Geophysical Variables as Predictors of Megabenthos Assemblages from the Northern Great Barrier Reef, Australia

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Abstract

The question as to whether geophysical data from habitats can be used to predict the occurrence of benthic biodiversity is becoming more important with the increase in the use of Marine Protected Areas (MPAs) as tools for marine conservation. To help answer this question and to better understand the relationship between sediment, geomorphology and benthos, a multibeam sonar survey was conducted over two areas in the northern Great Barrier Reef–Gulf of Papua region. Multivariate statistical analyses (cluster, multi-dimensional scaling and BIO-ENV procedure) of the physical and biological datasets from both areas determined that the geophysical variables, slope and gravel percentage, were the best predictors for megabenthos assemblage patterns. In conjunction with Geographic Information System (GIS) models of the geomorphology and bathymetry, these geophysical variables were used to derive the spatial boundaries of benthic habitats for each study area. A hierarchical method of benthic-habitat mapping to the Secondary Biotope and Biological Facies levels was applied at the site (<10 km) scale. The combination of substrate type, sedimentary dynamics and physical processes related to near-seabed currents appear to be the dominant control on the benthic communities in the northern Great Barrier Reef–Gulf of Papua region. These results add confidence to the use of geophysical data from seabed habitats, such as geology, sediment and morphology, as predictors for benthos distribution and thus provide a basis for marine reserve selection.

Résumé

Le questionnement sur la pertinence des données géophysiques provenant des habitats dans la prédiction de la présence de biodiversité benthique devient de plus en plus important avec l'augmentation de l'utilisation des zones marines protégées comme outils de conservation marine. Afin d'aider à répondre à cette problématique et de mieux comprendre les *relations entre les sédiments, la géomorphologie et le benthos, un levé au sonar multifaisceaux a été réalisé dans deux zones de la partie nord de la Grande Barrière de corail, dans le golfe de la région de la Papouasie. Des analyses statistiques multidimensionnelles (amas, échelonnage multidimensionnel et procédure BIO-ENV) des ensembles de données physiques et biologiques des deux zones ont permis de déterminer que les variables géophysiques, la pente et le pourcentage de gravier, constituaient les meilleurs prédicteurs des patrons d'assemblage du mégabenthos. Conjointement aux modèles de Systèmes d'information géographique (SIG) de la géomorphologie et de la bathymétrie, ces variables géophysiques ont été utilisées pour déduire les limites spatiales des habitats benthiques de chaque zone d'étude. Une méthode hiérarchique de cartographie des habitats benthiques des couches de biotope secondaire et des faciès biologiques a été appliquée à l'échelle du site (<10 km). La combinaison du type de substrat, de la dynamique sédimentaire et des processus physiques liés aux courants près du fond marin semble constituer le contrôle dominant sur les communautés benthiques de la partie nord de la Grande Barrière de corail, dans le golfe de la région de la Papouasie. Ces résultats renforcent l'utilisation des données géophysiques des habitats du fond marin, comme la géologie, les sédiments et la morphologie, comme prédicteurs de la distribution du benthos et offrent donc une base pour la sélection des réserves marines.*

INTRODUCTION

One of the major obstacles posed for managers of marine environments to enable them to effectively discharge their responsibilities, has been knowledge of the benthic biodiversity. The vastness of the continental shelf seabed, let alone the deep abyssal seas, and the high cost of data collection are huge impediments for even developed countries. Over most of the continental shelf, there is an absence of biological data of the required quality and scale to map biological distributions (Stevens, 2002). Yet the trend toward Marine Protected Areas (MPAs) as zones of conservation of biodiversity demands a detailed knowledge of benthic habitats and associated biological communities. In the absence or paucity of biological data on which to base decisions on benthic habitat boundaries, MPAs rely upon abiotic or geophysical factors to characterize the seabed and water column, and thus provide a basis for reserve selection (Zacharias *et al.*, 1999; Roff *et al.*, 2003). Such questions as whether, and to what extent, the geophysical data from habitats can be used to predict the occurrence of assemblages of benthic organisms, will become increasingly important. However, there are few studies on the quantitative associations between habitats and the biological communities which depend on these habitats (Zacharias *et al.*, 1999).

A number of studies have attempted to answer this vexing question, often using multivariate or regression analysis to make quantitative associations on soft substrate (Schlacher *et al.*, 1998; Edgar and Barrett, 2002; Stark *et al.*, 2003; Giberto *et al.*, 2004; Rodil and Lastra, 2004), or on hard/complex substrate (Wilkinson and Cheshire, 1989; Schoch and Dethier, 1996; Bourget *et al.*, 2003). Typically, results show the patchiness of biological communities and habitats, and conclude that there is no single correct scale at which ecosystems can be described. In addition, each study must be clearly defined as to the scale of interest for comparisons to be made against similar areas (Shin and Ellingsen, 2004). At the broader scale, a number of studies have been made which successfully link regional-scale (100s of km) physical processes to biological patterns. For example, seabed current stress was used as a predictor of benthos distribution in the Torres Strait (Long *et al.*, 1995), and sediment type was found to be an important factor in the distribution of prawn species in the Gulf of Carpentaria (Somers, 1987). Zacharias and Roff (2001) were able to show that a combination of physical factors, related to environmental stability and disturbance, could explain patterns of intertidal species richness in coastal British Columbia.

Importantly, habitat should be considered as a surrogate for ecological structure within a hierarchy of scales (Greene *et al.*, 1999; Roff and Taylor, 2000). One such scheme used for the bioregionalization of Australia (Butler *et al.*, 2001) defined six levels: 1) Provinces, based upon broad-scale geological patterns and 1000s of km in extent, *e.g.*, continental blocks and abyssal basins; 2) Biomes, nested within provinces at the regional scale (100s of km), showing broad-scale geomorphology, *e.g.*, coast, continental shelf, slope and abyssal plain; 3) Geomorphic Units, within each biome at the local scale (10s of km), with areas of similar seabed geomorphology and usually having distinct biotas, *e.g.*, seamounts, canyons, rocky banks and coral reefs; 4) Primary Biotopes of soft, hard and mixed substrate-based units, together with their associated biological communities, also at the local scale (10s of km; maps to this level can generally be obtained by high-resolution acoustic surveys); 5) Secondary Biotopes which are substructural units within primary biotopes and are distinguished by the types of physical or biological substrate within soft, hard or mixed types at the site scale (<10 km), *e.g.*, limestone, granite, shelly sands or seagrasses (maps to this level are obtained by biological and physical ground-truthing); 6) Biological Facies being site scale (<10 km) units defined by a biological indicator, such as a species of seagrass, or group of hardcorals, sponges or other macrofauna linked to the facies.

To better understand the relationship between sediment, geomorphology and biological communities, a survey cruise was undertaken to the northern Great Barrier Reef–Gulf of Papua region between January and February, 2002 (Geoscience Australia Survey 234; Harris *et al.*, 2002). In this study, the Butler *et al.* (2001) habitat classification scheme was adopted to map a series of areas along a transect from the Fly River delta to the northern end of the Great Barrier Reef at the Secondary Biotope and Biological Facies levels. Multibeam sonar and a sub-bottom profiler were utilized; this was followed by collecting underwater video footage and grab samples at selected sites. This study contrasts two diverse areas within: 1) an inner shelf, low-relief, distal-deltaic zone; and 2) a high-relief, mid-shelf, incised valley zone (Harris *et al.*, 1996). These areas were selected from previous surveys by the author (PTH), and were considered typical of inner-shelf and mid-shelf areas in the northern Great Barrier Reef. The objective of the present study was to determine whether, in common with both areas, there is a combination of environmental variables which may be useful to quantitatively predict the distribution of megabenthos assemblages at the site scale (<10 km) in the northern Great Barrier Reef–Gulf of Papua region. The immediate objectives here are to: 1) describe the physical environment of the two areas; 2) determine the dominant megabenthos assemblage patterns; 3) examine which geophysical variables are the best predictors for megabenthos assemblages; and 4) derive maps of the secondary biotopes and biological facies of the two areas.

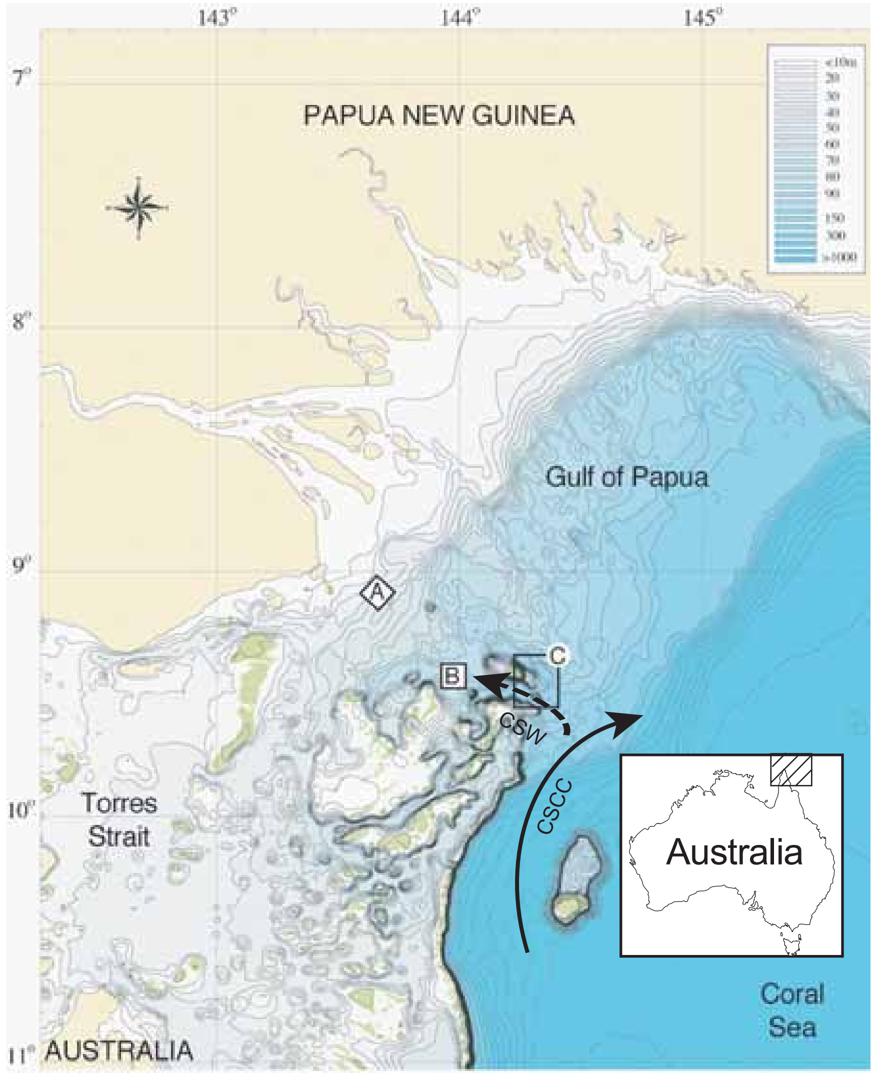


Figure 1. *Regional bathymetric map of the Gulf of Papua, Torres Strait and northern Great Barrier Reef based upon a new compilation of digital data provided by the Commonwealth Scientific and Industrial Reseach Organization (CSIRO) Division of Marine and Atmospheric Research and the Royal Australian Navy Hydrographic Office. Reefs are shaded green. Boxes show the location of surveys in Areas A and B reported in this paper from Geoscience Australia Survey 234 (Harris* et al.*, 2002). Only results from Areas A and B are reported in this paper. CSCC, Coral Sea Coastal Current; CSW, upwelling Coral Sea water.*

