

# El Niño induced local extinction of coral reef bryozoan species from Northern Bahia, Brazil

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Received 25 March 2003; received in revised form 25 September 2003; accepted 12 October 2003

## Abstract

The 1997–1998 El-Niño Southern Oscillation was the most severe on record and dramatically impacted corals worldwide. However, the effect of this event on the associated community of reef organisms has received much less attention. The composition of the bryozoan assemblage from the coral reefs of Northern Bahia, Brazil were monitored annually from 1995 to 2000, allowing the investigation of the effects of this large-scale stressor on an important, diverse, yet understudied component of the coral reef system. Bryozoan samples (35 replicates/reef) were collected during April/May from four shallow bank reefs (10–40 m depth) located a few kilometres off the coast, together with measurements of the associated environmental parameters. Currently 157 species have been recorded from the study area, but significant reductions in density and diversity were apparent between pre- and post El-Niño Southern Oscillation (ENSO) years, multivariate analysis denoting significant changes in assemblage composition. A total of 61 species were unrecorded following the 1997–1998 ENSO event (22 species from 1997; 25 further species from 1998 and 14 more from 1999). These included several species endemic to Brazil, suggesting that the 1997–1998 ENSO has had a marked influence on the reef bryozoan community, resulting in the local extinction of several species. Bryozoan mortalities were probably initiated by elevated temperatures, but continued disappearance of species for 2 years after ENSO suggests other indirect factors are also influential. These results demonstrate that ENSO events can have severe long-term impacts on the biodiversity of coral reefs, with important conservation consequences.

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**Keywords:** ENSO; Bryozoa; Environmental impact; Global warming

## 1. Introduction

The Bryozoa is a relatively poorly known group of eurytopic sessile invertebrates recorded worldwide at all depths (Soule et al., 1995). Such a wide distribution is closely associated with the particular morphology and growth form of the colony, which are directly influenced by environmental variables such as hydrodynamics, depth, temperature, sedimentation rate, substrate, luminosity and oxygen availability (Souza, 1986; McKin-

ney and Jackson, 1989; Harmelin, 1988). Consequently, these organisms can play an important role in ecological and palaeoecological investigations (e.g. Anstey, 1986; Moissette, 1991; Smith, 1995).

To investigate the response of these organisms to environmental changes, a long-term monitoring study was started in 1995 throughout the coral reefs of northern Bahia, Brazil, where little is known of the bryozoan fauna (but see, for example, Marcus, 1941; Souza and Barbosa, 1994). Such quantitative monitoring was designed to record spatial and temporal patterns in bryozoan biodiversity and assemblage structure from four shallow-bank reefs: Abaí, Guarjuba, Itacimirim and Praia do Forte. However, the monitoring period subsequently included the severe 1997–1998 El-Niño

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Southern Oscillation (ENSO), which resulted in global seawater temperature increases (Pittock, 1999; Kumar et al., 2001; Pezzi and Cavalcanti, 2001) and consequent large-scale bleaching of the world's coral reefs (Aronson et al., 2000; Glynn et al., 2001). Despite the scale of bleaching being well reported, there has been little information on the effect, and conservation implications, of the 1997–1998 ENSO on other invertebrates associated with coral reefs. In this paper we describe the impact of this global event on the bryozoan populations of Bahian reefs, and assess the scale of any recovery in subsequent years.

## 2. Methods

### 2.1. The study area

The studied reefs are 70 km from the city of Salvador and extend for 20 km between the beaches of Abaí and Praia do Forte, an area under the influence of river discharge (Fig. 1). They are located in the narrowest part of the Eastern Brazilian Continental Shelf (average width 15 km between the São Francisco and Doce Rivers), the shelf edge being approximately

70 m deep (DHN, 1993). The investigated shallow-bank reefs are located a few kilometres off the coast and date from the Holocene (Nolasco, 1987). Their dimensions vary from 500 to 1800 m (long) and 400 to 500 m (wide). Water depth was between 10 and 40 m. The lateral contours of these structures are highly irregular, presenting sometimes well-developed spur and groove systems on the fore reef side, whilst the back-reef is usually less irregular. The irregular reef tops, eroded due to sea-level fluctuations, possess thin columnar structures, cavities, meandering channels and small caves. A small river (Pojuca) discharges in the proximity of these reefs (between Praia do Forte and Itacimirim), supplementing the sedimentary load from the two major rivers in the area (Kelmo et al., 2003). Due to these specific environmental conditions and comparative isolation due to the Amazon barrier, the coral species present on the Bahian reefs include a high proportion of endemics (39%) and no branching taxa (e.g. *Acropora*).

