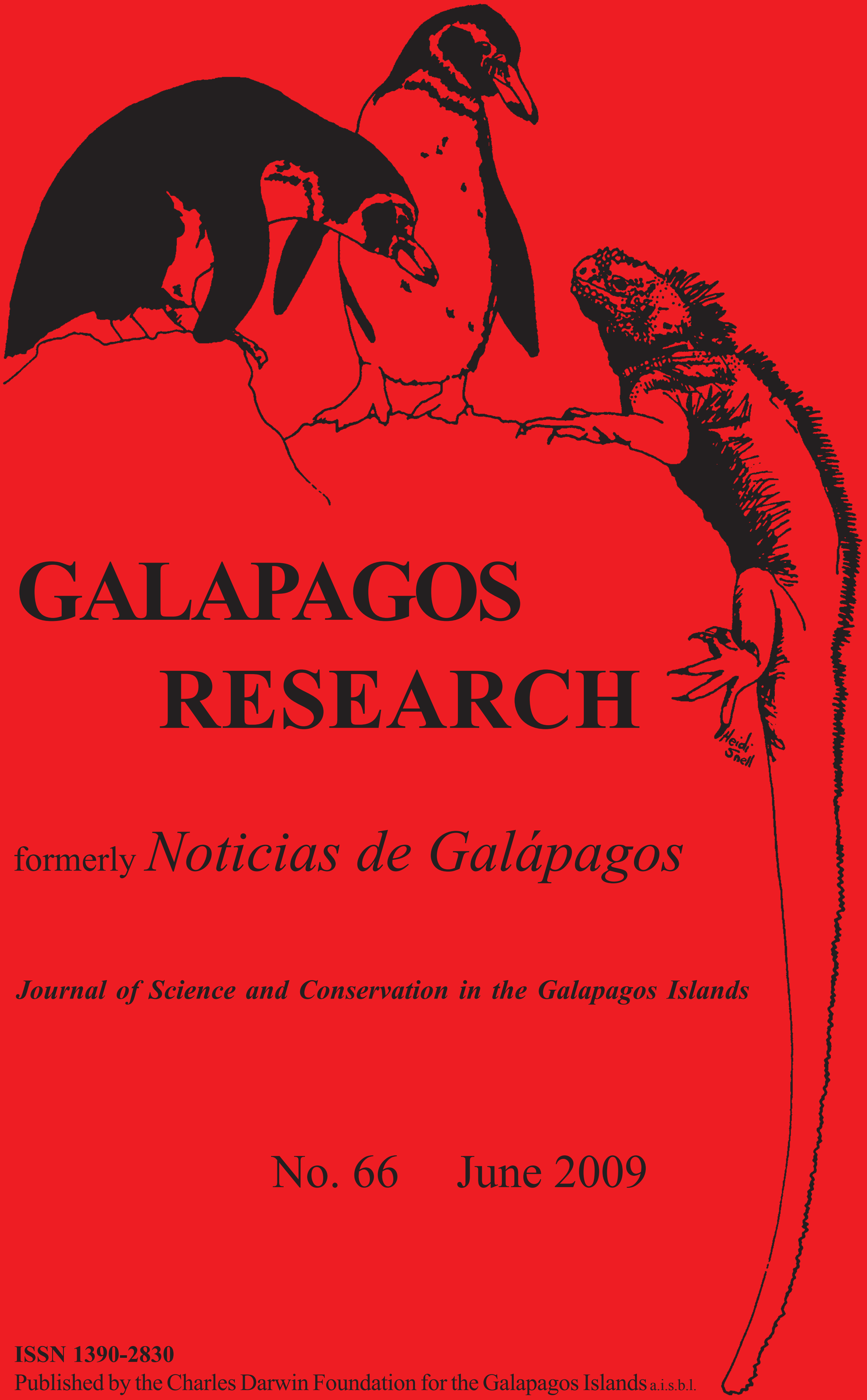


GALAPAGOS RESEARCH

formerly *Noticias de Galápagos*

Journal of Science and Conservation in the Galapagos Islands

No. 66 June 2009

ISSN 1390-2830
Published by the Charles Darwin Foundation for the Galapagos Islands a.i.s.b.l.

FUNDACIÓN CHARLES DARWIN PARA LAS ISLAS GALÁPAGOS
CHARLES DARWIN FOUNDATION FOR THE GALAPAGOS ISLANDS
FONDATION CHARLES DARWIN POUR LES ILES GALAPAGOS

Puerto Ayora, Isla Santa Cruz, Galápagos, Ecuador
AP 17-01-3891, Quito, Ecuador
cdrs@fcdarwin.org.ec www.darwinfoundation.org

INFORMATION FOR SUPPORTERS

The Charles Darwin Foundation for the Galapagos Islands (CDF) is an "*association internationale sans but lucrative*" (international non-profit organisation) registered under Belgian law. It is supported by national and international institutions but remains dependent on the generosity of individuals for the funds needed to finance its programmes. Funds go to work for science, conservation, and education in the Islands.

To contribute to CDF or to offer your support, please contact: Charles Darwin Foundation, Department of Information & Development, Puerto Ayora, Galapagos. Email: <cdrs@fcdarwin.org.ec>. Tel: +593 (0)5 2526146. PAYPAL online: <http://www.darwinfoundation.org/en/get-involved/donate-now>. Website: <www.darwinfoundation.org>. Contributions may also be sent to any of the following "Friends of Galapagos" organisations (FOGOs), independent non-profit organisations that support CDF by raising funds worldwide. It is easy to join a FOGO, and they will make sure that you get the most of your investment, keeping you up to date on what is happening in Galapagos and how your contribution is helping. Friends of Galapagos may also elect to receive *Galapagos Research* for no extra cost. Depending on relevant laws in each FOGO country, FOGOs may offer tax deductibility or other ways of increasing the value of your donation. The FOGOs are:

Canada:
Charles Darwin Foundation of Canada, 55 Avenue Road,
Suite 2250, Toronto, ON M5L 3L2.
Email: <garrett@lomltd.co>. Tel/fax: +1 416 964 4400.

Germany:
Zoologische Gesellschaft Frankfurt, Alfred-Brehm Platz 16,
D-60316 Frankfurt a.M. Web: <www.zgf.de>.
Email: <info@zgf.de>. Tel: +49 (0)69 9434460.

Japan:
Japan Association for Galapagos, Kita-Aoyama 3-15-13-403,
Minato-ku, Tokyo 107-0061. Web: <www.j-galapagos.org>.
Email: info@j-galapagos.org. Tel: +81 70 6429 4770.

Luxembourg:
The Galapagos Darwin Trust, Banque Internationale à
Luxembourg, 2 Boulevard Royal, L-2953 Luxembourg.
Donations marked "for Galapagos" may be made to
Account 1-100/9071.

Netherlands:
Stichting Vrienden van de Galapagos Eilanden, Binnenweg
44, 6955 AZ Ellecom. Web: <www.galapagos.nl>.
Email: <fin.galapagos@planet.nl>. Tel: +31 313 421940.

New Zealand:
Friends of Galapagos New Zealand, PO Box 11-639,
Wellington. Web: <www.galapagos.org.nz>.
Email: <info@galapagos.org.nz>. Tel/fax: +64 4 476 3241.

Nordic countries:
Nordic Friends of Galapagos, Korkeasaari, 00570 Helsinki,
Finland. Web: <www.galapagosnordic.org>.
Email: <k.kumenius@kolumbus.fi>. Tel: +358 50 5644279.

Switzerland:
Freunde der Galapagos Inseln (CH), c/o Zoo Zürich,
Zürichbergstr. 221, CH-8044 Zürich. Web: <www.galapagos-ch.org>. Email: <galapagos@zoo.ch>. Tel: +41 (0) 1 254 2670.

United Kingdom:
Galapagos Conservation Trust, 5 Derby Street, London W1Y
7AB. Web: <www.savegalapagos.org>.
Email: <gct@gct.org>. Tel: +44 (0)207 629 5049.

United States of America:
Galapagos Conservancy, 407 North Washington Street,
Suite 105, Falls Church, Virginia 22046, U.S.A.
Web: <www.galapagos.org>.
Email: <comments@galapagos.org>. Tel: +1 703 538 6833.

We express our grateful appreciation to all those supporters whose generosity has made it possible to achieve so much for the conservation of Galapagos.

GALAPAGOS RESEARCH (formerly *Noticias de Galápagos*)

Journal of Science and Conservation in the Galapagos Islands

Published by the Charles Darwin Foundation for the Galapagos Islands, an international organization created under the auspices of the Government of Ecuador, UNESCO and the International Union for Conservation of Nature (IUCN).

Number 66 June 2009

CONTENTS

GUEST EDITORIAL

RESEARCH ARTICLES

GALAPAGOS COMMENTARY

***Galapagos Research* (formerly *Noticias de Galápagos*)** is the research journal of the Charles Darwin Foundation for the Galapagos Islands. Back issues are available for purchase, and all except the most recent may be found online at: http://www.darwinfoundation.org/en/library/pubs/gal-research.

Information for subscribers: Please contact the Charles Darwin Foundation <cdrs@fcdarwin.org.ec> or your local Friends of Galapagos organisation with questions about subscriptions (addresses inside front cover). Annual or lifetime individual, and annual institutional subscriptions are available. *Galapagos Research* is sent free to current Friends of Galapagos, on request to their Friends of Galapagos organisation.

Information for authors: Manuscripts for consideration for publication in *Galapagos Research* should be submitted to the Editor (addresses below). Instructions for Authors are inside the back cover and online at: http://www.darwinfoundation.org/en/library/pubs/gal-research/instructions.

Editor: Dr Alan Tye
Postal address: SPREP, PO Box 240, Apia, Samoa
Email: galapagosresearch@fcdarwin.org.ec

Back cover map: Tom Giermakowski & Howard Snell (University of New Mexico)

The work presented in this special edition of *Galapagos Research* was supported by the U.K.'s Darwin Initiative grant 14-048 entitled *Galapagos Coral Conservation: Impact Mitigation, Mapping and Monitoring* and implemented through a collaborative effort between the Charles Darwin Foundation, Conservation International and the Universities of Edinburgh and Southampton.

These institutions are grateful to the Galapagos National Park Service for supporting this work, to the Darwin Initiative for funding it, and to Galapagos fishermen, guides and tour operators for participating in workshops and field activities.

We hope and expect that the Galapagos Marine Reserve will benefit from this research and cooperation

GUEST EDITORIAL

GALAPAGOS CORAL CONSERVATION: IMPACT MITIGATION, MAPPING AND MONITORING

By: T.P. Dawson[1], S.J. Henderson[2] & S. Banks[3]

[1]School of Geography, University of Southampton, Highfield, Southampton SO17 1BJ, U.K.
<t.p.dawson@soton.ac.uk>
[2]Conservation International, Puerto Ayora, Santa Cruz Island, Galapagos, Ecuador
[3]Charles Darwin Foundation, Charles Darwin Research Station,
Puerto Ayora, Santa Cruz Island, Galapagos, Ecuador

This special edition of Galapagos Research is devoted to research outcomes from the U.K. Government's Darwin Initiative project 14-048 entitled *Galapagos Coral Conservation: Impact Mitigation, Mapping and Monitoring*. The Darwin Initiative was established in 1992, to assist countries rich in biodiversity but poor in resources to meet their obligations under the Convention on Biological Diversity (CBD). Projects supported from Darwin Initiative funding link U.K. institutions with public and voluntary sector institutions in partner countries.

Marine and Coastal biodiversity is a major thematic programme within the CBD, since 1995. Coral reefs provide significant ecological services and social, economic and environmental benefits to society, including storm protection, fisheries production, erosion control and the cycling of carbon, nutrients and sediments, as well as biodiversity resources and tourism opportunities (MEA 2005). Global climate change is identified as one of five major impacts on coral reefs. Although degradation resulting from direct human impacts, including overfishing and coastal development, is the primary problem in some regions (*e.g*. Caribbean), the increasing number and severity of coral bleaching events induced by climate change is a major cause of concern (Fig. 1). Hermatypic (reef building) corals are sensitive to elevated temperatures, which have been linked to coral bleaching (loss of symbiotic zooxanthellae), with many studies reporting significant decline and mortality of corals during El Niño events (Stone *et al*. 1999).

As a result, the seventh meeting of the Conference of the Parties (COP-7) to the CBD in 2004 revised the work plan on coral bleaching to make it increasingly oriented towards management action and strategies to support reef resilience, rehabilitation and recovery (CBD 2004). The amendments to the plan recognize the need to manage coral reefs for resistance and resilience to, and recovery from, episodes of raised sea temperatures and/or coral bleaching, including taking such factors into account in marine protected area network design. One of the goals of the Marine and Coastal Protected Areas programme is the establishment and maintenance of protected areas that are effectively managed using an ecosystems approach and that contribute to a global network of marine and coastal protected areas.

The coral reefs of the Galapagos Islands contribute significantly to species richness and diversity in the Galapagos Marine Reserve (GMR). They support thousands of species, including many rare and endemic corals. However, their distribution has been strongly affected by extreme climatic events over the last 30 years, especially El Niño events where extensive coral reefs were reduced by 95% in 1982–3, with further mortality in 1997–8. Following these losses, the northern islands of Wolf and Darwin harbour > 95% of the coral species in the GMR including rare corals (*e.g*. *Leptoseris* sp.) that may become locally and indeed globally extinct, and demand special conservation attention.

In fact, their importance as part of Ecuador's natural heritage seems disproportionate to their size. The coral reef fringe in Wolf and Darwin represents a tiny fraction (*c*. 0.9 %) of the overall shallow (<20 m) Galapagos coastal habitat, yet its ecological contribution as a distinguishing biogeographic subunit is considerable. These productive oceanic pinnacles surrounded by the deep abyssal plain and largely low-productivity, blue-water "deserts" are potential stepping stones for many transitory Indo-Pacific, Panamic and circumtropical species uncommon in the rest of the islands. The unique confluence of currents that connect within the archipelago and between other neighbouring marine protected areas such as Cocos Island (Costa Rica) and Malpelo (Colombia) may well connect refuge habitats afforded to coral reef communities. In addition, these reef ecosystems are major pelagic species hotspots with remarkable aggregations of sharks, tuna,

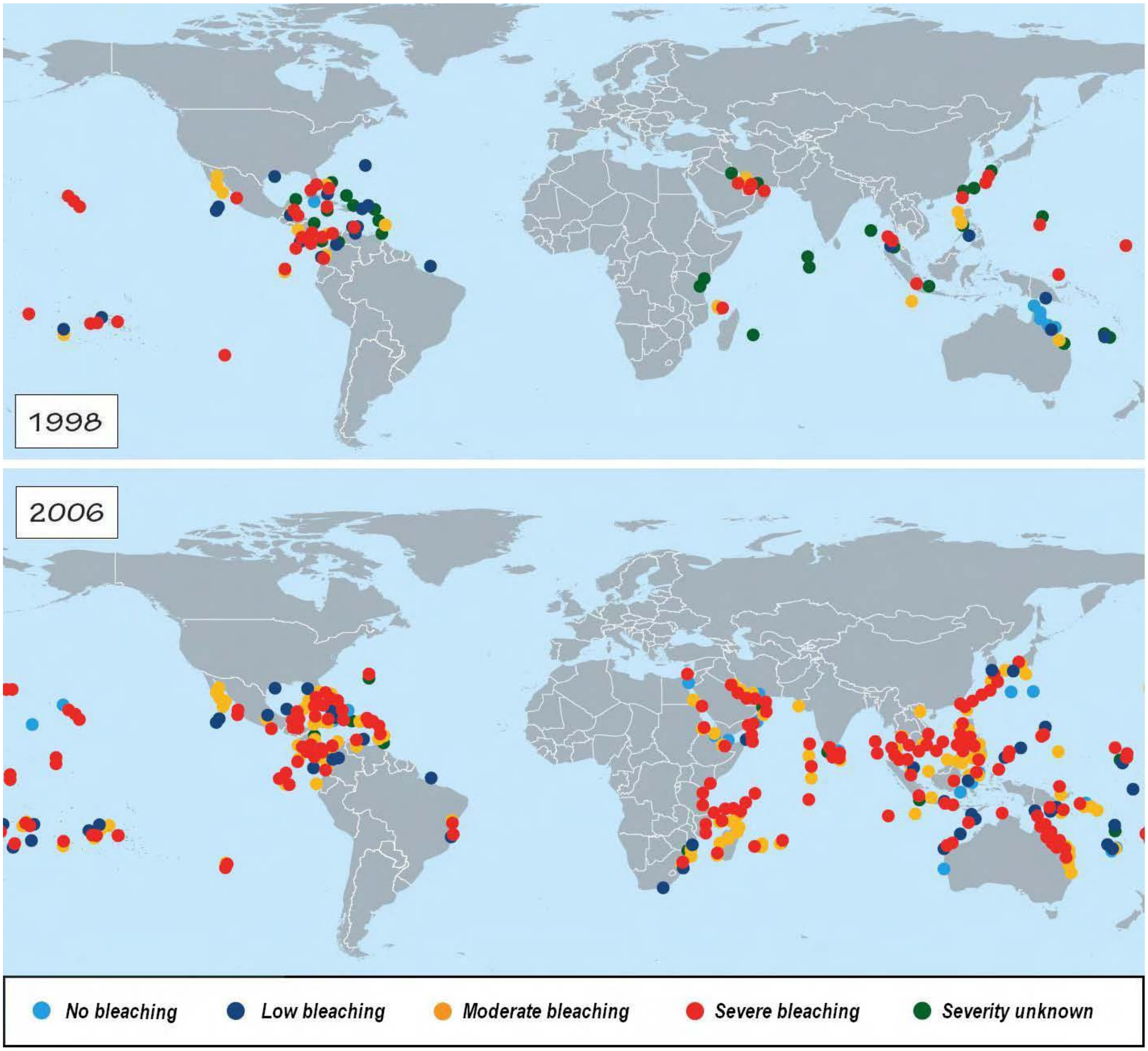


Figure 1. Global trends in the extent and severity of mass coral bleaching, 1998–2006 (adapted from Marshall & Schuttenberg 2006).

turtles, dolphins and other cetaceans, all ecologically linked to the area's reef complexes.

The economic value of the local live-aboard dive tourism industry attracted by such a fascinating natural seascape is considerable. Two sites in Wolf and Darwin accounted for more than half of the registered dives in 2007 across Galapagos. This raises urgent questions as to what represents an appropriate level of use and how best to mitigate adverse effects, such as anchor damage. The Galapagos National Park Service (GNPS) views this with concern and has embraced the concept of low-impact anchorages which was developed within this Darwin Initiative project. With strong industrial fishing pressure across adjacent unprotected regions, it would seem common sense to prioritise conservation measures across such small yet clearly vital, productive oases for tropical marine life.

The purpose of this project was therefore to assist the Ecuadorian Government, through the Galapagos National Park, in protecting the last remaining extensive Galapagos coral reefs of the northern islands as a crucial step to helping Ecuador meet its obligations under the CBD. This was achieved through the following outputs:

1. improved baseline knowledge of coral reefs and associated biodiversity of the northern GMR;
2. reduced coral damage due to the installation and establishment of permanent boat moorings;
3. training, workshops and other capacity-building exercises, to increase the knowledge of the stakeholders participating in coral monitoring and conservation.

Great advances in regional coral research from the early 1970s were led by key figures including many of the participants in this project and authors of papers in this issue. However, the present project constitutes the most comprehensive study using innovative mapping and rapid assessment techniques undertaken to date in the remote northern Galapagos islands. It has helped put important historical observations and the large body of recent field research into the context of pressing contemporary management issues. The papers in this special issue report on the outcomes and analysis of coral survey and monitoring expeditions conducted over the period 2005–7, as well as providing some updated review material. The project has brought input from a large number of international and local marine and coral scientists, including from other regional marine protected areas, and Charles Darwin Research Station scientists, to address the particular conservation challenge faced by Wolf and Darwin Islands. The project has discovered new species both to science and to Galapagos, including zooanthid species from the genera *Hydrozoanthus*, *Parazoanthus, Antipathozoanthus* and possibly *Epizoanthus*, although the latter may be an entirely new genus as yet undescribed. Other reef-building corals have been identified, which are new to Galapagos, including *Pocillopora effusus*, *P. inflata*, and *Pavona chiriquiensis*. In addition, a possible new gorgonian of the genus *Pacifigorgia* (*Octocorallia: Gorgoniidae*) species has been collected, together with a new reef-building coral, *Leptoseris* sp. All collections are currently being prepared for systematic morphological and molecular analyses. Further scientific publications are anticipated.

In addition to the establishment of comprehensive baseline biodiversity data sets, the project engaged the fishing and tourism industries for improved management of the marine environment through capacity-building of tourism and dive guides and fishers, and established permanent mooring buoys to avoid boat anchor damage.

Responsible stewardship of such a fascinating natural resource demands a combination of objective science-based recommendations with clear outreach, training and well-informed actions such as impact mitigation methods, plus the establishment of policies, such as zoning rules, that regulate uses, diving practices and sustainable fishing codes. A previous Darwin Initiative marine project (no. 162/6/174, 1997–2000) supported crucial early decisions to determine no-take zones and tourism and fishing practices. These moves were motivated by the goal of achieving UNESCO World Heritage status for Galapagos marine areas to complement this status for terrestrial areas, through establishing sound management practices, and resulting in the declaration of the GMR in 1998. A first biodiversity catalogue helped underpin discussions leading to a marine management plan. A decade later, the contributions in this volume improve our knowledge and appreciation of the value and current condition of the Galapagos's northerly coral communities and establish conservation measures and stakeholder commitments to protect these valuable habitats. This step forward demonstrates how relatively modest external aid can empower applied marine research and lead to management policy. Such results of research for conservation support the GNPS as it navigates the changeable, often difficult seascape in search of the holy grail of sustainable development. Such steps are critical if natural ecosystem function is to be conserved to maintain Galapagos's intrinsic value and contribution to the wellbeing of future generations.

LITERATURE CITED

CBD. 2004. *Decisions adopted by the Conference of the Parties to the Convention on Biological Diversity at its seventh meeting* (UNEP/CBD/COP/7/21/Part 2), Decision VII/30.

Marshall, P. & Schuttenberg, H. 2006. *A Reef Manager's Guide to Coral Bleaching*. Great Barrier Reef Marine Park Authority, Townsville.

MEA. 2005. *Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington DC.

Stone, L., Huppert, A., Rajagopalan, B. Bhasin, H. & Loya, Y. 1999. Mass coral bleaching: a recent outcome of increased El Niño activity? *Ecology Letters* 2: 325–330.

RESEARCH ARTICLES

RAPID RECOVERY OF A CORAL REEF AT DARWIN ISLAND, GALAPAGOS ISLANDS

Peter W. Glynn[1], Bernhard Riegl[2], Adrienne M.S. Correa[3] & Iliana B. Baums[4]

[1]Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, U.S.A.
<pglynn@rsmas.miami.edu>
[2]National Coral Reef Institute, Oceanographic Center, Nova Southeast University, U.S.A.
[3]Department of Ecology, Evolution and Environmental Biology, Columbia University, U.S.A.
[4]Department of Biology, The Pennsylvania State University, U.S.A.

SUMMARY

Surveys at Darwin Island in 2006 and 2007 have demonstrated that this northernmost Galapagos Islands coral reef has recovered significantly since the 1982–3 El Niño event. When first surveyed in 1975, this structural reef exhibited actively accreting frameworks of pocilloporid and poritid corals. The coral suffered severe mortality in 1983, resulting in the near total loss of pocilloporids and extensive partial mortality of poritid corals. Large sections of the reef had not recovered by 1992 and dead frameworks were subject to bio-erosion, although small numbers of sexual recruits of pocilloporid corals and numerous recruits plus regenerating patches of *Porites lobata* were present in some areas. An increase in live coral cover and recruitment was apparent through 2000 and 2002. Recent sampling at three sites along the reef has demonstrated mean (± 1 SD) live coral cover of 21.9 ± 1.7 % with *P. lobata* as the predominant species. *Pocillopora* spp. were present, but not so abundant as in earlier surveys. In spite of moderate erosion by echinoid and fish grazers, much of the original coral framework remained intact, providing a substrate for coral regeneration and recruitment. Recovery can be attributed to the original reef structure remaining intact, asexual regrowth of surviving tissues and sexual recruitment of poritid corals from surviving source populations.

RESÚMEN

Recuperación rápida de un arrecife de coral en la Isla Darwin, Islas Galápagos. Investigaciones en la Isla Darwin en 2006 y 2007 han demostrado que en esta isla, la más al norte del archipiélago de las Galápagos, los arrecifes de coral se han recuperado de una manera significativa desde el advenimiento del fenómeno de El Niño de 1982–3. Cuando se realizaron las primeras observaciones en 1975, este arrecife mostraba crecimiento activo de corales, especialmente de las familias Pocilloporidae y Poritidae. En 1983 los corales sufrieron mortandad severa lo que resultó en la pérdida casi absoluta de pocilopóridos y una mortandad generalizada de los porítidos. Grandes porciones del arrecife aún no se habían recuperado en 1992, y las estructuras coralinas muertas habían sido afectadas por la bio-erosión, aun que un número pequeño de reclutas sexuales de corales pocilopóridos y numerosos reclutas y parches regenerativos de *Porites lobata* se avistaron en algunas áreas. La recuperación continuó en marcha tanto en el 2000 como en el 2002. Recientemente, muestreos llevados a cabo en tres localidades a lo largo del arrecife han demostrado un promedio (± 1 DE) de cobertura de coral vivo de 21,9 ± 1,7 % y una dominancia de *P. lobata. Pocillopora* spp. estaban presentes, pero no tan abundantes como en muestreos anteriores. A pesar de erosión ocasionados por erizos y peces, la mayoría de la estructura coralina permaneció intacta y esto ha proporcionado un sustrato para la regeneración del coral y el reclutamiento. La recuperación se puede atribuir a que la estructura coralina ha permanecido intacta, el crecimiento asexual del tejido sobreviviente, y el reclutamiento sexual de los corales porítidos provenientes de las poblaciones sobrevivientes de coral.

INTRODUCTION

The resistance and resilience of member species influence the recovery of biotic communities affected by disturbances. Community resistance, the ability to avoid displacement by alternate species assemblages, is greater if member species can withstand perturbations. Resilience, the ability of a community to recover from a

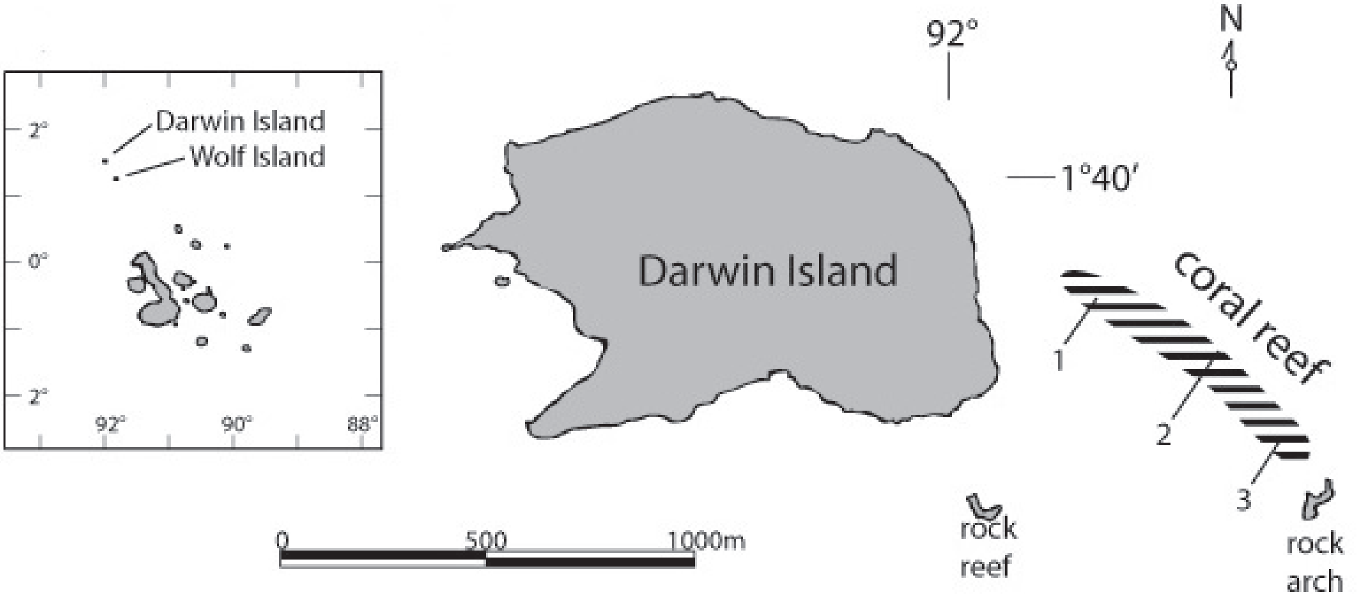


Figure 1. Location of Darwin and Wolf Islands in the Galapagos Archipelago, and approximate position of the Darwin Island coral reef and sampling sites.

disturbance, is enhanced by species that can quickly re-establish populations to pre-disturbance levels. In E Pacific reef-building coral communities, certain species can survive periods of elevated temperature anomalies (*e.g. Porites lobata* and *Pavona clavus*), and others colonize communities through sexual recruitment after such disturbances (*e.g. Pocillopora* spp. and *Psammocora stellata*). Related to resilience is the availability of surviving source populations that can supply propagules capable of recruiting to degraded communities. This study centers on these aspects of community dynamics, focusing on a Darwin Island coral reef that was seriously degraded by sea warming episodes during the past two decades.

Like many coral reef ecosystems worldwide (*e.g.* Hoegh-Guldberg 1999, Gardener *et al.* 2003, Bellwood *et al.* 2004, Wilkinson 2004), the coral reefs of the Galapagos Islands have suffered severe declines since the early 1980s (Robinson 1985, Glynn 1994, Wellington & Glynn 2007). The 1982–3 El Niño event was accompanied by high sea temperatures that caused extensive coral bleaching (loss of symbiotic zooxanthella photobionts and their photosynthetic pigments) and mortality throughout the archipelago (Robinson 1985, Glynn 1990). The objectives of this study are to describe the location, geomorphology and coral species composition of the Darwin Island coral reef, and to assess its recovery over the 25 years following the 1982–3 El Niño disturbance.

MATERIALS AND METHODS

Darwin or Culpepper Island is centered at 1°39′20′′N, 92° 0′30′′W. A structural coral reef is located on the insular shelf at 8–18 m depth, with its long axis trending NW–SE between the island's east shore and Darwin's rock arch (Fig. 1). The reef was surveyed in 1975, but only briefly described (Glynn & Wellington, 1983). Subsequent surveys were conducted on 26 Mar 1992, 18 Aug 2000, 18 May 2002, and 21–23 May 2006. More recently, the extent of the reef and quantitative sampling of the epibenthic cover along its length were initiated on 6 and 7 Mar 2007. The location of the reef and sampling sites were determined from a Quickbird satellite image with 2.4 m multispectral resolution, taken on 25 Feb 2005, and hand-held differential Global Positioning System (GPS) fixes (*c.* 5 m precision) at various positions along the reef. From this image, we obtained the reef's general outline.

Dead coral framework heights were measured in 1992, 2000 and 2007 to determine the extent of erosion following the 1982–3 El Niño disturbance. This was accomplished by two divers, one holding a weighted tape measure at the summit of a formation and the other sighting and signaling the horizontal elevation from the adjacent sand plain. Framework formations adjacent to the reef floor or with skeletal shafts leading to the reef base were selected for measurement. Sampling was biased toward the higher framework elevations.

Live coral cover was quantified in 2007 from 10 photographs of 0.25 m^2 quadrats laid at predetermined random locations along each of 15, 10 m length transects. Three sets of 5 transects, each running perpendicular to the long axis of the reef and separated by 5 m, were completed at sites 1, 2 and 3 (Fig. 1).

During the reef surveys in 2000 and 2007, the height and diameter of *Porites lobata* Dana colonies first encountered at sampling sites 1 (2000) and 1–3 (2007) (Fig. 1) were measured, and percentage estimates of the live and dead surface areas of each colony were recorded. The dead areas were further classified as "old dead" (OD) and "new dead" (ND), where OD were defined as dead patches serving as substrates for large barnacles, azooxanthellate corals and/or thick crusts of coralline algae, with skeleton highly eroded, and ND were dead patches overgrown by filamentous algae and/or thin crusts of coralline algae, with skeleton not highly eroded and fine structure of calices still visible.

During the 2006 survey, tissues from *Porites lobata* and its endosymbiotic algae (*Symbiodinium* spp.) were collected from 15 colonies at Darwin and Wolf (Wenman) Islands (Fig. 1). Samples were collected from the upper surfaces of colonies and fixed in 95 % ethanol. DNA was extracted using an organic protocol (Rowan & Powers 1991, Baker *et al*. 1997), and the Internal Transcribed Spacer region 2 (ITS-2) was amplified using primers designed by LaJeunesse & Trench (2000). Distinct amplicons within the reaction products of each sample were then separated using Denaturing Gradient Gel Electrophoresis (DGGE) on a 35–75 % gradient gel according to the general methods described by LaJeunesse (2002). Individual bands were excised from DGGE gels, the DNA was extracted and reamplified, and the PCR products were directly sequenced using the BigDye terminator method and an automated DNA sequencer (Applied Biosystems 3730xl). Edited sequences were then identified by BLAST searches in GenBank (http://www.ncbi.nlm.nih.gov/BLAST/).

RESULTS

The estimated length of Darwin reef is *c.* 700 m, with the westernmost terminus located *c.* 225 m off Darwin Island's east shore at *c.* 10 m depth (Fig. 1). In its eastward extension, the reef bends gradually toward the southeast and ends *c.* 100 m from Darwin's rock arch at 18 m depth. At its center, the reef is *c.* 90 m wide. Calcareous sand flanks both the shallow shelf and deeper (N–NE) sides of the reef. A large fraction of the coral rubble on the reef floor and in off-reef sediments consists of pocilloporid branches commonly ranging from 10–20 cm in length.

Eleven zooxanthellate coral species were observed on the reef: *Porites lobata*, *Pavona clavus* Dana, *Pavona gigantea* Verrill, *Pavona chiriquiensis* Glynn, Maté & Stemann, *Pavona varians* Verrill, *Pocillopora elegans* Dana, *Pocillopora damicornis* (Linnaeus), *Pocillopora eydouxi* Milne-Edwards & Haime, *Pocillopora meandrina* Dana, *Pocillopora* sp., and *Psammocora stellata* (Verrill). *Tubastrea coccinea* Lesson, an azooxanthellate species, was also present and common on exposed reef substrates. Crustose coralline algae, turf algae and leathery macroalgal crusts covered most of the reef substrate not occupied by scleractinian corals. Other noticeable epifaunal species nearly always present in Galapagos coral reef communities included the echinoid bio-eroders *Diadema mexicanum* A. Agassiz and *Eucidaris galapagensis* Döderlein, and the acorn barnacle *Megabalanus peninsularis* (Pilsbry), a competitor for space on dead and live coral skeletons. The Guineafowl Puffer *Arothron meleagris* (Bloch & Schneider) was a common obligate corallivore and Yelloweye Filefish *Cantherhinus dumerilii* (Hollard), another corallivore, was also present. *Acanthaster planci* (Linnaeus) was sometimes observed feeding on coral during our surveys. However, it has been seen only at Darwin Island.

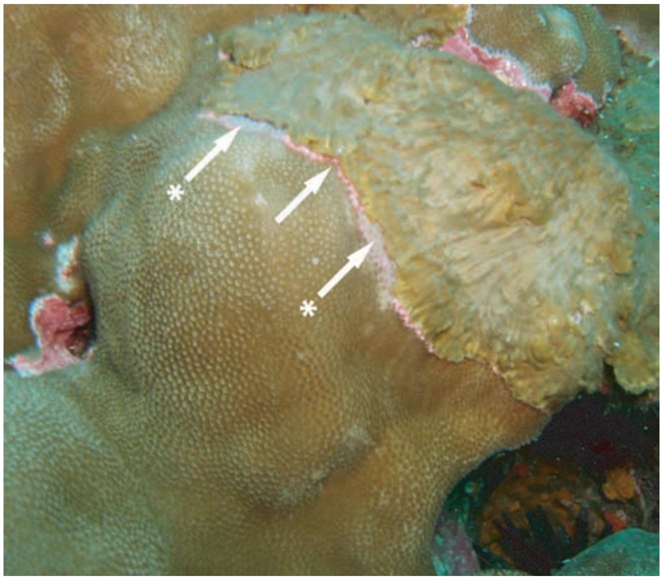


Figure 2. *Peyssonnelia boergesenii* Weber-van Bosse, an encrusting brown alga apparently overgrowing live *Porites lobata* tissues. Arrows point to the coral-algal interface. * = pink margin between coral tissue and alga. Diameter of alga *c.* 20 cm. Darwin reef, 12 m depth, 6 Mar 2007.

Several interphyletic species interactions were observed. *Peyssonnelia boergesenii* Weber-van Bosse, a brown macroalgal crust, commonly occurred and evidently grew over the living tissues of *Porites lobata* (Fig. 2). The coral skeletons underlying the alga were recently dead and retained their detailed structure, suggesting recent overgrowth by the alga. Pink pustules along the peripheral growing edges and neoplasms were also commonly seen on poritid colonies. *Megabalanus peninsularis* occurred in patches on many of the larger live colonies of *P. lobata* (Fig. 3). The rasping scars of echinoids were prominent, but generally on dead algal-covered substrates and not live corals. The puffer and filefish were both observed biting off pieces (0.5–1.0 cm) of live *P. lobata*.

Many colonies of zooxanthellate coral species exhibited mild to moderate bleaching in deeper and cooler waters on Darwin reef, other sites around Darwin Island and at Wolf Island (about 40 km SE of Darwin Island). The species exhibiting bleaching at 10–15 m were *Porites lobata*, *Pocillopora* spp., *Pavona clavus* and *P. gigantea*. This bleaching was first observed in early March 2007 during a cold shock event of upwelled water following slightly elevated and protracted temperatures from a moderate El Niño up to March. There was a 12ºC decline (28º to 16ºC) at 15 m depth over a six-day period at the end of February, and another cold event of similar magnitude in May (S. Banks pers. comm.).

Mean poritid reef framework structures ranged in height from 1.97 m in 2007 to 3.67 m in 2000 (Table 1). Due

Table 1. Dead *Porites lobata* framework heights in four years on the western sector (near site 1) of Darwin Island coral reef. Measurements are in meters and biased toward the higher elevations encountered in the sampling areas.

Year	N	Range	Mean (SE)
1992	5	1.8–3.4	2.46 (0.32)
2000	3	2.0–5.0	3.67 (0.88)
2006	6	1.0–4.0	2.73 (0.44)
2007	15	1.0–2.7	1.97 (0.12)

to small sample sizes and inconsistent interannual site sampling, it is not possible to test for temporal changes. However, these data indicate that, although the tallest structures seem to have disappeared by 2007, the dead poritid frameworks are largely still intact and have retained much of their relief following two severe El Niño events (1982–3, 1997–8). Pocilloporid coral frameworks, present in 1975, were absent from all surveyed areas. Instead, numerous dead pocilloporid branches were present on the sand bottom among dead standing poritid frameworks and in areas immediately surrounding the reef. The *Pocillopora* spp. colonies observed during surveys from 2000 to 2007 were isolated, not growing in juxtaposition.

Total reef-wide coral cover amounted to 21.1 % in 2007 (Table 2). *Porites lobata* predominated, contributing 19.5 % to the total (Fig. 3). *Pavona clavus*, *Tubastrea coccinea* and *Pocillopora* spp. each contributed < 0.4 % to the total cover. The differences in total coral cover were not significant among transects or sites ($P > 0.05$, F1 = 2.89, F2 = 2.91,

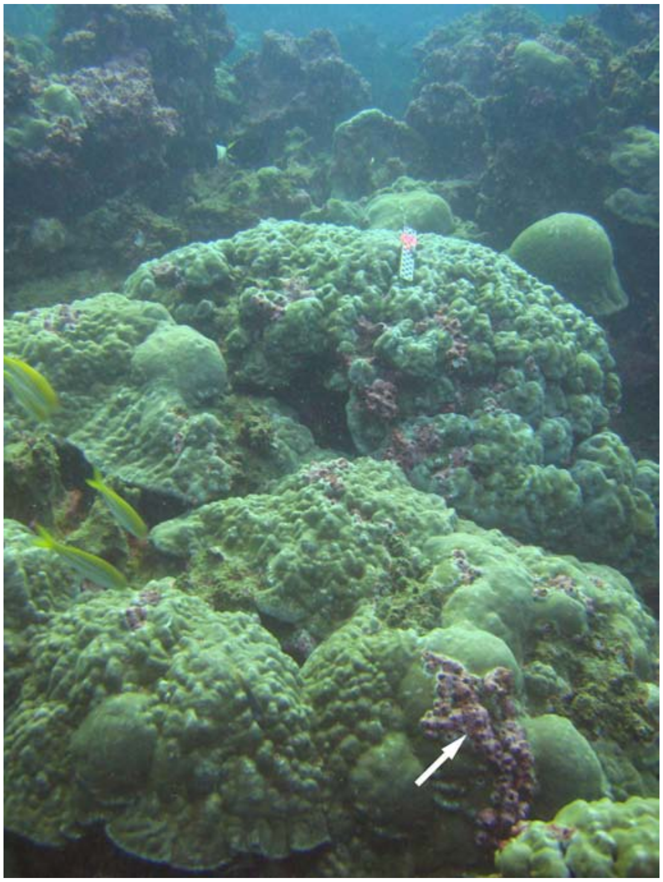


Figure 3. *Porites lobata* colonies that survived the 1982–3 El Niño event. Most colonies are encrusted with patches of the acorn barnacle *Megabalanus peninsularis* (arrow). Scale resting on coral colony in background is 20 cm in length. Darwin reef, 12 m depth, 6 Mar 2007.

Table 2. Live coral cover (% ± 1SD of 0.25 m^2 sample squares) of key species on Darwin Island reef in 2007. S1–3 = sample sites 1–3, Fig. 1; T1–5 = transects 1–5 at each sample site.

	Porites lobata	*Pavona clavus*	*Tubastrea coccinea*	*Pocillopora* spp.	Site mean live cover
S1: T1	18.86 ± 24.73	0	0.35 ± 0.40	0	16.58
T2	20.33 ± 15.42	0	0.10 ± 0.17	0	
T3	8.61 ± 18.53	0	0.86 ± 0.61	0	
T4	17.49 ± 18.64	0	0.51 ± 0.61	0	
T5	15.08 ± 14.30	0	0.74 ± 0.84	0	
S2: T1	13.38 ± 22.36	0	0.86 ± 1.89	3.97 ± 12.57	20.59
T2	8.63 ± 8.18	4.73 ± 14.95	0.11 ± 0.31	0	
T3	24.93 ± 18.66	0	0.20 ± 0.41	0	
T4	33.55 ± 28.41	0	0	0	
T5	11.51 ± 14.11	0	0.70 ± 0.89	0.36 ± 1.15	
S3: T1	35.78 ± 23.77	0	0.06 ± 0.16	0	26.14
T2	7.58 ± 8.16	0	0	0	
T3	21.05 ± 17.49	0	0.06 ± 0.11	0	
T4	47.31 ± 27.74	0	0.18 ± 0.25	0	
T5	18.61 ± 25.03	0	0.03 ± 0.07	0	
				Overall reef mean	**21.10**

Figure 4. Several live *Porites lobata* colonies on eroded colonies killed during the 1982–3 El Niño event. Scale is 20 cm in length. Darwin reef, 12 m depth, 6 Mar 2007.

nested ANOVA). The reef framework consisted of large dead massive *P. lobata* colonies with smaller live colonies affixed to the upper surfaces of the former (Fig. 4). Although it was not possible to identify the species of *Pocillopora* in the phototransects, the majority of the colonies sampled were *P. elegans* and *P. eydouxi*. Pocilloporid species and all other non-poritid zooxanthellate species were more abundant or only observed along the deeper (15–18 m) reef edge.