MATERIALS AND METHODS

Study Areas

Area A (Figure 1) is located on the distal-delta of the Fly River along the western margin of the Gulf of Papua. The Fly River is rated as the 17th largest river in the world, based upon a pre-industrial sediment discharge of 85 million tonnes year^{-1}, due to abundant rainfall in the Papua New Guinea highlands (Harris *et al.*, 1993). The distal-delta lies in 20 to 50 m of water, and is deep enough to escape reworking except by the largest wind-driven waves (Harris *et al.*, 1993). Wind-driven currents in the area reflect the seasonal variation in winds, from the northwest during the monsoon period, November to April, and from the southeast during the trade-wind season, May to October (Wolanski *et al.*, 1988). The distal-delta sediment facies are millimetre- to decimetre-thick sand/mud alternations occurring with a limited amount of bioturbation (Harris *et al.*, 2004b). Despite the proximity to the Fly River mouth, the distal-delta experiences a slow rate of sediment accumulation at the present time (Harris *et al.*, 2002; Walsh *et al.*, 2004). Brackish water plumes derived from the Fly River are known to extend over this area (Wolanski *et al.*, 1984; Davies, 2004).

Area B (Figure 1) lies on an incised valley zone on the middle shelf, just north of the Great Barrier Reef (Harris *et al.*, 1996). The seabed shows a complex, east–west valley-dominated bathymetry of approximately 50 to 130 m water depth. The area experiences the same seasonal variation in winds as the distal-delta region. A branch of the South Equatorial Current gives rise to a clockwise rotating current within the Gulf of Papua called the Coral Sea Coastal Current, which sweeps north along the outer shelf but reduces toward the coast (Wolanski *et al.*, 1995). Oceanographic observations in Area B indicate that the valleys provide a conduit onto the shelf for cool and saline upwelled Coral Sea water (Harris *et al.*, 2002). The surficial sediment reflects a Great Barrier Reef shelf facies with a calcium carbonate content that increases toward the south, and which contain less than 50% mud (Harris *et al.*, 1993).

Bathymetry Data

A Reson™ SeaBat 8101 240 kHz multibeam sonar recorded bathymetry using a line spacing of 250 m in both Areas A and B. Navigation was maintained with a differential GPS to a horizontal accuracy of better than 5 m. Tidal corrections were performed at Geoscience Australia using predicted tidal heights provided by the

National Tidal Facility at Flinders University, South Australia. The tidal heights were derived from a computer tidal model and related to the centre positions of Areas A and B. ASCII XYZ (easting/northing/depth) point data at 10 m intervals were extracted from the raw files using Caraibes seafloor mapping software (http://www.ifremer.fr/fleet/equipements_sc/logiciels_embarques/caraibes/) and interpolated using the ESRI™ ArcInfo program Topogrid to generate a 5-m resolution bathymetric model of each area. The resulting bathymetry grids were analyzed for artificial drainage flow and slope within ESRI™ ArcGIS, and viewed as a 3-D digital terrain model. The slope model was created by fitting a plane with a 3 x 3 cell neighbourhood around each processing or centre cell. Thus, slope was averaged over a distance of 15 m for each cell of the bathymetry model to derive a 5-m resolution slope model for each area.

In conjunction with the multibeam sonar, a Datasonics™ DSP 661/66 3.5 kHz Chirp sub-bottom profiler and towfish TTV170S recorded high-resolution seismic data throughout the survey with a trigger interval of 0.25 seconds. The high-resolution sub-bottom profiles were recorded as CGM images for each survey line, then examined in the viewing program ZEHPlot-PE™ for echo-character types based upon Damuth (1980). At each one-minute interval (about 150 m equivalent distance), an echo-character type was assigned within a spreadsheet. The resulting spreadsheet was converted to an ArcGIS point shapefile, and then polygon boundaries were digitized to match the spatial distribution of echo-character types, which was then used to help create a GIS model of the geomorphology for each study area.

Underwater Video Data

Within each study area, 21 sites were selected for ground-truth sampling based upon variation observed in bathymetric and sub-bottom profiles. The aim was to ground-truth as much seabed surface and sub-bottom diversity as possible to observe the variation in geomorphology and any associated biological communities. A sled-mounted analog video camera was towed along the seabed for about five minutes at each station to obtain a transect averaging approximately 75 m long. A scaled ruler was mounted on the sled within view of the camera to obtain a crude size of features on the seabed. Real-time video images were fed to the vessel and recorded onto VHS tape through a monitor, with the differential GPS position and time recorded automatically on the video. Underwater video footage was viewed frame-by-frame (approximately every two seconds or an equivalent 0.5 m distance range) and a megabenthos category assigned based on the predominant assemblage in the frame. Megabenthos is defined as organisms readily visible in photographs (Solan *et al.*, 2003). Categories were: no fauna, small sponge, mixed garden, softcoral, mobile, bioturbator. The softcoral category included softcorals, gorgonians and sea whips (*Alcyonacea*). The mixed garden category comprised both softcorals and sponges, and other dense fauna. Mobile megabenthos was typically echinoderms and excluded fish. The bioturbator category comprised mounds or burrows as indicators of the indirect presence of infauna.

The resolution of the analog video precluded taxonomic classification of individual organisms to a specific level, and so these broad categories were considered detailed enough to capture the variation of biological assemblages associated with benthic habitat at the scale of this study. For each transect, counts were made of the number of times a megabenthos category was recorded, and then standardized into the percentage occurrence. Thus, each transect had a ratio of the megabenthos categories observed and provided the data to conduct multivariate statistical analysis. Using the statistical program Primer Ver. 5 (Clarke and Warwick, 2001), Bray–Curtis similarity coefficients were computed on the square root-transformed percentage megabenthos data, the purpose of the transformation being to reduce the emphasis on dominant components. The resulting similarity matrix from each study area was analyzed using group-averaged cluster analysis and displayed as a non-metric, Multi-Dimensional Scaling (MDS) ordination plot to establish the similarity in megabenthos occurrence between transects.

Environmental Data

While in position at each station, a Sea-Bird Electronics™ SBE911 conductivity/temperature/depth (CTD) profiler was deployed along with a SeaTech transmissometer, calibrated to measure suspended sediment concentration in the water column. At each station, surficial sediment grabs were obtained by Smith-McIntyre grab, collecting approximately 10 litres of sediment. Sediments from grab samples were analyzed for percentage gravel, sand and mud content by the wet sieve method, using nested 2 mm and 63 µm analytical sieves. The carbonate content of the gravel fraction was estimated visually, within approximately ± 5%. The carbonate content of the sand and mud fractions were determined separately in a carbonate bomb, where a known weight of dried and crushed sediment is placed in a sealed chamber (Müller and Gastner, 1971). Dilute hydrochloric acid is released inside the chamber and the dissolution of the calcite produces CO_2 gas. The mass of calcium carbonate was then determined by a calibration curve.

To test which environmental variables were the best predictors for the megabenthos assemblage patterns observed in video transects at each station, a spreadsheet was compiled with the following categories: depth (m), slope (º), gravel weight (%), sand weight (%), mud weight (%), gravel $CaCO_3$ (%), sand $CaCO_3$ (%), mud $CaCO_3$ (%), total $CaCO_3$ (%), temperature (ºC), salinity (psu), and transmission (%). The data for the oceanographic variables of temperature, salinity and transmission were obtained from near-seabed at each cast. Because of the requirement to obtain a single depth and slope value at each sample site for comparison against the megabenthos data, the video transect lines were overlaid on the slope and bathymetry grid models within a GIS. The cell values from the depth and slope models intersected by each transect were examined in a histogram and the mean was used to derive the single depth and slope value at each sample site. The resulting spreadsheet of environmental variables of each area provided data for multivariate statistical analysis.

Using the statistical program Primer, a Principal Component Analysis (PCA) was conducted on the untransformed environmental data to establish trends in environmental variables across the sites. PCA ordination using normalized Euclidean distance to measure dissimilarity of samples is a suitable method of analyzing relationship trends for environmental variables (Clarke, 1993). The BIO-ENV procedure in Primer was then used to explore the subset of environmental variables which best matched the observed megabenthos patterns. The BIO-ENV routine simply calculates a measure of agreement between the two (dis)similarity matrices. For each survey area, the Bray–Curtis similarity matrix of square root-transformed megabenthos data was compared against the normalized Euclidean distance (dissimilarity) matrix of untransformed environmental data. Spearman's rank correlation coefficients quantifies the match between the biotic and abiotic matrices, and chooses the subset of environmental variables which maximize the correlation coefficient. This subset of environmental variables was given priority for overlay in a GIS, and in conjunction with models of the geomorphology and bathymetry, assisted in deriving the spatial boundaries of the secondary biotopes and biological facies of each area. These boundaries were then digitized as polygon shapefiles within ArcGIS for overlay on the 3-D digital terrain models.

