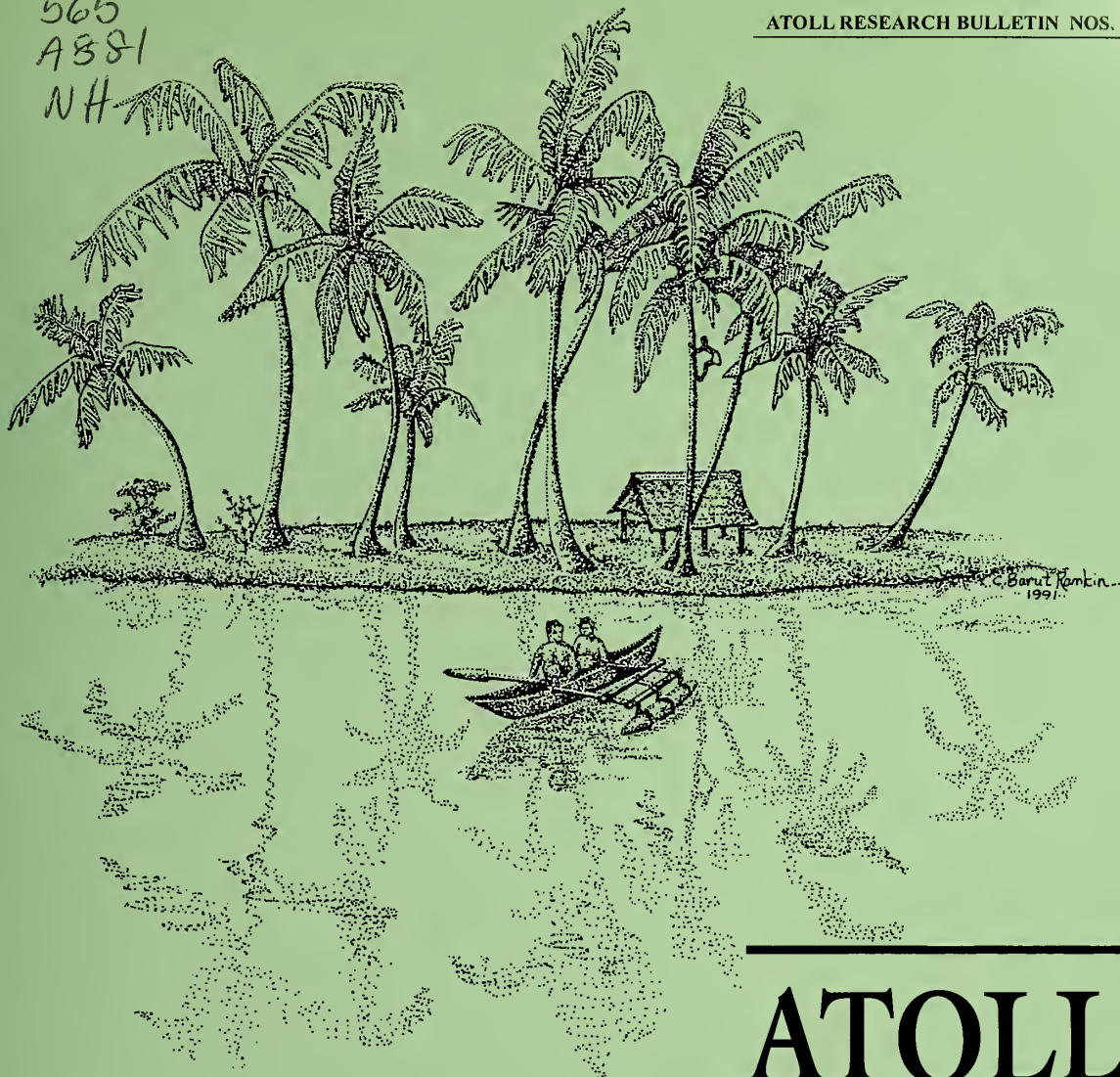


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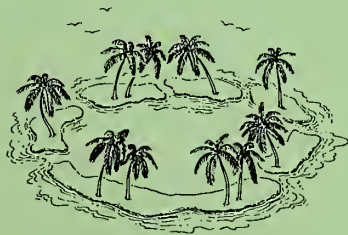
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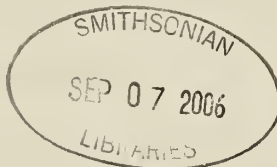
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ATOLL RESEARCH BULLETIN

NO. 531

**EVALUATING CORAL REEF BENTHIC COMMUNITIES IN REMOTE
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BIOSPHERE RESERVE**

BY

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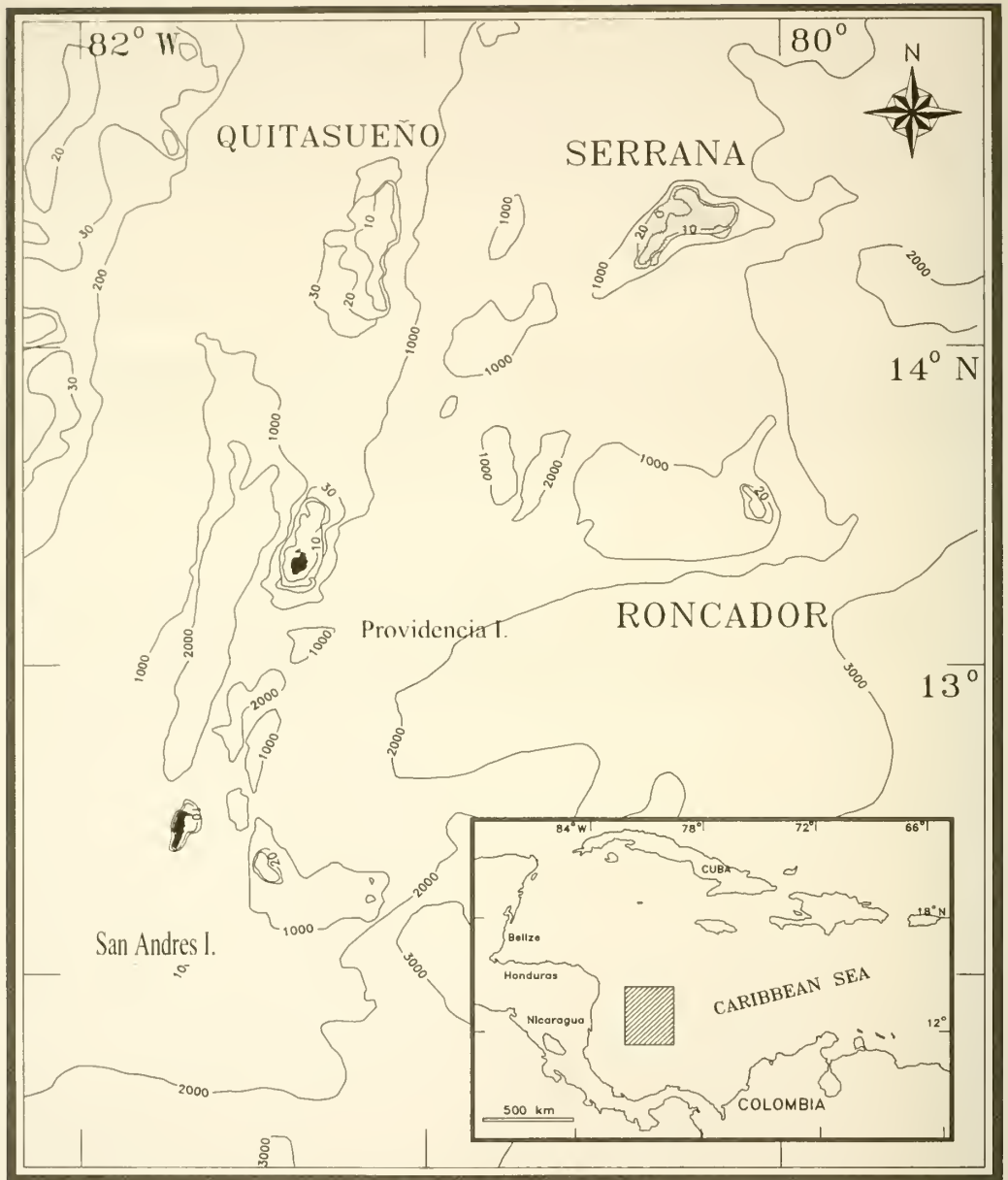


Figure 1. Southwestern Caribbean showing the location of the Northern banks (Colombia).

EVALUATING CORAL REEF BENTHIC COMMUNITIES IN REMOTE CARIBBEAN ATOLLS (QUITASUEÑO, SERRANA, AND RONCADOR BANKS) TO RECOMMEND MARINE-PROTECTED AREAS FOR THE SEAFLOWER BIOSPHERE RESERVE

BY

JUAN ARMANDO SÁNCHEZ,¹ VALERIA PIZARRO,² ALISON R. ACOSTA-DE-SÁNCHEZ,¹ PAULA A. CASTILLO,³ PILAR HERRON,² JUAN CAMILO MARTÍNEZ,² PHANOR MONTOYA,³ AND CARLOS OROZCO²

ABSTRACT

Three remote oceanic atolls, the Northern Cays (Quitassueño, Serrana, and Roncador Banks, Archipelago of San Andres and Providencia, Colombia) were intensively surveyed during April and May, 2003 through a multilevel quantitative study of the benthic communities (substrate cover: coral-benthos; densities: octocorals and urchins; frequencies: coral diseases). This study is the first approach towards the design of a network of Marine Protected Areas (MPAs) in these Caribbean reefs. We found between 66 and 73 categories of substrates in the benthic communities, including 43-to-46 species of reef-building corals and 38 species of octocorals. Ample ranges of coral cover (2-52 %) and octocoral densities (0-15 col. m⁻²) were observed among stations. The community structure corresponded to shared species-specific environmental preferences, perceptible as minor gradients such as windward-leeward and/or shallow-deep, and to physical/topographical characteristics, which in most habitats were products of the reef-building corals themselves (e.g., '*Montastraea*' or '*Acropora palmata* - *Diploria*' habitats).

Depth was the major structuring force. Species abundance distribution followed the pattern that few species are dominant whereas most of them are rare. Common species were *Montastraea* spp. (reef-building corals), *Pseudopterogorgia bipinnata* (an octocoral) and *Lobophora variegata* (fleshy macroalgae). Sea urchins and coral diseases had a heterogeneous distribution being absent in many stations and frequent in a few. Higher densities of sea urchins (*Diadema antillarum* and *Echinometra viridis*) were encountered in Quitassueño Bank. There were areas of high coral abundance and diversity in the three atolls which can be important for the MPA design. The particular assemblages had mean values of coral cover > 32% (most of them >38%), coral species >16, octocoral densities >0.6 col. m⁻² (usually >2.9 col. m⁻²), and octocoral diversity > 4 (usually >8), which are within the ranges of the best-conserved reefs in the Caribbean. Some areas of special concern were identified that could need special management.

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Difficult management challenges are the high density/diversity areas of endangered and/or rare octocorals (Roncador and Serrana Banks: *Gorgonia* spp. and *P. elisabethae*) as well as heterogeneous shallow patch reefs of endangered corals and highly productive coralline algae (*A. palmata* and *Porolithon pachydermum*) intermingled with *Montastraea* spp. reefs exhibiting disease outbreaks (white plague, bleaching, and dark spots) in Serrana Bank.



Figure 2. Coral reefs at the *Montastraea* spp. habitat in Roncador Bank, Southwestern Caribbean, Colombia. Upper: Organisms with most of their biomass above the substrate such as gorgonian octocorals (*Pseudopterogorgia* spp.). Below: Organisms covering the reef substrate; dominant coral in the photo is *Montastraea franksi*.

INTRODUCTION

Quitasueño, Serrana and Roncador Banks (Northern Cays) are some of the few true oceanic atolls of the Atlantic surrounded by depths of thousands of meters (Díaz et al., 1996a). The coral-reef banks belong to the Archipelago of San Andrés and Providencia (Colombia) in the southwestern Caribbean (Fig. 1). This area been declared a biosphere reserve by UNESCO (Seaflower Biosphere Reserve) and the local environmental authority (CORALINA) is proceeding with the design of a network of MPAs in the area including the Northern Cays (e.g., Friedlander et al., 2003). However, very little information on the benthic communities of these atolls is available to design a series of MPAs. This study comprises the first detailed and quantitative study of the benthic communities of the coral reefs on Quitasueño, Serrana and Roncador Banks that will contribute to the zoning and design of the MPAs. Ultimately, local authorities will have these recommendations, in addition to parallel studies on fish communities and Queen Conch populations (*Strombus gigas*), to confront with stake-holder needs and finally design a network of MPAs in these banks.

The Archipelago of San Andrés and Old Providence comprises a series of oceanic islands, barrier-reef complexes, atolls and coral shoals on a volcanic basement (Fig. 1) aligned in a north-northeasterly direction over nearly 500 km along the Lower Nicaraguan Rise off the Central American continental shelf (Geister, 1983, 1992; Díaz et al., 1995; Díaz et al., 1996a, 1996b, 2000). Both geomorphological and habitat distribution patterns are similar among these reef complexes mainly due to the strong wave action generated by trade winds. The upper platform of these atolls is surrounded by a rather even 20m-deep terrace. On its windward, fore-reef side it has low relief due to the strong abrasion which allows only sparse growth of encrusting and mound-shaped corals but permits profuse gorgonian development (Sánchez et al., 1997, 1998). This windward, fore-reef terrace gradually slopes upwards emerging on a reef crest which is variably developed as a spur-and-groove system of hydrocorals (*Millepora* spp.), zoanthids and crustose coralline algae (corallinaceae). The crest forms an almost continuous barrier to the waves and fringes the eastern, northern and southern internal margins of the upper platform.

Behind the barrier there is an extensive, sinuous and shallow (1-3 m) sand-and-rubble lagoonal terrace that is connected to the lagoonal basin by an abrupt sandy slope. There is no reef formation behind the crest (e.g., back reef) as in the traditional Caribbean fringing reef (e.g., Jamaica). The mid-depth (12-18 m) lagoonal basin is usually covered by a dense patch-reef network (e.g., Díaz et al., 1996b). These patch reefs are mostly dominated by massive scleractinian corals, especially *Montastraea annularis* and *M. faveolata*. The reefs are irregular in topography with sand patches occurring among the coral heads (e.g., large massive reef-building corals). Bordering the western margin of the lagoon there is a leeward terrace, often times crowned with a discontinuous band of peripheral shallow reefs, inner sand bars and algal ridges that partially enclose the lagoon (e.g., Díaz et al., 1997). The leeward terrace gradually slopes down towards the 20-30m deep break on the outer-slope margin supporting moderate relief reefs with variable live-coral cover (see more details in Milliman, 1969; Díaz et al., 1996a, 2000). The benthic

community structure of these oceanic reef complexes, including Serrana and Roncador, is considerably different than coastal coral reefs (Diaz-Pulido et al. submitted).

The most conspicuous sessile benthic organisms of Caribbean coral reefs are localized at two overlapping layers (Fig. 2). One layer comprises organisms that are covering the substrate, principally scleractinian and milleporinan corals, zoanthids, sponges, and algae, referred to here as the benthic community. The other layer is composed of erect or bushy organisms, present just above the substrate, such as gorgonians, octocorals and black corals, which we refer to as the octocoral community. Typically, these layers have been studied separately and little is known about the joint distribution patterns of the two layers. With a few exceptions (Florida: Goldberg 1973; Wheaton and Jaap, 1989) little is known about the distribution patterns of the benthic and octocoral communities, information which could provide valuable clues on the processes governing the community structure of Caribbean reefs.

Ecological communities or assemblages are composed of individuals of different species that co-occur and potentially interact with one another as determined by past and continuing evolutionary processes (McPeck and Miller, 1996). In the coral-reef benthic community there are several species guilds that coexist over a wide range of environmental conditions. The most conspicuous guilds of benthic sessile organisms show particular morphological adaptations related to precise life-history strategies (Jackson, 1977). Many scleractinian coral species occur over a wide bathymetric range but with similar wave-energy conditions (e.g., Geister, 1977; Graus and Macintyre, 1989). On the other hand, gorgonian octocorals, due to their bushy physiognomy and position in the upper layer, have advantages such as a near absence of competition for space or colonial expansion such as occurs in the coral-reef community. However, they are more affected by drag forces associated with water movement (Jackson, 1977) and thus the octocoral community patterns more closely reflect the influence of wave energy (Kinzie 1973; Alcolado, 1981; Jordán, 1989; Yoshioka and Yoshioka, 1989; Sánchez et al., 1997). This study presents information collected at the same time on both benthic and octocoral communities as two semi-independent sources of community structure information.

The aim of this study was to survey the community/habitat structure and reef condition on Serrana, Roncador and Quitasueño Banks. The specific goals included obtaining quantitative information on: (1) the community of organisms that cover the reef substrate or benthic community; (2) the community of gorgonian octocorals that colonize space above the substrate or octocoral community (a part of the benthic community that is underrepresented using benthic cover methods); (3) the populations of keystone urchin species; (4) the topographical complexity or rugosity of the habitat; and (5) marine diseases affecting reef-building corals.

METHODS

The Northern Cays were intensively surveyed during April 24 to May 11, 2003 on board the M/V Spree and M/N Anglonamar II using enriched air SCUBA techniques

(EANx-Nitrox, O₂ up to 32%). A total of 118 stations were sampled (48 on Quitasueño, 48 on Serrana, and 22 on Roncador). We tried to survey as many habitats as possible, thoroughly covering the reef platform with the guidance of existing habitat maps (Diaz et al. 1996a, 2000). The surveyed habitats included shallow lagoonal sites (e.g., *Acropora–Diploria* or *Montastraea* spp patch reefs and algal mat habitats), leeward terrace sites (e.g., *Montastraea* spp, scattered corals or mixed-coral habitats), and fore-reef terrace sites (e.g., gorgonian octocorals and scattered corals habitat) (see details in results section). The fore-reef terrace, however, was surveyed on Quitasueño Bank. Bad weather prevented access to the habitats on Serrana and Roncador.

The abundance of the organisms covering the reef substrate was estimated as percent cover using the planar point-intercept method (PPI) (Dodge et al., 1982). This method is a modification of the point-intercept method of Loya (1978) in which the points are surveyed within a grid instead of along a line. It has the advantages of both plot and plotless methods as well as typically producing less inter-observer variation than occurs with traditional quadrant methods. Sampling stations consisted of 10 randomly chosen one-square-meter plots out of 50 potential positions along both sides of a 25 m- linear transect. At each position we surveyed the benthic species, genera (for some common algae), functional groups (for particular algae types and sponges), and types of inert substrate on a grid of 64 points. We tried to record 640 points per station, with 500 points being considered the minimum number required to obtain a representative survey of the station. Due to diving safety limits, the number of points varied slightly among stations with a mean of 628 (sd=44, min>500) and no differences detected among the means for the three banks (ANOVA, $P=0.25$, $df=2$, 115). A total of 74,127 points were surveyed at the 118 stations which was equivalent to 7412.7 linear meters of transect with points every 10 cm concentrated within 1158 square meters of grid using 64 points per square meter. Environmental variables recorded at each station were depth and topographic complexity or bottom rugosity. Rugosity, which is an indicator of wave-motion energy and the chronic disturbance effect of waves (Aronson and Precht, 1995), was estimated from the ratio of linear length of a chain that was laid out in a straight line along the bottom following all the vertical relief to its length when stretched out (10 m; e.g., Sánchez et al., 1997).

The transect line was established by a team of three divers surveying fish populations (Dalgreen et al., in prep.) that preceded the benthic team at each station. Each benthic survey was conducted by one of two teams of four observers that alternated dives. Within each team, two divers estimated substrate cover and the other two performed the remaining tasks. One surveyed gorgonian octocorals, urchins, and, if possible, substrate cover. The fourth diver measured bottom rugosity, looked for rare species to estimate more completely coral species diversity (alpha diversity) and examined diseased coral colonies visually identifying the coral species, the disease and estimating the percentage of affected tissue. Gorgonian octocoral density per species was estimated using the same 10 square-meter plots in which all colonies were counted and identified to the species or genus level (e.g., Sanchez, 1999). We counted and identified 4,828 colonies of octocorals at the 118 stations. Sea urchin densities (1,710 counted at the 118 stations), particularly of *Diadema antillarum* and *Echinometra viridis*, were estimated by counting the number

of urchins within 1m along both sides of the 25 m-long transect (50m²). All divers were fully trained previously for underwater identifications and data collection.

The species distribution patterns and community structure were analyzed using a variety of multivariable methods. Classification methods identify the similarity of cases (e.g., stations) according to their variable composition (e.g., species). Ordination methods allow the variation from several variables to be concentrated or expressed in a few composite, variance-rich variables to enable the detection of whole-community patterns. Classification and ordination methods can be combined to identify both structure and gradient patterns in the community (Flury & Riedwyl, 1988). Initially the database was organized into species-per-station matrices. For both substrate cover and gorgonian density, stations were classified by normal (Q-mode) cluster analysis using species cover, same as substrate cover, or density data ($\log_{10} [X+1]$ transformed), the Bray-Curtis dissimilarity index, and the Unweighted Pair Group Method (UPGMA) for building dendrograms (Field et al., 1982). Ordination analyses with the same data were obtained by a multivariate eigen-vector procedure, Detrended Correspondence Analysis (DCA) (Ter Braak 1986), which identifies gradients among stations and/or environmental variables. Potential environmental interpretations of the DCA axis values were found through correlation with depth and rugosity (e.g., Sánchez et al., 1997).

Previously, this suite of methods has been applied successfully to similar benthic assessments within the studied Archipelago (Friedlander et al., in press, in prep.). To further understand the relationship between groups or clusters of stations and community variables (e.g., coral cover, octocoral density, urchin density, frequency of coral diseases, etc.) or environmental variables (depth and rugosity), the magnitudes and mean location of these variables were superimposed on DCA 1 vs DCA 2 station ordination plots. Finally, the characteristic species of each successively nested cluster within a dendrogram were determined by recalculating substrate cover or density for each minimal cluster and then accumulating their abundance and successively marking those minimal clusters which contained at least 70% of the species' total abundance (R-mode). Species were then reordered and grouped according to membership within a given cluster or nest of clusters (Kaandorp, 1986; e.g., Sánchez et al., 1998).

RESULTS

Quitasueño Bank

A total of 73 benthic categories among species, genera, and functional groups of sessile organisms were recorded in Quitasueño Bank. There were a total of 46 species of milleporids and scleractinian corals observed qualitatively, 12-to-30 (min-max) coral species recorded quantitatively per station, and a coral cover ranging from 18-to-50%. Overall, analysis of the major functional groups showed that hard corals (Scleractinia and Milleporidae) were the most abundant organisms (18-50% cover), followed by fleshy macroalgae (4-39%), calcareous macroalgae (4-25%), encrusting algae (0.8-10%), and octocoral bases (0-10%), with lesser amounts of filamentous algae and invertebrates

being recorded (Fig. 3). The classification and cluster analyses showed a division of the 48 stations in two minimal groups with less than 40% dissimilarity (I and II), and with two and four major sub-clusters respectively (Figs. 4-5). Station 22 did not cluster with any other station. This station was situated in a typical rubble and algae (*Avrainvillea* spp.) patch in the leeward margin (e.g., Fig. 6 C-D). The most important result from this cluster analysis is that the classification of the stations revealed significant spatial structure on Quitasueño where apparently homogeneous habitats (e.g., habitat map: Fig. 5) had different sub-clusters that correspond to the reef windward-leeward edges (Fig. 5A: clusters D and C). Similarly, some lagoonal-leeward habitats had a spatial differentiation depending on whether they were north or south with respect to the lagoonal basin (Fig. 5A: clusters A and B respectively). Therefore, a characterization of the benthic communities based on the habitat mapping, as observed only with aerial photographs (Diaz et al., 1996, 2000), is not entirely a realistic view of the quantitative benthic community structure. The latter, nevertheless, is not completely disparate with respect to the major habitats (e.g., cluster F: Fig. 5A); these are hypotheses of community structure and for zoning and management purposes the results from the classification analysis and consequent ordination and inverse analyses should be taken in account (see discussion).

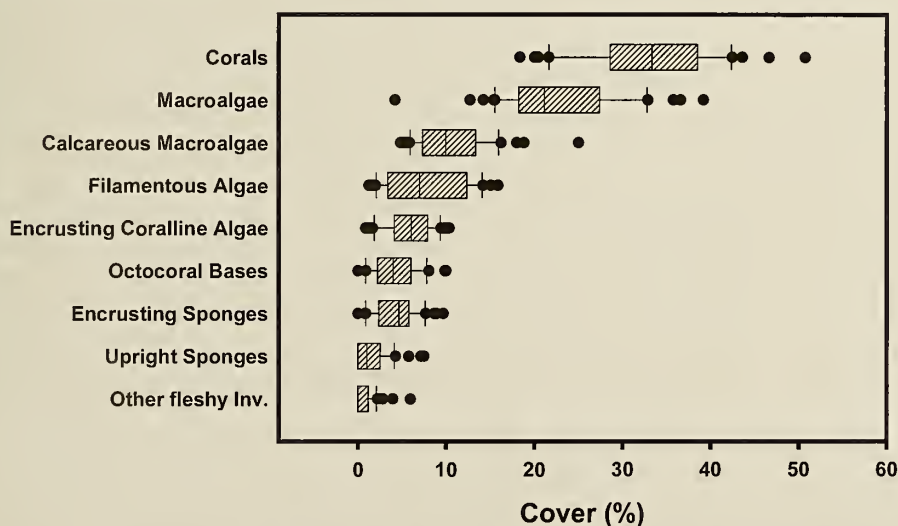


Figure 3. Box plots from the data distribution per station of the major functional benthic groups in the benthic community. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars. Quitasueño Bank.

Of the two main station clusters, cluster I is made up of leeward reef stations including sites in the lagoon and on the leeward margin that always had a protected position with respect to the reef crest (Fig. 5: clusters A and B; Fig. 4). As presented in Table 1 and Figures 4-5, sub-cluster A from the 'protected cluster I' is composed of shallow and intermediate depth stations in the lagoon, and sub-cluster B consists of some intermediate depth leeward reefs.

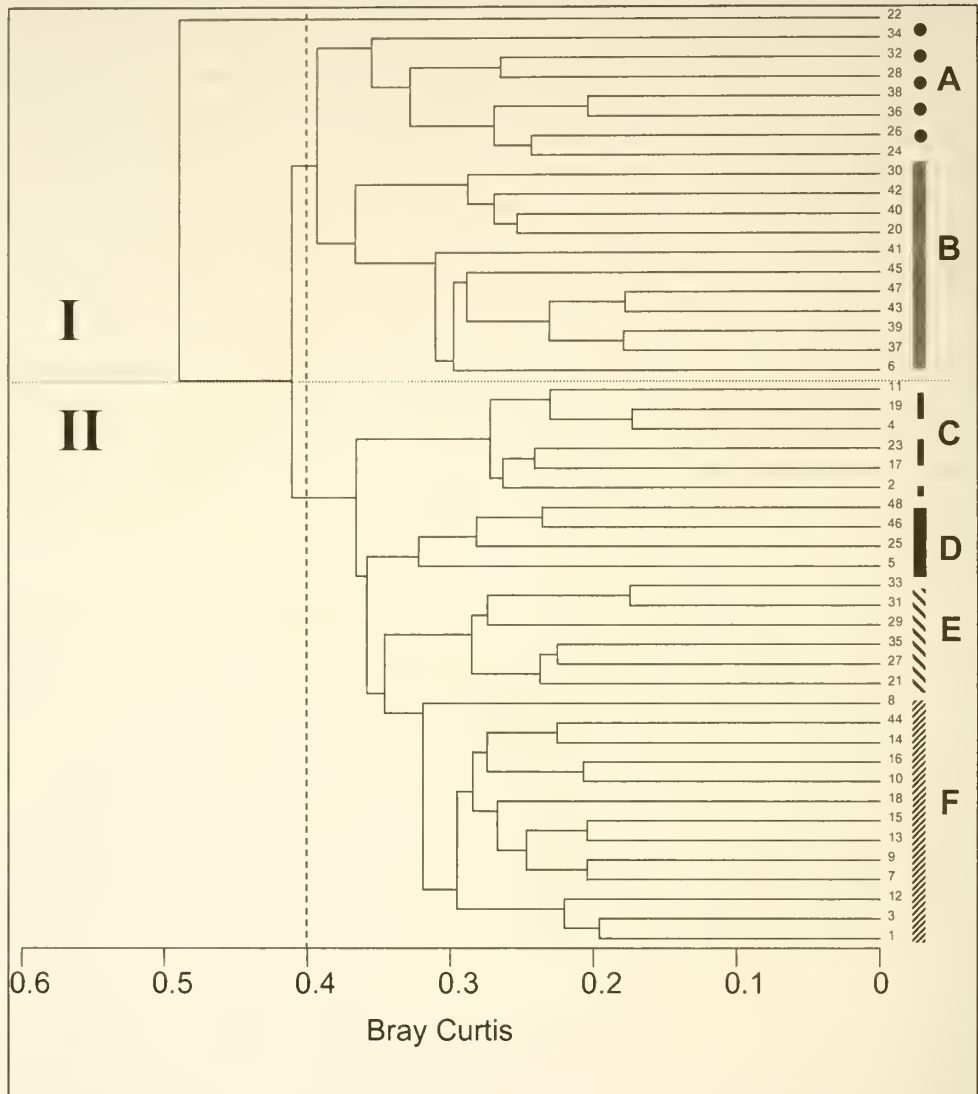


Figure 4. Dissimilarity (Bray-Curtis) dendrogram of the 48 benthic stations on Quitasueño Bank. The dashed line shows the 40% dissimilarity division among groups.

Both sub-clusters A and B had stations placed indiscriminately in three different habitats, '*Acropora - Diploria*', '*Montastraea*', and mixed corals. Cluster II is composed of a mixture of fore-reef and leeward stations that are either windward or well leeward at a greater distance from reef crest compared to cluster I stations. The 'terraces cluster-II' had sub-clusters of stations exclusively from the fore reef and leeward terraces (Fig. 5A [cluster E]; Fig. 4; Fig. 7 A-B) and two sub-clusters (C and D) with stations located

at both north and south ends of the barrier-terrace system (Fig. 5A). Sub-clusters C and F had stations at 'mixed coral' and 'encrusting corals and hard bottom' habitats whereas sub-clusters D and E were on 'mixed coral habitats' (Fig. 5A) which revealed a great deal of sub-habitat divisions in the 'mixed corals' habitats according to the windward, leeward or windward-leeward positioning.

Table 2 presents the community structure according to the cluster analysis discussed above. This analysis presents the species that had their highest peak abundances chosen arbitrarily here as >70 % of the species abundance after totaling all the points of a given species as 100% and then calculating the percentage of each cluster at any given cluster or nest of clusters from Fig. 4. Table 2 represents substrate cover data (totalled by cluster) to visualize the most abundant benthic reef dwellers. Species sharing boxes of peak abundances are expected to group somewhat in an R-mode inverse cluster analysis. For instance, cluster A only had two taxa that had their 70% abundance peak: the algae *Penicillus* spp. and *Turbinaria* spp. (Table 2). *Turbinaria* spp. had high substrate cover (>10%) and was indeed a dominant species in the north lagoonal reefs. Overall, algae with higher abundances (>5% of substrate cover), such as *Dictyota* spp., *Sargasum* spp., filamentous algae, and *Lobophora variegata*, did not have their high distribution peaks in a particular cluster or nest of clusters; they were distributed in most of the groups. Coral species with high abundances (e.g., *Montastraea* spp.), on the other hand, were restricted to cluster B (*M. franksi*) and A+B (*M. faveolata* and *M. annularis*) suggesting a clear correspondence to 'leeward cluster I' and habitats such as '*Montastraea*', '*Acropora-Diploria*' and protected 'mixed corals'. Although other clusters, with the exception of D, also harbored species with their highest abundances in them, they did not have more than 5% of substrate cover (usually less than 1%) but they are mostly scleractinian coral species. Overall, only 19 out of 73 species, genera, functional groups, and/or types of substrate were present only in one cluster of stations, whereas 31 of them were distributed widely on Quitasueño (Table 2) which explains the high degree of similarity among all stations (~50%). There is a "background" assemblage that was found in most stations including inert substrates (excluded from cluster analyses: bare hard ground, sand, rubble), at least 15 species of reef-building corals, and several invertebrates and algae ("all groups": Table 2).

In addition to the presence of stations from different habitats grouping together as described above, the ordination analysis showed a continuum gradient among groups using the two main axes of the DCA (Fig. 8A). The ordination biplot shows, as expected, maximum separation between fore reef (sub-cluster F) and lagoonal reefs (sub-cluster A) with narrow distances between leeward terrace stations and other lagoonal stations in the middle showing overlap with respect to each of the DCA axes (Fig. 8A). The DCA biplot was used to discern ordination and correspondence patterns. Coral cover and alpha diversity appeared to be uniformly distributed among all clusters (Table 1). Lowest rugosity values appeared to be present in groups C and F from the fore- and windward-leeward-reef terraces (Table 1). The urchin *Diadema antillarum* (0-1 individuals m⁻²) was more abundant on lagoonal and leeward stations (B and E groups: Table 1). *Echinometra viridis* (0-10 individuals m⁻²) was very abundant on the leeward terrace on stations from cluster E (Table 1). Urchins were nearly absent on fore-reef terrace stations. The cover

of sessile invertebrates also had a certain correspondence among stations. Upright and encrusting sponges, octocoral bases and encrusting species such as *Erythropodium caribaeorum* had their higher abundances in the fore-reef and leeward terraces (Table 1). Other fleshy invertebrates, such as tunicates, zoanthids, corallimorpharians, and anemones, were more abundant in leeward reefs (e.g., cluster B: Table 1). Functional groups of algae were distributed haphazardly on the different groups of stations except for calcareous macroalgae which were more abundant on lagoonal stations (cluster I: Table 1).

The most frequent coral diseases and abnormalities encountered during the survey of the three banks were white plague, dark spots, and bleaching. On Quitasueño, white plague was found at over one-half of the survey sites and affected up to three species per site with up to 5% (tissue species⁻¹) of any one species being affected. White plague was much more abundant at two lagoonal stations (Table 1) which were less than 4% of the stations. Dark spots affected corals in a larger number of stations with up to four species per station being affected. Bleaching was also present in most stations but the percentage per species was overall low (Table 1). The highest abundance of these three coral diseases did not correspond at the same stations and no concomitant effects were noted. In each case the diseases affected between 4 and 10% of the tissue species⁻¹; otherwise infection rates were very low. Other diseases such as white and yellow band were also observed with even lower frequencies than white plague.

A total of 38 species or genera of gorgonian octocorals were identified with up to 16 species observed per station. Octocoral densities varied between 0.01 to 12 colonies m⁻². A major difference of the octocoral community was that the minimal clusters, harboring the largest dissimilarity among clusters, had >50% of dissimilarity showing a higher level of structure in terms of species characteristic of each cluster, which is higher than the near 40% observed in the benthic community (Fig. 9). Clusters A and B corresponded to shallow-to-mid-depth stations in the lagoonal basin and leeward margin indiscriminately on 'mixed corals', '*Acropora-Diploria*' and '*Montastraea*' habitats (Figs. 5B, 9). Cluster C was just two shallow fore-reef stations towards the north end of the barrier reef on 'encrusting corals on hard bottom' habitat (Figs. 5 B, 9). Cluster D had stations on two north and south spots at the leeward margin and a few in the south lagoonal basin spanning the same habitat types of clusters A and B but monopolizing most of the south lagoonal stations (Figs. 5B, 9). Clusters E and F had mostly fore-reef stations but cluster F also had a few located on the leeward terrace (Figs. 5B, 9). Station 22 was an outlier of the overall pattern. Table 3 shows the octocoral community structure according to the cluster analysis from Figure 9. As expected, more structuring, i.e. number of species showing a high degree of habitat specificity, of the octocoral community was found than in the benthic community. Cluster B can be characterized by the high abundance of *Plexaura homomalla*, a common gorgonian octocoral from shallow protected reefs (Table 3). Cluster D presented the high-peak abundances of rare and uncommon species such as *Muricea pinnata* and *Eumicea clavigera* (Table 3). Cluster F presented an almost select but inconspicuous, i.e. low density, mixed assemblage of over 10 species: *Eumicea* spp., *Muricea* spp., *Pterogorgia* spp. and *Plexaurella* spp. (Table 3). Clusters D and E presented a close similarity (Fig. 9) and shared the high-peak abundances of the most

dense species of the survey such as *Pseudopterogorgia bipinnata* and *Muriceopsis flavida*, as well as lesser amounts of *Gorgonia mariae* (Table 3). The topological relationships of the dendrogram of Figure 9 for clusters D,E,F,C, and B shared a number of both abundant and habitat generalist species such as the sea candelabra *E. mammosa* and *E. succinea* and the soft octocoral *Briareum asbestinum* (Table 3).

The ordination analysis showed three major groupings, one containing clusters C, D, E, and F (as they are related in the dendrogram from Figure 9 and shared a number of important species) and two corresponding to clusters A and B respectively (Fig. 8B). Except for a few fore-reef stations (cluster F) that had low rugosity (small circles), some leeward places with high octocoral species diversity and cluster A with low octocoral density values, no clear correspondence among the variables could be observed. Because the coral cover was so uniform in Quitasueño Bank as well as the overall rugosity (mean 0.39, sd=0.03), no correspondence was found with the ordination or clustering of the gorgonian community. The cover of encrusting coralline algae, a substrate on which many octocoral recruits settle, was fairly uniform across all stations and no particular correspondence to a particular cluster was detected.

The first DCA axes from the benthic and octocoral communities of Quitasueño, which predominately had information on the variation of the entire species assemblage (i.e., overall patterns or structuring forces as explained in the above analyses), were significantly correlated with both depth and rugosity. Whereas the two variables explained a very low proportion of the benthic variation (multiple $r^2=0.27$; $p<0.001$), depth and rugosity did explain a large proportion of octocoral community variability ($r^2=0.62$; $p<0.001$). Other variables, such as urchin density for both the whole benthic community and octocoral community and coralline algae (for octocoral community only), did not have any significant correlation with the first DCA axis.

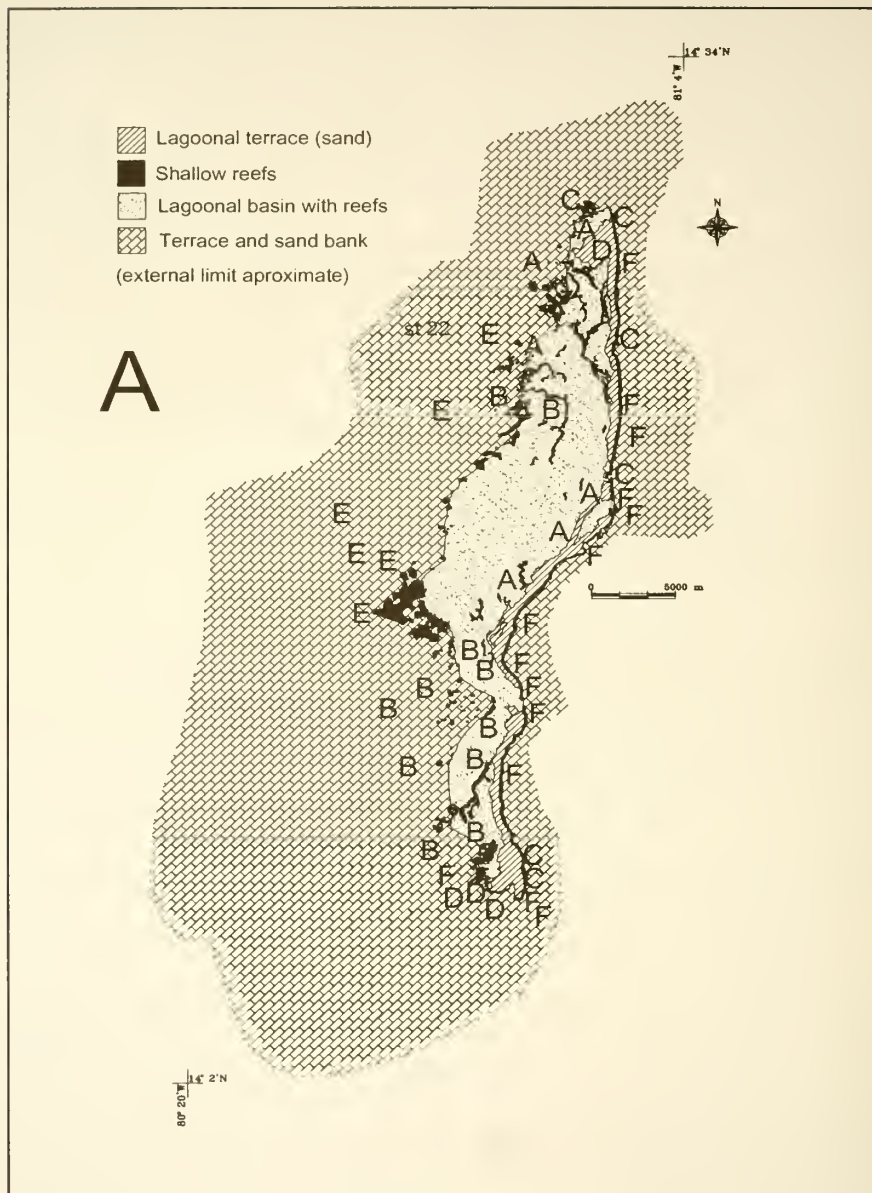


Figure 5 (A). Quitasueño Bank (habitats map: modified from Diaz et al., 2000) with locations of stations. Lagoonal basin presented deep habitats such as *Montastraea* spp. Shallow reefs in the lagoon basin where *Acropora palmata* – *Diploria* and rubble with coralline algae and *Turbinaria* spp. habitats. Terraces presented scattered corals and octocorals in the fore reef and mixed corals, *Montastraea* spp., or algae meadows in the Leeward terrace. Printed scale does not allow seeing more details. A. Distribution of stations according to cluster from Fig. 4. Location of stations approximate.

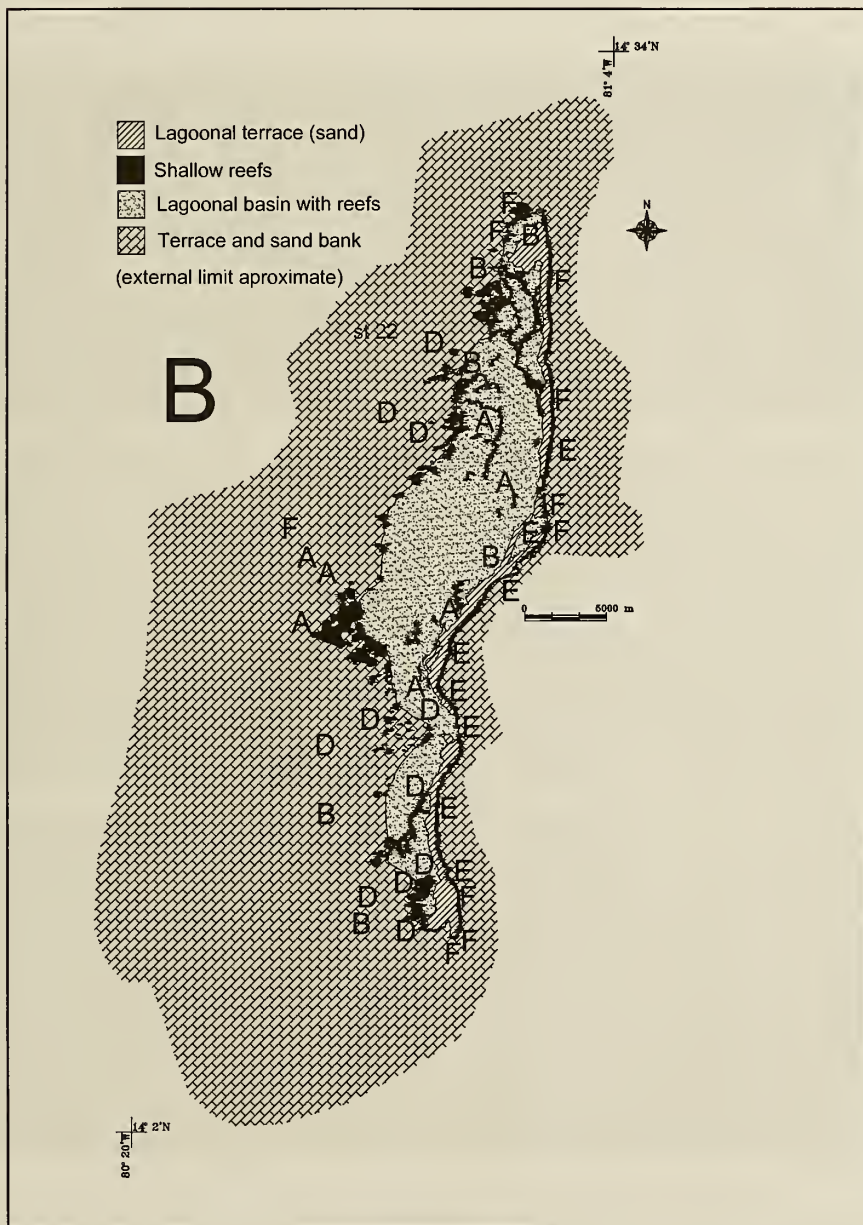


Figure 5 (B). Distribution of stations according to cluster from Fig. 9 (octocoral community).



Figure 6. Quitasueño Bank environments. A. Fore-reef terrace (*Pseudopterogorgia bipinnata*); B. *Turbinaria* spp. on shallow lagoonal reefs; C-D. Fleshy macroalgae, *Avrainvillea* habitat in the leeward margin; E. Urchin *Diadema antillarum* underneath *Montastraea faveolata*; F. *Acropora cervicornis* and *Eunicea fusca* (octocoral) in the leeward margin.

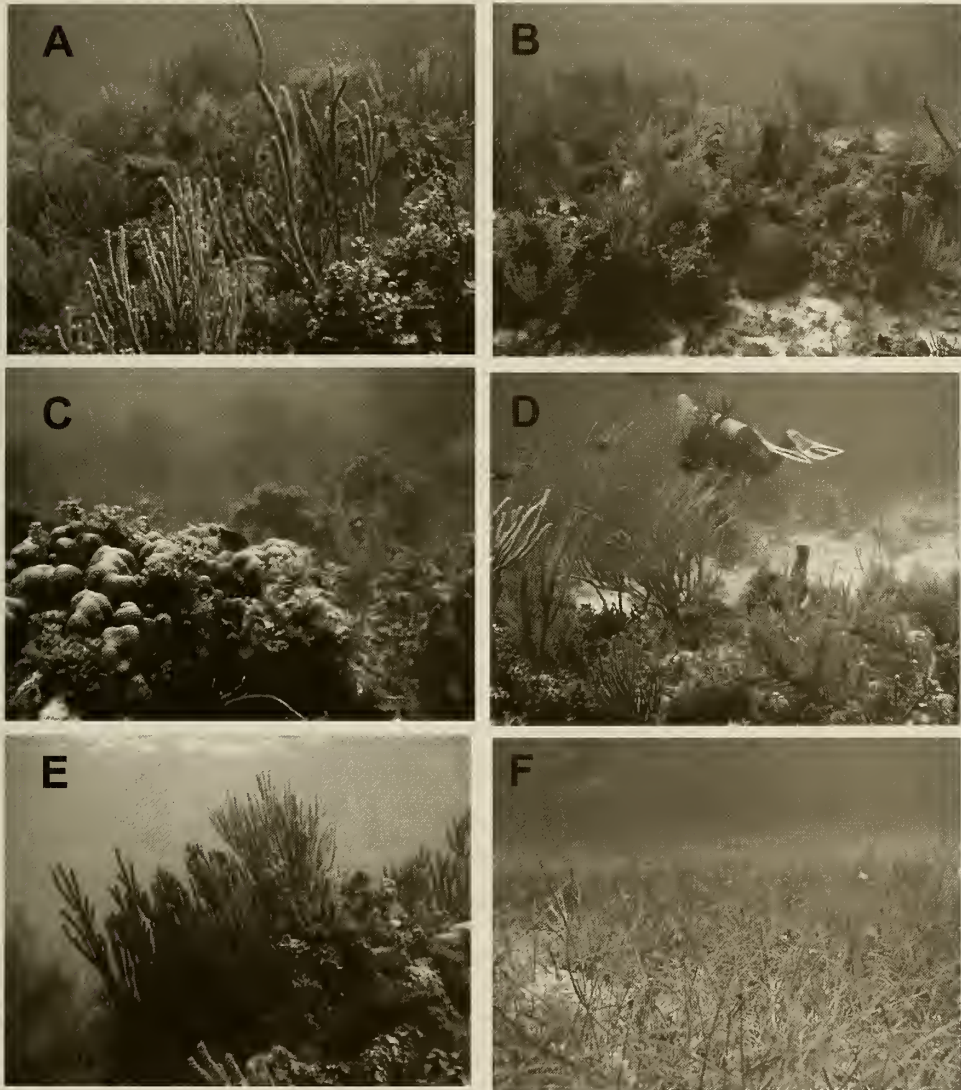


Figure 7. Quitasueño Bank environments. A. Plexaurid octocorals at the leeward terrace; B. *Pseudopterogorgia* spp. on the leeward margin; C. *Montastraea annularis* and fleshy macroalgae in the lagoon; D. Sand canal in the leeward terrace; E. *Plexaura homomalla* and *P. kukenthalii* in a shallow patch reef; F. Sea grass in the lagoon basin (*Halodule* and *Syringodium*).

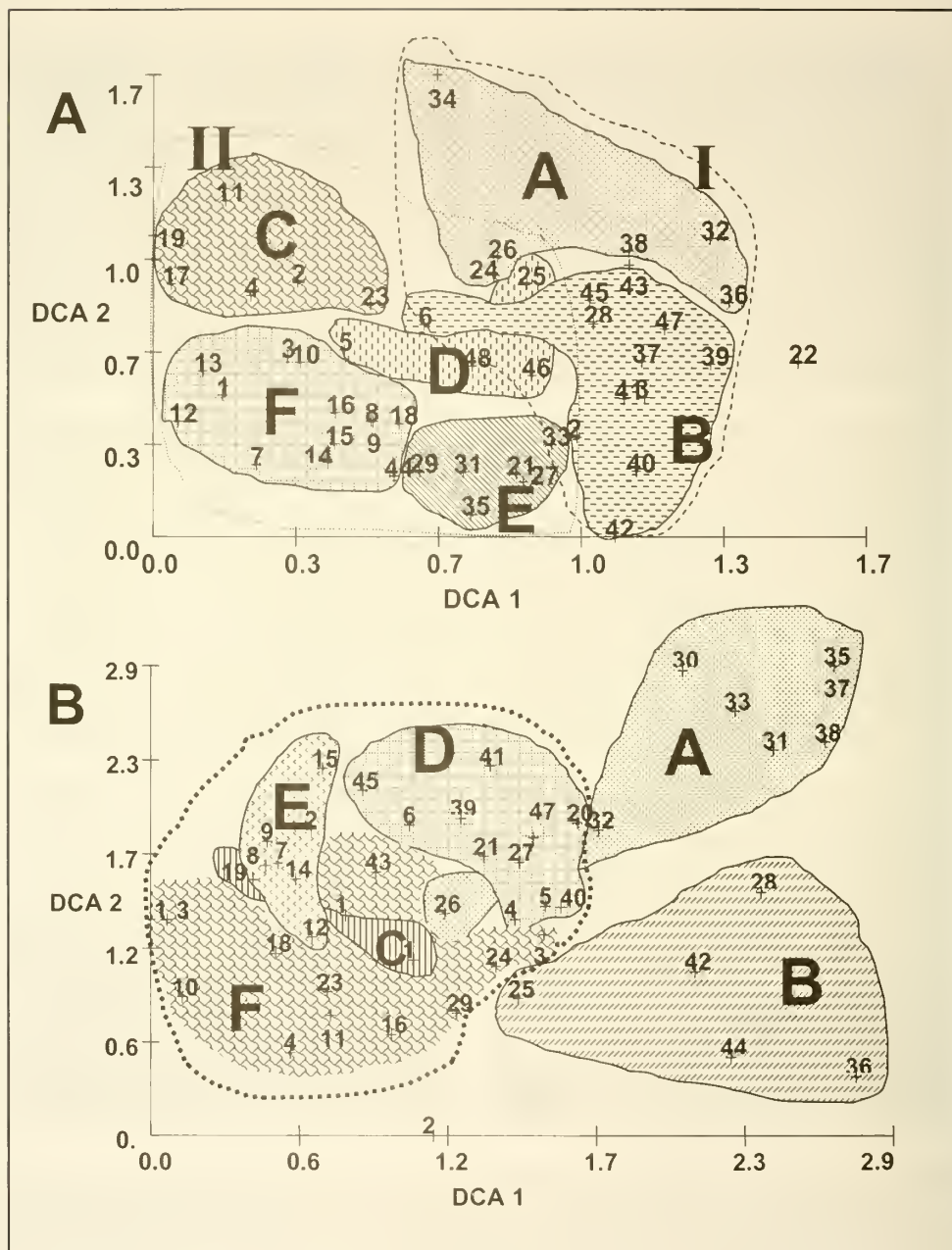


Figure 8. Quitasueño benthic DCA biplots and community structure according to the groups from the cluster analysis of Figures 4 (A. benthic community) and 9 (B. gorgonian community).

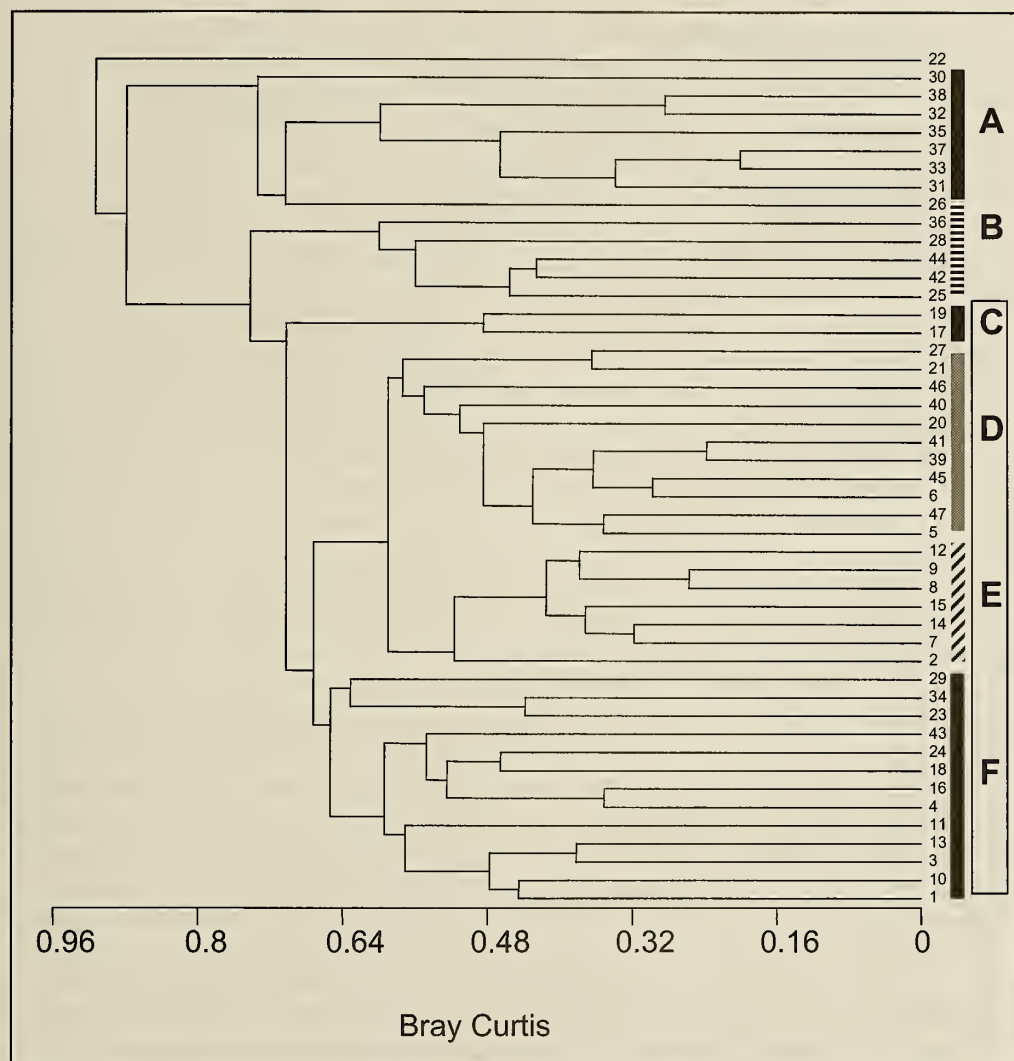


Figure 9. Dissimilarity (Bray-Curtis) dendrogram of the 47 stations Quitasueño Bank with presence of octocorals.

Scrana Bank

Sixty-seven benthic categories among species, genera, functional groups of sessile organisms, and types of inert substrate were found in the Serrana Bank benthic community. The stations were located on the platform including the lagoon basin and the leeward margin of the reef (the fore-reef terrace was not visited because of adverse weather conditions). A total of 48 species of scleractinian corals were observed qualitatively whereas the quantitative stations had between 10 and 30 (min.-max.) coral species and coral cover between 2.8 and 52% (see Table 4 for means and standard deviations). The distribution of substrate cover values per station showed that fleshy macroalgae (e.g., *Dictyota* spp., *Lobophora* spp., *Sargassum* spp. and *Turbinaria* spp.) were usually the most abundant (0.4-59% cover, min.-max.) followed by corals (2.81-52%), filamentous algae (0.152-31%), calcareous macroalgae (1.4-26%), and lesser amounts of other algae and invertebrates (Fig. 10). The cluster analyses produced five minimal clusters and one outlier station (Fig. 11). Clusters A, B, and C corresponded to the stations on patch reefs in the lagoon (1.5-3.0 m, one station 12 m) mostly distributed on '*Acropora palmata* - *Diploria*' habitats (Fig. 3A). Cluster D included stations both in the 'mixed corals' (down to 24 m) and '*Montastraea*' (down to 15 m) habitats on the leeward margin corresponding to the two elbow-like lagoonal basins at the east and north portions of the bank (Fig. 12A). Cluster E included mid-depth stations (7-14 m) mostly in the southwest portion of the lagoon (Fig. 11, Fig. 12A) on '*Montastraea*' habitat or 'scattered *Montastraea*' habitat (Diaz et al., 1996).

In summary, habitats surveyed on Serrana Bank included shallow patch reefs of '*Acropora palmata* - *Diploria*' (frequently with some colonies of *A. cervicornis* and algal ridges of *Porolithon pachydermum*, *Porites furcata* and/or *Millepora complanata*) (e.g., clusters A, B, and C: Fig. 13 A-B and D; Fig. 14 E) and a number of lagoonal reef formations dominated by *Montastraea* spp. (Figs. 13 E-F, 14 F), some dense (e.g., cluster D) or scattered on sand (e.g., cluster E). Other habitats included particular gorgonian-dominated patch reefs in the lagoon that were intermeshed with algal mats (*Lobophora variegata*) (e.g., cluster C: Fig. 13 C) and 'mixed coral' habitats at the leeward margin of the reef (Fig. 14 A).

The inverse analysis of species peak abundances in determined clusters or nests of clusters showed that a few groups presented exclusive species (i.e., species with their >70 peak abundance). Cluster B, for instance, had only two species corresponding to uncommon scleractinian corals (*Agaricia fragilis* and *Mycetophyllia aliciae*: Table 5). Cluster C had peak abundances of two important reef-building corals, *Montastraea faveolata* (>10 % of substrate cover) and *Acropora cervicornis*, whereas Cluster D had 14 species including 10 reef-building corals including *A. palmata* and *Millepora complanata*, two fast-growing corals, and >6% cover values of cyanophyta algae (Table 5; Fig. 14 D). Most other benthic species were distributed within the combined clusters C and D or C-D-E (Table 5). Clusters C and D shared the highest abundance of two important habitat- and reef-building corals, *M. annularis* and *M. franksi* (Table 5). The most abundant species in all the groups were algae species such as *Halimeda* spp., *Lobophora variegata*, *Sargassum* spp., *Dictyota* spp., encrusting coralline algae, and filamentous algae (Table 5).

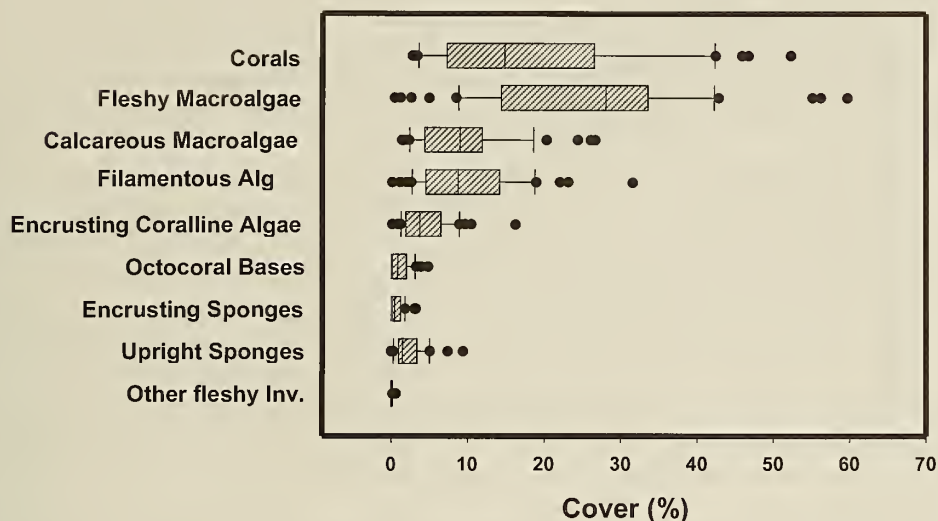


Figure 10. Box plots from the data distribution per station of the major functional benthic groups in the benthic community of Serrana Bank. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars.

The ordination analysis showed an overlap among stations of clusters A and B and among three clusters (C, D, and E) but a separation between these two major groups of clusters (Fig. 15A). Interestingly, clusters D and E overlapped in a number of stations whereas not much spatial overlapping was noted (Fig. 12A). Likewise clusters A and B also had overlap of stations in the ordination (Fig. 15A) but no spatial overlapping. Higher coral cover values were observed in clusters C and D, whereas E had low coral cover. Inversely, C and D had less coral species than cluster E (Table 4). Clusters A and B did not have a representative number of stations from which to draw similar observations, but a major proportion of the variance in the DCA axis 1 of the benthic community analysis was significantly explained in terms of rugosity and depth ($r^2 = 0.724$, $P < 0.001$). With the exception of one shallow station, most urchins were distributed at a few stations from clusters C and E (Table 4). It is important to notice that urchin densities at the sampled environments of Serrana Bank were overall low (*D. antillarum* 0-0.76 individuals m^{-2} , *E. viridis* 0-0.56 ind. m^{-2}). In general, most invertebrate species also had their higher abundances on the deeper stations of cluster E where sponges and octocoral bases had very similar distributions (Table 4). Algae functional groups were also more abundant towards deeper clusters with their major abundances on the border between clusters D and E (Table 4).

Coral diseases were particularly noticeable on Serrana Bank. Minor white plague outbreak areas were observed throughout the Serrana Bank on lagoonal coral habitats deeper than 7 m where the disease was primarily observed. However, on Station 18 (14°

27° 53.24" N and 80° 14' 22.27" W; 12 m depth) mass coral mortality was observed in the northern portion of the bank on some shallow *Montastraea* patch reefs (see details in: Sanchez et al., in prep.). Nonetheless, excluding Station 18, the percentage of affected tissue per species was relatively low (white plague 0-13%; dark spots 0-5%; bleaching 0-2.5%: Table 4). Due to the incidence of disease encountered during the expedition in Serrana, recently dead coral had up to 27% of the cover in Station 18 but usually less than 4%.

The gorgonian octocoral community can be divided into four minimal clusters with a certain spatial coherence at ~75% dissimilarity (Fig. 16). Cluster A only had two stations which were in the lagoon. Cluster B consisted of stations on the shallower patch reefs of the lagoon, mostly on '*Acropora palmata*-*Diploria*' habitat (Fig. 12 B). Cluster C stations were distributed mostly on the leeward margin including '*Montastraea*' and 'mixed corals' habitats down to 24 m. The last cluster D, which consisted of mid-depth stations of lagoonal patch reefs ('scattered *Montastraea*' in Diaz et al. [1996]; '*Montastraea*': Fig. 12 B), was distributed on the southwest end of the reef and the sand bank in algal-mat habitat as well (7-12 m). Although not a perfect match, the structure of the gorgonian dendrogram reminds one of the benthic community structure (Figs. 12 A-B).

Octocoral community cluster A had the peak abundances of *Gorgonia mariae* and *Eunicea* sp. (*E. colombiana* n. sp.: Sánchez, submitted) which were absent in the rest of the stations (Table 6: please note that fore-reef terrace habitats were not sampled). The most abundant species on Serrana Bank had their peak abundances in cluster C, *Pseudopterogorgia bipinnata*, with densities of up to three colonies m⁻² (Table 6). Cluster C also had the peak abundances of *P. elisabethae*, a species of commercial importance elsewhere in the Caribbean, and *Briareum polyanthes*, an encrusting soft coral. Cluster D had peak abundances of 19 species with particular high densities of *Pseudoplexaura* spp. (Table 6), and with colonies reaching over 2 m in height (Fig. 13 C). This highly diverse cluster D corresponded to the 'scattered *Montastraea*' habitat from Diaz et al. (1996) which is a combination of rubble, sand, hard ground and scattered corals that seemed the most suitable habitat for complex octocoral assemblages in the leeward and lagoonal habitats of Serrana Bank.

The ordination analysis for the octocoral community exhibited an interesting continuum gradient along the DCA axis 1 (clusters C, D, and B in that order: Fig. 15B). The gradient seems to be correlated to depth with the highest density of species occurring at the deeper sites (14-24 m). Depth explained a large proportion of the variation in the DCA axis 1 (multiple $r^2 = 0.563$; $P < 0.001$). A correspondence of high octocoral density with high coral cover was noticed (Table 4) which also was significant in a bivariate scheme ($r^2 = 0.357$, $P < 0.001$). Cluster A was largely separated from B-C-D (composed of only two stations, not shown in Fig. 15B). Stations 33 and 35 comprised outliers.

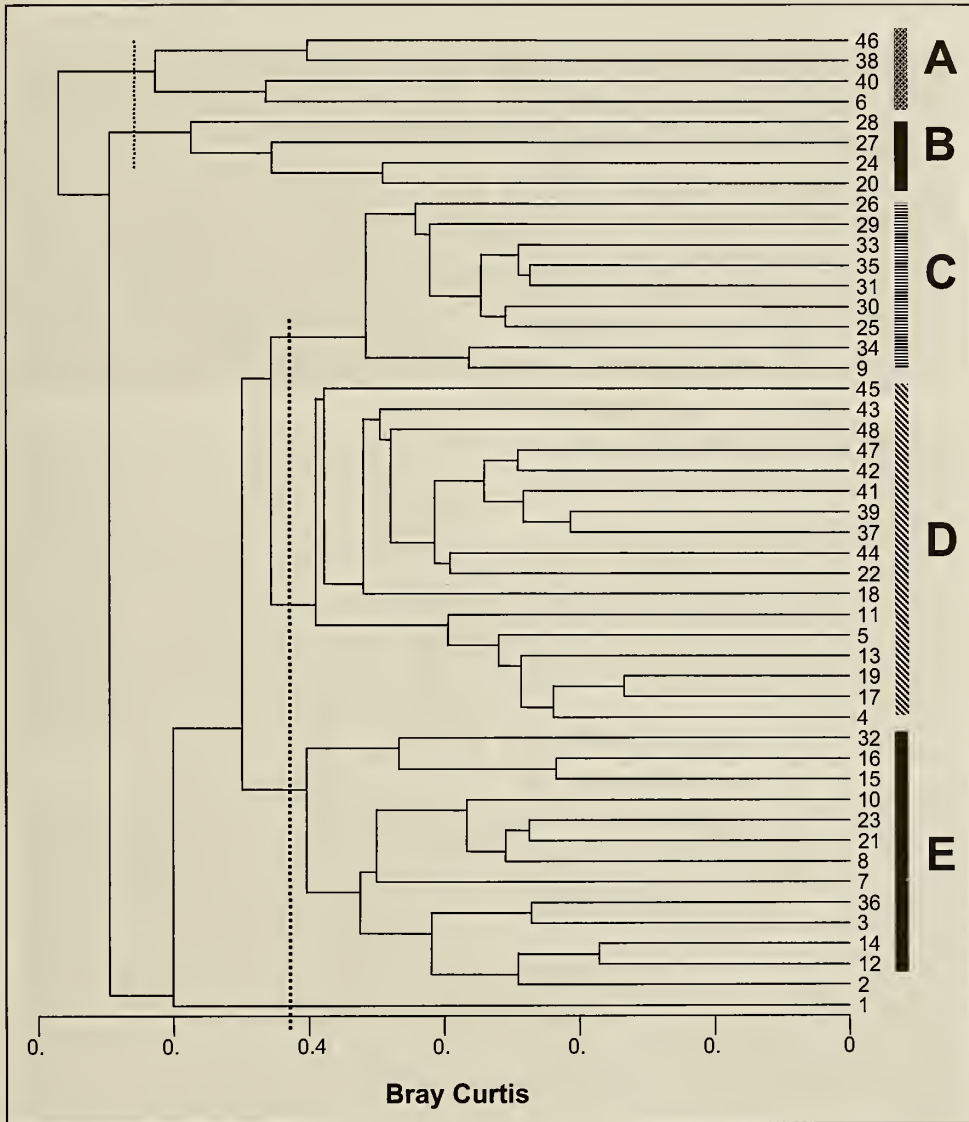


Figure 11. Dissimilarity (Bray-Curtis) dendrogram of the 48 from the benthic stations on Serrana Bank. The dashed line shows dissimilarity division among chosen groups.

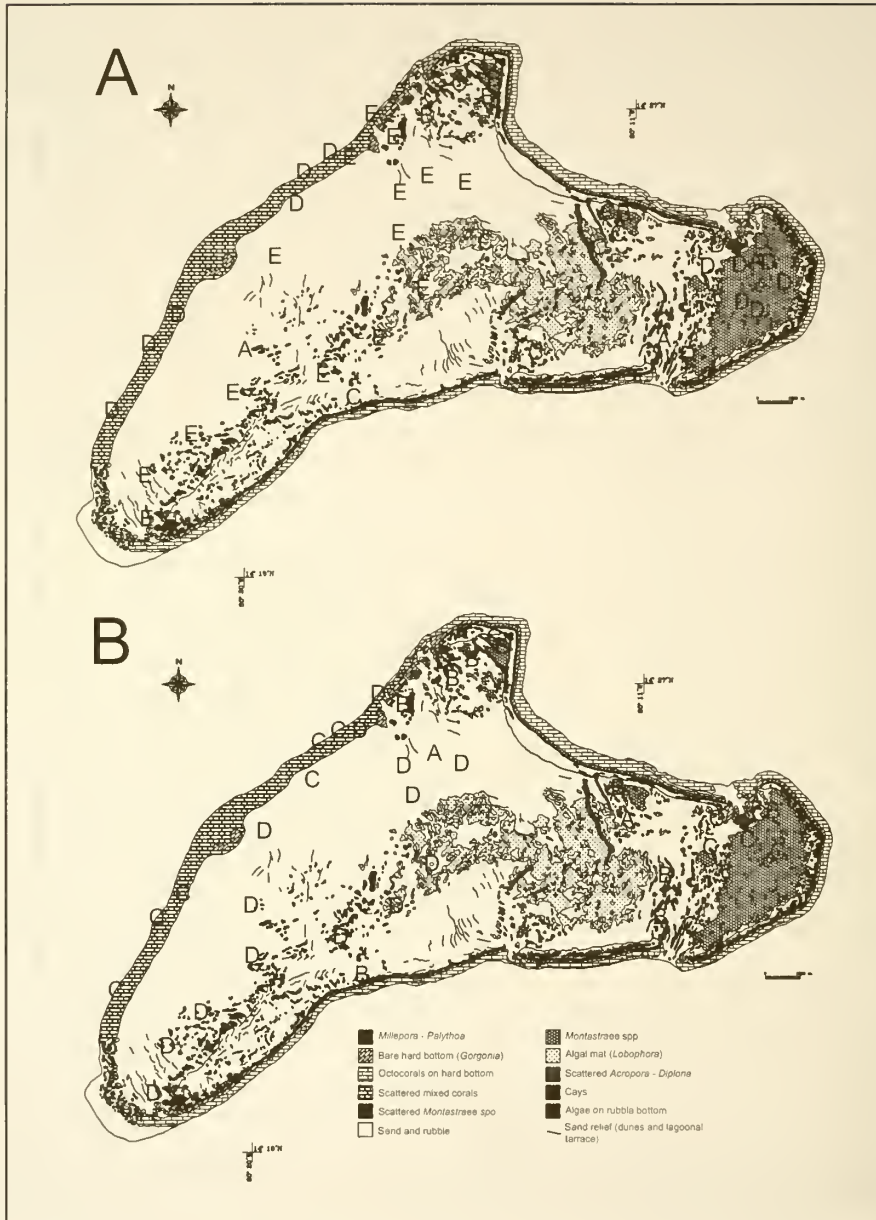


Figure 12. Serrana Bank habitats (modified from Diaz et al., 1996) with locations of stations (approximate). A. Distribution of stations according to cluster from Fig. 11. B. Distribution of stations according to cluster from Fig. 15.

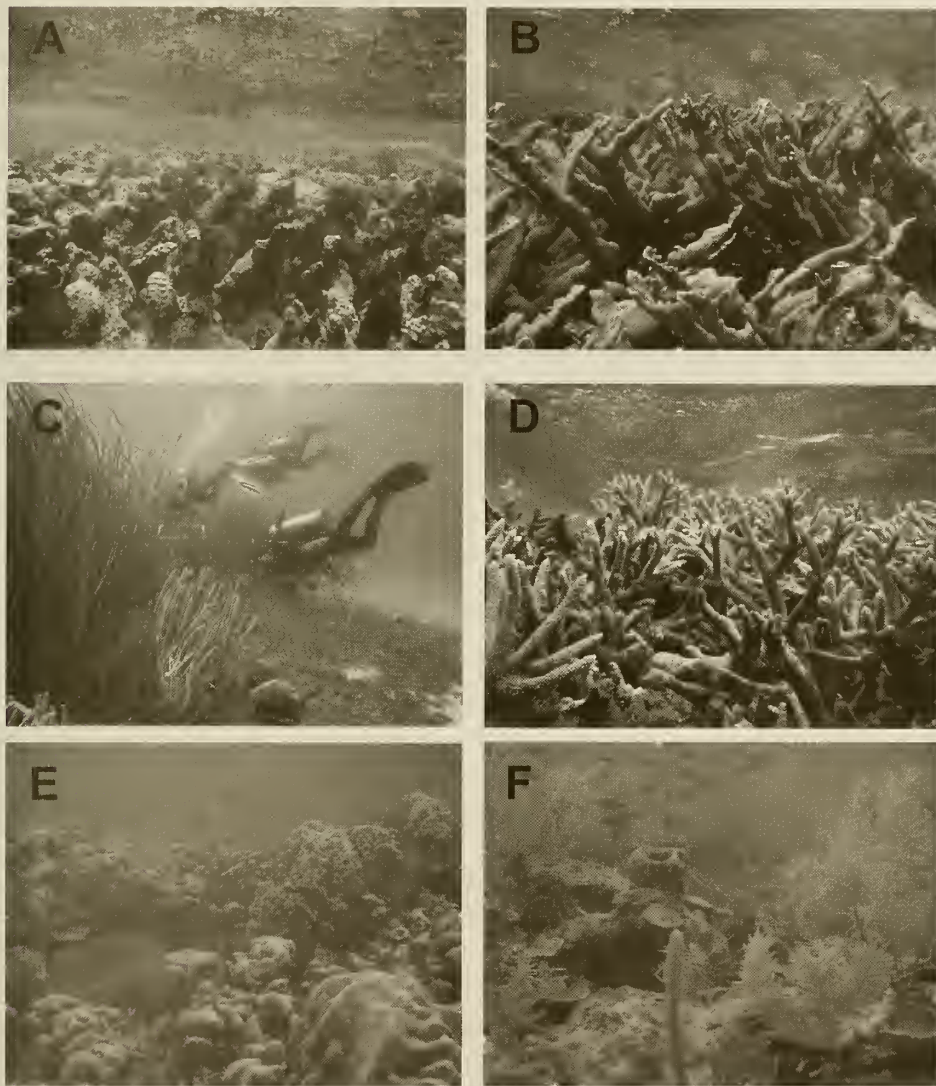


Figure 13. Serrana Bank environments. A. *Porolithon pachydermum* ridge on dead *Acropora palmata*; B. *A. palmata*; C. *Pseudoplexaura* spp. in the lagoon; D. *A. cervicornis*, E. *Montastraea* spp. patch reefs; F. deep leeward margin (*Pseudopterogorgia bipinnata*).

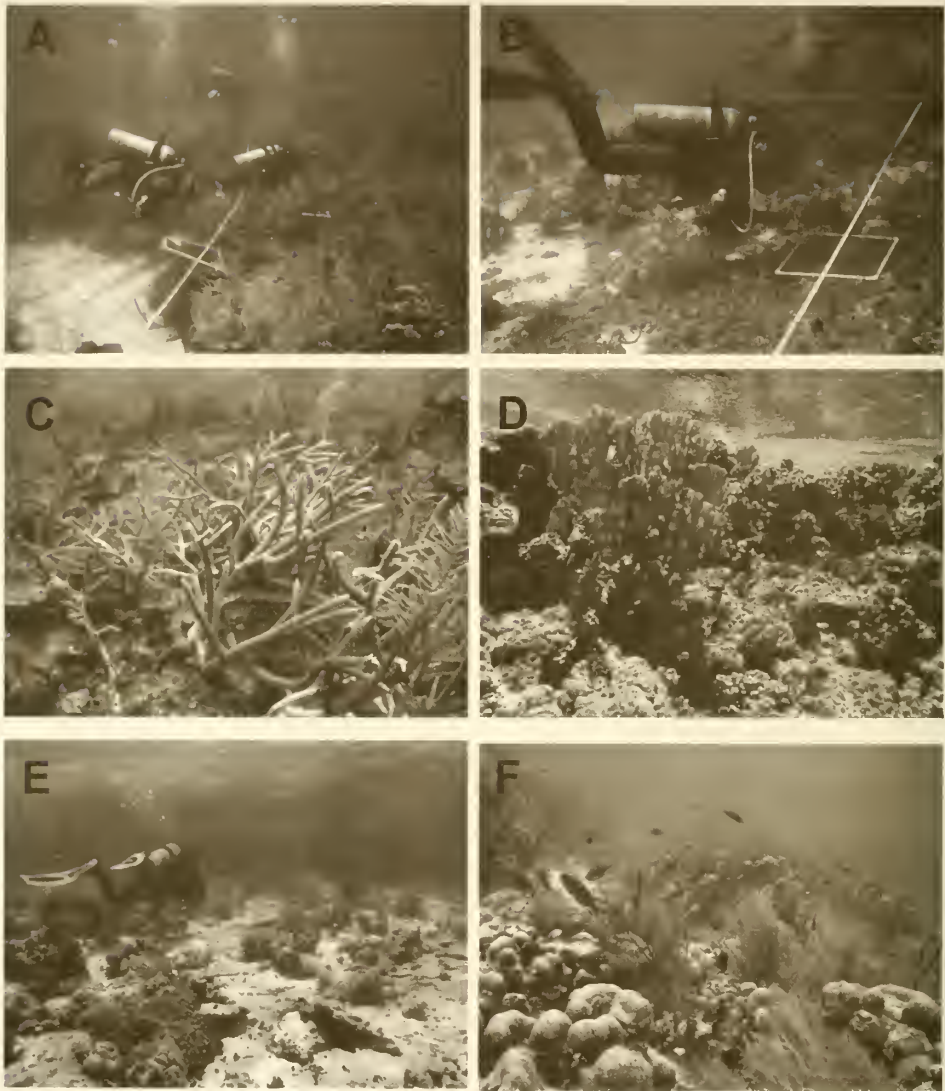


Figure 14. Serrana Bank environments. A. Leeward terrace; B. lagoon basin with *Lobophora variegata* mat; C. *Acropora cervicornis* on the leeward terrace; D. *Millepora complanata* on top of *A. palmata* reef; E. shallow lagoonal patch reefs; F. *Montastraea annularis* in the lagoon and gorgonians (*Pseudopteroorgia bipinnata*).

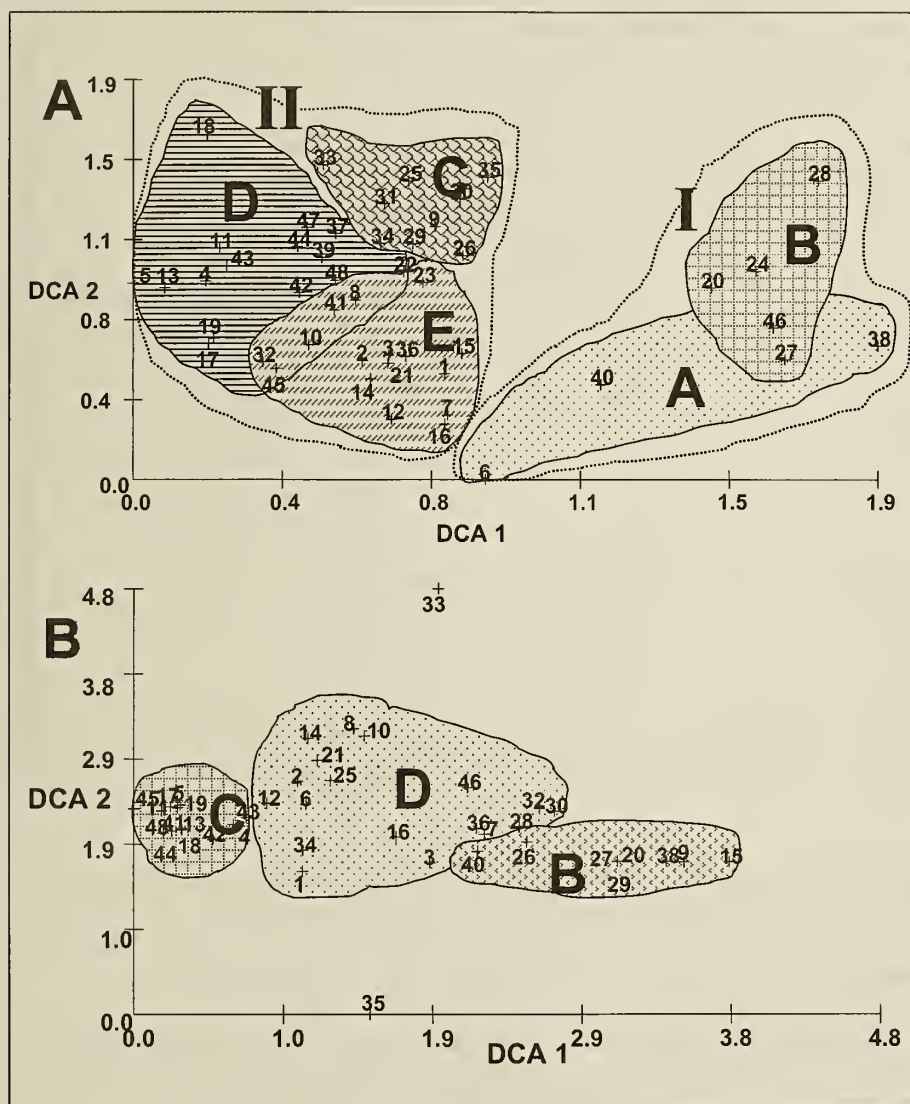


Figure 15. Serrana Bank DCA biplots and community structure according to the groups from the cluster analysis of Figures 11 (A. benthic community) and 16 (B. octocorals, cluster A not shown).

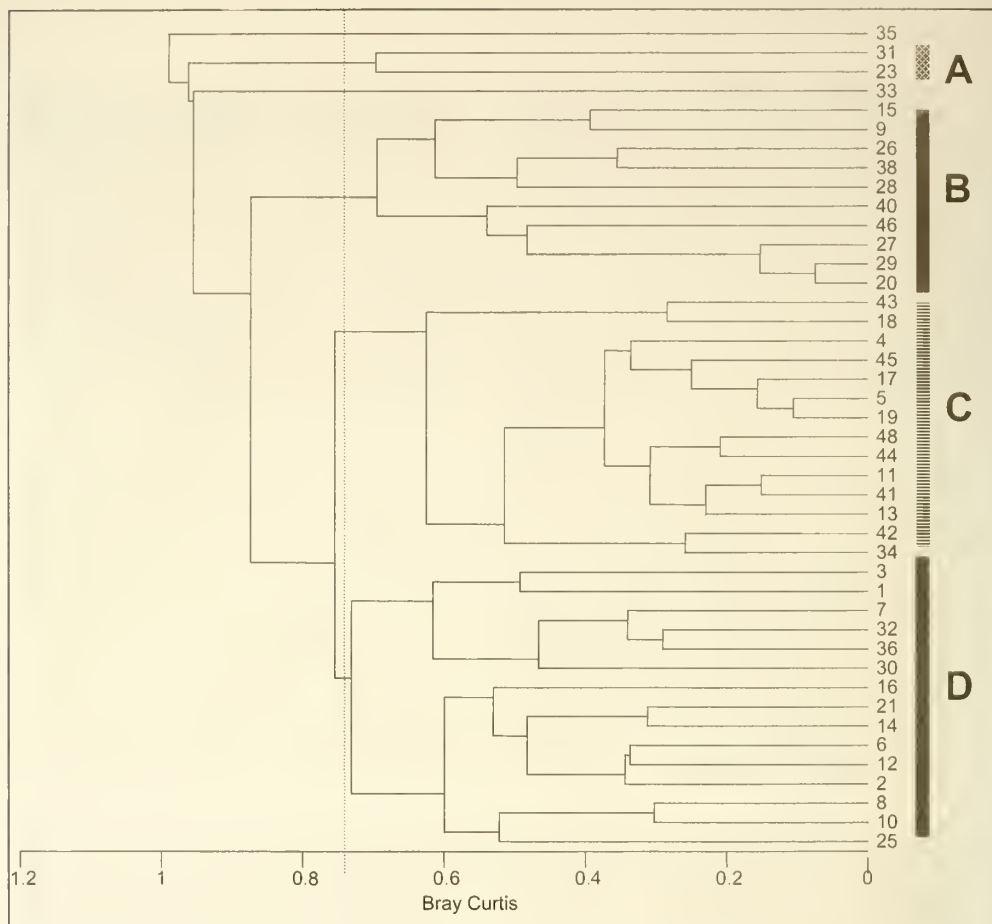


Figure 16. Dissimilarity (Bray-Curtis) dendrogram of the 47 stations on Serrana Bank with presence of gorgonian corals. The dashed line shows the dissimilarity division among groups.

Roncador Bank

Sixty-six benthic categories among species, genera, and functional groups of sessile organisms were found on Roncador Bank lagoonal and leeward reefs; fore-reef habitats could not be visited due to rough sea conditions. We observed 43 species of reef-building corals, 12-29 (min.-max.) species recorded per station, and coral cover from 3.5 to 41%. Overall, fleshy macroalgae were the most abundant sessile reef dweller on the sampled stations (10-59%) followed by hard corals (3.5-41%), filamentous algae (2.5-36%), calcareous macroalgae (1.4-18%), and lesser amounts of other sessile benthic organisms (Fig. 17: Table 7). The benthic community cluster analysis revealed three minimal groups with less than 40% dissimilarity (Fig. 18). Cluster A only had two stations corresponding to shallow (1.8-3 m) lagoonal reefs, probably on small not-mapped '*Acropora palmata-Diploria*' habitats intermingled with '*Montastraea*' (Fig.

19A). Cluster B was a clear group of stations on a deep leeward terrace corresponding to the 'mixed coral' habitat (22-28 m) (cluster B: Figs. 18-19A). Most of the stations were grouped within cluster C with mid-depths typical of the leeward upper platform or lagoonal basin including 'Montastraea' and 'mixed coral' habitats (6-16 m, st. 20 with 1.2 m, Figs. 18 C-19, see also Figs. 20, 21).

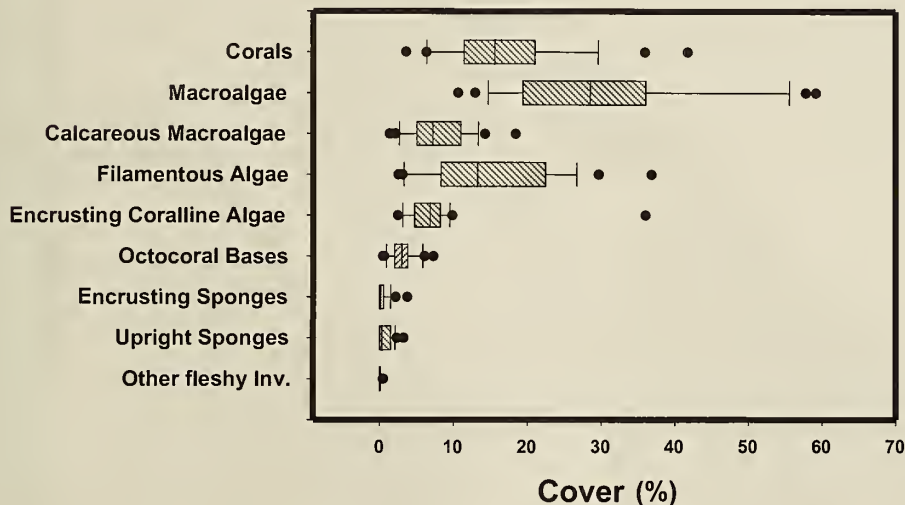


Figure 17. Box plots from the data distribution per station of the major functional benthic groups in the benthic community of Roncador Bank. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars.

Group A presented the peak abundances of the hydrocoral *Millepora complanata* and the coralline alga *Porolithon pachydermun*, two fast growing reef builders with low substrate cover (<3%; Tables 8-9). These are species typical of old and/or dead *A. palmata* stands on shallow lagoonal reefs. Cluster B presented only the peak abundances of some rarely encountered corals such as *Scolymia* spp. and plate corals (*Agaricia* spp.), which were present in high relief areas and under overhangs (e.g., Fig. 20D), whereas cluster C had the peak abundances from 17 coral species, including *Montastraea* spp., *Diploria* spp., and many other sessile organisms typical of a complex and mixed-species zone (Tables 8-9; Figs. 20, 21). As observed in the other banks, the dominant organisms covering the substrate were algae such as *Halimeda* spp., filamentous and encrusting coralline algae (Table 7).

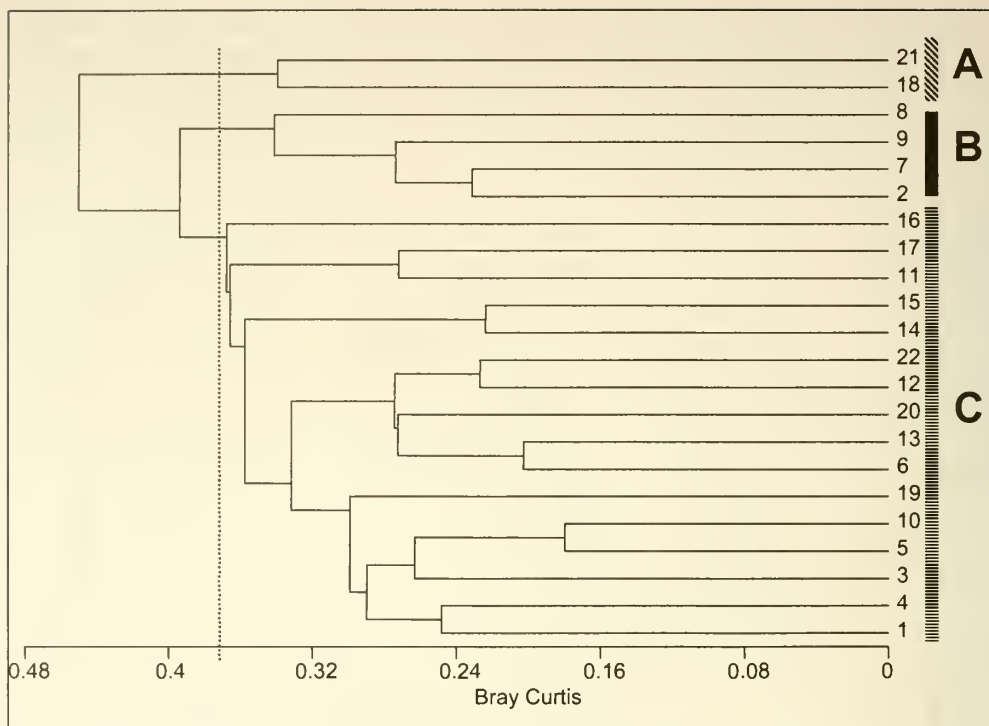


Figure 18. Dissimilarity (Bray-Curtis) dendrogram of the 22 from the benthic stations on Roncador Bank. The dashed line shows dissimilarity division among groups.

The studied habitats on Roncador Bank (please note that fore-reef habitats were not sampled) had two particularities: high bottom rugosity as well as the highest abundance of octocorals among the three banks (Figs. 20 and 21). The ordination analysis presented a fairly discrete distribution of the clusters, with clusters B and C very close to each other in the DCA axes 1 and 2 biplot (Fig. 22A), which is a similar result as the cluster analysis (Fig. 18). Coral cover appeared to correspond with high rugosity (Table 7) and was somewhat statistically correlated ($r^2=0.244$, $P<0.05$). Depth, on the other hand, explained a significant proportion of the DCA axis 1 variation ($r^2 = 0.41$, $P<0.01$). Urchins had low abundances in Roncador Bank with the presence of only a few individuals in lagoonal habitats (*D. antillarum* 0-0.12 ind. m⁻²; *E. viridis* 0-0.56 ind. m⁻²; Table 7). Sponges were particularly abundant on the deeper stations of cluster B and octocoral bases on cluster C (Table 7). Higher abundances of fleshy, filamentous, and calcareous algae were encountered on the lagoonal stations of cluster C which also presented overall low values of coralline algae (Table 7). Coral diseases were also present on Roncador Bank in relatively low proportions in the affected species (e.g., white plague 0-5% average affected tissue per species; dark spots 0-10%; bleaching 0-5%), which were usually less than four affected species per station (Table 7).