Mean *Porites lobata* colony sizes, expressed as the heights of the linear skeletal growth axes, demonstrated significant increases ($P = 0.0023$, Mann Whitney U test) from August 2000 to March 2007 (Fig. 5). The incremental increase in the sample colony sizes over the nearly 7-year period was 19.9 cm (54.5 ± 39.1, SD, n = 53, 2007; 34.6 ± 36.1, SD, n = 32, 2000). The size-class distributions in both years contained relatively high proportions of young colonies. Relatively higher proportions of colonies were 35 cm or larger in 2007 compared with the sampled population in 2000. The two colonies in the 91+ cm size class in 2000 had skeletal growth axes of 150 and 160 cm. In 2007, seven colonies were sampled in this largest size class, and two of them had growth axes of 170 and 200 cm.

All but three colonies sampled in 2000 contained dead patches, indicative of a high incidence of partial mortality (Fig. 5, Table 3), while only three colonies in 2007 showed signs of partial mortality. Contrasting the relative ages of these scars, in 2000 78.1 % of colonies exhibited old dead patches, and in 2007 no old dead patches were sampled. The three colonies exhibiting partial mortality (new dead) in 2007 represented only 5.7 % of the sample.

Five unique symbiont band profiles were detected by DGGE analysis within the 15 *Porites lobata* colonies sampled (Fig. 6); three of the profiles contained previously unreported sequences. All *Symbiodinium* identified were members of clade C, with sequences exactly or nearly matching type C15 (at most, three base pairs different). The C15 type and a novel band profile (C15-1) were most common, detected from five and six of the colonies sampled, respectively.

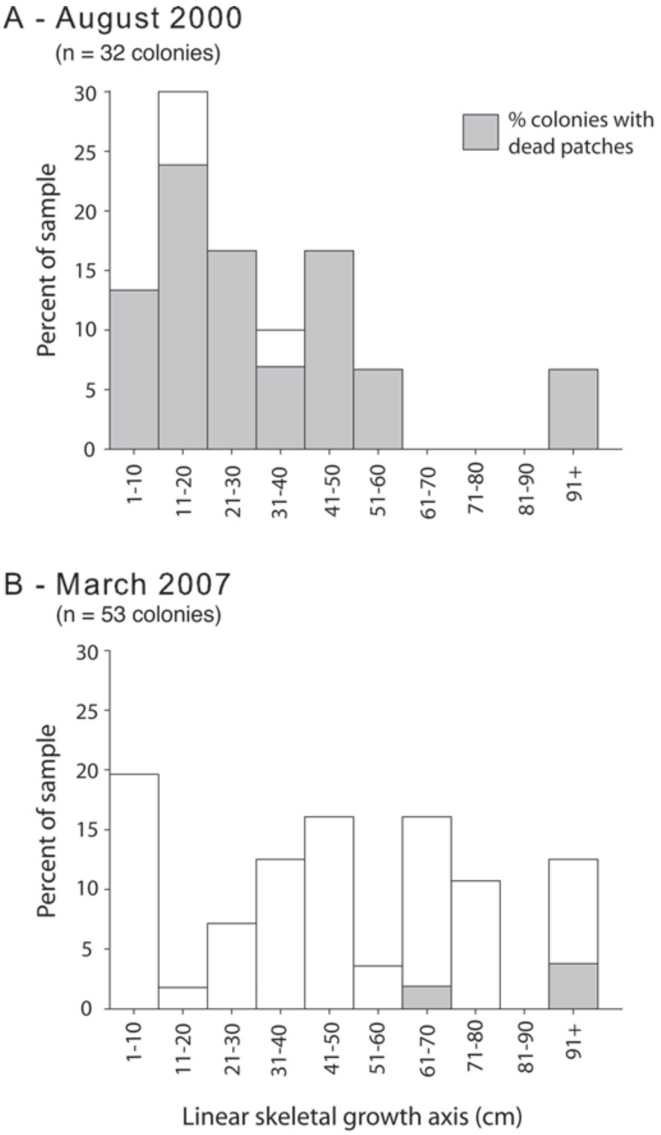


Figure 5. Size-class frequency distributions of the linear skeletal growth axes of *Porites lobata* on Darwin reef in August 2000 and March 2007.

Table 3. Numbers of *Porites lobata* colonies on Darwin reef with old (OD) and new (ND) dead patches sampled in March 2000 and 2007. Because some colonies contained both old and new dead surfaces, the total number of scars may exceed the number of sampled colonies.

		Colony condition		Relative age	
Year	n colonies	No scars	Scars present	OD	ND
2000	32	3	29	25	12
2007	53	50	3	0	3

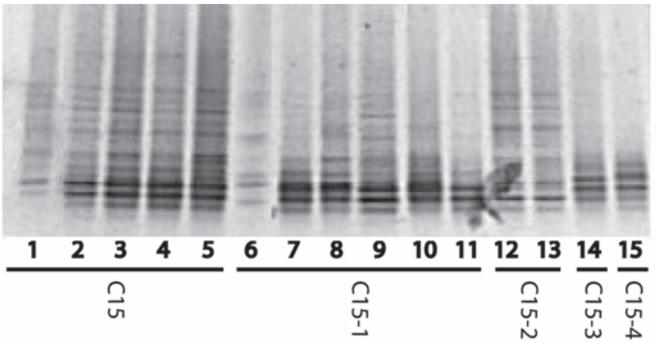


Figure 6. DGGE analysis of the ITS-2 region (285 base pairs) of *Symbiodinium* sampled from *Porites lobata* colonies (numbered 1–15) from Darwin and Wolf Islands in 2006. Sampled colonies containing symbionts with identical band profiles are each grouped by a horizontal bar, with the *Symbiodinium* type (C15 to C15-4) identified from that band profile shown below the bar. Collection depths for each *Symbiodinium* type (C15 to C15-4) were 7–15, 12–20, 11–13, 11 and 6 m, respectively.

DISCUSSION

All coral reefs in the central and southern Galapagos Islands that experienced high mortality (*c.* 95 %) during the 1982–3 El Niño event were further degraded by several years of intense bio-erosion (Glynn 1988, Reaka-Kudla *et al.* 1996). Reef frameworks were converted to rubble and sand by internal and external bio-eroders. Among the latter, *Eucidaris galapagensis* has been the most destructive. It erodes about ten times the mass of coral and coralline algae as *Diadema mexicanum*, and its population density was commonly 15–30 m^{-2} on dead coral substrata (Glynn *et al.* 1988). *Diadema* was present only at low densities (< 1 m^{-2}) on dead reef structures. In contrast, the northern islands of Darwin and Wolf support relatively few *Eucidaris* and higher abundances of *Diadema*. For example, the highest mean abundances were: *Diadema* (sampled at night) 3.5 m^{-2} and *Eucidaris* (day sampling) 0.54 m^{-2} (Bustamante *et al.* 2002). It is highly likely that the intact coral frameworks at Darwin Island owe their existence to the relatively low levels of bio-erosion. In the long term, the persistence and growth of coral reefs depend on the presence of former structures that can support coral regeneration and recruitment. Colgan (1990) attributed the modest reef buildups in the Galapagos Islands to intermittent El Niño-induced bleaching and death, and then the bio-erosion and loss of limestone substrates.

Pocilloporid reef frame bio-erosion was also high in Panamá following the 1982–3 El Niño event (Glynn 1990, Eakin 1996). This was caused chiefly by *Diadema mexicanum*, which dramatically increased in abundance after 1984, from <10 m^{-2} pre-event to 50–90 m^{-2} through the mid-1990s. Since 2000, *Diadema* abundances have declined to <10 m^{-2} (Eakin 2001), and live *Pocillopora* spp. patches are now present on remnant framework substrata. Coral mortality in Panamá was significantly lower following the 1997–8 bleaching event, 13 % compared with 75 % in 1982–3 (Glynn et al. 2001). Reef recovery, *i.e.* an increase in live coral and initiation of framework growth, is presently occurring on many reefs in Panamá (Glynn & Fong 2006).

High abundances of *Tubastrea coccinea* were commonplace on open (upper) reef substrates. This azooxanthellate species is generally cryptic in the E Pacific, occurring on the undersides of massive corals and other stable structures. Even though it contributed little (0.32 %) to the total live cover, hundreds of colonies were present in the photoquadrats. Colonies are typically small, *c.* 3–8 cm in diameter (2–12 polyps). It is possible that the large numbers of *T. coccinea* settled and grew in response to the available habitat space resulting from the high coral mortality in the early 1980s.

In 1975, the west end of Darwin reef, the only reef sector surveyed at that time, consisted of large sections of live pocilloporid frameworks. These were about 1 m in vertical thickness and covered massive pavonid and poritid colonies. No pocilloporid buildups, live or dead, were observed at any of the survey sites in 2006 or 2007. Pocilloporid rubble, however, was scattered over the bottom across the entire reef. Since the chief frame-building species in March 2007 was *Porites lobata*, the reef is presently diminished in terms of its structural diversity. Several sites sampled in the Galapagos Islands during the 1997–8 El Niño event showed *P. lobata* to have lower mortality rates than pocilloporid corals (Glynn *et al.* 2001). Thus, the prominence of *P. lobata* is likely due to its resistance to elevated temperatures and subsequent renewed growth of surviving tissues (Glynn & Fong 2006). In addition, the numerous young colonies (2–10 cm, skeletal growth axis) are indicative of successful recruitment, an attribute of species resilience.

Photophysiological differences between *Symbiodinium* spp. within coral species and individuals contribute to variations in bleaching response (Warner *et al.* 1996, Iglesias-Prieto *et al.* 2004), and this has been linked to symbiont genetic diversity (*e.g.* Berkelmans & Van Oppen 2006, Warner *et al.* 2006). Corals that can flexibly host different symbiont types may therefore be better able to cope with environmental perturbations. Although *Symbiodinium* clades C and D have previously been detected within *Porites lobata* (Baker 1999), only clade C symbionts were detected within the individuals sampled in 2006 from the northern Galapagos Islands. Furthermore, ITS-2 sequence differences between the symbiont band profiles from these colonies are minimal and likely to represent intraspecific variation. Ongoing analysis of additional coral colonies will be useful in understanding *Symbiodinium* spp. distributions within the Galapagos Islands, and how these distributions may influence the persistence and current dominance of *P. lobata* in this region, despite recurrent El Niño bleaching events.

Corallivore feeding scars, caused primarily by the pufferfish *Arothron meleagris* and the filefish *Cantherhinus dumerilli*, were commonplace on *Porites* colonies. The bite scars were usually concentrated along colony ridges or protuberances. The scars ranged from recently bitten to various stages of regeneration. In no instance was a colony entirely consumed. The gastropod *Coralliophila violacea* (Kiener) was also observed grazing on some *Porites* colonies. A single *Acanthaster planci*, a seastar corallivore, has been observed feeding on corals at Darwin Island, but in areas away from the coral reef. *Acanthaster* is rare in the Galapagos region (Glynn 2003). Therefore, corallivore concentration on remnant corals surviving El Niño disturbances or small recruits does not seem to have been an important factor in the recovery of the Darwin Island coral reef. The recovery of coral reefs at Cocos Island, Costa Rica also has not been thwarted by corallivores (Guzman and Cortés 2007).

Based on an analysis of skeletal density bands by X-radiography, the mean elongation rate of *Porites lobata* over a 12-year period at Marchena Island, in the thermally highest sector (Harris's zone 3, see Banks 2002) of the mid-Galapagos Islands region, was 8.9 (± 1.0 SE) mm yr^{-1} (Glynn 1994). Applying this mean growth rate to the modal size class sampled in 2000, colonies in this cohort likely recruited from 22 to 12 years previously, *i.e.* from 1978 to 1988. The largest size class sampled in 2007 consisted of smaller colonies that probably recruited from 11 to *c.* 1 year ago. Since seawater temperatures are generally higher at the northernmost islands of Wolf and Darwin compared to Marchena, with likely commensurately higher growth rates, the skeletal extension rates used here may overestimate the age of coral recruits. Nonetheless, these size classes and the relatively abundant larger and older size classes in both years suggest that the recruitment of *P. lobata* has continued over the past 25 years and longer in spite of severe El Niño events.

The high abundance of colonies with dead patches in 2000 (93.8 %) compared with 2007 (5.7 %) is indicative of the regeneration and healing of surviving coral tissues over this 7-year period. In addition, the proportion of colonies in 2000 with old dead (78.1 %) compared with new dead (37.5 %) scars implies that coral mortality was greater during the 1982–3 than the 1997–8 El Niño event. Indeed, Glynn *et al.* (2001) documented higher mortality rates for *Porites lobata* during the earlier event.

Darwin reef is one of the few coral reefs in the Galapagos that has not lost its structural integrity through bioerosion (Glynn 2003). Its persistence and stability have allowed the regeneration of surviving coral patches and the settlement of coral recruits following recent El Niño disturbances. The coral reefs at Cocos Island (Costa Rica), located on the Cocos Ridge about 440 km NE of Darwin Island, have experienced a similar degree of recovery as Darwin Island (Guzman & Cortés, 2007). Overall coral cover of five reefs at Cocos Island was 23 % in 2002, compared with 21 % at Darwin Island in 2007. The dominant species in both regions was *Porites lobata*. In an earlier report on the recovery potential of reefs at Cocos Island, Guzmán & Cortés (1992) predicted that full recovery (including attainment of the original, pre-1983 reef framework thickness) would require centuries. The present state of reefs at Cocos and Darwin Islands indicates that significant recovery is in progress, including the initiation of coral framework construction.

ACKNOWLEDGMENTS

Thanks are due to the following for help with recent and past surveys: Heather Balchowsky, Leandro Castillo, Ángel Chiriboga, Joshua Feingold, Juan Carlos Moncayo, Carlos Alberto Vasconez Medina, Alejandro Muentes, Fernando Rivera, Diego Ruiz, and Mariana Vera. Lenin Cruz offered support aboard the *Pirata* on earlier surveys. The opportunity to participate in the 2006 and 2007 Darwin Initiative cruises was facilitated by Stuart Banks, Scott Henderson and Terence Dawson. Thanks are due to Mark and Diane Littler for identifying the alga. Chris Elvidge, National Oceanic and Atmospheric Administration (NOAA), kindly prepared a Quickbird image of Darwin Island under funding from the NOAA Coral Reef Conservation Program. Rafael Araujo kindly composed the Spanish summary. We thank Craig Starger and Rob DeSalle for sequencing support through the Sackler Institute for Comparative Genomics at the American Museum of Natural History. We thank Ian Enochs for help with the figures. We also appreciate the recommendations of Joshua Feingold and Stuart Banks; the latter supplied temperature observations. Research funding was provided by the U.K.'s DEFRA Darwin Initiative Project 14-048, Conservation International, the National Geographic Society, and US National Science Foundation grant OCE-0526361 and earlier awards. A.M. Romanski was supported by grants to Andrew Baker from the Wildlife Conservation Society and the Pew Institute for Ocean Science. I.B. Baums was supported by NSF grant OCE 0550294. Logistical support and permits were provided by the Charles Darwin Research Station and the Galápagos National Park Service.

LITERATURE CITED

Baker, A.C., Rowan, R. & Knowlton, N. 1997. Symbiosis ecology of two Caribbean acroporid corals. *Proceedings of the 8th International Coral Reef Symposium*, Panama 2: 1295–1300.

Baker, A.C. 1999. *Symbiosis Ecology of Reef-building Corals*. Ph.D. dissertation, University of Miami.

Baker, A.C., Starger, C.J., McClanahan, T.R., Glynn, P.W. 2004. Corals' adaptive response to climate change. *Nature* 430: 741.

Banks, S. 2002. Ambiente físico. Pp. 22–37 *in* Danulat, E. & Edgar, G.J. (eds) *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Puerto Ayora.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. 2004. Confronting the coral reef crisis. *Nature* 429: 827–833.

Berkelmans, R., Van Oppen, M.J.H. 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London B*. 273: 2305–2312.

Bustamante, R.H., Vinueza, L.R., Smith, F., Banks, S., Calvopiña, M., Francisco, V., Chiriboga, A. & Harris, J. 2002. Comunidades submareales rocosas I: organismos sésiles y mesoinvertebrados móviles. Pp. 38–97 *in* Danulat, E. & Edgar, G.J. (eds.) *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Puerto Ayora.

Cohen, D.M. 1985. Notes on a cruise in the Galapagos Islands — May 1984. *Terra* 23: 21–24.

Colgan, M.W. 1990. El Niño and the history of eastern Pacific reef building. Pp. 183–232 *in* Glynn, P.W. (ed.) *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation.* Oceanography Series 52, Elsevier, Amsterdam.

Cortés, J. & Jiménez, C. 2003. Corals and coral reefs of the Pacific of Costa Rica: history, research and status. Pp. 361–385 *in* Cortés, J. (ed.) *Latin American Coral Reefs.* Elsevier, Amsterdam.

Eakin, C.M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño. *Coral Reefs* 15: 109–119.

Eakin, C.M. 2001. A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panamá. *Bulletin of Marine Science* 69: 171–186.

Gardener, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301: 958–960.

Glynn, P.W. 1988. El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7: 129–160.

Glynn, P.W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. Pp. 55–126 *in* Glynn, P.W. (ed.) *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation.* Oceanography Series 52, Elsevier, Amsterdam.

Glynn, P.W. 1994. State of coral reefs in the Galápagos Islands: natural vs anthropogenic impacts. *Marine Pollution Bulletin* 29: 131–140.

Glynn, P.W. 2003. Coral communities and coral reefs of Ecuador. Pp. 449–472 *in* Cortés, J. (ed.) *Latin American Coral Reefs*. Elsevier, Amsterdam.

Glynn, P.W. & Fong, P. 2006. Patterns of reef coral recovery by the regrowth of surviving tissue following the 1997–98 El Niño warming and 2000, 2001 upwelling cool events in Panamá, eastern Pacific. *Proceedings of the 10th International Coral Reef Symposium, Okinawa* 2: 624–630.

Glynn, P.W. & Wellington, G.M. 1983. *Corals and Coral Reefs of the Galápagos Islands*. University of California Press, Berkeley, CA.

Glynn, P.W., Maté, J.L., Baker, A.C. & Calderón, M.O. 2001. Coral bleaching and mortality in Panamá and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69: 79–109.

Guzmán, H.M. & Cortés, J. 1992. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982–83 El Niño disturbance. *Revista de Biología Tropical* 40: 309–324.

Guzman, H.M. & Cortés, J. 2007. Reef recovery 20 years after the 1982–1983 El Niño massive mortality. *Marine Biology* 151: 401–411.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50: 839–866.

Iglesias-Prieto, R., Beltran, V.H., LaJeunesse, T.C., Reyes-Bonilla, H. & Thome, P.E. 2004. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. *Proceedings of the Royal Society of London Series B* 271: 1757–1763.

LaJeunesse, T.C. & Trench, R.K. 2000. The biogeography of two species of *Symbiodinium* (Freudenthal) inhabiting the intertidal anemone, *Anthopleura elegantissima* (Brandt). *Biological Bulletin* 199: 126–134.

LaJeunesse, T.C. 2002. Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology* 141: 387–400.

Reaka-Kudla, M.L., Feingold J.S. & Glynn P.W. 1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. *Coral Reefs* 15: 101–107.

Robinson, G. 1985. The influence of the 1982–83 El Niño on Galápagos marine life. Pp. 153–190 *in* Robinson, G. & Pino, E.M. del (eds.) *El Niño in the Galápagos Islands: the 1982–1983 Event*. Fundación Charles Darwin, Quito.

Rowan, R. & Powers, D.A. 1991. Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). *Marine Ecology Progress Series* 71: 65–73.

Warner, M.E., LaJeunesse, T.C., Robison, J.D., Thur, R.M. 2006. The ecological distribution and comparative photobiology of symbiotic dinoflagellates from reef corals in Belize: potential implications for coral bleaching. *Limnology and Oceanography* 51: 1887–1897.

Warner, M.E., Fitt, W.K., Schmidt, G.W. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae *in hospite* from four different species of reef coral: a novel approach. *Plant Cell and Environment* 19: 291–299.

Wellington, G.M. & Glynn, P.W. 2007. Responses of coral reefs to El Niño-Southern Oscillation sea-warming events. Pp. 342-385 *in* Aronson, R.B. (ed.) *Geological Approaches to Coral Reef Ecology*. Ecological Studies 192, Springer, New York.

Wilkinson, C. (ed.) 2004. *Status of Coral Reefs of the World: 2004*, vols 1 & 2. Australian Institute of Marine Science, Townsville.

PRELIMINARY SURVEY OF ZOOXANTHELLATE ZOANTHIDS (CNIDARIA: HEXACORALLIA) OF THE GALAPAGOS, AND ASSOCIATED SYMBIOTIC DINOFLAGELLATES (*SYMBIODINIUM* SPP.)

By: James D. Reimer[1,2,3] & Cleveland P. Hickman, jr[4]

[1]Biological Institute on Kuroshio, 560 Nishidomari, Otsuki, Kochi 788-0333, Japan.
[2]Research Program for Marine Biology and Ecology, Extremobiosphere Research Center, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima, Yokosuka, Kanagawa 237-0061, Japan.
[3]Correspondence: MISE (Molecular Invertebrate Systematics and Ecology) Lab., Rising Star Program, TRO-SIS, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 901-0213, Japan. <jreimer@sci.u-ryukyu.ac.jp>
[4]Department of Biology, Washington and Lee University, Lexington, VA 24450, U.S.A.

SUMMARY

Despite their presence in almost all marine ecosystems, the zoanthids (Cnidaria: Hexacorallia: Zoantharia) are poorly studied, in large part due to a lack of useful morphological identification characters. Recent research combining morphology with DNA markers has begun to shed new light on diversity and distribution of the order Zoantharia. Here, preliminary findings on the diversity and distribution of zooxanthellate zoanthid species from the genera *Zoanthus* and *Palythoa* are presented, documenting these genera in the Galapagos for the first time. A brief description of the species found is provided. *Zoanthus* and *Palythoa* appear to be limited in the Galapagos to rocky shores in warm shallow sublittoral and infralittoral waters (minimum temperature >18°C), isolated from the colder water that dominates much of the archipelago. Preliminary results from the internal transcribed spacer region of ribosomal DNA sequences of symbiotic dinoflagellates suggest that both *Zoanthus* and *Palythoa* spp. in the Galapagos possess only *Symbiodinium* clade C. Brief descriptions of the zooxanthellate zoanthid species found in the Galapagos are provided.

RESUMEN

Estudios preliminares de zoántidos zooxantelados (Cnidaria: Hexacorallia) de las Galápagos, y dinoflagelados simbiontes asociados (*Symbiodinium* spp.). A pesar de su presencia en casi todos los ecosistemas marinos, los zoántidos (Cnidaria: Hexacorallia: Zoantharia) están pobremente estudiados, en gran parte debido a una falta de caracteres de identificación morfológica útiles. Investigaciones recientes combinando morfología con marcadores de DNA han empezado a dar nuevas luces sobre la distribución y diversidad del orden Zoantharia. Aquí son presentados hallazgos preliminares sobre la distribución y diversidad de especies de zoántidos zooxantelados de los géneros *Zoanthus* y *Palythoa*, documentando estos géneros en las Galápagos por primera vez. Una breve descripción de las especies encontradas es proporcionada. *Zoanthus* y *Palythoa* parecen estar limitados en las Galápagos a costas rocosas del sublitoral e infralitoral en aguas cálidas y someras (temperatura mínima >18°C), aisladas de las aguas más frías que dominan mayormente el archipiélago. Resultados preliminares de la región de los espaciadores internos transcriptos de la secuencia del ADN ribosomal de los dinoflagelados simbióticos sugieren que ambos *Zoanthus* y *Palythoa* spp. en las Galápagos poseen solamente *Symbiodinium* clado C. Se presentan breves descripciones de las especies de zoántidos zooxantelados en las Galápagos.

INTRODUCTION

The Galapagos Islands are world-famous for their terrestrial biodiversity and wealth of endemic species. However, the biological richness of the Galapagos marine ecosystem is equally exceptional but only recently has begun to be comprehensively investigated. In particular, marine invertebrate diversity was understudied until recently. While some groups of Anthozoans (Cnidaria) such as scleractinian corals (Cairns 1991, Glynn 2003), hydroids (Calder *et al*. 2003) and anemones (Fautin *et al*. 2007) are now relatively well documented in the Galapagos, others such as the order Zoantharia (zoanthids) remain to be described. Zoanthids, characterized by two rows of tentacles, one siphonoglyph and a (usually) colonial way of life, have long been taxonomically neglected, due in large part to their lack of useful morphological identification characters (Reimer *et al*. 2004, Sinniger *et al*. 2005). Additionally, most zoanthids use mineral particles (sand and detritus, foraminifer tests, spicules from sponges, sclerites from octocorals, *etc*.) taken from the water column to help make their structure, making dissection and cross-sectioning to access the few useful identification characters (sphincter muscle structure, mesentery count *etc*.) even more difficult.

Recent integrated taxonomic approaches combining traditional morphology with molecular DNA markers have proven useful in documenting the diversity of zoanthids (Reimer *et al*. 2004, 2006b, 2006c), examining their phylogeny (Sinniger *et al*. 2005, 2007) and describing new taxa (Reimer *et al.* 2006b, 2007a). Here, preliminary integrated taxonomic results from surveys undertaken between 2001 and 2007 are presented, documenting for the first time the presence of the genera *Zoanthus* and *Palythoa* in the Galapagos. Additionally, zoanthid distribution patterns are examined, as well as symbiotic dinoflagellate diversity (*Symbiodinium* spp.).

MATERIALS AND METHODS

Zooxanthellate zoanthids were searched for by hand intertidally or by SCUBA on most major islands in the Galapagos, and specimens collected from three locations (Fig. 1) in 2001, 2002 and 2007. Before collection, *in situ* photographs were taken to assist in identification and for morphological data (oral disk/polyp diameter, color, polyp form *etc*.). Specimens were then stored in 75% alcohol at ambient temperature. Samples were assigned numbers based on the sample year; thus: sample 07-01 is sample 1 from 2007.

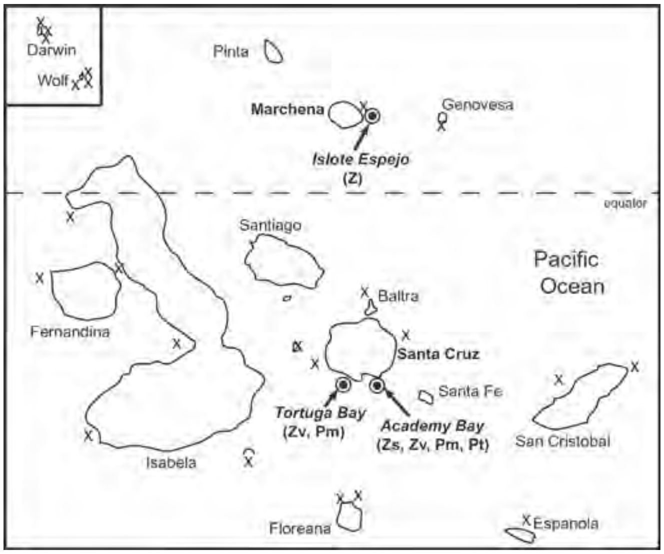


Figure 1. Map of Galapagos and sampling locations. Filled circles indicate presence of zooxanthellate zoanthids (with observed species in parentheses), "X" indicates locations examined where no zooxanthellate zoanthids found. Zs = *Zoanthus* cf. *sansibaricus*, Zv = *Z.* cf. *vietnamensis/kuroshio*, Z = unidentified *Zoanthus* sp., Pm = *Palythoa* cf. *mutuki*, Pt = *P.* cf. *tuberculosa*.

All specimens were identified by morphology, following descriptions in Reimer *et al*. (2006b) and Reimer (2007). Seventeen samples were also examined by using two mitochondrial DNA markers, cytochrome oxidase subunit I (COI) and 16S ribosomal DNA (mt 16S rDNA), following procedures for DNA extraction, PCR amplification, and subsequent analyses outlined in Reimer *et al.* (2004, 2006c).

Species identifications are preliminary, as few records of *Zoanthus* and *Palythoa* exist for the E Pacific, where undescribed species with morphological and DNA characteristics matching those of the species listed here might exist. There are also poorly described Pacific species for which no specimens are available (thus no DNA and no good morphological information). Specimens and DNA data from the W coast of S America and other islands in the E Pacific would help to identify the Galapagos specimens with more confidence; nevertheless, these are at least closely related to the species listed. Descriptions of the species to which Galapagos specimens are referred are given in Appendix 1.

No means exist for reliably identifying *Symbiodinium* spp. clades by morphology, so 15 samples had their *Symbiodinium* spp. internal transcribed spacer of ribosomal DNA (ITS-rDNA) sequences examined (see Rowan & Powers 1991). *Symbiodinium* DNA extraction, ITS-rDNA PCR amplification, and subsequent analyses followed procedures explained in Reimer *et al.* (2006e). All *Symbiodinium* names follow LaJeunesse (2005).

Novel DNA sequences for both host zoanthid specimens (mitochondrial 16S ribosomal DNA, cytochrome oxidase subunit I, and ITS-rDNA) and *Symbiodinium* spp. (ITS-rDNA) will be discussed in detail elsewhere.

RESULTS

Zooxanthellate zoanthids of the genera *Zoanthus* (family Zoanthidae) and *Palythoa* (Sphenopidae) were found at only three and two sites respectively (Fig. 1): Tortuga Bay and Academy Bay on Santa Cruz Island (both genera at both sites), and Islote Espejo, Marchena Island (*Zoanthus* only). No zooxanthellate zoanthids were found at most sites investigated, although some locations were investigated only by SCUBA and not intertidally. All specimens were found in the low infralittoral zone or shallow sublittoral zone, often in tidepools (Table 1).

All *Zoanthus* found were attached to hard substrate, usually large rocks, in the low infralittoral to shallow sublittoral (<1.5 m depth) zones. Species found were *Zoanthus* cf. *sansibaricus* (Tortuga Bay only) and *Zoanthus* cf. *vietnamensis/kuroshio* species group (all three sites). Specimens of *Zoanthus* cf. *vietnamensis/kuroshio* species group were quite common at Academy Bay and Tortuga Bay, usually in locations with warm ocean temperatures (>18ºC), high wave or current activity and high light levels.

Palythoa spp. in Galapagos were mostly found in the same warm, high wave/current, high light levels and

Table 1. Zooxanthellate zoanthid specimens collected from the Galapagos. Sites are: AB = Academy Bay (Santa Cruz Island); TB = Tortuga Bay (Santa Cruz); E = Islote Espejo (Marchena Island). *P. m.* = *Palythoa mutuki*; *P. t.* = *P. tuberculosa*; *Z. s.*= *Zoanthus sansibaricus*; *Z. v./k.* = *Z. vietnamensis/kuroshio*. Pre-2007 collections were by CPH, 07-30 by JDR and B. Riegl, all others by JDR.

Specimen number	Site	Date	Depth (m)	Morphological identification	COI identification	mt 16S rDNA identification	*Symbiodinium* clade	Identity conclusion
01-05	TB	14 Jun 2001	Low infralittoral tidepool	*Z.* sp.	*Z. s.*	*Z. s.*	C1/C3 related	*Z.* cf. *s.*
01-105	AB	22 Jul 2001	Low infralittoral	*Z.* sp.	*Z. v./k.*	*Z. v./k.*	C1/C3 related	*Z.* cf. *v./k.*
01-106	AB	22 Jul 2001	Low infralittoral	*P. t.*	*P.* spp.	*P. t.*	C1/C3 related	*P.* cf. *t.*
02-122	TB	27 Jun 2002	Low infralittoral tidepool	*P. m.*	*P.* spp.	*P. m.*	C1/C3 related	*P.* cf. *m.*
07-01	TB	1 Mar 2007	+0.5	*Z.* sp.				*Z.* cf. *v./k.*
07-02	TB	1 Mar 2007	0	*Z.* sp.				*Z.* cf. *v./k.*
07-03	TB	1 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-04	TB	1 Mar 2007	0	*Z.* sp.			C	*Z.* cf. *v./k.*
07-05	TB	1 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-06	AB	2 Mar 2007	+0.5	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-07	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-08	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*			*Z.* cf. *v./k.*
07-09	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-10	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-11	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*		C	*Z.* cf. *v./k.*
07-12	AB	2 Mar 2007	0	*Z.* sp.	*Z. v./k.*			*Z.* cf. *v./k.*
07-13	AB	2 Mar 2007	0	*P. m.*	*P.* spp.		C1/C3 related	*P.* cf. *m.*
07-14	AB	2 Mar 2007	0	*P. m.*	*P.* spp.		C1/C3 related	*P.* cf. *m.*
07-15	AB	2 Mar 2007	0	*P. m.*	*P.* spp.		C1/C3 related	*P.* cf. *m.*
07-15b	AB	2 Mar 2007	0	*P. m.*	*P.* spp.			*P.* cf. *m.*
07-30	E	3 Mar 2007	-1.0	*Z.* sp.				*Z.* sp.

hard substrate conditions as *Zoanthus*. Species were *Palythoa* cf. *tuberculosa* (infralittoral zone in Academy Bay, only observed in 2001, not found in 2007), and *Palythoa* cf. *mutuki* (Academy Bay and Tortuga Bay), which was sympatric with but not as common as *Z.* cf. *vietnamensis/kuroshio* (Fig. 2b).

All specimens examined, regardless of host species or genus, possessed *Symbiodinium* clade C (Table 1).

DISCUSSION

Distribution in Galapagos

Although the presence of zooxanthellate zoanthids at both Academy Bay and Tortuga Bay had been known for many years (Hedgpeth 1969), they had not been conclusively identified to species. The presence of *Zoanthus* and *Palythoa* was not unexpected, because they are by far the two most common zooxanthellate zoanthid genera, found worldwide in subtropical and tropical waters. Both genera possess *Symbiodinium* and are thus limited to ocean waters above *c.* 15–16°C (Reimer *et al.* 2006e, 2007b), similar to reef-building corals. Although the Galapagos Islands are situated over the equator, the cold Peru Oceanic Current brings water as cold as 18°C and, in the western archipelago, the Equatorial Undercurrent produces localized upwelling as cold as 14°C on the west coasts of Fernandina and Isabela (Chávez & Brusca 1991). Thus, zooxanthellate corals and other zooxanthellate colonial anthozoans are most likely limited to shallow, warm (>18°C) waters more common in the eastern archipelago and/or east coasts of islands, as well as the northern islands of Darwin and Wolf.

Occasional El Niño-Southern Oscillation (ENSO) events may severely affect zooxanthellate-hosting organisms in Galapagos. Protracted elevated sea temperatures during the 1982–3 and 1997–8 events resulted in widespread coral bleaching and mortality throughout Galapagos, including at Darwin and Wolf where coral communities have flourished in the past (Glynn 2003). Recent surveys confirm the recovery of reef structure around these northern islands, but no zooxanthellate zoanthids were found there despite numerous shallow-water surveys. Zooxanthellate zoanthids are negatively affected by ENSO high ocean temperature (>30°C) conditions similar to zooxanthellate Scleractinia (S. Ono *et al.* unpubl. data, Reimer *et al.* 2007b), and it is possible that ENSO disturbances may explain the apparent absence of zooxanthellate zoanthids at many sites where we should expect to find them (Fig. 1). Future surveys may find additional *Zoanthus* and *Palythoa* populations in shallow or infralittoral waters with rocky substrates in warm-water areas.

Origin of Galapagos zooxanthellate zoanthids

While data on mobile azooxanthellate larvae of *Palythoa* (zoanthellae) are sparse, it is known that *Zoanthus* *sansibaricus* in Japan reproduces sexually during summer in apparent mass spawning events (Ono *et al*. 2005), with swimming azooxanthellate larvae (zoanthinae) that survive at least 60 days without settling (S. Ono pers. comm.). Such larvae may have been able to colonize Galapagos from the west coast of S or central America. Unfortunately, there are few historical records on the distribution of *Zoanthus*, *Palythoa* and other zooxanthellate zoanthids from the E Pacific: *Palythoa* and *Zoanthus* from Easter Island (Carlgren 1922), *Palythoa* and *Zoanthus* from the Bay of Panama (Verrill 1869, Carlgren 1951), and *Palythoa* from French Polynesia (Boone 1938), the west coast of El Salvador and Mexico (Verrill 1869). Therefore comparisons of species diversity are not yet possible.

All specimens examined possessed *Symbiodinium* of clade C, as previously seen in *Palythoa* spp. (Reimer *et al*. 2006d) and *Zoanthus* spp. (Reimer *et al*. 2006e, 2007b). In particular, several specimens had *Symbiodinium* C1/C3, which is a host generalist found in a wide variety of corals throughout the Pacific and Atlantic Oceans (LaJeunesse 2005), and is also theorized to be an environmental generalist. *Symbiodinium* such as C1/C3 may be suited for the unusually variable environments found in the Galapagos.

Both *Zoanthus* spp. and the majority of *Palythoa* spp. have azooxanthellate larvae, acquiring *Symbiodinium* at settlement and attachment (both genera) or during the free-swimming zoanthinae stage (*Zoanthus* only) (Ryland *et al*. 2000). The Galapagos results suggest symbiont flexibility for both *Z.* cf. *sansibaricus* and *Z.* cf. *vietnamensis/kuroshio*, as specimens of both species groups possessed generalist C1/C3 or closely related types, which were not previously seen in *Zoanthus* spp. in Japan. *Z. sansibaricus* has previously been found to be flexible in its association with *Symbiodinium*, either possessing a specific subclade of *Symbiodinium* (designated C1z: C1/C3-related but different from types seen here, see Reimer *et al*. 2006e, 2007c), or clade A (Reimer *et al*. 2006e), while *Z. vietnamensis* in Japan possesses subclade C15 and related types (Reimer *et al*. 2007c). It may be that azooxanthellate larvae of *Zoanthus* spp. acquired C1/C3, the most common type of *Symbiodinium* in the Pacific (LaJeunesse 2005), upon colonization of the Galapagos.

Palythoa specimens also possessed C1/C3 *Symbiodinium*, as previously seen in *Palythoa* spp. (Reimer *et al*. 2006d), and thus it is impossible to speculate if these species arrived in the Galapagos as a result of sexual or asexual reproduction. However, these preliminary results reinforce findings from Japan that in the Pacific *P. tuberculosa* and *P. mutuki* associate only with C1/C3 (Reimer *et al*. 2006d).

Conclusions and future research

An examination of other locations in the Galapagos and the west coast of S and central America would help clarify our understanding of the distribution and diversity of these understudied genera (and their *Symbiodinium* spp.). As global warming increases, such records may also help in documenting the potential spread of these warm-water (>18ºC) organisms, as seen with the first sighting of the Crown-of-thorns starfish *Acanthaster planci* at Darwin Island in 1995, a species that may have arrived with the ENSO event of 1982–3 (Hickman 1998).

ACKNOWLEDGMENTS

This work forms part of the Galapagos Marine Life Series undertaking. We thank the following for assistance during sample collection: Dr William C. Ober, Angel Chiriboga, Dr Dale Calder, Dr Daphne Fautin (Academy Bay and Tortuga Bay, 2001), Dr Bernard Riegl (Islote Espejo, 2007), Dr Fred Liss, Dr Odalisca Breedy (both Tortuga Bay, 2007), and the captain and crew of the *Tip Top IV* (March 2007, Marchena Island). Dr Shusuke Ono kindly provided information on *Zoanthus* larvae. Specimen collection was partially funded by DEFRA Darwin Initiative project 14-048. JDR was partially financed by a Japan Society for the Promotion of Science post-doctoral fellowship (#P04868) at JAMSTEC (Yokosuka, Japan), the Fujiwara Natural History Foundation, and the Biological Institute on Kuroshio (Otsuki, Japan). Masaru Kawato (JAMSTEC) is acknowledged for his assistance in DNA sequencing.

LITERATURE CITED

Boone, L. 1938. Scientific results of the world cruises of the yachts "Ara" 1928–1929, and "Alva" 1931–1932, "Alva" Mediterranean Cruise 1933, and "Alva" South American Cruise 1935, William K. Vanderbilt, Commanding. Part II, Coelenterata. *Bulletin of the Vanderbilt Marine Museum* 7: 29–76.

Cairns, S.D. 1991. A revision of the Ahermatypic Scleractinia of the Galápagos and Cocos Islands. *Smithsonian Contributions to Zoology* 504.

Calder, D.R., Mallinson, J.J., Collins, K. & Hickman, C.P. 2003. Additions to the hydroids (Cnidaria) of the Galápagos, with a list of species reported from the islands. *Journal of Natural History* 37: 1173–1218.

Carlgren, O. 1922. Actiniaria und Zoantharia von Juan Fernandez und der Osterinsel. Pp. 145–160 *in* Skottsberg, C. (ed.) *The Natural History of Juan Fernandez and Easter Island*. Almquist & Wiksells, Uppsala.

Carlgren, O. 1951. The actinian fauna of the Gulf of California. *Proceedings of the United States National Museum* 101: 415–449.

Chávez, F.P. & Brusca, R.C. 1991. The Galápagos Islands and their relations to oceanographic processes in the tropical Pacific. Pp. 9–33 *in* James, M.J. (ed.), *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Fautin, D.G., Hickman, C.P. Jr., Daly, M. & Molodtsova, T. 2007 Shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria) and tube anemones (Cnidaria: Anthozoa: Ceriantharia) of the Galápagos Islands. *Pacific Science* 61: 549–573.

Glynn, P.W. 2003. Coral communities and coral reefs of Ecuador. Pp. 449–472 *in* Cortes, J. (ed.), *Latin American Coral Reefs*. Elsevier, Amsterdam.

Hedgpeth, J.W. 1969. An intertidal reconnaissance of rocky shores of the Galápagos. *The Wasmann Journal of Biology* 27: 1–24.

Hickman, C.P. Jr. 1998. *A Field Guide to Sea Stars and Other Echinoderms of Galápagos.* Sugar Spring Press, Lexington, VA.

LaJeunesse, T.C. 2005. "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution* 22: 570–581.

Ono, S., Reimer, J.D. & Tsukahara, J. 2005. Reproduction of *Zoanthus sansibaricus* in the infra-littoral zone at Taisho Lava Field, Sakurajima, Kagoshima, Japan. *Zoological Science* 22: 247–255.

Pax, F. 1910. Studien an westindischen Actinien. *Zoologische Jahrbucher* Suppl. 11: 157–330.

Reimer, J.D. 2007. Preliminary survey of zooxanthellate zoanthid diversity (Hexacorallia: Zoantharia) from southern Shikoku, Japan. *Kuroshio Biosphere* 3: 1–16 + 7 pls.

Reimer, J.D., Ono, S., Takishita, K., Fujiwara, Y. & Tsukahara, J. 2004. Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecifity within four previously presumed species. *Zoological Science* 21: 517–525.

Reimer, J.D., Ono, S., Iwama, A., Tsukahara, J. & Maruyama, T. 2006a. High levels of morphological variation despite close genetic relatedness between *Zoanthus* aff. *vietnamensis* and *Zoanthus kuroshio* (Anthozoa: Hexacorallia). *Zoological Science* 23: 755–761.

Reimer, J.D., Ono, S., Iwama, A., Tsukahara, J., Takishita, K. & Maruyama, T. 2006b. Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan with description of two new species. *Zoological Science* 23: 261-275.

Reimer, J.D., Ono, S., Takishita, K., Tsukahara, J. & Maruyama, T. 2006c. Molecular evidence suggesting species in the zoanthid genera *Palythoa* and *Protopalythoa* (Anthozoa: Hexacorallia) are congeneric. *Zoological Science* 23: 87–94.

