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Report 21

Benthic Community Structure and Sea Urchin Distribution

The Bay of Diego-Suarez

Mrowicki, R.J., & Fanning, E. (eds)

Frontier-Madagascar:
Institut Halieutique et des Sciences Marines (IH.SM)
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Frontier-Madagascar

Madagascar is renowned for its high biological diversity, characterised by a high abundance of endemic species. It is one of the poorest nations in the world and very dependent on the resources that its natural environment provides. As a result, conservation and development work is of paramount importance as efforts are made to preserve an environment under pressure from unsustainable exploitation. Frontier-Madagascar is in the process of undertaking baseline survey work in the coastal region of the Antsiranana province, at the northern tip of Madagascar, to contribute biological and resource utilisation data to the preparation of sustainable management initiatives for the area.

L'Institut Halieutique et des Sciences Marines (IH.SM)

L'Institut Halieutique et des Sciences Marines (IH.SM) is a department of the University of Toliara in southwest Madagascar. It is a centre of learning and research for the field of marine sciences and runs courses for both undergraduate and postgraduate students. IH.SM also provides consultations to government institutions, non-government organisations and individuals.

The Society for Environmental Exploration (SEE)

The Society for Environmental Exploitation (SEE) is a non-profit making company limited by guarantee and was formed in 1989. The objectives of The Society are to advance field research into environmental issues and implement practical projects contributing to the conservation of natural resources. Projects organised by The Society are joint initiatives developed in collaboration with national research agencies in co-operating countries.

Frontier-Madagascar Coastal Research Programme (FMCRP)

The SEE and IH.SM have been conducting collaborative research into environmental issues since 2000 under the banner of Frontier-Madagascar, of which one component is the Frontier-Madagascar Coastal Research Programme (FMCRP). Frontier-Madagascar conducts research into biological diversity and resource utilisation of both marine and terrestrial coastal environments. Since relocating to the Antsiranana region in April 2005, the FMCRP has begun working in collaboration with the University of Antsiranana in addition to IH.SM.

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EXECUTIVE SUMMARY

The Bay of Diego-Suarez, considered to be one of the finest and largest natural harbours in the world, is located towards the northernmost tip of Madagascar in the Antsiranana province. Despite its historical and current use as a port, much of its convoluted perimeter is still somewhat untouched, harbouring pristine shorelines and subtidal coral reefs. The position of the bay between other regions in which high marine biodiversity has already been revealed suggests that it may also harbour high biodiversity. However, the relatively long coastline and limited connectivity of the bay with the Indian Ocean, in combination with existing anthropogenic activities, potentially make its marine environments susceptible to a range of environmental impacts including sedimentation, nutrification and pollution.

The Frontier-Madagascar Marine Research Programme (FMMRP) became involved in conducting marine ecological survey work in the Bay of Diego-Suarez, north Madagascar, in April 2005, having relocated from its previous base at Anakao in southwest Madagascar. The rationale for the survey programme stemmed from the affiliation of the FMMRP with the Malagasy organisations Association Nationale pour la Gestion des Aires Protégées (ANGAP) and Service d'Appui a la Gestion de l'Environnement (SAGE), who were interested in identifying areas of the bay with particularly healthy coral reef systems. Additional environmental interest in the bay has arisen as a result of its proximity to surrounding terrestrial protected areas such as the newly managed Ramena complex, incorporating Orangea and Montagne des Français, and also Montagne d'Ambre.

Since its relocation to the Diego-Suarez area, the FMMRP has compiled over two years' worth of marine ecological data relating to benthic community composition, fish species abundance and population size structure, frequency of algae and invertebrate indicator species, and physical environmental parameters. Thus there exists an extensive dataset for the Bay of Diego-Suarez, from which details of the current condition of its marine habitats can be investigated and a baseline for temporal monitoring can be established.

The primary purpose of this report is to signify the initial detailed dissection of the dataset and demonstrate the conclusions that can be made regarding the ecological status of coral reef systems within the bay. This has mostly involved the examination of benthic data, focusing upon variations in percentage cover of substrata and coral community characteristics as useful structural indicators of reef condition. Additionally, the report includes an assessment of the abundance and distribution of sea urchins and their relation to benthic community patterns, as a demonstration of the ability to interrelate different aspect of the FMMRP dataset to enhance the conclusions that can be drawn.

Benthic community data were obtained from 380 line intercept transects conducted in different sectors of the Bay of Diego-Suarez between October 2005 and December 2007, representing a combined distance of 7,600 m. Sediment occupied the greatest overall proportion of the benthos (around 38%), especially in the western areas of the bay. Overall mean hard coral cover was around 15%, and tended to co-vary with other 'hard' substrata such as rock and rubble. In total, 38 scleractinian coral genera were recorded during survey work, in addition to a number of unidentified genera. The coral communities of the bay were dominated by *Acropora* and *Porites* spp., which comprised around 33% and 20% of total recorded hard coral cover, respectively.

Hard coral cover and generic diversity appeared to be positively related. These indicators were greatest in the northeast area opposite the mouth of the bay, reaching mean values of around 37% and 6.8 genera, respectively. Here, the hard coral community was dominated by *Acropora* spp. and comprised a relatively high proportional cover of *Galaxea* spp. In the northwest of the bay, coral cover was approximately half as great and consisted primarily of species belonging to the genera *Porites* and *Millepora*. Habitats in this area were highly similar in terms of their overall coral community composition. Hard coral cover and diversity were generally lower in the southern portion of the bay, especially in more immediate proximity to the population centre of Diego-Suarez (around 2% and 1.5-5.5 genera, respectively). Coral community composition was considerably more variable than in the northern portion of the bay.

After sediment and ‘hard’ substrata, seagrass formed the next major interplaying component of the benthic environment (around 10% overall proportional cover). The easternmost areas adjacent to the mouth of the bay were characterised by high seagrass cover, which reached around 48%. Little or no seagrass was encountered elsewhere, except at one locality in the northwest (around 13% cover). Macroalgae cover was low and less variable, reaching a maximum value of around 10% adjacent to Diego-Suarez. There were no differences between island and mainland sites in terms of overall benthic substratum characteristics, yet soft coral cover was significantly greater amongst island sectors.

Sea urchin abundance data were obtained from 498 belt transects conducted between April 2006 and December 2007, representing a total area of 49,800 m^2. A total of 6 species were recorded, of which *Diadema setosum* comprised by far the greatest relative abundance (96%) and observation frequency (55%). The greatest population densities of this species were encountered in the more exposed areas in the west and northwest, reaching around 1.5 m^{-2}, and very few individuals were recorded in the eastern reaches. Data suggest a possible seasonal increase in *D. setosum* densities, corresponding with an increase in water temperature towards the end of the year.

No significant correlation existed between *D. setosum* population density and coral cover, although these seemed to be inversely related in the central northern area of the bay. There was also no significant correlation with macroalgae cover. However, *D. setosum* density was positively and negatively associated with rubble and seagrass cover, respectively. There was a lack of a clear pattern amongst sectors with respect to overall benthic community characteristics, let alone between the density of *D. setosum* and benthic substratum composition.

In conclusion, a relatively detailed map of benthic community composition has been produced for the Bay of Diego-Suarez, which shall be useful in elucidating the primary factors determining the condition of marine environments within the bay and developing effective sustainable management strategies. Further analysis, incorporating additional components of the FMMRP dataset, is required in order to further clarify our understanding of the key issues surrounding the current status of these coral reef systems. It is hoped that continued survey work will enable important long-term ecological monitoring of the marine environment of the bay and assessment of the effectiveness of any management initiatives that may be implemented.

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1. INTRODUCTION

1.1 Bay of Diego-Suarez

Located towards the northernmost tip of Madagascar, the town of Diego-Suarez is the fifth largest in Madagascar, with a population of approximately 80,000 (URL 1). It is situated on a promontory jutting out into the Bay of Diego-Suarez, which is considered to be one of the finest natural harbours in the world (Figure 1). The bay has long been recognised as a port of importance. It was named after the Portuguese navigator Diego Suárez who arrived in 1543. Ever since this time, the bay was regarded as a desirable strategic base. In 1885, after the first Franco-Hova War, a treaty was signed by Queen Ranavalona III to give France a protectorate over the bay and surrounding area (URL 2).

During the Second World War, Diego-Suarez was a key point of invasion for Allied forces, and British naval forces wrested control of the bay from the Vichy French. However, France continued to use the town as a military base after the Malagasy independence in 1960 until the socialist revolution of 1973 (Pitcher and Wright, 2004; Bradt, 2005; URL 2). In recent times, its main industry has been ship construction and repair, in addition to the production of goods such as salt, chemicals and processed foods (URL 1), yet the remote location and inaccessibility of the town has made it relatively unimportant for freight traffic. Fishing is widespread across the bay, primarily at an artisanal subsistence level.

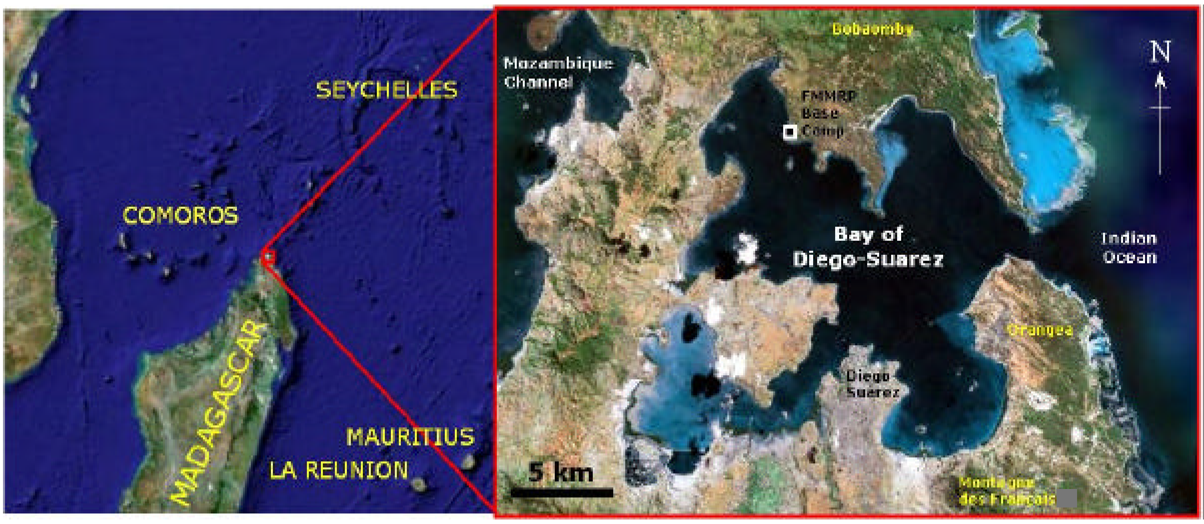

Figure 1. Map displaying the location and geographical features of the Bay of Diego-Suarez in northern Madagascar. Images obtained from Google Earth.

The Bay of Diego-Suarez is believed to have originated from a submerging coastline or drowned river valley, resulting in a convoluted coastline with many peninsulas that can be seen today (Figure 2). It opens to the east into the Indian Ocean via a deep-water channel running through a narrow inlet, which provides some shelter from the prevailing winds (URL 2; URL 3). The benthic topography of the bay is characterised by a deep central section with an average depth of approximately 40 m, which extends from the inlet to the north and west portions. The peripheral bays to the south and east exhibit shallower topographies ranging from 10 to 20 m (Frontier-Madagascar, 2007).

This region exhibits a strongly tropical climate, comprising pronounced seasonal fluctuations. The dry season, which normally extends from April to November each year, is accompanied by the strongest of the easterly winds originating in the Indian Ocean. The rainy summer months between November and April are characterised by short, localised storms producing rainfall of up to 350 mm per month, calmer prevailing winds and higher surface water temperatures, sometimes exceeding 30°C (pers. obs.), compared to a minimum of approximately 23°C in winter months (Frontier-Madagascar, 2007).

The large size of the Bay of Diego-Suarez relative to its seaward inlet means that water circulation and exchange with the open ocean is substantially reduced, making it susceptible to pollution and the effects of coastal sedimentation (Larcombe *et al.*, 1995) and freshwater input. The influence of terrestrially derived inputs, most notably those arising from a combination of anthropogenic land use practices and heavy summer rainfall, upon the marine ecosystems of the bay is further intensified by its long (~130 km) coastline and the protrusion into the bay of the population centre Diego-Suarez. Despite the historical use of the bay as a port and the aforementioned considerations, much of its perimeter is still somewhat untouched, harbouring pristine shorelines and undiscovered subtidal reefs. There is a great deal of interest in this region due to its proximity to terrestrial protected areas such as Montagne d'Ambre, Orangea and the newly managed Montagne des Français, in addition to the potentially high marine biodiversity in the area.

Figure 2. Panoramic view of the northwest area of the Bay of Diego-Suarez, overlooking Nosy Fano.

Studies conducted on the west coast of Madagascar have already highlighted high marine biodiversity (Ahamada *et al.*, 2002) despite there being a relatively high level of environmental impact resulting from anthropogenic activities in this area. Marine environments that are of similar nature and in close proximity but experiencing lower levels of anthropogenic impact would therefore be expected to harbour even greater biodiversity. Indeed, a rapid assessment of the Nosy Hara region to the west of Diego-Suarez in 2002 identified a greater number of endemic marine species in the northwest and, additionally, survey work undertaken within the Masoala region has revealed high biodiversity around the northeast coast (Frontier-Madagascar, 2007). The position of the Bay of Diego-Suarez between these areas suggests that it also potentially contains a large number of species. Also, its location makes it susceptible to influxes of dispersing species from mainland Africa and the wider Indian Ocean via the Southern Equatorial Current (URL 4).

1.2 Frontier-Madagascar Marine Research Programme (FMMRP)

As a result of both potentially high marine biodiversity and a steadily growing regional tourism industry, supported by a recently improved infrastructure, there is great incentive for the implementation of conservation work and associated funding within the Bay of Diego-Suarez. The reef systems of the bay face a number of threats, including terrestrial sedimentation and nutrient input, pollution from anthropogenic sources, overfishing and direct physical damage from boat-based activities. On top of these factors, there are potential climatic threats such as elevated water temperatures, which can act to trigger coral bleaching (Glynn, 1996), and storm damage. There appears to be the need for the development of an integrated strategy for the sustainable management of the resources of the bay and for the mitigation of the aforementioned negative environmental impacts. An important first step in this process is to gather substantial information regarding the condition of the marine habitats under consideration.

