

El Niño, grazers and fisheries interact to greatly elevate extinction risk for Galapagos marine species

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Abstract

Comparisons between historical and recent ecological datasets indicate that shallow reef habitats across the central Galapagos Archipelago underwent major transformation at the time of the severe 1982/1983 El Niño warming event. Heavily grazed reefs with crustose coralline algae ('urchin barrens') replaced former macroalgal and coral habitats, resulting in large local and regional declines in biodiversity. Following recent threat assessment workshops, a total of five mammals, six birds, five reptiles, six fishes, one echinoderm, seven corals, six brown algae and nine red algae reported from coastal environments in Galapagos are now recognized as globally threatened. The 2008 International Union for the Conservation of Nature (IUCN) Red List includes 43 of these species, while two additional species (Galapagos damsel *Azurina eupalama* and 24-rayed sunstar *Heliaster solaris*) not seen for >25 years also fulfil IUCN threatened species criteria. Two endemic species (Galapagos stringweed *Bifurcaria galapagensis* and the damselfish *A. eupalama*) are now regarded as probably extinct, while an additional six macroalgal species (*Dictyota galapagensis*, *Spatoglossum schmittii*, *Desmarestia tropica*, *Phycodrina elegans*, *Gracilaria skottsbergii* and *Galaxaura barbata*) and the seastar *H. solaris* are possibly extinct. The removal of large lobster and fish predators by artisanal fishing probably magnified impacts of the 1982/1983 El Niño through a cascade of indirect effects involving population expansion of grazing sea urchins. Marine protected areas with adequate enforcement are predicted to ameliorate but not eliminate ecosystem impacts caused by increasing thermal anomalies associated with El Niño and global climate change.

Keywords: climate change, effects of fishing, marine protected area, sea urchin, threatened species, trophic cascade

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Introduction

Through experimentation and ecosystem monitoring, the Galapagos Archipelago potentially provides a glob-

ally unique 'field laboratory' for assessing impacts of extreme oceanographic warming on marine biodiversity. Galapagos sits near the centre of the most intense El Niño events (Glynn & Ault, 2000) and is less impacted by human activity than other large tropical and temperate archipelagos.

Dating back to the voyage of the *Beagle* in 1835 (Grove & Lavenberg, 1997), Galapagos historically has also attracted disproportionate scientific attention because

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of its fragmented landscapes, endemic flora and fauna, isolation on the equator and reputation as a living laboratory of evolution (Bensted-Smith, 2002). Endemism rates for marine species are taxonomically variable (8–67%) but generally much higher than most other archipelagos for major marine groups (Bustamante *et al.*, 2000a; Hickman, 2009).

El Niño events appear to have strengthened in the eastern tropical Pacific over the past millennium, with unprecedented heating recorded over the past 50 years (Conroy *et al.*, 2009). Whether or not these changes are directly caused by global warming, recent extreme El Niño events provide case studies for assessing likely impacts of climate change on ecosystems. Global warming will presumably affect communities primarily through increasing magnitude and frequency of extreme events comparable to El Niño rather than through gradual changes in ocean climate (Reaser *et al.*, 2000; Boer *et al.*, 2004).

Despite the comparative regularity of El Niño, field observations indicate that Galapagos marine ecosystems are not well adapted for extreme thermal impacts. Intertidal shores and shallow rocky and coral reef habitats across Galapagos changed substantially at the time of the 1982/1983 El Niño (Robinson, 1985; Glynn, 1994). Although probably not unprecedented at the 100-year scale (Enfield, 2001), this extreme thermal anomaly was characterized by water temperatures up to 5° C above long-term averages (Barber & Chavez, 1986). Elevated temperatures persisted for over 12 months generating clear oceanic waters, major declines in dissolved nutrients and a decline in phytoplankton productivity that ultimately resulted in a prolonged reduction of biomass at the base of the marine food chain (Robinson & Del Pino, 1985).

Vertebrate animals were much affected by changes to the food web associated with the 1982/1983 El Niño. Populations of endemic Galapagos penguins (*Spheniscus mendiculus*), flightless cormorants (*Phalacrocorax harrisi*), Galapagos fur seals (*Arctocephalus galapagoensis*) and Galapagos sea-lions (*Zalophus wollebaeki*) were estimated to have declined by 78%, 45%, 60% and 35%, respectively (Robinson & Del Pino, 1985; Trillmich & Limberger, 1985).

Habitat changes on shallow Galapagos reefs catalysed by the 1982/1983 El Niño included loss of coral reefs through bleaching and subsequent sea urchin bioerosion (Glynn & Wellington, 1983; Glynn, 1990, 1994), and loss of most macroalgal beds (Robinson & Del Pino, 1985). A total of 95–99% of reef coral cover was lost from Galapagos between 1983 and 1985. All known coral reefs based on calcareous frameworks died and subsequently disintegrated to rubble and sand (Glynn, 1994).

Oceanographic warming associated with both El Niño and global climate change can operate directly on species' populations (Thomas *et al.*, 2004, 2006; Helmuth *et al.*, 2006), or indirectly through interaction with other factors (Occhipinti-Ambrogi, 2007; Poertner & Knust, 2007; Crain *et al.*, 2008), including factors associated with human activity (Hughes *et al.*, 2005). In the marine context, interactions between climate change and fishing have been suggested to have far-reaching consequences for species persistence (Hughes *et al.*, 2003; Harley & Rogers-Bennett, 2004; Edgar *et al.*, 2005; Pandolfi *et al.*, 2005).

In Galapagos, published studies and our local observations extending over 40 years suggested that populations of many marine species had not recovered since catastrophic declines at the time of the 1982/1983 El Niño (see Robinson, 1985). Anecdotal observations also indicated that Galapagos reefs had been ecologically affected by excessive fishing pressure (Ruttenberg, 2001; Sonnenholzner *et al.*, 2009). We here consider the validity of these observations by assessing the hypothesis that extreme heating events can cause regime shifts in marine ecosystems and extinction of species. We use historical data and reports, quantitative field surveys, directed searches for threatened taxa and outcomes of threat assessment workshops involving Galapagos experts to document the spatial and temporal scale of recent changes in species' distributions and important benthic habitat types.

