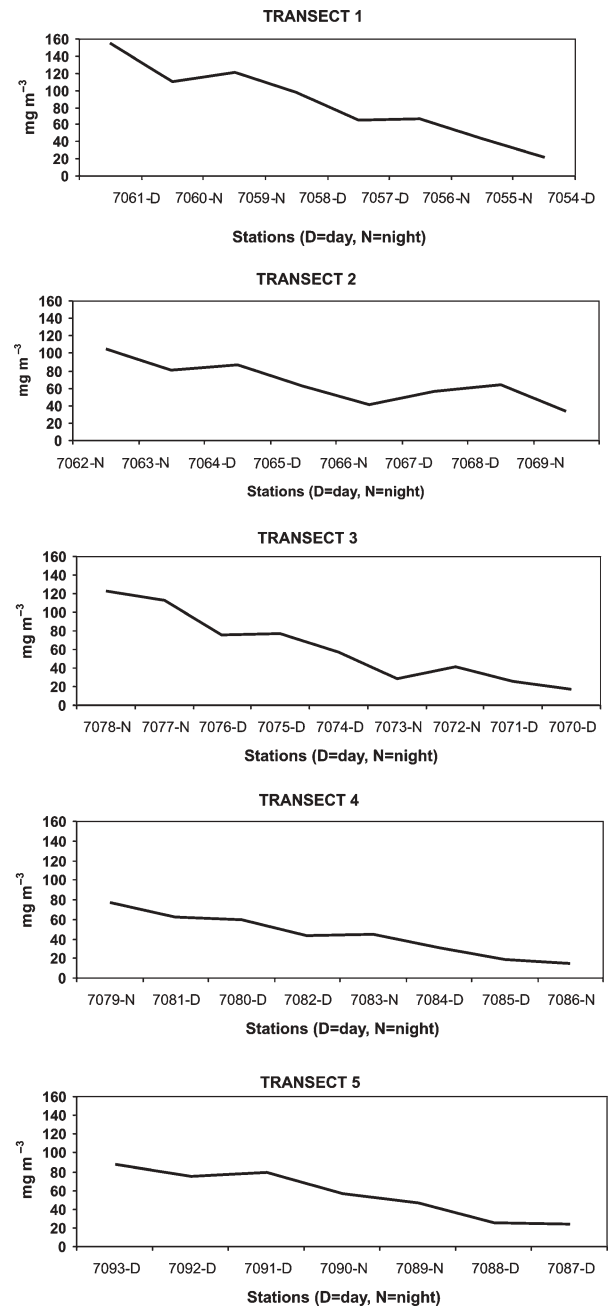


Fig. 3. Biomass of mesozooplankton off northeastern Brazil, June 1986.

DISCUSSION

The mesozooplankton species composition was very diverse. We attribute this to the stable conditions in the TW present in the area, environmental stability being characterized by a low range of environmental variation such as salinity, temperature and frequency of storm events (Levinton, 1995). Physically stable environments