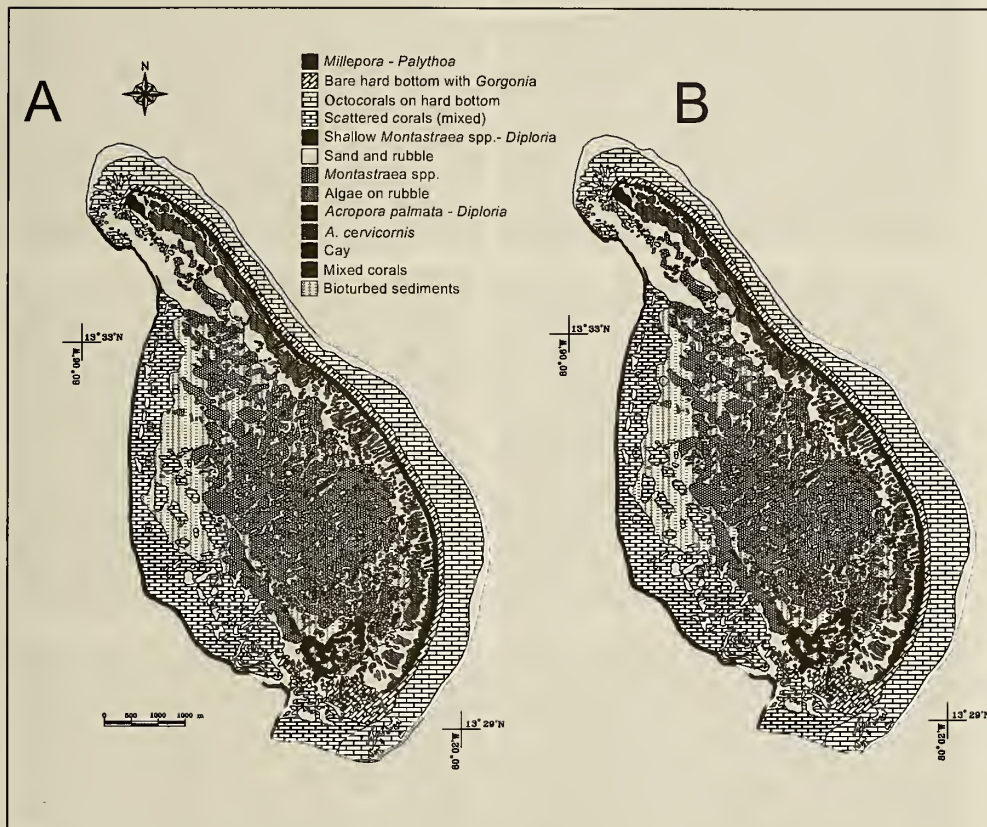


Figure 19. Roncador Bank habitats map (modified from Diaz et al., 1996) with locations of stations. A. Distribution of stations according to cluster from Fig. 18; B. Distribution of stations according to cluster from Fig. 23.

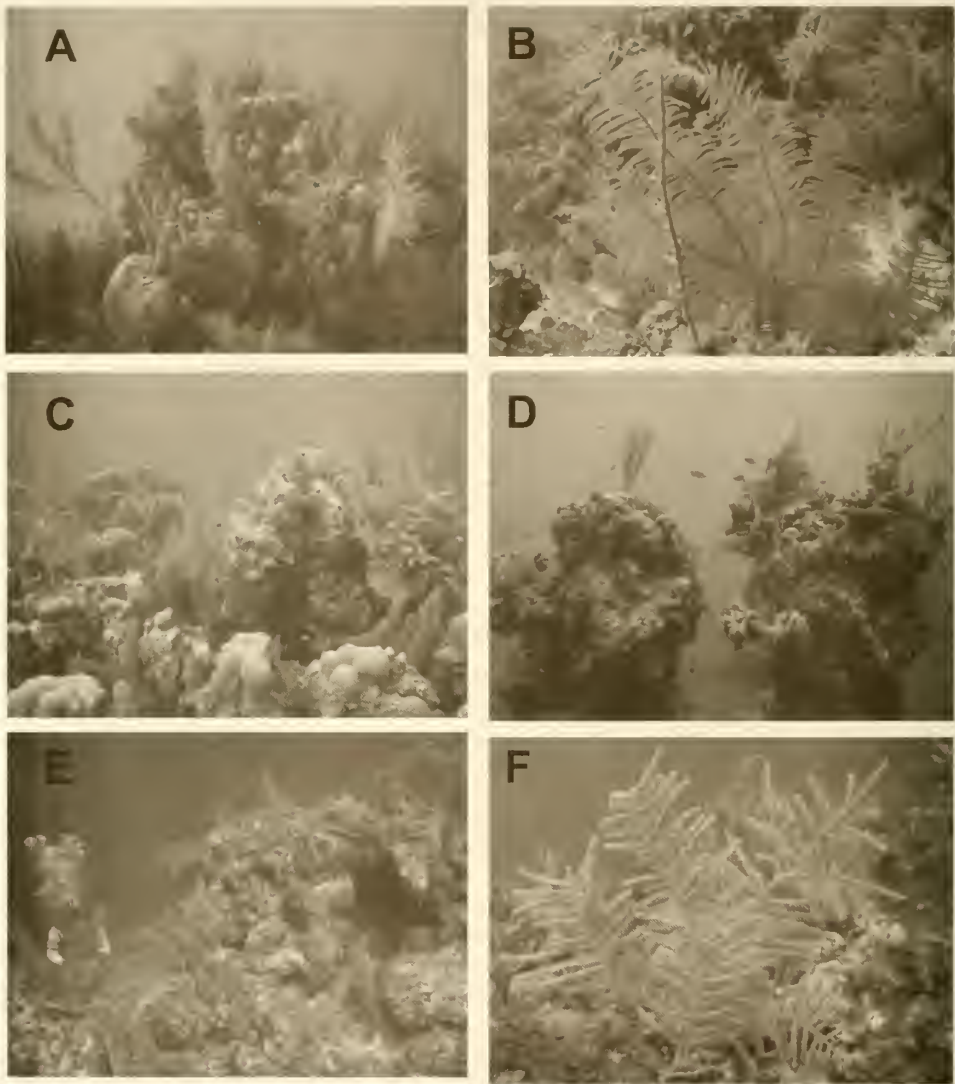


Figure 20. Roncador Bank environments. A. High relief lagoonal patch-reef; B. Leeward margin (*Pseudopterogorgia bipinnata*); C. Lagoonal reef (*Briareum asbestinum*); D. Old pinnacle-like coral head in the lagoon; E. Leeward drop-off; F. *P. elisabethae* in the leeward margin.

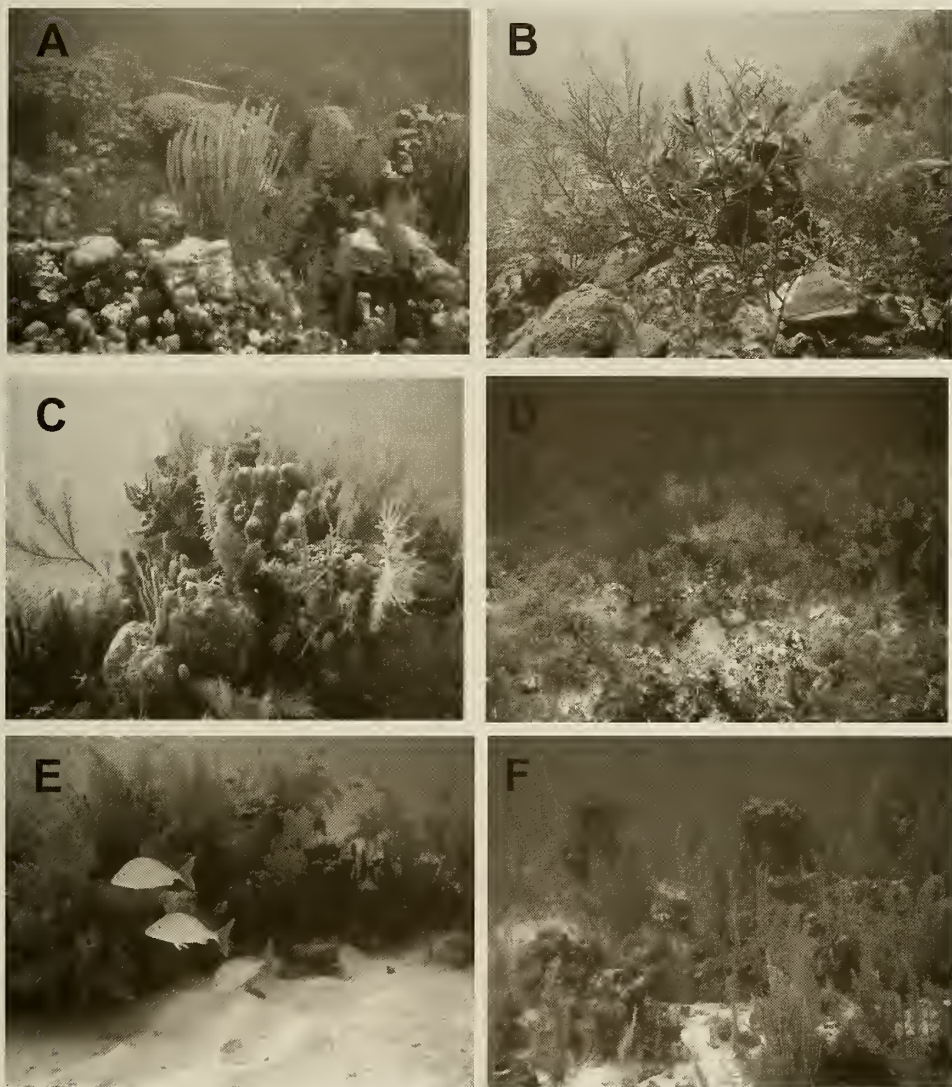


Figure 21. Roncador Bank environments. A. Lagoonal patch-reef; B. Leeward terrace; C. High relief lagoonal reef; D. Leeward terrace; E. Patch reef on sand channel; F. Gorgonians in the leeward margin (*Pseudopterogorgia* spp.).

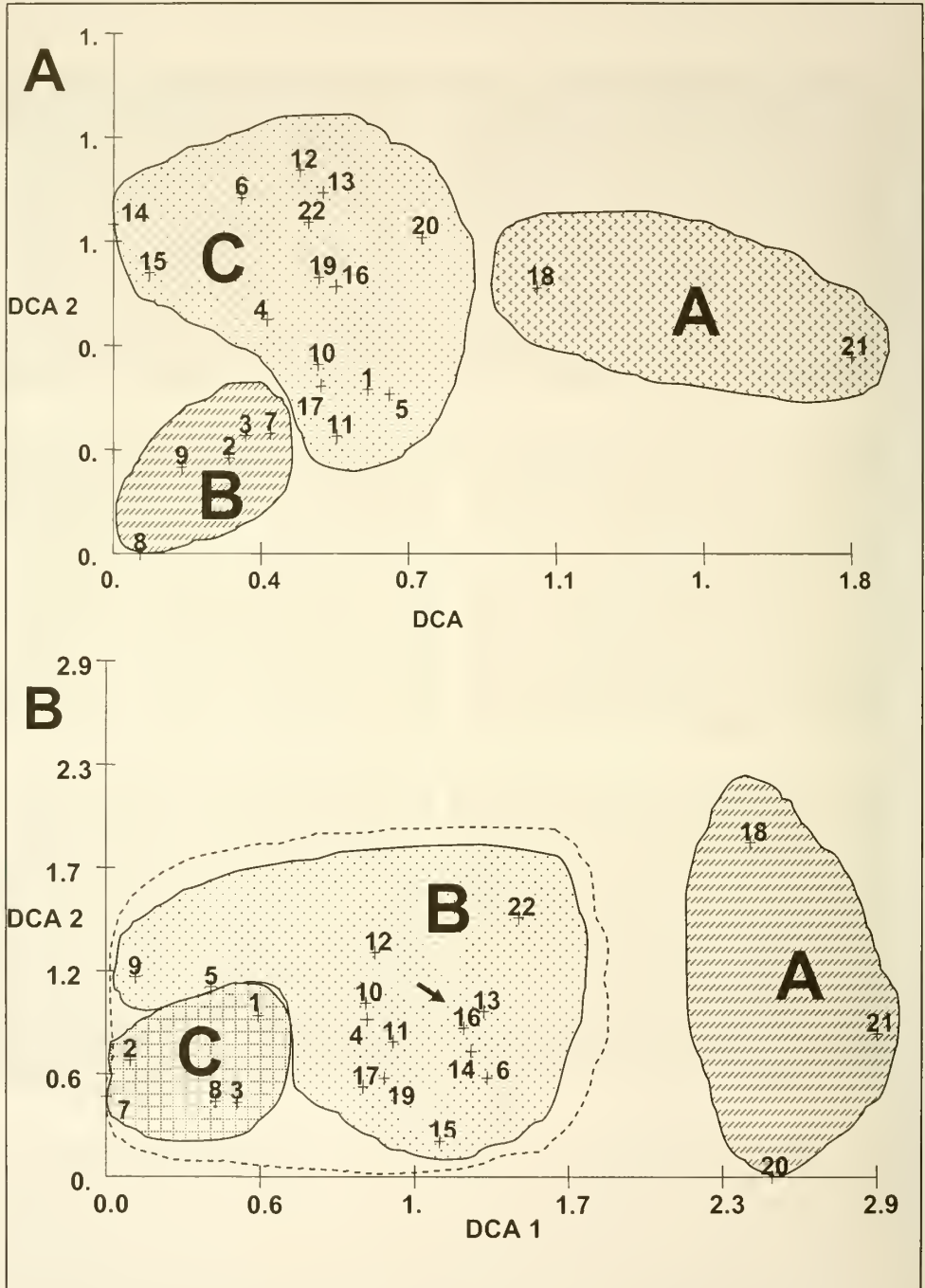


Figure 22. Roncador Bank benthic DCA biplots and community structure according to the groups from the cluster analyses of Figs. 18 and 23.

The octocoral community was also structured in three major minimal clusters of stations with less than 60% of dissimilarity (Fig. 23). Cluster B and C were nearly 50% dissimilar. The groups were somewhat similar to what was found in the benthic community. For instance, clusters B and C (Fig. 23) had almost the same stations as clusters C and B, respectively, in Figure 18 (see also Fig. 19A-B). Eight species such as *Plexaura homomalla*, *Plexaurella grisea* and *Eunicea laxispica* had their peak abundances in cluster A which corresponds to shallow lagoonal patch reefs (Table 9; Fig. 21A). Cluster B had an assemblage of 14 octocoral species corroborating again the 'mixed coral' nature of those stations in the leeward upper platform and some lagoonal reefs (Table 9). Cluster B also included the high peak abundances of the densest species in the sample habitats such as *Briareum asbestinum* and *Pseudopterogorgia bipinnata* (>1 colony m^{-2} ; Table 9; Fig. 21B). The ordination analysis also showed a gradation between clusters B and C, which are composed of stations that overlap in environmental conditions and geographically (Fig. 22B). A large proportion of the DCA axis 1 variation was significantly explained with depth ($r^2=0.762$; $P<0.001$). Octocoral density seemed to correspond to high rugosity and coral cover values (Table 7) but only correlated significantly with the latter ($r^2=0.230$; $P<0.001$).

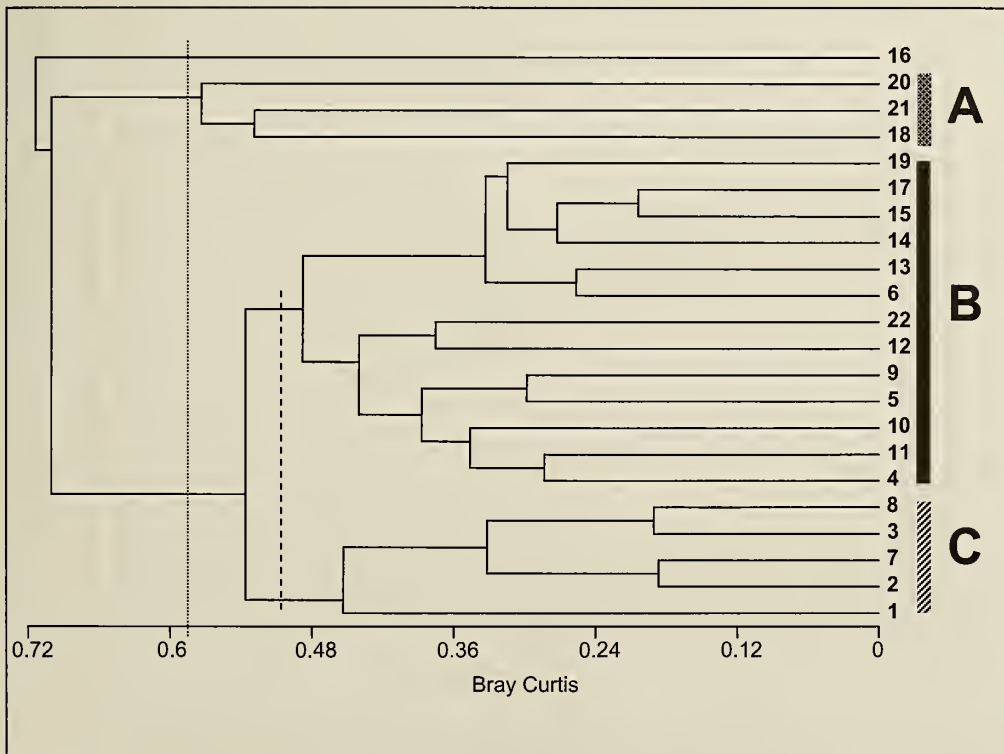


Figure 23. Dissimilarity (Bray-Curtis) dendrogram of the 22 stations on Roncador Bank with presence of gorgonian corals. The dashed line shows the dissimilarity division among groups.

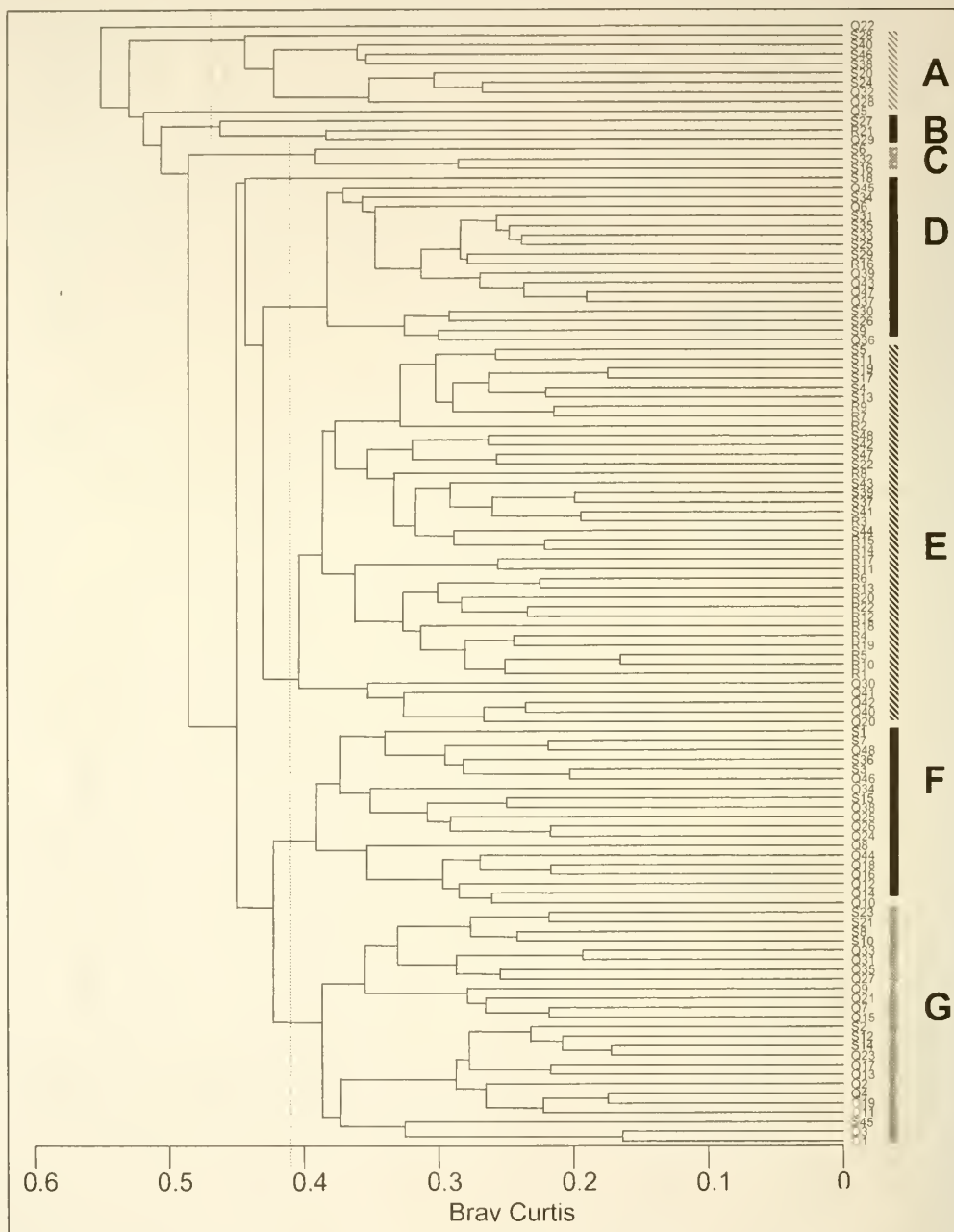


Figure 24 (A). Dissimilarity (Bray-Curtis) dendrogram of the 118 stations from the benthic stations including the three banks (Q. Quitasueño, S. Serrana, and R. Roncador). The dashed line shows dissimilarity division among groups.



Figure 24 (B). Dissimilarity (Bray-Curtis) dendrogram of the 118 stations on the three banks (octocoral data). The dashed line shows dissimilarity division among groups.

Northern Cays

Analyzing the 118 stations of the three banks as one whole community, it was found that there is some structure in terms of major reef (e.g., Serrana, Quitasueño and Roncador Banks) at both benthic (substrate cover) and octocoral assemblages (colonies density) (Figs. 24A-B). A larger number of minimal clusters was found using the same dissimilarity criterion than the analysis of each particular bank (<40%; Fig. 24A) which was expected given that there are many more stations and a much wider geographic range. In the benthic community, most of Roncador stations grouped almost exclusively with Serrana Bank stations but Quitasueño Bank grouped with only a few Serrana stations distributed in every cluster except C (Fig. 24A). A similar pattern was found using the data from the octocoral community (Fig. 24B). The results may be affected by an artifact because we sampled neither the fore-reef terraces on Serrana and Roncador Banks nor the leeward slope margin of Quitasueño Bank. Nonetheless, Roncador and Serrana Banks were similar since a large number of their stations grouped together.

DISCUSSION

The results presented here show once again the great complexity in the organization and structure of coral-reef communities. In spite of this, overall patterns were identified, which explained some aspects of the benthic community organization affecting the three studied Caribbean atolls (Northern cays: Quitasueño, Serrana, and Roncador Banks). Differences and particularities of each coral bank with respect to the others were also distinguished. Our results comprise the most recent survey (April, 2003) in these extensive coral reef areas and some historical differences were noted when comparing with studies from the previous decades. Nonetheless, several high coral- and octocoral-diversity/abundance areas were also recognized which provides flexibility and basis for the design and management of a network of MPAs in the Northern banks.

Patterns in the Northern Cays Benthic Communities

The Northern Cays had between 66 and 73 types of substrates as part of the benthic communities including 43-to-46 species of reef-building corals and 38 species of octocorals. Large ranges of coral cover (2-52%) and octocoral densities (0-15 col. m⁻²) were observed among stations. Octocoral diversity could certainly have been higher since we did not collect specimens and some species could not be differentiated visually to the species level *in situ*, such as most *Pseudoplexaura* spp. (3) and some of the *Eumicea* (3) and *Muricea* (2) species. The octocoral fauna seems to be similar to what is found in the nearby Providencia island barrier-reef complex which comprises 44 species, the highest in the Western Caribbean (Sánchez et al., 1998). The coral diversity is similar to that of any other well-developed Caribbean reef (e.g., Cairns, 1982) or Colombian coast reef (c.g., Sánchez, 1995). High coral-octocoral diversity and abundance were located on wave-protected and mid-depth environments in leeward zones. As suggested by Bak and

Povel (1988, 1989), coral diversity and abundance are arranged (min.-max.) according to prevailing environmental conditions from 'exposed' to 'sheltered' sites. Leeward terraces, including part of the 'mixed coral' habitat, in the Northern Cays represent a suitable environment for both coral and octocoral growth exhibiting almost all coral-octocoral species within a small reef portion which has also been called the 'edge effect' (Porter, 1972; Liddell and Ohlhorst, 1987). Long-term evidence shows that the deeper environments remain as the most constant habitat as opposed to the potentially disturbed shallower reef portions (Bak and Nieuwland, 1995) which in turn allows high coral and octocoral diversity in the 'mixed coral' habitat.

In general, species assemblages within each community structure (e.g., benthic or only octocorals) corresponded to shared species-specific environmental preferences, perceived as minor gradients such as windward-leeward and/or shallow-deep, and, of course, to physical/topographical characteristics which in most habitats were the product of the reef-building corals themselves (e.g., '*Montastraea*' or '*Acropora palmata-Diploria*' habitats). Species-abundance distribution followed the pattern found everywhere in natural communities: few species are highly abundant as compared to most of the species which are rare (see review in Marrugan and Henderson, 2003) which has been called the "inherent rarity" property of ecological communities (e.g., Maina and Howe, 2000). Highly abundant species in the benthic community, i.e., from the three banks and most habitats, were *Montastraea* spp. (reef-building corals), *Pseudopterogorgia bipinnata* (octocoral), and *Lobophora variegata* (fleshy macroalgae). These species are also highly abundant in the southern cays and Providencia Island (Sanchez et al., 1997, 1998; Friedlander et al., in press) and seem to be particular features of the Archipelago region. Other algae can also be considered highly abundant functional groups, which comprised a generalized "background assemblage" that was present in most stations; however, it is expected that a few species, that were treated here at the generic or functional level, are more abundant within each functional group. Nonetheless, since highly abundant species are also known to have a larger geographical distribution than rare species (e.g., Brown, 1995), local abundance of rare species also should be considered important in terms of conservation priorities. Locally abundant species in terms of a particular bank and/or habitat will also be discussed below.

The community structure always separated shallow vs. deeper habitats and exposed from protected environments usually exhibited a continuum which was better explained in terms of depth as the major structuring force in the Northern cays. Certain unpredictable patchiness, though, was found in some shallow habitats. For instance, the north vs. south habitats in Quitasueño Bank presented certain structure independently of the habitat type. This could be due to the heterogeneous effects of past physical disturbances such as hurricanes (e.g., 1987 Joan) and the seasonal effect of the 'Northern's', winds that are potential chronic disturbance events at the Archipelago of San Andres and Providencia (Geister, 1992) and which can irregularly affect leeward portions of the reef. Studies on gorgonians have elucidated that their communities could be distributed along an environmental continuum due to topographic relief and wave-exposure (e.g., Yoshioka and Yoshioka, 1989). This pattern has been found in the gorgonian community of the Southern Cays, where the most contrasting habitats (lagoon

and fore-reef terrace) have a gradual change with the leeward terrace as intermediate in terms of species composition and structure (Sanchez, et al., 1997). Octocoral axes have a determined content of elastic fibers and carbonate depending upon the turbulence regime that each species withstands (Lewis et al., 1992) which explains specificity in contrasting environments. The mix of assemblages seems to occur thanks to the plasticity of some species such as *Pseudopterogorgia bipinnata*, a super abundant species, distributed from 1-to-45 m and with a wide range of wave-exposure as well (Sánchez, in prep.). A reef-building coral example can be observed with species such as the *Montastraea annularis* complex, *M. annularis*, *M. faveolata* and *M. franksi*, where some are found shallower whereas some sustain more sediment exposure (e.g., Van Veghel, 1994). It is important to notice that *Montastraea* spp. provide a high topographic complexity with elevated rugosity and multiple refuges for vagile invertebrates and fish. Consequently, *Montastraea*-dominated reefs in the Northern Cays should be considered among the conservation priorities.

The community-structure patterns found here have also been observed in other ecological communities from the northern banks and the islands of San Andres and Providencia. Similar ordination and classification patterns, as presented here, were observed at the algae community level of Serrana, Roncador and the Southern Cays (Diaz-Pulido and Diaz, 1997). In communities such as reef fish of Serrana and Roncador Banks there were greater differences among reef habitats than among banks and contrasting habitats such as fore-reef terrace and lagoon were not significantly different (Mejia and Garzon-Ferreira, 2000). Likewise, Dahlgren et al. (in prep., this report), in a parallel study including the three banks surveyed here, found an evident fish-community structure among the habitats and also among the banks exhibiting a higher heterogeneity compared to the benthic community structure presented here. Dahlgren et al. (in prep., this report) discuss in detail the likely causes for such heterogeneity in the fish community, which could be of anthropogenic origin. Sponges show even greater heterogeneity among the banks of the archipelago (Roncador, Serrana and Albuquerque), probably due to disparate founder populations and the differential effect of physical disturbance (Zea, 2001). Nonetheless, Zea (2001) noted that the sponge density in the archipelago was lower than in continental areas, possibly due to lower suspended matter in these oceanic banks. We also found low sponge abundance in the northern banks.

Current State of the Benthic Communities

Overall, coral cover in Quitasueño Bank was the highest among the three studied atolls with a mean of 32.9 % (min.-max.: 18.3- 50.7%) versus 19.2 % (2.8-52.3%) in Serrana and 16.9 % (3.5- 41.7) in Roncador Banks. However, it is important to note that the fore-reef terrace habitats were not visited at Serrana and Roncador banks. A survey on the fore-reef terrace by Diaz-Pulido et al. (submitted) of the latter banks revealed a mean coral cover of 19.7 (7.4 SD) which is certainly low compared to 32.9% mean coral cover (cluster F: 18-50% min.-max., Table 1) found at Quitasueño Bank in this study. Coral cover values in other leeward areas of the reef during 1995 had values of 19.4 % (10.4 SD) on the leeward terrace, 37.4% (6.5 SD) in the mid-depth lagoon (< 8m), and 46%

(14.5 SD) in the shallow '*Montastraea*' habitat (Diaz-Pulido et al., submitted), which are values within the range of what was found in Serrana and Roncador Banks during 2003 in this study (Tables 4 and 7). For instance, the leeward terrace of Serrana Bank (e.g., Table 4, Fig. 12A: cluster D) had 11.6 % (5.3 SD) of coral cover, in the analogous habitat in Roncador Bank there was 16.3 % (2.1 SD) (e.g., Table 7, cluster B). Fairly high coral covers were also found in the mid-depth (7-9 m) lagoon sites of Roncador (mean 41.9%, Table 7, Fig. 18A: cluster C). Nonetheless, the same habitat at Serrana Bank had lower coral cover (mean 21.3%; 10.4 SD; Table 4; Fig. 12A: cluster D) than Roncador Bank and the data from 1995 suggest certain reduction in the coral cover at the Serrana Bank lagoon.

Shallow habitats had a more heterogeneous structure among the banks and, since the exact location of the Diaz-Pulido et al. (submitted) stations as well as ours could not be matched exactly due to GPS incompatibilities, accurate comparisons between the two studies could not be made. It was clear that, overall, Quitasueño Bank exhibited the highest coral cover values throughout shallow habitats and Roncador had the highest coral cover in a particular habitat, whereas Serrana Bank presented a reduction in coral cover in the lagoon. It is important to note that the edge of the leeward terrace, where most of the stations were placed at Serrana and Roncador Banks, was not surveyed at Quitasueño Bank. It is unknown if there is such a habitat or if there is a different type of environment. Indeed, one of the stations at the leeward most region of the bank (st 22 Quitasueño) was situated in an atypical rubble and algae (*Avrainvillea* spp.) environment patch in the leeward margin (e.g., Fig. 6 C-D), which also had an atypical fish community (Dahlgren et al. in prep.). Due to time constraints and the enormous size of Quitasueño Bank, a limited number of stations were surveyed and more exploration should be done on the leeward most areas of the bank to depict both geomorphology and benthic communities.

Decline in coral cover and the effects of mass mortalities have been noted in nearby areas of the archipelago (San Andres Island: Zea et al., 1998; Providencia Island: Sanchez et al., 1998). Besides, during 1988 hurricane 'Joan' had affected this area and *Acropora* species have declined abruptly in the coral reefs of San Andres (Zea et al., 1998). Particularly, the urchin mortality associated with the Caribbean-wide die-off in 1983-84 provoked algae blooms with the further loss of coral cover in many areas due to competition and suffocation by algae (e.g., Hughes et al., 1987; Hughes, 1989, 1994; Coyer et al., 1993). An important part of the benthic community in the Northern Cays was indeed dominated by highly opportunistic algae such as *Lobophora variegata* and *Dictyota* spp. These turnovers in the dominant algae species could provoke changes in the normal algae community structure of coral reefs (Steneck and Dethier, 1994) and, indeed, more coral reef-benign types of algae (e.g., coralline, calcareous, and filamentous) were affected and reduced in abundance, which was particularly notable in Serrana and Roncador (fleshy-algae dominated) compared to Quitasueño (coral dominated). It is worth noting that the highest, though very localized and heterogeneous, sea urchin densities were observed in Quitasueño Bank, which suggests a link for a coral-dominated benthic community. In any case, fleshy fish-unpalatable (e.g., *Lobophora* and *Dictyota*) algae were the dominant functional algal group in the three banks.

Besides the multiple aspects enhancing macroalgae dominance in the Northern Cays at present, it is possible to speculate on the degradation of their coral reefs due to coral diseases. The latter was particularly noticeable in the lagoonal habitats of Serrana Bank towards the semi-enclosed lagoonal basins from the north and east elbow-like ends. White-plague (e.g., Dustan, 1977; Dustan & Halas, 1987; Richardson et al., 1998), bleaching, and dark spots (Gil-Agudelo & Garzon-Ferreira, 2001) were observed on several habitats throughout the banks. These diseases have been observed in these areas of Colombian reefs since the mid 1990s (see review in Garzon-Ferreira et al., 2001 and references therein). Effects from white plague were particularly serious in a localized but extensive area of Serrana Bank (Sánchez et al, submitted).

Coral diseases and bleaching have been observed for over two decades in the area of the archipelago and still coral reefs exhibit some high coral cover habitats as signs of resilience in the system (e.g., Providencia: Friedlander et al., in press; San Andres: Friedlander et al., in prep.). The answer to this interesting behavior can be found in coral reefs that have been under a steady state of stressors (e.g., hot temperatures, sediments, nutrients, etc.) which exhibit mean coral cover >40% (e.g., Imelda Bank, Cartagena: Sánchez, 1999; Bocas del Toro, Panama: Guzman and Guevara, 1999). Another substantial amount of evidence comes from the concept of "adaptive" bleaching hypothesis (Buddemeier and Fautin, 1993) and zooxanthellae (coral symbiotic microscopic dinoflagellate algae) specificity and "naïve" reefs (see reviews in Rowan, 1997; Baker, 2003). Corals acclimatize (= "adapt") to changing ocean conditions by changing their symbionts for more resistant species (=clades) of zooxanthellae (clade D: Baker, 2003). Coral reefs from regions that have not been affected by bleaching are considered "naïve" reefs, which in turn can acclimatize and prevent further bleaching. As a hypothesis, remote and oceanic reefs, such as the Northern Cays, are increasingly affected by global change (e.g., global warming) and their coral populations have started to acclimatize which was noticed by the heterogeneous distribution of bleaching throughout the habitats. Nonetheless, it is unknown if the pattern of bleaching as acclimatization appears as heterogeneous as we saw it or if it is a massive event. Further studies on this, including zooxanthellae genotyping, should address this question and the Northern Cays provide an interesting situation for that. It is still unknown if the observed diseases (e.g., white plague and dark spots) could be due to similar complex interactions, but in this case, within the coral microbial flora. In summary, the evaluation of the current state of the Northern Cays coral reefs is optimistic when observing different states of conservation among habitats with a noticeable degree of decline in some semi-enclosed lagoonal reefs in Serrana Bank. Described below are those highly conserved habitats as well as habitats that deserve further observation.

Areas of Special Ecological Interest: Concluding Remarks

Besides the overall patterns of community structure, it is important to highlight areas with high coral abundance and diversity, which in turn will contribute to the planning and zoning of a network of MPAs in the Northern Cays. In addition, some areas of special concern were also identified that could need special management and/or further

monitoring. The areas of high coral abundance and diversity had mean values of coral cover > 32% (most of them >38%), coral species >16, octocoral densities >0.6 col. m⁻² (usually >2.9 col. m⁻²), and octocoral diversity > 4 (usually >8) (Table 10), which are within the ranges of the best conserved coral reefs on the Colombian coast (e.g., Imelda Bank, Colombia: Sánchez, 1999) and southern Caribbean (Bocas del Toro, Panama: Guzman & Guevara, 1999). In the Caribbean Sea, areas with coral cover >32% are considered of high coral abundance (e.g., Edmunds, 2002). Therefore, these identified areas in the Northern Cays, exceeding coral cover >32%, are among the most conserved in Colombia and the Caribbean Sea but in need of protection. Unfortunately, not all the habitats fall in this category but probably more than half of the coral areas in the Northern Cays do. Apparently, these habitats have endured the coral reef decline of the last two decades. In addition, since most of the coral reef areas of the Northern Cays belong to Quitasueño (1320 km² vs. 321 km² [Serrana Bank] and 50 km² [Roncador Bank]: Diaz et al., 2000) and it was the bank with the highest coral abundance and diversity areas, it is recommended that a good portion of the MPAs' network covers this bank (e.g., Fig. 25 A).

The highest gorgonian density ever found in the Colombian Caribbean with up to 22 colonies m⁻² (compare to Sánchez, 1999; Sánchez et al., 1997; 1998), as well as the highest mean coral cover found in the Northern Cays (41.9 %), was observed in the '*Montastraea*' habitats in the lagoon and leeward margin of Roncador Bank. The habitats of high coral abundance and diversity were distributed in the three atolls, but Quitasueño Bank had the largest extent and number of stations in these areas (Table 10; Fig. 25). Overall the areas with high coral/octocoral abundance and diversity were always distributed on '*Montastraea*' and/or 'mixed corals' (one case included '*Acropora palmata* – *Diploria*') and with the exception of the Quitasueño fore-reef terrace, all of them were distributed in the lagoonal basin or the leeward terrace. In terms of choosing ecologically important habitats (i.e., those with high abundance of habitat-forming organisms plus high diversity) the zones described in Table 10 and Figure 25 comprise the best options within the surveyed habitats of the Northern Cays.

Areas of especial interest or concern included those habitats that harbor particular species, or group of species, that are somewhat endangered or are considered rare nowadays in the Caribbean. For instance, sea fans *Gorgonia ventalina* and *G. flabellum* have undergone mass mortalities and in other regions of the archipelago they are very scarce (Southern Cays: Sánchez et al., 1997; San Andres island: Zea et al., 1998; Providencia island: Sanchez et al., 1998). The fore-reef terraces from Serrana and Roncador particularly harbored among the most dense and abundant sea-fan zones, just as observed in 1995 (Diaz et al., 1996a; Sánchez, unpublished). Together with Bushnell shoal off the Colombian coast (Diaz et al., 1996c), Roncador and Serrana comprise some of the few places that were not affected by the sea fan mortality that occurred in the 1980s (Smith et al., 1996; Nagelkargen et al., 1997). The fore-reef terrace habitat in these two banks is largely inaccessible due to high seas and rough conditions which was the reason we could not survey such habitats during this study. Nonetheless, it is a habitat of importance due to the luxuriant sea fan populations observed during 1995, which could be a natural reservoir of this species for the Archipelago of San Andres and Providencia

and the southwestern Caribbean as well. A further exploration of this habitat is necessary.

Gorgonian octocorals, which are distributed worldwide, have been for many years harvested as precious and semiprecious jewels (e.g., red coral in the Mediterranean, gold and pink coral in Hawaii, Grigg, 1994; sea fans and sea candelabrams in the Caribbean, pers. obs., etc.). In the nearby islands of San Andres and Providencia as elsewhere in the Caribbean (e.g., Bahamas, Mexico, Puerto Rico, Belize, Panama, Trinidad and Tobago, pers. obs. J. A. Sanchez and A. R. Acosta-de-Sanchez), native handicrafts ("artesanias") containing gorgonian octocoral axes are commonly encountered. It is unknown what the effects of this type of extraction is on the populations of gorgonian octocorals, but in some regions of mainland Colombia, such as Isla Grande, Rosario Islands (pers. obs. J. A. Sanchez), octocorals are locally extinct due to past extractive activities whereas protected nearby islands harbor luxuriant communities (e.g., isla Tesoro: Sánchez, 1995). The success of a network of marine reserves is found in the conservation of the integrity of the ecosystem (e.g., McClanahan and Arthur, 2001). Therefore, octocoral rich habitats should also be considered among the areas of high coral abundance and diversity. Nonetheless, there are also some important reasons to consider some octocoral-rich areas special. For instance, Caribbean gorgonian octocorals (sea fans, feathers, candelabrams, etc.) also harbor a great diversity of secondary metabolites in their soft tissues, which have been demonstrated to have a strong anti-inflammatory, anti-carcinogenic, and anti-tumor activity in the laboratory (see review in Rodriguez, 1995). Gorgonians are the dominant component of the underwater landscape in southwestern Caribbean atolls (Sánchez et al., 1997). Some Caribbean gorgonians, such as *Pseudopterogorgia elisabethae*, have been harvested for the extraction of anti-inflammatory metabolites by the cosmetic industry (e.g., Mayer et al., 1998), which has brought along economic benefits for local communities in the Bahamas. Some areas of Roncador and Serrana banks (Table 10, Fig. 25 B-C) distributed on the leeward margin, in the drop-off edge particularly, presented a high abundance of this species (up to 2.4 col. m⁻²), which could be a potential zone for the study or exploitation of this species. Nevertheless, a proper survey of the populations is necessary to access the potential risk of that kind of extractive activity.

The largest concentration of reefs in the Northern Cays is the reticulate network of *Montastraea* spp. patch reefs on the north and east elbow-like lagoonal basins of Serrana Bank (Diaz et al., 1997). Although there were over 10 species of reef-building corals with their highest peak abundances in this area, the distribution of coral cover was highly heterogeneous (Table 10; Fig. 25 B). The community seemed the same as in the leeward margin (Fig. 12 A, cluster D) with dominance of algae (cyanophyceae, filamentous, and *Lobophora variegata*), which we could speculate as the aftermath of recurrent disease and/or bleaching outbreaks. This scenario was observed in some of the stations that presented acute white plague disease outbreak despite *Montastraea* spp. have shown high resilience and regeneration rates in other Caribbean reefs (e.g., Sánchez et al., 2004). The dominant reef-building coral in most stations was *Montastraea franksi*. Surprisingly, the shallow habitats or "flats" of some of these patch reefs exhibited very healthy small aggregations of *Acropora palmata* (sometimes together with *A. cervicornis* and *Porites furcata*), particularly towards the west lagoonal basin. This kind of habitat harbors a rich fish community (Lerman, 1999; see also Dahlgren et al., this report). It is

worth noting than the *A. palmata* ridges were observed in isolation of each other, 100-200 m apart in the closest cases, and usually small (< 100 m²) including depths ranging from 10-to-20 m in the sandy areas between the patches. It is known that the main spatial propagation strategy of Caribbean acroporids is fragmentation (e.g., Lerman, 2000) which in turn generates clonal dominance. This has been considered as a weakness of Caribbean reefs where just a few species and a few genotypes dominate extensive reef areas, which make them vulnerable due to poor genetic diversity. Susceptible genotypes, to disease for instance, could perish resulting in a population collapse. In Serrana Bank we are most likely have the scenario where multiple genotypes of *A. palmata* co-occur due to the heterogeneous distribution of shallow patch-reef flats in the lagoonal basin. Hypothetically, higher genetic diversity could be found in this patch reef as compared to fringing coastal reefs. In addition, dead skeletons of *A. palmata* were observed colonized by *Porolithon pachydermum* and its symbiotic chiton *Choneplax lata*, which comprise one of the fastest reef-building systems known (Littler et al., 1995). In brief, both the vulnerability to disease of the deep parts and the ecological importance of the heterogeneous shallow *Acropora* habitats made the reticulate patch-reef network of Serrana an area of special concern deserving of further detailed studies and complex management.

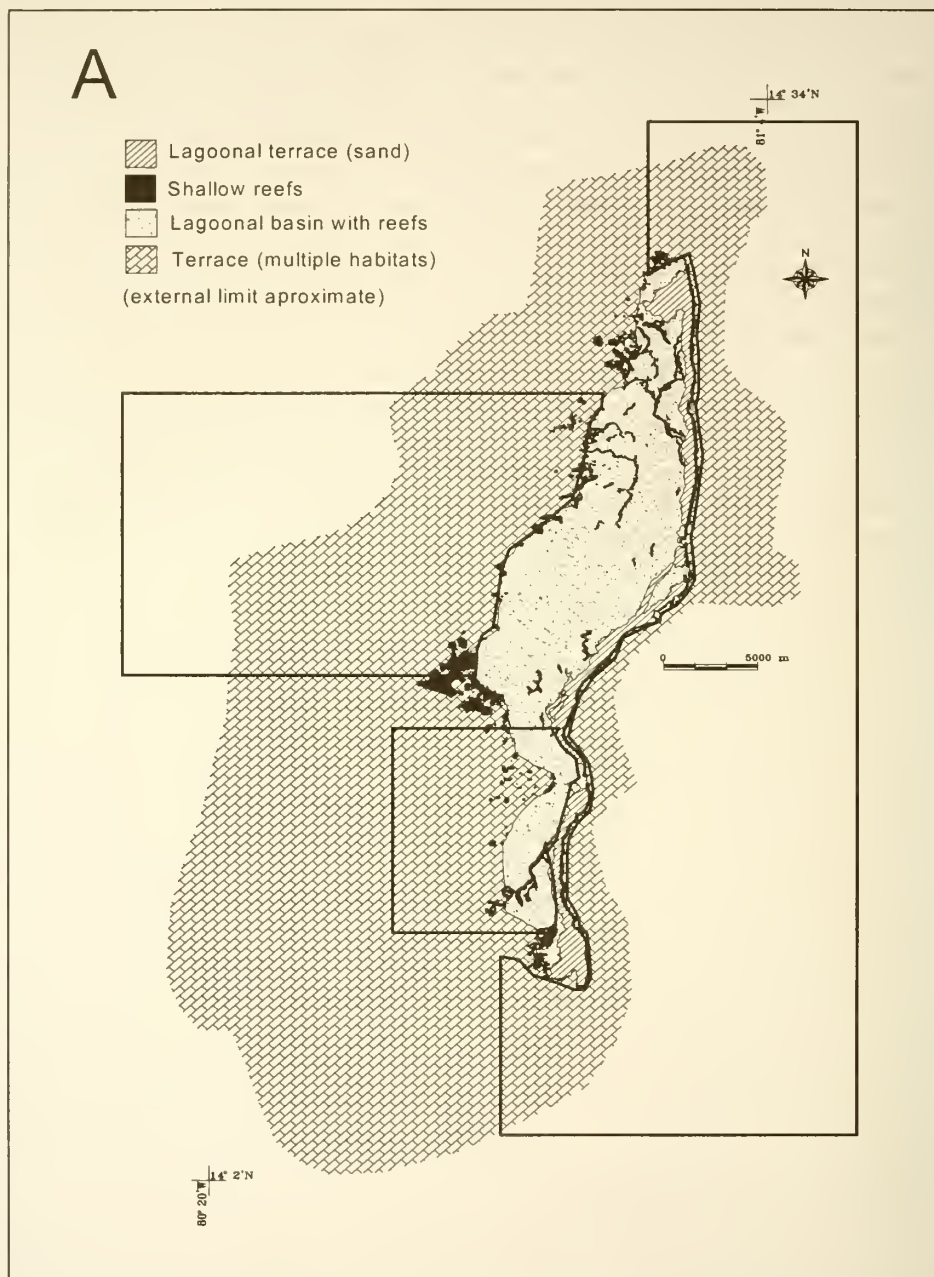


Figure 25 (A). Areas of particular interest. A. high coral and abundance and diversity areas in Quitasueño Bank (see details in Table 10).



Figure 25 (B). Areas of particular interest. B. high coral and abundance and diversity areas in Serrana Bank (open polygon) and areas of particular concern (hatched polygons) (see details in Table 10). 'Bare hard bottom *Gorgonia*' habitat is also an area of particular concern.

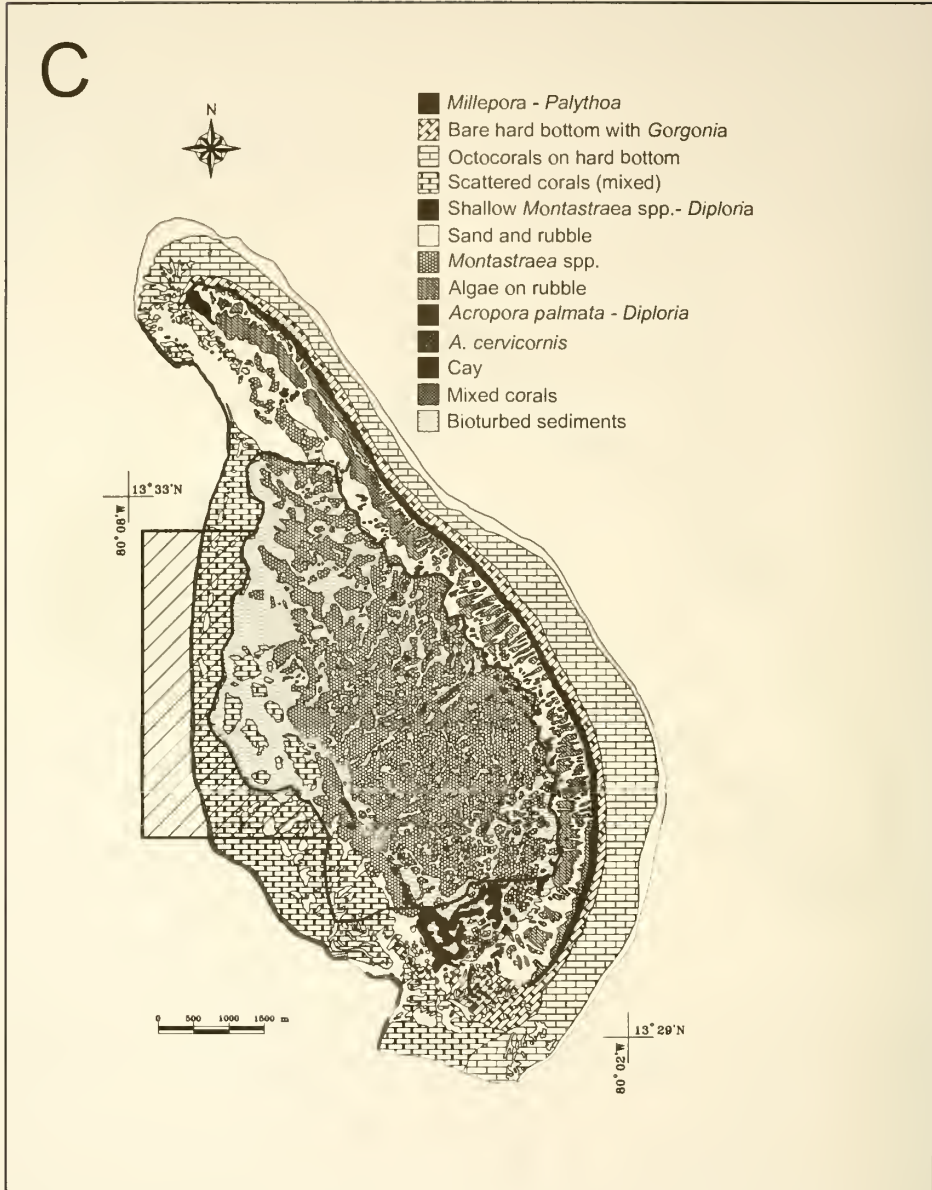


Figure 25 (C). Areas of particular interest. C, high coral and abundance and diversity areas in Roncador Bank (open polygon) and areas of particular concern (hatched polygon) (see details in Table 10). 'Bare hard bottom with *Gorgonia*' habitat is also an area of particular concern.

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Table 1. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Quitasucño bank according to the classification of Figure 4.

Cluster	A		B		C		D		E		F	
	X	sd	X	sd	X	sd	X	sd	X	sd	X	sd
Rugosity index	0.370	0.198	0.610	0.169	0.122	0.084	0.461	0.036	0.507	0.135	0.267	0.121
Depth (m)	6.267	4.407	10.109	5.855	16.401	2.339	14.700	7.596	12.136	3.768	19.240	4.948
Coral species	18.571	3.155	20.364	4.105	16.500	3.271	19.750	2.630	23.667	4.274	22.538	3.230
Octocoral species	6.000	4.967	8.727	2.412	9.333	1.751	11.250	1.708	11.833	3.545	10.692	2.810
SUBSTRATE COVER (%)												
Coral cover	26.859	5.361	35.666	5.365	22.263	4.121	36.277	10.201	39.678	5.486	35.664	4.423
Encrusting algae	4.951	2.762	5.979	1.902	7.812	1.739	4.712	2.955	8.882	0.997	4.775	2.470
Calcareous macro algae	15.695	4.923	11.953	3.501	10.197	1.856	8.757	3.645	9.793	2.019	7.302	2.246
Fleshy macro algae	26.849	7.883	19.290	3.566	32.674	4.820	19.237	6.451	15.298	5.930	22.877	4.152
Filamentous algae	3.633	1.883	8.900	5.406	13.930	1.175	4.065	2.850	9.070	2.077	5.938	3.443
Other fleshy invertebrates	0.523	0.921	1.148	1.384	-	-	1.156	0.833	0.636	0.774	0.215	0.424
Encrusting sponges	0.590	1.011	1.190	1.290	0.831	1.250	0.216	0.431	4.095	2.528	2.229	1.528
Erect Sponges	3.542	2.121	1.988	1.434	4.203	1.744	4.731	2.630	3.039	1.209	6.915	1.651
Octocoral bases	1.767	2.365	3.644	1.994	2.781	1.691	5.542	2.900	4.350	3.503	6.287	1.972
Bare hard ground	7.605	0.878	2.701	2.788	0.293	0.455	4.019	2.975	1.620	0.458	4.696	3.742
Rubble	2.900	0.753	1.376	1.681	-	-	2.245	2.417	0.269	0.421	0.535	0.776
Sand	5.087	1.510	6.164	2.896	5.016	2.458	9.042	1.315	3.270	2.235	2.565	2.224
DENSITIES												
Octocorals (colonies m ⁻²)	2.186	4.536	2.955	1.664	2.500	0.772	4.050	0.676	4.450	4.333	4.431	2.184
Diadema antillarum (individuals m ⁻²)	0.143	0.361	0.124	0.159	-	-	0.005	0.010	0.127	0.192	0.003	0.008
Echinometra viridis (ind. m ⁻²)	0.029	0.046	0.304	0.369	-	-	-	-	3.617	3.948	0.002	0.006
CORAL DISEASES												
White Plague-WP (No. affected spp.)	0.857	0.900	1.000	0.775	0.667	0.516	0.250	0.500	1.333	1.211	0.385	0.650
WP-average of percentage affected tissue	1.002	1.825	1.136	1.518	0.667	0.516	0.003	0.005	0.778	0.655	0.232	0.438
Dark Spots-DS (No. affected spp.)	0.857	1.069	1.273	1.009	1.333	1.366	1.500	0.577	2.167	1.329	1.385	0.506
DS-average of percentage affected tissue	0.147	0.376	2.017	2.870	1.000	0.843	1.754	1.751	2.972	1.714	0.852	0.981
Bleaching (No. affected spp.)	0.571	0.787	1.000	0.632	1.000	1.095	0.750	0.957	1.667	0.816	0.923	1.188
BL-average of percentage affected tissue	0.146	0.377	1.910	2.844	0.667	0.516	0.503	0.998	1.333	0.516	0.425	0.639

Table 2. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 6 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Quitasueño Bank. Shaded cells represent values >5% of coral cover.

SPP	A	B	C	D	E	F	s22
Cluster A							
Penicillus spp.	0.45	0.03	-	0.04	-	-	-
Turbinaria spp.	12.12	0.49	0.67	5.05	0.10	0.13	-
B							
Dyctiosoma sanctitomae	-	0.03	-	-	-	-	-
Isophyllia sinuosa	-	0.01	-	-	-	-	-
Hydroids	-	0.01	-	-	-	-	-
Caulerpa spp.	-	0.14	-	-	0.03	-	0.16
Montastraea franksi	-	1.67	0.03	0.66	0.68	0.08	-
A+B							
Diploria clivosa	0.07	0.11	0.03	-	-	0.01	-
Agaricia humilis	0.02	0.04	-	-	-	0.01	-
Montastraea faveolata	2.72	6.35	0.03	5.50	0.31	0.75	-
Montastraea annularis	4.17	7.22	0.06	0.66	3.09	0.70	-
Favia fragum	0.14	0.11	-	-	-	0.01	-
Diploria labyrinthiformis	0.50	0.28	-	-	0.18	0.14	-
Ventricaria spp.	0.02	0.03	-	-	-	-	0.16
C							
Anadyomene spp.	0.05	-	0.39	-	-	-	-
Padina spp.	-	0.08	0.56	-	-	0.01	-
E							
Mycetophyllia aliciae	-	-	-	-	0.10	-	-
F							
Agaricia lamarcki	-	-	-	-	-	0.03	-
Mycetophyllia sp.	-	-	-	-	-	0.01	-
Palythoa spp.	-	-	-	-	-	0.01	-
Porolithon pachydermum	-	-	-	-	-	0.06	-
Agaricia spp. (plate-like)	-	0.01	-	-	-	0.09	-
Madracis decactis	-	-	-	-	0.03	0.08	-
Leptoseris cucullata	-	0.04	-	-	0.03	0.23	-
E+F							
Montastraea cavernosa	-	-	0.22	-	1.07	1.18	-
Colpophyllia natans	-	0.20	-	-	0.44	0.44	-
Mycetophyllia ferox	-	-	-	-	0.10	0.04	-
Stephanocoenia intersepta + Solenastrea hyades	0.09	0.03	0.06	-	1.40	0.19	0.16
E+F+D							
Millepora alcornis	0.09	0.08	0.70	0.49	0.55	0.91	0.16
Acropora cervicornis	-	0.06	-	0.08	0.10	0.09	-
E+F+D+C							
Wrangellia spp.	-	-	0.03	-	-	0.03	-
Meandrina meandrites	-	-	0.14	0.04	0.05	0.10	-
Neomeris spp.	0.05	-	0.08	-	-	0.06	-
Styopodium zonale	0.79	0.03	5.28	0.66	-	3.10	-
Erect sponges	1.22	0.59	2.18	1.52	1.07	3.54	4.82
Siderastrea siderea	0.93	0.60	1.93	2.01	2.39	2.62	0.93
Octocoral bases	0.97	1.00	0.98	1.35	2.37	2.39	0.62
Encrusting sponges	0.11	0.25	0.48	0.16	1.51	0.79	3.11
Dictyota spp.	11.33	4.60	28.45	16.63	7.33	11.44	2.49
Other Algae	0.02	0.01	0.11	0.04	-	0.03	-
Laurencia spp.	-	0.21	0.92	-	-	0.10	-
Anadyomene spp.	0.05	-	0.39	-	-	-	-
St. 22							
Dictyoteris spp.	-	-	-	-	-	-	3.89
Avranvillea spp.	0.02	-	0.03	-	0.03	-	14.77
All groups							
Dichocoenia stokesi	-	-	-	0.08	0.05	0.09	0.78
Diploria strigosa	0.79	0.03	0.11	0.41	0.13	0.80	-
Ricordea florida	-	0.03	-	0.12	0.03	-	-
Sargassum spp.	7.61	10.39	8.64	8.54	16.31	10.99	-
Rhipocephallus spp.	0.07	0.07	0.17	0.12	-	0.06	-
Scolymia spp.	-	0.04	0.03	-	0.10	-	-
Manicina aerolata	-	0.03	0.03	-	-	0.03	-
Filamentous algae	4.76	10.29	13.08	5.25	10.30	4.88	1.71
BARE HARD GROUD	15.88	3.34	0.25	5.01	0.75	16.17	14.15
Isophyllastraea rigida	-	0.04	-	-	-	0.05	-
Cyanophyceae	0.27	2.70	4.58	-	0.96	0.93	0.93
Lobophora variegata	5.78	20.83	12.02	3.28	15.50	17.34	25.04
Porites astreoides	0.43	1.25	0.17	1.03	0.91	0.89	0.16

Table 2. continued.

SAND	9.40	10.81	7.24	25.04	3.59	6.36	8.55
Halimeda spp.	4.67	4.15	2.91	1.68	7.57	2.40	5.91
Eusmilia fastigiata	-	0.13	0.03	0.04	0.13	0.04	-
Agaricia agaricites	3.29	3.11	0.73	3.69	2.81	2.36	-
Porites furcata	0.32	0.31	-	0.21	0.21	0.32	-
Scolymia wellsi	-	0.03	-	-	-	0.03	-
Mussa angulosa	-	0.01	0.03	-	-	-	-
Udotea spp.	1.00	0.14	0.03	1.15	0.44	0.05	0.16
Mycetophyllia lamarckiana	-	0.07	-	-	-	0.06	0.16
Agaricia fragilis	0.02	0.04	-	-	0.08	-	-
Porites porites	0.32	0.85	0.03	1.15	0.29	0.18	-
RUBBLE	3.44	1.84	-	5.13	0.08	0.49	-
Sea Anemones	0.11	0.13	-	0.08	0.08	0.04	-
Galaxaura spp.	0.09	0.18	0.17	0.08	0.03	-	-
Tunicates	0.07	0.03	-	0.04	0.16	-	2.33
Amphiroa spp.	1.02	0.35	0.17	-	0.13	0.18	1.09
Agaricia humilis	0.02	0.04	-	-	-	0.01	-
Jannia spp.	1.52	0.60	0.50	0.04	0.16	0.16	6.38
Porites divaricata	0.02	0.28	-	-	0.13	-	0.78

Table 3. Octocoral community assemblages (colonies m^{-2} per group letter). Boxes mark the species characteristic of each successively nested cluster as in Figure 14 (R-mode analysis, 70% relative abundance of each species in determinate cluster[s]). Quitasueño bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

SPP	A	B	C	D	E	F	St22
Cluster B							
Briareum polyanthes	-	0.060	-	-	-	-	-
Eunicea laxispica	-	0.080	-	0.009	-	-	-
Plexaura homomalla	-	0.920	-	0.127	-	0.023	-
D							
Muricea pinnata	-	-	-	0.009	-	-	-
Eunicea clavigera	-	-	-	0.073	-	0.023	-
F							
Plexaurella spp.	-	-	-	-	-	0.015	-
Muricea spp.	-	-	-	-	-	0.008	-
Pseudopterogorgia acerosa	-	-	-	-	-	0.069	-
Pterogorgia anceps	-	-	-	-	-	0.008	-
Plexaura kuna	-	-	-	-	-	0.008	-
Eunicea tourneforti	-	-	-	0.009	0.071	0.146	-
Pterogorgia citrina	-	0.040	0.150	-	0.029	0.162	-
Eunicea fusca	-	-	-	0.045	0.043	0.185	-
Muricea atlantica	-	-	-	0.009	-	0.023	-
Muricea muricata	-	-	-	0.018	-	0.038	-
D+E							
Pseudopterogorgia bipinnata	0.025	-	0.150	1.882	3.057	0.077	-
Gorgonia mariae	-	-	-	0.082	0.186	0.031	-
Muriceopsis flavida	-	-	-	0.527	0.529	0.231	-
Eunicea colombiana*	-	-	0.100	0.118	0.029	0.031	-
D+E+F							
Plexaurella fusifera	-	-	-	0.018	0.086	0.054	-
Eunicea tayrona*	-	-	-	0.036	0.186	0.077	-
Pseudopterogorgia americana	0.013	0.060	0.250	0.027	0.500	0.554	0.100
Muricea elongata	-	0.020	0.050	0.045	0.014	0.046	-
Plexaura flexuosa	0.013	0.180	-	0.055	0.086	0.231	-
Pseudoplexaura spp.	-	0.280	0.250	0.264	0.129	0.231	-
Eunicea pallida	-	0.020	-	0.009	-	0.015	-
Gorgonia ventralina	0.050	0.080	0.200	0.036	0.186	0.138	-
Plexaurella nutans	-	0.040	-	0.018	0.029	0.008	-
Plexaura kukenthali	0.013	0.460	0.050	0.236	0.014	0.246	-
Plexaurella grisea	0.013	0.520	0.200	0.445	0.043	0.146	-
D+E+F+C							
Eunicea calyculata	-	-	0.100	0.009	0.014	-	-
Eunicea laciniata	0.013	-	0.100	0.009	-	0.015	-
D+E+F+C+B							
Eunicea mammosa	-	0.240	-	0.127	0.043	0.062	-
Eunicea asperula	-	0.040	-	0.009	-	0.023	-
Briareum asbestinum	0.338	0.380	-	0.627	-	0.100	-
Plexaurella dichotoma	-	0.120	-	0.018	0.029	0.023	0.200
Eunicea succinea	0.050	0.840	-	0.109	0.100	0.015	-
Pseudoplexaura crucis	0.038	0.120	-	-	-	0.031	-

* Sánchez (submitted).

Table 4. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Serrana bank according to the classification of Figure 11.

Cluster	A		B		C		D		E	
	X	sd	X	sd	X	sd	X	sd	X	sd
Rugosity index	0.230	0.132	0.643	0.318	0.672	0.187	0.516	0.211	0.306	0.184
Depth (m)	5.839	4.379	4.875	5.318	8.226	1.088	15.681	6.234	10.497	2.032
Coral species	7.500	4.722	3.000	2.160	4.778	1.856	4.882	3.059	11.818	4.119
Octocoral species	14.000	2.608	13.750	0.957	17.556	3.046	21.235	5.142	17.545	4.034
SUBSTRATE COVER (%)										
Coral cover	6.844	4.551	14.394	5.779	38.931	12.137	21.321	10.461	8.873	7.075
Encrusting algae	2.801	2.170	7.149	6.452	3.932	1.694	4.750	3.400	4.317	2.494
Calcareous macro algae	6.826	4.207	8.565	2.853	12.974	7.660	12.413	5.706	4.234	2.676
Fleshy macro algae	17.098	17.838	23.781	15.679	18.561	6.734	22.901	11.208	39.926	12.587
Filamentous algae	2.913	2.093	14.568	6.444	9.708	5.051	12.157	7.270	9.813	6.514
Other fleshy invertebrates	0.026	0.063	-	-	0.101	0.167	0.113	0.206	0.028	0.063
Encrusting sponges	0.363	0.635	0.752	0.670	0.881	0.617	1.260	1.142	0.399	0.255
Erect Sponges	2.026	1.850	0.765	1.032	1.387	0.635	2.713	2.728	3.576	1.698
Octocoral bases	1.661	1.229	0.199	0.300	0.376	0.477	1.324	1.315	1.530	1.318
Bare hard ground	6.316	8.127	7.758	9.029	4.662	6.352	4.143	5.082	4.858	8.107
Rubble	12.741	13.282	8.836	9.952	1.141	2.331	2.970	6.074	2.083	4.187
Sand	40.386	28.154	13.233	7.402	7.347	5.792	13.935	12.136	20.361	12.940
Recently dead coral	-	-	-	-	0.801	1.423	1.639	6.556	-	-
DENSITIES										
Octocorals (colonies m ⁻²)	1.783	1.566	0.150	0.191	0.656	0.606	3.500	3.659	2.209	1.424
Diadema antillarum (individuals m ⁻²)	-	-	0.205	0.371	0.042	0.045	0.008	0.014	0.004	0.008
Echinometra viridis (ind. m ⁻²)	-	-	0.085	0.114	0.236	0.308	0.015	0.030	-	-
CORAL DISEASES										
White Plague-WP (No. affected spp.)	0.333	0.516	0.500	0.577	2.556	2.128	3.118	3.160	0.182	0.405
WP-average of percentage affected tissue	0.333	0.516	0.500	0.577	2.556	2.128	3.118	3.160	0.182	0.405
Dark Spots-DS (No. affected spp.)	0.500	0.837	-	-	0.778	0.972	0.765	1.091	2.000	1.342
DS-average of percentage affected tissue	0.333	0.516	-	-	0.391	0.781	0.903	1.484	1.510	1.112
Bleaching (No. affected spp.)	0.333	0.516	0.500	0.577	0.222	0.441	0.588	0.939	0.455	0.688
BL-average of percentage affected tissue	0.003	0.005	0.253	0.498	0.002	0.004	0.461	0.807	0.185	0.602

Table 5. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 18 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Serrana bank. Shaded cells represent values >5% of coral cover.

SPP	A	B	C	D	E	St 1
B						
Agaricia fragilis	-	0.04	-	-	-	-
Mycetophyllia aliciae	-	0.04	-	-	-	-
C						
Acropora cecicornis	-	-	0.16	-	-	-
Montastraea faveolata	0.16	0.20	10.12	0.72	0.95	2.27
D						
Galaxaura spp.	-	-	-	0.02	-	-
Isophyllastraea rigida	-	-	-	0.02	-	-
Mussa angulosa	-	-	-	0.02	-	-
Mycetophyllia ferox	-	-	-	0.01	-	-
Solenastraea bourroni	-	-	-	0.01	-	-
Avranvillea spp.	-	-	-	0.07	0.01	-
Acropora palmata	0.18	-	-	0.38	-	-
Agaricia spp. (plate-like)	-	-	-	0.10	0.03	-
Eusmilia fastigiata	-	-	0.02	0.09	0.01	-
Manicina aerolata	-	-	-	0.05	0.01	-
Mycetophyllia lamarckiana	-	0.08	-	0.12	-	0.15
Recently dead coral	-	-	0.79	1.68	-	-
Cyanophyceae	0.23	2.26	0.95	6.35	0.83	0.15
Scolymia spp.	-	-	-	0.03	-	0.15
Millepora complanata	0.21	-	-	0.21	-	-
E						
Laurencia spp.	-	-	-	-	0.03	-
C+D						
Anadyomene spp.	-	-	0.05	0.04	-	-
Penicillus spp.	0.18	0.04	0.79	1.13	-	-
Agaricia lamarcki	-	0.08	0.14	0.23	0.01	-
Colpophyllia natans	-	0.16	0.84	1.07	0.03	1.52
Caulerpa spp.	-	-	0.09	0.04	0.01	-
Jania spp.	-	0.40	1.03	0.27	0.01	0.15
Tunicates	-	-	0.09	0.02	0.01	-
Porites furcata	0.29	0.12	1.17	0.25	0.04	-
Montastraea franksi	0.03	5.81	2.76	7.01	0.36	-
Montastraea annularis	0.70	2.30	15.96	1.86	2.99	-
Encrusting Sponges	0.36	0.48	0.88	1.32	0.40	-
Amphiroa spp.	-	0.44	0.59	0.12	0.07	-
Riphocephalus spp.	0.10	0.12	0.07	0.23	0.04	-
Porites porites	0.26	0.69	2.22	4.07	0.40	1.36
Agaricia agaricites	0.52	1.94	2.09	3.00	1.12	2.73
Porolithon pachydermun	0.08	0.12	0.07	0.11	-	-
Agaricia humilis	-	0.04	0.02	0.04	-	0.15
Halimeda spp.	6.36	7.95	10.13	10.16	3.70	2.27
C+D+E+st. 1						
Leptoseris cucullata	-	-	0.05	0.05	0.01	0.45
Ricordea florida	-	-	-	0.02	0.01	-
Other macroalgae	-	-	0.03	0.03	0.04	-
Styopodium zonae	-	-	-	0.11	0.12	-
Stephanocoenia intersepta	-	-	-	-	-	-
+ Solenastraea hyades	-	-	0.07	-	0.01	0.15
Montastraea cavernosa	-	0.08	0.09	0.18	0.24	-
Diploria labyrinthiformis	0.03	0.48	0.79	0.14	0.47	1.52
Upright Sponges	2.02	0.97	1.38	2.71	3.54	0.91
Filamentous algae	2.67	9.04	8.70	6.61	8.89	5.76
Lobophora variegata	5.58	13.80	8.74	15.84	13.86	0.30
Sargassum spp.	3.89	3.15	3.53	2.10	12.22	-
Dictyota spp.	6.41	4.84	5.57	2.92	12.31	31.52
Encrusting corallinaceae	2.73	5.28	3.88	4.97	4.29	4.85
Udotea spp.	0.18	0.40	0.29	0.28	0.35	0.15
Millepora alcicornis	0.39	0.12	0.09	0.36	0.40	0.30
Favia fragum	0.05	0.12	0.03	0.12	0.01	0.15
Siderastraea siderea	1.12	0.65	0.72	0.51	1.24	2.42
Octocoral bases	1.66	0.85	0.38	1.15	1.54	4.85
Dichocoenia stokesi	0.08	-	-	0.03	0.04	0.45
Bare Hard ground	6.33	7.91	4.79	4.15	4.94	22.58

Table 5. continued.

C+D+E+st. 1+B						
Erythropodium caribaeorum	-	0.16	-	0.04	-	-
Turbinaria spp.	1.22	8.47	0.52	0.29	1.28	-
Siderastraea radians	0.05	0.08	-	0.01	0.07	0.15
Porites astreoides	1.64	1.82	0.78	1.55	0.24	1.36
Diploria strigosa	0.70	1.17	0.02	0.41	0.13	0.91
Sand	40.32	8.39	7.25	15.01	20.48	8.48
All groups						
Porites divaricata	0.23	0.16	-	0.10	0.01	-
Rubble	12.77	8.75	1.19	3.03	2.12	1.82
Madracis decactis	0.10	-	-	0.04	-	-
Anemones	0.03	-	0.02	-	-	-
Diploria clivosa	0.13	-	0.09	-	-	-

Table 6. Octocoral community assemblages (data as colonies m^{-2} per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 28 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Serrana bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

SPP	A	B	C	D	E	F
A						
Eunicea colombiana*	0.050	-	-	-	-	-
Gorgonia mariae	0.100	-	-	-	-	-
C						
Pseudopterogorgia bipinnata	-	-	3.179	0.173	-	-
Pseudopterogorgia elisabethae	-	-	0.271	0.027	-	-
Briareum polyanthes	-	-	0.043	0.013	-	-
D						
Eunicea asperula	-	-	-	0.020	-	-
Eunicea calyculata	-	-	-	0.007	-	-
Eunicea clavigera	-	-	-	0.007	-	-
Eunicea fusca	-	-	-	0.073	-	-
Eunicea mammosa	-	-	-	0.033	-	-
Eunicea pallida	-	-	-	0.007	-	-
Eunicea succinea	-	-	-	0.047	-	-
Eunicea tayrona*	-	-	-	0.013	-	-
Eunicea tourneforti	-	-	-	0.013	-	-
Muricea atlantica	-	-	-	0.020	-	-
Plexaurella fusifera	-	-	-	0.020	-	-
Plexaurella grisea	-	-	0.007	0.193	-	-
Pseudoplexaura spp.	-	0.040	-	0.413	-	-
Plexaura flexuosa	-	0.010	-	0.120	0.100	-
Plexaura kukenthalii	0.050	0.020	-	0.173	-	-
Plexaurella nutans	-	-	0.007	0.053	-	-
Muricea muricata	-	0.010	-	0.033	-	-
Plexaurella dichotoma	-	-	-	0.033	-	0.100
Eunicea laciniata	-	-	0.007	0.027	-	-
C+D						
Pseudopterogorgia americana	0.050	0.010	0.193	0.387	-	-
Briareum asbestinum	-	0.060	0.393	0.620	-	-
Muriceopsis flavida	-	0.030	0.114	0.047	-	-
C+D+B						
Plexaura homomalla	-	0.120	-	0.047	-	-
Gorgonia ventalina	-	0.320	0.036	0.060	-	-
Outliers						
Muricea spp.	-	-	-	0.007	0.100	-
Plexaura kuna	0.100	0.010	-	-	-	-

* from Sánchez (submitted).

Table 7. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Roncador Bank according to the classification of Figure 17.

CLUSTERS	A		B		C	
	X	sd	X	sd	X	sd
Rugosity index	0.584	0.379	0.664	0.096	0.729	0.339
Depth (m)	2.437	0.862	24.754	3.734	11.748	4.037
Coral species	16.000	4.243	24.250	2.986	22.313	4.527
Octocoral species	11.500	2.121	7.000	1.826	10.875	4.884
SUBSTRATE COVER (%)						
Coral cover	8.714	3.345	15.615	2.330	18.260	10.424
Encrusting algae	20.360	22.164	7.231	2.868	6.148	2.157
Calcareous macro algae	10.460	0.876	6.930	1.438	7.976	4.985
Fleshy macro algae	24.251	6.685	31.276	19.301	30.612	14.151
Filamentous algae	19.053	6.053	17.918	11.966	13.829	8.891
Other fleshy invertebrates	-	-	0.039	0.077	0.078	0.127
Encrusting sponges	1.976	2.593	1.089	0.855	0.224	0.301
Erect Sponges	-	-	1.756	1.160	0.598	0.790
Octocoral bases	3.610	3.533	1.788	0.802	3.496	1.728
Bare hard ground	0.071	0.100	3.663	2.781	2.020	2.827
Rubble	0.071	0.100	0.859	1.335	1.389	1.827
Sand	11.435	16.171	11.835	12.894	15.369	12.527
DENSITIES						
Octacorals (colonies m ⁻²)	4.550	2.475	5.725	2.980	11.256	4.930
Diadema antillarum (individuals m ⁻²)	0.020	0.028	0.005	0.010	0.030	0.048
Echinometra viridis (ind. m ⁻²)	-	-	0.005	0.010	0.028	0.055
CORAL DISEASES						
White Plague-WP (No. affected spp.)	1.000	-	0.250	0.500	0.438	0.512
WP-average of percentage affected tissue	1.000	-	0.003	0.005	0.689	1.447
Dark Spots-DS (No. affected spp.)	1.000	-	0.500	0.577	0.938	1.340
DS-average of percentage affected tissue	15.000	7.071	1.000	1.155	1.261	2.561
Bleaching (No. affected spp.)	1.000	-	1.000	0.816	0.500	0.730
BL-average of percentage affected tissue	0.505	0.700	0.503	0.574	0.502	1.316

Table 8. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 32 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Roncador Bank. Shaded cells represent values >5% of coral cover.

SPP	A	B	C
A			
Laurencia spp.	1.50	-	-
Millepora complanata	1.05	-	-
Porolithon pachydermun	2.47	-	-
B			
Agaricia fragilis	-	0.04	-
Scolymia cubensis	-	0.04	-
Scolymia wellsii	-	0.12	-
Tunicates	-	0.04	-
Agaricia spp. (plate-like)	-	0.23	0.02
C			
Agaricia humilis	-	-	0.01
Anemones	-	-	0.02
Caulerpa spp.	-	-	0.03
Diploria clivosa	-	-	0.07
Isophyllastraea rigida	-	-	0.01
Manicina aerolata	-	-	0.04
Mycetophyllia ferox	-	-	0.07
Meandrina meandrites	-	-	0.01
Other macroalgae	-	-	0.02
Porites divaricata	-	-	0.01
Ricordea florida	-	-	0.05
Styopodium zonale	-	-	0.03
Wrangelia spp.	-	-	0.01
Zoanthids	-	-	0.01
Diploria labyrinthiformis	0.07	-	0.39
Montastraea annularis	2.10	0.04	7.23
Amphiroa spp.	0.07	0.04	0.45
Porites porites	0.37	-	1.04
Diploria strigosa	-	0.12	0.60
Porites furcata	0.15	-	0.33
Riphocephalus spp.	-	0.04	0.12
Colpophyllia natans	-	0.27	0.83
Penicillus spp.	0.22	0.23	0.77
Siderastraea siderea	-	0.39	0.77
Sargassum spp.	0.30	0.39	0.98
Porites astreoides	0.90	0.43	1.53
Rubble	0.07	0.86	1.32
Jania spp.	0.37	0.04	0.30
Octocoral bases	3.75	1.79	3.47
Sand	12.07	11.79	15.16
Scolymia spp.	-	0.04	0.03
Agaricia lamarcki	0.07	-	0.03
Dictyota spp.	21.74	1.01	9.42
Lobophora variegata	0.97	29.93	20.38
Galaxaura spp.	0.15	-	0.05
Millepora alcornis	0.22	0.66	0.47
Montastraea faveolata	-	1.28	0.77
B+C			
Dichocoenia stokesi	-	0.04	0.02
Upright Sponges	-	1.75	0.61
Montastraea cavernosa	-	0.39	0.12
Mycetophyllia lamarckiana	-	0.43	0.12
Avranvillea spp.	-	0.04	0.01
Eusmilia fastigiata	-	0.19	0.05
Mycetophyllia aliciae	-	0.04	0.01
Montastraea franksi	-	9.46	2.24
Leptoseris cucullata	-	0.12	0.02
Madracis decactis	-	0.23	0.04
Stephanocoenia intersepta + Solenastrea hyades	-	0.12	0.02
Bare Hard ground	0.07	3.66	2.07

Table 8. continued.

All Groups			
Udotea spp.	0.22	0.51	0.37
Cyanophyceae	3.22	7.51	3.77
Filamentous algae	15.59	10.35	9.87
Halimeda spp.	9.45	6.07	6.01
Favia fragum	0.07	0.12	0.03
Encrusting corallinaceae	17.02	7.24	6.12
Agancia aganicites	3.82	0.82	1.38
Encrusting Sponges	1.87	1.09	0.23

Table 9. Octocoral community assemblages (data as colonies m^{-2} per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 41 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Roncador bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

SPP	A	B	C	St.16
A				
Eunicea succinea	0.033	-	-	-
Eunicea tourneforti	0.033	-	-	-
Muricea elongata	0.100	-	-	-
Muricea spp.	0.033	-	-	-
Plexaura homomalla	0.200	-	-	-
Eunicea tayrona*	0.133	-	0.020	-
Plexaurella grisea	0.967	0.062	0.020	-
Eunicea laxispica	0.400	0.031	-	-
B				
Eunicea asperula	-	0.015	-	-
Eunicea clavigera	-	0.008	-	-
Eunicea fusca	-	0.608	-	-
Eunicea knighti	-	0.038	-	-
Eunicea pallida	-	0.008	-	-
Muricea atlantica	-	0.015	-	-
Muricea laxa	-	0.015	-	-
Plexaura kuna	-	0.008	-	-
Pseudoplexaura spp.	-	0.008	-	-
Muriceopsis flavida	-	0.108	0.020	-
Briareum polyanthos	0.067	0.185	-	0.100
Briareum asbestinum	0.767	1.854	0.100	0.400
Pseudopterogorgia bipinnata	1.967	8.331	5.020	0.100
Eunicea colombiana*	-	0.023	0.020	-
C				
Pseudopterogorgia elisabethae	-	0.100	0.900	-
B+C				
Plexaurella dichotoma	-	0.015	0.040	-
Plexaurella nutans	-	0.031	0.060	-
Pseudopterogorgia americana	-	0.400	0.700	-
Plexaurella fusifera	-	0.015	0.020	-
Eunicea laciniata	0.033	0.023	0.020	-
B+C+A				
Muricea muricata	0.033	0.008	0.020	-
Plexaura flexuosa	0.067	0.023	0.020	-
Gorgonia mariae	0.033	0.015	-	-
Gorgonia ventalina	0.533	0.154	-	-
Eunicea mammosa	0.200	0.038	-	-
Plexaura kukenthalii	0.367	0.054	0.040	-

* from Sánchez (submitted).

Table 10. Areas of especial ecological interest (benthic communities) in the Northern Cays; mean values (min-max).

Location	Important feature	Habitat distribution	Coral spp.	Coral cover (%)	Octocoral spp.	Octocoral density col. m ⁻²
High coral abundance and diversity areas						
Roncador bank: Fig. 19 A; cluster C; Fig. 24C	Mixed corals and highest gorgonian densities and coral cover. Dominant spp.: <i>Pseudopterogorgia bipinnata</i> & <i>Montastraea annularis</i>	' <i>Montastraea</i> '	22 (12-29)	41.9 (23.2-52.3)	10 (3-22)	11.2 (0.6-22.4)
Serrana bank Fig. 12 A; Clt. C; Fig. 24 B	<i>M. faveolata</i> and scattered <i>Acropora cervicornis</i> populations.	' <i>Acropora palmata-Diploria</i> '	17 (13-22)	38.9 (14.6-52.3)	4 (3-8)	0.65 (0.1-1.6)
Quitasuño Bank Fig. 5A: clt. F; Fig. 24A	Extensive mixed coral area at exposed fore-reef terrace. (naturally protected)	'mixed corals'	22 (17-28)	32.9 (18.3-50.7)	10 (6-16)	4.4 (2.2-9.7)
Quitasuño Bank Fig. 5A: clt. B; Fig. 24A	South lagoonal-leeward terrace patch reefs (<i>Montastraea</i> spp.)	' <i>Montastraea</i> '	20 (12-27)	35.6 (25.3-42.9)	8 (4-12)	2.9 (0.3-5.6)
Quitasuño Bank Fig. 5A: clt. E; Fig. 24A	Extensive leeward mixed coral areas.	'mixed corals'	23 (18-30)	39 (33.3-46.6)	11 (7-15)	4.45 (0.4-10.6)
Areas of particular concern (Fig. 24 B-C)						
Roncador & Serrana banks fore-reef terrace (Fig. 24 B-C)	High densities of endangered sea fan species <i>Gorgonia ventalina</i> and <i>G. flabellum</i> .	'Octocorals and mixed corals' high relief spur & groove	19.7* ±7.4 SD	~13*	~14**	5.8** (2.6-9)
Roncador bank: Fig. 19 A: clt. B (see also Serrana bank: Fig. 12 B, clt. C)	Mixed corals and high densities of a commercially important octocoral: <i>P. elisabethae</i>	'Mixed coral'	24 (20-27)	15 (13.2-18.1)	7 (5-9)	5.7 (2.3-9.5)
Serrana bank*** Fig. 12 A; Clt. D.	<i>Montastraea</i> spp. patch reefs, shallow area with <i>A. palmata</i> and coralline algae.	<i>Acropora palmata-Diploria</i> ' ' <i>Montastraea</i> '	21 (12-30)	21.3 (7.1-41.8)	4 (1-14)	3.5 (0-13.9)

* From Diaz-Pulido et al. (submitted), ** From Sánchez J.A. (unpublished, 1995)

*** Heterogeneous area showing both degradation in deeper parts and active *A. palmata* reefs in the shallow parts.

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**GUIDE TO THE DOMINANT MACROALGAE OF THE STROMATOLITE
FRINGING REEF COMPLEX, HIGHBORNE CAY, BAHAMAS**

BY

**DIANE S. LITTLER, MARK M. LITTLER, IAN G. MACINTYRE,
EMILY BOWLIN, MIRIAM S. ANDRES, AND R. PAMELA REID**

**ISSUED BY
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Figure 1. Location of Highborne Cay, Bahamas showing the fringing reef and stromatolite areas prominent along the eastern shore. T's mark the 10 established research transects across the Highborne Cay stromatolite fringing reef complex.

GUIDE TO THE DOMINANT MACROALGAE OF THE STROMATOLITE FRINGING REEF COMPLEX, HIGHBORNE CAY, BAHAMAS

BY

DIANE S. LITTLER,^{1,2} MARK M. LITTLER,¹ IAN G. MACINTYRE,³ EMILY BOWLIN,⁴ MIRIAM S. ANDRES⁴, AND R. PAMELA REID⁴

ABSTRACT

This is the first description of macroalgae documented from a stromatolite reef complex. Because of the sediment stress conditions that promote the development of stromatolites in this open marine environment, macroalgae are generally limited in species diversity and are sparse except for the crustose coralline alga *Neogoniolithon strictum*, which forms the elevated reef crest behind which the sediments and stromatolites accumulate. At the 10 sites sampled, a total of 22 species were encountered, 10 Rhodophyta, 9 Chlorophyta, 2 Phaeophyta and 1 Cyanobacteria.

INTRODUCTION

Stromatolites, which are laminated microbial deposits, have a unique geologic history that dates back to more than three billion years and extends right up to the present day. Dravis (1983) was the first to report modern marine stromatolites on the northeastern margins of Exuma Sound. Following this initial discovery, marine stromatolites were reported at numerous locations throughout the Exuma Cays, on the western margin of Exuma Sound (Dill et al., 1986; Dill, 1991; Reid and Brown, 1991; Reid et al., 1995). These stromatolites all occur in tidal channels with the exception of those off Stocking Island, Darbay Island and Highborne Cay (Fig. 1) where they form part of a fringing reef that has a reef crest formed by the sediment-tolerant crustose coralline algal

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Neogoniolithon strictum (Steneck et al., 1997). The facies pattern of these fringing reefs is well illustrated in a series of cores collected off Stocking Island to study their growth history (Macintyre et al., 1996).

For modern stromatolites to exist, the environmental conditions have to be under severe stress to eliminate most other benthic organisms that can out-compete and destroy these microbially laminated sedimentary structures. In the marine environment this stress is usually hyper-saline conditions or, as found off Highborne Cay, stress associated with the constant movement and inundation of sediments (Andres and Reid, 2005). As macroalgae are one of the competitors with stromatolite growth, little attention has been paid to the limited numbers of macroalgae species that can survive these severe conditions of sediment stress. This is the first description of the macroalgae that are found in a stromatolite-reef complex. A complete description of this complex ecosystem is found in Reid et al., 1999 with ample photographs of the area and thorough documentation of the internal and external structures of the microbial buildup and surface mats characteristic to this unique habitat.

SETTING

Off the east-facing beach of Highborne Cay ($76^{\circ}49'W$; $24^{\circ}43'N$), an island in the northern Exuma Cays, a fringing mixed microbial-coralline-algal reef extends along this windward coast for about 2.5 km (Fig. 1). The shelf, with average water depths of 10–20 m, extends seaward for 1–2 km before dropping off into the Exuma Sound with depths of up to 20 km.

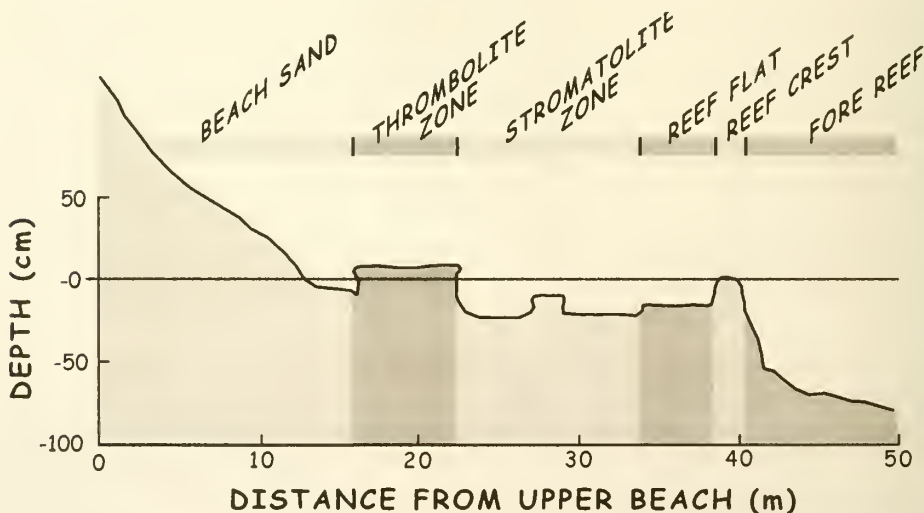


Figure 2. Schematic profile of the near shore reef at Highborne Cay, Bahamas. The above zones serve as a location reference in reporting the distribution of macroalgal species. (modified from Reid et al. 1999, Fig. 3)

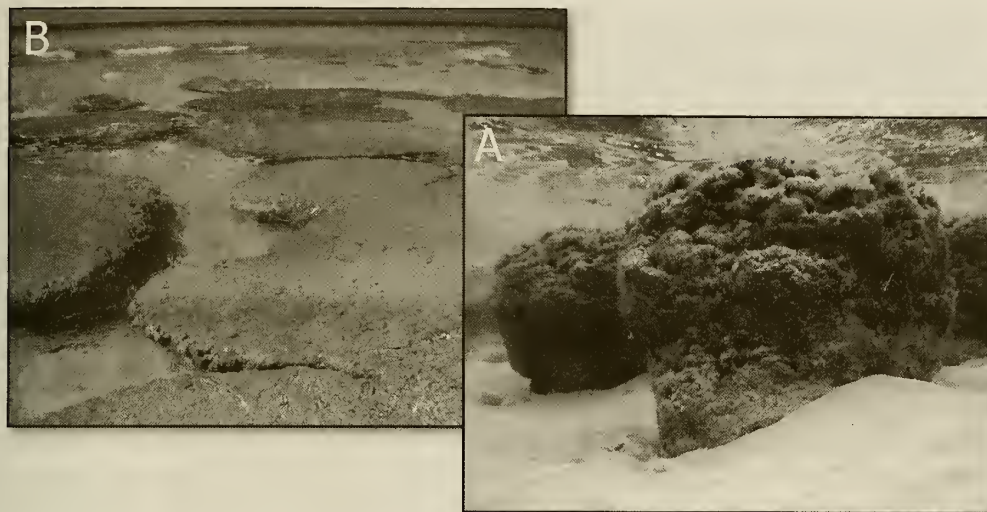


Figure 3. A. Thrombolites forming in shallow-inshore, heavily sand-inundated areas. B. Surface view of thrombolites (formed by irregular internal microstructures) showing their irregular shape and often flattened top.

