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ESTABLISHING REFERENCE POINTS TO ASSESS LONG-TERM CHANGE IN ZOOXANTHELLATE CORAL COMMUNITIES OF THE NORTHERN GALAPAGOS CORAL REEFS

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SUMMARY

Dramatic reduction in zooxanthellate corals through bleaching during the 1982–3 El Niño event and subsequent bio-erosion have resulted in archipelago-wide loss and fragmentation of coral habitat. Slow natural recovery and the risk to corals from global climate change raise important coral conservation questions in a multi-use reserve. The largest coral reef communities remaining at Wolf, Darwin and Marchena islands were surveyed, to provide information on the condition of these last persisting reef systems as a basis for future evaluation of the effects of climate change, human use and management upon them. Over the period September 2005 to February 2007, 2250 m of subtidal habitat were surveyed at 15 m and 6 m depth at four study sites. At each site we recorded substrate heterogeneity, zooxanthellate coral diversity and relative abundance, simple measurements of colony size, reef relief and health, and relative abundances and size distributions of the associated subtidal marine community (sessile macro-invertebrates and algae, mobile macro-invertebrates and reef fish). Given the high level of tourism visitation, restricted range of the coral reef, considerable small scale between-site differences in coral species composition and associated subtidal assemblages, high subtidal species diversity unique to the northerly islands, and strong frequent climatic stress, appropriate additional protective measures, such as low impact fixed moorings, are recommended. Such measures will help conserve the ecosystem function of these key habitat-forming species both in the north and for the archipelago as a whole.

RESUMEN

Estableciendo puntos de referencia para evaluar cambios a largo plazo en las comunidades de corales zooxantelados de los arrecifes de corales del norte de Galápagos. La dramática reducción de los corales zooxantelados durante los eventos de blanqueamiento y bio-erosión durante El Niño 1982–3 han resultado en una amplia pérdida y fragmentación del hábitat de coral en el archipiélago. La lenta recuperación natural y los riesgos hacia los corales a través del cambio climático global plantean importantes preguntas de su conservación dentro de una reserva multi-uso. Los más grandes arrecifes de coral remanentes a través de las islas Wolf, Darwin y Marchena fueron evaluadas con la finalidad de proveer información de su condición actual, como una base para futuras evaluaciones de efectos de cambio climático, uso humano y el manejo, sobre estos últimos sistemas de arrecifes. Sobre el período septiembre 2005 a febrero 2007, 2250 m de hábitat submareal fueron evaluados a través de dos estratos de profundidad 15 m y 6 m en cuatro sitios de estudio. En cada sitio registramos la heterogeneidad del sustrato, la diversidad y abundancia relativa de los corales zooxantelados, registros simples de la talla de las colonias, el relieve y la salud del arrecife, así como también la abundancia relativa y distribución de tallas de la comunidad marina submareal (macro-invertebrados sesiles y algas, macro-invertebrados móviles y peces de arrecife). Dado el alto grado de las visitas turísticas, el rango restringido del arrecife coralino, las diferencias considerables a escala reducida en la composición de especies de coral y los ensamblajes submareales asociados en cada sitio, el grado alto de diversidad submareal única a las islas del norte, y el fuerte y frecuente estrés climático, se recomiendan medidas adicionales para su adecuada protección, tales como la fijación de fondeaderos de bajo impacto, enfocadas hacia la conservación de la función de estas especies claves formadoras de hábitat dentro del ecosistema en el norte y en todo el archipiélago.

INTRODUCTION

Surveys from the 1970s describe a widespread coral reef network across the Galapagos archipelago (Glynn & Wellington 1983), which contrasts sharply with the rocky reef substrate that today predominates over an estimated 90% of the coastal subtidal habitat of the Galapagos Marine

Reserve (GMR). Such a drastic change during the short documented history of the reserve is associated with 95–99% coral bleaching from strong regional climatic events, especially the strong El Niño Southern Oscillation (ENSO) events of 1982–3 and 1997–8 (Glynn *et al.* 2001, Feingold 2001), as well as with the concurrent and near-exponential increase in human activity and exploitation.

After the last strong ENSO-related bleaching events, few continuous coral reefs persisted. Those that have survived are fragmented and spatially reduced (Danulat & Edgar 2002) with the largest reefs now located in the far northern islands of Wolf and Darwin.

Given known ENSO periodicity we would expect another strong event in the near future. New environmental stressors, including human visitation, have dramatically increased, bringing with them increased risk of pollution, invasive marine species, and damage by divers and anchors. In order to mitigate these risks, GMR managers require up-to-date indicators of coral recovery or decline. Management is also increasingly being examined in the context of global climate change. Gradual warming is likely to cause serious extinction risk to corals, from intensified thermal stress and ocean acidification. Impacts to the most susceptible coral communities will be exacerbated by human practices in the coastal zone (IPCC 2007, Carpenter *et al.* 2008).

One of the greatest challenges for Galapagos marine research and a priority for the conservation of biodiversity in the GMR has been to characterize the wide diversity of marine communities present. In order to support and improve protection of threatened habitats, communities and species, it was imperative to characterize the biota and undertake analyses aimed at producing recommendations for sustainable use and management. Divers have

conducted > 3800 subtidal community survey transects at two depths (15 m and 6 m) since 1994, representing more than 190 km of linear survey or about 5 % of the 1670 km coastline, and including fished, tourism and protected zones.

The far northerly islands of Wolf and Darwin harbour species assemblages unique to the archipelago, having a strong affinity with Panamic and Indo-Pacific biogeographic regions (including Cocos Island to the northeast), and communities that are extremely spatially restricted and closely associated with the only surviving continuous coral reef structures over rocky substrate (Bustamante *et al.* 2002, Edgar *et al.* 2002, Edgar *et al.* 2004). This is not unexpected considering that Wolf and Darwin are the surface expression of a chain of submerged volcanic pinnacles approximately 200 km north of the equator. They are isolated from the central Galapagos platform and lie between it and Cocos Island (Costa Rica) and Malpelo Island (Colombia), 700 km and 1180 km respectively to the northeast of Wolf (Fig. 1). This makes them important stepping stones in the oligotrophic deep ocean for many migratory species, and sites where many tropical species could establish, even if temporarily. New work on connectivity has begun to explore this. Tagging of Scalloped Hammerhead Sharks *Sphyrna lewini*, for example, showed that individuals can migrate from Wolf to Cocos in 15 days (A. Hearn pers. comm). Rare sightings

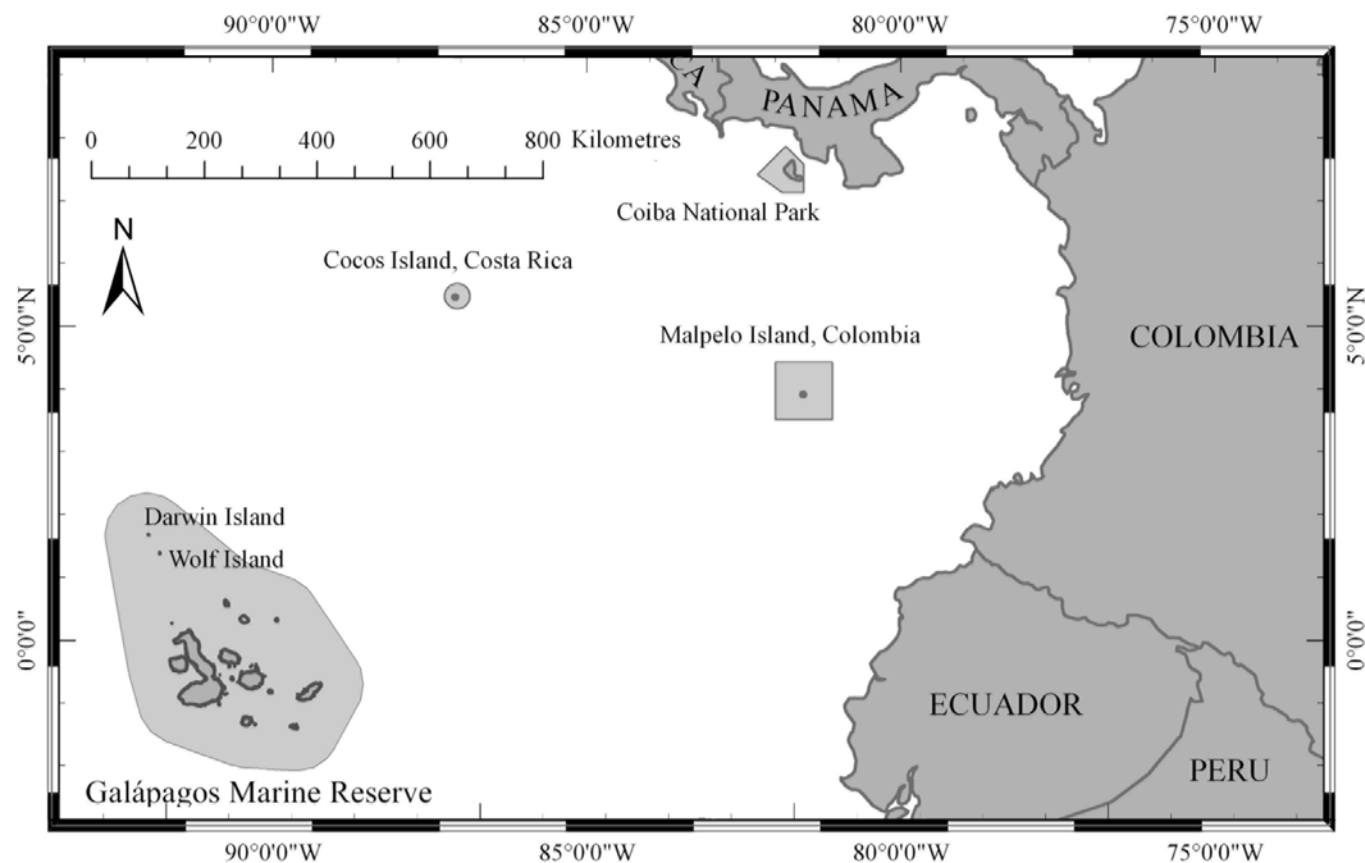


Figure 1. Marine protected areas within the Eastern Tropical Pacific (shaded).

of tropical species such as certain butterfly fish are more common in the north during strong El Niño years when the influence of the Panama Bight current is strengthened. Recruitment patterns of Indo-Pacific species such as the spiny lobsters *Panulirus* are hypothetically linked to increased surface transport from the northeast and reinforced geostrophic flow from source populations in the W Pacific during these times. The same may be true with respect to some coral propagules. To date however few planulae have been detected in the upper mixed layer of the water column. Seasonal plankton surveys (*c.* 240 oblique plankton tows to 100 m depth over 60 fixed open water and coastal survey stations across the entire GMR) recorded just six coral planulae during 2004–7. Although coral larvae can remain viable for 100 days in the water column, research with some groups such as *Pocillopora* suggests that they may successfully settle locally (Richmond 1987). Much remains unclear as to the dispersal frequency and recruitment mechanism in the GMR.

The bathymetry of Wolf and Darwin plunges > 1000 m sharply on all sides towards the abyssal plain, mixing deep open water and a narrow coastal fringe. The prevailing westward-flowing surface currents around the islands result in often strong near-shore currents that support a highly productive mix of resident and migratory pelagics, large schooling fish and hammerhead shark aggregations, mixing coastal resident species with normally tropical species. These islands are also important seabird nesting and foraging sites, and support marine mammals, including small Galapagos Sealion *Zalophus wollebaeki* colonies. These assemblages are remarkable given the small sizes of the islands (Wolf 1.3 km², Darwin 1.1 km²) and their relative isolation.

Outside of strong ENSO warm and cold extremes, Wolf and Darwin are bathed in a predominantly westward to southwest flow, which is consistently 2–3°C warmer than the southeastern part of the archipelago (Banks 2002). A deviation of the North Equatorial Counter Current (NECC) extending down from the Panama Bight forms the northerly component of the Southern Equatorial Current (Kessler 2006). Normally strengthened during the hot season (November–May), a reinforced compensatory NECC flow from the W Pacific during strong ENSO warm events raises and homogenises surface temperatures across Galapagos. There are strong multiple effects on the marine ecosystem as the thermocline deepens and the Equatorial Undercurrent, which normally brings nutrients into the euphotic zone, is depressed.

Wolf and Darwin, situated towards the low-pressure intertropical convergence zone experience less drastic positive temperature anomalies compared to other parts of the archipelago, perhaps promoting species conditioning to warmer events over generations. Some evidence for this was provided by recent analysis of zooxanthellae clades (Glynn *et al.* 2001, Glynn *et al.* 2009). Recent observations of internal wave passage across the

region suggest that short-lived negative temperature anomalies also play an important role in structuring Galapagos and other E Tropical Pacific (ETP) coral communities particularly with respect to *Porites lobata* and *Pocillopora* sp. (pers. obs., J. Cortes pers. comm).

In addition to their biodiversity value as an ecologically distinct region in Galapagos, tourism in the northern islands is important economically. Recreational dive operations promote Wolf and Darwin, which are renowned for consistent sightings of Whale Sharks *Rhincodon typus* and schooling Scalloped Hammerheads. In 2007, 12,496 tourism dives were recorded by the Galapagos National Park Service (GNPS) at Darwin Arch and the El Derrame site in Wolf alone, representing 56.2 % of all registered dives in 2007 across the entire GMR. These two sites receive approximately five times more visitation than their recommended capacity (Cubero *et al.* 2007, GNPS pers. comm.). This has increased anchor damage and physical abrasion to remaining reefs.

High reef species interdependence and slow coral growth rates suggest that effects of rapid coral mortality could propagate quickly throughout the community, causing significant shifts in equilibrium. Anchor and diver damage can easily reduce decades of coral growth to rubble (Richmond 2005). The over-fishing of reef predators such as lobsters and groupers may also cause the explosion of herbivorous fish and urchin populations, which rapidly bio-erode reef frameworks before they can recover from short-term bleaching events. As with diverse terrestrial zones such as rainforests, any process that affects habitat-forming species alters the capacity to sustain a variety of ecological niches and associated species. Being small zones of great strategic importance for the GMR both biologically and economically, the northern coral reefs are a priority for improved protection and impact mitigation.