We also test the prediction that reef communities exhibit changes along a spatial gradient of fishing pressure. We use distance from port as a metric of cumulative fishing pressure because fishers progressively operate further and further from ports as stocks are overfished (i.e., serial depletion). Effort near Galapagos home ports has traditionally been greater than at distance because relatively few fishers are prepared to undertake multiday trips except for the lucrative sea cucumber fishery (Born *et al.*, 2003). Fishing in Galapagos is primarily undertaken using small open fibreglass and wooden boats, which are associated with larger wooden motherships for travel on multiday trips to outlying islands (Born *et al.*, 2003).

In deciding on an appropriate index of fishing pressure, we also considered direct measures of fishing effort, as recorded in logbooks and by fishery observers on board Galapagos fishing vessels (Danulat & Edgar, 2002). However, fishing effort is not independent of the distribution of reef communities. Following tradeoffs involving time and travel costs, fishers target sites where they expect highest catch rates (i.e., sites with highest perceived densities of fishery species). As a consequence, no clear prediction could be made regarding whether sites with high current fishing effort should

show positive or negative relationships with resource species. Heavily fished sites could potentially possess high densities of resource species because such sites attract fishers, or low densities because fishing pressure has depleted resource species at those sites.

We calculated Pearson's correlation coefficients between distance from nearest fishing port and six ecological metrics to test predictions of the hypothesis that fishing has affected benthic community types. Predictions tested were as follows:

- (i) densities of large predatory fishes (sharks, serranid groupers, carangid jacks, scombrid tunas and mackerel and lutjanid snappers) decline with fishing effort (i.e., tend to be lowest off islands nearest to ports),
- (ii) densities of spiny lobsters (*Panulirus penicillatus* and *Panulirus gracilis*) and slipper lobsters (*Scyllarides astori*) increase with distance from fishing port,
- (iii) catch per unit effort (CPUE) of spiny lobsters, as recorded by observers in 2001 on board commercial fishing vessels (Toral *et al.*, 2002), increases with distance from port,
- (iv) densities of sea urchins (primarily *Euclidaris galapagensis*, *Triploneustes depressus*, *Lytechinus semituberculatus*, *Echinometra vanbrunti* and *Diadema mexicanum*) decrease with distance from fishing port because of increased levels of predation,
- (v) coral cover increases with distance from fishing port because of third-order trophic effects associated with decreased predator numbers and increased grazer numbers, and
- (vi) cover of foliose macroalgae increases with distance from fishing port because of third-order trophic effects.

In addition to lobster numbers sighted on underwater transects, we included CPUE of lobsters as a proxy for lobster density because of the high degree of patchiness in lobster distribution. Numbers recorded on transects were greatly affected by stochastic sightings of groups of individuals, particularly off islands with low lobster densities. We nevertheless recognize that interpretation of CPUE data also requires caution. The relationship between CPUE and lobster density may not be linear because commercial divers avoid areas with few lobsters, causing 'hyperstability' in catch rates (Harley *et al.*, 2001).

Methods

Data sources

All available historical and contemporary sources of marine ecological data for Galapagos dating back to the

Allan Hancock and Templeton-Crocker (California Academy of Sciences) expeditions of 1932 (Setchell, 1937; Setchell & Gardner, 1937; Taylor, 1945) were searched for distribution and abundance data on threatened species, corals, macroalgae, sea urchins, reef fishes and lobsters. Limited information from earlier expeditions was noted (1873 Hassler expedition, 1888, 1891 and 1904–1905 Albatross expeditions, 1898–1999 Hopkins Stanford expedition, 1905–1906 California Academy of Science Expedition, 1925 Arcturus Expedition, and 1926 and 1928 Vanderbilt expeditions); however, these were excluded from temporal analyses because few marine species were recorded on those expeditions, and because a 50-year historical time slice to 1982 was considered most relevant for comparisons with recent patterns rather than applying an open-ended historical time period.

Historical data sets that form the basis of threat assessments presented here are summarized in Edgar *et al.* (2008). Unpublished long-term data sets compiled by the authors include (i) data on marine algae, invertebrates and fishes obtained by S. Earle during the 1966 Anton Bruun and 1972 Searcher expeditions (Mead *et al.*, 1972); (ii) results of an archipelago-wide study of intertidal and subtidal fishes, invertebrates and plants in 1973–1974 (Wellington, 1975); (iii) coral monitoring data obtained at intervals of 1–4 years at 30 sites established in 1975 and 1976, plus 14 additional sites added in 1985 (Glynn & Wellington, 1983; Glynn, 1994, 2003); (iv) observations and >2000 archived underwater photographs on fishes, invertebrates and macroalgae obtained before, during and after the 1982/1983 El Niño (Grove, 1985); (v) archipelago-wide fish observations since 1987 (222 sites in total), including annual quantitative transect data from 1994 to 2003 at >20 sites (F. Rivera, unpublished results); and (vi) quantitative surveys of fishes, mobile macroinvertebrates, sessile invertebrates and floral communities at two depths at ca. 70 sites per year from 2000 to 2008 that were aimed at assessing baseline conditions (Danulat & Edgar, 2002) and population trends (S. Banks, unpublished results) following establishment of the Galapagos Marine Reserve (GMR).

Additional data on threatened species and habitat cover were obtained during two 10-day expeditions undertaken between 26 November 2004 and 17 December 2004. A total of 56 sites were specifically searched for 49 species considered potentially threatened, with an average of five dive surveys per site. Sites were selected to encompass the range of biogeographic and environmental conditions across the archipelago, with emphasis on locations with historical ecological data or records of threatened taxa. In addition, while descending perpendicular to the shore, divers mapped the

distribution of habitat types by recording the depth at which habitat types changed from the low water mark down to the reef edge or 30 m depth if reef habitat extended passed that depth.