The Frontier-Madagascar Marine Research Programme (FMMRP) became involved in conducting marine ecological survey work in the Bay of Diego-Suarez in April 2005, creating a coastal research base located in the northwest region of the bay (S12°10.450, E049°13.800; see Figure 1), having relocated from its previous base at Anakao in southwest Madagascar. The rationale for the original survey programme stemmed directly from the affiliation of the FMMRP with the Malagasy non-governmental organisations Association Nationale pour la Gestion des Aires Protégées (ANGAP) and Service d'Appui à la Gestion de l'Environnement (SAGE), who were mainly interested in identifying areas of the bay with particularly healthy coral reef systems. In addition to assisting with scientific research, the primary objectives of the FMMRP were to build capacity for conservation within the local community and to contribute directly to regional conservation (Frontier-Madagascar, 2007).

During the first year of operation in the Bay of Diego-Suarez, the focus of the programme was on the completion of a baseline ecological assessment of the marine habitats in the bay. The initial analysis of the resulting data enabled the investigation of biological, physical and chemical features and the production of broad marine habitat maps of the bay. Subsequent collection of comparable data using refined methodology has allowed, and will continue to allow, long-term temporal ecological monitoring of marine ecosystems within the bay, in addition to the ongoing expansion of an already large ecological database that will prove highly useful for the detailed investigation of various aspects of the marine ecological environment. Furthermore, the diversification of the research programme to include additional themes, such as seagrass and mangrove surveys, and the inclusion of socio-economic studies and community work (Frontier-Madagascar, 2007) has helped even more to establish the FMMRP as a potential authority in the development of sustainable management recommendations for the Bay of Diego-Suarez.

1.3 Coral Reef Health and Sea Urchin Abundance

It is important to establish regional patterns of coral reef condition in order to determine the extent and severity of decline and to develop hypotheses about the causes of decline. Reef health involves the response of structural and functional components of the ecosystem (Kramer, 2003) and thus can be characterised by using a selection of indicators related to these components. A key factor for determining the long-term integrity of reef ecosystems is the condition of the principal corals that contribute to the structure of the coral reef framework (Done, 1997). This includes aspects such as coral cover, colony size, species composition, mortality and recruitment. Marine macroalgal abundance and species composition are also crucial facets of coral reef condition, especially when considered in relation to the delicate balance between the levels of live coral and algae within reef ecosystems (Done, 1992).

Since its relocation to the Diego-Suarez region, the FMMRP has compiled over two years' worth of ecological data, which can provide us with a detailed description of the condition of marine habitats within the bay. This information may be fed into future sustainable management recommendations and also forms a baseline for the assessment of long-term changes in the condition of reef ecosystems in the bay. The primary purpose of this report is to signify the initial dissection of the dataset and to demonstrate the conclusions that can be drawn from it regarding the ecological status of coral reefs in the Bay of Diego-Suarez. The first part of this shall involve the examination of benthic data, which includes useful structural indicators of reef condition, to investigate patterns in benthic composition within the bay.

Reef health is not merely dependent on the condition of corals in a particular ecosystem, but is a product of interaction between ecosystem components including corals, algae and predatory or grazing fish, invertebrates and other fauna. Herbivorous fishes and sea urchins have particular influences upon the balance between macroalgae and corals, and changes in the populations of these regulatory organisms can have dramatic impacts upon coral reef structure and composition (Roberts, 1995). It has already been shown that high population densities of sea urchins belonging to the genus *Diadema* can alter reef conditions in a top-down manner by decreasing algal biomass and species diversity (e.g. Sammarco, 1982; Levitan, 1988; Aronson and Precht, 2000). They are also known to prey upon living coral surfaces, with *Acropora* spp. being the most heavily attacked (Bak and Van Eys, 1975).

The sea urchin species *Diadema setosum* is often abundant on shallow Indian Ocean reefs, having diverged first from the other extant members of the genus (Lessios *et al.*, 2001). Within the Bay of Diego-Suarez, *D. setosum* constitutes the vast majority of sea urchin biomass and exhibits characteristically high population densities in various parts of the bay (pers. obs.; Figure 3). It seems likely that this species is having a considerable impact upon the condition of reefs in the bay via grazing of macroalgae, competition with other herbivores, predation of corals and bioerosion of coral skeletons.

Another aim of this report is to utilise data collected by the FMMRP to investigate the abundance and distribution of sea urchins within the Bay of Diego-Suarez and relate these aspects to the findings relating to the variation of benthic composition around the bay. This shall enable useful conclusions to be made about the nature of the impact of herbivorous sea urchins upon the reef communities in the bay. Additionally, it shall contribute further to the preliminary dissection of the two-year ecological dataset and the demonstration of the general ability to interrelate different aspects to explain the condition of the marine ecosystems of the region.

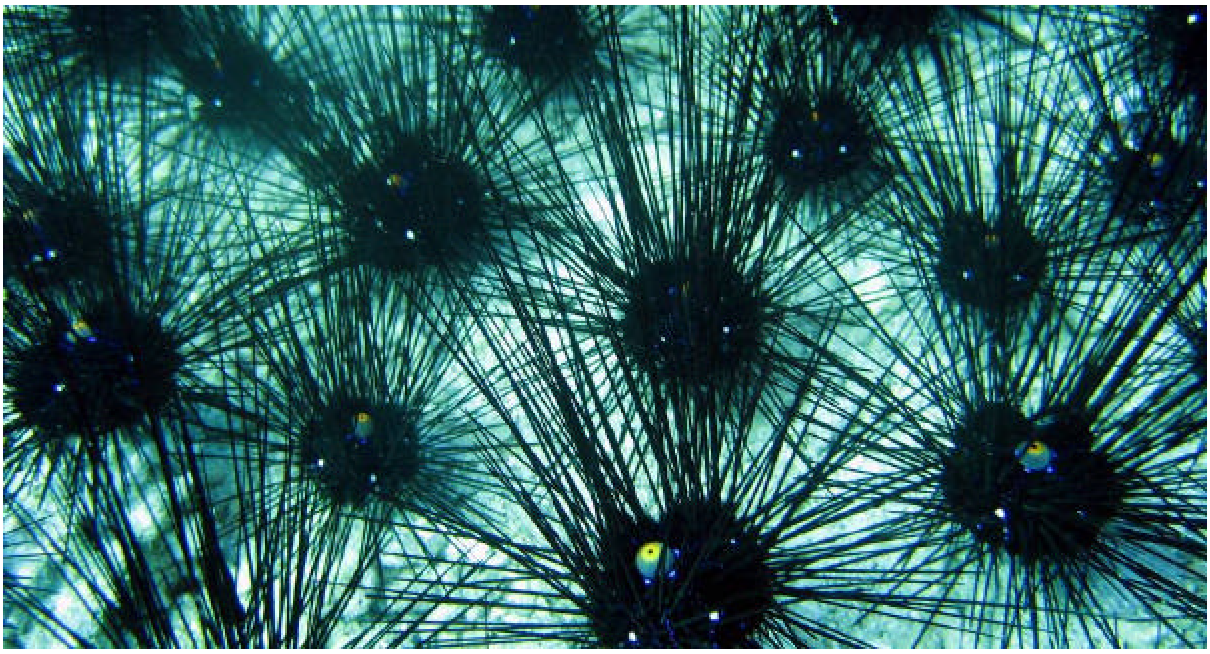

Figure 3. A high population density of sea urchins (*Diadema setosum*) at a shallow site dominated by coral rubble at Nosy Boka in the Bay of Diego-Suarez.

1.4 Study Aims and Objectives

Thus, as stated previously, the key aims of this study are as follows:

- To investigate spatial patterns in benthic community structure and, in particular, hard coral community composition, within the Bay of Diego-Suarez;
- To examine the abundance and spatial distribution of sea urchins within the bay, and relate these aspects to observed patterns in benthic community structure.

These aims are to be achieved by utilising the marine ecological dataset collected by the FMMRP over the past two years, specifically those components regarding the proportional cover of different benthic substratum categories and coral genera at different survey sites and the corresponding abundance of invertebrate species.

The main desired outcomes of this study are twofold:

- The production of an initial picture of the ecological condition of marine habitats in different areas of the Bay of Diego-Suarez, to be used as a baseline for temporal monitoring and input into integrated sustainable management plans;
- The demonstration of the ability to utilise the extensive FMMRP dataset and interrelate its different components in order to draw useful conclusions regarding the marine habitats of the bay.

2. MATERIALS AND METHODS

2.1 Overview

The primary method utilised by the FMMRP to survey and monitor subtidal marine biodiversity was a compilation of a number of well-known survey techniques into one standardised procedure, the Baseline Survey Protocol (BSP). This technique, developed in 2005 to be undertaken by trained volunteers working with the FMMRP, aimed to provide data on the basic benthic coverage, fish species abundance and population size structure, frequency of algae and invertebrate indicator species and an account of the physical and environmental conditions of the site, thus allowing all aspects of the marine environment to be directly related to each other at known locations. Subsequently, the large biological database formed via the continued implementation of the BSP technique may be used to provide potential explanations for the status of coral reef health within the Bay of Diego-Suarez.

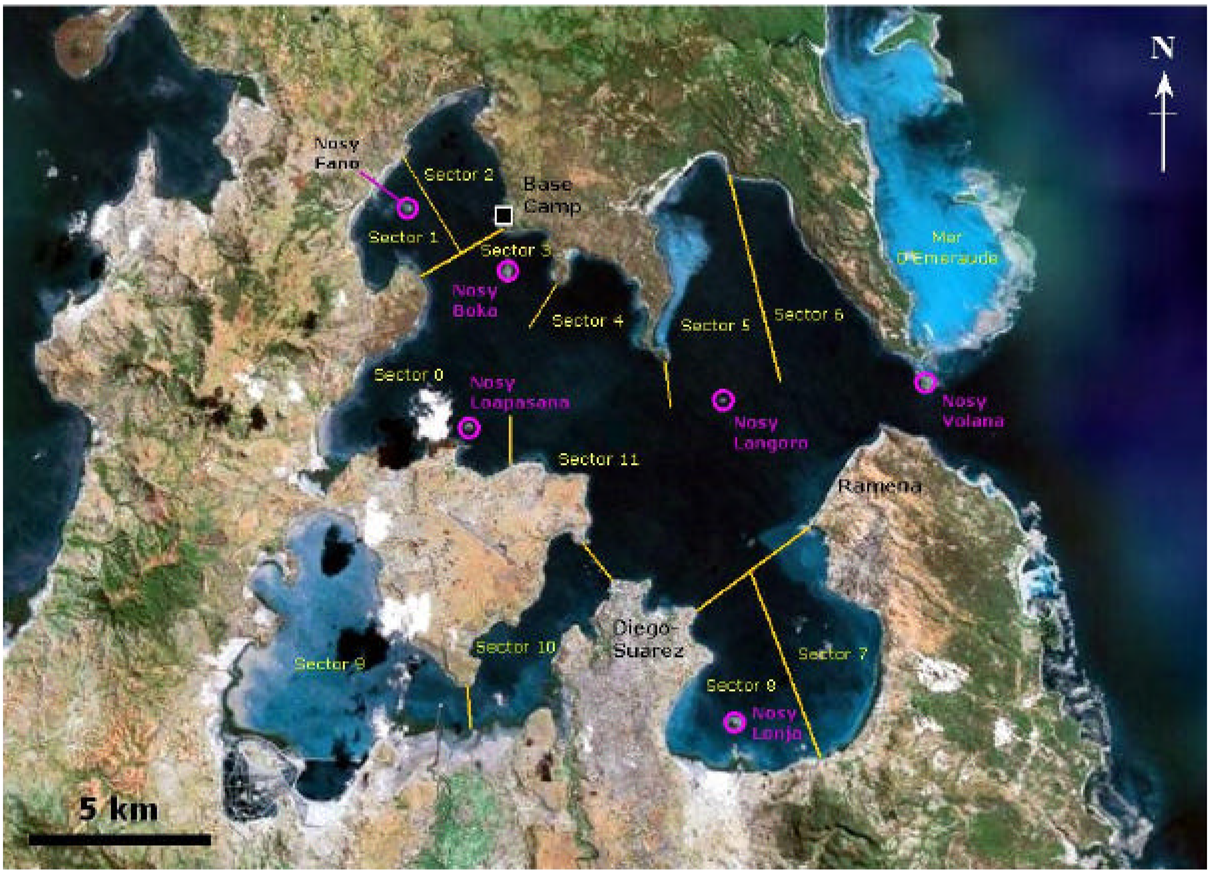

Figure 4. Satellite image of the Bay of Diego-Suarez displaying key locations relevant to the Frontier Madagascar Marine Research Programme (FMMRP) and the sectors within which survey work was undertaken. Yellow = mainland sectors; purple = island sectors. Image obtained from Google Earth.

As shown in Figure 4, the mainland coast of the bay was divided into 13 arbitrary sectors, including the region adjacent to Ramena. The division of the area in this way was designed to reflect potential differences in conditions and characteristics amongst the smaller sub-bays within the Bay of Diego-Suarez itself and allow the according stratification of sampling. The bay contains 6 major islands, 5 of which were designated island survey sectors, with the notable exception of Nosy Lonja located in sector 8. This island is regarded in local culture as a highly sacred site and so was inaccessible.

Designated survey sites were located around the coastline of the bay in water 15 m or shallower and were distributed evenly within sectors. In the case of island sectors, survey sites were distributed around the circumference of the island, again in water 15 m or shallower. The sites represent a wide spectrum of situations with respect to environmental conditions, disturbance levels and extent of anthropogenic impact.

The BSP survey was designed as a four-person technique to be conducted at a variety of depths (less than 15 m) using either SCUBA or snorkel equipment as appropriate. As hinted at previously, the surveys incorporated four aspects, namely physical attributes, fish species size and abundance, algae and invertebrate species frequency and, finally, benthic substrate composition. Each of the four aspects was examined by a separate surveyor within the underwater survey team and on each occasion all personnel entered the water and began actively surveying at the same time. For the purposes of this report, data concerning only invertebrate species frequency and benthic composition were investigated, and the methodological procedures for these two aspects are considered in turn below.

2.2 Benthic Composition Surveys

Benthic compositional data were collected using a line intercept transect (LIT) technique along two 20-m transects per site. To conduct such a survey at a particular site, a weighted 50-m tape measure was laid underwater so that it followed a depth contour and was parallel to the shore. Along the tape measure were designated two zones, namely *a*, from 0-20 m, and *b*, from 25-45 m. These two zones were treated as two independent transects, thus creating two replicates for each survey carried out.

Table 1. Categories of substratum and their codes used in the collection and processing of baseline benthic composition data from subtidal line intercept transect (LIT) surveys conducted in the Bay of Diego-Suarez.