In response to these concerns, a project was designed to document the state, diversity and health of corals and the associated marine community, map the extent of coral formations and provide a benchmark for future measures of management success in the northerly islands. Here we present one component of this work, habitat mapping, to summarise the distribution and composition of these remaining coral communities.

MATERIALS AND METHODS

The four surveyed areas were Wolf Anchorage and the protected coral bay Bahía Tiburón (Wolf Island), Darwin Anchorage extending towards the Darwin Arch platform, and Punta Espejo in the SE corner of Marchena Island (Fig 2). We conducted three expeditions (September 2005, May 2006, February 2007), and evaluated various techniques during the early phase. Representatives from the science, conservation, fisheries and dive tourism sectors were involved in all research cruises. The survey work complements detailed colony-specific information taken

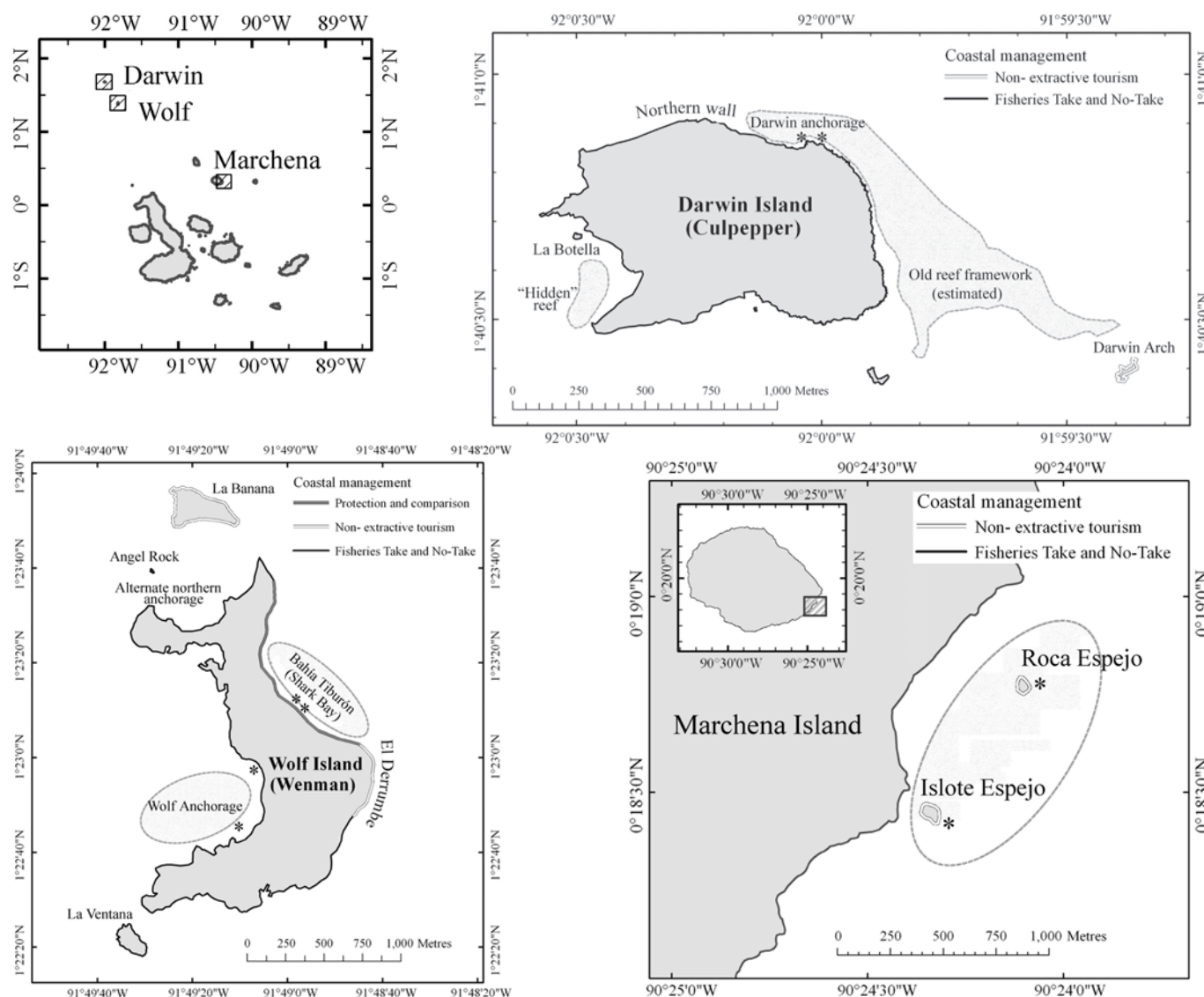


Figure 2. Coral survey sites (hatched areas) at the islands of Wolf, Darwin and Marchena. Long term subtidal community monitoring sites are indicated by *.

over fixed monitoring plots in the same localities. The survey objective was to cover as much area as possible, thereby providing a broad assessment of coral assemblages and maximising the possibility of recording rare species and spatial heterogeneity.

In the Results, “corals” implies zooxanthellate species throughout. Table 1 provides a reference summary of zooxanthellate corals recorded from Galapagos. Four types of survey data are presented.

1. Coral point-intercept transects

For point-intercept coral measurements and habitat mapping, 100-m transects were laid by divers in parallel at 15 m and 6 m isobaths across the four principal survey sites (where bottom profile permitted). To map the approximate transect path and facilitate dive work between the various working groups, surface buoys were deployed at 50 m or 100 m intervals. Global Positioning

System (GPS) positions were taken (WGS84 datum) for all survey transects. The total linear extensions surveyed underwater were 350 m across Wolf Anchorage, 845 m in Bahía Tiburón, 354 m across Darwin Anchorage and 700 m SW to NE at Punta Espejo, Marchena. The transect segments and lengths that correspond to the different types of monitoring described across the three islands are indicated by numerals and letters alongside the transect lines on the island maps (Figs 3–5, 8, 11, 12, 15, 16).

To characterise the species composition and take simple morphometric measures of coral colonies, coral species, substrate type and community data were recorded by three diver-pairs along each transect at each depth. In each pair a coral specialist worked with an assistant with a measuring stick to record, for each colony on the transect line, the centroid point, maximum diameter and coral height from colony base. Time and expertise permitting, other coral health data (bleaching,

Table 1. Zooxanthellate corals registered in Galapagos (from Charles Darwin Research Station registry 2007). Fungiid free-living corals *Cycloseris curvata* and *Diaseris distorta* are not included. C = Cosmopolitan; CP = Central Pacific; EP = East Pacific; IP = Indo-Pacific; IWP = Indo-West Pacific; WP = West Pacific.

Family and species	Galapagos distribution	World distribution
Thamnasteriidae		
<i>Psammocora stellata</i>	Devils Crown, Floreana; Wolf; Darwin Bay, Genovesa; Gardner Bay, Española; Marchena (Hickman 2008, Wells 1983, Glynn 2003, Glynn & Ault 2000, Glynn 1997, Reyes-Bonilla 2002, Reyes-Bonilla <i>et al.</i> 2005; G. Edgar pers obs).	EP; IP; WP; CP
<i>Psammocora superficialis</i>	Throughout, except W Isabela and Fernandina.	EP; IP; WP; CP
<i>Psammocora profundacella</i>	Darwin; Pinzón (Glynn & Ault 2000, Glynn & Wellington 1983, Glynn 1997, Glynn 2003).	EP; IP; WP; CP
Pocilloporidae		
<i>Pocillopora verrucosa</i>	Recently considered conspecific with <i>P. elegans</i> . Shallow water habitats (Hickman 2008).	IWP; EP
<i>Pocillopora damicornis</i>	Throughout (Glynn <i>et al.</i> 2001, Glynn 2003, Hickman <i>et al.</i> 2005, Glynn <i>et al.</i> 2009).	IWP; EP
<i>Pocillopora meandrina</i>	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
<i>Pocillopora elegans</i>	Throughout, except Fernandina and W Isabela (Glynn 2003, Hickman <i>et al.</i> 2005).	C; IP; EP
<i>Pocillopora capitata</i>	Throughout, except Fernandina and W Isabela (Glynn 2003).	EP
<i>Pocillopora eydouxi</i>	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
<i>Pocillopora effusus</i>	Darwin; Wolf (Hickman 2008).	EP
<i>Pocillopora inflata</i>	Throughout central archipelago (Hickman 2008).	EP
<i>Pocillopora ligulata</i>	Possibly present but requires confirmation (Hickman 2008).	IWP; EP
<i>Pocillopora woodjonesi</i>	Possibly present Darwin and Wolf, but requires confirmation (Hickman <i>et al.</i> 2005).	IWP; EP
Agariciidae		
<i>Pavona varians</i>	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
<i>Pavona chiriquiensis</i>	Throughout, except Fernandina and W Isabela (Hickman <i>et al.</i> 2005, Hickman 2008).	EP
<i>Pavona clavus</i>	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
<i>Pavona gigantea</i>	Throughout, except Fernandina and W Isabela (Glynn 2003, Hickman <i>et al.</i> 2005).	EP
<i>Pavona maldivensis</i>	Central archipelago plus Darwin and Wolf (Glynn & Ault 2000, Glynn 2003, Hickman 2008).	IWP; EP
<i>Pavona duerdeni</i>	Possibly present at Punta Estrada, Santa Cruz; but requires confirmation (A. Chiriboga pers. obs.).	IWP; EP
<i>Gardineroseris planulata</i>	Champion, Floreana; Punta Estrada, Santa Cruz (this colony not found since 1998); Darwin; Wolf (G. Edgar pers. comm.).	IWP; EP
<i>Leptoseris scabra</i>	Darwin; Wolf (Hickman 2008).	IWP; EP
Poritidae		
<i>Porites lobata</i>	Throughout, except Fernandina and W Isabela (Glynn & Wellington 1983, Glynn 2003, Glynn & Ault 2000, Hickman <i>et al.</i> 2005).	IWP; EP

predation, infection *etc.*) were also collected for each colony. These measurements are time consuming in coral-rich areas, so 10-m sampled segments were alternated with 10-m non-sampled intervals, allowing representation of coral distributions over longer distances. The non-sampled areas are indicated by shaded areas in Figs 5, 8, 12 and 16.

The area of an individual colony was represented as the upper surface area of a cone, crudely estimated from colony height from base and maximum colony diameter. Estimated colony surface coverage (averaged per 100 m along the 15 m and 6 m isobaths) was calculated for each of the four study areas, as well as average colony size per coral species. Colony surface cover data were log-transformed and ranked in abundance plots for each site. Reef profiles and species distributions were determined by plotting colony midpoints along the transect against maximum colony diameter and height from base.

2. Small scale habitat mapping

Relative proportions of substrate and habitat-forming species were mapped in a continuous 2-m-wide swath along the transect. Every 10 m (or less where a marked transition was observed) an estimate was made of bottom cover for a predetermined list of substrate types, epiphytes and epifauna in broad taxonomic groups against this scale: 0 = absent; 1 = solitary individual; 2 = occasional (>0–2 %); 3 = common (2–25 %); 4 = abundant (25–75 %); 5 = complete (75–100 %).

In order to represent these semi-quantitative estimates as relative cover it was necessary to standardise the observations. For each transect a minimum and maximum area for each substrate type was calculated using the area (length × 2 m swath width) multiplied by the minimum and maximum percentage range limits defined in the corresponding scale category. The sum of each maximum area and minimum area for each substrate class was then

corrected against the total area surveyed (since there was a tendency for some overlapping of semi-quantitative coverage estimates, resulting in > 100 % total cover). Midpoint values were then taken from the resulting minimum and maximum possible areas for each substrate class. The associated error in estimating coverage of each substrate type was taken as the difference between the midpoint and the upper and lower area limits.

3. Community level sub-tidal surveys

Species richness, relative abundance and population size structure data have been collected for subtidal marine communities at 15m and 6m depths across the GMR using a standardised methodology since 2001 (and in some localities since 1994). A subset of more than 60 sites has been routinely monitored since 2004 as part of a long-term evaluation of the changing state of coastal marine communities under different management measures. Eight of these long-term monitoring sites fall within the coral survey transects at Darwin, Wolf and Marchena and are included in this analysis, two sites within each of the four survey areas, as indicated in Fig. 2. Each site was surveyed at hot season (Feb–Apr) and cold season (Sep–Oct) extremes (*i.e.* twice per year) during 2005 and 2006.

Observations of fish, macro-invertebrate and algal species richness collected on the 100-m transects were supplemented by detailed reef community data collected at these eight long-term monitoring transects (two 50-m long transects at each depth at each island site) established within the 100-m point-intercept transects. The 50-m transects were deployed at 15 m and 6 m depths and surveyed by a three-diver group, to register species richness, relative abundance and population size structure of benthic sessile species, reef-associated mobile macro-invertebrates and fish.

Survey methods follow Edgar *et al.* (2004). Species, abundance and size of all fish are counted in an estimated corridor extending 5 m on either side of the 50 m transect (= 500 m² total coverage). A 1-m band transect is applied for non-cryptic mobile macro-invertebrates (100 m² total coverage). Percentage cover of sessile macro-invertebrate and algae is calculated from ten 0.25 m² quadrats spaced every 5 m along the 50 m transect line, with 81 equidistant intersection sample points per quadrat.

The survey data were summarised graphically for each site in ranked log abundance plots averaged at each locality. A Detrended Correspondence Analysis (DECORANA) was used to assess similarities in community composition between sites for each monitored group together with the coral survey data.

4. Oceanographic sampling

Given the sensitivity of corals to environmental perturbations it was considered important to characterise the climatic variability influencing coral dynamics and health, to help determine the environmental forcing of subtidal community composition.

Oceanographic information was collected by both an *in-situ* conductivity-temperature-depth YSI-Sonde with integrated fluorometer (CTD-Fl) installed at 15 m depth within the reef at Bahía Tiburón (Wolf), and by Onset Stowaway temperature loggers at 20 m and 10 m depths in Wolf Anchorage. Additional water profile information was collected to 100 m depth by a Seabird 19 Plus v1 CTD-Fl as part of both coral survey expeditions and seasonal oceanographic monitoring cruises with the GNPS. Downloaded instrument data were transformed into temperature time-series and depth profiles for temperature, salinity and inferred chlorophyll-a (productivity) from fluorescence.