A total of 14 categories were recognized in the habitat analysis – sand, open rock (including urchin barrens), scleractinian (reef-building) corals, antipatharian (black) corals, nonscleractinian corals, barnacles, anemones, gorgonians, sponges, other sessile invertebrates, *Sargassum* spp., other brown algae, red algae and green algae. Along the depth profile, habitat types were scored on an underwater slate using a semiquantitative habitat density scale – 0: absent; 1: single individual; 2: occasional (0–2% cover, mode 1%); 3: common (2–25% cover, mode 10%); 4: abundant (25–75% cover, mode 50%); 5: complete (75–100% cover, mode 100%). Mean percentage cover of the different habitat types at different depths was estimated by back-transforming semiquantitative values using modes. Divers mapped an average of four profiles at each site.

Assessment of threatened species and habitat change following 1982/1983 El Niño

Threatened marine species in Galapagos were identified by, firstly, compiling a list of taxa recorded from Galapagos that were included on the 2004 International Union for the Conservation of Nature (IUCN) Red List, then adding species belonging to groups not previously assessed but which qualified as threatened using IUCN Red List criteria (IUCN, 2001). The latter were identified by (i) tabulating endemic Galapagos marine species, (ii) gathering all available distribution and population trend data for these species, (iii) undertaking a preliminary assessment to determine whether these species fulfil IUCN Red List criteria as globally threatened, (iv) instigating directed field surveys at sites where species on this list had been recorded historically or their presence suspected and (v) reassessing the list of threatened species in the light of new field data.

Scientists with expert local knowledge formally assessed the threat status of tropical eastern Pacific corals and endemic Galapagos macroalgae at IUCN Red List Marine Threat Assessment Workshops in Galapagos (28–31 May 2006). Endemic Galapagos corals and macroalgae identified as threatened were added to the 2007 Red List following these workshops, and an additional four nonendemic corals added to the 2008 Red List following additional workshops facilitated worldwide by IUCN and the Global Marine Species Assessment (Carpenter *et al.*, 2008).

Changes in habitat types during the course of the 1982/1983 El Niño were quantified using digitized

information on habitats present in the background of underwater images photographed across the GMR by J. Grove. Of >2000 images available, a total of 239 were considered suitable for analysis, comprising 71, 46 and 122 images photographed in the years 1982, 1983 and 1984, respectively. These images, which were photographed at sites distributed haphazardly across the archipelago, included background areas of benthic habitat sufficiently sharp to be classified into 16 classes (green foliose algae, red foliose algae, *Sargassum* spp., other foliose brown algae, crustose coralline algae, fine mixed turf algae, sponges, barnacles, gorgonians, *Pocillopora* spp., *Pavona* spp., other scleractinian corals, *Tubastraea* spp., other nonscleractinian corals, black corals and bare rock). The point intercept method based on a grid with 50 points overlaid on each image was used to estimate the percentage cover of different taxa and substratum types. The image subject, generally a fish, was ignored.

The significance of changes in mean density from 1982 to 1984 were assessed using one-way analysis of variance (ANOVA), with significant outcomes further analysed using *a posteriori* Tukey's test (Zar, 1996) to identify individual years of significant change. Habitat-level changes were investigated using nonmetric multidimensional scaling (nMDS), a graphical procedure that provides the best depiction of faunal relationships possible within a two-dimensional plot (Carr, 1996), based on mean cover of major habitat groups in different years. In order to allow comparison with data obtained during threatened species surveys in 2004, taxa were grouped into ten functional categories: green foliose algae, red foliose algae, brown foliose algae, open reef (crustose coralline algae, fine mixed turf algae plus bare rock), sponges, barnacles, gorgonians, scleractinian corals, nonscleractinian corals and black corals. The similarity matrix used in the nMDS, which described pairwise patterns of faunal similarity between years, was calculated using the Bray-Curtis index (Faith *et al.*, 1987).

The set of 239 underwater images was also used to assess changes in density of the abundant urchins *Eucidaris galapagensis* and *Lytechinus semituberculatus*. Abundance of each urchin species was counted within the largest rectangular area of reef substratum clearly discernible within the image. An estimate was made by eye of the area of the rectangle using sizes of organisms present as references. To reduce bias, all image counts were made by a single person, whose overall accuracy in estimating distances was $97.5 \pm 15.7\%$ (mean estimated distance across image/measured distance \pm SD) using a set of 22 images with a calibrated survey tape that was concealed on the image when the distance estimate was made.

Assessment of impact of fishing

We tested the prediction that densities of predatory fishes, spiny lobsters and urchins vary with distance from fishing port using data obtained between 13 May 2000 and 13 December 2001 during GMR baseline surveys (Danulat & Edgar, 2002; Edgar *et al.*, 2004a, b). Data comprised densities of fishes and mobile macroinvertebrates sighted along 50 m transect lines set at two depths (5–16 m) at >250 sites during underwater visual censuses. Two transect blocks (50 m × 5 m for fishes; 50 m × 1 m for macroinvertebrates) at two depths were generally surveyed at each site. Overall, a total of 1158 and 1138 transect blocks were surveyed archipelago-wide for fishes and macroinvertebrates, respectively. Data on estimated coral and macroalgal cover were obtained from 111 sites visited during threatened species surveys undertaken in 2004 plus 118 sites visited in 2000–2001 during the GMR baseline surveys.