Reimer, J.D., Takishita, K. & Maruyama, T. 2006d. Molecular identification of symbiotic dinoflagellates (*Symbiodinium* spp.) from *Palythoa* spp. (Anthozoa: Hexacorallia) in Japan. *Coral Reefs* 25: 521–527.

Reimer, J.D., Takishita, K., Ono, S., Maruyama, T. & Tsukahara, J. 2006e. Latitudinal and intracolony ITS-rDNA sequence variation in the symbiotic dinoflagellate genus *Symbiodinium* (Dinophyceae) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia). *Phycological Research* 54: 122–132.

Reimer, J.D., Hirano, S., Fujiwara, Y., Sinniger, F. & Maruyama, T. 2007a. Morphological and molecular characterization of *Abyssoanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a northwest Pacific methane cold seep. *Invertebrate Systematics* 21: 255–262.

Reimer, J.D., Ono, S., Furushima, Y. & Tsukahara, J. 2007b. Seasonal changes in the morphological condition of symbiotic dinoflagellates (*Symbiodinium* spp.) of *Zoanthus sansibaricus* (Anthozoa: Hexacorallia) over a latitudinal range in southern Japan. *South Pacific Study* 27: 1–24.

Reimer, J.D., Ono, S., Tsukahara, J., Takishita, K. & Maruyama, T. 2007c. Non-seasonal clade-specificity and subclade microvariation in symbiotic dinoflagellates (*Symbiodinium* spp.) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia) at Kagoshima Bay, Japan. *Phycological Research* 55: 58–65.

Reimer, J.D., Takishita, K., Ono, S. & Maruyama, T. 2007d. Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) utilizing nuclear ITS-rDNA. *Coral Reefs* 26: 399–410.

Rowan, R. & Powers, D.A. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbiosis. *Science* 251: 1348–1351.

Ryland, J.S. & Lancaster, J.E. 2003. Revision of methods of separating species of *Protopalythoa* (Hexacorallia: Zoanthidea) in the tropical West Pacific. *Invertebrate Systematics* 17: 407–428.

Ryland, J.S., Putron, S. de, Scheltema, R.S., Chimonides, P.J. & Zhadan, D.G. 2000. Semper's (zoanthid) larvae: pelagic life, parentage and other problems. *Hydrobiologia* 440: 191–198.

Sinniger, F., Montoya-Burgess, J.I., Chevaldonne, P. & Pawlowski, J. 2005. Phylogeny of the order Zoantharia (Anthozoa: Hexacorallia) based on mitochondrial ribosomal genes. *Marine Biology* 147: 1121–1128.

Sinniger, F., Chevaldonne P. & Pawlowski, J. 2007. Mitochondrial genome of *Savalia savaglia* (Cnidaria, Hexacorallia) and early metazoan phylogeny. *Journal of Molecular Evolution* 64: 196–203.

Uchida, H. 2001. *Sea Anemones in Japanese Waters* (in Japanese). TBS Britannica, Tokyo.

Verrill, A.E. 1869. Review of the corals and polyps of the west coast of America. *Transactions of the Connecticut Academy of Arts and Sciences* 1(6).

APPENDIX 1

DESCRIPTIONS OF ZOOXANTHELLATE ZOANTHIDS IN THE GALAPAGOS (ADAPTED FROM REIMER 2007)

FAMILY ZOANTHIDAE

The only family within the Order Zoantharia not to be sand-encrusted. All three genera (*Zoanthus*, *Isaurus*, *Acrozoanthus*) are zooxanthellate.

Genus *Zoanthus*
Distinguished in Galapagos by its lack of sand and/or detritus. *Zoanthus* polyps are uniformly smooth on the outer surface. Can also often be distinguished from *Palythoa* by often having brightly colored oral disks, although green and brown forms (similar to *Palythoa* spp.) exist. The external surface of polyps and the coenenchyme is mainly light to dark purple, although pale green polyps are sometimes observed.

***Zoanthus* cf. *sansibaricus* Carlgren 1900 (Fig. 2a).** Often forms large colonies with polyps well clear and free of the coenenchyme ("liberae") (Reimer *et al*. 2006b; see Pax 1910). Adult polyps 3–12 mm in diameter, up to 20 mm in length. External polyp surface generally uniform light to dark purple, no markings, sometimes slightly paler around edge of oral disk. Tentacles 40–58, mesenteries 48–54. Wide variation in oral disk color: red, green (most common), brown, purple, white, blue (common), often fluorescent. Genetic data show it to consist of many different color morphotypes (Reimer *et al*. 2004, 2006b).

***Zoanthus* cf. *vietnamensis* Pax and Mueller 1957/*Zoanthus* cf. *kuroshio* Reimer and Ono 2006 species group.** *Z.* cf. *vietnamensis* has polyps up to 30 mm in length, up to 20 mm in diameter (Uchida 2001, Reimer *et al*. 2006a). Polyps "liberae". Oral disk pale to dark pink, occasionally mint green, often with white oral opening. Tentacles 55–64. Morphs of *Z.* cf. *vietnamensis* with pink or green oral disk often are very hard to distinguish from *Z.* cf. *sansibaricus*.

Molecular data suggest that *Z.* cf. *kuroshio* is simply a morphotype of *Z.* cf. *vietnamensis* (Reimer *et al.* 2006a), although their morphology is clearly different. *Z.* cf. *kuroshio* usually has oral disk pale pink, although white and pale blue varieties observed. Tentacles 50–64, mesenteries 42–48. Polyps deeply embedded, barely extend from coenenchyme ("immersae"). Oral disk 6–12 mm in diameter when expanded. Polyps narrower in diameter towards oral opening than at base. Edge of coenenchyme tongue-like in form. Colonies often intertidal and in tide pools on wave-exposed shoreline, can be very large and encrusting, forming a mat over substrate (rock or dead coral).

FAMILY SPHENOPIDAE

Differs from Zoanthidae in that it is sand-encrusted. Includes the colonial genus *Palythoa* with many species worldwide, as well as the solitary genus *Sphenopus*.

Genus *Palythoa*

Palythoa species can be distinguished from *Zoanthus* in Galapagos by their sand and detritus structures. Colony and polyp tissues are usually tan or brown, sometimes green. Patchy bleaching may sometimes be observed in larger *P. tuberculosa* colonies.

***Palythoa* cf. *tuberculosa* Delage and Herouard 1901.** Polyps immersae, barely extending above large, well-developed coenenchyme (Uchida 2001, Reimer *et al*. 2006c). Oral disks up to 20 mm in diameter, though often closed in daytime. Coenenchyme dark brown, generally uniform although some patchiness often observed. Colonies small to large, encrust substrate. Tolerates more marginal environments (reef lagoons, tide pools *etc*.) than many other colonial cnidarians (Reimer *et al*. 2006d).

***Palythoa* cf. *mutuki* Carlgren 1937 (Fig. 2b).** Polyps liberae, up to 40 mm in length (Ryland & Lancaster 2003, Reimer *et al*. 2006c). Oral disk up to 30 mm diameter, green. Radii often visible (white, pale brown). Colonies generally small (<100 polyps). Closely related to *P. tuberculosa*, and may have undergone reticulate evolution with it in the past (Reimer *et al*. 2007d).

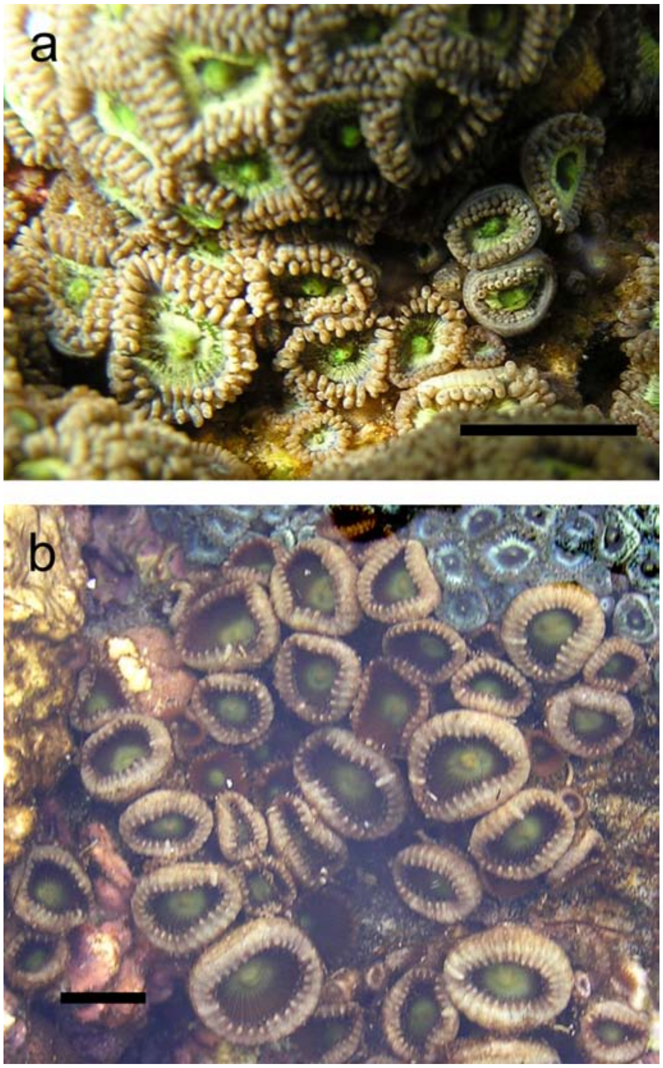


Figure 2. Zooxanthellate zoanthids *in situ* in the Galapagos, March 2007: (a) *Zoanthus* cf. *vietnamensis/kuroshio* (depth 0 m), Tortuga Bay, Santa Cruz Island; (b) *Palythoa* cf. *mutuki* (with interspersed *Z.* cf. *vietnamensis/kuroshio* at top of image), tidepool at low tide, Academy Bay, Santa Cruz Island. Black bars = 1 cm.

A HABITAT SUITABILITY MODEL FOR PREDICTING CORAL COMMUNITY AND REEF DISTRIBUTIONS IN THE GALAPAGOS ISLANDS

By: Terence P. Dawson[1], Felicity Jarvie[2] & Femke Reitsma[2]

[1]School of Geography, University of Southampton, UK. <t.p.dawson@soton.ac.uk>
[2]School of Geosciences, University of Edinburgh, UK

SUMMARY

The coral communities and coral reefs of the Galapagos Marine Reserve support tens of thousands of species, including many rare and endemic species. Reef-building corals are sensitive to elevated temperatures, which have been linked to coral bleaching (loss of symbiotic zooxanthellae) and therefore their distribution around the islands has been strongly affected by extreme climatic events over the last 30 years. Following the 1982–3 El Niño-Southern Oscillation event, coral cover was reduced by 95 %, with further mortality in the 1997–8 event. Although there has been significant recovery of the communities in recent years, there is concern that by 2100 the global climate system and sea surface temperatures will warm by between 1.4° and 5.8°C, which could result in 100% mortality of Galapagos corals. This paper reports a temperature and depth bioclimatic envelope (or niche) model of potential coral distribution, developed using an historical analysis of monthly sea surface temperatures, derived from the NOAA AVHRR over the period 1985–2001, and a near-shore bathymetry data set derived from Shuttle Radar Topography Mission digital topographic data integrated with ship-based depth sounding surveys and digitised hydrographic maps. The model was validated against known coral community and coral reef localities. Application of the model can support the identification of potential new areas where conditions for coral growth are favourable and enable predictions of the effects of future climate change.

RESUMEN

Un modelo de hábitat apropiado, para predecir la distribución de comunidades y arrecifes de coral en las islas Galápagos. Las comunidades y arrecifes de corales en la Reserva Marina de Galápagos mantienen decenas de miles de especies, incluidas muchas especies raras y endémicas. Los corales formadores de arrecifes son sensibles a temperaturas elevadas, las cuales han sido ligadas al blanqueamiento de corales (pérdida de algas simbióticas zooxanteladas) y por lo tanto su distribución alrededor de las islas ha sido fuertemente afectada por eventos climáticos extremos durante los últimos 30 años. Después del evento de El Niño-Oscilación Sur de 1982–3, la cobertura de corales fue reducida en un 95 %, con una mortalidad adicional en el evento de 1997–8. Aunque ha habido una significante recuperación de las comunidades en los años recientes, hay la preocupación que para el 2100 el sistema climático global y la temperatura superficial del mar se calentarán entre 1.4° y 5.8°C, lo cual podría resultar en la mortalidad del 100 % de los corales de Galápagos. Este artículo reporta un modelo "sobre" o "nicho" bio-climático de temperatura y batimetría, de la distribución potencial de corales, desarrollado usando un análisis de datos históricos de la temperatura superficial mensual del mar, derivados de la NOAA AVHRR sobre el período de 1985–2001, y un juego de datos de batimetría costera derivado de datos topográficos digitales de la Misión del Transbordador espacial de Radar Topográfica integrados con estudios de sondas de profundidad a bordo de barcos y mapas hidrográficos digitalizados. El modelo fue validado contra las localidades de comunidades y arrecifes de coral conocidas. La aplicación del modelo puede sostener la identificación de nuevas áreas potenciales donde las condiciones para el crecimiento de corales son favorables, y permitir predicciones de los futuros efectos del cambio climático.

INTRODUCTION

Coral reefs form one of the richest and most diverse marine ecosystems in the world. Although corals do not form reefs in Galapagos except at the northern islands of Darwin and Wolf, coral communities exist throughout the archipelago, resulting in increased diversity compared to areas without corals. Hermatypic or reef-building corals containing photosynthetic dinoflagellates (zooxanthellae) are only located in warm tropical and subtropical regions of the world in a limited physical, chemical and biological range. For example, coral reefs cannot develop below 18°C whilst coral bleaching, the expulsion of the coral's symbiotic zooxanthellae pigments under stress, is associated with extended periods of elevated sea temperatures above 30–35°C. The symbiotic association between corals and dinoflagellates is mutualistic, with zooxanthellae providing oxygen and food (e.g. glucose, amino acids), whilst the coral host provides carbon dioxide, nutrients and living space. Zooxanthellate corals are limited to clear, well-lit shallow water because of their phototrophic symbionts. This study uses our knowledge of these constraints to develop a habitat suitability model based on bathymetry and sea surface temperature (SST) data, which can be used to predict the coral's spatial distribution around the Galapagos Islands. The Galapagos Marine Reserve, created in 1998, covers *c.* 133,000 km^2, and the whole archipelago has been designated as a World Heritage Site by UNESCO. However, the vulnerability of the Galapagos Islands and their coral communities, in particular to El Niño-Southern Oscillation (ENSO) events, is well documented. During the past three decades coral research in Galapagos has demonstrated that widespread coral bleaching and subsequent mortality resulted from increases in sea temperature during the events of 1982–3 and 1997–8 (Fitt *et al.* 2001, Glynn 2001, Reaser *et al.* 2000). This has heightened concern regarding the effects of global warming on the marine environment (Glynn 1993, Hoegh-Guldberg 1999, Obura 2005, Stone *et al.* 1999). Indeed, West & Salm (2003) suggested that "climate change may now be the single greatest threat to [coral] reefs worldwide". This paper presents a method for predicting coral distributions in the Galapagos Islands using depth and SST, which can facilitate research on the impacts of climate change on coral communities and reef habitats and be useful for predicting the distribution of hermatypic coral across the study area. Based upon the concept that species distributions can be described by a range of environmental conditions (biological and physical), this approach has been widely applied in terrestrial and more recently marine ecosystems (Pearson & Dawson 2003, Guinotte *et al.* 2006).

METHODS

The potential coral habitat model was developed by integrating a wide range of satellite and survey data, including SST data from an analysis of AVHRR imagery and bathymetric data from ship surveys (Fig. 1). Ecophysiological parameters were used to set acceptable limits for each variable.

The bathymetric component of the model included extensive data from a range of remotely sensed sources, specifically:

1. Data from ship surveys and digitised hydrographic maps *c.* 1994 provided by W. Chadwick (http://www.pmel.noaa.gov/vents/staff/chadwick/galapagos.html, accessed 16 May 2008), including high resolution mapping data and all known measurements for this area (Fig. 2).
2. A 3 arc-second resolution digital elevation model of the islands derived from the Shuttle Radar Topography Mission (SRTM) (Global Land Cover Facility, http://glcfapp.umiacs.umd.edu:8080/esdi/index.jsp, 16 May 2008). These data allowed the terrestrial topography of the islands to be included in determining the slope gradient transition from land to water at a high spatial resolution.
3. The coastlines of the islands, provided by the Charles Darwin Research Station (CDRS) to force a clear delineation between the marine and terrestrial environments, through the assignment of a weighted value.

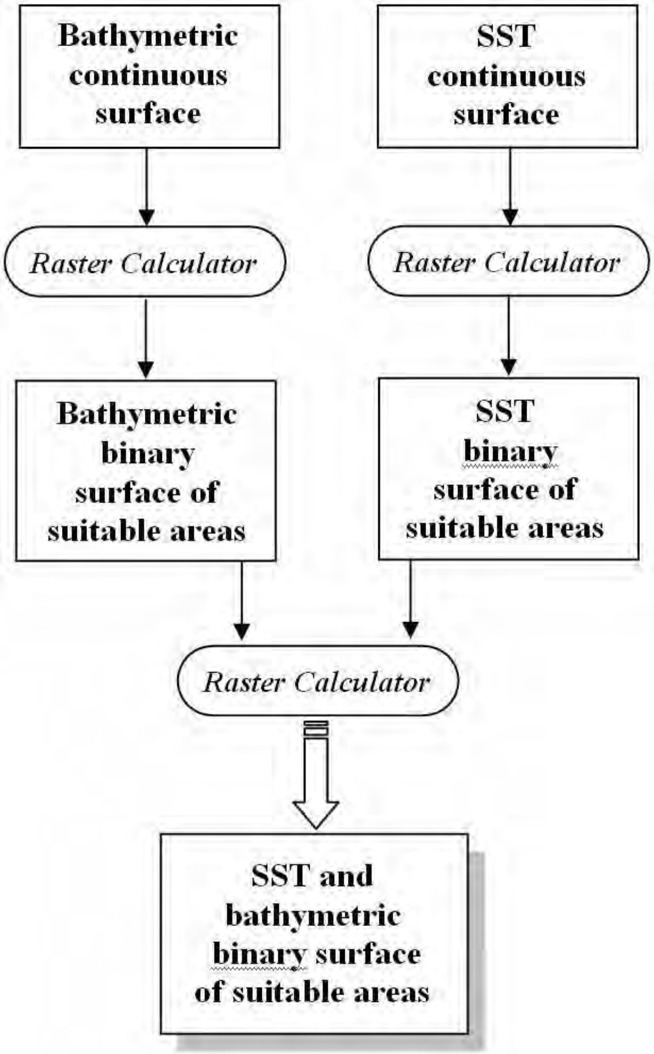


Figure 1. Steps in producing the habitat suitability map.

After integrating all the data, interpolation using ordinary kriging was deployed to generate a regular gridded bathymetric data set where pseudo-depths were estimated in locations where measurements had not been recorded. However, the accuracy of the resultant bathymetric map depends strongly upon the density of ship survey data, and the distribution of ship track data was very uneven and sparse across much of the archipelago (see W. Chadwick website for further information).

The interpolated bathymetric data were then bounded to depths suitable for coral formation. Nybakken (2001) determined that coral reefs worldwide are limited to

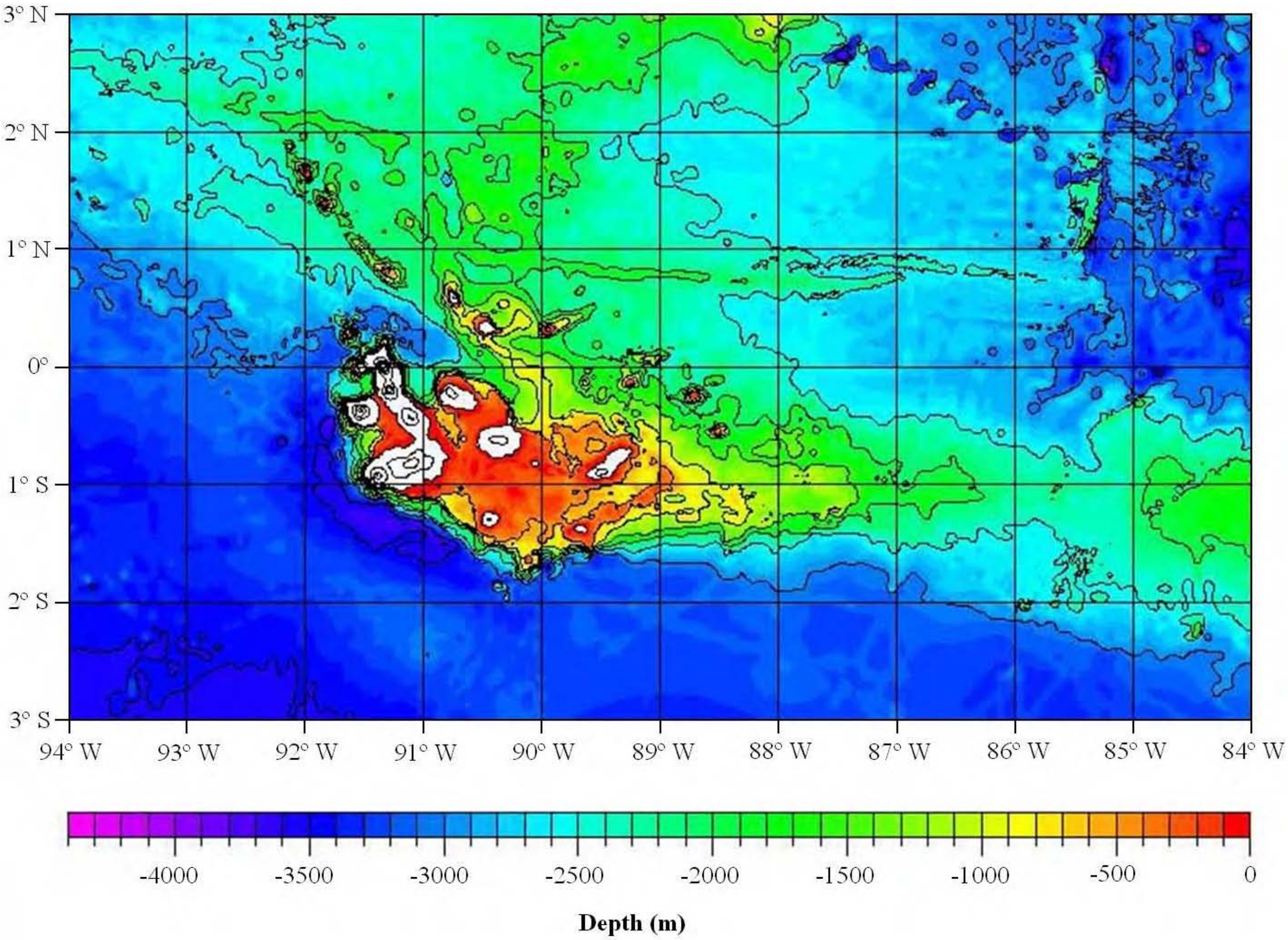


Figure 2. Interpolated ship-survey bathymetry data.

≤ 80 m depth. However, Glynn (2003) discovered that many of the hermatypic coral communities around the Galapagos Islands were found in < 20 m, which may reflect the high water turbidity (and low light penetration) in the Galapagos Islands compared to other regions of the world, due to high zooplankton concentrations during the period from June to October, when the nutrient-rich Humboldt Current runs up the west coast of South America from Antarctica. The bathymetry constraints were therefore conservatively set at 1–50 m depth.

The SST component of the model was based on AVHRR data at 4 km resolution for the area 88–93°W and 3°N to 3°S, acquired through the NASA Physical Oceanography Distributed Active Archive Center (PO.DAAC) utilising the Ocean ESIP Tool (http://poet.jpl.nasa.gov/ accessed 23 July 2006). Monthly averages for 1985–2001 were used to calculate the absolute minimum, maximum and average SST over this period. It was necessary to take into consideration the influence of ENSO events on our analysis; the SST anomalies during the well-documented 1997–8 event were therefore considered separately. The AVHRR data provided a record of SSTs throughout the study area. Because of missing data due to pixel removal as a result of coastal–terrestrial contamination, an inverse distance weighting of the SSTs was undertaken to fill missing values. A mosaic of three Landsat ETM+ images for March 2001 was also used to compare the coastal effect on SSTs at high resolution (60 m) with the AVHRR coastal pixels. Digital number (DN) values from the Landsat ETM+ thermal band were converted to radiances in degrees C using the following equations (see Trisakti *et al.* 2004, Lu 2005):

$$L_\lambda = \frac{(Lmax_\lambda - Lmin_\lambda)}{(DNmax - DNmin)} . (DN - DNmin) + Lmin_\lambda \quad (1)$$

$$T_{Landsat} = \frac{K2}{\ln((K1/L_\lambda) + 1)} - 273 \quad (2)$$

Where:

L_λ = Spectral radiance ($W.sr^{-1}.m^{-2}$)
DN = Digital Number
$Lmin_\lambda$ = Spectral radiance that correlates to DNmin ($W.sr^{-1}.m^{-2}$)

Lmax_λ = Spectral radiance that correlates to DNmax ($\text{W.sr}^{-1}.\text{m}^{-2}$)
DNmin = Minimum value of DN (1 or 0)
DNmax = Maximum value of DN = 255
T_{Landsat} = Effective temperature (Celsius)
K1 = 666.09 ($\text{W.sr}^{-1}.\text{m}^{-2}$), constant
K2 = 1282.71 ($\text{W.sr}^{-1}.\text{m}^{-2}$), constant

Six 4-km transect profiles, chosen at random to reflect different coastal depth gradients and temperature variation across the region, were delimited on the ETM+ images perpendicular to the coast of the islands to evaluate within-pixel variability and the coastal effect of SSTs on the AVHRR data.

To determine the most suitable SST range around the Galapagos Islands, known coral sites were overlaid on a map of average SST. The suitable range was found to be 23–25°C. However, as individual daily SSTs exceed the monthly mean values during the period from March to June, and in consideration of the optimum figures suggested by Kaiser *et al*. (2005), a range of 18–28°C was chosen as acceptable for coral reef habitats. Values beyond this range were classified as unsuitable, where stress and bleaching may be evident.

The location of known coral communities and coral reefs around the islands was acquired from a number of sources including 1-km polygons from the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) and point data provided by the CDRS. Other sources included extrapolation from maps, literature and field surveys from around the Galapagos Islands (Glynn 2003). The mortality of corals caused by the 1982–3 and 1997–8 ENSO events has undoubtedly changed their current status compared to earlier observations. Consequently, the integration of these records in the model was limited to the addition of depth and localities of known coral communities to the bathymetry database and testing of the baseline habitat suitability map.

RESULTS

The interpolated AVHRR SST imagery for the Galapagos Islands shows considerable differences in SSTs between the 1997–8 ENSO event and the whole period excluding the 1997–8 period (Fig. 3). Many of the thermal patterns are evident in both images, including the cool ocean upwelling in the southwest and the latitudinal temperature gradient. However, the pattern of warm water regions on the southern coasts of several islands (Marchena, Santiago, Santa Cruz, San Cristóbal, Fernandina, Isabela, Floreana and Española) during the 1997–8 ENSO event was not evident in the non-ENSO years.

Excluding during El Niño events, areas in the southwest were found to experience temperatures as low as 16°C due to upwelling, thus making them uninhabitable for hermatypic corals. The maximum SST divided the study area, with the northern section exceeding the temperature tolerance for reef growth and the south remaining suitable. The duration of extreme fluctuations in temperature will also affect coral survival, with prolonged periods causing stress, possible bleaching and mortality.

Investigation of the coastal effect on SSTs showed variation in SST across the 4-km transects, with most profiles experiencing the greatest deviation very close to

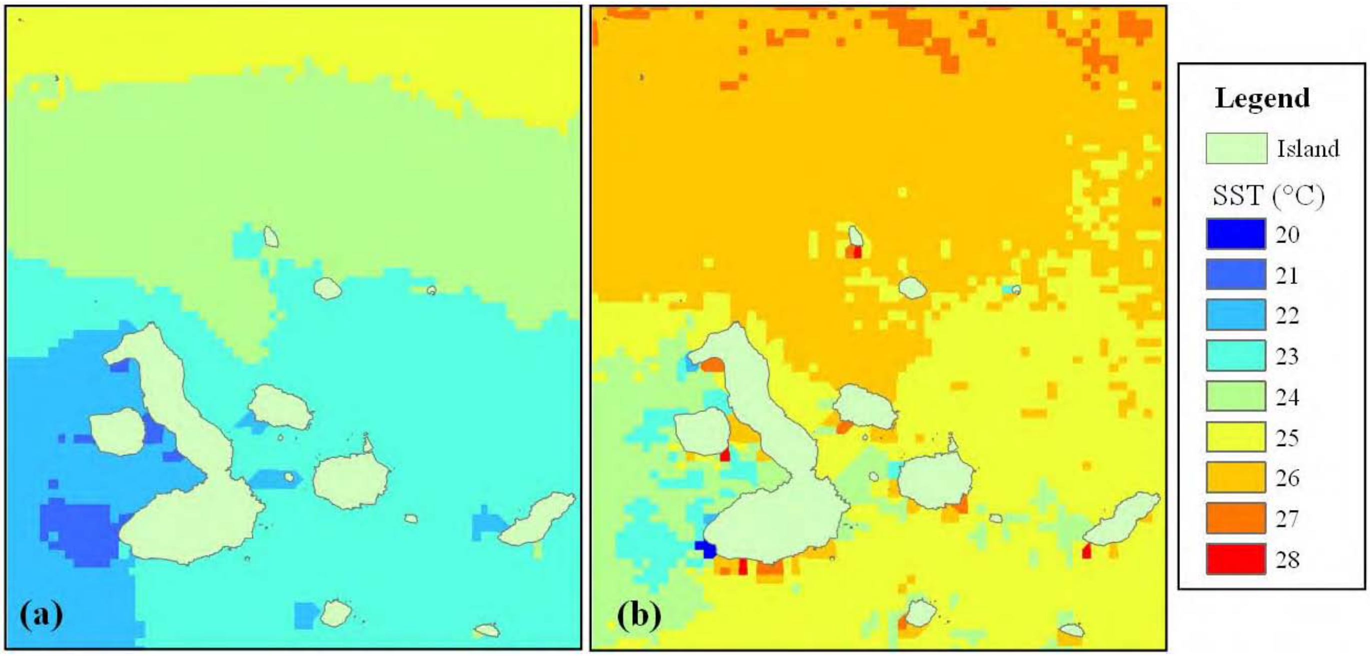


Figure 3. Mean SSTs (a) excluding El Niño records (1985–2001) and (b) during El Niño events (1997–1998).

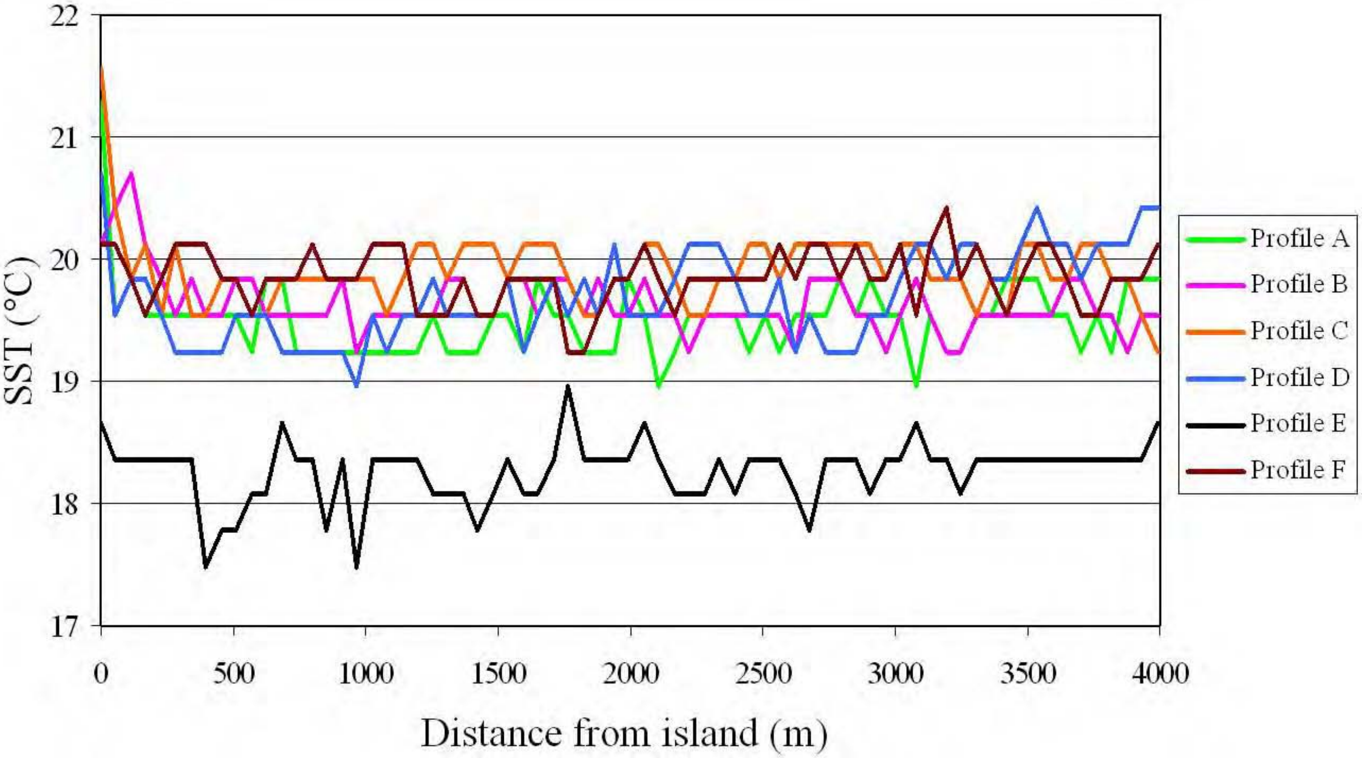


Figure 4. Variation in SST over six 4-km transects perpendicular from the coastline around the Galapagos Islands.

the coast (Fig. 4). Profile E recorded generally lower temperatures, as it was located in a cool upwelling region. However, all SSTs were within ± 1°C variability across the 4 km profile of the AVHRR pixel, so we remain confident that the AVHRR SST data are adequate for delineating coral temperature suitability.

With mean monthly SSTs within 18–28°C, the baseline historical habitat map was subsequently constrained by the bathymetry (Fig. 5), and compared against known coral distributions. Results were good, with all the known coral sites captured within the predicted suitable habitat areas. However, the model over-predicted for many potentially suitable areas where corals have not been recorded.

DISCUSSION

A coral reef habitat suitability model based upon a bioclimatic envelope approach is applied in the Galapagos Islands, illustrating that extensive potentially suitable coral habitat exists around all of the islands, with a greater abundance in the central area where a shallow plane links the islands. The non-existence of coral reefs in many of the over-predicted areas of potential suitability can be attributed to the absence of a hard benthic substrate, which is essential for corals to establish. Most of these areas have sandy or soft sediment substrates, although it is conceivable that new reefs might be found in such areas where surveys have not yet been carried out. Recent El Niño events have caused extensive bleaching and subsequent mortality throughout the archipelago and field research remains necessary to determine the current extent and scope of recovery for these critical habitats.

SSTs of up to 31°C in both the 1982–3 and 1997–8 ENSO events (Glynn *et al*. 2001) resulted in extensive bleaching and coral mortality across the archipelago, particularly in the shallow plane linking the central islands. Significant coral reefs in the south and west sectors of the archipelago were at Devil's Crown and Champion Island (off Floreana), east of Puerto Villamil (southern Isabela), Punta Baquerizo (western point of Santiago) and in tidal pools near Punta Espinosa (east Fernandina). These were lost due to coral mortality and subsequent bio-erosion by urchins following the 1982–3 ENSO event with only a few isolated coral communities remaining.

Glynn *et al*. (2001) estimated that over 95% of coral populations were killed in the 1982–3 event. However, recent surveys in Darwin Island reported significant recovery, with actively accreting reef structures (Glynn *et al*. 2009). This suggests that corals are resilient to episodic extreme temperatures given enough time for recovery and where the original reef structures remain intact and there remains a source of coral propagules.

Kaiser *et al*. (2005) suggested that the latitudinal range of coral reefs corresponds with a temperature range of 18–36°C, with optimum reef development occurring at 26–28°. The average temperatures during the 1997–8 El Niño event verged on the upper 28° tolerance limit. Coral reefs tend to live at the upper limit of their temperature

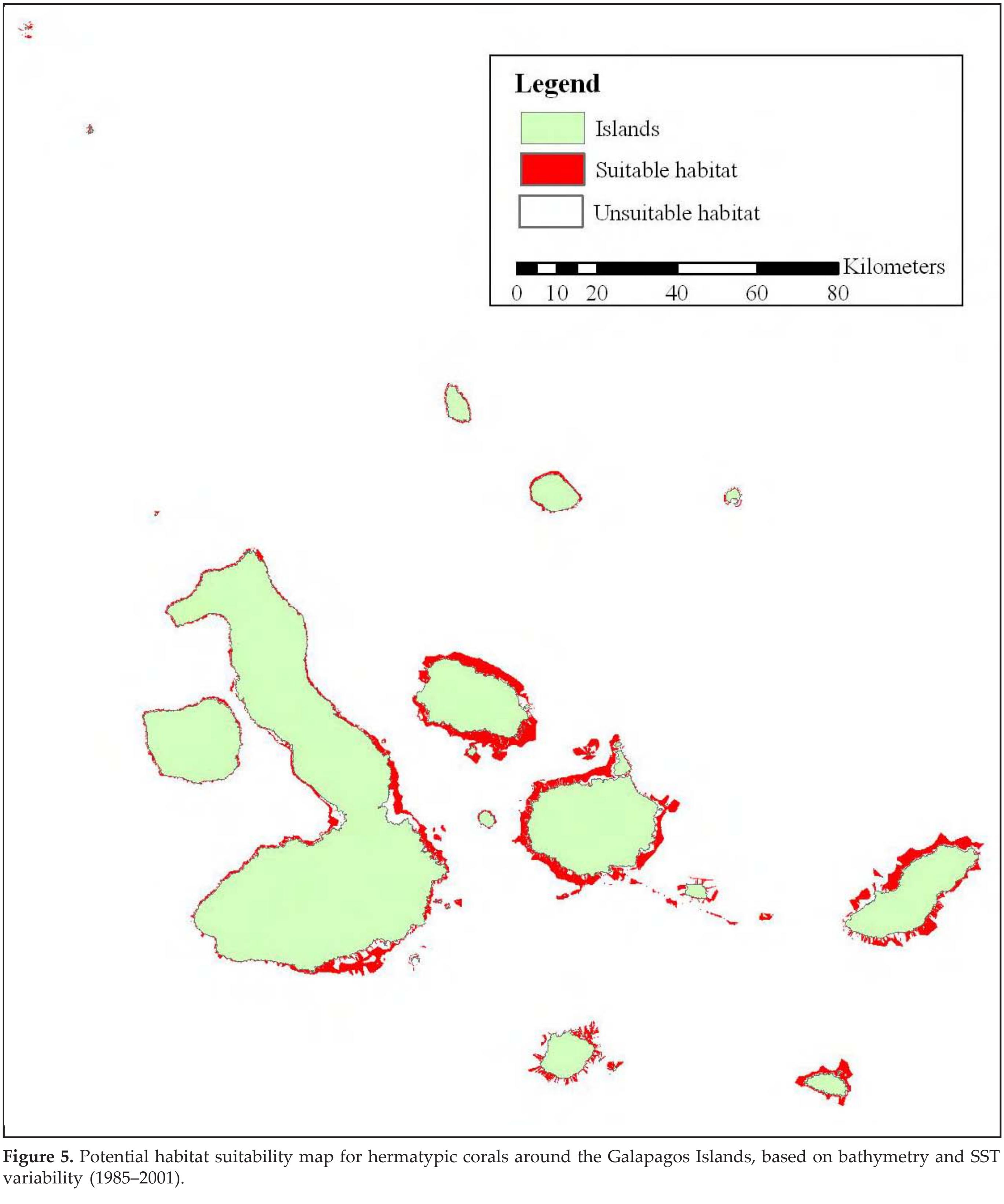


Figure 5. Potential habitat suitability map for hermatypic corals around the Galapagos Islands, based on bathymetry and SST variability (1985–2001).

tolerance and bleaching may result from slight increases (1–2°C) over a sustained period of time (Hoegh-Guldberg 1999). Other studies have identified the significance of temperature anomalies rather than absolute temperatures in determining the temperature tolerance of corals (Goreau *et al*. 1993, Goreau & Hayes 1994). For example, the absolute temperatures in Panama were higher than those in Galapagos during the 1982–3 ENSO event, yet mortality was lower in Panama since the anomaly was less (Glynn *et al*. 2001).

The potential habitat suitability map (Fig. 5) does not account for substrate, which can determine coral presence, as they require a hard foundation for establishment. Maps of hard substrates in the coastal zone of the Galapagos Islands would significantly improve the potential habitat suitability model.

ACKNOWLEDGMENTS

This research was funded under theDEFRA Darwin Initiative project 14-048 *Galapagos Coral Conservation: Impact Miti-gation, Mapping and Monitoring*. We thank Stuart Banks (CDRS), Peter Glynn (University of Miami) and UNEP-WCMC for providing coral mapping, survey data and other materials.

LITERATURE CITED

Fitt, W.K., Brown, B.E., Warner, M.E. & Dunne, R.P. 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20: 51–65.

Glynn, P.W. 1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12: 1–17.

Glynn, P.W. 2003. Coral communities and coral reefs in Ecuador. Pp. 449–472 *in* Coatés, J. (ed.), *Latin American Coral Reefs*. Elsevier, Amsterdam.

Glynn, P.W., Maté, J.L., Baker, A.C. & Calderón, M.O. 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation Event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69: 79–109.

Glynn, P.W., Riegl, B., Romanski, A.M. & Baums, I.B. 2009. Rapid recovery of a coral reef at Darwin Island, Galapagos Islands. *Galapagos Research* 66: 6–13.

Goreau, T.J. & Hayes, R.L. 1994. Coral bleaching and ocean "hot spots". *Ambio* 23: 176–180.

Goreau, T.J., Hayes, R.L., Slarke, J.W., Basta, D.J. & Robertson, C.N. 1993. Elevated sea surface temperatures correlate with Caribbean coral reef bleaching. Pp. 225–255 *in* Geyer, R. (ed.) *A Global Warming Forum: Scientific, Economic, and Legal Overview*. CRC Press, Boca Raton.

Guinotte, J.M., Bartley, J.D., Iqbal, A., Fautin, D.G. & Buddemeier, R.W. 2006. Modeling habitat distribution from organism occurrences and environmental data: case study using anemonefishes and their sea anemone hosts. *Marine Ecology Progress* 31: 269–283.

Hoegh-Guldberg, O. 1999. Climate change: coral bleaching and the future of the world's coral reefs. *Marine Freshwater Research* 50: 839–866.

Kaiser, M.J., Attrill, M., Jennings, S., Thomas, D.N., Barnes, D., Brierley, A., Polunin, N., Raffaelli, D. & Williams, P. 2005. *Marine Ecology: Processes, Systems, and Impacts*. Oxford University Press, Oxford.

Lu, D. 2005. Urban classification using full spectral information of landsat ETM+ imagery in Marion Country, Indiana. *Photogrammetric Engineering and Remote Sensing* 71: 1275–1284.

Nybakken, J.W. 2001. *Marine Biology, an Ecological Approach* (5th ed.). Benjamin Cummings, San Francisco.

Obura, D.O. 2005. Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science* 63: 353–372.

Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361–371.