RESULTS

Geomorphology

Approximately 68 km^2 of seabed was mapped in Area A to 100% coverage. The bathymetry of Area A shows a gradual seaward-dipping ramp forming the distal section of the Fly River delta (Figure 2A). Water depths range from 22 to 38 m over a flat seabed with isolated knolls and pockmarks. The knolls are up to 4 m above the surrounding seabed and the pockmarks are less than 1 m deep. Knolls and ridges with a similar relief above the surrounding flat seabed have been recognized in other studies within the distal delta. The knolls and ridges are generally flat-topped and described as 'mesa-like' in profile (Harris *et al.*, 1996). There are seabed surface expressions of two shallow channels trending normal to the general slope of the area, which average approximately 550 m in width. Sub-bottom profiles reveal these features to be infilled channels (Figures 3A and 3B). The channels are now infilled to approximately 10 to 15 m deep. A third infilled channel with little surface expression was detected across the middle of the sur-

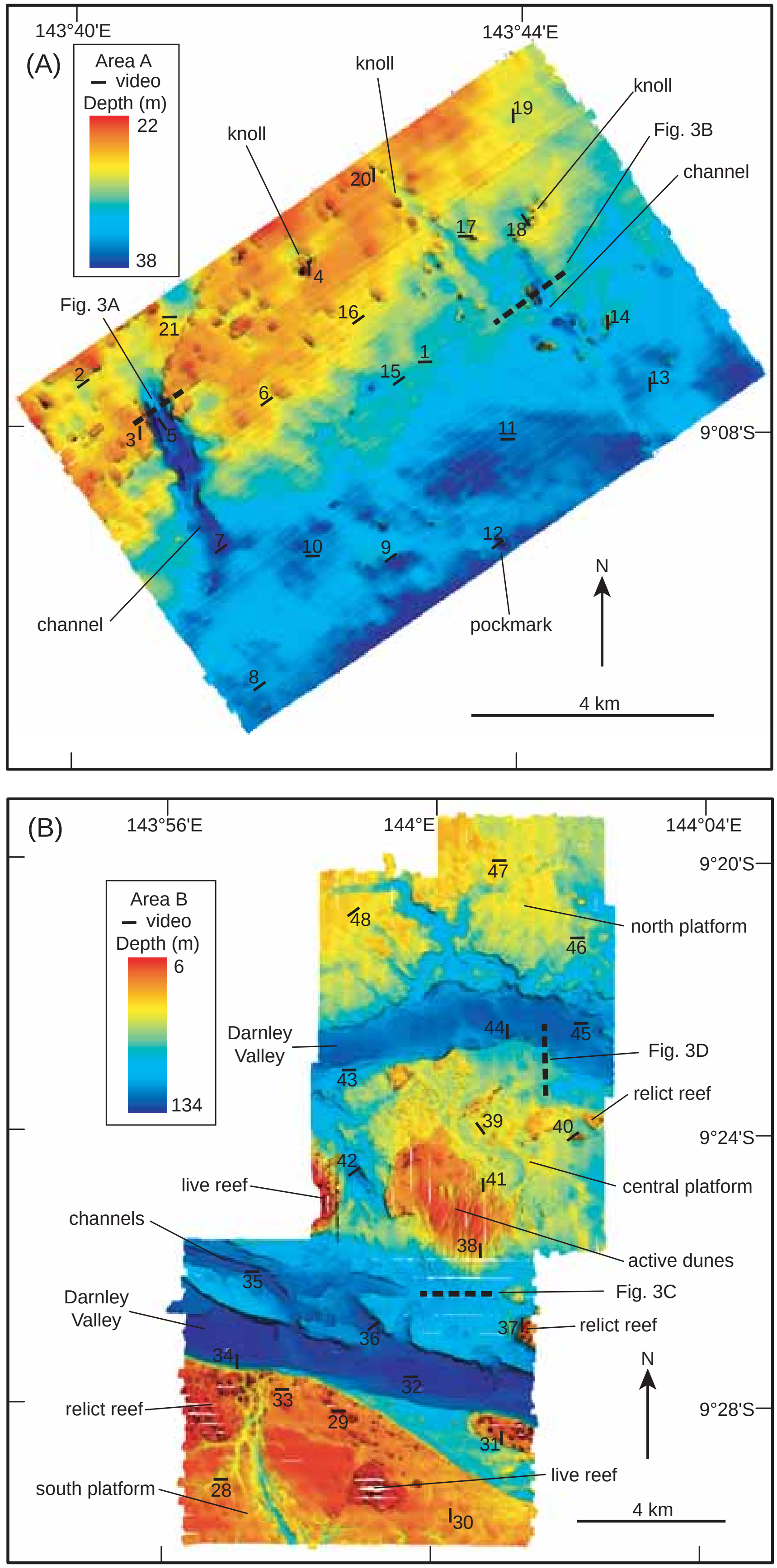


Figure 2. *Sun-shaded bathymetric maps of the survey areas. (A) Area A on the Fly River distal-delta. Note the shallow channels aligned normal to the isobaths and the numerous low-relief knolls. (B) Area B on the northern Great Barrier Reef shelf. Note the presence of deep submarine valleys as two limbs of the Darnley Valley separate around a live reef in the west-central platform. Numbers refer to the video transect stations. Dashed lines refer to the positions of sub-bottom profiles in Figure 3.*

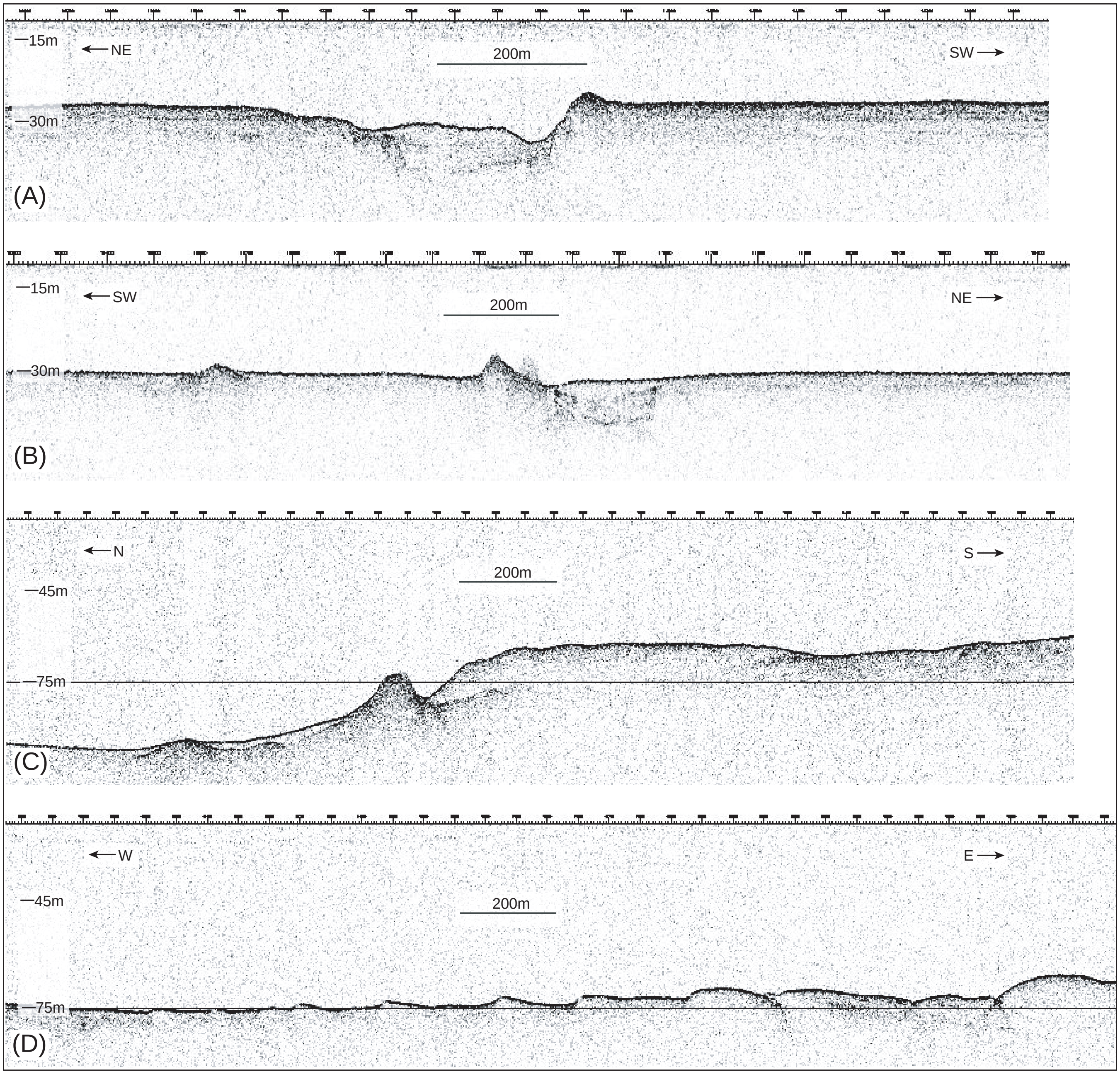


Figure 3. *Example Chirp sub-bottom profiles. (A) Area A, showing an infilled channel. (B) Area A, showing sub-surface reflectors and infilled channel. (C) Area B, showing sub-surface reflectors on the margin of the north arm of the Darnley Valley. (D) Area B, showing an active dune field. See Figure 2 for locations.*

vey area. Seismic profiles revealed that isolated knolls lay either side of the infilled channels, and look much like relict versions of the ridge and channel morphology characteristic of modern tide-dominated deltas (Walker, 1984). Pockmarks are located around the base of a number of these low-relief knolls.

Approximately 165 km^2 was mapped in Area B to nearly 100% coverage. The survey confirmed the presence of a submarine valley system, trending east–west across the shelf dividing the survey area into three platforms (Figure 2B). Depths in the valleys are about 130 m in the south valley and 90 m in the north valley. Multibeam survey results show that the two valleys are separate limbs of the Darnley Valley, which branches around an unnamed live reef in the west-central study area. These valleys are considered to have been formed by high-energy, tidal current scour during mid-stand sea levels in the late Quaternary and are now relict features (Harris *et al.*, 2005). In the north of the survey area is a relatively flat and channel-incised platform about 55 m deep. On the central platform, sub-bottom profiles also reveal numerous meandering channels, now infilled to maximum depths of approximately 20 m with little or no seabed surface expression (Figure 3C). A large seabed surface feature of the central platform is an active dune field at depths of approximately 40 to 70 m, with crest to trough heights averaging 2 m, and wavelengths of approximately 180 m (Figure 3D). Dune crests are sinuous, often sharp, and in cross-section the lee slope faces west, suggesting net westerly current flow (Harris *et al.*, 2005). A live reef on the south platform extends to approximately 6 m below the water surface from platform depths of about 50 m. Scattered around the southern and central platforms are numerous submerged or relict reefs showing karst-erosion surfaces in sub-bottom profiles between depths of 30 to 42 m, and averaging 36 m.