The coastal belt along the State of Bahia has a tropical humid climate. In the study area, rainfall ranges between 1300 mm per year, at its northernmost part, to 1900 mm per year around Salvador City (Leão et al., 1997). Average air temperature ranges from 23 °C

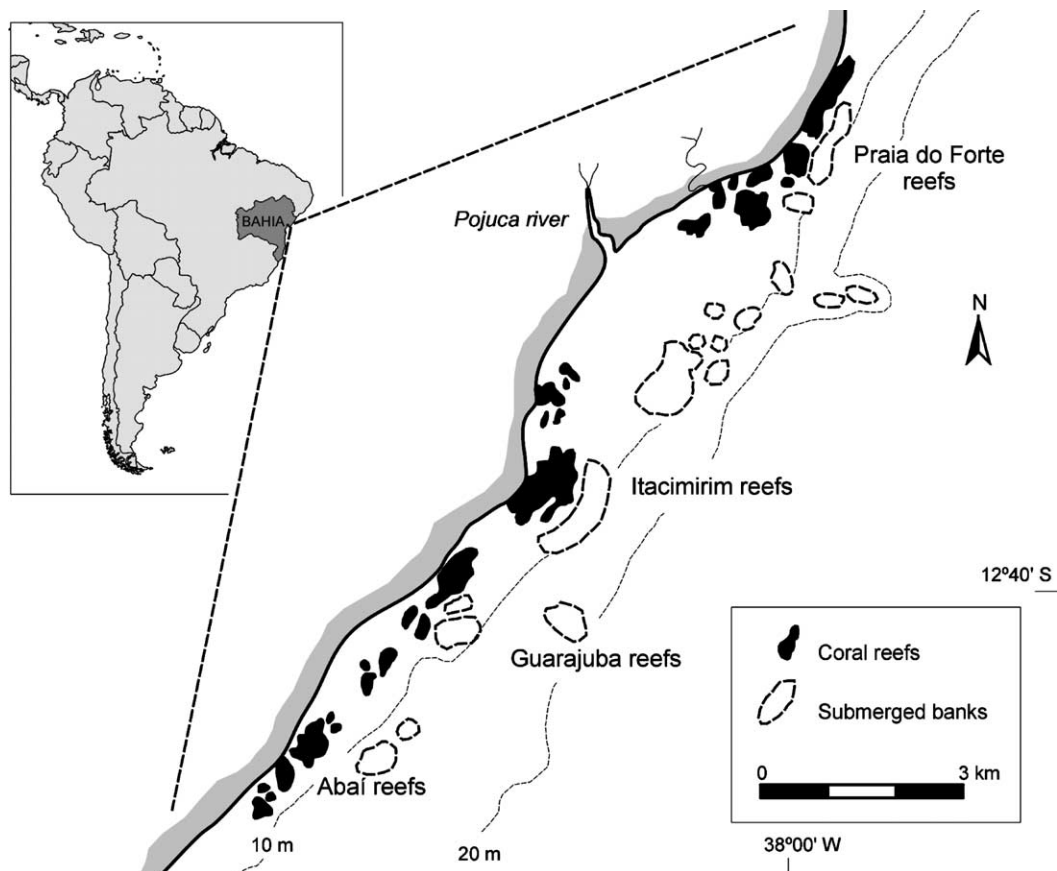


Fig. 1. Location map showing the four shallow bank reefs sampled from 1995 to 2000.

(winter) to 28 °C (summer) (Leão et al., 1997). Mean surface water temperatures range from 25 °C (in winter) to 28 °C (in summer). Salinity and pH values vary little, with no seasonal patterns. In January and September dominant easterly winds occur. North-easterly winds are frequent from October to December and from February to March, whilst stronger South-easterly winds occur during storms (April–August) (DHN, 1993).

## 2.2. Sampling methods

Since 1995, data on the bryozoan community of the submerged shallow-bank reefs of Northern Bahia (Fig. 1) have been collected annually (between April and May) by scuba diving. Quantitative samples were taken from 35 1 m<sup>2</sup> quadrats positioned randomly on each reef. All colonies were counted in situ; however, fragments or entire colonies were collected for confirmatory identification in the laboratory. Voucher specimens of all species, collected each year, are stored at the scientific collection of the Department of Zoology – University Federal of Bahia (address as for first author).

Sea surface temperature, sunlight irradiation, air temperature, rainfall and cloud cover were obtained from the Brazilian Meteorological Institute (INMET). Complementary data on physical parameters (i.e. sea-water temperature, salinity and pH) were taken on each sampling visit, and measured with a pH/conductivity/TDS/Temperature meter Hanna<sup>®</sup> model HI 991300. Turbidity was estimated with a Secchi disc.

## 2.3. Data analysis

ANOVA and Kruskal–Wallis tests were used to identify any significant variations between pre- and

post-El-Niño periods. Data were normalised and fourth-root transformed where necessary. Post hoc pairwise comparisons were undertaken using Tukey–Kramer and Dunn's multiple comparison tests.

A triangular matrix of similarities between the bryozoan samples was constructed using the Bray–Curtis similarity coefficient on density data. The similarity matrix was subjected to clustering and ordination analyses using the PRIMER (Plymouth Routines in Multivariate Ecological Research) package (Carr, 1996). Clustering was by a hierarchical agglomerative method using group-average linking and ordination by non-metric multidimensional scaling (MDS). Formal significance testing of differences in community composition between years was tested using ANOSIM (Clarke and Green, 1988). To investigate the relationship between environmental variables and the bryozoan community data the BIOENV method (Clarke and Ainsworth, 1993) was used. This method correlates the similarity matrix derived for the bryozoan communities with an equivalent for the suite of environmental measurements taken at each site, defining which variables “best explain” the observed changes in community composition.