Reaser, J.K., Pomerance, R. & Thomas, P.O. 2000. Coral bleaching and climate change: scientific findings and policy recommendations. *Conservation Biology* 14: 1500–1511.

Stone, L., Huppert, A., Rajagopalan, B., Bhasin, H. & Loya, Y. 1999. Mass coral bleaching: a recent outcome of increased El Niño activity? *Ecology Letters* 2: 325–330.

Trisakti, B., Sulma, S. & Budhiman, S. 2004. Study of sea surface temperature (SST) using Landsat-7 ETM. Pp. 1–5 *in*: *Proceedings, Thirteenth Workshop of OMISAR — validation and application of satellite data for marine resources conservation*. Asia-Pasific Economic Cooperation, Bali.

West, J.M. & Salm, R.V. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology* 17: 956–967.

OCTOCORALS IN THE GALAPAGOS ISLANDS

By: Odalisca Breedy[1], Cleveland P. Hickman, Jr[2] & Gary C. Williams[3]

[1]Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica 2060,
San José, Costa Rica
[2]Department of Biology, Washington & Lee University, Lexington, VA 24450, U.S.A.
[3]Department of Invertebrate Zoology and Geology, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118, U.S.A.

SUMMARY

The Galapagos octocorals were almost unknown until recent years. Of the three orders within the subclass Octocorallia (Anthozoa, Cnidaria), the Pennatulacea (sea pens) and Alcyonacea (soft corals and gorgonians) occur in the Galapagos. Recent collections and research bring the total known octocorallian fauna to three sea pens (*Virgularia galapagensis, Ptilosarcus undulatus* and *Cavernulina darwini*) and 15 gorgonians. Of the 13 gorgonians that we have collected, several are new species. *Pacifigorgia* is widely distributed in the archipelago, with four named species (*P. dampieri, P. symbiotica, P. rubripunctata*, and *P. darwinii*), three of them recently described, and two others yet to be described. The genus *Muricea* contains three widely distributed undescribed species, one of which appears in three chromotypes, and one deep-water species that has not been collected recently. Two species of *Heterogorgia* occur in the central archipelago, *H. verrucosa* and the recently described and widely distributed *H. hickmani.* The remaining gorgonians are *Eugorgia daniana, Leptogorgia alba* and *Adelogorgia telones.*

RESUMEN

Octocorales en las Islas Galápagos. Hasta hace pocos años, los octocorales de las Islas Galápagos eran muy poco conocidos. De los tres órdenes que comprende la subclase Octocorallia (Anthozoa, Cnidaria), los Pennatulacea (plumas de mar) y Alcyonacea (corales suaves y gorgonias) aparecen en las Galápagos. Por medio de investigación y recolectas recientes se ha encontrado que la fauna de octocorales está compuesta por tres plumas de mar (*Virgularia galapagensis, Ptilosarcus undulatus* y *Cavernulina darwini*) y por 15 gorgonias. Nosotros hemos recolectado 13 gorgonias y de ellas, algunas son especies nuevas. El género *Pacifigorgia* con cuatro especies descritas (*P. dampieri, P. symbiotica, P. rubripunctata* y *P. darwinii*), tres de estas descritas recientemente, más dos probablemente nuevas, se encuentra ampliamente distribuido en el archipiélago. El género *Muricea* contiene tres especies que no se han descrito y que están ampliamente distribuidas, de las cuales una presenta tres cromotipos, más una especie de profundidad que no ha sido recolectada recientemente. Del género *Heterogorgia*, dos especies aparecen en el archipiélago central, *H. verrucosa* y *H. hickmani*. Esta última, ha sido descrita recientemente y se encuentra ampliamente distribuida. Las otras gorgonias son *Eugorgia daniana, Leptogorgia alba* y *Adelogorgia telones.*

INTRODUCTION

The marine faunas of oceanic islands are of great biogeographical interest, providing insights into endemism, dispersal patterns, and evolution through comparisons with mainland faunas (Quammen 1996, Hickman 2009). There are five main oceanic islands or archipelagos in the tropical E Pacific: Cocos Island, Costa Rica; Malpelo Island, Colombia; the Revillagigedo Islands, Mexico; Clipperton Island, France; and the Galapagos, Ecuador. Each is separated from the mainland by at least 435 km (Malpelo) and up to 1300 km (Clipperton), and also by abyssal depths (Kaiser & Bryce 2001). Numerous expeditions have yielded a considerable literature on certain taxonomic groups on these islands. However some groups of marine invertebrates, including the Octocorallia, have received little attention. Although several octocoral species have been photographed and collected from these islands, published records exist only from Cocos and Galapagos. The Galapagos are the largest group of islands in the tropical E Pacific, and the subject of considerable research, but the marine fauna, especially the octocorals, was almost unknown until recently. This paper summarises our knowledge of the octocorals of Galapagos.

THE OCTOCORALS

The subclass Octocorallia (class Anthozoa) comprises sedentary, mostly colonial marine animals, distinguished from the true, or stony, corals by their octoradial symmetry, pinnate tentacles, and skeletal elements of calcium carbonate, called sclerites, in their tissue. Many taxa also have proteinaceous and calcified axial skeletons. The Octocorallia comprise three orders: Helioporacea (blue corals), Pennatulacea (sea pens), and Alcyonacea (soft corals and gorgonians). Sea pens and gorgonians occur in the Galapagos.

The Pennatulacea have colonies formed by a very large primary polyp called the oozooid, on the wall of which the coenenchyme spreads with numerous small (secondary) polyps. The primary polyp may be additionally supported by a horny axis, and part of it forms the peduncle that anchors the colony in sand or soft substrates. The other part of the oozooid forms the rachis, which bears other kinds of polyps: autozooids and siphonozooids. In some species the emergent part looks like a feather (thus the name sea pens) (Williams 1990, Fabricius & Alderslade 2000).

Alcyonacean soft corals have not been reported in the Galapagos. Gorgonians, the most abundant octocorals in the Galapagos, include sea rods, sea whips, sea candelabra, sea feather plumes and sea fans. They present very diverse growth forms: encrusting colonies, upright fans and bushes with slender branches, or simple whips. Gorgonian colonies have a central axial skeleton composed of a collagenous matrix called gorgonin, and calcifications within the collagen interstitial spaces (Jeyasuria & Lewis 1987). A layer of coenenchyme with sclerites and polyps surrounds it.

There are an estimated 2900 species of octocorals worldwide although new species and even genera continue to be described at a rapid rate. In Galapagos, nine shallow-water (<50 m) and one deep-water octocoral species have been reported in the literature and eight more shallow-water species are reported here (Table 1). The species listed in the table, except *Adelgorgia telones*, which has not been collected since it was described by Bayer (1978), are described in more detail, with photographs, in Hickman (2008).

Main identification sources are Bayer (1981) and Williams (1995). There is also a key to octocoral families, complete bibliography of octocoral literature and listing of current genera by G. Williams at http://www.calacademy.org/research/izg/isg_researchl_ink.htm. Octocoral species are identified by colony morphology

Table 1. Distribution of shallow-water (< 50 m) octocoral species in the Galapagos Islands. * indicates records not previously published.

Species	Sites
Order Pennatulacea:	
Cavernulina darwini Hickson 1921 (Veretillidae)	San Cristóbal.
Virgularia galapagensis Hickson 1930 (Virgulariidae)	Isabela (Tagus Cove). Santiago (James Bay).
Ptilosarcus undulatus (Verrill 1865) (Pennatulidae)	Wolf, Isabela (Tagus Cove).
Order Alcyonacea: Suborder Holaxonia: Family Gorgoniidae:	
Pacifigorgia dampieri Williams & Breedy 2004[1]	Darwin, Wolf, Roca Redonda.
Pacifigorgia darwinii (Hickson 1928)[1]	Isabela (Cuatro Hermanos islets, Tagus Cove, Punta Moreno, Punta Vicente Roca), Fernandina (Punta Espinosa), Floreana (La Botella rock), San Cristóbal (and Kicker Rock), Pinzón.
Pacifigorgia symbiotica Williams & Breedy 2004[1]	Darwin, Wolf, Isabela (Caleta Iguana, Cabo Rosa).
Pacifigorgia rubripunctata Williams & Breedy 2004[1]	Bartolomé, Española, Rábida, Nameless, Santiago, Floreana (Gardner islet), Isabela (Cuatro Hermanos islets), Genovesa.
**Pacifigorgia* sp. 1 (*P.* cf. *symbiotica*)[1]	Wolf.
**Pacifigorgia* sp. 2 (*P.* cf. *rubripunctata*)[1]	Nameless.
**Eugorgia daniana* Verrill 1868	Genovesa, Nameless, Pinzón.
Leptogorgia alba (Duchassaing & Michelotti 1864)	Darwin, Wolf.
Order Alcyonacea: Suborder Holaxonia: Family Plexauridae:	
Adelogorgia telones Bayer 1979[1]	San Cristóbal (Kicker Rock).
**Muricea* cf. *fruticosa* Verrill 1868	Isabela (Cuatro Hermanos islets, Punta Vicente Roca), Nameless, San Cristóbal (Punta Pitt, Whale Rock), Darwin.
**Muricea* sp. 1[1]	Fernandina (Cabo Douglas), Isabela (Punta Albermarle, Punta Vicente Roca, Tagus Cove, Tortuga islet), Nameless, Pinzón, Floreana (La Botella rock, Gardner islet), Santiago (Bainbridge Rocks), San Cristóbal (Kicker Rock).
**Muricea* sp. 2 purple variety[1]	Darwin, Genovesa.
**Muricea* sp. 2 yellow/orange variety[1]	Darwin, Genovesa, Floreana (Devil's Crown islets).
**Muricea* sp. 2 white variety[1]	Darwin, Floreana (Devil's Crown islets), Santa Fe (NW), San Cristóbal (Whale Rock).
Heterogorgia hickmani Breedy & Guzman 2005[1]	Pinzón, Floreana (La Botella rock, Devil's Crown islets), San Cristóbal (Kicker Rock, Five Fingers rocks), Isabela (Las Marielas islets, Caleta Black, Tagus Cove and south of there, Punta Albemarle, Caleta Iguana, Tortuga islet), Santa Fe (NW), Rábida, Santa Cruz (Gordon Rocks), Española.
**Heterogorgia verrucosa* Verrill 1869	Santa Cruz (Gordon Rocks).

[1] Known only from Galapagos.

(branching pattern, colour and shape) and sclerite morphology (sizes, colours, forms and abundance of the different types of sclerite). However, morphological characteristics can be modified by the environment, and intergrading forms may confound some identifications (Breedy & Guzman 2003, 2007). For identification and molecular studies, specimens ideally should be collected complete and preserved in 70–95% ethanol (never formalin as this dissolves the sclerites). However, most octocorals can be identified on sclerite morphology using a much smaller sample, as little as a few polyps. For the study of sclerites, fragments from colonies are treated with sodium hypochlorite to dissociate sclerites from tissue, washed several times in distilled water, dehydrated with 100% ethanol, then air or oven dried and prepared for scanning electron microscopy or light microscopy. For further details of the methodology, see Breedy & Guzman (2002) and http://www.calacademy.org/research/izg/OctoResearchTech.htm.

RESULTS

The first octocoral specimen from Galapagos was a fragment of probably *Pacifigorgia darwinii* collectedby Charles Darwin in 1835 (Hickson 1921, 1928), which was deposited in the University Museum of Zoology, Cambridge, U.K. Unfortunately this specimen was misplaced or lost (R. Preece pers. comm.). Two species of Pennatulacea and three species of *Pacifigorgia* (under the name *Gorgonia*) were reported from the C. Crossland S.Y. St George voyage (Hickson 1928, 1930, Stiasny 1941, 1943), and one alcyonacean, described as *Muricea galapagensis*, came from the Presidential Cruise of 1938 (Deichmann 1941). Bayer (1978) described *Adelogorgia telones* from collections by W.D. Hope in 1978. Several specimens collected during the R.V. Anton Bruun Cruise in 1966 were deposited in the Museum of Comparative Zoology of Harvard University and later identified as *Pacifigorgia rubripunctata* (Williams & Breedy 2004). Collections made by the 1986 Harbor Branch Oceanographic Institution expedition to the Galapagos, Cocos, and Pearl Islands contain a number of octocorals from deep waters that may yield new species. Collections made by the 1994 California Academy of Science Marine Expedition to the Galapagos, periodic marine surveys by the Charles Darwin Research Station, Galapagos, and numerous collections by CPH from 1996 to 2007 have produced three new species of *Pacifigorgia* (Williams & Breedy 2004), one new species of *Heterogorgia* (Breedy & Guzman 2005), specimens of the pennatulid *Ptilosarcus*, one species of *Eugorgia*, one of *Leptogorgia*, and probably three or four species of *Muricea*. Several are expected to represent species new to science (Table 1).

Geographic distribution of Galapagos shallow-water species is shown in Table 1. In addition to the species in the table, *Muricea galapagensis*, a deep-water species (> 50 m) collected in 1938 at Isabela Island (Deichmann 1941), has not been reported since.

Figure 1. *Leptogorgia alba*, Darwin´s Arch, Darwin Island. Photograph: CPH.

Although sea pens were believed to have disappeared from Galapagos following the 1982–3 El Niño event, all three species have been observed recently at depths below 40 m (S. Banks pers. comm.).

Among the Gorgoniidae, *P. dampieri*, *P. symbiotica* and *Leptogorgia alba* (Fig. 1) have been found at the northernmost islands of Darwin and Wolf. A species similar to *P. symbiotica* was also found at these islands but its status is not yet resolved. *P. rubripunctata* was found mostly at the central and eastern islands, while a similar species, *Pacifigorgia* sp. 2 was found coexisting with *P. rubripunctata* at Santa Cruz. *P. darwinii* (Fig. 2) was found throughout the central and western archipelago. It is the species with the widest range, but is not reported for Darwin and Wolf. *Eugorgia*

Figure 2. *Pacifigorgia darwinii*, Roca Onan, Pinzón Island. Photograph: Angel Chiriboga.

Figure 3. *Eugorgia daniana*, Darwin Bay, Genovesa Island. Photograph: CPH.

Figure 4. *Muricea* cf. *fruticosa*, Cuatro Hermanos islets, Islabela. Photograph: CPH.

daniana (Fig. 3) was found at Genovesa, Pinzón and Nameless.

Of the Plexauridae, two of the *Muricea* spp. are probably new to science. *Muricea* sp. 2 comprises three chromotypes (purple, yellow/orange, and white), found together in Darwin. *M.* cf. *fruticosa* (Fig. 4) is distributed throughout the archipelago, while *Muricea* sp. 1 is restricted to the central and southern archipelago. *Heterogorgia hickmani* occurs throughout the central and southern archipelago, while *H. verrucosa* has been reported only from Santa Cruz. No specimens of *Adelogorgia telones* have been recovered since the initial report by Bayer (1978).

DISCUSSION

Studies of octocoral diversity at other E Pacific oceanic islands are scarce; only records from Cocos are available for comparison, where only three species of gorgonians have been reported, in shallow waters: *Pacifigorgia curta* (Breedy & Guzman 2003), *Leptogorgia alba* (Breedy & Guzman 2007) and a new, unnamed species of *Leptogorgia*. Only *L. alba*, which is a widespread species, is present in both Cocos and Galapagos. The pennatulid *Ptilosarcus undulatus* that was reported for Cocos (Deichmann 1941) needs validation, owing to an inadequate description of the Cocos specimen. Because Galapagos has a wider range of biotopes and is much larger than Cocos, its diversity is higher, at least in shallow waters.

The Galapagos octocoral fauna includes more species than reported from Ecuador's mainland coast. The few published records for the mainland include two species of *Leptogorgia* and two of *Eugorgia* (Bielschowsky 1929), although many others have been observed in recent explorations (S. Luna, D. Ruiz, pers. comm.). At present, all of the thirteen largest islands and many of the smaller islands of the Galapagos have been searched for shallow water species of octocorals, but other sites remain to be explored and new records and new species are expected. Meaningful comparison of gorgonian diversity in Galapagos, the Ecuador mainland and other oceanic islands will only be possible when comprehensive surveys equivalent to those in the Galapagos are completed.

ACKNOWLEDGMENTS

We are especially grateful to the Charles Darwin Research Station whose sustained support of CPH's research over the years has made possible the collections that formed a large part of OB's taxonomic research on Galapagos octocorals. Although many people assisted in the field, we are especially grateful to Angel Chiriboga, Bill Ober and Fred Liss for assistance in sample collection, and the captain and crew of the *Tip Top IV* during the 2007 collections. We also are grateful to Jorge Cortés who read and offered helpful comments on this manuscript. The authors would like to thank the U.K. Department for Environment, Food and Rural Affairs' Darwin Initiative Project 14-048 *Galapagos Coral Conservation: Impact Mitigation, Mapping and Monitoring* for supporting the 2006–7 expeditions to the northern islands of Galapagos, where some of the recent specimens were collected.

LITERATURE CITED

Bayer, F.M. 1978. *Adelogorgia telones*, a new species of Gorgonacean coral (Coelenterata: Octocorallia) from the

Galapagos Islands. *Proceedings of the Biological Society of Washington* 91: 1026–1036

Bayer, F.M. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. *Proceedings of the Biological Society of Washington* 94: 901–947.

Bielschowsky, E. 1929. Die Gorgonarien Westindien. 6. Die Familie Gorgoniidae, zugleich eine Revision. *Zoologische Jahrbücher*, Suppl. 16: 63–234.

Breedy, O. & Guzman, H.M. 2002. A revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Proceedings of the Biological Society of Washington* 115: 787–844.

Breedy, O. & Guzman, H.M. 2003. The genus *Pacifigorgia* (Octocorallia:Gorgonacea) in Costa Rica (Coelenterata: Octocorallia: Gorgoniidae). *Zootaxa* 281: 1–60.

Breedy, O. & Guzman, H.M. 2005. A new species of alcyonacean octocoral from the Galapágos Archipelago. *Journal of the Marine Biological Association* 85: 801–807.

Breedy, O & Guzman, H.M. 2007. A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. *Zootaxa* 1407: 1–90.

Deichmann, E. 1941. Coelenterates collected on the Presidential Cruise of 1938. *Smithsonian Miscellaneous Collections* 99(10): 1–17.

Fabricius, K. & Alderslade, P. 2000. *Soft Corals and Sea Fans: a Comprehensive Guide to the Tropical Shallow Water Genera of the Central-west Pacific, the Indian Ocean and the Red Sea.* Australian Institute of Marine Sciences, Townsville.

Hickman, C.P. Jr. 2008. *A Field Guide to Corals and Other Radiates of Galapagos*. Sugar Spring Press, Lexington.

Hickman, C.P., Jr. 2009. Evolutionary responses of marine invertebrates to insular isolation in Galapagos. *Galapagos Research* 66: 32–42.

Hickson, S.J. 1921. Some Alcyonaria in the Cambridge Museum. *Proceedings of Philosophical Society* 20: 369.

Hickson, S.J. 1928. The Gorgonacea of Panama Bay together with a description of one species from the Galapagos Islands and one of Trinidad. *Videnskavelige Meddelelser fra den naturhistoriske Forening i Kovenhavn for Aarene* 85: 325–422.

Hickson, S.J. 1930. Some Alcyonarians from the eastern Pacific Ocean. *Proceedings of the Zoological Society of London* 14: 209–227.

Jeyasuria, P. & Lewis, J.C. 1987. Mechanical properties of the axial skeleton in gorgonians. *Coral Reefs* 5: 213–219.

Kaiser, K.L. & Bryce, C.W. 2001. The recent molluscan marine fauna of Isla Malpelo, Colombia. *The Festivus* 33: 1–11.

Quammen, D. 1996. *The Song of the Dodo.* Simon and Schuster, New York.

Stiasny, G. 1941. Studien über Alcyonaria und Gorgonaria I–V. (Parerga und Paralipomena). *Zoologische Anzeiger* 133: 268–271.

Stiasny, G. 1943. Gorgonaria von Panama. Aus der Sammlung Dr. Th. Mortensen, Zoologisk Museum, Kopenhagen. *Videnskavelige Meddelelser fra den naturhistoriske Forening i Kovenhavn for Aarene* 107: 59–103.

Williams, G.C. 1990. The Pennatulacea of southern Africa (Coelenterata, Anthozoa). *Annals of the South African Museum* 99: 31–119.

Williams, G.C. 1995. Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. *Zoological Journal of the Linnean Society* 113: 93–140.

Williams, G.C. & Breedy, O. 2004. The Panamic genus *Pacifigorgia* (Octocorallia: Gorgoniidae) in the Galápagos Archipelago. *Proceedings of the California Academy of Sciences* 55: 54–87

EVOLUTIONARY RESPONSES OF MARINE INVERTEBRATES TO INSULAR ISOLATION IN GALAPAGOS

By: Cleveland P. Hickman, Jr

Dept of Biology, Washington & Lee University, Lexington, Virginia 24450, U.S.A. <hickman.c@rockbridge.net>

SUMMARY

I examine the natural barriers to distribution and colonization that have shaped the Galapagos marine invertebrate biota. While diversity is high for some groups, such as hydroids and bryozoans, it is low for many others. Porcelain crabs and molluscs are examples with reduced or unbalanced representation in Galapagos, resulting from their dependency on dispersal of relatively short-lived planktonic larvae by ocean currents and on habitat limitations in Galapagos. Because Galapagos shorelines are predominantly rocky, without the wide expanses of silt typical of much of the Ecuadorian mainland that are favored by infaunal bivalves, gastropod diversity in Galapagos far exceeds that of bivalves. Nearly all hermatypic corals in Galapagos are members of the Panamic province; none is endemic to Galapagos. This suggests that colonization occurred by larval dispersal from there. The ahermatypic (azooxanthellate) coral fauna of Galapagos, with 43 species, is richer and more diverse than the hermatypic corals, with 29% of the shallow-water ahermatypes endemic and the remainder with Panamic, Indo-Pacific, and cosmopolitan affinities. The 73 verified species of Galapagos shallow-water echinoderms are dominated by Panamic species, with additional affinities to the Indo-Pacific and the California province; 8% are cosmopolitan and 8% endemic. With species richness roughly equivalent to that of Pacific Colombia, Galapagos echinoderm representation is not depauperate, but is sufficiently distinctive to characterize it as an isolated, insular biota. Hydroids and bryozoans, two groups with high diversity in Galapagos, accomplish long-distance transport mainly as adults on floating debris and hulls of ships, rather than by the free-swimming reproductive stage. Endemism among marine invertebrates averages 18.3 %, but varies widely among major taxa, from 0% for reef corals to 71% for gorgonians. Unlike the Galapagos terrestrial biota, in which endemic genera are common, the absence of endemic genera among marine invertebrates may be attributed to low isolation arising from greater dispersal and gene flow in the marine environment.

RESUMEN

Respuestas evolutivas al aislamiento insular de los invertebrados marinos en Galápagos. En este reporte examino las barreras naturales para la distribución y colonización que han modelado la biota de los invertebrados marinos de Galápagos. Mientras la diversidad es alta en algunos grupos, tales como hidroides y briozoos, es baja en muchos otros. Los cangrejos porcelana y moluscos son ejemplos con representación reducida o no balanceada en Galápagos, resultante de su dependencia en la dispersión por corrientes oceánicas de su larva planctónica de relativamente corta vida, y de limitaciones de hábitat en Galápagos. Debido a que las costas de Galápagos son predominantemente rocosas, sin las amplias extensiones de limo típicas de muchas de las costas ecuatorianas que son favorecidas por la infauna de bivalvos, la diversidad de gasterópodos en Galápagos excede por mucho la de los bivalvos. Casi todos los corales hermatípicos en Galápagos son miembros de la provincia Panámica; ninguno es endémico para Galápagos. Esto sugiere que la colonización ha ocurrido por dispersión larval desde dicha provincia. La fauna de corales ahermatípicos (azooxantelados) de Galápagos, con 43 especies, es más rica y más diversa que en los corales hermatípicos, con un 29% de especies de poca profundidad endémicas y las otras con afinidades Panámicas, Indopacíficos y cosmopolitas. Las 73 especies de equinodermos de poca profundidad verificadas para Galápagos están dominadas por especies Panámicas, con afinidades adicionales para el Indopacífico y la provincia de California; 8% son cosmopolitas y 8% endémicas. Con una riqueza de especies aproximadamente equivalente a la del Pacífico colombiano, la representación de los equinodermos de Galápagos no está depauperada, pero es lo suficientemente distintiva como para caracterizarla como una biota insular aislada. Hidroides y briozoos, dos grupos con alta diversidad en Galápagos, logran ser transportados largas distancias, principalmente como adultos sobre restos flotantes y cascos de barcos, más que por el estado reproductivo de libres nadadores. El promedio de endemismo entre invertebrados marinos es de 18.3%, pero varia ampliamente entre las principales taxas, desde el 0 % para corales hermatípicos hasta 71% para gorgonias. En contraste a la biota terrestre de Galápagos, la cual cuenta con muchos géneros endémicos, la ausencia de géneros endémicos entre los invertebrados marinos puede ser atribuida al bajo aislamiento que resulta de la mayor dispersión y flujo genético en los ambientes marinos.

INTRODUCTION

It has long been recognized that the flora and fauna of the Galapagos terrestrial environment are unbalanced compared to South American mainland biota. While some animal groups, such as reptiles, seabirds, marine mammals and land snails are well represented, others, such as amphibians, song birds, land mammals, aquatic insects, and freshwater fish are poorly represented or absent (Jackson 1993). Groups with obvious adaptations for dispersing long distances tend to be disproportionately common. Is this disharmonic representation also present in the marine environment of Galapagos? Answering this is hampered by uneven taxonomic investigations in the marine environment of the equatorial east Pacific, where some invertebrate groups have received much more attention than others. Before the introduction of scuba diving in the 1950s, explorations of subtidal life depended mainly on dredging, a notoriously clumsy and non-selective way to collect marine invertebrates. Nevertheless, the extensive collections of earlier expeditions, together with more recent surveys, allow us to begin to compare the marine biota of Galapagos with that of the South American mainland coast.

Diversity is high for groups with good dispersal, such as hydroids (Calder *et al* 2003), bryozoans (Banta 1991), cirripedians (Zullo 1991) and caridean shrimps (Wicksten 1991, Wicksten & Hendrickx 2003), but considered low for many other groups, such as molluscs (Finet 1991, 1994), echinoderms (Maluf 1991), benthic polychaetes (Blake 1991), hermatypic corals (Glynn 2003), and porcelain crabs (Haig 1960, Harvey 1991). Table 1 summarizes the number of species and degree of endemism in Galapagos marine groups. The proportion of both shore-dwelling and deep-water endemic marine organisms totals about 18%; this is comparable to other oceanic islands and archipelagoes, which range from 0 to 20% (Bustamante *et al.* 2002).

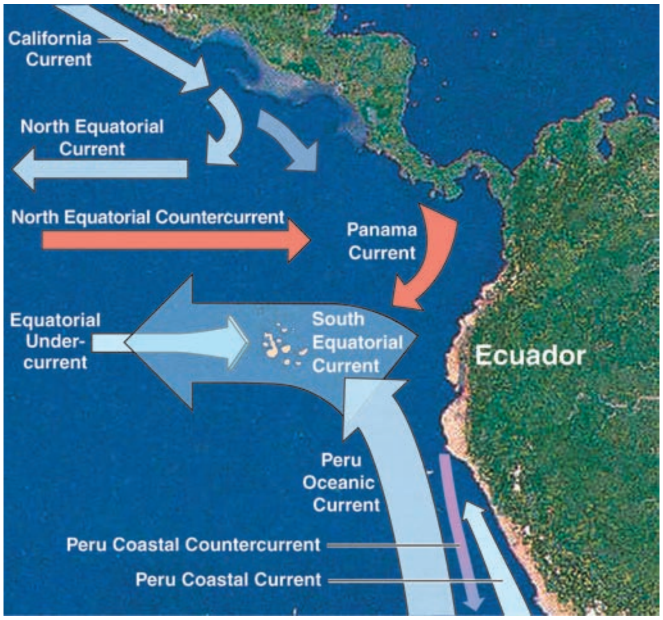


Figure 1. Currents of the east Pacific.

Trans-oceanic dispersal is heavily influenced by oceanic currents and the distribution of islands that may act as stepping stones. The Galapagos archipelago lies at the confluence of three oceanic currents (Fig. 1). The main current is the South Equatorial Current (SEC) which is fed principally by the cool (20–24°C) Peru Oceanic Current (POC). The Peru Coastal Current (PCC) carries cold water (as low as 13°C) but is separated from the POC by the Peru Coastal Countercurrent. When the POC reaches Galapagos its temperature is 18–22°C. The SEC is supported throughout the year by southeasterly trade winds that vary in strength seasonally. It is a strong current during much of the year, traveling 80–160 km per day. The Equatorial Undercurrent upwells along the western wall of the Galapagos Platform, bringing cold water (14–16°C) to the western islands. It is also nutrient rich, producing great productivity in this area. The Panama Current, a composite of the California Current and the North Equatorial Countercurrent, is a slow-moving current bringing to Galapagos warm water (26–29°C), low in salinity and low in nutrients, usually in January when the southeasterly trade winds slacken (Banks 2002, Chavez & Brusca 1991, Wyrtki 1985). During El Niño years, this current is believed to transport Panamic species to the Galapagos. A consequence of this complex current system is marked variation in oceanographic conditions across the archipelago. During El Niño years, regional variation in conditions disappears as water temperatures rise above 25°C.

Oceanic currents make possible the dispersal of species between widely separated areas, especially species capable of long-distance larval transport. Currents also serve as barriers to dispersal. The principal barriers to east–west distribution are the Central American land barrier to the east and the E Pacific Barrier to the west (Fig. 2). The

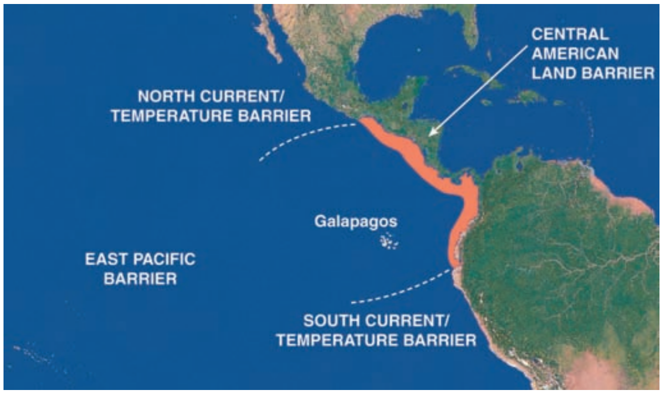


Figure 2. Barriers to larval dispersal in the Pacific.

latter, often referred to as Ekman's East Pacific Barrier (Ekman 1953), is an enormous expanse of water between the Indo-Pacific and east Pacific, presenting virtually no opportunity for island hopping. The Line Islands, the central Pacific islands closest to Galapagos, are more than 7500 km away. The major eastward-flowing current is the North Equatorial Countercurrent (NEC) with a mean flow of about 35 km/day (Wyrtki & Kilonsky 1984), although highly variable seasonally.

PORCELAIN CRABS

The porcelain crabs (Decapoda: Anomura: Porcellanidae) provide insights into the origins of Galapagos marine invertebrates. Because they are among the most abundant crustaceans in sheltered cobble or boulder coastal habitats, porcelain crabs have been considered ideal for studies of congeneric physiological adaptation and distribution (Villalobos Hiriart *et al.* 1992, Stillman 2002). Despite their resemblance to brachyurans, they are anomuran decapods with huge claws in relation to body size and three pairs of usable walking legs, the fourth pair much reduced and folded forward over the abdomen. They feed by trapping plankton on highly setose mouth appendages which they wave through the water (Fig. 3). They are common in the intertidal and shallow subtidal zones of Galapagos, clinging to the underside of stones or associated with corals or sponges. The 14 recognized species, eight of which are considered common in Galapagos (Hendrickx & Harvey 1999, Hickman & Zimmerman 2000), are a homogeneous group: all are filter feeders, with similar ecology and morphology. Three of the 14 are endemic to Galapagos (Table 1).

Figure 3. Porcelain crab *Pachycheles biocellatus*, showing the setose mouth appendages used in feeding.

Of the *c.* 250 known species of porcelain crabs worldwide, approximately 180 occur in the Pacific (Table 2). Of these, about 90 species are in the Indo-Pacific and 92 in the east Pacific with no overlap between the two regions (Haig 1960, Harvey 1991, Hiller *et al*. 2004). The affinity of

Table 1. Number of marine species in major taxonomic groups of Galapagos, after Bustamante *et al*. (2002), expanded and updated to include additional groups.

Group	No. of species	No. of endemics	Percent endemic	Species richness	Level of study
Mammals	24	2	8.3	High	Good
Marine birds	19	5	26.3	High	Good
Fishes	447	51	11.4	Intermediate	Moderate
Polychaetes	192	50	26	Intermediate	Poor
Amphipods	50	19	38	Intermediate	Good
Brachyurans	120	23	19.2	Intermediate	Poor
Caridea & Stenopods	65	10	15.4	High	Poor
Porcelain crabs	14	3	21.5	Low	Moderate
Barnacles	18	4	22.2	Low	Moderate
Molluscs	780	141	18.1	Low	Moderate
Opisthobranchs	49	18	36.7	Low	Poor
Echinoderms	200	34	17.0	Low	Moderate
Bryozoans	184	34	18.5	High	Poor
Sea anemones	15	2	13.3	Low	Poor
Zoanthids	7	?	?	Low	Poor
Gorgonians	14	10	71.4	Intermediate	Poor
Sea pens	4	2	50	Low	Poor
Cerianthids	2	0	0	Low	Poor
Hydroids	96	14	14.5	High	Moderate
Corals, hermatypic	23	0	0	Low	Good
Corals, ahermatypic	43	17	39.5	Intermediate	Poor
Algae	333	130	39	High	Poor
Soft bottom meiofauna communities	390	?	?	High	Poor
Overall	**3089**	**569**	**18.3**		

Table 2. Comparing Galapagos porcellanids to other regions. Adapted from Harvey (1991).

Region	No. of species	Shared species
Pacific total	180	14
Indo-West Pacific	90	0
Eastern Pacific	92	14
Alaskan–Oregonian	4	0
Californian	26	0
Cortez–Mexican	41	7
Panamanian	61	13
Peruvian–Chilean	14	1

Table 3. Representation of Panamic genera of porcelain crabs in Galapagos, Ecuador and Colombia.

Genus	Galapagos[1]	Ecuador[2]	Colombia[3]	Panama[4]
Petrolisthes	8[5]	15	19	20
Pachycheles	2	7	7	8
Neopisosoma	2	2	3	2
Clastotoechus	1	1	2	1
Polyonyx	1	1	1	1
Megalobrachium	0	2	4	5
Euceramus	0	1	0	2
Porcellana	0	1	2	3
Pisidia	0	1	1	1
Ortochela	0	1	1	1
Minyocerus	0	0	1	0
Ulloaia	0	0	0	1
Totals	14	32	41	45

[1] From Haig (1960), Hickman (2000)

[2] From Haig (1960), Hiller *et al.* (2004)

[3] From Hiller *et al.*(2004), Lazarus-Agudelo (2006)

[4] From Gore & Abele (1976)

[5] Added in proof. A ninth species, *Petrolisthes donadio* Hiller and Werding 2007, was discovered among my specimens after completion of this manuscript.

the 11 non-endemic Galapagos porcellanids is overwhelmingly with the Panamic province, which extends from the Gulf of Tehuantepec (southern Mexico) to the Gulf of Guayaquil (southern Ecuador) or Paita in northern Peru (Briggs 1974) (Fig. 4). Seven of these 11 are shared with the Cortez–Mexican province and one is shared with the Peruvian province. None of them occurs north of the Cortez–Mexican province.

Of the 92 species of porcellanids in the east Pacific, 32 occur in Ecuador and 41 in Pacific Colombia (Table 3). If we accept these as the major source pool for the Galapagos fauna, with a combined 42 species, we can ask why only 14 species occur in Galapagos. Harvey (1991) describes two principal elements that could have contributed. One is the short dispersal phase during larval development; compared to other decapod crustaceans, porcellanids produce few large eggs with accelerated larval development and are thus poorly suited for long-distance oceanic transport. Second, dispersal of porcellanid larvae, like any planktonic larvae, is wholly dependent on the pattern of oceanic currents. Porcellanid larvae hatched in the central Pacific would have to be transported at least at 10 times the rate of the NEC to reach Galapagos or any other islands in the east Pacific (Harvey 1991). For porcelain crabs, the East Pacific Barrier is complete: no Indo-Pacific porcellanids have established populations in the east Pacific and no east Pacific porcellanids are known to have successfully established populations in the Indo-Pacific.

Figure 4. Marine provinces of the east Pacific.

Additional barriers are the north and south current-temperature barriers (Fig. 2). From California southwards, the current is unfavorable most of the year and the water too cold for tropical porcelain crabs. From the south, the only Galapagos porcelain crab with Peruvian affinity, *Petrolisthes armatus,* is known from a single record and considered "extralimital" by Haig (1960). It has not appeared in recent collections. A possible explanation for the absence of porcellanids of Peruvian affinity is that the POC, which gives rise to the SEC that flows directly through Galapagos, is separated from the PCC by the Peru Coastal Countercurrent (Fig. 1), which acts as a barrier to larval dispersal northward from coastal Peru (Fig. 2). Also, because the continental shelf along Peru is narrow and strong currents sweep offshore, pelagic larvae would be swept out to sea beyond a site for safe settlement. Consequently there has been selection for more direct development with fewer, larger eggs, and for reduction or complete omission of prolonged, free-swimming larval stages that might be distributed as far as Galapagos.

Ten of the 14 Galapagan porcelain crabs are of just two genera (Table 3), *Petrolisthes* and *Pachycheles*, which are the most specious, both within the Panamic province and worldwide (Harvey 1991, Stillman & Reeb 2001), suggesting that the porcelain crabs of Galapagos have passed through a dispersal filter that allowed only species with good dispersal and colonizing ability to become established there. Additionally, habitat diversity is limited in Galapagos as compared to coastal mainland Ecuador and Colombia. For example, Bahía Málaga in Pacific Colombia, with 32 species of porcellanids, has high coastal habitat diversity with extensive mangroves, mudflats, intertidal rocky shores and depositional sand beaches (Lazarus-Agudelo & Cantera-Kintz 2007). Galapagos shorelines, consisting mainly of sloping rocky lava fields with interspersed sand and gravel pockets and occasional shoreline mangroves, offer more limited habitat resources for porcellanids, for which the Galapagos can be considered a diminutive outpost of the Panamic province, the apparent exclusive source of its porcellanid fauna.

MOLLUSCS

The marine molluscs of Galapagos have been thoroughly sampled and described, the result of several expeditions over the past century, as well as extensive collecting by the De Roy and Angermeyer families of Puerto Ayora. There are *c.* 780 shallow-water marine molluscs in Galapagos (Kaiser 1997), as compared with *c.* 1200 in continental Ecuador, based on recent surveys by the Nazca Institute for Marine Research (K. Clark, pers. comm.) and more than 3000 species in the Panamic Province (Keen 1971).

Molluscs of the Panamic province exhibit the greatest diversity of all east Pacific provinces (Roy *et al*. 1994) but distributional patterns differ significantly between the northern and southern reaches of the province. Dispersal is by pelagic larvae and, unlike the porcelain crabs, many gastropod groups have teleplanic larvae with sufficiently long pelagic life to cross the East Pacific Barrier (Finet 1991). Some adults may cross this barrier on floating debris, especially during El Niño years when, for example, the grapsoid crab *Plagusia immaculata* and the swimming crab *Euphylax dovii*, the latter often in enormous numbers, appear in Galapagos (Hickman & Zimmerman 2000).

Table 4. Zoogeographical affinities of the marine molluscs in Galapagos (from Finet 1991).

Affinity	No.	%
Endemic	125	21
Pure Panamic	337	57
Panamic + Californian	46	8
Pure Californiana	0	0
Panamic + Peruvian	42	7
Pure Peruvian	3	0.5
Panamic + Caribbean	10	1.7
Pure Indo-Pacific	13	2
Circumtropical	14	2.2

Table 5. Numbers of species and percentage of the respective total marine molluscan fauna in Galapagos and continental Ecuador.

	Galapagos[1]		Ecuador[2]	
Class	Number	%	Number	%
Cephalopoda	8	<1	6	<1
Scaphopoda	8	<1	6	<1
Bivalvia	201	26	347	39
Gastropoda	537	70	527	59
Polyplacophora	13	2	5	<1

[1] From Kaiser, 1997

[2] Numbers are minimal, representing incomplete analysis of collections (K. Clark pers. comm.).

Some 13 species of Galapagos molluscs have pure Indo-Pacific affinities (Table 4). For north–south distribution, mollusc dispersal is limited by the same thermal-current barriers that operate against the porcellanids. No Galapagos molluscs have pure Californian affinity and only three have pure Peruvian affinities. However, some 46 Galapagos species have a Panamic–Californian distribution. As Finet (1991) suggests, these are probably Panamic species that have been carried north when coastal currents flow northward during the northern summer.

Compared to the mainland, Galapagos is rich in gastropods and relatively poor in bivalves (Table 5). On the Ecuadorian coast, the ratio of gastropods to bivalves is approximately 1.5:1 (K. Clark pers. comm.), while in Galapagos it approaches 3:1 (Table 5). There also has been clear selection against bivalves that burrow or live in sand compared to those living on top of, or attached to, the benthos: on the mainland coast there are nearly four times as many infaunal bivalves as epifaunal, whereas in Galapagos these are approximately equal in number (Kay 1991). A principal reason for the prominence of gastropods is that Galapagos shores are rocky, dropping away quickly to deep water. There is a scarcity of the wide expanses of silty, sandy ocean bottom, typical of the mainland coast (Fig. 5), that are required to support large numbers of infaunal bivalves.

Approximately 18% (141 of 780 species) of the Galapagos shallow-water molluscs are considered endemic (Finet 1991) and most of these are gastropods. Endemism is strictly at the species level. Establishing endemism is not a simple matter. Species thought to be endemic to their region of occurrence are later frequently found elsewhere. The percentage of endemism for Galapagos molluscs will doubtless decline as coastal field studies now underway in Ecuador and Colombia bring results. Future molecular genetic studies also may reveal some presumed endemics to be east Pacific species obscured by phenotypic differences between island and mainland populations.

SCLERACTINIAN CORALS

The reef-building (hermatypic or zooxanthellate) coral fauna of the equatorial east Pacific is impoverished and patchy in distribution compared to the central and west Pacific, with a pronounced pattern of increasing species richness from east to west (Veron 1995). From the equatorial east Pacific with 32 species (excluding the *Millepora* hydrocorals) diversity increases just west of the East Pacific Barrier to approximately 100 species in the central Pacific. Species richness increases steadily to 450 species in the Philippine and north Indonesian archipelagoes. More than 500 west and central Pacific hermatypic coral species have been described (Veron 2000).

The reef-building corals of Galapagos, while locally abundant in the north, are restricted by limited shallow-water habitat required for reef development, by an abundance of bio-eroding organisms and, especially, by periodic El Niño events. In recent years, Galapagos reefs were almost entirely destroyed by the 1982–3 and 1997–8 El Niño events. Recovery has been slow and several species that were once abundant are now uncommon (Glynn 2003). None has become extinct, however. Galapagos, with 22 species of reef-building corals, shares with the Panamic province a coral fauna dominated by two genera: *Pocillopora* (9 species) and *Pavona* (5 species) (Table 6). The remaining seven species, belonging to six genera, are uncommon, with the exception of *Porites lobata*, a resilient reef-building species that has rapidly recovered from the 1982–3 and 1997–8 El Niño events to become the dominant coral in Darwin and Wolf. Despite periodic El Niño disturbances, Galapagos supports as many coral species as Ecuador and Colombia and only slightly fewer than Panama (22 in Galapagos, 26 in Panama), the latter considered a more favorable coral habitat. For hermatypic corals, Galapagos is a remarkable exception to the effect of island impoverishment compared to mainland source areas.