RESULTS

Habitat description by study site

Wolf Anchorage. Tourism, fishing and park vessels anchor between the western and (to a lesser extent) northern bays, which are partially protected from prevailing westward-flowing surface currents. Nonetheless, the sharp bathymetry of the island can rapidly shoal oceanic wave trains into a strong swell over the narrow rocky reef fringe when current and winds shift.

Occasional coral patches over small rocks and boulders at 3–6 m were replaced at 16–25 m by occasional boulders over a sandy bottom upon which most boats anchor. Much rubbish was often found, including marine batteries, plates and jars, rope and lost dive equipment. Strong upwelling of colder water from the west and productive chlorophyll plumes observed from satellite imagery suggest that the Equatorial Undercurrent may deviate this far north, or that the steep bathymetric gradient brings deep equatorial waters up around the island, providing limiting nutrients and promoting productivity. Divers often observed a well developed vertical thermocline moving up from depth into the western anchorage shallows, suggesting that periodic internal waves may force cold deep water up into the mixed surface layer around the island pinnacle. Since the Anchorage is in the lee of the island, partially protected from the prevailing westward flow, there was usually an obvious temperature and visibility difference between the west and Bahía Tiburón on the opposite east coast.

Rocky substrate dominated both the 6 m and 15 m transects with some sandy incursions at depth (Fig. 3). Coral cover was approximately half that found in Bahía Tiburón and had a different species composition, with *Pavona clavus* and *P. gigantea* dominating among the 12 species identified at 6 m. *Porites lobata* and *Pavona gigantea* were prevalent among the ten species observed at 15 m, with coral cover five times greater than at 6 m. Individual *Porites* colonies at 15 m were found to be on average six times larger than at 6 m (Fig. 4: A1 and A2). “Massive” corals (*i.e.* the growth form exhibited by *Pavona* and *Porites*) showed a tendency to cluster by species, with a relatively

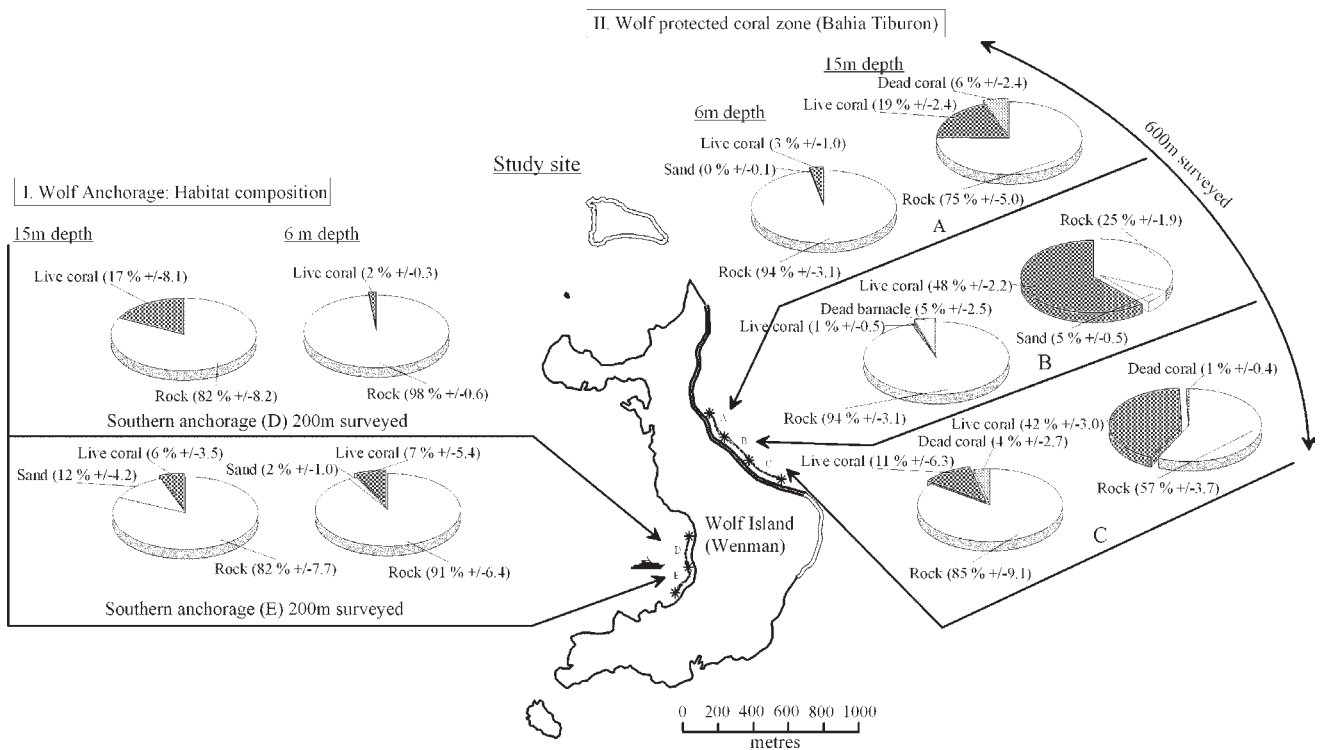


Figure 3. Habitat composition over 200 m transect segments at 15 m and 6 m depth across (I) Wolf Anchorage and (II) Bahía Tiburón (associated error in parentheses).

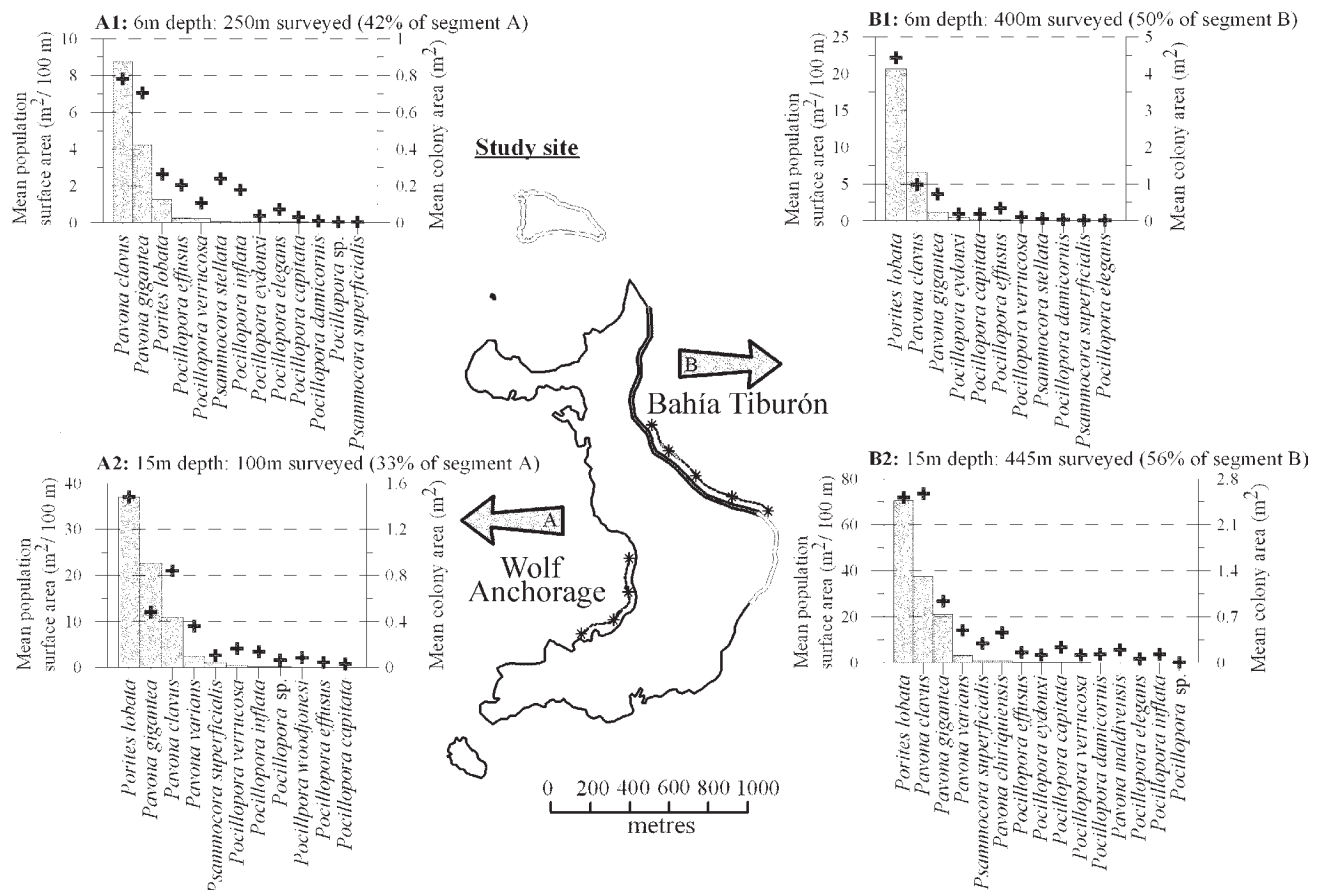


Figure 4. Hermatypic coral species ranked by estimated surface area over 100 m linear transects, with mean colony size (indicated by +) at 6 m and 15 m depth for Wolf Anchorage (A) and Bahía Tiburón (B). Transect segments are indicated by *

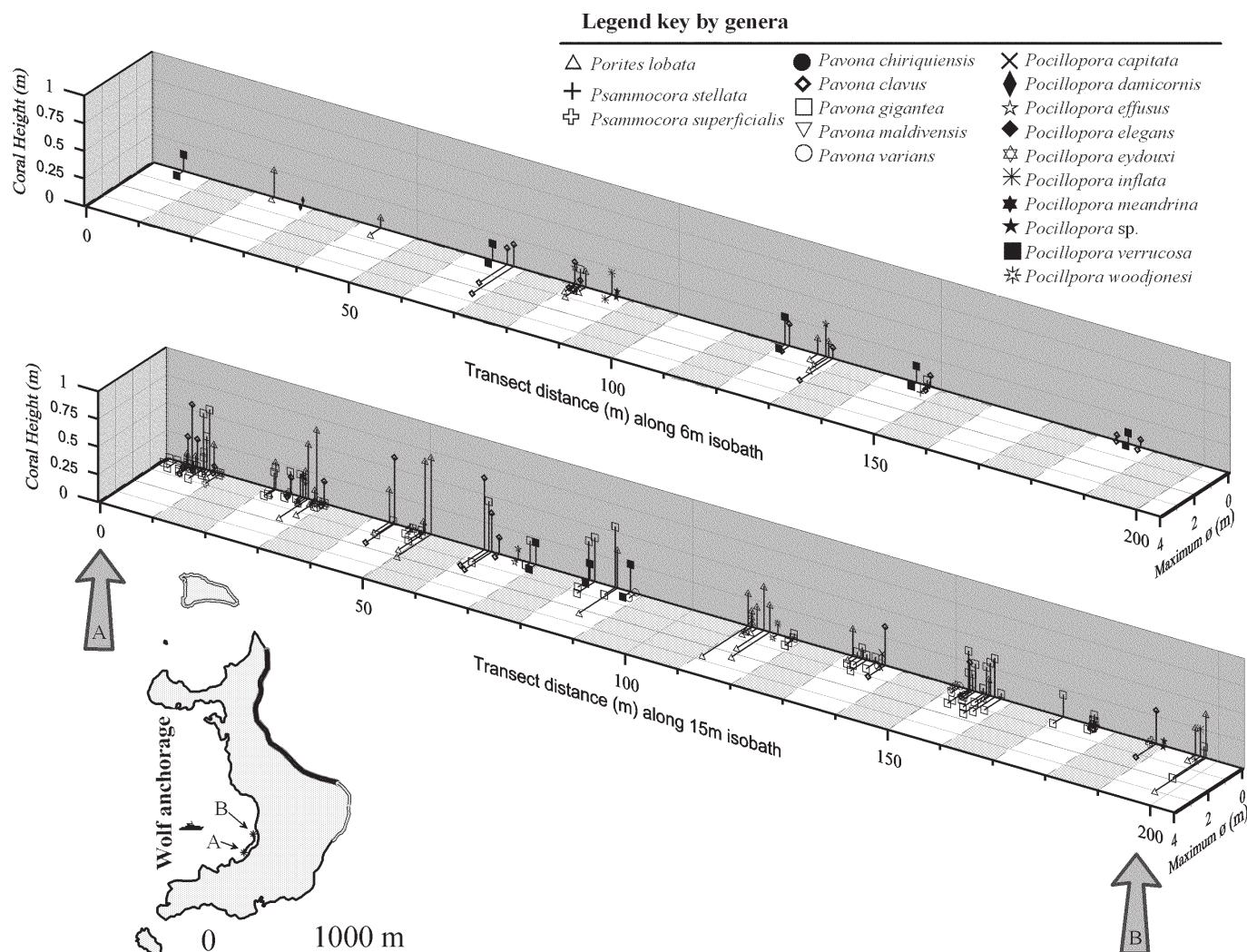


Figure 5. Zooxanthellate coral relief within Wolf Anchorage. Species, mid-point colony position, colony height from base and maximum diameter (\varnothing) across a 200 m transect segment at 15 m and 6 m depth in the southern region of the bay. Shaded areas represent “skipped” 10 m blocks along the non-continuous intercept transect.

low overall reef profile (average 0.19 m) due to numerous encrusting colonies (Fig. 5).

Wolf Anchorage and all other sites in the northern islands have abundant clusters of the long-spined urchin *Diadema mexicanum* at shallower depths. The pencil urchin *Eucidaris galapagensis*, ubiquitous in the archipelago, dominated the mobile macrofauna at 15 m depth (Fig. 6). The encrusting algae *Lithothamnium* sp., *Gymnogongrus* sp. and *Hildenbrandia* dominate the benthos. The foliose, closely adpressed algae *Ralfsia* sp. often partially covers coral (Figure 7A). The general impression is of an urchin barren, although green and white urchins *Lytechinus* and *Triplaneustes* were largely absent. The barnacle *Megabalanus peninsularis* was found at both depths but with greater coverage at 6 m.