Megabenthos

Table 1 gives the percentage occurrence of megabenthos categories for Area A transects 1 through 21 (Figure 2A). For 19 out of the 21 video transects, the substrate appears as a muddy sand, and mostly flat to undulating topography. Only the occasional small bushy softcoral or small tube sponge was observed as sessile megabenthos. Rare holothurians or asteroids were the only mobile megabenthos observed on the sand flat, however, there were moderate to abundant burrows and mounds. These were likely the result of Ghost shrimps (*Callinassidae*) biogenically working the seabed. In contrast to the predominantly flat seabed, the seafloor at Stations 4, 14 and 18 (Figure 2A) was noticeably more gravelly and revealed low-relief (<4 m in vertical change) knolls above the surrounding flat seabed. Cores targeting the knolls obtained a compacted grey mud and scattered shell debris. Wherever the low-relief limestone knolls were observed in video transects, prolific mixed gardens of fan-shaped sponges, gorgonian fan corals, large bushy softcorals and sea whips appeared as sessile fauna attached to the hard surface of the knolls. Soldier fish (*Holocentridae*) and large cod (*Serranidae*) congregated around the low-relief knolls. Station 12, which targeted a pockmark adjacent to a knoll, recorded the substrate becoming coarse and with a prominent change in gradient as the video sled travelled into the depression. Only the occasional small bushy softcoral was observed with no bioturbation on the seabed.

Table 2 gives the percentage occurrence of megabenthos categories for Area B transects 28 through 48 (Figure 2B). Most of the stations sampled the flat to gently undulating extensive platforms. On the seabed was sparse sessile benthos, with just the occasional small bushy softcoral observed. Only infrequent mounds or burrows were recorded, in contrast to the more heavily bioturbated seabed of Area A. Rare individual ophiuroids and echinoids were seen moving along the seabed. On the central platform, transects obtained at stations 38 and 41 on the active dune field showed a seabed of mostly sand and few gravel clasts. Small ripples, about 10 cm apart, were superimposed on the stoss slope of the dunes. Burrows and sessile megabenthos were rarely observed in this dynamic area. Transects at stations 34 and 44 sampled the sides of the valleys and found the high-gradient seabed to have abundant cobbles and boulders scattered on the gravelly sand. Sessile benthos was moderate to abundant, with the scattered boulders providing the attachment substrate for large softcorals and sea whips.

Transects at stations 32 and 45 (Figure 2B) sampled the valley floors at approximately 129 m and 88 m, respectively, and the seabed became notably more muddy, indicating an increase in finer grained sediment in these deeper areas. In contrast to the valley sides, the flat valley floors were much reduced in biota. Scattered around the south and central platforms were high-relief (>4 m in vertical change) submerged or relict reefs. When video transects ran directly over the relict reefs at stations 29, 37 and 40 (Figure 2B), the karst-style erosion was obvious. Weathered limestone outcrop

Table 1. Underwater video transect megabenthos descriptors for Area A. Counts were made of the various descriptors at two-second intervals along each transect and standardized into percentage occurrence. See Figure 2A for locations

Video number	No fauna (%)	Small sponge (%)	Mixed garden (%)	Soft-coral (%)	Mobile (%)	Bioturbator (%)
1	52.48	0.00	0.00	0.71	0.00	46.81
2	81.58	0.00	0.00	0.00	0.00	18.42
3	71.11	0.74	0.00	9.63	0.00	18.52
4	17.28	0.62	35.19	46.91	0.00	0.00
5	95.00	0.00	0.00	0.00	0.00	5.00
6	62.73	0.00	0.00	0.91	0.00	36.36
7	72.22	0.00	0.00	2.78	0.00	25.00
8	78.26	1.09	0.00	1.09	1.09	18.48
9	80.58	1.94	0.00	4.85	0.97	11.65
10	88.78	0.00	0.00	0.00	0.00	11.22
11	84.38	1.04	0.00	0.00	0.00	14.58
12	97.30	0.00	0.00	2.70	0.00	0.00
13	89.51	0.70	0.00	0.00	0.00	9.79
14	75.74	0.37	6.99	9.56	0.37	6.99
15	89.25	0.00	0.00	0.00	0.00	10.75
16	85.84	0.00	0.00	0.00	0.00	14.16
17	91.23	0.00	0.00	0.88	0.00	7.89
18	78.13	1.25	9.38	9.38	0.00	1.88
19	90.40	0.00	0.00	0.80	0.00	8.80
20	83.48	0.00	0.00	0.87	0.00	15.65
21	95.58	0.00	0.00	0.00	0.00	4.42

Table 2. Underwater video transect megabenthos descriptors for Area B. Counts were made of the various descriptors at two-second intervals along each transect and standardized into percentage occurrence. See Figure 2B for locations

Video number	No fauna (%)	Small sponge (%)	Mixed garden (%)	Soft-coral (%)	Mobile (%)	Bioturbator (%)
28	89.50	0.00	0.00	0.00	0.00	10.50
29	72.45	0.51	22.45	0.00	0.00	4.59
30	97.95	0.00	0.00	1.37	0.68	0.00
31	95.00	0.00	0.00	5.00	0.00	0.00
32	97.06	0.00	0.00	0.00	1.18	1.76
33	95.83	0.00	0.00	2.78	0.00	1.39
34	63.00	2.00	0.00	35.00	0.00	0.00
35	90.55	0.00	0.00	4.72	0.00	4.72
36	86.33	0.72	0.00	10.07	0.00	2.88
37	39.33	0.00	52.81	7.87	0.00	0.00
38	99.28	0.00	0.00	0.72	0.00	0.00
39	93.81	0.00	0.00	0.00	0.00	6.19
40	28.06	0.00	38.13	33.81	0.00	0.00
41	96.55	0.00	0.00	2.76	0.00	0.69
42	99.51	0.00	0.00	0.49	0.00	0.00
43	95.51	0.00	0.00	3.37	1.12	0.00
44	75.63	0.00	3.13	20.63	0.00	0.63
45	93.03	1.00	0.00	5.97	0.00	0.00
46	91.12	0.00	0.00	5.92	2.37	0.59
47	98.44	0.00	0.00	0.52	0.00	1.04
48	93.96	0.00	0.00	4.70	0.00	1.34

revealed numerous holes and caves, providing a favourable attachment habitat for dense gardens of large softcorals, sponges and sea whips. Within Area B, two unnamed live reefs were surveyed in the south platform and western-central platform. Both these two reefs came within approximately 10 m of the water surface and had abundant live hardcorals observed from the deck of the vessel. However, neither reef was sampled by video or grab sample and so were excluded from statistical analysis.

The non-metric, MDS ordination plots of square root-transformed percentage megabenthos occurrence data in Tables 1 and 2 show distinct groups of samples. In Area A (Figure 4A), dense mixed gardens of softcorals, sponges and sea whips occur only on the limestone knolls observed at stations 4, 14 and 18, with the latter two stations also being bioturbated due to flat seabed along the transects. Station 12 has no bioturbation and only softcorals, and appears dissimilar compared to the other stations. In contrast, most of the stations in Area A are grouped together showing a similar high bioturbated assemblage, reflecting the presence of abundant infauna in the muddy sand. The MDS plot for megabenthos in Area B (Figure 4B) shows a group of mixed garden assemblage at stations 29, 37 and 40, which were sampled over the relict reefs. Softcorals dominate at stations 44 and 34, obtained on the relatively steep valley sides. Figure 4B shows a group of the remaining stations as predominantly sparse fauna. These stations included the infilled channel sites, active dune field, valley floors and on the extensive platforms.

Environmental Variables

Tables 3 and 4 show the environmental data for Areas A and B, respectively. In Area A, slope ranged from nearly 0º to 3º, highlighting the generally flat study area. Gravel percentage ranged from approximately 2% to as high as 70% (Figure 5A). Total calcium carbonate varied from 37% to 92%. In Area B, slope varied from nearly 0º to over 11º, reflecting an increase in relief and gradient compared to Area A. Gravel percentage ranged from less than 1% to nearly 32% (Figure 5B). The total calcium carbonate ranged from approximately 34% to greater than 95%.

Ordination plots of PCA on the untransformed environmental descriptors in Tables 3 and 4 show distinct groups of similarity. In Area A (Figure 6A), a group of stations 4, 12, 14 and 18 shows relatively higher slope and were obtained at the knoll and pockmark sites. A second group of the remaining stations were obtained from the predominantly flat muddy sand of Area A. In Area B (Figure 6B), there are three groups of similarity. One group, with a relatively high slope, are the relict reef samples at stations 29, 37 and 40. Another group of relatively high slope are the valley sides and adjacent channel samples at stations 34, 36, 42 and 44. The remaining stations are grouped into samples obtained from the predominantly flat platforms, dune field and valley floors.

BIO-ENV Procedure

To explore the subset of environmental variables which best matches the observed megabenthos patterns in Area A, the BIO-ENV procedure was applied to the biotic data in Table 1 and abiotic data in Table 3. Reducing the environmental variables to a manageable subset of three, the best combination is slope, gravel weight and sand $CaCO_3$ at a Spearman's rank correlation of 0.747. For Area B, the BIO-ENV procedure on biotic data in Table 2 and abiotic data in Table 4 results in a best combination of slope, gravel weight and transmission at a Spearman's rank correlation of 0.62. Both correlation coefficients are relatively high (1.0 would be a perfect match) suggesting that these subsets of abiotic variables are good matches for the patterns of megabenthos assemblages observed in the MDS plots of Figure 4.