Figure 5. A sand-silt beach of mainland Ecuador, important habitat for infaunal molluscs.

The origin of the coral reef fauna of the east Pacific has been a matter of controversy (Glynn & Wellington 1983, Veron 1995, Glynn & Ault 2000). A long-distance dispersal hypothesis (Dana 1975) holds that the east Pacific corals are comparatively recent immigrants, by long-distance larval transport and recolonization from the central Pacific following massive extinction of east Pacific corals

Table 6. Presence/absence of hermatypic corals of the equatorial east Pacific in Galapagos (G), mainland Ecuador (E), Colombia (C), Panama (P), central Pacific (CP) and Indo-Pacific (IP). + = present; – = not recorded

E Pacific species that occur in:	**G[1]**	**E[2]**	**C[3]**	**P[4]**	**CP[5]**	**IP[6]**
Pocillopora damicornis	+	+	+	+	+	+
Pocillopora verrucosa[7]	+	+	+	+	–	+
Pocillopora elegans[7]	+	+	+	+	+	+
Pocillopora eydouxi	+	+	+	+	+	+
Pocillopora ligulata	+	–	–	+[8]	+	–
Pocillopora meandrina	+	–	–	+	+	+
Pocillopora capitata	+	+	+	+	–	+
Pocillopora inflata	+	–	–	+	–	–
Pocillopora woodjonesi	+	–	–	–	+	+
Pocillopora effusus	+	+[8]	–	–	–	–
Pocillopora danai	–	–	+	–	?	+
Acropora valida	–	–	+	–	+	+
Porites lobata	+	+	+	+	+	+
Porites panamensis	–	+	+	+	–	–
Psammocora stellata	+	+	+	+	+	+
Psammocora superficialis	+	+	+	+	+	+
Psammocora brighami	–	+	–	+	-–	–
Psammocora obtusangula	–	–	+	+	+	+
Gardineroseris planulata	+	+	+	+	+	+
Siderastrea glynni	–	–	–	+	-–	–
Leptoseris scabra	+	–	–	–	+	+
Leptoseris papyracea	–	+	+	+	+	+
Leptoseris foliosa	–	+	-–	–	–	+
Pavona clavus	+	+	+	+	+	+
Pavona frondifera	–	–	+[8]	+	–	+
Pavona gigantea	+	+	+	+	+	–
Pavona maldivensis	+	–	+	+	+	+
Pavona varians	+	+	+	+	+	+
Pavona chiriquiensis	+	+[8]	+	+	-–	–
Pavona cf. *duerdeni*	–	–	–	+-	+	+
Cycloseris curvata	+	+	+	+	–	+
Diaseris distorta	+	+	+	+	+	+
Totals	22	20	22	26	20	21

[1] From Glynn (2003), Hickman (2008).
[2] From Glynn (2003), Reyes-Bonilla (2002).
[3] From Zapata & Vargas-Ángel (2003), Glynn & Ault (2000), Reyes-Bonilla (2002).
[4] From Maté (2003), Glynn & Ault (2000), Guzman et al. (2008), Reyes-Bonilla (2002).
[5] From Glynn & Ault (2000), Glynn (2003).
[6] From Veron (2000).
[7] *P. verrucosa* and *P. elegans* considered conspecific by P. Glynn and counted as one species in the totals.
[8] Needs verification.

during the unsettled Neogene period. An alternative vicariance hypothesis (McCoy & Heck 1976, Heck & McCoy 1978) proposed that the east Pacific coral communities are derived from a widespread pan-Tethyan coral biota that was widely distributed across the Central American seaway. After the Pliocene closure of the seaway *c.* 3.5–3 million years ago, surviving fauna were modified by tectonic events, speciation and extinction. The vicariance hypothesis has been criticized by several authors and rejected by Veron (1995 and references cited) but Glynn & Ault (2000) caution that it seems premature to dismiss the hypothesis at this time. It is also possible that remnants of the extensive Neogene fauna may have survived in the east Pacific following closure of the Central American seaway, to be augmented by dispersal from the west (Glynn & Wellington 1983), a view that favors contributions from both vicariance and long-distance dispersal to the modern east Pacific coral fauna.

There seems little question that long-distance dispersal of pelagic, planktotrophic larvae has contributed to the recovery of equatorial east Pacific reefs destroyed by recent El Niño events. As evidence, Guzman & Cortes (2007) point to the recent appearance at Cocos Island of several coral species that had not been reported before the mid-1990s. The Line Islands are considered the principal source of east Pacific corals by way of the NEC. While this current lies well north of Galapagos (Fig. 1), several lines of evidence attest to the dispersal of coral larvae (and both larvae and adults of other marine taxa) by warm gyres from the NEC to the islands, especially during El Niño activity. "Dispersal pulses" that could provide rapid transport of coral larvae to the Galapagos would be favored during such anomalous conditions (Glynn & Wellington 1983). Glynn & Ault (2000), recognizing that the East Pacific Barrier is more a hindrance to eastward larval dispersal than a complete impediment, suggest that the barrier should more appropriately be termed an east Pacific filter bridge.

The ahermatypic (azooxanthellate) corals of the equatorial east Pacific represent a much richer and more diverse fauna than the hermatypic corals. Approximately 105 species are recognized from the east Pacific and 43 are recorded from the Galapagos (Cairns 1991 and pers. comm.). Unlike the hermatypic corals, none of which is endemic to Galapagos, 17 of the 43 ahermatypic species (39.5%) are peculiar to the Galapagos (Table 1). Twenty-three of the 43 species are deep water. If shallow-water ahermatypes only are considered, the percentage of endemicity drops to 29%. Twenty ahermatypes (47%) have Panamic affinity and 14 (33%) have Indo-Pacific affinity. Six (14%) are cosmopolitan. These percentages contrast markedly with the hermatypic corals, which have 86% Panamic affinity and 86% Indo-Pacific or Central Pacific affinity.

As a distinct faunal group, ahermatypes occur worldwide, exploit a wide range of ecological niches, and are not limited to shallow, sunlit waters as are the hermatypic corals. Many thrive in deep ocean, under rocks, and in ledges and caves where light is absent or minimal. The faunistic affinities of Galapagos ahermatypes resemble those of molluscs with a high endemic component and strong Panamic affinities, followed by Indo-Pacific and cosmopolitan affinities. Because an ahermatypic faunal analysis from Ecuador and Pacific Colombia comparable to that from Galapagos is not yet available, we can only speculate that the ahermatypic composition of Galapagos appears well represented as compared to the mainland.

ECHINODERMS

Echinoderms are well represented in Galapagos with nearly 200 species, although nearly two-thirds of these are deep-water species that do not appear in shallow-water surveys. Surveys (Hickman 1997) and published information (Maluf 1988, 1991) yield a total of 84 species in shallow-water Galapagos. Removing species that have not appeared in recent surveys, single records that may be strays, and suspected mistaken literature reports, the total is reduced to 73 verifiable species. This exceeds the 65 verified species of the Colombian Pacific coast, where both the basic taxonomic work and shallow-water ecosystems parallel those of Galapagos (Table 7). The results of recent surveys from the Ecuadorian coast were not available at this writing. Species shared by Galapagos and Pacific Colombia range from 29% for ophiuroids and echinoids, to 43% for asteroids and 50% for holothuroids. Holothuroids are especially well represented in Galapagos, with 18 shallow-water species compared to 12 in Colombia. The 26 echinoids of Galapagos compare with Colombia's 16 species (Neira & Cantera 2005) and the 33 species found in Panama (Lessios 2005). Of the 33 Panama species, 20 occur in Galapagos, attesting to the strong Panamic affinity of Galapagos echinoderms. Oddly, ten echinoid species shared between Panama and Galapagos have not been recorded from Pacific Colombia.

Approximately 8% of Galapagos shallow-water echinoderms are endemic (one asteroid, three ophiuroids

Table 7. Representation of shallow-water (<30 m) echinoderms of Galapagos, Pacific Colombia and the east Pacific.

Class	Galapagos[1]	Colombia[2]	E Pacific[3]
Asteroidea	20	22	62
Ophiuroidea	13	16	86
Echinoidea	21	16	55
Holothuroidea	18	13	71
Crinoidea	1 (?)	0	1
Totals	**73**	**67**	**275**

[1] From Maluf (1988, 1991), Hickman (1997).

[2] From Neira & Cantera (2005), M. Cohen (pers. comm.).

[3] E Pacific = Central East Pacific of Maluf (1988), *i.e.* between Pt Conception, California and S Peru (34°30′N to *c.* 18°S).

and two echinoids), although collecting has not been as methodical along the Ecuadorian mainland coast as it has in Galapagos. The inclusion of deep-water endemics brings total endemism to 18% (Maluf 1991), a higher percentage than in other east Pacific islands, where it varies from 0% for Clipperton to 9% for Cocos (Maluf 1991). The higher percentage in Galapagos may be an archipelago effect, with greater opportunity for isolation and speciation. However, currents probably distribute larvae throughout the islands, suggesting that there is little opportunity for allopatric speciation within the archipelago. Additionally, sampling effort has been very uneven among the east Pacific islands, suggesting caution in evaluating comparisons of endemism. As with the molluscs, echinoderm endemism is at the species level; there are no endemic echinoderm genera in the Galapagos Islands.

Like the marine molluscs, the Galapagos echinoderms have affinities with neighboring Pacific regions but are dominated by Panamic species. In general echinoderms have been more successful in long-distance colonization than marine molluscs and porcelain crabs. All echinoderm classes except the crinoids are well represented in Galapagos. Of the shallow-water (<200 m) echinoderms, 12% have Indo-Pacific affinities, 8% are cosmopolitan, and 8% are shared with the California province (Maluf 1991).

HYDROIDS AND BRYOZOANS

The preceding examples suggest that for Galapagos, as for other oceanic islands, three agents act as determinants for colonization of marine invertebrates that are dependent primarily upon larval dispersal: habitat substrate, currents and temperature, and isolation. However, these conditions may not be limiting to groups less dependent upon larval dispersal, such as hydroids of the phylum Cnidaria and bryozoans of the phylum Ectoprocta. All marine species within these two groups are colonial.

Although the hydroid fauna along several areas of the mainland east Pacific coastline is poorly known, 125 species have been identified from the Panamic province. Diversity is high in Galapagos, with 96 known species and 14 (14.5%) considered endemic (Calder *et al*. 2003), a relatively high percentage for a group with good dispersal potential. Hydroids are poorly equipped for long-distance dispersal by medusae or larvae. Instead they attach to floating objects, such as logs, debris, and hulls of ships. Long-range dispersal in this manner by the "sessile" benthic stage of the animal is much more successful than by its free-swimming reproductive stage.

Bryozoans are tiny, sessile, colony-building animals that are ubiquitous in the marine environment. Some form erect, branching colonies that resemble seaweed but most form limy encrustations on almost any solid surface. Fig. 6, showing the underside of a rock collected from Cousins islet in 2002, emphasizes the widespread presence of bryozoans in Galapagos. On this 30 cm rock were 12 species of bryozoans, in addition to numerous ascidians, hydroids, and sponges.

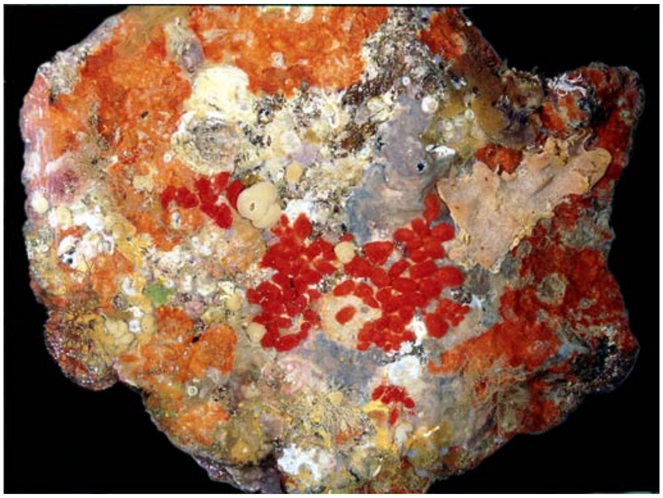


Figure 6. Underside of a rock recovered at Cousins Island, on which were growing 12 species of bryozoans, as well as sponges, ascidians and hydroids.

Surveys and collections made before 1990 yielded 184 species of bryozoans in Galapagos (Banta & Redden 1990). This impressive total, which almost certainly is an underestimate, is comparable to the most diverse bryozoan faunas known (Banta 1991). The greatest affinity is with the Panamic province, but with good representation of both northern (California, 85 species) and southern (Peru–Chile, 24 species) provinces (Table 8), while 28% have affinities with the Indo-Pacific, which attests to the effective dispersal of bryozoans. Eighteen percent are endemic, compared with 14–16% for shore fishes (McCosker 1998), 19% for brachyuran crabs (Garth 1991), 14.5% for hydroids, and 19% for molluscs (Finet 1991).

Only two families of bryozoans with six species have planktotrophic larvae, but they are not better represented than those with other larval types. So, as with hydroids, dispersal is mainly by rafting on floating debris or transport on the hulls of ships in the adult stage, as well as by larvae. Adults are planktotrophic, making

Table 8. Zoogeographic affinities of Galapagos bryozoans (184 species) (from Banta 1991).

Affinity	No. of species	%[1]
Panamic	148	80
California	85	46
Peru–Chile	24	13
Endemic	34	18
Indo-Pacific	51	28

[1] Percentages total more than 100 because many species have affinities with more than one province.

survival more likely and increasing the chance of establishment of a permanent population once transport is accomplished.

EVOLUTION OF GALAPAGOS ENDEMICS

Endemism among Galapagos invertebrates occurs by one of two processes. When a species colonizes the islands from a distant source and then becomes extinct outside the archipelago, the Galapagos population represents a biogeographic relict (allochthonous endemic). The alternative is allopatric speciation, when a species colonizes the islands and its population there diverges through drift and/or selection (creating autochthonous endemics). Given the short life of oceanic islands due to erosion and subsidence, we might expect there to be insufficient time for the extinction of all conspecific populations of a species found outside the archipelago, especially in the case of species that were sufficiently abundant elsewhere to have managed to colonize the islands in the first place. Consequently, the allopatric model leading to autochthonous endemics is usually assumed to be the more common of the two processes on oceanic islands. Since the Galapagos islands are separated by deep ocean, repeated rounds of allopatric speciation could occur within the archipelago itself, by infrequent dispersal from island to island. In this case, the result would be a cluster of sister species, all endemic to the archipelago and, at least at first, with endemic congeners on separate islands. Such a pattern is seen in many of the terrestrial animals (*e.g.* mockingbirds *Nesomimus* and tortoises *Geochelone*) and plants (*e.g. Scalesia*) of Galapagos.

Terrestrial plant and animal genera found on the Galapagos and other oceanic islands are commonly represented by many endemic sister species. Many genera of vascular plants and several animal groups have undergone such radiations on the islands. In contrast, among the marine invertebrates no genus comprises more than one endemic species. The failure of marine invertebrates to experience archipelago speciation may reflect slower speciation of marine invertebrates, a claim made by paleontologists (*e.g.* James 1984), as well as the greater gene flow between shallow water habitats. The absence of any marine invertebrate genera that are endemic to Galapagos, in contrast to the land fauna, may also reflect these factors.

ACKNOWLEDGMENTS

I am grateful to Rodrigo Bustamante, Graham Edgar and Terrence Dawson for reviewing an early draft of the manuscript and offering many helpful suggestions. The comments of two anonymous reviewers also greatly improved the manuscript. I am much indebted to John Knox, Lawrence Hurd, Peter Glynn, Graham Edgar and Alan Tye, who offered many valuable comments on later drafts of the manuscript that greatly improved its content. This project was funded in part by the Department for Environment, Food and Rural Affairs' Darwin Initiative Project 14-048 *Galapagos Coral Conservation: Impact Mitigation, Mapping and Monitoring*.

LITERATURE CITED

Banks, S. 2002. Ambiente físico. Pp. 22–35 *in* Danulat, E. & Edgar, G.J. (eds) *Reserva Marina de Galápagos, Linea Base de la Biodiversidad*. Fundación Charles Darwin/Servicio Parque Nacional Galápagos, Puerto Ayora.

Banta, W.C. 1991. The Bryozoa of the Galápagos. Pp. 371–389 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands.* Plenum, New York.

Banta, W.C. & Redden, J. 1990. A checklist of the Bryozoa of the Galápagos. *Proceedings of the Biological Society of Washington* 103: 789–802.

Blake, J.A. 1991. The polychaete fauna of the Galápagos Islands. Pp. 75–96 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Briggs, J.C. 1974. *Marine Zoogeography*. McGraw-Hill, New York.

Bustamante, R.H., Wellington, G.M., Branch, G.M., Edgar, G.J., Martinez, P., Rivera, F., Smith, F. & Witman, J. 2002. Outstanding Marine Features. Pp. 60–71 *in* Bensted-Smith, R. (ed.) *A Biodiversity Vision for the Galapagos Islands*. Charles Darwin Foundation and World Wildlife Fund, Puerto Ayora.

Cairns, S.D. 1991. A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands. *Smithsonian Contributions to Zoology* 504: 1–32 + 12 plates.

Calder, D.R., Mallinson, J.J., Collins, K. & Hickman, C.P. 2003. Additions to the hydroids (Cnidaria) of the Galápagos, with a list of species reported from the islands. *Journal of Natural History* 37: 1173–1218.

Chavez, F.P. & Brusca, R.C. 1991. The Galápagos Islands and their relation to oceanographic processes in the tropical Pacific. Pp. 9–33 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Dana, T.F. 1975. Development of the contemporary eastern Pacific coral reefs. *Marine Biology*, 33: 355–374.

Edgar, G.J., Banks, S., Fariña, J.M., Calvopiña, M. & Martinez, C. 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. *Journal of Biogeography* 31: 1107–1124.

Ekman, S. 1953. *Zoogeography of the Sea.* Sidgwick & Jackson, London.

Finet, Y. 1991. The marine molluscs of the Galápagos Islands. Pp. 253–280 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Finet, Y. 1994. *The Marine Mollusks of the Galápagos Islands: a documented faunal list.* Muséum d'Histoire Naturelle, Geneva.

Garth, J. 1991. Taxonomy, distribution, and ecology of Galápagos Brachyura. Pp. 123–145 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Glynn, P.W. 2001. Eastern Pacific coral reef ecosystems. *Ecological Studies* 144: 281–305.

Glynn, P.W. 2003. Coral communities and coral reefs of Ecuador. Pp. 449–472 *in* Cortes, J. (ed.) *Latin American Coral Reefs*. Elsevier Science, Amsterdam.

Glynn, P.W. & Ault, J.S. 2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs*, 19: 1–23.

Glynn, P.W. & Wellington, G.M. 1983. *Corals and Coral Reefs of the Galápagos Islands*. Univ. of California Press, Berkeley.

Gore, R.H. & Abele, L.G. 1976. Shallow water porcelain crabs from the Pacific coast of Panama and adjacent Caribbean waters (Crustacea: Anomura: Porcellanidae). *Smithsonian Contributions to Zoology* 237: 1–30.

Guzman, H.M. & Cortés, J. 2007. Reef recovery 20 years after the 1982–1983 El Niño massive mortality. *Marine Biology* 151: 401–411.

Guzman, H.M., Benfield, S., Breedy, O. & Mair, J.M. 2008. Broadening reef protection across the Marine Conservation Corridor of the eastern tropical Pacific: distribution and diversity of reefs in Las Perlas Archipelago, Panama. *Environmental Conservation* 35: 46–54.

Haig, J. 1960. The Porcellanidae (Crustacea Anomura) of the eastern Pacific. *Allan Hancock Pacific Expeditions* 24: 1–440.

Harvey, A.W. 1991. Biogeographic patterns of the Galápagos porcelain crab fauna. Pp. 157–172 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Heck, K.L., Jr. & McCoy, E.D. 1978. Long-distance dispersal and the reef-building corals of the eastern Pacific. *Marine Biology (Berlin)* 48: 349–356.

Hendrickx, M.E. & Harvey, A.W. 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Belgian Journal of Zoology* 129: 363–389.

Hickman, C.P., Jr. 1997. *A Field Guide to the Sea Stars and Other Echinoderms of Galápagos.* Galápagos Marine Life Series, Sugar Spring Press, Lexington, VA.

Hickman, C.P., Jr. 2008. *A Field Guide to the Corals and other Radiates of Galápagos*. Galápagos Marine Life Series, Sugar Spring Press, Lexington, VA.

Hickman, C.P., Jr. & Zimmerman, T.L. 2000. *A Field Guide to the Crustaceans of Galápagos*. Galápagos Marine Life Series, Sugar Spring Press, Lexington, VA.

Hiller, A. & Werding, B. 2007. Redescription of *Petrolisthes edwardsii* (de Saussure) and description of a new, sibling species from the eastern Pacific based on different colour, morphology and genetic identity (Crustacea: Anomura: Porcellanidae). *Organisms, Diversity & Evolution* 7: 181–194.

Hiller, A, Lazarus, J.F. & Werding, B.. 2004. New records and range extensions for porcellanid crabs in the eastern Pacific (Crustacea: Anomura: Porcellanidae). *Contributions to the Study of East Pacific Crustaceans, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico* 3: 127–138.

Jackson, M.H. 1993. *Galápagos: A Natural History Guide.* University of Calgary Press, Calgary.

James, M.J. 1984. A new look at evolution in the Galápagos: evidence from the late Cenozoic marine molluscan fauna. *Biological Journal of the Linnean Society* 21: 77–95.

Kaiser, K.L. 1997. The recent molluscan marine fauna of the Islas Galápagos. *The Festivus* 29 Suppl. 1–67.

Kay, E.A. 1991. The marine mollusks of the Galápagos: Determinants of insular marine faunas. Pp. 235–252 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Keen, A.M. 1971. *Sea Shells of Tropical West America*, 2nd ed. Stanford University Press, Palo Alto.

Lazarus-Agudelo, J.F. 2006. *Composición Taxonómica y Estructura Poblacional de Porcelánidos (Crustacea: Decapoda: Porcellanidae) en las Bahías de Buenaventura y Málaga (Pacífico Colombiano).* Thesis, Universidad del Valle, Cali, Colombia.

Lazarus-Agudelo, J.F. & Cantera-Kintz, J.R. 2007. Crustáceos (Crustacea: Sessilia, Stomatopoda, Isopoda, Amphipoda, Decapoda) de Bahía Málaga, Valle del Cauca (Pacífico colombiano). *Biota Colombiana* 8: 221–239.

Lessios, H.A. 2005. Echinoids of the Pacific waters of Panama: status of knowledge and new records. *Revista de Biología Tropical* 53 Suppl. 3: 147–170.

McCosker, J.E. 1998. Review of: The Fishes of the Galápagos Islands, by J.S. Grove and R.J. Lavenberg. *Copeia* 1998: 809–812.

McCoy, E.D. & Heck, K.L., Jr. 1976. Biogeography of corals, sea grasses, and mangroves: an alternative to the center of origin concept. *Systematic Zoology* 25: 201–210.

Maluf, L.Y. 1988. *Composition and Distribution of the Central Eastern Pacific Echinoderms.* Technical Report 2, Natural History Museum of Los Angeles County, Los Angeles, CA.

Maluf, L.Y. 1991. Echinoderm fauna of the Galápagos Islands. Pp. 345–367 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Maté, J.L. 2003. Corals and coral reefs of the Pacific coast of Panamá. Pp. 387–417 *in* Cortes, J. (ed.) *Latin American Coral Reef.,* Elsevier Science, Amsterdam.

Neira, R. & Cantera, J.R. 2005. Composición taxonómica y distribución de las asociaciones de equinodermos en los ecosistemas litorales del Pacifico Colombiano. *Revista de Biología Tropical* 53 Suppl. 3: 195–206.

Reyes-Bonilla, H. 2002. Checklist of valid names and synonyms of stony corals (Anthozoa: Scleractinia) from the eastern Pacific. *Journal of Natural History* 36: 1–13.

Roy, K., Jablonski, D. & Valentine, J.W. 1994. Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for "Rapoport's rule." *Proceedings of the National Academy of Science* 91: 8871–8874.

Stillman, J.H. 2002. Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. *Integrative and Comparative Biology* 42: 790–796.

Stillman, J.H. & Reeb, C.A. 2001. Molecular phylogeny of Eastern Pacific porcelain crabs, genera *Petrolisthes* and *Pachycheles,* based on the mtDNA 16S rDNA sequence: phylogeographic and systematic implications. *Molecular Phylogenetics and Evolution* 19: 236–245.

Veron, J.E.N. 1995. *Corals in Space and Time: the biogeography and evolution of the Scleractinia.* Cornell University Press, Ithaca.

Veron, J. E. N. 2000. *Corals of the World*, 3 vols. Australian Institute of Marine Science, Queensland.

Villalobos Hiriart, J.L., Cantu Diaz-Barriga, A., Valle Martinez, M.D., Flores Hernandez, P., Lira Fernandez, E. & Nates Rodriquez, J.C. 1992. Spatial distribution and zoogeographical aspects of intertidal decapod crustaceans of the islands in the Gulf of California, Mexico. *Proceedings of the San Diego Society of Natural History* 11: 1–13.

Wicksten, M.K. 1991. Caridean and stenopodid shrimp of the Galápagos Islands. Pp. 147–156 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

Wicksten, M.K. and Hendrickx, J.E. 2003. An updated checklist of benthic marine and brackish water shrimps (Decapoda: Penaeoidea, Stenopodidea, Caridea) from the eastern tropical Pacific. Pp. 49–76 *in* Hendrickx, M.E. (ed.) *Contri-butions to the Study of East Pacific Crustaceans*, vol. 2. Universidad Nacional Autonoma de Mexico, Mazatlan.

Wyrtki, K. 1985. Water displacements in the Pacific and the genesis of El Niño cycles. *Journal of Physical Oceanography* 4: 91–103.

Wyrki, K. & Kilonsky, B. 1984. Mean water mass and current structure during the Hawaii-to-Tahiti Shuttle Experiment. *Journal of Physical Oceanography* 14: 242–254.

Zapata, F.A. & Vargas-Ángel, B. 2003. Corals and coral reefs of the Pacific coast of Colombia. Pp. 419–447 *in* Cortés, J. (ed.) *Latin American Coral Reefs*. Elsevier Science, Amsterdam.

Zullo, V.A. 1991. Zoogeography of the shallow-water cirriped fauna of the Galápagos Islands and adjacent regions in the tropical eastern Pacific. Pp. 173–192 *in* James, M.J. (ed.) *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands*. Plenum, New York.

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

By: Stuart Banks[1,2], Mariana Vera[1] & Angel Chiriboga[3]

[1]Charles Darwin Foundation, Puerto Ayora, Ecuador. [2]Corresponding author: <sbanks@fcdarwin.org.ec>
[3]Brown University, Rhode Island, U.S.A.

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 conditionof 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 perdida 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 informacion 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-inveretebrados 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 unica a las islas del norte, y el fuerte y frecuente estrés climático, se recomiende 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 & Wellingon 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 north east), 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

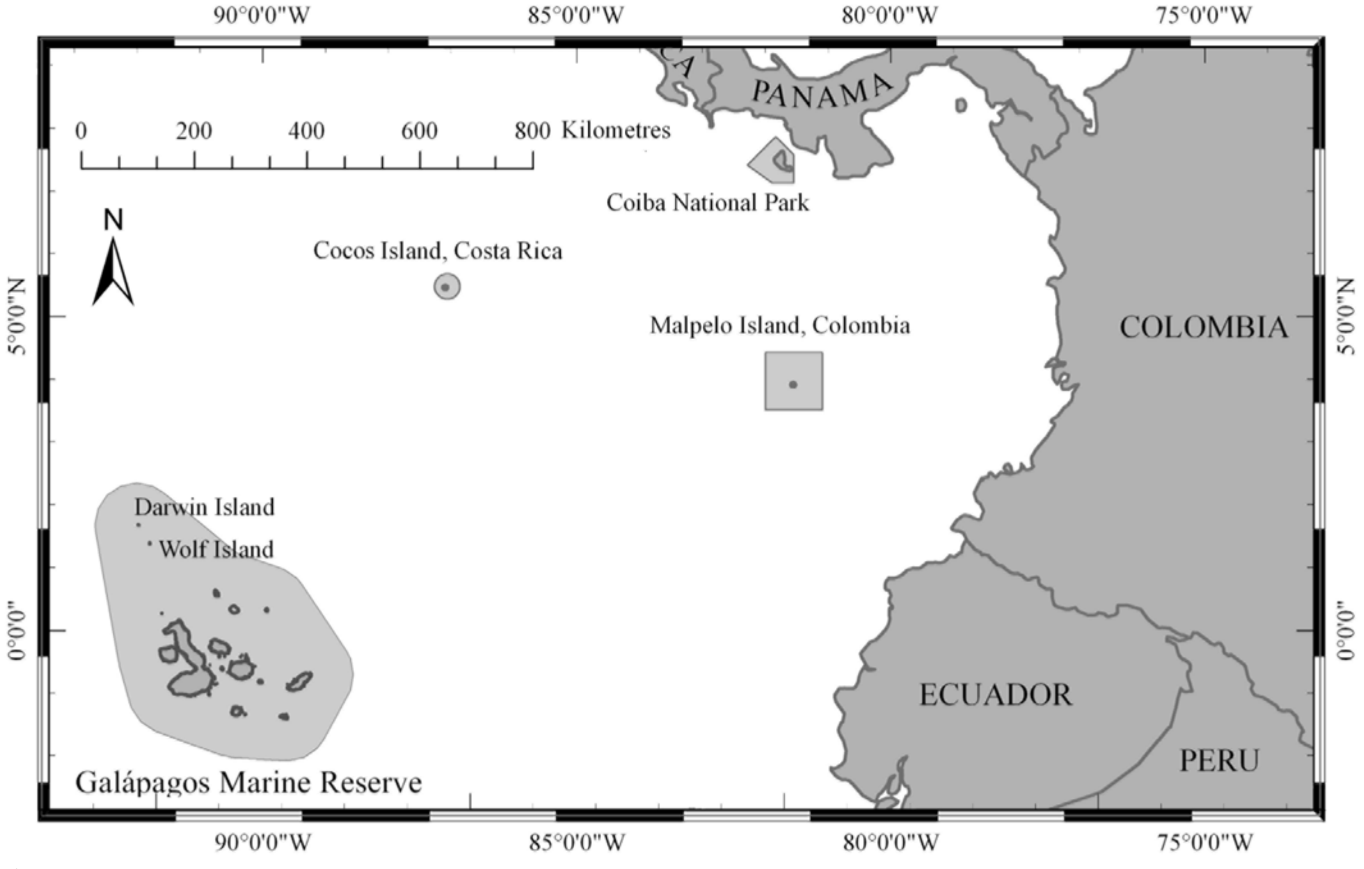


Figure 1. Marine protected areas within the Eastern Tropical Pacific (shaded).

of tropical species such as certain butterfly fish are more common in the north during strong El Niño years when the influenceof 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 km^2, Darwin 1.1 km^2) 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 *Rhyncodon 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

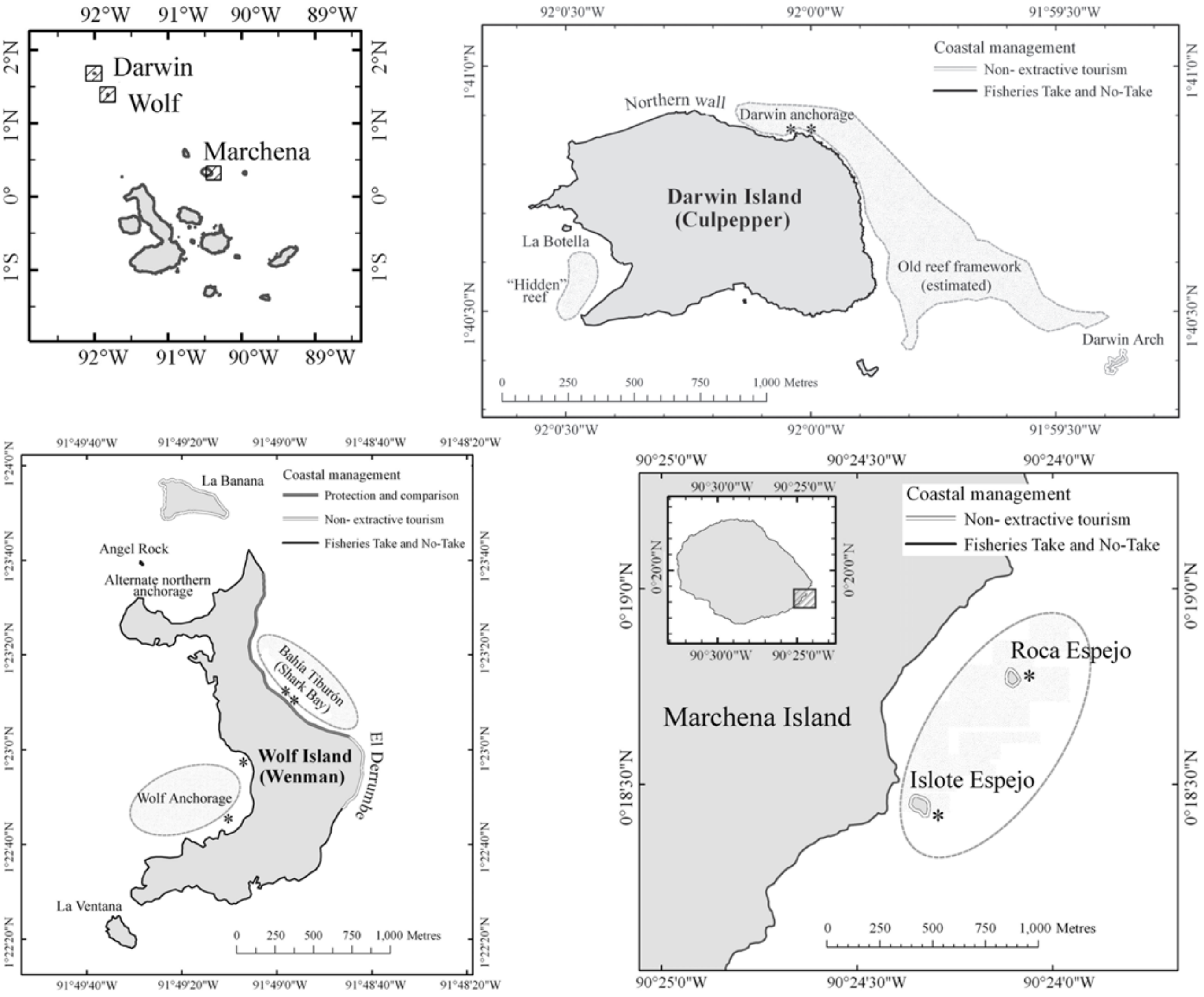


Figure 2. Coral survey sites (hatched areas) at the islands of Wolf, Darwin and Marchena. Long term subtidal community monitoring sites are indicated by *.

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		
Psammocora stellata	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 *et al*. 2005; G. Edgar pers obs).	EP; IP; WP; CP
Psammocora superficialis	Throughout, except W Isabela and Fernandina.	EP; IP; WP; CP
Psammocora profundacella	Darwin; Pinzón (Glynn & Ault 2000, Glynn & Wellington 1983, Glynn 1997, Glynn 2003).	EP; IP; WP; CP
Pocilloporidae		
Pocillopora verrucosa	Recently considered conspecific with *P. elegans*. Shallow water habitats (Hickman 2008).	IWP; EP
Pocillopora damicornis	Throughout (Glynn *et al.* 2001, Glynn 2003, Hickman *et al.* 2005, Glynn *et al*. 2009).	IWP; EP
Pocillopora meandrina	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
Pocillopora elegans	Throughout, except Fernandina and W Isabela (Glynn 2003, Hickman *et al.* 2005).	C; IP; EP
Pocillopora capitata	Throughout, except Fernandina and W Isabela (Glynn 2003).	EP
Pocillopora eydouxi	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
Pocillopora effusus	Darwin; Wolf (Hickman 2008).	EP
Pocillopora inflata	Throughout central archipelago (Hickman 2008).	EP
Pocillopora ligulata	Possibly present but requires confirmation (Hickman 2008).	IWP; EP
Pocillopora woodjonesi	Possibly present Darwin and Wolf, but requires confirmation (Hickman *et al.* 2005).	IWP; EP
Agariciidae		
Pavona varians	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
Pavona chiriquiensis	Throughout, except Fernandina and W Isabela (Hickman *et al.* 2005, Hickman 2008).	EP
Pavona clavus	Throughout, except Fernandina and W Isabela (Glynn 2003).	IWP; EP
Pavona gigantea	Throughout, except Fernandina and W Isabela (Glynn 2003, Hickman *et al.* 2005).	EP
Pavona maldivensis	Central archipelago plus Darwin and Wolf (Glynn & Ault 2000, Glynn 2003, Hickman 2008).	IWP; EP
Pavona duerdeni	Possibly present at Punta Estrada, Santa Cruz; but requires confirmation (A. Chiriboga pers. obs.).	IWP; EP
Gardineroseris planulata	Champion, Floreana; Punta Estrada, Santa Cruz (this colony not found since 1998); Darwin; Wolf (G. Edgar pers. comm.).	IWP; EP
Leptoseris scabra	Darwin; Wolf (Hickman 2008).	IWP; EP
Poritidae		
Porites lobata	Throughout, except Fernandina and W Isabela (Glynn & Wellington 1983, Glynn 2003, Glynn & Ault 2000, Hickman *et al.* 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 x 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 m^2 total coverage). A 1-m band transect is applied for non-cryptic mobile macro-invertebrates (100 m^2 total coverage). Percentage cover of sessile macro-invertebrate and algae is calculated from ten 0.25 m^2 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

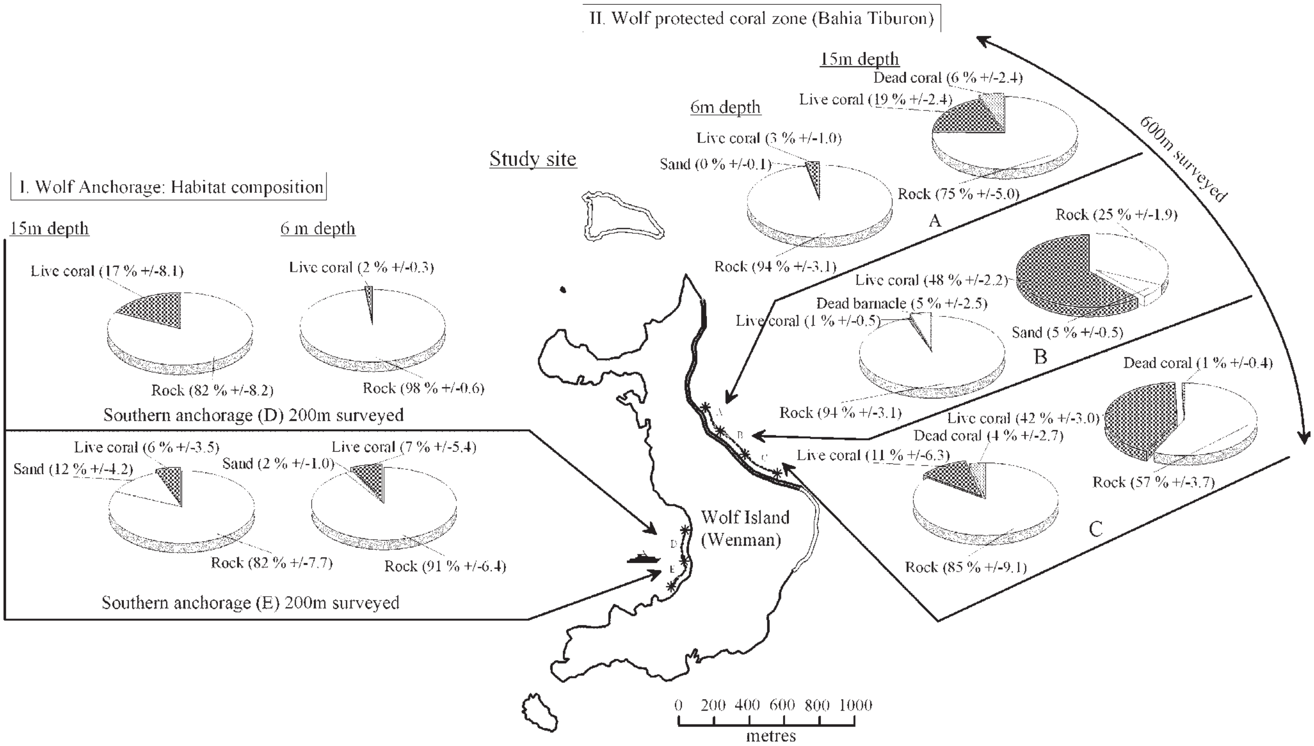


Figure 3. Habitat composition over 200 m transect seg ments at 15 m and 6 m depth across (I) Wolf Anchorage and (II) Bahía Tiburón (associated error in parentheses).