Survey data were aggregated as the mean of transects for each of the 15 major islands to reduce the likelihood of spatial autocorrelation confounding analyses, as occurs when sites equally contribute data to probability tests but with numerous sites concentrated in a particular location (Legendre, 1993). Because of the great distance around the largest island (Isabela) from the populated south to the unpopulated north (ca. 120 km north–south), data from this island were subdivided into independent north and south components using a boundary at 0.68°S latitude. Distance to port for each island was calculated as minimum sea distance from nearest port to sites surveyed, with mean of distances to sites surveyed calculated for each island. The four recognized fishing ports in Galapagos are Puerto Baquerizo Moreno (San Cristobal), Puerto Ayora (Santa Cruz), Puerto Villamil (southern Isabela) and Canal Itabaca (Santa Cruz).

Results

Threatened species and habitat change following 1982/1983 El Niño

Initial analysis based on data to 2004 indicated a total of 49 Galapagos marine species as potentially globally threatened. Nineteen of these species had been listed on the 2004 IUCN Red List (the mammals, birds, reptiles and two fishes), with the other thirty species considered to fulfil IUCN-threatened species criteria on preliminary screening.

Two expeditions undertaken in 2004 in search of threatened species successfully located seven endemic algae on the preliminary threatened species list that had not been observed for over 30 years. None of these algae (*Eisenia galapagensis*, *Sporochmus rostratus*, *Chondria flex-*

icaulis, *Laurencia oppositoclada*, *Myriogramme kylinii*, *Pseudolaingia hancockii* and *Schizymenia ecuadoreana*) were found in high densities. The other taxa on the preliminary list that were not seen since the 1982/1983 El Niño were not encountered despite searches at their historic locations.

The preliminary list of threatened species was modified following targeted searches. Macroalgal species recorded at more than one site (*Sporochmus rostratus* and *Chondria flexicaulis*) were removed from the list under the assumption that rare species observed at two or more sites were also likely to be present at multiple additional sites not searched by divers, and hence were best regarded as data deficient (sensu IUCN, 2001) until population trend information was available. Survey and historical data were presented at expert threat assessment workshops for corals and macroalgae, leading to the addition of three endemic Galapagos corals and 15 macroalgae to the 2007 IUCN Red List. A total of 45 Galapagos marine species are currently recognized as threatened, comprising five mammals, six birds, five reptiles, six fishes, one echinoderm, seven corals, six brown algae and nine red algae (Table 1). Two of these species, the damselfish *Azurina eupalama* and sunstar *Heliaster solaris*, remain to be added to the Red List, but clearly fulfil criteria as they have not been sighted during the past 30 years despite searches.

The nMDS two-dimensional display of relationships between habitat types present in the background of underwater photographs indicated major ecosystem-level changes between 1982 and 1983, with subsequent relative stability of ecosystems in 1983 and 1984 (Fig. 1). The stress value associated with this plot is extremely low ($P < 0.01$), indicating that the plot provides an extremely good two-dimensional depiction of multivariate patterns (Clarke, 1993). Habitat data obtained by divers in 2004 showed much greater similarity to data digitized from underwater photographs in 1983 and 1984 than data from 1982, despite the very different methods of assessment.

Among the major habitat classes examined, the cover of fine mixed turf algae increased significantly from 1982 to 1983, the cover of foliose brown algae and sponges declined precipitously over the same period, the cover of barnacles increased greatly between 1983 and 1984, and the amount of bare rock was significantly higher in 1983 than in either 1982 or 1984 (Fig. 2). Other sessile taxa showed no significant trends when assessed using one-way ANOVA. The density of the urchin *Eucidaris galapagensis* increased significantly by a factor of about two from 1982 to 1984 (Fig. 2).

Although significant changes in coral cover were not detected for the 1982–1984 period (Fig. 2), long-term

Table 1 Threatened Galapagos marine and shoreline species included on the 2008 IUCN Red List, plus two additional endemic species that, although not yet formally evaluated, qualify for listing as they have not been sighted for >25 years and are possibly extinct

	Threat	Threat	Threat	Threat	
Critically endangered species		Endangered species		Vulnerable species	
<i>Camarhynchus heliobates</i> Mangrove finch*	X	<i>Balaenoptera musculus</i> Blue whale	F	<i>Arctocepalus galapagoensis</i> Galapagos fur seal*	E,F
<i>Pterodroma phaeopygia</i> Galapagos petrel*	F,I	<i>Zalophus wollebaeki</i> Galapagos sea lion*	E,F	<i>Physeter macrocephalus</i> Sperm whale	F
<i>Dermodelphys coriacea</i> Leatherback turtle	F	<i>Spheniscus mendiculus</i> Galapagos penguin*	E	<i>Megaptera novaeangliae</i> Humpback whale	F
<i>Eretmochelys imbricata</i> Hawksbill turtle	F	<i>Phalacrocorax harrisi</i> Flightless cormorant*	E	<i>Larus fuliginosus</i> Lava gull*	X
<i>Azurina eupalama</i> Black-spotted damselfish†	E	<i>Chelonia mydas</i> Green turtle	F,I	<i>Phoebastria irrorata</i> Waved albatross*	F
<i>Helianter solaris</i> 24-rayed sun star†	E	<i>Lepidochelys olivacea</i> Olive ridley turtle	F	<i>Amblyrhynchus cristatus</i> Marine iguana*	E,I
<i>Rhizopsammia wellingtoni</i> coral*	E	<i>Sargassum setifolium</i> String sargassum*	EF [§]	<i>Rhincodon typus</i> Whale shark	F
<i>Tubastraea floreana</i> coral*	E			<i>Mycteroperca olfax</i> Bacalao grouper	F
<i>Bifurcaria galapagensis</i> Galapagos stringweed*	EF [§]			<i>Sphyrna mokarran</i> Giant hammerhead	F
<i>Desmarestia tropica</i> Tropical acidweed*	EF [§]			<i>Hippocampus ingens</i> East Pacific seahorse	F
<i>Dictyota galapagensis</i> brown alga*	EF [§]			<i>Taeniura meyeni</i> Speckled stingray	F
<i>Spatoglossum schmittii</i> brown alga*	EF [§]			<i>Polycyathus isabellae</i> coral*	E
<i>Phycodrina elegans</i> red alga*	EF [§]			<i>Pocillopora elegans</i> coral	E
<i>Laurencia oppositoclada</i> red alga*	EF [§]			<i>Pocillopora inflata</i> coral	E
<i>Myriogramme kylinii</i> red alga*	EF [§]			<i>Fungia curvata</i> coral	E
<i>Schizymenia ecuadoreana</i> red alga*	EF [§]			<i>Psammocora stellata</i> coral	E
<i>Gracilaria skottsbergii</i> red alga*	EF [§]			<i>Eisenia galapagensis</i> Galapagos kelp*	EF [§]
<i>Galaxaura barbata</i> red alga*	EF [§]			<i>Acrosorium papenfussii</i> red alga*	EF [§]
				<i>Pseudolaingia hancockii</i> red alga*	EF [§]
				<i>Austrofolium equatorianum</i> red alga*	EF [§]