All sites in Wolf and Darwin, including Wolf Anchorage, showed unusually high abundance of large Fine-spotted Moray Eels *Gymnothorax dovii*, closely associated with rocky and coralline reef crevices. Such sites also harbour cryptic cardinalfish *Apogon* sp., soldierfish and Glasseye Snapper

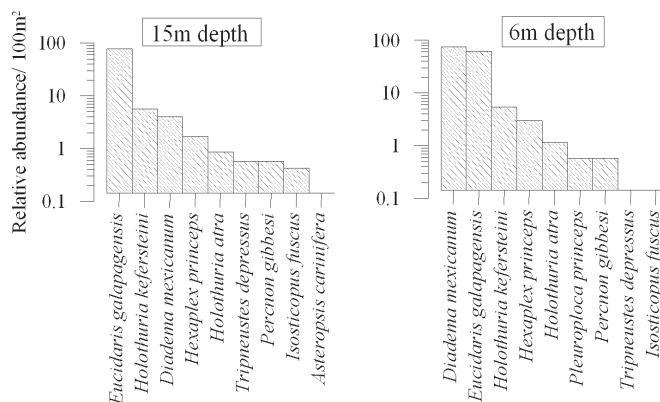


Figure 6. Rank-ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at two long-term replicate monitoring sites at Wolf Anchorage, over 100 m² transects at 15 m and 6 m depth.

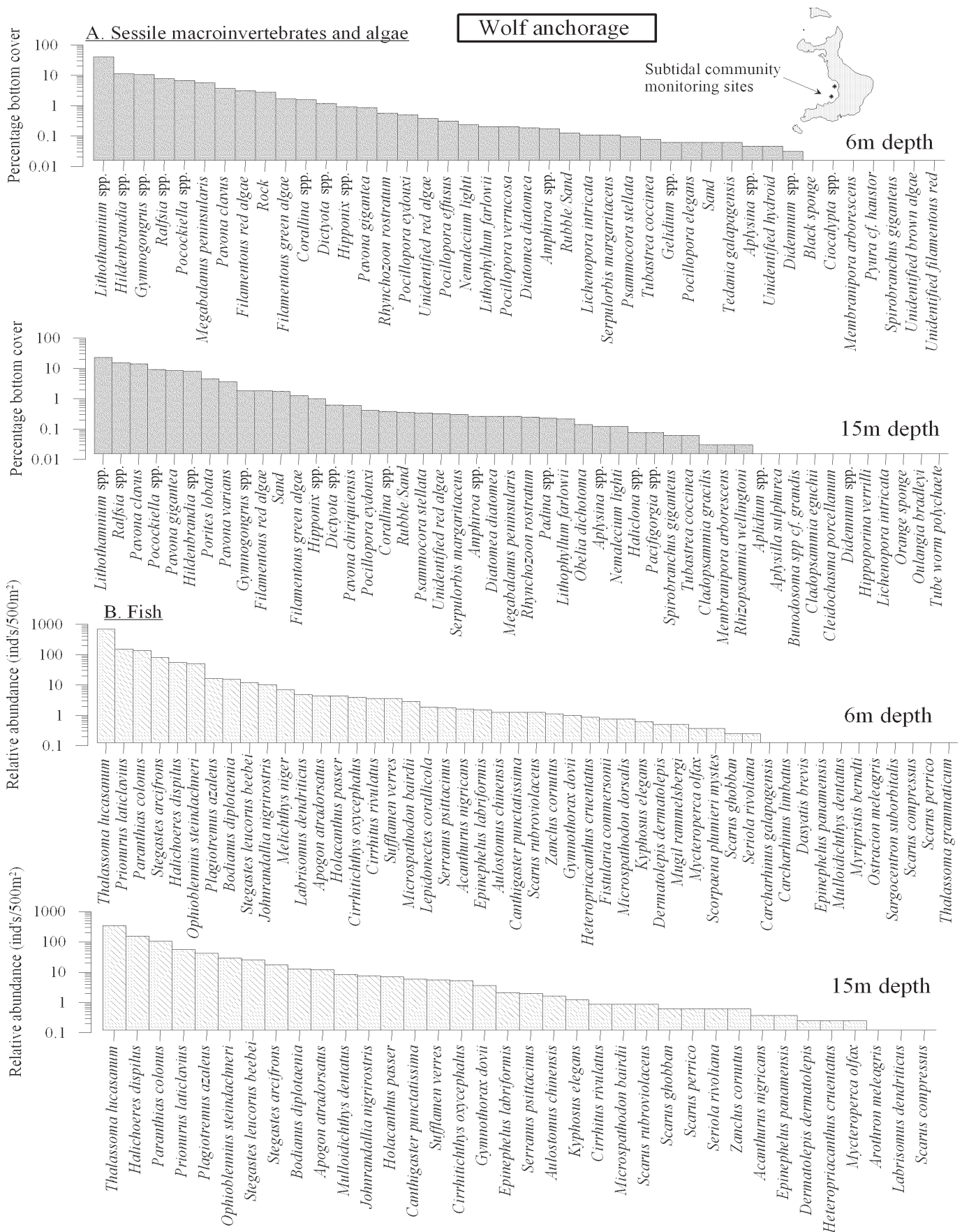


Figure 7. A Rank-ordered cover of sessile benthic macro-invertebrates and algae and B relative abundance of reef fish, averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Wolf Anchorage at 15 m and 6 m depth.

Heteropriacanthus cruentatus (Fig. 7B). At 6 m depth, patches of turf algae “gardens” were maintained by Yellowtail Damselfish *Stegastes arcifrons* and to a lesser extent the less territorial Whitetail Damselfish *S. beebei*. The Giant Damselfish *Microspathodon dorsalis* and Bumphead Damselfish *M. bairdii* were also common and territorial at shallower depths.

The Galapagos and Black-tip Reef Sharks *Carcharhinus galapagensis* and *C. limbatus* were observed as solitary individuals over the shallow reef, with occasional schooling hammerheads in deeper water. Pods of dolphins and juvenile (3 m) Whale Shark were occasionally observed in the surface of the bay. Red-lip Batfish *Ogcocephalus darwini* were on the sand at depths > 20 m, below the transect surveys. Within the sand at 32 m depth a remotely operated vehicle discovered the octo-coral *Ptilosarcus undulates*, which had not been recorded from Galapagos since the 1982–3 El Niño event.

Bahía Tiburón protected coral bay, Wolf Island. Upon reaching the exposed east coast, westward-flowing surface currents diverge to the south (from the popular tourism site “El Derrumbe”) and up across the northern

protected bay. At the northeast edge, current rapidly funnels through the channel between the main island and Isote Banana. The bay between the two points is relatively calm. Denominated a protected non-extractive zone, it harbours one of the most extensive coral reef communities remaining in Galapagos. Coral cover was 1.83 times higher across the two sampled depths than in the western Anchorage. *Pavona lobata*, *P. clavus* and *P. gigantea* dominated the coral benthos with occasional pocilloporids (Fig. 4B). Average *P. lobata* colony size was also larger, often extending across the reef bathymetry. Coral species richness was higher at 15 m (15 identified species compared to 10 in the Anchorage) with both *Pavona chiriquiensis*, *P. maldivensis*, and the more challenging to identify *Pocillopora* groups, with at least *P. eydouxi* observed. Reef profile at 15 m depth was significantly elevated (maximum height 2.7 m above rocky basal substrate, averaging 0.42 m) compared to the Anchorage, with near-continuous *Porites* coverage. *Porites* cover was much less at 6 m (c. 20 % cover) with only occasional large “massive” colonies and outcrops of *Pocillopora* (Fig. 8).

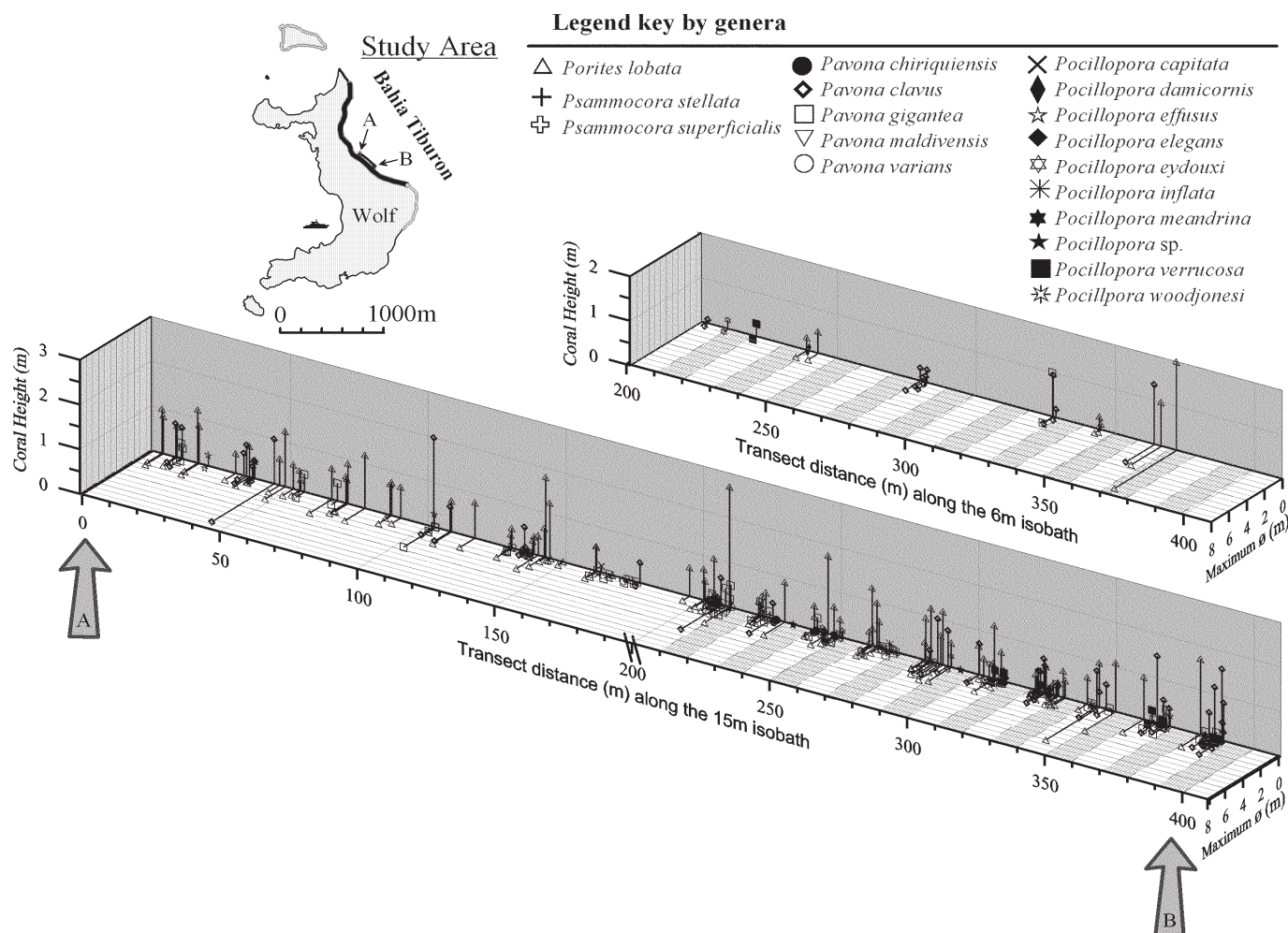


Figure 8. Coral relief within Bahía Tiburón, Wolf. Species, midpoint colony position, colony height from base and maximum diameter (Ø) across a 400 m transect segment at 15 m depth and 200 m over 6m depth in the central region of the bay. Shaded areas represent “skipped” 10 m blocks along the non-continuous intercept transect.

In terms of benthic composition, at 6m the algae *Ralfsia*, *Hildenbrandia*, *Pocockiella* and *Lithothamnium* sp. were prevalent, with the barnacle *Megabalanus peninsularis*, and followed

by the massive *Porites* sp. and *Pavona* sp. corals. At 15m, the massive corals dominated (Fig. 9A). *Diadema* urchins were found in highest densities at 6m, with greater mobile

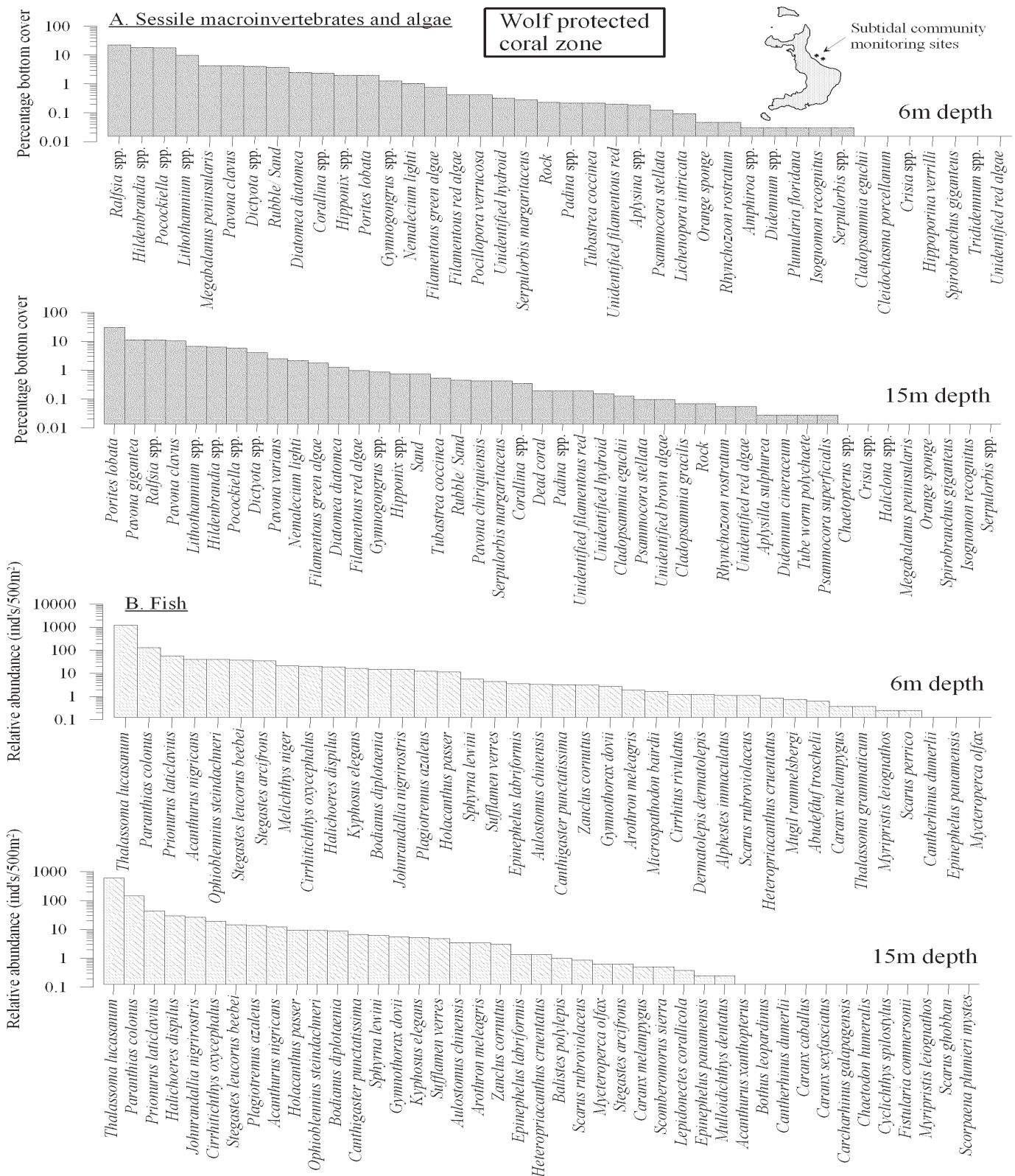


Figure 9. Rank ordered cover of sessile benthic macro-invertebrates and algae (A) and relative abundance of reef fish (B) averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Bahía Tiburón, Wolf at 15 m and 6 m depth.