Substratum	Code	Comments
Hard coral	HC	Including *Millepora* spp.
Soft coral	SC	
Recently killed coral	RKC	Dead hard coral retaining structural integrity
Macroalgae	AG	
Seagrass	SG	
Rock	RK	Diameter ≥ 15 cm, including dead hard coral
Rubble	RB	0.5 cm ≤ diameter < 15 cm, including dead hard coral
Sediment	SD	Including sand and silt
Other	OT	Including sponges

For each transect, the surveyor swam along the tape measure and examined the substrata directly underlying the tape. Substrata were classified into pre-designated categories, explained in Table 1. At each point along the transect that there was a transition from one substratum category into another, the distance on the tape measure at which this occurred was recorded to the nearest centimetre. Thus the resulting data could be used to calculate the total 'length' occupied by each substratum category on a transect and so obtain a value for the percentage cover of different substrata. In the case of hard coral, the genus of coral was also recorded in order to obtain information about the coral community composition at each site.

Any surveys for which benthic composition was entirely sediment were not included in the subsequent analysis. While it is important to sample randomly, it is also important that collected data impart information about marine fauna and flora. The substratum across the majority of the Bay of Diego-Suarez consists of sediment and these areas reveal very little about reef ecosystems, which the BSP methodology is specifically tailored for.

2.3 Sea Urchin Density Surveys

Invertebrate abundance data were gathered using a belt transect technique incorporating two 20×5 m areas per site. The transects utilised were the same as for the sea urchin density surveys so that, again, two replicate datasets were obtained per survey. The invertebrate surveyor carefully examined the substrate 2.5 m to either side of the tape measure in each of the two zones in a methodical way and recorded the presence and abundance of any invertebrates that were found within these areas. In the case of sea urchins, individuals were identified to genus level only and then tallied in order to obtain abundance and, subsequently, population density values. The surveyor was trained to identify six sea urchin genera, encompassing the most common species within the Bay of Diego-Suarez (see Figure 5).

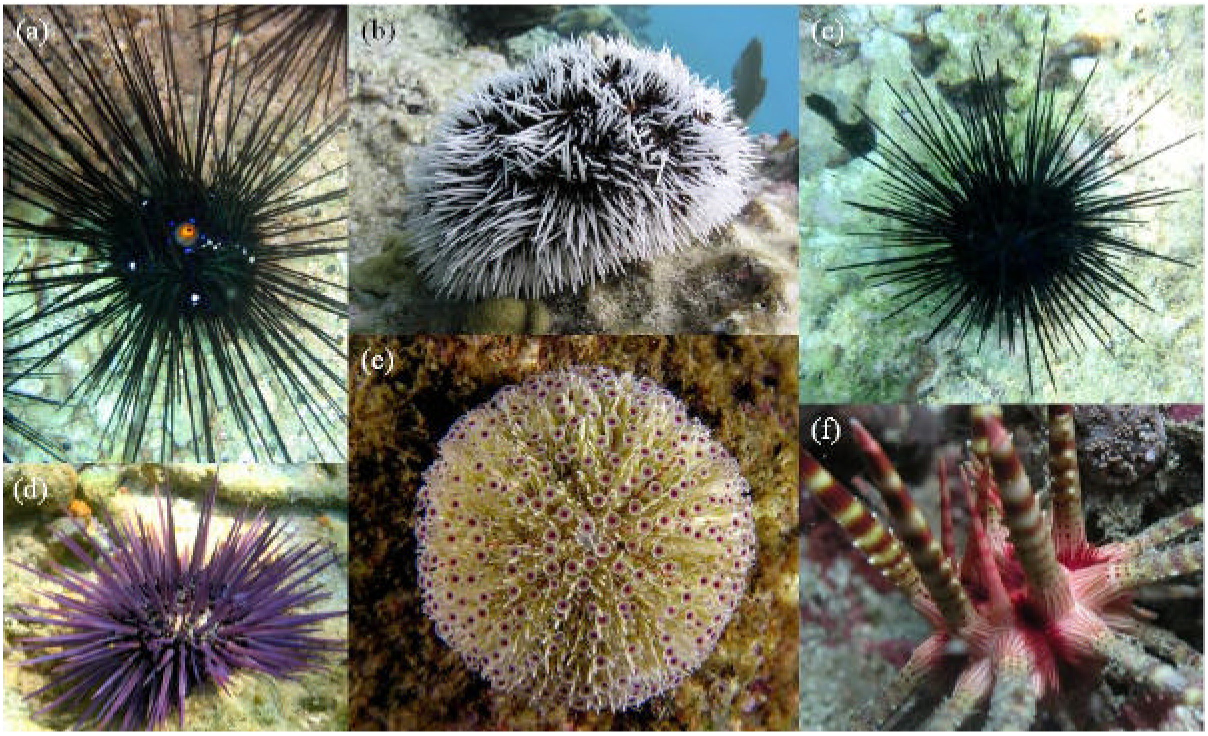

Figure 5. Representatives of sea urchin genera identified and recorded during subtidal invertebrate surveys conducted between April 2006 and December 2007. (a) *Diadema* sp.; (b) *Tripneustes* sp. (www.inkbox.net); (c) *Echinothrix* sp. (www.reef-guardian.com); (d) *Echinometra* sp.; (e) *Toxopneustes* sp. (www.scuba-equipment-usa.com); (f) *Eucidaris* sp. (www.starfish.ch).

2.4 Data Entry and Analysis

Recorded data were entered into Microsoft Excel 2000 electronic worksheets, with separate sheets used for benthic and invertebrate data. Benthic data were organised into columns for bay sector, survey site, transect number, benthic substratum category, coral species (if applicable) and length occupied upon transect. Sea urchin data were represented by columns for bay sector, survey site, transect number, sea urchin species and abundance.

Datasets were extracted and input into the Minitab Release 14 statistical software package in order to obtain descriptive statistics and to carry out univariate statistical tests. Mean values and corresponding standard errors of variables calculated for particular sectors have been based upon the number of 20-m transects conducted within those sectors. Where statistical tests were performed, datasets were initially assessed for their suitability for parametric analysis of variance (ANOVA) to ensure that they met the criteria of normality of error and equality of variance. This was achieved by conducting Anderson-Darling normality tests and equal variance tests, respectively. In cases where data did not exhibit normality of error and the situation could not be rectified by applying a square root, logarithm or inverse transformation, a non-parametric Kruskal-Wallis test was performed. If the criterion of equality of variance could not be met, despite attempts at resolution via transformation, a non-parametric Mood's Median test was implemented.

Multivariate statistical analyses of benthic community data were performed using the PRIMER v.6 statistical software package, using transformations appropriate to the type of data. The MapInfo Professional 6.0 geographical information systems (GIS) package was used to produce summary maps displaying data in a more accessible manner. Summary data were input via a Microsoft Excel 2000 worksheet and georeferenced according to sector location.

3. RESULTS

3.1 Benthic Community Structure

3.1.1 Sampling Effort

A total of 380 line intercept transect (LIT) surveys conducted between October 2005 and December 2007, representing a combined distance of 7,600 m, contributed to the analysis of the variation of subtidal benthic characteristics within the Bay of Diego-Suarez. Table 2 shows the number of surveys undertaken according to both sector and annual quarter. The number of surveys carried out varied widely amongst sectors, ranging from a mere two for sector 9 to a maximum of 56 for sector 5. This was also true amongst quarters, with the number of surveys ranging from 14 for July-September 2007 to 97 for October-December 2005. Only sectors 0, 2 and 3 are represented in the dataset for all quarters, whereas, for example, sectors 7, 8, 9, 10, R, NL and NV were surveyed in only three or fewer quarters throughout the entire time period.

Table 2. The number of 20-m subtidal line intercept transect (LIT) surveys undertaken in different annual quarters from October 2005 to December 2007 in different sectors of the Bay of Diego-Suarez, from which benthic composition baseline data was obtained. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana.

Quarter	Sector																		Total
	0	1	2	3	4	5	6	7	8	9	10	11	R	NB	NF	NL	NLS	NV	
054	7	6	12	6	14	12	0	13	15	0	0	0	3	1	6	0	1	1	*97*
061	9	4	5	5	9	11	15	1	3	0	0	0	0	0	0	0	0	0	*62*
062	2	0	4	2	3	0	0	0	0	2	3	0	2	0	3	0	3	0	*24*
063	4	5	3	2	3	11	0	0	0	0	0	5	0	1	3	1	1	0	*39*
064	3	8	8	5	10	7	2	0	1	0	1	1	3	3	0	0	2	0	*54*
071	8	4	2	5	0	7	1	0	0	0	0	1	0	0	0	2	0	0	*30*
072	6	4	4	2	7	3	4	0	0	0	0	1	0	3	2	0	1	4	*41*
073	1	0	1	3	2	2	0	0	0	0	0	0	0	2	0	1	2	0	*14*
074	1	0	3	4	2	3	0	0	0	0	0	1	0	2	2	0	1	0	*19*
Total	*41*	*31*	*42*	*34*	*50*	*56*	*22*	*14*	*19*	*2*	*4*	*9*	*8*	*12*	*16*	*4*	*11*	*5*	*380*

3.1.2 General Benthic Community Structure

Figure 6 displays the mean proportional cover of different benthic substratum types for all surveyed sectors around the bay. In most cases, sediment comprised the greatest proportion of the seabed (overall mean 37.72 ± 1.73%, ± SE), which was especially the case in the sheltered southwest (> 83%) and, to a lesser extent, northwest portions of the bay. Percentage cover of sediment correlated negatively with that of all other benthic substratum categories (Pearson correlation p-values ≤ 0.001), with the sole exception of 'Other'.

Overall mean hard coral cover was 15.49 ± 0.92% and was at its greatest in the mainland sector 5 and the island sectors NL and NV close to the eastern mouth of the bay. There were significant positive correlations between hard coral cover and that of the other 'hard' substrata, specifically recently killed coral ($R = 0.180$, $p < 0.001$) and rock ($R = 0.172$, $p = 0.001$). Additionally, hard and soft coral cover correlated positively ($R = 0.102$, $p = 0.047$).

Another aspect of the benthos that showed a pattern was the percentage cover of seagrass, which had an overall mean percentage of 10.16 ± 1.22%. The highest proportion of seagrass was encountered in the sheltered and semi-sheltered eastern areas of the bay (Figure 6), reaching above 42% in sectors 6 and R. Proportional seagrass cover correlated negatively with the 'hard' substratum types of hard coral ($R = -0.306$, $p < 0.001$), recently killed coral ($R = -0.140$, $p = 0.006$) and rock ($R = -0.204$, $p < 0.001$), in addition to the 'soft' substratum category of sediment ($R = -0.169$, $p = 0.001$). Thus, it appears that within the bay of Diego-Suarez, there is a general inverse relationship and interplay between three main types of substratum, namely 'soft' sediment, 'hard' substrates such as coral, recently killed coral and rock, and finally, seagrass.

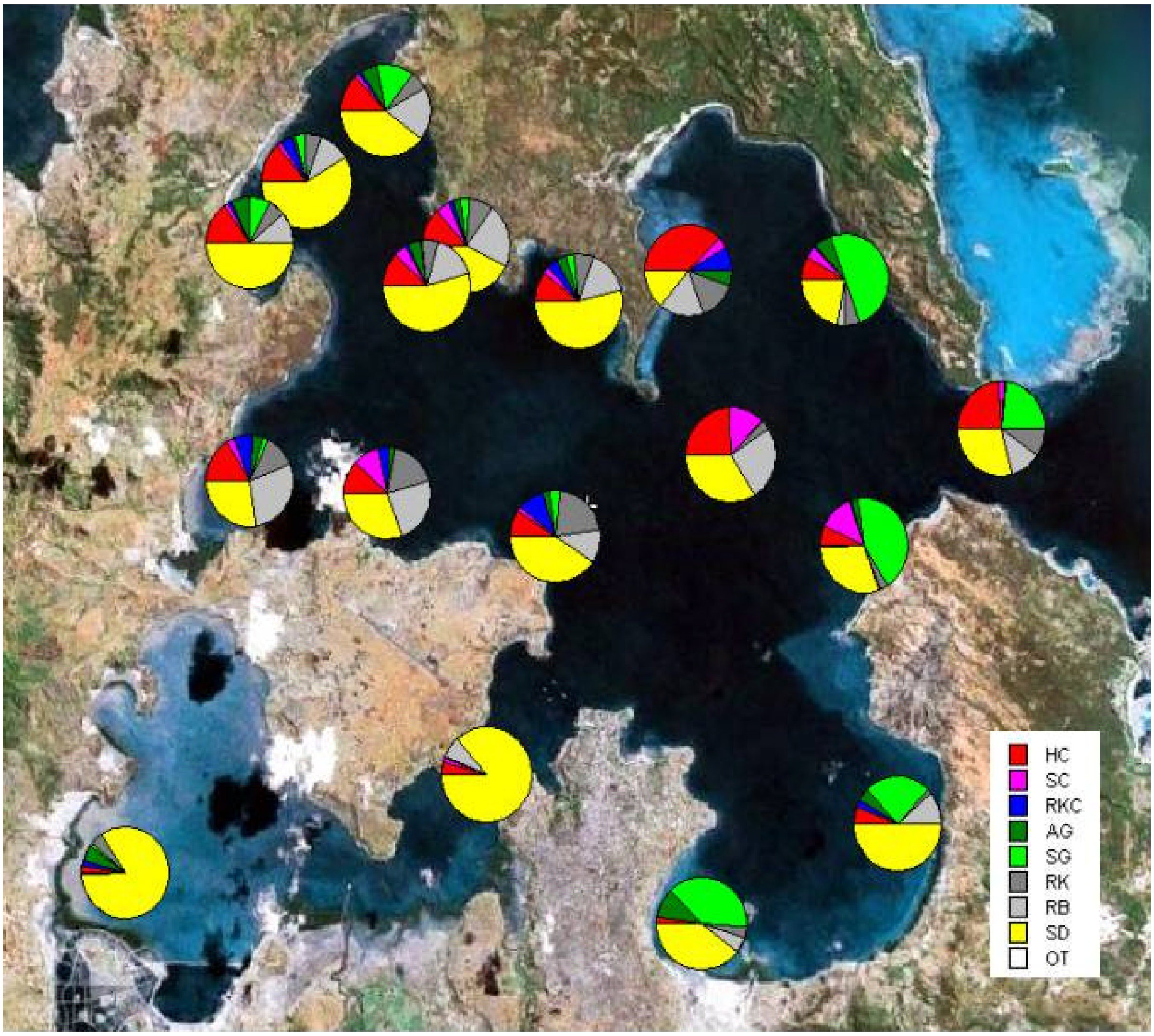

Figure 6. Thematic map of the Bay of Diego-Suarez displaying the mean proportional cover of different benthic substratum types in different sectors, as ascertained from 20-m subtidal line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. Benthic substrata codes are explained in Table 1.