The most probable threats to species survival are also shown. (E, El Niño; F, overfishing; EF[§], herbivore overgrazing associated with interactions between El Niño and overfishing; I, predation by introduced species; X, unknown threatening process that probably includes predation by introduced species.)

*Endemic and near endemic (>99% of known global population) Galapagos marine species;

†Endemic species that qualify but have not yet been placed on the International Union for the Conservation of Nature (IUCN) Red List.

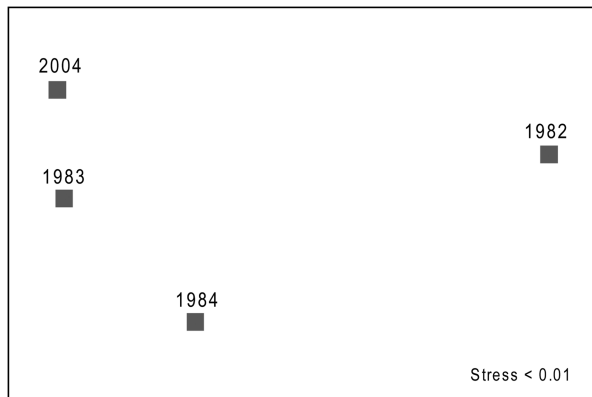


Fig. 1 Results of nonmetric multidimensional scaling showing biotic relationships between communities of sessile benthic organisms in different years.

monitoring indicated a precipitous decline in reef corals over the subsequent 3-year period (Fig. 3, Glynn, 1990, 1994). Little regeneration of surviving corals or establishment of new colonies >20 cm diameter have since occurred (P. Glynn and G. Wellington, unpublished results), with corals now covering significant areas (i.e., patches of tens or hundreds of square metres) only off the northern islands of Darwin and Wolf, and Marchena in the central region (Table 2). Solitary corals have also declined greatly in recent decades, including the endemic taxon *Madrepora oculata f. gamma*, which was recorded as abundant until the 1982/1983 El Niño (Glynn & Wellington, 1983; Robinson & Del Pino, 1985), but has not been seen in any surveys since.

Recent data also contrast with historical observations extending back to 1932 and photographs (Fig. 4) that indicate lower intertidal and shallow subtidal habitats of the central and western archipelago were densely covered by large furoid algae before 1983, most conspicuously by *Bifurcaria galapagensis* and *Sargassum* spp. (Houvenaghel & Houvenaghel, 1974; Wellington, 1975). Foliose macroalgae are now highly localized in Galapagos, with patches of *Sargassum* spp. virtually absent outside the cool western upwelling region (Table 2).

Diverse red algal beds grew luxuriantly at many sites in depths >15 m before the 1980s (Taylor, 1945; Mead *et al.*, 1972; Wellington, 1975). Large red algae are now uncommon, while urchin 'barrens' composed of open reef with encrusting coralline algae and cropped algal turfs have predominated since at least 1987 (Kendrick, 1988) across most of the archipelago (Table 2).

The present distribution of threatened Galapagos species coincides with loss of macroalgal habitat from the central and southeastern region of the archipelago. Species now recognized as threatened were recorded as present off many more islands before 1983 than since that year (Fig. 5), despite a 20-fold increase in search

effort in terms of diver hours between the periods pre- and post-1983 (~ 300 h cf. ~ 6000 h underwater). Since the 1982/1983 El Niño, macroinvertebrate and macroalgal species now recognized as threatened have largely disappeared from the central archipelago, with greatest losses at the four islands with human habitation (Floraena, Santa Cruz, San Cristobal and Isabela). Most remnant populations of threatened species now persist only in the relatively isolated western region of the archipelago. Few threatened species reside in the northern region.

Impact of fishing

Based on data from the 2000–2001 GMR baseline surveys, densities of large predatory fishes and lobsters were both significantly lower at islands located near fishing ports than at more distant islands (Fig. 6). The opposite relationship was found for sea urchins. Coral cover was significantly positively correlated with distance of islands from port, while macroalgal cover was not significantly affected, albeit trending in a positive direction (Fig. 6).

The above relationships were strongly influenced by data from the two most distant islands of Darwin and Wolf (Fig. 6). Most notably, lobster densities were very high at Darwin and Wolf while low and variable elsewhere. If the islands of Darwin and Wolf are removed from analyses, the power of statistical tests declines, with only the correlation between predatory fishes and distance among the plots shown in Fig. 6 remaining significant for two-tailed tests ($R = 0.59$, $0.05 > P > 0.01$). A much stronger trend is indicated for macroalgal density, albeit one that is only marginally significant if a one-tailed test (i.e., for a positive correlation) is applied ($R = 0.44$, $0.01 < P < 0.05$).