## 3. Results

### 3.1. Environmental parameters

Although the physico-chemical parameters varied little between reefs, mean temperature, turbidity and cloud cover variation were significantly different in 1998 compared with other years (Table 1).

Table 1  
Summary of wide-scale and locally measured physico-chemical data recorded from the shallow bank reefs throughout the sampling period

Parameter recorded	Mean value ± SE						F value	P (1998)
	1995	1996	1997	1998	1999	2000		
<i>Wide-scale</i>								
Sea surface temperature (°C)	25.55 ± 0.05	25.45 ± 0.03	25.57 ± 0.03	<b>27.70 ± 0.06</b>	25.47 ± 0.13	25.50 ± 0.04	195.62	***
Sunlight irradiation (h/yr)	2110 ± 2.5	2080 ± 2.5	2190 ± 2.5	<b>2410 ± 7.5</b>	2100 ± 2.5	2050 ± 7.1	80.485	***
Air temperature (°C)	26.37 ± 0.11	26.17 ± 0.05	26.47 ± 0.03	<b>28.62 ± 0.23</b>	26.62 ± 0.10	26.50 ± 0.04	58.421	**
Annual rainfall (mm <sup>3</sup> )	1410 ± 2.5	1950 ± 2.5	1350 ± 4.8	<b>1150 ± 2.9</b>	1480 ± 2.5	1950 ± 2.5	11.530	*
Annual cloud cover (Dec)	4.57 ± 0.03	4.55 ± 0.03	4.52 ± 0.03	<b>3.97 ± 0.03</b>	4.77 ± 0.06	5.57 ± 0.09	116.68	***
<i>Local</i>								
Sea-water temperature (bottom) (°C)	25.05 ± 0.03	25.05 ± 0.03	25.27 ± 0.08	<b>27.17 ± 0.10</b>	25.22 ± 0.08	25.12 ± 0.09	128.34	***
Salinity	36.32 ± 0.11	36.30 ± 0.04	36.40 ± 0.17	36.65 ± 0.10	36.45 ± 0.17	36.47 ± 0.15	0.9279	NS
pH	8.27 ± 0.03	8.22 ± 0.02	8.22 ± 0.03	8.27 ± 0.03	8.32 ± 0.03	8.25 ± 0.03	2.179	NS
Turbidity (Secchi clarity, m)	1.65 ± 0.09	1.65 ± 0.12	1.85 ± 0.06	<b>2.47 ± 0.05</b>	1.62 ± 0.06	1.57 ± 0.03	21.436	***

Significance of difference between 1998 and other years (highlighted in bold): \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; NS, not significant. (ANOVA/K–W with post hoc testing – see Section 2).

### 3.2. Bryozoan assemblage

A total of 1014 colonies and 157 species of bryozoan were recorded from the four shallow bank reefs assessed. The most abundant species were *Aetea ligulata*, *Discoporella umbellata*, *Hippothoa flagellum*, *Bugula ditrupae* and *Hippaliosina imperfecta*, whilst *Cellaria*, *Hippopori-dra*, *Membranipora*, *Nolella*, *Onychocella*, *Palmicellaria*, *Pasuthea*, *Proboscina*, *Syphonophora*, *Smittipora*, *Stylopoma*, *Synnotum*, *Terebripora*, *Tremogasterina* and *Tremoschizodina* were the least abundant genera.

All species experienced a significant decline in their densities (including local extinction) one year after ENSO has started (Appendix, Fig. 2(a)). Local extinction took place at different times as follows: 22 species by 1997; 25 further species by 1998 and 14 more by 1999 (Appendix). Most importantly, these local extinctions included several bryozoan species endemic to Brazil: *Exochonella brasiliensis* (disappeared in 2000 – was endemic but has since expanded its distribution), *Rhynchozoon arborescens* (disappeared in 1997), *Celleporaris aschubarti* (disappeared in 2000) and *C. carvalhoi* (disappeared in 1997 and unrecorded since except a single colony 1999). Two endemic species, *H. imperfecta* and *Utinga castanea* (endemic to Bahia) have, however, been recorded in all years. Conversely, new additions have been made to the species list after the 1997–1998 ENSO and eight species previously unrecorded to the area were found: *Nolella dilatata*, *Palmicellaria skenei*, *Proboscina robusta*,

*Reptadeonella bipartita*, *Schizoporella pungens*, *Smittipora tuberculata*, *Stylopoma aurantiacum* and *Victorella sibogae*, although all in very low densities (Appendix). The dramatic loss of species is illustrated by the number of species of bryozoan recorded on each reef over the survey period (Fig. 2(b)).

Differences in density, species number and diversity between 1998 and the previous three years were significant (ANOVA all  $F > 17.1$ ,  $P < 0.001$ ; Fig. 2), although there was no significant change in evenness (ANOVA  $F = 1.43$ ,  $P > 0.05$ ). Similarly, there were continued significant declines in density, species number and diversity after 1998 (Fig. 2).