Of interest in the BIO-ENV results is the inclusion of the environmental variables, slope and gravel weight, from both survey areas despite the obvious contrast in marine landscapes. The relatively high correlations indicate that these two environmental variables, slope and gravel weight, are potentially useful as predictors for megabenthos assemblage patterns in this study. For example, sites with high slope and gravel weight values appear to correlate with the presence of relatively dense mixed gardens of softcorals, sponges and sea whips on both the knolls of limestone in Area A and the relict reefs in Area B. Sites with low slope and gravel weight values correlate with bioturbated muddy sand in Area A and the sparse fauna

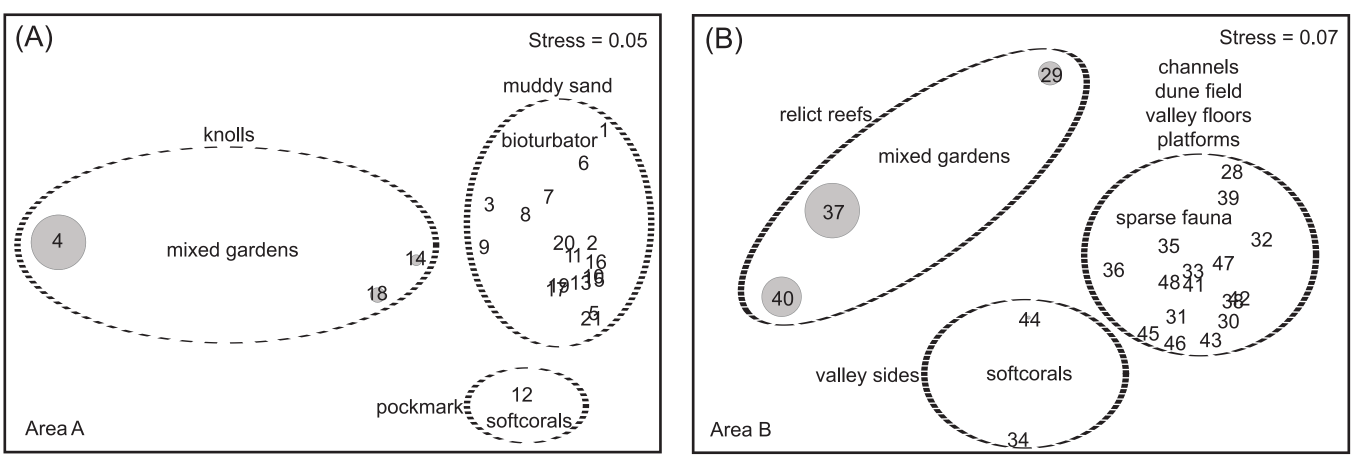


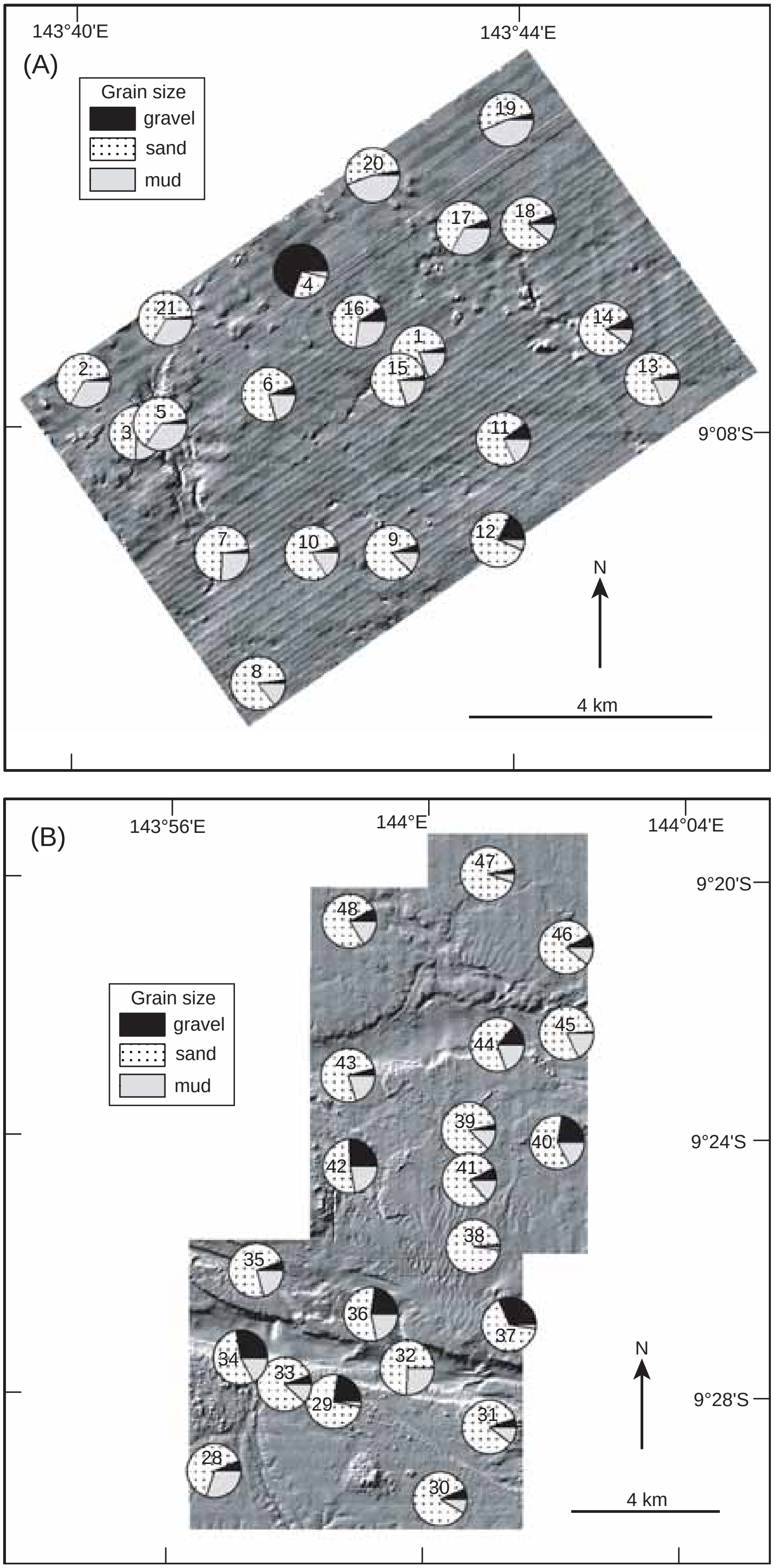
Figure 4. *Two-dimensional ordination plots using non-metric MDS on Table 1 and Table 2 megabenthos data, showing circles of the relative size of mixed garden percentage at sites. (A) Area A transects are clustered into three groups: mixed gardens, softcorals, and predominantly bioturbator. (B) Area B transects are clustered into three groups: mixed gardens, softcorals, and predominantly sparse fauna.*

Table 3. Environmental data for Area A. See Figure 2A for locations

Station number	Depth (m)	Slope (°)	Gravel weight (%)	Sand weight (%)	Mud weight (%)	Gravel $CaCO_3$ (%)	Sand $CaCO_3$ (%)	Mud $CaCO_3$ (%)	Total $CaCO_3$ (%)	Temp. (°C)	Salin. (psu)	Trans. (%)
1	29.66	0.11	2.92	77.76	19.32	95.00	47.00	13.00	41.83	28.32	34.51	83.66
2	28.60	0.17	2.68	63.66	33.66	95.00	63.00	9.00	45.68	28.94	34.45	83.42
3	27.13	0.38	18.33	55.84	25.83	60.00	75.00	14.00	56.49	28.86	34.49	83.87
4	22.27	2.91	69.60	26.73	3.68	97.50	89.00	12.00	92.09	28.93	34.48	83.10
5	32.50	1.25	3.03	62.18	34.79	95.00	70.00	12.00	50.58	28.91	34.46	81.21
6	27.90	0.26	5.45	73.74	20.81	75.00	70.00	14.00	58.62	28.93	34.44	81.24
7	32.37	0.32	2.53	71.80	25.66	95.00	75.00	15.00	60.11	28.85	34.46	83.62
8	31.42	0.37	2.09	83.26	14.65	85.00	63.00	22.00	57.45	28.77	34.51	85.21
9	30.72	0.19	4.93	83.10	11.97	85.00	60.00	21.00	56.56	28.70	34.53	85.66
10	31.65	0.28	3.98	80.22	15.80	90.00	63.00	23.00	57.75	28.72	34.53	85.56
11	31.85	0.15	9.77	72.27	17.97	85.00	57.00	17.00	52.55	28.56	34.56	84.60
12	32.72	2.33	18.13	75.05	6.83	95.00	88.00	18.00	84.49	28.44	34.58	81.72
13	30.96	0.61	3.77	77.59	18.64	90.00	56.00	14.00	49.45	28.27	34.61	81.21
14	29.32	2.33	7.52	82.56	9.92	85.00	73.00	14.00	68.05	28.24	34.62	78.70
15	30.04	0.07	2.73	77.28	19.99	90.00	68.00	16.00	58.20	28.51	34.58	81.27
16	28.23	0.15	8.73	64.08	27.19	70.00	61.00	12.00	48.46	28.65	34.55	82.46
17	28.88	0.49	5.20	62.42	32.38	85.00	68.00	9.00	49.78	28.79	34.52	79.53
18	27.55	2.72	5.81	82.75	11.45	95.00	81.00	10.00	73.69	28.84	34.51	77.25
19	28.71	0.11	3.86	52.91	43.23	95.00	61.00	7.00	38.97	29.07	34.37	65.75
20	27.50	0.31	2.50	53.19	44.31	90.00	61.00	6.00	37.36	29.14	34.33	71.26
21	28.14	0.05	1.98	64.41	33.61	95.00	59.00	7.00	42.23	29.15	34.31	77.67

Table 4. Environmental data for Area B. See Figure 2B for locations

Station number	Depth (m)	Slope (°)	Gravel weight (%)	Sand weight (%)	Mud weight (%)	Gravel $CaCO_3$ (%)	Sand $CaCO_3$ (%)	Mud $CaCO_3$ (%)	Total $CaCO_3$ (%)	Temp. (°C)	Salin. (psu)	Trans. (%)
28	51.08	0.87	5.92	64.61	29.47	75.00	67.00	77.00	70.42	27.78	34.81	86.68
29	38.93	8.74	22.83	74.12	3.05	97.50	96.00	75.00	95.70	27.83	34.81	88.42
30	48.01	0.43	6.32	84.89	8.79	90.00	57.00	80.00	61.11	27.66	34.83	88.98
31	46.46	2.27	5.31	84.32	10.37	80.00	89.00	77.00	87.28	27.69	34.86	90.02
32	128.64	1.83	0.25	73.61	26.15	97.50	63.00	76.00	66.48	27.60	34.88	89.19
33	46.86	0.96	5.77	82.57	11.66	60.00	63.00	76.00	64.34	27.66	34.87	89.88
34	83.02	11.54	27.57	55.54	16.89	55.00	78.00	76.00	71.32	27.72	34.85	89.41
35	100.31	0.28	5.70	74.07	20.23	80.00	62.00	67.00	64.04	27.67	34.82	88.29
36	81.03	11.08	23.04	55.31	21.64	65.00	47.00	63.00	54.61	27.67	34.86	90.28
37	144.89	4.22	31.90	65.49	2.60	95.00	91.00	70.00	91.73	27.73	34.89	89.87
38	50.70	3.44	1.16	96.58	2.26	90.00	21.00	63.00	22.75	27.61	34.91	88.27
39	53.23	1.84	3.27	83.98	12.75	75.00	37.00	63.00	41.56	27.53	34.92	87.02
40	51.45	6.19	22.35	60.58	17.07	75.00	75.00	63.00	72.95	27.55	34.93	86.59
41	51.82	4.67	7.37	78.88	13.75	40.00	41.00	24.00	38.59	27.57	34.93	88.74
42	72.82	5.79	25.69	52.00	22.31	70.00	35.00	66.00	50.91	27.55	34.91	88.96
43	75.37	2.67	4.39	75.12	20.49	70.00	64.00	60.00	63.44	27.50	34.94	89.70
44	86.31	9.82	13.80	66.53	19.67	75.00	38.00	47.00	44.88	27.51	34.93	89.65
45	88.37	2.09	1.39	80.37	18.23	60.00	49.00	42.00	47.88	27.59	34.93	90.81
46	58.02	1.16	7.50	81.27	11.23	80.00	51.00	54.00	53.51	27.45	34.91	89.83
47	51.96	1.35	3.50	91.36	5.14	70.00	32.00	54.00	34.46	27.37	34.90	89.25
48	51.66	0.09	7.40	76.47	16.13	85.00	60.00	59.00	61.69	27.45	34.88	89.57



on the platforms, dune field and valley floors in Area B.