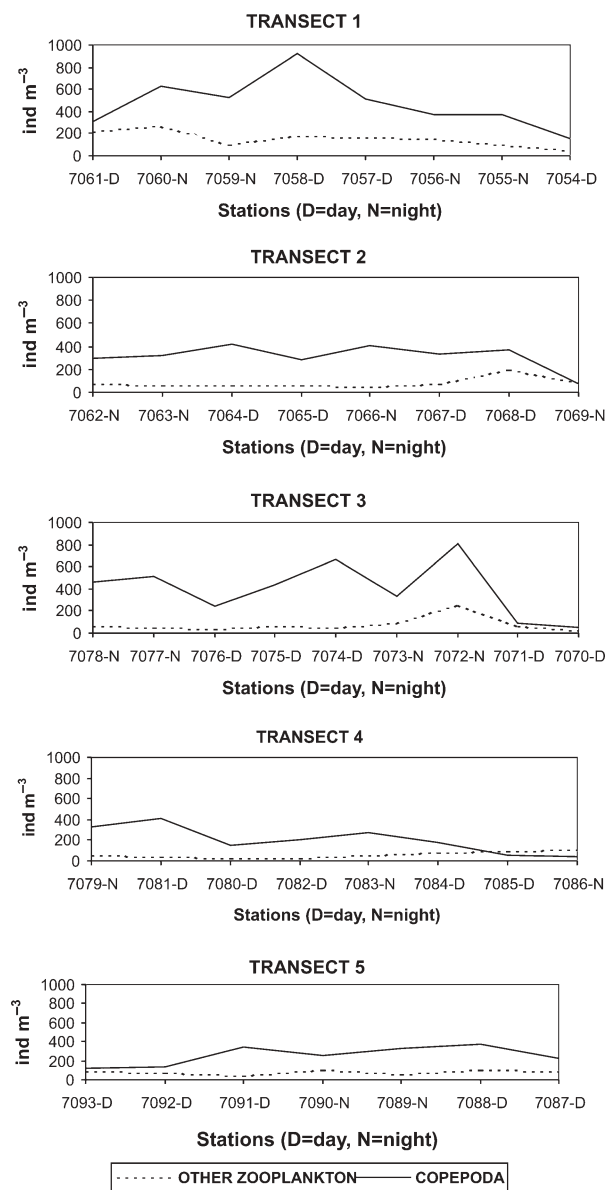


Fig. 4. Numerical abundance of mesozooplankton off northeastern Brazil, June 1986.

may accommodate more species than variable environments (Giller, 1984).

The dominance of Copepoda in the TW of the SWA has been described by (Boltovskoy, 1981, 1999). The most abundant species found in the present work are apparently epipelagic, oceanic and widespread in tropical and subtropical waters of the Atlantic, Pacific and Indian oceans, except for *U. vulgaris*, which is neritic (Björnberg, 1981; Bradford-Grieve *et al.*, 1999). *Undinula vulgaris* was the dominant copepod species in oceanic samples from the Northeastern Brazil exclusive economic zone (Cavalcanti and Larrazábal, 2004) and was

observed in the tropical oceanic area off West Africa (Champalbert *et al.*, 2005). As young stages, this species was also abundant in oceanic samples in the present study, suggesting that it also inhabits oceanic regions. It is suggested that the ecology of this species merits further study.

In general, most of the dominant copepods throughout the study area were of smaller size and accounted for 71% of the total abundance. Smaller species and developmental stages are important components of planktonic communities in oligotrophic areas, where microbial components are dominant (Calbet *et al.*, 2001; Turner, 2004). Also, these small-sized copepods are intermediates between the classical and the microbial food web (Nakamura and Turner, 1997; Hopcroft *et al.*, 1998; Turner, 2004), have a much higher growth rate (Peterson *et al.*, 1991; Hopcroft *et al.*, 1998) and have a greater influence on the efficiency of trophic coupling between the primary producers and the protozooplankton than do the larger species in low chlorophyll environments such as SWA due to their high clearance rates on microzooplankton (Zervoudaki *et al.*, 2007).

The wide spatial distribution of many Copepoda (*C. pavo*, *U. vulgaris*, *O. plumifera*, *O. venusta*, *M. gracilis*, *M. rosea* and *C. speciosus*), Chaetognatha (*S. enflata* and *S. serratodentata*) and Larvacea (*Oikopleura* spp.) is chiefly the result of the fact that for pelagic plankton, circum-global distribution patterns are more common than endemism (Boltovskoy *et al.*, 2002). Exceptions to this pattern are taxa with high percentages of neritic forms, and benthopelagic groups (Angel, 1993).