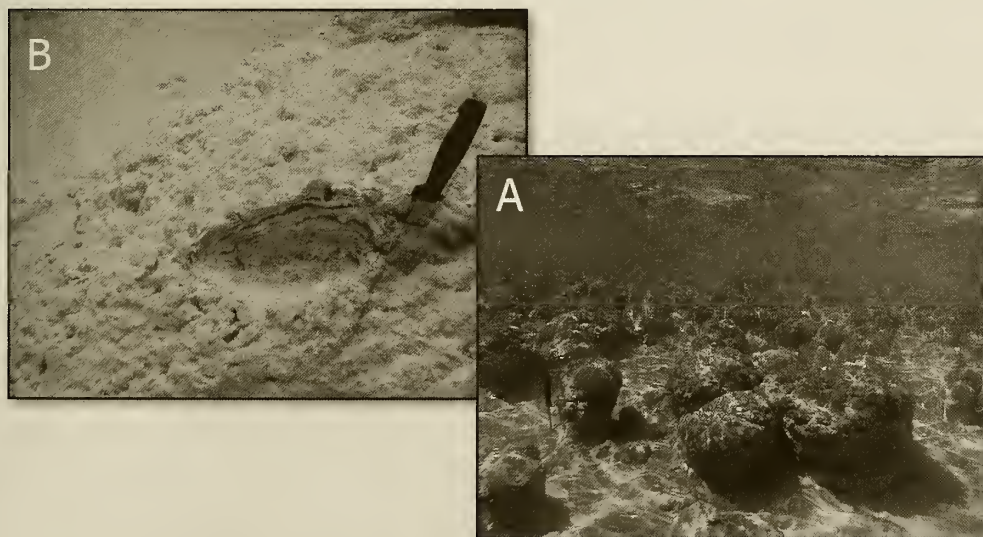


Figure 4. A. Stromatolites (formed by laminated internal microstructure) generally occurring in deeper water than the thrombolites. B. Close-up of a stromatolite showing the distinctly differentiated layers that create the structure.

Oceanographic conditions are characterized by normal salinity, approximately 35 ‰, with sea-surface temperatures ranging from 20–28° C in winter and summer, respectively. The water is saturated with respect to both aragonite and calcite. Tides are diurnal with a range of ~1 m. The climate is dominated by the trade winds blowing on average 10–15 knots from a southeast to easterly direction.

Although the reef system extends along the entire length of the beach, it is most extensively developed in the southern to central sections and in the very northern part. For research purposes this part of the reef system is subdivided into sites, numbered Site 1 in the south to Site 10 in the north (Fig. 1).

The reef tract is divided into distinct morphological zones (Fig. 2): beach sand, thrombolite (irregular internal microstructure) zone (Fig. 3); stromatolite (laminated internal microstructure) zone (Fig. 4); reef flat (Fig. 5); reef crest (*Neogoniolithon* zone, Fig. 6); and fore reef. Whereas most of these zones are found throughout all transects, the thrombolite zone occurs only at a few sites. Furthermore, the individual width and lateral extension of these zones is highly variable. In overview, this reef system is widest in the southern part of the eastern beach extending over 20–50 m with a maximum width of 54 m within Site 2 (Fig. 1). The *Neogoniolithon* zone is more shoreward at Site 3, resulting in decreased width to 25–35 m at Sites 3 and 4, narrowing further to 10 m and less at Sites 5–8. Although interrupted by cuts and channels, the outer reef edge is continuously traceable from Sites 1–6, whereas Sites 7 and 8 comprise a series of discontinuous narrow reefs. Sites 9 and 10 are isolated crescent-shaped reefs with extensive open sand areas in between (Fig. 1).

METHODS

From 30 January to 2 February 2005, Emily Bowlin and Ian G. Macintyre collected the dominant macroalgae from 10 established research transects across the Highborne Cay stromatolite fringing reef complex. Samples were collected from the *Neogoniolithon strictum* zone, the reef flat, the stromatolite zone, and finally the thrombolite zone, which did not occur in some transects (Fig. 1).

Samples were then taken to the laboratory in the R/V Walton Smith where they were photographed and then pressed and dried. Both photographs and pressed material were transferred to the Smithsonian Institution's National Museum of Natural History where the macroalgae were studied, identified and described by Diane S. Littler and Mark M. Littler. Highborne Cay photographs were sharpened and cropped in Adobe Photoshop but otherwise remain untouched. In air photographs of the Highborne Cay specimens were taken by Emily Bowlin with the assistance of Ian G. Macintyre. Drawings of internal structures and *in situ* photographs are from "Caribbean Reef Plants", used with the permission of the publisher and are not specifically from Highborne Cay or Highborne Cay material. However, they provide a representation of comparable *in situ* plants that occurred in the transects.

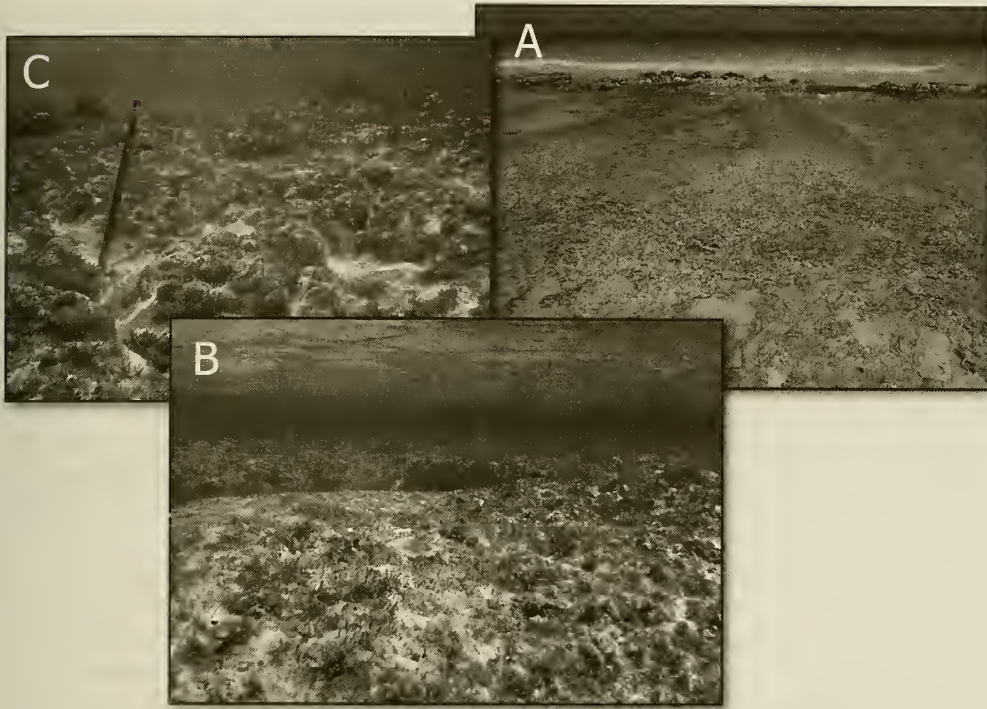


Figure 5. A. Surface view of the reef flat at low tide. B. Underwater view of the reef flat showing the sparse algal and seagrass cover presumably due to the turbulent sand scouring and intermittent sand inundation. C. Closer view of reef flat habitat.



Figure 6. The reef crest zone dominated by large heads of the sediment tolerant crustose coralline algal *Neogoniolithon strictum*.

RESULTS AND DISCUSSION

The marine flora of the Bahamas has been extensively studied over a long time period beginning at the turn of the 19th century when M.A. Howe began focusing his efforts on collecting there (e.g., Howe, 1904, 1905a, 1907, 1909, 1920, 1924). The myriad of algal habitats have not been intensively investigated in terms of coverage. Historical treatments in the past 75 years are limited to mostly ecological works and more limited floras and monographs (e.g., Jensen, 1985; Littler et al., 1985, 1986, 1988, 1991; Littler and Littler, 1990a, 1990b, 1991, 1992, 2000, 2004; Lapointe et al., 1992, 2004, in press a, in press b). Bahamian specimens and distributional records were also used to produce field guides such as Littler et al. (1989) and Littler and Littler (2000). Consequently, the present work adds a floristic dimension to a unique Bahamian ecosystem.

Twenty-two marine macroalgae commonly occurred on the stromatolite reefs of Highborne Cay. Of these, 10 were Rhodophyta (red algae), with 9 Chlorophyta (green algae), 2 Phaeophyta (brown algae) and 1 Cyanobacteria (blue-green algae). The often overlooked brown algal species *Padina haitiensis* was present. This species is commonly mistaken for *P. sanctae-crucis* and, consequently, has been rarely reported.

The reef crest was the most diverse site with 13 species present (Fig 7). The reef flat had 12 species while the stromatolite zone maintained 11 species. The thrombolite zone was the most depauperate in terms of species richness with only five species present. The latter paucity is presumably due to the constant and turbulent sand inundation in the shallow subtidal adjacent to the beach.

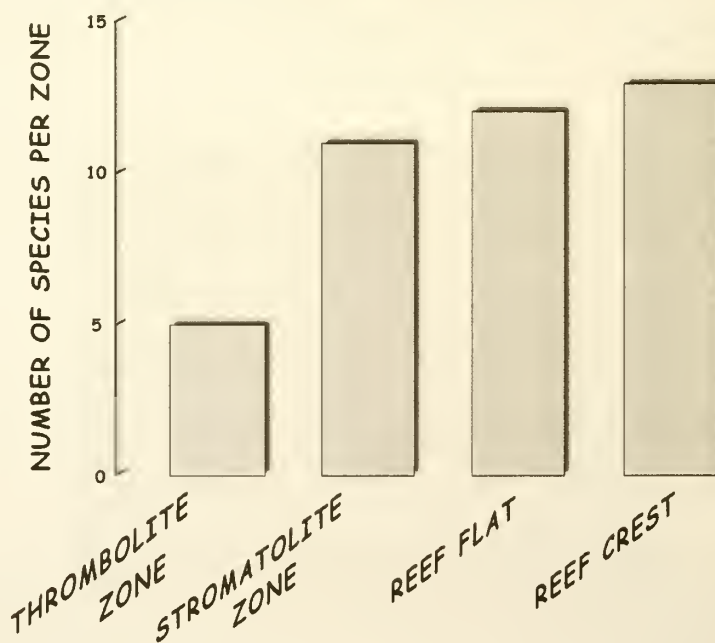


Figure 7. Histogram showing the number of species for the four zones.

The green alga *Batophora occidentalis* was the only species that occurred in every transect (Table 1). This species was the dominant macroalga in the thrombolite and/or the stromatolite zone and occasionally appeared on the reef crest and reef flat. The red alga *Laurencia obtusa* was present in all 10 transects on the reef crest or reef flat except at site 3 but was never found in either the stromatolite or thrombolite zones. The red alga *Lophosiphonia obscura* and the blue-green alga (cyanobacteria) *Dicothrix fucicola* were only present in the thrombolite zone, while *Neosiphonia sphaerocarpa* was present in the thrombolite and stromatolite zone; none of the three were found on the reef flat or reef crest. Two samophytes, the green algae *Udotea flabellum* and the closely related *U. norrisii*, were found only in the stromatolite zone. The brown alga *Dictyota cervicornis* is a common species on the reef flat and reef crest and is also present in the northernmost stromatolite zone. Species that were restricted to the reef flat and reef crest were *Avrainvillea digitata*, *Caulerpa paspaloides* var. *compressa*, *Chondrophyucus gemmifera*, *Halimeda incrassata*, *Jania capillaceae*, *Laurencia obtusa* and *Rhipocephalus phoenix*, presumably species that are more susceptible to damage by sand scouring and inundation (Table 1).

ACKNOWLEDGEMENTS

We gratefully acknowledge Ana Patricia Gaspar for providing precise locations of the 10 transects in Figure 1. Funding for field work was provided from National Science Foundation Grant EAR-0221796 and funding for laboratory work was provided by the Smithsonian Marine Station at Fort Pierce, Florida (SMSFP Contr. No. 622). RIBS Contr. No. 34. HBOI Contr. No. 1609.

Table 1. List of species occurring at Highborne Cay study area according to Transect Sites 1–10. Sites show where individual species occurred on the RC = reef crest, RF = reef flat, SZ = stromatolite zone and TZ = thrombolite zone. The epiphyte *Pneophyllum fragile* is not included since it occurs on various species.

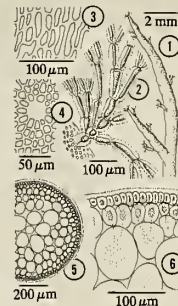
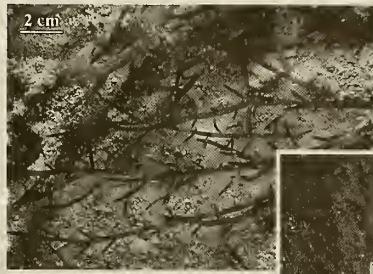
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10
<i>Acetabularia crenulata</i>				RF,SZ	RF	RF				
<i>Avrainvillea digitata</i>		RC								
<i>Batophora occidentalis</i>	SZ	RF,SZ	RC,SZ	RC,RF,SZ	RC,RF,SZ, TZ	RC,RF,SZ, TZ	TZ	RF,SZ	SZ	TZ
<i>Caulerpa paspaloides</i>	RC									
<i>Chondria littoralis</i>		RC	SZ	SZ	RF	RF,SZ		RF,SZ	RF,SZ	RC,RF
<i>Chondrophycus gemmifera</i>		RF			RC	RC			RC	
<i>Dichothrix fucicola</i>					TZ					
<i>Dictyota cervicornis</i>	RC,RF	RC	RC,RF	RC,RF		RC,RF	RF,SZ	SZ	RF,SZ	SZ
<i>Digenia symplex</i>			RF,SZ							
<i>Halimeda incrassata</i>			RC							RF
<i>Jania capillaceae</i>	RC		RF	RC	RF					
<i>Laurencia obtusa</i>	RF	RC,RF		RF	RC	RC,RF	RC	RC,RF	RC,RF	RC,RF,SZ
<i>Lophosiphonia obscura</i>				TZ	TZ	TZ	TZ	TZ		
<i>Neogoniolithon strictum</i>	RC	RC	RC	RC	RC	RC	RC	RC	RC	RC
<i>Neosiphonia sphaerocarpa</i>				TZ	SZ		TZ			SZ
<i>Padina haitiensis</i>	RF			RC,RF,SZ			RC,RF			
<i>Rhypocephalus phoenix</i>			RC							
<i>Udotea flabellum</i>			SZ						SZ	SZ
<i>Udotea norrisii</i>			SZ							
<i>Valoniopsis pachynema</i>	RC,RF	RF	RF	RC				RC,RF		RC,RF, TZ
<i>Wrangelia penicillata</i>			SZ		RF		RC,RF,SZ			RC,SZ

Chondria littoralis Harvey 1853: 22

Thallus: sparsely branched, to 35 cm high, brown-yellow or pale to dark red; branching irregular. *Branches* cylindrical, to 2.0 mm diam. proximally (main axis to 2.2 mm diam.), tapering to 0.8 mm distally; pericentral cells 5-6. *Branchlets* only present on outer branches, to 0.5 mm diam., tapered at both ends, mainly unbranched, decidedly pinched at base; apices pointed; apical filaments fine, to 1.5 mm long, dichotomously branched (often at every segment for rst 5-6 divisions), densely tufted, persistent; apical cell exposed. *Surface cells* to 18 μm diam., rectangular, 1-4 diameters long.

Common: firmly attached to coral, rock fragments or other hard surfaces on shallow sand or mud ats, occasionally intermingled with other small algae in short turfs; to 15 m deep.

Highborne Cay distribution: generally found on the reef at and in the stromatolite zone; only once was it found on the reef crest.



1. Branch with branchlets abruptly thinner than main axis.
2. Persistent apical filaments.
3. Surface cells of mature branch.
4. Surface cells of branchlet with lamenent scar.
5. Transverse section of branch.
6. Transverse section of cortex.



Highborne Cay US# 209060

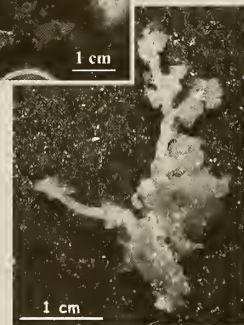
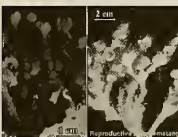
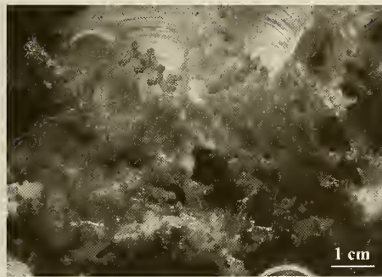
Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae

Chondrophycus gemmiferus (Harvey) Garbary & Harper 1998: 194

Thallus: bushy, sti , wiry, 2-5(-15) cm high, yellow-brown, occasionally with red-brown tips; branching dense, alternate to irregular. *Branches* cylindrical, somewhat flattened with age, 1.0-2.2 mm diam., tapering to 0.5 mm diam. at apices. *Branchlets* numerous, cylindrical, 0.2-0.9 mm diam., 0.2-1.0(-3.0) mm long, blunt, wart-like, often swollen; apices tufted with fine deciduous, dichotomously branched laments extending just beyond rim of terminal depression. *Surface cells* oval to angular, 40-50(-130) μm diam., with surface projection near apices, deeply pigmented; medullary cells large, colorless; apical cell sunken in terminal depression. Holdfast disc-like or spreading to pad-like.

Uncommon: on hard surfaces of shallow reef ats or attached to dead coral rubble on shallow sand plains; to 20 m deep.

Highborne Cay distribution: in most stations limited to the reef crest, in one instance on the reef at.



1. Habit.
2. Transverse section of immature branchlet showing pointed surface cells.
3. Branchlet apex.
4. Surface cells of mature branch.

Highborne Cay US# 209056

Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae

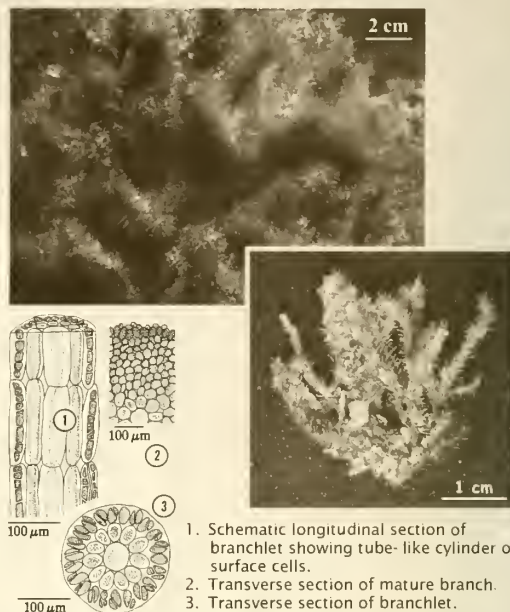
Digenea simplex (Wulfen) C. Agardh 1822 [1822-1823]: 389

Thallus: sti, wiry, often gregarious, to 8(-25) cm high, light pink to dull, dark brown-red; branching dichotomous to irregular. **Branches** naked proximally, covered with numerous short branchlets distally; in transverse section, large central cells grading smaller toward surface. **Branchlets** 3-5(-15) mm long, unbranched, sti, wiry, often with fine, deciduous hairs near apices. **Surface cells** of branchlet 25-35 μm diam., in 20-24 longitudinal cylinders; pericentral cells 10-12, 25-38 μm diam.; central filament distinct, 40-55 μm diam. **Holdfast** of coarse, short rhizoids descending from thicker disc-like base.

Common: on hard surfaces, often overgrown by filamentous epiphytes, abundant in heavy-surf conditions, when buried by sand dwarfed and denuded; lower intertidal to 20 m deep.

Highborne Cay distribution: only present at Site #10 both on the reef flat and in the stromatolite zone; generally a species commonly occurring throughout the Bahamas.

Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae



1. Schematic longitudinal section of branchlet showing tube-like cylinder of surface cells.
2. Transverse section of mature branch.
3. Transverse section of branchlet.

Highborne Cay US# 209062

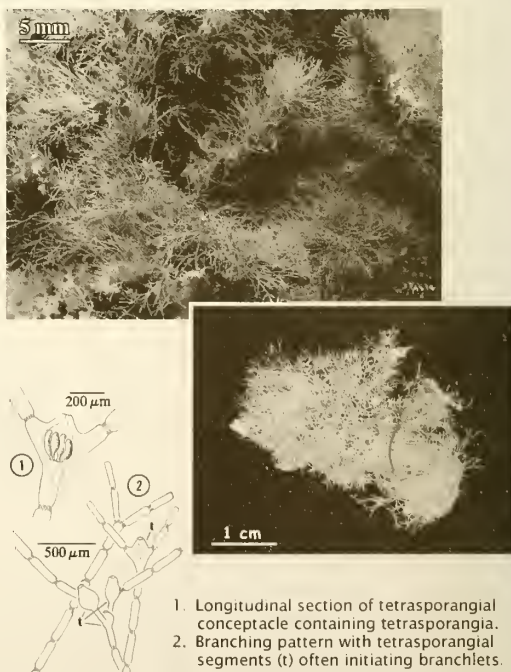
Jania capillacea Harvey 1853: 84-85

Thallus: delicate, as tightly packed clumps or small cushions, 4-10 mm high, rose-red; branching widely dichotomous (angled 30°-45°). **Branches** cylindrical, 45-100 μm diam., often recurved; apices pointed to occasionally rounded. **Segments** calcified, 300-600 μm long; medullary cells tiered, parallel, elongated, 26-42 μm long; cortical cells roundly rectangular, 5-8 μm diam., densely pigmented. **Joints** exible, uncalcified, occurring at base of branches and at regular intervals between branches; cells elongated, 42-77 μm long, parallel, in one tier; cortex lacking. **Holdfast** crust-like or disc-like. **Tetrasporangial conceptacles** solitary, vase-shaped, with central pore, formed in swollen apical segments, eventually initiating new branchlets; tetrasporangia oval, zonately divided.

Common: epiphytic on other marine plants, in calm waters; to 15 m deep.

Highborne Cay distribution: on the reef crest or reef flat.

Phylum Rhodophyta Class Florideophyceae Order Corallinales Family Corallinaceae



1. Longitudinal section of tetrasporangial conceptacle containing tetrasporangia.
2. Branching pattern with tetrasporangial segments (t) often initiating branchlets.

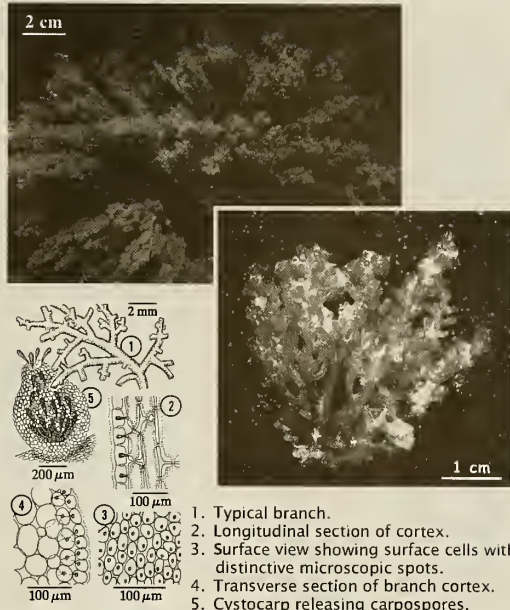
Highborne Cay US# 209067

Laurencia obtusa (Hudson) J.V. Lamouroux 1813: 130

Thallus: compact, often clumped, 8–15(–26) cm high, dark to olive- green with maroon tips; branching alternate, sparse below, numerous and crowded above. *Branches* cylindrical, proximally 0.7–1.8 mm diam. *Branchlets* generally spiral to occasionally opposite, 0.5–0.8 mm diam., 1–2 mm long; apices tufted with the deciduous laments forming in shallow terminal depression. *Surface cells* 24–30 μm diam., somewhat spherical, heavily pigmented, with distinctive colorless spherical bodies (“corps en cerise”) present in live or recently preserved specimens only; medullary cells large, colorless; apical cell sunken in shallow terminal depression. *Tetrasporangia* tetrahedrally divided.

Common: in shallow wave- dashed habitats or areas of strong currents; to 8 m deep.

Highborne Cay distribution: extremely common on the reef crest and reef flat in shallow water near low tide mark, found only once in the stromatolite zone.



Highborne Cay US# 209070

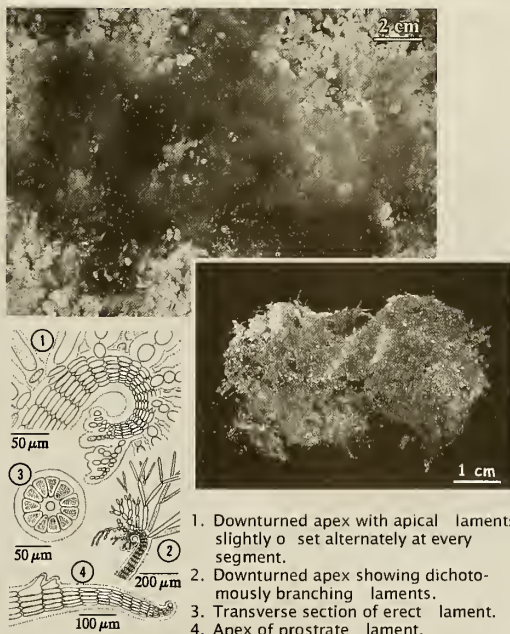
Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae

Lophosiphonia obscura (C. Agardh) Falkenberg in Schmitz & Falkenberg 1897: 46

Thallus: as filamentous turfs, to 1.5(–2) cm high, of indeterminate area, red- brown; prostrate branching irregular; branching of erect laments infrequent, lateral. Prostrate axis to 140 μm diam., bearing single upright every (4)–8–10 or more joints; apices upcurved. Erect branchlets to 100 μm diam., tapering at apices; mature segments slightly longer than wide; pericentral cells (6)–9–13, thick- walled; apices downturned. Apical laments crested on outer margin, slightly alternately set on every segment when mature, soon deciduous, pseudodichotomously branched; basal cell often spherical. Rhizoids single- celled, 30–50 μm diam., as extension of pericentral cell, partitioning cell wall absent, terminating in nger- like attachment pad.

Uncommon: inconspicuous, on hard surfaces, in calm protected areas; lower intertidal to 2 m deep.

Highborne Cay distribution: only recorded from the thrombolite zone adjacent to the beach in very shallow water.



Highborne Cay US# 209055

Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae

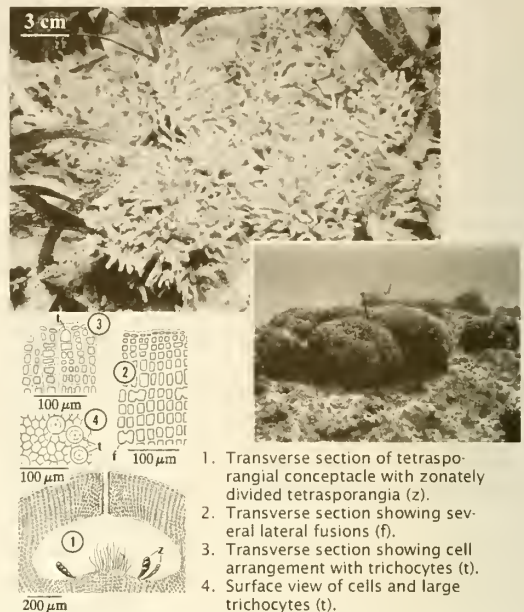
Neogoniolithon strictum (Foslie) Setchell & L.R. Mason 1943: 92

Thallus: stony, heavily calcified, forming brittle clumps or nodules, to 14(-20) cm diam., chalky rose-pink; branching abundant, irregular, often cervicorn. *Branches* cylindrical, rigid, to 1.5 mm diam., tapered, roughened with reproductive structures when fertile. *Cells* of surface layer lens-shaped to oval, 15-20 μm diam., synchronous sloughing of surface layer common; subsurface stratum of many layers, gently curving to medulla, lateral pit connections absent, lateral fusions common; medullary cells thick-walled, rectangular, tiered, 15-20 μm wide, 20-40 μm thick. *Trichocytes* large, thick-walled, solitary or in vertical clusters, scattered in surface layer.

Common: often lying free in shallow seagrass beds on reef flats, occasionally fusing to create massive reef structures on turbulent reefs; to 3 m deep.

Highborne Cay distribution: dominant alga of the reef crest zone.

Phylum Rhodophyta Class Florideophyceae Order Corallinales Family Corallinaceae



1. Transverse section of tetrasporangial conceptacle with zonately divided tetrasporangia (z).
2. Transverse section showing several lateral fusions (f).
3. Transverse section showing cell arrangement with trichocytes (t).
4. Surface view of cells and large trichocytes (t).

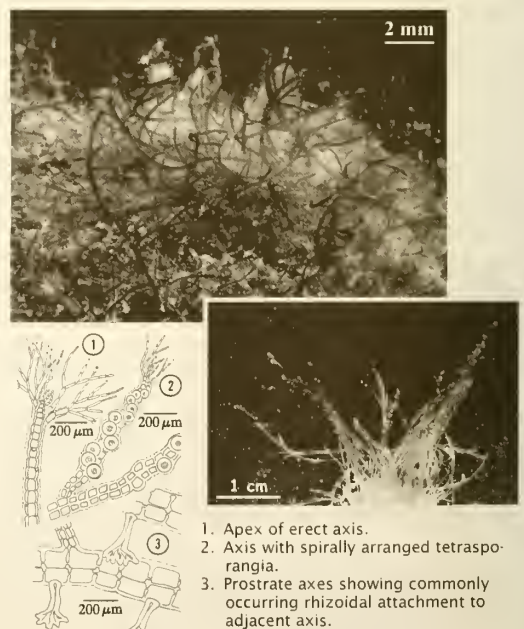
Neosiphonia sphaerocarpa M.S. Kim & I.K. Lee 1999: 280

Thallus: filamentous, fine, tufted, bushy, to 2 cm high, light brown to rose-red to maroon; branching alternate to somewhat dichotomous. *Prostrate axis* 100-210 μm diam. *Erect axis* 60-150 μm diam., of four pericentral cells; lateral branches 60-125 μm diam., often basally constricted, replacing apical laments; cortication absent; lament scar cells common; segments 0.5-1.5(-3.0) diameters long. *Apical filaments* deciduous, rarely to 800 μm long. *Holdfast* initially disc-like, later attached by unicellular rhizoids; rhizoids separated from parent cell by wall, distal on pericentral cells, commonly attaching to nearby branches creating mesh-like net which traps sand. *Tetrasporangia* spherical, 50-60 μm diam., tetrahedrally divided, as swollen spiral series in outer branchlets.

Common: inconspicuous, epiphytic on larger plants or on hard surfaces, in wave-exposed areas; lower intertidal to 8 m deep.

Highborne Cay distribution: only occurring in the stromatolite and thrombolite zones.

Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Rhodomelaceae



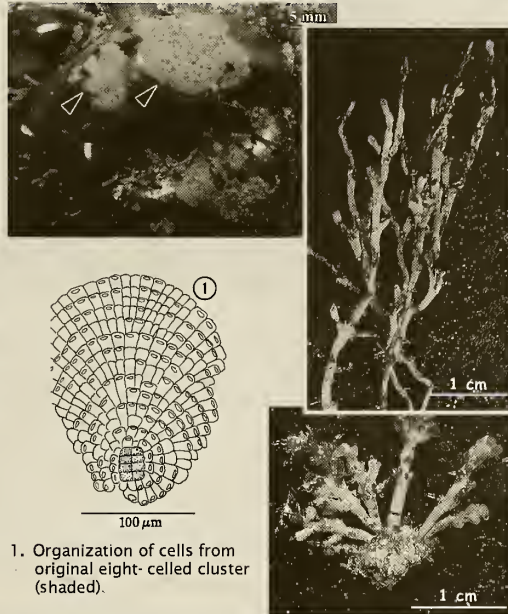
1. Apex of erect axis.
2. Axis with spirally arranged tetrasporangia.
3. Prostrate axes showing commonly occurring rhizoidal attachment to adjacent axis.

Pneophyllum fragile Kützing 1843: 385

Thallus: prostrate, fragile, forming thin calci ed crusts, 0.5–2.0 mm diam., 15–30 μm thick, with older thalli often merging together, rose, pale pink to white. *Cells* square to rectangular, 5–10 μm wide, 5–20 μm long, radiating from original eight-celled structure; one cell thick, older crusts up to four cells thick; surface cells 6.5–12.0 μm wide, 3.5–11.5 μm long, 17–20 μm thick; cap cells wider than long, 3.4–8.0 μm wide, 1.5–3.5 μm long, 2–3 μm thick, at distal ends of surface cells. *Trichocytes* intercalary, rare, 8.5–13.5 μm diam., 11–16 μm long. *Conceptacles* at or slightly raised, with central pore; cystocarpic and sporangial conceptacles (60–)150–250(–300) μm diam.; spermatangial conceptacles (13–)75–100 μm diam.

Common: inconspicuous, epiphytic on macroalgae or seagrasses; to 10 m deep.

Distribution: common epiphyte on most species occurring on the reef crest and reef at.



1. Organization of cells from original eight-celled cluster (shaded).

Highborne Cay US# 209071

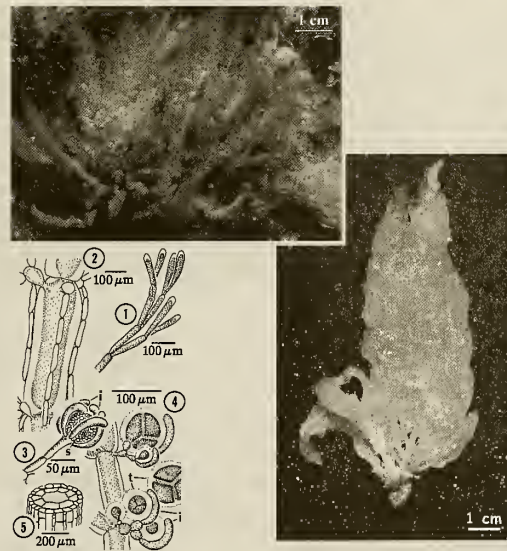
Phylum Rhodophyta Class Florideophyceae Order Corallinales Family Corallinaceae

Wrangelia penicillata (C. Agardh) C. Agardh 1828: 138

Thallus: nely branched, bush-like, to 8 cm high, light pink; main branching alternate or irregular; secondary branching alternate at every segment, mainly in one plane. *Main filaments* cylindrical, 180–200 μm diam., completely corticated proximally; cells to 800 μm long. *Branchlets* soft, thin, in whorls at joints, dichotomously divided; apical cells blunt tipped, often deciduous. Rhizoids clustered, nely branched. *Tetrasporangia* abundant, spherical, 75–100 μm diam., tetrahedrally divided, at joints near branchlet tips, loosely clasped by short, slender, involucrel laments. *Spermatangia* similar to above but clustered, 55–60 μm diam. *Cystocarps* to 400 μm diam., terminal on short branchlets, surrounded by many short, slender, incurved laments.

Common: generally epiphytic on seagrasses or other larger algae; to 15 m deep.

Highborne Cay Distribution: on the reef crest, reef at and stromatolite zones.



1. Branchlet apices.
2. Main branch segment showing descending corticating laments.
3. Spermatangial cluster (s) loosely surrounded by involucrel cells (i).
4. Tetrasporangia (t) clasped by solitary involucrel laments (l).
5. Transverse section of main branch in oblique view.

Highborne Cay US# 209061

Phylum Rhodophyta Class Florideophyceae Order Ceramiales Family Ceramiaceae

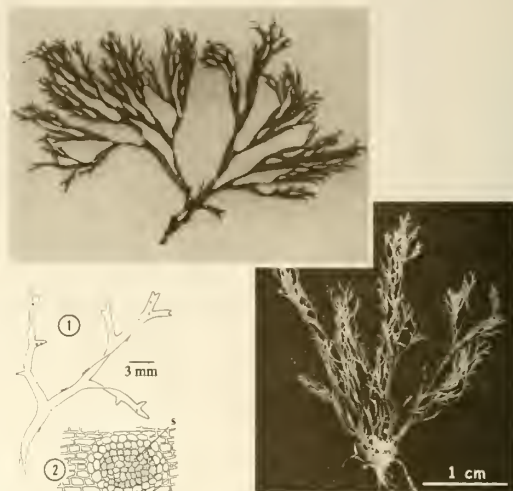
Dictyota cervicornis Kützing 1859: 11, pl. 24, g. 2

Thallus: bushy, to 20 cm high, olive-brown; branching dichotomously asymmetrical, cervicorn. *Branches* 1.0–2.5 mm wide (very old thalli with proliferating blades to 3 mm wide); 180–220 μm thick, 10–25 medullary cells wide, often twisted or spiral, small surface hooks often present in Indian River Lagoon specimens; apices pointed. *Medullary cells* in one layer, rectangular, 140–180 μm thick, arranged in longitudinal rows. *Surface cells* rectangular, 15–20 μm thick. *Surface hairs* in tufts, scattered near central axis. *Holdfast* brous, mat-like; marginal rhizoids common. *Sporangia* scattered, solitary, to 120 μm diam., surrounded by paraphyses. *Oogonial sori* scattered.

Common: attached to rocks, shell fragments or large plants in sandy shallow areas; to 3 m deep.

Highborne Cay distributin: common on the reef crest and reef flat, occasionally in the stromatolite zone.

Phylum Heterokontophyta Class Phaeophyceae Order Dictyotales Family Dictyotaceae



1. Habit of blade.
2. Surface view of antheridial sorus (s) surrounded by paraphyses (a).
3. Transverse section of blade margin showing antheridial sori (s) and marginal rhizoids (r).

Highborne Cay US# 209065

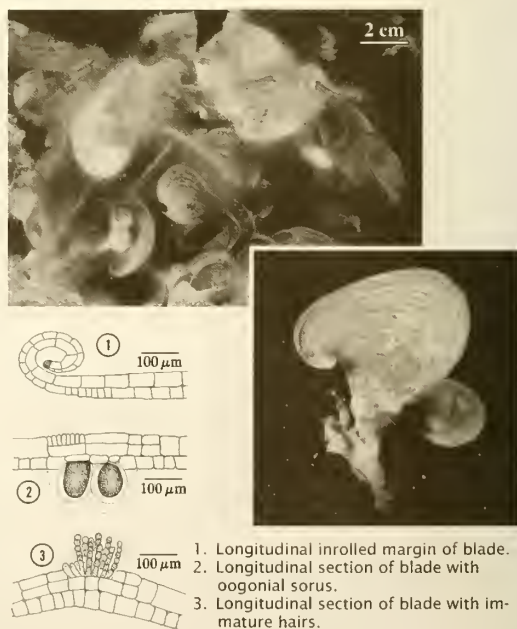
Padina haitiensis Thivy in W.R. Taylor 1960: 235, 632, pl. 75, g. 1

Thallus: in leaf-like clusters, rounded, to 6 cm high, upper surface chalky white alternating with light yellow-brown bands, lower surface less calcified with darker brown bands. *Blades* fan-shaped, to 8 cm broad, concentrically zoned, substantially calcified; to 65 μm thick distally, 105 μm thick proximally, generally of two cell layers, three cell layers only where surface hairs are produced or reproductive structures are formed; dorsal cells rectangular, 30–80 μm wide, to 60 μm thick; ventral cells smaller, rectangular, 20–60(–80) μm wide, to 30 μm thick; margins inrolled. *Surface hairs* to 15 μm diam., 130 μm long, in concentric zones. *Rhizoidal base* matted. *Reproductive sori* alternating with bands of sterile hairs.

Rarely reported: in the Bahamas, often misidentified as *Padina sanctae-crucis*, on hard substrates such as beach rock; lower intertidal to 3 m deep.

Highborne Cay distribution: generally on the reef crest and reef flat, only collected once from the stromatolite zone.

Phylum Heterokontophyta Class Phaeophyceae Order Dictyotales Family Dictyotaceae



1. Longitudinal inrolled margin of blade.
2. Longitudinal section of blade with oogonial sorus.
3. Longitudinal section of blade with immature hairs.

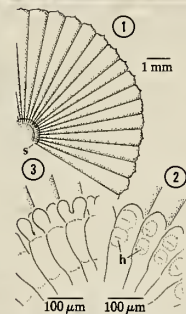
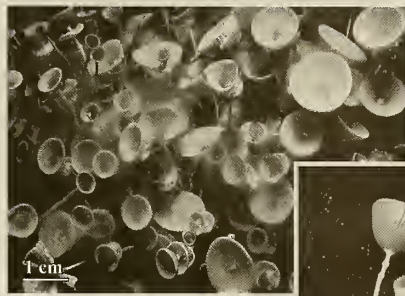
Highborne Cay US# 209068

Acetabularia crenulata J.V. Lamouroux 1816: 249, pl. 8, g. 1

Thallus: solitary or in clusters, parasol-shaped, moderately calcified, 2–8 cm high, white-green. Axes 200–300 μm diam., heavily calcified, occasionally bearing several whorls of laments; laments colorless, pale green when young, rapidly deciduous. *Discs* one or more in succession, flat or cup-shaped, 12–20 mm diam., of 30–80 rays; outer margin of ray with centered tooth or spine; corona superior (at base of rays) of short inconspicuous projections, with rounded or slightly lobed apices and two exceedingly faint hair scars; corona inferior (underside, base of rays) of short inconspicuous projections with forked apices. *Gametangia* are mature rays, producing up to 500 cysts per ray; cysts spherical, 65–80 μm diam.

Common: growing on mangrove prop roots, rocks, shells or coral fragments in protected areas; to 3 m deep.

Highborne Cay Distribution: mainly found on the reef flat, only found once in the stromatolite zone.



1. Disk of rays with corona superior (s) at base.
2. Corona superior with two hair scars (h).
3. Corona inferior.



Highborne Cay US# 209054

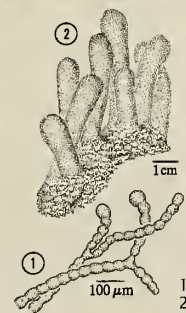
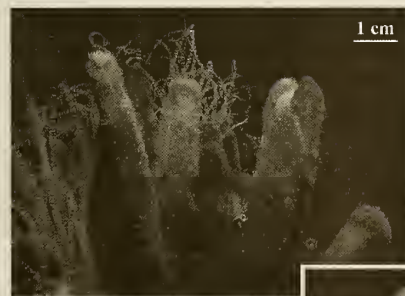
Phylum Chlorophyta Class Ulvophyceae Order Dasycladales Family Polyphysaceae

Avrainvillea digitata D.S. Littler & M.M. Littler 1992: 379, g. 3

Thallus: gregarious, finger-like, occasionally club-shaped or pointed, to 6 cm high, 1.5 cm diam., dull dark brown-green. *Blades* loosely woven, spongy; zonation absent; interior and surface siphons strong-walled, 40–55 μm (to 75 μm at growing margins) diam., slightly moniliform (bead-like), apices bulbous or rounded. *Stipe* absent. *Rhizoidal mass* large, prostrate.

Common: on carbonate sediments or mangrove peat, growing as large mats in shallow waters (less than 1 m), often interspersed among *Thalassia testudinum* or at the edges of mangrove islands; deeper forms (greater than 3 m) have narrow uprights with bluntly pointed apices, Puerto Rican specimens have more club-shaped uprights; to 5 m deep.

Highborne Cay Distribution: only encountered on the reef flat.



1. Surface siphons of blade.
2. Habit.



Highborne Cay US# 209059

Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Udoteaceae

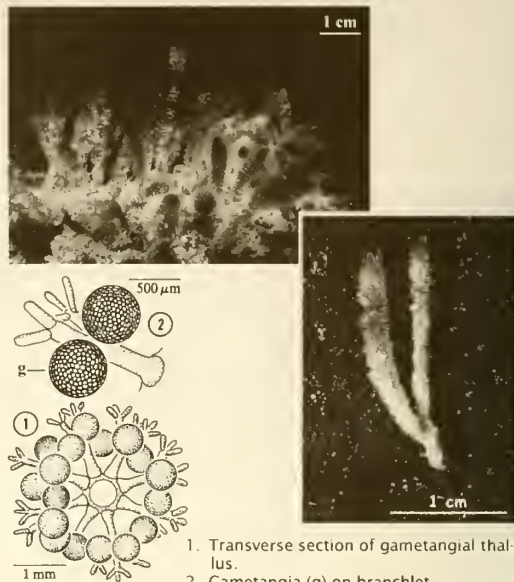
Batophora occidentalis* var. *largoensis

(J.S. Price & S. Baker) S. Berger & Kaever ex M.J. Wynne 1998: 108

Thallus: fuzzy, soft, cylindrical, solitary or most often gregarious, 4-6 mm diam., 3-4(-6) cm high, green to brown-green, releasing bright yellow stain when crushed. *Main axis* of loosely whorled branchlets every 1 mm or less; whorls of 8-13 branchlets; branchlets dichotomously forked 1-7 times, initial branch to 400 μ m diam., dw eciduous on older fertile thalli, lower 0.5 cm of axis often naked. *Gametangia* spherical, 500-800 μ m diam., bright yellow-green, clustered near base of branchlet; reproductive bodies oval to oblong, 40-60 μ m diam.

Common: in lagoons, especially around mangroves, also in brackish-water habitats, often on rubble or dead seashells; to 8 m deep.

Highborne Cay Distribution: common and most abundant species, occurring throughout the study area. A dominant on stromatolites and thrombolites.



1. Transverse section of gametangial thallus.
2. Gametangia (g) on branchlet.

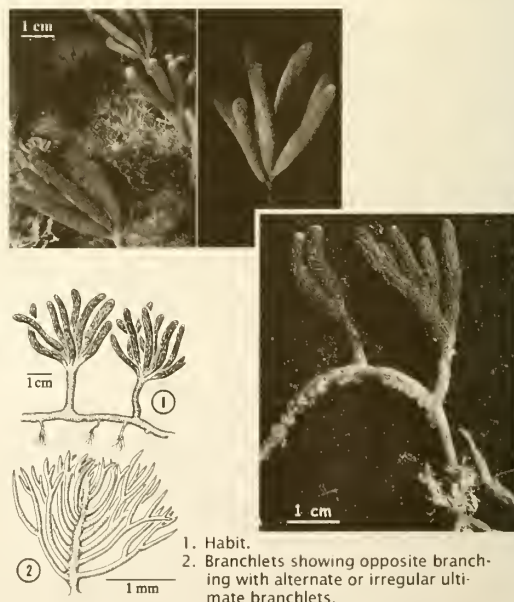
Phylum Chlorophyta Class Ulvophyceae Order Dasycladales Family Dasycladaceae

Caulerpa paspaloides* var. *compressa (Weber-van Bosse) M. Howe 1920: 609

Thallus: erect, to 8 cm high; summit branches 3-5 mm diam., 3-4 cm long, dark green, densely covered with the branchlets not set in vertical rows, cylindrical in configuration when viewed from tip. *Branchlets* cylindrical, 80-100 μ m diam., 1-2 mm long, angling 75-90° from axes, stipe; branching opposite to alternate in two rows opposite one another; ultimate branchlets alternate or irregular, angling 45° or more from one another. *Stalk* naked, green, generally unbranched, to 4 mm diam., to 2 cm long; summit whorled with 3-12 branches. *Stolons* creeping, to 4 mm diam.; rhizoids numerous, white-yellow, stalked, to 2 mm diam. at stolons, branching to slender apices.

Uncommon: in shallow seagrass communities; to 12 m deep.

Highborne Cay Distribution: found only once on the reef crest in the study area, but a species commonly occurring the Bahamas.



1. Habit.
2. Branchlets showing opposite branching with alternate or irregular ultimate branchlets.

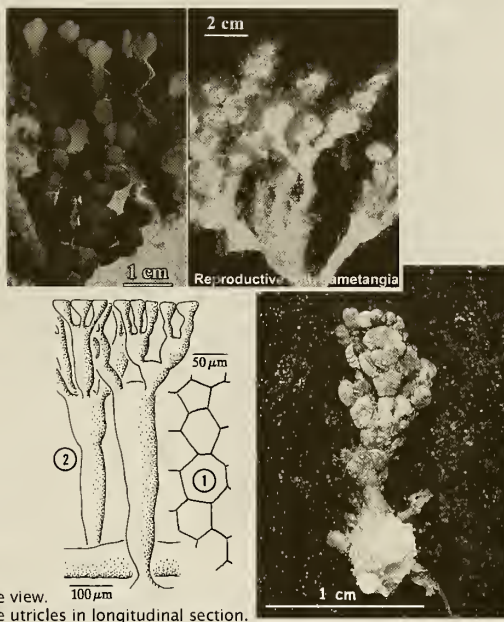
Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Caulerpaceae

Halimeda incrassata (J. Ellis) J.V. Lamouroux 1816: 307

Thallus: erect, to 25 cm high, light to dark green; branching somewhat dichotomous, initial branching in one plane. *Segments* heavily calcified, hard, brittle, disc-like, oval to kidney-shaped, to 14 mm wide, 10 mm long, 0.7–1.5 mm thick, often ribbed and/or lobed; basal segments fused. *Utricles* in 3–5 layers; surface utricles 34–90(–105) μm diam., 40–125 μm long, 2–4 supported by each subsurface utricle; subsurface utricles oval, swollen, 23–90 μm diam., 30–115 μm long. *Joint siphons* uniting as single group, uncalcified. *Rhizoidal mass* bulbous. *Sporangia* spherical to oval, bright green, 200–380 μm diam. on dichotomously forked stalk, densely clustered at margins of fertile segments.

Common: associated with seagrasses or on shallow sand flats; to 12(–65) m deep.

Highborne Cay Distribution: common on the reef flat.



1. Surface view. 100 μm
2. Surface utricles in longitudinal section.

Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Halimedaceae

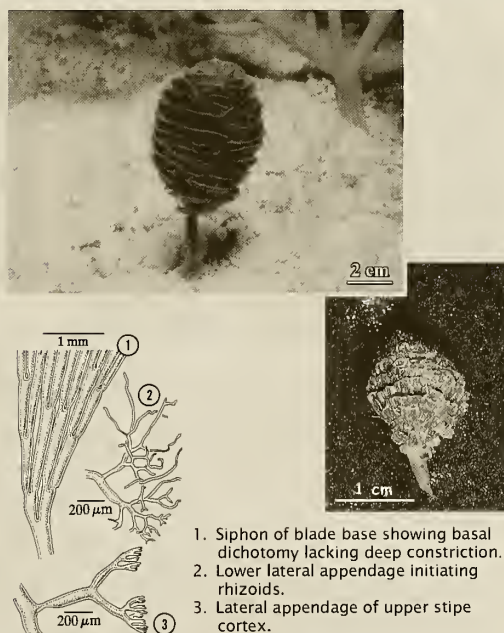
Highborne Cay US# 209051

Rhypocephalus phoenix (J. Ellis & Solander) Kützing 1843: 311

Thallus: lightly calcified, to 10 cm high, dark green. *Cap* oval, of small blades in close proximity to main stalk. *Blades* 2–3 cm long, concentric, attenuated, symmetrical; siphons cylindrical, parallel, fused laterally, 200–250 μm diam. proximally, 50–100 μm diam. distally; dichotomies equal distances from base, lower one or two dichotomies not constricted after decalcification, others evenly constricted. *Stipe* cylindrical, 3–5 mm diam., 2–5 cm long; cortical appendages tightly packed, repeatedly branched with blunt, finger-like apices. *Rhizoidal mass* compact.

Common: on rock or sand, often among seagrasses; to 20 m deep.

Highborne Cay Distribution: only found on the reef crest.



1. Siphon of blade base showing basal dichotomy lacking deep constriction.
2. Lower lateral appendage initiating rhizoids.
3. Lateral appendage of upper stipe cortex.

Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Udoteaceae

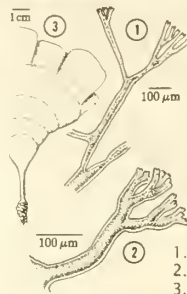
Highborne Cay US# 209057

Udotea flabellum (J. Ellis & Solander) M. Howe 1904: 94

Thallus: fan-shaped, moderately calcified, solitary, to 30 cm high, pale green to dark green. **Blade** variable, undivided to highly divided, size variable, 0.8–1.5 mm thick, leathery, corticated; zonation distinct; siphons 30–50 μm diam., constrictions above infrequent dichotomies absent or slightly uneven; lateral appendages irregularly spaced, long stemmed, dichotomously branched with crowded, short, rounded apices, apices appear shrunken or at when dried. **Stipe** cylindrical below, attenuated above, 5–7 mm diam., 2–4 cm long, unbranched; surface unmodified in transition to blade; siphons 20–80 μm diam.; lateral appendages similar to blade. **Rhizoidal mass** bulbous to elongated.

Common: widespread, occurring in sandy areas or seagrass beds; to 10 m deep.

Highborne Cay Distribution: only in the stromatolite zone.



1. Blade siphon with lateral appendages.
2. Blade lateral appendage.
3. Habit.



Highborne Cay US# 209058

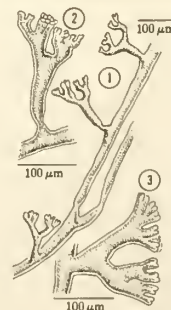
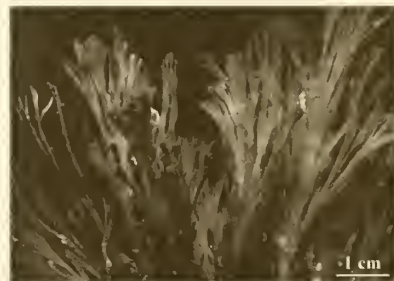
Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Udoteaceae

Udotea norrisii D.S. Littler & M.M. Littler 1990a: 235, g. 17

Thallus: coarse, bushy, heavily calcified, to 11 cm high, gray-green. **Blades** irregularly dissected into long linear segments, 1–3 mm wide, 1–2 mm thick, corticated; zonation distinct; siphons 40–80 μm diam., unevenly constricted above dichotomies; lateral appendages widely spaced, irregular, long-stemmed, apices attenuated or rounded. **Stipe** often branched, 2–3 mm diam., 1–2 cm long, surface unmodified in transition to blade; lateral appendages repeatedly branched with attenuated, blunt apices. **Rhizoidal mass** bulbous, tangled.

Rare: on sand plains or sandy patches around coral pinnacles; 3–30 m deep.

Highborne Cay Distribution: only in the stromatolite zone.



1. Blade siphon with lateral appendages.
2. Blade lateral appendage.
3. Stipe lateral appendage.



Highborne Cay US# 209069

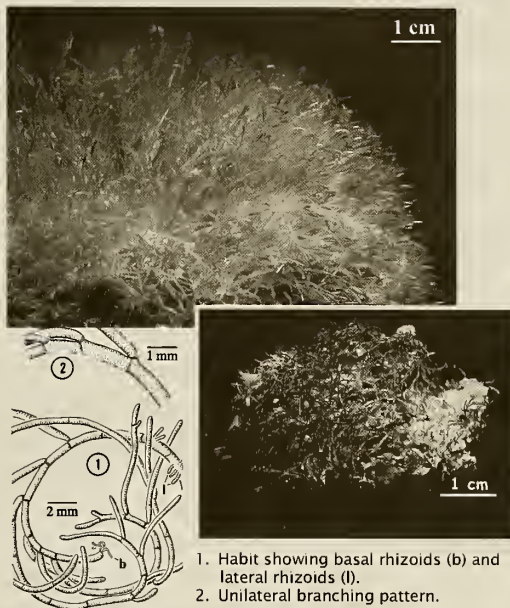
Phylum Chlorophyta Class Bryopsidophyceae Order Bryopsidales Family Udoteaceae

Valoniopsis pachynema (G. Martens) Børgesen 1934: 10, gs. 1, 2

Thallus: filamentous, coarse, stiff, loose, forming pad-like cushions, to 10 cm diam., 5 cm thick, glossy green; branching generally unilateral. *Filament cells* cylindrical, (0.3-)0.5-1.0 mm diam., 2-10 or more diameters long. *Branchlets* cylindrical, with no or little taper, originating from upper ends of parent cells; wall formation basal to main filament. *Rhizoids* short, sparse; older branches often secondarily attached by short lateral rhizoids.

Common: forming stiff masses or clumps in calm shallow habitats; to 5 m deep.

Highborne Cay Distribution: on the reef crest, reef flat and thrombolite zones, but not present in the stromatolite zone.



1. Habit showing basal rhizoids (b) and lateral rhizoids (l).
2. Unilateral branching pattern.

Phylum Chlorophyta Class Ulvophyceae Order Cladophorales Family Anadyomenaceae

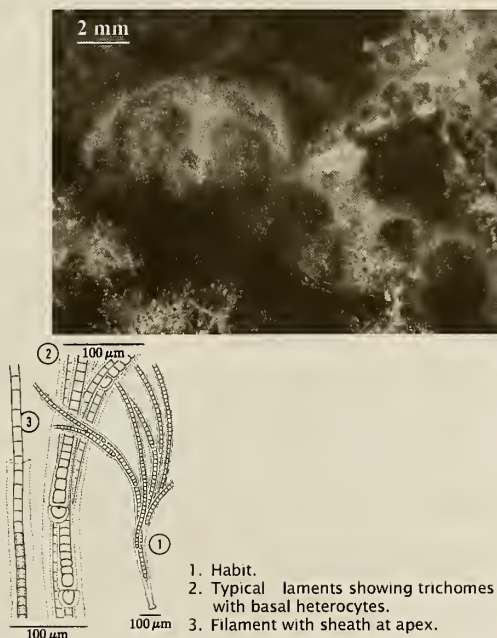
Highborne Cay US# 209064

Dichothrix fucicola (Kützting) Bornet & Flahault 1886: 379

Thallus: forming small erect tufts or soft fuzzy patches, to 8 mm high, lavender-red to dark olive-green. *Filaments* 20-40 μm diam., forming false branching. *Trichomes* one per sheath, merging with age, tapering from base, ending in a long hair. *Cells* 9-13 μm diam., swollen base 13-22 μm diam., 10-60 μm long; not constricted at cross walls. *Sheaths* clear, colorless or yellowish, striated, 8-20 μm thick. *Heterocytes* spherical, cone-shaped to elongated, 20-25 μm diam., 20-60 μm long, basal or intercalary.

Common: generally epiphytic on other marine plants, forming small pads or fuzzy clumps; intertidal to 2 m deep.

Highborne Cay Distribution: found intermixed with other species in all zones.



1. Habit.
2. Typical filaments showing trichomes with basal heterocytes.
3. Filament with sheath at apex.

Phylum Cyanophyta Class Cyanophyceae Order Nostocales Family Rivulariaceae

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ATOLL RESEARCH BULLETIN

NO. 533

**PLANKTONIC PROTOZOAN POPULATIONS ON FIVE
WEST INDIAN REEFS**

BY

JOHN A. FORNSHELL

**ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
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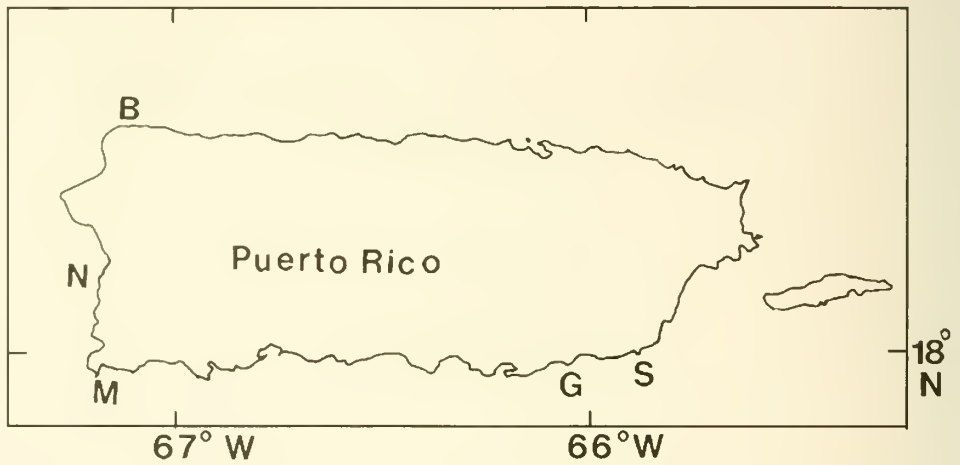


Figure 1. The positions of the five reefs where plankton samples were collected in this study: B = Bujuras Reef; G = Guayama Reef; M = Margarita Reef; N = Negro Reef; S = Sargente Reef.

PLANKTONIC PROTOZOAN POPULATIONS ON FIVE WEST INDIAN REEFS

BY

JOHN A. FORNSHELL¹

ABSTRACT

A study of the Protozoan plankton on five West Indian reefs was conducted from August to November 1982 and in June 1983. Plankton tows were collected in five areas: Sargente Reef, Guayama Reef, and Margarita Reef from the northeastern Caribbean Sea, Negro Reef from Mona Passage between the Islands of Puerto Rico and Hispaniola, and Bujuras Reef in the tropical Atlantic Ocean. The Protozoan plankton were identified along with benthic Foraminifera collected in the plankton tows. Thirty-eight different species of armored Dinoflagellata were found on the five reefs in this study. Benthic Foraminifera and Radiolaria were also found in the plankton samples from all five reefs. Armored Dinoflagellata accounted for 62%, 72%, 22%, 28% and 45% on Bujuras Reef, Negro Reef, Margarita Reef, Guayama Reef and Sargente Reef, respectively. On Margarita Reef and Guayama Reef, Tintinnids were more abundant than armored Dinoflagellata, 30% and 38% respectively. Distinctiveness and diversity indices were calculated based on the armored Dinoflagellata populations on the reefs in this study. There was greater seasonal than spatial variation in the distinctiveness of the populations of armored Dinoflagellata in the study area. The populations were all typically diverse as would be expected in the tropics.

INTRODUCTION

A study of the abundance and variability of planktonic Protozoans on five West Indian reefs in the northeastern Caribbean Sea and adjacent tropical Atlantic Ocean was conducted during the summer and fall of 1982 and summer of 1983. In addition to armored Dinoflagellata, other Protozoans were enumerated from the samples. This helped to determine the relative abundance of the armored Dinoflagellata in the microplankton of the reefs. In earlier works on the planktonic Protozoa in the study area, armored Dinoflagellata were reported as having a significant population density in coastal waters close to mangroves (Margalef, 1961). Glynn (1973) considered armored Dinoflagellata to be uncommon on reef flats. Marshall (1973) surveyed the Protozoa in

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open waters of this area during the winter month of January. He listed several armored Dinoflagellata, some of which he considered to have wide distribution in the northeastern Caribbean Sea. Armored Dinoflagellata have been studied in the southeastern Caribbean Sea on the Venezuelan coast by Halim (1967) and the western Caribbean Sea by Faust (2000). Faust (2000) found the armored Dinoflagellata to make up as much as 95% of the plankton in some areas on the Barrier Reef of Belize. Morton (2000), also working on the Barrier Reef of Belize, found considerable variability in biomass and diversity of the Protistan plankton in three ponds which he studied. General surveys of the microplankton, including armored Dinoflagellata in the Caribbean Sea, are found in Wood (1968) and Marshall *et al.* (1982). An ocean-wide analysis of the distribution of the genus *Ceratium* can be found in Dodge and Marshall (1994).

MATERIALS AND METHODS

The plankton-sampling program was conducted on a noninterference basis during a project to conduct Lagrangian current measurements along the Caribbean shore of Puerto Rico (Fornshell *et al.*, 1984). Between August 29 and November 13, 1982 microplankton samples were taken from three Caribbean reefs along the southern shore of Puerto Rico: Sargente Reef, Guayma Reef and Margarita Reef. During this time period, microplankton samples were also taken from a fourth reef, Negro Reef, in Mona Passage between Puerto Rico and the island of Hispaniola. A fifth reef on the Atlantic coast of Puerto Rico, Bujuras Reef, was sampled in July 1983 (Fig. 1 and Table 1).

The length of each tow was adjusted to minimize the effects of clogging. As a result, different quantities of water were sampled on each reef. The volumes of water sampled on each reef in cubic meters were determined using a Tsukishima Kikai flowmeter. They are as follows: Sargente Reef, 43.2 m³; Guayma Reef, 35.3 m³; Margarita Reef, 49.6 m³; Negro Reef, 24.7 m³; and Bujuras Reef, 45.2 m³. All of the plankton tows were made in the fore-reef zone following the 20 m-depth contour on Sargente, Guayama, Margarita, and Bujuras Reefs. Because of the steepness of the reef front, this was very close to the reef crest. On Negro Reef the plankton tows were made in the back-reef lagoon.

The Protozoan plankton and the benthic Foraminiferans that were collected in the plankton net were identified. All five of the reefs can be characterized as having a significant surf breaking over the reef. As a result of this wave action, a large number of benthic Foraminifera are lifted into the water column and are collected along with the plankton.

The distinctiveness and diversity indices of the armored Dinoflagellata populations were calculated. The armored Dinoflagellata were selected because they were abundant on all five reefs and good taxonomic data was available for this group. The distinctiveness index described in Menzies *et al.* (1974) is given by the formula:

$$\frac{(\text{Total number of species} - \text{number of species in common}) \times 100}{(\text{Total number of species})}$$

The distinctiveness index gives a quantitative measure of the difference in the composition of two populations. The index represents the distinctiveness of the population as a percentage. It does not measure differences in relative abundance.

The diversity index provides a measure of the diversity of a single population. The diversity index as described in Menzies *et al.* (1974) is given by the formula:

$$\frac{(\text{Total number of species})}{(\text{Total number of individuals})}$$

Table 1. Dates and positions of the five reefs where plankton tows were made.

Reef	Sampling Dates	Location
Sargente Reef	3 tows on Aug. 29, 1982	17-58N; 65-54W Off Punta Tuna, P.R.
	2 tows on Nov. 13, 1982	
Guayama Reef	2 tows on Aug. 29, 1982	17-50N; 66-04W Off Punta Figuras, P. R.
	3 tows on Nov. 13, 1982	
Margarita Reef	5 tows on Sept. 2, 1982	17-56N; 67-13W Off Cabo Rojo, P. R.
Negro Reef	5 tows on Sept. 20, 1982	18-10N; 67-13W Off Punta Guanajibo, P. R.
Bujuras Reef	3 tows on July 8, 1983	18-32N; 67-12W Off Punta Agujereada, P. R.

RESULTS

The data are summarized in Tables 2 and 3. Thirty-eight species of armored Dinoflagellata were found on the five reefs. Only seven species of armored Dinoflagellata were found on all five reefs: *Ceratium contortum*; *C. declinatum*; *C. furca*; *C. macroceros*; *C. massiliense*; *C. trichoceros*; and *C. tripos* (Table 2). *Globigerinoides ruber* was the only Foraminiferan found on all five reefs. Benthic Foraminifera were a significant component of the Protozoans sampled at each reef. Tintinnids were present in the samples from Bujuras, Guayama, and Sargente Reef, but not on Margarita and Negro Reefs. Radiolaria were found on all five reefs (Table 3). The armored dinoflagellate population on Bujuras Reef was 160/cubic meter; on Negro Reef, 641/cubic meter; on Margarita Reef, 80/cubic meter; on Guayama Reef, 168/cubic meter; and on Sargente Reef, 133/cubic meter. These numbers represent 62%, 72%, 22%, 28%, and 43% of the total Protozoan plankton on each reef.

On three of the five reefs, Bujuras, Negro, and Sargente, the armored

Dinoflagellata are the largest single component of the net microplankton. On two of the reefs, Margarita and Guayama, Tintinnids were the largest single component of the microplankton, 30% and 38% respectively.

The samples from Guayama and Sargente Reefs, taken in August and November 1982 (Table 1), showed significant intra-reef difference in their distinctiveness (indices 71 and 92 respectively). Since these values are larger than inter-reef values (see Table 4), the seasonal variations are greater than the spatial variations observed in this study.

The distinctiveness indices show relatively little difference among the three reefs on the south coast, Sargente, Guayama and Margarita, and Negro Reef in Mona Passage. The distinctiveness indices between these four reefs and Bujuras Reef on the Atlantic coast are larger, an average of 56.5 vs. an average of 40 among the first four named reefs. This may be due to seasonal variations given the large amount of time, 10 months, between the sampling of Bujuras Reef and the other four reefs.

The diversity indices for the five reefs were as follows: Bujuras Reef, 0.055; Negro Reef, 0.0015; Margarita Reef, 0.038; Guayama Reef, 0.0027; and Sargente Reef, 0.0048. While these are small numbers in absolute terms, they are typical of diverse populations of marine organisms.

DISCUSSION

Armored Dinoflagellata are not abundant in an absolute sense; however, they are a major component of the net microplankton. The benthic Foraminifera are believed to be suspended in the water column near the reef by the action of breaking waves. As such, they are available as food to plankton-feeding organisms. The armored dinoflagellates were found to be the largest single component in the microplankton on three of the five reefs surveyed.

There do not appear to be any significant differences in the armored dinoflagellate populations on the five reefs of this study. The intra-reef indices of distinctiveness observed on Sargente and Guayama Reefs over a period of 76 days, 71 and 92 respectively (Table 4), were larger than those between the reefs. The time spread of 10 months between the survey of the four Caribbean Sea reefs and the one tropical Atlantic reef could account for temporal or seasonal variations.

Table 2. Species of armored Dinoflagellata on the five reefs. The numbers of organisms per cubic meter are given.

Species	Bujuras Reef	Negro Reef	Margarita Reef	Guayama Reef	Sargente Reef
<i>Ceratium</i> sp.	0	4	0	1.1	0.9
<i>C. belone</i>	0	0.8	0	0.6	0.5
<i>C. breve</i>	0	0	0	0.6	0
<i>C. buceros</i>	0	0	0	2.8	1.4
<i>C. candelabrum</i>	0.9	0	0.4	2.3	0.9
<i>C. concilians</i>	0	0	0	0.6	0.4
<i>C. contrarium</i>	1.8	0	0	1.7	0
<i>C. contortum</i>	7.5	0.8	2.8	12.5	2.3
<i>C. declinatum</i>	4.4	4.6	8.9	5.9	3.7
<i>C. eurarcuatum</i>	0	0	0.4	2.8	4.6
<i>C. fatulipes</i>	0	3.2	0	0	0
<i>C. furca</i>	1.3	122.3	0.8	12.5	6.5
<i>C. fusus</i>	2.2	13	0	0.6	4.6
<i>C. geniculatum</i>	0	3.2	0	0	0
<i>C. karstent</i>	22.1	0	0	0	1.4
<i>C. kofoid</i>	0	1.6	0	0.6	1.8
<i>C. longinum</i>	4	2.4	0	24.4	1.4
<i>C. linula</i>	1.3	0	0	1.2	0.6
<i>C. macroceros</i>	29.2	157.9	8.9	30.1	12.5
<i>C. massiliense</i>	44.2	98	18.1	64.2	37
<i>C. minutum</i>	0	0	10.5	0.6	0.5
<i>C. pavillardi</i>	0.4	0.8	0	0	0
<i>C. pentagonum</i>	0	1.6	0.4	0.6	0.5
<i>C. setaccum</i>	0	0	0	0.6	0.5
<i>C. teres</i>	0	0.8	0.4	2.8	3.2
<i>C. trichoceros</i>	14.6	102	4	39.2	0.5
<i>C. tripos</i>	15.9	18.6	16.9	67.6	16.2
<i>C. vultur</i>	3.5	1.6	3.2	17	5.1
<i>Gambierdiscus toxicus</i>	0	0	0	0	0.5
<i>Goniaulax dicantha</i>	0	17	2	6.2	5.1
<i>G. polygrama</i>	0	34.8	3.2	19.9	12.5
<i>Heterodinium</i> sp.	0	0	0	2.3	0.9
<i>Ornithocercus magnificans</i>	0	0	0	0.6	0
<i>Phalocoma argus</i>	0.4	0	0	0	0
<i>Peridinium</i> sp.	0	2.4	0	0	0
<i>P. depressus</i>	1.8	23.5	0	5.6	1.8
<i>P. divergens</i>	1.8	17	0	1.7	1.8
<i>P. fatulipes</i>	0	0	0	1.7	0
<i>P. grande</i>	2.6	0	0	0.6	0

Table 3. Protozoan microplankton on the five reefs. The numbers given are the number of organisms per cubic meter.

Microplankton	Bujuras Reef	Negro Reef	Margarita Reef	Guayma Reef	Sargente Reef
<i>Globergerinoides ruber</i>	5.8	30.8	82.2	79	19.4
<i>Pulleniantina obliquiloculata</i>	0.9	6.5	13.1	7	0
<i>Benthic Foraminiferans</i>	68.1	157.9	77	108	34.2
<i>Tintinnids</i> sp.	0	42.1	111.3	8.5	1.8
<i>Condonellopsis indica</i>	0	0	0	24.4	0
<i>Favella fistulicauda</i>	0	0	0	2.3	0
<i>F. markusorszkyi</i>	1.8	0	0	24.4	5.6
<i>F. panamensis</i>	4.4	0	0	9.1	22.2
<i>F. serata</i>	0.9	0	0	0	0
<i>Parafavella elegans</i>	1.8	0	0	4	4.2
<i>P. media</i>	0	0	0	2.3	1.8
<i>P. enflata</i>	0	0	0	1.1	0
<i>P. lata</i>	0	0	0	52.8	0
<i>Rabdonella</i> sp.	0	0	0	84.1	0
<i>R. amor</i>	0	0	0	0	72.2
<i>R. brandtei</i>	0	0	0	11.4	0.5
<i>R. quantula</i>	0.9	0	0	0	0
<i>R. spiralis</i>	0.9	0	0	0	0
<i>Radiolaria</i> sp.	1.8	0.8	2.4	4.5	5.6
<i>Heliosphaera actinota</i>	0.4	0	0	0	0
<i>Acanthara</i> sp.	12	10.5	0	0	0

When compared with the studies of the eastern Caribbean Sea, we find that the first two species considered having wide distribution by Marshall (1973), *C. tripos* and *C. trichoceros*, were present in relatively large numbers on all five of the reefs in this study but the last named species, *C. fusus*, was present on all but one of the reefs. Thirteen of the 38 species found in this study were listed in the southeastern Caribbean Sea by Halim (1967). Six of the 38 species in our study were also listed by Faust (2000) in the western Caribbean. This implies greater variation in the east-west axis of the Caribbean Sea than in the north-south direction. Dodge and Marshall (1994) created six zones of distribution for the genus *Ceratium* in the North Atlantic and Caribbean Sea. Their warm temperate and tropical zones are essentially the same as these findings.

The armored Dinoflagellata populations are typical of tropical and warm

temperate seas. They show no significant variations over the geographical range of this study. This is not surprising given the small horizontal variation in physical properties (Wust, 1964 and Fornshell, 1984). There are similarities with other studies from other parts of the Caribbean Sea but these similarities decrease with increasing distance

Table 4. Distinctiveness Indices for the five reefs. The numbers represent the percent distinctiveness of the population on each reef relative to the other reefs.

	Bujuras Reef	Negro Reef	Margarita Reef	Guayama Reef	Sargente Reef
Bujuras Reef	0.0	53.6	66.7	55.2	57.6
Negro Reef	53.6	0.0	54.2	44.8	30.8
Margarita Reef	66.7	54.2	0.0	50.0	46.2
Guayama Reef	55.2	44.8	50.0	0.0	33.3
Sargente Reef	57.6	30.8	46.2	33.3	0.0

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ATOLL RESEARCH BULLETIN

NO. 534

**DINOFLAGELLATE DIVERSITY AND ABUNDANCE IN TWO
BELIZEAN CORAL-REEF MANGROVE LAGOONS: A TEST OF
MARGALEF'S MANDALA**

BY

**MARIA A. FAUST, R. WAYNE LITAKER, MARK W. VANDERSEA,
STEVEN R. KIBLER, AND PATRICIA A. TESTER**

**ISSUED BY
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NOVEMBER 2005**

Research Area of Twin Cays and Douglas Cay

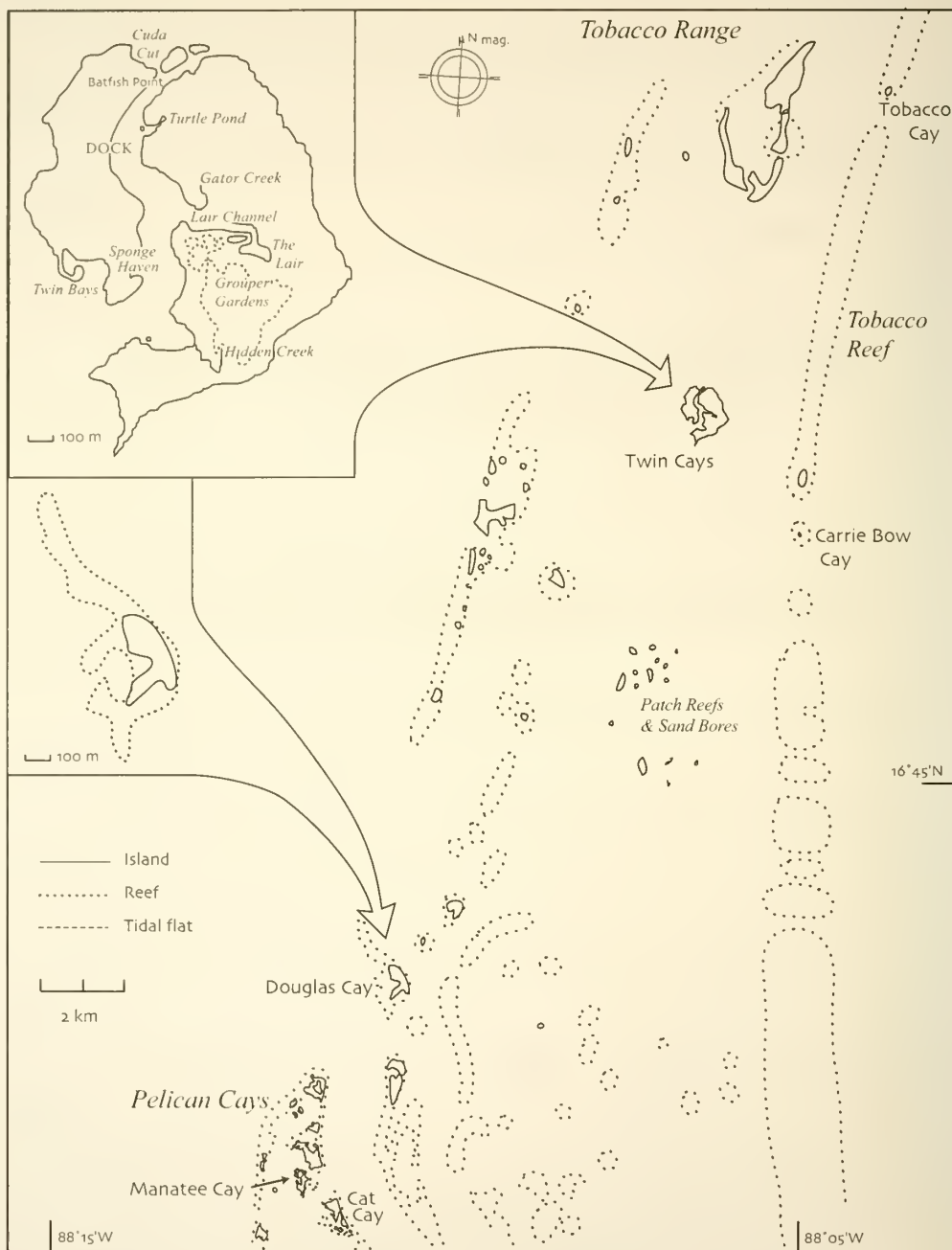


Figure 1. Map showing The Lair at Twin Cays, and Douglas Cay sample sites and surrounding cays.

DINOFLAGELLATE DIVERSITY AND ABUNDANCE IN TWO BELIZEAN CORAL-REEF MANGROVE LAGOONS: A TEST OF MARGALEF'S MANDALA

BY

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ABSTRACT

Dinoflagellates are frequently abundant in the coral-reef mangrove lagoons off the coast of Belize. Margalef predicted that marine environments with low turbulence and high nutrient inputs would favor dinoflagellates. A long-term study of coral-reef mangrove embayment cays of Belize, including this study, has shown that these systems contain abundant dinoflagellate species. Consistent with Margalef's prediction, these habitats are protected from wind mixing, show a high degree of stratification, and have restricted water exchange with surrounding oligotrophic waters of the open barrier-reef system. This limited water exchange favors retention of dinoflagellate cells and the trapping of nutrient rich organic material that is rapidly recycled providing a relatively high-nutrient environment. Species-specific blooms are a common feature of these systems. In the study, the ecology and diversity of dinoflagellate species from two nutrient-enriched habitats, Douglas Cay and The Lair at Twin Cay, were examined in detail. A comparison of the species composition from both sites showed that Douglas Cay contained coastal planktonic and offshore oceanic dinoflagellates while The Lair at Twin Cay contained mainly benthic dinoflagellates. A total of 19 bloom-forming species were observed in these systems during three two-week studies. The morphology of eight of these bloom-forming species is illustrated in Scanning Electron Microscopy (SEM) photographs. These include *Bysmatrum caponii*, *Dinophysis caudata*, *Gonyaulax grindleyi*, *Peridinium quinquecorne*, *Gonyaulax polygramma*, *Gonyaulax spinifera*, *Lingulodinium polyedrum*, and *Pyrodinium bahamense* var. *bahamense*. Approximately half of the bloom-forming dinoflagellates are known toxin producers. The congruence between Margalef's prediction and the distribution of dinoflagellates in these naturally eutrophic systems suggests that increased nutrient inputs in oligotrophic portions of the Caribbean will favor a shift in species dominance toward dinoflagellate species. The effect will be most pronounced in bays or other regions where turbulence is likely to be reduced. This species shift may have consequences for food web dynamics and the prevalence of dinoflagellate toxins in the food chain.

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INTRODUCTION

Dinoflagellates constitute one of the dominant groups of oceanic phytoplankton and are responsible for a significant portion of overall primary productivity. Many species are bloom formers, and a subset of these is known to produce potent toxins that accumulate in the food chain causing mass mortalities of fish, birds and mammals, as well as human illness and death. These blooms frequently reach densities sufficient to discolor the water and can release enough organic material to result in hypoxia or other forms of water-quality degradation including noxious odors and unsightly foams. Occurrences of harmful algal blooms (HABs) near shore regions cause severe economic impact, have major environmental and human health problems, and cause losses to fisheries and tourism operations (Smayda, 1997; Ajani et al., 2001). Often these blooms are characterized by the proliferation and dominance of a particular species (Hallegraeff, 1993). Globally, HABs are increasing in scale and frequency and currently threaten most coastal regions of the world. Many reasons for this increase in bloom frequency have been postulated, ranging from anthropogenic nutrient inputs to increased awareness and improved surveillance (Pitcher and Cockroft, 1996).

Extensive research has been conducted to identify the physical, chemical and biological mechanisms responsible for dinoflagellate bloom formation (Smayda, 1997). One of the earliest and most robust hypotheses put forward is Margalef's Mandala (Margalef, 1978; Margalef et al., 1979). This hypothesis predicts that low turbulence and high nutrient environments favor dinoflagellate dominance. Work with mid- and upper-latitude species does indeed seem to confirm that substantial nutrient inputs and low turbulence conditions coincide with dinoflagellate blooms. These conditions also include blooms that are enhanced by accumulation in stable frontal zones which represent regions of lowered turbulent dispersion. There is, however, a paucity of available information about HAB dinoflagellate blooms that occur in tropical regions including the Atlantic barrier coral-reef mangrove ecosystems of Belize (Hernández-Becerril and Becerril, 2004). Preliminary surveys have found that although some HAB dinoflagellates are found in low abundance throughout the Belizean barrier-reef system, the greatest diversity and highest number of bloom-forming species appear restricted to mangrove cay embayments or similar environments (Faust, 2000, 2004; Morton and Villareal, 1998; Morton, 2000). In this publication, we report the occurrence of 59 dinoflagellate species from two lagoonal embayments located at Douglas Cay and Twin Cays, Belize. Fifteen of the species identified formed substantial blooms. The ecology and morphology of eight of these are described in detail and an evaluation of how well the prevailing conditions and dinoflagellate abundance agree with the predictions of Margalef's Mandala is presented.

METHODS

Study Area

Douglas Cay, Belize is situated north of The Pelican Cays ($16^{\circ} 42.5' N$ $88^{\circ} 10.3' W$, Figure 1) and is part of the largest barrier-reef mangrove ecosystem in the new world (Macintyre and Rützler, 2000). The reefs in this system are characterized by channels that form a number of shelf atolls (James and Ginsburg, 1979) which are separated by an unusual network of reef ridges, both submerged and exposed, which were formed during the Holocene (Macintyre et al., 2000). Many of these lagoon reefs have been colonized by red mangroves, *Rhizophora mangle* Linnaeus (Purdy, 1994). When the morphology of these lagoonal reefs is favorable, the developing mangrove islands will encompass an internal lagoon like that found at Douglas Cay. These lagoons range from 1-10 m depth at their center. They have eroded peat banks around the margin with an abundant growth of mangrove prop roots. The entrance to these lagoons is frequently characterized by a sill or other morphological feature that restricts water exchange with the surrounding oceanic fore-reef systems. As a result, these lagoons are considered separate water masses and are characteristically warmer and more saline than the open waters of the surrounding central lagoon (Villareal et al., 2000). The mangrove prop roots that line the edge of these lagoons are colonized by abundant corals, sponges and tunicates (Rützler and Feller, 1996). The hydrographic isolation of these systems, and low tidal amplitude (<20 cm) allows retention of nutrient and carbon-rich detrital material supplied by the surrounding mangrove trees. These conditions promote a high microbial biomass and the rapid rates of nutrient recycling.

Twin Cays, the second system studied (located 7 km north of Pelican Cays ($16^{\circ} 49.4' N$ $88^{\circ} 6.1' W$), consists of a shallow intertidal mangrove island characterized by a series of lagoons, channels, mud flats and ponds. The "Lair", the specific location where samples were taken, is a shallow lagoon (0.5 to 3 m deep) located at the end of The Lair channel. Though The Lair has a poorly developed sill, the <20 cm tide and long narrow Lair channel which separates The Lair from surrounding waters, help restrict water exchange with the surrounding waters. Overall water exchange, however, is greater than observed for Douglas Cay (Kibler et al., 2005). The Lair is also high in organic matter originating from mangroves, meadows of turtle grass, *Thalassia testudinum* Bank ex Konin, as well as benthic production associated with the soft sediments.

Physical Parameters and Chlorophyll a Biomass

Temperature, salinity, dissolved oxygen and irradiance were measured in the water column at three depths with a Yellow Spring Instrument profiling unit (model 6600). Irradiance was estimated by the integrating quantum scalar irradiance meter, Biospherical Instruments # QSI-140 meter (Tester et al., 2003). Ammonia was measured fluorometrically using the method of Holmes et al. (1999). Samples for chlorophyll a analysis were vacuum-filtered through 25mm GF/F filters (< 10 cm Hg) and were immediately frozen in liquid nitrogen. Samples were subsequently extracted with 7.5

ml 90% acetone and were macerated with a tissue grinder before being analyzed using the acidification method for chl *a* described by Parsons et al. (1984). The water column conditions at Douglas Cay and The Lair were similar in 2002, 2003 and 2004. In 2004, we formally quantified stratification at each station using the Brunt-Väisälä frequency (*N*), which describes the oscillation that results when the pycnocline is displaced (Mann and Lazier, 1996). This metric was calculated at mid-depth in the water column using the expression $N \text{ (rad s}^{-1}\text{)} = (g/\bar{\sigma}'z)^{1/2}$, where *g* is the gravitational constant (m s^{-2}) and $\bar{\sigma}'$ is density (Kg m^{-3}). To simplify comparisons, *N* was converted to units of cycles h^{-1} using $N/2\pi$. Strong stratification is indicated by frequencies in excess of 20 cycles h^{-1} (Macintyre et al., 2002).

Dinoflagellate Sampling

The dinoflagellate assemblages were characterized annually at both Douglas Cay and Lair habitats during a two-week period in each May from 2002 to 2004 (Fig. 1). A total of 42 water samples were collected from Douglas Cay and 20 water samples were collected from The Lair. Subsurface water was collected using a 20 μm pore size nylon plankton net towed by a small boat operating at its lowest speed for 1-2 minutes. Large pieces of floating detritus were also collected (Faust, 2004). Samples were concentrated to 100 ml volume and fixed with glutaraldehyde at 1% final concentration for light microscopy and SEM species identification (Faust, 1990). Both the Douglas Cay and "Lair" habitats were characterized by a diverse community of dinoflagellates (Faust, 2004).

Enumeration and Identification of Dinoflagellates

To enumerate microalgae, cell concentrations of three replicates for each water sample were estimated at 100x magnification in a Palmer-Maloney cell chamber or in settling chambers (Guillard, 1973). Dinoflagellates were identified under differential interference contrast illumination with Carl Zeiss Axiophot microscope. The relative abundance of dinoflagellates was determined as the proportion of organisms present in a total of 500 cells.

For SEM, glutaraldehyde (1% concentration)-preserved dinoflagellates were isolated using a capillary pipette under a compound microscope. Cells were concentrated onto a polycarbonate filter at room temperature, rinsed six to eight times with deionized water, dehydrated in a graded series of ethanol concentrations and critical point dried. The preparation was coated with carbon and by a layer of gold-palladium (Faust, 1990). Cell dimensions were determined from SEM photographs of at least 10 cells; values given represent the mean. Kofoidian nomenclature was used for identifying dinoflagellate species (Kofoid, 1909). Samples of this investigation are deposited in The Dinoflagellate Collection of the U.S.A. National Herbarium, Smithsonian Institution, Washington D.C.

RESULTS

Physical environment

Both temperature and salinity were high in Douglas Cay and The Lair and varied only slightly over the course of all three May study periods (Table 1). Both lagoons were protected from prevailing winds by the surrounding mangrove trees. Stable temperature and salinity conditions, low tidal exchange and reduced wind mixing resulted in a low turbulence environment (Table 2).

Table 1. Range of environmental variables measured in Douglas Cay and The Lair, Twin Cays during the three two week study periods.

Study Site	Dissolved NH ₄ ⁺ µmole.L ⁻¹	Temperature °C	Salinity psu	Dissolved O ₂ ppm	Light µE.m ⁻² . s ⁻¹	Chlorophyll a µg.L ⁻¹
Douglas Cay	0.6-6.0	28.3-29.3	35.6-36.1	2.2-6.5	1500-2000	5.0-15.0
The Lair	0.1-0.8	29.1-31.2	37.5-38.0	2.0-5.0	1200-2000	0.8-15.0

Table 2. Brunt-Vaisala frequency calculated at Douglas Cay and at The Lair

The Lair 2004		
Date	Time	B-V Frequency (cycles h ⁻¹)
12 May 04	1530	37.6
13 May 04	0800	23.5
13 May 04	1415	34.2
17 May 04	0830	28.3
17 May 04	1430	33.8
18 May 04	1000	34.3
18 May 04	1615	40.7

Douglas Cay 2004		
Date	Time	B-V Frequency (cycles h ⁻¹)
10 May 04	0630	10.3
11 May 04	0645	25.0
11 May 04	1400	48.6

Dissolved oxygen varied from hypoxic to supersaturated depending on the time of day. This fluctuation is due to the balance between bacterial respiration and photosynthetic oxygen production. In these shallow systems, midday photosynthetically active radiation is sufficient to saturate photosynthesis in the water column (Table 1) and at the benthic surface as well. Dissolved NH₄⁺ is higher in Douglas than in The Lair, but both are on

average approximately an order of magnitude greater than concentrations found in the surrounding oligotrophic lagoon. The Brunt-Väisälä numbers exceeded 20 cycles h^{-1} during each period measured except one, indicating that the water column is highly stable (Table 2).

Distribution and Diversity of Dinoflagellates Observed in Douglas Cay and The Lair

The dinoflagellate assemblage present in Douglas Cay during 2002 was quite diverse. There were 45 dinoflagellate species present. Twenty-one of these were planktonic, 11 benthic and 5 benthoplanktonic. Thirty-three of the species are known autotrophs, 6 were heterotrophs and 3 mixotrophs. Fifteen are known to form toxic blooms in other regions (Table 3). A comparison of the dinoflagellate species present in Douglas Cay and The Lair in 2004 demonstrated that dinoflagellate communities were similarly diverse to that observed in 2002, and that they shared approximately 65% of the species in common. Overall, benthic species were common in The Lair than in Douglas Cay (Tables 3 and 4). A compilation of the data from all three years identified a total of 19 bloom-forming species from Douglas Cay and The Lair (Table 5). Some of these species were more persistent in time and space than others. Of these 19 species, 11 are known toxin producers (Table 6). A detailed description of the ecology and morphology for 8 of these 19 bloom-forming species follows:

Gonyaulax grindleyi Reinecke 1967

Synonym: *Protoceratium reticulatum* (Claparède & Lachmann) Bütschli, 1885: p. 1000, pl. 52.

Figures 2-6

Morphology: Cells conical with a rounded hypotheca; cells (30-45 μm L, and 28-43 μm W) (Fig. 2). Surface is deeply areolate (Fig. 3). Apical pore complex is oblong with the apical pore in the center covered by a mucus plug (Fig. 4). Sulcus is oblong and narrow (Fig. 5). Morphology of the dissociated plates is in line drawings (Fig. 6): species-specific feature the intercalary plate 1a and the ventral pore situated in right margin on apical plate 1' (Fig. 6b). Forms cysts.

Ecology: Cells present in Cat Cay, Douglas Cay, Elbow Cay, and Manatee Cay (Faust, 2000). Bloom of 9.85×10^4 cells L^{-1} caused brown water discoloration at Tobacco Range (Fig. 1) in May 2000. Cysts in the sediment germinate that initiated the bloom (Reinicke, 1967).

Distribution: neritic, estuarine; cold temperate to subtropical waters.

Toxicity: Producer of paralytic toxin affecting shellfish beds (Table 6).

Peridinium quinquecorne Abé 1927

Synonym: *Protoperidinium quinquecorne* (Abé) Balech, 1974: p. 59.

Figures 7-10

Morphology: Epitheca is conical with a pointed apex, cells (23-40 μm L and 20-36 μm W) (Fig. 7); Hypotheca is angular, 4 antapical spines variable in length. Intercalary plates 1a pentagonal and 2a heptagonal (Fig. 8). Apical plate is a round chamber with a Po plate and X canal plate (Fig. 9). Cell shape is rhomboid (Fig. 10b- c). Red eye-spot present.

Ecology: Identified in floating detritus at Douglas Cay and The Lair, cell shape, and length variable. Forms red tides (1.15×10^4 cells L^{-1}), cells adapted to both benthic and planktonic shallow-tropical waters. Cells tolerate high temperatures (38 to 42 $^{\circ}\text{C}$). Present in tropical tide pools (Horiguchi and Pienaar, 1991).

Toxicity: During very high cell numbers this species can cause anoxia and fish kills (Fukuyo et al., 1990).

Bysmatrum caponii (Horiguchi et Pienaar) Faust and Steidinger 1998

Synonym: *Peridinium gregarium* Lombard et Capon, 1971a: p. 184-187.

Figures 11-12

Morphology: Epitheca is conical and hypotheca trapezoidal; epitheca and hypotheca almost equal (Fig. 11). Cells are 35 μm L to 30 μm W and cell surface vermiculate. Hypotheca is indented (Fig. 12a). Apical intercalary plates 1a and, 2a adjacent and 3a separated (Fig. 12b). Apical pore complex is chamber-like Fig. 12b). Sulcus is wide four sulcal platelets present (Fig. 12c). Red stigma is present.