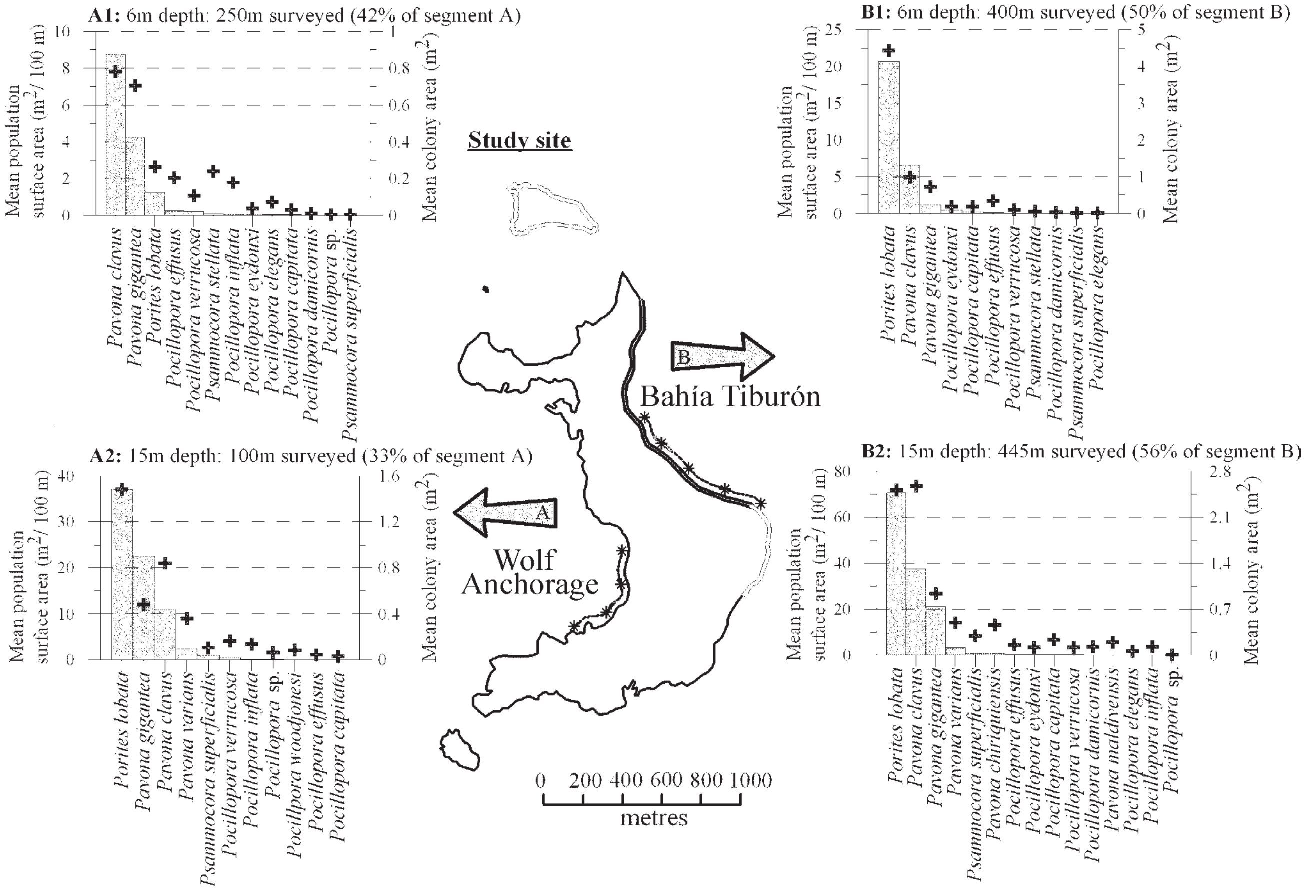


Figure 4. Hermatypic coral species ranked by estimated surface area over 100 m linear transects, with mean colony size (indicated by +) at 6 m and 15 m depth for Wolf Anchorage **(A)** and Bahía Tiburón **(B)**. Transect segments are indicated by *

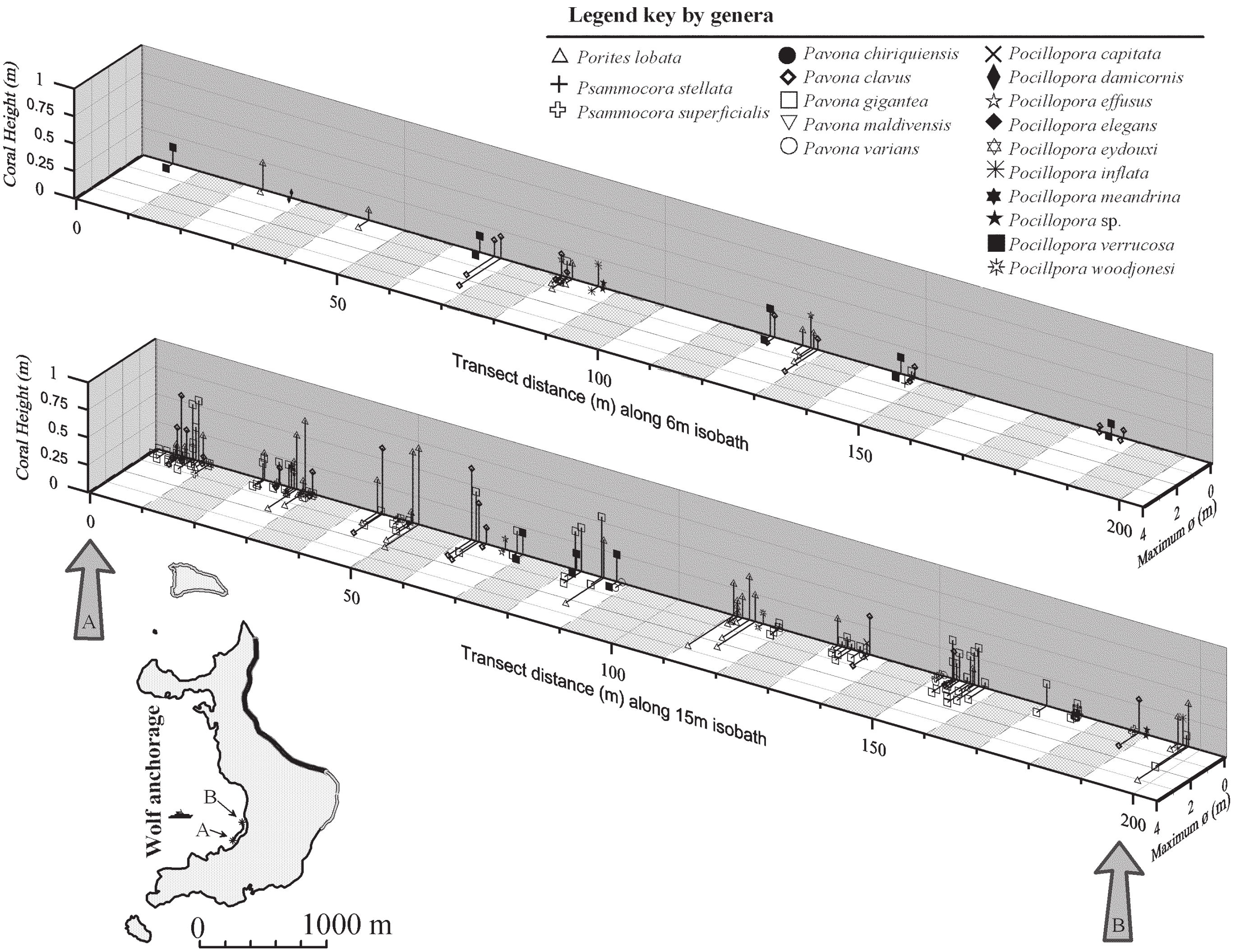


Figure 5. Zooxanthellate coral relief within Wolf Anchorage. Species, mid-point colony position, colony height from base and maximum diameter (Ø) across a 200 m transect segment at 15 m and 6 m depth in the southern region of the bay. Shaded areas represent "skipped" 10 m blocks along the non-continuous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

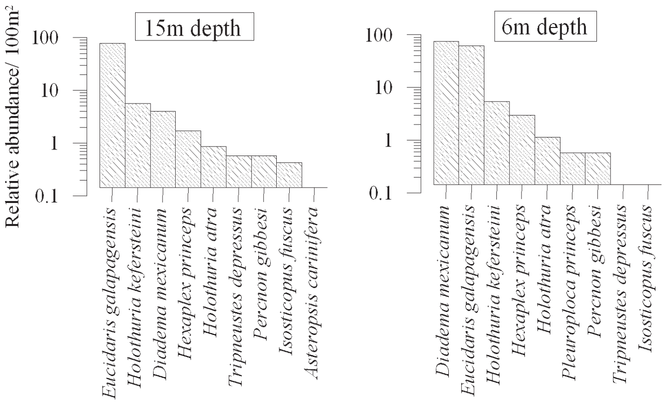


Figure 6. Rank-ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at two long-term replicate monitoring sites at Wolf Anchorage, over 100 m^2 transects at 15 m and 6 m depth.

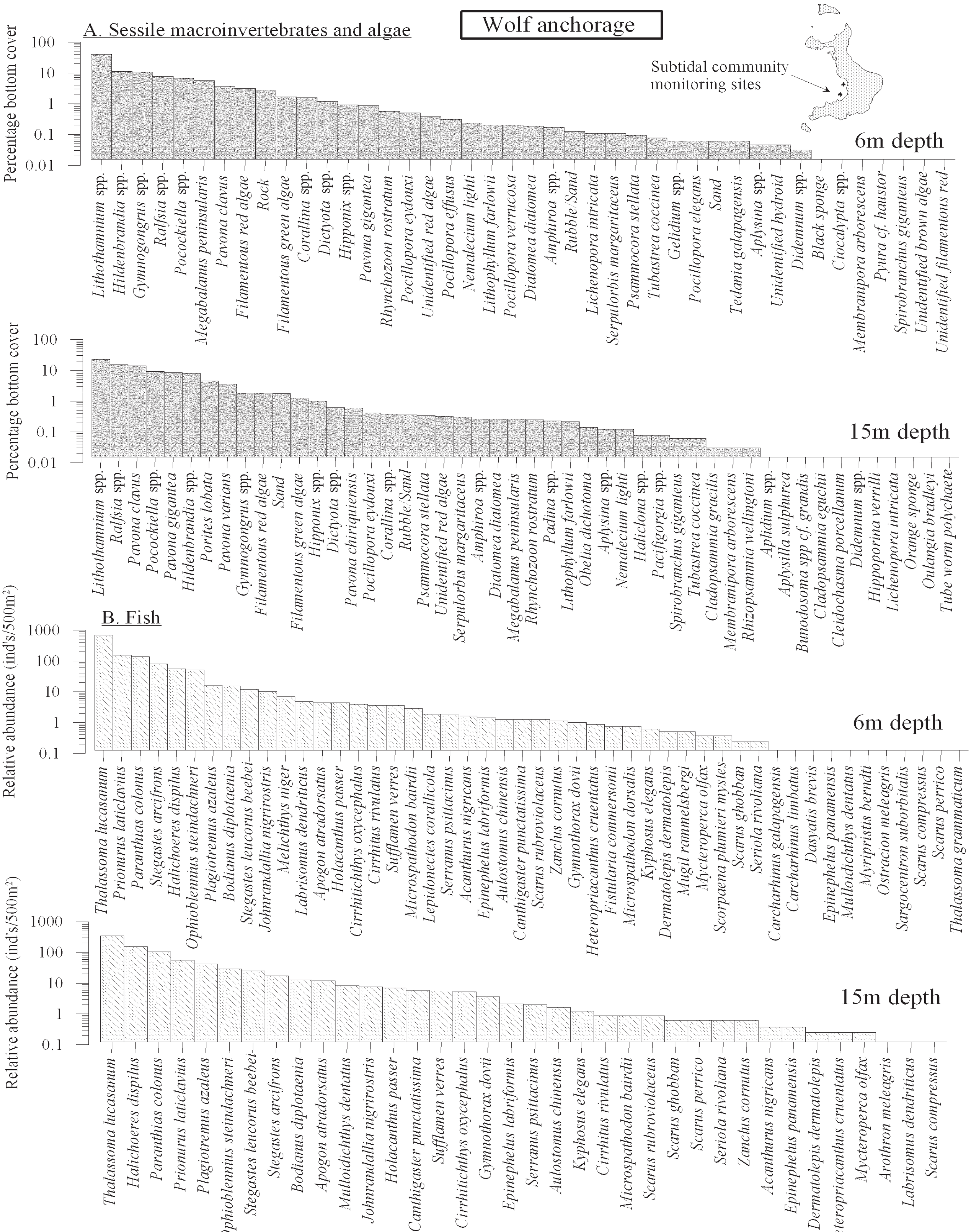


Figure 7. A Rank-ordered cover of sessile benthic macro-invertebrates and algae and **B** relative abundance of reef fish, averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Wolf Anchorage at 15 m and 6 m depth.

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 Damsel *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 octocoral *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 Islote 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).

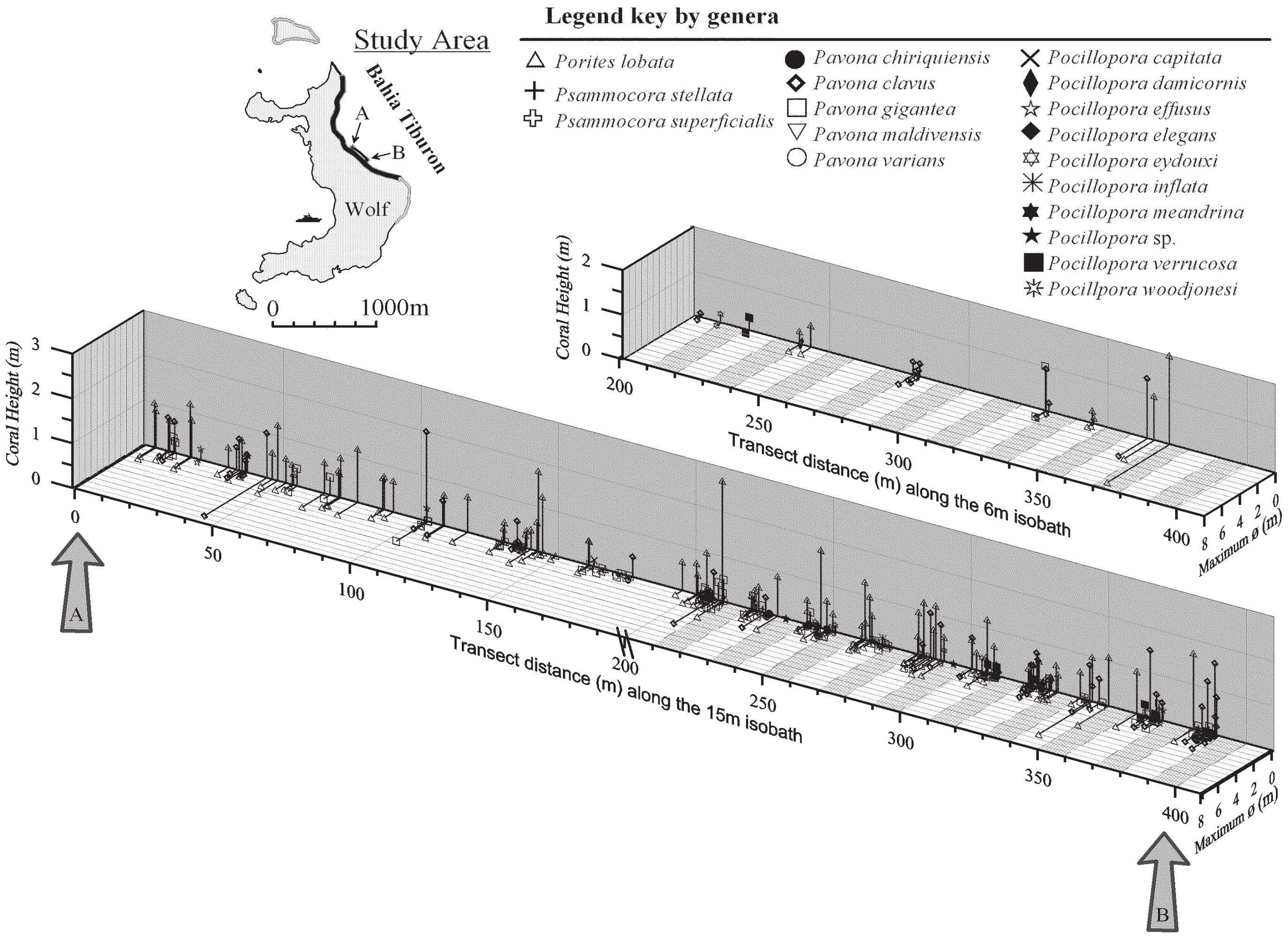


Figure 8. Coral relief within Bahía Tiburón, Wolf. Species, midpoint colony position, colony height from base and maximum diameter (Ø) across a 400 m transect segment at 15 m depth and 200 m over 6m depth in the central region of the bay. Shaded areas represent "skipped" 10 m blocks along the non-continuous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

In terms of benthic composition, at 6m the algae *Ralfsia, Hildenbrandia, Pocokiella* and *Lithothanium* 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 6 m, with greater mobile

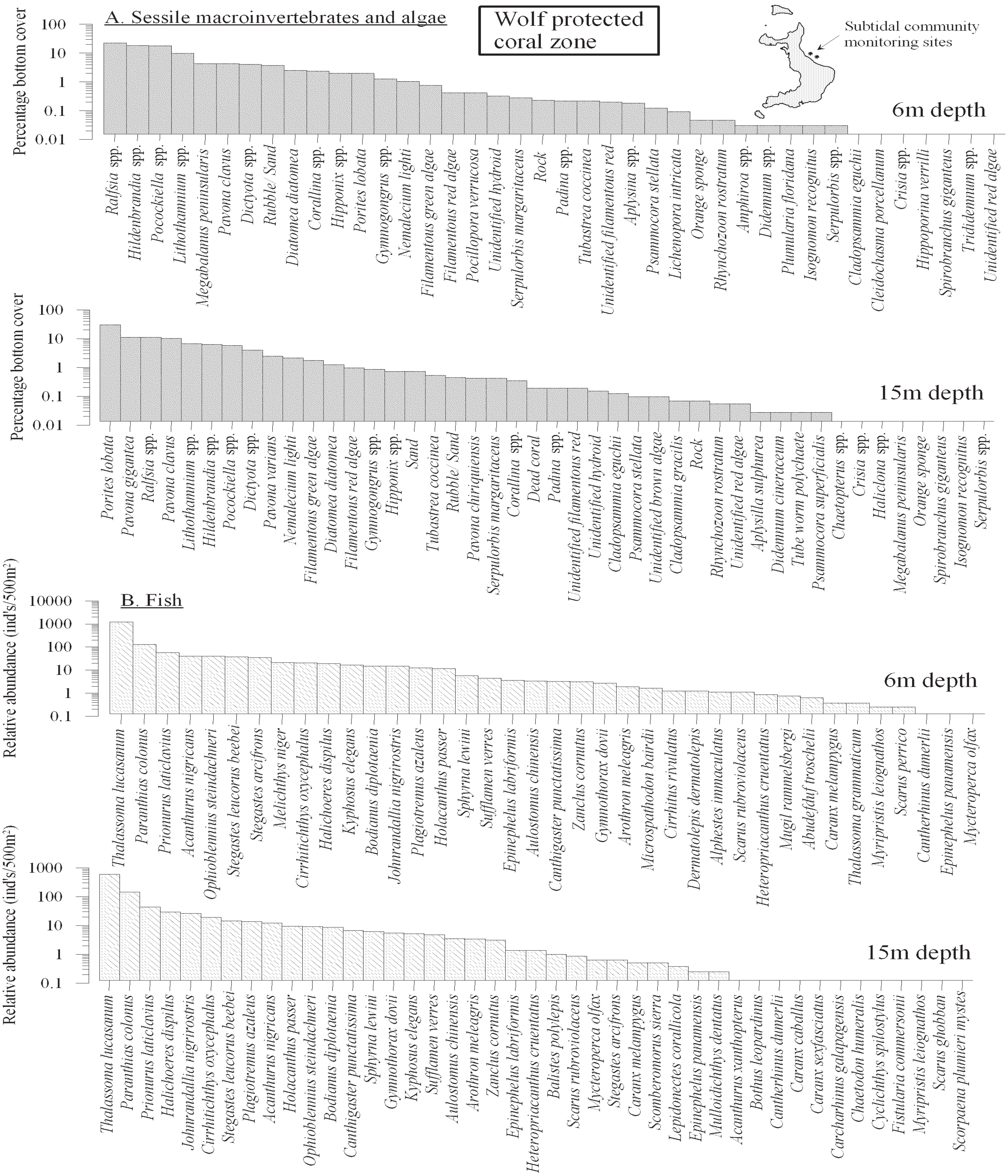


Figure 9. Rank ordered cover of sessile benthic macro-invertebrates and algae **(A)** and relative abundance of reef fish **(B)** averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Bahía Tiburón, Wolf at 15 m and 6 m depth.

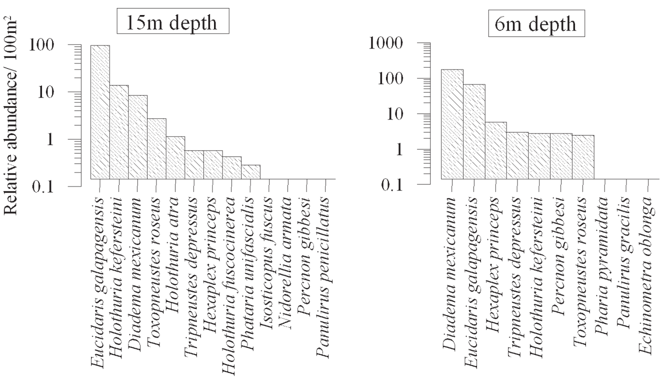


Figure 10. Rank ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at two adjacent monitoring sites in Bahía Tiburón, Wolf over 100 m² transects at 15 m and 6 m depth.

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 dispilus*, Yellow-tailed Surgeon *Prionurus laticlavius*, White-tail Damsel and Pacific Creolefish *Paranthias colonus* were evident in all sites. High abundance of cryptic coral dwellers such as the Coral Hawkfish *Cirrhitichthys oxycephalus*, Trumpet Fish *Aulostomus chinensis* and Guineafowl Puffer *Arothon meleagris* distinguished these high coral-cover sites from other parts of the GMR (Fig. 9B). Barberfish *Johnrandallia nigirosiris* 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 *Melichtys 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*.

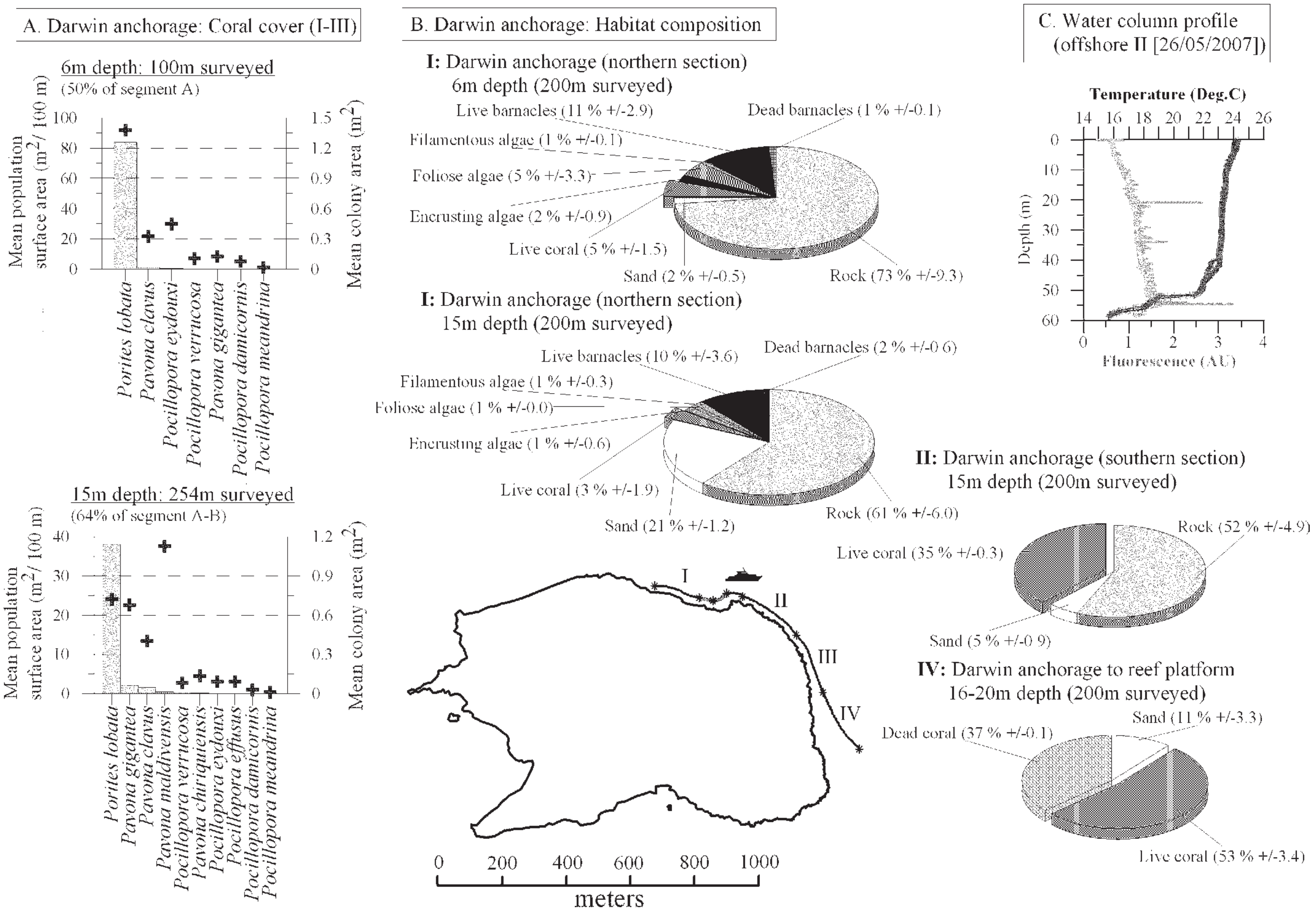


Figure 11. Darwin Anchorage. **A** Coral species ranked by estimated surface area over a 100 m linear transect, with mean colony size (indicated by +) at 6 m and 15 m depth. **B** Habitat composition by transect segments I, II & IV (associated error in parentheses). **C** Water temperature and fluorescence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

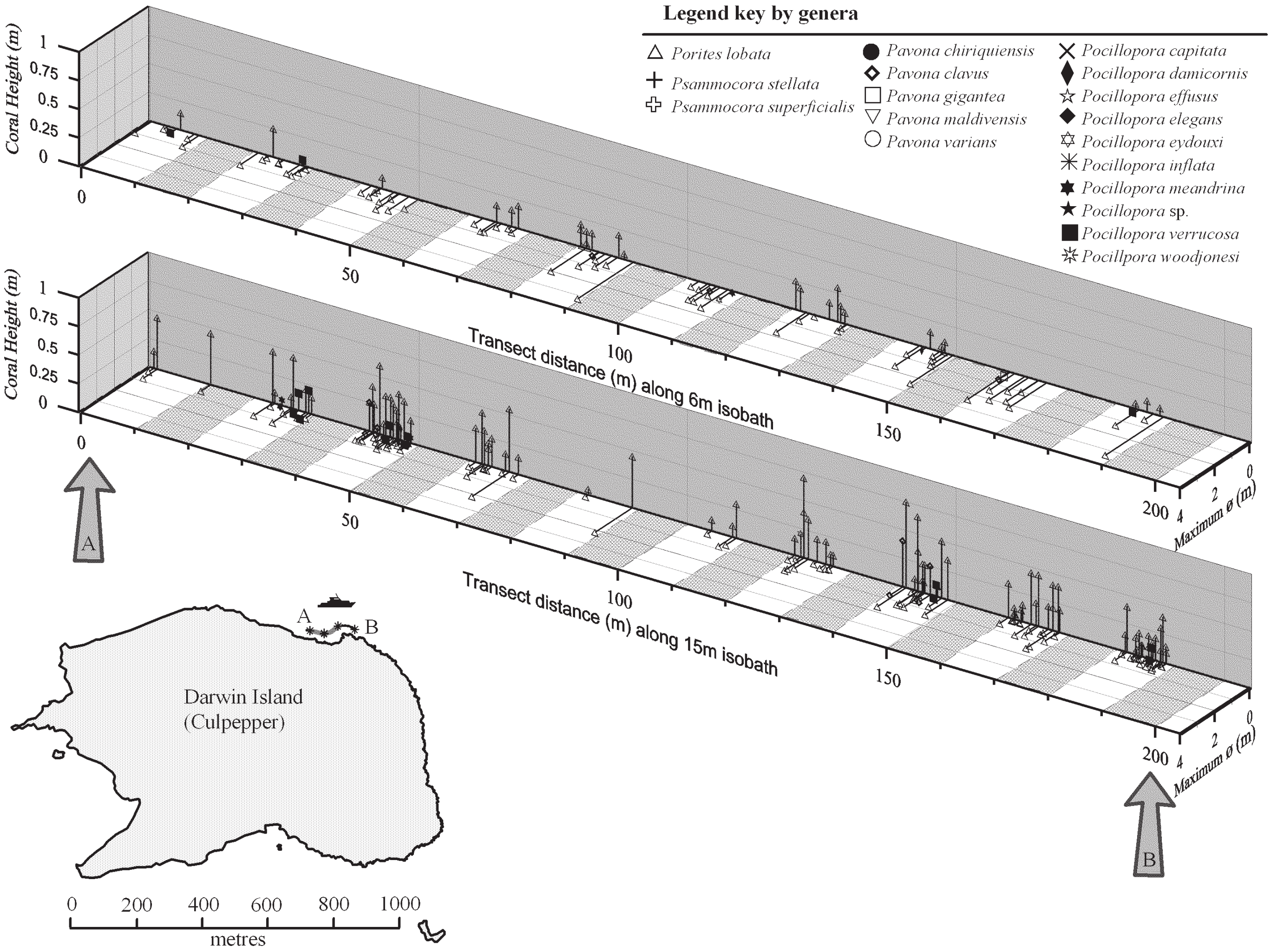


Figure 12. Coral relief at Darwin Anchorage. Species, colony midpoint position, colony height from base and maximum diameter (Ø) across a 200 m transect segment at 15 m and 6 m depth. Shaded areas represent "skipped" 10 m blocks along the non-continuous intercept transect.

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

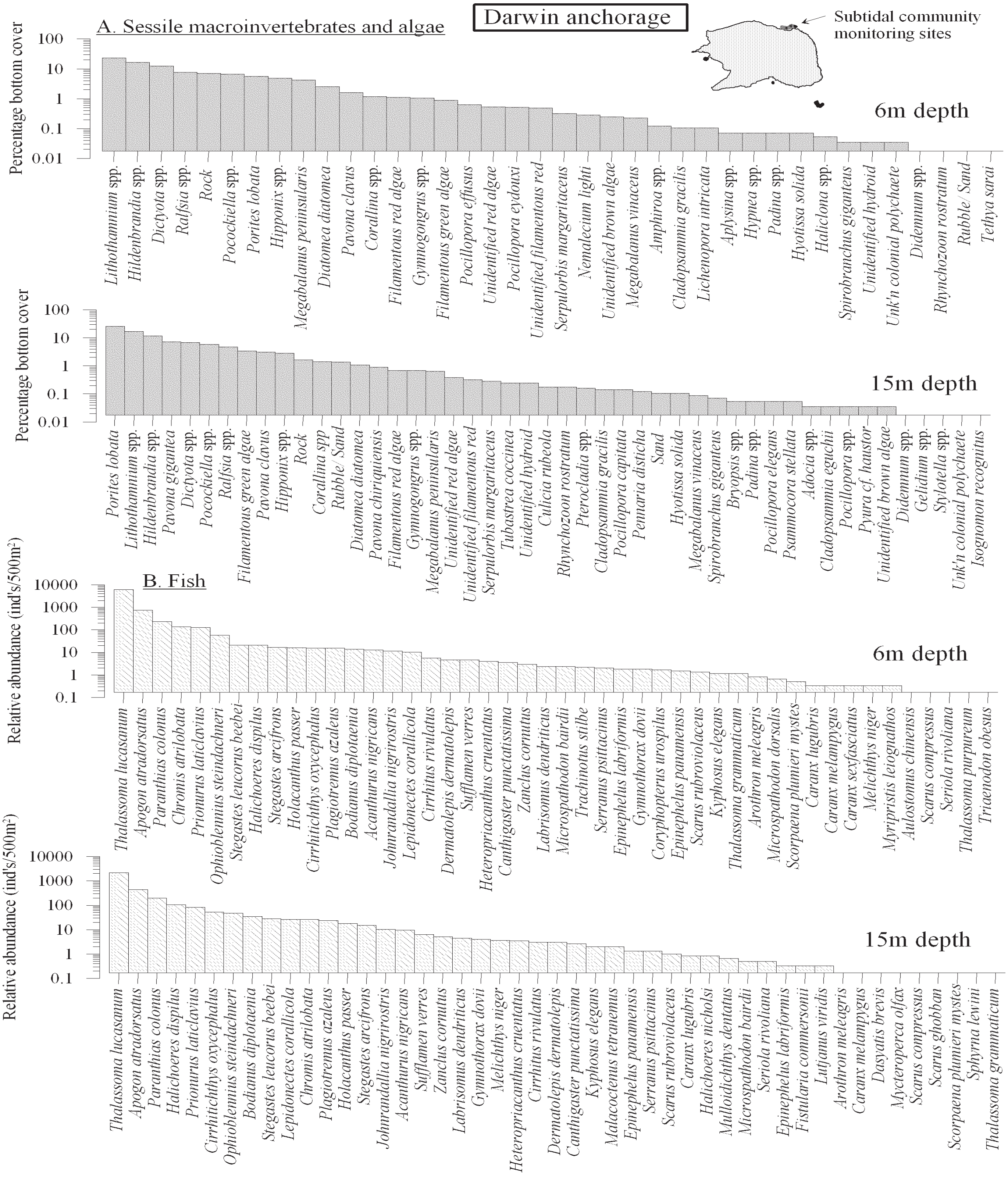


Figure 13. Rank ordered cover of sessile benthic macro-invertebrates and algae **(A)** and relative abundance of reef fish **(B)** averaged across 2005–6 seasonal sampling at two adjacent monitoring sites within Darwin Anchorage at 15 m and 6 m depth.

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 planckii*, 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* 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.

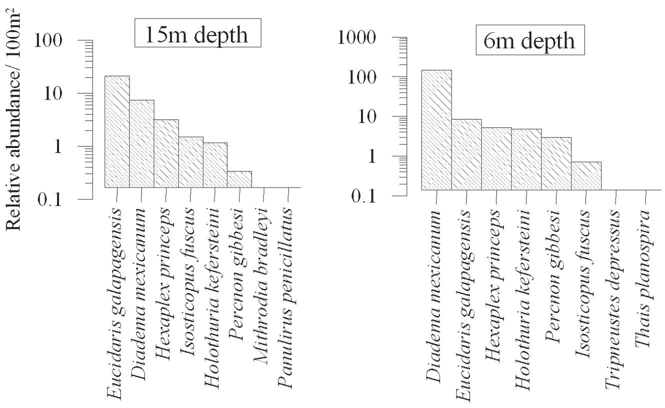


Figure 14. Rank ordered mobile macro-invertebrate relative abundance averaged across 2005–6 seasonal sampling at two adjacent monitoring sites in Darwin Anchorage over 100 m² transects at 15 m and 6 m depth.

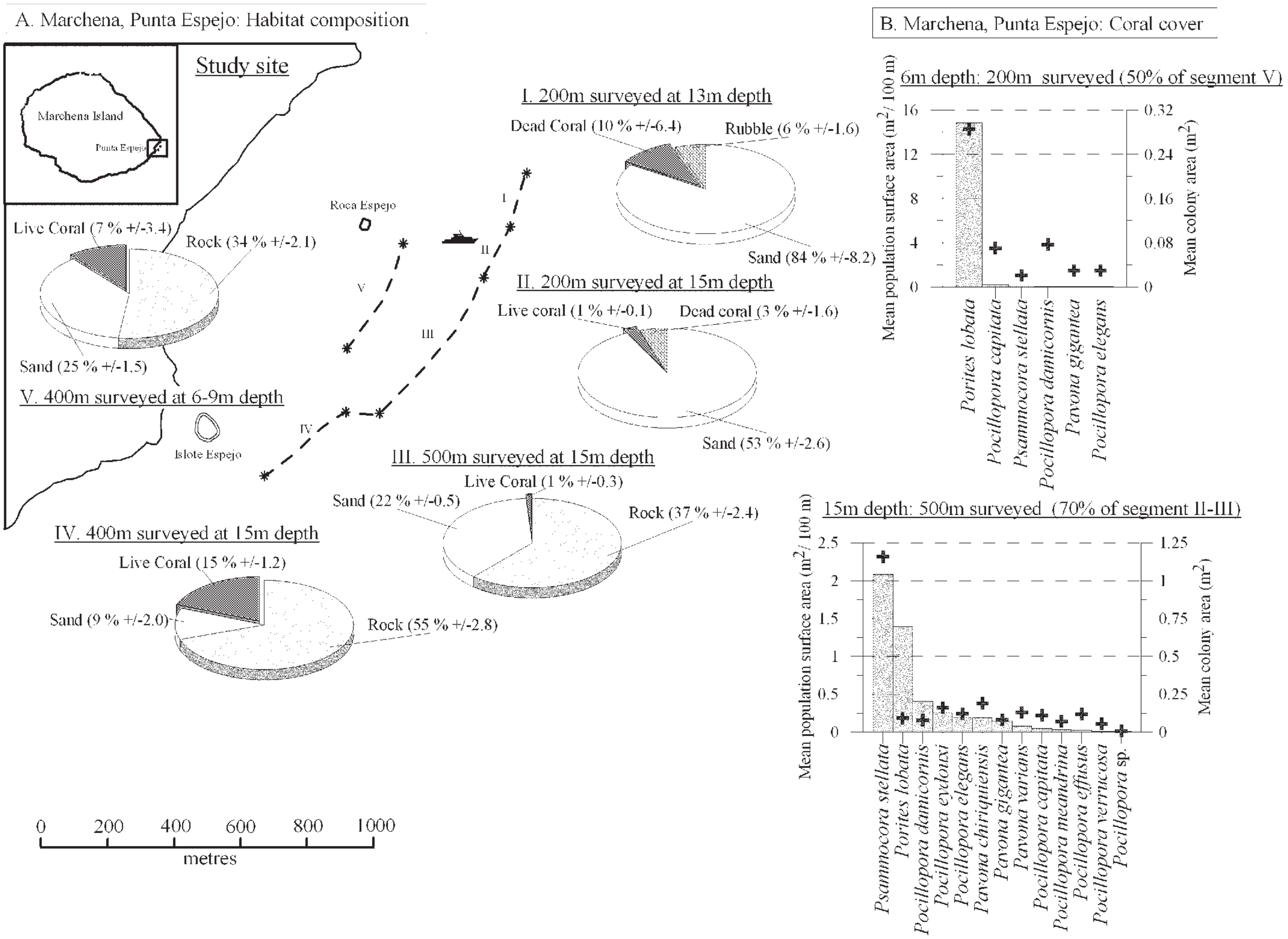


Figure 15. A Habitat composition by transect segments (I–V) across Punta Espejo, Marchena (associated error given in parentheses). **B** Coral species ranked by estimated surface area over a 100 m transect, with mean colony size (indicated by +) at 6 m and 15 m depth (across transect segments II, III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

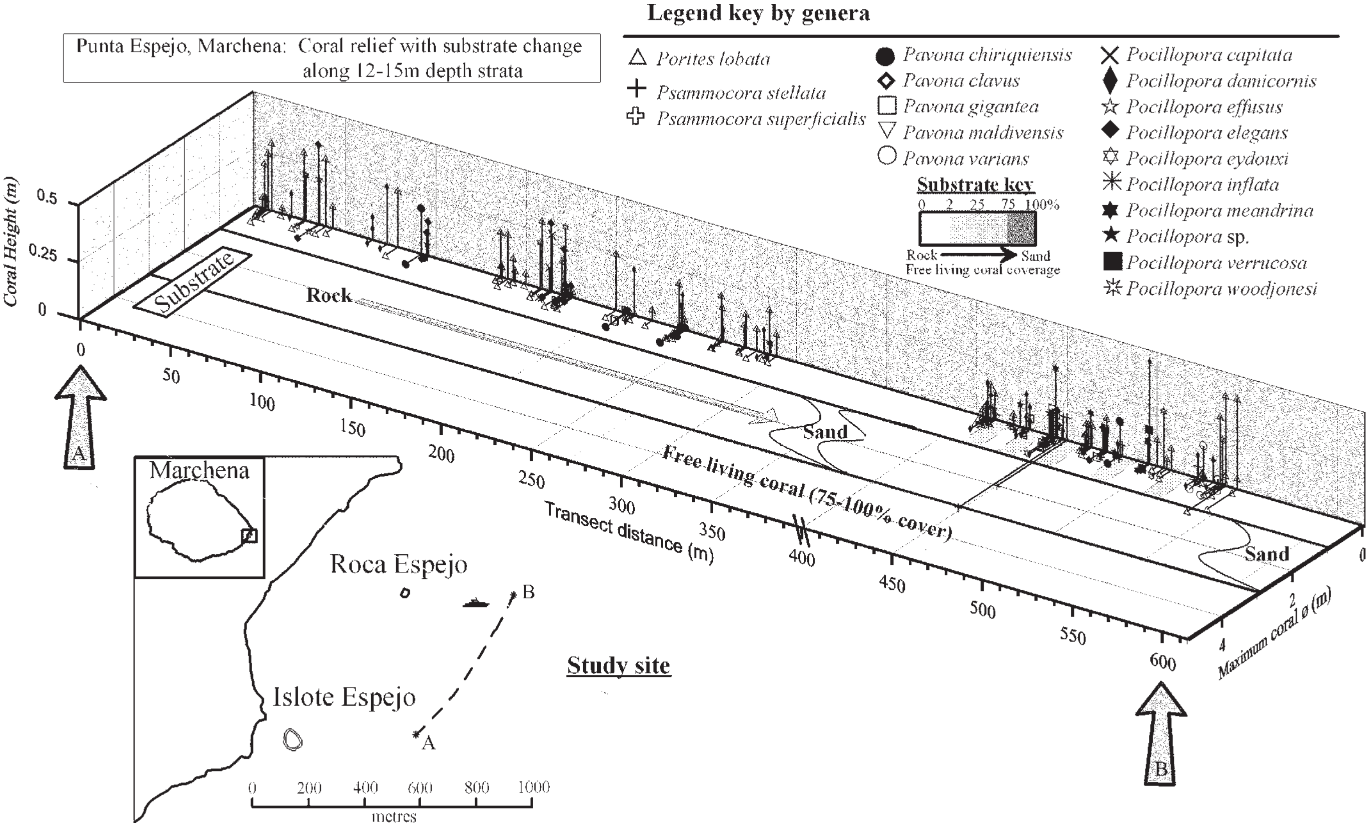


Figure 16. Coral relief at Punta Espejo, Marchena. Species, colony midpoint position, colony height from base and maximum diameter (Ø) over a 600 m transect at 12–15 m depth. Shaded areas represent "skipped" 10 m blocks along the non-continuous intercept transect. Substrate transition from rock to sand 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).

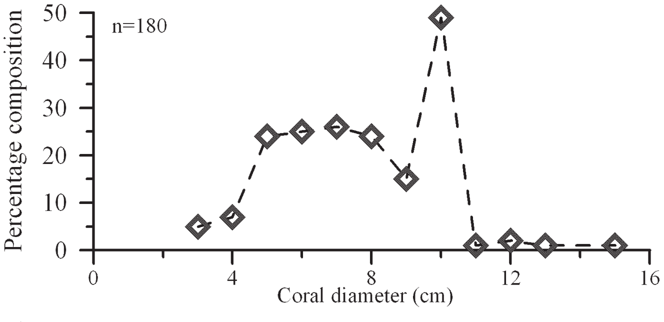


Figure 17. Size distribution of free living *Psammocora stellata* on sand substrate taken from three sampling periods (2005, 2006, 2007) at Roca Espejo, Marchena.

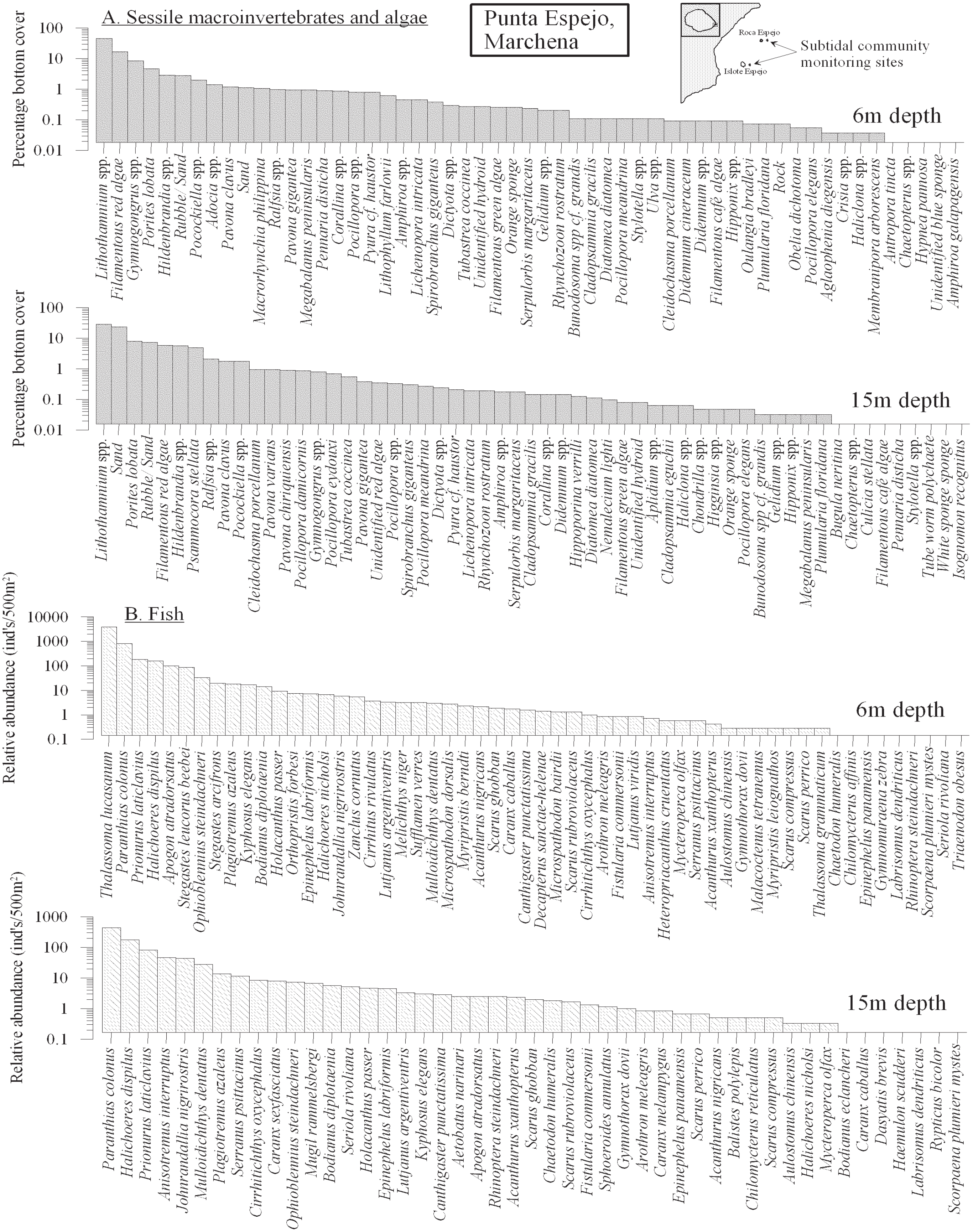


Figure 18. A Rank ordered cover of sessile benthic macro-invertebrates and algae and **B** relative abundance of reef fish averaged across 2005–6 seasonal sampling at two adjacent long-term monitoring sites at Punta Espejo, Marchena at 15 m and 6 m depth.