Young Chaetognatha showed a mixture of oceanic and neritic species, with a predominance of oceanic species. *Sagitta enflata*, *S. serratodentata*, *S. hexaptera*, *S. bipunctata* and *Krohnia subtilis* are TW indicators, whereas *S. tenuis* and *S. helenae* are coastal-water indicators. *Pterosagitta draco* occurs in both water masses (Boltovskoy, 1981). The higher numerical abundance of *S. enflata* is a common feature of the study area. Boltovskoy (Boltovskoy, 1981, 1999) and Gusmão (Gusmão, 1986) found similar results.

In general, the mesozooplankton abundance in the study area was very low. Boltovskoy (Boltovskoy, 1981) noted that the maximum zooplankton biomass in the SWA occurs in neritic waters, with values reaching 100 mg m^{-3} in the upper 200 m. In general, biomass (considering all seston) decreased from neritic to oceanic stations due to the presence of suspended material from continental drainage and the higher presence of large-sized taxa (Decapoda larvae, Echinodermata larvae, Hydromedusae, *O. dioica* houses, among others); however, the general tendency of

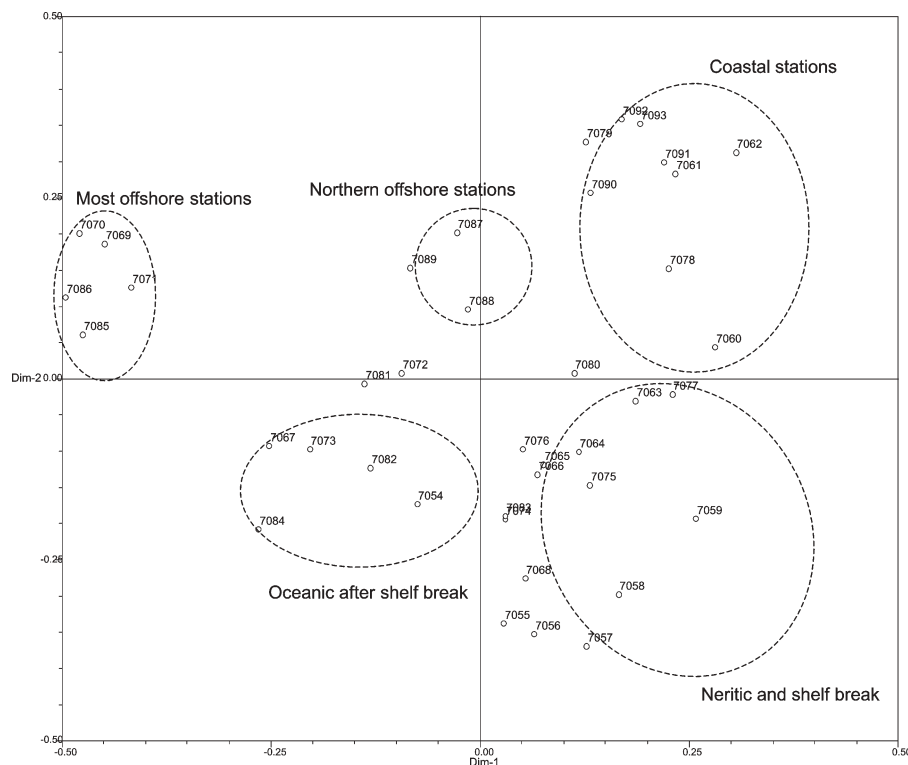


Fig. 5. PCA showing site similarity of mesozooplankton composition (based on Copepoda) off northeastern Brazil, June 1986, based on Bray–Curtis index.

numerical abundance to decrease from coastal to offshore stations was not observed. An increase in zooplankton abundance near the shelf break and close to Rocas Atoll (Station 7072) is caused by local topographic upwelling (Strama *et al.*, 1990) and in these areas a higher number of small-sized copepods (*Nannocalanus minor*, *Clausocalanus furcatus* and *U. vulgaris* copepodites) occurred.