Ecology: Species is a new red tide-forming dinoflagellate from Belize. Cell concentrations, 1.85×10^2 cells L^{-1} , observed in Douglas Cay. Cells also present in Elbow and Manatee Cays (Faust, 2000). Species sand dwelling, attach to particles via mucus strands emerging from the apical pore (Po).

Distribution: coastal, warm, tropical and estuarine tide pools.

Toxicity: Not toxic (Table 6).

Dinophysis caudata Saville-Kent 1881

Synonym: *Dinophysis homunculus* Stein, 1883: p. 3, 24, pl. 21, figs. 5-7.

Figures 13-14

Morphology: Epitheca very small and hidden, cells flattened and 110 μm L to 80 μm W (Fig. 13). Hypotheca is prominent with a long ventral finger-like projection. Left sulcal list extends the length of the main body; right sulcal list is shorter. Cell surface is delicately areolated. Cells may occur in pairs, dorsally attached (Fig. 14).

Ecology: Species is a new red tide-forming dinoflagellate species from Belize. Concentrations of *D. caudata* $2.8\text{-}3.2 \times 10^2$ cells L^{-1} observed in Douglas Cay, and 550-

2010 cells L⁻¹ in Manatee Cay (Morton, 2000); dinoflagellates also present in Cat Cay and Fisherman Cay (Faust, 2000). The 'bloom' population in Douglas Cay may suggest that high organic nutrients enhanced growth of *D. caudata* to a red tide level in Douglas Cay that is an unusual occurrence (Maestrini, 1998).

Distributions: Neritic and estuarine in warm temperate to tropical waters worldwide except in cold water, cosmopolitan.

Toxicity: Producer of ichthyotoxins that may cause massive fish mortality (Table 6).

***Gonyaulax polygramma* Stein 1883**

Figures 15-18

Morphology: Cell elongate with tapered epitheca; epitheca angular with a short horn (Fig. 15). Cell size (42-65 µm L and 26-56 µm W). Hypotheca rounded or truncate (Fig. 16) with three short antapical spines. Theca is ornate with reticulae, longitudinal ridges and striae (Fig. 17). Line drawings of plates are characterized by longitudinal raised and serrated reticulae extending from apex to antapex (Fig. 18).

Ecology: Species is a new red tide-forming dinoflagellate species from Belize. Cell concentrations 1.2 x 10³ cells L⁻¹ observed in Douglas Cay. The first reported of a dense red tide of 3.5 x 10⁶ cells L⁻¹ and caused brown discoloration of the water in Manatee (Morton and Villareal, 1998).

Distribution: neritic, oceanic, cosmopolitan in cold temperate to tropical waters, worldwide distribution.

Toxicity: Non-toxin producing species (Table 6); causing anoxia and fish kills during the microalgal cells decomposition and release of high sulfide and ammonia concentrations (Koizumi et al., 1996).

***Gonyaulax spinifera* (Claparède et Lachmann) Diesing 1866**

Synonym: *Peridinium spiniferum* Claparède et Lachmann, 1859: p. 405, pl. 20, figs 4-5.

Figures 19-22

Morphology: Epitheca elongate, conical with a short apical horn (Fig. 19), cells (35-40 µm L and 21-33 µm W). Cell and hypotheca rounded; two short antapical spines present (Fig. 20). Apical pore complex is oblong, Po elliptical. Apical plate 1' bears a ventral pore (Vp) (fig. 22a). Cingulum is excavated, descending with an overhang (Fig. 21). Cell surface is ornate, characterized by reticulae, extending from the apex to antapex. Striac associated with round trichocyst pores. Thecal plate morphology illustrated in line drawing (Fig. 22). The shape of *G. spinifera* is variable and difficult to identify. Forms cysts.

Ecology: *Gonyaulax spinifera* formed red tide 1.5 x 10³ cells L⁻¹ in Douglas Cay, was also

observed in Cat Cay, Manatee Cay and Lagoon Cay reef-mangrove ponds.
Distribution: neritic, oceanic, estuarine, cosmopolitan.

Toxicity: Non-toxic (Table 6).

Lingulodinium polyedrum (Stein) Dodge 1989

Synonym: *Gonyaulax polyedra* Stein, 1883: p. 13, pl.4, figs. 7-9.

Figures 23-26

Morphology: Cells polyhedral shaped without antapical spines and apical horn (Fig. 23). Cell size (40-50 μm L and 37-53 μm W). Epithea is pointed and hypotheca round to flat; sulcus long, narrow and excavated (Figs. 24, 26a). The APC oblong and the apical pore plate Po appears as a lattice inside with raised ridge (Fig. 25). Surface of thecal plates sculptured, reticulation includes ring-shaped ridges round trichocysts pores in depressions (Fig. 25). Line drawings describe morphology of thecal plates (Fig. 26). Forms cysts.

Ecology: Species is a new red-tide-forming dinoflagellate from Belize. *L. polyedrum* formed red tides 1.8×10^3 cells L^{-1} outside Douglas Cay, and species present in Cat Cay, Fisherman Cay and Manatee Cay (Faust, 2000). Cells during the night display brilliant phosphorescence.

Distribution: neritic oceanic coastal warm temperate to tropical waters.

Toxicity: Species producer of paralytic shellfish poison and saxitoxin (Table 6).

Pyrodinium bahamense var. bahamense Plate 1906

Figures 27-30

Morphology: Cell shape nearly round, epithea and hypotheca about equal in size; prominent apical horn and apical spine with a list (Fig. 27). Cell size (33-47 μm L and 37-52 μm W); in bloom condition cell size larger (34-77 μm L and 38-67 μm W). Apical pore plate triangular shaped and composed of the Po plate and closing plate (cp) (Fig. 30). Cingulum equatorial, lists well developed (Fig. 27). Plate sutures with a crest arising between plates (Fig. 29); and thecal surface laced with spinulae of round tip (Fig. 28). Forms cysts.

Ecology: Species formed red tide 2.5×10^3 cell L^{-1} outside the Douglas Cay and species present outside Cat Cay, Fisherman Cay and Manatee Cay. This species may confine to mangrove-fringed coastal waters of the Atlantic and Indo-West Pacific and causes red-brown water discoloration under bloom condition (Hallegraeff, 1993).

Distribution: Species present worldwide in Caribbean, Atlantic and Pacific Oceans in subtropical to tropical waters.

Toxicity: *P. bahamense var. bahamense* producer of DSP and paralytic shellfish poison (Table 6).

Table 3. Characteristics of the 45 dinoflagellate species identified in 2002 at Douglas Cay.

Dinoflagellate species	Benthic, Planktonic or Both	Autotroph Heterotroph, or Mixotroph	Bloom Forming
<i>Akashijo sanguinea</i>	Both	Autotroph	-
<i>Amphidinium carterae</i>	Benthic	Autotroph	+
<i>Bysmatrum caponii</i>	Both	Autotroph	+
<i>Ceratium furca</i>	Planktonic	Autotroph	+
<i>Ceratium pulchellum</i>	Planktonic	Autotroph	-
<i>Ceratium trichoceros</i>	Planktonic	Autotroph	+
<i>Ceratium tripos</i>	Planktonic	Autotroph	-
<i>Cochlodinium polykrikoides</i>	Planktonic	Mixotroph	+
<i>Coolia monotis</i>	Benthic	Autotroph	-
<i>Dinophysis caudata</i>	Planktonic	Autotroph	-
<i>Dinophysis rotundata</i>	Planktonic	Mixotroph	-
<i>Diplopelta symmetrica</i>	Planktonic	Mixotroph	-
<i>Diplosalis bomba</i>	Planktonic	Mixotroph	-
<i>Gambierdiscus australes</i>	Benthic	Autotroph	-
<i>Gambierdiscus polynesiensis</i>	Benthic	Autotroph	-
<i>Gambierdiscus toxicus</i>	Benthic	Autotroph	-
<i>Goniodoma sphaericum</i>	Planktonic	Autotroph	-
<i>Gonyaulax digitale</i>	Benthic	Autotroph	-
<i>Gonyaulax grindleyi</i>	Both	Autotroph	+
<i>Gonyaulax polygramma</i>	Planktonic	Autotroph	+
<i>Gonyaulax spinifera</i>	Planktonic	Autotroph	+
<i>Gonyaulax verior</i>	Planktonic	Autotroph	-
<i>Heterocapsa triquetra</i>	Planktonic	Autotroph	+
<i>Lingulodinium polyedrum</i>	Planktonic	Autotroph	+
<i>Ostreopsis labeus</i>	Benthic	Mixotroph	-
<i>Ostreopsis lenticularis</i>	Benthic	Mixotroph	-
<i>Ostreopsis ovata</i>	Benthic	Autotroph	-
<i>Ostreopsis siamensis</i>	Planktonic	Autotroph	-
<i>Peridinium quinquecorne</i>	Planktonic	Autotroph	+
<i>Peridinium venestrum</i>	Planktonic	Heterotroph	+
<i>Plagonidium belizeanum</i>	Benthic	Autotroph	-
<i>Prorocentrum caribbeanum</i>	Benthic	Autotroph	-
<i>Prorocentrum elegans</i>	Planktonic	Autotroph	+
<i>Prorocentrum hofmanianum</i>	Benthic	Autotroph	-
<i>Prorocentrum lima</i>	Benthic	Mixotroph	-
<i>Prorocentrum mexicanum</i>	Both	Autotroph	-
<i>Prorocentrum rhathymum</i>	Both	Autotroph	+
<i>Protoperidinium depressum</i>	Planktonic	Heterotroph	-
<i>Protoperidinium divergens</i>	Planktonic	Heterotroph	-
<i>Protoperidinium oblongum</i>	Planktonic	Heterotroph	-
<i>Protoperidinium oceanicum</i>	Planktonic	Heterotroph	-
<i>Protoperidinium pallidum</i>	Planktonic	Autotroph	-
<i>Protoperidinium steidingerae</i>	Planktonic	Heterotroph	-
<i>Pyrodinium bahamense v. b.</i>	Both	Autotroph	+
<i>Pyrophacus steinii</i>	Planktonic	Autotroph	-

Table 4. Biodiversity of dinoflagellates in detritus at Douglas Cay and The Lair, Twin Cays (2004) including whether species producing toxin (*) were present (+) or (-) absent.

Dinoflagellate species	Douglas Cay	The Lair	Benthic, Planktonic or Both	Autotroph, Heterotroph or Mixotroph
<i>Akashiwo sanguinea</i>	+	+	Both	Autotroph
<i>Alexandrium balechii</i>	-	+	Planktonic	Autotroph
<i>Bysmatrum caponii</i>	-	+	Both	Autotroph
<i>Bysmatrum subsalsum</i>	-	+	Benthic	Autotroph
<i>Ceratium furca</i>	+	-	Planktonic	Autotroph
<i>Ceratium pulchellum</i>	+	-	Planktonic	Autotroph
<i>Ceratium trichoceros</i>	+	-	Planktonic	Autotroph
<i>Ceratium tripos</i>	+	-	Planktonic	Autotroph
<i>Cochlodinium polykrikoides*</i>	+	-	Planktonic	Autotroph
<i>Coolia monotis*</i>	+	+	Benthic	Autotroph
<i>Coolia tropicalis</i>	-	+	Planktonic	Autotroph
<i>Dinophysis accuminata*</i>	-	+	Planktonic	Autotroph
<i>Dinophysis caudata*</i>	+	+	Planktonic	Autotroph
<i>Dinophysis rotundata*</i>	+	-	Planktonic	Mixotroph
<i>Gambierdiscus belizeanus*</i>	-	+	Benthic	Autotroph
<i>Gambierdiscus polynesiensis*</i>	-	+	Benthic	Autotroph
<i>Gambierdiscus toxicus*</i>	+	+	Benthic	Autotroph
<i>Gonyaulax grindleyi</i>	+	-	Benthic	Autotroph
<i>Gonyaulax monocanta</i>	+	-	Planktonic	Autotroph
<i>Gonyaulax reticulatum*</i>	+	-	Planktonic	Autotroph
<i>Gonyaulax polygramma*</i>	+	-	Planktonic	Autotroph
<i>Gonyaulax spinifera</i>	+	-	Planktonic	Autotroph
<i>Heterocapsa triquetra</i>	+	+	Planktonic	Autotroph
<i>Ostreopsis labens*</i>	+	+	Benthic	Mixotroph
<i>Ostreopsis marina</i>	-	+	Benthic	Mixotroph
<i>Ostreopsis siamensis*</i>	+	-	Benthic	Mixotroph
<i>Peridinium quinquecorne</i>	+	+	Planktonic	Autotroph
<i>Peridinium quinquecorne</i>	+	+	Planktonic	Autotroph
<i>Peridinium venestrum</i>			Planktonic	Heterotroph
<i>Plagodinium belizeanum</i>	+	+	Planktonic	Autotroph
<i>Prorocentrum belizeanum*</i>	+	+	Benthic	Autotroph
<i>Prorocentrum elegans</i>	-	+	Planktonic	Autotroph
<i>Prorocentrum emarginatum</i>	+	-	Benthic	Autotroph
<i>Prorocentrum hoffmannianum*</i>	-	+	Benthic	Autotroph
<i>Prorocentrum mexicanum*</i>	+	+	Both	Autotroph
<i>Prorocentrum micans</i>	+	-	Planktonic	Autotroph
<i>Prorocentrum lima*</i>	+	-	Benthic	Autotroph
<i>Prorocentrum rathymum</i>	-	+	Both	Autotroph
<i>Prorocentrum ruetzlerianum</i>	-	+	Benthic	Autotroph
<i>Prorocentrum tropicalis</i>	-	+	Benthic	Autotroph
<i>Protoceratium spinulosum</i>	+	-	Planktonic	Autotroph
<i>Protoperidinium crassipes</i>	+	+	Planktonic	Heterotroph
<i>Pyrodinium bahamense v. b</i>	+	-	Planktonic	Autotroph
<i>Scrippsiella trochoidea</i>	-	+	Planktonic	Autotroph
<i>Scrippsiella tiftida</i>	+	+	Planktonic	Autotroph

Table 5. Relative abundance of bloom-forming dinoflagellate species at Douglas Cay and The Lair, Twin Cays in different years. * Cell concentrations L-1 are: cells + (<10²), ++ (<10³) and +++ (<10⁴). * Species present (+) and species absent (-).

Dinoflagellate species	Douglas Cay		The Lair Twin Cays		Reference
	2002	2003	2003	2004	
<i>Akashivo sanguinea</i>	-*	++	++	++	Faust, M.A., 2004
<i>Bysmatrum caponii</i>	++	+	-	+	Faust M.A. & K.A. Steidinger, 1998
<i>Bysmatrum subsalsum</i>	-	++	++	++	Faust M.A. & K.A. Steidinger, 1998
<i>Ceratium furca</i>	-	-	-	++	Steidinger K.A. & K. Tangen, 1996
<i>Cochlodinium polykrikoides</i>	++	++	++	++	Sournia, A., 1986
<i>Coolia monotis</i>	+	+	-	+	Faust, M.A., 1992
<i>Dinophysis caudata</i>	+	++	+	+	Balech, E., 1988
<i>Gonyaulax grindleyi</i>	+	++	-	-	Balech, E., 1988
<i>Gonyaulax polygramma</i>	+	++	-	-	Balech, E., 1988
<i>Gonyaulax spinifera</i>	+	+	-	-	Balech, E., 1988
<i>Heterocapsa triquetra</i>	-	-	++	+	Horiguchi, T. & Pienaar, R. N., 1991
<i>Lingulodinium polyedra</i>	+	++	-	-	Dodge, J.D., 1989
<i>Peridinium quinquecorne</i>	+++	++	++	++	Horiguchi, T. & Pienaar, R.N., 1991
<i>Plagodinidium belizeanum</i>	++	-	-	++	Faust M.A. and E. Balech, 1993
<i>Prorocentrum belizeanum</i>	-	+	-	+	Faust, M.A., 1993
<i>Prorocentrum caribbeanum</i>	+	-	++	+	Faust, M.A., 1993
<i>Prorocentrum elegans</i>	++	++	+++	+	Faust, M.A., 1993
<i>Prorocentrum mexicanum</i>	+	++	++	++	Martin, G.W., 1929
<i>Pyrodinium bahamense</i>	++	++	-	-	Steidinger, K.A., 1983

Table 6. Toxin and non-toxin producing dinoflagellates at Douglas Cay and The Lair, Twin Cays. Abbreviations: DSP =diarrhetic shellfish poisoning; FAT=fast acting toxins; PSP=paralytic shell-fish poisoning; and STX=saxitoxin.

Dinoflagellate species	Produced Toxins	Reference
<i>Akashivo sanguinea</i>	Ichthyotoxins	Carlson, R.D. & D.R. Tindall, 1985
<i>Bysmatrum caponii</i>	Non toxic	Faust, M.A. & K.A. Steidinger, 1998
<i>Bysmatrum subsalsum</i>	Non toxic	Faust, M.A. & K.A. Steidinger, 1998
<i>Ceratium furca</i>	Non toxic	Steidinger, K.A. & T. Tangen, 1996
<i>Cochlodinium polykrikoides</i>	Ichthyotoxins	Yuki, K. & S. Yoshimatsu, 1989
<i>Coolia monotis</i>	Cooliatoxin	Holmes M.J. et al., 1995
<i>Dinophysis caudata</i>	Ichthyotoxin, DSP	Okaichi, T., 1967
<i>Gonyaulax grindleyi</i>	Paralytic toxin	Reinecke, P., 1967
<i>Gonyaulax polygramma</i>	Fish kills due to anoxia	Koizumi, Y. et al., 1996
<i>Gonyaulax spinifera</i>	Non toxic	Steidinger, K.A. & K. Tangen, 1996
<i>Lingulodinium polyedrum</i>	PSP toxins: STX	Bruno, M.P. et al., 1990
<i>Peridinium quinquecorne</i>	Fish kills due to anoxia	Fukuyo, Y. et al., 1990
<i>Plagodinidium belizeanum</i>	Non toxic	Faust, M.A. & E. Balech, 1993
<i>Prorocentrum belizeanum</i>	DSP toxins: DTX1, OA	Morton, S.L. et al., 1998
<i>Prorocentrum caribbeanum</i>	Non toxic	Faust, M.A., 1993
<i>Prorocentrum elegans</i>	Non toxic	Faust, M.A. & E. Balech, 1993
<i>Prorocentrum mexicanum</i>	FAT	Tindall D.R. et al., 1984
<i>Pyrodinium bahamense</i>	DSP, Ichthyotoxin	Hallegraeff, G.M. 1993

DISCUSSION

Mandala's Prediction Validated for Tropical Mangrove Lagoons

The hydrographic and residual ammonia data from both Douglas Cay and The Lair are consistent with these lagoonal systems being stable, low turbulence environments with high rates of nutrient regeneration (Fig. 2, Tables 1-2, Kibler et al., 2005). Elevated nutrients in these systems likely result from the rapid recycling of organic matter by bacteria (Chróst and Faust, 1999). This organic matter is contributed by the surrounding mangrove forest, seagrasses, macroalgal meadows and the dense assemblage of filter-feeding invertebrates and sponges that colonize the peat walls and mangrove prop roots (Rützler and Feller, 1996). These relatively higher nutrient levels are reflected in the 4 to 40 times higher chlorophyll a biomass in the lagoons compared to the surrounding oligotrophic waters of the central Belizean reef system which are generally $<0.2 \mu\text{g chl a L}^{-1}$ (Table 1). Both lagoons are also protected from wind mixing due to prevailing winds by the surrounding mangrove trees which further promote the stability of the water column. Margalef's Mandala predicts that these low-turbulence, high-nutrient environments would favor dinoflagellate species (Margalef, 1978; Margalef et al., 1979; Smayda, 1997; Smayda and Reynolds, 2001).

The reason is rooted in the basic biology of these organisms. Dinoflagellates are sensitive to physical disturbance with turbulence regimes disrupting their basic metabolism resulting in a significant decrease in division rates relative to other species such as diatoms (Sullivan et al., 2003). Dinoflagellates are also known to have slower growth rates at low nutrient concentrations than many other algal groups (Broekhuizen and Oldman, 2002). It is only at relatively higher nutrient concentrations that dinoflagellates have a competitive growth advantage. The low turbulence, high nutrient environment lagoons sampled in this study would therefore represent ideal environments for dinoflagellates.

Consistent with this prediction, both the Douglas Cay and Lair lagoons contained a rich assemblage of dinoflagellates with a total of 52 species being identified from Douglas Cay and 30 from The Lair (Tables 3-5). Interestingly, only 15 species were identified from both environments (Tables 4 and 5). Planktonic and autotrophic species common to more oceanic environments were dominant in Douglas Cay and include representatives from 7 genera: *Ceratium*, *Cochlodinium*, *Dinophysis*, *Gonyaulax*, *Lingulodinium*, *Peridinium*, and *Pyrodinium* (Tables 3 and 4). Of these, the armored dinoflagellate species were the most common with unarmored species such as *Akashiwo sanguinea*, *Amphidinium carterae*, *Cochlodinium polykrikoides*, and *Heterocapsa triquetra* representing a minor component (Table 3). In contrast, benthic dinoflagellates composed a greater proportion of the species observed in The Lair (Tables 3 and 4). Because dinoflagellates tend to be niche specialists (Smayda, 1997), the large diversity of dinoflagellate species recovered from both Douglas Cay and The Lair imply that these environments contain a diverse array of temporally and spatially varying niches. That a majority of species are unique to each environment also implies that there are different source populations for Douglas Cay and The Lair, or that the selection regime is significantly different.

Differences in the water exchange in these semienclosed mangrove lagoons may account to some extent for these observed differences in species composition (Levasseur et al., 1984). Douglas Cay has a predominant sill that may restrict exchange to a greater extent than occurs in Lair which is mainly restricted due to the length of The Lair Channel and the low tidal amplitude (<20 cm) (Macintyre and Rützler, 2000). A lower rate of exchange in Douglas would favor retention of dinoflagellate cells (Villareal et al., 2000) and a larger portion of incoming organic matter, thereby increasing the nutrient recycling capacity of the system. Douglas Cay is also a larger lagoon with a more complicated geomorphology (unpublished data). Furthermore, Douglas Cay received nutrient inputs from the abundant pelicans that come to fish in the lagoon and roost in the mangroves. Trees surrounding the lagoon were consequently streaked with guano. These highly mobile pelican populations feed on a wide range of food sources and thus import nutrients daily to the lagoon. All these conditions combine to foster the greater diversity of dinoflagellate species in Douglas Cay. Despite the richer environment, Douglas Cay still provides sufficient confinement and nutrient supply to enhance the proliferation of species-specific dinoflagellate blooms (Table 5; Smayda and Reynolds, 2001). The observed diversity is also higher than generally reported at any given time for the deep offshore waters of the Eastern Caribbean Sea (Halim, 1967; Hulburt, 1968; Marshall, 1973).

Another low-turbulence, high-nutrient microenvironment, which exists to a much larger extent in The Lair than in the Douglas Cay, are the loose detrital mats which cover much of the benthos. These flocculent mats sit on top of the sediments where nutrient fluxes are likely to be high. Evidence for this nutrient flux can be found in the rich assemblage of dinoflagellate and other algal species that occupy these mats. In the afternoon, oxygen production by algae in the mat causes large sections to detach and begin floating upward in the water column. This floating biodetritus carries large numbers of dinoflagellates into the water column and can account for the higher proportion of benthic dinoflagellates observed in The Lair compared to those in Douglas Cay, where the benthos is dominated to a greater extent by attached macrophytes and sea grasses (Tables 3 and 4; Faust, 2004).

Bloom-forming Dinoflagellates

In addition to high diversity, we observed a number of dinoflagellate blooms in both lagoonal systems. In Douglas Cay, 14 bloom-forming species were observed in 2002 and 15 in 2003. The Lair experienced a slightly smaller number of blooms involving 9 species in 2003 and 13 in 2004 (Table 5). The most intense bloom-forming species were *Peridinium quinquecorne* in Douglas Cay and *Prorocentrum elegans* in The Lair. Blooms of *Gonyaulax grindleyi* in Douglas Cay were also sufficiently high to discolor the water. Similar *G. polygramma*, blooms have been reported in Manatee Cay (Morton and Villarcal, 1998; Morton, 2000). Previous studies in Douglas Cay conducted in May 1997, 1999 and 2000 also found one or more >20 μm dinoflagellates bloomed in each of these studies reaching cell concentrations in excess of 1×10^3 cells L^{-1} . Frequent blooms therefore can be considered a persistent feature of these systems from year-to-year during the May study period.

Of the 19 bloom-forming species observed, the most consistent species between sites were *Akashivo sanguinea*, *Bysmatrum subsalsum*, *Cochlodinium polykrikoides*, *Dinophysis caudata*, *Peridinium quinquecorne*, *Prorocentrum elegans* and *P. mexicanum*. Blooms typically varied in intensity and duration with many lasting only a few days. A potential reason for the rapid decline of many of these blooms is predation by the large number of heterotrophic ciliates, nematodes, and dinoflagellates such as the *Protoperidinium* species. Mixotrophic species, such as those that belong to the genera *Prorocentrum* and *Ostreopsis*, were also common and are known to feed heterotrophically on other small microalgae (Faust, 1998). The rapid growth and decline of these blooms, in conjunction with elevated nutrient concentrations, may imply a tight coupling between bottom-up nutrient driven growth and top-down control by predators.

Toxin-producing Species

Approximately half of the 19 bloom-forming species found in either Douglas Cay or The Lair are known toxin producers (Table 6). This implies that the natural eutrophication present in these lagoons favors selection of toxic bloom formers. It is not currently known if these potentially toxic bloom-forming species actually are producing toxin. There is growing evidence that HAB toxins can serve an anti grazing function (Teegarden et. al., 2001). This would lead to the prediction that, in instances of intense grazing pressure, blooms producing toxin will be favored. Further research is needed to address this possibility. If grazers find these species unpalatable or toxic, it can lead to significant and often adverse alterations of the food web (Pitcher and Cockroft, 1996). It should be noted that all the toxic bloom-forming species were phototrophs as are most reported HAB taxa (Smayda and Reynolds, 2001).

Margalef's Madala, and the results for Douglas Cay and The Lair, also have profound implications for ecosystem health. Both the theory and the species found in these naturally eutrophied systems (Tables 3-5) would predict that as anthropogenic inputs into the oligotrophic waters of the Caribbean increase, so will the proportion of dinoflagellates in the assemblage. This species shift would likely be most pronounced in sheltered bays or other regions where turbulence and hydrodynamic dilution are minimized and in the very regions most likely to be receiving increased nutrient inputs. (Smayda, 1997). If the toxic dinoflagellate species are favored due to selective grazing pressures or other factors, their toxins will likely accumulate in the food web. It is now known that all trophic compartments of marine food web are vulnerable to the chronic, sublethal impacts of these HAB toxins (Hallegraeff, 1993). In cases where toxin accumulation is significant, acute impacts including alteration of food-web dynamics sufficient to result in trophic dysfunction, as well as adverse effects on fisheries and human health, can result.

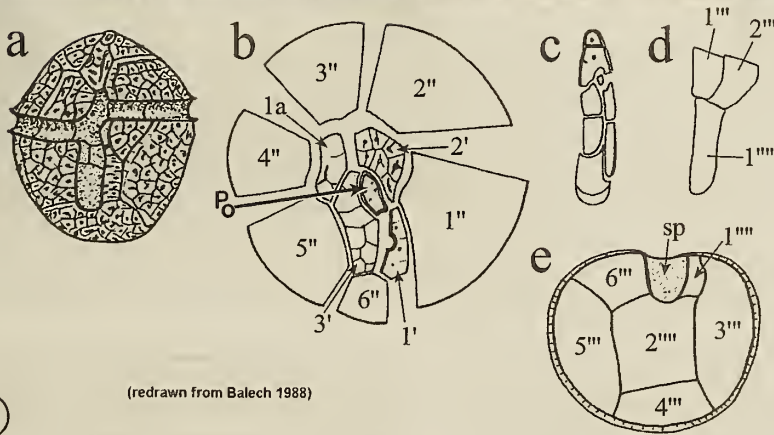
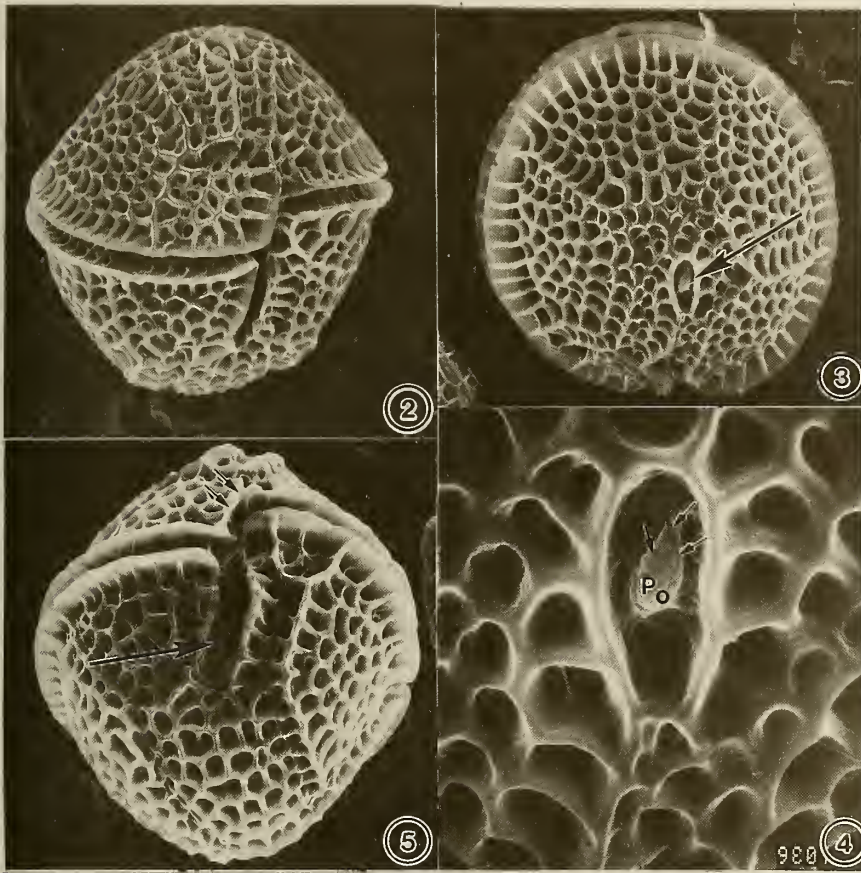
Even if the nontoxin-producing bloom-forming dinoflagellates come to predominate, they can still cause problems (Alongi, 1998). Though these blooms pose no serious threat in the environment, they often discolor the water and are considered to be aesthetically unpleasant and noxious. Anoxia formation resulting from the degradation of organic-rich material derived from phytoplankton blooms can also cause fish kills (Pitcher and Cockroft, 1996; Koizumi et al., 1996). High ammonia concentration released after cell lysis can adversely affect fish as well (Ajani et al., 2001).

CONCLUSIONS

The results of this study demonstrate that the phytoplankton species composition of two naturally eutrophic lagoonal systems in the Belizean Barrier Reef system conform to the predications of Margelf's Mandala. This theory predicts that high nutrient, low turbulence marine environments, such as those examined in this study, will favor the diversity and abundance of dinoflagellates. Consistent with this prediction, a rich assemblage of dinoflagellates is found in both lagoonal systems. Approximately 19 of these species were consistent bloom formers, and of these bloom formers, approximately half were known toxin producers. The ecology and taxonomy of eight of these bloom formers were described in detail. If the predictions of Margalef's Mandala hold true, then increased anthropogenic nutrient inputs into the oligotrophic Caribbean waters may favor a shift in species composition toward potentially toxic dinoflagellate species. This shift could profoundly alter the food-web dynamics as well as adversely affecting fisheries and human health.

ACKNOWLEDGEMENTS

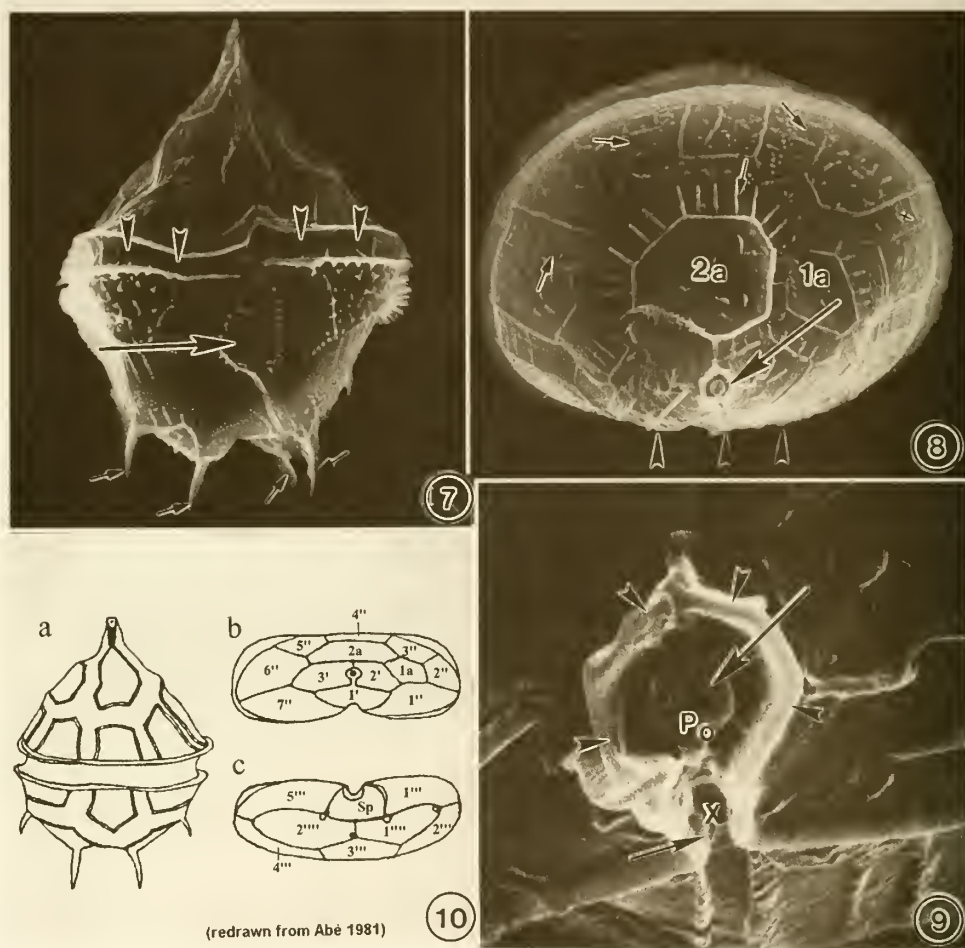
We thank Dr. Klaus Rützler at the National Museum of Natural History (NMNH), Smithsonian Institution, for use of the facilities at Carrie Bow Cay Field Station, Belize. We are also grateful to numerous individuals who contributed to its success and deserve credit here: Dr. Ian G. Macintyre for his valuable comments on this manuscript; Ms. Molly Ryan for her artwork and graphics; and Mrs. Judit A. Quasney for photographic layouts that paved the way for publishing this research paper. I convey a special thanks to Scott Whitaker in the SEM laboratory for technical assistance and Mike Carpenter for logistic support, NMNH. This investigation was supported by grants from the Caribbean Coral Reef Ecosystem program (CCRE) at the National Museum of Natural History. This paper is Contribution No. 729 from the CCRE Program.



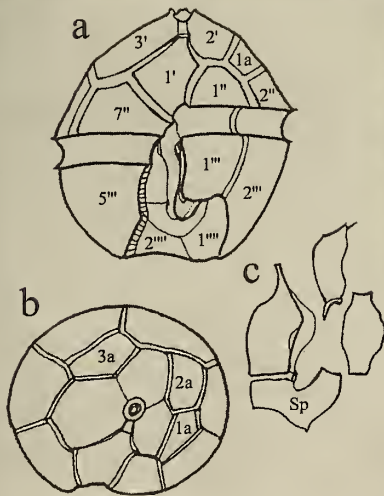
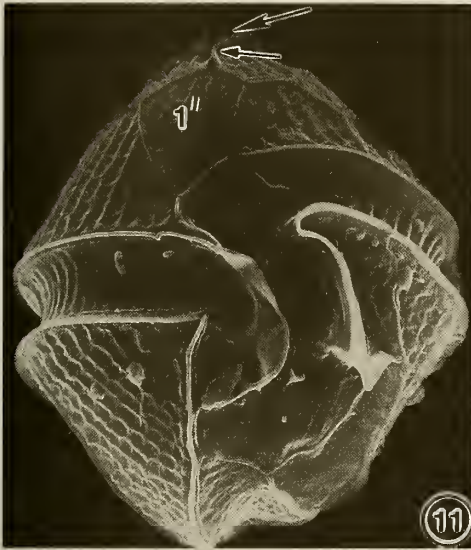
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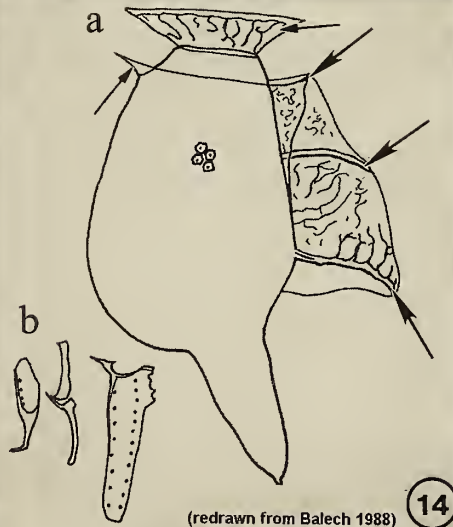
Figures 2-6. Morphology of *Gonyaulax grindleyi* dinoflagellate species causing water discoloration in sampling areas illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.



Figures 7-10. Morphology of *Peridinium quinquecorne* dinoflagellate species associated in floating detritus in The Lair at Twin Cays illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.



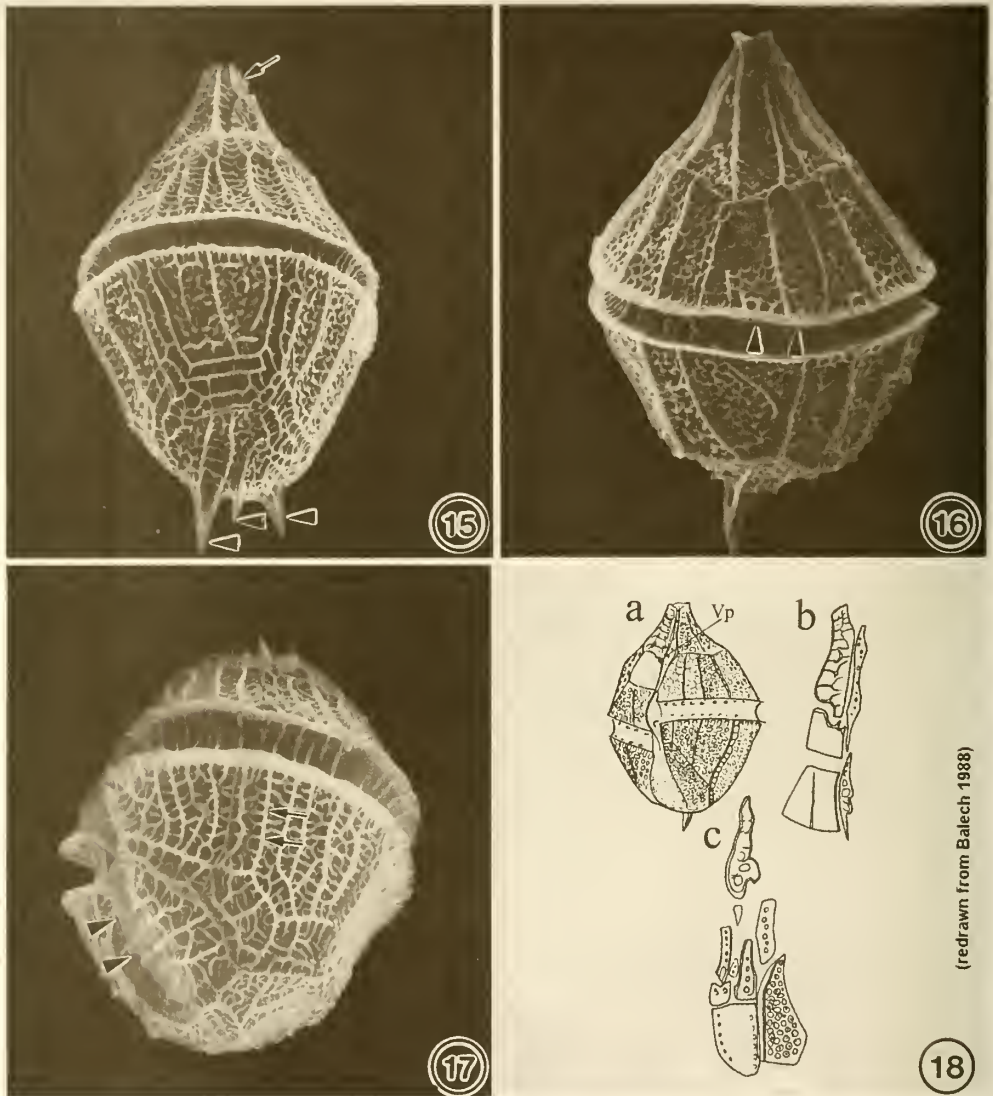
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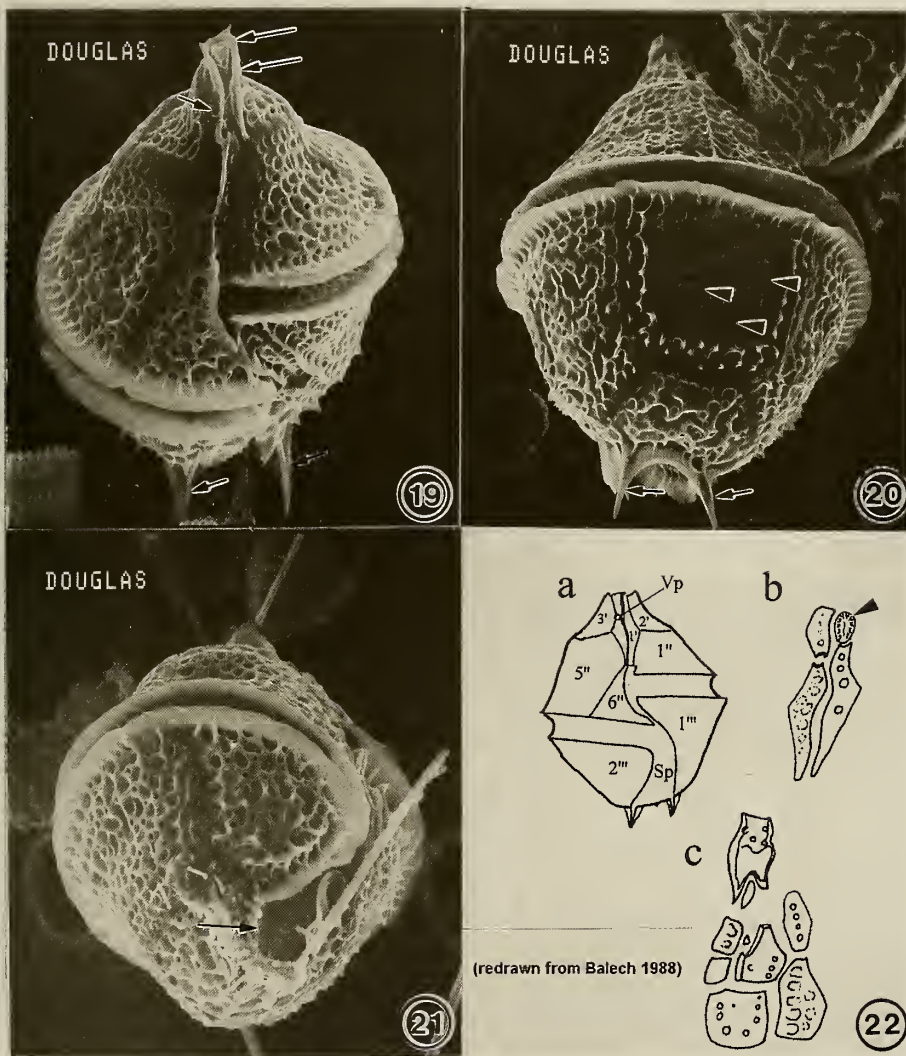
Figures 11-12. Morphology of *Bysmatrum caponii* sand dwelling dinoflagellate species identified from Douglas Cay and The Lair at Twin Cays sampling areas illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.

Figures 13-14. Morphology of *Dinophysis caudata* planktonic dinoflagellate species identified from Douglas Cay and The Lair at Twin Cays sampling areas illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.

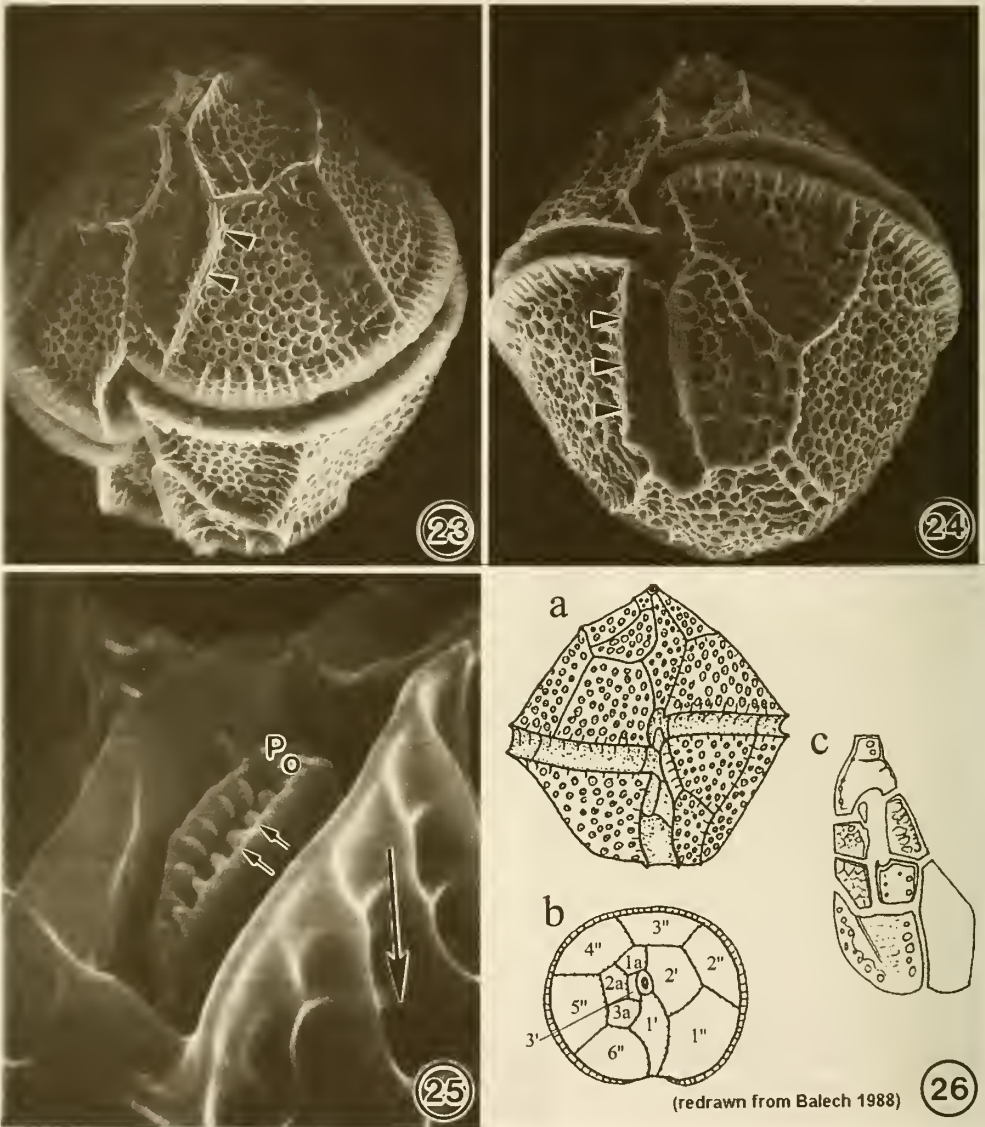


Figures 15-18. Morphology of *Gonyaulax polygramma* cosmopolitan oceanic, red-tide dinoflagellate species identified from Douglas Cay illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.

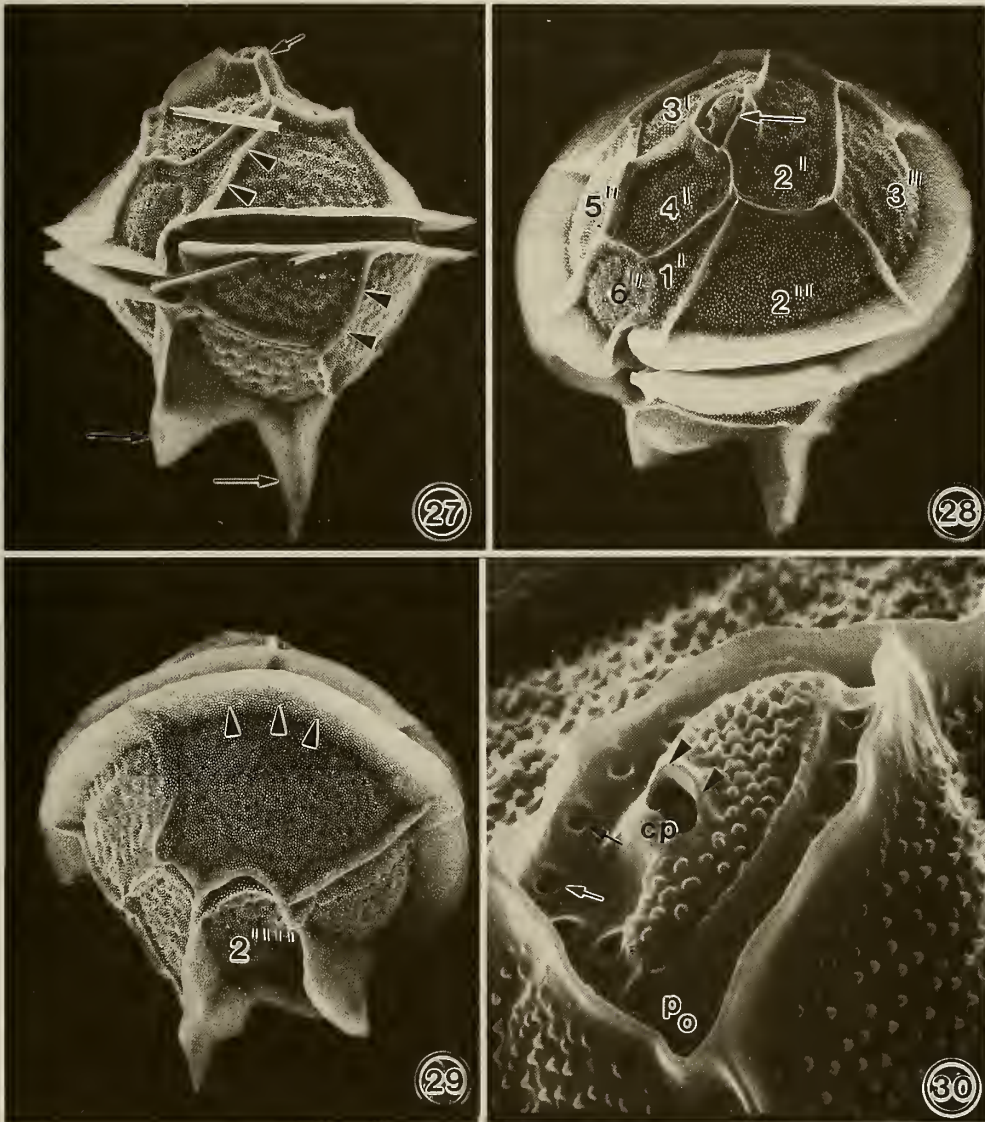
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Figures 19-22. Morphology of *Gonyaulax spinifera*, an oceanic red-tide dinoflagellate species identified from Douglas Cay sampling area, illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.



Figures 23-26. Morphology of *Lingulodinium polyedrum* oceanic bioluminescent dinoflagellate species identified from Douglas Cay sampling area illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.



Figures 27-30. Morphology of *Pyrodinium bahamense* var. *bahamense* planktonic worldwide distributed dinoflagellate species identified from Douglas Cay sampling area illustrated in scanning electron micrographs.

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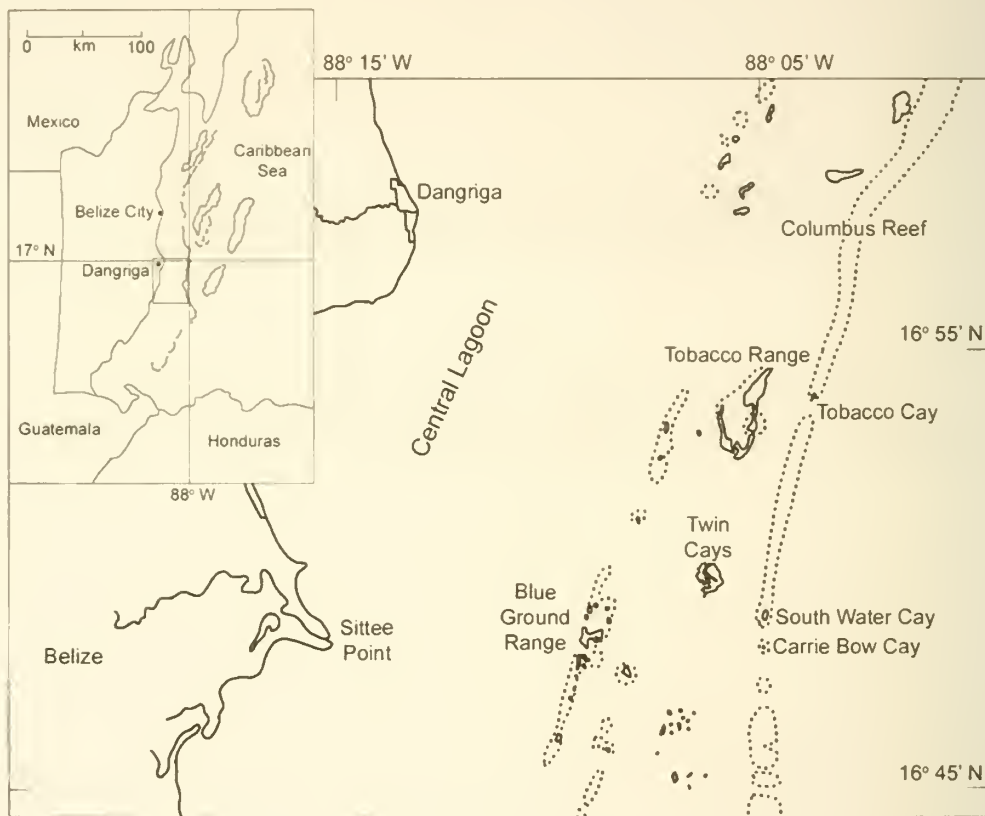


Figure 1. Regional map of the Belizean central lagoon showing Twin Cays and surrounding islands. Map drawn by M. Ryan, Department of Invertebrate Zoology, NMNH, Smithsonian Institution, Washington, D.C.

WATER COLUMN STRUCTURE AND CIRCULATION IN THE MAIN CHANNEL, TWIN CAYS, BELIZE

BY

STEVEN R. KIBLER,¹ MARIA A. FAUST,² MARK W. VANDERSEA,¹ SABRINA M. VARNAM,¹ R. WAYNE LITAKER,¹ AND PATRICIA A. TESTER¹

ABSTRACT

The hydrographic structure of the Main Channel at Twin Cays, Belize was surveyed in the morning and on the afternoon of 18 May 2004. Transects conducted along the channel revealed the northern and southern portions of the system were characterized by very different hydrographic conditions. In the afternoon, the deeper southern portion of the Main Channel was characterized by two-layer circulation in which warm ($\sim 30\text{ }^{\circ}\text{C}$) surface water flowed outward from the Main Channel and cooler ($28.6\text{-}28.7\text{ }^{\circ}\text{C}$) bottom water moved northward from the lagoon. The southern channel was also characterized by a plume of high temperature ($\sim 29\text{ }^{\circ}\text{C}$) and high salinity (~ 37.4) bottom water from the neighboring Lair Channel.

Strong afternoon stratification occurred in the southern channel as evidenced by Brunt-Väisälä frequencies of $20\text{-}50\text{ cycle h}^{-1}$. In contrast, the northern part of the channel was characterized by more shallow ($< 2\text{ m}$), poorly stratified waters ($0\text{-}10\text{ cycle h}^{-1}$) that were divorced from the surrounding lagoon by shoals and patch reefs. Average water temperatures were lower in the southern channel due to inflow of lagoon water and more rapid diel heating of the shallow waters to the north. The shallow bathymetry in the north also prevented cooler bottom waters from entering the northern channel. Salinity was lower (~ 36.6) in the northern channel due to input of rainwater from the interior of the islands. The hydrographic structure of the Main Channel also influenced the distribution of chlorophyll and dissolved oxygen. The southernmost part of the Main Channel was characterized by relatively high chlorophyll fluorescence ($> 25\text{ RFU}$) at the surface, which was attributed to a phytoplankton bloom fueled by outwelling of nutrients from the mangrove fringe. In contrast, relative fluorescence was highest ($20\text{-}30\text{ RFU}$) along the bottom of the northern channel due to an abundance of subsurface microalgae. Shallow areas in the northern channel were marked by the high rates of photosynthetic O_2 production ($22\text{ }\mu\text{mol O}_2\text{ L}^{-1}\text{ h}^{-1}$) resulting in O_2 saturation in excess of 150%.

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INTRODUCTION

The mangrove islands in the central lagoon of Belize are surrounded by a complex fringe environment that includes channels, ponds, coves and other small embayments. These shallow (< 4 m) habitats are characterized by a mixed assemblage of fish, corals, sponges, macroalgae and other organisms (Macintyre et al., 2000). Water flow among these habitats supplies nutrients, food particles and dissolved oxygen to fringe biota and eliminates wastes. Flow is also crucial for transport of organic matter that supports the extensive detrital food web in the mangrove fringe (Alongi et al., 1989; Ambler et al., 1994). However, circulation between fringe habitats and the surrounding central lagoon waters is often restricted because of the dense mangrove vegetation that dampens wind stress and prevents mixing. This situation is compounded by lack of tidal mixing because of the minimal tides in the region (~20 cm). As a result, the mangrove embayments and ponds in the central lagoon are often poorly flushed, exhibiting stratified and sometimes stagnant conditions (Urish, 2000; Villareal, 2000).

Twin Cays (16° 49.4' N; 88° 6.1' W) is a group of small peat-based islands located 12 km from the Belizean mainland (Fig. 1). This site is characterized by a series of bays and channels (Fig. 2), some of which are poorly flushed. Twin Cays are largely covered with mangroves (*Rhizophora mangle* L.; *Avicennia germinans* L.) and are bisected by the relatively deep Main Channel (Fig. 2) (McKee et al., 2002). While much is known about the ecology of the mangroves at Twin Cays, very little is known about the hydrography of the Main Channel and how water circulation relates to the distribution of aquatic biota. The few hydrographic data available represent attempts to measure flow rates within the mangrove channels or to characterize flushing of water from the interior of the islands (ex., Wright, 1991; Ferrari et al., 2003). On 18 May 2004, we undertook a hydrographic survey of the Main Channel at Twin Cays as part of a more extensive investigation into factors controlling productivity in the nearby Lair and Lair Channel (Fig. 2) (Kibler et al., in preparation). Here we report the results of our survey with respect to vertical structure and circulation within the Main Channel and how environmental conditions varied over the course of a single day during the Belizean dry season.

METHODS

Study Site

The Main Channel at Twin Cays (Fig. 2) is a system encompassing 0.1-0.2 km² and is navigable by small boats along most of its length. Water depth varies from 4-5m near the southern end of the Main Channel (Stas. TL-MC2) to 1-3 m in the northern channel (Fig. 2, Table 1). The northern terminus of the channel is narrow (10-15 m) and is obstructed by shoals and patch reefs that restrict exchange with the lagoon. In contrast, the southern end of the Main Channel is significantly wider (> 100 m) and opens into a wide bay covered in seagrass and small patches of coral. In this study, the southern end of

the Main Channel is referred to as the mouth because of the greater depth and breadth in this part of the system.

Most of the Main Channel is protected from the prevailing NE trade winds (meteorological convention) by mangroves that overhang the channel in many locations. Because of the small tidal range (~ 20 cm), currents are normally less than 20 cm s^{-1} . The prevailing current is southward ($\sim 5 \text{ cm s}^{-1}$) in the northern part of the channel and is strongest in Cuda cut, the first of two openings along the northwestern side of the channel (Rützler et al., 2004). South of the Lair Channel (Fig. 2), currents are tidally driven northward during flood ($\sim 5 \text{ cm s}^{-1}$) and southward during ebb ($\sim 5 \text{ cm s}^{-1}$) (Ferrari et al., 2003).

Hydrographic Data

Hydrographic data were collected at Twin Cays using a model 6600 Sonde in profiling mode (YSI Inc., Yellow Springs, Ohio). The unit was equipped with sensors to measure temperature and conductivity (YSI model 6560) as well as dissolved O_2 (model 6562) and chlorophyll fluorescence (model 6025). Because in situ fluorometric measurements were not calibrated to absolute chlorophyll concentrations, data collected with the YSI fluorometer were termed chlorophyll fluorescence and represent a relative measure of phytoplankton abundance (RFU, relative fluorescence units). All other sensors were calibrated in accordance with the instructions provided by the instrument manufacturer. Irradiance was quantified with a model LI-1925A PAR sensor (Li-Cor Inc., Lincoln, Nebraska) fixed on a side arm to the instrument. Hydrographic data were collected at a series of 10 stations situated along a transect between the northern terminus of the Main Channel (Sta. 10) and the lagoon to the south (Sta. TL, Fig. 2). Vertical profiles were collected at each of these stations in the morning and afternoon of 18 May 2004.

Data Analyses

Hydrographic data from each station were compiled and MATLAB 7.04 (The Mathworks Inc., Natick, Massachusetts) was used to create vertical sections of the Main Channel. Data were cubic spline interpolated and gridded using depth measurements from each station. Distance was estimated using a spatially referenced aerial photograph of Twin Cays (Rodriguez and Feller, 2004). An electronic image of the map was spatially calibrated with Metamorph 5.0 software (Universal Imaging Inc., Downingtown, Pennsylvania). Distances between stations and surface area of the Main Channel were then calculated using the software's linear and area analysis functions.

RESULTS

Physical Conditions

The lowest average water temperatures were observed at Sta. TL in both morning (28.2 °C) and afternoon (29.0 °C) transects (Table 1). In the morning, temperature increased from the southern to the northern end of the channel with the highest water temperatures at Sta. 10. In contrast, afternoon temperatures were highest at the shallow sites in the northern channel between Stas. 6 and 9 (Table 1). To simplify comparisons among stations, depth, temperature and salinity values were averaged at each station with respect to both depth and time and were plotted versus station depth (Fig. 3). The results of a linear regression indicated temperature declined with station depth ($r^2 = 0.68$, $p = 0.003$) as a result of more rapid heating of shallow sites relative to deeper sites (Fig. 3A). Distribution of mean temperature data on the graph also suggested values were distributed among two groups, one comprised of shallow stations in the northern channel with high temperature (Stas. 5, 6, 7, 9, 10), and the other including deeper stations in the southern channel with cooler temperatures (Stas. TL, 1, 2, 4, MC2). A similar comparison of mean salinity among stations (Fig. 3B) revealed salinity was lower in the shallow northern part of the channel but the relationship was not significant ($p > 0.05$).

To better illustrate vertical structure of the water column along the length of the system, morning and afternoon vertical profile data were used to create vertical sections of temperature and salinity in the Main Channel (Figs. 4, 5). In the morning, the mouth of the channel was characterized by an outflow of relatively warm (> 28 °C) surface water and a subsurface inflow of cooler (< 28.5 °C) lagoon water (Fig. 4A). Pockets of warmer surface water also were evident near the midpoint of the Main Channel and at its northern extent. A narrow band of warm bottom water was also present at MC2, reflecting outflow of bottom water from the Lair Channel. After entering the Main Channel, this plume moved southward along the bottom before mixing with cooler water near Sta. TL (arrows, Fig. 4A). Morning salinities ranged from 36.6 to 36.7 along the surface, increasing to ~ 36.9 near the Lair Channel (Fig. 5A). Water with the lowest salinity was present in northern Main Channel where salinity declined to ~ 36.6 . This low salinity lens was attributed to outflow from the interior of the islands following rainfall on the morning of 18 May. High salinity water was present in two regions of the Main Channel. The first of these was at the bottom of Sta. MC2 as a result of high salinity (~ 37.4) water from the Lair Channel which moved southward along the bottom (arrows, Fig. 5A). Salinity was also high at the bottom of Sta. 10 reflecting the restricted exchange at the north end of the Main Channel (Fig. 5A).

By afternoon, water temperatures increased along the length of the Main Channel. Stations 5-9 exhibited the greatest increase in temperature, which averaged 5-7% higher in the afternoon versus the morning hours (compare Figs. 4A, B). The two-layer structure in the southern channel was more pronounced in the afternoon, a strong thermocline being present southward of Sta. MC2 (Fig. 4B). Outwelling of warm surface water, which was evident along most of the southern Main Channel, was balanced by inflow along the bottom. The difference between surface and bottom temperatures increased from < 0.5 °C

in the morning to >1 °C (Stas. 1-4) by the afternoon. The warmest water (> 30 °C) was present between Stas. 5 and 10 with a slightly cooler subsurface inflow from Cuda Cut evident at Sta. 7 (Fig. 4B).

Transect data showed that outflow from the Lair Channel continued through the afternoon (arrows, Figs. 5A, B). High salinity (> 37) bottom water along the southern Main Channel was overlain by a lens of low salinity (< 36.7) water extending from the surface to ~ 2 m (Fig. 5B). This low salinity lens represents surface water from the northern channel that was advected southward by the ebbing tide. Low salinity water was also observed in the Lair and Lair Channel during the same part of the day (data not shown), suggesting surface outflow from the Lair Channel may have been significant in reducing salinity in the southern Main Channel.

Comparison of morning and afternoon density structure in the channel (Fig. 6) revealed the effect of bathymetry as well as diel heating upon circulation between the Main Channel and the lagoon. Contours of σ_t illustrated a low-density region in the northern portion of the channel and a high-density region in the southern half of the channel. In the northern channel, this partitioning was partly governed by bathymetry where the shallows between Stas. 5 and 6 prevented subsurface exchange. Longitudinal density gradients prevented low salinity water at Stas. 5-6 from mixing with the higher salinity water to the north and south (Fig. 6). The bathymetry of the channel also restricted circulation further north resulting in a pool of high density water at the bottom of Sta. 10 (Fig. 6A, B). The outflow from the Lair Channel was also evident in morning and afternoon sections as high-density bottom water at Sta. MC2 (Fig. 6).

In order to better illustrate the influence of salinity and temperature upon the vertical structure of the water column at each station, a comparison of thermal and salinity gradients was made using profile data from morning and afternoon transects. The influence of temperature ($\alpha\partial T/\partial z$) and salinity ($\beta\partial S/\partial z$) upon stratification was quantified (Table 2), where α , β , $\partial T/\partial z$ and $\partial S/\partial z$ are the thermal expansion coefficient, haline contraction coefficient, vertical temperature gradient, and vertical salinity gradient (respectively). In the morning, positive vertical salinity gradients dominated the structure at Stas. 4, MC2 and 10 due to high-salinity bottom water at these sites (Table 2, Fig. 5A). Strong negative thermal gradients dominated vertical structure in the morning at Stas. 6 and 9. The remaining stations exhibited slight-to-moderate temperature and salinity gradients in the morning (Table 2). In contrast, afternoon structure was mostly dominated by temperature that greatly exceeded salinity effects in the southern half of the Main Channel (Stas. TL-4). Stations MC2 and 10 were characterized by strong negative vertical temperature gradients combined with strong positive vertical salinity gradients (Table 2). The effect of these gradients upon the vertical stratification of the water column is evident in Fig. 6.

Stratification was quantified at each station using the Brunt-Väisälä frequency (N) that describes the oscillation that results when the pycnocline is displaced (Mann and Lazier, 1996). This metric was calculated with the expression N (rad s^{-1}) = $(g/\rho \partial\rho/\partial z)^{1/2}$ where g is the gravitational constant ($m s^{-2}$) and ρ is density ($Kg m^{-3}$). To simplify comparisons, N was converted to units of cycles h^{-1} using $N/2\pi$. In general, the water column in the southern Main Channel was moderately stratified ($10 < N < 20$ cycles

h^{-1}) in the morning and more significantly stratified ($N \geq 20$ cycles h^{-1}) in the afternoon. In the morning, stratification was most evident at Sta. MC2 where high-salinity bottom water occurred in close proximity to low-salinity surface water (Fig. 7A). As a result of thermal stratification, Brunt-Väisälä frequencies were greatest in the afternoon at Stas. MC2, 4 and 2, and reached a maximum at a depth of $\sim 2\text{m}$ (Fig. 7B). Stratification was also evident at Sta. 10 due to warm surface waters and high-salinity bottom water in Cassiopea Cove.

Irradiance

Light penetration in the water column varied greatly along the Main Channel reflecting interaction between the visibly colored mangrove fringe waters and the more transparent waters of the lagoon. Irradiance data from vertical profiles collected at each station were used to calculate K_{PAR} , the attenuation coefficient with respect to PAR (300-700nm) using the expression $K_{\text{PAR}} (\text{m}^{-1}) = [-\text{Ln} (I_z / I_{0.1})] / z$, where z (m) is depth, $I_{0.1}$ and I_z represent irradiance ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) measured at 0.1 m and just above the bottom, respectively. Light attenuation was relatively low ($< 0.4 \text{ m}^{-1}$) at Stas. TL, 1 and 2 where lagoon waters were more prevalent (Fig. 8). Attenuation generally increased to 0.4-0.6 m^{-1} northward from Sta. 4 although K_{PAR} was $< 0.4 \text{ m}^{-1}$ at Sta. 5. The greater light attenuation in the northern Main Channel was attributable to plankton and particulates in the water column as well as to dissolved organic matter from the mangrove sediments that comprise the islands. The highest attenuation coefficient was observed in the afternoon at Sta. 4, where K_{PAR} exceeded 0.62 m^{-1} (Fig. 8). The results of a t-test indicated morning and afternoon attenuation were not significantly different ($p > 0.5$).

Dissolved Oxygen

Dissolved oxygen levels were relatively high throughout the Main Channel and were strongly impacted by solar radiation. The lowest average O_2 saturation levels were observed in the morning at Stas. 6 (89%) and 10 (90%, Table 3). The highest mean saturation occurred in the afternoon ranging from 112% at Sta. 10 to 170% at Sta. 7 (Table 3). Overall, O_2 concentrations averaged 37% higher in the afternoon relative to morning. Regression results showed a linear relationship between mean O_2 saturation and depth ($r^2 = 0.70$, $p = 0.001$), indicating deeper stations, on average, had higher levels of O_2 saturation than shallow stations (Fig. 9). This negative relationship was attributable to lower morning O_2 saturation in the northern Main Channel relative to the southern channel sites.

A vertical section of the Main Channel, created with profile data from each station, showed a significant longitudinal gradient in O_2 saturation and lesser variation with depth (Fig. 10). Low oxygen levels were evident in the morning, reaching minimum saturation along the bottom of the mid-to-northern Main Channel (Fig. 10A). Highest morning O_2 saturation ($\sim 110\%$) occurred along the bottom near Sta. TL reflecting mixing with lagoon waters. By afternoon all stations exhibited very high O_2 concentrations (6.4-10.5 mg L^{-1}). Afternoon oxygen concentrations were highest at Sta. 7 where saturation exceeded 160% near the surface and declined to 110-120% near the bottom (Fig. 10B).

Some of the lowest afternoon O_2 concentrations ($7-7.2 \text{ mg L}^{-1}$) were associated with the low salinity lens near the surface of Sta. 4. Similarly, O_2 saturation was low at the bottom of Sta. MC2 owing to outflow of high temperature, high salinity bottom water from the Lair Channel.

Chlorophyll Fluorescence

Similar to temperature, salinity and dissolved oxygen, fluorescence data indicated phytoplankton were distributed differently in the southern and northern portions of the Main Channel. In the morning, fluorescence was low ($<1 \text{ RFU}$) through most of the system but exceeded 25 RFU in the upper 0.5 m of the water column at Stas. TL and 1 (Fig. 11A). High fluorescence was also recorded along the bottom at Stas. 5, 6 and 10 ($20-30 \text{ RFU}$). This distribution suggests phytoplankton were largely concentrated near the surface at the mouth of the channel but showed a near-bottom distribution in the northern channel (Fig. 11A). Morning fluorescence was also moderately high ($4-6 \text{ RFU}$) at the bottom of Sta. MC2 reflecting the plume of bottom water from the Lair Channel (see Figs. 11A, 6A). Afternoon contours showed very low fluorescence ($< 1 \text{ RFU}$) throughout the system with very narrow bands of higher fluorescence at the bottom of Stas. 2, 4, 9 and 10 (Fig. 11B). Unlike in the morning, the surface waters at the mouth of the Main Channel were characterized by low fluorescence (compare Figs. 11A, B). This low fluorescence may be attributed to the advection of phytoplankton cells out of the channel with the ebbing tide.

Diel Changes

The effect of solar radiation upon mean temperature, salinity and O_2 saturation at stations in the Main Channel was quantified using ΔT , the diel change in mean temperature, ΔS , the diel change in mean salinity, and ΔO_2 , the diel change in oxygen saturation (Fig. 12). Stations in the southern channel (Stas. TL-MC2) underwent a temperature increase of $2-3\%$ by afternoon while the shallow sites in the northern channel (Stas. 5-9) exhibited a diel increase of $6-8\%$. Similarly, northern channel sites increased in salinity by $\sim 1\%$ as opposed to those in the southern channel which increased very little or declined slightly (Fig. 12). Diel shifts in T and S at Sta. 10 were comparable to those near the mouth of the Main Channel, signifying exchange with the lagoon to the north. Oxygen saturation followed a similar pattern where saturation increased significantly at stations above MC2. The largest gain in O_2 saturation occurred at Stas. 6 and 7 where ΔO_2 exceeded 75% (Fig. 12).

DISCUSSION

The vertical and longitudinal structure of the Main Channel at Twin Cays is characterized by two distinct hydrographic zones. The first of these is the southern portion of the channel (Stas. TL-MC2) that is strongly influenced by exchange with the

waters of the central lagoon. In contrast, circulation is more restricted in the shallow northern part of the channel (Stas. 5-10) where environmental conditions are more closely governed by diel heating and outwelling of water from the interior of the islands. The distribution of chlorophyll and dissolved oxygen reflected the hydrographic structure of the Main Channel.

The southern portion of the Main Channel represents a transitional environment influenced by exchange of water between the channel and the lagoon. This exchange was most evident in the distribution of temperature and salinity at Stas. TL, 1, 2, and MC2. Both morning and afternoon transects demonstrated a distinct two-layer circulation pattern whereby an outflow of warm surface water from the channel is balanced by inflow of lagoon water along the bottom. The cooler, denser water from the lagoon is little influenced by diel heating thereby buffering the lower water column from the rapid shifts in temperature and salinity that characterize the northern channel sites. The benthic biota that reside in the southern channel benefit from this stability enabling reef-type organisms such as corals, seagrasses and sponges to survive in close proximity to the mangrove fringe. The interaction between lagoon and fringe waters in such environments may account for the high diversity of corals, sponges and other benthic biota that has been documented in similar mangrove bay habitats (Richardson, 2000; Rützler et al., 2000).

The two-layer structure that occurs in the southern Main Channel is influenced by outflow from the Lair Channel. Diel heating and evaporation in the sheltered waters of the Lair result in formation of high temperature and high salinity bottom water along the length of the Lair Channel. This dense bottom water spills into the Main Channel where it moves southward (Kibler et al., in preparation). Lair Channel water was visible in vertical sections of the Main Channel as a band of warm (~29 °C) saline water (37.1-37.2) that collected at the bottom of Sta. MC2 and moved southward at a depth of 3-4 m (Figs. 4, 5). The bottom water that emerges from the Lair Channel was also characterized by low oxygen and high chlorophyll (Figs. 10, 11), suggesting the outflow may be a significant source of benthic microalgae from the Lair (see Faust, 2004). The Lair Channel plume, which was detectable as far south as Sta. TL, may be a regular feature of circulation during the dry season.

In contrast to the mouth of the Main Channel, exchange between the northern portion of the channel and the lagoon is very limited. The region north of Sta. MC2 is more shallow than the rest of the system (Table 1). The shallow bathymetry restricts exchange by preventing intrusion of lagoon water along the bottom. More rapid heating of the shallow water column in the northern Main Channel also generates a steep longitudinal density gradient (Fig. 6) which further restricts exchange between the northern and southern channel. Although some inflow of lagoon water occurs through Cuda Cut, the flow rates are low and circulation is poor (Rützler et al., 2004).

The shallow part of the system is highly dynamic and is strongly impacted by diel heating and precipitation (Figs. 4, 5). The dynamic conditions in the northern channel were exemplified by moderate rainfall that developed over Twin Cays on the morning of 18 May. The rainfall resulted in a lens of low salinity surface water in the northern channel (Stas. 5-9, Fig. 5A). In contrast, salinity near the channel mouth was less affected by this precipitation indicating rainwater was directed into the northern

channel from the surrounding mangroves. The shallow ponds in the northwest quarter of East Island (Turtle pond, Candy's pond, Fig. 2) commonly collect rainwater that is then funneled into the Main Channel through Turtle creek and other outlets (Rützler et al., 2004). Similarly, outflow from the interior of West Island may enter the system through a channel near Sta. 5 (Wright et al., 1991). Rainfall, in concert with strong solar heating, caused rapid shifts in temperature and salinity in the shallow waters of the northern Main Channel. Organisms residing in this dynamic environment are likely to experience greater physiological stress than those residing elsewhere in the system. This physiological stress has the greatest impact upon sessile invertebrates and other benthic biota that are unable to migrate to more favorable habitats during periods of stress. The degree of environmental stress, in turn, has a direct impact upon diversity and distribution of benthic and epiphytic biota in the system (Goodbody, 2004; Rützler et al., 2004).

Circulation within the Main Channel was also influenced by vertical stratification. This stratification was reflected in the Brunt-Väisälä frequency where strong stratification was indicated by frequencies in excess of 20 cycle h^{-1} (MacIntyre et al., 2002). Stratification was weak (< 1) in the shallow portions of the northern Main Channel (Stas. 5, 6) where vertical salinity and temperature gradients were slight. Stratification increased slightly in the afternoon (Fig. 7B) with moderate Brunt-Väisälä frequencies at Cuda Cut (Sta. 7) and Cassiopea Cove (Sta. 10). In contrast, the two-layered circulation within the southern Main Channel resulted in a sharp afternoon pycnocline at mid-depth ($\sim 2 \text{ m}$) representing the boundary between outflowing Main Channel water and inflowing lagoon water (Fig. 7). Strong afternoon stratification occurred in the southern channel (Stas. TL, 1) as evidenced by Brunt-Väisälä frequencies of $20\text{-}30 \text{ cycle h}^{-1}$ (Fig. 8B). Further north, low salinity surface water combined with bottom water from the Lair Channel increased N to $40\text{-}50 \text{ cycle h}^{-1}$ (Fig. 5B). The strong vertical stratification observed in the southern Main Channel is more typical of estuaries where strong vertical salinity gradients result in classic estuarine circulation (Pritchard, 1989). Considering the depth of the system ($< 5 \text{ m}$), the degree of stratification observed in the Main Channel is therefore surprising and exemplifies the strong influence of solar heating upon vertical structure in mangrove fringe waters. Because salinity gradients across the entire system were relatively weak, thermal gradients had much more of an effect upon stratification (Table 2). A very similar pattern of thermal dominance occurs in lakes and reservoirs as well as other marine systems with near uniform salinity (Mann and Lazier, 1996; Talling, 2001).

In concert with bathymetry, water-column structure and circulation patterns in the Main Channel tend to segregate portions of the system into distinct zones. These zones encompass a spectrum of environmental conditions ranging from lagoonal reef-type habitats with clear water to those more typical of turbid mangrove ponds. The largest of these zones is the southern Main Channel which is characterized by low turbidity, low light attenuation and more constant temperature and salinity. Inflow of subsurface lagoon water buffers the southern water column from the rapid shifts in environmental conditions that occur closer to the mangrove fringe. As a result, the benthic organisms that reside in the southern Main Channel are typical of reef-and-seagrass communities elsewhere in the central lagoon. Some common examples of these organisms include numerous corals, macroalgae and sponges (Rützler et al., 2004). Conversely, the northern

portion of the water column is characterized by outflow of surface water from the Main Channel. In addition to having higher temperature and often lower salinity than lagoon water, the outflowing surface water is characterized by higher concentrations of dissolved nutrients and organic matter that may fuel productivity at the mouth of the Main Channel (Kibler et al., in preparation). Mangrove fringe water typically contains relatively high concentrations of dissolved nutrients due to remineralization of leaf litter and other organic matter (Moran et al., 1991). The high surface chlorophyll levels observed at the mouth of the Main Channel may reflect enrichment of phytoplankton by these nutrients.

Inflow of water from the mangroves may also represent a source of nutrients to the seagrasses and microalgae in the northern Main Channel. Both interstitial and surface waters in the interior of the islands contain high concentrations of nutrients (Feller, 1995; McKee et al., 2002), some of which undoubtedly leach into the Main Channel. Where outflow from the inland ponds occurs, seagrass density and biomass of associated epiphytes are elevated relative to other sites at Twin Cays (Richardson, 2004). Nutrient input may also promote phytoplankton growth as evidenced by the high subsurface chlorophyll levels observed at the northern channel sites (Fig. 11).

The greater abundance of seagrass and microalgae in the northern Main Channel may have also influenced O_2 saturation. Due to lower O_2 levels in the morning, average O_2 saturation tended to be slightly higher at deeper sites than shallow stations but diel O_2 production was dramatically higher in the northern channel (Fig. 9). The shallow stations in the northern channel (Stas. 5, 6, 7, 9) exhibited an average of 12% greater daytime oxygen production than stations in the southern channel (Stas. TL, 1, 2, MC2). The highest rate of oxygen production was observed at Sta. 7, where O_2 concentrations increased by 4.3 mg L^{-1} . This production was equivalent to a rate of $22 \text{ } \mu\text{mol } O_2 \text{ L}^{-1} \text{ h}^{-1}$. At best, stations in the southern channel produced no more than $1.1 \text{ } \mu\text{mol } O_2 \text{ L}^{-1} \text{ h}^{-1}$ during the same time period (Sta. MC2). The increased production in the northern channel could not be attributed to dissolution of atmospheric oxygen as water temperature and salinity, factors which would reduce gas solubility, were both higher in the afternoon. Instead, high O_2 saturation was attributable to in-situ production by seagrass and microalgae at these sites.

Unlike the remainder of the stations in the Main Channel, Sta. 10 exhibited low oxygen production relative to its depth (Figs. 10, 12). Cassiopea Cove is characterized by turbid, organic rich water similar to the Lair and other ponds at Twin Cays. Its muddy, flocculent sediment is unsuitable for seagrasses (Rützler et al., 2004) and oxygen production at this site was correspondingly low. The restricted circulation at this site promotes retention of organic matter, a factor which may increase the biochemical demand for oxygen in the water column. This demand is compounded by elevated water temperatures resulting from high levels of solar radiation.

Solar radiation is responsible for the physical structure of the water column and directly influences the distribution of dissolved oxygen and phytoplankton in the Main Channel. The effect of solar radiation is both direct, through solar heating of the water column, and indirect, by influencing the vertical distribution of phytoplankton and production of oxygen in Main Channel waters. The absorption of solar energy by fringe waters generates vertical temperature gradients and drives evaporation. The resulting

thermohaline structure governs circulation and controls the distribution of nutrients, dissolved oxygen and organic matter in the channels and bays at Twin Cays. Light attenuation, and therefore heat transfer, is greatest at the shallow stations in the northern channel (Fig. 4). The result is a very rapid increase in water temperature at these sites relative to the deeper, more transparent lagoon waters at the mouth of the Main Channel.

The greater light attenuation in the northern Main Channel may also govern oxygen production and phytoplankton distribution. Oxygen production and chlorophyll fluorescence were greatest at the stations where light attenuation was greatest (Figs. 8, 11). This pattern may be attributed to a reduction in photic stress at these sites. Photic stress is common in shallow tropical systems where high light levels may depress rates of photosynthesis and cause cellular damage (Fleischman, 1989; Lesser, 1996; Chróst and Faust, 1999). Increased photoproduction may therefore account for the very high O₂ levels in the northern Main Channel (Figs. 10, 12, Table 3). Similarly, the near-benthic distribution of chlorophyll may be a photoprotective strategy employed by microalgae to avoid photic stress near the surface.

Although the distribution of biota at Twin Cays and similar mangrove environments may be tied to meteorological forcing, the manifestation of such forcing may be subtle requiring a better understanding of variability occurring at short time scales (days, hours) and/or spatial scales (centimeters). For example, dinoflagellates and other phytoplankton associated with the mangrove fringe can be abundant in surface waters from the same portion of the Main Channel where lagoonal organisms like corals are found (Faust, unpublished; Rützler et al., 2004). These cells are advected from mangrove fringe waters with the low-density surface water via the channel. Alternatively, phytoplankton concentrations at the mouth of the Main Channel may develop in situ as a result of nutrients in the same surface layer. It is the structure of the water column in the southern Main Channel that makes this mix of lagoon and mangrove species possible. Clearly, both vertical and horizontal circulation are important determinants affecting the distribution of benthic and planktonic biota at Twin Cays. The vertical and longitudinal zonation of the Main Channel should be considered when future surveys of benthic and other biota are conducted at Twin Cays and elsewhere in the central lagoon.

CONCLUSIONS

This study represents one of the first attempts to characterize physical structure and thermohaline circulation in the Main Channel at Twin Cays. The data presented here demonstrate the manner in which the longitudinal density structure, vertical stratification and channel bathymetry act to create distinct zones in the Main Channel, each experiencing a different suite of environmental conditions. The southern portion of the Main Channel is characterized by a two-layer pattern of circulation in which warm surface water flows outward from the Main Channel and cooler bottom water moves northward from the lagoon. The surface outflow represents a source of nutrients and organic matter that promotes phytoplankton growth in the waters to the south of the island. The northern part of the Main Channel is characterized by shallow waters

divorced from the oligotrophic waters of the lagoon. These shallow sites are strongly influenced by diel heating, evaporation and rainfall and biota may undergo rapid shifts in environmental conditions. Nevertheless, this region of the channel is marked by the highest rates of photosynthetic O_2 production in the system. Restricted exchange in the northern channel may harbor microalgae, which were indicated by high chlorophyll levels along the bottom.

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We are very grateful to K. Rützler and M. Carpenter for the use of the Carrie Bow Cay field station and for the support we received, to K. Parson and B. Pfeiffer for their assistance with fieldwork, to J. Pinckney for HPLC analyses, and to C. Holland, A. Dubois and M. West for laboratory support while we were in Belize. This paper is contribution No. 730 from the Caribbean Coral Reef Ecosystem Program of the Smithsonian Institution.



Figure 2. Map of Twin Cays showing sampling stations in the Main Channel. Map drawn by M. Ryan, Department of Invertebrate Zoology, NMNH, Smithsonian Institution, Washington D.C. Gridlines represent nominal scale.

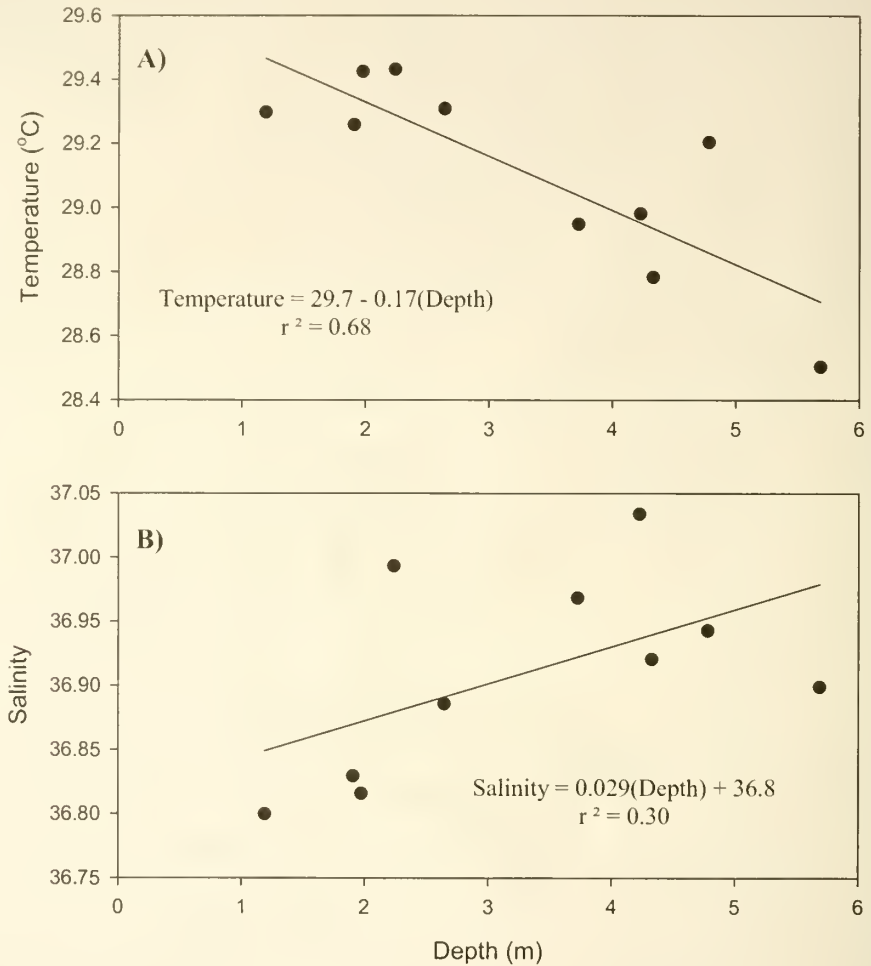


Figure 3. Linear relationship between A) temperature and depth and B) salinity and depth for stations in the Main Channel at Twin Cays, Belize. Temperature and salinity data were averaged with respect to depth and time.

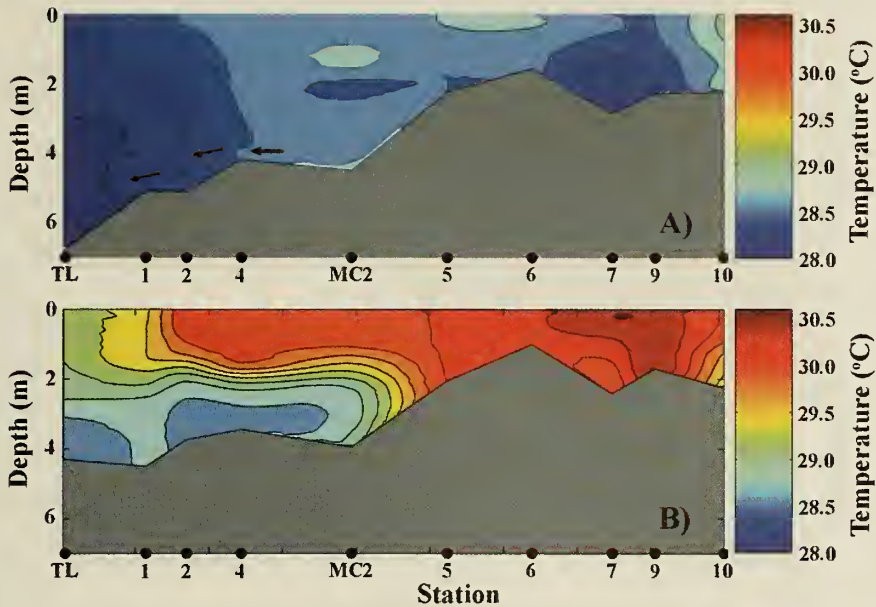


Figure 4. Morning vertical sections of (A) temperature ($^{\circ}\text{C}$) and (B) salinity from the Main Channel at Twin Cays, Belize. See Fig. 2 for stations. Arrows represent southward flow of bottom water from the Lair Channel (Sta. MC2).

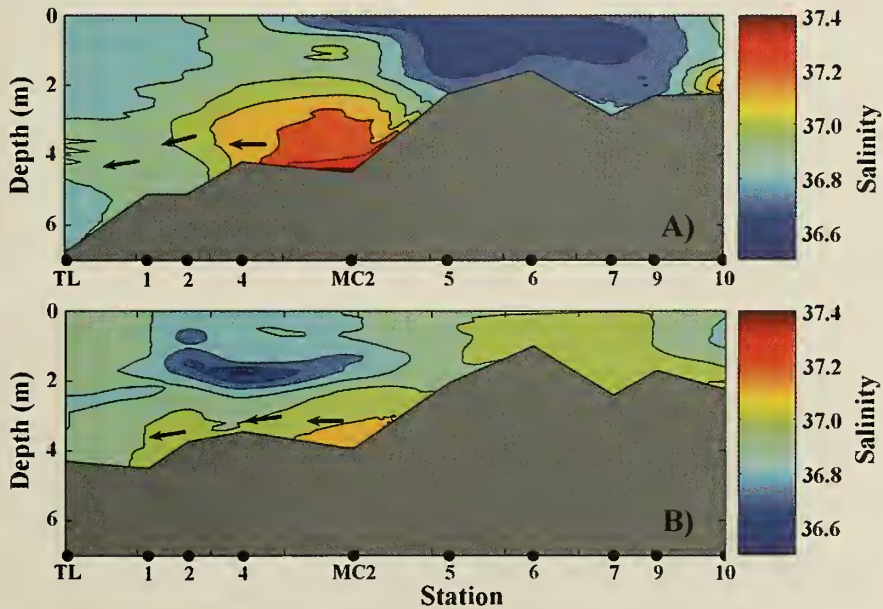


Figure 5. Afternoon vertical sections of (A) temperature ($^{\circ}\text{C}$) and (B) salinity from the Main Channel at Twin Cays, Belize. See Fig. 2 for stations. Arrows represent southward flow of bottom water from the Lair Channel (Sta. MC2).