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 *Tripnuestes* 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 *Phataria 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 forbes*. 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 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.

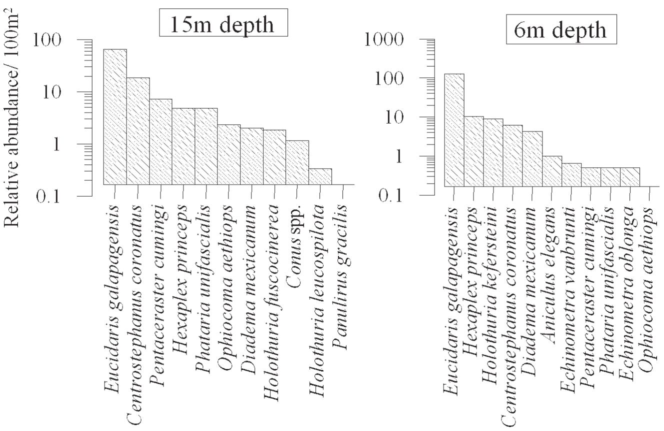


Figure 19. Rank ordered relative abundance of mobile macro-invertebrates averaged across 2005–6 seasonal sampling at 15 m and 6 m depth at two long-term monitoring sites at Punta Espejo, Marchena.

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.

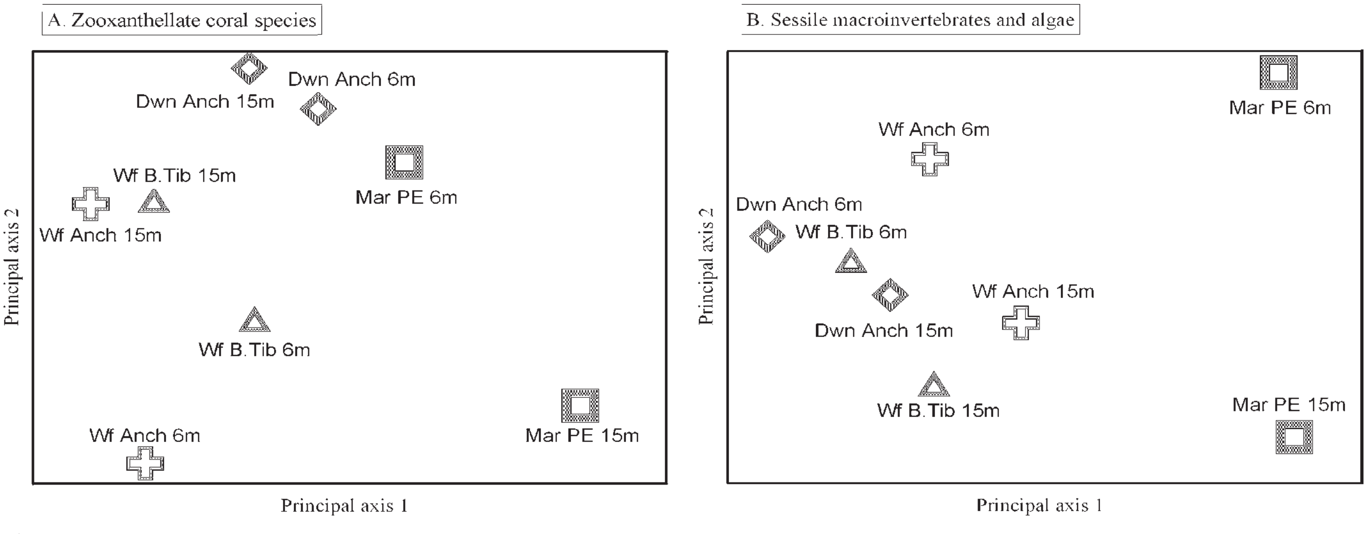


Figure 20. De-trended correspondence analysis (DECORANA) of northerly subtidal communities based on relative abundance/ cover of **A** zooxanthellate corals and **B** sessile macro-invertebrates and algae, surveyed synoptically during hot and cold seasons 2005–6 across 15 m and 6 m depth in the four 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 icthyofauna. 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 (Δ 6–8°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 26–28°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

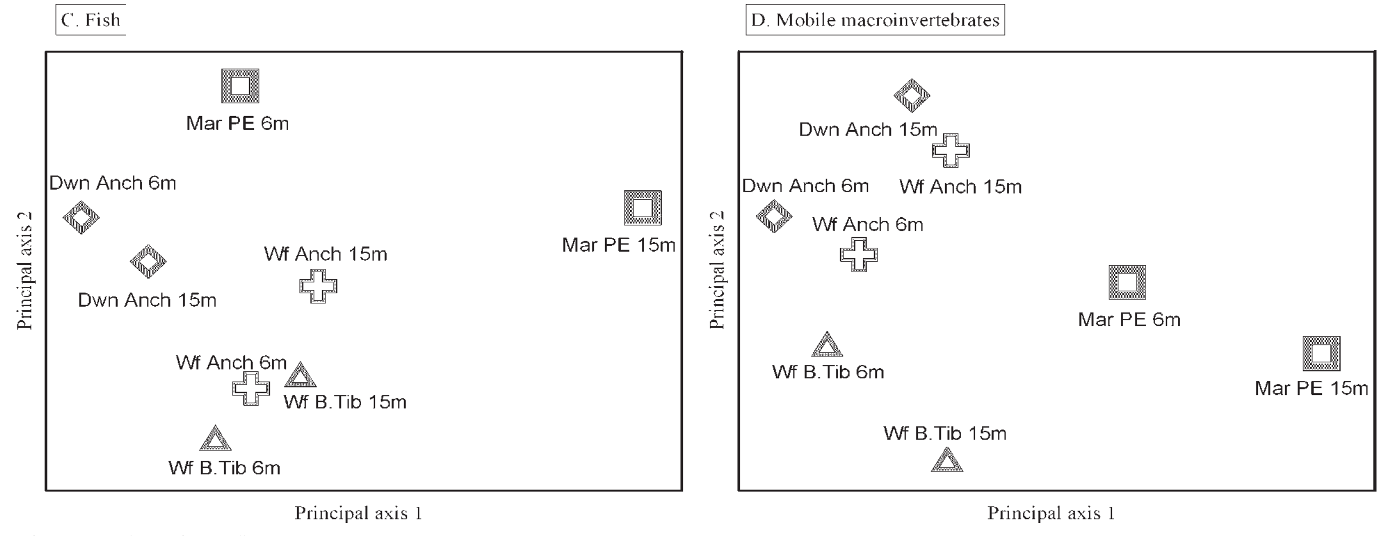


Figure 20 (continued). De-trended correspondence analysis (DECORANA) of northerly subtidal communities based on relative abundance/cover of **C** fish and **D** mobile macro-invertebrates, surveyed synoptically during hot and cold seasons 2005–6 across 15 m and 6 m depth in the four study sites.

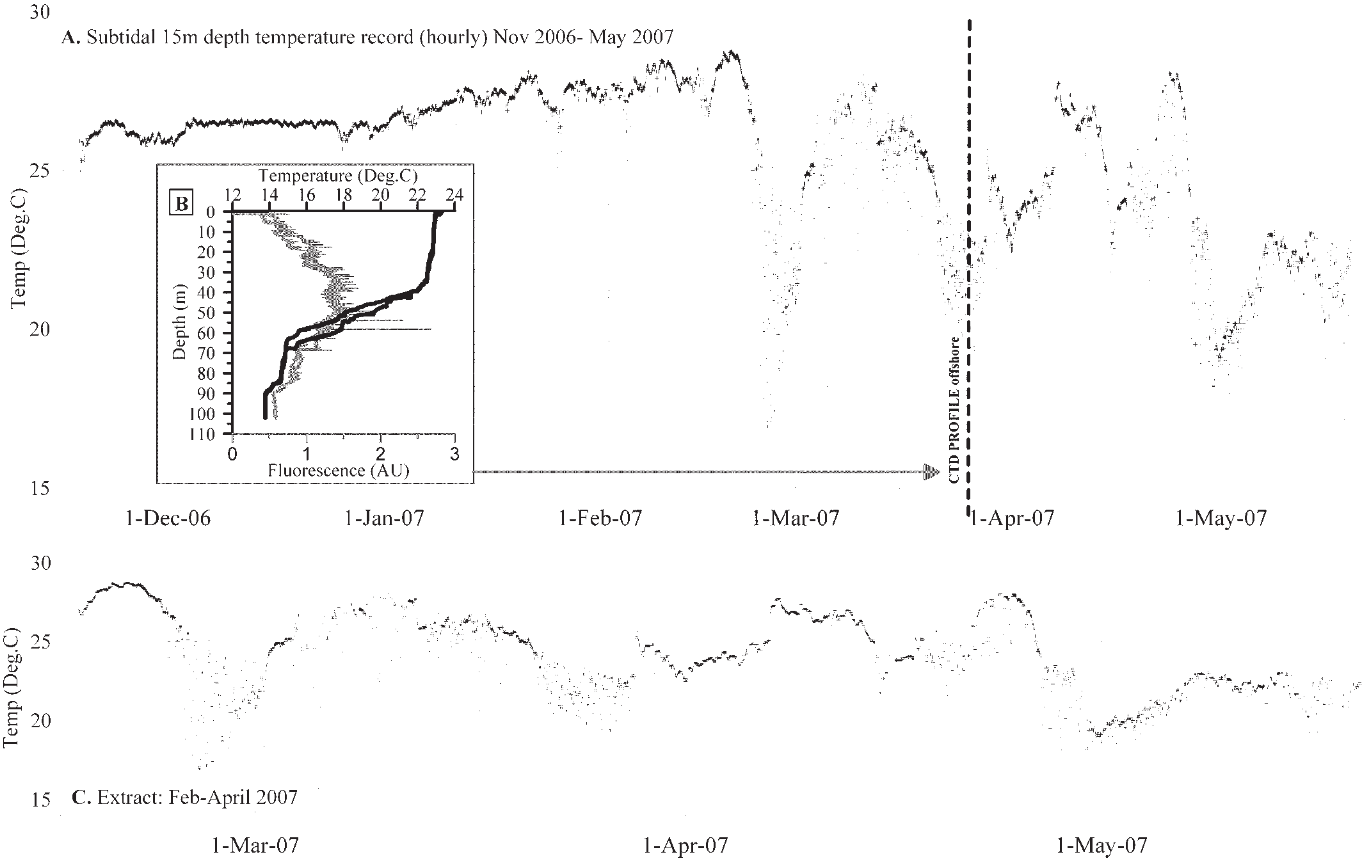


Figure 21. **A** Time series hourly temperature depth record from a YSI-CTD installed at 15 m depth in Bahía Tiburón, Wolf. Inset **B** shows the thermocline and chlorophyll maximum depth profile adjacent to the anchorage in deep water (taken 25 May 2007). **C** Extract of temperature record showing 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.

ACKNOWLEDGMENTS

The work described was completed through three expeditions financed by the UK DEFRA Darwin Initiative Project no. 14-048. Counterpart funding for equipment and salary were provided by EU-INCOFISH contract 3739, and NASA's Biodiversity and Ecological Forecasting grant NNG04 GL98G. We thank Dr Terry Dawson (University of Edinburgh) for coordinating the project and Rolf and Charles Wittmer for subsidised boat rental. We also thank Dr Cleveland Hickman, Dr Jorge Cortes, Dr Estrella Villamizar, Dr Silvia Earle, Dr Graham Edgar, Dr Fred Liss, Fernando Rivera, Fernando Pinillos and Roberto Pepolas for their participation, and Galapagos dive guides Leandro Castillo and Juan Carlos Moncayo, and fishermen Franklin Arreaga, Julio Rodriguez and William Chacon, for representing their respective sectors. This is Contribution number 1095 of the Charles Darwin Research Station.

LITERATURE CITED

Banks, S.A. 2002. Ambiente fisico Pp. 22–35 *in* Danulat, E & Edgar, G.J. (eds) *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin-Servicio Parque Nacional Galápagos, Puerto Ayora.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nystrom, M. 2004. Confronting the coral reef crisis. *Nature* 429: 827–833.

Bustamante, R.H., Vinueza, L.R., Smith, F., Banks, S.A., Calvopina, M., Francisco, V., Chiriboga, A. & Harris, J. 2002. Communidades submareales rocosas I: Organismos sesiles y mesoinvertebrados moviles. Pp. 38–67 *in* Danulat, E. & Edgar, G.J. (eds) *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin-Servicio Parque Nacional Galápagos, Puerto Ayora.

Carpenter, K.E., Livingstone, S.R., Abrar, M., Aeby, G., Aronson, R.B., Banks, S.A., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L., Edgar, G., Edwards, D.J., Fenner, D., Guzman, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J., Wallace, C., Weil, E. & Word, E. 2008. One third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321: 560–563.

Cubero Pardo P., González Pérez, F., Truelove, N., Green, V., Bauer, J. & Green, E. 2007. *Informe Anual de Resultados: Monitoreo del Impacto del Ecoturismo Marino en la Reserva Marina de Galápagos*. Fundación Charles Darwin, Puerto Ayora.

Danulat, E. & Edgar, G.J. (eds) 2002. *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Puerto Ayora.

Edgar, G.J., Fariña, J.M., Calvopina, M., Martinez, C. & Banks, S.A. 2002. Comunidades submareales rocosas II: Peces y macroinvertebrados moviles. Pp. 68–97 *in* Danulat, E. & Edgar, G.J. (eds) *Reserva Marina de Galápagos. Línea Base de la Biodiversidad*. Fundación Charles Darwin-Servicio Parque Nacional Galápagos, Puerto Ayora.

Edgar, G.J., Banks, S.A., Fariña, J.M., Calvopiña, M. & Martínez, C. 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galápagos archipelago. *Journal of Biogeography* 31: 1–18.

Feingold, J.S. 2001. Responses of three coral communities to the 1997–98 El Niño-Southern Oscillation: Galápagos Islands, Ecuador. *Bulletin of Marine Science* 69: 61–77.

Glynn, P.W. 1997. Eastern Pacific reef coral biogeography and faunal flux: Durhams dilemma revisited. *Proceedings of the 8th International Coral Reef Symposium, Panamá* 1: 371–378.

Glynn, P.W. 2003. Coral communities and coral reefs in Ecuador. Pp. 449–472 *in* Coates, J. (ed.) *Latin American Coral Reefs*. Elsevier Science, Amsterdam.

Glynn, P.W. & Ault, J.S. 2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19:1–23.

Glynn, P.W. & Wellington, G.M. 1983. *Corals and Coral Reefs of the Galápagos Islands*. University of California Press, Berkeley.

Glynn, P.W., Maté, J.L., Juan, L., Baker, A. & Calderón, M.O. 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation Event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69: 79–109.

Glynn, P.W., Riegl, B., Romanski, A.M. & Baums, I.B. 2009. Rapid recovery of a coral reef at Darwin Island, Galapagos Islands. *Galapagos Research* 66: 6–13.

Hickman, C.P. 2008. *A Field Guide to Corals and other Radiates of Galápagos.* Galápagos Marine Life Series, Sugar Spring Press, Virginia.

Hickman, C.P., Chiriboga A. & Ober, W.C. 2005. *A Field Guide to Corals of Galápagos.* Galápagos Marine Life Series, Sugar Spring Press, Virginia.

Kessler W.S. 2006. The circulation of the Eastern Tropical Pacific: A review. *Progress in Oceanography* 69: 181–217.

McClanahan, T. R., Ateweberhan, M., Muhando, C., Maina, J. & Mohammed, S.M. 2007. Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecological Monographs* 74: 503–525.

Podestá, G.P. & Glynn, P.W. 2001. The 1997–98 El Niño event in Panama and Galápagos: an update of thermal stress indices relative to coral bleaching. *Bulletin of Marine Science* 69: 43–59.

Reyes-Bonilla, H. 2002. Checklist of valid names and synonyms of the stony corals (Anthozoa: Scleractinia) from eastern Pacific. *Journal of Natural History* 36: 1–13.

Reyes-Bonilla, H., Calderón-Aguilera, L.E., Cruz-Piñón, G., Medina-Rosas, P., López-Pérez, R.A., Herrero-Pérezrul, M.D., Leyte-Morales, G.E., Cupul-Magaña, A.L. & Carriquiry-Beltrán, J.D. 2005. *Atlas de Corales Pétreos (Anthozoa: Scleractinia) del Pacífico Mexicano.* Centro de Investigación Científica y de Educación Superior de Ensenada, México.

Richmond, R.H. 1987. Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Marine Biology* 93: 527–533.

Richmond, R.H. 2005. Recovering populations and restoring ecosystems: restoration of coral reefs and related marine communities. Pp. 393–409 *in* Norse, E. & Crowder, L. (eds) *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity.* Island Press, Washington DC.

Wells, J.W. 1983. Annotated list of the scleractinian corals of the Galápagos Islands. Pp. 212–295 *in* Glynn, P.W. & Wellington, G.M. (eds) *Corals and Coral Reefs of the Galápagos Islands*. University of California Press, Berkeley.

HEALTH STATUS OF THE CORAL COMMUNITIES OF THE NORTHERN GALAPAGOS ISLANDS DARWIN, WOLF AND MARCHENA

By: Mariana Vera & Stuart Banks

Marine Ecosystem Research Programme, Charles Darwin Research Station, Galapagos, Ecuador
<mvera@fcdarwin.org.ec> <sbanks@fcdarwin.org.ec>

SUMMARY

Spatially reduced distributions of Galapagos corals and fragmented habitat, after recent strong El Niño Southern Oscillation events and greatly increased levels of human visitation, fisheries activities and dive tourism, raise important conservation questions as to the effects of compounding stress upon coral communities. A lack of knowledge concerning zooxanthellate coral disease in the Galapagos Marine Reserve, which could be used as an indicator of natural and/or anthropogenic stress prompted this characterisation of Galapagos coral health abnormalities. Colony condition was evaluated during research cruises conducted in September 2005, May 2006 and March 2007 at the northern islands of Wolf and Darwin, and in the north-central archipelago at Marchena. Observations of coral health and associated biota were taken for different coral species and sites, allowing characterisation of health anomalies that may indicate disease. Frequency of occurrence (FOC: the proportion of sites exhibiting a particular symptom) across sites and prevalence (the proportion of colonies presenting symptoms) were determined for six species-specific and three general anomalous health states. Over the eight coral reef communities sampled, the overall prevalence was 23.9 % (n = 973). The massive coral *Porites lobata* was found to be most affected, with 35 % showing symptoms of parasitism or illness. The most common health anomaly was identified as *Porites* trematodiasis, with 32 % overall prevalence within sites and found in all surveyed sites (FOC = 100 %).

RESUMEN

Estado de salud de las comunidades de corales de las islas del norte de Galápagos, Darwin, Wolf y Marchena. La reducción de la distribución espacial y la fragmentación de hábitats coralinos provocadas por los recientes eventos severos de El Niño-Oscilación Sur; conjuntamente con el enorme incremento de las visitas de turistas y las actividades de pesca comercial y buceo recreacional, plantean importantes preguntas de conservación tales como la identificación de los componentes de estrés sobre las comunidades existentes de corales. Una falta de conocimiento concerniente a enfermedades de corales zooxantelados en la Reserva Marina de Galápagos, que pueden servir como un indicador de stress natural y/o antropogénico, provocó esta caracterización de anomalías de salud en los corales de Galápagos. La condición de las colonias fue evaluada durante cruceros de investigación realizados en septiembre del 2005, mayo del 2006 y marzo del 2007 en las islas del norte Darwin y Wolf y en la parte del norte-central del archipiélago en Marchena. Observaciones de la salud de corales y la biota asociada entre especies de corales y sitios permitieron la caracterización de anomalias de salud que pueden indicar una posible enfermedad. La frecuencia de ocurrencia (FOC) (la proporción de sitios que muestran un síntoma en particular) a través de sitios y la prevalencia (proporción de colonias presentando síntomas) fueron determinadas para seis estados anormales de salud relacionados con especies en particular, y tres condiciones generales. La prevalencia total sobre las ocho comunidades de coral evaluadas fue de 23.9 % (n = 973). *Porites lobata*, un coral de crecimiento masivo, resultó ser el más afectado con 35 % de sus colonias mostrando síntomas de parasitismo o enfermedad. La anomalía de salud mas común fue identificada como *Porites* trematodiasis, con un 32 % de prevalencia dentro de sitios y encontrada en todos los sitios evaluados (FOC = 100 %).

INTRODUCTION

Coral disease is an increasing concern across diverse reef communities worldwide. Incidence and distribution of diseases in species of zooxanthellate coral have greatly increased over the last decade (Green & Bruckner 2000; Porter *et al*. 2001, Sutherland *et al*. 2004, Weil 2004). Caribbean reef monitoring data from 1996–8 for example show a 200 % increase in the different diseases registered (Porter *et al*. 2001). Symptoms of illness observed in coral communities occur as a response to biotic stressors such as bacteria, fungi and viruses and/or abiotic stressors such as increases in water temperature, UV radiation, sedimentation or localized pollution. The onset of most diseases is a response to multiple factors (Peters 1997), where one type of stress can exacerbate and compound effects from another (Santavy & Peters 1997). The increase in occurrence has caused extensive mortality across coral reefs worldwide. In the Caribbean it is implicated as the principal cause of coral decline, resulting in an apparent shift towards algae-based communities (Hughes 1994, Aronson & Precht 2001, Porter *et al*. 2001, Sutherland *et al*. 2004).

Coral communities in Galapagos constitute one of the key sensitive habitats subject to impact from not only natural disease, but also a complex interplay between climate change and anthropogenic activity. The Galapagos ecosystem, in comparison to other marine regions, is often cited as being in a near-pristine natural condition. Recently however, natural patterns of climatic stress are thought to have been exacerbated by resource over-exploitation, illegal fishing and increased dive tourism. Corals have persisted in Galapagos despite extreme archipelago-wide mortalities during El Niño Southern Oscillation (ENSO) warm events. In the 1982–3 event, coral mortality was higher in the Galapagos compared to other affected eastern Pacific study sites. Glynn *et al*. (1988) estimated a 95–99 % mortality of branching and massive coral species, and the coral mortality in the 1997–8 event was a further 26.2 % of remaining corals. Despite being of similar magnitude and duration, the coral responses during the two disturbance events were distinct (Glynn *et al*. 2001), having different spatial patterns of elevated sea temperature stress.

One might hypothesize that stress to corals through increased water temperatures would be exacerbated by a decrease in water quality through land run-off and pollution (*e.g.* during El Niño heavy rainfall), making coral more susceptible to disease. This may not be a driving factor in Galapagos, where pollution is still relatively localized around the three main urbanized ports and tourism anchorage zones. However, rain run-off from natural volcanic island deposits is rich in many minerals and may affect productive processes in low circulation coastal bays and lagoons. The causal factors behind the majority of the diseases observed for corals in Galapagos, as with many other sites in the Eastern Tropical Pacific (ETP), have yet to be elucidated, and work is needed to correctly identify them. It is strongly suspected that the change in coral habitat-forming species in Galapagos through ENSO stress has greatly altered marine ecosystem interactions over the last decades, although local observations are sparse, and largely anecdotal before 1982 (Robinson 1985, Glynn 1994). Coral populations once recorded across the archipelago are greatly reduced (Glynn 1994). Diseases are more likely to be a threat to such reduced fragmented populations.

The condition of a sample of zooxanthellate coral colonies across the range of native species present was recorded by diver survey along the coasts of Wolf, Darwin and Marchena Islands. The prevalence and significance of coral disease in Galapagos is an important indicator of their resilience to other stressors. This has local management implications for coral reefs and their associated sub tidal communities. In providing a reference point against which to measure future stress, health and conditioning of Galapagos coral species it should also be possible to compare Galapagos observations with other global and ETP regional studies. To that end, prevalence and frequency of occurrence (FOC) of possible symptoms as well as tissue anomalies were documented along with associated epibiota.

METHODS

Study area

Sites were selected based upon areas of known coral coverage from previous surveys, which included a range of zooxanthellate coral assemblages and associated biota (Danulat & Edgar 2002). Nine sites were surveyed, on the coastlines of Wolf, Darwin and Marchena. At Darwin, two sites (North Anchorage 1.68095°N, 92.001°W and

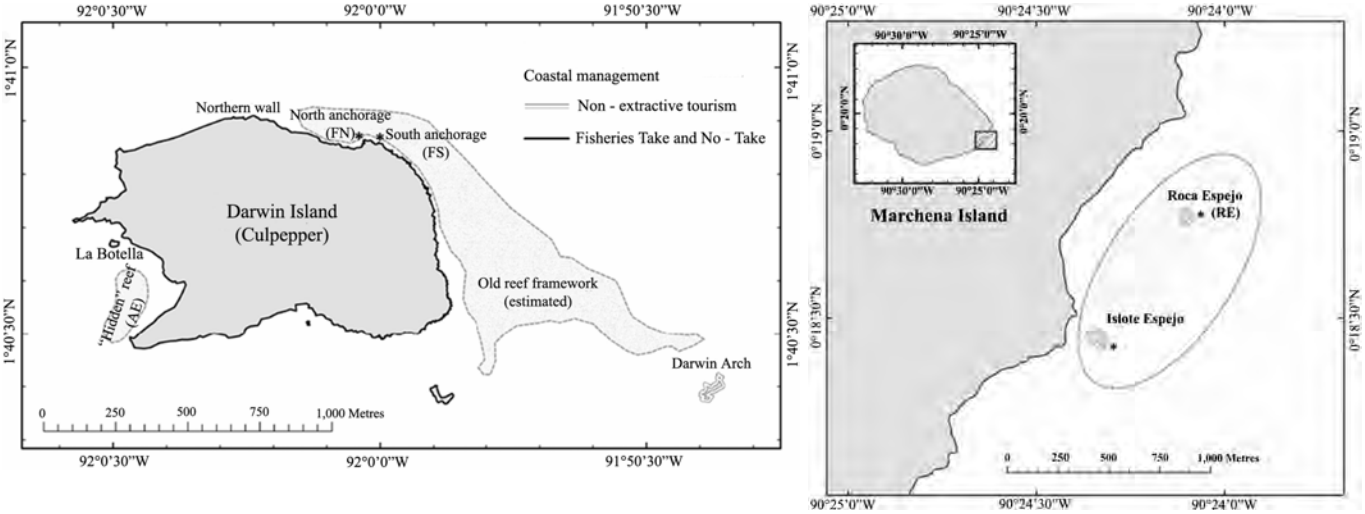


Figure 1. Darwin (left), Marchena (right) and Wolf (next page) monitoring sites (site codes defined in Table 1).

South Anchorage 1.68074°N, 91.9995°W) lay in the northeast and one in the rarely visited "Hidden Reef" (1.67683°N, 92.00752°W) to the west (Fig. 1). At Wolf, two sites (North Corals 1.38696°N, 91.8164°W and South Corals 1.387°N, 91.8166°W) were in Bahía Tiburón, the protected coral bay to the east, and one (the Anchorage 1.37867°N, 91.81940°W) to the west (Fig. 1). In Marchena, the three sites were next to Roca Espejo, separated from each other by *c.* 50 m (0.31283°N, 90.40129°W; Fig. 1). Surveyed sites correspond to habitat largely exposed to oceanic swell and current, with the exception of the more protected coral bay in eastern Wolf Island.

Surveys were undertaken at 6 m and 15 m depth, with the exception of Marchena where the platform extends at a uniform depth of 12 m. Details by research cruise and survey are summarised in Table 1. The data for 15 m (12 m at Marchena) are used in the present analysis due to low abundance at 6 m and occasional sampling problems in high surge. A deeper survey, at 20 m, was also performed at North Anchorage, Darwin, parallel to the other surveys there.

Study of coral illness

Coral illness was first documented in the Galapagos by Glynn (1983). The data presented here represent the most comprehensive revision to date, and complement efforts to map, monitor and mitigate impacts upon corals. Information presented was collected over three years during research cruises in September 2005, May 2006 and February–March 2007.

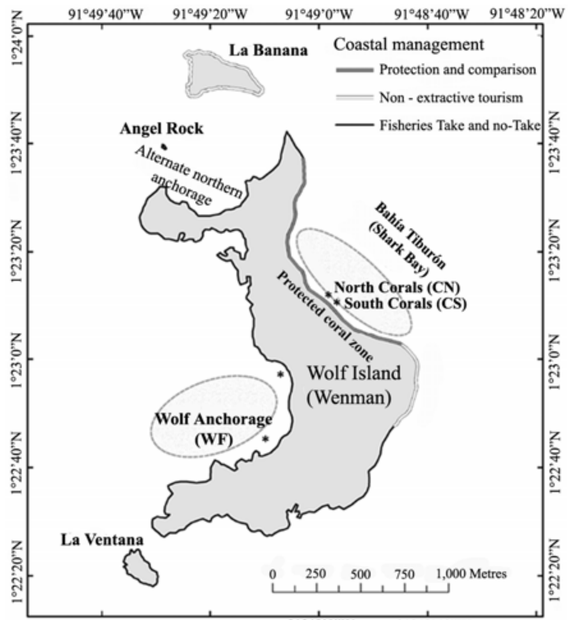


Figure 1 continued. Wolf Island monitoring sites.

Table 1. Coral monitoring effort at sampling sites in Darwin, Wolf and Marchena. Sites selected for long term comparisons are noted *. FS = Darwin South Anchorage (Fondeadero Sur); FN = Darwin North Anchorage (Fondeadero Norte); AE = Darwin Hidden Reef (Arrecife Escondido); FNp = Darwin North Deep Anchorage (Fondeadero Norte Profundo); CN = Wolf North Corals (Corales Norte); RE = Marchena Roca Espejo; CS = Wolf South Corals (Corales Sur); WF = Wolf Anchorage (Wolf Fondeadero).

Year	Island	Site	Depth (m)	% coral cover	n colonies evaluated	Transect m evaluated
2005	Darwin	*FN1	15	58.0	34	60
	Wolf	*CS	6/15	73.4	69	70
	Marchena	*RE1	12	31.8	67	30
		RE2	12	12.0	33	0
		RE3	12	16.7	49	0
2006	Darwin	AE	15	75.6	43	90
		*FN1	6/15	56.8	59	90
		FS	6/15	36.4	57	0
	Wolf	CN	6/15	56.8	69	90
		*CS	6/15	93.3	89	90
		WFP	6/15	40.6	83	90
	Marchena	*RE1	12	30.4	132	90
		RE2	12	14.2	43	90
2007	Darwin	AE	6/15	90.5	65	90
		*FN1	6/15	58.1	58	90
		FN2	6//15	49.6	46	90
		FNp	20-22	38.5	12	30
	Wolf	CN	15	51.2	69	0
		*CS	6/15	83.2	64	90
		WF1	6/15	36.3	60	60
	Marchena	*RE1	12	30.4	159	90
		RE2	12	9.5	20	30

At each of the nine sites, monitoring was undertaken by diver pairs installing a 50 x 4 m permanent plot (marked by short iron bars installed every 5–10 m), at 15 m and 6 m depths (12 m at Marchena). Each permanent plot contained three parallel 50-m transects separated by 2 m, centred on each of the 15 m and 6 m isobaths. Transects were denominated A (towards the coast), B (central) and C (towards open water). Because of trade-offs between diver experience and sampling coverage, sampling effort was divided between diver pairs recording just coral species composition and morphology and diver pairs collecting that same information, plus the more detailed health data presented here.

Along each transect (A, B and C), three 10-m segments (0–10 m, 20–30 m, 40–50 m) were surveyed, leaving unsurveyed 10-m intervals between each segment, resulting in 30 linear m per transect. Hence 90 linear m in total were surveyed at each depth at each of the nine plots. Detailed coral health data were collected on each cruise (total transect lengths evaluated for coral anomalies are given by site and cruise in Table 1).

A subset of these permanent plots may be used for future comparisons of coral cover and diversity, algal cover, macro-inverebrates and fish. We suggest that Darwin North Anchorage FN1 and FN2, Wolf North and South Corals CN and CS, and Roca Espejo RE1 be prioritised for such monitoring. Time-series community level data for fish, algae and macro-invertebrates collected since 2000 exist for these sites as part of a wider GMR evaluation.

Coral community structure was recorded by point intercept methods adapted from those used by the Atlantic Gulf Rapid Reef Assessment (AGRRA) in the Atlantic and Caribbean. Each diver recorded a set of measurements and observations for every coral colony falling under the transect line. These measures were: colony height from base (cm), maximum colony diameter (cm), % mortality (recent and old), % bleaching, associated fauna, % algae overgrowth, evidence of corallivory or grazing of algae, and the coral health observations presented here. In order to encourage robust comparable data we designated a pair of dedicated coral health inspectors who compared results after dives to check consistency. We also followed a consistent methodology between field trips, used a standard template for recording and used a shipside data coordinator and data format that facilitated rapid entry of information immediately after dive work. For each colony falling under the transect, all signs of illness were characterised, and photographed where possible, along with collection of morphometric measures for later comparison. Measurements of coral abnormalities used are based upon those applied in baseline studies of coral disease in the northwestern Hawaiian Islands (Aeby 2006).

Statistical analysis

Prevalence (or % incidence) of coral illness or infection was taken as the percentage of affected colonies among the total colonies sampled per transect. This was calculated grouping by condition, depth, and site and across all sites by dominant coral genera and species (*Pavona chiriquiensis, Pavona clavus, Pavona gigantea, Pavona varians, Pocillopora effusus, Pocillopora damicornis and Porites lobata*). Frequency of Occurrence (FOC) was calculated as the percentage of sites showing colonies with a particular infection among the total number of sites that harbour the coral genera affected by the condition.

FOC was used for descriptive comparisons between sites only. For Prevalence, a non-parametric Kruskal-Wallis test was performed across all sites and sampling visits between islands. Difference in overall Prevalence of disease between coral genera was tested with a χ^2 test for equality of distributions. We complemented this with an orthogonal one-way analysis of variance between islands for the three sites that were monitored at each of the three surveys in order to determine significant differences in Prevalence between islands.

RESULTS

Coral community structure

Relative abundance of coral taxa varied between islands and sites within islands (Table 2). Wolf and Darwin have a coastal margin dominated by large massive hermatypic coral colonies such as *Porites lobata* and, in lower pro-portion, *Pavona clavus* and *Pavona gigantea*, with greater net abundance at 15 m depth than at 6 m. A detailed coral inventory is presented separately (Banks *et al*. 2009).

Table 2. Percentages of sampled coral colonies by genus (*Pavona, Pocillopora, Porites, Psammocora*) for each site and survey.

Year	Island	Site	*Pav*	*Poc*	*Por*	*Psam*
2005	Darwin	FN1	50.0	8.8	38.2	2.9
	Wolf	CS	42.0	8.7	44.9	4.4
	Marchena	RE	2.7	14.8	57.1	25.5
2006	Darwin	AE	18.6	7.0	74.4	0
		FN1	76.3	1.7	22.0	0
		FS	0	3.5	96.5	0
	Wolf	CN	81.2	4.4	11.6	2.9
		CS	70.8	3.4	24.7	1.1
		WFP	71.1	6.0	9.6	13.3
	Marchena	RE	9.1	9.7	45.1	36.0
2007	Darwin	AE	12.3	3.1	84.6	0
		FN1	70.7	1.7	25.9	1.7
		FN2	56.5	2.2	34.8	6.5
		FNp	58.3	8.3	33.3	0
	Wolf	CN	72.5	5.8	15.9	5.8
		CS	50.0	6.3	42.2	1.6
		WF1	88.3	5.0	1.7	5.0
	Marchena	RE	1.1	7.3	40.2	51.4

The largest and by inference oldest colonies were concentrated in the Hidden Reef of Darwin and the North and South Anchorages, Wolf. Coral assemblages at Punta Espejo, Marchena, were dominated by *Porites lobata* and distinguished from any other site by large fields of small free living *Psammacora stellata* colonies.

Incidence of coral illness

Seven abnormal conditions were identified as possible coral malaise (Table 3). Other unclassified tissue anomalies were grouped into an additional class by coral genus (17.4 % of all disease observations). Examples of the characterised conditions are given in Fig. 2.

All sites showed tissue anomalies. Average Prevalence was 24.0 % across all colonies (n = 973) in all sites, with site mean of 22.6 % (n = 8, range 8.3–30.5 %). No relationship between host coral abundance and Prevalence was evident (Fig. 3).

Differences in Prevalence between islands were not statistically significant (Kruskal-Wallis, $\chi^2 = 0.27$, df = 2, $P = 0.8752$). Prevalence varied among sites (Table 4), but comparisons were not statistically significant (Kruskal-Wallis, $\chi^2 = 7.74$, df = 7, $P = 0.3561$). A one-way ANOVA (comparing pooled data from the three repeated sites over the three years) generated the same results: differences between islands were not significant (df = 2, F = 0.141, $P = 0.871$) and nor was between-site variation (df = 7, F = 0.326, $P = 0.898$).

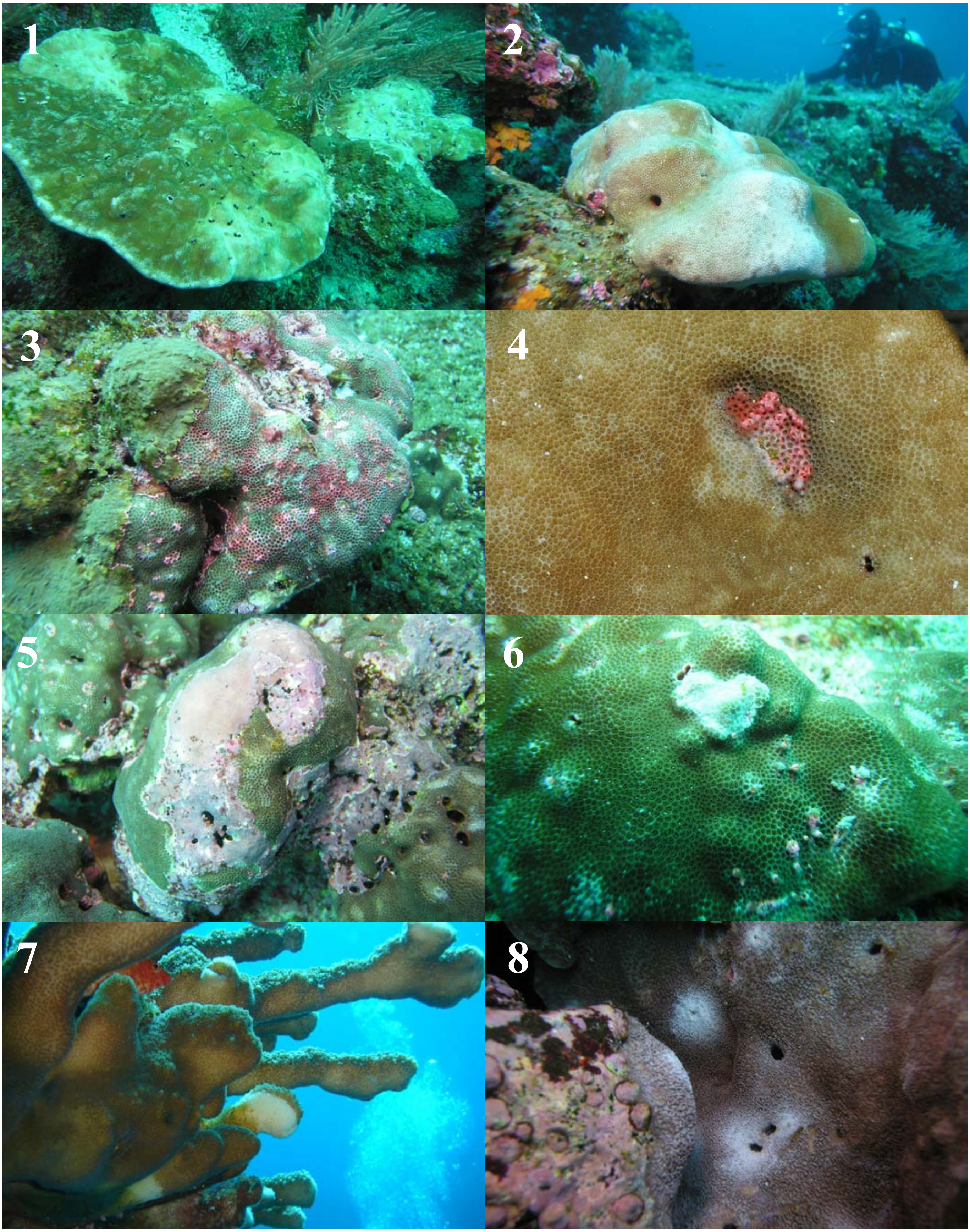


Figure 2. Corals showing some of the abnormal conditions recorded: 1, 2 *Porites* discoloration tissue thinning syndrome; 3, 4 *Porites* trematodiasis; 5 *Porites* uncharacterized disease; 6 *Porites* abnormal overgrowth; 7 *Pocillopora* white band; 8 *Pavona* white spot.

Table 3. Abnormal health conditions encountered on each coral genus at Darwin, Wolf and Marchena Islands (mean occurrence over three monitoring cruises). FOC = percentage of the sites containing the affected genera at which the disease was found.