A mixture of oceanic and neritic mesozooplankton was observed, making it difficult to separate both communities. These effects may result from across-shelf mixing due to the narrowness of the continental shelf and to the effect of inshore wind-driven advective processes. It is suggested that these processes favor a degree of homogeneity of the zooplankton community along the Brazilian tropical Atlantic. As expected, diversity did not increase from coastal locations to offshore. This pattern was described by Boltvoskoy (Boltvoskoy, 1981) and Neumann-Leitão *et al.* (Neumann-Leitão *et al.*, 1999) as a common feature of this area, although some meroplanktonic species have a marked preference for shallow waters, related to their adult reproductive requirements, such as Decapoda, Bryozoa, Echinodermata and Ascidea, among others.

The zooplankton bioindicator classification (Björnberg, 1963, 1981; Bradford-Grieve *et al.*, 1999)

showed that the most important group in our cluster analysis was composed of a high number of indicators (oceanic species) of the North Brazil Current, influenced by the shelf break (groups 1 and 2), and a smaller number (neritic species) of the warm coastal waters (group 3). Also, a smaller, offshore group was found (groups 4 and 5).

Copepods and other holoplanktonic organisms dominated at all stations, even in the coastal area. This pattern can be attributed to the lack of freshwater runoff from the continent because of the dry climate and geomorphology of the area, even during the rainy season. The same pattern was found by Neumann-Leitão *et al.* (Neumann-Leitão *et al.*, 1999) for this area. Mabesoone and Coutinho (Mabesoone and Coutinho, 1970) noted that the constant northeast tradewinds and dry climate in the coastal area of this state allow the formation of extensive beaches and dunes, which are in constant movement because of the lack of anchoring vegetation. These dunes block the free flow of rivers to the sea, and behind them a sequence of freshwater lakes is formed. The changes observed in these coastal areas seem to be principally driven by seasonal blooms of benthic invertebrate larvae.

According to Deevey and Brooks (Deevey and Brooks, 1977) and Webber and Roff (Webber and Roff, 1995),