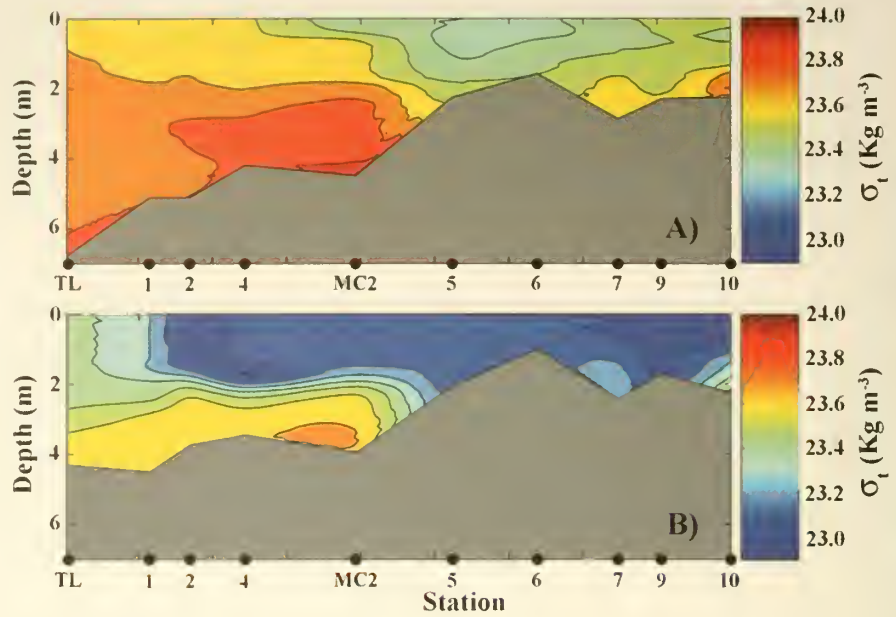


Figure 6. Density sections (σ_t) of the Main Channel created from (A) morning (am) and (B) afternoon (pm) profile data. See Fig. 2 for stations.

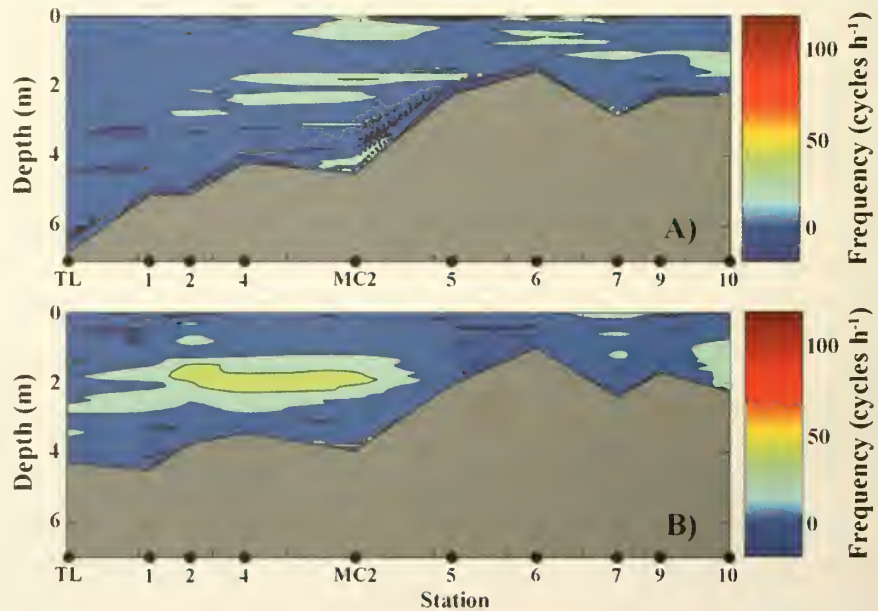


Figure 7. Vertical sections of the Brunt-Väisälä frequency (N) in the Main Channel created from (A) morning and (B) afternoon profile data. See Fig. 2 for station map.

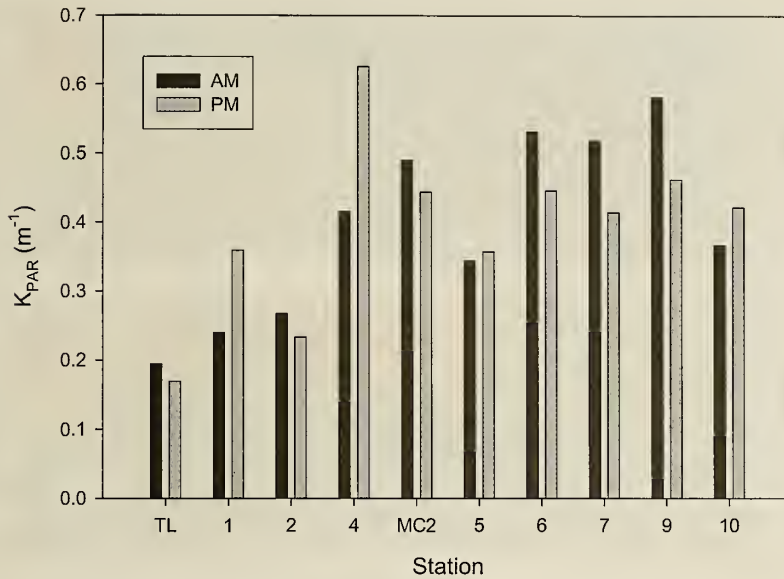


Figure 8. A comparison of light attenuation at stations in the Main Channel, Twin Cays. Attenuation was quantified as K_{PAR} , the light attenuation coefficient relative to PAR (400-700 nm) calculated from morning (AM) and afternoon (PM) profile data.

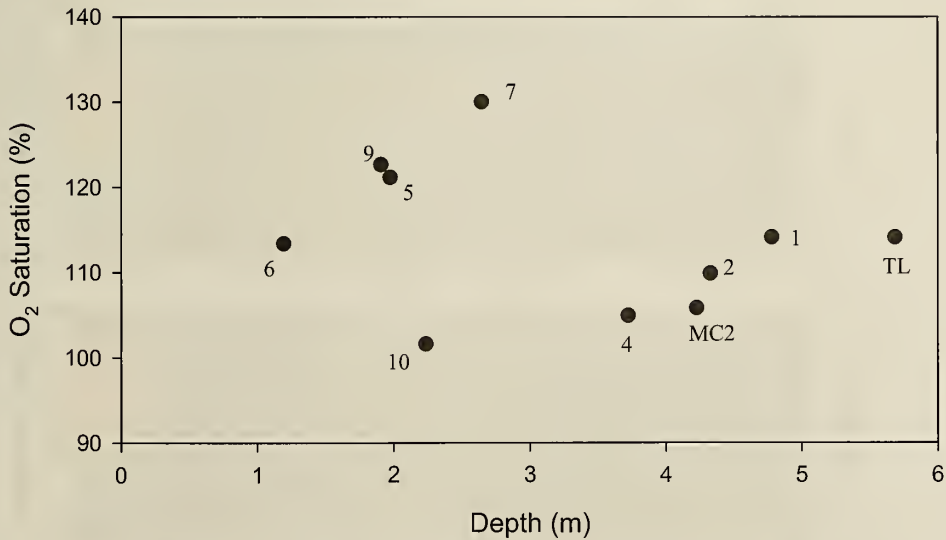


Figure 9. Relationship between mean dissolved O₂ saturation and depth at stations in the Main Channel. Data were averaged with respect to time.

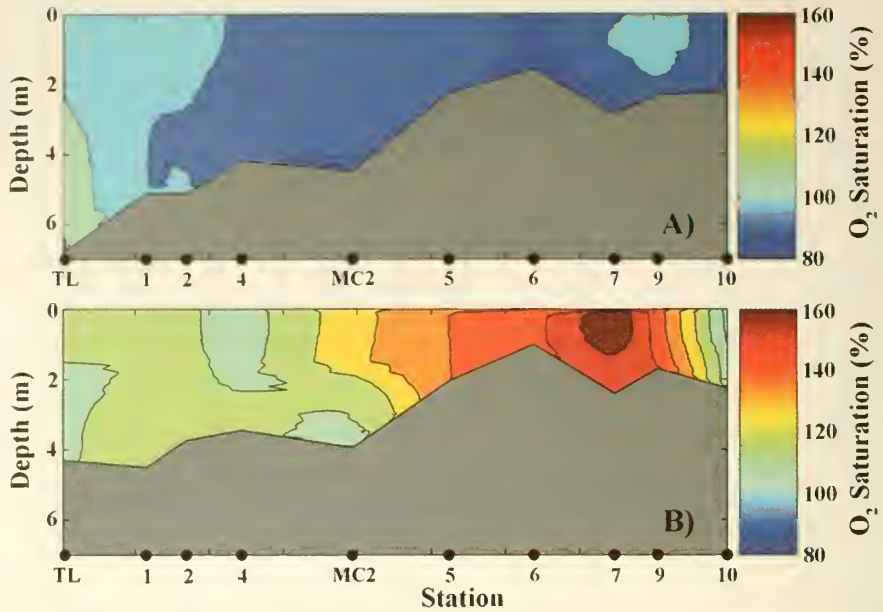


Figure 10. Dissolved O₂ saturation (%) sections of the Main Channel created from morning (am) and afternoon (pm) profile data. See Fig. 2 for station map.

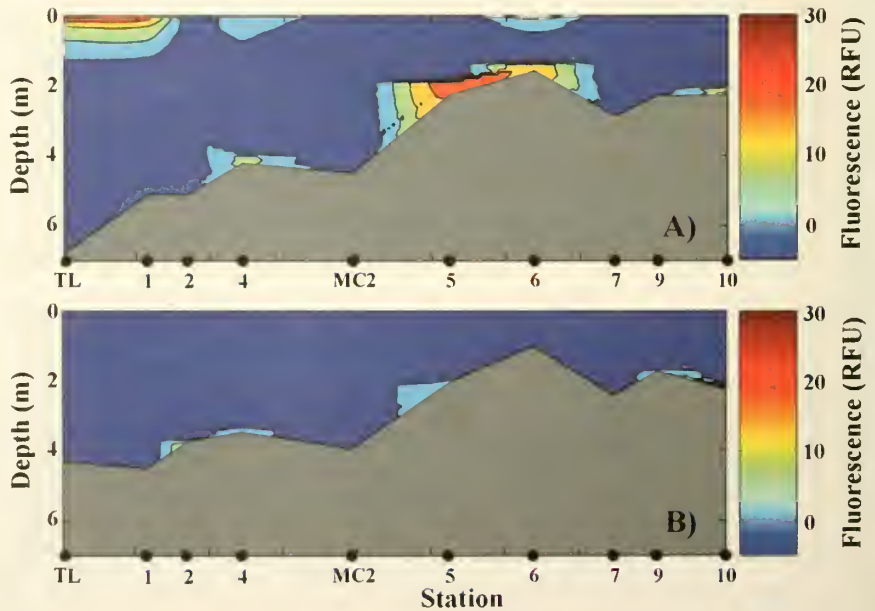


Figure 11. Vertical sections chlorophyll fluorescence (RFU) created from (A) morning and (B) afternoon profile data. See Fig. 2 for station map.

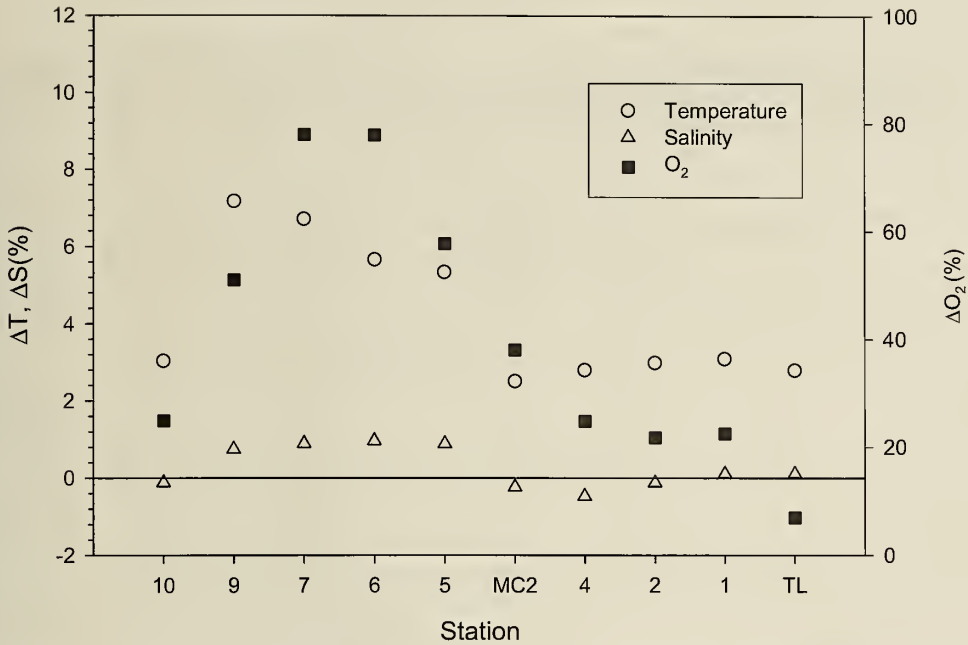


Figure 12. Diel shifts in temperature (ΔT), salinity (ΔS) and oxygen saturation (ΔO_2) at stations along the length of the Main Channel at Twin Cays, Belize. Data represent the difference between afternoon and morning values of mean (depth-averaged) temperature, salinity and O_2 saturation.

Table 1. Average depth (D), temperature (T) and salinity (S) at stations in the Main Channel, Twin Cays, Belize. Mean values represent depth-averaged data.

Station	D (m)	am		pm	
		T (°C)	S	T (°C)	S
10	2.2	28.96	37.018	29.84	36.973
9	1.9	28.52	36.730	30.56	37.004
7	2.6	28.42	36.734	30.33	37.061
6	1.2	28.73	36.678	30.36	37.030
5	2.0	28.70	36.663	30.23	36.985
MC2	4.2	28.72	37.066	29.44	36.980
4	3.7	28.64	37.037	29.44	36.862
2	4.3	28.45	36.939	29.30	36.893
1	4.8	28.33	36.903	29.20	36.943
TL	5.7	28.21	36.884	29.00	36.925

Table 2. Vertical gradients of temperature and salinity measured in the Main Channel, Twin Cays in the morning (am) and afternoon (pm) of 18 May 2004. Negative gradients indicate bottom values were higher than surface values.

Station	am	am	pm	pm
	$\alpha \frac{\partial T_z}{\partial z}$ (10^{-3} m^{-1})	$\beta \frac{\partial S_z}{\partial z}$ (10^{-3} m^{-1})	$\alpha \frac{\partial T_z}{\partial z}$ (10^{-3} m^{-1})	$\beta \frac{\partial S_z}{\partial z}$ (10^{-3} m^{-1})
10	7.87	86.6	-115	87.5
9	-44.8	5.36	8.75	32.4
7	-16.8	30.4	-46.7	-8.22
6	-132	21.4	0.00	0.00
5	-33.6	48.5	-3.04	-1.95
MC2	13.9	116	-82.4	62.1
4	-3.35	36.6	-143	34.0
2	-8.59	0.24	-105	36.3
1	-16.3	8.28	-38.0	12.8
TL	-12.3	-6.28	-53.7	1.13

Table 3. Average oxygen saturation in the Main Channel, Twin Cays in the morning (am) and afternoon (pm) of 18 May 2004. Values were averaged with respect to depth.

Station	am	pm
	O ₂ Saturation (%)	O ₂ Saturation (%)
10	89.6	112
9	104	156
7	95.4	170
6	88.6	158
5	95.1	150
MC2	92.9	128
4	95.7	119
2	101	123
1	101	124
TL	111	119

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ATOLL RESEARCH BULLETIN

NO. 536

**MEASUREMENTS OF THE GENERATION AND DISTRIBUTION OF
CARBONATE SEDIMENTS OF BUCK ISLAND CHANNEL, ST. CROIX,
U. S. VIRGIN ISLANDS, WITH OBSERVATIONS ABOUT SEDIMENTS IN
FRINGING LAGOONS**

BY

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**ISSUED BY
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Figure 1. Location map and bottom communities of the Buck Island Channel and nearby areas.

MEASUREMENTS OF THE GENERATION AND DISTRIBUTION OF CARBONATE SEDIMENTS OF BUCK ISLAND CHANNEL, ST. CROIX, U. S. VIRGIN ISLANDS, WITH OBSERVATIONS ABOUT SEDIMENTS IN FRINGING LAGOONS

BY

LEE C. GERHARD¹ AND TIMOTHY A. CROSS²

ABSTRACT

Sediments of the Buck Island platform northeast of St. Croix, U. S. Virgin Islands, are mostly fine-grained carbonate sands composed of *Halimeda*, molluscs, foraminifera, and coral, ratios of which are apparently related to current and depth dynamics. Sorting is controlled by organism ecology and water depth, modified by grass-bed entrapment. This paper adds to the knowledge of sedimentation on the St. Croix northeastern coast and complements earlier lagoon sediment descriptions.

Chance occurrence of severe rainstorms during a period when student research teams were present at the West Indies Laboratory of Fairleigh Dickinson University made it possible to track fresh runoff water into and out of a large lagoon facing Buck Island Channel. Fresh waters did not mix immediately with salt water. The effects of the rainfall could be tracked for 56 hours after cessation.

INTRODUCTION

Modern carbonate complexes in high-mechanical-energy settings are less commonly documented than those of evaporitic low-mechanical-energy settings. St. Croix, U.S. Virgin Islands (USVI), has an extensive shelf and platform as its northeastern quadrant terminating in the northeast in a reef (Lang Bank), which in turn marks a drop off to very deep waters (Fig. 1, Fig. 2). On the northern margin of the platform is Buck Island National Monument, eroded from Cretaceous age metaturbidites, with a fringing reef on the windward margin and a carbonate beach to the leeward. To the west, near Christiansted, the platform terminates in small reefs and grass beds west of which the water depth abruptly increases from 10 meters to 4000 meters. The northeastern margin of St. Croix, facing Buck Island and the Buck Island Channel, is a complex of banks and reefs with narrow lagoons. Predominant easterly trade winds drive currents and wave trains from the northeast and east with consequent strong east-to-west longshore drift (Hubbard et al, 1981). The maximum tide range is about 0.33 meters.

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This paper characterizes the setting and characteristics of the carbonate sediments of part of the northeastern quadrant of the St. Croix shelf, U. S. Virgin Islands, the Buck Island Channel and an associated lagoon of northeastern St. Croix.

During the period of 1971 through 1986, Fairleigh Dickinson University, Madison, NJ, USA, operated the West Indies Laboratory (WIL) on St. Croix. This laboratory was a teaching and research facility dedicated to study of the shallow marine and tropical terrestrial environments. The data from which this paper is drawn were accumulated by the writers and by some of the many students from many academic institutions who participated in research projects and course work at the West Indies Laboratory. The facility was destroyed by Hurricane Hugo in 1986 and never rebuilt. Much data, many records, and extensive collections were lost in that disaster. This paper is compiled from data taken while the senior author was resident at the WIL from 1972-1975 and on two subsequent research expeditions terminating in 1979. Ninety-eight sample locations and 15 transects provide the primary new data for this study. Major changes occurred in the reefs post-1979. Black-band and white-band coral disease and an unknown pathogen decimated reefs and the grazing sea urchin, *Diadema antillarum*, by 1984. In 1986, Hurricane Hugo created storm waves and currents that changed the character of reefs and of some bottom communities (Hubbard et al, 1991).

BUCK ISLAND CHANNEL SEDIMENTS

The open shelf between Buck Island National Park (Fig. 1) and the mainland of St. Croix is called the Buck Island Channel (B.I.C). Water depth in the channel ranges from 15 feet (5 meters) at the western margin to about 50 feet (17 meters) where the shelf deepens onto the main St. Croix platform in the east (Fig. 3). Water depth on the eastern main platform averages about 80 feet (26 meters). Wave trains approach from the east and northeast, varying seasonally, as do the trade winds (as summarized by Fuller, 1978). During November, December and January, winds tend to be ENE (the "Christmas Winds"), whereas during the rest of the year, winds are easterly.

The result of this wind- and wave-train geometry is that a steady current moves water from east-to-west through the channel, transporting fine-grained sediment that apparently becomes trapped by grass beds on the western terminus of the channel resulting in shallower water depths. Longshore drift behind the bay-barrier reefs on the southern margin of the channel is also east-to-west with current velocities up to about 0.33 meters per second (Fuller, 1978). Channel velocities are similar to the longshore velocities, although they have not been recorded.

Bottom communities of the channel are open sand, grass beds, coralgall reef, and scattered coral and sand (Fig. 1). Open sand areas contain standing crops of alcyonarians and are covered with thin filamentous algal mats that stabilize the sediment in gentle current regimes, but can be disrupted during storm events. Hummocky topography occurs where these sand bodies are burrowed; where shallow, the sand bodies may be rippled. Much of the open sand is coarse-grained (Fig. 4) and poorly sorted (Fig. 5).

Although statistical measures of sorting and size are not normally applied to carbonate sediments, we have found both size analysis and sorting to be useful in describing noneefal carbonate sediment bodies that are subject to mechanical transportation through extensive bioturbation, waves, and currents. These measures should not be used to compare carbonate sediment bodies to detrital sediment bodies, since transportation of carbonates is usually much less important to the resultant rock body than for detrital sediments. However, statistical comparison of carbonate to carbonate bodies is useful, since qualitative information about the role of transportation in carbonate settings can be extracted from the data. For instance, it appears that the bathymetry of the Buck Island Channel has resulted from the transportation of fine carbonate grains from east-to-west. These grains are trapped in grass beds and along a fringing coralgall reef community. Excess sediments eventually slide into deeper water off the western edge of the shelf. An easterly current regime can be detected by the shoaling of water from east-to-west and by the constituent particles of the sediment body (Fig. 2). Sorting of the sediment indicates a greater degree of winnowing in the shoaler portions of the Buck Island Channel (Fig. 5), although sorting of carbonate sediments is rarely good except in very strong currents or where the particles are derived from one organism source, such as the cropping of *Halimeda*. Sorting is very poor in grass beds no matter the current regime, reflecting the trapping of a wide variety of fine-grained particles which are added to the *in situ*-produced sediment.

Halimeda, mollusks, and coral are the three most abundant constituent particles in the Buck Island Channel (Fig. 2). Coral is a major constituent only where the sediment samples are adjacent to coralgall reefs along the margins of the channel and at the western termination of the B.I.C, where *Porites* coral gardens line the drop-off into the Christiansted submarine canyon. In general, coral/mollusc sands are indicative of the presence of nearby coral reefs, whereas *Halimeda*/mollusc sands are indicative of open sand and grassbed sediments. An occasional near-reef sample will contain significant amounts of coralline algae and the occasional sample from a grassbed contains significant amounts of foraminifers.

East of the main study area, the St. Croix northeastern shelf is sediment-deficient. Hardgrounds, thin sands, and scattered coral constitute the major bottom types. Water depth averages 80 feet (27 meters) in contrast to the average 50 feet and shoaler of the BIC. A framework reef (Burke and Gerhard, 1987; Gerhard, 1989; Gerhard and Burke, 1990), Lang Bank, marks the eastern extremity of the island shelf. It does not break the surface.

Although no coring was done to establish the cause of the shoaling to the west, it is likely that current-dominated sediment accumulation is a primary cause of the shoaling (Hubbard et al, 1981). Cretaceous metaturbidites of the Caledonia Formation (Whetten, 1966) crop out both on the mainland opposite the BIC and on Buck Island. Burke et al (1989) suggest that the floor of the BIC is well-indurated Pleistocene limestone although it has not been sampled except directly in front of Tague Bay Reef.

Burke et al (1989) demonstrate that the associated bank barrier reef on the northern margin of St. Croix has grown on a limestone substrate of presumable Pleistocene Age and that substrate dips to the east. It is possible that the abrupt shoaling

in the Buck Island Channel from east-to-west is related to the relict topography on the Pleistocene limestone rather than to the accumulation of modern sediments, or a combination of both.

CORALGAL REEFS AND BANKS

The term "reef" as used in this paper includes reefs of varying types ranging from true framework reefs that bound the St. Croix platform through the abundant biodetrital reefs that fringe nearshore lagoons and in the quieter bays and estuaries hydromechanical banks (Burke and Gerhard, 1987; Gerhard and Burke, 1990; Gerhard, 1991).

The reefs of the St. Croix north shore are most mature to the west and least mature to the east, reflecting bottom topography that is either relict or the result of a general tilting down to the east of the island (Adey, 1975; Burke et al, 1989). These reefs are well-developed biodetrital reefs with higher energy mechanical forms in the east into the prevailing wind and wave trains. The main reef system is about four miles long from the east tip of the island to the termination at Sand Cay (Candlelight Reef). The best-documented of these reefs is the Tague Bay Reef (Burke et al, 1989; Ogden, 1974). Reef development is also pronounced around the east end and southern side of Buck Island, part of Buck Island National Monument, but these are small compared to the Tague Bay complex.

LAGOONS

Shoreward of the barrier reefs on the north shore of St. Croix are lagoons separated from each other by points of land jutting northward from the island. The lagoons are hydraulically connected, the separations being spatial constrictions of rock points that reduce the distance between the reef and the island, thus increasing velocity of longshore flow (see Fuller, 1978). The most easterly-studied lagoon is Boiler Bay, named for its relict coralline algal "boilers" (Gerhard and Stolzman, 1974), and the largest one, Tague Bay, is located just west of Boiler Bay (Fig. 6 A, B.) separated by Cottogarden Point (see Fuller, 1978). Several studies of other lagoons and estuaries that describe nearshore sedimentary facies of St. Croix have been previously published (Gerhard and Petta, 1974; Gerhard, 1978; and Gerhard, 1981).

Tague Bay's central portion averages over six meters deep (Fig.7). Tague Bay lagoon contains medium-to-fine-grained sand, except at the entrance and exits of longshore currents where coarser grained sands predominate (Cottogarden and Tague Points, respectively) (Fig. 8). At the eastern end, near Cottogarden Point, there is a gap in the reef and here the bottom sediments are strongly rippled in response to longshore drift, wave impingement, and tidal change.

Constituents of the sands are predominantly coral near the barrier reef and near shoreline, as in Boiler Bay, but the major portion of the lagoon is a mixture of *Halimeda* with various amounts of mollusks, coralline algae and foraminifers (Fig. 9,

Fig. 10). Insoluble residues are present in a pattern that appears to reflect transport from the strandline through the bay to the west, are most abundant in a triangular arc in the southwest of the bay, and are mostly near-absent in the northeastern portion of the bay (Fig. 11). Grass beds (mostly *Thalassia testudinum*) cover much of the lagoon bottom with *Calianassa* mounds dotting the open sand areas.

The current regime is reflected in the sorting of the sediments. Near the pass between the lagoon and the Buck Island Channel, where the tidal currents and movement of water into the lagoon is highest, sorting is best, deteriorating into the leeward western end of the lagoon (Fig. 11). Near shore wave-dominated settings are better sorted than the main portion of the lagoon. Insoluble residues in the sediments reflect both proximity to shoreline sources and trapping in grass beds as contrasted to the dynamic winnowing of open sand areas (Fig. 12).

A two-meter-long sediment core taken in roughly the center of the lagoon in a sand bottom contained mostly *Halimeda* with abundant mollusks; the lack of foraminifera suggests that grass beds were never present at the core location while the sediment was accumulating. The cored sediments were coarse sand at the bottom with the median size decreasing to fine sand at the top of the core. If preserved as a rock sequence, this would be a fining upward skeletal packstone.

Storm Event Observations in Tague Bay Lagoon

Two intense thunderstorms occurred when observations of the relationship of tidal stage to runoff into the marine environment could be made. The first occurred on a falling tide and the second on a rising tide. In the first, 2.95 inches of rain fell in a short thunderstorm on a falling tide. Sediment-laden runoff through Great Pond, a major watershed on the south shore of St. Croix, streamed into the Great Pond lagoon and out through the reef pass without mixing as a density current lighter than the sea water. It left no trace in the sedimentary record of the lagoon.

The second rain storm, following 16 inches of precipitation over the preceding 45 days that saturated the thin soils and leaked ground water directly into Tague Bay lagoon, was 4.74 inches over 5 hours on a rising tide. Study of the impacts of the rainstorm was possible owing to the presence of students in a sedimentology class at the research site (Table 1).

Runoff from that rainstorm was highly turbid, carrying coarse sediment into the shallowest waters, but more important, suspended sediment was transported into the lagoon where it ponded on the rising tide. No mixing took place; clear water "shadows" around pilings and boats demonstrated that mixing was minimal. After the rainstorm event, transects were measured across the exit of Tague Bay lagoon. Water was sampled at the surface and at the sediment-water interface at intervals of 14 hours after rainfall, 34 hours, 39 hours, and 56 hours. In the initial measurements, pH was reduced to 7.8, and fully recovered to 8.1 only after 39 hours and only at the bottom; at 56 hours the surface had recovered except at the shore where dilution by seepage of freshwater still reduced pH.

Salinity was mismeasured in the first set of measurements. By 34 hours it was 32 ppt at the surface and recovered to 33 ppt by 39 hours and 34 ppt by 56 hours. The

nearshore recovery lagged the offshore recovery. In addition, the salinity and pH values show that the bottom waters recovered faster than surface waters in a wedge-shaped profile as the fresh water lay on the saline marine waters.

SUMMARY

Sediments on the northern St. Croix shelf are almost entirely carbonate skeletal remains. The sedimentary package is the result of in situ skeletal degradation of mollusks, foraminifera, coral, and *Halimeda*. In lagoons, coralline algae are also sediment contributors near reefs, particularly in the back reef environment. On the shelf, trade wind-driven current sweeps sediment from east to west. The sediment temporarily piles up on the edge of the shelf in grass beds, creating a shallow bar along the western edge of the Buck Island Channel. Effects of currents on the sediment body are ascertained by mapping sorting (Folk) and size, recognizing that these parameters cannot be directly compared to detrital sediments because of the organic origin of the sedimentary particles.

These observations add to the body of knowledge of modern carbonate sedimentary environments. Effects of storms on pH and salinity were noted owing to the fortuitous occurrence of severe storms when observations could be made. The stage of tide during severe rainfall events determines the rate at which sediment is trapped or transported through lagoons.

ACKNOWLEDGMENTS

This paper summarizes the work not only of the authors, but of numerous students who attended classes at the former West Laboratory of Fairleigh Dickinson University prior to its destruction by Hurricane Hugo. The reports of these students and their names have been destroyed along with the buildings, although much data was preserved in external files. Students who attended Field Sedimentology classes from 1973 through 1975 collected a significant portion of the data used in this report. Some of these data were previously published in West Indies Laboratory guidebooks or in other carbonate short-course manuals, but are no longer easily accessible after the destruction of that facility. Some of the data were recovered while unpacking libraries after several moves by both authors. The data have been compiled here at the request of other Caribbean researchers. We appreciate the assistance of the Kansas Geological Survey and Pat Acker who prepared the Buck Island Channel illustrations.

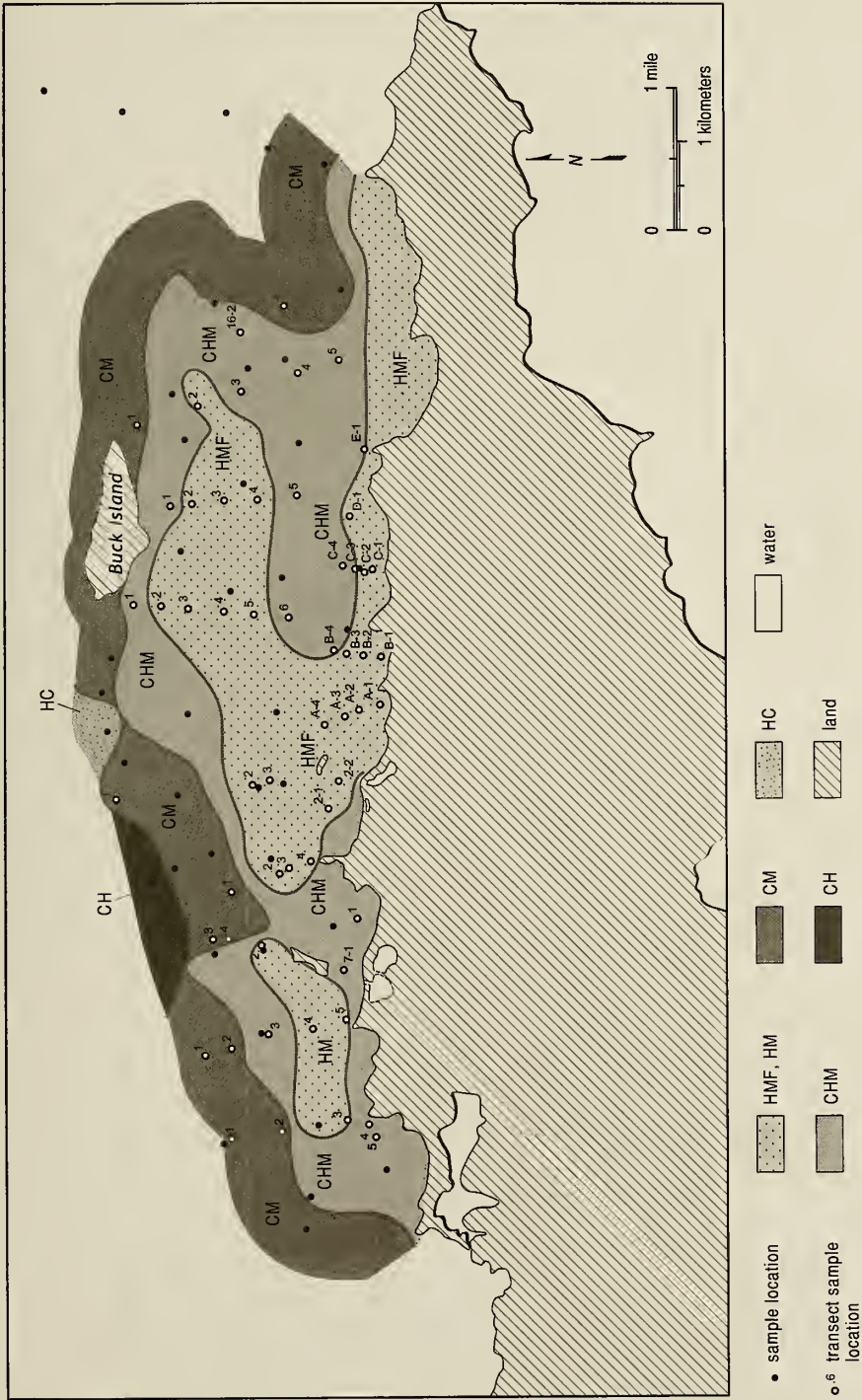


Figure 2. Constituent particles of Buck Island Channel surficial sediments.

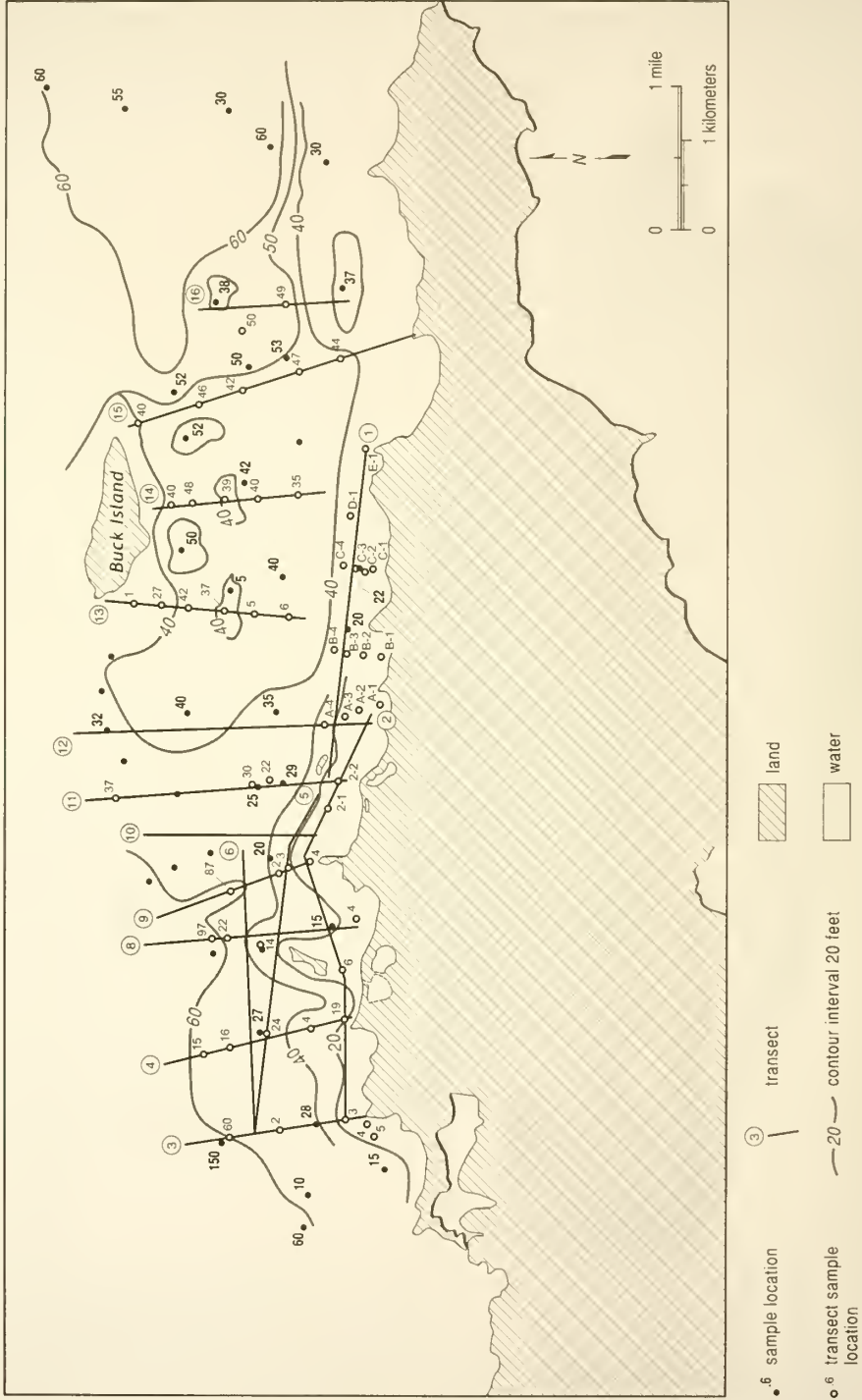


Figure 3. Bathymetry of the Buck Island Channel, showing location of sample points and transects.



Figure 4. Sediment grain size in the Buck Island Channel, in phi units.

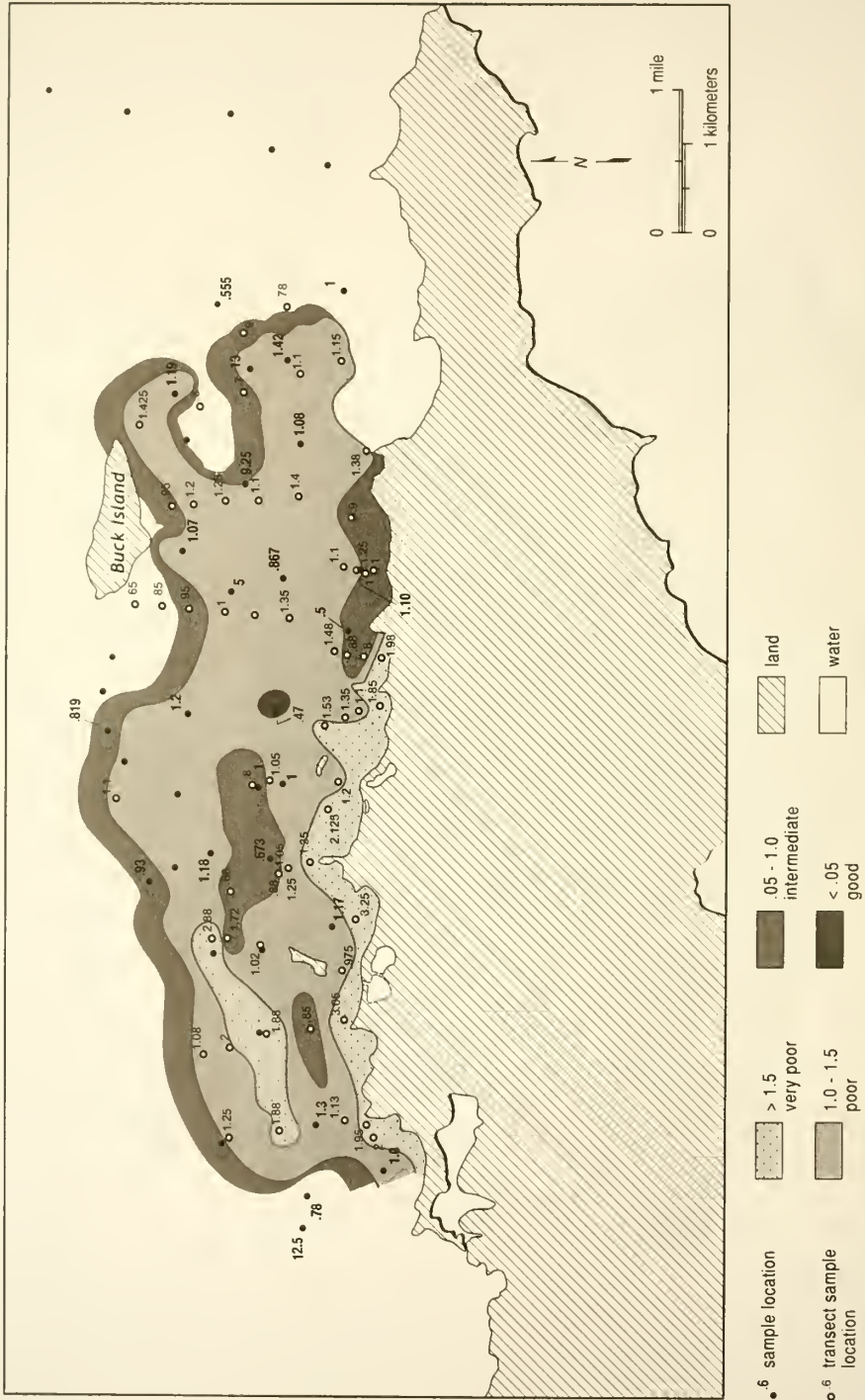


Figure 5. Sorting (Folk) of surficial sediments, Buck Island Channel.

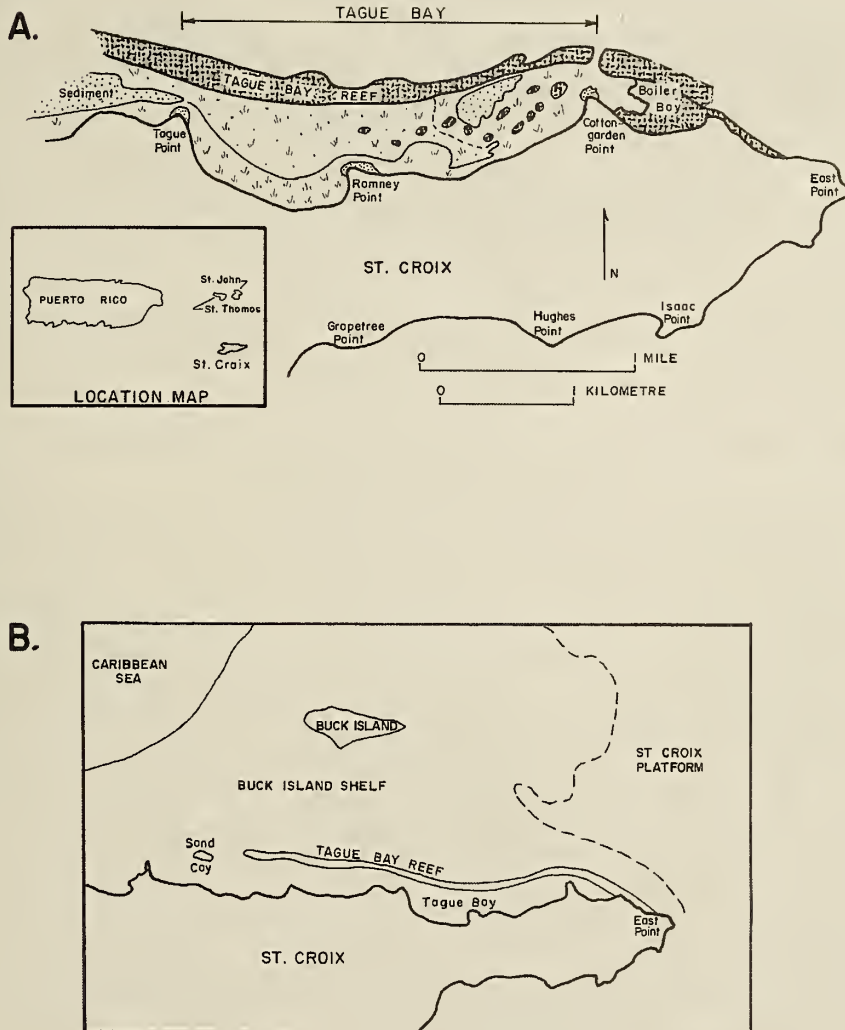


Figure 6. Location of Tague Bay (A, B) and composition of bottom communities (B). Grass symbol is *Thalassia*, grass and sand symbols are scattered grass and open sand, sand symbol is open sand, reefs are dense pattern.

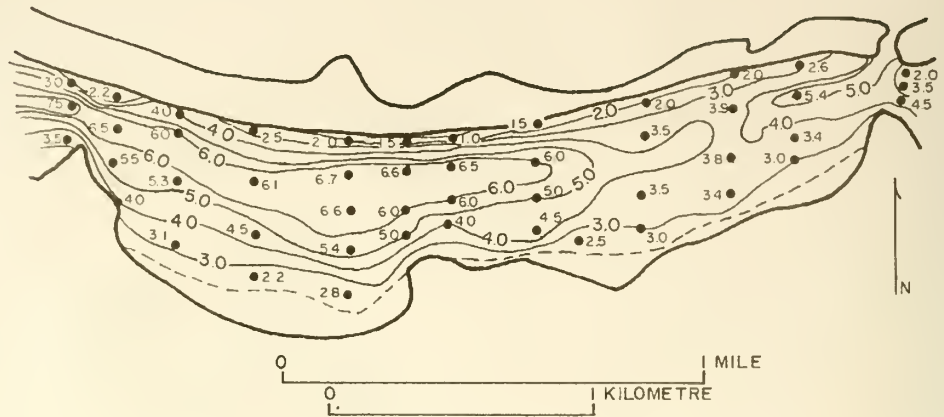


Figure 7. Tague Bay bathymetry. Contour interval is one meter. Datum July, 1974. Student data.

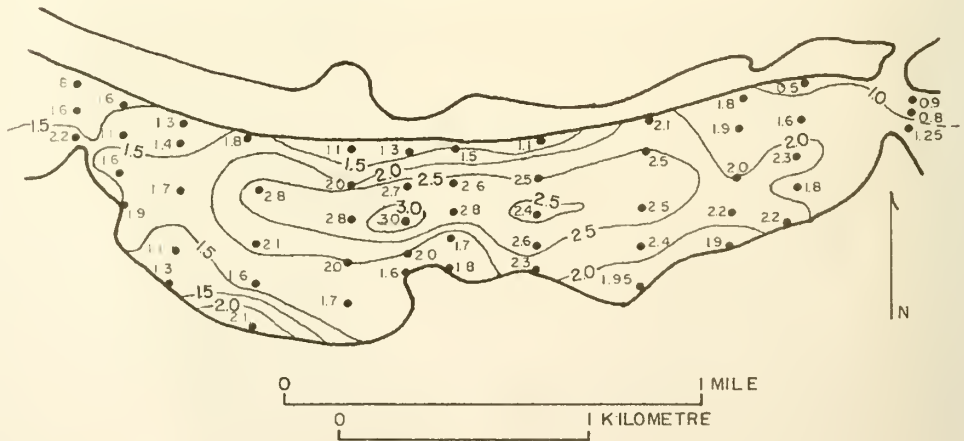


Figure 8. Surficial sediment grain size, Tague Bay lagoon. Data is graphic mean mapped at 0.5 phi interval. Student data.

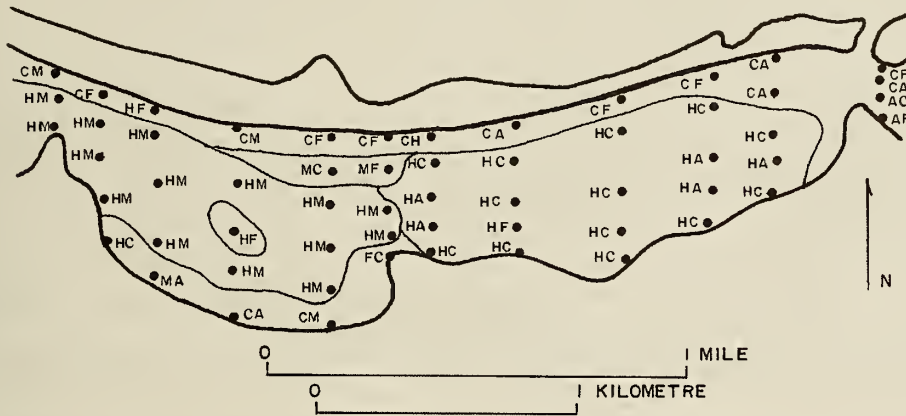


Figure 9. Constituent particles of surficial sediment in Tague Bay lagoon. The main skeletal constituents are *Halimeda* (H), coral (C), mollusc (M), foraminifera (F), and coralline algae (A). Boundaries separate major facies.

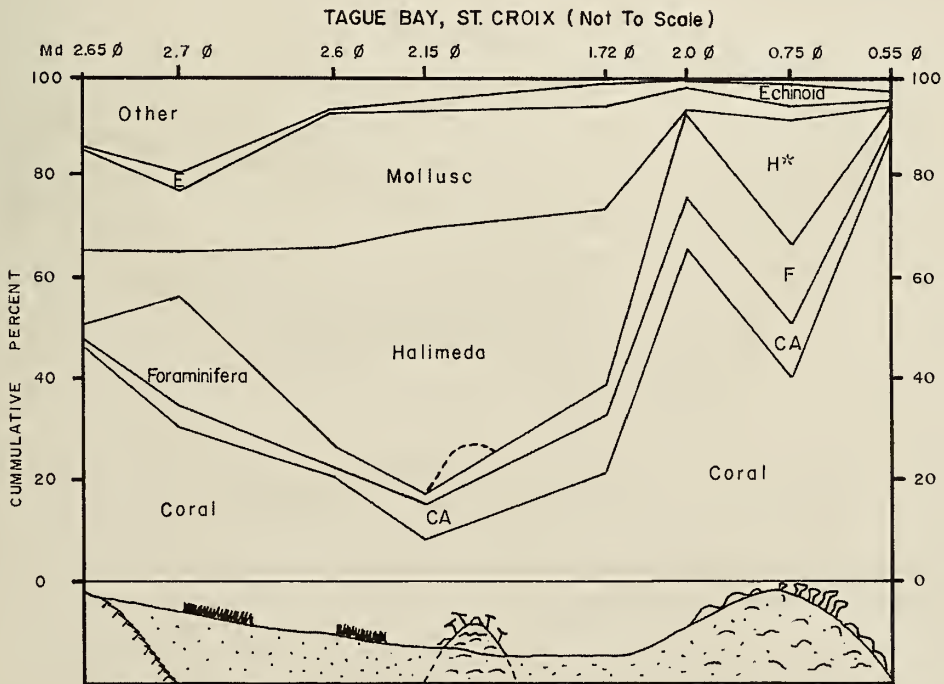


Figure 10. Shoreline to forereef transect across Tague Bay lagoon, showing constituent particles abundance. Data portrayed as percentages of total. Student data.

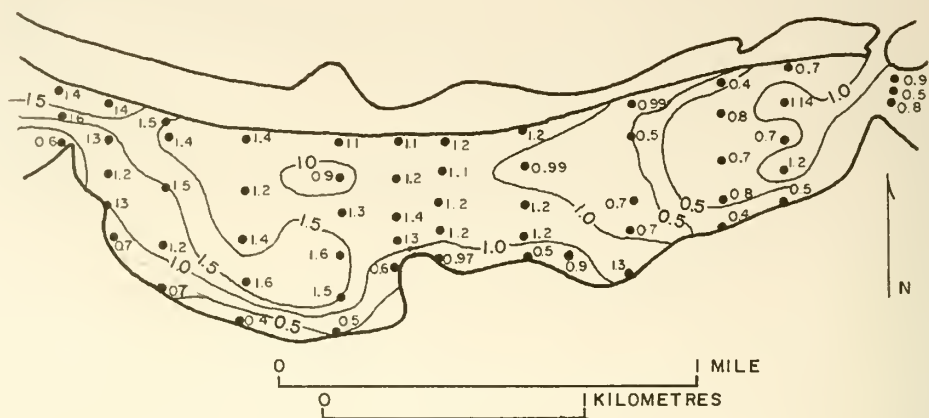


Figure 11. Sorting (Folk) of Tague Bay surficial sediments. Contour interval is 0.5. 0.5 is well sorted, 1.5 is poorly sorted. Student data.

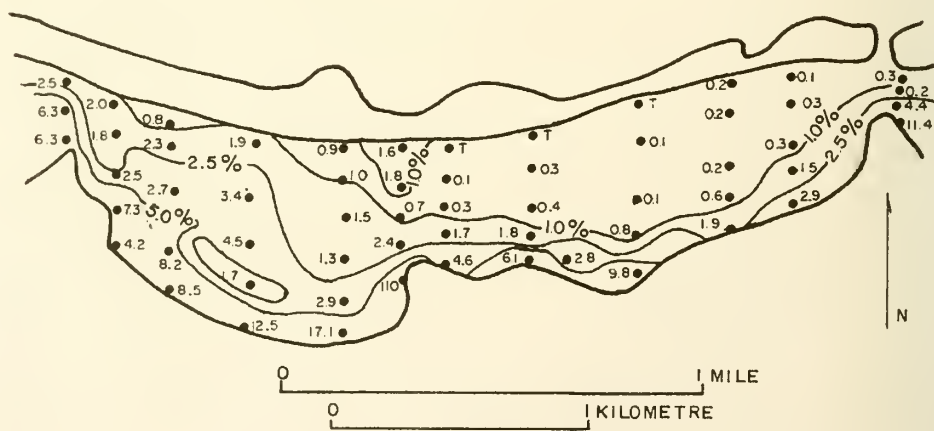


Figure 12. Insoluble residues map showing influence of terrestrial sediments in Tague Bay lagoon. Contours represent 5%, 2.5%, and 1%. Student data.

Table 1. Storm rainfall amounts at St. Croix in 1974.

Rainfall amounts from rain gauge at West Indies Laboratory, East End, St. Croix

January	2.56 (in inches)
February	0.87
March	3.57
April	1.37
May	0.26
June	0.8
July	1.12
August	6.95
September	3.85
October	7.64
November	13.72
December	na

Largest one day event: November 13, 1974, 4.74 inches.

Table 2. Salinity and pH Along Transect from Tague Point to Tague Bay Reef, November 13-15, 1974

Station	Distance from shore (meters)	Date	Hours after storm	Salinity 0/00
1 Surface	25	13-Nov	14 misrun	
1 Bottom	25	13-Nov	14 misrun	
3 Surface	85	13-Nov	14 misrun	
3 Bottom	85	13-Nov	14 misrun	
6 Surface	200	13-Nov	14 misrun	
6 Bottom	200	13-Nov	14 misrun	
1 Surface	25	14-Nov	34	32
1 Bottom	25	14-Nov	34	32
2 Surface	50	14-Nov	34	32
2 Bottom	50	14-Nov	34	32
3 Surface	90	14-Nov	34	32
3 Bottom	90	14-Nov	34	32
4 Surface	130	14-Nov	34	32
4 Bottom	130	14-Nov	34	32
5 surface	170	14-Nov	34	32
5 Bottom	170	14-Nov	34	33
6 Surface	200	14-Nov	34	33
6 Bottom	200	14-Nov	34	33
1 Surface	25	14-Nov	39	33
1 Bottom	25	14-Nov	39	33
2 Surface	50	14-Nov	39	33
2 Bottom	50	14-Nov	39	32.5
3 Surface	90	14-Nov	39	33
3 Bottom	90	14-Nov	39	33
4 Surface	130	14-Nov	39	33
4 Bottom	130	14-Nov	39	33
5 surface	170	14-Nov	39	33
5 Bottom	170	14-Nov	39	33
6 Surface	210	14-Nov	39	33
6 Bottom	210	14-Nov	39	33
NOTE BENE: EBB TIDE				
1 Surface	25	15-Nov	56	33
1 Bottom	25	15-Nov	56	33
2 Surface	50	15-Nov	56	33
2 Bottom	50	15-Nov	56	33
3 Surface	95	15-Nov	56	33
3 Bottom	95	15-Nov	56	33
4 Surface	130	15-Nov	56	33
4 Bottom	130	15-Nov	56	34
5 surface	170	15-Nov	56	33
5 Bottom	170	15-Nov	56	34
6 Surface	210	15-Nov	56	34
6 Bottom	210	15-Nov	56	34
Additional sample at 5 meters from shore, .7 meters deep (shows drainage from shoreline rocks still occurring)				32.5

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**NEW DATA ON THE LOCATIONS OF SEAGRASS SPECIES
IN THE INDIAN OCEAN**

BY

N.A. MILCHAKOVA, R.C. PHILLIPS, AND V.G. RYABOGINA

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NOVEMBER 2005**

NEW DATA ON THE LOCATIONS OF SEAGRASS SPECIES IN THE INDIAN OCEAN

BY

N.A. MILCHAKOVA, R.C. PHILLIPS,[†] AND V.G. RYABOGINA

ABSTRACT

Localities and depths are described for seven seagrasses (*Syringodium isoetifolium*, *Halodule uninervis*, *Cymodocea rotundata*, *Thalassodendron ciliatum*, *Halophila decipiens*, *Halophila stipulacea* and *Enhalus acoroides*) collected in the Indian Ocean during four expeditions. These data are compared with those reported from the literature. Maps showing the formerly unknown localities are given.

INTRODUCTION

The number of seagrasses growing in the Indian Ocean varies from 17 to 24 species (Phillips, Menez, 1988; Short, Coles, 2001; Mangroves and seagrasses of the Indian Ocean, CD, SIDCA). The numerical discord is due to different taxonomic approaches used in species identification, to the uncertainty in defining the geographical limits of the Indian Ocean, and to the habitat characteristics of a specific area. In this paper, we accept the boundaries of the Indian Ocean as they are defined in the electronic catalogue "Mangroves and seagrasses of the Indian Ocean", CD, SIDCA, i.e., the eastern coast of Africa, the coast of the Red Sea, to India, Malaysia, and northeastern Australia. Most of the relevant publications give evidence that seagrasses occupy vast areas in every part of the ocean. However, data on the ecology and the depth of occurrence are few (den Hartog, 1970, World Seagrass Atlas, 2003). This paper is an endeavor to fill in the gap in the knowledge about the localities and the borders of occurrence of the seagrasses prevailing in the Indian Ocean.

Seven seagrasses, *Syringodium isoetifolium*, *Halodule uninervis*, *C. rotundata*, *Thalassodendron ciliatum*, *Halophila decipiens*, *H. stipulacea* and *Enhalus acoroides* were collected in different parts of the Indian Ocean during four research cruises and are reported in this study.

MATERIALS AND METHODS

Four research cruises were made: 1) to the Red Sea in 1966, R/V Academician Kovalevsky; 2) to the Seychelles Archipelago in 1981; 3) to the Mascarena subwater mountain range in 1984, R/V Academician Vernadsky; and 4) to the Seychelles Islands

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in 1989, R/V Academician Nesmeyanov. The most comprehensive floristic study was conducted in 1989 during the joint (Institute of Biology of the Sea, Vladivostok, IBSS and Smithsonian Institute of Natural History, USA) research cruise on board the R/V Academician Nesmeyanov. The resulting data comprise the detailed description of the algal flora found at 12 large island groups of the Seychelles: the islands Mahe, Praslin, La Digue, Desroches and Providence, and the atolls Cœtivy, African, Farquhar, Aldabra, St. Joseph, Cosmoledo and Astov (Kalugina-Gutnik, Perstenko, Titlyanova, 1992).

Seagrass specimens collected are deposited in the herbarium of the Institute of Biology of the Southern Seas (IBSS), National Academy of Sciences of Ukraine, Sevastopol.

The investigation of bottom vegetation growing in the Indian Ocean was conducted along transects using scuba equipment to collect algal and seagrass samples from the upper-to-the lower margins of growth.

The herbarium contains 593 samples of seagrass specimens from the Indian Ocean. Four hundred and twenty-two of the samples represent seven species described in this paper. Formerly unknown localities and depths of occurrence are given for most of the seagrasses. The species arrangement is in accord with the recent taxonomic guide (Kuo and den Hartog, 2001).

RESULTS AND DISCUSSION

Syringodium isoetifolium (Ascherson) Dandy

Location and sampling sites. Seychelles. Northwestern coast of the Desroches, 12 m depth (Fig. 1), 6 February 1989, three plants, collected by Yu.Ya. Latypov; Aldabra atoll, mid-littoral zone, 29 January 1989, three plants collected by Yu.Ya. Latypov.



Figure 1. Herbarium specimen of *Syringodium isoetifolium* (Ascherson) Dandy, northeastern coast of Desroches Island, Seychelles, 12 m depth.

S. isoetifolium is widely found in the tropical Indian Ocean (den Hartog, 1970; Bandeira and Gall, 2003). The following localities are new for this species: Desroches Island, Cœtivy and Aldabra atolls of the Seychelles Archipelago (Kalugina-Gutnik, Perstenko, Titlyanova, 1992) (Fig. 2). Apparently, the 12 m depth near Desroches Island closely approximates the lower limit of the occurrence of the species that was found near Cuba, i.e., 16.5 m (Duarte, 1991). den Hartog (1970) reported the depth of the species as 6 to 10 m in the Indian Ocean.

Halodule uninervis (Forsskal) Ascherson

Location and sampling sites. Felidy atoll, littoral zone, Maldives, 6 November 1981, one plant collected by A.A. Kalugina-Gutnik, Socotra Island, littoral, 11 November 1981, four plants collected by A.A. Kalugina-Gutnik; Seychelles, Cœtivy atoll, western coast, mid-littoral, 18 January 1989, 25 plants collected by N.I. Selin; Aldabra atoll, littoral,

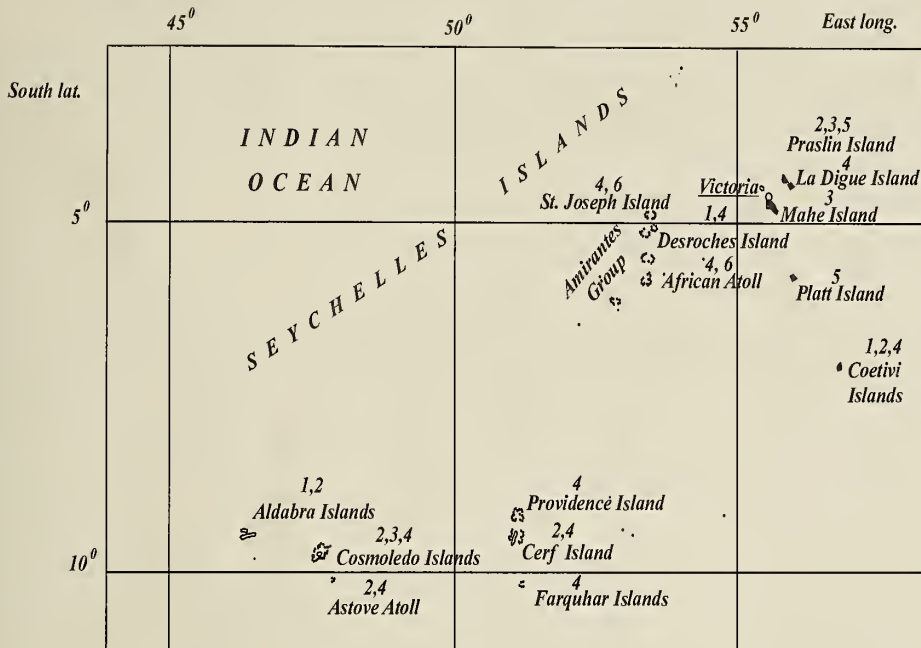


Figure 2. The new localities in the Seychelles for: 1 – *Syringodium isoetifolium*, 2 – *Halodule uninervis*, 3 – *Cymodocea rotundata*, 4 – *Thalassodendron ciliatum*, 5 – *Halophila decipiens*, 6 – *Halophila stipulacea*.

29 January 1989, two plants collected by A. A. Kalugina-Gutnik; Astov atoll, littoral, 10 March 1989, two plants collected by L.P. Perestenko; Praslin Island, mid-littoral, 11 February 1989, two plants collected by N.A. Milchakova; Cerf Island (adjacent to Mahé), mid-littoral, 17 February 1989, two plants collected by L.P. Perestenko.

H. uninervis is often found along the eastern coast of Africa and the Red Sea (den Hartog, 1970; Phillips and Menéz, 1988; Bandeira and Gell, 2003). Based on the herbarium specimens and published data (Kalugina-Gutnik et al., 1992), the area occupied by *H. uninervis* in the Indian Ocean has been extended to several localities not listed in earlier publications, i.e., Felidy atoll, the Maldivé Islands (Fig. 3), Socotra Island (Fig. 4), the Seychelles: Coetivy, Aldabra, Astov atolls, Praslin, Cosmoledo and Cerf Islands (den Hartog, 1970; Phillips and Menéz, 1988; Bandeira and Gell, 2003, Mangroves and seagrasses of the Indian Ocean, CD, SIDCA) (Fig. 2).

***Cymodocea rotundata* Ehrenberg and Hemprich ex Ascherson**

Location and sampling sites. Felidy atoll, the northern shallow-water lagoon, Maldives, 0.5 m depth, 4 November 1981, five plants collected by A.A. Kalugina-Gutnik.

This species is widely known in the Indian Ocean (den Hartog, 1970; Lipkin et al. 2003; Bandeira and Gell, 2003). There are no data regarding the occurrence of

Cymodocea rotundata near the Seychelles and Maldives (den Hartog, 1979; Phillips and Menéz, 1988; Bandeira and Gell, 2003; Mangroves and scagrasses of the Indian Ocean, CD, SIDCA). The only exception is one paper (Kalugina-Gutnik et al., 1992), in which this species is described for some islands of the Seychelles Archipelago. Among the new localities where *C. rotundata* was found in the Indian Ocean are the islands of the Seychelles Archipelago named here (Fig. 2) and the atoll Felidu in the Maldives (Fig. 3).

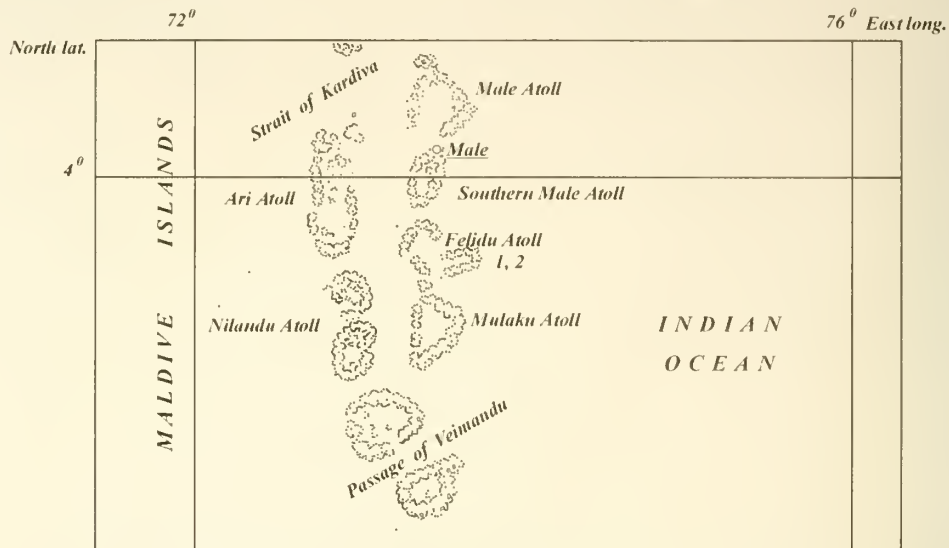


Figure 3. The new localities in the vicinity of the Maldives for: 1 - *Halodule uninervis*, 2 - *Cymodocea rotundata*.



Figure 4. The new localities in the Red Sea and near Socotra for: 1 - *Halodule uninervis*, 2 - *Halophila decipiens*.

***Thalassodendron ciliatum* (Forsskal) den Hartog**

Location and sampling sites. Saya de Malha Bank, Mascarene subwater ridge, 20 m depth, 25 July 1981, four plants; 50 m depth, 4 August 1981, nine plants (Fig. 5), collected by E.Z. Gabrielian.



Figure 5. Herbarium specimen of *Thalassodendron ciliatum* (Forsskal) den Hartog, Saya de Malha Bank, Mascarene subwater ridge, 50 m depth.

Seychelles. Cœtivy atoll, eastern coast, 3 March 1984, 50 m depth, eight plants, collected by Yu. M. Latypov; Cœtivy atoll, western coast, 14 January 1989, 20 m depth, one plant, collected by N. I. Selin; Desroshes Island, northwestern coast, littoral zone, 6 February 1989, 14 plants, collected by E.V. Titlyanov; Astov atoll, 1.5 m depth, to March 1989, one plant, collected by N. I. Selin; La Digue Island, north-western extremity near Praslin Island, lower littoral zone, 26 February 1989, four plants, collected by N. I. Selin; Farquhar atoll, 3 m depth, 23 January 1989, four plants, collected by N. I. Selin; Providence Island, 1.5 m depth, 5 March 1989, four plants, collected by N. I. Selin.

Th. ciliatum has a discontinuous distribution. This species is common in the Red Sea and in the eastern and western Indian Ocean (den Hartog, 1970) at Mascarene subwater ridge (Kalugina-Gutnik et al., 1992). In the northeastern part of Cœtivy atoll, *Th. ciliatum* grows at a depth of 17 to 25 m. Total community biomass, including *Halimeda* spp., constitutes 1,640 – 2,319 gm⁻² (wet weight) with 10% coverage over the bottom. *Th. ciliatum* grows most extensively at African Bank, South Island. At depths from 10 to 31 m, biomass varies from 440 to 2,240

gm⁻² wet weight with the coverage estimated from 50 to 90 %, with an almost complete absence of associated seaweeds.

Though generally common for the Seychelles, *Th. ciliatum* has only recently been found at the Desroshes, La Digue, Providence, Cerf Islands and Astov, African, Cœtivy, Farquhar, St. Joseph, Cosmoledo atolls (Kalugina-Gutnik et al., 1992) (Fig. 2). The depth at which this species grows varies widely from the shallows to 33 m (Lipkin, 1977; Hulings, 1979; Pärnik et al., 1992; Lipkin et al., 2003; Titlyanova and Butorin, 1978). Based on herbarium records, the lower depth for this species is apparently 50 m (Cœtivy atoll and Saya de Malha Bank). We report that this depth constitutes a new lower depth record for *Th. ciliatum*.

***Halophila decipiens* Ostenfeld**

Location and sampling sites. Saya de Malha Bank, Mascarene subwater ridge, 20 m depth, one plant and 40 m depth, 19 March 1981, four plants, collected by E.Z. Gabrielian.

The Red Sea, the southern part of the Hodeida port, 0,5 depth, 3 September 1966, two plants, collected by A.A. Kalugina-Gutnik.

Grande Anse Bay, littoral zone, Praslin Island, Seychelles, 12 February 1989, one plant collected by N.A. Milchakova; Platt Island, 20 m depth (Titlyanova and Butorin, 1978).

This species is widely found in the Indian Ocean. There is little evidence regarding *H. decipiens* at the Seychelles, Mascarene subwater ridge and the southern Red Sea (den Hartog, 1970; Kalugina-Gutnik et al., 1992; Bandeira and Gell, 2003; Lipkin et al., 2003; Mangroves and seagrasses of the Indian Ocean, CD, SIDCA). According to our collections, the localities new for the species are the port of Hodeida, the Red Sea (Fig. 4), the coastal seawater of Praslin Island, Seychelles (Fig. 2) and Saya de Malha Bank (Fig. 6). According to Titlyanova and Butorin (1978), it is also found at Platt Island, Seychelles.

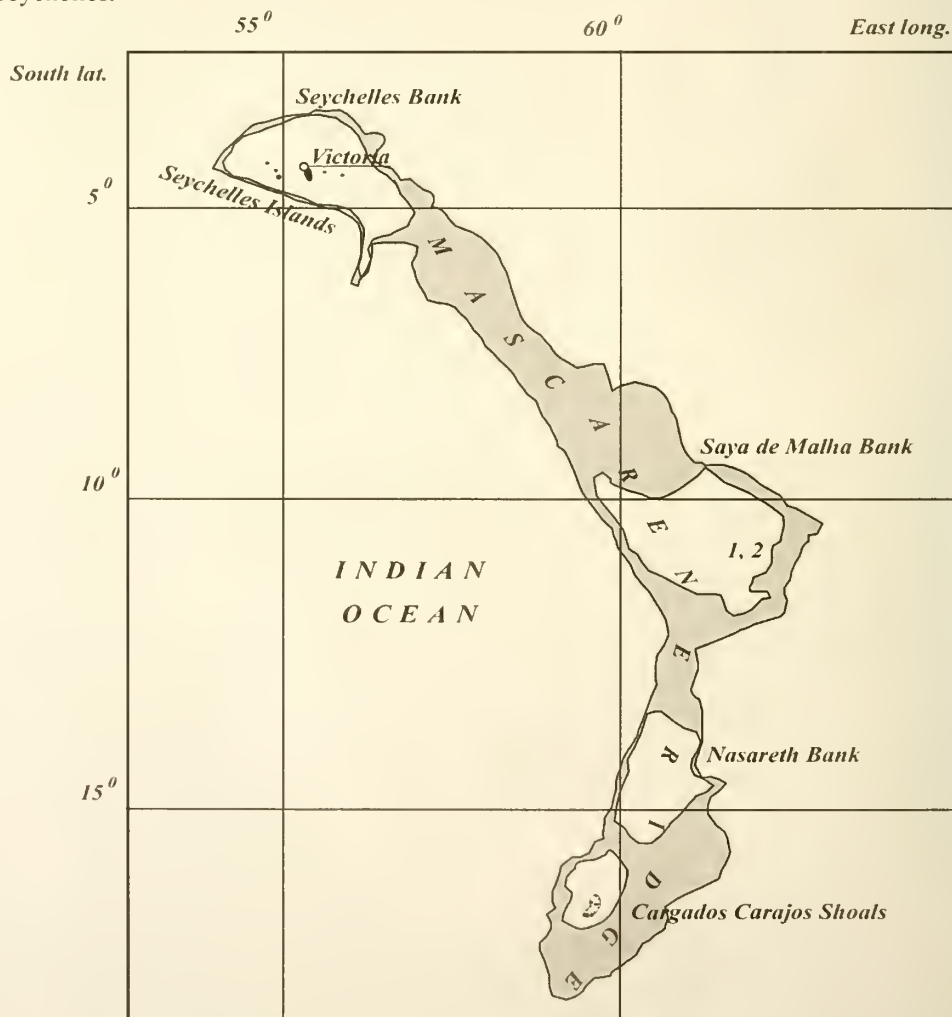


Figure 6. The new localities at the Mascarene ridge between the Seychelles and Mauritius Island for: 1 - *Halophila decipiens*, 2 - *Enhalus acoroides*.

***Halophila stipulacea* (Forsskal) Ascherson**

Location and sampling sites. Southeastern coast of St. Joseph atoll, Seychelles, 37 m depth, 3 March 1989, one plant (Fig. 7), collected by M. and D. Littler; African atoll, South Island, southeastern coast, 31 m depth, 28 February 1989, one plant, collected by N. I. Selin.



Figure 7. Herbarium specimen of *Halophila stipulacea* (Forsskal) Ascherson, southeastern coast of St. Joseph atoll, Seychelles, 37 m depth.

H. stipulacea is widely known in the Indian Ocean. The species has never been mentioned for the African and St. Joseph atolls in the Seychelles (Fig. 2) in the literature (Bandeira and Gell, 2003; Seagrasses of the Indian Ocean, CD, SIDCA) until recently and are places new for this species. There, at depths from 3 to 17 m, *H. stipulacea* grows together with solitary plants of *Th. ciliatum*, *Halimeda* spp. and other algae (Kalugina-Gutnik et al., 1992).

H. stipulacea grows at depths varying from 0 to 70 m, mostly from 0 to 18 m (den Hartog, 1970; Phillips and Menéz, 1988; Mangroves and seagrasses

of the Indian Ocean, CD, SIDCA). Duarte (1991) wrote that the lowest depth of *H. stipulacea* is 50 m. However, in the Gulf of Elat, the Red Sea, plants of *H. stipulacea* were found growing at 50 to 70 m deep (Lipkin, 1977; Hulings, 1979; Lipkin et al., 2003). The growth of this species at depths of 31 to 37 m along the Seychelles is new ecological data for *H. stipulacea* from the Indian Ocean (Kalugina-Gutnik et al. 1992).

***Enhalus acoroides* (L.) Royle**

Location and sampling sites. Saya de Malha Bank, Mascarene subwater ridge, 20 m depth, 25 July 1981, six plants (Fig. 8), collected by E. Z. Gabrielian.



Figure 8. Herbarium specimen of *Enhalus acoroides* (L.) Royle, Saya de Malha Bank, Mascarene subwater ridge, 20 m depth.

In the Indian Ocean, this species is sparsely found (den Hartog, 1970). About a century ago, *E. acoroides* was registered at Mahé and Praslin islands, Seychelles (den Hartog, 1970). More recent publications (Kalugina-Gutnik et al., 1992; Bandeira and Gell, 2003) gave little evidence. The species was reported for the Seychelles in "Mangroves and seagrasses of the Indian Ocean", CD, SIDCA. Saya de Malha Bank and the Mascarene ridge are, apparently, new localities for this species (Fig. 2).

E. acoroides usually grows at depths from 0.5 to 6 m. The lower boundary for this species is 20 m (Saya de Malha Bank, Mascarene ridge). Little evidence is available about the ecology of this seagrass. It seems to be insufficiently studied (den Hartog, 1970).

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ATOLL RESEARCH BULLETIN

NO. 538

**HUMPHEAD WRASSE (*CHEILINUS UNDULATUS*) ABUNDANCE AND SIZE
STRUCTURE AMONG CORAL REEF HABITATS IN MALDIVES**

BY

ROBERT D. SLUKA

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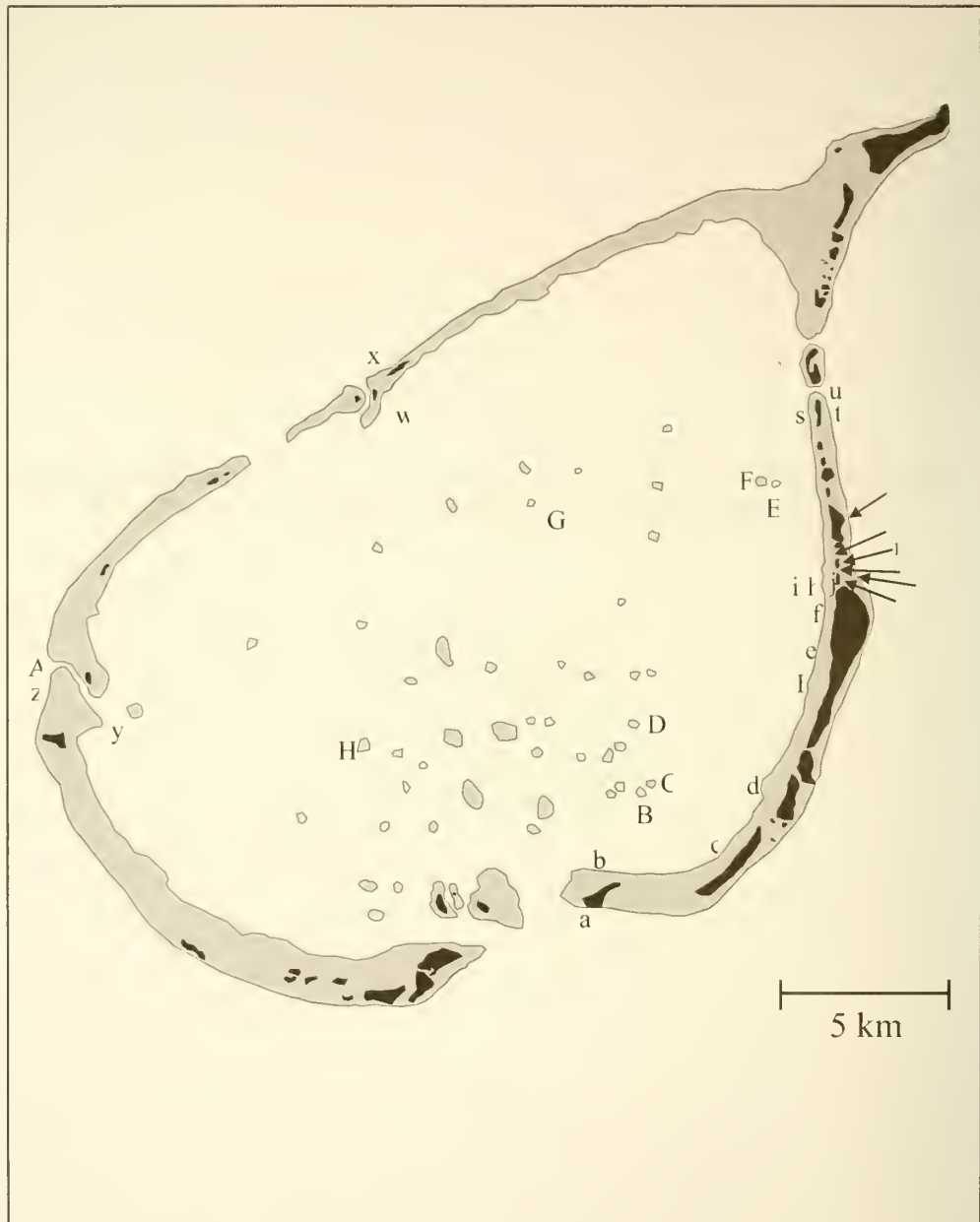


Figure 1. Map of study sites within Laamu Atoll. Line surrounding shaded (lagoon and shallow coral reef) and black (island) areas indicates the reef crest. Codes reference sites listed in Table 1.

HUMPHEAD WRASSE (*CHEILINUS UNDULATUS*) ABUNDANCE AND SIZE STRUCTURE AMONG CORAL REEF HABITATS IN MALDIVES

BY

ROBERT D. SLUKA¹

ABSTRACT

The abundance and size of humphead wrasse (*Cheilinus undulatus*) among 36 sites comprising five habitat types at one atoll in the Republic of Maldives were assessed through underwater visual observation. Humphead wrasse were observed more often in channel habitats than all others. The average size of sited individuals was not significantly different among the three habitats where size data was available.

INTRODUCTION

Fishing to supply the live-fish food trade has been implicated in the demise of coral-reef fisheries for grouper and humphead wrasse (*Cheilinus undulatus*) in many areas of the Indo-Pacific (Erdmann and Pet-Soede, 1996; Johannes and Riepen, 1995; Donaldson and Sadovy, 2001; Sadovy and Vincent, 2002). Humphead wrasse, also known as the Napoleon or Maori wrasse, are one of the most highly sought after species. Little is known about the biology of humphead wrasse. This is one of the largest of all reef-dwelling teleosts, only smaller than a few grouper species (Randall et al., 1978). The largest reliably recorded specimen was 229 cm long (Randall et al., 1990). This species ranges from 0.5 - 60 m in depth and occurs from the east coast of Africa and Red Sea across the Indian Ocean to the central Pacific Ocean (Debelius, 1993; Gomon, 1984). Juvenile humphead wrasse have been observed in shallow sandy areas adjacent to coral-reef lagoons and in lagoonal staghorn coral thickets (*Acropora* spp) (Debelius, 1993; Randall, 1955; Randall et al., 1978). Adults tend to be more common offshore and deeper, especially in outer-reef slopes and channels, but can also be found in lagoons (Randall, 1955; Randall et al., 1978; Sluka, 2001). This species eats mollusks, fishes, sea urchins, crustaceans, and other invertebrates (Randall et al., 1978; Randall et al., 1990). Humphead wrasse exhibit paired spawning in small groups or larger aggregations (Donaldson, 1995).

This study was conducted to examine the large-scale distribution patterns of the humphead wrasse in Laamu Atoll, Republic of Maldives.

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METHODS

Habitat Description

The Republic of Maldives is a chain of coral-reef atolls stretching from about 7°N to 2°S at 73°E. The southern atolls of the Maldives, such as Laamu, are distinctly different from the northern ones including fewer channels and, consequently, larger unbroken coral-reef structures (Anderson, 1992). There is a typical zonation to most reefs progressing from inshore-to-offshore with a shallow sandy lagoon, reef flat, reef crest, and reef slope. The outside atoll-rim reef slope drops precipitously to about 30-45 m, slopes gently for about a half kilometer, then drops again to abyssal depths (Anderson et al., 1992). The inner reef slope drops steeply to about 20-30 m and then grades into a sandy bottom which occupies the inner portion of the atoll. Laamu Atoll has the deepest inner lagoon of all Maldivian atolls reaching to 73 m. A unique feature of these atolls is the circular reef rings which rise from the atoll's inner floor called faros. Many are similar in zonation with a reef flat, crest, and slope.

Data Collection and Analysis

Surveys were completed by noting humphead wrasse observed during the course of diving for other studies from November 1996 to June 1997. These dives were mostly focused on completing visual censuses of other fish species and lent themselves well to noting the presence of humphead wrasse. The total dive time was noted as well as the number and size of any humphead wrasse observed. Two sites were surveyed by snorkeling (J and K); all other were surveyed on scuba. Five habitat types were identified (Fig. 1): 1) reef slopes on the outside of the atoll rim (sites: a, g, r, t, x, and z, Fig. 1 and Table 1); 2) reef slopes on the inside of the atoll rim (sites: b, c, d, e, f, h, i, j, q, s, v, y, and w); 3) channels that lead from the inside to the outside of the atoll rim (sites: u, A, J, and K); 4) faros (sites: B-H); and 5) shallow (< 2m) reef crest and lagoonal patch reefs (mostly branching acropid patches). Due to only zero values in faro and shallow sites, these two habitats were not used in the analysis.

The number of wrasse observed per hour was plotted by habitat type and tested for significant differences using a Kruskal-Wallis ANOVA. A non-parametric ANOVA was selected due to the highly skewed distribution resulting from numerous zero values. Size was estimated visually after training. Parametric analysis of variance was used to test for significant differences in mean size among the three habitats.

RESULTS

Thirty-six sites were studied (Table 1) yielding a total of 51 fish observed during 103 hours and 43 minutes of sampling. Humphead wrasse were observed more often in channels than in any other habitat (Fig. 2). The mean number of humphead wrasse per hour of observation was significantly higher in channels than inside atoll-rim reef slopes ($p < 0.05$). Fish occurrence at outside atoll-rim reef slope sites was not significantly different than either those at the inside atoll-rim sites or the channel sites. More

replication would be necessary to ascertain differences between this habitat and the other two as there was high variability in the data. Average size was not significantly different among the three habitat types where this species was observed (Fig. 3, $p > 0.05$). Sizes ranged from 30-140 cm with a mean ($\pm 1SE$) of 80.2 (4.8) (Fig. 4).

Table 1. Survey sites, including site codes which reference Fig.1. The time surveyed, number of humphead wrasse observed, and average size of individuals are given for each site. The two sites marked with an + were surveyed using snorkel; all others by scuba.

Site	Site code	Time surveyed (h:min)	No. observed	Size (cm \pm 1SE)
Gaadhoo outside	a	1:26	10	95 (10)
Gaadhoo inside	b	0:50	2	65 (35)
Fonadhoo	c	0:30	0	
Kadhdhoo	d	0:39	0	
Matimatidhoo	e	6:15	0	
Gamu inside	f	6:14	0	
Gamu outside	g	1:55	0	
Bodufinalhu slope	h	25:24	0	
Bodufinalhu deep	i	1:41	0	
Bodufinalhu shallow	j	11:30	0	
Bodufinalhu lagoon	k	2:00	0	
Bodufinalhu channel	l	2:00	0	
Gaskandufinalhu lagoon	m	1:00	0	
Baresdhoo channel	n	4:00	0	
Bodufinalhu reefcrest	o	3:00	0	
Baresdhoo reefcrest	p	2:30	0	
Baresdhoo inside	q	4:36	1	100 (-)
Baresdhoo outside	r	2:40	0	
Mundo inside	s	1:28	0	
Mundu outside	t	0:50	0	
Mundu channel	u	0:56	9	78 (10)
Maabaidhoo	v	1:46	4	70 (6)
Fushi channel	J	1:00 ⁺	3	93 (7)
Vadinalhoo inside	w	0:59	0	
Vadinalhoo outside	x	1:44	3	65 (9)
Vadinalhoo channel	K	1:00 ⁺	4	65 (13)
Maava inside	y	1:54	0	
Maava outside	z	1:40	0	
Maava channel	A	1:23	15	5 > 100
Gaadhoo faro	B	0:38	0	
Fonadhoo faro	C	2:16	0	
Mundu faro	D	1:21	0	
Baresdhoo faro 1	E	4:36	0	
Baresdhoo faro 2	F	0:20	0	
Vadinalhoo faro	G	2:03	0	
Maava faro	H	1:39	0	

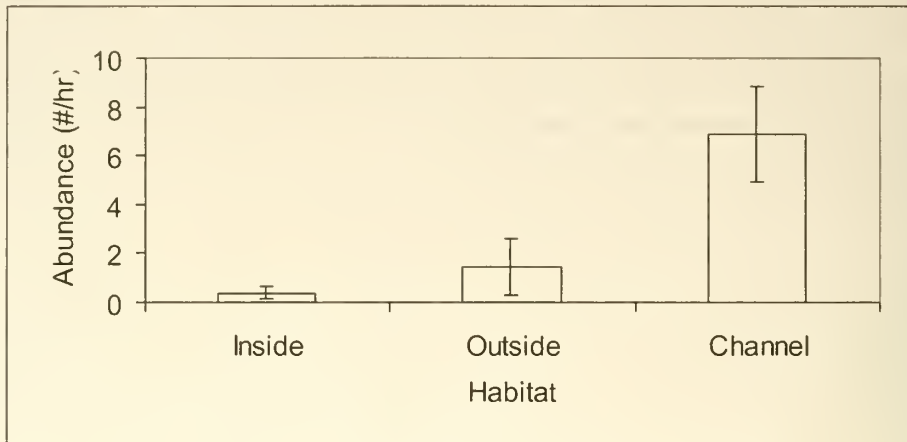


Figure 2. Mean humthead wrasse abundance (number/hour \pm 1 SE) among three habitat types: reef slopes inside the atoll rim; reef slopes outside the atoll rim; and channels connecting the inside and outside of the atoll rim.

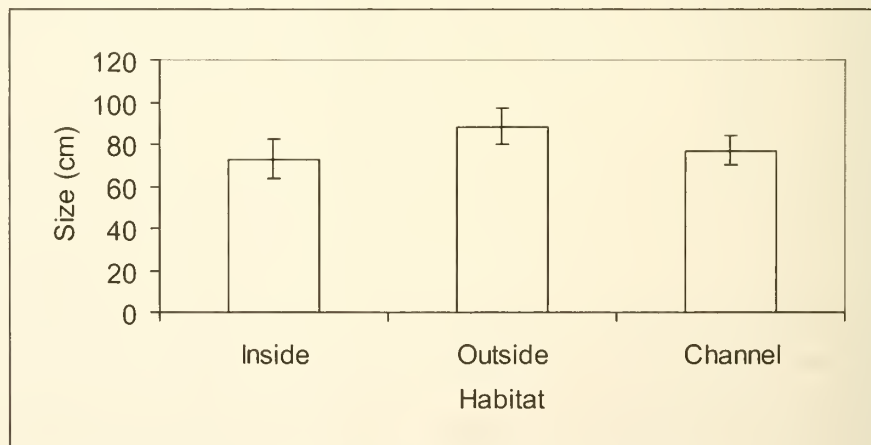


Figure 3. Mean size (cm \pm 1 SE) of humthead wrasse observed among three habitat types: reef slopes inside the atoll rim, reef slopes outside the atoll rim, and channels connecting the inside and outside of the atoll rim.

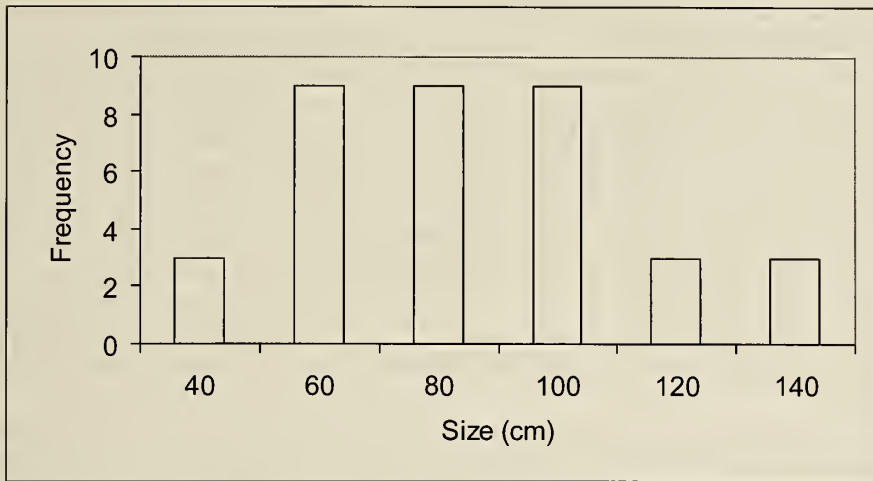


Figure 4. Size-frequency distribution of all humphead wrasse where size data were available (n=31).

DISCUSSION

Humphead wrasse preferentially occupied channel habitats in Laamu Atoll, Maldives. This species was also observed in three reef-slope sites inside the atoll rim and two reef-slope sites outside the atoll rim. However, two of three inside sites and both outside sites were adjacent to channel habitats. Only one humphead wrasse was observed at a site located a significant distance from a channel. It is unknown why this species prefers this type of habitat. Comparative data are only available from one other central Indian Ocean site (Sluka and Lazarus, in press). The relative abundance of this species at the study sites in Maldives (0.49 fish/hr) was approximately three times higher than at sites on the west coast of India (0.18 fish/hr). However, the Indian sites were mainly non-carbonate reefs with high structural complexity but low coral cover (Sluka, Mary, and Lazarus, unpublished data) and thus of a significantly different habitat type.