The mean percentage cover values for hard coral and soft coral within each sector are shown in Figure 7. As mentioned previously, the highest level of hard coral cover was found in sector 5 (37.73 ± 2.63%, ± SE); in fact, it was significantly greater in this sector than in any other mainland sector (Mood's Median ?$^{2}_{17}$ = 76.29, $p < 0.001$). The island sectors NL and NV also exhibited relatively high hard coral cover (24.76 ± 4.44% and 23.68 ± 6.71, respectively).

In the case of mainland sectors in the northern half of the bay, there seemed to be a decline in percentage cover of hard coral from the westernmost sector 0 (16.09 ± 2.52%) to the easternmost sector 6 (7.59 ± 2.38%), with the obvious exception of sector 5. The opposite appeared to be true for the island sectors, where hard coral cover was elevated on the islands close to the mouth of the bay compared to those situated further west, such as sector NLS (11.92 ± 3.98%).

Hard coral cover was considerably lower in the southern half of the bay closer to the population centre of Diego-Suarez, with lowest values encountered in sectors 8 and 9 (2.26 ± 2.10% and 1.82 ± 1.44%, respectively). Adjacent to the second main town on the shore of the bay, Ramena, hard coral cover was also relatively low (6.75 ± 5.24%).

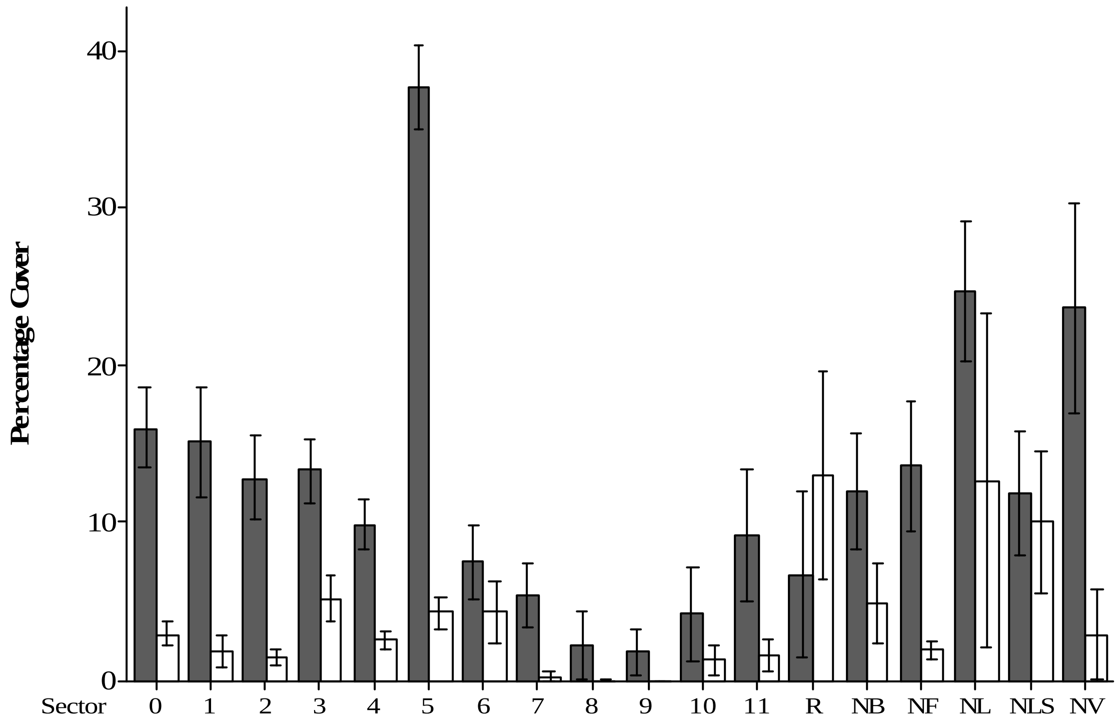

Figure 7. The mean percentage cover of hard coral (■) and soft coral (□) within different sectors of the Bay of Diego-Suarez as ascertained from subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. Error bars represent one standard error from the mean.

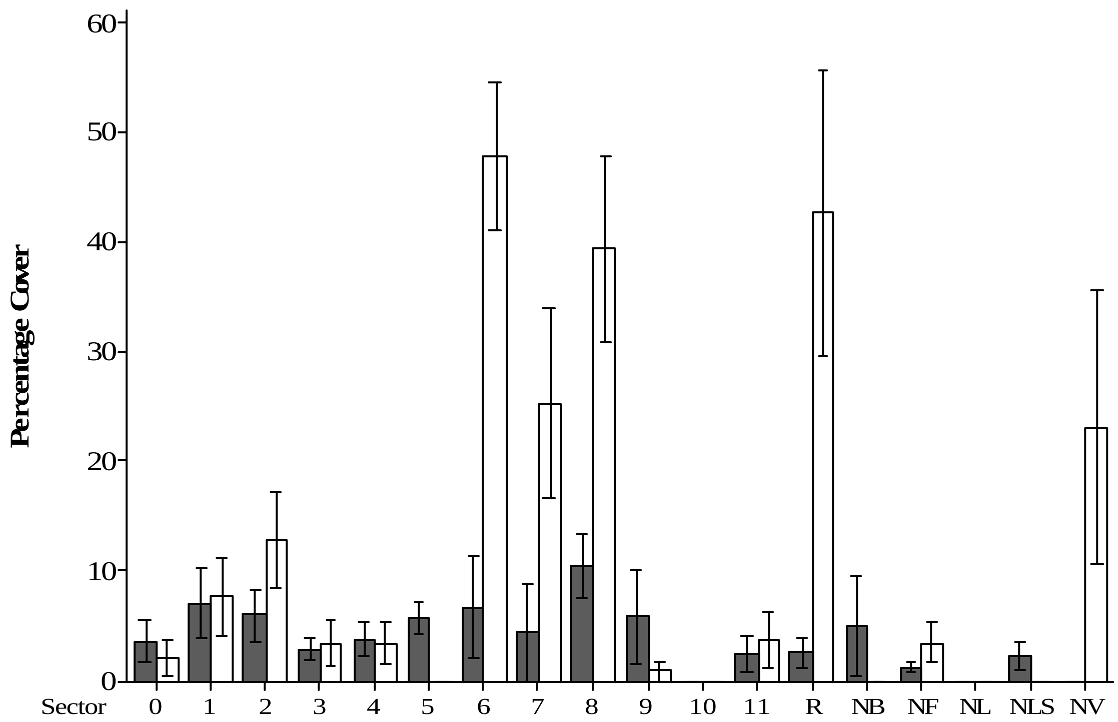

Figure 8. The mean percentage cover of macroalgae (■) and seagrass (□) within different sectors of the Bay of Diego-Suarez as ascertained from subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. Error bars represent one standard error from the mean.

Proportional cover of soft coral was less than that of hard coral in all sectors, with the exception of sector R which displayed the greatest soft coral cover in the bay (13.05 ± 6.53%, ± SE). Notably high soft coral cover was also found at the island sectors NL and NLS (12.80 ± 10.60% and 10.05 ± 4.49%, respectively). There was less of a clear pattern in the variation of this substratum type than that of hard coral, yet the lowest proportional cover of soft coral was recorded in sectors 7 and 8 in the southern portion of the bay around Diego-Suarez (0.28 ± 0.28% and 0.05 ± 0.05%, respectively). No soft coral was encountered in sector 9 in the southwest region.

Patterns in the percentage cover of other benthic substratum categories within the Bay of Diego-Suarez were also examined. Figure 8 shows the mean percentage cover of macroalgae and seagrass for different sectors of the bay. Macroalgae cover was highest in the relatively sheltered sector 8, adjacent to Diego-Suarez (10.48 ± 2.98%, ± SE), whilst no macroalgae was recorded in sector 10, adjacent to the other side of the Diego-Suarez peninsula. In the northern half of the bay, moderately high cover was exhibited by sectors 1 and 2 (7.06 ± 3.12% and 6.00 ± 2.39%, respectively) and 5 and 6 (5.74 ± 1.46% and 6.73 ± 4.64%, respectively). The lowest recorded proportional cover of macroalgae was encountered at sector NF (1.18 ± 0.49%), and no macroalgae was recorded at either of the two exposed island sectors NL or NV.

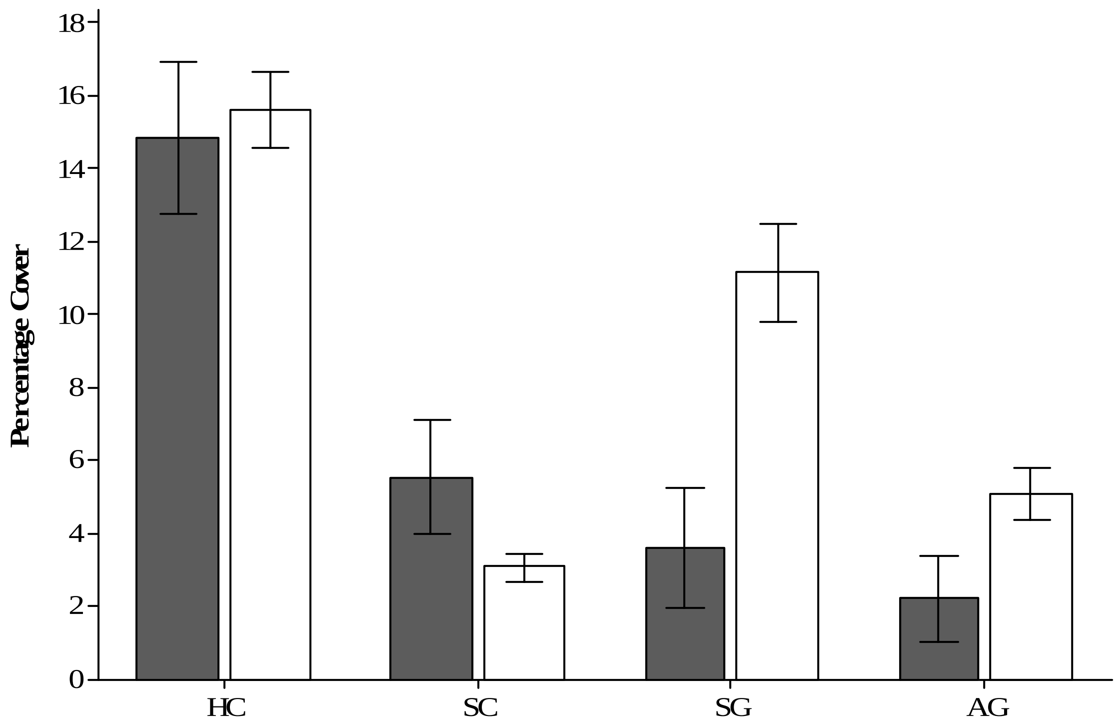

Figure 9. The mean percentage cover of hard coral (HC), soft coral (SC), seagrass (SG) and macroalgae (AG) at island (■) and mainland (□) coastal sites in the Bay of Diego-Suarez as ascertained from subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. Error bars represent one standard error from the mean.

The mean percentage cover of seagrass varied widely throughout the bay. As mentioned previously, the highest levels of cover were to be found in the far east of the bay, most notably in sectors R (42.60 ± 13.00%, ± SE) and 6 (47.92 ± 6.83%), where seagrass cover was significantly greater than that in all other mainland sectors except 7 and 8 (Mood's Median $?^{2}_{17}$ = 122.91, $p < 0.001$). High percentage cover of seagrass was also encountered in the sheltered mainland sectors 7 and 8 (25.29 ± 8.61% and 39.39 ± 8.48%, respectively) and the easternmost island sector NV (23.20 ± 12.50%). At these sites, seagrass was by far the dominant form of marine vegetation.

There was no seagrass recorded in sectors 5, 10 or NL, and exceptionally low cover was found in sector 9 (0.88 ± 0.88%), where macroalgae prevailed as the dominant form of vegetation. The cover of macroalgae was also greater than that of seagrass in sector 0 (3.52 ± 1.89% and 2.17 ± 1.60%, respectively). Throughout the rest of the northern portion of the bay, seagrass cover was low, but seemed to peak in sector 2 in the northwest (12.95 ± 4.40%).

Figure 9 compares the mean percentage cover of hard coral, soft coral, seagrass and macroalgae for mainland and island sectors. There was no significant difference between hard coral cover recorded in island sectors and that recorded in mainland sectors (Kruskal-Wallis H_{adj} = 0.51, p = 0.473). On average, seagrass cover was found to be higher for mainland sectors than for island sectors (11.11 ± 1.36% and 3.59 ± 1.65%, ± SE, respectively), yet this difference was not significant for square root transformed data (Kruskal-Wallis H_{adj} = 1.87, p = 0.172). Macroalgae cover was also greater in mainland sectors (5.08 ± 0.72%) than island sectors (2.21 ± 1.17%) but again this did not present a significant difference (Kruskal-Wallis H_{adj} = 3.66, p = 0.056).

A multivariate analysis of similarities (ANOSIM) randomisation procedure showed no significant difference between island and mainland sectors in terms of their overall benthic substratum characteristics (Global R = -0.033, p = 0.590). However, there was a significant difference between the two groups of sectors in terms of square root transformed percentage soft coral cover (Kruskal-Wallis H_{adj} = 7.59, p = 0.006), with island sectors (5.56 ± 1.54%) exhibiting a greater mean cover than mainland sectors (3.07 ± 0.36%).

3.1.3 Hard Coral Community Structure

A total of 38 hard coral genera were identified and recorded in the Bay of Diego-Suarez on the benthic LIT surveys, in addition to a number of other unidentified or novel genera. These are given in Appendix I, along with the total recorded length occupied by each genus across all transect surveys undertaken. The overall proportions of the total hard coral cover constituted by the 15 most common genera across the bay as a whole are shown in Figure 10.