Discussion

Threatened species and habitat change following 1982/1983 El Niño

Of a total of 45 Galapagos marine species now recognized as Vulnerable, Endangered or Critically Endangered (Table 1), the majority were assessed as threatened because of their susceptibility to El Niño events, at least in part. Information provided during threat assessment workshops and now included with entries on the Red List (<http://www.iucnredlist.org/>) indicates that the major threatening processes affecting marine species are overfishing (15 species threatened), El Niño (14 species threatened) and interactive effects between these two factors (15 species threatened; Table 1). Although climate change interacts with both El Niño

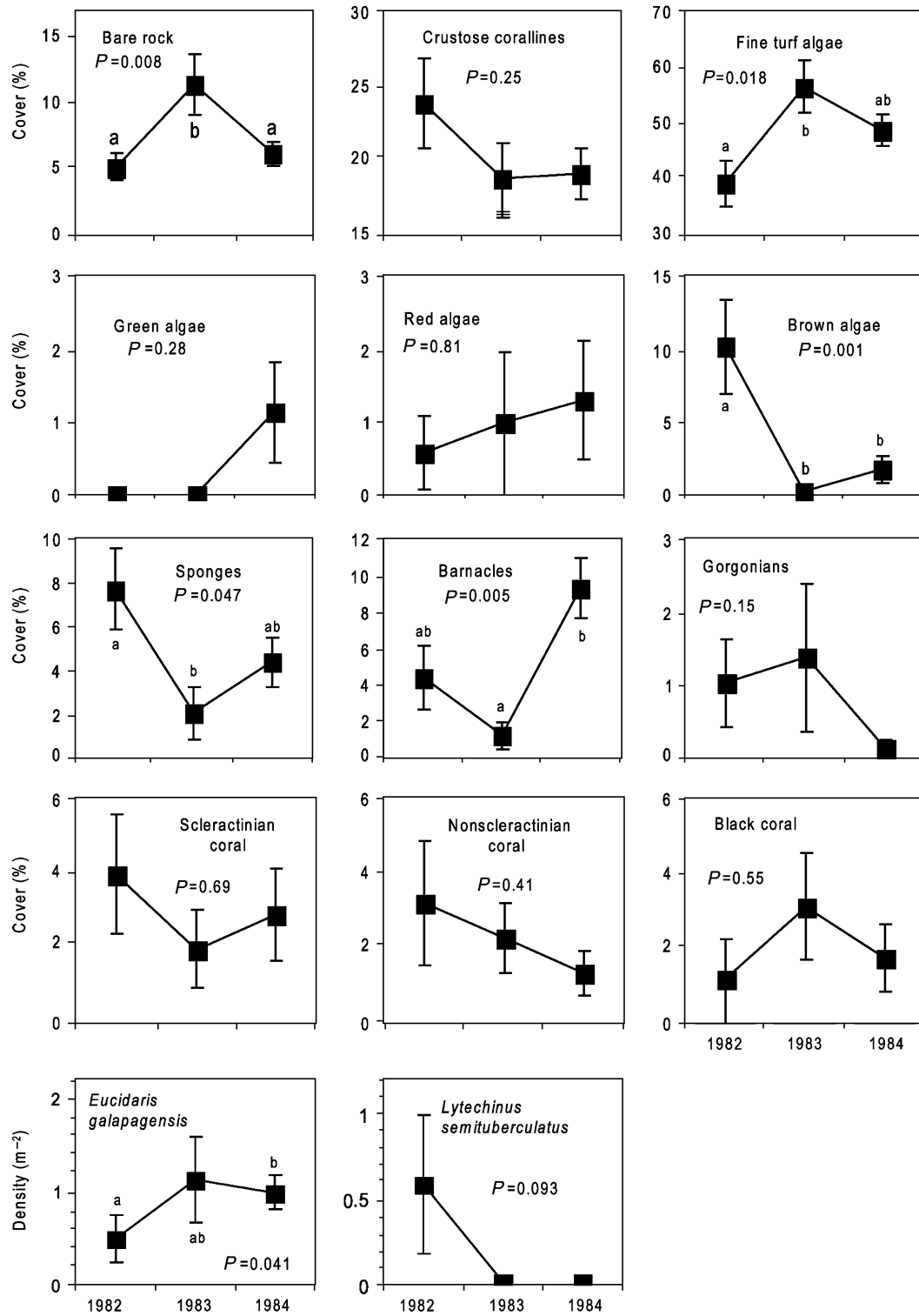


Fig. 2 Changes between years in mean cover (\pm SE) of bare rock and major sessile floral and functional groups, and mean density (\pm SE) of the urchins *Eucidaris galapagensis* and *Lytechinus semituberculatus*. Probability values associated with one-way analysis of variance *F*-tests are also shown (density data log transformed), with significant differences between years indicated by differing associated letters.