Little is known about humphead wrasse biology which can be used to infer causative agents of distribution patterns. This species eats a wide range of prey including mollusks, fish, and sea urchins, and the crown-of-thorns starfish, *Acanthaster planci* (Randall et al., 1978). The reef-slope habitats of Laamu Atoll have high coral cover and tend to have high spatial complexity, including vertical relief (R. Sluka and M.W. Miller, unpublished data), while the channels tend to have lower vertical relief and spatial complexity (Sluka, pers. obs.). It may be that food items are easier to find due to the relative lack of hiding places and more exposed nature of the channel coral reefs. However, the humphead wrasse observed in the channels tended to be found near the outer edge of the channel adjacent to the point at which the channel drops off and turns into the reef slope. It is unknown if this species switches ends of the channel with the changing of the tide (i.e., in outgoing tides it is located primarily at the outer end of the channel and in ingoing tides, the inner end). If this were the case, it would seem likely that humphead wrasse were making use of the currents for foraging activity.

Knowledge of habitat preferences of humphead wrasse is important for the management of this species. While a total ban on export is the ideal situation as far as the resource is concerned, some level of exploitation may be possible once the biology and ecology of this species are better known. Where other management strategies need to be used, protection of spawning aggregations within a system of marine fishery reserves appears to be the best strategy for long-term sustained exploitation of long-lived, slow growing coral-reef species (Roberts et al., 1995). Johannes (1980) suggested that protecting spawning aggregations by limiting fishing, either spatially or temporally, could be one of the most effective management strategies. Humphead wrasse have been observed to aggregate in large numbers to spawn (Johannes and Riepen, 1995). By protecting these spawning events, the larger individuals which have higher fecundity than smaller fishes are allowed to reproduce and potentially supply recruits to surrounding areas.

It is clear that there is intense pressure on the humphead wrasse resources of the Indo-Pacific. The Maldivian Government banned the export of humphead wrasse in 1995 owing to concerns of the recreational diving industry. However, effective enforcement of these regulations is lacking as import statistics show that Maldives is still exporting significant quantities of humphead wrasse to Hong Kong (Lau and Parry-Jones, 1999). Until we learn more concerning habitat requirements and population biology of this species, it is unknown what impact this exploitation has on these fishes in this region.

ACKNOWLEDGEMENTS

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ATOLL RESEARCH BULLETIN

NO. 539

**DEMOGRAPHIC CHARACTERISTICS OF SELECTED EPINEPHELINE
GROUPERS (FAMILY: SERRANIDAE; SUBFAMILY: EPINEPHELINAE) FROM
ALDABRA ATOLL, SEYCHELLES**

BY

BY EDWIN GRANDCOURT

**ISSUED BY
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DEMOGRAPHIC CHARACTERISTICS OF SELECTED EPINEPHELINE GROUPERS (FAMILY: SERRANIDAE; SUBFAMILY: EPINEPHELINAE) FROM ALDABRA ATOLL, SEYCHELLES

BY

BY EDWIN GRANDCOURT¹

ABSTRACT

Sagittal otoliths were extracted from samples of six species of groupers (Serranidae: Epinephelinae) caught with hand lines around the periphery of Aldabra atoll (southwest Indian Ocean) in December 2000: *Epinephelus fuscoguttatus* ($n=26$), *Epinephelus multinotatus* ($n=33$), *Epinephelus polyphekadion* ($n=77$), *Epinephelus tukula* ($n=62$), *Plectropomus laevis* ($n=22$) and *Variola louti* ($n=101$). Growth increments consisting of alternating translucent and opaque bands were observed in transverse sections of sagittae. The von Bertalanffy growth function was fit to size and increment number data, values of the growth coefficient (k) ranged from 0.13 for *E. tukula* to 0.48 for *V. louti*, with a mean value of 0.24 for all species. Estimates of the annual instantaneous rate of natural mortality ranged from 0.13 yr⁻¹ for *E. polyphekadion* to 0.28 yr⁻¹ for *V. louti*. The maximum number of putative annuli observed in transverse sections of sagittae ranged from 15 for *V. louti* to 31 for *E. polyphekadion*. While the study demonstrates the utility of structural increments in sagittal otoliths for establishing key demographic characteristics, parameters derived from age estimates are preliminary given the need to validate the periodicity of increment formation. Nevertheless, the results suggest that groupers in general are long-lived, slow-growing species that have low rates of natural mortality. The findings are important to fisheries management and conservation authorities as they support the contention that these species have a low resilience to exploitation and their populations may be particularly vulnerable to overfishing.

INTRODUCTION

Progress in understanding the dynamics of tropical fish populations has been hindered by the misconception that banding patterns do not form in the otoliths or other hard parts of reef fish due to a lack of seasonality in the tropics (Longhurst and Pauly, 1987). As a result, fisheries resource assessments in the southwest Indian Ocean region have been based predominantly on the analysis of length frequency data (eg., Sanders *et al.*, 1988). A principal constraint of length-based techniques is the inability of modal analyses to discriminate older age classes, especially for long-lived, slow-growing species, resulting in unreliable growth rate and longevity estimates (eg., Goeden, 1978; Langi, 1990).

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The assumptions that tropical fish have rapid continuous growth and short life spans has been dispelled by studies that have shown annual banding patterns in sagittal otoliths (see Fowler, 1995 for review). The utility of seasonally deposited increments for deriving growth rates, longevity and other key demographic characteristics has been demonstrated for representative species of families important in reef fisheries, eg: Lethrinidae (Pilling *et al.*, 2000); Lutjanidae (Newman *et al.*, 1996); Serranidae (Ferreira and Russ, 1992; Ferreira and Russ, 1994); and Scaridae (Lou, 1992; Choat *et al.*, 1996). While growth has been investigated for *Epinephelus fuscoguttatus* and *Variola louti* by Wright *et al.* (1985), longevity, natural mortality and other fundamental life history characteristics have yet to be established for some of the larger groupers such as *Epinephelus tukula*.

The Epinepheline groupers, family Serranidae and subfamily Epinephelinae, occur in shallow tropical and subtropical seas of the Indo-Pacific region. They are usually at the top of food chains playing a major role in the structure of coral-reef communities (Randall, 1987) and are relatively abundant on the reefs of Aldabra atoll (Teleki *et al.*, 2000). Since groupers are favored for consumption or sale in commercial and subsistence fisheries, they are commonly targeted by fishermen (Munro, 1983). Their aggressive nature and relatively large size make them more vulnerable to fishing gears (Munro and Williams, 1985) and aspects of their reproductive biology and demography predispose them to overexploitation (see Sadovy, 1996 for review). These factors may explain the sequential reduction in abundance of groupers on the Seychelles Bank to the northeast of Aldabra atoll over the last decade (Grandcourt and Cesar, 2002).

Reliable estimates of demographic characteristics such as growth and mortality rates are vital to the evaluation of fisheries resources. Given the declining status of these species and problems associated with the use of size-frequency data, age-based investigations are required in order to improve the integrity of stock assessments. In this context, objectives of this study were to establish age-based demographic parameters including size at age-specific growth rates, natural mortality rates, longevity, otolith growth rates and parameters of the von Bertalanffy growth function, assuming an annual pattern of growth increment formation. The absence of any significant fishery in the waters around Aldabra atoll presents a unique opportunity for the collection of these data, much of which is unavailable for the majority of the selected study species.

MATERIALS AND METHODS

Study Site and Species Selection

Aldabra is situated in the southwest of the exclusive economic zone of the Republic of Seychelles (9°24' S, 46°20' E), 420 km to the north of Madagascar (Fig. 1). Samples were obtained from locations around the perimeter of the atoll during a research cruise in December 2000. Representatives of the family Serranidae selected for sampling based on their relative abundance in the catch included: *Epinephelus fuscoguttatus*, *Epinephelus uultinotatus*, *Epinephelus polyphkadion*, *Epinephelus tukula*, *Plectropomus laevis* and *Variola louti*.

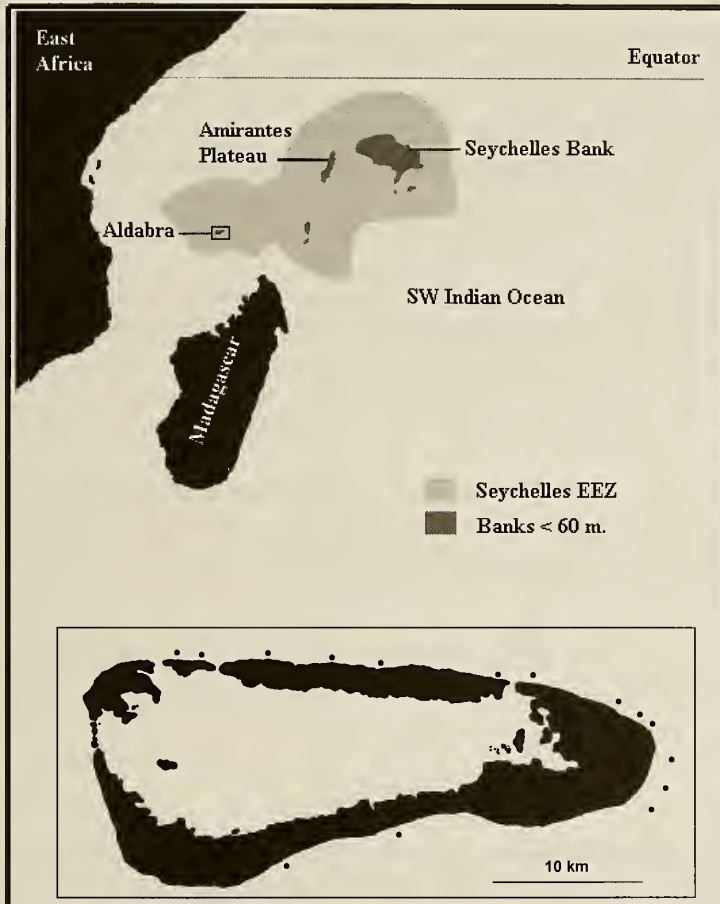


Figure 1. The position of Aldabra atoll in the southwest Indian Ocean, showing locations (●) from which fish were caught (insert).

Sampling and Otolith Processing

Fish were caught during December 2000 using hand lines with baited hooks set between 30 m. and 70 m. Total (L_T) and fork length (L_F) measurements were obtained using a measuring board and recorded to the nearest mm. As all samples were taken on completion of the research cruise when fish were landed, sex could not be determined as fish had been gutted and cleaned. Eviscerated weight was determined using an electronic balance and recorded to the nearest g. Sagittal otoliths were removed from samples, cleaned in water and stored dry in paper envelopes.

One of each pair of sagittae was weighed to the nearest 0.1 mg. The nucleus was then marked and the otolith embedded in epoxy resin. Resin blocks were mounted on glass slides using thermoplastic glue. Transverse sections 200 to 300 μm thick were made through the core using a low speed Buehler Isomet jewelry saw. Sagittal sections were ground using 400 grit wet and dry abrasive paper. Processing of otoliths was based on methods of Secor *et al.* (1991).

Increment counts in sectioned otoliths were made using a dissecting microscope and reflected light with a black field. Otoliths were read once by the author. Sections were smeared in immersion oil prior to examination in order to reduce scatter and improve contrast. In order to reduce bias, slides were coded so that no information relating to the size of the fish was available when increment counts were made.

Data Analyses

Growth. Growth was investigated by fitting the von Bertalanffy growth function (von Bertalanffy, 1938) to size and increment number data from otoliths. The von Bertalanffy growth function is defined as follows:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

Where L_t is length at time t , L_∞ is the asymptotic length, k is the growth coefficient and t_0 is the hypothetical time at which length is equal to 0. Because juvenile fish were under-sampled, the growth model was constrained through the origin ($t_0 = 0$) in order to obtain biologically tenable parameters.

Natural Mortality. Estimates of the annual instantaneous rate of natural mortality (M) were obtained for each species using the empirical equation derived by Hoenig (1983):

$$\ln(Z) = 1.46 - 1.01 \ln(t_{\max})$$

Where Z is the total mortality rate, which is analogous to M in an unexploited population, and t_{\max} is the age of the oldest fish, taken as the maximum number of increment counts in sagittal otolith sections.

Sagittal Weight-increment Number Relationships. Relationships between sagittal weights and numbers of increments observed were determined using least-squares linear regression with sagittal weight as the independent variable and increment number as the dependent variable. The regression equation ($y = b.x + a$) was fitted to sagittal weight and increment number data.

Length-weight Relationships. Parameters of the length-weight relationship were obtained by fitting the power function $W = a.L^b$ to length and weight data where: W is the weight, a is a constant determined empirically, L is the length and b is close to 3.0 for species with isometric growth. Because fish were sampled in a gutted state, the weight was raised by a factor of 1.15 to represent the ungutted condition. This value was derived from a subjective estimation of the weight of organs removed from the body cavity during gutting which occurred directly after capture.

RESULTS

Catch

A total of 5,390 kg of fish were caught on patch reefs around the periphery of Aldabra atoll. The catch was composed of nine species from six genera and four families (Table 1). While *Lutjanus bohar* was the most abundant species in terms of weight, representatives of the family Serranidae made up 61% of the total catch, 54% of which was sampled for length-weight measurements and otoliths. Sample sizes and size ranges for the study species were: *Epinephelus fuscoguttatus* ($n=26$, 49.5-76.7 cm L_T); *Epinephelus multinotatus* ($n=33$, 44.8-62.0 cm L_T); *Epinephelus polyphekadion* ($n=77$, 37.6-62.0 cm L_T); *Epinephelus tukula* ($n=62$, 72.3-128.4 cm L_T), *Plectropomus laevis* ($n=22$, 72.2-108.1 cm L_F); and *Variola louti* ($n=101$, 33.9-57.8 cm L_F).

Table 1. Total catch weights, sample weights and numbers for species caught around Aldabra atoll, December 2000.

Species	Catch (kg)	Sample weight (kg)	Number sampled
<i>Cheilinus undulatus</i>	88	0	0
<i>Epinephelus fuscoguttatus</i>	414	130	26
<i>Epinephelus multinotatus</i>	131	84	33
<i>Epinephelus polyphekadion</i>	613	193	77
<i>Epinephelus tukula</i>	1,486	875	62
<i>Lethrinus nebulosus</i>	67	0	0
<i>Lutjanus bohar</i>	1,941	0	0
<i>Plectropomus laevis</i>	383	272	22
<i>Variola louti</i>	267	228	101
Total	5,390	1,782	321

Otolith Structure

Transverse sections of sagittal otoliths showed defined structural increments consisting of alternating opaque and translucent bands when viewed with reflected light under low-power magnification (Fig. 2). Distances between bands became smaller from the core towards the outer edge of the otolith. The contrast of the banding pattern was variable between species. Opaque increments were most distinct in sagittal sections from representatives of the genus *Epinephelus*: *E. fuscoguttatus*, *E. multinotatus*, *E. polyphekadion*, *E. tukula* and less well defined in sections from *Plectropomus laevis* and *Variola louti*. The maximum number of opaque increments observed in sagittal otolith sections (considered to represent longevity) ranged from 15 for *V. louti* to 31 for *E.*

polyphekadion; other values obtained were 30 (*E. fuscoguttatus*), 27 (*E. multinotatus*), 26 (*E. tukula*) and 20 (*P. laevis*).

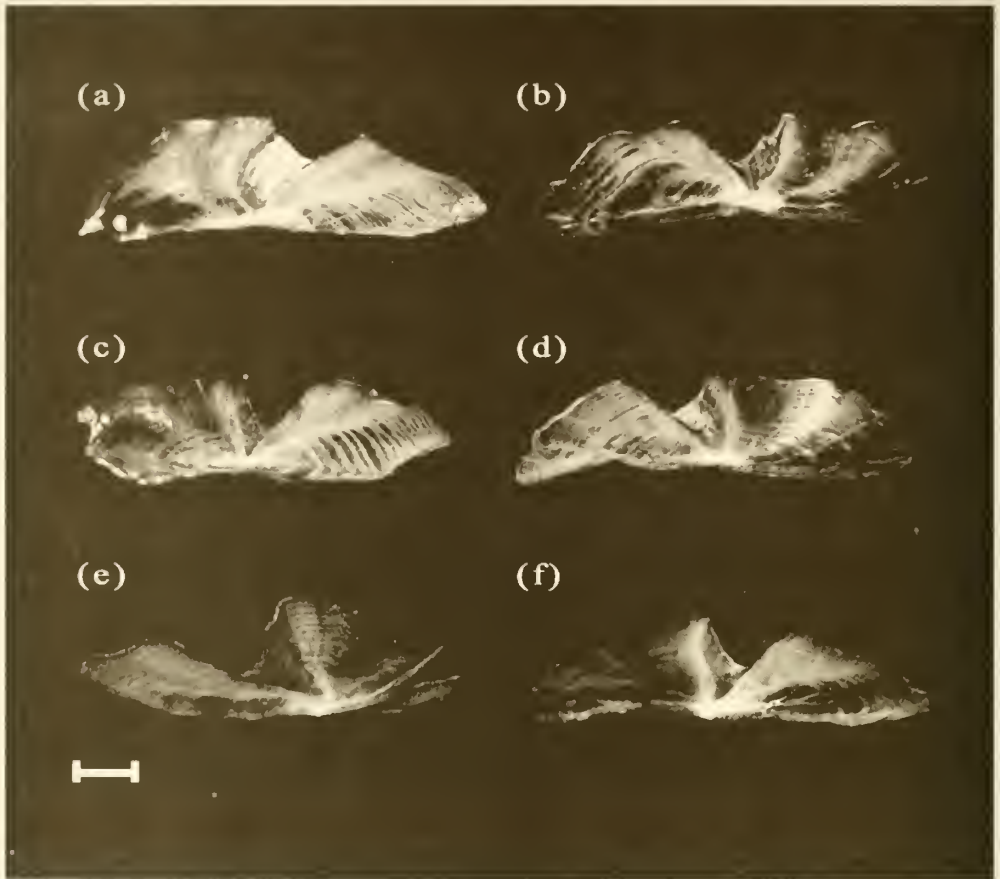


Figure 2. Photomicrographs of transverse sections through sagittal otoliths of six species of groupers collected at Aldabra atoll, December 2000: (a) *Epinephelus fuscoguttatus* (69.7 cm L_T); (b) *Epinephelus multinotatus* (49.6 cm L_T); (c) *Epinephelus polyphekadion* (52.6 cm L_T); (d) *Epinephelus tukula* (88.7 cm L_T); (e) *Plectropomus laevis* (102 cm L_T); (f) *Variola louti* (56.9 cm L_T). (Scale bar = 1 mm).

Growth

Relationships between fish size and number of increments in otolith sections were predominantly asymptotic in form (Fig. 3). The von Bertalanffy growth function provided a good fit to the data with coefficients of determination ranging from 0.74 for *E. tukula* and *V. louti* to 0.95 for *E. fuscoguttatus*. Parameter estimates of the growth coefficient (k) ranged from 0.13 for *E. tukula* to 0.48 for *V. louti*, with a mean of 0.24 for all species. Parameters of the von Bertalanffy growth function are summarized in Table 2.

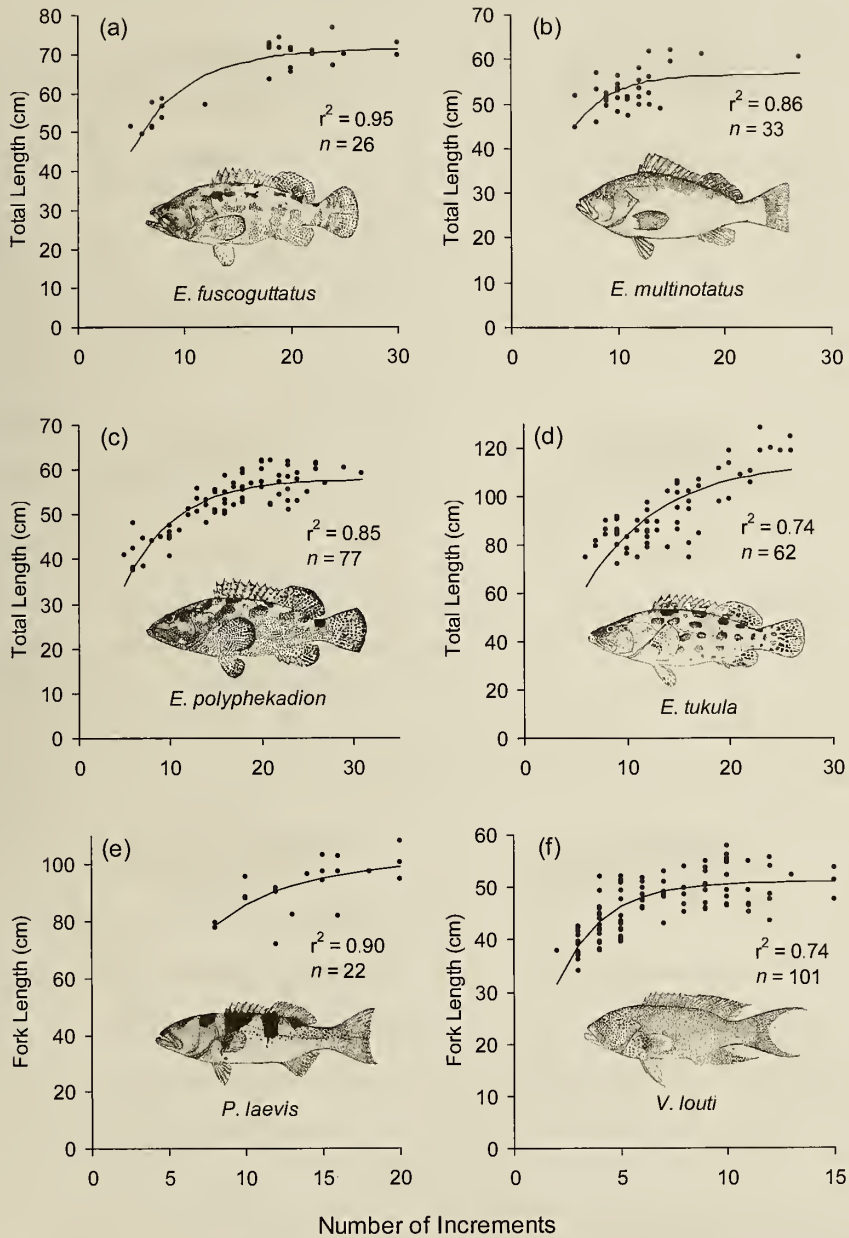


Figure 3. The von Bertalanffy growth function: $L_t = L_\infty (1 - e^{-k(t-t_0)})$ fitted to the relationship between size and increment number, the model has been constrained through the origin ($t_0 = 0$). (a) *Epinephelus fuscoguttatus*, (b) *Epinephelus multinotatus*, (c) *Epinephelus polyphekadion*, (d) *Epinephelus tukula*, (e) *Plectropomus laevis*, (f) *Variola louti*.

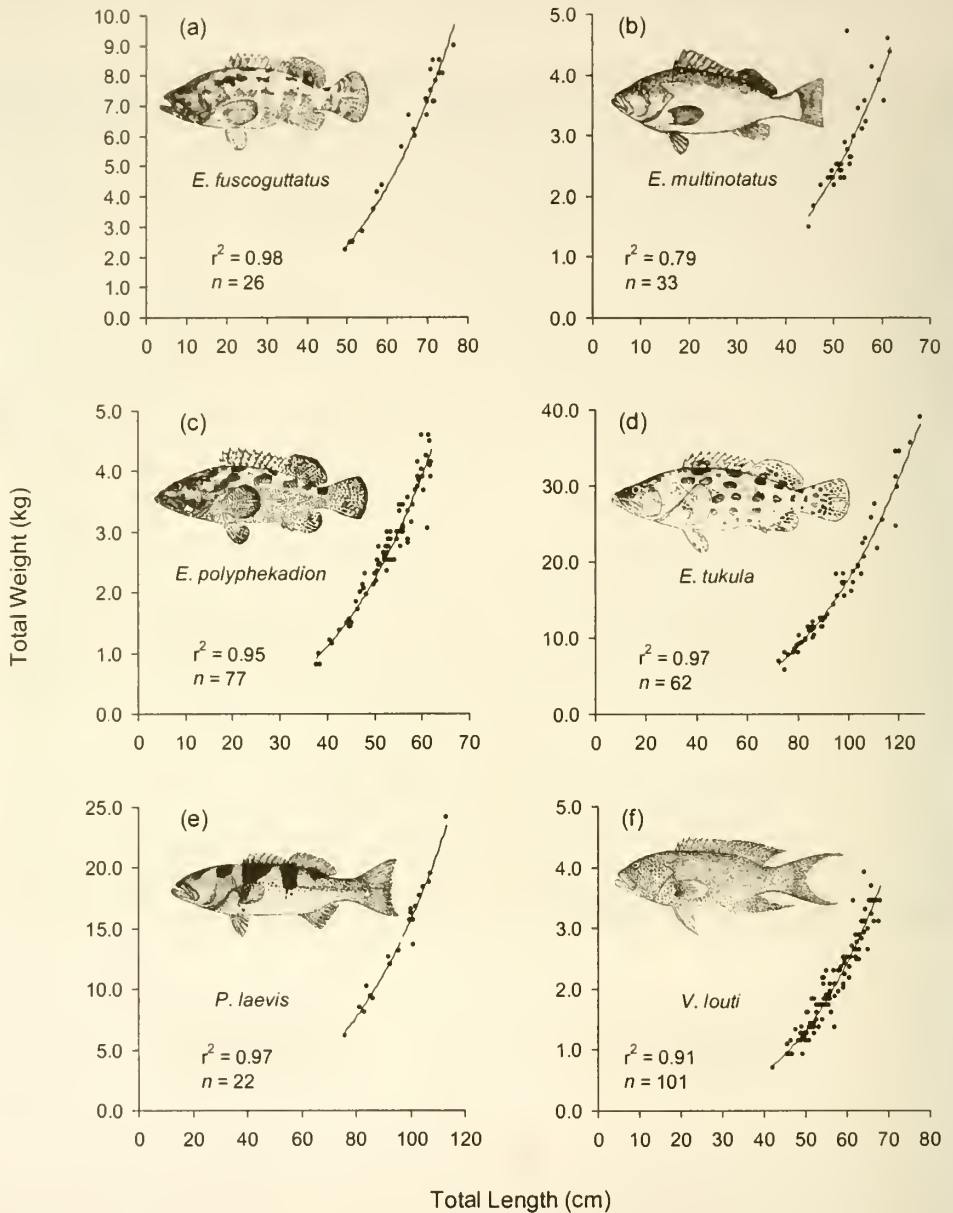


Figure 4. Length-weight relationships showing the power function: $y = a \cdot x^b$ fitted to the data. (a) *Epinephelus fuscoguttatus*: $y = 6.0^{-6} \cdot x^{3.28}$ (b) *Epinephelus multinotatus*: $y = 2.0^{-5} \cdot x^{3.01}$ (c) *Epinephelus polyphekadion*: $y = 1.0^{-3} \cdot x^{3.11}$ (d) *Epinephelus tukula*: $y = 1.0^{-5} \cdot x^{3.07}$ (e) *Plectropomus laevis*: $y = 6.0^{-6} \cdot x^{3.20}$ (f) *Variola louti*: $y = 3.0^{-6} \cdot x^{3.35}$.

Table 2. Parameters of the von Bertalanffy growth function $L_t = L_\infty (1 - e^{-k(t-t_0)})$ and maximum fish lengths (L_{\max}) recorded for six species of groupers collected at Aldabra atoll, December 2000. Note: as the model has been constrained through the origin, $t_0 = 0$ for all species. All lengths are total (L_T) except those of *Plectropomus laevis* and *Variola louti* for which fork lengths (L_F) are given.

Species	k	L_∞ (cm)	L_{\max} (cm)
<i>Epinephelus fuscoguttatus</i>	0.20	71.3	76.7
<i>Epinephelus multinotatus</i>	0.27	57.0	62.0
<i>Epinephelus polyphkadion</i>	0.18	57.9	62.0
<i>Epinephelus tukula</i>	0.13	114.9	128.4
<i>Plectropomus laevis</i>	0.19	101.5	108.1
<i>Variola louti</i>	0.48	51.0	60.0

Natural Mortality

Annual instantaneous rates of natural mortality derived using the Hoenig (1983) empirical equation ranged from 0.13 yr^{-1} for *E. polyphkadion* to 0.28 yr^{-1} for *V. louti* (Table 3). The mean natural mortality rate for all species was 0.18 yr^{-1} .

Table 3. Estimates of annual instantaneous rates of natural mortality (M) derived from the Hoenig (1983) empirical equation for six species of groupers collected at Aldabra atoll, December 2000.

Species	Natural mortality rate ($M \text{ yr}^{-1}$)
<i>Epinephelus fuscoguttatus</i>	0.14
<i>Epinephelus multinotatus</i>	0.15
<i>Epinephelus polyphkadion</i>	0.13
<i>Epinephelus tukula</i>	0.16
<i>Plectropomus laevis</i>	0.21
<i>Variola louti</i>	0.28

Length-Weight Relationships

The length-weight relationship ($W = a.L^b$) provided a good fit to length and weight data for all species (Fig. 4). Values of the coefficient of determination ranged from 0.79 for *E. multinotatus* to 0.98 for *E. fuscoguttatus*. Values of b ranged from 3.01

for *E. multinotatus* to 3.35 for *V. louti*, and were close to 3.0 for all species examined indicating that isometric growth occurs in these groupers.

Sagittal Weight-Increment Number Relationships

Linear relationships between sagittal weights and increment numbers indicated that otoliths increased in mass at a constant rate throughout the life of all species (Table 4).

Table 4. Parameters of the regression equation and coefficients of determination derived from the relationships between otolith weight and the number of increments observed in sagittal otolith sections for six species of groupers collected at Aldabra atoll, December 2000.

Species	<i>a</i>	<i>b</i>	<i>r</i> ²
<i>Epinephelus fuscoguttatus</i>	2.53	60.34	0.91
<i>Epinephelus multinotatus</i>	1.27	64.51	0.68
<i>Epinephelus polyphekadion</i>	0.06	54.23	0.76
<i>Epinephelus tukula</i>	3.71	38.29	0.80
<i>Plectropomus laevis</i>	2.76	95.21	0.57
<i>Variola louti</i>	0.67	85.32	0.72

DISCUSSION

Due to their importance in tropical fisheries around the world (Ralston, 1987), a number of studies have focused on the age and growth of representatives of the family Serranidae, in particular on members of the subfamily Epinephelinae, commonly known as groupers. These investigations have confirmed the utility of seasonally deposited increments in sagittal otoliths for estimating demographic parameters of these fishes. Age structures, growth rates, longevity estimates and other population characteristics have been established for a range of exploited grouper species (see Manooch, 1987; Munro and Williams, 1985 for reviews). This study extends the geographic and taxonomic range for which growth increments in sagittal otoliths have been observed for groupers and further demonstrates their utility in establishing key population parameters for the species examined.

Formation of alternating translucent and opaque growth increments in fish otoliths has been associated with a variety of factors including seasonal variations in water temperature, photoperiod, feeding, and reproduction (Manickchand-Heileman and Philip, 2000; Moe, 1969; Morales-Nin and Ralston, 1990; Panella, 1980; Reay, 1972). High amplitudes of seasonal growth oscillations observed for *Epinephelus chlorostigma* were attributed to the annual variation in water temperature of about 10 °C caused by the

seasonal presence of a thermocline on the Seychelles Bank (Sanders *et al.*, 1988). It is plausible that seasonal growth oscillations associated with rhythmic annual fluctuations in environmental conditions could be the causal factor of alternating opaque and translucent bands observed in sagittal otoliths of the Serranids examined in this study.

With exception of *V. louti*, all the study species had low values of k , with parameters of the growth coefficient of the von Bertalanffy growth function ranging from 0.13 for *E. tukula* to 0.27 for *E. multinotatus*. While the relationships between size and the number of increments were predominantly asymptotic in form, the growth of *E. tukula* was largely indeterminate as size increased with age throughout the lifespan, resulting in the large maximum size that was reached by this species. Conversely, the growth of *V. louti* was highly asymptotic in form with the majority of growth being achieved during the first six years of life. As the growth coefficient describes the rate at which the asymptotic length is approached, the high value of k by comparison with the other species was associated with its smaller asymptotic size and, in particular, reduced longevity, which is about half that of the other Serranids examined. The mean value of the growth coefficient (0.24) for all species in the present study compared well to the mean value of 0.22 reported by Manooch (1987) for 31 species of Serranidae.

Growth coefficients have previously been reported for *E. fuscoguttatus* and *V. louti* by Wright *et al.* (1985). Their value of k for *E. fuscoguttatus* (0.20) is the same as the estimate obtained here. Conversely, the growth coefficient for *V. louti* of 0.18 was considerably less than the estimate obtained here (0.48). The large difference in k for *V. louti* could be due to methodological differences as the previous estimate was derived using size frequency data. Given the inability of modal analyses to discriminate older age classes, especially for long-lived, slow-growing species, the growth parameter estimates obtained here are probably more reliable in this context. The growth coefficient estimate for *E. multinotatus* of 0.27 occurring in the northern Arabian Gulf (Mathews and Samuel, 1987), which was also derived from sections of sagittal otoliths, was the same as the estimate obtained in this study. Nevertheless, growth parameters could have been improved with larger sample sizes that covered the entire size range, especially those for *E. fuscoguttatus*, *E. multinotatus* and *P. laevis* for which sample sizes were small. Additionally, given the possibility that growth may differ among sexes, particularly as the species investigated are protogynous hermaphrodites, sex-specific growth characteristics should be determined in future studies.

Estimates of the annual instantaneous rates of natural mortality for *V. Louti* and *E. fuscoguttatus* of 0.48 yr^{-1} (Wright *et al.*, 1985) were considerably greater than the estimates obtained here (0.28 and 0.14 yr^{-1} respectively). Nevertheless, the values estimated in the present study are in line with the trend for Serranids which in general have low rates of natural mortality (eg., Manooch, 1987).

Maximum ages for Serranid species determined using otolith microstructures range from 9 yrs. for *E. cruentatus* (Nagelkerken, 1979) to 41 yrs. for *Mycteroperca interstitialis* (Manickchand-Heileman and Philip, 2000). The provisional longevity estimates obtained in the present study, based on the maximum number of putative annuli (between 15 yrs. and 31 yrs.) are within the range estimated for groupers from other areas and suggest that the selected species examined from Aldabra atoll are generally long-lived. As with the growth rate, the maximum age of *E. multinotatus* in the northern

Arabian Gulf of 28 yrs. estimated by Mathews and Samuel (1987) compares well with the maximum obtained here (27 yrs.). Life history characteristics can be used to classify the resilience of a species to fishing pressure (Musick, 1999) and the level of productivity within the population. Growth parameters and longevity estimates derived here suggest that the Epinepheline groupers examined have low resilience to exploitation. This would explain the sequential reduction in abundance of groupers on the Seychelles bank that has occurred over the last decade (Grandcourt and Cesar, 2002) and demonstrates the need for a precautionary approach to the management of these species.

Parameters derived from length-weight relationships have utility in fishery independent methods of biomass estimation such as underwater visual census surveys (eg., Jennings *et al.*, 1995). These methods improve assessments of reef-fishery resources (Connell *et al.*, 1998) and reporting length-weight relationships is especially important for species for which no published parameter estimates exist (Manooch, 1987). Given the relative abundance of Serranid species on the reefs of Aldabra atoll (Teleki *et al.*, 2000), it is anticipated that the parameters provided here will be used in biomass estimation and monitoring studies of these fishes in the future.

The relationships between otolith weights and increment numbers indicate that the otoliths of the species examined grow throughout the life of the fish, fulfilling one of the fundamental criteria required for aging (Fowler and Doherty, 1992). However, structures used for aging should be shown to correspond to a regular time scale of known duration (Beamish and McFarlane, 1983; Fowler and Doherty, 1992). Validation studies have confirmed the annual nature of increment formation in the otoliths of *Lethrinus mahsena* on the Seychelles Bank using oxytetracycline injection/mark-recapture (Grandcourt, 2002) and marginal increment/edge analysis (Pilling *et al.*, 2000). While this study has confirmed the presence of discernible banding patterns, further work is required to authenticate the periodicity of increment formation. The results are nevertheless important in that they offer an insight into the demographic characteristics of these species from populations that have not been modified by intensive exploitation. Moreover, the patterns of age, growth, longevity and natural mortality observed adhere to the general trends for other Epinepheline groupers across the Indo-Pacific.

This study confirms the presence of banding patterns in the sagittal otoliths of a selection of Serranid species, extending the taxonomic and geographical range over which such observations have been made. Furthermore, evidence is provided suggesting that *Epinephelus fuscoguttatus*, *Epinephelus multinotatus*, *Epinephelus polyphkadion*, *Epinephelus tukula* and *Plectropomus laevis* are long-lived, slow-growing species that have low rates of natural mortality. These results are important to fisheries management and conservation authorities as they support the contention that groupers have a low resilience to exploitation and their populations may be particularly sensitive to fishing.

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NO. 540

**DIEL CHANGES IN NUMBERS OF SEABIRDS OCCUPYING CAYS ON THE
SWAIN REEFS, GREAT BARRIER REEF, AUSTRALIA**

BY

MENNA JONES, HAROLD HEATWOLE, AND PAUL O'NEILL

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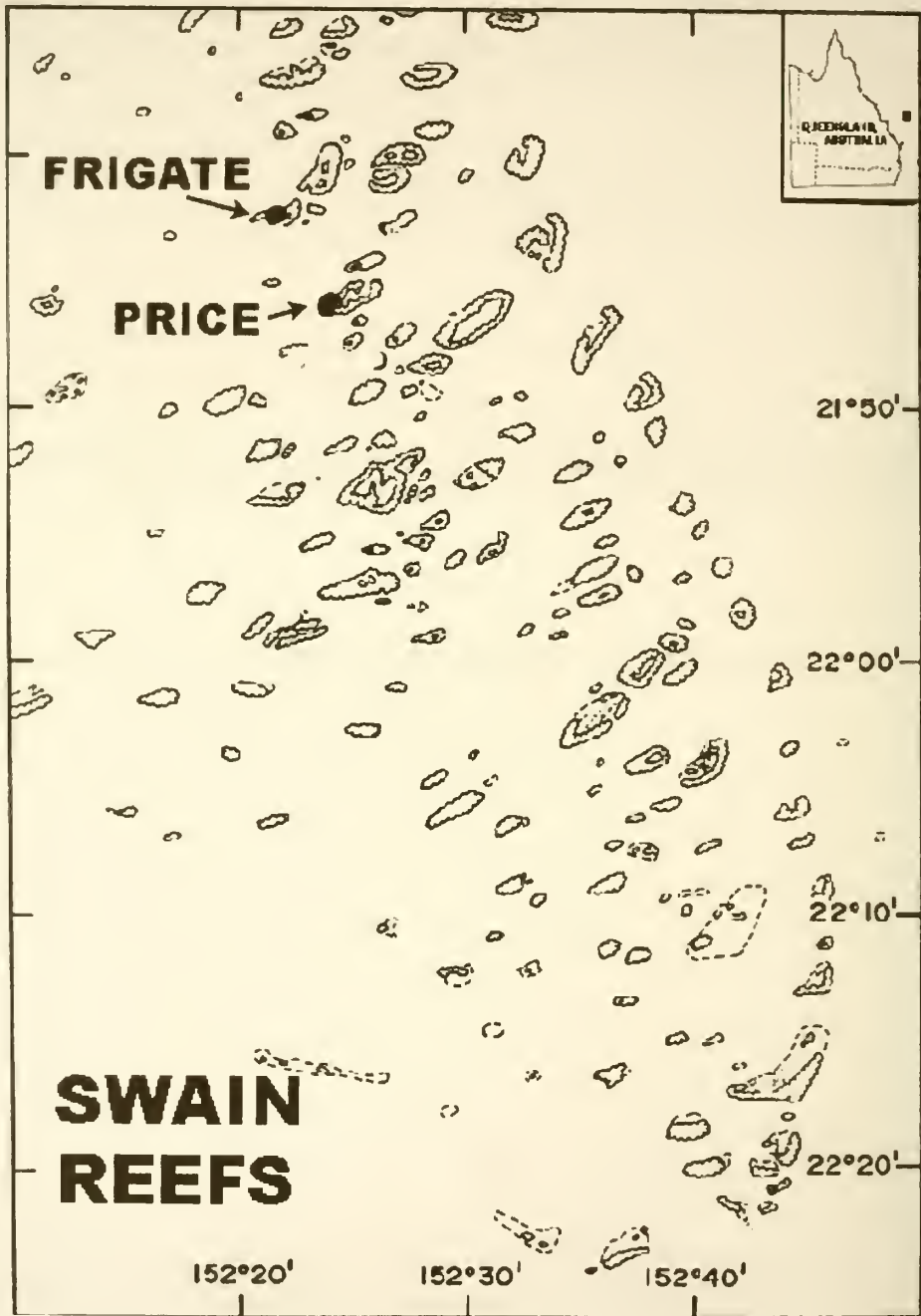


Figure 1. Map of the Swain Reefs showing Frigate and Price Cays. The black rectangle in the small inset in the upper right hand corner shows the location of the Swain Reefs in relation to Australia.

DIEL CHANGES IN NUMBERS OF SEABIRDS OCCUPYING CAYS ON THE SWAIN REEFS, GREAT BARRIER REEF, AUSTRALIA

BY

MENNA JONES,¹ HAROLD HEATWOLE,² AND PAUL O'NEILL³

ABSTRACT

Seabirds were counted during four 24-hour periods, two in summer and two in winter, on each of two cays (Price Cay and Frigate Cay) in the Swain Reefs, Great Barrier Reef, Australia. There were six breeding species of seabirds and 13 nonbreeding ones. Each species showed its own pattern of diel change in number of individuals on the islands, some being more numerous by day, others by night. For a given species, there were differences between seasons and between islands.

INTRODUCTION

There is a kaleidoscope of both positive and negative ecological interactions between seabirds and coral cays on the Great Barrier Reef (Heatwole, 1976, 1989, 1990, 1994; Heatwole and Saenger, 1989; Heatwole and Walker, 1989). Islands provide roosting and nesting platforms, and the structural variability of insular vegetation meets the nesting requirements for an array of bird species of varying habitat requirements (Heatwole *et al.*, 1981).

Seabirds are a major link in the nutrient cycling of coral cays. They capture organic matter in the form of fish and marine invertebrates over a wide expanse of sea and concentrate it, as guano, carrion and food scraps, on the cays thereby permitting the establishment of a scavenger-based food chain of terrestrial animals (Heatwole, 1971) and enriching the soil to levels allowing establishment of plants not otherwise able to colonize. Birds also act as agents for dispersal of many plant species to cays. Finally, birds destroy plants by trampling and overenrichment with nutrients. Because of this multiplicity of interactions, assessment of the size and variability in bird populations is an important contribution toward an understanding of insular ecosystems. Such assessment is an essential ingredient in the formulation of management plans for the coral cays of the Great Barrier Reef, many of which are threatened with ecological deterioration due to escalating encroachment by humans.

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As part of a long-term investigation of the community ecology of the Swain Reefs, Great Barrier Reef, periodic daytime counts of seabird populations were conducted on seven islands over a number of years (Heatwole *et al.*, 1996; O'Neill *et al.*, 1996). These were thought to be underestimates because at any one time a proportion of the population would be foraging at sea. Furthermore, some seabirds forage by night (Martin, 1990) and interspecific differences in foraging schedules could lead to variation in species composition and/or relative abundances among species over the diel cycle and seasonally. Appropriate corrections may need to be applied to data obtained diurnally. Indeed, Hunter and Morris (1976) suggested that restriction of observations to diurnal periods was inappropriate for studies of seabird colonies in view of the probable importance of nocturnal events. The present study was designed to: (1) describe the diel pattern of change in numbers of seabirds occupying two cays; and (2) assess whether that pattern changed seasonally.

STUDY AREA AND METHODS

Counts of all species of birds were carried out at varying intervals, but usually every four hours over part or all of the diel cycle. Two islands, Frigate Cay and Price Cay, each were investigated both in summer (January) and in winter (July). Observations on 28 January 1988 were carried out five days before the full moon, and those on 22 January 1987 seven days after the full moon. The two observation periods in July were conducted on nights two-to-three days from the dark of the moon.

Both islands are small, oblong cays of coral sand, each located on its own patch reef in the Swain Reefs, a complex lying in the Coral Sea at the southern end of the Great Barrier Reef about 200 km northeast of Cape Clinton on the central Queensland coast (Fig. 1). Frigate Cay is the second largest of the seven major cays in the Swain Reefs and has an area of 35,100 m² with a vegetated center of about 16,900 square meters. Price Cay lies 6 km to the southeast of Frigate Cay. It is 29,700 m² in area with the vegetated part 10,800 m². Except for a few shrubs of Octopus Bush, *Argusia argentea*, the vegetation mostly is low (30 cm or less) and consists primarily of *Boerhavia diffusa*, a perennial herb, and the grasses, *Lepturus repens* and *Thuarea tomentosa*. Plant cover on the vegetated part of Frigate Cay is 60-90%; plants are more sparsely distributed on Price Cay (cover 50-60%).

Upon arrival at an island, before anyone else was allowed ashore, a party of four persons circled the island in a dinghy, one person to operate the motor, one to record data, and two with binoculars to make independent counts of birds on the beaches. When those counts were completed, the party landed and completed the census by walking slowly from one end of the island to the other and counting the birds in the central, vegetated part. Counts for each section of beach or central area were compared between the two observers. Small differences between them were averaged. Large discrepancies (rare) resulted in a recount. Nocturnal censuses differed only by use of headlights to make counts and birds on the beach were counted from the island rather than from a dinghy.

RESULTS AND DISCUSSION

Total bird counts (Fig. 2) represent the composite of the patterns of abundance of the various component species. Total numbers were higher on both cays in the Austral summer than in winter and for both seasons higher on Frigate than on the smaller island, Price. The same applies to some of the counts of individual species described below. In summer, the total number of birds was highest at night or in early morning and decreased during the day. The changes were less marked in winter. On Frigate there was a decrease from the earliest count, but for the rest of the day numbers fluctuated at levels below 1000 birds. On Price, numbers remained relatively stable all day.

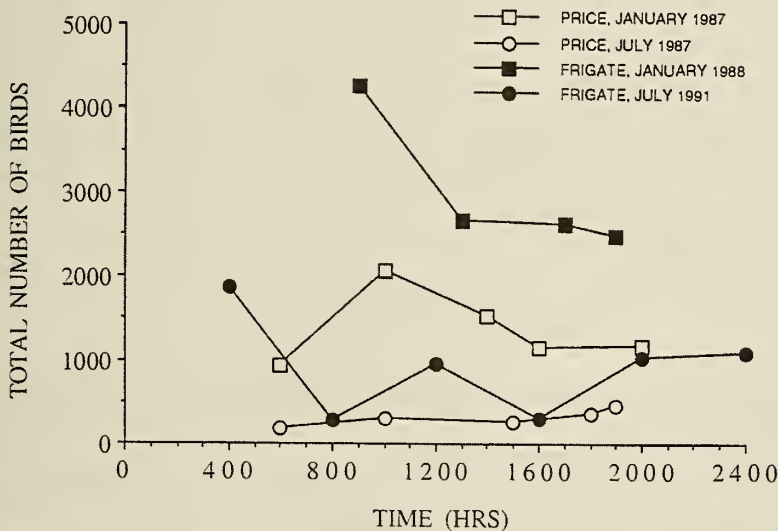


Figure 2. Total numbers of seabirds counted at different times of day and at different seasons on Price Cay and Frigate Cay.

The contributions to these patterns of each of the six species that nested during one or both seasons are now examined individually.

The Brown Booby (*Sula leucogaster*)

The numbers of Brown Boobies showed marked diel changes in summer (Fig. 3), their time of peak nesting in the Swains (Table 1). Numbers on Frigate were relatively low during the day as partners shared nesting duties, alternating between tending eggs of young and fishing at sea. With the return of many of the foraging birds in the evening, including unmated individuals that aggregated on the beach, and occupancy of the nest site by both members of mated pairs, numbers more than doubled (Fig. 3). In the winter, the resident population was smaller and the nocturnal increase was slight. On Price, there was even a decline in numbers in late evening. The decrease in numbers of Brown Boobies at night on Price Cay may be linked to the unusually high nocturnal increase

Table 1. Number of birds of breeding species roosting on vegetation compared to total numbers on cays during 24-hour censuses. Data on number of nests derived from Jones and Heatwole (in preparation).

			NUMBER OF BIRDS ROOSTING ON VEGETATION / TOTAL NUMBER OF BIRDS																
LOCATION/DATE	SPECIES/TIDE	N.O. OF NESTS	0400	0600	0800	0900	1000	1200	1300	1400	1500	1600	1700	1800	1900	2000	2400		
PRICE CAY 22 Jan '87	Brown Booby	200	119/210	219/416						212/290	121/135						144/356		
	Masked Booby	5	258/299	256/2						11/22	6/9						7/159		
	Silver Gull	0	0/22	2/32						3/19	14/26						1/1		
	Crested Tern	0	0/57	300/354						353/456	404/536						1/56		
	Common Noddy	85	250/295	400/580						310/332	922/36						600/660		
PRICE CAY 23 July '87*	Bridled Tern	8	5/5	40/40						2/26	18/18						156/156		
	STATE OF TIDE		Falling	Low						Rising	High						Falling		
	Brown Booby	0	1/109	Low							2/114						13/45		
	Masked Booby	24	51/53	6/11						19/19	High						55/165		
	Silver Gull	1	0/12	26/31						10/14							49/92		
FRIGATE CAY 28 Jan '88	Crested Tern	0	0/1	0/7						0/48							0/0		
	Common Noddy	2	0/0	0/20						2/13							0/0		
	Bridled Tern	0	6/6	7/37						0/0	0/0						315/315		
	STATE OF TIDE		Rising	High						Low							0/0		
	Brown Booby	79	119/232														Rising		
FRIGATE CAY 14 July '91**	Brown Booby	11	15/30	96/261						11/23/1496	Low						High		
	Silver Gull	0	0/15	10/16						96/261							60/20		
	Crested Tern	0	0/68	2/30						10/16							0/19		
	Common Noddy	603	930/1150	0/81						2/30							0/0		
	Bridled Tern	19	171/542	75/48						1123/1496							0/18		
FRIGATE CAY 14 July '91**	STATE OF TIDE		High	Falling													Falling		
	Brown Booby	56***	130/149	96/184						370/1300							197/207		
	Masked Booby	42***	172/258	68/74						657/1006							82/124		
	Silver Gull	***	117/139	2/7						99/285							113/120		
	Crested Tern	***	0/3	0/57						High							0/0		
FRIGATE CAY 15 July '91***	Common Noddy	***	0/1553	0/311													0/1		
	Bridled Tern	***	0/0	0/0													0/18		
	STATE OF TIDE		0/0	0/0													0/0		

*Observations at 0600 and 1000 hours were made on 24 July

**Observations at 0400 and 0600 hour made on 15 July

***Search for nests was not as thorough as on previous occasions because of gulls following humans and threatening nests. Where values are listed, they are minimum ones.

on nearby Frigate Cay high nocturnal increase on nearby Frigate Cay. Perhaps for this species, Frigate has better nocturnal roosting habitat for nonbreeding birds, e.g., broader beaches, and therefore at night attracts some of the individuals from Price.

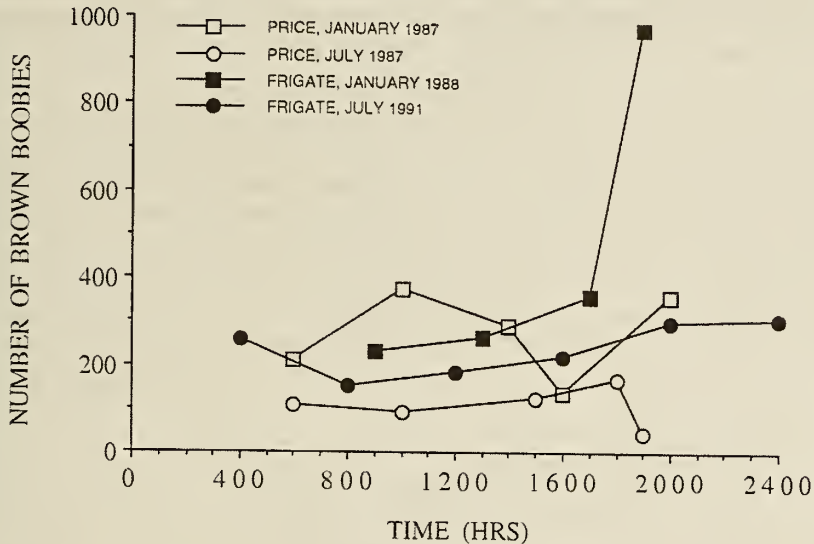


Figure 3. Numbers of Brown Boobies counted at different times of day and at different seasons on Price Cay and Frigate Cay.

The Masked Booby (*Sula dactylatra*)

The numbers of Masked Boobies were higher on Price during the Austral summer than in winter but the opposite was true for Frigate. In winter, Frigate had more birds than did the smaller island, Price, but this was reversed in summer. In both seasons the total number of birds tended to be higher at night and dwindle during the day to rise again after 1600 hours. These changes were less marked in the season with the lesser number of birds (winter on Price and summer on Frigate). Breeding of the Masked Booby in the Swains peaks in winter rather than in summer (Table 1; note that these results differ from those of King, 1993). A large number of nonbreeding individuals had assembled on Frigate in summer and, because few of them were attending nests at that time of year, numbers were low on the island by day but many returned in the evening from foraging at sea and were on the island at night (Fig. 4). Frigate had more Masked Boobies during the season of lowest breeding (summer) than during the winter peak of breeding, suggesting it may be more suitable as a roosting station than as a breeding ground. The opposite is true for Price where numbers were highest at the winter breeding peak. This species favors bare sand for nesting and the more open vegetation on Price may make a better breeding habitat than the denser vegetation on Frigate.

When Masked Booby chicks are small, one parent attends them during the day while the other forages. Radiotracking shows that adults do not forage at night although part of the return trip may take place after dark (Anderson and Ricklefs, 1992). Most delivery of food to young by returning adults occurs during the two-hour period preceding nightfall or just after dark (Anderson and Ricklefs, 1992). Accordingly, adults returning with food and then remaining on land accounted for the net accumulation of birds on the islands after 1600 hrs (Fig. 4).

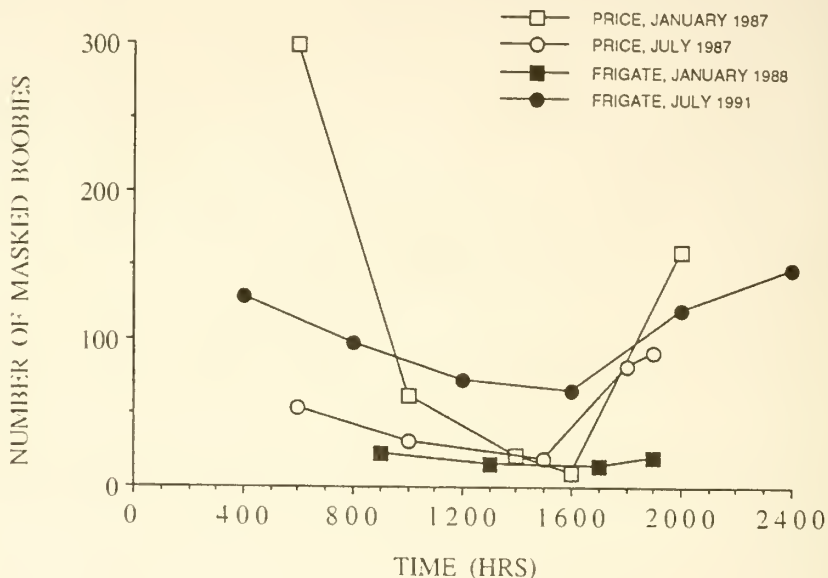


Figure 4. Numbers of Masked Boobies counted at different times of day and at different seasons on Price Cay and Frigate Cay.

An accumulation of birds at night in summer questions the validity of the migratory and/or seasonally dispersive behavior usually reported for the species (Marchant and Higgins, 1990). Analysis of 10 years of mark-recapture data for both Masked and Brown Boobies at the Swain Reefs (O'Neill *et al.*, 1996) suggests that it is largely the young birds that disperse and that fidelity to breeding sites is strong.

Bird numbers were not related to the state of the tide in either summer or winter (Table 1), probably because Masked Boobies forage at greater distances at sea (Nelson, 1970; Anderson and Ricklefs, 1987) and would be less affected by tides than would inshore feeders such as some terns (see Hulsman and Smith, 1988; Domm and Recher, 1973). Birds left the island progressively during the day so numbers reached their lowest value just prior to the mass return after 1600 hrs (Fig. 4).

The Silver Gull (*Larus novaehollandiae*)

Gulls were present on the islands in greater numbers by day than by night. Indeed, during much of the night no gulls were present at all and must either have gone to sea or moved to a different island to roost. Alternatively, they may have been disturbed by the researchers before detection and may have flown to another island. Silver Gulls were found to be very sensitive to human disturbance at night during banding activities (M. Jones, personal observations).

Generally, numbers gradually increased during the day and then declined again toward evening (Fig. 5). The gulls were exceptional in consistently having as large a population on Price Cay as on Frigate Cay. On both cays, numbers in winter were lower than in summer, perhaps reflecting differences in their general abundance in the Swains at these times of year. Silver Gulls move among islands and between mainland and islands, tracking temporary food sources (Walker, 1988). They are predators of eggs and small chicks at tern and booby colonies (Walker, 1988) and consequently may have been attracted to these cays by the summer peak of breeding of terns and Brown Boobies (Table 1; Figs. 3, 5-7).

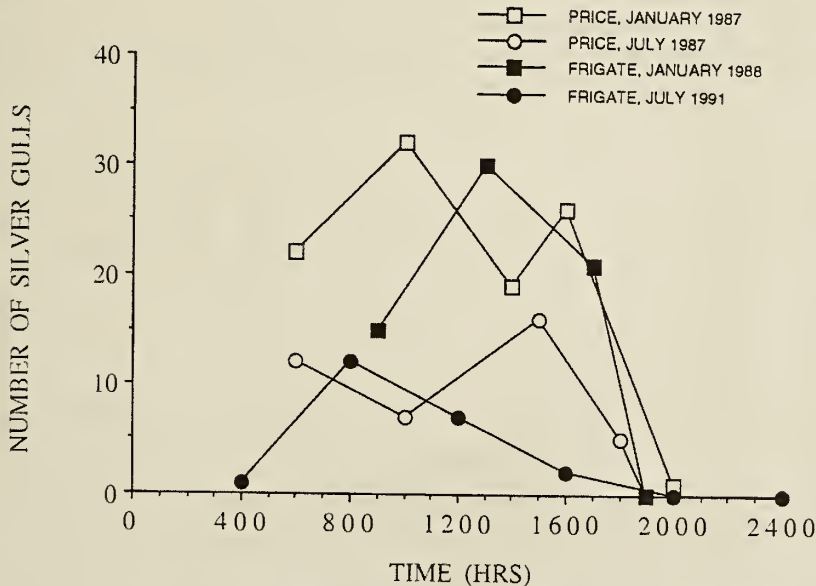


Figure 5. Numbers of Silver Gulls counted at different times of day and at different seasons on Price Cay and Frigate Cay.

Gulls were mostly scattered around the beach, singly or in twos and threes. This distribution may have provided them good vantage points from which to view birds returning with fish to feed their chicks (Hulsman, 1976). The exceptions were aggregations of gulls in the vegetated zone in the middle of the afternoon, the hottest

part of the day (Table 1). On Price in January and July 1987 and on Frigate in January 1988, such aggregations coincided with nesting species (Brown Boobies and Common Noddies in summer and Masked Boobies in winter) (Figs. 3-5, 7) having large numbers away from nests while foraging at sea. All eggs and small chicks of all nesting seabirds and the older chicks of small larids are vulnerable to predation by gulls.

The Crested Tern (*Sterna bergii*)

Unlike the other breeding species, Crested Terns nested in dense, localized colonies and roosted in large aggregations. They, like the gulls, were present during the day but absent, or in low numbers, at night (Fig. 6). Again, this may be because nonbreeding terns leave an island in response to disturbance by lights. The roosting pattern closely followed the tidal cycle with terns resting on the island during high tide. Hulsman (1974, 1977) found similar behavior in Crested Terns on One Tree Island. Crested Terns forage on shallow reefs close to the islands (Diamond and Prys-Jones, 1986). The resident population was much larger on Price Cay in January than at other times or places because about 500 terns were establishing a breeding colony. They were settling tenaciously in one patch on the edge of the vegetated zone but no eggs had been laid. Crested Terns will nest year-round in the Swains although fewer nest in winter (Walker and Jones, 1986). Gulls are an ever-present threat to eggs and nestlings by day and the terns may tend to feed at night when it is safer to leave their nests.

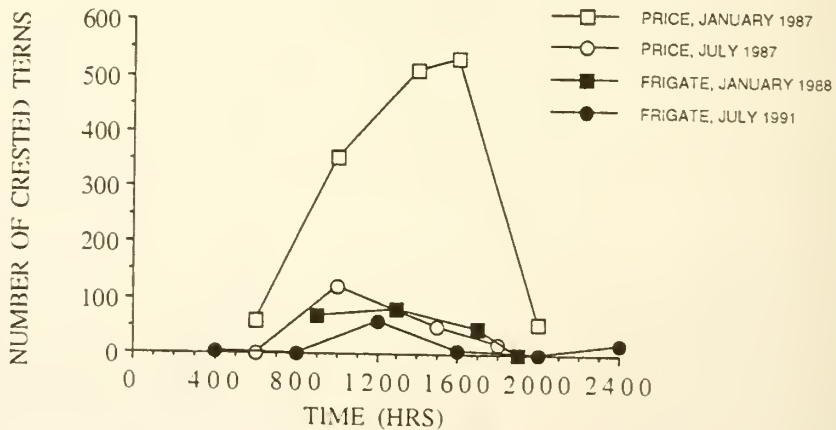


Figure 6. Numbers of Crested Terns counted at different times of day and at different seasons on Price Cay and Frigate Cay.

The Common Noddy (*Anous stolidus*)

Common Noddies are especially easy to count at night. Unlike many other larids, they do not fly away when spotted with dim light. Numbers were higher on both cays during summer breeding (peak nesting is November to March) than in winter, with many more birds and nests on Frigate than on Price during both seasons (Fig. 7), probably because Frigate provides denser vegetation in which nests can be concealed (Jones, unpublished). Common Noddies foraged in the early morning and afternoon and rested on the island in the hot, middle part of the day (Fig. 7). In contrast to many terns (Hulsman, 1974, 1977), numbers during the day were not related to the tidal cycle. This pattern of activity is similar to that of the closely related Black Noddies (*Anous minutus*) on One Tree Island (Hulsman, 1977). Common Noddies showed a distinct preference for roosting in the vegetation zone. For daylight roosting, this trend was more marked in the summer nesting season than in winter. Nearly all birds present at night on Price roosted in the vegetation during both seasons. Large numbers of nonbreeding Common Noddies roosted on the beach on Frigate in summer, although all breeding birds roosted at their nests (Table 1).

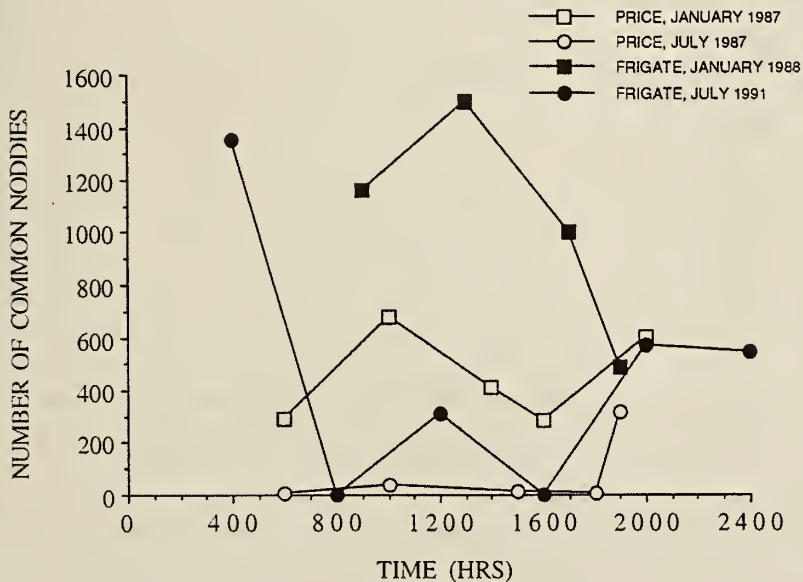


Figure 7. Numbers of Common Noddies counted at different times of day and at different seasons on Price Cay and Frigate Cay.

The Bridled Tern (*Sterna anaetheta*)

Bridled Terns were not present in winter but bred on both islands during summer (Fig. 8). Like Common Noddies, they were easy to see at night and generally stayed still when spotted by dim light. There were relatively few nests on either island but the large number of roosting birds on Frigate in summer (Table 1) suggests that they were preparing to nest there. In the absence of other shelter commonly used by this species for nesting elsewhere (e.g., rock crevices, under dead turtles), Bridled Terns on the cays of the Swain Reefs create small blind tunnels under the dense vegetation and lay their eggs there. This habit could significantly reduce the chance of gulls finding the nests. The denser vegetation on Frigate provided more suitable nesting habitat than occurs on Price. Numbers on Frigate were lower during the day when birds were away foraging, but increased dramatically at night. Numbers on Price were low at all times and actually decreased at night. Perhaps birds use Price as a daytime roost while fishing but roost at night on Frigate where they are preparing to nest. However, with only one exception, there were always more birds present in the vegetated zone of both islands than there were on nests (Table 1). There was a distinct preference for roosting in the vegetated zone regardless of island or time of the diel cycle.

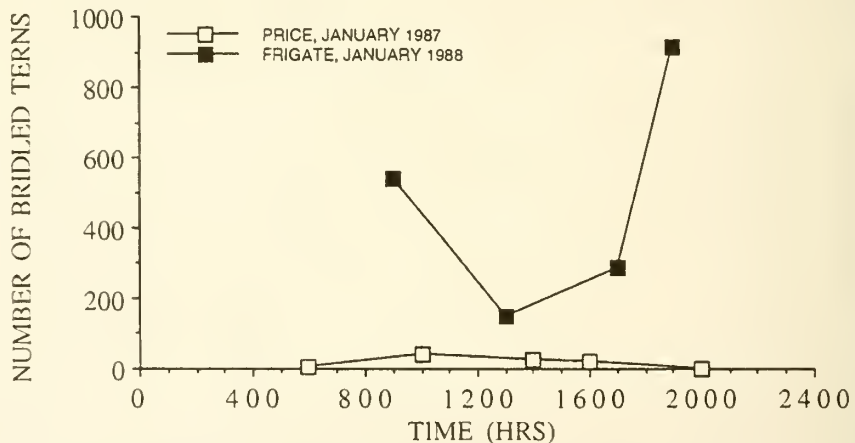


Figure 8. Numbers of Bridled Terns counted at different times of day in summer on Price Cay and Frigate Cay.

Nonbreeding Species

Counts of species that were present on these islands but did not nest there are presented in Table 2. Unlike other species, the Least Frigatebird (*Fregata ariel*) was found at night but not by day. In winter there were momentary influxes of groups of particular species that otherwise were usually absent or in low numbers. Most of these visits were by small numbers, although two (on Frigate) involved more than 100 birds:

Roseate Terns (*Sterna dougalli*) at noon and Black Noddies at 0400 hrs. In summer, counts of nonbreeders of several species were higher and some of the species maintained a more constant association with the island.

Lesser Golden Plovers (*Pluvialis dominica*), Ruddy Turnstones (*Arenaria interpres*), Black-naped Terns (*Sterna sumatrana*) and Little Terns (*Sterna albifrons*) were only recorded during the day. The lack of nocturnal observations may result from the sensitivity of these species to disturbance by lights at night. They may have flown to another island before they were detected. While not breeding during the time of these counts, Black-naped Terns do occasionally nest on the cays of the Swain Reefs (Limpus and Lyon, 1981; Moverley, 1985; Walker, 1986). Roseate Terns occurred on the island in greater numbers by day than by night in both seasons (Table 2). This pattern is opposite to that displayed by this species when wintering in Guyana where they feed offshore by day and come to land mainly at night (Nisbet, 1984). As the numbers of Roseate Terns in all surveys fluctuated dramatically from count-to-count, they were probably quite mobile, roosting on a number of the nearby cays in this part of the Swains. This pattern also has been observed in the longer-term counts on Swain Reef islands (Heatwole *et al.*, 1996). In summer, Black Noddies were found on the islands only by day. However, in winter on Frigate they were present in greater numbers by night than by day. The greater numbers of Black Noddies on Frigate and their almost complete absence on Price is probably because only Frigate had shrubs (two sizable *Argusia* bushes); Black Noddies prefer trees or shrubs for nesting and roosting.

Nonbreeding species were relatively constant in number throughout a particular diel cycle on only one island and during only one season; otherwise, they occurred merely as sporadic visitors (e.g., Lesser Crested Tern, *Sterna bengalensis*; Great Frigatebird, *Fregata minor*; Whitefaced Heron, *Ardea novaehollandiae*). Whereas Lesser Crested Terns were only recorded as sporadic visitors in this survey, it should be noted that they do breed occasionally in small numbers on the Swain Reefs in mixed colonies with Crested Terns (M. Jones, unpublished data). Finally, there were species that seldom occurred and then in very low numbers (Least Frigatebird, *Fregata ariel*; Sooty Tern, *Sterna fusca*; Eastern Reef Egret, *Egretta sacra*).

There was no clear relationship between the numbers of roosting birds and tidal cycles for any of the nonbreeding tern species or between numbers of nonbreeding Black Noddies and time of day, such as Hulsman (1974, 1977) found. Perhaps these nonbreeding birds, not being attached to a particular nest site, were moving frequently between islands so that tidal and diel patterns of roosting were obscured.

A total of 13 nonbreeding species was recorded during the counts of which 11 species occurred in summer on the two islands collectively and nine species in winter. In summer, there were nine species on each island, seven in common between the two islands and two species unique to each (Table 1). In winter, Price had five species and Frigate seven, with three species in common between them and two unique to Price and four unique to Frigate.

The higher number of Bar-tailed Godwits (*Limosa lapponica*), Lesser Golden Plovers and Ruddy Turnstones in summer than in winter is because populations overwintering in Australia are supplemented in summer by migrants from the northern hemisphere (Cayley, 1970).

In general, seabirds on Frigate and Price Cays roosted in mixed-species aggregations, mostly small and scattered around the beach, but with some large aggregations consistently in one spot. Nonbreeding species roosted almost exclusively on the beach. Exceptions to this generalization were Common Noddies and Bridled Terns which roosted in the vegetation regardless of whether they were nesting or not, and Black Noddies which showed a preference for roosting in the only bushes available, the two *Argusia* shrubs on Frigate. Black-naped Terns showed a preference for roosting on spits and nonbreeding Brown Boobies often roosted on exposed beachrock at night regardless of the direction and strength of the wind. When nesting, birds of all species roosted near their nests in the vegetated zone of the island, both by day and night. An exception occurred during the storm on the night of the summer count on Frigate. All nesting adult boobies, except those directly involved in brooding eggs or small chicks, congregated on the beach on the lee side of the island.

Diel patterns of activity are not well documented for seabirds. It is known, however, that various species of terns engage in "social flights" at twilight during the breeding season (Marshall, 1942). Desertion of nests for all or part of the night (when the risk of predation on eggs is lower) while maintaining nest attentiveness during the day has been recorded in several gull species, e.g., Ring-billed Gulls (*Larus delawarensis*), Chardine and Morris, 1983) and Black-headed Gulls (*L. ridibundus*) (Beer, 1962). In a review of nocturnal nest desertion by colonially nesting seabirds, Chardine and Morris (1983) found that desertion is most common early in the breeding season, both before and after egg-laying, and involves numbers ranging from a few individuals to nearly all of the colony. In the latter case, movements often were synchronous with virtually all birds departing and returning simultaneously. Such nocturnal nest desertion is thought to function in promoting synchrony in hatching. This type of nocturnal nest desertion must be distinguished from that caused by the risk of predation to the brooding adults. Nest desertion has been recorded in Ring-billed Gulls threatened by predation (Emlen *et al.*, 1966) and in Common Tern (*Sterna hirundo*) colonies (Hunter and Morris, 1976; Nisbet and Welton, 1981; Shealer and Kress, 1991) in response to threat of predation by owls or Night Herons. In the study by Nisbet and Welton (1981), nests were deserted for 6.5 to 8 hours each night throughout the nesting season. Clearly, nocturnal desertion can be an important factor affecting diel changes in numbers of seabirds on islands. Differences in the extent of nest desertion at different stages of the nesting cycle could introduce a seasonal effect as well.

A number of other factors need to be taken into account when counting seabirds. It is important to conduct surveys at a consistent time of the year when bird species are at a similar stage of the nesting cycle. Even a few weeks can make a large difference in numbers if birds are just arriving to breed or if chicks are just fledging (del-Nevo *et al.*, 1993). As the present study has shown, it is possible to obtain reliable counts of Brown and Masked Boobies, Common and Black Noddies and Bridled Terns at night, but gulls, charadriid waders and some species of terns are highly sensitive to lights and human activity at night and are likely to fly away before being counted; they are much more sensitive to disturbance at night than during the day and are particularly sensitive on moonlit nights. Schreiber and Chovan (1986) found that a census 10 minutes after

sunset gave an accurate count of the numbers of Redfooted Boobies (*Sula sula*) and Great Frigatebirds that roosted on an island for the night. This time-frame does not apply to all species, however. In the present study, Brown and Masked Boobies and Common Noddies continued to increase in numbers for several hours after sunset and, in the case of the Black Noddy, all night long. Finally, weather conditions at the time of the count can influence the number of birds roosting. Wind has a major influence on foraging activity of oceanic birds. Calm conditions reduce the area covered and may prolong the time away from the nest (Jouventin and Wiemerskirch, 1990). By contrast, species that forage inshore, such as terns, seek shelter in high wind (Hulsman, 1977). Long periods of severe weather, such as cyclones, can dramatically reduce breeding success in colonies because strong winds prevent adults from foraging or reduce their foraging success and chicks starve (Hulsman, 1984). The present study found that, in strong winds, nonbreeding birds, partners of brooding or incubating adults, and parents of large chicks congregated on the leeward beach where some shelter could be obtained. On calmer nights, birds were distributed more evenly around the island, even on the windward side, and remained near their brooding mate or large chick wherever located.

In summary, it is clear that on the cays of the Swain Reefs numbers of birds change both during the diel cycle and seasonally. Any measure of the impact of birds on islands should take such changes into consideration. The variation in numbers, even during the daytime, means that counts on different islands at different times of day are not strictly equivalent and techniques for taking censuses need to be standardized if precise comparative information is to be gleaned. The confounding factors of nocturnal desertion, differences between species in sensitivity to human disturbance at night, and weather conditions need to be recognized.

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**THE BIRDS OF THE SOUTHERN CORAL SEA INCLUDING OBSERVATIONS
BY HMS HERALD IN 1858-60**

BY

W.R.P. BOURNE, A.C.F. DAVID, AND I.A.W. McALLAN

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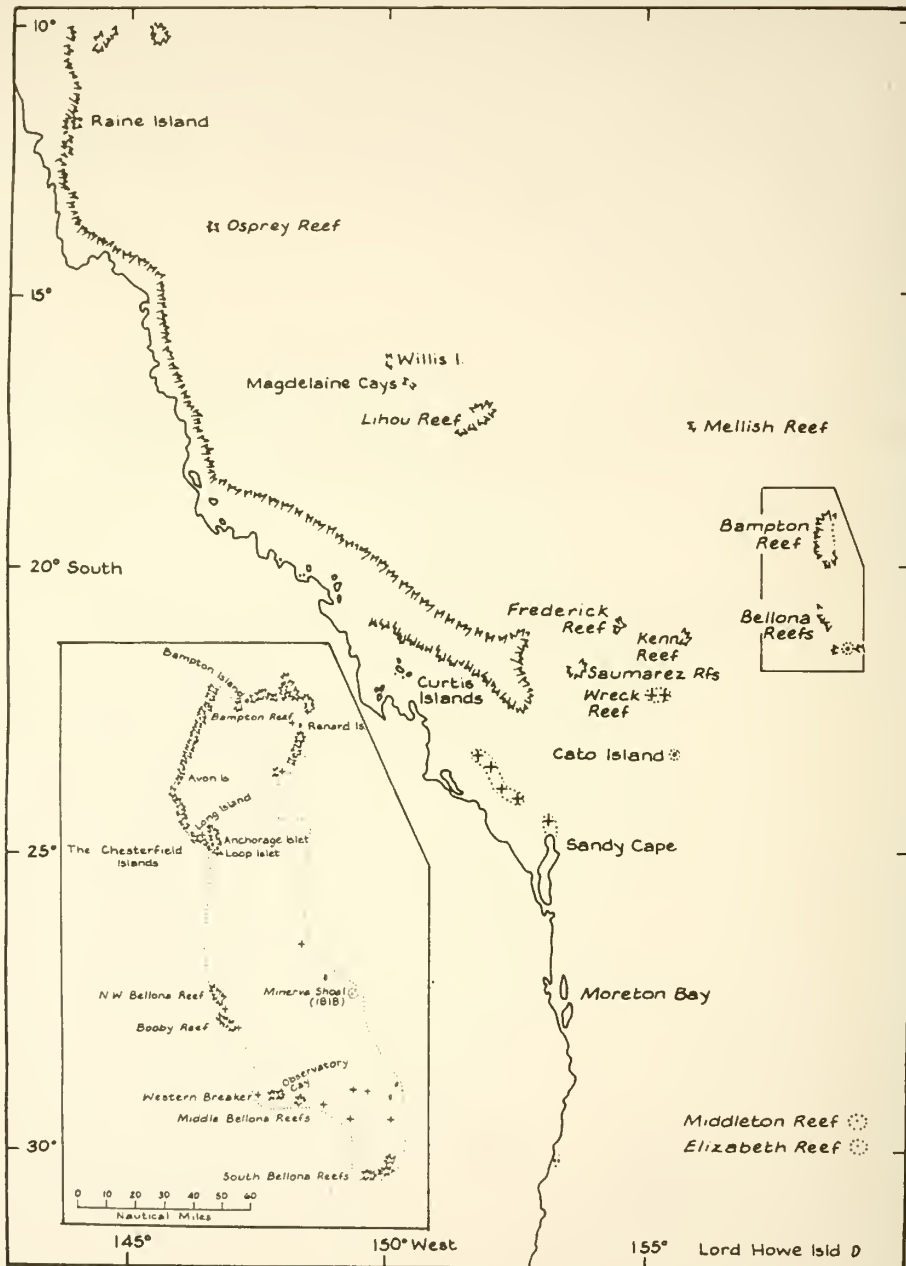


Figure 1. Index map of the Coral Sea showing details of the Chesterfield Islands.

THE BIRDS OF THE SOUTHERN CORAL SEA INCLUDING OBSERVATIONS BY HMS HERALD IN 1858-60

BY

W.R.P. BOURNE,¹ A.C.F. DAVID,² AND I.A.W. McALLAN³

It was hoped to include Terry Walker, who had visited most of the remoter islands in the Coral Sea in the course of preparing a seabird atlas, among the authors of this work until he failed to return from a trip in the Gulf of Carpentaria in May 1992 (Ogilvie and Hulsman, 1993). This contribution is therefore dedicated to his memory.

ABSTRACT

The log of HMS *Herald* when surveying reefs in the southern Coral Sea in 1858-60 shows that the little-known islands in this area were an important site for whales, turtles and seabirds (possibly including the Herald Petrel, *Pterodroma (arminjoniana) heraldica*, named after the ship) before they were devastated by whalers and guano-digging soon afterwards. This information is compared with more recent observations. While the slow-breeding, surface-nesting Herald Petrels and most of the Red-tailed Tropicbirds, *Phaethon rubricauda*, have not been found again, the vegetation and other more numerous bird populations appear to have largely recovered. While some birds may breed more or less continuously, there appears to be a peak for both birds and turtles in the spring in the south of the area and also in the autumn for the birds farther north, possibly due to the northward movement and increase in strength of the southeast trade wind in the winter. Individual birds' apparently erratic breeding behaviour may help them to avoid predators and parasites.

INTRODUCTION

One of the minor mysteries of marine ornithology concerns the origin of two identical medium-sized gadfly petrels, *Pterodroma* sp., said to have been collected on the Chesterfield Islands by John MacGillivray in the middle of the 19th century and eventually named *Oestrelata heraldica* by Salvin (1888). Presumably this was on the assumption that they must have been collected while MacGillivray was the naturalist in the *Herald*. During a study of the surveying voyage by Captain H.M. Denham in the *Herald* (David, 1995), WRPB and ACFD therefore looked for evidence for their origin.

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In 1995, IAWM independently examined a series of specimens from this voyage, apparently labelled by F.M. Rayner, surgeon in the *Herald*, and supplied by John Gould with a letter dated 13 August 1862 to Muscum Victoria in Melbourne, and found another specimen. These separate lines of research have revealed some other useful additional information about the islands.

The Chesterfield Reefs or Islands, and sometimes Group, are the most important of a number of uninhabited coral sand cays, some still awash and liable to shift with the wind and others stabilized by the growth of grass, creepers and low trees, lying on a series of reefs comprising the Chesterfield Reefs and extending from 19° to 22° S between 158-160 E in the southern Coral Sea halfway between Australia and New Caledonia (Fig. 1). The Chesterfield Reefs are now part of the territory of New Caledonia while the islands farther west are now part of the Australian Coral Sea Territory. They include the following main islets from south to north (Thiercelin, 1866; Anon., 1916; Hindwood et al., 1963):

Cato Island (23° 15' S, 155° 32' E), which lies 152 nautical miles (nm) NE of Sandy Cape and about 150 nm ESE of the southern end of the Great Barrier Reef, is a mound of coral debris measuring some 800m by 250m and 6m high covered in grass and creepers up to 1m high.

Bird Islet (22° 11' S, 155° 28' E), 64 nm to the north at the east end of Wreck Reef, is another mound measuring some 500m by 250m and 6m high with a bare centre surrounded by a ring of herbage. There are three other cays of which the first, Porpoise Cay, is 275m long, 90m across and 3m high with a few low plants, and the others are up to 120m long and 2m high lying about four miles apart along the reef to the west.

Observatory Cay (21° 16' S, 155° 48' E), at the south end of Kenn Reef 60 nm farther north, is about 100m by 50m and 2m high with a little vegetation and there are a number of other bare outlying cays scattered across this reef. There is a similar Observatory Cay (21° 02' S, 154° 23' E) on Frederick Reefs to the west and some cays on the Saumarez Reefs farther south.

Another Observatory Cay (21° 24' S, 158° 51' E), 800m long and 2m high, lies on the Middle Bellona Reefs at the southern end of the Chesterfield Reefs and 180 nm east of Kenn Reef.

Loop Islet (19° 59' S, 158° 28' E), which lies 85 nm farther north near the south end of the central islands of Chesterfield Reefs, is a small, flat, bushy islet 3m high where a permanent automatic weather station was established by the Service Météorologique de Nouméa in October 1968. Terry Walker reported the presence of a grove of *Casuarinas* in 1990.

Anchorage Islets are a group of islets five nautical miles north of Loop Islet. The third from the north, about 400m long and 12m high, shelters the best anchorage.

Long Island (19° 53' S, 158° 19' E), 10 nm NW of Loop Islet, is the largest of the Chesterfield Islands, and is 1400 to 1800m long but no more than 100m across and 9m high. Although wooded in the 1850s, it was stripped during guano extraction in the 1870s and was said to be covered in grass with only two coconut trees and some ruins at the south end early in the last century (Anon., 1916). The vegetation was growing again by 1957 when the remaining ruins were confused with those of a temporary automatic

meteorological station established in the same area by the Americans between 1944-48 (Pisier, 1979, Godard, nd). Terry Walker reported that by 1990 there was a ring of low *Tournefortia* trees growing around the margin, herbs, grass and shrubs in the interior, and still a few exotic species including coconuts.

One-to-three nautical miles south of Long Island and Loop Islet there are three small low islets up to 400m across followed, after a narrow channel, by Passage or Bennett Island, which is 12m high and was a whaling station in the first half of the last century. Several sand cays lie on the reef southeast of the islet.

The two Avon Isles (19° 32' S, 158° 15' E), some 188m in diameter and 5m high to the top of the dense vegetation, are situated 21 nm north of Long Island.

Renard Island (19° 14' S, 158° 58' E) lies 45 nm NE of the Avon Isles and is 273m long, 180m across and also 6m high to the top of the bushes.

Bampton Island (19° 08' S, 158° 38' E) lies on Bampton Reefs 20 nm NW of Renard Island. It is 180m long, 110m across and 5m high. It had trees when discovered in 1793, but has seldom been visited since then except by castaways.

Herald's Beacon Islet (17° 25' S, 155° 52' E), 170m by 120m and 2m high, lies on Mellish Reef 180 nm NW of Bampton Island.

There are also many cays on Lihou Reef halfway between Mellish Island and the coast of Queensland and more reefs to the northwest where a particularly useful comparative study has been carried out on Northeast Herald Cay (Comben, 2001).

HISTORY

Booby Reef in the centre of the eastern chain of reefs and islets comprising Chesterfield Reefs appears to have been discovered first by Lt. Henry Lidgbird Ball in HMS *Supply* on the way from Sydney to Batavia in 1790 (Collins, 1798; Findlay, 1851, 2: 1161). The reefs to the south were found next by Mathew Boyd (ms) in the convict ship *Bellona* on his way from Sydney to Canton in February-March 1793. The following June, William Wright Bampton (ms) became embayed for five days in the reefs at the north end of Chesterfield Reefs in the Indiaman *Shah Hormuzeer* with Mathew Bowes Alt (ms) in the whaler *Chesterfield*, and reported two islets with trees and "a number of birds of different species around the ships, several of them the same kind as at Norfolk Island" (Collins, 1798; Flinders, 1814; Pisier, 1979).

Cato Island, and then Bird Islet, were found by Captain John Park in the Indiaman *Cato* and Lt. Robert Fowler in HMS *Porpoise* on 17 August 1803. The latter ran aground on Wreck Reef. Matthew Flinders (1814) on the *Porpoise* reports that all the cays held many birds, laying in the period August-October. On Bird Islet they included gannets, boobies, man-of-war birds, tropic birds and noddies. There were also turtles of up to 208 kg and many Humpbacked Whales in the lee of the reef.

The reefs continued to present a hazard to shipping plying between Australia and Canton or India (where cargo was collected on the way home to Europe) and in due course the southern reefs were surveyed by Captain H.M. Denham (ms, 1860) in the *Herald* in 1858-60, who made natural history notes discussed below, and the northern

ones by Lt G.E. Richards in HMS *Renard* in 1878 (Richards, 1878) and the French the following year (Chevron, 1880; Rageau and Vervent, 1958).

The area was also visited by increasing numbers of whalers during the off-season in New Zealand in search of the many wintering Humpbacked and fewer Sperm Whales (Townsend, 1935) in the middle of the 19th century as described by Thiercelin (1866). He reports that in July 1863 the islets only had two or three plants, including a bush 3-4 m high, and were frequented by turtles weighing 60-100 kg, paille-en-queues, fous, pétrels 'etc.', a petit oiseau noir (noddy?), and a coq de bruyère (rail?). Many eggs were being taken regularly by several English, two French and one American whaler. On another occasion there were no less than eight American whalers (*Moniteur de la Nouvelle Calédonie*, 5 July 1863, quoted by Pisier, 1979). A collection of birds said to have been made by Surgeon Jourde of the French whaler *Général d'Hautpoul* on the Brampton Shoals in July 1861 was subsequently brought by Gerard Krefft (1862) to the Australian Museum, but clearly not all the specimens came from there.

On 27 October, 1862, the British Government granted an exclusive concession to exploit the guano on Lady Elliot Island, Wreck Reef, Swain Reefs, Raine Island, Bramble Cay, Brampton Shoal, and Pilgrim Island (not located, possibly somewhere off Western Australia?) to the Anglo-Australian Guano Company organised by the whaler, Dr. W.L. Crowther in Hobart, Tasmania. They were apparently most active on Bird Islet (Wreck Reef) and Lady Elliot and Raine Islands (Hutchinson, 1950), losing five ships at Bird Islet between 1861 and 1882 (Crowther 1939). It is not clear that they ever took much guano from the Chesterfield Islands unless it was obtained from Higginson, Desmazures et Cie, discussed below.

When in 1877 Joshua William North also found guano on the Chesterfield Reefs, Alcide Jean Desmazures persuaded Governor Orly of New Caledonia to send the warship *La Seudre* to annex them. There were estimated to be about 185,000 cu m of guano on Long Island and a few hundred tons elsewhere, and 40-62% phosphate (Chevron, 1880), which was extracted between 1879-88 by Higginson, Desmazures et Cie of Nouméa (Godard, nd), leaving Long Island stripped bare for a time (Anon., 1916).

Apparently the islands were then abandoned until Commander Arzur in the French warship *Dumont d'Urville* surveyed the Chesterfield Reefs and erected a plaque in 1939 (Cohic, 1959). In September 1944, American forces installed a temporary automatic meteorological station at the south end of Long Island, which was abandoned again at the end of World War II (Rageau and Vervent, 1958).

The first biological survey was made of Long Island by Cohic (1959) during four hours ashore on 26 September, 1957. It revealed among other things a variety of avian parasites including a widespread *Ornithodoros* tick (Rageau & Vervent, 1958) belonging to a genus carrying arboviruses capable of causing illness in man (Bourne, 1989). This island and the Anchorage Islets were also visited briefly during a survey of New Caledonian coral reefs in 1960 and 1962 (Chevalier, 1964). Those islands belonging to Australia and their birds and parasites were surveyed in September-October 1960 and October-November 1961 by Hindwood et al. (1963).

An aerial magnetic survey was made of the Chesterfield area in 1966 (Pisier, 1979), and a seismic survey in 1972 (Godard, nd), which apparently have not been followed up

yet. In November 1968 another automatic meteorological station was installed on Loop Islet where 10 plants were collected by A.E. Ferré (Guillaumin & Veillon, 1969). Since then the Centre de Nouméa of the Office de la Recherche Scientifique et Technique Outre-Mer has arranged for periodic surveys by Rancurel (1974a,b), Condamin (1977) and others when this installation is serviced. The ornithological observations are summarized by Naurois & Rancurel (1978a,b).

Since 1982, Terry Walker had been carrying out methodical surveys of the Coral Sea islets with the intention of producing a seabird atlas, including a visit to the central islands of the Chesterfield Reefs in December 1990 (Heatwole & Ménez n.d., Tables 1 and 2). It appears from his records to have been about half finished when he was lost, and the Department of Environment and Heritage, which has his records, has made a commitment to complete it (Ogilvie and Hulsman, 1993).

The Observations by HMS *Herald*

The *Herald* left Britain in 1852 and had been surveying in the southwest Pacific area for over five years by the time she reached the Coral Sea (David, 1995). In this time her officers and crew had clearly become very familiar with insular wildlife and appear to have collected birds at every opportunity. Every boat that went ashore would also take 'upwards of a hundred dozen' eggs when available. Although the official naturalist, John MacGillivray (Ralph, 1993), had been dismissed in Sydney in April 1855, Captain Denham was still recording natural history observations in his own journal and the species seen were also listed on the track chart by someone whose writing differs from that of others mentioned.

According to MacGillivray, the surgeon F.M. Rayner was also collecting birds for the Royal Naval museum at Haslar Hospital (later including the type of *Procellaria macgillivrayi* of Gau, Fiji: Watling and Lewanavanua, 1985). Alternatively they, and later a new Assistant Surgeon, G.B. Beale, may have sent them to the Hydrographer of the Navy, Admiral Sir Francis Beaufort. Wherever they originally sent their specimens, they eventually reached one of Beaufort's correspondents, John Gould, who passed some of the most interesting, such as the types of the Tristan Thrush *Nesocichla eremita* and Fiji Petrel *Pseudobulweria macgillivrayi*, to the British Museum. Most or all of the remaining specimens were acquired by Frederick McCoy, founder of the National Museum of Victoria (now Museum Victoria), including at least 14 collected in the SE Coral Sea by Rayner in September- November 1858 and five collected there by Beale in May-September 1859. One is a Herald Petrel *Pterodroma (arminjoniana) heraldica*, presumably taken with the two now in the (British) Natural History Museum.

Surveys by Denham in the Coral Sea

3 September- 19 December 1858: Sydney, South and Middle Bellona Reefs, Wreck Reef, Cato Island, Cape Moreton, Sydney.

11 April- 14 October 1859: Sydney, Middle Bellona Reef north to Bampton Reef, Kenn Reef, Frederick Reefs, Saumarez Reefs, Percy Isles, Cato Island, Wreck Reef and Bird Islet, Mellish Reef, Lihou Reef. running survey of Great Barrier Reef, Moreton Bay, Sydney.

21 January- 23 May 1860: Sydney, Mellish Reef, Lihou Reef, Willis Islets, Osprey Reef, Raine Island, Herald Cays, Magdelaine Cays, Mellish Reef, Sydney.

17 August- 19 September 1860: Homeward bound, Kenn Reef, Frederick Reefs, running survey of outer edge of Great Barrier Reef, Herald's Surprise, Holmes Reefs, Raine Island.

Since the inner islands are better-known and the marine biology and lesser plants still comparatively undisturbed, we shall confine our attention to the larger wildlife of the seldom-visited outer islands devastated by guano extraction shortly afterwards, citing the scientific names used at the time, and discuss the identity of the birds later.

Denham reports that around the Bellona Reefs in September 1858 they saw many sharks *Carcharinus* (one that was caught had a Hawksbill Turtle in its stomach), Humpbacked Whales *Megaptera*, Sperm Whales *Catodon*, Finner Whales *Physalus*, Blackfish *Globiocephalus*, Boatswain Birds *Phaeton phoenicurus*, Masked and Brown Gannets *Sula personata* and *S. fusca*, man-of-war birds *Tachypetes* and "common" terns *Sterna* at sea. They found only 18 Green Turtles *Chelonia marmorata* weighing 1615 kg, Masked and Brown gannets, Sooty Terns *Onychoprion fuliginosus* and the tern *Sternula nereis* breeding on the bare sand cay where all the guano had been washed away by storms. The following April, while there were still turtles at sea, there were now only hatching turtle eggs ashore and many fewer birds, which were just starting to lay again.