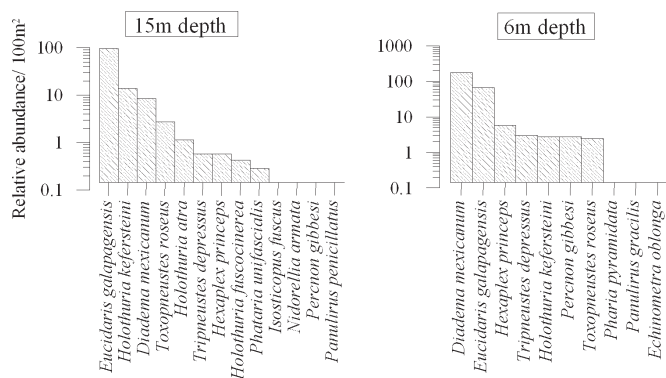


Figure 10. Rank ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at two adjacent monitoring sites in Bahía Tiburón, Wolf over 100 m² transects at 15 m and 6 m depth.

macro-invertebrate species diversity compared to all other sites, and including the less common Rose Urchin *Toxopneustes roseus* (Fig. 10).

Widespread fish species such as the Rainbow Wrasse *Thalassoma lucasanum*, Chameleon Wrasse *Halichoeres*

disipulus, Yellow-tailed Surgeon *Prionurus laticlavus*, White-tail Damsel and Pacific Creolefish *Paranthias colonus* were evident in all sites. High abundance of cryptic coral dwellers such as the Coral Hawkfish *Cirrhichthys oxycephalus*, Trumpet Fish *Aulostomus chinensis* and Guinea fowl Puffer *Arothron meleagris* distinguished these high coral-cover sites from other parts of the GMR (Fig. 9B). Barberfish *Johnrandallia nigrosirris* were associated with cleaning stations for the large schooling pelagics. Yellow-rim Surgeonfish *Acanthurus nigricans* were closely associated with the reef at 3–8 m, whereas the less common Redtail Triggerfish *Xanthichthys mento* was observed below 25 m. Black Durgon *Melichthys niger* were inshore, feeding in the upper water column. Solitary or occasional schooling Cortez Chub *Kyphosus elegans* with occasional larger pelagic jacks such as *Caranx sexfasciatus* were slightly offshore in the upper 20 m. Scalloped Hammerheads were commonly seen cruising along the reef. Frequently observed sealions complemented occasional sightings of dolphins, usually slightly offshore and towards the southern point El Derrumbe. The area was occasionally frequented by transient Whale Sharks, Orcas *Orcinus orca* and Humpback Whales *Megaptera novaeangliae*.

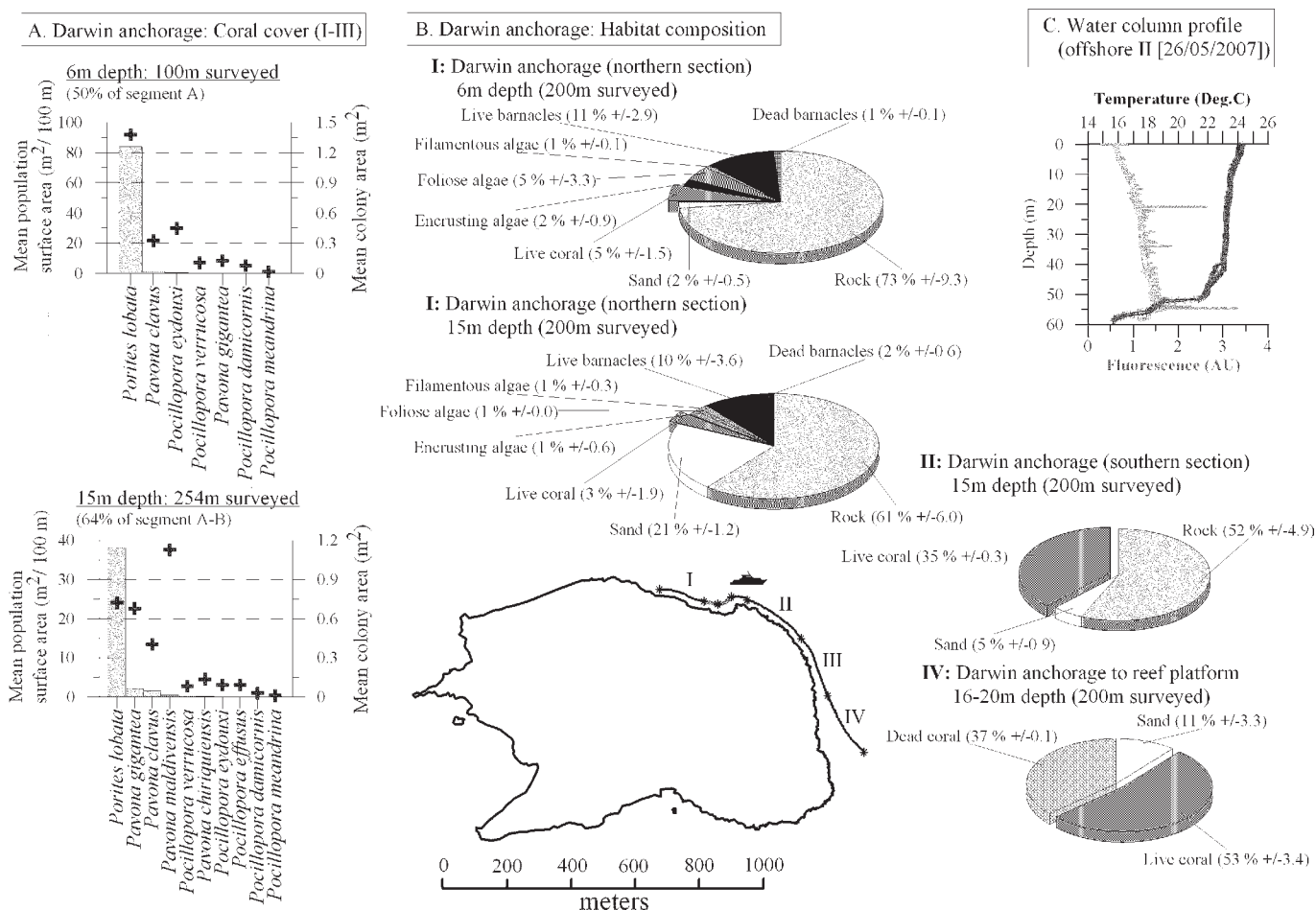


Figure 11. Darwin Anchorage. A Coral species ranked by estimated surface area over a 100 m linear transect, with mean colony size (indicated by +) at 6 m and 15 m depth. B Habitat composition by transect segments I, II & IV (associated error in parentheses). C Water temperature and fluorescence (chlorophyll) depth profiles.

Darwin Anchorage. The area surveyed was in the northeast of the island, from the central northern shore passing southeast around the eastern coastal fringe then offshore towards Darwin Arch across the old reef framework (a platform at 15–20 m depth to the southeast). Boats typically anchor over large sandbanks and rocky outcrops at 30–60 m depth, slightly offshore from the coast, due to moderate to strong swell. Strong westward-flowing surface currents pass over rock and sand platforms that drop off sharply to the northwest. Coral reef was almost exclusively dominated by *Porites* colonies, with higher coverage at 6 m depth than at 15 m over the surveyed northern segment: the opposite of that recorded at other sites (Fig. 11A). Whether this was the case towards the south of the anchorage is unclear; numerous *Porites* colonies that were seen across a large shallow platform over the southern segments were not studied because of a strong swell (F. Rivera pers. comm.). There were fewer large colonies at 15 m depth compared to Bahía Tiburón. Other uncommon species included *Pavona*

maldivensis (at 6 m) and *Pocillopora meandrina*. The latter was not observed in the Wolf transects. Although not detected on the transects, broader searches revealed the rare cryptic zooxanthellate coral *Leptoseris scabra* and a possible new *Leptoseris* sp. (C. Hickman pers. comm.).

At 15 m depth, rock and sand gave way to increasing coral coverage around the northeast point of the island, extending towards the south (Fig. 11B). The benthic cover of live and dead coral increased to >90 % across the southeastern platform (towards Darwin Arch) where Glynn & Wellington (1983) documented one of the largest reefs in the archipelago before the 1982–3 El Niño. The reef showed considerable epiphyte overgrowth and bio-erosion, yet retained its structural complexity and height, also exhibiting some signs of recovery (Glynn *et al.* this volume).

Reef profile at Darwin was distinct from that at Wolf, with a similar average colony height (0.31 m overall). Wider encrusting colonies of *Porites* were recorded in the often turbulent surge zone at 6 m compared to those at 15 m depth (Fig. 12).

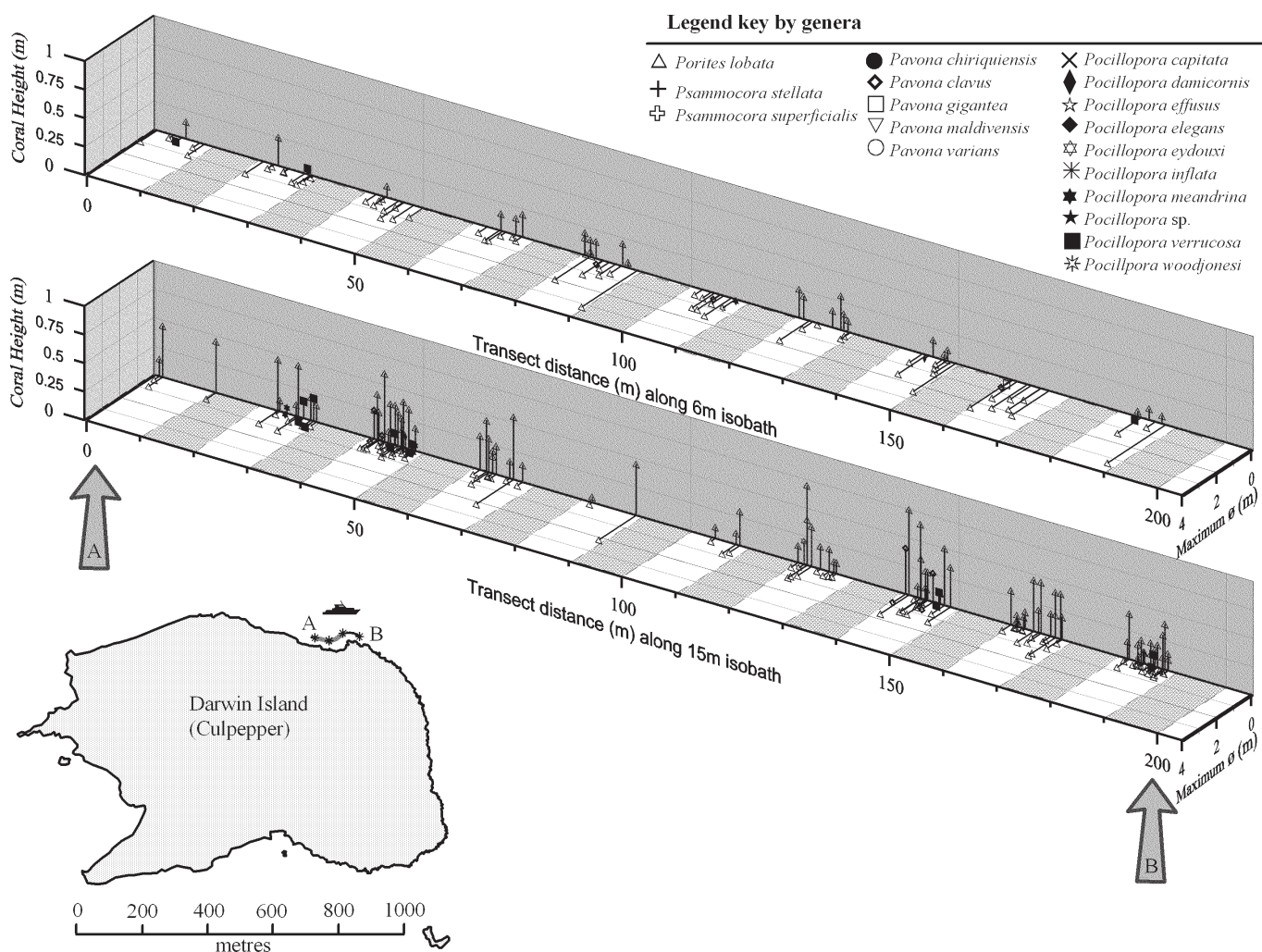


Figure 12. Coral relief at Darwin Anchorage. Species, colony midpoint position, colony height from base and maximum diameter (Ø) across a 200 m transect segment at 15 m and 6 m depth. Shaded areas represent "skipped" 10 m blocks along the non-continuous intercept transect.