Multivariate analysis grouped all the sampled reefs from 1995 to 1997 into one cluster, denoting similarity between assemblages in these years. All the samples taken from 1998 to 2000 formed separate clusters for each year (dendrogram not shown). This is illustrated by the MDS ordination (Fig. 3) which clearly separates the sampled community into three distinct groups: (1) samples taken before 1998, (2) samples collected in 1998 and (3) samples obtained after 1998. ANOSIM revealed overall significant differences in assemblage composition ( $R = 0.704$ ,  $P < 0.01$ ) consistent with the patterns exhibited on the ordination.

BIOENV analysis indicated a combination of increased mean temperature, reduced cloud cover and turbidity ( $R = 0.683$ ) as the main environmental variables best explaining the investigated community patterns.

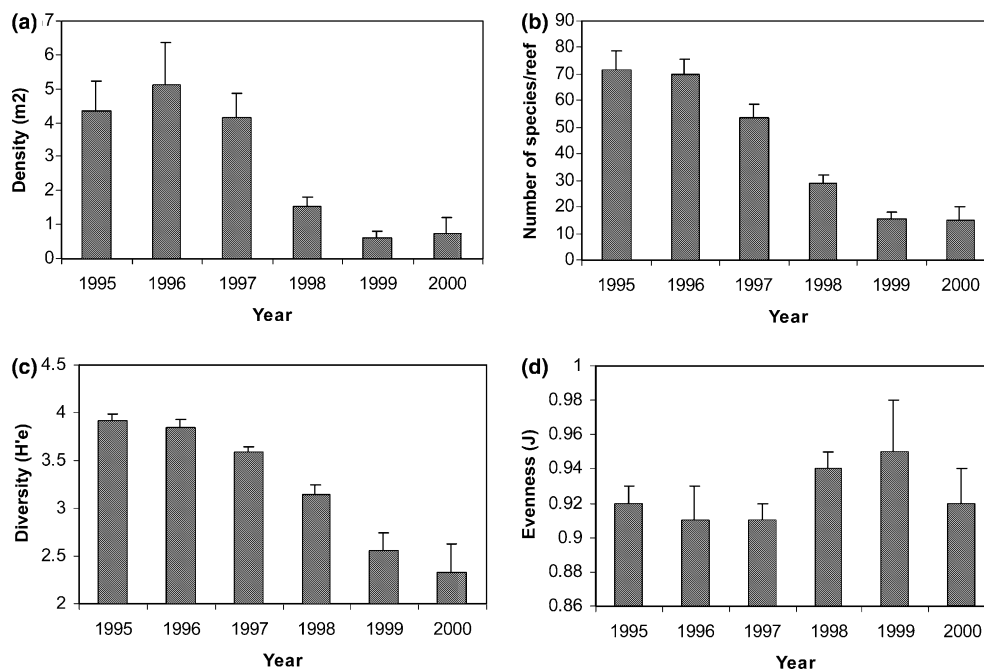


Fig. 2. Histograms illustrating the change in univariate measures of the bryozoan assemblage from 1995 to 2000, with the ENSO event occurring between the 1997 and 1998 surveys: (a) density; (b) number of species; (c) diversity; (d) evenness. All values are means  $\pm$  SE.

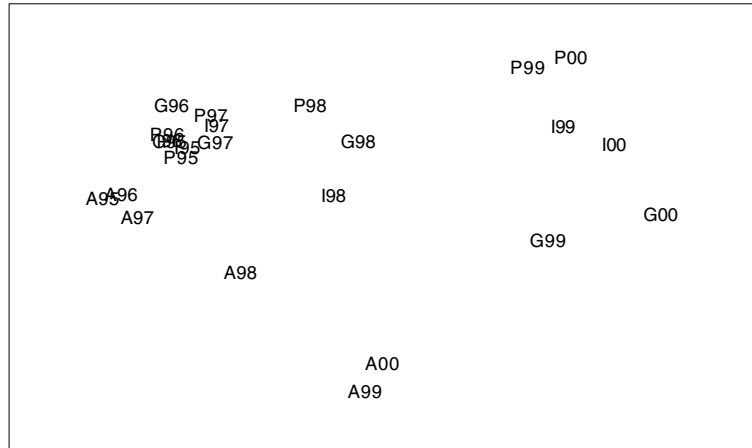


Fig. 3. MDS ordination of the bryozoan assemblage data for each reef 1995–2000. P = Praia do Forte; I = Itacimirim; G = Guarajuba and, A = Abaí. Year codes are from 1995 (95) to 2000 (00).

#### 4. Discussion

During the 1997–1998 El-Niño Southern Oscillation (ENSO) both north (Kumar et al., 2001) and south America (Pezzi and Cavalcanti, 2001) experienced extensive sea surface warming, resulting in increased and prolonged temperatures for the entire period unprecedented in recent times (Kumar et al., 2001). The dramatic reduction in bryozoan species densities recorded in 1998 was associated with abnormal records of increased seawater temperature, reduced turbidity and low cloud cover observed throughout the investigated reefs in the same period. This suggests a causative link with the 1997–1998 ENSO, which had notable documented effects on coral reef communities' worldwide (e.g. Wilkinson and Hodgson, 1999).