When they visited Bird Islet, Wreck Reef, on 9 October 1858, Denham reported that it was composed of pale grit, half a mile round and 12 ft high, with a bare centre surrounded by tufts of rank grass *Rottboilla* of Endliche and creepers of the families Portulacaceae and Nyctaginaceae etc, with polluted fresh water seeping from crevices. It was covered with nesting gannets, man-of-war birds, terns and noddies breeding in separate groups so that the colony was divided into five sections. There were a few Hawksbill Turtles *Caretta imbricata* in the lagoon and many Humpback and Finner whales and a school of Sperm Whales offshore. Rayner identified the birds as *Puffinus carneipes*, *Sula australis*, *S. personata*, *S. fusca*, *S. piscator* or *rubripes*, *Tachypetes*, *Phaeton phoenicurus*, a *Limosa*, *Sterna melanorhyncha*, *S. gracilis*, *Onychoprion fuliginosa*, *Anous cinereus* and *A. leucopillus*.

Three days later Denham reported Cato Island was more substantial than other cays in the area, measuring 1/3 by 1/6 miles, rising to 19 ft, and covered in coarse tufted grass *Rottboilla*, a creeping plant *Nyctagin portulaca* and a sort of buttercup *Senebiera crucifera* undermined and fertilised by burrowing mutton-birds, the only species that the sailors wished to eat. There were again dense colonies of gannets, man-of-war and Boatswain Birds, terns and noddies, with eggs and chicks, and he shot a godwit and a brace of plovers. There were records of repeated visits by whalers but now only one

Humpback offshore. Rayner also recorded a *Limosa*, *Charadrius*, *Strepsilas interpres*, and a landrail. When they returned with plants from the Percy Isles and seeds from Sydney to provide succour for castaways in August, 1859 Denham again reported that the birds formed a cloud hovering 60 feet above the island, though “a few visits like ours would tend to check the accumulation in proportion to each boat bringing off upwards of 100 dozen eggs at a three hours gleaning!”

In May 1859, Denham found Long Island was “a heap of “foraminifera” densely covered with stunted bush-trees with leaves as large as cabbage plants, spreading 12 feet (3.7 m) and reaching as high, upon trunks 9 inches (23 cm) diameter... The trees around the margin of this island were leafless, as if from the sea-fowl (gannet, man-of-war bird and boatswain bird) roosting and nesting, instead of laying upon the ground as at Cato Island and Bird Islet, which would seem to be a habit on account of the ground being too much shaded for sun-hatching, as also in some degree, perhaps, to avoid the snakes (presumably breeding sea snakes). The mutton-birds burrowed, and were more successfully bagged by our boats’ crews, than at the open-surface islets... A land-bird (a rail), of the size of a plover, black and scantily speckled, was found in numbers feeding on insects...”

The Avon Isles to the north were also “densely covered with stunted trees and creeping plants and grass, and... crowded with the like species of birds... the small tern *Sterna gracilis*... the Sooty Tern *Onychoprion fuliginosus*... the Black Noddy *Anous stolidus*... the gannets, some with red legs, *Sula fusca*, *S. australis* and *S. piscator*... with the man-of-war birds *Tachypetes ariel* and *T. aquila*. We also found the land-bird already described and of which I retained good specimens. These isles afforded but few mutton birds, but as the boats’ crews became adept at birds’ nesting, and as this was evidently the laying season, each boat (brought) on board three or four buckets of eggs. At first they were chiefly addled, but after clearing all the nests a fresh lay took place...”

The list of the fauna observed on the *Herald*’s Track Chart includes a *Procellaria*, *Puffinus carneipes*, *Attagen ariel*, *Phaeton phoenicurus*, *Sula australis*, *S. personata*, *S. rubripes*, *Rallus pectoralis*, *Charadrius xanthocheilus*, *Limosa uropygialis*, *Strepsilas interpres*, a *Sterna*, *Onychoprion fuliginosus*, *Anous stolidus*, *A. cinereus*, *A. leucocapillus*, *Chelonia marmorata*, *Catadon australis*, *Globicephalus macrorhynchus*, *Megaptera* and *Physalus*. In addition to the rail, Denham reports that a sooty tern, a noddy and a booby were collected. There are two sooty terns from the Avon Isles, a buff-banded rail from the Chesterfield Reefs, and a bar-tailed godwit, black noddy and tree martin *Hirundo nigricans* from Observatory Islet on Middle Bellona Reefs in Museum Victoria.

The *Herald* next surveyed Kenn Reef “and its bare white sand cays” between 25 May- 6 June. “At present these cays are scarcely six feet above high-water level but, nevertheless, are so protected from the ocean surge by the rim of the outer reef as to allow vegetation, which, though not discernible afloat, consists of the like creeping plant which we had seen on the windward cays and whereupon the Black Noddy *Anous stolidus*, the only bird I saw there, lays eggs...”. Surveys were carried out on Frederick Reefs between 10-13 June, which also had some vegetation, eggs and chicks of Black Noddies *Anous leucocapillus*, sharks, and a middle-sized Green Turtle.

A visit to Saumarez Reefs between 17-20 June was interrupted by a storm during which they retired to Kenn Reef. When they returned to Saumarez Reefs during 24-30 June they found gannets, noddies and frigate-birds occupying the cays. Finally, when they visited Herald Beacon Cay on Mellish Reef in August the ship's rigging was covered in roosting boobies, which returned throughout their stay.

Denham's conclusions are engraved on British Admiralty Chart 349:

"These Plans and a mast-head Lookout will enable a Ship to round to under the lee of the Reefs where she may caulk topsides, set up rigging, rate Chronometers, [and] obtain turtle, fish and seafoal eggs. On some of the more salient reefs, beacons were erected by Captn Denham, and for the sake of castaways, cocoa-nuts, shrubs, grasses & every description of seed likely to grow, were sown in the way to promote the superstructure; and it is most desirable that these Refuge- spots should be held sacred for universal benefit and not ruthlessly destroyed by the Guano-seeker."

THE BIRDS

Diomedea exulans Wandering Albatross. Hindwood et al (1963) saw an immature near Cato Island on 6 October 1960.

Daption capense Cape Petrel. One followed the *Herald* from Breaksea Spit off Sandy Cape, south Queensland, to Cato Island in August 1859.

Pachyptila vittata Broad-billed Prion? A 'Broad-billed Whalebird *Prion vittatus*' was reported by Denham off the south end of the South Bellona Reef on 17 September 1858. There may have been confusion with the smaller gadfly petrels discussed below which appear to have been mistaken for more southerly species at a number of other places in the tropical Pacific.

Pterodroma (arminjoniana) heraldica Herald Petrel. For a long time this form was only known from two specimens in the pale phase in the (British) Natural History Museum said to have been taken by the *Herald* on the Chesterfield Islands. They were identified by Murphy and Pennoyer (1952) as a poorly-defined small South Pacific population of the southern Indo-Atlantic Trindade Petrel *P. arminjoniana*, though molecular analyses now suggest the systematics of these birds is more complicated (Brooke and Rowe, 1996). A few arc now also known to breed on Raine Island towards the north end of the Australian Great Barrier Reef, possibly laying about August (King and Reimer, 1991). It is said to occur in the New Caledonian area (Barré and Dutson, 2000), but details have yet to be published in full (Spaggiari and Barré, 2005), and it is seen at intervals in the western Coral Sea including one north of Cato Island on 16 May 1981 (Stokes and Corben, 1985). Most appear to lay a little later, in September, in the South Atlantic (Olson, 1981) and South Pacific (Bourne and David, 1983), and not until November on Round Island off Mauritius (Gardner et al., 1985).

In fact, one of these specimens (62.6.22.10) was originally found among 32 skins

of unknown origin in other parts of the world obtained by the Natural History Museum from John Gould on 22 June 1862. The museum acquired the similar type (88.5.18.110), said to have been taken by MacGillivray (Salvin, 1888), in the Salvin-Godman collection in 1888 and Museum Victoria has another (B.17189 "*Procellaria phillipi*"), also in the light phase, among the specimens obtained by the *Herald* in the Coral Sea received from Gould in 1862. They may be the "*Procellaria*" listed opposite the central islands of the Chesterfield Reefs on *Herald's* track chart but, if so, they cannot have been taken by MacGillivray who had by then left the ship.

Alternatively, they may have been obtained by MacGillivray during a simultaneous trip from Australia to Vanuatu where he presumably collected two Collared Petrels *Pterodroma (leucoptera) brevipes* on Aneityum in February and March 1859, now in the Natural History and Leiden Museums, which he named *Procellaria torquata* (MacGillivray 1860), three undated specimens of the last form in the Salvin-Godman Collection, and seven White-throated Storm-petrels *Nesofregatta fuliginosa* obtained on Aneityum in January 1860 distributed between these collections and Museum Victoria. But if so, they cannot have come from the *Herald*. The simplest solution, however, seems to be to accept the traditional origin, collection by the *Herald* in the Chesterfield Islands.

Pterodroma rostrata Tahiti Petrel. A dark petrel with a white belly seen by Hindwood et al (1963) several times off the Australian coast has subsequently been identified as this species was thought to move south with warm Coral Sea waters in January and February (Holmes, 1981; Stokes and Corben, 1985). Possible birds were described by J.B. Mitchell over the Lord Howe Seamounts at 20°45' S, 158° E on 24 October 1963, and two next day at 22° S, 156° 15' E (Bourne, 1964). One has recently been seen by Neil Cheshire at 18° 00' S, 160° 10' E, 93 nm ENE of Bampton Reef on 14 October 1985, another at 22° 30' S, 159° 03' E, 35 nm SW of South Bellona Reef, on 9 October and a third at 24° 53' S, 159° 24' E, 176 nm south of South Bellona Reef on 10 October 1988. Stokes and Corben (1985) are incorrect in stating it breeds in the Chesterfield Islands. In addition to the breeding data for New Caledonia cited by Naurois (1978), there is a chick with sprouting feathers in the (British) Natural History Museum obtained by E.L. Layard at Woodin Pass, New Caledonia on 3 November 1877. It has also been reported breeding on Îles Belep at the northwestern end of New Caledonia (V. Bretagnolle in Barré and Dutson 2000) which is thus the closest breeding point to the Chesterfield Reefs.

Pterodroma leucoptera Gould's Petrel. This species, which breeds in New Caledonia in one direction and New South Wales in the other, was reported at sea on 17 April 1974 a day before arriving at Loop Islet from New Caledonia (Rancurel, 1974a) and one was seen north of Cato Island on 16 May 1981 (Stokes and Corben, 1985). In addition to the breeding data for New Caledonia cited by Naurois (1978) there is a downy chick in the (British) Natural History Museum obtained by E.L. Layard in New Caledonia on 11 April 1877. (The similar Black-winged Petrel *Pterodroma nigripennis* is also likely to occur as it has been recorded breeding on islets farther east in New Caledonian waters, Barré and Dutson, 2000).

Puffinus carneipes Flesh-footed Shearwater. While this species was reported by Rayner at Bird Islet and on *Herald's* track chart, the next species is not, so they may have been confused. Hindwood et al (1963) also saw a few off the western reefs, presumably feeding birds from Lord Howe Island to the south.

Puffinus pacificus Wedge-tailed Shearwater. "Mutton- birds" have been seen offshore or their burrows found on at least Cato Island, Bird Islet, Long Island, the Avon Isles and Loop Islet by most visitors. While Denham failed to record them around Bellona Reefs in September 1858, apparently they had arrived at Cato Island by mid-October. Condamin (1977) also saw birds at sea but found the burrows still unused ashore on Loop Islet in early October 1977 though he reports that Ferré saw them ashore at the end of October. Rancurel (1974a) found large chicks here on 18 April 1974 and Denham found a few still present on Long Island and the Avon Isles in April-May 1859, thus it appears that, as usual, they must breed in the summer and leave in the winter. Terry Walker reported it still breeds commonly on Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Pelagodroma marina White-faced Storm-petrel. Stokes and Corben (1985) saw one near Cato Island on 16 May 1981.

Fregatta tropica Black-bellied Storm-petrel. Neil Cheshire saw one at 18 00 S, 160 10 E, 93 nm ENE of Bampton Reef on 14 October 1985, presumably returning from wintering farther north.

Fregatta grallaria White-bellied Storm-petrel. Hindwood et al (1963) report about 10 off Cato Island on 6 October 1960 and others to the south. Norris (1967) saw one at 22 S, 156 E on 23 August 1961, and Stokes and Corben (1985) saw two north of Cato Island on 16 May 1981, presumably from Lord Howe Island.

Sula dactylatra Masked Booby. Denham recorded *Sula personata* breeding on Observatory Cay on Middle Bellona Reefs in September 1858. It was listed as occurring at Bird Islet the following month and Denham listed it again on the central islands of the Chesterfield Reefs the following April-May. Cohic (1959) found them breeding on Long Island on 26 September 1957 on the ground among clumps of *Triumfetta*, *Boerhavia* and *Lepturus* and Rancurel (1973, 1974a) found them starting to breed on the Anchorage Islets in April 1973. By 18 April 1974 they had finished incubating on Loop Islet and the adults were away by day and only returned to feed large chicks on flying fish in the evening. Naurois and Rancurel (1978a) report they lay one or two eggs near *S. leucogaster* at the top of the beach on the edge of the *Sesuvium* but normally rear only one chick and conclude that most must nest seasonally in the spring as appears to be usual in this area (Marchant and Higgins, 1990). Condamin (1977) found 55 breeding on Loop Islet on 2-3 October 1977 (when one regurgitated a flying fish *Prognichthys*) and a few more outnumbered by *S. leucogaster* on the Anchorage Islets and Long Island next day. Terry Walker reported it still breeds commonly on Cato Island, Bird Islet and the

central islands of the Chesterfield Reefs and Hindwood et al (1963) that it also breeds on Herald's Beacon Islet on Mellish Reef, Porpoise Cay on Wreck Reef, and was seen on North Cay on Mellish Reef and Observatory Cay on Kenn Reef. A chick ringed on the Chesterfield Islands by H. Heatwole on 10 December 1990 was recovered dead on Nafinua Island in the Solomons (10°40' S, 162°15' E) on 27 November 1992 (*Corella* 17:163). The birds breeding on the Chesterfield Islands, and presumably elsewhere in the area, are the yellow-eyed subspecies *S.d. personata* (see photograph in Hannecart & Letocart, 1983). However, it is likely that nonbreeding members of the dark-eyed subspecies *S.d. tasmani* are regular visitors as there are many recoveries of birds ringed at Lord Howe Island and Norfolk Island from Raine Island, New Caledonia and Vanuatu.

Sula leucogaster Brown Booby. Denham found *Sula fusca* nesting on Observatory Cay on South Bellona Reefs in September 1858, Rayner lists it as occurring at Bird Islet in the following month, and it is listed again on the track chart off the central islands of the Chesterfield Reefs in the following April-May. Cohic (1959) reported that they appeared to lay two or three eggs but only rear one chick on Long Island on 26 September 1957. Condamin (1977) found only 21 on Loop Islet on 2-3 October 1977 although they were the commonest booby on the Anchorage Islets and Long Island next day. Rancurel (1974a) saw many young at sea and found old birds starting to nest again ashore on 18 April 1974. Naurois and Rancurel (1978a) report that they lay two eggs in scattered nests and conclude that unlike the other sulids they must breed continually. Terry Walker reported it still breeds commonly on Cato Island, Bird Islet and the central islands of the Chesterfield Reefs and Hindwood et al (1963) that it breeds on Southwestern Extreme Cay off Kenn Reef, Herald's Beacon Islet on Mellish Reef and Porpoise Cay on Wreck Reef. It was also seen on West Islet and an unnamed cay on Wreck Reef.

Sula sula Red-footed Booby. *S. piscator* or *rubripes* were listed at Bird Islet in October 1858, when Rayner took male and female young birds now in Museum Victoria. Denham also noted the presence of gannets "with red legs" at Long Island and the Avon Isles in April-May 1859 when *Sula rubripes* appeared on the track chart. On 26 September 1957, Cohic (1959) found nests with single eggs in *Sophora tormentosa* and *Scaevola sericea* on Long Island. Rancurel (1973, 1974a) reported eggs and young present in April 1973 when many young attended the fishing offshore and some birds were building on Loop Islet. Few had eggs or young in April 1974. Naurois and Rancurel (1978a) reported both the white and brown morphs, which may help explain some of the confusion on the *Herald* over the sulids occurring in the area. Condamin (1977) reported 300 nests in all stages of the breeding cycle in *Argusea argentea* on Loop Islet on 2-3 October 1977 and a few on the Anchorage Islets and Long Island next day. Thus it would appear that most must nest in the spring. The adults regurgitated the squid *Symplectoteuthis oualaniensis* and flying fish. Terry Walker reported a few still breed on Cato Island and Bird Islet and more on the central islands of the Chesterfield Reefs, and Hindwood et al (1963) also saw it on Observatory Cay on Kenn Reef and Mellish Reef.

Morus serrator Australasian Gannet. Flinders (1814) reported that both gannets and boobies were present at Bird Islet on its discovery in 1803 and Rayner includes *Sula australis* among birds seen there in October 1858. Denham also includes it among those present around the central islands of the Chesterfield Reefs in April-May 1859 when it was listed on *Herald's* track chart for that area though absent off Raine Island farther north. While even Bird Islet and the Chesterfield Reefs seem unusually far north for *S. serrator*, all the other local sulids were also reported. This species is usually found close to the coast in Queensland, with records as far north as 19°14' S (Storr, 1984).

Phalacrocorax sulcirostris Little Black Cormorant. Condamin (1977) saw a small group on Loop Islet on 2-3 October 1977 and probably the same 10 on the Anchorage Islets next day.

Fregata minor Great Frigatebird. This is presumably a species recorded by Denham as *F. aquila* in the central islands of the Chesterfield Reefs in April-May 1859. Rancurel (1973, 1974a) found eggs and young on Long Island and the Anchorage Islets in April 1973 and thought it was starting to breed on Loop Islet on 18 April 1974. Cohic (1959) found nests in *Scaevola sericea* and grass clumps in the open on Long Island on 26 September 1957 and Condamin (1977) found 60 nests with eggs and young in *Abutilon indicum* and *Argusia argentea* there on 4 October 1977. Terry Walker said it breeds commonly on the central islands of the Chesterfield Reefs with a few on Cato Island.

Fregata ariel Lesser Frigatebird. Denham saw man-of-war birds at sea around the Bellona Reefs in September 1858 and breeding at both Bird Islet and Cato Island the following month. Both *Tachypetes ariel* and *T. aquila* had red pouches on the northern islands in April-May 1859 while *Attagen ariel* was listed on *Herald's* track chart. F.M. Rayner collected a male, now in Museum Victoria on Bird Islet on Wreck Reef, in October 1858. It was found with eggs and young on "Brampton Shoals" in July 1861 (Kreffit, 1862). Hindwood et al. (1963) found it breeding on Bird Islet and Cato Island and Cohic (1959) found nests with eggs in *Sophora tomentosa* on Long Island on 26 September 1957. Rancurel (1973) only saw it flying over the Anchorage Islets in April 1973 and, although Condamin (1977) saw none on Long Island in early October 1977, frigates were said to be breeding again on one of the Anchorage Islets. Thus it seems possible that they may breed in the spring although Rancurel (1974a) also thought that they might be starting to breed on Loop Islet on 18 April 1974. Terry Walker reported it still breeds commonly on Cato Island, Bird Islet on Wreck Reef and the central islands of the Chesterfield Reefs.

Phaethon rubricauda Red-tailed Tropicbird. Denham reported *P. phoenicurus* at sea around the Bellona Reefs in September 1858 and breeding on Cato Island the following month. It was listed again on *Herald's* track chart off the central islands of the Chesterfield Reefs in April-May 1859 and there are two collected by F.M. Rayner during the voyage of the *Herald* on Bird Islet on Wreck Reef in October 1858 in Museum Victoria. Jourde found small young on "Brampton Shoals" in July 1861 (Kreffit,

1862). Thiercelin (1866) reports paille-en-queues in the Chesterfield Islands in 1863. *P. rubricauda* has been reported to occur again more recently by Pisier (1979) and Rancurel (1973, 1974a) saw a probable bird over Long Island in April 1973 and one at sea on 17 April 1974 the day before arriving at Loop Islet. Terry Walker also thought it may breed on the central islands of the Chesterfield Reefs. Thus, although Naurois and Rancurel (1978b) say it has not been found breeding any nearer than Surprise Island on the d'Entrecasteaux reefs to the north and Walpole, Mathew and Hunter Islands to the east, it may also survive in this area as well although it has apparently gone from most of the inshore islands except northeast Herald Cay (King, 1993; James; 2001).

Phaethon lepturus White-tailed Tropicbird. Seen at sea by Hindwood et al (1963) on 9 October 1960 at 23 10 S, 154 E, between Cato Island and the mainland, by Rancurel (1974a) on 17 April 1974 a day before arriving at Loop Islet, again by Condamin (1977) on the way to the islands in early October 1977, and two by Neil Cheshire at 18 00 S, 160 10 E, 93 nm ENE of Bampton Reef on 14 October 1985 though Naurois and Rancurel (1978b) report that it does not breed nearer than Walpole, Mathew and Hunter Islands.

Gallirallus philippensis Buff-banded Rail. Rayner reported a "landrail" on Cato Island on 12 October 1858 and G.B. Beale in the *Herald* collected a female, now in Museum Victoria, in the central Islands of the Chesterfield Reefs in May 1859. Denham recorded the presence of an agile rail, which fed on insects on Long Island and the Avon Isles in April-May 1859, identified as *Rallus pectoralis* (then used for *R. philippensis*) on the track chart. Joude found it on "Brampton Shoals" in July 1861 and a darker bird thought to be a female (Kreffit, 1862). Thiercelin (1866) also reported hunting a coq de bruyère there in 1863. Rancurel (1974a) saw a number on Loop Islet on 18 April 1974 but Condamin (1977) could only find one here on 2-3 October 1977 with another on the Anchorage Islets and several on Long Island the next day. Terry Walker reported that a few breed on Cato Island and Bird Islet and more on the central islands of the Chesterfield Reefs. Schodde and Naurois (1982); Marchant and Higgins, 1993) made Long Island the type locality of the debatable race of *G. p. tounelieri* found on islets on the Great Barrier Reef and in the Coral Sea.

Pluvialis fulva Pacific Golden Plover. Denham shot a brace of plovers on Cato Island on 12 October 1858 and *Charadrius xanthocheilus* is listed on *Herald's* track chart. Froude took one on "Brampton Shoals" in July 1861 (Kreffit, 1862). Hindwood et al. (1963) saw over 20 on Bird Islet and Condamin (1977) four on the Anchorage Islets on 4 October 1977. It had also been recorded by A.E.Ferré. Terry Walker reported them from Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Arenaria interpres Ruddy Turnstone. *Streptilas interpres* was reported by Rayner on Cato Island on 12 October 1858 and was listed again on the *Herald's* track chart. Hindwood et al (1963) found it the commonest shorebird on the islands with a maximum of 60 on Cato Island. Condamin (1977) saw 12 on Loop Islet on 2-3 October 1977 and others on the Anchorage Islets and Long Island next day. Terry Walker reported them from Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Heteroscelus brevipes/incanus Tattler sp. Froude took *Totanus griseopygius* on "Brampton Shoals" in July 1861 (Kreffit, 1862) and there is an *incanus* of uncertain origin in the Australian Museum that could be the specimen concerned. Hindwood et al (1963) report tattlers from Bird Islet and West Islet on Wreck Reef and Condamin (1977) from the Anchorage Islets on 4 October 1977. Terry Walker reported them from Cato Island, Bird Islet and the central Islands of the Chesterfield Reefs. *H. incanus* is the common tattler on the islands east of Australia.

Calidris alba Sanderling. Condamin (1977) saw one among the shorebirds on the Anchorage Islets on 4 October 1977.

Limosa lapponica Bar-tailed Godwit. Denham reported *Limosas* on Observatory Cay on Middle Bellona Reefs in September 1858 and on Cato Island and Bird Islet the following month. A body now in the Australian Museum was taken by F.M. Rayner on Observatory Cay on Middle Bellona Reefs in September and another on Cato Island in October 1858. *L. uropygialis* is also listed on the *Herald's* track chart. Froude took birds on "Brampton Shoals" in July 1861 (Kreffit, 1862). Hindwood et al. (1963) reported it from Observatory Cay on Kenn Reef, Bird Islet and Cato Island, and Terry Walker from Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Numenius minutus Little Whimbrel. Hindwood et al (1963) found a body on *Herald's* Beacon Islet, Mellish Reef, on 26 November 1961.

Sterna bergii Crested Tern. Hindwood et al (1963) saw it on Wreck Reef. Rancurel (1974a) found five to six birds with eggs on Loop Islet on 18 April 1974 and Condamin (1977) saw two there on 2-3 October 1977. Terry Walker reported they occurred on Cato Island and Bird Islet and a few bred on the central islands of the Chesterfield Reefs.

Sterna hirundo and/or *S. dougallii* Common or Roseate Terns. Denham reported "common" terns over South Bellona Reefs in September 1858, Rayner both *Sterna melanorhyncha* (Common Tern *S. hirundo*) and *S. gracilis* (Roseate Tern *S. dougallii*) at Bird Islet the following month and Denham *S. gracilis* again around the central islands of the Chesterfield Reefs in April-May 1859 when a *Sterna* was listed on the track chart. While these may have been Black-naped Terns, possibly both breeding and wintering Roseate and wintering Common Terns might occur.

Sterna sumatrana Black-naped Tern. These may be the small terns reported by Denham and noted on his track chart on the Avon Isles. Hindwood et al (1963) reported it bred on a cay on Wreck Reef and was seen on Porpoise Cay and Cato Island. Rancurel (1973) saw it on the Anchorage Islets in April 1973 and Condamin (1977) found two there 4 October 1977. Terry Walker reported it on Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Sterna nereis/albifrons Fairy/Little Tern? The small local race of Fairy Tern *S. n. exsul* breeding in New Caledonia and reported along the Australian Great Barrier Reef (McKean, 1978) has a dark tip to the bill similar to the Little Terns *S. albifrons* nesting along the Great Barrier Reef so the identification of small terns in this region presents problems (Hitchcock, 1959; Higgings and Davies, 1996). Denham reported *Sternula nereis* nesting on Observatory Cay on Middle Bellona Reefs in September 1858. Rancurel (1973, 1974b) saw birds resembling *S. nereis* with dark marks on the bill around New Caledonia and in the Chesterfield Islands from 1973, Naurois and Rancurel (1978b) found unidentified birds and 20 nests with 1-2 eggs or young in the Chesterfield Islands on 25 June 1976, and Condamin (1977) found 12 on the Anchorage Islets and several on Long Island on 4 October 1977. Terry Walker also saw terns of this group in the central islands of the Chesterfield Reefs.

Sterna fuscata Sooty Tern. Denham found many *Onychoprion fuliginosus* breeding on Observatory Cay on Middle Bellona Reefs in September 1858 and on Bird Islet and Cato Island the following month when F.M. Rayner collected a male now in Museum Victoria. Returning on 21 April 1859, Denham again saw streams passing west at 23 04 S, 158 05 E towards Cato Island 200 km away. They were also reported around the central islands of the Chesterfield Reefs and on the track chart and Beale collected a pair now in Museum Victoria on the Avon Isles in May 1859. Froude took "*O. panaya*?" (usually applied to Bridled Terns *S. anaethetus* but surely *S. fuscata*?) near the "Brampton Shoals" in July 1861 (Krefft, 1862). Rancurel (1973) found large chicks, many dead, on Loop Islet in April 1973 and Naurois and Rancurel (1978b) found thousands breeding again in the Chesterfield Islands in September 1973 and speculated that they may nest at intervals of less than a year. Condamin (1977) found several off the Bellona Reefs and 2-3000 with young on Loop Islet in early October 1977. These young regurgitated small reddish squid. He also saw some Sooty Terns on the Anchorage Islets and Long Island next day. Rancurel (1974a) found them less common on 18 April 1974 although some large chicks were still being fed in the evening. Most may nest in the spring. Terry Walker reported it still breeds commonly on Cato Island, Bird islet and on the central islands of the Chesterfield Reefs where he found 3650 breeding on North Avon Isle in December 1990.

Anous stolidus Common Noddy. Denham reported noddies breeding on Observatory Cay on Middle Bellona Reefs in September and on Bird Islet and Cato Island in October in 1858 and present (and possibly breeding?) around the central islands of the Chesterfield Reefs in April-May 1859 when *A. stolidus* was listed on the track chart. In June he reported first "Black Noddies *A. stolidus*" breeding on bare Kenn Reef but then "Black Noddies *A. leucocapillus*" breeding on similar Frederick Reefs nearby. These seem most likely to have been *A. stolidus* since *A. minutus* normally nests in trees in this area (Hindwood et al., 1963). There is a record of a specimen of *A. stolidus* taken on Frederick Reefs by G.B. Beale in June 1859 in Museum Victoria. Froude took an *Anous* resembling *A. melanogenys* Gray on "Brampton Shoals" in July 1861 (Krefft, 1862). This is presumably a Common Noddy specimen, P. 4519, in the Australian Museum collected at sea at 19° 05' S, 157° E on 16 June 1861. Thiercelin (1866) took many eggs from

his "petit oiscau noir" in the Chesterfield Islands in July 1863. Naurois and Rancurel (1978b) found eggs and chicks of *A. stolidus* in nests a few cm above the ground there in September 1973 and 1975, and Condamin (1977) saw 600 with a few large young on Loop Islet on 2-3 October 1977 and more noddies than Sooty Terns on the Anchorage Islets and Long Island. Rancurel (1974a) found many incubating in *Boerhavia* with no chicks yet on Loop Islet on 18 April 1974. Thus they may nest during much of the year. Hindwood et al. (1963) found it breeding on West Islet, Bird Islet and Porpoise Cay on Wreck Reef, Southwest Extreme and Observatory Cays on Kenn Reef and Herald's Beacon Islet on Mellish Reef. Terry Walker found it breeding commonly on Cato Island, Bird Islet and the central islands of the Chesterfield Reefs.

Auouis minutus Black Noddy. Male birds in Museum Victoria were taken on Observatory Cay on Middle Bellona Reefs by F.M. Rayner in November 1858 and G.B. Beale on Mellish Reef in September 1859. While Denham reported *A. leucocapillus* breeding on Fredrick Reefs in June 1859, see comment under *A. stolidus*. Rayner also reported the former on Bird Islet in October 1858 and it appears with *A. stolidus* on the track chart. Rancurel (1973) found eggs and chicks in the Chesterfield Islands in April 1973 and birds perching on the meteorological station and starting to incubate in Faux Tabacs *Argusia argentea* on Loop Islet, but no chicks, on 18 April 1974 (Rancurel, 1974a). Rancurel and Naurois (1978b) found them nesting again in September in *Pisonia* and *Messerschmidia*, and Condamin (1977) saw nests and young of all sizes on 2-3 October 1977. Hindwood et al. (1963) failed to mention it, but Terry Walker found it on Cato Island and Bird Islet and old nests commonly in the central islands of the Chesterfield Reefs on December 1990 where he thought it was the only species that bred at a different season from those in the western Coral Sea. It may be one of the species affected by the destruction of vegetation in the guano-digging era? The nearest breeding colonies are on Norfolk and Matthew Islands.

Procelsterua cerulea Grey Noddy. Although it is not mentioned in Denham's journal, Rayner reports *Auouis cinereus* on Bird Islet on 9 October 1878 and it is also listed opposite the central islands of the Chesterfield Reefs on the *Herald's* track chart. Terry Walker did not know of it in the area and there may have been confusion with the Little or Fairy Terns not mentioned in these lists.

Cuculus pallidus Pallid Cuckoo. A male in Museum Victoria was collected by F.M. Rayner off Cato Island in October 1858.

Eudynamis taitensis Long-tailed Cuckoo. Seen on Cato Island on 28 November 1961 (Hindwood et al., 1963).

Hirundo nigricans Tree Martin. One in Museum Victoria was collected by F.M. Rayner on Observatory Cay on Middle Bellona Reefs in September 1858. Stokes and Corben (1985) give other records on offshore islands including a body found on North Reef Cay on Frederick Reefs on 29 April 1980.

DISCUSSION

The presence of many fish, cetaceans and turtles around the islands in the southern Coral Sea implies that this must be a biologically productive area, presumably as a result of turbulence in the westbound south equatorial current and its southern branch, the East Australian Current (Burrage, 1993), around the reefs. The birds play an unusually important role in the ecosystem (Smith, 1993) by carrying marine nutrients ashore so that Hutchinson (1950: 362) reports that the Chesterfield Reefs and Huon islands were originally estimated to have over 500,000 cum of guano. The guano was said to consist of about two feet of loose "alluvial guano" over about two feet of "cement guano" composed of phosphatised coral sand and shell grit in the centre of Surprise Island in the Huon group (Power, 1925) and doubtlessly elsewhere. The observations by the *Herald* are interesting here because they are the best record of the situation in the middle of the 19th century before the islands were devastated by guano-diggers liable to take both the animals for food and the plants for fuel.

Apparently there were then many more whales than until recently, especially Humpbacks *Megaptera novaeangliae* inshore and Sperm Whales *Physeter macrocephalus* out at sea although rorquals *Balaenopteridae* and pilot whales *Globicephala* sp. were also present. They apparently occurred all around the islands although they were commonest off the south end of the Bellona Reefs. There were also many birds, including most species found today, and others not reported recently such as the Herald Petrel, one or two tropicbirds, the Roseate Tern and Grey Noddy. While some may have been misidentified in the past or overlooked until recently, as with two recent discoveries, the Crested and Black-naped Terns, the scarce species may have suffered from past predations whereas the commoner ones survived and all are now increasing again.

The local annual cycles of the seabirds seem particularly interesting. The islands lie between the area where most (but by no means all) seabirds normally lay in the local spring off south and east Australia, and where most lay in the autumn when the northward movement of the southeast tradewinds and development of the southerly Asiatic monsoons lead to seasonal upwelling in the winter off north and west Australia. Thus Serventy et al (1971) comment on the lack of information but suggest there may be double spring-and-autumn laying seasons in the central Coral Sea. Now that Naurois and Rancurel (1978a,b) have also discussed the area farther east around New Caledonia, it is possible to discern some trends.

So far most visits to the area have been made in the spring and autumn, producing few consistent results. However, while Denham is vague about individual species, he must have been able to assess the total amount of local seabird breeding activity fairly accurately because his crew was collecting the birds and especially their eggs for food. He remarks that though many birds were breeding on the southern islands in September and October 1858, when the Green Turtles *Chelonia mydas* were also laying, there were fewer birds breeding in April 1859 when the last young turtles were also leaving. On the other hand, although his crew does not appear to have found many chicks, apart from the fledging mutton-birds on Long Island and the Avon Isles 300 km

farther north, soon afterwards when they destroyed any set eggs they were soon replaced by fresh ones. In common with several more recent observers he deduced that some birds must also have been starting to lay again in the autumn. Thiercelin (1866) also appears to have found at least noddies breeding in July 1863. Terry Walker found some Wedge-tailed Shearwaters, boobies and frigates and one colony of Sooty Terns breeding in December 1990, but few other terns or noddies.

Unfortunately, it is still uncertain whether the breeding seasons of the individual species show any equally consistent pattern since several have been found breeding erratically in both the spring and autumn. This might be due to a variety of causes, such as the occurrence of "niño" years due to fluctuations in the south equatorial current, the passage of cyclones, variations in the food supply, the disturbance by people, or because the birds do not breed at annual intervals. Also these highly social birds may not all breed together but in a fluctuating stream that gives rise to a succession of synchronised breeding groups of different sizes dispersed around the available habitat providing an important means of avoiding both interactions between birds in different stages of the breeding cycle and also between some of the numerous predators and parasites ranging from seamen to ticks that infest seabird colonies.

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Table 1: Number of bird sites reported on the Chesterfield Islands (excluding Bampton and Bellona Reefs) by Walker & Savage (n.d.) in December 1990 compared with Walker's ms maxima since the survey by Hindwood et al (1960) for the main colonies in the western Coral Sea, and estimates for NE Herald Cay farther north (Comben and Beruldsen 2001).

Location:	Chesterfield Is	Cato Id	Wreck Reef		Kenn Reef		Herald Cays
			Porpoise Cay	Bird It	Obsy Id	SW Cay	NE Cay
Character:	S-B	V	V	V	V	S	B
Wedge-tailed Shearwater	35000	13000		Large			62250+
<i>Puffinus pacificus</i>							
Great Frigatebird	630	46					100s
<i>Fregata minor</i>							
Lesser Frigatebird	118	550	1	+		1	1000s
<i>Fregata ariel</i>							
Brown Booby	302	1200	80	1275	61	53	10
<i>Sula leucogaster</i>							
Red-footed Booby	914	25		Small			1000+
<i>Sula sula</i>							
Masked Booby	464	700	54	200	22	20	53
<i>Sula dactylatra</i>							
Red-tailed Tropicbird	?						386
<i>Phaethon rubricauda</i>							
Crested Tern	+	7	9	4	7	7	+
<i>Sterna bergii</i>							
Black-naped Tern	+	6	25	7		16	12
<i>Sterna sumatrana</i>							
Sooty Tern	7800	50000	6	4500		100	+
<i>Sterna fuscata</i>							
Common Noddy	3300	8000	300	400	340	80	100s
<i>Anous stolidus</i>							
Black Noddy	1700	+			+	+	10000s
<i>Anous minutus</i>							

Character: S - Sand, V - Low vegetation, B - Bushes and trees, + - species present

Table 2: Birds recorded on the central islands and cays of the Chesterfield Reefs by Terry Walker (ms) and numbers estimated to be nesting on 11 of these islands and cays by Walker and Savage (nd) in December 1990.

Species:	WTS	GF	LF	BB	MB	RFB	BNT	ST	CN	BN
Long Island	on			650	300	199	2	1	200	300
Loop Islet	1		8	10	100	50	15	300		on
Passage Island	+	12	200	239	22	141	3	12	300	100
Passage) 1	+	30	3	65	6	131	2	2	250	150
Island) 2				48	3	2	16	2	200	
Cays) 3				6	8		2			
4				100						
N Anchorage 1.	b++	17		29	22	180	2	50	700	1
S Anchorage 1.	b	78		57	11	142		2	400	250on
Islets 1		2		32	50	23	20	1	150	
2	b			3	103	14	10		450	350on
3		55		11	170	9	6	2	200	400on
4				20	86	8	6	8	on	on
5				9	2	4	16		100	
S Avon Isle		2	1	20		14	3	500	10	
N Avon Isle	3b		16	42	22	34	180	3650	500	200on
Numbers estimated nesting	35000b	630	118	302	464	914		7800	3300	1700

Species:

WTS Wedge-tailed Shearwaters, GF Greater Frigatebirds, LF Lesser Frigatebirds, BB Brown Boobies, MB Masked Boobies, RFB, Red-footed Boobies, BNT Black-naped Terns, ST Sooty Terns, CN Common Noddies, BN Black Noddies; + - species present, b - burrow, on - old nests. Only three pairs of Common Noddies had active nests, and there were only old nests of Black Noddies. Not all the Shearwater burrows were occupied, and no Herald Petrels were found.

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ATOLL RESEARCH BULLETIN

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**INVENTAIRE BIBLIOGRAPHIQUE DES MOLLUSQUES MARINS
DE L'ARCHIPEL DES MARQUISES (POLYNÉSIE FRANÇAISE)**

PAR

JEAN TRÖNDLÉ AND RUDO VON COSEL

**ISSUED BY
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Polynésie française

INVENTAIRE BIBLIOGRAPHIQUE DES MOLLUSQUES MARINS DE L'ARCHIPEL DES MARQUISES (POLYNÉSIE FRANÇAISE)

PAR

JEAN TRÖNDLÉ¹ AND RUDO VON COSEL²

ABSTRACT

The published records of marine molluscs from the Marquesas are compiled and critically examined. A total of **391** species are referenced. Presence of **365** species is verified or probable: **5** polyplacophores, **37** bivalves, **2** cephalopods and **321** gastropods. **29** species (7,95 %) are currently regarded as endemic to the archipelago and a further **6** species are represented by endemic subspecies. Three nominal species are treated as new synonyms: *Natica nukahivensis* Jardin, 1858 is regarded as a synonym of *Natica orientalis* Gmelin, 1791, *Mitra obliqua* Lesson, 1842 as a synonym of *Mitra aurantia* (Gmelin, 1791) and *Mitra modesta* Reeve, 1845 as a synonym of *Vexillum virginalis* (Lesson, 1842).

RÉSUMÉ

Cette publication donne un inventaire des mollusques marins actuellement connus des Îles Marquises au travers de la littérature. Sont citées, au total, **391** espèces dont la présence de **365** est avérée ou vraisemblable: **5** polyplacophores, **37** bivalves, **2** céphalopodes et **321** gastéropodes. **29** espèces (7,95%) et **6** sous-espèces sont mentionnées comme endémiques. **3** nouvelles synonymies sont établies: *Natica nukahivensis* Jardin, 1858 est placé en synonymie de *Natica orientalis* Gmelin, 1791, *Mitra obliqua* Lesson, 1842 est placé en synonymie de *Mitra aurantia* (Gmelin, 1791) et *Mitra modesta* Reeve, 1845 est placé en synonymie de *Vexillum virginalis* (Lesson, 1842).

INTRODUCTION

L'Archipel des Marquises: brève présentation géographique et historique.

L'Archipel des Marquises se situe presque au centre de l'Océan Pacifique, entre 138°20' et 140°30' W et 7°50 et 10°35' S. Il comprend sept îles principales et plusieurs îlots, que l'on regroupe classiquement en deux ensembles géographiques distincts: le

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groupe Nord-Ouest avec les îles Nuku Hiva, Ua Huka et Ua Pou et les îlots Hati, Eiao et Hatutu; le groupe Sud-Est avec les îles Fatu Hiva, Hiva Oa, Tahuata, Motane et les îlots Thomasset et Fatu Huku. S'y ajoutent, dans les deux ensembles, quelques bancs et hauts-fonds. Les Marquises se situent à la bordure orientale de la province indo-pacifique qui s'étend de l'Afrique de l'Est et de la Mer Rouge jusqu'à la Polynésie. Les atolls des Tuamotu les plus proches sont distants de 500 km au sud; au nord-ouest, les Îles de la Ligne sont à 1000 km et les îles Hawaii à 3500 km; la côte mexicaine est à 5500 km au nord-est.

Ces îles hautes ont une origine volcanique, chacune constituée par un ou plusieurs anciens volcans et une caldera en partie effondrée (pour plus de détails, voir Brousse et al. [1978]). Elles sont quasiment dépourvues de barrière récifale et sont directement exposées à la houle océanique. Il existe cependant plusieurs constructions coralliennes isolées et quelques formations récifales, surtout en fond de baies, zones plus calmes (pour les détails, voir Brousse et al. [1978] et Chevalier [1978]). Les côtes sont essentiellement rocheuses et formées de très hautes falaises, accessibles seulement par la mer pendant de rares périodes de temps calme. Seules les baies ont, dans leurs parties les plus internes, de courtes plages de graviers, galets ou sable, avec en général très peu de laisses de mer.

Le premier voyageur européen à atteindre les Îles Marquises et plus précisément le groupe du Sud-Est est le navigateur espagnol Alvaro Mendana de Neira, qui arrive le 21 juillet 1595 à Fatu Hiva avec une flotte de quatre bateaux. Il donne à l'archipel le nom «Las Marquesas de Mendoza» (plus tard abrégé «Marquesas», en français «Marquises») en l'honneur de la Marquise de Mendoza, femme du vice-roi du Pérou Garcia Hurtado de Mendoza. Fatu Huku, du même groupe, n'est repéré que le 7 avril 1774 lors du deuxième voyage de James Cook qui lui donne le nom de Hood. Le groupe du Nord-Est reste encore ignoré des occidentaux jusqu'en 1791, lorsqu'il est découvert à son tour par le capitaine britannique Ingraham, commandant du «*Hope*» (Ua Huka, 19 avril 1791) et, deux mois plus tard, par le capitaine français Etienne Marchand, commandant du navire «*Le Solide*» (Ua Pou, 21 juin 1791). Le 1er mai 1842, au cours de son deuxième passage dans l'archipel, le contre-amiral Dupetit Thouars prend possession de l'archipel au nom de la France. Pour plus de détails sur l'histoire de ces contacts, on se reportera à Buck (1953), Jourdain (1970) et Deschamps & Laudon (1994).

Histoire de l'exploration Malacologique de l'Archipel des Marquises.

Pionniers. C'est sans aucun doute le capitaine James Cook et ses équipages à bord des deux navires «*Resolution*» et «*Adventure*» qui sont les premiers Européens à récolter des coquillages aux Marquises, où ils font escale à Tahuata en 1774, au cours de leur deuxième voyage autour du monde. Ces coquillages furent dispersés ou vendus dès le retour à Londres.

Un autre voyage à visée scientifique est celui de l'amiral russe Adam Johann von Krusenstern qui arrive à Nuku Hiva en 1804 avec une équipe de géographes et de naturalistes. Ils explorèrent l'île pendant dix jours, du 8 au 18 mai 1804, mais nous ne savons pas si des mollusques ont été récoltés.

Classiques. L'expédition suivante qui récolte des mollusques dans l'archipel est celle de la frégate «*Vénus*» sous le commandement de Abel Auber Dupetit-Thouars. Pendant son tour du monde, de décembre 1836 à juin 1839, la «*Vénus*» fait escale aux Marquises en août 1838. Les mollusques de ce voyage, récoltés par Dupetit-Thouars lui-même et son second, le capitaine Chiron, sont illustrés par Valenciennes en 1846 dans un atlas de 27 planches, numérotées de 1 à 24, sans texte. Ce matériel cédé par Dupetit-Thouars est aujourd'hui au MNHN. Trois exemplaires de *Nautilus pompilius* Linné, 1758 auraient été récoltés aux Marquises: cette espèce n'a jamais été signalée depuis en Polynésie Française et sa présence aux Îles Marquises n'est pas vraisemblable.

Simultanément, la deuxième expédition de Jules Dumont d'Urville avec les corvettes «*Astrolabe*» et «*Zélée*» fait escale à Nuku Hiva du 26 août au 3 septembre 1838. Des mollusques sont récoltés par le médecin du bord Jacques Bernard Hombron et le commandant de la «*Zélée*» Charles Hector Jacquinot. Ils sont publiés par Rousseau (1854), mais les noms des espèces nouvelles sont habituellement attribués à Hombron & Jacquinot. Une seule espèce provenant des Marquises est citée: *Coralliophila monodonta* (Blainville, 1832) (sous le nom *Purpura madreporarum* Sowerby, 1834, synonyme). Ce matériel est aujourd'hui au MNHN.

À peine deux ans plus tard, la dernière grande expédition «classique» visite l'archipel: le navire anglais «*Sulphur*» sous le commandement du capitaine Edward Belcher. Belcher lui-même est très intéressé par les mollusques et participe aux récoltes, mais le médecin du bord Richard Brinsley Hinds est le naturaliste officiel de l'expédition. Au cours de cette expédition autour du monde (1836-1842), le «*Sulphur*» arrive à Nuku Hiva le 20 janvier 1840 pour effectuer des dragages dans la baie de «Port Anna Maria» (aujourd'hui Taiohae), et des espèces endémiques comme *Cyrtulus serotinus* et *Conus marchionatus* sont découvertes. Les résultats sont publiés par Hinds en 1844. Ce matériel est aujourd'hui au BMNH.

De 1822 à 1825, René Primevère Lesson séjourne dans le Pacifique Sud (Tuamotu, Société, Tonga, Nouvelle Zélande) à bord de la «*Coquille*», mais ne s'arrête pas aux Marquises. C'est son frère Adolphe Lesson qui, au cours d'un séjour de deux ans «dans les mers du Sud», récolte aux Îles Gambier, aux Îles Marquises et à Tahiti. Ces espèces sont décrites peu de temps après, en 1842, par R.P. Lesson.

De mai 1853 à juillet 1854 Henri Jouan, officier de marine, est détaché aux Îles Marquises, puis nommé commandant particulier de ces îles à Taiohae (Nuku Hiva) où il séjourne dix-neuf mois de janvier 1855 à novembre 1856 (O'Reilly & Teissier, 1962). À son retour en France, Henri Jouan, membre de plusieurs sociétés savantes, publie en 1858 une note sur les Îles Marquises qui traite des mœurs marquisiennes, de la flore et de la faune. On y trouve une liste de mollusques, récoltés dans ces îles, dans laquelle ceux-ci sont mentionnés en langue marquissienne. Parmi une cinquantaine d'espèces citées, nous avons pu en reconnaître un certain nombre: *Chiton marquesanus* (mama), *Turbo setosus* (potea), *Cyrtulus serotinus* (pukava kekeo), *Cypraeacassis rufa* (pu tupe), *Tutufa bubo* (pu teuteu henua), *Cypraea tigris* (putoto eheke) ...

Désiré Édelestan Stanislas Aimé Jardin, aide-commissaire de marine, à la suite d'un séjour de quinze mois (1853-1854) à Nuku Hiva, est l'auteur de plusieurs écrits sur les Îles Marquises. En 1858, il publie un «Essai sur l'histoire naturelle de l'Archipel de

Mendana ou des Marquises» dans lequel il dresse une liste des mollusques terrestres et marins récoltés pendant son séjour. Les espèces ne sont pas figurées et nombre d'entre elles ne sont citées que sous un nom vernaculaire ou indigène. Nous n'avons retenu dans cet inventaire que les espèces clairement reconnues.

En 1933, dans le *Journal de Conchyliologie*, ce sont Philippe Dautzenberg & Louis-Joseph Bouge qui publièrent le premier inventaire des mollusques marins de Polynésie Française. Ph. Dautzenberg, malacologiste autodidacte belge, auteur de nombreux écrits sur les mollusques, obtint le matériel polynésien, et en particulier celui des Îles Marquises, par L.J. Bouge, amateur de coquillages averti, Chef de Cabinet à Tahiti de 1915 à 1919 et Gouverneur de la Polynésie Française de 1928 à 1931 (O'Reilly & Teissier, 1962).

Modernes. La première expédition moderne à travailler dans l'Archipel des Marquises est la «National Geographic Society-Smithsonian-Bishop Museum Marquesas Expedition», à bord du «*Pele*», le bateau de Mme Mariel King, une Américaine, amateur de coquillages. Placée sous la direction du malacologiste Harald A. Rehder, l'expédition travaille à Pitcairn et aux Marquises où, du 5 septembre au 2 novembre 1967, la faune est échantillonnée par dragages (jusqu'à 130 m), plongées en scaphandre autonome, et récoltes à pied autour des îles Nuku Hiva, Eiao, Hatutu, Ua Pou, Tahuata et Fatu Hiva. Un compte rendu avec une courte liste d'espèces est publié (Rehder, 1969), ainsi que la description de quatre nouvelles espèces (Rehder & Wilson, 1975; Houbriek, 1992), cependant, aucun rapport définitif comportant une liste des mollusques récoltés lors de cette expédition n'a vu le jour. Le matériel est au USNM.

La mission la plus complète pour un inventaire des mollusques des Marquises a lieu en 1997. Elle est composée de la campagne en mer MUSORSTOM 9 à bord du N/O «*Alis*» de l'ORSTOM (aujourd'hui IRD) entre le 18 août et le 11 septembre 1997, avec 168 stations de dragages et chalutages, et d'un atelier à terre à Ua Huka (16 septembre-19 octobre 1997) avec 40 stations échantillonnées à pied, en plongée libre et à la drague (voir Bouchet, 1998; Richer de Forges et al., 1999). Le matériel est conservé au MNHN.

Enfin, tout récemment a eu lieu une expédition de zoologistes professionnels et collectionneurs amateurs de plusieurs pays, qui ont travaillé du 17 au 31 octobre 1999 à Nuku Hiva et Ua Pou. Des récoltes ont été effectuées à pied, en plongée libre et en scaphandre autonome (Bryce, 2000). Une partie de ce matériel a été donnée au MNHN.

Parallèlement à ces grandes expéditions institutionnelles, les collectionneurs de coquillages ont depuis plusieurs décennies contribué à l'exploration de la faune malacologique des Îles Marquises: c'est ainsi qu'ont été découverts *Comus gauquini*, *Orania simonetae*, *Terebra troendlei*, ou *Hydatina exquisita*.

LISTE COMMENTÉE

La présente liste des mollusques marins des Îles Marquises est dressée exclusivement à partir de la littérature. Elle ne tient pas compte des occurrences non publiées, quelles que soient leurs sources. Pour chaque espèce, nous donnons les

références aux travaux concernant spécifiquement les occurrences marquisiennes et/ou illustrant des spécimens originaires de l'archipel. Les descriptions originales, les références synonymiques ne sont mentionnées que lorsqu'elles concernent des espèces réputées endémiques des Marquises, même si la localité-type est inconnue ou erronée.

Les espèces et sous-espèces endémiques sont signalées en **caractères gras**.

La présence aux Îles Marquises des espèces citées n'a pas pu être vérifiée systématiquement. Celles dont la présence aux Marquises est jugée erronée sont citées [entre crochets].

L'énumération des familles suit l'ordre systématique adopté par Beesley et al., 1998. Au sein de chaque famille, les genres sont énumérés par ordre alphabétique, de même que les espèces au sein des genres.

POLYPLACOPHORA

Mopaliidae

Plaxiphora gwenae Ferreira, 1987

Ferreira, 1987: 178, figs 1-5 (description originale, localité type: «Verao-Hapapani Bay, Nuku Hiva Id, Marquesas islands, French Polynesia (8°54'S, 140°06'W), intertidal zone»); Kaas & Van Belle, 1994: 288-289, fig. 117; Slieker, 2000: 92, 93, fig. 10.

Endémique.

Chitonidae

Acanthopleura gemmata (Blainville, 1825)

Salvat & Rives, 1975: 187 (figuré comme *Chiton* sp.); Ferreira, 1986: 225, fig. 113 C; 1987: 188; Slieker, 2000: 54.

Chiton marquesanus Pilsbry, 1893

Jardin, 1858: 196; Pilsbry, 1893: 170, pl. 36, figs 98-100 (description originale, localité type: «Marquesas Is.»); Rehder, 1969: 32; Lavondes et al., 1973: 132; Salvat & Rives, 1975: 187; Abbott & Dance, 1982: 288; Ferreira, 1987: 183, figs 6-7; Bullock, 1988: 179, figs 100, 105, 109, 116, 117, 120, 121; Planes et al., 1995: 69; Bouchet, 1998: 23; Kaas & Van Belle, 1998: 119; Slieker, 2000: 54, 55, fig. 18.

Jardin (1858) a sans aucun doute eu connaissance de *Chiton marquesanus* car il écrit: «Nous avons vu à Noukahiva deux espèces d'Oscabrions; l'une dont la coquille noirâtre est lisse et comme vernissée, et sillonnée de stries; [...]», ce qui correspond à l'espèce commune aux Îles Marquises *Chiton marquesanus* et à aucune autre espèce actuellement connue de l'archipel.

Endémique.

Rhyssoplax linsleyi Burghardt, 1973

Ferreira, 1987: 185, fig. 8; Slieker, 2000: 54.

Avant Ferreira (1987), l'espèce était considérée comme endémique des Îles Hawaii.

Tonicia sp.

Ferreira, 1987: 187.

BIVALVIA

Mytilidae

Lithophaga laevigata (Quoy & Gaimard, 1835)

Jardin 1858: 190, 197.

L'espèce, décrite de Nouvelle-Guinée a été citée de Rikitea par Seurat (Lamy, 1906: 312). Sa présence dans les Îles Marquises demande confirmation.

[*Lithophaga lithophaga* (Linné, 1758)

Jardin 1858: 190, 197.

L'espèce ne vit pas dans le Pacifique. Nous ne savons pas ce qu'a vu Jardin.]

Modiolus auriculatus Krauss, 1848

Richard, 1985a: 440.

Amygdalum beddomei (Iredale 1924)

Dautzenberg & Bouge, 1933: 435 (sous le nom *Modiolus beddomei* (Petterd), identification erronée vraisemblable).

Amygdalum beddomei est connu des côtes Ouest et Sud de l'Australie (Lamprell & Healy, 1998: 182). L'espèce est présente aux Îles Marquises et pourrait être synonyme de *Amygdalum peasei* (Newcomb, 1870) connu de Hawaï (Kay, 1979: 509). Plusieurs espèces proches les unes des autres vivent dans le Pacifique et leur relation n'est pas établie.

Arcidae

Arca plicata Dillwyn, 1817

Richard, 1985a: 440.

Pteriidae

Pinctada maculata (Gould, 1850)

Richard, 1985a: 441.

Pinctada margaritifera (Linné, 1758)

Jardin 1858: 190, Rehder, 1969: 31; Lavondes et al., 1973: 133; Planes et al., 1995: 69.

Pteria penguin (Röding, 1798)

Salvat & Rives, 1975: 369, fig. 412 (sous le nom *Pteria macroptera* (Lamarck, 1822), synonyme).

Isognomonidae

Les Isognomonidae de l'Indo-Pacifique n'ont pas fait l'objet d'une révision critique récente. Trois espèces sont citées des Îles Marquises, mais leur statut taxonomique est incertain.

Isognomon isognomum (Linné, 1758)

Richard, 1985a: 441.

Isognomon nucleus (Lamarck, 1819)

Richard, 1985a: 441.

Isognomon vulsella (Lamarck, 1819)

Richard, 1985a: 441.

Pinnidae

Streptopinna saccata (Linné, 1758)

Rehder, 1969: 31.

Limidae

Lima fragilis (Gmelin, 1791)

Richard, 1985a: 442.

Ostreidae

Saccostrea cucullata (Born, 1778)

Richard, 1985a: 442.

Pectinidae

Chlamys coruscans (Hinds, 1845)

Hinds, 1845: 61, pl. 17, fig. 3 (description originale de *Pecten coruscans*, localité type: «Port Anna Maria, Nuku Hiva, Marquesas Islands. In seven fathoms, on a sandy floor»); Paetel, 1883: 242; Waller, 1972: 231, pl. 1, figs 1-7, 12; Dautzenberg & Bouge, 1933: 426; Dijkstra, 1989: 12.

Cryptopecten bernardi (Philippi, 1851)

Dijkstra, 1989: 17.

Dijkstra pense que Dautzenberg & Bouge (1933: 427) se sont trompés en identifiant leur espèce «*Chlamys nux* Reeve». Nous ne savons pas ce que Dautzenberg & Bouge ont vu. De récentes missions ont permis de récolter les deux espèces dans les Îles

Marquises où *Cryptopecten bernardi* est généralement trouvé vivant entre 30 et 80 m, mais des valves ont été draguées jusqu'à 480 m. et où *Cryptopecten nux* est récolté vivant entre 60 et 120 m.

Cryptopecten nux (Reeve, 1853)

Paetel, 1883: 242; Dautzenberg & Bouge, 1933: 427.

Gloripallium pallium (Linné, 1758)

Jardin, 1858: 190; Waller, 1972: 239; Rehder, 1969: 31; Dijkstra, 1989: 14.

Propeamussiidae

Propeamussium malpelonium Dall, 1908

Rombouts, 1991: 65.

Spondylidae

Spondylus rubicundus Reeve, 1856

Richard, 1985a: 441.

Chamidae

Chama brassica Reeve, 1846

Dautzenberg & Bouge, 1933: 448.

Espèce connue du Japon et des Philippines. Sa présence aux Îles Marquises demande confirmation.

Chama iostoma Conrad, 1837

Lavondes et al., 1973: 133 (sous le nom *Chama imbricata* (Broderip, 1834), synonyme).

Chama pacifica Broderip, 1834

Richard, 1985a: 442.

Galeommatidae

Kellia delmasi Lamy, 1927

Lamy, 1927: 184-185 (description originale, localité type: «l'Ile Uahuka Hane» [= Baie de Hanc, Ua Huka, Marquises]); Dautzenberg & Bouge, 1933: 442.

Cardiidae

Vasticardium orbitum (Broderip & Sowerby, 1833)

Sowerby, 1897: 138, pl. 11, fig. 3 (description originale de *Cardium mendanaense*,

localité type: «Marquesas Is», sous-espèce [Vidal, 1997: 19]); Salvat & Rives, 1975: 374, fig. 430; Vidal, 1997: 19, pl. 1, fig. 5, pl. 2, figs 1a-b.

L'espèce est représentée aux Îles Marquises par la sous-espèce endémique *Vasticardium orbitum mendanaense* Sowerby, 1897.

Mesodesmatidae

Mesodesma striata (Schröter, 1788)

Dautzenberg & Bouge, 1933: 456.

Tellinidae

Tellina crebrimaculata Sowerby, 1868

Richard, 1985a: 443.

Tellina perna (Spengler, 1798)

Richard, 1985a: 443.

Tellina crucigera Lamarck, 1818

Richard, 1985a: 443 (sous le nom *Tellina tithonia* Gould, 1856, synonyme).

Tellina virgata Linné, 1758

Richard, 1985a: 443.

Semelidae

Semele australis (Sowerby, 1832)

Dautzenberg & Bouge, 1933: 466.

Veneridae

Irus crenatus (Lamarck, 1818)

Dautzenberg & Bouge, 1933: 455.

Lioconcha philippinarum (Hanley, 1844)

Lamy, 1906: 211; Dautzenberg & Bouge, 1933: 451.

Lioconcha ornata (Dillwyn, 1817)

Rehder, 1969: 31 (sous le nom *Lioconcha picta* (Lamarck, 1818), synonyme);

Harte, 1992: 8, fig. 12 (sous le nom *L. picta*).

Periglypta reticulata (Linné, 1758)

Fischer, 1891: 149 (sous le nom *Venus corbis* Lamarck, 1818, identification erronée); Rehder, 1969: 31; Lavondes et al., 1973: 133; Harte, 1992: 4, fig. 2; Planes et

al., 1995: 69.

Fischer (1891) met en synonymie *Venus reticulata* Linné, 1758 et *Venus corbis* Lamarck, 1818. À l'encontre des règles nomenclaturales il retient *Venus corbis* comme bonne espèce. En fait les deux espèces sont distinctes et *Venus corbis*, à notre connaissance, ne vit pas en Polynésie Française.

Pitar prora (Conrad, 1837)

Richard, 1985a: 443.

Pitar sp.

Harte, 1992: 7.

CEPHALOPODA

Octopodidae

Octopus cyanea Gray, 1849

Salvat & Rives, 1975: 205.

Argonautidae

Argonauta nouryi Lorois, 1852

Lorois, 1852: 9, pl. 1, fig. 5 (description originale, localité type: cinq cents lieues à l'Est des Marquises); Dunker, 1852: 48 (description originale de *Argonauta grumeri*, localité type: «Archipelago Australi, ad insulas Marquesas», synonyme *fide* Tryon, 1879); 1858: 29, pl. 9, figs 1-2; Tryon, 1879: 138, pl. 50, figs 126-127; Paetel, 1883: 1 (sous le nom *A. grumeri*), Paetel, 1888: 1.

GASTROPODA

Patellidae

Scutellastra flexuosa (Quoy & Gaimard, 1834)

Richard, 1985a: 414.

Powell (1973: 129) mentionne une répartition géographique s'arrêtant, à l'Est, à l'Archipel des Tuamotu. La présence aux Îles Marquises reste à confirmer.

Nacellidae

Cellana radiata (Born, 1778)

Powell, 1973: 151; Salvat & Rives, 1975: 255, fig. 9; Planes et al., 1995: 69.

L'espèce est représentée en Polynésie et, en particulier, aux Marquises où elle est commune, par la sous-espèce *Cellana radiata orientalis* Pilsbry, 1891 (Powell, 1973).

Haliotidae

[*Haliotis pulcherrima* Gmelin, 1791

Geiger, 2000: 84 (localité erronée).

Geiger mentionne les Îles Marquises et cite deux localités qui ne sont pas marquisiennes: Kiribati = Fanning Isl. (Archipel de la Ligne) et Lord Hood Isl. = Marutea du Sud (Archipel des Tuamotu) (confusion avec Hood Isl. = Fatu Huku, Marquises). À notre connaissance *H. pulcherrima* ne vit pas aux Marquises.]

Turbinidae

Turbo setosus Gmelin, 1791

Jardin, 1858: 188; Pilsbry, 1888: 195; Rehder, 1969: 30; Lavondes et al., 1973: 132; Planes et al., 1995: 69.

Neritidae

Clithon chlorostoma (Broderip, 1832)

Salvat & Rives, 1975: 262.

Nerita morio (Sowerby, 1832)

Recluz, 1841: 181 (description originale de *Nerita haneti*, localité type: «Les Îles Marquises», synonyme); 1850: 153; Martens, 1889: 104.

Nerita plicata Linné, 1758

Martens & Langkavel, 1871: 43; Fischer, 1891: 114; Rehder, 1969: 30; Salvat & Rives, 1975: 260; Planes et al., 1995: 69.

Nerita polita Linné, 1758

Rehder, 1969: 30; Salvat & Rives, 1975: 261.

Puperita bensoni (Récluz, 1850)

Recluz, 1850: 153, 162 (description originale de *Neritina desmoulinsiana*, localité type: «Nukahiva» [= Nuku Hiva], synonyme); Paetel, 1888: 520 (sous le nom *N. desmoulinsiana*); Dautzenberg & Bouge, 1933: 399 (sous le nom *Neritina reticulata* Sowerby, 1833, non Cristofori & Jan, 1832, non Karsten, 1789, synonyme).

Cerithiidae

Cerithium atromarginatum Dautzenberg & Bouge, 1933

Houbrick, 1992: 25.

Cerithium columna Sowerby, 1834

Richard, 1985a: 418.

Houbrick (1992: 49) donne une répartition géographique allant, à l'Est, jusqu'à l'Île de Pâques, mais excluant, au Nord, les Îles Marquises, où sa présence reste à confirmer.

Cerithium echinatum Lamarck, 1822

Rehder, 1969: 30 (sous le nom *Cerithium mutatum* Sowerby, 1834, synonyme); Salvat & Rives, 1975: 268; Houbrick, 1992: 77.

Cerithium nesioticum Pilsbry & Vanatta, 1906

Richard, 1985a: 418.

Houbrick (1992: 121) donne une répartition géographique allant, à l'Est, jusqu'à Pitcairn, mais excluant, au Nord, les Îles Marquises, où sa présence reste à confirmer.

***Cerithium rehderi* Houbrick, 1992**

Houbrick, 1992: 156, figs 112, 113 (description originale, localité type: "Haava Straits, between Tahuata and Hiva Oa, Marquesas, 56-72 m.").

Endémique.

Cerithium zebrum Kiener, 1841

Richard, 1985a: 417.

Rhinoclavis articulata (Adams & Reeve, 1850)

Salvat & Rives, 1975: 272 (sous le nom *Rhinoclavis gemmatus* (Hinds, 1844), espèce du Pacifique oriental, identification erronée); Houbrick, 1978: 48, pl. 20, fig. 2.

Rhinoclavis sinensis (Gmelin, 1791)

Richard, 1985a: 418.

Houbrick (1978: 53) donne une répartition géographique allant, à l'Est, jusqu'à Pitcairn, mais excluant, au Nord, les Îles Marquises, où sa présence reste à confirmer.

Dialidae

Diala semistriata (Philippi, 1849)

Ponder & de Keyser, 1992: 1022.

Planaxidae

***Angiola atra* (Pease, 1869)**

Pease, 1869: 72, fig. 4 (description originale de *Planaxis atra*, localité type: «Insl. Marquesas»); Salvat & Rives, 1975: 267 (mentionné, sans le nommer, comme étant «une variété toute noire» de *Planaxis lineatus* (Da Costa, 1776), espèce de l'Atlantique, identification erronée).

Les Planaxidae n'ont pas fait l'objet d'une révision récente. *Angiola fasciata* (Pease, 1868) décrit des Paumotus (= Archipel des Tuamotu) (Pease, 1868a: 102) est une

espèce indo-pacifique très variable qui a de nombreux synonymes et dont *Angiola atra* pourrait être la forme marquisienne.

Endémique.

Modulidae

Modulus candidus Petit de la Saussaye, 1853

Salvat & Rives, 1975: 267 (sous le nom *Modulus tectum* Gmelin, 1791, identification erronée); Tröndlé, 1989b: 16; Bouchet, 1998: 19, fig. 21 (sous le nom *M. tectum*).

Pease (1868b: 128) est le premier à considérer *Modulus candidus* comme synonyme de *Modulus tectum*. La plupart des auteurs récents ont suivi cette opinion, mais Abbott & Dance (1982: 63, figs) considèrent les deux formes comme distinctes. Tröndle (1989b: 16) suit ce dernier avis et met en évidence les différences qui séparent les deux formes et qui justifient le statut d'espèce à part entière pour chacune d'elle. En Polynésie, les deux espèces sont présentes dans tous les archipels hormis *Modulus tectum* qui, à notre connaissance, ne vit pas aux Marquises. Aucune forme intermédiaire n'a pu être observée sur les nombreux exemplaires examinés.

Littorinidae

Littoraria coccinea (Gmelin, 1791)

Richard, 1985a: 416.

Rosewater (1970) ne mentionne pas l'espèce pour les Îles Marquises. Elle est commune dans tous les archipels de Polynésie Française, **mais** sa présence aux Marquises, quoique vraisemblable, reste à confirmer.

***Nodilittorina cinerea* (Pease, 1869)**

Pease, 1869: 78, pl. 8, fig. 14 (description originale de *Littorina cinerea*, localité type: «Insl. Marquesas»); Rehder, 1969: 32; Rosewater, 1970: 505, pl. 386, figs 13-14 (lectotype), 15-18; Salvat & Rives, 1975: 264, fig. 42.

Endémique.

Nodilittorina pyramidalis (Quoy & Gaimard, 1833)

Martens & Langkavel, 1871: 40; Küster & Weinkauff, 1882: 98 (sous le nom *Littorina trochoides* Gray, 1839, synonyme); Weinkauff, 1983: 225 (sous le nom *L. trochoides*); Tryon, 1887: 258 (sous le nom *Tectarius nodulosus* (Gmelin, 1791), synonyme); Rehder, 1969: 30; Rosewater, 1970: 481; Salvat & Rives, 1975: 263, fig. 39.

Pickworthiidae

***Microliotia alvanioides* Le Renard & Bouchet, 2003**

Le Renard & Bouchet, 2003: 581, fig. 8 (description originale, localité type: «Marquesas Is, off Fatu Hiva, 10°34'S, 138°42'W, 1150-1250 m, MUSORSTOM 9, stn

DR1247»).

Endémique.

Strombidae

Lambis chiragra (Linné, 1758)

Abbott, 1961: 170.

Lambis crocata (Link, 1805)

Abbott, 1961: 158, pl. 128, figs 1-2 (description originale de *Lambis crocata pilsbryi*, localité type: «Nuku Hiva in the Marquesas Islands»); Rehder, 1969: 32; Cernohorsky, 1972: 84; Lavondes et al., 1973: 133; Kaicher, 1974: card 457; Salvat & Rives, 1975: 279, fig. 93; Abbott & Dance, 1982: 81, fig.; Bouchet, 1998: 20, fig. 26; Kreipl & Poppe, 1999: 21, pl. 17, figs 1-2, pl. 35, fig. 4; Bryce, 2000: 73, fig. 3.

L'espèce est représentée aux Îles Marquises par la sous-espèce endémique *Lambis crocata pilsbryi* Abbott, 1961.

Strombus dentatus Linné, 1758

Abbott, 1960: 84, pl. 59; Rehder, 1969: 30; Salvat & Rives, 1975: 276, fig. 86.

Strombus gibberulus Linné, 1758

Jardin, 1858: 189.

L'espèce est commune dans toute la Polynésie et y est représentée par la sous-espèce *Strombus gibberulus gibbosus* (Röding, 1798) (Abbott, 1960: 143). Abbott donne, pour la sous-espèce, une répartition géographique allant des Ryukyu à l'Indonésie et à l'Australie et donne les Tuamotu comme limite Est. Aucune récolte récente ne nous a été signalée et la présence de l'espèce aux Marquises, quoique vraisemblable, reste à confirmer.

Hipponicidae

Antisabia foliacea (Quoy & Gaimard, 1835)

Richard, 1985a: 420.

Pilosabia trigona (Gmelin, 1791)

Salvat & Rives, 1975: 281 (sous le nom *Hipponyx pilosus* Deshayes, 1831, synonyme).

Sabia conica (Schumacher, 1817)

Lavondes et al., 1973: 133; Salvat & Rives, 1975: 281.

Vanikoridae

Vanikoro cancellata (Lamarck, 1822)

Salvat & Rives, 1975: 281.

Calyptraeidae

Crepidula aculeata (Gmelin, 1791)

Garrett, 1878a: 335; Salvat & Rives, 1975: 282, fig. 101 (sous le nom *Crepidula* sp.).

Cypraeidae

Les avis sont partagés sur le bien-fondé d'utiliser différents noms de genre pour les Cypraeidae. Dans le cadre de la présente liste, nous avons par simplicité classé toutes les espèces dans le genre *Cypraea*, mais cela n'implique pas une décision taxonomique de notre part.

Cypraea arabica Linné, 1758

Jardin, 1858: 190; Hidalgo, 1906: 136, 185, 260; Lavondes et al., 1973: 133.

Cette espèce, à répartition indo-pacifique, est extrêmement rare en Polynésie Française et à Hawaïi. En Polynésie Française, elle a été récoltée avec certitude dans l'Archipel des Tuamotu (Marutea, Niau) et à Rapa (Richard & Hunon, 1991b: 13). Sa présence aux Marquises, quoique non confirmée par des récoltes récentes, est cependant vraisemblable.

Cypraea astaryi (Schilder, 1971)

Schilder, 1971: 297, pl. 1 (description originale de *Cribrarula fisheri astaryi*, localité type: «Marquesas-Inseln»); Salvat & Rives, 1975: 293, fig. 135 (sous le nom *Adusta esontropia* (Duclos, 1833), espèce de l'Océan Indien, identification erronée), fig. 136 (sous le nom *Adusta gaskoini* (Reeve, 1846), endémique de l'archipel hawaïen, identification erronée); Martin & Poppe, 1989: 6, figs, description originale de *Cribrarula lefaiti*, localité type: «Nuku Hiva, Archipelago of the Marquesas, French Polynesia», synonyme); Richard & Hunon, 1991a: 33, figs 19-20B; Burgess, 1993: 176, figs 5-7 (holotype); Lorenz & Hubert, 1993 et 2000: 181, pl. 70, figs 7-9, 11-12, 16-18; Lepetit, 1999: 16, figs 30-32; Bryce, 2000: 73, pl. 1, fig. B.

Burgess (1977a: 2) est le premier à reconnaître *Cypraea astaryi* comme bonne espèce, distincte de *Cypraea fisheri* et à considérer cette dernière comme synonyme de *Cypraea gaskoini* Reeve, 1846 [Burgess (1977b: 7)].

Lorenz & Hubert (1993 et 2000: 181) considèrent *Cypraea astaryi* comme une sous-espèce de *Cypraea cumingii* Sowerby, 1832.

Endémique.

Cypraea bistrinotata (Schilder & Schilder, 1937)

Salvat & Rives, 1975: 297; Richard & Hunon, 1991b: 35.

Lorenz & Hubert (1993 et 2000: 218) reconnaissent *Cypraea bistrinotata sublaevis* Schilder & Schilder, 1938 comme sous-espèce polynésienne.

Cypraea bouteti Burgess & Arnette, 1981

Salvat & Rives, 1975: 284 (sous le nom *Cypraea leviathan* Schilder & Schilder, 1937; identification erronée); Burgess & Arnette, 1981: 71 (description originale); Burgess, 1985: 252; Richard & Hunon, 1991b: 9.

Richard & Hunon (1991b) et Lorenz & Hubert (1993 et 2000: 70) considèrent *Cypraea bouteti* comme une sous-espèce de *Cypraea leviathan*.

Cypraea caputserpentis Linné 1758

Jardin, 1858: 190, 196; Garrett, 1879: 106; Fischer, 1891: 71; Rehder, 1969: 30; Bratcher, 1975: 4; Salvat & Rives, 1975: 286; Richard & Hunon, 1991a: 36; Lorenz & Hubert, 1993 et 2000: 206 (sous le nom *Cypraea caputophidii* Schilder, 1927, synonyme).

Nous suivons ici l'opinion générale et n'accordons pas à *Cypraea caputophidii* le statut de sous-espèce comme le font Lorenz & Hubert (1993).

L'examen d'un grand nombre d'exemplaires de *Cypraea caputserpentis* récoltés récemment aux Îles Marquises montre localement, comme dans le reste de la Polynésie, une très grande variabilité, en forme, taille et couleur. Celle-ci cependant est généralement d'un brun plus foncé pour les exemplaires récoltés aux Îles Marquises.

Cypraea carneola Linné, 1758

Jardin, 1858: 190; Garrett, 1879: 106; Fischer, 1891: 70; Hidalgo, 1906: 136, 189, 293; Dautzenberg & Bouge, 1933: 269 (sous le nom *Cypraea crassa* Gmelin, 1791 [= *Cypraea carneola carneola* Linné, 1758]); Schilder & Schilder, 1952: 224; Rehder, 1969: 30; Salvat & Rives, 1975: 283; Richard & Hunon, 1991b: 8; Bouchet, 1998: 17, fig. 2.

Nous suivons ici l'avis de Richard & Hunon (1991b) et Lorenz & Hubert (1993 et 2000: 68) et attribuons les populations de Polynésie Française à la sous-espèce *Cypraea carneola propinqua* Garrett, 1879. Burgess (1985:81) en fait une bonne espèce du Pacifique Central.

Cypraea contaminata Sowerby, 1832

Salvat & Rives, 1975: 391; Richard & Hunon, 1991b: 31, figs 83- 84; Bryce, 2000: 73.

[*Cypraea cumingii* Sowerby, 1832

Burgess, 1970: 181, pl. 13, fig B; Burgess, 1985: 240; Salvat & Rives, 1975: 293; Lorenz & Hubert, 1993 et 2000: pl. 70, fig. 1, 10.

Selon Richard & Hunon (1991b: 33), les citations de *Cypraea cumingii* pour les Îles Marquises ne sont pas fondées et correspondraient à des identifications erronées de *Cypraea astaryi* (Schilder, 1971).]

Cypraea depressa Gray, 1824

Garrett, 1879: 106 (sous le nom *Cypraea intermedia* Gray, 1824, identification erronée); Hidalgo, 1906: 138, 201, 368 (sous le nom *Cypraea gillei* Jousseaume, 1893,

synonyme); Salvat & Rives, 1975: 289; Richard & Hunon, 1991b: 13; Planes et al., 1995: 69.

Il ne fait aucun doute que la description que fait Garrett (1879) de *Cypraea intermedia* [= *C. arabica*] et la comparaison avec «*Cypraea reticulata* Martyn, 1784» [= *C. maculifera* (Schilder, 1932)] correspondent bien à *C. depressa* et non à *C. arabica*, d'autant qu'il signale par ailleurs que *C. intermedia* est plus abondante aux Tuamotu et aux Îles de la Société que nulle part ailleurs. *Cypraea arabica* est très rare en Polynésie Française.

Cypraea dillwyni Schilder 1922

Salvat & Rives, 1975: 299; Richard & Hunon, 1991a: 37.

Cypraea erosa Linné, 1758

Salvat & Rives, 1975: 286; Richard & Hunon, 1991a: 38.

Cypraea fimbriata Gmelin, 1791

Rehder, 1969: 30; Bratcher, 1975: 5; Salvat & Rives, 1975: 290, fig. 128; Richard & Hunon, 1991b: 32; Lorenz & Hubert, 1993 et 2000: 144, pl. 56, fig. 3; Lorenz, 2002: 82, pl. 21, figs 11-15 (description originale de *Purpuradusta fimbriata marquesana*, localité type: "Nuku Hiva, Marquesas Is.").

L'espèce est représentée aux Îles Marquises par la sous-espèce endémique

***Cypraea fimbriata marquesana* (Lorenz, 2002).**

Cypraea globulus Linné, 1758

Salvat & Rives, 1975: 298, fig. 152; Richard & Hunon, 1991b: 37.

Cypraea goodalli Sowerby, 183

Salvat & Rives, 1975: 295; Richard & Hunon, 1991a: 22.

Cypraea granulata Pease, 1862

Burgess, 1965: 38, pl. 4, figs E-H (description originale de *Cypraea cassiaui*, localité type: «Marquesas», sous-espèce); Burgess, 1970: 37, pl. 1, fig. C (sous le nom *C. cassiaui*); Burgess, 1985: 234 (sous le nom *C. cassiaui*); Rehder, 1969: 32 (sous le nom *C. cassiaui*); Cernohorsky, 1971: 104 et 1978: 58, pl. 16, fig. 3 (sous le nom *C. cassiaui*); Bratcher, 1975: 5 (sous le nom *C. cassiaui*); Salvat & Rives, 1975: 297, fig. 148 (sous le nom *C. cassiaui*); Abbott & Dance, 1982: 85; Richard & Hunon, 1991a: 41, figs 43-44; Cook B. & G., 1992: 5; Lorenz & Hubert, 1993: 216, pl. 101, figs 30-31, 33-34; Bouchet, 1998: 21 (sous le nom *C. cassiaui*).

Abbott & Dance (1982) mentionnent la présence de *Cypraea granulata* aux Îles Marquises et figurent la sous-espèce nominative: celle-ci ne vit pas aux Îles Marquises. C'est Richard & Hunon (1991a) qui les premiers traitent *Cypraea cassiaui* comme sous-espèce de *C. granulata*. Lorenz & Hubert (1993 et 2000) suivent cet avis. L'animal et son manteau, figurés pour la première fois par Cook B. & G. (1992), pourraient cependant donner raison à Burgess, qui considère *cassiaui* comme une bonne espèce dont la

répartition géographique s'étend aux Îles de la Ligne (Starbuck Island et Flint Island). Dans l'attente d'études plus approfondies, nous adoptons la position de Richard & Hunon.

Cypraea helvola Linné, 1758

Jardin, 1858: 190; Garrett, 1879: 106; Fischer, 1891: 73; Hidalgo, 1906: 139, 202, 376; Shaw, 1909: 311 (description originale de *Cypraea helvola* var. *callista*, localité type: Tahiti, erronée); Rehder, 1969: 30; Salvat & Rives, 1975: 286; Richard & Hunon, 1991a: 39, figs 37-38; Lorenz & Hubert, 1993 et 2000: pl. 84, figs 25-28; Bouchet, 1998: 17, fig. 3.

Aux Îles Marquises, l'espèce est représentée par la sous-espèce endémique *Cypraea helvola callista* Shaw, 1909 (Richard & Hunon, 1991a: 39). Shaw donne Tahiti comme localité et Lorenz & Hubert (1993 et 2000: pl. 84, fig. 34) illustrent un exemplaire supposé provenir des Tuamotu. Ces deux localités sont erronées.

Cypraea isabella Linné, 1758

Fischer, 1891: 69; Garrett, 1879: 106; Hidalgo, 1906: 139, 204, 389; Salvat & Rives, 1975: 296; Richard & Hunon, 1991b: 38; Planes et al., 1995: 69.

Lorenz & Hubert (1993 et 2000: 83) considèrent que l'espèce est représentée en Polynésie par la sous-espèce *Cypraea isabella controversa* Gray, 1824.

Cypraea lynx Linné, 1758

Jardin, 1858: 190; Hidalgo, 1906: 139, 207, 408; Salvat & Rives, 1975: 285; Richard & Hunon, 1991b: 10.

Cypraea maculifera (Schilder, 1932)

Garrett, 1879: 107 (sous le nom *Cypraea reticulata* Martyn, 1784, nom invalide, synonyme); Hidalgo, 1906: 141, 220, 499 (sous le nom *C. reticulata*); Rehder, 1969: 30; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 289; Richard & Hunon, 1991b: 14; Lorenz, 2002: 17, pl. 3, figs 3-7 (description originale de *Mauritia maculifera martybealsi*, localité type: "Taiohae Bay, Nuku Hiva, Marquesas Islands").

L'espèce est représentée aux Îles Marquises par la sous-espèce endémique *Cypraea maculifera martybealsi* (Lorenz, 2002).

Cypraea mappa Linné, 1758

Richard & Hunon, 1991b: 16; Martin & Laurens, 1995: 12-14, figs 1-2, 5; Bryce, 2000: 73; Lorenz, 2002: 24, pl. 6, figs 3-4.

Richard & Hunon, 1991b, Lorenz & Hubert 1993 et 2000: 64, considèrent que l'espèce est représentée en Polynésie Française par la sous-espèce *Cypraea mappa viridis* Kenyon, 1802. Lorenz, 2002 restreint l'aire de répartition géographique de *C. mappa viridis* à la Micronésie, à la Mélanésie, et au Queensland et décrit une nouvelle sous-espèce pour la Polynésie Française *Cypraea mappa aduirabilis*.

[*Cypraea mariae* (Schilder & Schilder, 1927)

Salvat & Rives, 1975: 299; Richard & Hunon, 1991b: 37.

L'espèce est peu commune en Polynésie Française. Les récoltes récentes aux Îles Marquises n'ont pas permis de confirmer sa présence.]

Cypraea mauritiana Linné, 1758

Jardin, 1858: 196; Garrett, 1879: 106, 115; Hidalgo, 1906: 140, 209, 420; Petrbook, 1932: 207, pl. 16, fig. 2 (description originale de *Mauritia mauritiana* var. *albiflora*, localité type: «Marquesas-Inseln», synonyme); Dautzenberg & Bouge, 1933: 282; Schilder & Schilder, 1952: 209; Rehder, 1969: 30; Lavondes et al., 1973: 133; Bratcher, 1975: 4; Salvat & Rives, 1975: 288, fig. 121; Richard & Hunon, 1991b: 14; Planes et al., 1995: 69.

Rarement récoltée dans les archipels de la Société, des Tuamotu et des Gambier, absente aux Îles Australes, *Cypraea mauritiana* est abondante aux Îles Marquises.

Cypraea moneta Linné, 1758

Garrett, 1879: 106; Fischer, 1891: 71; Dautzenberg & Bouge, 1933: 283; Salvat & Rives, 1975: 287, fig. 119; Richard & Hunon, 1991b: 17.

Cypraea nucleus Linné, 1758

Salvat & Rives, 1975: 297, fig. 147; Richard & Hunon, 1991a: 42.

Cypraea obvelata Linné, 1758

Jardin, 1858: 190 (sous le nom *Cypraea annulus* Linné, 1758; identification erronée); Hidalgo, 1906: 136, 184, 257 (sous le nom *C. annulus*); Salvat & Rives, 1975: 288; Richard & Hunon, 1991b: 17.

Il ne semble pas douteux que Jardin (1858) et Hidalgo (1906) se soient trompés. *Cypraea obvelata* remplace *Cypraea annulus* dans l'Est de la Polynésie, avec cependant une zone de sympatrie allant, du Nord-Est au Sud-Ouest, des Îles de la Ligne aux Îles Cook et aux Samoa. Les coquilles sont très proches et il est difficile de distinguer les juvéniles des deux espèces. L'animal semble cependant suffisamment différent pour justifier la reconnaissance de deux espèces distinctes (Burgess, 1985: 227, 230). Nous ne suivons pas ici l'avis de Richard & Hunon (1991b) qui traitent *Cypraea obvelata* comme sous-espèce de *Cypraea annulus*. Lorenz & Hubert (1993 et 2000: 204) considèrent *Cypraea obvelata* comme une bonne espèce, sans toutefois la citer des Îles Marquises.

Cypraea pellucens Melvill, 1888

Salvat & Rives, 1975: 295, fig. 141 (sous le nom *Erronea lator* (Melvill, 1888), identification erronée); Burgess, 1985: 264 (sous le nom *Cypraea alisonae* Burgess, 1983, synonyme); Richard & Hunon, 1991a: 21, figs 7-8 (sous le nom *Bistolida burgessi* (Kay, 1981), identification erronée); Lorenz & Hubert, 1993 et 2000: 164, pl. 73, figs 27-28, 30-31; Lorenz, 2002: 93, figs 2 et 5.

Cypraea poraria Linné, 1758

Salvat & Rives, 1975: 287; Richard & Hunon, 1991a: 40

En Polynésie Française, *Cypraea poraria scarabeus* Valenciennes in Bory de Saint Vincent, 1827, traitée comme synonyme par Lorenz & Hubert, 1993 et 2000: 203, est reconnue comme sous-espèce par Richard & Hunon (1991a).

Cypraea punctata Linné, 1758

Garrett, 1879: 107; Hidalgo, 1906: 141, 217, 482; Rehder, 1969: 30 (sous le nom *Cypraea atomaria* Gmelin, 1791 [= *Cypraea punctata punctata*]); Salvat & Rives, 1975: 291; Richard & Hunon, 1991b: 33.

L'espèce est représentée en Polynésie Française par la sous-espèce *Cypraea punctata trizonata* (Sowerby, 1870) (Richard & Hunon, 1991b, Lorenz & Hubert, 1993 et 2000: 184).

Cypraea schilderorum (Iredale, 1939)

Salvat & Rives, 1975: 284; Richard & Hunon, 1991b: 10; Planes et al., 1995: 69.

Cypraea scurra Gmelin, 1791

Garrett, 1879: 107; Salvat & Rives, 1975: 290; Richard & Hunon, 1991b: 15.

Lorenz & Hubert, 1993: 56, considèrent que l'espèce est représentée en Polynésie Française par la sous-espèce *Cypraea scurra indica* (Gmelin, 1791). Lorenz, 2002: 21 décrit une nouvelle sous-espèce *Cypraea scurra mundula* dont il limite la répartition géographique aux Îles de la Société et aux Tuamotu et pense que la population des Marquises pourrait représenter une nouvelle sous-espèce.

Cypraea subteres Weinkauff, 1880

Salvat & Rives, 1975: 294; Richard & Hunon, 1991a: 21.

Cypraea talpa Linné, 1758

Salvat & Rives, 1975: 295; Richard & Hunon, 1991b: 39.

Cypraea teres Gmelin, 1791

Garrett, 1879: 107 (sous le nom *C. tabescens* Dillwyn, 1817, synonyme); Hidalgo, 1906: 141, 218, 484 (sous le nom *C. punctulata* Gmelin, 1791, identification erronée); Richard & Hunon, 1991a: 20, figs 3-4.

***Cypraea thomasi* Crosse, 1865**

Crosse, 1865: 57 (description originale, sans localité); Rehder, 1969: 30 (sous le nom *C. beckii* Gaskoin, 1836, identification erronée *vide* Rehder, 1984: 1); Rehder, 1984: 1, figs 4-6, 10-12; Burgess, 1985: 121; Rehder, 1986: 12, figs 1-9; Burgess, 1994: 12, pl. 1; Richard & Hunon, 1991a: 41, figs 41-42; Poppe, 1993: 32, figs 1-7a (description originale de *Cypraea philmarti*, localité type: «Marquises», synonyme); Lillico, 1993: 3; Lorenz & Hubert, 1993 et 2000: 209, pl. 92, figs 31-35; Simonet, 1994: 1, 6-7, pl. 1; Bryce, 2000: 73.

Endémique.

Cypraea tigris Linné, 1758

Jardin, 1858: 190; Garrett, 1879: 107; Rehder, 1969: 30; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 283; Richard & Hunon, 1991a: 34; Planes et al., 1995: 69; Bouchet, 1998: 17, fig. 1.

Cypraea ventriculus Lamarck, 1810

Jardin, 1858: 190; Hidalgo, 1906: 143, 227, 551; Salvat & Rives, 1975: 284; Richard & Hunon, 1991b: 11.

Cypraea vitellus Linné, 1758

Garrett, 1879: 107; Fischer, 1891: 70; Hidalgo, 1906: 143, 228, 559; Salvat & Rives, 1975: 285; Richard & Hunon, 1991b: 12.

Ovulidae

***Phenacovolva carneopicta* Rehder & Wilson, 1975**

Rehder & Wilson, 1975: 6, figs 6, 9, 12 (description originale, localité type: "Haava Strait, between Tahuata et Hiva Oa, Marquesas Islands, on *Antipathes* sp., in 32 fms" [= 60 m]); Kaicher, 1991, card 5962 (holotype figuré).

Endémique.

Naticidae

Natica gualteriana Récluz, 1844

Salvat & Rives, 1975: 300, fig. 158.

Natica orientalis Gmelin, 1791

Jardin, 1858: 188, 193 (description originale de *Natica nukahivensis*, localité type: «Îles Marquises», synonyme).

Natica nukahivensis n'a jamais été figurée et sa validité est mise en doute par les auteurs ultérieurs. Jardin en donne une description succincte, mais suffisamment précise, nous semble-t-il, pour y reconnaître *Natica orientalis*, seule espèce des Îles Marquises qui corresponde à cette description. La synonymie est établie ici pour la première fois. Depuis Jardin, cette espèce indo-pacifique n'a jamais été citée de Polynésie Française, où elle est pourtant présente aux Tuamotu et aux Îles de la Société (Tröndle, inédit).

Polinices melanostoma (Gmelin, 1791)

Salvat & Rives, 1975: 301.

Bursidae

Charonia tritonis (Linné, 1758)

Jardin, 1858: 189 (sous le nom *Triton variegatum* Lamarck, 1822, synonyme, en partie); Lavondes et al., 1973: 125.

Bursa asperrima (Dunker, 1862)

Salvat & Rives, 1975: 307 (sous le nom *Bursa cruentata* (Sowerby, 1835), identification erronée).

L'espèce, souvent confondue avec *Bursa cruentata*, nous est connue des Îles de la Société et l'exemplaire représenté par Salvat & Rives (1975: fig. 180) provient de Makemo (Archipel des Tuamotu). Hormis la citation de Salvat & Rives, aucune découverte récente de l'espèce aux Marquises n'a été portée à notre connaissance. Cependant, sa présence à Hawaii et Clipperton (Beu, 1998: 146) et aux Îles Galapagos (Emerson, 1991: 68) laisse supposer que *Bursa asperrima* vit également aux Marquises.

Bursa bufonia (Gmelin, 1791)

Rehder, 1969: 31; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 308.

Bursa cruentata (Sowerby, 1835)

Rehder, 1969: 31.

Bursa granularis (Röding, 1798)

Jardin, 1858: 189 (sous le nom *Ranella granifera* Lamarck, 1816, synonyme); Rehder, 1969: 31; Salvat & Rives, 1975: 307; Planes et al., 1995: 69.

Bursa lamarckii (Deshayes, 1853)

Beu, 1998: 155.

Bursa latitudo Garrard, 1961

Beu, 1998: 157.

Bursa rhodostoma (Sowerby, 1835)

Salvat & Rives, 1975: 307, fig. 181; Bouchet, 1998: 17, fig. 9.