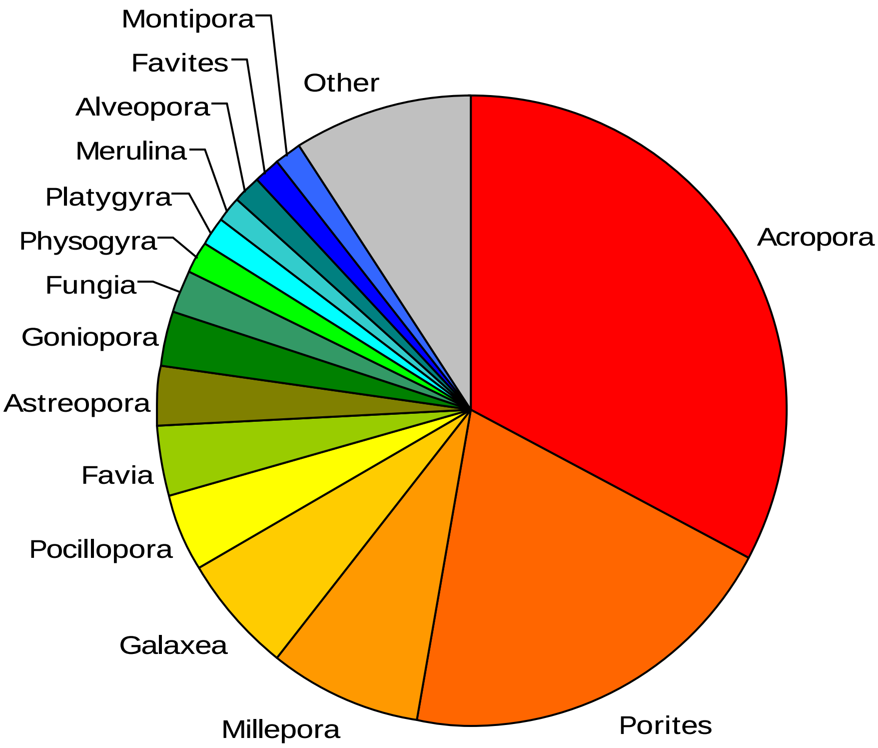

Figure 10. The overall proportions occupied by different hard coral genera of the total length of hard coral recorded across 380 subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007 within the Bay of Diego-Suarez. The "Other" category incorporates genera (n = 23) that each comprise less than 1.5% of the total recorded length of hard coral.

There were two scleractinian genera that dominated the coral communities of the bay, namely *Acropora* and *Porites*, which made up 32.85% and 19.97% of the total recorded hard coral cover, respectively. Species of the former create predominantly branching colonies, whereas those of the latter were primarily seen as massive or submassive colonies. The hydroid genus *Millepora*, recorded as a hard coral due to its reef building capacity, was the next most common, occupying 7.82% of coral cover. The next three most abundant genera were *Galaxea*, *Pocillopora* and *Favia*, constituting 6.08%, 3.84% and 3.72%, respectively. Only 1.60% of coral cover was composed of unidentified genera. The relative abundances of coral genera across the bay as a whole did not seem to be related to colony growth forms.

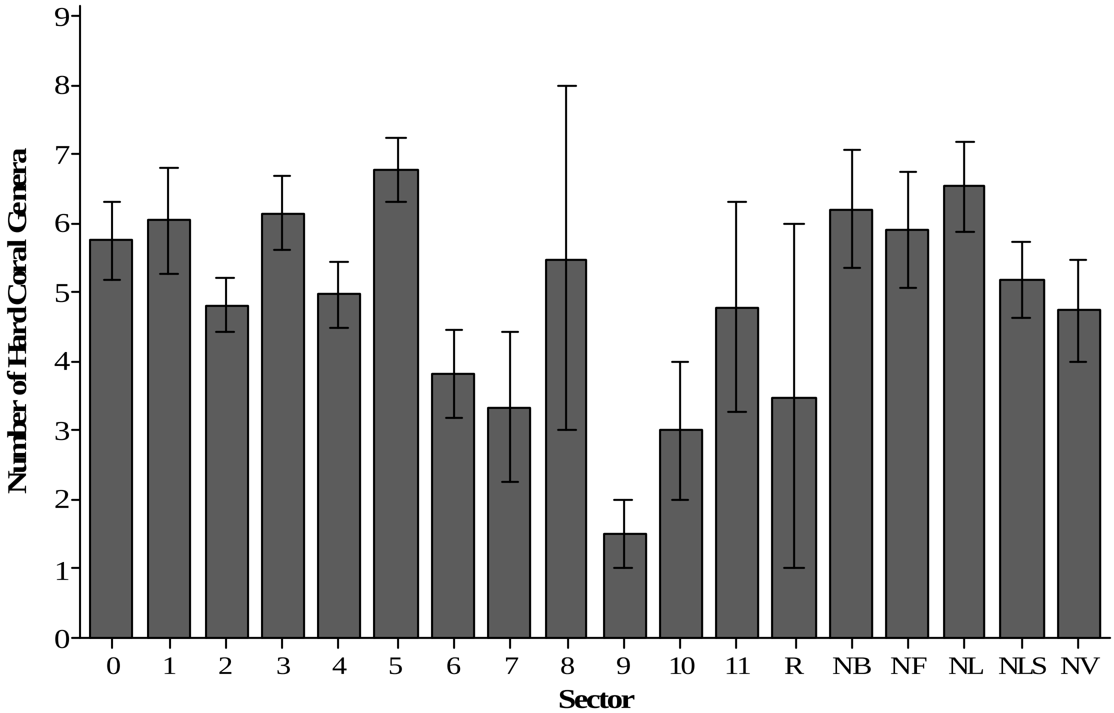

Figure 11. The mean number of hard coral genera recorded on subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007 within different sectors of the Bay of Diego-Suarez. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. Error bars represent one standard error from the mean.

Figure 11 displays the mean number of hard coral genera recorded during benthic surveys within each sector. Overall, the trend in coral diversity around the bay followed that of hard coral cover. The two sectors with the greatest coral cover, 5 and NL, also harboured the greatest coral diversity, with 6.79 ± 0.47 and 6.55 ± 0.65 genera (± SE) recorded on surveys. The fewest genera were recorded in sector 9 (1.50 ± 0.50 genera), which was the area with the lowest hard coral cover. In the northern portion of the bay, the relatively sheltered sectors 2 and 6 contained slightly fewer coral genera than other sectors in the same area (4.82 ± 0.40 and 3.82 ± 0.63 genera, respectively), for example the more exposed sector 3 (6.15 ± 0.55 genera). The number of genera recorded in sector 8, adjacent to Diego-Suarez itself, was surprisingly high (5.50 ± 2.50 genera), considering the low hard coral cover in this sector.

In the case of the island sectors, NV exhibited the lowest coral diversity (4.75 ± 0.75 genera) and, with the exception of sector NL, the number of coral genera increased towards the northwest reaches of the bay, with 6.21 ± 0.86 genera being recorded for sector NB. There was no significant difference between the mean number of coral genera recorded during surveys for island and mainland sectors (Kruskal-Wallis $H_{adj} = 1.14$, $p = 0.286$).

When hard coral community composition was compared between different sectors, some clear spatial patterns emerged (Figure 12). Coral cover in the northeast region of the Bay of Diego-Suarez was composed mainly of species belonging to the genus *Acropora*, which composed 53.20%, 52.84% and

45.83% of hard coral in sectors 5, NL and 6, respectively (Figure 13). However, sector NV, located in the eastern mouth of the bay, was where the greatest proportional cover of *Porites* corals was found (72.31%). With the exception of this latter sector, there was a clear trend in the northern half of the bay of hard coral cover becoming increasingly dominated by *Porites* spp. towards the northwest. For sectors 1, NF and 2, 50.38%, 47.45% and 39.99% of coral cover was composed of *Porites* coral, respectively.

The northwest region of the bay was also characterised by a relatively high proportional cover of *Millepora* spp. Hard coral cover in mainland sectors 1, 2 and 3 consisted of 14.30%, 15.32% and 18.31% *Millepora* cover, and for island sectors NB and NF, this parameter reached 13.07% and 18.46%, respectively. The highest value for the percentage cover of this genus was 59.56%, in sector 10. However, this may be unrepresentative due to the small number of surveys conducted in this sector. Cover of *Millepora* spp. in the northern portion of the bay was very low in sectors 5 and NL (3.24% and 0.42% of hard coral cover, respectively), but members of the genus *Galaxea* constituted a notably large proportion of the corals here (9.71% and 6.24%, respectively) compared to other northern sectors. Additionally, sector NL harboured the highest proportional cover of *Alveopora* spp. (19.61%), a genus that was only recorded in 5 other sectors, where it composed less than 0.70% of hard coral cover.

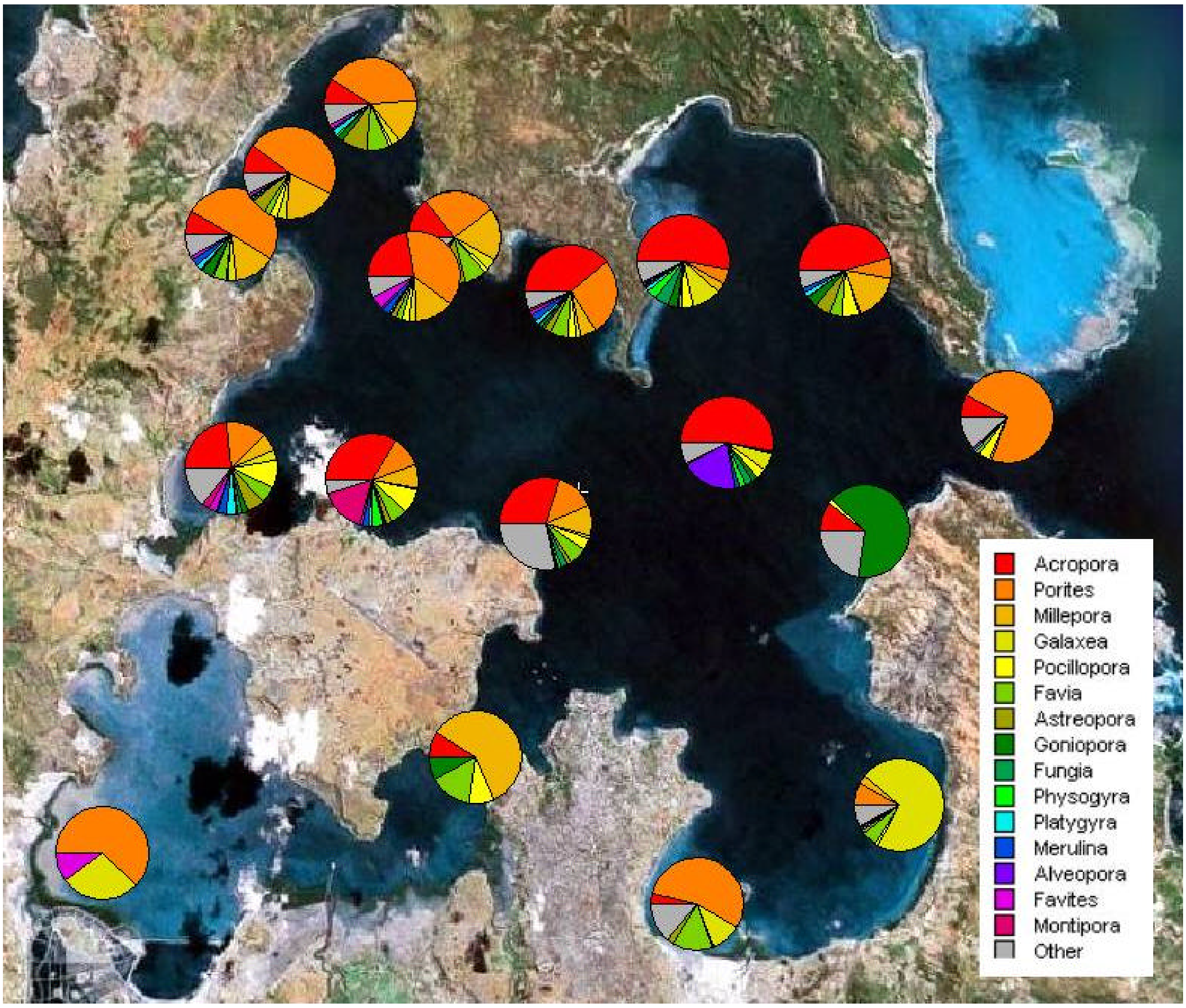

Figure 12. Thematic map of the Bay of Diego-Suarez displaying the overall relative proportional cover of different hard coral genera in different sectors, as ascertained from 20-m subtidal line intercept transect (LIT) surveys undertaken between October 2005 and December 2007.

In the southern portion of the bay, hard coral community characteristics varied widely. Overall, there was proportionally low cover of *Acropora*, which was not present in sectors 7 and 9 at all, and only composed 3.45% and 8.82% of coral cover in sectors 8 and 10, respectively. Exceptionally high proportional cover of *Porites* spp. was encountered in sectors 8 and 9 (55.17% and 62.07%, respectively), although in sector 10, the majority of coral cover (59.56%) was composed of *Millepora* spp. In sector 7, the dominant coral genus was *Galaxea*, making up 71.78% of the coral community, and in sector R, 64.82% of hard coral consisted of *Goniopora* spp. The highest proportional cover of species of the genus *Favia* was found in sectors 8 and 10, both adjacent to Diego-Suarez, at 13.79% and 14.71% respectively.

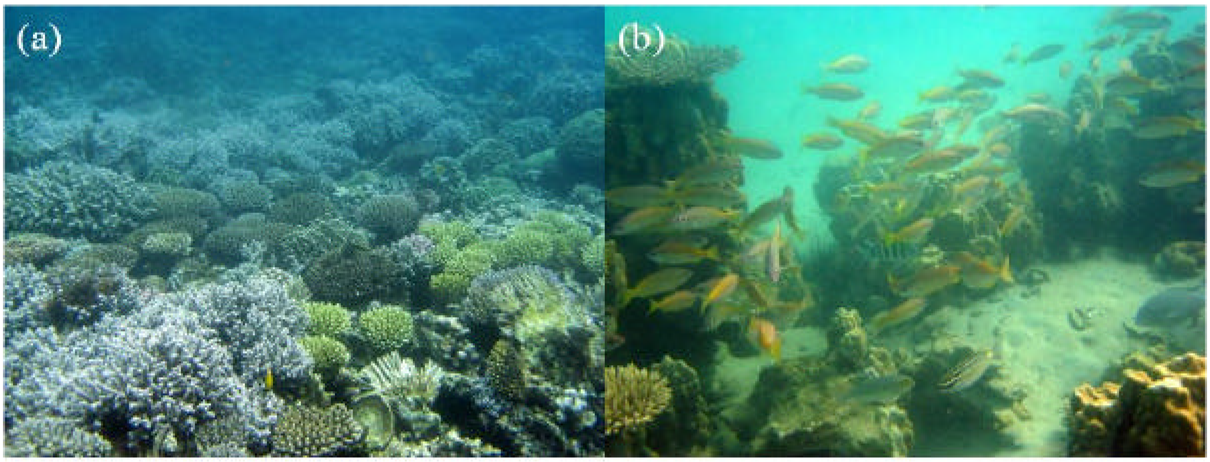

Figure 13. Differing coral reef ecosystems in the Bay of Diego-Suarez, characterised by high proportional cover of (a) *Acropora* spp., Nosy Langoro, and (b) *Porites* spp., Nosy Boka.