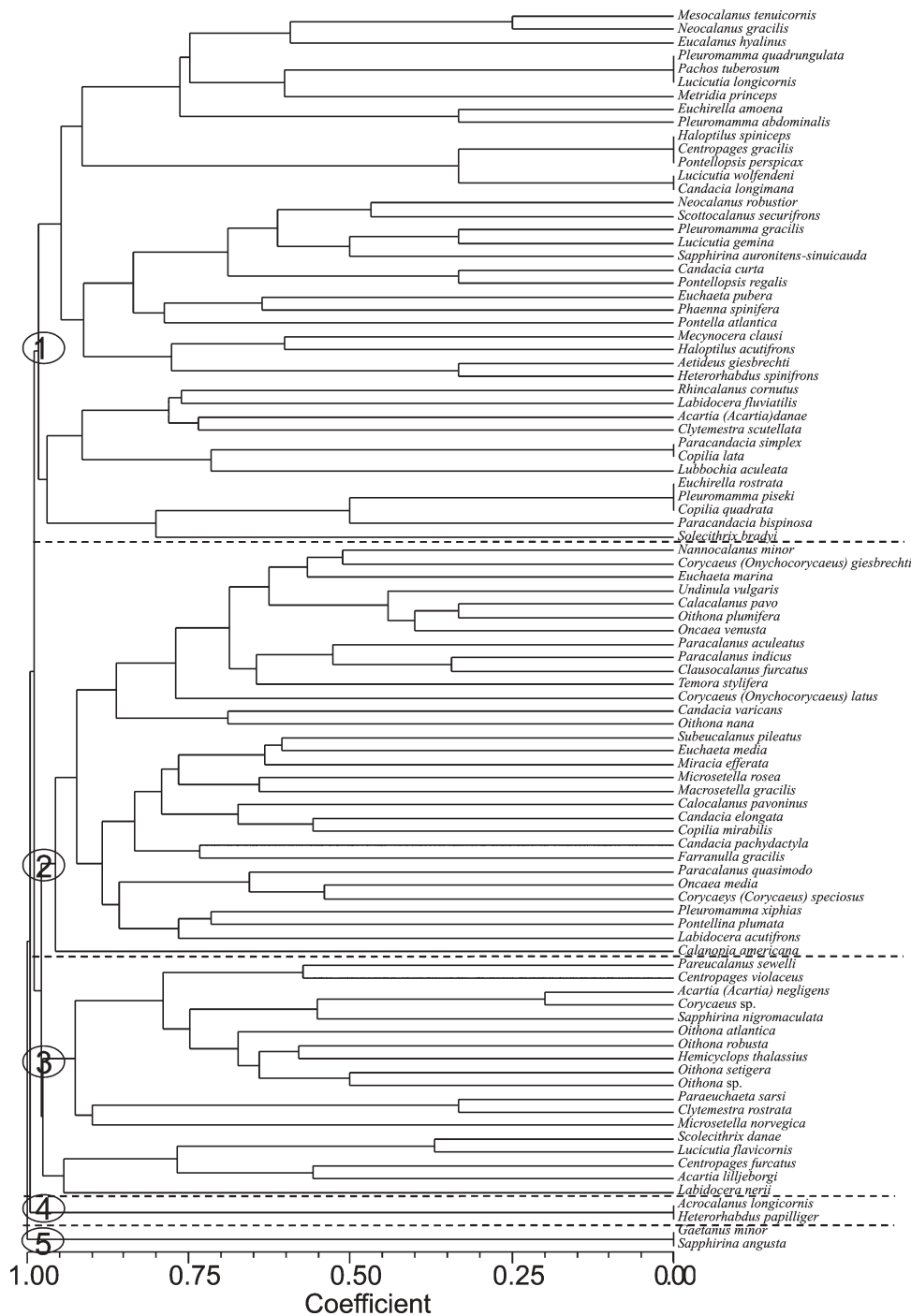


Fig. 6. Dendrogram showing species similarity of Copepoda in the waters off northeastern Brazil, June 1986, based on Bray–Curtis index. Linkage: WPGMA.

a vertical discontinuity in zooplankton abundance can take place in TW, since larger copepods occur mainly in phytoplankton-rich deep waters, whereas smaller species are more numerous at the surface. Nevertheless, studies by Gusmão *et al.* (Gusmão *et al.* 1998) from 100 and 50 m to the surface showed higher biodiversity and

abundance in deeper layers around 100 m, where Medeiros *et al.* (Medeiros *et al.*, 1999) found higher primary productivity. For the same area, Neumann-Leitão *et al.* (Neumann-Leitão *et al.*, 1999) confirmed higher biodiversity and productivity from samples from the upper 150 m. In our study, no

difference ($P > 0.5$) was found between day and night hauls. It seems that in the tropical Atlantic oligotrophic waters, there is upward vertical migration from 100 to 150 m. This may be an adaptation to save energy because of the small amount of food available in the surface layers. In general, most of the zooplankton community is concentrated around 100 m depth. Migration occurs only when increased food levels at the surface make upward migration worthwhile (Gliwicz and Pijanowska, 1988) or does not occur as the result of animals having located a food-rich stratum (Scrope-Howe and Jones, 1986). Champalbert *et al.* (Champalbert *et al.*, 2005) showed that the time of day (i.e. day or night) had no significant effect on the diversity of zooplankton in a tropical oceanic area off West Africa. However, the lack of samples from the deepest waters makes it difficult to ascertain the complete pattern of zooplankton biodiversity in the study area.

It can be concluded that the study area is characterized by high spatial homogeneity, high diversity and low numerical abundance. This is among the most oligotrophic marine habitats off Brazil, considering the abundance of mesozooplankton. Exceptions are some shelf-break and offshore stations influenced by topographic upwelling. The narrow shelf allows nearshore incursion of oceanic populations and vice versa, resulting in strong interaction between these communities. The connection between the oligotrophic oceanic water masses and the enriched coastal water is a key factor in the structure of the local food chain, contributing to the special pattern of zooplankton diversity in this region of the Southwest Atlantic.

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