At shallow depths, encrusting algae *Lithothamnium*, *Hildenbrandia*, *Ralfsia* and *Dictyota* sp. were dominant on rocky substrate. Sessile macrofauna comprised intermittent

massive coral, occasional limpets *Hipponix* sp. and well distributed barnacle growth (Fig. 13A). As with the Wolf sites, Coral Hawkfish were abundant, associated with

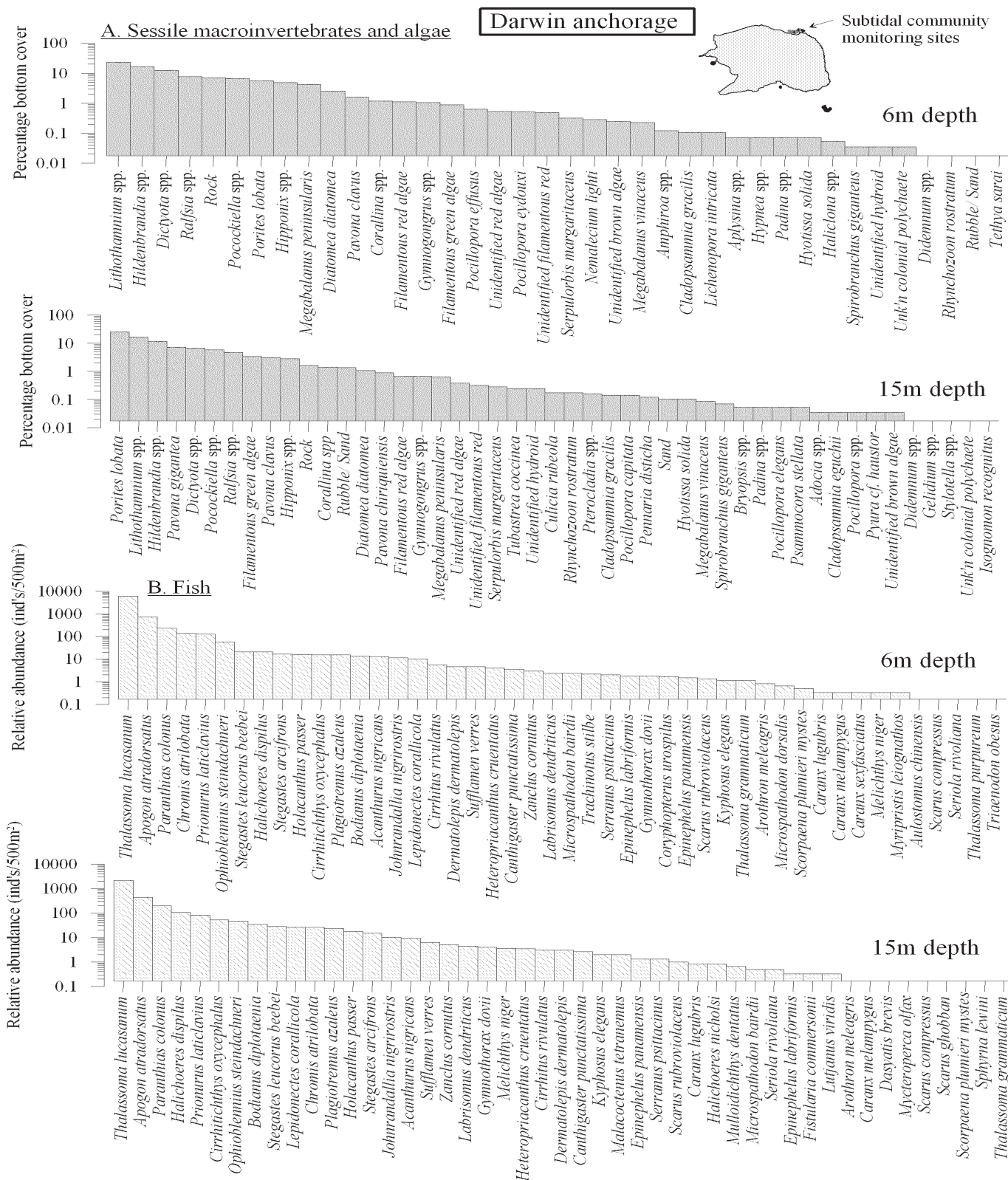


Figure 13. Rank ordered cover of sessile benthic macro-invertebrates and algae (A) and relative abundance of reef fish (B) averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Darwin Anchorage at 15 m and 6 m depth.

the coral. Scissor Chromis *Chromis atrilobata* were observed at 6 m. Cryptic species such as the cardinalfish *Apogon atradorsatus* and Glasseye Snapper were associated with large boulder crevices (Fig. 13B). Larger predatory fish normally associated with ETP coral reefs, such as *Dermatolepis dermatolepis*, were rare. Various pelagics not commonly seen in the coastal fringe such as the Almaco *Seriola rivoliana*, Bigeye *Caranx sexfasciatus* and Bluefin Trevally *C. melampygus* were also recorded rapidly crossing the reef, along with occasional White-tip *Triaenodon obesus*, Black-tip, Scalloped Hammerhead and Whale Sharks. The Crown of Thorns Sea-star *Acanthaster planci*, considered a voracious corallivore, was uncommon; it was never observed in other sites. Macro-invertebrate diversity and species composition were similar to those of Wolf Anchorage. Large boulders were colonised by the mollusc *Hexaplex princeps*, swimming crabs *Percnon gibbesi* and low densities of the commercial sea cucumber *Isosticopus fuscus* that were nonetheless higher than those observed in other sites at 15 m depth (Fig. 14). A single specimen of the long-spined urchin *Echinothrix cf. diadema*

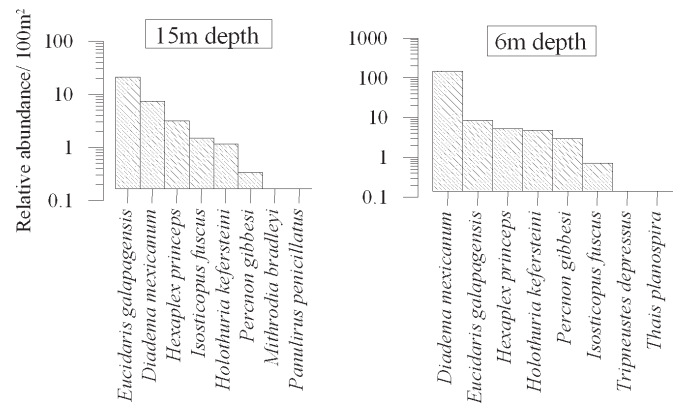
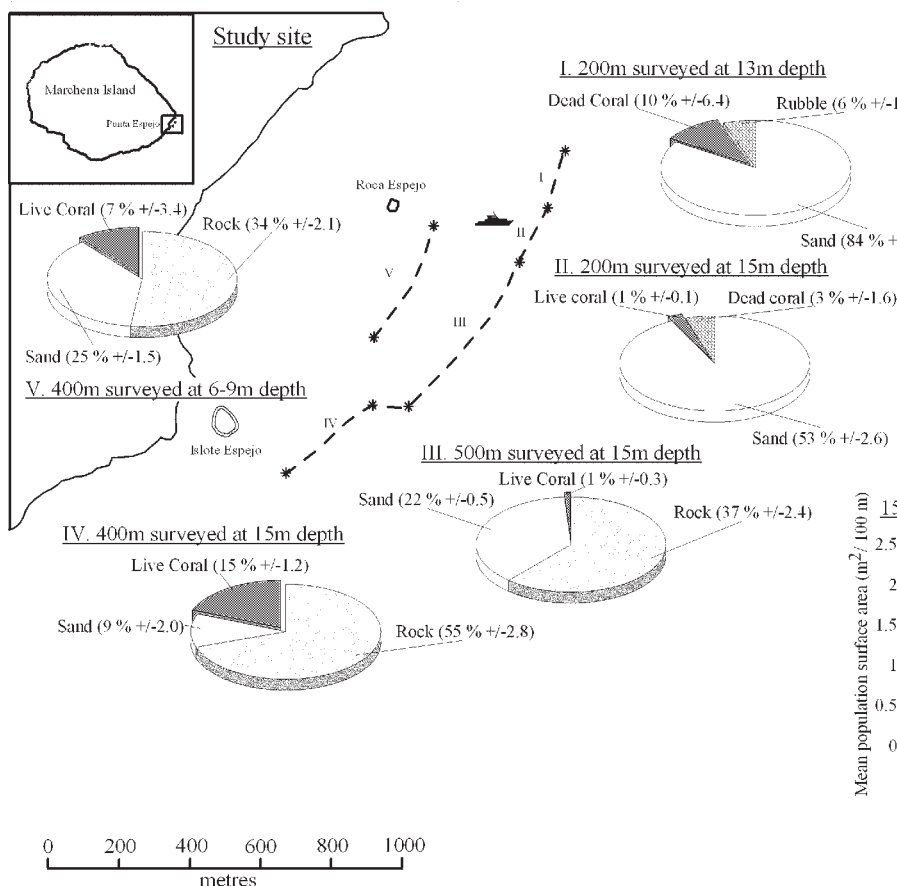


Figure 14. Rank ordered mobile macro-invertebrate relative abundance averaged across 2005–6 seasonal sampling at two adjacent monitoring sites in Darwin Anchorage over 100 m² transects at 15 m and 6 m depth.

was collected at 8 m depth. *E. diadema*, with a mainly Indo-Pacific distribution, was previously unrecorded in Galapagos but is found in Cocos Island.

A. Marchena, Punta Espejo: Habitat composition



B. Marchena, Punta Espejo: Coral cover

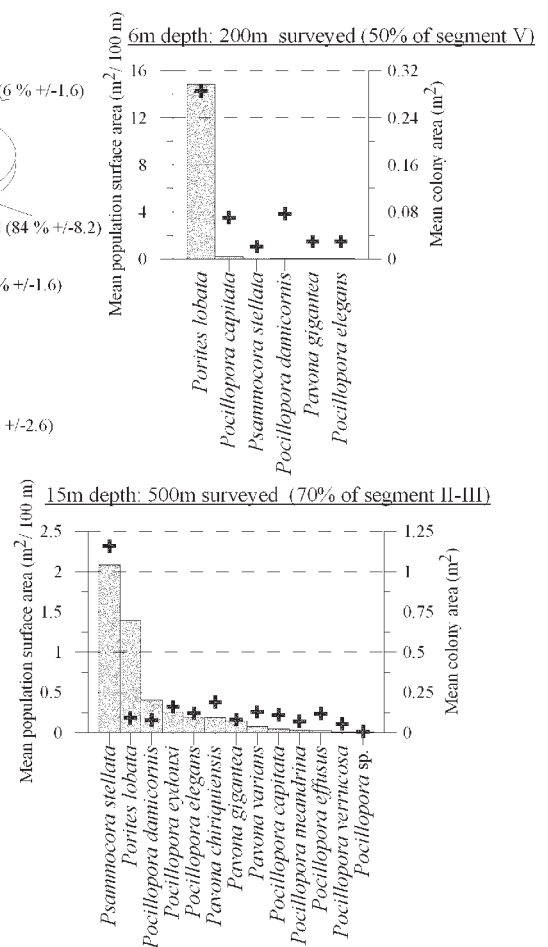


Figure 15. A Habitat composition by transect segments (I–V) across Punta Espejo, Marchena (associated error given in parentheses). B Coral species ranked by estimated surface area over a 100 m transect, with mean colony size (indicated by +) at 6 m and 15 m depth (across transect segments II, III and V).

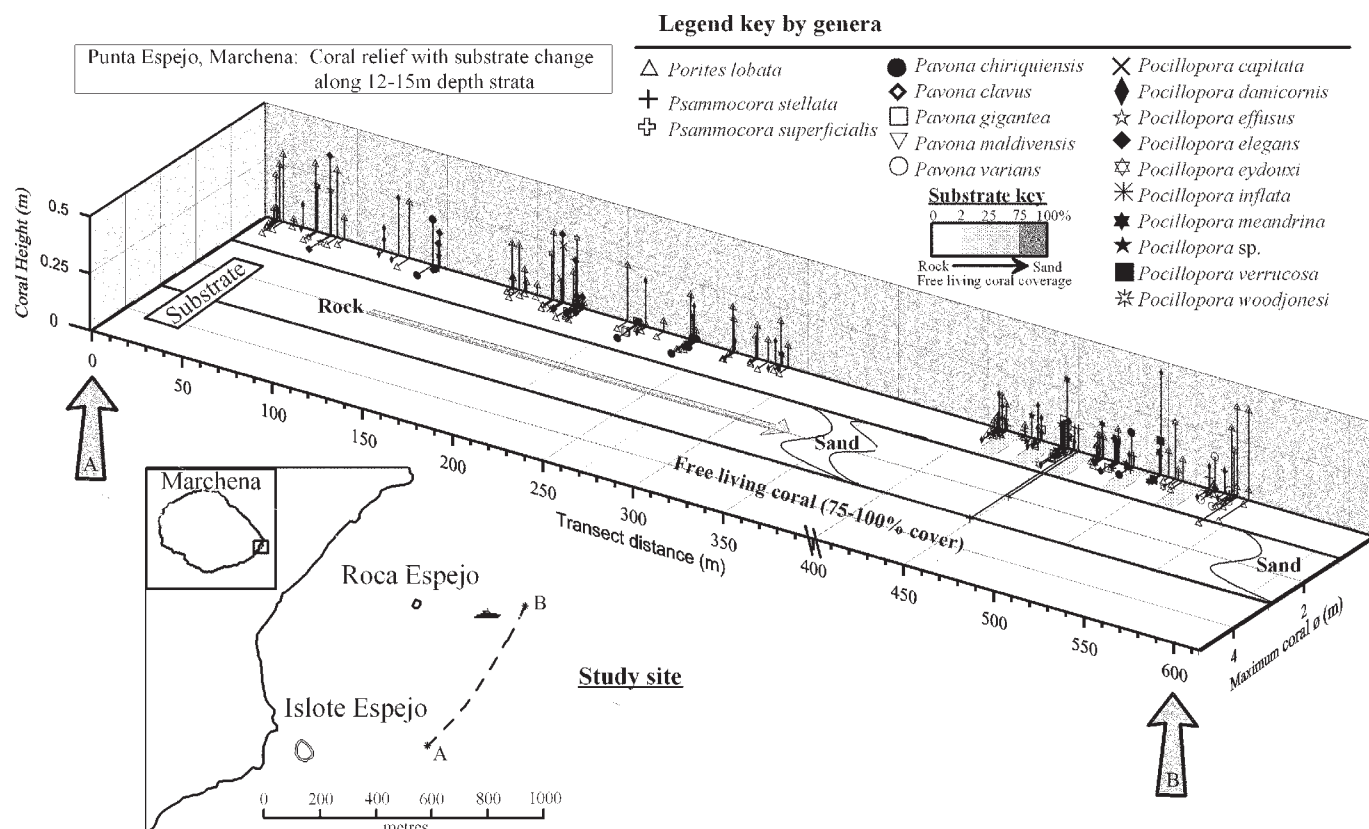


Figure 16. Coral relief at Punta Espejo, Marchena. Species, colony midpoint position, colony height from base and maximum diameter (\varnothing) over a 600 m transect at 12–15 m depth. Shaded areas represent “skipped” 10 m blocks along the non-continuous intercept transect. Substrate transition from rock to sand is indicated, along with estimations of *Psammocora stellata* and *Porites lobata* free-living coral cover.