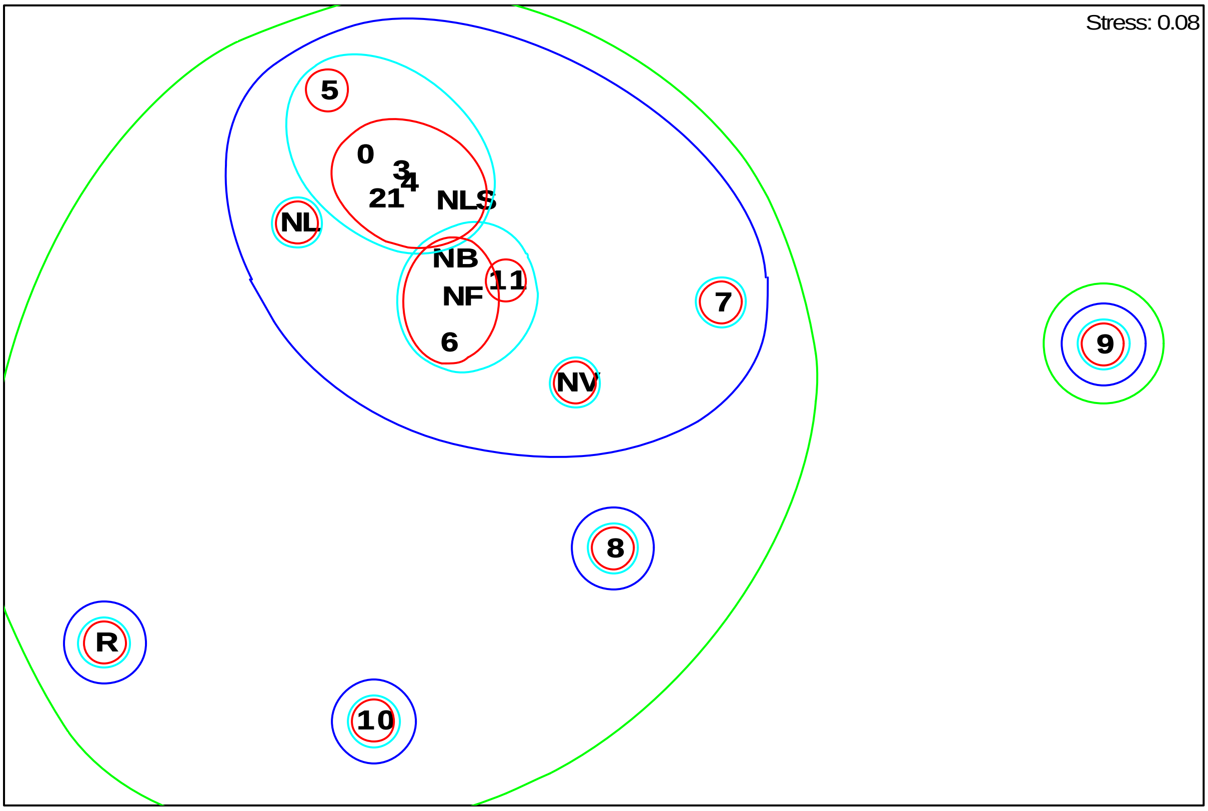

Figure 14. Two-dimensional MDS plot for the mean genera composition of the hard coral community within different sectors of the Bay of Diego-Suarez, as ascertained from subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. Based on a Bray-Curtis similarity matrix computed for fourth root transformed absolute benthic cover data for different hard coral genera. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. Overlay lines represent 20%, 45%, 66% and 72% similarity boundaries.

The similarities between sectors with respect to their overall hard coral community compositions at the genus level are displayed graphically in Figure 14. It can be seen that the northwest mainland sectors

0-4 shared highly similar coral cover characteristics, grouping together at over 78% similarity. The comparable coral genus composition of the island sector NLS, located adjacent to sector 0, also grouped it with these sectors at over 72% similarity. However, the other northwest island sectors NB and NF exhibited greater similarity (68%) with sectors 6 and 11 in terms of hard coral community characteristics than with this initial group (under 62% similarity). It appears that the hard coral community composition became increasingly dissimilar further away from this northwest group, as shown by the positions of sectors 5, NL, 6 and NV on the plot.

In the case of the sectors in the southern portion of the bay, including sector R, there was little evidence of any defined relationships relating to coral community characteristics and sectors exhibited high dissimilarity with each other and with the aforementioned northern groupings. Sector 9 formed a distinct outgroup with less than 17% similarity to any other sector with respect to hard coral genus composition. Sectors R, 8 and 10, despite bearing a greater resemblance to other sectors (around 40%), did not form part of any coherent grouping. Sector 7 was most similar to sector NV in terms of its coral community structure (58%). Overall, there was no significant difference between the hard coral genus composition of mainland and island sectors, as revealed by a multivariate analysis of similarities (ANOSIM) test (Global R = -0.171, p = 0.126).

3.2 Sea Urchin Distribution

3.2.1 Sampling Effort

A total of 498 subtidal 20 × 5 m belt transect invertebrate surveys were conducted between April 2006 and December 2007, enabling the investigation of sea urchin population densities and distribution within the Bay of Diego-Suarez. The number of surveys per sector and annual quarter are given in Table 3. As with the benthic line intercept transect surveys, the number of invertebrate surveys from which data were obtained for this analysis varied greatly amongst both sectors and quarters. In terms of quarters, the number of surveys ranged from 10 conducted in 073 to 128 conducted in 064. Sectors 7 and 8 are represented by just two surveys but, for example, 68 surveys were conducted in sector 2. Only sectors 0, 3 and 5 are represented in the dataset for all quarters, whereas sectors 7, 8, 9, 10, R and NV were surveyed in three or fewer quarters throughout the entire time period.

Table 3. The number of subtidal 20 × 5 m belt transect surveys undertaken in different annual quarters from April 2006 to December 2007 in different sectors of the Bay of Diego-Suarez, from which invertebrate density baseline data was obtained. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana.

Quarter	Sector																		Total
	0	1	2	3	4	5	6	7	8	9	10	11	R	NB	NF	NL	NLS	NV	
062	10	0	16	8	8	2	2	0	0	8	6	0	0	2	8	0	6	0	*76*
063	2	4	10	4	8	18	0	0	0	0	0	14	0	2	6	6	4	0	*78*
064	14	22	18	8	16	16	4	2	2	0	2	2	10	6	0	2	4	0	*128*
071	14	16	6	8	4	10	4	0	0	0	0	4	0	0	0	4	2	0	*72*
072	12	10	10	6	14	6	8	0	0	0	0	2	0	6	2	0	4	8	*88*
073	2	0	0	4	0	2	0	0	0	0	0	0	0	0	0	2	0	0	*10*
074	4	0	8	10	6	6	0	0	0	2	0	2	0	2	4	0	2	0	*46*
Total	*58*	*52*	*68*	*48*	*56*	*60*	*18*	*2*	*2*	*10*	*8*	*24*	*10*	*18*	*20*	*14*	*22*	*8*	*498*

3.2.2 Sea Urchin Distribution

Six main genera of sea urchin were recorded during the invertebrate surveys (Table 4). Sea urchin communities in shallow water areas of the bay were dominated by *Diadema* spp., namely *D. setosum*, with a relative abundance of 96.00% and an overall mean density of 0.829 ± 0.069 m^{-2} (± SE). This species was widespread, being observed at over 55% of all sites surveyed.

Table 4. The mean (± SE) densities, relative abundances (RA = total number of individuals of one species / total number of individuals of all species) and observation frequencies (OF = number of sites at which a species was observed / total number of sites) of different sea urchin species within the Bay of Diego-Suarez, as ascertained from subtidal 20 × 5 m belt transect surveys undertaken between April 2006 and December 2007.

Genus	Density (/100 m^2)	RA (%)	OF (%)
Diadema spp.	82.880 ± 6.880	96.000	55.020
Echinothrix spp.	1.823 ± 0.530	2.112	8.433
Echinometra spp.	1.568 ± 0.293	1.816	16.064
Eucidaris spp.	0.036 ± 0.025	0.042	0.602
Toxopneustes spp.	0.012 ± 0.010	0.014	0.402
Tripneustes spp.	0.006 ± 0.003	0.007	0.602
Other	0.008 ± 0.005	0.009	0.602

The next most abundant genera were *Echinothrix* spp., with a relative abundance 2.11% and a mean density of 0.018 ± 0.005 m^{-2}, and *Echinometra* spp., with a relative abundance of 2.11% and a mean density of 0.016 ± 0.003 m^{-2}. Despite being uncommon, these genera were relatively widespread, with *Echinometra* spp. found at 16.06% of sites and *Echinothrix* spp. found at 8.43%. Other urchin genera were rarely recorded, and their relative abundances did not exceed 0.04%.

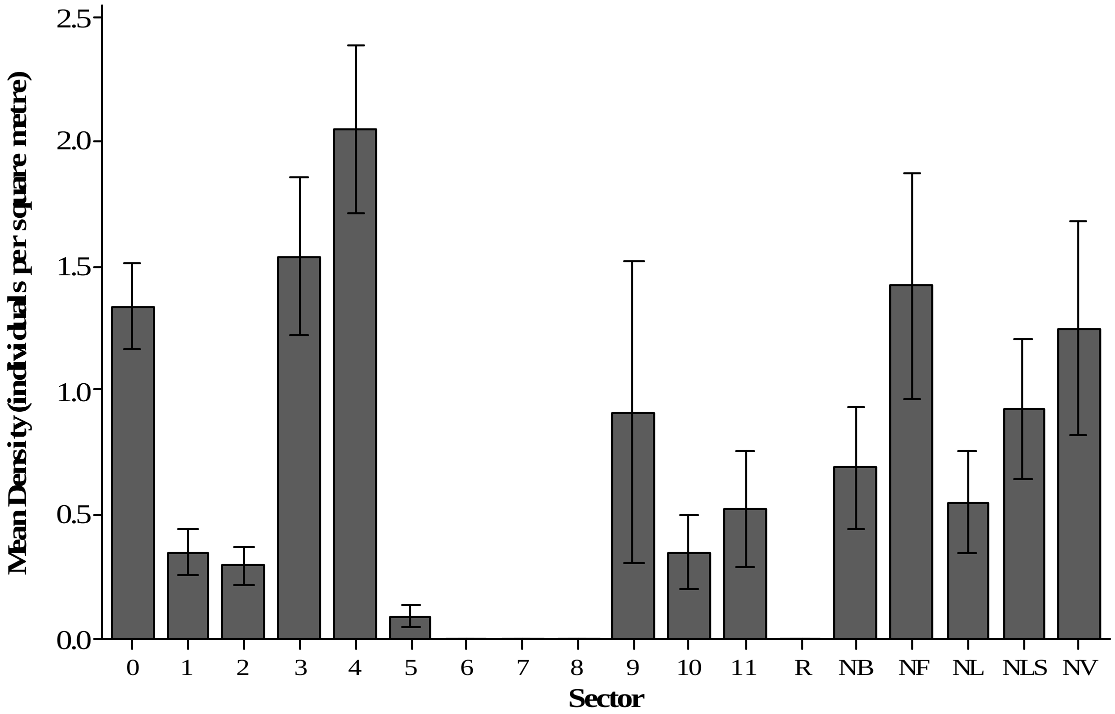

Figure 15. The mean density of *Diadema setosum* within different sectors of the Bay of Diego-Suarez as ascertained subtidal 20 × 5 m belt transect surveys undertaken between April 2006 and December 2007. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. Error bars represent one standard error from the mean.

The mean density of *Diadema setosum* in different sectors of the bay is shown in Figure 15. On average, the highest population densities seemed to be found in the more exposed sectors of the west and northwest regions of the bay, namely the mainland sectors 0, 3 and 4 (1.34 ± 0.17 m^{-2}, 1.54 ± 0.32 m^{-2} and 2.05 ± 0.34 m^{-2}, ± SE, respectively) and around the island NF (1.42 ± 0.45 m^{-2}). These were similar sectors in terms of coral community composition (Figure 12), characterised by moderate coral cover with a relatively high proportion of *Millepora* spp., and also moderate vegetation cover. Sectors

1 and 2, sheltered in the northwest corner of the bay, exhibited much lower densities of 0.35 ± 0.09 m^{-2} and 0.30 ± 0.07 m^{-2}, respectively.

D. setosum densities were at their lowest in the easternmost region of the bay. No individuals were recorded in sectors 6, 7, 8 and R. However, a density of 1.25 ± 0.43 m^{-2} was encountered in sector NV, located in the mouth of the bay. Other island sectors, namely NB, NL and NLS, harboured moderate densities of *D. setosum* (0.55-0.92 m^{-2}).

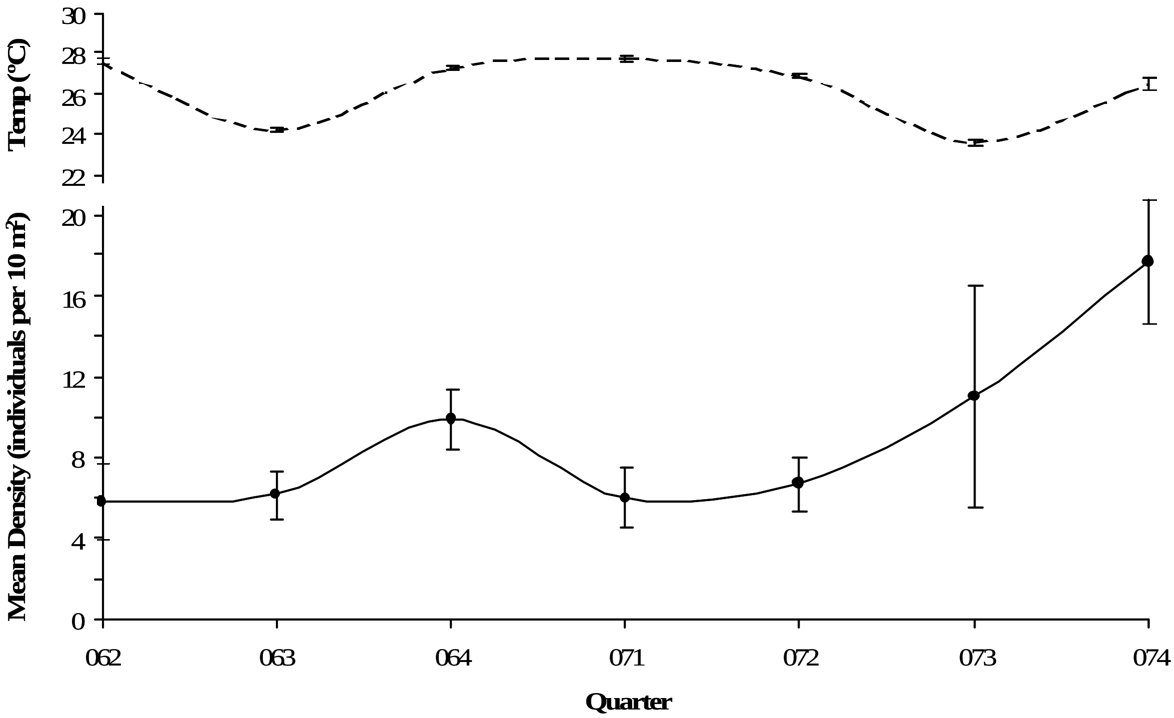

Figure 16. The overall mean density of *Diadema setosum* and mean temperature recorded at depth in the Bay of Diego-Suarez in different annual quarters from April 2006 to December 2007, as ascertained from subtidal 20 × 5 m belt transect surveys undertaken throughout this period. Error bars represent one standard error from the mean.