Our results clearly demonstrate a considerable impact of this event on the bryozoan community of northern Bahia, with comparatively large scale extinction of species omnipresent before the 1997–1998 ENSO. Conversely, species have been recorded since 1998 that are apparently new to the fauna. Whilst the initial mortality of species is likely to be as a direct response to the environmental conditions accompanying ENSO, namely elevated sea temperatures, this does not explain the continued loss of species, and lack of recruitment, over subsequent years. The most plausible causative explanation probably involves indirect effects on biological processes (Glynn, 1988, 1990), particularly influences on larval survival and settlement (such as delayed harmful effects of increased UV light – Kelmo et al., 2003) and disruption of trophic links impacting fitness of surviving individuals (Kelmo et al., 2003).

In summary, the 1997–1998 ENSO has had a marked effect on the bryozoan assemblage of Bahian reefs, with a large-scale loss of species from the fauna (including endemics) that has continued during sub-

sequent years. It is therefore clear that the environmental conditions associated with El Niño can have severe consequences for coral reef systems additional to the well reported bleaching of corals, even in regions such as Brazil where the influence of ENSO is indirect (Kelmo and Attrill, 2001; Kelmo et al., 2003). Coral reefs are perhaps the most high-profile marine system in terms of conservation, due to the high diversity of associated organisms as much as the corals themselves. The results of this study demonstrate that this diversity can be greatly impacted by ENSO events, including the potential disappearance of endemic taxa, and highlight the need for further such work on non-coral invertebrates. As the frequency and intensity of ENSO events is predicted to increase with global warming (Timmermann et al., 1999), the conservation consequences for coral reef biodiversity are paramount. Three years after the ENSO there is little evidence of recovery within the Bahian coral reef bryozoan assemblage, and continued monitoring is required to assess the longer-term consequences of this global event.

#### Acknowledgements

This investigation was made possible by financial support from CNPq-Brazil. Thanks to Dr. José Maria Landin Dominguez – Laboratory of Coastal Studies, and to Dr. Marlene Campos Peso Aguiar – Laboratory of Malacology and Benthic Ecology, both from Universidade Federal da Bahia, Brazil, for the technical facilities provided during the early years of this research. F.K. extends particular gratitude to Carlos Neves, Larissa de Siqueira, Simone Souza de Moraes and Yonara Souza Braga for encouragement over a number of years, and for all their help and assistance during the fieldwork.

## Appendix

Quantitative inventory of densities (mean  $m^{-2}$ ) of the Bahian bryozoan community from the four shallow bank reefs assessed throughout the sampling period, 1995–2000