Tutufa bubo (Linné, 1758)

Rehder, 1969: 31 (sous le nom *Bursa lampas* (Linné, 1758), synonyme, en partie); Lavondes et al., 1973: 133 (sous le nom *B. lampas*); Salvat & Rives, 1975: 307, fig. 178.

Cassidae

Casmaria erinaceus (Linné, 1758)

Abbott, 1968: 190, pl. 14, figs 7-12, 17, pl. 179; Salvat & Rives, 1975: 302.

L'espèce est représentée en Polynésie Française par la sous-espèce *Casmaria erinaceus kalosmodix* (Melvill, 1883).

Cypraecassis rufa (Linné, 1758)

Jardin, 1858: 188; Rehder, 1969: 30; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 302.

Personidae

Distorsio amus (Linné, 1767)

Salvat & Rives, 1975: 306.

Distorsio graceiellae Parth, 1989

Beu, 1998: 188, figs 60k, o-p.

Ranellidae

Cymatium aquatile (Reeve, 1844)

Rehder, 1969: 31.

[*Cymatium armatum* (Sowerby, 1897)

Sowerby, 1897: 137, pl. 11, fig. 1 (description originale, localité type „Marquesas Is.“); Kaicher, 1982: card 3293 (holotype figuré).

Beu (1998: 115) estime que la localité type de cette espèce peu commune est vraisemblablement erronée: Les seuls exemplaires connus à ce jour ont été récoltés dans le Nord du Queensland, en Nouvelle Calédonie et au Vanuatu.]

Cymatium hepaticum (Röding, 1798)

Salvat & Rives, 1975: 305, fig. 170, droite; Beu, 1987: 282.

Cymatium intermedium (Pease, 1869)

Beu & Kay, 1988: 200; Salvat & Rives, 1975: 305, fig. 172 gauche (sous le nom *C. pileare* Linné, 1758, identification erronée).

Cymatium lotorium (Linné, 1758)

Salvat & Rives, 1975: 304, fig. 168.

Cymatium mundum (Gould, 1849)

Salvat & Rives, 1975: 305, fig 173 (sous le nom *C. gemmatum* Reeve, 1844; identification erronée).

Cymatium muricinum (Röding, 1798)

Richard, 1985a: 422.

Cymatium nicobaricum (Röding, 1798)

Rehder, 1969: 31.

Cymatium peasei Beu, 1987

Beu, 1987: 287, figs 46-47, 50-51 (description originale, localité type: „inside patches of living and dead coral in 1.2-2.4 m, Taiohae Bay, north coast of Nuku Hiva, Marquesas Islands“); Salvat & Rives, 1975: 305, fig. 170 gauche (sous le nom *C. hepaticum* (Röding, 1798), identification erronée); Henning & Hemmen, 1993: 95.

Cymatium pileare (Linné, 1758)

Jardin, 1858: 189; Rehder, 1969: 31; Salvat & Rives, 1975: 305, fig. 172, droite.

Cymatium rubeculum (Linné, 1758)

Rehder, 1969: 31.

Epitoniidae

***Amaea boucheti* Garcia, 2003**

Garcia, 2003: 3, figs 13-15 (description originale, localité type: „Marquesas Islands, off Fatu Hiva, 10°34' S, 138° 424 W, in 1150-1250 m [MUSORSTOM 9, sta. DR1247]“).

Endémique.

Cylindriscala humerosa (Schepman, 1909)

Garcia, 2003: 11, fig. 50.

Epitonium stigmaticum (Pilsbry, 1911)

Garcia, 2003: 14, fig. 62.

Eulimidae

Pulicicochlea faba Ponder & Gooding, 1978

Ponder & Gooding, 1978: 171.

Muricidae

[*Azumamorula mutica* (Lamarck, 1816)

Jardin, 1858: 189.

L'espèce ne vit pas en Polynésie. C'est une espèce de l'Océan Indien. Nous ne savons pas ce que Jardin a vu.]

Aspella producta (Pease, 1861)

Tröndlé & Houart, 1992: 81.

Chicoreus maurus (Broderip, 1833)

Tryon, 1880: 89; Rehder, 1969: 32 (sous le nom *Chicoreus steeriae* (Reeve, 1845), synonyme); Lavondes et al., 1973: 133 (sous le nom *C. steeriae*); Salvat & Rives, 1975: 311, fig. 192 (sous le nom *C. steeriae*), fig. 193 (sous le nom *C. torrefactus* Sowerby, 1841, identification erronée); Radwin & D'Attilio, 1976: 39; Fair, 1976: 78, pl. 8, fig. 106 (sous le nom *C. steeriae*); Cernohorsky, 1978a: 72, figs 18-19; Cernohorsky, 1978b: 65, pl. 18, fig. 2; Abbott & Dance, 1982: 136, fig.; Tröndlé & Houart, 1992: 72, fig. 1; Houart, 1992: 51, figs 289, 291; Bouchet, 1998: 20, fig. 27.

Longtemps considérée comme endémique des Îles Marquises (Salvat & Rives,

1975, Cernohorsky, 1978a, 1978b), l'espèce a une répartition Pacifique plus large (Abbott & Dance, 1982) et a notamment été récoltée dans l'Archipel des Tuamotu (Anaa, Kaukura), à Tahiti (Tröndlé & Houart, 1992) et en Nouvelle Calédonie (MNHN). La localité type de *Chicoreus maurus* («Ad Insulam Annaam in Oceano Pacifico» [= Anaa, Archipel des Tuamotu] n'est donc pas nécessairement erronée comme le suppose Cernohorsky (1978a).

[*Chicoreus microphyllus* (Lamarck, 1822)

Richard, 1985a: 423.

Hormis la citation de Richard, l'espèce n'a jamais été mentionnée pour la Polynésie où sa présence n'est pas vraisemblable. Houart (1992: 59) donne les Îles Fiji comme limite Est.]

Chicoreus ramosus (Linné, 1758)

Jardin, 1858: 189; Rehder, 1969: 3; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 311, fig. 191; Tröndlé & Houart, 1992: 73; Houart, 1992: 43.

Chicoreus rubescens (Broderip, 1833)

Tröndlé & Houart, 1992: 73.

***Chicoreus thomasi* (Crosse, 1872)**

Crosse, 1872: 212 (description originale, localité type: «Nouka- Hiva, insularum "Marquises" dictarum Oceaniae» [= Nuku Hiva]); Crosse, 1873: 249, pl. 11, fig. 4; Kobelt, 1877: 150; Paetel, 1888: 29; Rehder, 1969: 32; Salvat & Rives, 1975: 312, fig. 194; Radwin & D'Attilio, 1976: 39 (sous le nom synonyme de *C. maurus*, erreur); Fair, 1976: 81, fig. 62; Cernohorsky, 1978a: 74, figs 20 (holotype), 21; Cernohorsky, 1978b: 65, pl. 18, fig. 4; Tröndlé & Houart, 1992: 74, figs 15-16; Houart, 1992: 86, figs 388-389; Bouchet, 1998: 20, figs 22-23; Bryce, 2000: 73.

Endémique.

Chicoreus venustus Rehder & Wilson, 1975

Rehder & Wilson, 1975: 7, figs 4-5 (description originale, localité type: «off SW coast of Tahuata, 36-39 fms» [= 66-71 m]); Cernohorsky, 1978: 65, fig. 5 (holotype); Tröndlé & Houart, 1992: 75, fig. 18 (holotype); Houart, 1992: 124, figs 225 (holotype); Bouchet, 1998: 21; Kaicher, 1978: card 1596.

Cronia avenacea (Lesson, 1842)

Tröndlé & Houart, 1992: 86.

L'espèce, à large distribution indo-pacifique, a souvent été figuré dans la littérature sous le nom *Vexilla fusconigra* Pease, 1860, qui est un synonyme (Tröndlé & Houart, 1992). En Polynésie, l'espèce est connue des Tuamotu, des Gambier (localité type de *Purpura avenacea*) et essentiellement des Marquises, où elle est commune.

Cronia margariticola (Broderip, 1833)

Lesson, 1842c: 186 (description originale de *Purpura violacea* Lesson, 1842, non Kiener, 1836, localit  type:  les Gambier et Marquises, synonyme); Tryon, 1880: 192, 261 (sous le nom *P. violacea*).

Dautzenberg & Bouge (1933: 219) n'ont pas reconnu l'esp ce et la trouvent « douteuse ». Tryon dit qu'elle est voisine de *Thais marginatra* (Blainville, 1832),  galement pr sent aux  les Marquises, mais bien diff rent. L'esp ce est tr s variable et a eu de nombreux synonymes (Cernohorsky, 1982a: 116). Tr ndl  & Houart (1992: 85), apr s examen du type de *Purpura violacea*, conserv  au MNHN, et comparaison avec une centaine d'exemplaires de *Cronia margariticola* des diff rents archipels polyn siens, ont mis les deux taxons nominaux en synonymie.

Cronia submissus (E. A. Smith, 1903)

Tr ndl  & Houart, 1992: 87, fig. 42.

Cytharomorula cf. *grayi* (Dall, 1889)

Tr ndl  & Houart, 1992: 88, fig. 48.

Drupa clathrata (Lamarck, 1816)

Emerson & Cernohorsky, 1973: 31, pl. 2, figs. 16-18; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 316; Tr ndl  & Houart, 1992: 110, figs 97, 106-107; Bouchet, 1998: 17, fig. 7.

Drupa elegans (Broderip & Sowerby, 1829)

Salvat & Rives, 1975: 315; Tr ndl  & Houart, 1992: 107.

Drupa grossularia R d ng, 1798

Rehder, 1969: 31; Emerson & Cernohorsky, 1973: 35; Tr ndl  & Houart, 1992: 112.

Drupa morum R d ng, 1798

Lesson, 1840: 355 (description originale de *Purpura iodostoma*, localit  type: «Nova-Zelandia» [= Nouvelle Z lande], erreur, sous-esp ce selon Emerson & Cernohorsky, 1973); Lesson, 1842: 102 (correction de la localit  type: «exclusivement des  les Marquises <»); Jardin, 1858: 188 (sous le nom *Ricinula horrida* Lamarck, 1816 [= *Drupa morum* R d ng, 1798], esp ce nominative absente aux Marquises), 189 (sous le nom *Ricinula iodostoma*); Rehder, 1969: 32 (sous le nom *Drupa iodostoma*); Lavondes et al., 1973: 133 (sous le nom *D. iodostoma*); Emerson & Cernohorsky, 1973: 18, pl. 2, figs 4-5 (sous le nom *D. morum iodostoma*, restriction de la localit  type : «Taiohae, Nuku Hiva Island, Marquesas Islands»); Salvat & Rives, 1975: 314, fig. 204; Cernohorsky, 1978: 68, pl. 19, fig. 7; Kaicher, 1980: card 2397 (sous le nom *D. iodostoma*); Abbott & Dance, 1982: 150; Tr ndl  & Houart, 1992: 108, fig. 96; Planes et al., 1995: 69; Bouchet, 1998: 17, fig. 8.

L'esp ce est repr sent e aux  les Marquises par la sous-esp ce end mique *Drupa morum iodostoma* (Lesson, 1840).

Drupa ricinus (Linné, 1758)

Jardin, 1858: 188 (sous le nom *albolabris* Blainville, 1832 et *arachnoidea* Lamarck, 1816, synonymes); Rehder, 1969: 31; Emerson & Cernohorsky, 1973: 19; Tröndlé & Houart, 1992: 109; Planes et al., 1995: 69.

Drupa rubusidaeus Röding, 1798

Crosse, 1862: 47, pl. 1, fig. 3 (description originale de *Ricinula reeveana* Crosse, 1862 non C.B. Adams, 1852, localité type: «Nouhiva insularum Marqueses» [= Nuku Hiva], synonyme); Paetel, 1883: 20 (sous le nom *R. reeveana*); Salvat & Rives, 1975: 315; Tröndlé & Houart, 1992: 111.

Drupa speciosa (Dunker, 1867)

Salvat & Rives, 1975: 315, fig. 208; Tröndlé & Houart, 1992: 111.

Drupella cornus (Röding, 1798)

Rehder, 1969: 31; Tröndlé & Houart, 1992: 95.

Habromorula porphyrostoma (Reeve, 1846)

Reeve, 1846: pl. 2, fig. 7. (description originale, localité type: "Marquesas Islands (on the reefs at low water)"); Paetel, 1883: 19; Dautzenberg & Bouge, 1933: 243 (sous le nom *Purpura dumosa* Conrad, 1837, *nomen dubium fide* Tröndlé & Houart, 1992), 247; Cernohorsky, 1982b: 126, figs 6-9 (sous le nom *Morula dumosa*); Tröndlé & Houart, 1992: 106, fig. 89; Houart, R. 1994: 27, fig. 13 (lectotype).

[*Habromorula biconica* (Blainville, 1832)

Richard, 1985a: 424.

Hormis la citation de Richard, l'espèce n'a jamais été mentionnée pour la Polynésie Française et aucune récolte récente n'a été signalée (Tröndlé & Houart, 1992: 70). Nous pensons que *Habromorula biconica* ne vit pas aux Îles Marqueses.]

Homalocantha anatomica (Perry, 1811)

Rehder, 1969: 31; Salvat & Rives, 1975: 313, fig. 198; Tröndlé & Houart, 1992: 80, fig. 31.

Maculotrion serriale (Deshayes, 1830)

Lesson, 1842f: 200 (description originale de *Columbella pulicaris*, localité type: Îles Marqueses, synonyme); Lesson, 1842c: 185; Hinds, 1844b: 21 (description originale de *Triton bracteatus*, localité type composite: «Marquesas; New Ireland; Straits of Malaca: on the shores and in seventeen fathoms, mud», synonyme); Paetel, 1883: 12 et 1888: 98 (sous le nom *T. bracteatus*), 212 (sous le nom *C. pulicaris*); Hedley, 1899: 456 (sous le nom *Tritonium digitale*, Reeve, synonyme); Lamy, 1926: 382; Rehder, 1969: 31; Salvat & Rives, 1975: 317, fig. 217; Cernohorsky, 1982b: 130 (restriction de la localité type de *Triton bracteatus* à Straits of Malaca, Indonesia); Tröndlé & Houart, 1992: 90, fig. 56 (syntype de *C. pulicaris*).

Tröndlé & Houart (1992: 90), après examen des deux syntypes de *Columbella pulicaris*, conservé au MNHN, et comparaison avec une centaine d'exemplaires de *Maculotriron serriale* des différents archipels polynésiens, ont mis les deux taxons nominaux en synonymie.

[*Mancinella aculeata* Deshayes & Milne Edwards, 1844
Astary, 1973: 7.

Hormis la citation d'Astary, sans localité précise, cette espèce, à large répartition indo-pacifique et connue en Polynésie dans les archipels de la Société, des Tuamotu et des Gambier, n'a jamais été mentionnée des Marquises. Les récoltes récentes aux Îles Marquises n'ont pas permis de confirmer sa présence.]

Mancinella tuberosa (Röding, 1798)

Lesson, 1842: 103 (sous le nom *Purpura pica* Blainville, 1832, synonyme);
Tröndlé & Houart, 1992: 99.

[*Morula anaxeres* (Kiener, 1835)

Richard, 1985a: 424.

Bien que l'espèce ait été citée par Tryon (1880) et Dautzenberg & Bouge (1933) pour la Polynésie Française, aucune récolte récente nous a été signalée et sa présence aux Îles Marquises est douteuse.]

Morula granulata (Duclos, 1832)

Rehder, 1969: 31; Tröndlé & Houart, 1992: 100.

Morula uva (Röding, 1798)

Jardin, 1858: 189 (sous le nom *Ricinula morus* Lamarck, 1816, synonyme);
Dautzenberg & Bouge, 1933: 246 (sous le nom *Ricinula nodus* Lamarck, 1816,
synonyme); Rehder, 1969: 31; Tröndlé & Houart, 1992: 104, figs 82.

Murexiella rosamiae (d'Attilio & Myers, 1985)

Houart & Tröndlé, 1997: 3.

Nassa tuamotuensis Houart, 1996

Rehder, 1969: 31 (sous le nom *Nassa sertum* (Bruguière, 1789), identification erronée); Salvat & Rives, 1975: 318 (sous le nom *Nassa francolinus* (Bruguière, 1789), identification erronée); Tröndlé & Houart, 1992: 113, fig. 13 (sous le nom *N. francolinus*).

Les exemplaires récoltés aux Marquises par Rehder (1969) sont conformes à ceux figurés par Salvat & Rives (1975: 318, fig. 219) (Rehder, communication personnelle) et sont identifiables à *Nassa tuamotuensis*. *Nassa sertum* semble n'être présent en Polynésie Française que dans l'Archipel des Australes (Tröndlé & Houart, 1992; Houart, 1996: 53), actuellement considéré comme la limite Est de son aire de répartition., et *Nassa francolinus* vit exclusivement dans l'Océan Indien (Houart, 1996: 52).

Orania pacifica (Nakayama, 1988)

Tröndlé & Houart, 1992: 102, fig. 81; Houart, 1995: 272.

***Orania simonetae* Houart, 1995**

Houart, 1995: 272, figs 140-141 (description originale, localité type: «Nuku Hiva, Marquesas Islands, living at 30 m»); Houart & Tröndlé, 1997: 3, figs 1-2 (holotype).
Endémique.

Pascula muricata (Reeve, 1846)

Salvat & Rives, 1975: 316 (sous le nom *Drupella ochrostoma* (Blainville, 1832), identification erronée); Tröndlé & Houart, 1992: 114 (sous le nom *Pascula* sp.).

Pascula ozenneana (Crosse, 1861)

Dautzenberg & Bouge, 1933: 247; Tröndlé & Houart, 1992: 88, fig. 43.

Phyllocoma convoluta (Broderip, 1833)

Tryon, 1880: 25; Salvat & Rives, 1975: 309, fig. 187.

Pteryarchia bouteti (Houart, 1990)

Houart, 1990: 9 (description originale); Tröndlé & Houart, 1992: 77.

Pteryarchia tripterus (Born, 1778)

Salvat & Rives, 1975: 312, fig. 195; Tröndlé & Houart, 1992: 79.

Pterynotus loebbeckei (Kobelt, 1879)

Tröndlé & Houart, 1992: 78, fig. 24.

Purpura persica (Linné, 1758)

Lavondes et al., 1973: 133; Salvat & Rives, 1975: 314, fig. 202; Tröndlé & Houart, 1992: 95, fig. 66; Planes et al., 1995: 69.

Spinidrupa euracantha (A. Adams, 1853)

Tröndlé & Houart, 1992: 105.

Thais armigera (Link, 1807)

Lesson, 1842d: 211; Lesson, 1842f: 206; Dautzenberg & Bouge, 1933: 232; Lavondes et al., 1973: 133; Tröndlé & Houart, 1992: 92.

Thais foliacea (Conrad, 1837)

Tröndlé & Houart, 1992: 92.

Thais marginatra (Blainville, 1832)

Tröndlé & Houart, 1992: 93, fig. 63.

Vexilla vexillum (Gmelin, 1791)

Salvat & Rives, 1975: 317, fig. 218.

(Coralliophilinae)

Coralliophila bulbiformis (Conrad, 1837)

Salvat & Rives, 1975: 310 (sous le nom *Coralliophila costularis* (Lamarek, 1816), identification erronée); Rehder, 1985: 98; Trondlé, 1989a: 19.

Coralliophila clathrata (A. Adams, 1854)

Robertson, 1981: 8, figs 8,9 (lectotype); Trondlé, 1989a: 19.

Coralliophila violacea (Kiener, 1836)

Jardin, 1858: 188; Rehder, 1969: 31.

Coralliophila monodonta (Blainville, 1832)

Hombroun & Jaquinot, 1852: 92, pl. 22, figs 34-35 (sous le nom *Purpura madreporarum* Sowerby, 1834, synonyme); Jardin, 1858: 188, 194 (sous le nom *P. madreporarum*); Rehder, 1969: 31 (sous le nom *Quoyula madreporarum*).

Rhizochilus antipathum Steenstrup, 1852

Trondlé, 1989a: 25.

Buccinidae

Caducifer decapitata (Reeve, 1844)

Rehder, 1969: 31, 1980: 81.

L'espèce est représentée en Polynésie par la sous-espèce *Caducifer decapitata cylindrica* (Pease, 1868).

[*Caducifer truncata* (Hinds, 1844)

Richard, 1985a: 425.

Cernohorsky (1971b: 147) et Richard (1985a: 425) considèrent *Caducifer decapitata* (Reeve, 1844) synonyme de l'espèce. Nous suivons ici l'avis de Rehder (1980: 81) qui estime *Caducifer decapitata* différent et donne Ryukyu, les Îles Fiji et Samoa comme aire de répartition géographique pour *Caducifer truncata*. Cette espèce n'est pas présente en Polynésie Française.]

Clivipollia fragaria (Wood, 1828)

Salvat & Rives, 1975: 319, fig. 224 (sous le nom *Engina bella* (Reeve, 1846), synonyme).

Colubraria nitidula (Sowerby, 1833)

Richard, 1985a: 423.

Colubraria cf. obscura (Reeve, 1844)

Salvat & Rives, 1975: 308, fig. 184 (sous le nom *Colubraria nitidula* (Sowerby, 1833), identification erronée).

Colubraria souverbii (Reeve, 1844)

Bouchet, 1998: 20, figs 24-25.

Colubraria tortuosa (Reeve, 1844)

Jardin, 1858: 189 (sous le nom *Triton distortum* Schubert & Wagner, 1829 (non Lamarck, 1816), synonyme).

Hormis cette citation, aucune découverte récente de l'espèce aux Marquises n'a été portée à notre connaissance. Cependant l'espèce a une large répartition indo-pacifique et est connue de la Société et des Tuamotu. Sa présence aux Marquises est vraisemblable.

[*Engina alveolata* (Kiener, 1836)

Richard, 1985a: 425.

L'espèce a souvent été confondue avec *Engina siderea* (Reeve, 1846). Elle est commune dans tout l'Indo-Pacifique, mais rare en Polynésie Française, où elle nous a été signalée sans que nous ayons personnellement examiné le matériel. Nous pensons que *Engina alveolata* n'est pas présent aux Îles Marquises.]

Engina siderea (Reeve, 1846)

Cernohorsky, 1975: 180, figs 12-13.

En Polynésie Française *Engina sidera* est présent dans tous les archipels.

Phos dumale (Philippi, 1851)

Philippi, 1851a: 60 (description originale, localité type: «Insulae Marquesas»); Paetel, 1888: 117.

Pollia undosus (Linné, 1758)

Rehder, 1969: 31; Salvat & Rives, 1975: 318; Planes et al., 1995: 69.

Prodotia iostomus (Gray in Griffith & Pidgeon, 1834)

Petit de la Saussaye, 1853: 239, 244, pl. 8, fig. 5 (description originale de *Phos billeheusti*, localité type: «Nouka-Hiva» [= Nuku Hiva], synonyme); Cernohorsky, 1986: 59, fig. 8.

Columbellidae

Metanachis marquesa (Gaskoin, 1851)

Gaskoin, 1852: 8 (description originale, localité type: «Marquesas»); Paetel, 1883: 24, 1888: 92; Sleurs, 1985: 271 (sous le nom *Metanachis jaspidea* (Sowerby, 1844)).

Nous ne suivons pas ici l'avis de Sleurs (1985) qui traite *Metanachis marquesa* comme synonyme de *Metanachis jaspidea*. Les coquilles sont proches, cependant les

caractères de *Metanachis marquesa* sont constants et suffisamment différents de ceux de *Metanachis jaspidea*, nous semble-t-il, pour justifier la reconnaissance de deux espèces distinctes.

Pyrene flava (Bruguière, 1789)

Richard, 1985a: 426.

Pyrene livescens (Reeve, 1859)

Richard, 1985a: 426.

Pyrene obtusa (Sowerby, 1834)

Salvat & Rives, 1975: 320 (sous le nom *Pyrene flava* (Bruguière, 1789), identification erronée); Kaicher, 1984: card 3838.

[*Pyrene scripta* (Lamarck, 1822)

Richard, 1985a: 426.

Hormis cette citation, l'espèce n'a jamais été mentionnée pour la Polynésie Française. Nous ne pensons pas que *Pyrene scripta* soit présent aux Marquises.]

Pyrene turturina (Lamarck, 1822)

Salvat & Rives, 1975: 320, fig. 226.

Pyrene varians (Sowerby, 1832)

Salvat & Rives, 1975: 320 (sous le nom *Pyrene scripta* (Lamarck, 1822), identification erronée).

Nassariidae

Nassarius candens (Hinds, 1844)

Hinds, 1844: 35, pl. 9, figs 6-7 (description originale, localité type: "Marquesas"); A. Adams, 1852: 95; Paetel, 1883: 16, 1888: 122 ; Salvat & Rives, 1975: 321; Cernohorsky, 1978b: 81, pl. 24, fig. 7; Richard et al., 1984: 8, fig. 5 (syntypes), 6; Cernohorsky, 1984: 84, pl. 8, figs 5-6 (lectotype), 7; Kaicher, 1983: card 3481 (syntype figuré).

Malgré l'illustration d'un exemplaire par Salvat & Rives (1975, fig. 232), la présence à l'Australian Museum (Sydney) et à la Smithsonian Institution (Washington) de spécimens donnés comme provenant de Tahiti, nous pensons que cette provenance est erronée et que l'espèce est endémique des Îles Marquises, où elle est abondante.

Endémique.

Nassarius dijki (Martin, 1895)

Cernohorsky, 1992: 72, figs 9-10.

Nassarius gaudiosus (Hinds, 1844)

Salvat & Rives, 1975: 321, fig. 231; Richard et al., 1984: 10, fig. 15; Cernohorsky, 1984: 113.

Nassarius glans (Linné, 1758)

Salvat & Rives, 1975: 321, fig. 230; Richard et al., 1984: 10, fig. 17; Cernohorsky, 1991a: 188.

Nassarius haldemanni (Dunker, 1847)

Cernohorsky, 1991a: 201, fig. 12.

Nassarius hirtus (Kiener, 1834)

Cernohorsky, 1984: 64.

[*Nassarius olivaceus* (Bruguière, 1789)

Lesson, 1842e: 237.

Lesson n'a pas figuré son matériel. L'espèce n'est pas connue, à l'Est, au-delà des Îles Fidji. La description qu'en fait Lesson semble indiquer une erreur d'identification pour *Nassarius gaudiosus* (Hinds, 1844).]

Nassarius papillosus (Linné, 1758)

Lesson, 1842e: 237; Salvat & Rives, 1975: 320, fig. 229 (haut); Rehder, 1969: 31; Richard et al., 1984: 12, fig. 23; Cernohorsky, 1984: 60.

Nassarius vittatus (A. Adams, 1851)

Dautzenberg & Bouge, 1933: 212 (sous le nom *Nassa glabrata* A. Adams, 1851, synonyme), 216; Richard et al., 1984: 14, fig. 34; Cernohorsky, 1984: 192.

Cette espèce à répartition indo-pacifique n'est connue en Polynésie que des Îles Marquises où elle est abondante.

[Melongenidae]

[*Semifusus lacteus* (Reeve, 1847)

Dautzenberg & Bouge, 1933: 206.

Reeve décrit *Pyrula lactea* des Îles Philippines et hormis la citation de Dautzenberg & Bouge, l'espèce n'a jamais été mentionnée pour la Polynésie Française.]

Fasciolaridae

***Cyrtulus serotinus* Hinds, 1843**

Hinds, 1843: 257 (description originale, localité type: «Port Anna Maria, Nuku Hiva, I. Marquises»); Jardin, 1858: 189, 195; Dautzenberg & Bouge, 1933: 199; Salvat & Rives, 1975: fig. 237; Bouchet, 1998: 21. Bryce, 2000: 73, 74, fig. 5. Bryce, 2000: 73, 74, fig. 5.

Endémique.

Fusinus undatus (Gmelin, 1791)

Richard, 1985a: 427.

[*Fusus bernardianus* Philippi, 1851

Philippi, 1851b: 76 (description originale, localité type: «Insulae Marquesas»); Kobelt, 1881: 214; Paetel, 1888: 35.

L'espèce, non figurée, n'a pas été reconnue et doit être traitée comme *nomen dubium*.]

[*Fusus frondosus* Lesson, 1842

Lesson, 1842d: 214 (description originale, localité type: «Îles Marquises»).

L'espèce, non figurée, n'a pas été reconnue et doit être traitée comme *nomen dubium*.]

Latirus amplustris (Dillwyn, 1817)

Richard, 1985a: 427.

L'espèce, rare en Polynésie Française, n'est représentée au MNHN que par quelques exemplaires récoltés dans les Tuamotu. Sa présence aux Marquises demande confirmation.

***Latirus fallax* (Kobelt, 1876)**

Kobelt, 1876a: 80, pl. 19, fig. 3 (description originale, localité type: „unbekannt, vermuthlich in Polynesian“); Lavondes et al., 1973: 124; Kaicher, 1978: card 1829; *non* Rehder, 1969: 32 (identification erronée vraisemblable pour *Latirus sanguifluus*, Rehder communication personnelle).

L'espèce semble rare et n'a pu être examinée dans aucune collection récente.

Endémique (*vide* Kaicher, 1978).

Latirus iris (Lightfoot, 1786)

Richard, 1985a: 427.

L'espèce est rare et n'a pu être examinée dans aucune collection récente.

Cernohorsky (1972: pl. 46, fig. 10) figure un exemplaire de l'Île Jarvis (Îles de la Ligne). Sa présence aux Îles Marquises est vraisemblable.

Latirus nodatus (Gmelin, 1791)

Rehder, 1969: 31; Lavondes et al., 1973: 124; Salvat & Rives, 1975: 322.

Latirus sanguifluus (Reeve, 1847)

Rehder, 1969: 32 (sous le nom *Latirus fallax*, identification erronée vraisemblable pour *L. sanguifluus*, Rehder communication personnelle); Salvat & Rives, 1975: 323.

Peristernia sp. aff. *iricolor* (Hombron & Jacquinot, 1854)

Dautzenberg & Bouge, 1933: 202; Salvat & Rives, 1975: 323, fig. 242 (sous le nom *Peristernia usulata* (Reeve, 1847), identification erronée).

***Peristernia lirata* (Pease, 1868)**

Pease, 1868c: 152 (description originale, localité type: «Insl. Marquesas»);
 Reeve, 1847: pl. 12, fig. 61a-b (sous le nom variété de *Latirus gemmatus* Reeve, 1847,
 identification erronée); Kobelt, 1876b: 23; Paetel, 1888: 164; Lavondes et al., 1973: 124;
 Salvat & Rives, 1975: 323, fig. 240; Cernohorsky, 1980: 115, figs 6-7 (syntypes), 8.

Endémique.

***Peristernia marquesana* (A. Adams, 1855)**

A. Adams, 1855: 315 (description originale, localité type:»Marquesas«); Kobelt,
 1876b: 24; Paetel, 1888: 164; Dautzenberg & Bouge, 1933: 203.

Tryon (1881: 84) considère *Peristernia marquesana* (A. Adams, 1855) comme
 synonyme de *Peristernia ustulata* (Reeve, 1847) et la plupart des auteurs ont par la suite
 suivi cet avis. Une grande confusion existe entre les espèces nominales *ustulata* Reeve,
 1847, *caledonica* Petit de la Saussaye, 1851, *iricolor* Hombron & Jacquinot, 1854 et
marquesana A. Adams, 1855. Les Fasciolariidae n'ont pas fait l'objet d'une révision
 approfondie récente et nous préférons ici considérer *Peristernia marquesana* comme une
 bonne espèce, connue actuellement uniquement des Îles Marquises.

Endémique

***Peristernia nassatula* (Lamarck, 1822)**

Richard, 1985a: 427.

Olividae

***Oliva amethystina* (Röding, 1798)**

Salvat & Rives, 1975: 324 (sous le nom *Oliva annulata* (Gmelin, 1791), *nomen
 dubium*).

***Oliva jaspidea* Duclos, 1835**

Dautzenberg & Bouge, 1933: 145 (sous le nom *Oliva duclosi* Reeve, 1850,
 synonyme); Salvat & Rives, 1975: 325 (sous le nom *O. duclosi*); Tursch & Greifeneder,
 2001: 318.

***Oliva nitidula* Duclos, 1835**

Salvat & Rives, 1975: 324 (sous le nom *Oliva paxillus* Reeve, 1850, synonyme).

***Oliva panniculata* Duclos, 1835**

Salvat & Rives, 1975: 325, fig. 248; Planes et al., 1995: 69; Petuch & Sargent,
 1986: 26, 63, pl. 2, figs 3-6 (description originale de *Oliva marquesana*, localité type:
 «150 meters depth off southern coast of Fatu Hiva Island, Marquesas Island, French
 Polynesia», synonyme), 1986: 26, 64, pl. 2, figs 9-10 (sous le nom *Oliva nitidula*
 Duclos, 1835, identification erronée), 1986: 26, 65, pl. 2, figs 7-8 (sous le nom *Oliva
 polita* Duclos, 1835, identification erronée); Tursch & Greifeneder, 2001: 318, pl. 7,
 figs 6-7. Sterba, 2003: 80. pl.. 27, figs. 11, 12; 13, 14 (les deux derniers sous le nom

Oliva panniculata forma *polita* Marrat, 1867); 15 (sous le nom *Oliva panniculata* forma *marquesana* Petuch & Sargent, 1986).

Harpidae

Harpa amouretta Röding, 1798

Jardin, 1858: 188, 194 (sous le nom *Harpa gracilis* Broderip & Sowerby, 1829; identification erronée vraisemblable); Rehder, 1969: 31; Rehder, 1973: 240; Salvat & Rives, 1975: 326; Poppe & Brulet in Poppe, Brulet & Dance, 1999: pl. 2, fig. 1.

Harpa gracilis est connu des Îles Ellice, aux Tuamotu et à Clipperton et n'a, semble-t-il, jamais été collecté dans les Îles hautes (Rehder, 1973: 243). Pour ces raisons et aussi parce que Jardin dit que "*Harpa gracilis*" est commun à Noukahiva [= Nuku Hiva], nous pensons qu'il s'est trompé et qu'il a vu *Harpa amouretta*.

Harpa major Röding, 1798

Jardin, 1858: 188, 194 (sous le nom *Harpa nobilis* Lamarck, 1816 [= *Harpa articularis* Lamarck, 1822], identification erronée vraisemblable); Rehder, 1973: 245, pl 183 bas; Salvat & Rives, 1975: 326; Frydman, 1990.

Il ne semble faire aucun doute que Jardin ait fait une erreur: *Harpa articularis* n'est connu à l'Est que jusqu'aux Îles Fidji (Rehder, 1973: 249).

***Morum clatratum* Bouchet, 2002**

Frydman, 1991: 13 (sous le nom *Morum* sp.); Bouchet, 2002: 534, fig. 1 (description originale, localité type: «Off Nuku Hiva, Marquesas Is., 08°45.1' S, 140°14.1' W, 108-112 m [MUSORSTOM 9: sta.CP1177]»).

Endémique.

Morum roseum Bouchet, 2002

Bouchet, 2002: 537, fig. 2 (A-E) (description originale, localité type: «Off Fatu Hiva, Marquesas Is., 09°44.6' S, 138°51.1' W, 115-120 m»).

Mitridae

Domiporta granatina (Lamarck, 1811)

Dautzenberg, 1935: 80; Cernohorsky, 1991: 95.

Imbricaria conovula (Quoy & Gaimard, 1833)

Philippi, 1850: 29 (description originale de *Mitra eburnea*, localité type: «Insulae Oceani Pacifici, quae Marquesas dicuntur», synonyme); Philippi, 1851: 84 (sous le nom *M. eburnea*); Paetel, 1888: 177 (sous le nom *Mitra eburnea*).

Cernohorsky (1991b: 137) reconnaît la synonymie de *Mitra eburnea* Philippi, mais ne retient pas les Îles Marquises dans la répartition géographique de l'espèce. Celle-ci est connue de Hawaii et sa présence dans l'Archipel des Marquises, si elle demande confirmation, est vraisemblable.

Mitra ambigua Swainson, 1829
Richard, 1985a: 428.

Mitra ancillides Broderip, 1836
Turner, 1993: 4.

Mitra assimilis Pease, 1868
Garrett, 1880: 3, 12 (*assimilis*), 5, 32 (sous le nom *Strigatella auriculoides* Reeve [= *Mitra auriculoides* Reeve, 1845], identification erronée); Cernohorsky, 1976: 486, fig. 2.

Mitra aurantia (Gmelin, 1791)
Garrett, 1880: 3, 14 (sous le nom *Mitra caeligena* Reeve, 1845, synonyme); Paetel, 1883: 27 et 1888: 174 (sous le nom *M. caeligena*).

Cernohorsky (1976: 425) donne pour limite Est les Îles de la Société. Mais l'espèce est connue jusqu'aux Îles Gambier: *Mitra obliqua* Lesson, 1842 (localité type: Îles Gambier, nouvelle synonymie), dont le type est conservé au MNHN; celui-ci mis en synonymie par erreur avec *Mitra testacea* Broderip, 1836, par Cernohorsky (1976: 434), est un exemplaire juvénile en tout point semblable aux exemplaires adultes récoltés aux Gambier et conservés au MNHN. *Mitra aurantia*, peu commune en Polynésie française, a une très large répartition indo-pacifique et bien qu'actuellement nous n'ayons pas d'information concernant des récoltes récentes de l'espèce aux Îles Marquises, il n'y a pas de raison de douter de sa présence.

Mitra auriculoides Reeve, 1845
Dautzenberg & Bouge, 1933: 155; Cernohorsky, 1976: 484.

Mitra aurora Dohrn, 1861
Richard, 1985a: 428.
Cernohorsky (1976: 440) ne mentionne pas la présence de cette espèce aux Îles Marquises. L'espèce est largement indo-pacifique, et vit aux Îles Hawaii. Sa présence, quoique vraisemblable aux Marquises, reste à confirmer.

Mitra cardinalis (Gmelin, 1791)
Cernohorsky, 1976: 312, pl. 264 (carte de distribution).
Cernohorsky mentionne les Îles Marquises sans préciser ses sources. La présence de l'espèce est confirmée par un exemplaire originaire de Nuku Hiva dans les collections du MNHN.

Mitra coronata Lamarck, 1811
Salvat & Rives, 1975: 330; Cernohorsky, 1976: 437.

[*Mitra doliolum* Küster, 1839
Dautzenberg & Bouge, 1933: 187 (sous le nom *M. rotundilirata* Reeve, 1844,

synonyme, identification erronée vraisemblable).

L'espèce a également été citée de «Paumotu» [= Tuamotu] par Martens & Langkavel (1871: 19), mais aucune récolte récente ne nous a été signalée et il semble que la limite Est connue de sa répartition géographique soit les Îles Samoa (Cernohorsky, 1976: 413).]

Mitra edentula Swainson, 1823

Crosse, 1858: 160 (description originale de *Dibaphus philippii*, localité type: «Nuku Hiva ?»), synonyme).

Nuku Hiva est cité avec réserve par Crosse. La présence dans l'Archipel des Marquises n'a pas été confirmée par des récoltes récentes, mais il s'agit d'une espèce rare en Polynésie et par ailleurs connue de Hawaii (Kay, 1979: 306) et de Clipperton (Hertlein & Allison, 1960: 14). Si sa présence demande confirmation, elle est cependant vraisemblable.

Mitra fastigium Reeve, 1845

Cernohorsky, 1976: 494.

Mitra ferruginea Lamarck, 1811

Rehder, 1969: 31; Cernohorsky, 1976: 397.

Mitra fraga Quoy & Gaimard, 1833

Lesson, 1842b: 141.

L'espèce n'est pas citée des Îles Marquises par Cernohorsky (1976: 404), mais celui-ci la mentionne de Hawaii et des Îles de la Ligne et elle est connue de l'Archipel des Tuamotu. Sa présence vraisemblable aux Marquises reste à confirmer.

[*Mitra inca* d'Orbigny, 1841

Dautzenberg & Bouge, 1933: 180 (sous le nom *Mitra nucleola* Lamarck, 1811, synonyme? nom douteux).

Le nom *Mitra nucleola* a été diversement interprété par les auteurs, rattaché tantôt à des espèces caraïbe ou panaméenne, tantôt à des espèces indo-pacifiques. Parmi les auteurs modernes, Cernohorsky (1967: 144, 1970a: 93) traite *Mitra nucleola* comme une bonne espèce mais figure sous ce nom *Mitra turgida* Reeve, 1845. Plus tard, le même auteur (Cernohorsky, 1969: 984; 1970b: 36) figure le type et montre la priorité de *Mitra nucleola* sur *M. inca*, considéré alors comme synonyme. Cependant, afin de conserver la stabilité nomenclaturale, Cernohorsky (1976: 457) déclare *Mitra nucleola* douteux et conserve *Mitra inca* pour une espèce du Pacifique américain.

L'espèce ne vit pas aux Marquises et nous ne savons pas ce que Dautzenberg & Bouge ont vu.]

Mitra incompta Lightfoot, 1786

Richard, 1985a: 429.

Cette grande espèce, à large répartition indo-pacifique, est peu commune en

Polynésie Française et n'est pas signalée aux Îles Marquises par Cernohorsky (1976: 322). Sa présence reste à confirmer.

Mitra litterata Lamarck, 1811

Salvat & Rives, 1975: 331; Cernohorsky, 1976: 482.

Mitra luctuosa A. Adams, 1853

Cernohorsky, 1976: 443.

Mitra papalis (Linné, 1758)

Richard, 1985a: 429.

Cernohorsky (1976: 308) mentionne l'espèce des Îles de la Société et de l'Archipel des Tuamotu, mais ne signale pas sa présence aux Îles Marquises. *Mitra papalis* est connue de Hawaï (Cernohorsky, 1976: 308; Kay, 1979: 296) et de Clipperton (Hertlein & Allison, 1960: 14). Sa présence aux Îles Marquises est vraisemblable, mais demande confirmation.

Mitra paupercula (Linné, 1758)

Richard, 1985a: 429.

La présence de l'espèce reste à confirmer. Elle n'est pas citée des Îles Marquises par Cernohorsky (1976: 477), mais est présente aux Îles de la Ligne et à Hawaï.

Mitra pellisserpentis Reeve, 1844

A. Adams, 1853: 132 (description originale de *Mitra serotina*, localité type: «Marquesas», synonyme); Garrett, 1880: 3, 10 (sous le nom *Mitra astricta* Reeve, 1844, synonyme); Dautzenberg & Bouge, 1933: 190 (sous le nom *M. serotina*); Cernohorsky, 1970: pl. 4, figs 4-5; 1976: 495, pl. 447, figs 3, 7, 9.

Garrett (1880) cite *Mitra astricta* des Îles Marquises et de Hawaï, qu'il différencie de *pellisserpentis* récolté dans le reste de la Polynésie. Cernohorsky (1976) considère *Mitra astricta* comme sous-espèce de *Mitra pellisserpentis*, endémique des Îles Hawaï, tout en précisant: «The Hawaiian form of *M. pellisserpentis* is a weak subspecies and differs from the nominate subspecies only in colour ornamentation.». Constatant que tous les intermédiaires sont présents dans les eaux marquisiennes, nous ne suivons pas ici l'avis de Cernohorsky et estimons que *astricta* est un synonyme strict de *pellisserpentis*.

[*Mitra scutulata* (Gmelin, 1791)

Duval, 1852 (description originale de *Mitra sertum*, localité type: Les Îles Marquises?, synonyme); Paetel, 1883: 29 et 1888: 187 (sous le nom *M. sertum*).

Cernohorsky (1976: 488) ne cite pas *Mitra scutulata* des Îles Marquises. La présence de cette espèce, rare en Polynésie Française, est douteuse, d'autant que Duval lui-même nous dit : «elle vient des Îles Marquises, ou de quelques-unes des îles de l'Océan Pacifique». Nous ne connaissons pas de récoltes récentes.]

Mitra stictica (Link, 1807)

Garrett, 1880: 4 (sous le nom *Mitra pontificalis* Lamarck, 1811, synonyme).

***Neocancilla arenacea* (Dunker, 1852)**

Dunker, 1852: 51 (description originale, sans localité); A. Adams, 1853: 138 (description originale de *Mitra formosa*, localité type: «Marquesas», synonyme); Paetel, 1883: 28 et 1888: 179 (sous le nom *M. formosa*); Dautzenberg & Bouge, 1933: 169 (sous le nom *M. formosa*); Cernohorsky, 1978b: 103, pl. 33, fig. 2; Cernohorsky, 1991b: 107, pl. 102, figs 2-3 (lectotype de *M. formosa*), 4-5 (paralectotype de *M. formosa*), 6-7; Abbott & Dance, 1982: 203, fig.. Robin & Martin, 2004: 19, pl. M-31.

Le type de *Mitra arenacea* Dunker n'a pas été retrouvé, mais la diagnose et l'illustration originales ne laissent aucun doute sur l'identité du nom. Dunker ne mentionne pas de localité et Cernohorsky (1991b) désigne «Marquesas Islands» comme localité type.

Endémique.

Neocancilla clathrus (Gmelin, 1791)

Cernohorsky, 1991: 105.

Neocancilla papilio (Link, 1807)

Cernohorsky, 1991: 103.

Scabricola casta (Gmelin, 1791)

Garrett, 1880: 3, 16 (sous le nom *Mitra fasciata* Martyn, 1784, nom non disponible).

Scabricola variegata (Gmelin, 1791)

A. Adams, 1853: 270 (description originale de *Mitra marquesana*, localité type: «Marquesas», synonyme); Paetel, 1888: 182 (sous le nom *M. marquesana*); Dautzenberg & Bouge, 1933: 175 (sous le nom *M. marquesana*); Cernohorsky, 1978b: 101; Cernohorsky, 1991b: 115, pl. 110, figs 2-3 (lectotype de *M. marquesana*); Abbott & Dance, 1982: 202, fig.

«*Ziba*» *annulata* (Reeve, 1844)

Cernohorsky, 1991b: 59.

“*Ziba*” *interlirata* (Reeve, 1844)

Cernohorsky, 1991b: 54.

Costellariidae

Vexillum cadaverosum (Reeve, 1844)

Richard, 1985a: 430.

Vexillum cavea (Reeve, 1844)

Cernohorsky, 1978b: 116.

Vexillum cremans (Reeve, 1845)

Salvat & Rives, 1975: 340, fig. 302 (sous le nom *Vexillum pisolinum* Lamarck, 1811, identification erronée); Turner, 1989: 15, pl. 7, fig. 24.

Vexillum crocatum (Lamarck, 1811)

Planes et al., 1995: 69.

Vexillum leucozonias (Deshayes in Laborde & Linant, 1834)

Cernohorsky, 1978b: 113.

Vexillum pacificum (Reeve, 1845)

Richard, 1985a: 431.

Vexillum piceum (Pease, 1860)

Cernohorsky, 1978b: 117; Turner, 1993: 21.

[*Vexillum pisolinum* (Lamarck, 1811)

Richard, 1985a: 431.

L'espèce est rare et est connue du Pacifique de l'Ouest (Cernohorsky, 1971a: 184). Aucune récolte récente ne peut confirmer sa présence en Polynésie Française. Nous pensons que l'espèce ne vit pas aux Îles Marquises.]

Vexillum unifascialis (Lamarck, 1811)

Dautzenberg & Bouge, 1933: 155 (sous le nom *Mitra aureolata* Reeve, 1844, synonyme), 178 (sous le nom *Mitra multicostrata* (Broderip, 1836), synonyme).

Vexillum virginalis (Lesson, 1842)

A. Adams, 1853: 139 (description originale de *Mitra pallida*, localité type: «Marquesas», synonyme); Paetel, 1888: 184 (sous le nom *M. pallida*); Salvat & Rives, 1975: 338 (sous le nom de *Vexillum modestum* (Reeve, 1845), nouvelle synonymie); Cernohorsky, 1978: 111.

L'examen du type de *Vexillum virginalis*, conservé au MNHN, et sa comparaison avec plus d'une centaine d'exemplaires de *Vexillum modestum* provenant des différents archipels polynésiens permettent de mettre les deux taxons en synonymie.

Turridae

***Gymnobela virgulata* Sysoev & Bouchet, 2001**

Sysoev & Bouchet, 2001: 309, fig. 129, 171 (description originale, localité type: «Marquesas Island», 08°44' S, 140°15' W [musorstom 9, sta. DW 1173]).

Endémique

***Iotyrris marquesensis* Sysoev, 2002**

Medinskaya & Sysoev, 2001: 7, Fig. 1 D (sous le nom *Xenuroturris cerithiformis*

Powell, 1964, identification erronée); Sysoev, 2002: 169, fig. 1 (description originale, localité type: «Marquesas Island», 9°44.6' S, 138°51.1' W, 115-120 m.).

Endémique

Lovellona atramentosa (Reeve, 1849)

Richard, 1985a: 433.

Xenroturris cingulifera (Lamarck, 1822)

Dautzenberg & Bouge, 1933: 93; Sysoev, 2002: 171.

Terebridae

Hastula celidonota (Melvill & Sykes, 1898)

Trondle, 1983: 14, fig. 34 (sous le nom *Hastula* cf. *contigua* Pease, 1871, identification erronée); Bratcher & Cernohorsky 1987: 182.

Hastula hectica (Linné, 1758)

Jardin, 1858: 189 (sous le nom *Terebra caerulescens* Lamarck, 1822, synonyme).
Aucune récolte récente nous a été signalée. L'espèce a une large répartition indo-pacifique. Sa présence aux Marquises est vraisemblable.

Hastula lanceata (Linné, 1767)

Salvat & Rives, 1975: 363, fig. 395; Trondle, 1983: 14.

Hastula penicillata (Hinds, 1844)

Salvat & Rives, 1975: 364, fig. 396; Trondle, 1983: 14, fig. 37 (droite).

Hastula philippiana (Deshayes, 1859)

Deshayes, 1859: 289 (description originale, localité type: «Îles Marquises?»);
Paetel, 1888: 253; Trondle, 1983: 15; Bratcher & Cernohorsky, 1987: 181.

Hastula strigilata (Linné, 1758)

Jardin, 1858: 190.

Aucune récolte récente nous a été signalée. L'espèce a une large répartition indo-pacifique. Présente à Hawaii, l'espèce est connue en Polynésie Française de la Société et des Gambier. Sa présence aux Marquises est vraisemblable.

Hastula stylata (Hinds, 1844)

Dautzenberg & Bouge, 1933: 64 (sous le nom *Terebra confusa* E. A. Smith, 1877 [= *Hastula inconstans* (Hinds, 1844), endémique de l'archipel hawaïien], identification erronée); Salvat & Rives, 1975: 364, fig. 398 (haut); Trondle, 1983: 15.

Hastula stylata est largement distribué dans le Pacifique tropical et est remplacé dans l'archipel hawaïien par *Hastula inconstans* (Bratcher & Cernohorsky, 1987). Les deux espèces ont souvent été confondues et il n'est pas douteux que Dautzenberg & Bouge ont eu en main *Hastula stylata*.

***Duplicaria trochlea* (Deshayes, 1857)**

Deshayes, 1857: 89, pl. 5, fig. 6 (description originale, localité type: Zanzibar, erronée); Reeve, 1860: pl. 13, sp. 54; Bratcher, 1969: 334, pl. 52, figs 1-4; Salvat & Rives, 1975: 362, fig. 391; Trondle, 1983: 13, fig. 30; Bratcher & Cernohorsky, 1987: 207, pl. 65, figs 253a-b. (localité type désignée: «Marquesas Islands»); Bouchet, 1998: 17, fig. 5; Bryce, 2000: 73, fig. 4.

Endémique.

***Terebra affinis* Gray, 1834**

Dautzenberg & Bouge, 1933: 61; Salvat & Rives, 1975: 360, 363, fig. 394 (sous le nom *Terebra* sp. B); Trondle, 1983: 7, fig. 2.

Aux Îles Marquises, *Terebra affinis* se rencontre le plus souvent sous des formes où les ponctuations situées entre les rides axiales sont très prononcées (*Terebra puncticulata* Deshayes, 1859, *Terebra peasei* Deshayes, 1859 sont des synonymes).

***Terebra argus* Hinds, 1844**

Hinds, 1844a: 160 (description originale, localité type: "Tahiti, Society Islands; Nukuhiva, Marquesas"); 1845: 154; Salvat & Rives, 1975: 359; Trondle, 1983: 8; Bratcher & Cernohorsky, 1987: 42 (localité type: réduite à "Tahiti, Polynésie Française").

***Terebra babylonia* Lamarck, 1822**

Fischer, 1891: 45; Dautzenberg & Bouge, 1933: 62; Salvat & Rives, 1975: 361; Trondle, 1983: 9.

***Terebra cerithina* Lamarck, 1822**

Hinds, 1844a: 151 (description originale de *Terebra pulchra*, localité type: «Marquesas, in seven fathoms», synonyme), 1845: 178, pl. 45, fig. 129 (sous le nom *T. pulchra*); Paetel, 1883: 41 (sous le nom *T. pulchra*); Salvat & Rives, 1975: 359; Trondle, 1983: 9.

***Terebra chlorata* Lamarck, 1822**

Trondle, 1983: 9.

***Terebra cingulifera* Lamarck, 1822**

Reeve, 1860: sp. 44a-b; Salvat & Rives, 1975: 361; Trondle, 1983: 9.

***Terebra crenulata* (Linné, 1758)**

Jardin, 1858: 189; Hinds, 1844a: 160; 1845: 153, pl. 42, fig. 32; Martens & Langkavel, 1871: 27; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 358; Trondle, 1983: 9, figs 12; Bouchet, 1998: 17, fig. 4 (sous le nom *Terebra guttata* Röding 1798, identification erronée).

***Terebra funiculata* Hinds, 1844**

Reeve, 1860: pl. 12, sp. 48; Paetel, 1883: 41, 1888: 250; Trondle, 1983: 10.

Terebra guttata (Röding, 1798)

Lavondes et al., 1973: 133; Trondle, 1983: 11.

***Terebra ligata* Hinds, 1844**

Hinds, 1844a: 153 (description originale, localité type: „Marquesas, in seven fathoms, sandy mud“); 1845: 166, pl. 45, figs 117-118 ; Paetel, 1888: 251.

Tryon (1885: 26) considère *Terebra ligata* synonyme de *Terebra tessellata* Gray, 1834, mais Bratcher & Cernohorsky (1987: 36) ont montré que *T. ligata* est différent. L'holotype de *Terebra ligata* (BMNH 1979128) mesure 31,1 mm. Des récoltes récentes confirment la présence de l'espèce aux Marquises et les exemplaires correspondent en tout point à l'espèce décrite par Hinds. Elle vit entre 50 et 150 m. de profondeur et y est représentée par une population dont la taille est comprise entre 30 et 70 mm.

Endémique.

Terebra maculata (Linné, 1758)

Rehder, 1969: 31; Lavondes et al., 1973: 133; Salvat & Rives, 1975: 358; Trondle, 1983: 11.

Terebra nitida Hinds, 1844

Hinds, 1844a: 152 (description originale, localité type: „Marquesas; in seven fathoms, sandy mud“); 1845: 164, pl. 45, fig. 103; Paetel, 1883: 41, 1888: 252; Salvat & Rives, 1975: 363; Trondle, 1983: 12.

[*Terebra orizoides* Lesson, 1842

Lesson, 1842f: 203 (description originale, localité type: „Îles Marquises“).

L'espèce non figurée par Lesson est considérée comme douteuse par Bratcher & Cernohorsky (1987: 232).]

Terebra punctatostriata Gray, 1833

Deshayes, 1857: 87, pl. 4, fig. 3 (description originale de *Terebra pallida*, localité type: “Îles Marquises”, synonyme); 1859: 311 (sous le nom *T. pallida*); Paetel, 1888: 253; Cernohorsky & Bratcher, 1976: 134, fig. 11 (lectotype de *Terebra pallida*); Bratcher & Cernohorsky, 1987: 52, pl. 8, fig. 24b (lectotype de *Terebra pallida*); Trondle, 1983: 12, fig. 27 (11) (d'après Cernohorsky & Bratcher, 1976).

Terebra quoygaimardi Cernohorsky & Bratcher, 1976

Deshayes, 1859: 312 (sous le nom *Terebra monile* Quoy & Gaimard, 1833, synonyme); Reeve, 1860: sp. 42a (sous le nom *T. monile*); Paetel, 1883: 41 et 1888: 252 (sous le nom *T. monile*).

Bratcher & Cernohorsky (1987) donnent comme limite Est de répartition géographique la Micronésie. Couturier (1907: 125) signale la présence de «*Terebra monilis* Quoy» à Marutea (Tuamotu). Richard (1985a: 436) mentionne l'espèce des Îles de la Société.

Il semble que l'espèce soit rare en Polynésie Française. Aucune récolte

récente aux Îles Marquises n'a été portée à notre connaissance. Sa présence demande confirmation.

[*Terebra tessellata* Gray, 1834

Richard, 1985a: 436.

Dautzenberg & Bouge (1933: 69) font référence à «Hinds, 1843: 163» (erreur de date de publication pour 1844) pour signaler la présence de l'espèce aux Îles Marquises. Hinds (1844a: 163, 1845: 166) ne mentionne pas les Marquises. Gray (1834: 61) ne donne pas de localité. Ni Trondle (1983: 16), ni Bratcher & Cernohorsky (1987: 36) ne confirment une présence aux Marquises.

Cette espèce indo-pacifique est peu commune et connue à l'Est jusqu'à Padang, Sumatra, localité type de *Terebra decorata* Deshayes, 1857, synonyme.

À notre connaissance, *Terebra tessellata* Gray ne vit pas aux Marquises.]

***Terebra troendlei* Bratcher, 1981**

Salvat & Rives, 1975: 362, fig. 392 (sous le nom *Terebra* sp. A: holotype de *Terebra troendlei*, désigné ultérieurement par Bratcher, 1981); Bratcher, 1981: 330, figs 3-4 (description originale, localité type: «Entrance to Hana Hevane Bay, Tahuata Island, Marquesas, depth 10 meters, sand bottom»); Trondle, 1983: 13, fig. 31 (holotype); Bratcher & Cernohorsky, 1987: 47, pl. 6, figs 18a-b; Bouchet, 1998: 17, fig. 6.

Endémique.

Conidae

Conus adamsonii Broderip, 1836

Richard, 1985b: 6; Hart, 1992: 1, 5; Röckel et al., 1995: 213, pl. 43, fig. 7.

[*Conus arenatus* Hwass in Bruguière, 1792

Salvat & Rives, 1975: 347; Walls, 1979: 123.

Richard (1985b: 6), tout en confirmant la présence de l'espèce dans les Îles de la Société, nous dit qu'elle ne vit pas aux Marquises où elle a été confondue avec *Conus pulicarius* Hwass in Bruguière 1792 et *Conus vautieri* Kiener, 1846. *Conus arenatus* n'est pas repris pour les Îles Marquises par Röckel et al. (1995: 83).]

Conus auricomus Hwass in Bruguière, 1792

Planes et al., 1995: 69.

Röckel et al. (1995: 307) ne citent pas expressément l'espèce des Îles Marquises, mais incluent ces Îles sur la carte de répartition géographique. *Conus auricomus* a une large répartition indo-pacifique, des côtes africaines à l'Ouest, à l'Archipel des Tuamotu et Hawaii à l'Est. En Polynésie Française, l'espèce est rare.

Conus bandanus Hwass in Bruguière, 1792

Jardin, 1858: 189 (sous le nom de *Conus marmoreus* Linné, 1758, identification erronée).

Conus bandanus, longtemps considéré comme synonyme de *C. marmoreus*, a une large répartition indo-pacifique et est présent dans les Îles de la Société, les Tuamotu et les Gambier. Il n'est pas douteux que c'est bien cette espèce que Jardin a vue.

Conus betulinus Linné, 1758

Salvat & Rives, 1975: 356, fig. 362; Richard, 1985b: 8, fig. 18.

Bien que Röckel et al. (1995: 92) limitent à la Nouvelle-Calédonie, à l'Est, la répartition géographique de l'espèce, celle-ci est représentée en Polynésie Française par une population isolée et connue uniquement des Marquises (Salvat & Rives, 1975, Richard, 1985b).

Conus bullatus Linné, 1758

Rehder, 1969: 31; Salvat & Rives, 1975: 356; Richard, 1985b: 9; Röckel et al., 1995: 214, pl. 43, fig. 12; Bouchet, 1998: 19, figs 16-17; Bryce, 2000: 73, pl. 1, fig. A.

Conus cf. *canonicus* Hwass in Bruguière, 1792

Marsh & Rippingale, 1964: 108, pl. 14, fig. 18 (sous le nom *Conus panniculus* Lamarck, 1810 (= *Conus textile* Linné, 1758); identification erronée); Salvat & Rives, 1975: 355, fig. 359 (sous le nom *Gastridium panniculus* (Lamarck)); Kaicher, 1977: card 1146 (sous le nom *C. panniculus*); Walls, 1979: 39, 42 (fig.), 49 (fig.) (sous le nom *Conus abbas* Hwass in Bruguière, 1792); Richard, 1985b: 29, fig. 85 (sous le nom *Conus textilinus* Kiener, 1845 (= *C. textile*); identification erronée); Röckel et al., 1995: 308, pl. 68, figs 10-12 (sous le nom *C. textile* f. *textilinus*); Bouchet, 1988: 19, fig. 18 (sous le nom *C. textilinus*).

Cette espèce a longtemps été citée des Îles Marquises sous le nom *Conus panniculus* Lamarck, 1810, considéré par les auteurs comme endémique de l'archipel. Or ce nom est un synonyme de *Conus textile* Linné, 1758. De plus, l'espèce appelée *Conus panniculus* dans la littérature n'est pas endémique des Marquises, mais est également présente dans les Îles de la Société et l'Archipel des Tuamotu (Richard, 1985b: 9, sous le nom *Conus canonicus*).

Le nom qui doit être employé pour désigner cette espèce n'est pas clair. Richard (1985b) lui attribue le nom *Conus textilinus* Kiener. Röckel et al (1995: pl. 68, fig. 9) illustrent l'holotype de cette espèce nominale, qui est clairement un synonyme de *Conus textile* (ce dernier est également présent aux Marquises, où il est différenciable de *Conus* cf. *canonicus*, sans intermédiaire.) L'espèce marquisienne nous semble également proche de *Conus abbas* de l'Océan Indien si ce n'est par la couleur de l'ouverture généralement blanche pour *abbas*, rose pour l'espèce marquisienne. Le test de cette dernière possède des coloris et une ornementation semblables à celle de *Conus canonicus* et ne s'en différencie que par la forme; celle-ci plus épaulée et triangulaire chez les jeunes exemplaires, plus ventrue et atteignant généralement une taille supérieure pour les exemplaires adultes, rapprocherait les exemplaires marquisiens de *Conus abbas*.

Des recherches complémentaires sont nécessaires pour se prononcer plus clairement sur le nom et le statut de cette forme marquisienne.

Conus catus Hwass in Bruguière, 1792

Rehder, 1969: 31; Lavondes et al. 1973: 133; Bratcher, 1975: 5; Salvat & Rives, 1975: 348, fig. 336; Walls, 1979: 197 (fig.); Coomans et al., 1983: 98; Richard, 1985b: 9, fig. 21; Planes et al., 1995: 69; Röckel et al., 1995: 103; figs 18-28.

Conus chaldaeus (Röding, 1798)

Garrett, 1878b: 356 (cité comme *Conus vermiculatus* Lamarck, 1810, synonyme); Fischer, 1898: 48 (cité comme *C. vermiculatus*); Salvat & Rives, 1975: 346; Richard, 1985b: 10.

Conus coronatus Gmelin, 1791

Salvat & Rives, 1975: 346; Richard, 1985b: 11.

Conus cylindraceus Broderip & Sowerby, 1830

Richard, 1985b: 11.

Conus distans Hwass in Bruguière, 1792

Richard, 1985b: 11.

Conus ebraeus Linné, 1758

Salvat & Rives, 1975: 345; Richard, 1985b: 11.

Conus eburneus Hwass in Bruguière, 1792

Fischer, 1891: 46; Salvat & Rives, 1975: 345; Richard, 1985b: 11.

***Conus encaustus* Kiener, 1845**

Kiener, 1845: pl. 14, fig. 2, 1846: 54 (description originale, sans localité); Reeve, 1848: pl. 2, fig. 277 (description originale de *Conus praetextus* Reeve, 1848, localité type: "Marquesas Islands", synonyme); Garrett, 1878b: 354, 359; Tryon, 1884: 21, pl. 5, figs 82-83; Paetel, 1883: 48, 1888: 296; Rehder, 1969: 32; Marsh & Rippingale, 1964: 147, pl. 21, fig. 14; Rehder, 1969: 32; Cernohorsky, 1971: 220, pl. 56, fig. 420; 1972: 193, pl. 55, fig. 9; Salvat & Rives, 1975: fig. 325; Walls, 1979: 284 (fig.), 430; Abbott & Dance, 1982: 259 (fig.); Richard, 1983: 13, 15; 1985b: 12, figs 31 (holotype), 32; Coomans et al., 1986: 115 (sous le nom sous-espèce de *Conus miliaris* Hwass in Bruguière, 1792, localité type désignée: "Marquesas Islands"); Planes et al., 1995: 69; Röckel et al., 1995: 65, pl. 7, figs 18-21; Bouchet, 1998: 19, fig. 19.

Nous suivons ici l'avis général des auteurs qui est de considérer *Conus encaustus* comme espèce à part entière et non pas comme sous-espèce de *Conus miliaris* (Coomans & al., 1986). Par ailleurs, Lewis (1979: 11) signale la présence de *Conus encaustus* à Viti Levu, Fiji. Les exemplaires ont été trouvés morts sur une plage de la côte sud de l'île, occupés par des pagures, et la présence de l'espèce n'a pas été, à nouveau, mentionnée pour la région. Kiener ne donne pas de localité. La localité type est désignée par Coomans & al. (1986). L'espèce est ici considérée comme endémique des Îles Marquises où elle est commune.

Endémique.

Comus flavidus Lamarck, 1810

Garrett, 1878b: 354; Salvat & Rives, 1975: 352; Richard, 1985b: 18.

Comus frigidus Reeve, 1848

Salvat & Rives, 1975: 352; Richard, 1985b: 13.

Dautzenberg & Bouge (1933: 83) cite *Comus maltzaniannus* Weinkauff, 1873, qui est un synonyme, mais font référence à Tryon (1884, pl. 13, fig. 48) qui représente *Comus muriculatus* Sowerby, 1833.

***Comus gauguini* Richard & Salvat, 1973**

Richard & Salvat, 1973: 25, figs 1-3 (description originale, localité type: «Îles Marquises»); Salvat & Rives, 1975: 352, fig. 351; Walls, 1979: 199 (sous le nom synonyme de *Comus barthelemyi* Bernardi, 1861; identification erronée); Richard, 1981: 12 (holotype figuré); 1983: 15; 1985b: 14, fig. 35 (holotype); Röckel et al., 1995: 218, pl. 44, figs 13-17; Bouchet, 1998: 21; Bryce, 2000: 73, pl. 1, fig. C.

Endémique

Comus imperialis Linné, 1758

Jardin, 1858: 189; Garrett, 1878b: 354; Rehder, 1969: 31; Salvat & Rives, 1975: 344; Richard, 1985b: 15.

Comus legatus Lamarck, 1810

Planes et al., 1995: 69.

Röckel et al. (1995: 307, carte 132) n'incluent pas les Marquises dans l'aire de répartition géographique de l'espèce. L'espèce est peu commune en Polynésie Française et sa présence est vraisemblable.

Comus litoglyphus Hwass in Bruguière, 1792

Richard, 1985a: 434.

Comus litteratus Linné, 1758

Richard, 1985b: 16.

L'espèce a une large répartition indo-pacifique, excepté Hawaii et la Mer Rouge (Röckel et al., 1995: 79), mais elle est rare en Polynésie Française, et n'y est représentée que sur les pentes externes des îles hautes (Richard, 1985b).

Comus lividus Hwass in Bruguière, 1792

Garrett, 1878b: 354; Fischer, 1891: 50; Dautzenberg & Bouge, 1933: 81; Salvat & Rives, 1975: 347; Richard, 1985b: 16.

Comus magnificus Reeve, 1843

Salvat & Rives, 1975: 354, fig. 357; Richard, 1985b: 17, fig. 48; Röckel et al., 1995: 291, pl. 62, figs 2.

***Conus marchionatus* Hinds, 1843**

Hinds, 1843: 256 (description originale, localité type: "Port Anna Maria, Nuku Hiva, Marquesas, dredged from a sandy floor in 7 to 10 fathoms"), 1844: 6, pl. 1, figs 6-7; Weinkauff, 1874: 244; Garrett, 1878b: 355, 361; Tryon, 1884: 9, pl. 2, fig. 16, pl. 27, fig. 3 (introduction du nom *eudoxus* "Melvill"; synonyme); Paetel, 1883: 49, 1888: 300; Dautzenberg & Bouge, 1933: 84; Marsh & Rippingale, 1964: 20, pl. 1, fig. 11; Rehder, 1969: 32; Bratcher, 1975: 5; Salvat & Rives, 1975: fig. 315; Kaicher, 1977: card 1201; Cernohorsky, 1978: 126, fig. 2; Walls, 1979: 501 (fig.), 766 (sous le nom synonyme de *Conus nobilis* Linné, 1758; identification erronée); Abbott & Dance, 1982: 247 (fig.); Richard, 1983: 15, 1985b: 18, fig. 51; Röckel et al., 1995: 188, pl. 36, figs 18-20; Bouchet, 1998: 18, figs 10-15; Bryce, 2000: 73, pl. 1, fig. D (sous le nom *C. nobilis marchionatus*, identification erronée).

Endémique.

***Conus miles* Linné, 1758**

Jardin, 1858: 189, 196; Richard, 1985b: 19.

***Conus moluccensis* Küster, 1838**

Rehder & Wilson, 1975: 14, fig. 10 (description originale de *Conus marielae* Rehder & Wilson, 1975, localité type: «One-half mile off Baie Motu-Hee, Nuku Hiva, 35 fms» (= 65 m.), sous-espèce); Kaicher, 1977: card 1349 (sous le nom *C. marielae*); Walls, 1979: 440 (fig.), 691 (sous le nom *C. marielae*); Abbott & Dance, 1982: 261 (sous le nom *C. marielae*, holotype figuré); Richard, 1983: 15 (sous le nom *C. marielae*); 1985b: 18, fig. 52 (sous le nom *C. marielae*, holotype figuré); Röckel et al., 1995: 231, pl. 48, figs 10 (paratype), 11; Bouchet, 1998: 19, fig. 20 (sous le nom *C. marielae*).

Suivant l'avis de Röckel et al. (1995) l'espèce est représentée aux Marquises par la sous-espèce *Conus moluccensis marielae*. Celle-ci, considérée dans un premier temps comme endémique des Îles Marquises, a également été signalée dans l'Archipel des Australes (Richard, 1985b) et récoltée à Tahiti (Laurens, 1994: 32) et aux Îles Marshall (Röckel et al., 1995).

***Conus moreleti* Crosse, 1858**

Bratcher, 1875: 5; Salvat & Rives, 1975: 347, fig. 330; Richard, 1985b: 19, fig. 57; Röckel et al., 1995: 53, figs 17-18.

***Conus muriculatus* Sowerby, 1833**

Dautzenberg & Bouge, 1933: 83 (sous le nom *maltzanianus* Weinkauff, 1873 (= *frigidus* Reeve 1848), identification erronée).

L'espèce à large répartition indo-pacifique est connue des Îles de la Société et de Tuamotu sous sa forme lisse, mais n'a pas été signalée récemment des Îles Marquises; sa présence demande confirmation.

***Conus nussatella* Linné, 1758**

Jardin, 1858: 189, 196 (sous le nom «*Conus mussatella* [sic] L., *C. drap piqueté*»);

Richard & Salvat, 1973: 28; Salvat & Rives, 1975: 356, fig. 366; Richard, 1985b: 21, fig. 61.

Conus obscurus Sowerby, 1833

Richard & Salvat, 1973: 28; Bratcher, 1975: 5; Salvat & Rives, 1975: 353, fig. 353; Richard, 1985b: 21, figs 62-63.

Conus pennaceus Born, 1778

Bratcher, 1975: 5.

Conus pennaceus est connu en Polynésie Française des Îles de la Société, des Tuamotu et des Gambier (Richard, 1995b: 22). L'espèce vit à Hawaii (Kay, 1979: 376; Röckel et al., 1995: 296) dont la faune est bien connue de Bratcher. Bien qu'aucune récolte ne nous ait été signalée depuis, il semble vraisemblable que cette espèce, rare en Polynésie Française et non mentionnée par Röckel et al (1995), soit présente dans les Îles Marquises.

Conus pertusus Hwass in Bruguière, 1792

Salvat & Rives, 1975: 350; Richard, 1985b: 22.

Conus pulicarius Hwass in Bruguière, 1792

Jardin, 1858: 189, 196; Garrett, 1878b: 355; Fischer, 1891: 48; Richard, 1985b: 23.

L'espèce est rare dans le Nord des Tuamotu et aux Marquises (Richard, 1985b: 30) et il est surprenant que Jardin (1858: 196) nous dise: «On ramasse souvent le *C. pulicarius*». Ce dernier auteur ne semble pourtant pas confondre l'espèce avec *Conus vautieri* Kiener, 1849, qu'il cite par ailleurs (Jardin, 1858: 189).

Conus quercinus Solander in Lightfoot, 1786

Garrett, 1878b: 355; Rehder, 1969: 31; Salvat & Rives, 1975: 356, fig. 363; Richard, 1985b: 24, fig. 73.

Conus rattus Hwass in Bruguière, 1792

Jardin, 1858: 189 (sous le nom *Conus taitensis* Hwass in Bruguière, 1792, synonyme); Garrett, 1878b: 355 (sous le nom *Conus Tahitensis* [sic]); Rehder, 1969: 31; Bratcher, 1975: 5; Salvat & Rives, 1975: 350, fig. 342; 350, fig. 343 (sous le nom *C. taitensis*); Richard, 1985b: 24, 27; Planes et al., 1995: 69 (sous le nom *C. taitensis*); Röckel et al., 1995: 139, pl. 24, fig. 22 (sous le nom *C. rattus* f. *taitensis*).F

Nous suivons ici l'avis général des auteurs et considérons *Conus taitensis* comme une variété de *Conus rattus*. Celle-ci décrite de Tahiti est de couleur violacée, pointillée de blanc et ornée de deux bandes blanches plus ou moins régulières, l'une à l'épaule, l'autre plus discrète au milieu du dernier tour (Kohn, 1968: 485, pl. 9, fig. 113; figure type désignée et figurée). Il est à noter que cette forme est présente des Îles Carolines, à Hawaii et la Polynésie (Garrett, 1878: 354, 364); elle est relativement rare en Polynésie.

Des études plus approfondies pourraient permettre de démontrer que la forme aux

coloris sensiblement différents, brun foncé et peu marqué de blanc (Salvat & Rives, 1975: 350, fig. 343), relativement fréquente dans l'Archipel des Marquises, représente une espèce différente.

Conus retifer Menke, 1829

Richard & Salvat, 1973: 28; Salvat & Rives, 1975: 355; Richard, 1985b: 25; Röckel et al., 1995: 305, pl. 65, fig. 23.

Conus sanguinolentus Quoy & Gaimard, 1834

Salvat & Rives, 1975: 347; Richard, 1983: 15 (sous le nom *Conus unicolor* Sowerby, 1833, *nomen dubium*, *fide* Kohn, 1992: 242); 1985b: 30, fig. 89 (sous le nom *C. unicolor*); Planes et al., 1995: 69; Röckel et al., 1995: 52, pl. 4, figs 11-12.

Conus sponsalis Hwass in Bruguière, 1792

Jardin, 1858: 189 (sous le nom *Conus musicus* Hwass in Bruguière, 1792; identification erronée vraisemblable); Garrett, 1878b: 355 (sous le nom *Conus sponsalis*, mais également sous le nom *Conus nanus* Sowerby, 1833, synonyme); Rehder, 1969: 3; Salvat & Rives, 1975: 346; Richard, 1985b: 20 (sous le nom *C. nanus*), 26.

Nous suivons ici l'avis de Röckel et al. (1995: 68) qui considèrent *Conus nanus* comme une variété unicolore de *Conus sponsalis* dotée parfois d'une bande bleutée sur le dernier tour et/ou quelques traces de couleur rouge. Tous les intermédiaires se rencontrent en Polynésie Française.

Conus striatus Linné, 1758

Salvat & Rives, 1975: 352; Richard, 1985b: 26.

Conus tenuistriatus Sowerby, 1858

Salvat & Rives, 1975: 357, fig. 371; Richard, 1985b: 27, fig. 80.

Conus terebra Born, 1778

Röckel et al., 1995: 171, pl. 31, fig. 16.

Conus tessulatus Born, 1778

Jardin, 1858: 189 (sous le nom *Conus tesselatus* Hwass in Bruguière, 1792, synonyme); Salvat & Rives, 1975: 345; Richard, 1985b: 28.

Conus textile Linné, 1758

Rehder, 1969: 31; Salvat & Rives, 1975: 355; Walls, 1979: 188 (fig. en bas à gauche), 270 (sous le nom *Conus canonicus* Hwass in Bruguière, 1792, identification erronée); Richard, 1985b: 28.

Le cône figuré par Walls (1979) représente la variété de *Conus textile* des Marquises que Kiener (1845) a appelée *Conus textilinus*.

Conus tulipa Linné, 1758
Garrett, 1878b: 355.

***Conus vautieri* Kiener, 1845**

Kiener, 1845: pl. 100, fig. 3, 1849-1850: 350 (description originale, sans localité); Jardin, 1858: 189; Weinkauff, 1874: 248, 1875: 201, pl. 31, figs 8-9; Garrett, 1878b: 356, 365 (sous le nom *Conus Santieri* [sic]); Paetel, 1883: 51, 1888: 308; Rehder, 1969: 32; Bratcher, 1975: 4; Salvat & Rives, 1975: fig. 334; Richard 1983: 15; 1985b: 30, fig. 90; Röckel et al., 1995: 84, pl. 11, figs 13-14 (sous le nom sous-espèce de *Conus pulicarius* Hwass in Bruguière, 1792).

Kiener (1849-1850: 350) ne donne pas de localité pour *Conus vautieri*. Röckel et al. (1995) considèrent *Conus vautieri* comme sous-espèce de *Conus pulicarius* Hwass in Bruguière, 1792. Nous ne suivons pas cet avis mais l'opinion générale des auteurs, et en particulier celui de Richard (1985b) qui différencie clairement *Conus vautieri* de *Conus pulicarius*. Cet auteur précise que, bien que rare aux Marquises *Conus pulicarius* est bien présent et sympatrique de *Conus vautieri*. Notons par ailleurs que Jardin (1858) et Garrett (1878) citent les deux espèces distinctement.

Endémique.

Conus vexillum Gmelin, 1791

Jardin, 1858: 196 (sous le nom *Conus sumatrensis* (= *Conus vexillum sumatrensis* Hwass in Bruguière, 1792, sous-espèce du Nord-Ouest de l'Océan Indien); Rehder, 1969: 31; Salvat & Rives, 1975: 350, fig. 341; Richard, 1985b: 31, fig. 91; Röckel et al., 1995: 131, pl. 23, fig. 1.

Conus virgo Linné, 1758
Richard, 1985b: 31.

Architectonicidae

[*Architectonica maxima* (Philippi, 1849)

Jardin, 1858: 188, 194 (sous le nom «*Solarium perspectivum* Lamarck») (non *Trochus perspectivus* Linné, 1758), synonyme; identification erronée vraisemblable).

Aucune récolte récente ne confirme la présence de *Architectonica maxima* dans les Îles Marquises. Bieler (1993: 52) cite les Îles de la Société comme limite Est de distribution géographique. Jardin a pu confondre avec *Architectonica perspectiva* (Linné, 1758), espèce commune aux Îles Marquises.]

Architectonica modesta (Philippi, 1849)

Salvat & Rives, 1975: 265: fig. 46 (bas) (sous le nom *Architectonica perspectiva* (Linné, 1758), *fide* Bieler, 1993; identification erronée); Bieler, 1993: 80, fig. 63 (carte de distribution géographique).

Architectonica perspectiva (Linné, 1758)

Salvat & Rives, 1975: 265, fig. 46 (haut); Bieler, 1993: 44, fig. 30 (carte de distribution géographique).

Architectonica trochlearis (Hinds, 1844)

Bieler, 1993: 48, fig. 34 (carte de distribution géographique).

Heliacus areola (Gmelin, 1791)

Bieler, 1993: 195, fig. 161 (carte de distribution géographique).

Heliacus implexus (Mighels, 1845)

Bieler, 1993: 212, fig. 179 (carte de distribution géographique).

Heliacus infundibuliformis (Gmelin, 1791)

Bieler, 1993: 270, fig. 220 (carte de distribution géographique).

Bieler cite l'espèce avec doute. Aucune récolte récente n'a été signalée à notre attention. La présence de l'espèce est connue des Îles de la Société et des Tuamotu, mais reste à confirmer pour les Îles Marquises.

Heliacus sterkii (Pilsbry & Vanatta, 1908)

Bieler, 1993: 226, fig. 189 (carte de distribution géographique).

Heliacus trochoides (Deshayes, 1830)

Bieler, 1993: 201, fig. 165 (carte de distribution géographique).

Heliacus variegatus (Gmelin, 1791)

Salvat & Rives, 1975: 265, fig. 48; Rehder, 1969: 30; Bieler, 1993: 189, fig. 158 (carte de distribution géographique).

Psilaxis radiatus (Röding, 1798)

Salvat & Rives, 1975: 265, fig. 47; Bieler, 1993: 123, fig. 100 (carte de distribution géographique); Rehder, 1969: 30 (sous le nom *Philippia hybrida* (Linné, 1758), espèce méditerranéenne et atlantique; identification erronée); Robertson, 1970: 76, fig. 5.

Philippia hybrida et *Psilaxis radiatus* ont souvent été confondus par les auteurs dans la littérature (Bieler, 1993). Il n'est pas douteux que Rehder ait commis la même erreur.

Pyramidellidae

Pyramidella sulcata (A. Adams, 1854)

Dautzenberg & Bouge, 1933: 392.

Pyramidella dolabrata (Linné, 1758)

Salvat & Rives, 1975: 175 (sous le nom *Pyramidella terebellum* (Müller, 1774), synonyme).

Hydatinidae

Hydatina amplustre (Linné, 1758)

Rehder, 1969: 31.

***Hydatina exquisita* Voskuil, 1995**

Salvat & Rives, 1975: 177 (sous le nom *Aplustrum amplustre* (Linné, 1758), identification erronée *vide* Voskuil, 1995); Voskuil, 1995: 37, pl. 1, fig. 13-14 (description originale, localité type: «Marquesas Islands, Pacific»).

Endémique.

Bullidae

[*Bulla adamsi* Menke, 1850

Dautzenberg & Bouge, 1933: 53.

Espèce de Mazatlan, Pacifique de l'Est: identification erronée vraisemblable.]

Bulla conspersa Pease, 1869

Pease, 1869: 72, pl. 8, fig. 9 (description originale, localité type: «Insl. Marquesas»); possible synonyme de *Bulla vernicosa* Gould, 1859).

Bulla vernicosa Gould, 1859

Salvat & Rives, 1975: 177.

Dendrodorididae

Dendrodoris nigra (Stimpson, 1855)

Richard, 1985a: 439.

Phyllidiidae

Fryeria guamensis Brunckhorst, 1993

Bryce, 2000: 74, pl. 1, fig F

Phyllidia tula Marcus & Marcus, 1970

Bryce, 2000: 74, pl. 1, fig E

Ellobiidae

Les Ellobiidae de l'Indo-Pacifique n'ont pas fait l'objet d'une révision récente. Six espèces sont citées des Îles Marquises, mais leur statut taxonomique (espèce? sous-espèce? variante phénotypique?) est incertain.

- Melampus caffer* (Küster, 1844)
Dautzenberg & Bouge, 1933: 45.
- Melampus crassidens* Gassies, 1869
Dautzenberg & Bouge, 1933: 45.
- Melampus cylindroides* Paetel, 1869
Paetel, 1883: 171; Dautzenberg & Bouge, 1933: 45.
- Melampus flavus* (Gmelin, 1791)
Hedley, 1899: 487 (sous le nom *Melampus fasciatus* Deshayes, 1830, synonyme);
Dautzenberg & Bouge, 1933: 46 (sous le nom *M. fasciatus*).
- Melampus philippii* (Küster, 1844)
Garrett, 1887: 46; Dautzenberg & Bouge, 1933: 48.
- Melampus zonatus* (Anton, 1847)
Paetel, 1883: 171; Garrett, 1887: 47.

Espèces nominales dont la localité-type est l'Archipel des Marquises et leur statut actuel.

<i>Plaxiphora gwenae</i> Ferreira, 1987	valide - endémique
<i>Chiton marquesanus</i> Pilsbry, 1893	valide - endémique
<i>Pecten coruscans</i> Hinds, 1845	valide [<i>Chlamys</i>]
<i>Kellia delmasi</i> Lamy, 1927	valide
<i>Cardium mendanaense</i> Sowerby, 1897	ssp. de <i>Vasticardium orbitum</i> - endémique
<i>Argonauta nouryi</i> Lorois, 1852	valide
<i>Nerita haneti</i> Récluz, 1841	syn. de <i>N. morio</i>
<i>Neritina desmoulinsiana</i> Récluz, 1850	syn. de <i>Puperita bensoni</i>
<i>Cerithium rehderi</i> Houbriek, 1992	valide - endémique
<i>Planaxis atra</i> Pease, 1869	valide - endémique
<i>Littorina cinerea</i> Pease, 1869	valide [<i>Nodilittorina</i>] - endémique
<i>Microliotia alvanioides</i> Le Renard & Bouchet, 2003	valide - endémique
<i>Lambis crocata pilsbryi</i> Abbott, 1961	ssp. valide - endémique
<i>Cribrarula fischeri astaryi</i> Schilder, 1971	syn. de <i>C. astaryi</i> - endémique
<i>Cribrarula lefaiti</i> Martin & Poppe, 1989	syn. de <i>C. astaryi</i>
<i>Cypraea cassiaui</i> Burgess, 1965	ssp. de <i>C. granulata</i>
<i>Cypraea philmarti</i> Poppe, 1993	syn. de <i>C. thomasi</i> - endémique
<i>Phenacovolva carneopicta</i> Rehder & Wilson, 1975	valide - endémique
<i>Natica nukahivensis</i> Jardin, 1858	syn. de <i>N. orientalis</i>
<i>Cymatium peasei</i> Beu, 1987	valide
<i>Amaea boucheti</i> Garcia, 2003	valide - endémique
<i>Murex thomasi</i> Crosse, 1872	valide [<i>Chicoreus</i>] - endémique
<i>Chicoreus venustus</i> Rehder & Wilson, 1975	valide
<i>Purpura violacea</i> Lesson, 1842	syn. de <i>Cronia margariticola</i>
<i>Ricinula reeveana</i> Crosse, 1862	syn. de <i>Drupa rubusidaeus</i>
<i>Ricinula porphyrostoma</i> Reeve, 1846	valide [<i>Habromorula</i>]

<i>Columbella pulicaris</i> Lesson, 1842	syn. de <i>Maculotriron serriale</i>
<i>Triton bracteatus</i> Hinds, 1844	syn. de <i>Maculotriron serriale</i>
<i>Orania simonetae</i> Houart, 1995	valide - endémique
<i>Buccinum dumale</i> Philippi, 1851	valide [<i>Phos</i>]
<i>Phos billeheusti</i> Petit de le Saussaye, 1853	syn. de <i>Prodotia iostomus</i>
<i>Columbella marquesa</i> Gaskoin, 1852	valide [<i>Metanachis</i>]
<i>Nassa candens</i> Hinds, 1844	valide [<i>Nassarius</i>] - endémique
<i>Cyrtulus serotinus</i> Hinds, 1843	valide - endémique
<i>Fusus bernardianus</i> Philippi, 1851	<i>nomen dubium</i>
<i>Fusus frondosus</i> Lesson, 1842	<i>nomen dubium</i>
<i>Turbinella fallax</i> Kobelt, 1876	valide [<i>Latirus</i>] - endémique
<i>Latirus liratus</i> Pease, 1868	valide [<i>Peristernia</i>] - endémique
<i>Latirus marquesanus</i> A. Adams, 1855	valide [<i>Peristernia</i>] - endémique
<i>Oliva marquesana</i> Petuch & Sargent, 1985	syn. de <i>O. pammiculata</i>
<i>Morum clatratum</i> Bouchet, 2002	valide - endémique
<i>Morum roseum</i> Bouchet, 2002	valide
<i>Dibaphus philippii</i> Crosse, 1858	syn. de <i>Mitra edentula</i>
<i>Mitra serotina</i> A. Adams, 1853	syn. de <i>M. pellisserpentis</i>
<i>Mitra sertum</i> Duval, 1852	syn. de <i>M. scutulata</i>
<i>Mitra eburnea</i> Philippi, 1850	syn. de <i>Imbricaria conovula</i>
<i>Mitra formosa</i> A. Adams, 1853	syn. de <i>Neocancilla arenacea</i>
<i>Mitra marquesana</i> A. Adams, 1853	syn. de <i>Scabricola variegata</i>
<i>Mitra pallida</i> A. Adams, 1853	syn. de <i>Vexillum virginalis</i>
<i>Gymnobela virgulata</i> Sysoev & Bouchet, 2001	valide - endémique
<i>Iolyris marquesensis</i> Sysoev, 2002	valide - endémique
<i>Terebra argus</i> Hinds, 1844	valide
<i>Terebra pulchra</i> Hinds, 1844	syn. de <i>T. cerithina</i>
<i>Terebra nitida</i> Hinds, 1844	valide
<i>Terebra orizooides</i> Lesson, 1842	<i>nomen dubium</i>
<i>Terebra pallida</i> Deshayes, 1857	syn. de <i>T. punctatostriata</i>
<i>Terebra ligata</i> Hinds, 1844	valide - endémique
<i>Terebra troendlei</i> Bratcher, 1981	valide - endémique
<i>Terebra philippiana</i> Deshayes, 1859	valide [<i>Hastula</i>]
<i>Conus praetextus</i> Reeve, 1848	syn. de <i>C. encaustus</i>
<i>Conus gauguini</i> Richard & Salvat, 1973	valide - endémique
<i>Conus marchionatus</i> Hinds, 1843	valide - endémique
<i>Conus marielae</i> Rehder & Wilson, 1975	ssp. de <i>C. moluccensis</i>
<i>Conus vautieri</i> Kiener, 1849	valide - endémique
<i>Hydatina exquisita</i> Voskuil, 1995	valide - endémique
<i>Bulla conspersa</i> Pease, 1869	valide

Espèces endémiques de l'Archipel des Marquises décrites sans localité ou avec une localité erronée.

<i>Cypraea helvola callista</i> Shaw, 1909	Tahiti
<i>Cypraea thomasi</i> Crosse, 1865	sans localité
<i>Drupa morum iodostoma</i> (Lesson, 1840)	New Zealand
<i>Neocancilla arenacea</i> (Dunker, 1852)	sans localité
<i>Duplicaria trochlea</i> (Deshayes, 1857)	Zanzibar

Espèce absente dont la localité type Archipel des Marquises est erronée.

Lotorium armatum Sowerby, 1897

Espèces endémiques.

Sur les **365** espèces présentes aux Marquises, recensées dans la littérature, **29** espèces (**7,95%**) sont considérées comme endémiques de la région. Parmi les espèces récemment récoltées (MUSORSTOM 9 - Atelier de Ua Huka) un premier examen des protoconques des espèces de gastéropodes encore inconnues de Polynésie Française tend à montrer un niveau d'endémisme supérieur qui pourrait atteindre les 10%.

Plaxiphora gwenae Ferreira, 1987
Chiton marquesanus Pilsbry, 1893
Cerithium rehderi Houbbrick, 1992
Angiola atra (Pease, 1869)
Nodilittorina cinerea (Pease, 1869)
Microliotia alvanioides Le Renard & Bouchet, 2003
Cypraea astaryi (Schilder, 1971)
Cypraea thomasi Crosse, 1865
Phenacovolva carneopicta Rehder & Wilson, 1975
Amaea boucheti Garcia, 2003
Chicoreus thomasi (Crosse, 1872)
Orania simonetae Houart, 1995
Nassarius candens (Hinds, 1844)
Cyrtulus serotinus Hinds, 1843
Latirus fallax (Kobelt, 1876)
Peristernia lirata (Pease, 1868)
Peristernia marquesana (A. Adams, 1855)
Morum clatratum Bouchet, 2002
Neocancilla arenacea (Dunker, 1852)
Gymnobela virgulata Sysoev & Bouchet, 2001
Iotyrris marquesensis Sysoev, 2002
Duplicaria trochlea (Deshayes, 1857)
Terebra ligata Hinds, 1844
Terebra troendlei Bratcher, 1981
Conus encaustus Kiener, 1845
Conus gauquini Richard & Salvat, 1973
Conus marchionatus Hinds, 1843
Conus vautieri Kiener, 1845
Hydatina exquisita Voskuil, 1995

Sous-espèces endémiques:

Vasticardium orbitum mendanaense Sowerby, 1897
Lambis crocata pilsbryi Abbott, 1961
Cypraea fimbriata marquesana (Lorenz, 2002)
Cypraea helvola callista Shaw, 1909
Cypraea maculifera martybealsi (Lorenz, 2002)
Drupa morum iodostoma (Lesson, 1840)

CONCLUSIONS

Jardin (1858) cite **120** espèces; nous avons reconnu **45** espèces marines, **3** d'entre elles ne vivant pas aux Marquises. Dautzenberg & Bouge (1933) citent **45** espèces dont **5** ne vivent pas aux Marquises. Richard (1985a) cite **229** dont seules **48**, considérées comme des citations nouvelles, sont reprises dans cette étude et nous pensons que **7** d'entre elles ne vivent pas aux Îles Marquises.

Nous avons recensé au total **391** espèces valides citées dans la littérature pour l'Archipel des Marquises. Sur ces **391** espèces nous avons pu vérifier la présence de **340** espèces. Pour **25** espèces leur présence aux Îles Marquises est possible mais non confirmée; en revanche pour **26** espèces nous pensons qu'il s'agit d'erreurs d'identification et qu'elles sont absentes des Îles Marquises.

Les récoltes récentes effectuées lors de la campagne MUSORSTOM 9 et de l'atelier de Ua Huka, et dont l'inventaire et l'identification des espèces sont en cours, permettent d'ors et déjà d'évaluer le nombre d'espèces littorales à plus de 500 et d'estimer, avec les collectes profondes, à 700 le nombre total d'espèces actuellement récoltés aux Îles Marquises.

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