Secondary Biotopes and Biological Facies

Through an examination of the patterns of the megabenthos assemblages and environmental variables, the results of the BIO-ENV procedure and in conjunction with models of the geomorphology and bathymetry, Area A was divided into three secondary biotopes and three biological facies at the site scale (<10 km), showing a high correlation between the predominant substrate and the types of biological assemblages associated with this substrate (Figure 7A). Area B was divided into four secondary biotopes and four biological facies, and includes the live reefs observed, but not sampled for quantitative analysis (Figure 7B). The spatial boundaries of these units reflect the patterns observed using the available datasets, and are consistent within the context and scales of the hierarchical habitat classification scheme of Butler *et al.* (2001).

The construction of these maps was assisted by raster reclassification of the high-resolution bathymetric and slope models using GIS. For instance, an examination of the histograms of slope and depth grid values found that the limestone knoll features in Area A were greater than 1º slope and less than 4 m above the surrounding seabed. The relict reefs of Area B were greater than 4º slope and generally over 4 m above the surrounding seabed. Therefore, reclassification of the slope and depth raster grids using these limits highlighted the exact boundaries of these significant geomorphic features. A description of each secondary biotope and the corresponding biological facies is given for each survey area. Conceptual model diagrams of the association between the secondary biotopes and biological facies of Areas A and B are shown in Figure 8.

Area A – 'Low-relief Limestone' and 'Mixed Garden'

The 'low-relief limestone' Secondary Biotope stands out from the predominantly flat distal-

Figure 5. *Gravel, sand and mud weight proportions from grab samples. (A) Area A. (B) Area B. Numbers refer to station numbers in Tables 3 and 4, respectively. There is a pattern of higher gravel proportions in samples obtained from low-relief limestone and pockmarks in Area A, and relict reefs, valley sides and channels in Area B.*

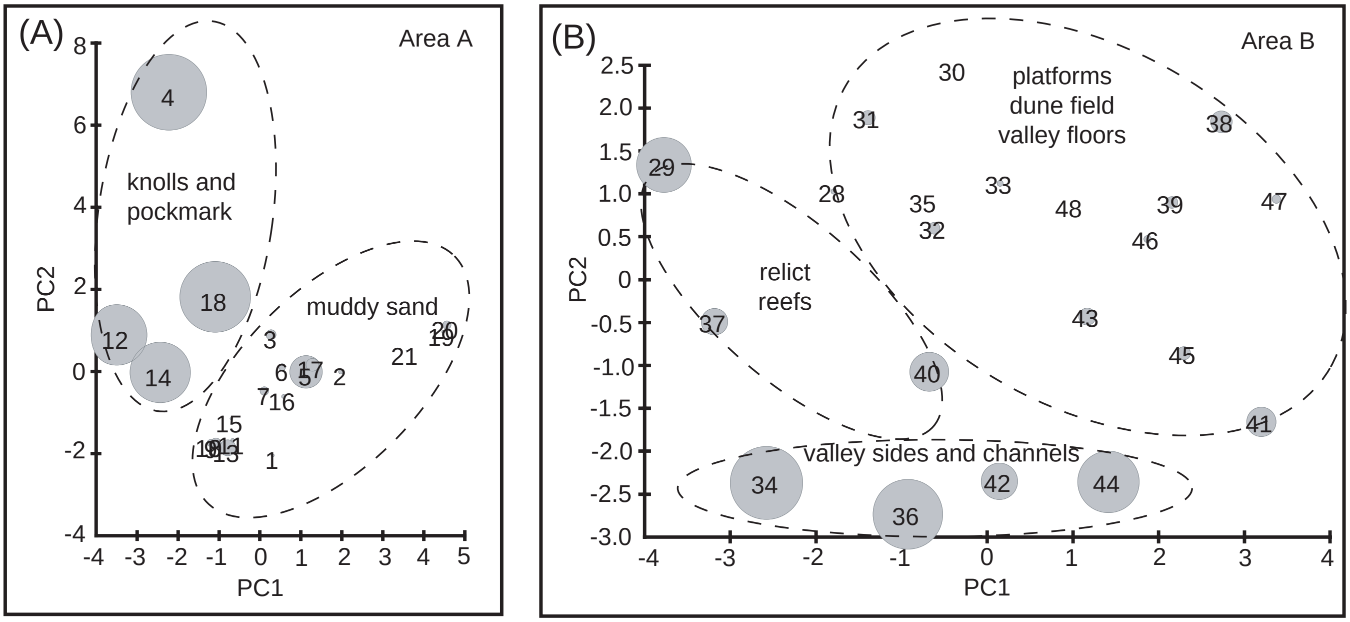


Figure 6. *Ordination plots of PCA using Euclidean distance on Table 3 and Table 4 environmental data, showing circles of the relative size of slope at each station. (A) Area A variables are clustered into two groups: knolls and pockmarks, and muddy sand. (B) Area B variables are clustered into three groups: relict reefs, valley sides and channels, and platforms, dune field and valley floors.*

delta zone as numerous (at least 30) small knolls. There is a distinct pattern of knolls located along the edges of the shallow infilled channels. Even channels filled and showing little seabed surface expression had knolls located at the edges, confirming the strong link between the knolls and palaeochannels. The low-relief features are interpreted to be relict Pleistocene deltaic deposits (Harris *et al.*, 2005), and may have originally been levee banks deposited while draining the Fly River during lower sea levels. After transgression, the levee banks were drowned and compacted into a hard limestone substrate, and the scattered knolls are now the eroded remnants of these levees. Underwater video reveals a ‘mixed garden’ Biological Facies strongly associated with this biotope. The hard substrate has a structurally complex surface with overhangs and small crevices. Dense fauna covered the limestone knolls and comprised a mixed garden of fan-shaped sponges, gorgonian fan corals, large bushy softcorals and sea whips. The knolls also provide favourable habitats for reef- and rocky-bottom-dwelling fish, such as invertebrate/fish-feeding soldierfish and cod (Randall *et al.*, 1990).

Area A – ‘Infilled Channel’ and ‘Patchy Softcoral’

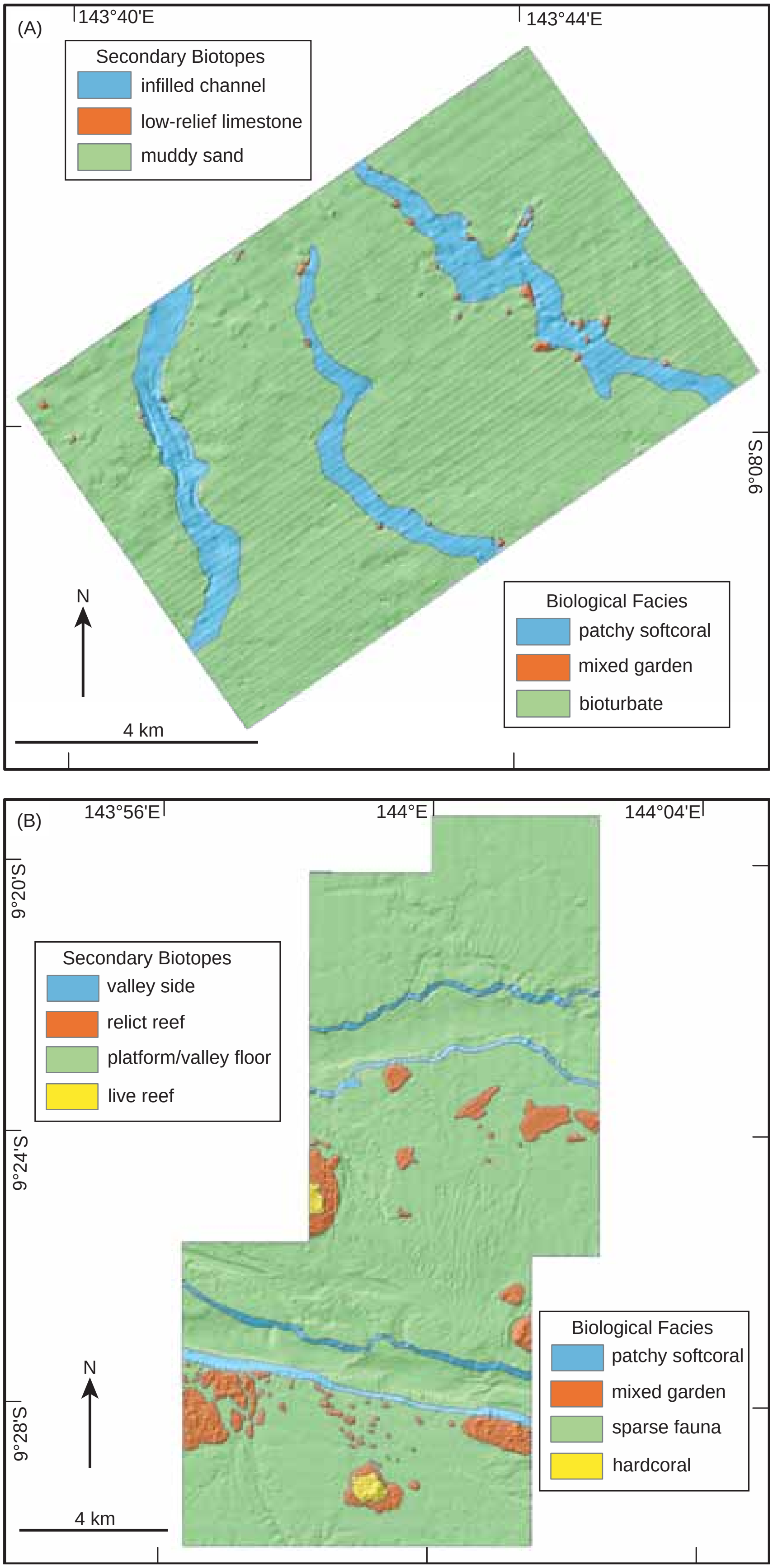
The ‘infilled channel’ Secondary Biotope represents the three palaeochannels which trend across Area A. They are similar to palaeochannels observed elsewhere on the distal-delta that once drained part of the Fly River (Crockett *et al.*, 2005). Surficial sediments in the channels are a dark grey muddy sand and calcareous gravel similar to the predominantly flat seabed either side of the channels (Harris *et al.*, 2002). However, the present study found localized pockmarks closely associated with the knolls and channels, and surficial sediment that became relatively coarser. The ‘patchy softcoral’ Biological Facies is named after the occasional small bushy softcoral observed in pockmarks. Because of the lack of bioturbation and increase in gravel content compared to the surrounding flat muddy sand, the pockmarks are the result of near-seabed currents, inducing a local bottom-stress maxima and associated zone of bottom scour around the knolls. In this area, tidal currents up to approximately 50 cm sec^{-1} were observed during the duration of the survey (Harris *et al.*, 2002). The current scour around the knolls and channel edges favours suspension-feeding sessile fauna over deposit-feeding infauna.