Species	1995	1996	1997	1998	1999	2000
<i>Aetea ligulata</i> Busk 1852	1.12	1.45	0.35	0.12	0	0
<i>Aetea sica</i> Couch 1884	0.49	0.77	0.43	0	0	0
<i>Aetea truncata</i> Landsborough 1852	0.32	0.36	0.12	0.03	0.03	0
<i>Alcyonidium mamillatum</i> Alder 1857	0.18	0.18	0.25	0.22	0.06	0
<i>Alcyonidium polyom</i> Hassall 1841	0.12	0.18	0.18	0.29	0.06	0
<i>Alderina irregularis</i> Smitt 1873	0.6	0.52	0.46	0.09	0	0.17
<i>Amanthia convoluta</i> Busk 1886	0.55	0.15	0.06	0.03	0	0
<i>Amanthia distans</i> Busk 1886	0.15	0.12	0.2	0	0	0
<i>Anguinella palmata</i> Van Beneden 1845	0.24	0.21	0.32	0.17	0	0
<i>Antropora granulifera</i> Hincks 1880	0.03	0.03	0	0	0	0.03
<i>Antropora parvus</i> Canu & Bassler 1928	0.34	0.12	0.23	0	0.03	0
<i>Antropora typica</i> Canu & Bassler 1928	0.2	0.29	0.06	0.03	0.03	0.03
<i>Aptonella violacea</i> Canu & Bassler 1928	0.21	0.24	0.65	0	0	0
<i>Arachnoidea evelinae</i> Marcus 1937	0.18	0.24	0.35	0	0	0
<i>Anthropoma cecilii</i> Audouin 1826	0.2	0.15	0.03	0.06	0.03	0.03
<i>Beania australis</i> Busk 1852	0.27	0.43	0.32	0	0	0
<i>Beania hirtissima</i> Heller 1867	0.26	0.4	0.26	0.23	0.2	0.12
<i>Beania intermedia</i> Hincks 1881	0.03	0	0	0.03	0	0
<i>Bowerbankia caudata</i> Hincks 1880	0.03	0	0	0.03	0.03	0.03
<i>Bowerbankia gracilis</i> Leidy 1855	0.12	0.18	0.06	0.03	0	0.06
<i>Bugula californica</i> Roberts 1905	0.18	0.15	0.09	0.03	0	0
<i>Bugula carvalhoi</i> Marcus 1949	0.12	0.09	0.12	0.03	0.03	0.03
<i>Bugula ditrupae</i> Busk 1858	0.46	0.4	0.64	0.12	0.17	0.37
<i>Bugula flabellata</i> Thompson 1868	0.18	0.23	0.2	0.32	0	0
<i>Bugula neritina</i> Linnaeus 1758	0.18	0.29	0.2	0.09	0.09	0
<i>Bugula stolonifera</i> Ryland 1960	0.15	0.32	0.95	0.12	0.03	0
<i>Bugula turrita</i> Desor 1848	0.34	0.18	0.24	0.12	0	0
<i>Bugula uniserialis</i> Hincks 1884	0.48	0.28	0.2	0.06	0.03	0
<i>Buskia nitens</i> Hincks 1880	0.03	0.06	0.06	0.03	0	0
<i>Buskia repens</i> O'Donoghue 1923	0.06	0	0.09	0	0.03	0.03
<i>Buskia setigera</i> Hincks 1887	0.15	0	0	0.03	0	0
<i>Canda philipinensis</i> Canu & Bassler 1929	0.4	0.09	0.03	0	0	0
<i>Canda retiformis</i> Pourtales 1867	0.15	0.2	0.06	0	0	0
<i>Catenicella contei</i> Audouin 1826	0.06	0	0	0	0	0.03
<i>Caulibugula armata</i> Verrill 1900	0	0.15	0.09	0.03	0	0
<i>Cellaria</i> sp. Ellis-Solander 1786	0	0.03	0	0	0	0
<i>Celleporaria carvalhoi</i> Marcus 1939	0.03	0.12	0	0	0.09	0
<i>Celleporaria mordax</i> Marcus 1947	0.09	0.6	0	0	0	0
<i>Celleporaria shubarti</i> Marcus 1939	0.23	0.12	0.03	0.03	0.03	0
<i>Cleidochasma contracta</i> Waters 1899	0.23	0.2	0	0	0	0
<i>Cleidochasma porcellana</i> Busk 1860	0.15	0.12	0.06	0	0.03	0
<i>Cleidochasma porcellana</i> var <i>granulifera</i> Canu & Bassler 1929	0.03	0.35	0.17	0	0	0
<i>Cleidochasma porcellana</i> var <i>tuberculata</i> Osburn 1952	0	0.03	0	0.03	0	0
<i>Coleopora corderoi</i> Marcus 1949	0.09	0.12	0.09	0.03	0	0
<i>Colletosia radiata</i> Moll 1803	0.09	0	0.06	0	0	0
<i>Copidozoum tenuirostre</i> Hincks 1880	0.12	0.12	0	0	0	0
<i>Crassimarginatella exilimargo</i> Canu & Bassler 1929	0.26	0.52	0.14	0	0	0