In addition to spatial variability in the population density of *Diadema setosum*, data revealed some temporal variation. Figure 16 suggests that population densities of this species peaked in October-December in both years that surveys were undertaken, reaching 0.99 ± 0.15 m^{-2} (± SE) in quarter 064 and a maximum of 1.77 ± 0.31 m^{-2} during 074. These two periods corresponded with seasonal water temperature rises from 24.29 ± 0.12°C (± SE) to 27.30 ± 0.11°C in 2006 and 23.63 ± 0.13°C to 26.49 ± 0.35°C in 2007, as determined from mean temperature measurements obtained during the same surveys. However, these population density peaks also correspond with increases in both the total number of surveys conducted during that quarter compared to the previous quarter and also the proportion of surveys undertaken in the 'urchin-rich' northwest areas of the bay.

3.2.3 Relation to Benthic Community Structure

A thematic map relating the population density of *Diadema setosum* with the mean percentage cover of coral and macroalgae within different sectors of the bay is shown in Figure 17. There appeared to be a general trend of decreasing *D. setosum* density and increasing coral cover from western to eastern sectors, although there was no significant correlation between *D. setosum* density and cover of hard coral ($R = 0.094$, $p = 0.231$) or soft coral ($R = -0.059$, $p = 0.457$), perhaps due to the relatively large variation in *D. setosum* density in the west and northwest region of the bay in comparison to that of coral cover. The only area in which there seemed to be a negative correlation between these factors was that surrounding sectors 3, 4, 5 and NL.

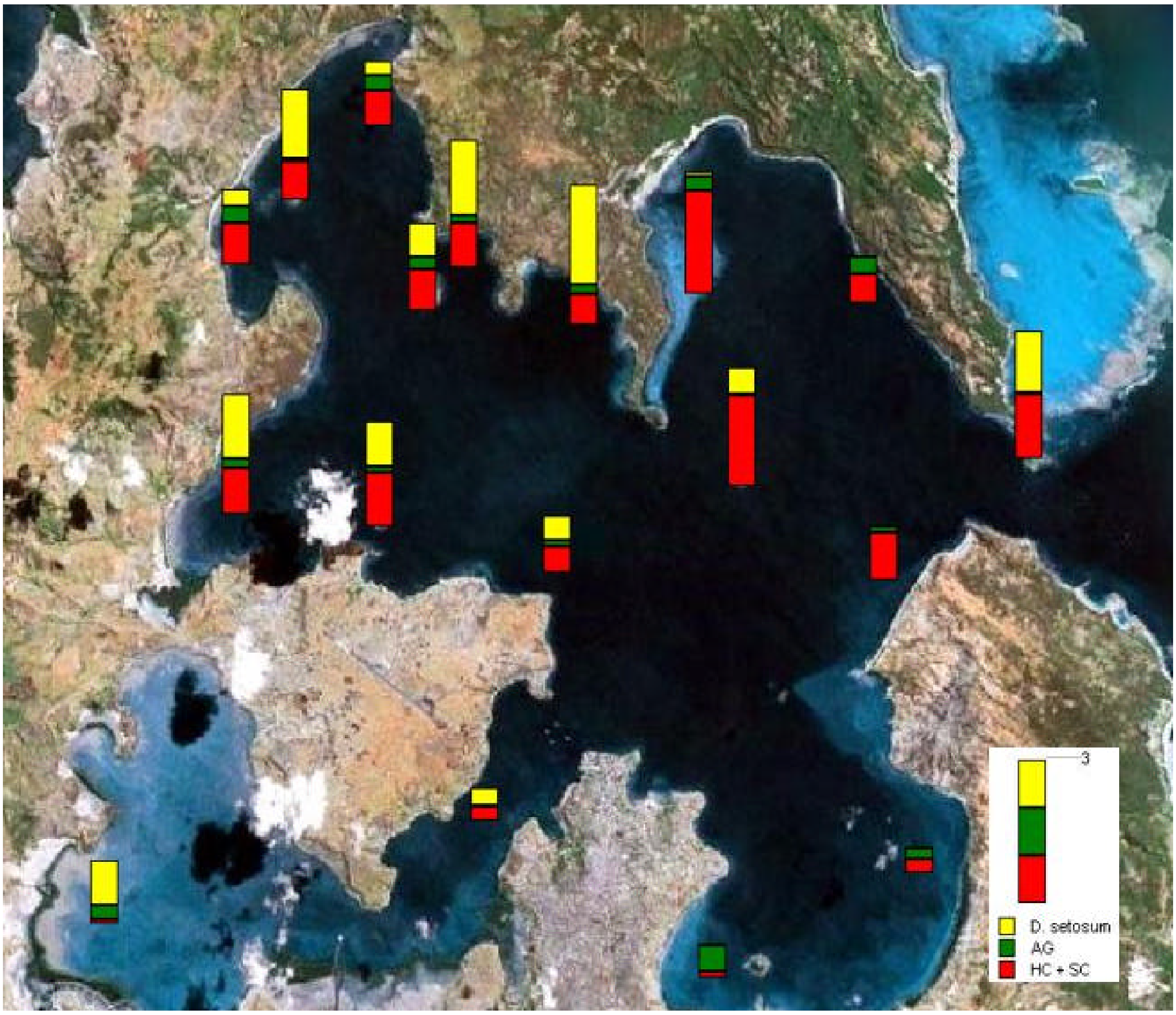

Figure 17. Thematic map of the Bay of Diego-Suarez displaying the mean density of *Diadema setosum* (/m^2), as ascertained from subtidal 20 × 5 m belt transect surveys, together with the mean percentage cover (/20) of hard (HC) and soft (SC) coral and macroalgae (AG) benthic substratum types, determined from subtidal 20-m line intercept transect (LIT) surveys, in different sectors. Surveys were undertaken between April 2006 and December 2007.

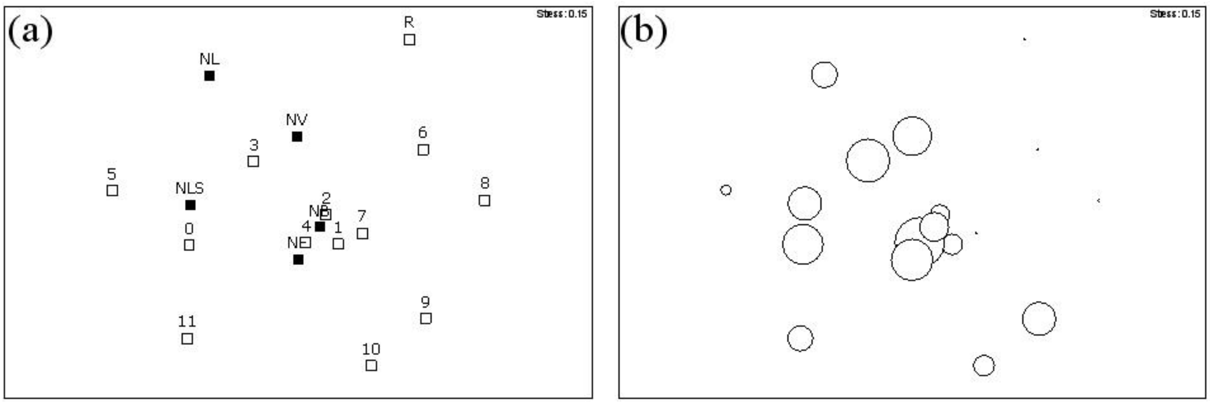

Figure 18. (a) Two-dimensional MDS plot for benthic characteristics of different sectors of the Bay of Diego-Suarez, as ascertained from subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007. Based on a Euclidean distance similarity matrix computed for normalised mean percentage cover data for different benthic substratum categories. □ = mainland sector, ■ = island sector. R = Ramena, NB = Nosy Boka, NF = Nosy Fano, NL = Nosy Langoro, NLS = Nosy Loapasana, NV = Nosy Volana. (b) The same MDS plot but with superimposed circles representing the mean relative density of Diadema setosum within each sector, determined from subtidal 20 × 5 m belt transect surveys undertaken between April 2006 and December 2007.

The population density of the species exhibited some negative correlation with macroalgae cover. The sectors with elevated percentage cover of macroalgae, such as 1, 2, 5, 6 and 8, also harboured low densities of *D. setosum*. However, this correlation was not significant (R = -0.118, p = 0.133). The two substratum types with which the density of *D. setosum* was significantly related were seagrass (R = -0.175, p = 0.025) and rubble (R = 0.221, p = 0.005) cover.

The lack of a clear relationship between the population density of *Diadema setosum* and benthic substratum composition around the Bay of Diego-Suarez is compounded in Figure 18. Sectors 1, 2, 4, NB and NF formed a relatively tight cluster (Figure 18(a)), indicating that they exhibited similar overall benthic composition characteristics. However, Figure 18(b) shows that the density of *D. setosum* was highly variable within this group of sectors. With the exception of most of the sectors in this group, the sectors in the bay tended not to cluster according to neither geographic juxtaposition nor whether they were island or mainland sectors.

4. DISCUSSION

This report describes the outcomes of the initial detailed evaluation of the marine ecological dataset compiled by the FMMRP since its relocation to the Bay of Diego-Suarez in 2005. In addition to providing an overview of the features of subtidal habitats around the bay, the results have enabled conclusions to be drawn regarding the current condition of the habitats and the factors responsible for their ecological status.

4.1 Sampling Effort

Although the dataset examined was very large, comprising 380 benthic and 498 invertebrate surveys, it was shown that there was an uneven distribution of sampling effort, both spatially and temporally. For example, there was relatively little data representing the southern and eastern parts of the bay and island sectors compared to the well-surveyed northwest region. As the FMMRP base camp is located in the northwest area of the bay due to practical and logistical reasons, it might be expected that sampling effort has been concentrated around this region. As well as distance considerations, parts of the bay that are further away from the base camp were often relatively inaccessible as a result of poor weather conditions, especially during the windy season.

Variation between annual quarters in terms of volumes of data collected can be partly attributed to seasonal changes in weather conditions, as demonstrated by a decrease in the number of surveys carried out in the second quarter, which was within the windy season, compared to the fourth quarter of each year. Also, the nature of the operation of the FMMRP, which is primarily funded and run by volunteer members, means that the number of available personnel to conduct survey work has not been constant from one annual quarter to the next.

During the continued expansion of the long-term ecological dataset for the Bay of Diego-Suarez, work should be focused more upon those areas that have been thus far underrepresented in the survey programme in order to ensure a more even spatio-temporal distribution of sampling effort. This shall enable even more reliable conclusions about the condition of marine ecosystems in the bay to be drawn, which can ultimately be used to determine suitable sustainable management strategies for the bay, and also enhance the effectiveness of any long-term monitoring.

4.2 Benthic Community Structure

The vast majority of the benthic habitats of the Bay of Diego-Suarez were dominated by sediment, as coral has grown only in the relatively shallow margins around the edge of the bay and adjacent to islands. This is why the surveys were primarily conducted near the coast. Even amongst those areas that were surveyed, sediment comprised the greatest overall proportion of benthic cover. The high amount of sediment within the bay is likely to be the result of extensive terrestrial runoff, enhanced by the large length of convoluted coastline around the bay combined with a restricted water exchange with the open ocean. In turn, this has greatly decreased the extent of light penetration through the water column, especially in more sheltered areas, which has a negative effect on coral growth and reduces their depth limit. Within the reefs themselves, sedimentation can have detrimental effects upon ecosystem condition by smothering organisms (Rogers, 1990).

Hard coral cover and species composition provide indications as to the condition of the components of a coral reef framework, and are related to other elements of the ecosystem, for example, fish species abundance and diversity (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984). Factors such as these help us to determine the long-term integrity of reef ecosystems (Kramer, 2003). Another aspect of the benthos that can be significantly associated with fish population characteristics is reef topographic complexity (McClanahan, 1994), and it is suggested that some measure of this be included in future studies utilising FMMRP benthic data.

In the case of the current study, hard coral cover and species composition were roughly correlated. The seemingly healthiest and most extensive reefs in the Bay of Diego-Suarez, as shown by high coral cover and diversity, were to be found in sector 5 and at the nearby Nosy Langoro, as well as, to a lesser degree, Nosy Volana. These areas, all exposed to oceanic water currents from the mouth of the bay, would receive outside nutrients and planulae larvae that act to sustain and restock their resident coral reefs (Brooks and Mrowicki, 2007). The currents would act to remove residual suspended sediment from the water column, enhancing light penetration and promoting coral growth. Also, as the bay constitutes a relatively closed system, the water temperature inside the bay may be slightly elevated above that outside the mouth, and so influxes of cooler water from the ocean may maintain healthier corals in this area.

Although hard coral cover was low in sector 8, the coral genus diversity was high compared to nearby regions. The generic composition of the hard coral community on the northern edge of this sector may have been influenced via oceanic currents that bypass the centres of good reef health in the northeast of the bay, due to its location directly opposite the middle of the bay.

The lower coral cover and diversity around the rest of the coast of the bay may largely reflect reduced exposure to the sustaining oceanic currents and greater susceptibility to the adverse effects of sedimentation and nutrient input. In the case of island sectors, it may be expected that the primary factor governing the condition of associated coral reef systems would be exposure to oceanic currents. Indeed, coral cover in island sectors generally decreased with increasing distance from the mouth of the bay with the exception of Nosy Volana. The greater exposure of this island to the ocean and prevailing weather conditions may have contributed to the slightly reduced coral cover and diversity at this locality, via the effects of increased environmental disturbance (Connell, 1978; Done, 1982). Yet land runoff can influence marine habitats that are many kilometres from shore (Lough *et al.*, 2002). Therefore it is not surprising that there is a lack of significant differences between island and mainland sectors in terms of benthic characteristics, especially when considering the enclosed nature of the bay.

The lowest average hard coral cover and number of coral genera were recorded in southern sectors adjacent to the population centres of Diego-Suarez and Ramena. Sector 9, an extremely sheltered and shallow peripheral bay with a very narrow inlet running past Diego-Suarez and a salt manufacturing plant located on its southern shore, harboured the lowest hard coral cover and diversity. This provides evidence for the detrimental effects of anthropogenic activity upon coral reefs in the bay, arising primarily from pollution, urban and industrial development and, in the case of Ramena, destructive fishing practices (Frontier-Madagascar, 2007). The latter may account for some of the apparent decline in coral cover within northern sectors from west to east, with the exception of sector 5 and Nosy Langoro. However, further work is needed in order to quantify such anthropogenic environmental influences around the bay.