Area A – ‘Muddy Sand’ and ‘Bioturbate’

Most of Area A is a ‘muddy sand’ Secondary Biotope. The seabed is predominantly flat, interrupted only by the presence of low-relief limestone knolls and the infilled channels. Surficial sediments are dark grey muddy sand with calcareous gravel. The mud content is highest in the northern corner and generally decreases to the east and south, reflecting the Fly River delta as the source of terrigenous material (Harris *et al.*, 2002). The ‘bioturbate’ Biological Facies is strongly associated with this habitat, showing moderate to abundant burrows and mounds as evidence of an environment favouring infauna. An earlier survey on the inner to middle shelf of the Gulf of Papua using a variety of cores found that the macroinfauna was dominated generally by small seabed surface deposit-feeding polychaetes, followed by amphipod crustaceans (Aller and Aller, 2004). The presence of relatively high bioturbation seaward of the Fly River delta clinoform is also consistent with the bioturbation observations of Alongi *et al.* (1992) and Walsh *et al.* (2004). Sessile fauna, such as small softcorals and tube sponges, are present but were few in number in comparison to a seabed dominated by deposit-feeding infauna.

Area B – ‘Relict Reef' and ‘Mixed Garden’

The ‘relict reef’ Secondary Biotopes of Area B were a surprising discovery in this study. They appear as numerous (at least 50) submerged reefs of various sizes across the southern and central plat-



forms. Underwater video reveals a structurally complex surface with high-relief and karst-type erosion into holes and caves. The 'mixed garden' Biological Facies is strongly associated with this habitat. The limestone provides a hard stable substrate for the attachment of a dense mixed garden comprising softcorals, sponges and sea whips. It is interesting that the dense softcoral is mostly found on the relict reefs because these were once sites of hardcoral growth when the sea level was between 30 to 42 m below present sea level, which is the approximate range of upper surface depths. An examination of the eustatic sea-level curve over the past 140 kyr BP (Pillans *et al.*, 1998; Lambeck and Chappell, 2001), reveals a sea level at, or less than, 30 to 42 m below present sea level for approximately 38 kyr during the last glacial/interglacial cycle, when hardcorals may have lived. When the sea level dropped more than 42 m below present sea level (approximately 90 kyr of the past 140 kyr BP), reefs were exposed to karst-type erosion. When eustatic sea level rose through the Holocene, reef growth lagged the rapid rate of sea-level rise, growth ceased and the reefs drowned (*i.e.*, 'give-up reefs'; Neumann and MacIntyre, 1985).

Area B – 'Live Reef' and 'Hardcoral'

In Area B, two unnamed 'live reef' Secondary Biotopes were mapped in the west-central platform and in the centre of the southern platform. The seabed rises nearly to the water surface and was clearly associated with a 'hardcoral' Biological Facies, typical of zooxanthellate fauna found on other northern Great Barrier Reef platform reefs (Veron, 1993). Bathymetric data shows that these live reefs rose from the upper surfaces of relict reefs. The limited extent of the live reefs in comparison to the relict reefs show that only two live coral reefs were able to grow and track Holocene sea-level rise, or later catch-up to the water surface (*i.e.*, 'keep-up' and 'catch-up reefs' respectively; Neumann and MacIntyre, 1985). Most of the Torres Strait platform reefs grow on an antecedent foundation of Pleistocene reefs (Davies *et al.*, 1989; Woodroffe *et al.*, 2000), and further dating of coral framework from the relict and live reefs is required to establish the exact timing of reef growth or demise.

Figure 7. *Secondary biotopes and biological facies of the study areas (A) and (B).*

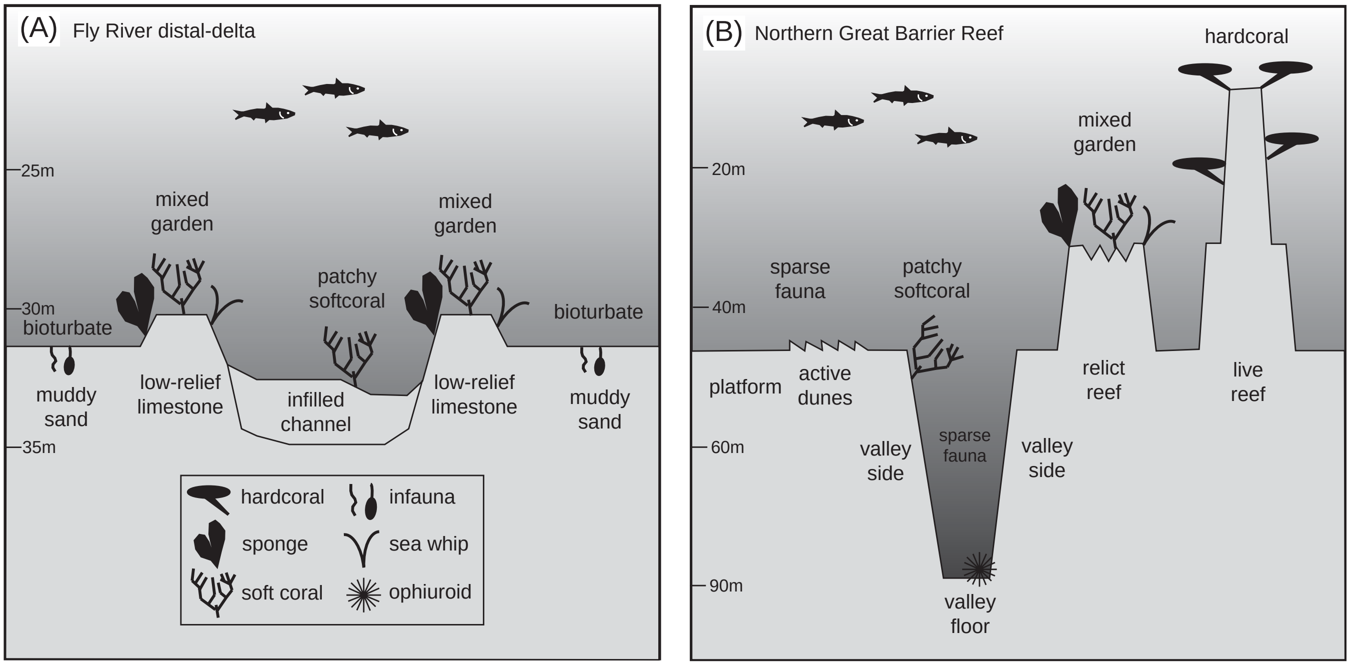


Figure 8. *Conceptual model diagrams of the association between the secondary biotopes and biological facies. A) Area A on the Fly River distal-delta. B) Area B on the northern Great Barrier Reef shelf.*

Area B – 'Platform/Valley Floor' and 'Sparse Fauna'

Most of Area B is the 'platform/valley floor' Secondary Biotope, which is predominantly flat and divided by some of the deepest submarine valleys found on the northeast Australian shelf (Harris *et al.*, 2002). Surficial sediments on the platforms range from gravelly muddy sands to gravelly sands, and a moderate to high carbonate content in the mud fraction, showing a gradual increase from the north to south platforms (Harris *et al.*, 2002). A localized variation in surficial sediments on the central platform occurs in the active dune field. Surficial sediments are slightly gravelly sand, with a lack of mud, indicating winnowing of finer grained sediments by relatively stronger currents in this area. This biotope also includes the predominantly undulating to flat valley floors, and surficial sediments are slightly gravelly, muddy sand. The increased depth reflects a slight increase in mud content compared to the relatively shallower platforms. The 'sparse fauna' Biological Facies corresponds with this predominantly flat habitat. Underwater video reveals a seabed with sparse sessile benthos, and the occasional individual small bushy softcoral. Mobile fauna were mostly ophiuroids and echinoids. In contrast to the high bioturbation in Area A, the platforms of Area B show limited mounds or burrows.

Area B – 'Valley Side' and 'Patchy Softcoral'

Thin, linear 'valley side' Secondary Biotopes are found on the sides of the two limbs of the Darnley Valley and show a high gradient environment. Underwater video reveals the seabed to have abundant cobbles and boulders scattered on the gravelly sand, presumably as a result of debris flows down the steep slope of the valley sides. The 'patchy softcoral' Biological Facies is clearly associated with this habitat as moderate to abundant large softcorals and sea whips are attached to the cobbles and boulders. The preference for soft fauna on the valley sides may also be due to the Coral Sea water upwelling through the deep shelf valleys and these suspension-feeders taking advantage of the increased nutrients and food particles.

DISCUSSION

This study has shown a quantitative association between geophysical data from seabed habitats and the biological communities which depend on these habitats. Such findings are helpful when asking whether geophysical data can be used to predict the occurrence of benthic biodiversity, particularly with the increase in MPAs as tools for marine conservation. In this study, the geophysical variables, slope and gravel weight, were highlighted as useful predictors for megabenthos assemblages, and in conjunction with models of the geomorphology and bathymetry, were used to derive the spatial boundaries of benthic habitats at the site scale (<10 km). These findings add confidence to the use of abiotic or geophysical factors, such as sediment and high-resolution bathymetry, as predictors for benthos distribution and thus provide a basis for reserve selection. Future studies should be conducted which prioritize the collection of slope and gravel weight to explore whether they are potentially useful as universal predictors or are relevant only to the northern Great Barrier Reef–Gulf of Papua region under study.