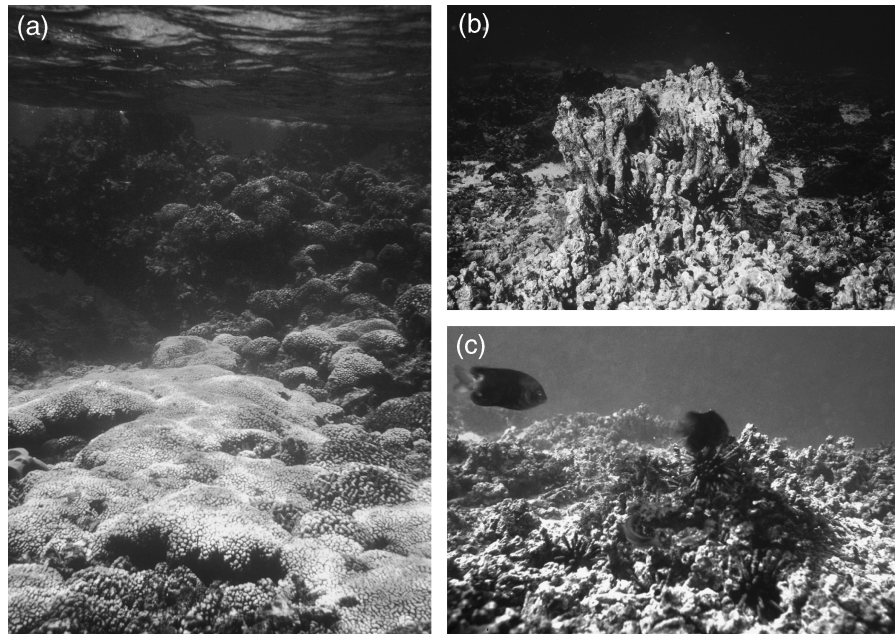


Fig. 3 Sheltered embayment at Devils Crown, Floreana, showing well developed *Pocillopora damicornis* reef in 1982 with calcareous framework extending for 0.6–0.8 m below photographed reef surface (a; photo P. Glynn); and remnants of coral framework and rubble with numerous urchins (*Eucidaris galapagensis*) in 1986–1987 (b; photo P. Glynn; c; photo F. Rivera). The seabed at this site now consists of sand and coral fragments (most <5 cm long) overlaying basalt.

Table 2 Estimated mean percentage (\pm SE) cover of habitat-forming reef corals, macroalgae and open reef (including bare rock, fine algal turf and crustose coralline algae) for sites studied from 0 to 30 m depth in 2004 within the three major Galapagos marine biogeographical zones (Fig. 5, Edgar *et al.*, 2004a)

Zone	Reef corals (%)	<i>Sargassum</i> spp. (%)	Other foliose algae (%)	Open reef (%)
Northern	5.8 \pm 2.6	0	2.6 \pm 2.5	76.3 \pm 4.7
Central	2.3 \pm 0.6	0.02 \pm 0.01	3.3 \pm 1.1	82.7 \pm 2.3
Western	0.02 \pm 0.01	2.2 \pm 0.5	14.9 \pm 2.6	75.2 \pm 2.7

Macroalgal species recognized as habitat-forming are foliose species with fronds >5 cm length. Percentage cover data relate to sites visited during threatened species surveys in 2004, where all sites with known concentrations of corals and macroalgae were visited, hence mean estimates for corals and macroalgae are inflated compared with true archipelago-wide means.

and fishing, and potentially represents the gravest threat of all, this process was not considered during assessments because of the magnitude of current uncertainties, as has also been the case with most other IUCN threat assessments (Akcakaya *et al.*, 2006).

The probable extinction of the Galapagos damsel *Azurina eupalama* is particularly notable given that the IUCN Red List has yet to recognize a fully marine fish as 'Extinct' (Edgar *et al.*, 2005). This endemic planktivorous species was formerly common in localized aggregations on the islands of Floreana, Española, Isabela, Marchena, Santiago, San Cristobal, Santa Cruz, and Santa Fe, but declined precipitously in 1983 (Robinson & Del Pino, 1985). It has not been sighted since, neither in Galapagos nor Isla del Coco, the extra-limital location

for one museum record 600 km north of Galapagos (Grove & Lavenberg, 1997) that is possibly misattributed.

The five threatened species most widely encountered during recent surveys (Galapagos sea lion, green turtle, marine iguana, bacalao grouper and Galapagos penguin) are all higher vertebrates that have been comparatively well studied and were placed on the Red List because of documented population declines. If population trend data were available for fishes, invertebrates and macroalgae, many more threatened species would likely be recognized. Numerous cryptic reef-associated species undoubtedly declined with the loss of coral reefs, as did populations of inconspicuous algal epiphytes and grazing invertebrates associated with *Bifurcaria galapagensis* and other macroalgal beds



Fig. 4 The rocky intertidal shore in front of the Charles Darwin Research Station in 1974 (left; photo G. Wellington) and 2003 (right; photo F. Rivera). The dominant brown algae in the left photo is *Bifurcaria galapagensis*, an endemic species that once formed extensive growths from the low intertidal to 6 m depth on moderately exposed coasts of southern and central islands (Wellington, 1975). Despite extensive searches archipelago-wide, this alga has not been observed since dieback and catastrophic decline between January and March 1983 (Robinson & Del Pino, 1985). It is now probably extinct.

(Houvenaghel & Houvenaghel, 1974; Robinson & Del Pino, 1985).

The majority of threatened plants and animals within the region are endemic Galapagos taxa (Table 1). The trend for endemic species to show disproportionately large population declines compared with nonendemic taxa is indicated by the 2008 IUCN Red List, which currently lists as threatened nine of 10 endemic Galapagos marine mammals, birds and reptiles, compared with only five of the 33 nonendemic marine species belonging to these higher vertebrate groups that regularly frequent the archipelago.

Following the 1982/1983 El Niño, much of the Galapagos region underwent major ecosystem changes that have apparently persisted to date. These changes are reflected in the nMDS plot (Fig. 1), where biotic patterns in 2004 much more closely approach patterns at the end of the 1982/1983 El Niño, and also during the 1984 La Niña, than they do patterns at the start of the warming event. The similarity of observed patterns in 1983 with 2004 was unexpected given the different techniques used to assess cover of habitat classes in those 2 years, emphasizing the magnitude of real differences between either of those years and 1982.

Major habitat changes detected over the 1982–1984 period include substantial declines in cover of sponges and foliose brown algae, particularly *Sargassum*, and an increase in the cover of a layer of mixed turf algae (intermingled diatoms, *Hildenbrandia*, *Hincksia*, *Jania*

and other algae forming a fine turf <10 mm tall) on exposed reef surfaces (Fig. 2). Barnacle cover increased substantially in 1984, presumably a consequence of the strong La Niña in that year and the rapid population responses shown by barnacles in periods with cool upwelling conditions (Witman & Smith, 2003). Although not found to be significant, the greatly increased cover of foliose green algal species in 1984 was also probably real given parallels with the massive increase in cover of *Ulva* (including *Enteromorpha*) that was documented in lower intertidal habitats during the transition into La Niña conditions at the end of the 1997/1998 El Niño (Vinuela *et al.*, 2006).