4.2.1 Hard Coral Community Composition

The numbers of coral genera and species identified during BSP surveys since 2005, despite being large, do not represent a comprehensive list of the corals within the Bay of Diego-Suarez. The data were collected by non-expert volunteers who were trained to identify only a certain subset of species and genera, which was determined by a trade-off involving the extent of training that they received and the reliability and accuracy of the resulting survey data. However, the examination of these data in the current study has provided a relatively detailed overview of the nature of coral communities in the bay.

In the northern section of the bay, there appeared to be two broad types of coral community, distinguishable by both component coral genera and geographic location. Mainland sectors in the west and northwest of the bay, with the addition of Nosy Loapasana, were highly similar in terms of their coral reef systems that were characterised by high proportional cover of species belonging to the genera *Porites* and, to a lesser extent, *Millepora*. These could be defined as rock reefs, dominated by large boulders and rocky outcrops (Rajasuriya *et al.*, 1998), rather than coral reefs. Sectors in the northeast of the bay, namely those in which coral cover and diversity was greatest, did not fall into this grouping and were shown to have coral communities that were dominated by *Acropora* spp. and also harboured a relatively high proportional cover of the genus *Galaxea*.

The unique similarity amongst coral reefs in the northwest in terms of their constituent genera might be attributable to their position within a sheltered basin that has been relatively isolated from the rest of the bay and the open ocean in terms of water circulation. The physical environment of this area is vulnerable to input via terrestrial runoff, involving sedimentation. Strong winds during the winter months may also heavily influence suspended sediment concentrations in this shallow region (Larcombe *et al.*, 1995). It is likely that these factors have shaped the coral community composition of the reefs in this particular locality, in relation to that of other coral reefs in the bay, via the alteration of physical and biological processes (Rogers, 1990). Observed faunistic differences between the coral communities are maintained as the reefs, especially in the northwest, are probably mostly self-seeded (Done, 1982). In the northeast of the bay, greater exposure to oceanic influences relative to terrestrial and/or anthropogenic influences, as mentioned previously, is the likely determinant of the status of the richer coral communities associated with this area, promoting and sustaining the growth of the faster growing species found here.

Compared to sectors in the northern half of the Bay of Diego-Suarez, there was less of a coherent pattern amongst southern sectors and, overall, they appeared relatively disparate in terms of their constituent coral communities. The inability to uncover a pattern is perhaps partly due to the reduced sampling effort in this area of the bay. However, it appears that the differential impact of anthropogenic activities between the sectors in the south might be significantly influencing the coral reefs in this area. These varying influences have arisen from the salt manufacturing plant in sector 9, the town of Diego-Suarez between sectors 8 and 10, and the town of Ramena towards the mouth of the bay. Sector 9 appeared to be the greatest outlier in terms of the nature of its subtidal habitats, probably due to its physically isolated nature compared to other parts of the bay, as discussed previously.

4.2.2 Benthic Substratum Distribution

Considering all benthic substratum types, there appeared to be three main, interacting groups of substrata that characterised particular sites in the bay according to their relative dominances. These were 'soft' sediment, 'hard' coral and rock and, finally, 'green' seagrass and algae. As mentioned, sediment constituted the most common substratum type, especially towards the western reaches of both northern and southern portions of the bay. The easternmost areas of the north and south parts of the bay were characterised by high cover of seagrass. The region encompassing sector 5 and Nosy Langoro may be classified as the centre of hard coral within the bay. The relative dominances of these three main groups of substrata have been found to be useful in giving an overall picture of the distribution of general shallow marine habitat types in the Bay of Diego-Suarez. Such a picture may be reflected by variation in other biotic components such as fish and invertebrate abundance and diversity (Bell and Galzin, 1984), yet this is yet to be revealed by subsequent analysis of the ecological dataset.

Seagrass was by far the dominant form of vegetation in shallow marine habitats in the bay and displayed relatively high variability with respect to proportional benthic cover. This reached notably high levels in the eastern reaches including sectors 6, 7, 8, adjacent to Ramena and around Nosy Volana, thus replacing hard coral and/or sediment as the primary substratum. These areas were not directly exposed to the prevailing currents from the east, and this may have provided the environmental conditions and substrate characteristics necessary for the development of extensive seagrass beds. At the same time, the lower water turbidity in this region as a result of the influence of oceanic currents and water flushing through the mouth of the bay may have promoted seagrass growth. It could also be the case that the reduction of populations of sea urchins or herbivorous fish species such as parrotfish and surgeonfish (Ogden *et al.*, 1973) may have resulted in extensive seagrass cover.

Proportional cover of macroalgae was generally low and varied relatively little around the bay. Algal cover was greatest in sector 8, where there was relatively low hard coral cover. The opposite was true for Nosy Langoro and Nosy Volana, which exhibited very low algal cover and some of the highest levels of cover of hard coral in the bay. In other sectors, proportional cover of macroalgae and hard coral were moderate. Thus, there was some inverse relationship between macroalgae and coral in terms of average benthic cover within sectors, as may be expected from the competition for space that exists between these two biotic components of the benthos (Tanner, 1995) and also the phenomenon of the algal-coral phase shift. The pattern is, however, not straightforward, and the balance between macroalgae and hard coral may be affected by the levels of many factors including nutrient input, herbivore populations and physical habitat characteristics, and the impact of anthropogenic activities upon them (Done, 1992). It is suspected that nutrient enrichment is not the primary cause of shifts in coral-algal abundance, but that the impact of this factor is merely exacerbated by increased coral death or reduced levels of herbivory (McCook, 1999; Szmant, 2002).

In more general terms, when similarities between sectors with respect to overall benthic composition were examined, there was little clustering or patterning of sectors according to geographical juxtaposition or whether sectors were island or mainland. This emphasises that the benthic composition and condition of subtidal habitats in the bay was regulated by a multitude of natural and anthropogenic factors that vary in a complex manner, including those discussed previously. Important natural processes seem to be related to hydrodynamics and sedimentation (Rajasuriya *et al.*, 1998), although there are many other determinants of reef status in the bay.

Also, these results reflect the highly patchy and variable nature of marine habitats, which should be perpetually taken into consideration when interpreting the findings of the current study. It is probably true that comparing the average results of entire bay sectors with each other may mask more informative patterns that occur at smaller spatial scales (Edmunds and Bruno, 1996). In order to encompass the high variability that exists within sectors, differences at a higher resolution, such as between survey sites within sectors, should be examined. This would produce a more precise picture of the patterns in general reef condition within the bay and lead to a reduction in any biases or skewing factors, thus enhancing the conclusions that can be drawn.

4.3 Sea Urchin Distribution

Characterising the current condition of coral reefs is a complex problem since there are likely multiple influencing factors operating over several spatial and temporal scales (Kramer, 2003). The impact of sea urchin populations was considered previously as one aspect that may partially explain variations in subtidal benthic characteristics within the Bay of Diego-Suarez. This is due to the notably high population densities of *Diadema setosum* observed in certain areas. The subsequent investigation of this factor, as well as providing some useful conclusions, demonstrated the interrelation of different components of the FMMRP ecological dataset to help explain the condition of marine ecosystems in the bay.

Sea urchins were common and widespread in the bay, being recorded at most survey sites. The six main genera that one would expect to find in tropical Indo-Pacific waters were present, yet the vast majority of individuals encountered, over 96%, belonged to the species *D. setosum*. The highest population densities of this species were observed in the more exposed sectors of the northwest region of the bay that were shown to be highly similar in terms of their coral community composition, comprising coral species predominantly of the genus *Porites* and a substantial degree of cover of *Millepora* spp. This would seem to indicate either a direct or indirect link between coral community composition and sea urchin abundance. Additionally, herbivorous fish and sea urchins compete for algae as their food source and outbreaks of sea urchins have been attributed to overfishing of competitive grazers (Carpenter, 1990b; McClanahan and Shafir, 1990; Szmant, 2002), which may be the case here, where fish populations are smaller than in more eastern regions of the bay (Frontier-Madagascar, 2007). The more sheltered sectors 1 and 2, with their slightly differing hard coral community characteristics, harboured far lower average densities of *D. setosum*. These results appear contrary to previous findings that *Diadema* spp. may be limited by water turbulence (Alves *et al.*, 2001).

This species is known to feed on algae and, to a lesser extent, coral polyps (Bak and Van Eys, 1975). However, where one might expect a negative relationship between the mean population density of *D. setosum* and the proportional cover of macroalgae or hard coral within sectors (Alves *et al.*, 2001), there was little or none, except perhaps in sectors 3-5 and Nosy Langoro in the centre of the northern portion of the bay. If correlations amongst these parameters were to actually exist, it is possible that they are somewhat masked by the variability and highly patchy nature of the benthic environment within sectors themselves, as discussed above.

One benthic parameter that the population density of *D. setosum* did correlate with, even at the spatial scale utilised, was the proportional cover of rubble. In the Bay of Diego-Suarez, the benthic substratum classified as rubble for the purposes of BSP survey work, whether it was coral or rock, often incorporated a high cover of turf algae, which was the case for most areas of the bay (pers. obs.). Being the major food source of this urchin species, this would explain the correlation. *D. setosum* density also correlated negatively with the proportional cover of seagrass, which is likely to be a by-product of the inverse relationship between cover of 'hard' substrata, including rubble, and marine vegetation. Additionally, the physical environmental conditions in the eastern reaches of the bay may have led to reduced sea urchin densities here by influencing the marine habitat characteristics or the sea urchin population numbers themselves (Alves *et al.*, 2001).

Overall, there is a general lack of evidence for the strong, top-down regulatory effect upon the condition of marine ecosystems that herbivorous invertebrates such as *D. setosum* are sometimes shown to exert (e.g. Sammarco, 1982; Liddell and Ohlhorst, 1986; Levitan, 1988; Carpenter, 1990a). In other cases, interrelationships between sea urchins and substrate characteristics have been difficult to resolve and the regulatory processes occurring may be a combination of top-down and bottom-up effects (McClanahan, 1994; Aronson and Precht, 2000). Due to their large numbers, it is likely that sea urchins are affecting the state of coral reefs within the Bay of Diego-Suarez via herbivory (Thacker *et al.*, 2004) and that any major changes in the population density of *D. setosum* could have dramatic implications for benthic community composition. This relationship still needs to be clarified by examining it at a higher spatial resolution. Also, other natural and anthropogenic environmental influences are in evidence, as has already been demonstrated by variations in the benthic environment, and it appears that sea urchin populations have a smaller part to play in determining the condition of marine habitats around the bay.

Some evidence for seasonal variation in populations of *D. setosum* was uncovered, with mean population densities exhibiting slight peaks in the fourth quarter of each year, corresponding with a rise in water temperature. This could be partly attributed to an increase in survey numbers both within the 'urchin-rich' sectors in the northwest area of the bay and in general across the bay as a whole during both fourth annual quarters. Thus, here it is emphasised again that a more even spatio-temporal distribution of sampling effort is preferable in order to enable more reliable conclusions to be drawn. If it were the case that sea urchin population densities across the bay did increase during summer months, this could be explained by a seasonal rise in algal biomass resulting from spring algal blooms that are known to occur in the tropics (Longhurst, 1993), representing an increase in the food source of sea urchins. Also, temperature changes may directly affect the rates of reproduction of sea urchin species in some way. Either way, data from a longer time period would be required to determine whether or not the apparent seasonal variation held true.

4.4 Conclusions

In conclusion, a relatively detailed map of the benthic compositional characteristics of subtidal habitats within the Bay of Diego-Suarez has been produced in the current study. The resulting initial picture of the condition of coral reef ecosystems shall be useful in determining the key factors influencing the marine environments of the bay. This in turn shall contribute to the development of effective sustainable management strategies for the region. The findings both compound and expand upon the initial results of the biological assessment conducted by the FMMRP (Frontier-Madagascar, 2007). It has also been demonstrated that different aspects of the dataset can be interrelated in order to enhance the conclusions that can be drawn regarding the status of subtidal habitats in the bay.

Key issues raised in this report that could be improved upon and incorporated into future work are the spatio-temporal evenness of sampling effort and consideration of patterns at a greater spatial resolution or through alternative stratification of sampling, such as examining differences between exposed and sheltered sites. More specific aspects of the current study that might be expanded upon include the relationship between macroalgal cover and other environmental factors and perhaps the characterisation of sea urchin population structure.

Yet the next main step in terms of marine research conducted by the FMMRP is the expansion of the ecological dataset via continued survey work in order to enable the examination of long-term trends in the condition of reef habitats in the bay. This will improve our understanding of the nature of the marine environment in the area and, if management initiatives are implemented, allow the assessment of the effectiveness of such measures. Of course, other aspects of the dataset, such as fish species size and abundance data and physical and chemical environmental data, should be incorporated in order to support and augment future work.

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5.2 Websites

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6. APPENDICES

Appendix I. The total recorded length occupied by different hard coral genera over 380 subtidal 20-m line intercept transect (LIT) surveys undertaken between October 2005 and December 2007 within the Bay of Diego-Suarez. The "Other" category incorporates novel or unidentified genera.

Genus	Length (m)	Percentage
Acropora	759.03	32.845
Porites	461.42	19.967
Millepora	180.60	7.815
Galaxea	140.41	6.076
Pocillopora	88.79	3.842
Favia	85.93	3.718
Astreopora	68.28	2.955
Goniopora	62.36	2.699
Fungia	54.08	2.340
Physogyra	37.31	1.615
Platygyra	33.74	1.460
Merulina	33.10	1.432
Alveopora	33.02	1.429
Favites	31.66	1.370
Montipora	28.16	1.219
Seriatopora	26.44	1.144
Pavona	19.30	0.835
Goniastrea	17.24	0.746
Turbinaria	16.91	0.732
Lobophyllia	15.04	0.651
Stylophora	12.74	0.551
Echinopora	10.66	0.461
Coscinarea	10.40	0.450
Cyphastrea	10.11	0.438
Montastrea	8.76	0.379
Hydnophora	7.32	0.317
Pachyseris	6.80	0.294
Diploastrea	4.94	0.214
Gardinesis	3.07	0.133
Plerogyra	2.24	0.097
Mycedium	1.70	0.074
Acanthastrea	1.55	0.067
Pectinia	0.30	0.013
Oulophyllia	0.20	0.009
Symphyllia	0.20	0.009
Leptastrea	0.17	0.007
Tubipora	0.10	0.004
Barbattoia	0.08	0.004
Other	36.80	1.592
Total	**2,310.96**	**100.000**