## Appendix (continued)

Species	1995	1996	1997	1998	1999	2000
<i>Crassimarginatella leucocypha</i> Marcus 1937	0	0.14	0	0	0	0
<i>Cribilaria floridana</i> Smitt 1873	0.12	0.18	0.15	0.03	0.03	0.03
<i>Cribilaria innominata</i> Couch 1844	0.06	0.17	0.17	0	0.23	0
<i>Cribilaria radiata</i> Moll 1803	0.06	0.09	0.12	0.23	0.09	0.2
<i>Crisia ficulnea</i> Buge 1979	0.11	0.2	0.71	0	0	0
<i>Crisia ramosa</i> Harmer 1891	0.09	0.09	0	0	0	0
<i>Cryptopolyzoon evelinae</i> Marcus 1941	0.03	0.03	0.06	0	0	0
<i>Cupuladria biporosa</i> Busk 1859	0.03	0.09	0	0	0.03	0
<i>Cupuladria canariensis</i> Busk 1859	0.12	0.06	0.09	0	0	0
<i>Cupuladria monotrema</i> Busk 1884	0.21	0.29	0.09	0.15	0	0
<i>Dakaria vaginata</i> Canu & Bassler 1930	0.09	0.06	0	0	0	0
<i>Discoporella umbellata</i> De France 1823	0.91	1.08	1.28	0.09	0	0
<i>Discoporella umbellata</i> var <i>conica</i> Canu & Bassler 1930	0.09	0.06	0.12	0.03	0	0
<i>Discoporella umbellata</i> var <i>depressa</i> De France 1823	0.06	0.09	0.03	0.03	0	0
<i>Discoporella buski</i> Harmer 1915	0.06	0.03	0.03	0.03	0	0
<i>Discoporella pila</i> Marcus 1955	0.03	0.03	0.09	0.03	0	0
<i>Electra bellula</i> Hincks 1881	0.18	0.26	0.34	0.03	0	0
<i>Electra pilosa</i> Linnaeus 1767	0.03	0.12	0.03	0.03	0	0
<i>Electra tenella</i> Hincks 1880	0.03	0.06	0.06	0	0	0
<i>Escharina parviseta</i> Canu & Bassler 1928	0.03	0.03	0.03	0	0	0
<i>Escharina pesanseri</i> Smitt 1873	0.03	0.06	0.06	0.06	0.03	0.03
<i>Escharina scopae</i> Canu & Bassler 1928	0.03	0.03	0.14	0	0	0
<i>Escharioides mariae</i> Marcus 1955	0	0.03	0.03	0	0	0
<i>Exechonella brasiliensis</i> Canu & Bassler 1928	0.26	0.38	0.59	0.4	0.09	0
<i>Exochella longirostris</i> Jullien 1888	0.12	0.2	0.12	0.06	0	0
<i>Gemelliporidra ornantissima</i> Canu & Bassler 1928	0.06	0	0	0.03	0	0
<i>Hippaliosina imperfecta</i> Canu & Bassler 1928	0.24	0.57	0.69	0.52	0.03	0.03
<i>Hippodiplosia otto-mulleriana</i> var <i>parva</i> Marcus 1938	0.03	0.06	0.03	0	0	0
<i>Hippodiplosia pertusa</i> Esper 1794	0.06	0	0	0.06	0	0
<i>Hippopodina feegeensis</i> Busk 1884	0.03	0.03	0.09	0.03	0	0
<i>Hippoporella gorgonensis</i> Hastings 1930	0.03	0.03	0.03	0	0	0
<i>Hippoporidra edax</i> Busk 1859	0.03	0	0	0	0	0
<i>Hippoporidra</i> sp. Canu & Bassler 1927	0	0.03	0	0	0	0
<i>Hippoporina americana</i> Verrill 1875	0.03	0.03	0	0	0	0
<i>Hippoporina cleidochasma</i> Smitt 1873	0	0.03	0.03	0	0	0
<i>Hippoporina porcellana</i> Busk 1860	0	0.03	0.03	0	0	0
<i>Hippothoa divaricata</i> Lamouroux 1821	0.03	0.03	0.03	0.03	0.06	0.06
<i>Hippothoa flagellum</i> Manzoni 1968	0.66	0.86	1.06	0.35	0.03	0.03
<i>Hippothoa hyalina</i> Linnaeus 1767	0.03	0.09	0.03	0	0	0
<i>Labioporella dipla</i> Marcus 1949	0.17	0.06	0.03	0	0	0
<i>Lepralia pulcherrima</i> Canu & Bassler 1928	0.15	0.03	0.03	0	0	0
<i>Mamillopora cupula</i> Smitt 1878	0.03	0.06	0.03	0	0	0
<i>Margaretta buskii</i> Harmer 1954	0.26	0.34	0.26	0.03	0.03	0.03
<i>Mecynoecia delicatula</i> Busk 1875	0.06	0.03	0.03	0	0	0
<i>Membranipora paulensis</i> Marcus 1937	0.03	0.03	0	0	0	0
<i>Membranipora savartii</i> Audouin 1826	0.03	0.03	0.09	0	0	0
<i>Membranipora serrata</i> Hincks 1882	0.03	0	0	0	0	0
<i>Membranipora tenuis</i> Desor 1848	0.03	0.06	0	0	0	0
<i>Membranipora tuberculata</i> Bosc 1802	0.03	0	0	0	0	0
<i>Membraniporella aragoi</i> Audouin 1826	0.03	0	0	0	0	0