Possible disease	Characteristics	Sites	FOC (%)	Host species
Porites				
Porites trematodiasis	Pink to pale, swollen nodules on coral colony. Nodules can be clustered or widely distributed on colony.	AE, FN, FS, RE, CS, CN, WF	100	*P. lobata*
Porites discoloration tissue thinning syndrome.	Areas of tissue thinning and discoloration that are poorly defined from surrounding healthy tissue. Polyps reduced or absent.	AE, CS, WF, FN	57.1	
Porites abnormal overgrowth	Abnormal skeletal growth.	CS, FN	33.3	
Porites mucus	Colonies show excessive mucus secretion.	AF, FN	28.6	
Porites yellow spot	Irregular yellow spots on colony.	CS	14.3	
Porites uncharacterized disease	Uncharacterized abnormal conditions.	CS, RE	25.0	
Pavona				
Pavona WRBS	Rings, bands and white spots of dead tissue in the coral colony.	CS, CN, FN, FNp, WF	83.3	*P. clavus*, *P. gigantea*
Pavona abnormal growth	Present abnormal skeletal growth.	CS, FN	33.3	*P .clavus*
Pavona mucus	Colonies show excessive mucus secretion.	FN	16.7	*P. chiriquiensis*
Pavona yellow spot	Irregular yellow spots on colony.	CS	16.7	*P. gigantea*
Pavona uncharacterized disease	Uncharacterized abnormal conditions.	AE, WF, CN, CS, FN	83.3	*P. clavus*, *P. gigantea*, *P. varians*
Pocillopora				
Pocillopora white band	White bands present on the coral branches.	WF	50.0	*P. damicornis*
Pocillopora uncharacterized disease	Uncharacterized abnormal conditions.	CS	50.0	*P. effusus*

Prevalence differed almost significantly between coral species ($\chi^2 = 18.32$, df = 6, $P = 0.055$) with *Porites lobata* having the highest Prevalence and *Pavona varians* the lowest (Fig. 4).

Darwin South Anchorage presented the greatest FOC and Darwin North Anchorage the least. Between islands, study sites in Darwin presented greater Prevalence of affected corals and Wolf the least (Fig. 5).

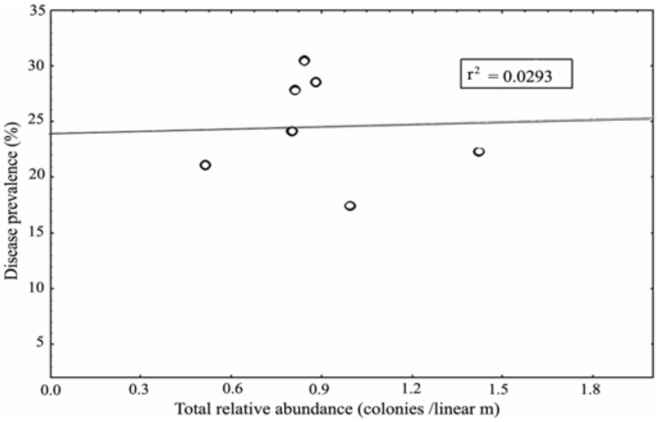


Figure 3. Total relative abundance of corals vs. disease prevalence across three sites in Darwin, three sites in Wolf and one in Marchena (at 12–15 m depth).

Distribution, FOC and Prevalence of abnormal conditions

Table 3 shows the distribution of the different abnormal colony conditions that could be differentiated (including possible infections, parasitism and tumours). Trematodiasis in *Porites lobata* (Cheng & Wong 1974, Aeby 1998a) was observed at all sites with the exception of Darwin North Anchorage at 20 m. *Porites* trematodiasis was by far the most common condition, affecting over 30 % of all *P. lobata* colonies, while undescribed conditions in *Pavona* spp. accounted for < 15 % of health problems (Fig. 6). The other characterised conditions were far less common (< 10 % of colonies presenting the other seven health

Table 4. Average Prevalence of affected coral health (all symptom types) by site.

Island	Reef profile	Site	Average Prevalence (%)
Darwin	Coastal reef	FN	21.1
		AE	22.3
		FS	30.5
		FNp	8.3
Wolf	Coastal reef	CN	28.6
		CS	27.8
		WF	17.4
Marchena	Reef platform	RE	24.2

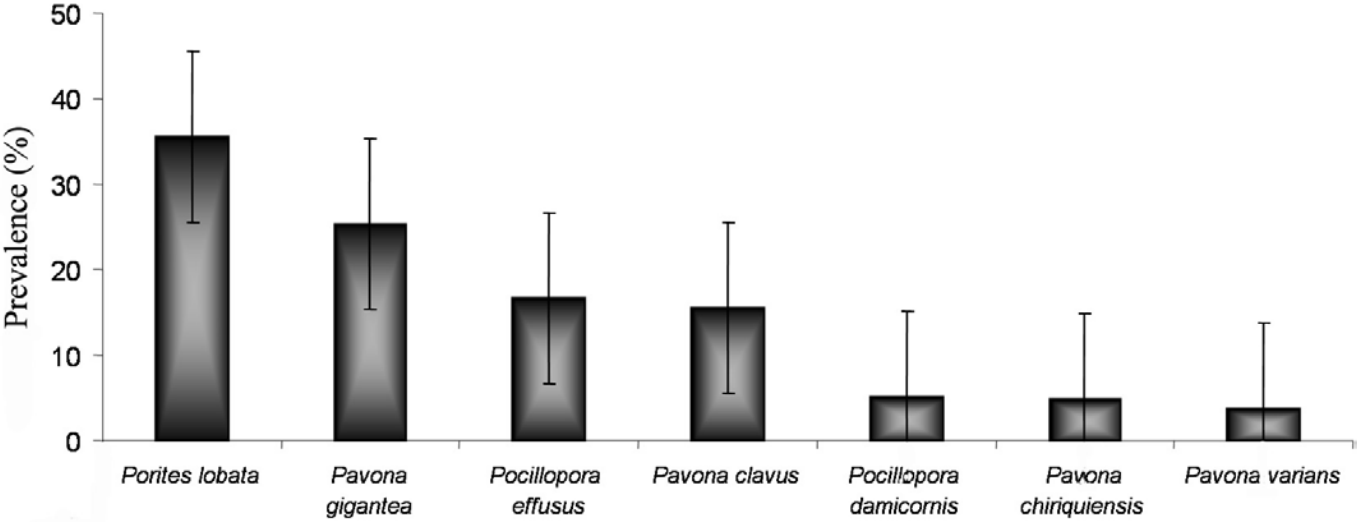


Figure 4. Mean Prevalence of all abnormalities registered for seven coral species across the seven study sites. This is the proportion of the colonies of a species that were diseased, out of the total number of colonies of the species sampled.

condition categories). Of all characterised conditions, that termed "yellow spot" was the least common.

Aside from having a greater proportion of affected colonies compared to other species, *Porites lobata* demonstrated symptoms of all observed conditions, while *Pavona varians* had both a lower relative abundance of colonies and the lowest Prevalence of health anomalies. Wolf South Corals, although showing relatively fewer affected colonies, presented all observed anomalies.

Occurrence of associated biota

Records of species associated with each colony (fish, mobile macro-invertebrates, sessile macro-invertebrates and algae) were collected to help evaluate the state of health of coral communities and improve understanding of species interdependence (Fig. 7).

Predation, as evidenced by the percentage of colonies with fish bite marks, was higher in Wolf than Darwin. Sessile bivalve and bio-eroder *Lithophaga* spp. were also more abundant around coral at Wolf. The mollusc corallivore *Coralliophillia violacea* was more abundant at Marchena than at the other two islands. Cryptic crabs were more abundant at Marchena. The crabs (*e.g. Trapezia* spp.) are typically beneficial endosymbionts and denote coral health, rather than disease (J. Feingold pers. comm.). The widespread bio-eroder pencil urchin *Eucidaris galapagensis* was most evident associated with coral colonies in Darwin and less abundant on colonies in Wolf.

DISCUSSION

An average 23.95 % of all evaluated zooxanthellate coral colonies showed tissue anomalies. This value is higher than found in other regions. In Colombia long-term coral reef monitoring programmes have been running since 1998 at San Andrés (five stations) and Providencia Islands

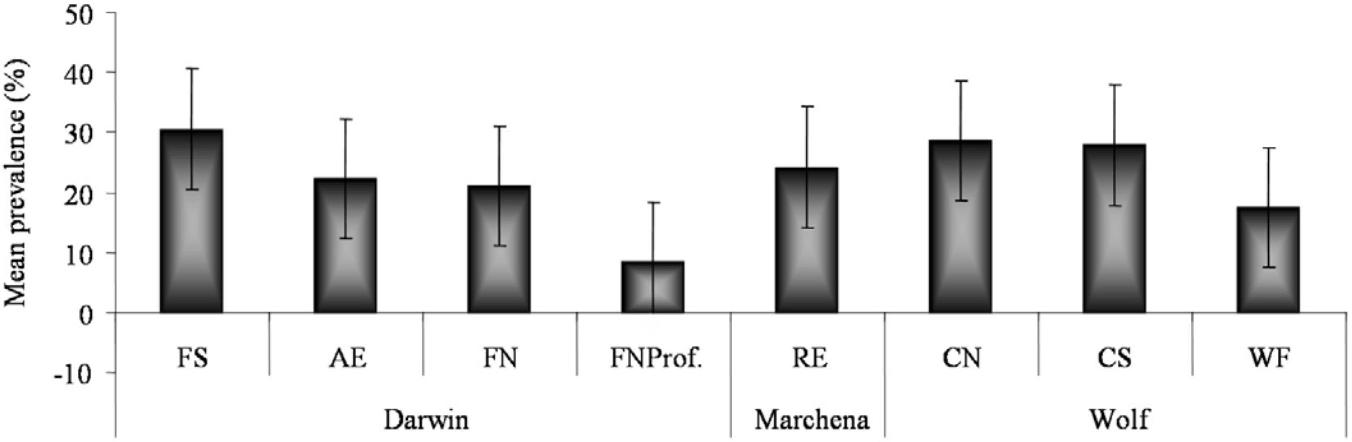


Figure 5. Mean Prevalence (± SE) of coral anomalies at the seven study sites over three cruises: September 2005, May 2006 and March 2007 (site codes defined in Table 1). Surveys were at 15 m depth with the exception of FNp at 20 m.

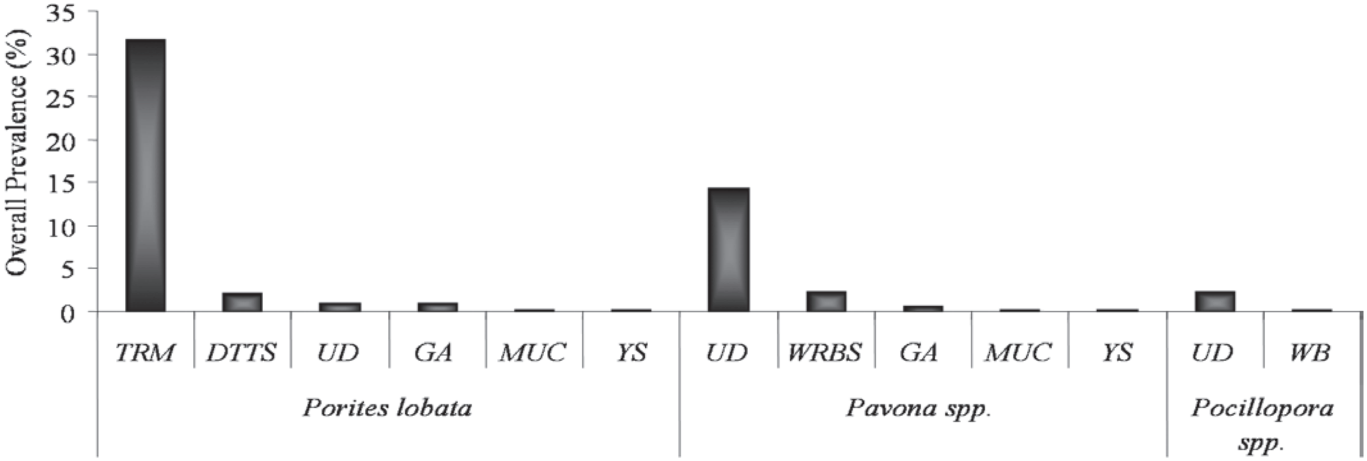


Figure 6. Mean Prevalance of all characterized coral symptoms, calculated as the % of affected colonies by species and genus. *Porites lobata*: TRM = Trematodiasis; DTTS = Discoloration tissue thinning syndrome; UD = Uncharacterized disease; GA = Growth anomaly; YS = Yellow spot; MUC = Mucus. *Pavona* spp.: WS = White spot; UD = Uncharacterized disease; GA = Growth anomaly; MUC = Mucus; YS = Yellow spot. *Pocillopora* spp.: WB = White band; UD = Uncharacterized disease.

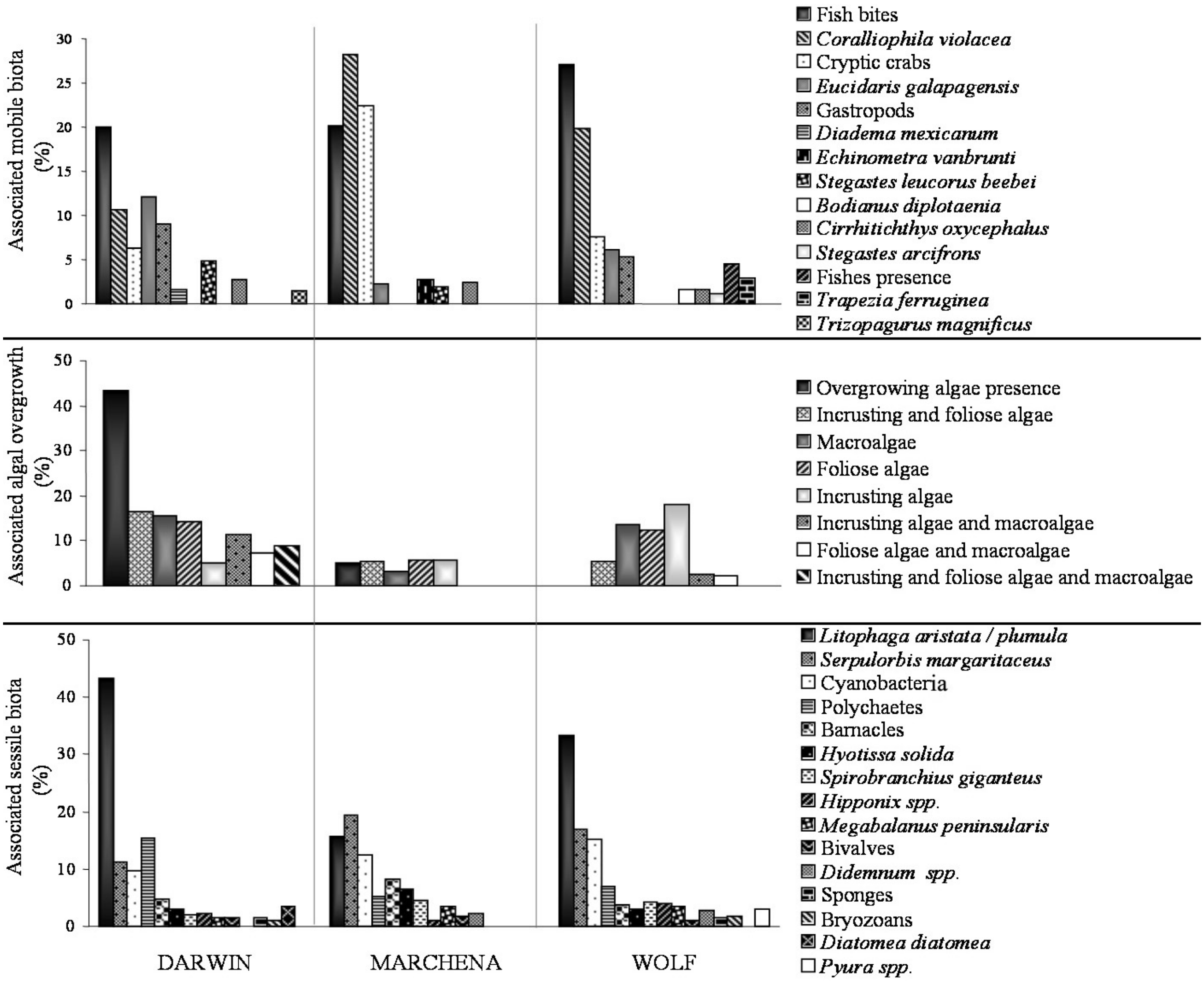


Figure 7. Mean occurrence of associated colony biota; evidence of fish predation, algae overgrowth, sessile and mobile macro invertebrates across the monitored sites.

(four stations) in the Caribbean. Coral condition was monitored from 1998–2003, and Prevalence of illness recorded at 5 %, with peaks in 1999 and 2001 in San Andrés of 9.1 % and 6.3 % respectively (Garzón-Ferreira *et al.* 2000). Santavy *et al*. (2001) surveyed coral disease across 32 stations in the Florida Keys, finding an average Prevalence of 9.6 %. Approximately 0.5 % of corals were reported to have signs of infection in the Hawaiian Islands across 73 sample sites (Aeby 2006), whereas Weil (2004) found an overall Prevalence of 5.3 % over 28 sites across islands in the Caribbean.

Including "uncharacterized", eight anomalous conditions were observed across the monitored islands: six for *Porites lobata*, five for *Pavona* spp. and two for *Pocillopora* spp. These do not all correspond to conditions reported in other regions. In the Indo-Pacific a similar number of diseases have been reported. Six states of coral malaise were described from the Philippines (Raymundo *et al*. 2005) and eight described for the Great Barrier Reef of Australia (Willis *et al*. 2004). Coral disease research in the Caribbean has a 30-year history, whereas Indo-Pacific research began during the past few years, and it is likely that the number of diseases recorded will increase with improved sampling effort in the region.

There are notable differences in the nomenclature of signs of disease, predation or parasitism. The condition characterized by swollen pink spots, termed here *Porites* trematodiasis, is known as *Porites* trematodiasis in Hawaii, pink spot in Australia and pink block *Porites* in Okinawa. Aeby (2006) recommends that nomenclature be standardised in the future. However, similarity between signs of illness described from different localities does not necessarily imply the same etiology.

Porites lobata is the dominant coral (in terms of bottom cover) over the communities evaluated, averaging 64.7 % across the three transect plot sites that were monitored each cruise. For species-specific anomalies, Prevalence depends on the density distribution of the host. This explains in part the relative FOC of each condition. *Porites* trematodiasis, the most ubiquitous condition, is for example closely linked to sites where *Porites* coral is most abundant. This condition is caused by the encystment of the larval stage of a digenetic trematode worm (of or related to *Digenea*) within the host colony (Cheng & Wong 1974, Aeby 1998a). The life cycle of this parasite is facilitated by corallivore fish ingesting infected polyps and the adult worm residing in the gills of the fish (Aeby 1998b). We inferred this condition, based on observations of tissue anomalies consistent with descriptions of the disease. Future microscopic/histological analysis should be applied to confirm this. The encysted stage of the parasite within the host coral is viable for many months before the parasite develops (Aeby 1998a). The pink coloration and swelling of infected polyps attract fish that preferentially graze upon them (Aeby 1992, 2002). These two attributes, the ability to maintain viability for long periods before transmission and the altered appearance of the host coral, promote successful dispersal via the host fish. Faecal liberation by the fish as a vector for the parasite eggs into the environment facilitates dispersal over the coral community as a whole.

Symptoms similar to four of the eight anomalies described in this study have been reported from other areas in the Indo-Pacific. *Porites* trematodiasis has a wide distribution across the Indo-Pacific, reported in Australia (Willis *et al*. 2004), the principal Hawaiian Islands (Aeby 1998a) and Okinawa, Japan (Yamashiro 2004). The white band disease inferred in *Pocillopora* in Wolf Anchorage is apparently similar to that described from the Caribbean. Future analysis isolating disease agents from corals displaying symptoms would help distinguish between denuded skeleton that could have resulted from corallivory and the inferred disease (J. Feingold pers. comm.). The other abnormal conditions registered in *Pavona* corals do not seem to have been reported from other regions.

As a region under extreme temperature stress and greatly increased anthropogenic activity in the coastal zone since the 1980s, the last remaining Galapagos zooxanthellate corals can be considered on the threshold of their natural tolerance. Estimating coral health and incidence of disease is important for assessing stress response and helps elucidate the possible compounding effects between recovery from strong climatic regional events such as El Niño, anchor damage, local pollution, physical diver damage and global climate change over larger scales. Given the recent tendency towards more frequent warm-water and cold-shock bleaching events and consequent greater susceptibility to pathogens and parasites (Hughes *et al*. 2003) the emphasis needs to turn towards how best to protect and manage the remaining Galapagos coral resources.

ACKNOWLEDGMENTS

This work was financed by the Darwin Initiative project 14-048 *Conservation of Galapagos Corals: Mitigation, mapping and monitoring* in coordination with the University of Edinburgh. We thank coral expert Dr Estrella Villamizar (Universidad Central de Venezuela) and the Rolf Wittmer M/V *Tip Top* operation for their support during the research cruises. This is Contribution number 1096 of the Charles Darwin Research Station.

LITERATURE CITED

Aeby, G.S. 1992. The potential effect the ability of a coral intermediate host to regenerate has had on the evolution of its association with a marine parasite. *Proceedings of the 7th International Coral Reef Symposium* 2: 809–815.

Aeby, G.S. 1998a. Interaction of the digenetic trematode, *Podoctyiloides stenometra*, with its coral intermediate host and butterfly fish definitive host: ecology and evolutionary implication. Ph.D. Dissertation, University of Hawaii, Honolulu.

Aeby, G.S. 1998b. A digenean metacercaria from the coral reef, *Porites compressa*, experimentally identified as *Podocotyloides stenometra*. *Journal of Parasitology* 84: 1259–1261.

Aeby, G.S. 2002. Trade-offs for the butterfly fish, *Chaetodon multicinctus*, when feeding on coral prey infected with trematode metacercariae. *Behavioural Ecology and Sociobiology* 52: 158–163.

Aeby, G.S. 2006. Baseline of coral disease in the Northwestern Hawaiian Islands. *Atoll Research Bulletin* 543: 471–488.

Aronson, R.B. & Precht, W.F. 2001. White-Band disease and the changing face of Caribbean coral Reef. *Hydrobiologia* 460: 25–38.

Banks, S.D., Vera, M. & Chiriboga, A. 2009. Characterizing the northern Galapagos coral reefs: establishing reference points to assess long-term change in zooxanthellate coral communities. *Galapagos Research* 66: 43–64.

Cheng, T.C. & Wong, A.K. 1974 Chemical, histochemical and histopathological studies on corals, *Porites* spp., parasitised by trematode metacercariae. *Journal of Invertebrate Pathology* 23: 303–317.

Danulat, E. & Edgar, G.J. (eds) 2002. *Reserva Marina de Galápagos. Linea Base de la Biodiversidad*. Fundación Charles Darwin/ Servicio Parque Nacional Galápagos, Puerto Ayora.

Garzón-Ferreira, J., Cortés, J., Croquer, A., Guzmán, H., Leão, Z. & Rodríguez-Ramírez, A. 2000. Status of coral reefs in southern tropical America: Brazil, Colombia, Costa Rica, Panama and Venezuela. Pp. 331–348 *in* Wilkinson, C. (ed.) *Status of Coral Reefs of the World.* Australian Institute of Marine Science, Townsville.

Glynn, P.W. 1994. State of coral reef in the Galápagos Islands: natural vs. anthropogenic impacts. *Marine Pollution Bulletin* 29: 131–140.

Glynn, P.W., Wellington, G.M. & Wells, J.W. 1983. *Coral and Coral Reefs of the Galápagos Islands*. University of California Press, Berkeley.

Glynn, P.W., Cortés, J., Guzmán, H.M. & Richmond, R.H. 1988. El Niño (1982–83) associated coral mortality and relationship to sea surface temperature deviation in the tropical eastern Pacific. Pp. 237–243 *in*: *Proceedings of the 6th International Coral Reef Symposium,* vol. 1. Australian Institute of Marine Science, Townsville.

Glynn, P.W., Maté, J.L., Baker, A.C. & Calderon, M.O. 2001. Coral bleaching and mortality in Panamá and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69: 79–109.

Green, E. & Bruckner, A. 2000. The significance of coral disease epizootiology for coral reef conservation. *Biological Conservation* 96: 347–361.

Hughes, T. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.

Hughes, T., Baird, A., Bellwood, A.D., Card, D.M., Connolly, M.S., Folke, S.C., Grosber, C.R., Hoegh-Guldberg, R.O., Jackson, O.J., Kleypas, J.J., Lough, J.J., Marshall, J.P., Nyström, P.M., Palumbi, M.S., Pandolfi, S.J., Rosen, B. & Roughgarden, J. 2003. Climate change, human impacts and the resilence of coral reefs. *Science* 301: 929–933.

Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16: S23–S32.

Nyström, M. & Folke, C. 2001. Spatial resilience of coral reefs. *Ecosystem* 4: 406–417.

Peters, E.C. 1997. Diseases of coral reef organisms. Pp. 114–139 *in* Bikerland, C. (ed.) *Life and Death of Coral Reefs*. Chapman & Hall, New York.

Porter, J., Dustan, P., Jaap, W., Patterson, K., Kosmynin, V., Meier, O., Patterson, M. & Parsons, M. 2001. Pattern of spread of coral disease in the Florida Keys. *Hydrobiologia* 460: 1–14.

Raymundo, L., Rosell, K., Reboton, C. & Kaczmarky, L. 2005. Coral disease on Philippine reefs: genus *Porites* is a dominant host. *Diseases of Aquatic Organisms* 64: 181–191.

Robinson, G. 1985. Influence of the 1982–1983 El Niño on Galápagos marine life. Pp. 153–190 *in* Robinson, G. & Del Pino, E.M. (eds), *El Niño in the Galápagos Islands: the 1982–1983 Event*. Charles Darwin Foundation, Quito.

Santavy, D.L. & Peters, E.C. 1997. Microbial pests: coral disease research in the western Atlantic. *Proceedings of the 8th International Coral Reef Symposium* 1: 607–612.

Santavy, D., Mueller, E., Peters, E., MacLaughlin, L., Porter, J., Patterson, K. & Campbell, J. 2001. Quantitative assessment of coral disease in the Florida keys: strategy and methology. *Hydrobiologia*. 460: 39–52.

Sutherland, K., Porter, J. & Torres, C. 2004. Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. *Marine Ecology Progress Series* 266: 273–302.

Weil, E. 2004. Coral reef disease in the wider Caribbean. Pp. 25–68 *in* Rosenberg, E. & Loya, Y. (eds) *Coral Health and Disease*. Springer-Verlag, Berlin.

Willis, B., Page, C. & Dinsdale, E. 2004. Coral disease on the Great Barrier Reef. Pp. 35–68 *in* Rosenberg, E. & Loya, Y. (eds) *Coral Health and Disease*. Springer-Verlag, Berlin.

Yamashiro, H. 2004. Coral disease. Pp. 56–59 *in* Tsuchiya, M., Nadaoka, K., Kayanne, H. & Yamano, H. (eds) *Coral Reefs of Japan*. Ministry of the Environment and Japanese Coral Reef Society, Tokyo.

GALAPAGOS COMMENTARY

PROTECTION OF SHALLOW MARINE ECOSYSTEMS IN GALAPAGOS BY PERMANENT MOORINGS

By: Godfrey Merlen[1], Fernando Ortiz Quevedo[2] & Roberto Pépolas[3]

[1]Puerto Ayora, Santa Cruz, Galapagos, Ecuador <merlenway@gmail.com>
[2]Conservation International, Puerto Ayora, Galapagos, Ecuador
[3]Charles Darwin Research Station, Puerto Ayora, Galapagos, Ecuador

SUMMARY

We describe a new system of permanent moorings designed for tour boats, to be installed throughout Galapagos, and the deployment of a research and monitoring vessel to Wolf Island.

RESUMEN

La protección de los ecosistemas costeros de Galápagos por los atracaderos permanentes. Describimos un nuevo sistema de atracaderos permanentes, diseñados para los barcos de turismo y para ser instalados a lo largo de las islas Galápagos, así que el despliegue de un barco de investigación y monitoreo a la isla Wolf.

GALAPAGOS CORALS AND THE NEED FOR FIXED MOORINGS

The tropical location of the Galapagos Islands might suggest that its underwater volcanic slopes should be covered with hard corals, as in the West Pacific. This is not the case due to the variable water temperatures, which do not provide the stable environment that corals thrive in. Notwithstanding, the Galapagos have 21 species of zooxanthellate corals, including 19 reef-forming species. Moreover, especially in the northern islands of Darwin and Wolf, some extensive coral reefs have developed.

In recent times, higher water temperatures and severe El Niño events, apparently associated with climate change, have led to extensive coral mortality. Growing awareness of the fragility of corals worldwide and in the Galapagos inspired the development of a project to locate coral reefs, study their diversity in Darwin and Wolf, and establish sustainable mechanisms to protect them for the long term. This was important given the growing dive tourism that has stimulated increasing and indiscriminate deployment of anchors in the archipelago. This work concentrated on the management of anchorage sites and the search for alternative methods of securing vessels.

Traditional mooring techniques (without use of the vessel's own anchors) utilizing heavy weights and chains, may still cause considerable bottom damage as the chains scrape across the bottom, creating a large circle of impact around the mooring centre. New techniques now available are designed to reduce such impact. These use methods of penetrating the sea floor and inserting solidly-fixed steel components, from which lines run to the surface where they are attached to mooring buoys. These techniques, specifically helix and Halas moorings, have been tested in various regions with considerable success.

MOORING DESIGNS

Calculations based on the type of vessels used at Darwin and Wolf (live-aboard dive vessels) and the most extreme oceanographic conditions likely to be encountered led to a decision to utilize in sandy bottoms two 3 m helix screws, driven deeply into the sand by a hydraulically powered reduction head coupled to a rotating socket. For rocky bottoms, stainless steel U-bolts (316 grade) of up to 25 mm diameter (a Halas design) were chosen for installation by using a hydraulic drill and bit to perforate the rock to a depth *c.* 35 cm. The two coarse-threaded shafts of the U-bolts are cemented into the substrate with epoxy glue.

THE ZERO ANCHORS PROJECT

Although the project was initially designed for the northern islands, it quickly became apparent that the problem was not unique to them. For example, it was estimated that 5500 anchors were deployed yearly at Bartolomé Island, on a bottom that is home to the endemic bat fish *Ogcocephalus darwini* and razor fish *Xyrichthys victori*, and native flatfish *Aseraggodes herrei*. In the archipelago as a whole, at least ten other species of endemic fish and invertebrates (Brittle Sea-Star *Ophionereis albomaculatus*, Green Sea-Urchin *Lytechinus semituberculatus*, Galapagos Sand Dollar *Encope galapagensis*, Galapagos Porgy *Calamus taurinus*, Blue and Yellow Snapper *Archosargus pourtalesii*, Yellow-mouth Blenny *Chaenopsis schimitti*, Galapagos Puffer-fish *Sphoeroides angusticeps*, Galapagos Garden Eel *Taenioconger klausewitzi*, Galapagos Tongue-Fish *Ophidion* sp., Galapagos Eel *Quassiremus evionthas*) and many native ones, such as the spectacular Blunt-head Triggerfish *Pseudobalistes naufragium*, inhabit, feed on or nest on sandy bottoms at the depth range (10–30 m) at which anchors are normally dropped. Thus the initial idea to conserve Wolf and Darwin led to the new concept of "Zero Anchors" for the whole archipelago, involving dozens of moorings. This idea now has the support of the Ecuadorian government and is being implemented by the Galapagos National Park Service (GNPS).

So far, five permanent moorings have been installed at an experimental pilot site at Bartolomé (Fig. 1). Bartolomé was chosen because, according to GNPS data, it is the uninhabited island with the highest visitation in the Galapagos group. Virtually every tour boat in the archipelago visits the island, so beginning there allowed for priority impact reduction along with high visibility and use, thus generating valuable feedback from users regarding mooring adequacy. Also, being relatively near to the GNPS base, the moorings can be monitored daily and inspected regularly for wear, tear and performance.

Both helix screw and stainless steel U-bolt moorings were employed. For experimental purposes the lines to the surface were of two types: a novel synthetic 20 mm fibre rope (French-manufactured DELTEX line), and 25 mm nylon rope utilizing an expandable section (Swedish-made SEAFLEX line) to reduce shocks on the mooring. Both systems have plastic mooring buoys equipped with solar-powered flashing lights and radar reflectors.

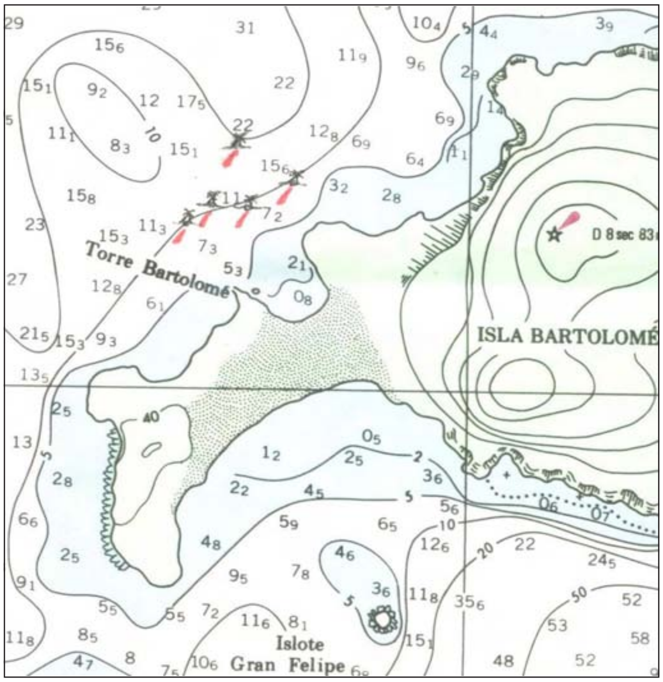


Figure 1. Permanent moorings at Bartolomé. This chart is the first of a series showing permanent moorings in Galapagos, generated by Ecuador's Oceanographic Institute of the Navy (INOCAR).

The moorings have been enthusiastically accepted by the tourism community, with captains and owners of vessels pleased with their efficiency and the saving of wear and tear on their ground gear. Preliminary monitoring results are already allowing selection of better materials for future permanent moorings.

COMPLEMENTARY PROTECTION FOR WOLF AND DARWIN ISLANDS

These two remote islands remain a priority and their coral reefs require urgent protection, complementary to the deployment of fixed moorings. These islands are a hub for large schools of Scalloped Hammerhead Shark *Sphyrna lewini*, and it is imperative not only to save the coral reefs with which these animals are associated, but also to end the slaughter of these creatures for their fins. These needs have resuscitated a project that was started seven years ago: the stationing of a live-aboard platform for science and management at Wolf Island. The vessel, the *Tiburon Martillo*, is a 23-m steel hull with living quarters for eight persons. It was successfully deployed in October 2008 to Wolf, where it will be permanently moored and from where expeditions will be made periodically to Darwin to ensure that corals are not being damaged and to control shark fishing there. The permanent moorings will be monitored regularly from the boat to ensure their safety for use and security from vandalism.

CONCLUSION

The state of the biodiversity of the Galapagos Islands is becoming more worrisome, especially with global climate change looming larger. Corals are at the forefront of these concerns. Permanent moorings will not only offer protection to the corals but will also help to conserve habitat for many other benthic organisms. At the same time their installation is helping to raise awareness of conservation issues and enabling tour operators and tourists to feel that their impact has been minimized.

ACKNOWLEDGMENTS

This work was partly financed by the UK DEFRA Darwin Initiative project 14-048. The Ecuadorian Oceanographic Institute of the Navy designed the buoys for this project and helped establish the Bartolomé pilot project. The Zero Anchors project receives financial and technical support from Conservation International and WildAid. This is Contribution number 1089 from the Charles Darwin Research Station.

Galapagos Research

INSTRUCTIONS FOR AUTHORS

***Galapagos Research* (formerly *Noticias de Galápagos*)** is the research journal of the Charles Darwin Foundation for the Galapagos Islands. It publishes Research Articles, archival value news items ("News from Academy Bay") and more general or popular articles ("Galapagos Commentary") covering any topic relevant to science or nature conservation in Galapagos, including natural history, biology, ecology, evolution, systematics, conservation biology, geology, geography, history, human activity, and the management of biological diversity. Material from other geographical areas may also be considered, if it is of immediate relevance to science or conservation in Galapagos.

Contributions are accepted in English. Editorial assistance will be made available to authors whose first language is not English, but this does not include full translation from other languages; it is the author's responsibility to have the paper translated into English prior to submission. Submission by email (Microsoft Word document as attached file) is preferred, to the Editor at <**galapagosresearch@fcdarwin.org.ec**>. Consult the Editor for further advice.

Research Articles must be original contributions that deal with subjects of relevance to Galapagos science or conservation (including all the subject areas listed above). Material published elsewhere, in whole or in part, will not normally be accepted. Wherever possible, manuscripts should have been critically scrutinised by at least one specialist in the relevant field, before submission to the journal. Papers from Charles Darwin Research Station staff and volunteers should be submitted to their Head of Department for review and approval prior to submission. Submitted manuscripts will be sent by the Editor to at least one relevant authority (normally two) for critical review.

News from Academy Bay items should not normally exceed 1000 words. News items may include notices of happenings in the islands that affect science or conservation, recent or forthcoming major events or publications about Galapagos (including book reviews), achievements in Galapagos science or conservation etc.

Galapagos Commentary items include opinion or discussion of Galapagos science or conservation issues, and more general or popular articles that have relevance to Galapagos science or conservation.

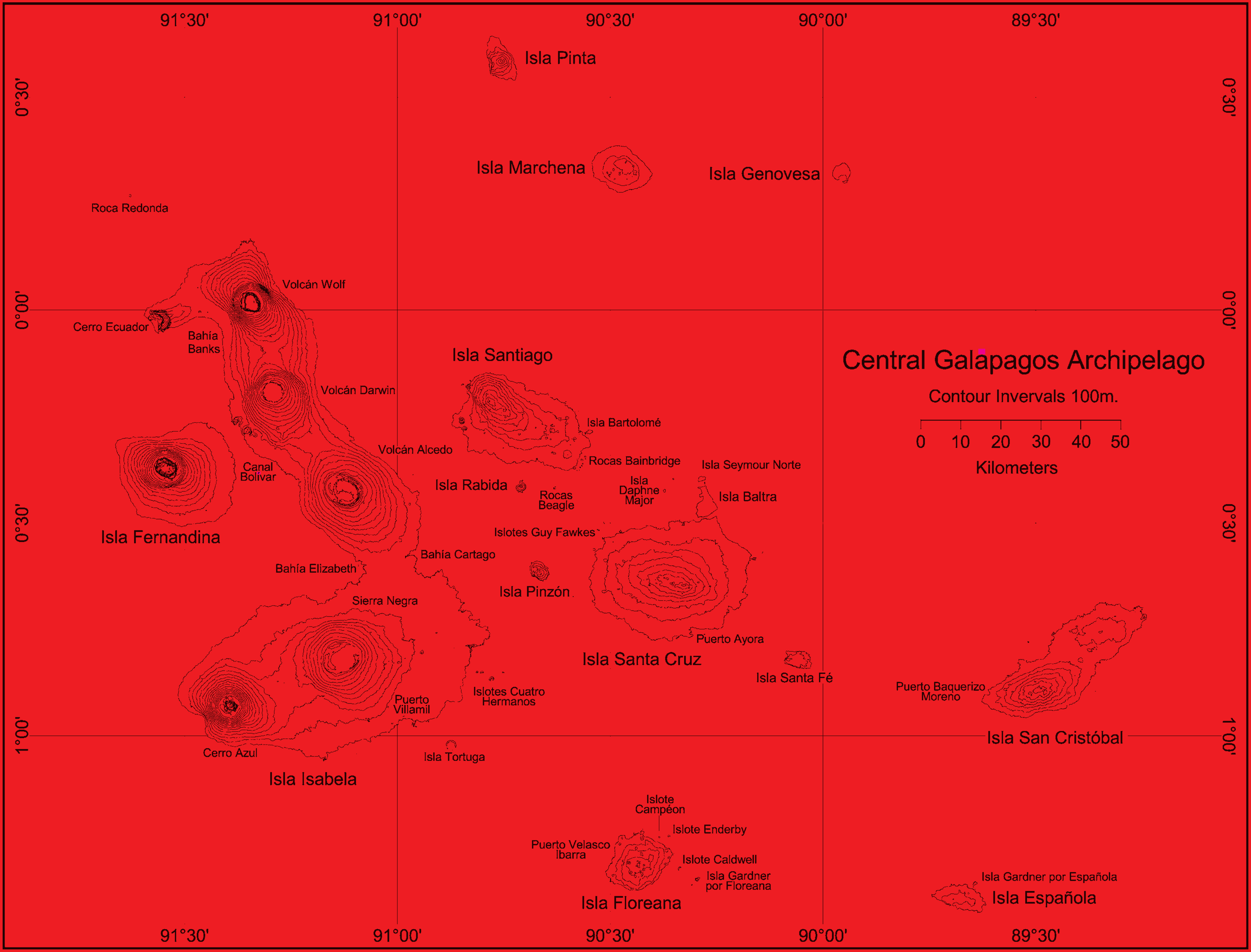
Format of tabular material, numbers, metric units, references, *etc*. should match recent issues. Note particularly: dates should be in the form 2 Feb 1990 but months standing alone in text may be written in full; times of day are written 6h45, 17h32 and coordinates in the form 0°46′N, 1°4′W (no leading zeros); numbers up to ten are written in full, except when followed by abbreviated units (*e.g.* 6 m), numbers from 11 upwards are written in figures except at the beginning of a sentence. All references mentioned in the article, and only such, must be entered in the bibliography.

Locality names should be widely recognised and in current use where possible. Articles citing older names, or localities that are not widely known, should contain a map or gazetteer, including all such localities mentioned. **Scientific names** should follow a recognised authority, which should be cited in papers dealing with taxonomic issues or lengthy species lists. Scientific names of **plants** should follow P.M. Jørgensen & S. León-Yánez (1999) Catalogue of the Vascular Plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75 (see http://www.tropicos.org/ for database), unless sound reasons for following a different scheme are presented.

Figures should be prepared as for final reproduction, allowing for reduction to fit column or page size. Figures prepared in or scanned into an appropriate graphics format, saved at high resolution and submitted electronically are preferred. Figures should not be included in a Word file. Low-resolution files or poor-quality scans will not be accepted. When designing Figures, pay attention to *Galapagos Research* column size and page-shape. Authors are encouraged to submit **photographs** that illustrate salient points of their articles. Photographs should be high-contrast (for publication in monochrome) and high resolution. Photographs should be supplied in graphics file format (*e.g.* jpg or tif) and should not be pasted into a Word file. Consult the Editor for further advice.

All Research Articles (but not News items or short Commentary notes) should include a **Summary**, not exceeding 5% of the paper's length. The Summary should briefly refer to the major findings of the paper and not simply outline what was done in the study. Summaries will be published in both English and Spanish and will be translated if necessary by the Editorial Board.

Offprints will not be supplied, but authors will be sent one copy of the issue in which their article appears, and a pdf file of their article, *gratis*.


Central Galapagos Archipelago
Contour Invervals 100m.
0
10
20
30
40
50
Kilometers
91°30'
91°00'
90°30'
90°00'
89°30'
0°30'
0°00'
0°30'
1°00'
Isla Pinta
Isla Marchena
Isla Genovesa
Roca Redonda
Volcán Wolf
Cerro Ecuador
Bahía Banks
Isla Santiago
Volcán Darwin
Isla Bartolomé
Volcán Alcedo
Rocas Bainbridge
Isla Seymour Norte
Canal Bolivar
Isla Rabida
Rocas Beagle
Isla Daphne Major
Isla Baltra
Isla Fernandina
Islotes Guy Fawkes
Bahía Cartago
Bahía Elizabeth
Isla Pinzón
Sierra Negra
Puerto Ayora
Isla Santa Cruz
Isla Santa Fé
Puerto Baquerizo Moreno
Islotes Cuatro Hermanos
Puerto Villamil
Isla San Cristóbal
Cerro Azul
Isla Tortuga
Isla Isabela
Islote Campéon
Islote Enderby
Puerto Velasco Ibarra
Islote Caldwell
Isla Gardner por Floreana
Isla Floreana
Isla Gardner por Española
Isla Española
91°30'
91°00'
90°30'
90°00'
89°30'
0°30'
0°00'
0°30'
1°00'