Limitations of the BIO-ENV Procedure

It should be noted that the use of the BIO-ENV procedure is best thought of as an exploratory tool, and that more detailed statistical analyses (beyond the scope of this study) are required to accurately assess how well biological community data are predicted by environmental variables. However, within this study, slope and gravel weight distribution alone provided a useful 'first cut' approximation of megabenthos patterns. An important consideration for the use of gravel weight as a predictor of megabenthos assemblages is the sampling density of the sediment samples. Note that an interpolation of widely-spaced gravel data points, in order to derive a map of the gravel content of the seabed, is unlikely to correlate well to the patchy distribution of megabenthos. Ideally, sediment grabs should be collected at a density which matches the scale of the geomorphic feature being investigated and also co-located with optical ground-truthing sites.

Another limitation in the use of the BIO-ENV procedure was the low resolution of the biological data. With the biological variables restricted to broad megabenthos categories, Bray–Curtis similarities could only detect gross variations between assemblages. Yet the variation between biological assemblages was sufficient to confidently predict the spatial distribution of assemblages when related to the 5 m horizontal resolution of the underlying slope and depth grids. Our results show that it is not necessary to categorize benthos to genus and species for Bray–Curtis similarity coefficients when the spatial distribution of broad assemblages over these scales is quite sufficient. An additional limitation for the BIO-ENV procedure was the horizontal resolution of the important slope and depth grids. Ideally, for the slope and depth data to be of use for comparison against the biological data observed in the relatively short video transects, they should be at the highest resolution possible. Reducing these slope and depth grids to lower resolution, say 10 m and larger, would decrease the effectiveness of the BIO-ENV procedure to detect similarities between biotic and abiotic datasets.

Geology-Benthos Relationships

The results of this study reinforce knowledge of the contrast between biological assemblages living on hard substrate and those in soft unconsolidated substrate. In the present study, there is a pattern of zooxanthellate hardcorals within the photic zone and suspension-feeding softcorals on hard substrate features, compared with detritus- and deposit-feeding fauna, such as echinoderms, crustaceans and polychaetes, on soft unconsolidated sediment. The variation in substrate is therefore an important factor in controlling the distribution of biological communities. Finer scale positive bathymetric features are also known to influence hydrodynamic processes, whereby the complex seabed surfaces interferes with current flow patterns to increase water turbulence and enhance particle capture by benthic suspension feeders (Gili *et al.*, 2001). The dense cover of suspension-feeders on the limestone knolls and relict reefs suggests that the availability of food particles is sufficiently high within the near-seabed currents passing over these seabed habitats to support such a rich and colourful sessile fauna.

Table 5 is a summary of area (km^2) and percentage of the secondary biotopes in Areas A and B. Given the strong relationship between the mixed garden assemblage and low-relief limestone or any hard substrate feature projected above the surrounding seabed in Area A, it is likely that the area of low-relief limestone at 0.54% is an underestimate. This small percentage of limestone knolls belies the fact that even in this predominantly flat deltaic zone, life does thrive, albeit in small patches associated with hard substrate. The strong association between low-relief limestone knolls and the mixed gardens of sessile fauna on the distal-delta adds to our knowledge of the fate of buried river channels in tropical shelf environments (Johnson *et al.*, 1982; Woolfe *et al.*, 1998; Fielding *et al.*, 2003; Crockett *et al.*, 2005). In Area B, the hard substrate is limited primarily to the relict limestone reefs and live reefs. It is worth noting that the surface area of the relict reefs is over an order of magnitude greater than the area of live reefs surveyed (6.18% vs. 0.53%), and suggests that the development of coral reefs in the northern Great Barrier Reef was more extensive in the past. Similarly, the strong relationship between sessile soft fauna and relict reefs contributes to a greater understanding of the fate of drowned reefs (MacIntyre, 1972; Adey *et al.*, 1977; Lightly *et al.*, 1978; Vora and Almeida, 1990; Grigg *et al.*, 2002; Harris *et al.*, 2004a).

Table 5. Area in km^2 (percentage) for the secondary biotopes of Areas A and B

Area A Secondary Biotopes	Area km^2 (%)
infilled channel	9.24 (13.64)
low-relief limestone	0.37 (0.54)
muddy sand	58.13 (85.82)
total	*67.74 (100)*
Area B Secondary Biotopes	**Area km^2 (%)**
live reef	0.88 (0.53)
platform/valley floor	148.02 (89.51)
relict reef	10.22 (6.18)
valley side	6.24 (3.77)
total	*165.36 (100)*

In the present study, the spatial boundaries between unconsolidated soft substrate habitats and their associated biological assemblages is not as sharp as the boundaries between hard substrate features and the associated dense sessile benthos. Yet there are distinct patterns unique to each area which relate to physical processes in addition to substrate type. On the inner shelf, distal deltaic zone, the predominantly flat seabed is the preferred habitat of deposit-feeding infauna within the muddy sand. Localized variations in this relationship occur with the presence of shallow pockmarks, possibly due to near-seabed currents scouring around knolls bordering the palaeochannels, similar to the scour pits found around shipwreck obstacles (Stride, 1982). The pockmarks are the preferred habitat of suspension-feeding softcoral at the expense of deposit-feeding infauna, therefore the dominant process is believed to be an increase in current strength on the seabed at this finer scale.

On the mid-shelf, incised valley zone, the unconsolidated soft substrate of the extensive platforms and valley floors are the preferred habitat of sparse sessile fauna. The presence of the active dunes and ripples between the two shelf valleys points to strong near-seabed currents as the dominant process controlling benthos in the dune field. In this case, high disturbance by mobile sand over a large area would be an important limiting factor to settlement by sessile benthos or infauna maintaining burrows, and is likely to favour mobile infauna such as errant polychaetes, heart urchins and sand-dwelling molluscs. The relative increase in sessile benthos on the valley sides may be a function of both a suitable substrate and upwelling Coral Sea water flowing through the valleys, taking advantage of an increased supply of food particles. In contrast to the valley sides, the flat valley floors were much reduced in sessile biota. No boulders or cobbles were observed on the seabed. The environment is relatively constant with little light and with reduced disturbance as the near-seabed currents decrease with depth. This habitat appears to favour detritus-feeding echinoderms over suspension-feeders. These physical processes are consistent with the observation by Aller and Aller (2004) that sedimentary dynamics and physical processes related to near-seabed currents, in addition to substrate type, appear to be a dominant control on the benthic communities in the northern Great Barrier Reef–Gulf of Papua region.

Assessment Techniques

The utility of high-density bathymetric data to image the seabed points to a new age of discovery of the oceans. Full ensonification of the seabed by multibeam sonar presents us with an unprecedented view of the true nature of the morphology of the seafloor and the variation in seabed sediment texture (Kostylev *et al.*, 2001). In addition, the ability to overlay a wide variety of physical and biological datasets as models using GIS now provides us with new insights to interpret the structure of benthic habitats and the processes influencing these patterns. The capability to examine the seabed as a 3-D digital terrain model at high-resolution is invaluable as other GIS models can then be draped and viewed at different scales of resolution and viewed at any angle. Where once there were contours, now there is complexity! And the complexity of the seabed, revealed by multibeam sonar, is the key to making links between the benthos and the dominant processes affecting the distribution. Because many benthic habitats are defined by substrate (sediment or rock), the new generation of bathymetric and geological maps derived from multibeam sonar provide a framework for remotely mapping the distribution of benthos or to accurately target distinct geomorphic features for ground-truth sampling (Greene *et al.*, 1995; Kostylev *et al.*, 2001).

The assessment techniques used in this study are recommended for future surveys requiring benthic habitat mapping. In priority, multibeam sonar data, with co-registered sidescan, is the most useful remote-sensed acoustic data. It produces high-resolution bathymetric and backscatter models to reveal geomorphology and sediment textural attributes of the seabed. Slope models, derived from bathymetry, are shown to be quite useful as predictors of megabenthos assemblage patterns. Another recommended remote-sensed acoustic technique is a sub-bottom profiler used to put into geological context the morphology of the seabed. As shown in this study, the events of the geological past have a profound influence on the present seabed, and an understanding of the long-term processes on a geological scale which have controlled the form of the seabed are very useful for interpreting benthic habitats.

Seabed ground-truthing priorities include optical techniques such as video, followed by physical sampling using sediment grabs, cores or water sampling devices. Single long video transects can give an indication of the composition and spatial arrangement of megabenthos on the seabed, which may be quite patchy. Sediment grabs and cores cannot provide the sampling area to discriminate megabenthos assemblages at this scale, and other than gravel weight as a potential proxy, are probably more useful to help describe the environment of deposition. Similarly, oceanographic variables such as temperature and salinity, which vary over broader scales, are probably more useful to help describe the hydrodynamic environment. The combination of both acoustic seabed classification methods and optical and physical ground-truthing is very effective in delineating the spatial patterns of seabed habitats and their associated biological assemblages.

CONCLUSION

This paper described the physical environment and megabenthos assemblage patterns of two study areas on the Fly River distal-delta and northern Great Barrier Reef of Australia. Multibeam sonar and a sub-bottom profiler data were utilized; this was followed by collecting underwater video footage and grab samples at selected sites. Multivariate statistical analysis (cluster, multi-dimensional scaling and BIO-ENV procedure) of the physical and biological datasets from both areas determined that the geophysical variables, slope and gravel percentage, were the most useful predictors for megabenthos assemblage patterns. In this paper, the slope and gravel percentage models were given priority for overlay in a GIS, and in conjunction with models of the geomorphology and bathymetry, maps were derived of the Secondary Biotopes and Biological Facies using the Butler *et al.* (2001) benthic habitat classification scheme. By characterizing the seabed at the Secondary Biotopes and Biological Facies levels, a better understanding of the association between the physical environment and the megabenthos assemblage patterns of the two study areas at the site scale (<10 km) was gained.

The variation in substrate was an important factor in controlling the distribution of biological communities in the study areas. Hard substrate habitats in both areas were associated with a dense and colourful sessile fauna of predominantly suspension-feeders. Soft substrate on the inner shelf, distal-deltaic zone, was the preferred habitat of deposit-feeding infauna. Shallow pockmarks, possibly due to near-seabed currents scouring around low-relief limestone knolls, were the preferred habitat of sessile suspension-feeders. On the mid-shelf, incised valley zone, the unconsolidated soft substrate was the preferred habitat of sparse sessile fauna. A relative increase in suspension-feeding sessile fauna on the steep valley sides may be a function of both a suitable substrate and upwelling Coral Sea water flowing through the valleys. The combination of substrate type, sedimentary dynamics and physical processes related to near-seabed currents appear to be a dominant control on the benthic communities in the northern Great Barrier Reef–Gulf of Papua region. Future surveys should combine high-resolution acoustic methods with optical assessment techniques to delineate seabed habitats and their associated biological assemblages.

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