Punta Espejo, Marchena. Punta Espejo is at the SE tip of Marchena Island, approximately 200 km southeast of Wolf and Darwin. It is an exposed bay between the exposed rock Roca Espejo and Islote Espejo further to the south, across a wide uniform platform descending gradually to the east (Fig. 2). Tidal currents channeled between the northern and central Galapagos islands are strong, often with considerable swell. The usual anchorage is c. 200 m to the east of Roca Espejo, on a rocky platform where much coral is interspersed with large sandy areas. Directly to the north and south of the anchorage, the depth is fairly uniform at 12–16 m. Much dead coral was observed across the anchorage zone, over predominantly sandy substrate. Towards the south and at shallower depth, surveys showed rockier substrate and a greater proportion of live coral (Fig. 15A).

The coral assemblage and complexity were distinct from those of Wolf and Darwin. Large expanses of sandy bottom were covered with extensive *Psammocora stellata* beds composed of hundreds of small 3–14 cm colonies (Fig. 16), as well as surviving *Porites lobata* coral fragments on the sand, rounded by frequent abrasion. The shorter transect surveyed at 6 m depth had far more extensive *Porites lobata* cover (Fig. 15B). At the ends of a NE–SW transect across the anchorage area (15 m depth) there

was a clear transition from relatively low-relief *Porites* and *Pocillopora* frameworks to a central sandbank with near complete *Psammocora* coral cover (Fig. 17).

Benthic communities were particularly diverse. In addition to the encrusting algae and some corals as commonly observed in Wolf and Darwin, varied sponges, bryozoans, hydroids and ascidians, which are more common in the southern and central archipelago, were present. *Psammocora* and *Pavona* coral species were most evident (Fig. 18A).

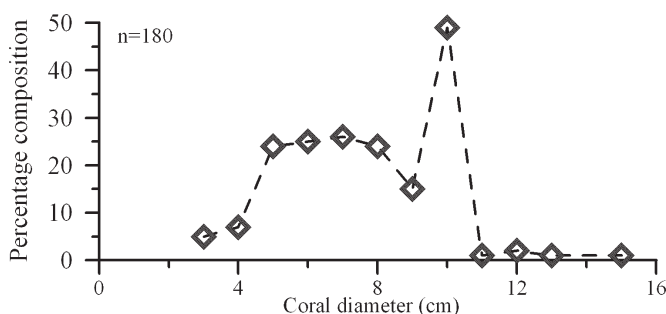


Figure 17. Size distribution of free living *Psammocora stellata* on sand substrate taken from three sampling periods (2005, 2006, 2007) at Roca Espejo, Marchena.

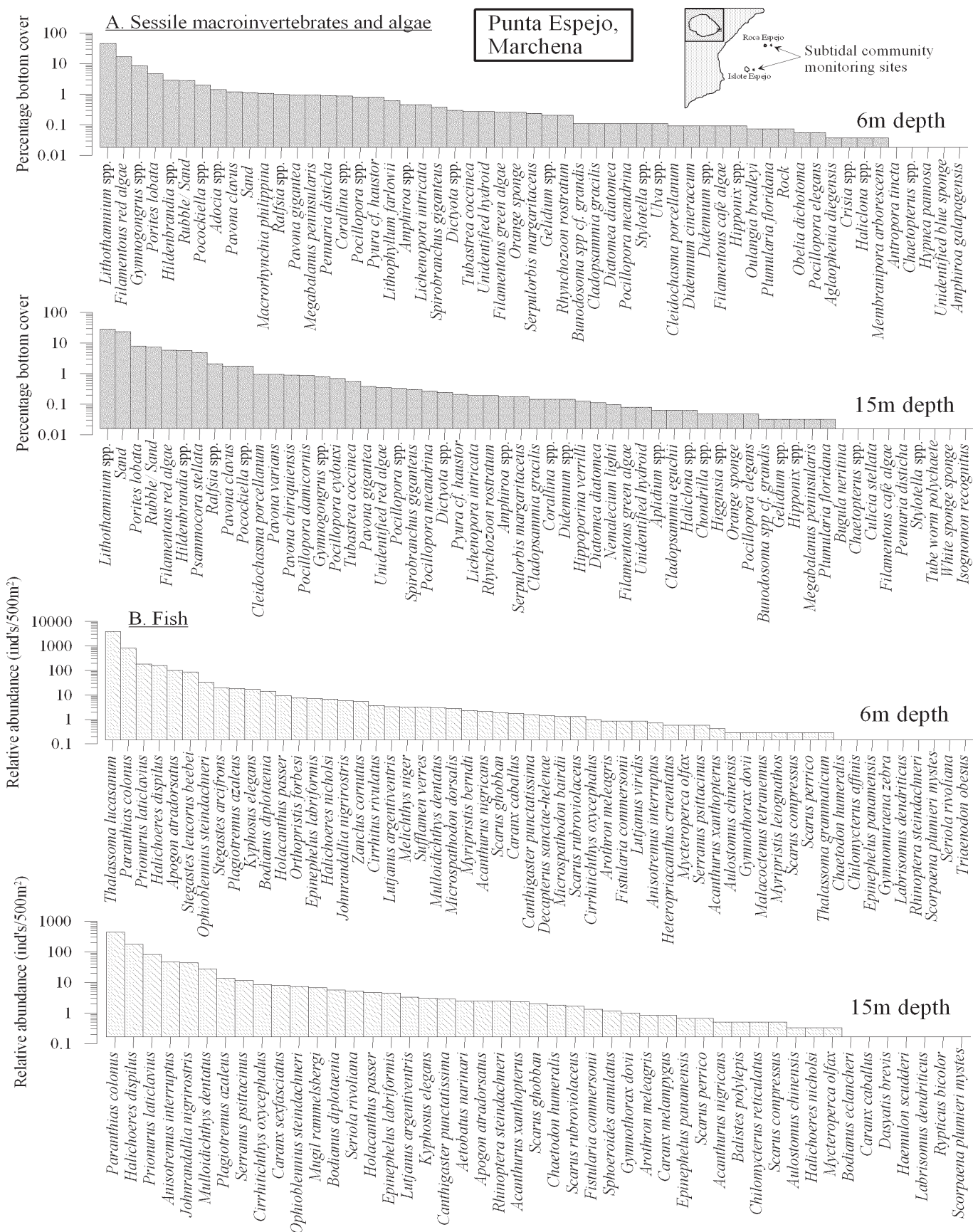


Figure 18. A Rank ordered cover of sessile benthic macro-invertebrates and algae and **B** relative abundance of reef fish averaged across 2005–6 seasonal sampling at two adjacent long-term monitoring sites at Punta Espejo, Marchena at 15 m and 6 m depth.

In contrast to Wolf and Darwin, *Eucidaris galapagensis* and the cryptic Crown Urchin *Centrostephanus coronatus* were more common than *Diadema*, whereas the white and green urchins *Tripluviesia* and *Lytechinus*, associated with overgrazing and normally common across the central archipelago, were absent. The Panamic Cushion Star *Pentaceraster cumungii* was often recorded feeding at the sand–rubble interface in deeper water. As at most sites in the central archipelago, the pencil urchin *Eucidaris galapagensis* dominated the mobile macrofauna. The Crown Urchin, the mollusc *Hexaplex princeps* and seastar *Phartaria unifascialis* were common across the rocky reef outcrops. Deposit feeders *Holothuria kefersteini* were common only at shallow depths (Fig. 19).

Many fish species of open water, coral reef, sandy bottom and rocky reef were resident. The spatially complex rocky reef habitat harbouring cryptic dwellers such as cardinalfish *Apogon* sp. contrasted with current-scoured sandy patches where schooling bottom feeders such as Mexican Goatfish *Mulloidichthys dentatus* were found (Fig. 18B). There were dense spawning aggregations of Rainbow Wrasse over reef outcrops. Other common schooling fish included Barberfish, Yellowtail Grunt *Anisotremus interruptus* and Galapagos Grunt *Orthopristis forbesi*. Jacks *Caranx* spp. and mullet *Mugil* sp. were in the upper water column. Fish with tropical distributions uncommon in the central archipelago included Yellowfin Surgeonfish *Acanthurus xanthopterus* and Gold-rim Surgeonfish *A. nigricans*. We commonly observed Eagle Ray *Aetobatus narinari*, Cow-nosed Ray *Rhinoptera steindachneri*, White-tip Shark, Fine-spotted Moray, and occasionally Scalloped Hammerheads and dolphins.

Community level analysis by taxa

A multivariate comparison of species richness and relative abundance of each of the four surveyed groups

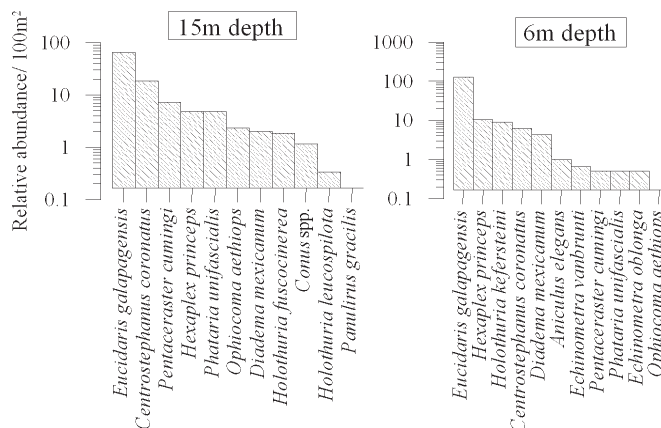


Figure 19. Rank ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at 15 m and 6 m depth at two long-term monitoring sites at Punta Espejo, Marchena.

reveals within-site variation between 15 m and 6 m depths at all sites (Fig. 20). This was most pronounced at Marchena because of the unique *Psammocora* coral communities at 15 m, and least pronounced at Darwin (Fig. 20A). Between-site comparisons show that Punta Espejo *Porites lobata* coral communities at 6 m were similar in composition to those at Darwin. The two Wolf sites had greater within-site differences between depths than between-site variation at the same depth; between-site differences were more pronounced at 6 m, perhaps reflecting the differing surge and exposure conditions on opposite sides of the island.

Sessile benthic species richness (all non-coral groups) at Marchena was much higher than at Wolf and Darwin, with a wider range of groups (Fig. 20B). This generated greater habitat complexity and presumably a more productive environment than at other sites.

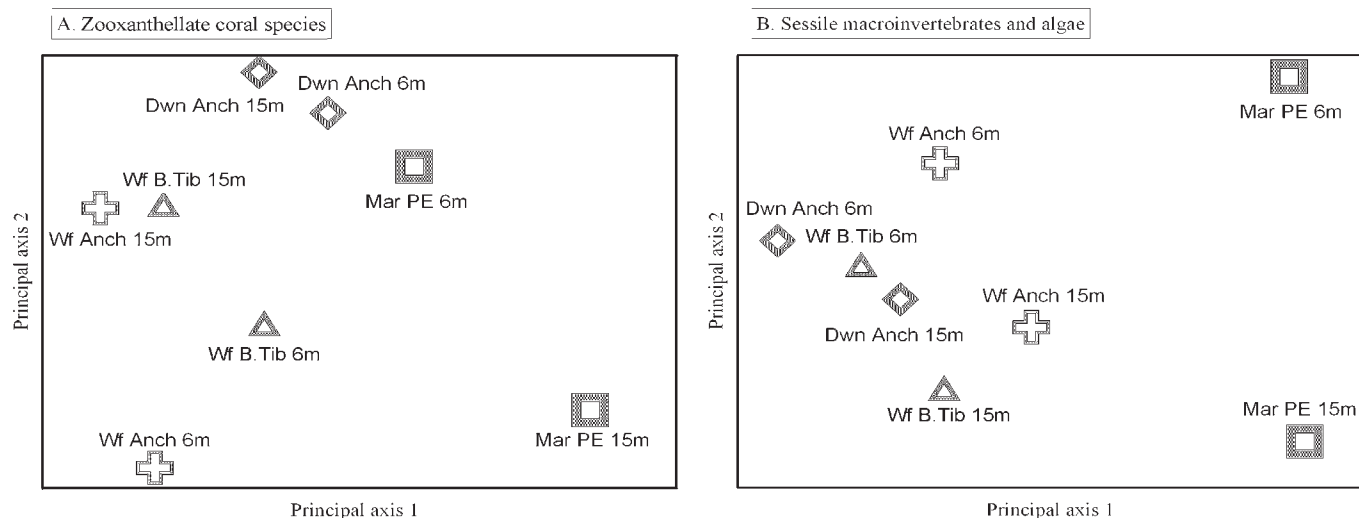


Figure 20. De-trended correspondence analysis (DECORANA) of northerly subtidal communities based on relative abundance/cover of **A** zooxanthellate corals and **B** sessile macro-invertebrates and algae, surveyed synoptically during hot and cold seasons 2005–6 across 15 m and 6 m depth in the four study sites.