## Appendix (continued)

Species	1995	1996	1997	1998	1999	2000
<i>Metrarabdotos tenue</i> Busk 1884	0.03	0.03	0	0	0	0
<i>Metrarabdotos tenue tenue</i> Busk 1884	0.03	0.03	0	0	0	0
<i>Metrarabdotos unguiculatum</i> Canu & Bassler 1928	0.06	0.03	0	0	0	0
<i>Metrarabdotos unguiculatum unguiculatum</i> Canu & Bassler 1928	0.12	0.18	0.11	0	0	0
<i>Micropora coreacea</i> Esper 1791	0.06	0.03	0	0	0	0
<i>Microporella ciliata var coronata</i> Audouin 1826	0.03	0.03	0	0	0	0
<i>Mimosella verticillata</i> Heller 1867	0.06	0.03	0	0	0	0
<i>Nellia oculata</i> Busk 1852	0.12	0.15	0.12	0.06	0.03	0.03
<i>Nevianipora rugosa</i> Osburn 1940	0.17	0.18	0.03	0	0	0
<i>Nolella dilatata</i> Hincks 1860	0	0	0	0	0.03	0
<i>Onychocella americana</i> Canu & Bassler 1928	0	0	0.03	0	0	0
<i>Palmicellaria skenei</i> Solander 1786	0	0	0	0	0.03	0
<i>Pasythea tulipifera</i> Ellis & Solander 1786	0	0	0.03	0	0	0
<i>Petraliella bisinuata</i> Smitt 1873	0.03	0	0	0	0	0.03
<i>Proboscina robusta</i> Canu & Bassler 1928	0	0	0	0	0	0.03
<i>Reptadeonella bipartita</i> Canu & Bassler 1928	0	0	0	0	0.03	0.03
<i>Reptadeonella costulata</i> Canu & Bassler 1928	0.03	0.03	0.03	0.06	0.03	0.03
<i>Reptadeonella heckeli</i> Canu & Bassler 1928	0.03	0.06	0	0	0	0
<i>Reptadeonella tubulifera</i> Canu & Bassler 1930	0.03	0	0	0	0	0.03
<i>Reptadeonella violacea</i> Johnston 1847	0.15	0.06	0.03	0.06	0	0.03
<i>Reteporellina denticulata</i> Busk 1844	0.03	0.09	0.03	0	0	0.03
<i>Rhyncozoom rostratum</i> Busk 1856	0.03	0.03	0.03	0.17	0	0
<i>Rhyncozoom arborescens</i> Canu & Bassler 1928	0	0.03	0.03	0	0	0
<i>Rhyncozoom phrynglossum</i> Marcus 1937	0.06	0.09	0.03	0.03	0	0.03
<i>Schizoporella carvalhoi</i> Marcus 1937	0.12	0.06	0.03	0	0	0.03
<i>Schizoporella horsti</i> Osburn 1927	0.03	0.03	0	0	0	0
<i>Schizoporella pungens</i> Canu & Bassler 1928	0	0	0	0	0	0.03
<i>Schizoporella trimorpha</i> Canu & Bassler 1928	0.03	0.03	0.09	0	0.03	0.03
<i>Schizoporella unicornis</i> Johnston 1847	0.21	0.23	0.2	0.03	0.03	0.09
<i>Scrupocellaria bertholletii</i> Audouin 1826	0.03	0.03	0.06	0.03	0	0.03
<i>Scrupocellaria cornigera</i> Audouin 1826	0.03	0.03	0.03	0.03	0.03	0.09
<i>Scrupocellaria drachi</i> Marcus 1855	0	0.03	0.17	0.09	0	0
<i>Scrupocellaria scrupea</i> Busk 1851	0.27	0.15	0.15	0.29	0.03	0.03
<i>Setosselina goesi</i> Silen 1942	0.03	0.03	0.12	0.03	0	0
<i>Siphonophorella granulosa</i> Canu & Bassler 1927	0	0	0.03	0	0	0
<i>Smittina areolata</i> Canu & Bassler 1927	0	0.15	0	0	0	0
<i>Smittina signata</i> Waters 1889	0.18	0.29	0.09	0.26	0	0
<i>Smittina trispinosa spathulata</i> Smitt 1873	0.03	0.03	0	0	0	0
<i>Smittipora acutirostris</i> Canu & Bassler 1928	0.06	0.03	0.03	0	0	0
<i>Smittipora tuberculata</i> Canu & Bassler 1928	0	0	0	0	0	0.03
<i>Steginoporella buskii</i> Harmer 1900	0.06	0.03	0.06	0.06	0.06	0.06
<i>Steginoporella connexa</i> Harmer 1900	0	0.03	0	0	0.03	0
<i>Steginoporella evelinae</i> Marcus 1949	0	0.03	0	0	0	0
<i>Steginoporella magnilabris</i> Busk 1854	0	0	0	0	0.15	0.2
<i>Steginoporella transversalis</i> Canu & Bassler 1928	0	0.11	0	0	0	0.06
<i>Stylopoma aurantiacum</i> Canu & Bassler 1928	0	0	0	0	0	0.09
<i>Stylopoma informata</i> Lonsdale 1845	0.03	0	0	0	0	0
<i>Synnotum aegyptiacum</i> Audouin 1826	0.03	0	0	0	0	0
<i>Terebripora fisheri</i> Jullien 1880	0	0	0.03	0	0	0
<i>Tremogasterina malleolus</i> Canu & Bassler 1928	0	0	0.03	0	0	0
<i>Tremogasterina mucronata</i> Smitt 1873	0.06	0	0	0	0	0
<i>Tremoschizodina lata</i> Smitt 1873	0	0.03	0	0	0	0



## Appendix (continued)

Species	1995	1996	1997	1998	1999	2000
<i>Trypostega venusta</i> Norman 1864	0.03	0.03	0	0	0	0
<i>Tubulipora brasiliensis</i> Buge 1979	0.06	0.26	0.06	0.06	0	0
<i>Tubulipora lunata</i> Marcus 1937	0.06	0.09	0.06	0	0	0
<i>Turbicellepora dichotoma</i> Hincks 1862	0	0.06	0	0.03	0.03	0
<i>Utinga castanea</i> Busk 1884	0.2	0.38	0.12	0.15	0.21	0.23
<i>Victorella sibogae</i> Harmer 1915	0	0	0	0.03	0.03	0.2
<i>Vitaticella contei</i> Audouin 1826	0	0	0.03	0.03	0.06	0.11
<i>Zoobotryon pellucidum</i> Ehrenberg 1831	0.03	0.03	0	0	0	0
Total density (m <sup>-2</sup> )	17.41	20.36	16.57	6.18	2.49	2.92
Total number of species	126	125	101	65	43	42

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