Different species were associated with each site and it is unclear whether this was due to habitat preference, species dispersal and pinnacle connectivity by currents, or both. For example, fish communities at 6 m depth in Punta Espejo were similar to those in Darwin Anchorage (Fig. 20C). Both sites were almost exclusively composed of *Porites lobata*, which may influence the associated ichthyofauna. All taxonomic groups in Punta Espejo at 15 m depth were distinctly different from the communities recorded at the other sites. This suggests that the *Psammocora* bed habitat type should be considered a distinct community. There were similarities in fish community structure at 6 m depth in Wolf Anchorage and 15 m in Bahía Tiburón.

Mobile macro-invertebrate assemblages at Wolf Anchorage and Darwin showed low between-site variation at each depth, with consistent differences between depths, and they were distinct from those at Bahía Tiburón and Punta Espejo (Fig. 20D). Mobile macro-invertebrate and fish diversity were both higher at Punta Espejo than at Wolf and Darwin.

Temperature effects

Periodic internal wave forcing around the oceanic pinnacles pushes the mixed layer thermocline ($\Delta 6\text{--}8^\circ\text{C}$), which is normally located around 50 m depth, up into the coastal fringe surface waters. The chlorophyll maximum from vertical profiles correlates well with the thermocline, suggesting nutrient limitation at the density interface. Water column profiles showed strong stratification at Darwin at 55 m depth (Fig. 11C). At Wolf we recorded less-stratified water with mixing over the 40–60 m depth interval (Fig. 21B). The temperature record at 15 m from January to June 2007 showed a distinct transition from a moderate El Niño warm event into a strong La Niña cold condition. At the apex of what is normally considered the

hot season, this produced an exaggerated thermocline between the surface and upwelled deep water. Temperatures remained consistently elevated, at $26\text{--}28^\circ\text{C}$, at 15 m depth in the mixed surface layer over the coral reef, until the end of February 2007, when temperatures fell to 16°C over just six days, with another cold event of similar magnitude in May at the end of the record (Fig. 21).

Great diurnal temperature variability reflects the migration of the thermocline under tidal forcing across the reef with large internal waves. Although surveys were completed in February, additional observations from May 2007 to January 2008 show widespread “cold shock” bleaching of *Porites lobata* and *Pocillopora* sp. across the entire archipelago. We noted greater bleaching at depth, associated with movement of the thermocline towards the surface. We observed relatively little bleaching of *Pavona* sp. colonies, which were often adjacent to completely bleached *Porites* colonies. Wolf and Darwin coral colonies appeared to have largely recovered by August 2007, with some algal overgrowth. However recent surveys of fragmented colonies in the central and southern islands show little recovery. These observations include *Pavona clavus* bleaching at depths >25 m in northern Floreana Island (unpubl. data, January 2008).

DISCUSSION

The remaining zooxanthellate coral reef communities in the far north, as well as the more fragmented communities that have persisted in other parts of the archipelago following the widespread impacts of the 1982–3 El Niño, are important in various ways. They represent the last remaining continuous reef structures and zooxanthellate species assemblages in the Galapagos region, sustaining a distinct community rich in species with Indo-Pacific and Panamic affinities. The contribution to GMR total

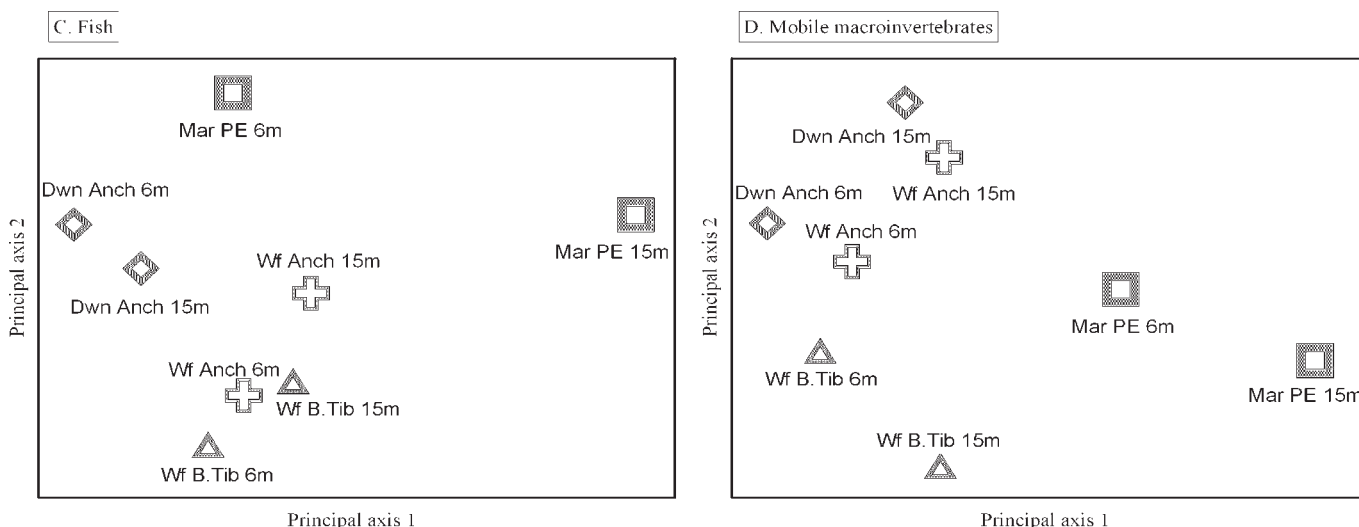


Figure 20 (continued). De-trended correspondence analysis (DECORANA) of northerly subtidal communities based on relative abundance/cover of **C** fish and **D** mobile macro-invertebrates, surveyed synoptically during hot and cold seasons 2005–6 across 15 m and 6 m depth in the four study sites.

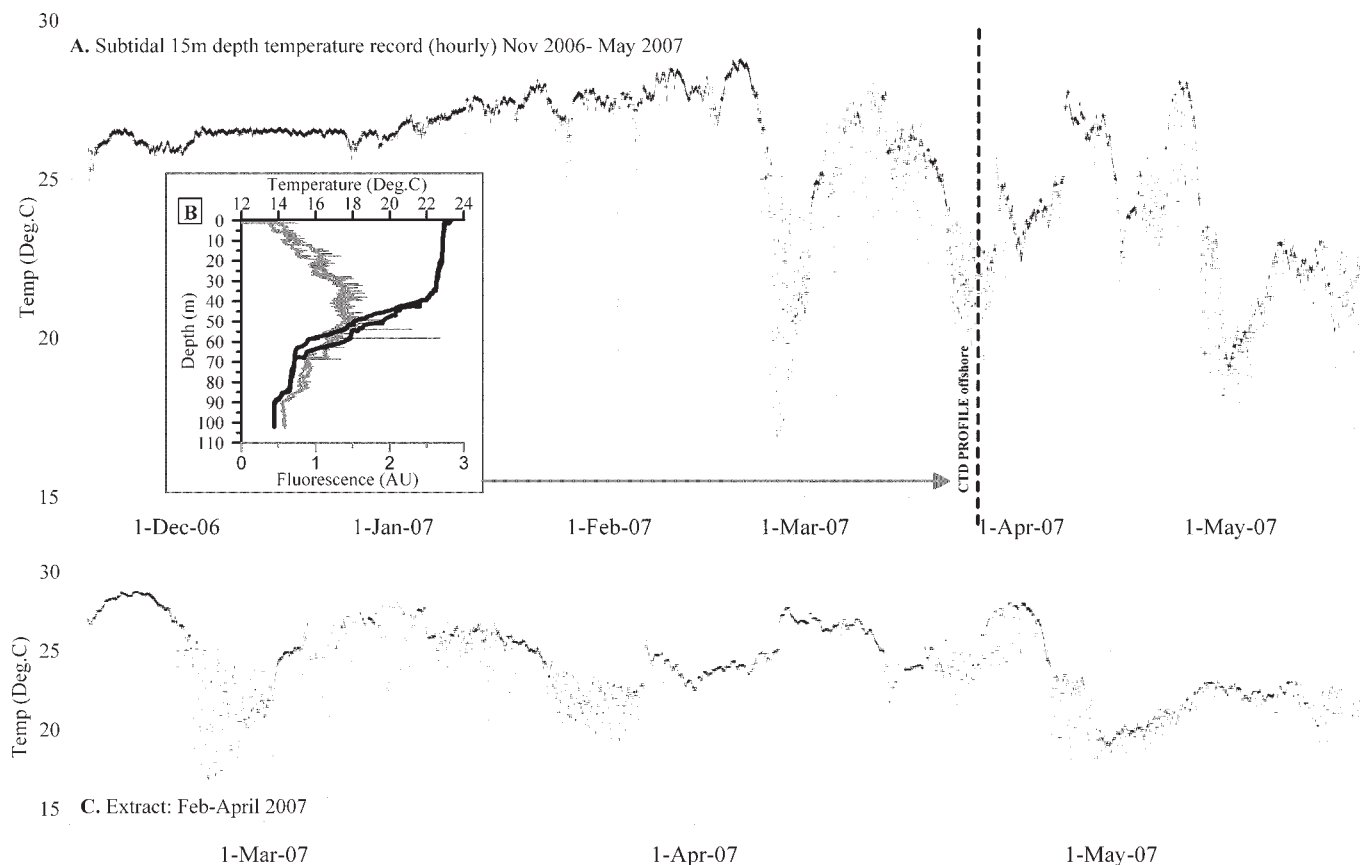


Figure 21. A Time series hourly temperature depth record from a YSI-CTD installed at 15 m depth in Bahía Tiburón, Wolf. Inset B shows the thermocline and chlorophyll maximum depth profile adjacent to the anchorage in deep water (taken 25 May 2007). C Extract of temperature record showing rapid decrease from a moderate El Niño state towards the beginning of the 2007 La Niña cold condition.

biodiversity is disproportionately large considering the small area of the coastal fringe in the north. Coral reefs are also highly productive refuge sites that afford protection from currents and surge for many cryptic species. They also provide niches within them, such as cleaning stations, species associations and nursery areas.

The reasons for the survival of northerly corals compared to those in the southeastern part of the GMR are complex. Coral and zooxanthellate physiological responses to oceanographic conditions have yet to be quantified. Differences in trophic interactions owing to climate and fisheries pressure may influence coral mortality. Algal overgrowth may vary between regions. Susceptibility to disease may vary within and between species and between fragmented populations. Settlement of new colonies may be affected by bio-eroder overgrazing. Changes in ETP circulation may alter source and sink larval connectivity for corals and the communities they support.

Despite uncertainty about the reasons, these areas have persisted despite 95–99 % losses across other areas in Galapagos. However, in addition to projected global climate and ocean acidification effects, the rapid development of fisheries and tourism over the last 20 years (as in

other parts of the world) now risks upsetting what appears to be an already tenuous balance between survival and local extinction.

The presence of large eroded frameworks and sporadic coralline biogenic sand beaches along the coast suggest that coral reef communities have persisted over long time periods. Given estimated growth rates, some *Porites lobata* colonies greater than 7 m in diameter to the west of Darwin are likely to be at least 200 years old. Over evolutionary timescales Galapagos zooxanthellate coral reefs may persist in climatic “refuge” areas afforded by cold periodic upwelling in warm periods and equatorial surface heating in protected bays during cold events. Surface currents from the Panamic province may facilitate exogenous recruitment in the far north of the GMR. Strong natural selection of resident populations driven by temperature stress and consistently higher temperatures in the northern isles might also explain a degree of natural resilience to periodic strong natural climatic stress events at the species level.

Long-term global climate forecasting needs to address possible impacts on coral reef systems (Podestá & Glynn 2001). The unique situation of Galapagos, with converging tropical, temperate and upwelling water masses, lends

insight into how communities persist at small spatial scales in the face of stress exerted by large ENSO and Pacific Decadal Oscillations. A combination of the strong biophysical gradients that exist over 100 km scales in the GMR, extremes at <1 km scale of cold upwelling and heated tidal bay “pockets”, and the very dynamic nature of incident currents intersecting the bathymetry, would support recruitment from neighbouring coral “hotspots” within and outside the GMR. Settling sites may shift as depth, light, temperature, sedimentation and chemical conditions change. Temperature differentials might allow pockets of fragmented reef to persist as cool-water refuges in the tropics in the event of climate change. Frequent ENSO-driven changes in the oceanographic regime (McClanahan *et al.* 2007), regularly pushing populations to their upper and lower temperature and thermal shock tolerances, may also select for more resilient colonies.

In addition to extensive coral bleaching through strong warming events, as observed towards the end of this study, regular cold upwelling may have depth-specific and coral-species-specific effects. This upwelling dynamic moderated by the tidal cycle interacts with larger internal wave oscillations across the Pacific during La Niña conditions. It is not uncommon for an almost vertical thermocline of 14–18°C deep water to pass inshore up over the reef and mix with and displace the 24–28°C surface layer. February–May 2007 marked the end of a moderate El Niño and an abrupt transition to upwelled cold water, with extensive bleaching of *Porites lobata* and *Pocillopora* species at 15–20 m, and graduated bleaching towards the shallows. *Pavona gigantea* and *P. clavus* appeared largely unaffected yet showed some bleaching at greater depths. Clearly cold-water shock is as important in determining coral health as warm-water bleaching for some species.

Globally, coral reef decline is considered a crisis (Bellwood *et al.* 2004). Galapagos coral reef systems are clearly very sensitive to short-term damage, with limited distributions and slow recovery rates. They are susceptible to climatic change and trophic cascade effects as a response to over-fishing (such as bio-erosion by urchins and over-grazing by corallivores).

CONCLUSION

The between-site comparison of coral habitat presented here can be used as part of an indicator system to follow recovery or decline of one of the most endangered marine habitat types in Galapagos. Future monitoring should help determine reef resilience and ability to resist degradation in the face of natural and human-induced disturbance.

Managers and the tourism industry have begun to adopt such information and to work to mitigate increased human impacts. Possible measures include restricting anchorages to certain sites, regulating marine visitation and installing low-impact fixed moorings, which would

prevent at least 400 anchors being deployed per year in Darwin Island alone. Climatic evidence and recent IUCN red-listing (IPCC 2007, Carpenter *et al.* 2008) suggest that coral stress due to ENSO and climate change will increase greatly in the next 20–100 years. Measures that reduce human impact will likely play important roles in determining regional coral reef survival.

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