Little scientific attention or management concern followed observations by Robinson (1985) during the course of the 1982/1983 El Niño that *Bifurcaria galapagensis*, *Sargassum* spp. and other canopy-forming algae had completely disappeared from all 16 sites studied. Any major reduction in Galapagos macroalgal habitat nevertheless represents a significant loss of global biodiversity. This diverse habitat comprises a small temperate ecosystem with a very high level of endemism that is isolated on the equator. Approximately 90 of 300 (33%) macroalgal taxa recorded from Galapagos have not been recorded elsewhere.

A total of seven large and conspicuous macroalgal species have not been sighted since the 1982/1983 El Niño. *Bifurcaria galapagensis* was assessed by specialists at the 2006 Galapagos threat assessment workshop as

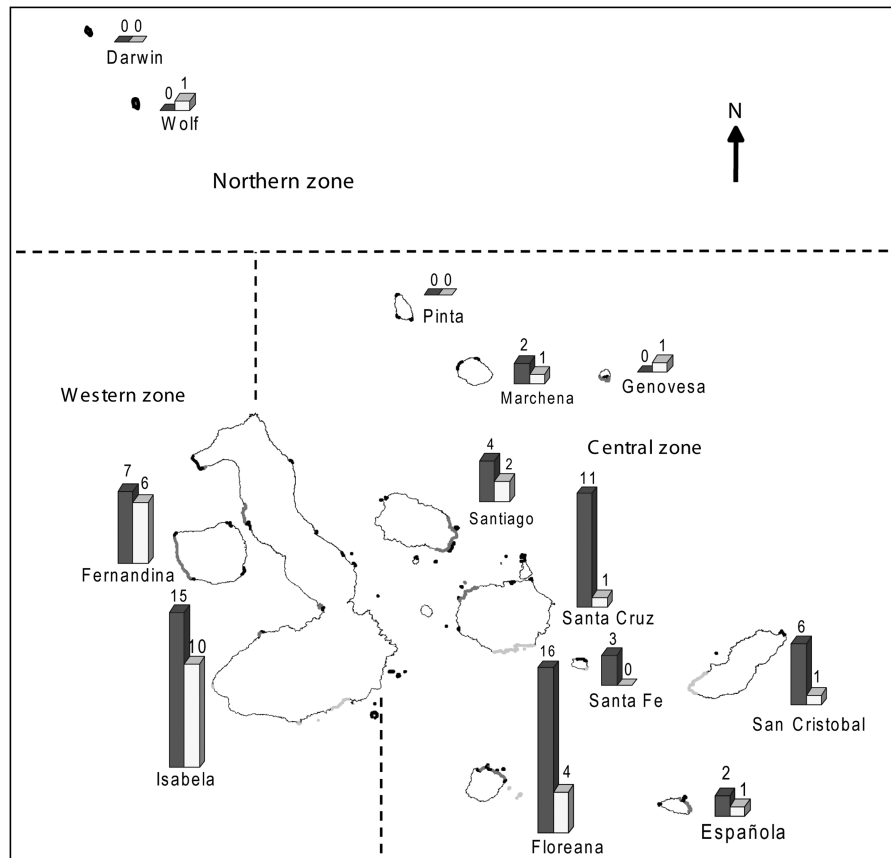


Fig. 5 Number of species on the current Galapagos threatened marine species list (Table 1) with historical records at different islands in the three major biogeographic zones before (dark bars) and after (light bars) the 1982/1983 El Niño. Threatened marine vertebrates and corals (*Pocillopora elegans* and *P. inflatus*) that are widely distributed across the archipelago have been excluded from totals. Conservation and tourism zones with prohibition on fishing are shown as darkened areas of coast.

probably extinct, while *Dictyota galapagensis*, *Spatoglossum schmittii*, *Desmarestia tropica*, *Phycodrina elegans*, *Gracilaria skottsbergii* and *Galaxaura barbata* were regarded as possibly extinct. Many other poorly known species were listed as data deficient, and may be threatened as well.

Some macroalgal species in Galapagos are clearly at great risk from extinction, a conclusion at odds with a recent suggestion that deep water macroalgal communities in Galapagos are resilient to impacts of El Niño (Graham *et al.*, 2007). That suggestion was, however, based on an estimated depression of about 20 m in the Galapagos thermocline during typical El Niño events, in which case most of the population of the kelp *Eisenia galapagensis* and other deepwater algae could persist within a refuge below the zone of El Niño nutrient depletion. However, the 20 m depression in the thermocline referred to by Graham *et al.* (2007) is based on a study of the mild 1991 El Niño (Kessler *et al.*, 1995), and is close to normal intra-annual variation (Wellington *et al.*, 2001). By contrast, during the extreme 1982/1983

El Niño, the thermocline declined by 50–70 m for many months (Halpern *et al.*, 1983), putting all known Galapagos kelp populations at risk.

In contrast to changes in macroalgal communities, changes in coral communities have been well documented in recent decades (see Feingold, 2001; Glynn, 2003). The major observed cause of coral loss following the 1982/1983 El Niño was bioerosion by the urchin *Eucidaris galapagensis*, which apparently increased in abundance (Fig. 2) and destroyed reef frameworks weakened by bleaching (Glynn *et al.*, 1979, 2001; Glynn, 1990, 1994). Although the 1997/1998 El Niño generated a thermal anomaly of similar magnitude to the 1982/1983 event (Wellington *et al.*, 2001), its ecological impact on corals was less severe, probably because no large coral reef frameworks remained in the archipelago in 1997, and because genotypes of remnant coral and associated zooxanthellae were more resilient to heat stress (Glynn *et al.*, 2001).

In addition to its role in accelerating coral bioerosion, the urchin *Eucidaris galapagensis* now appears to be

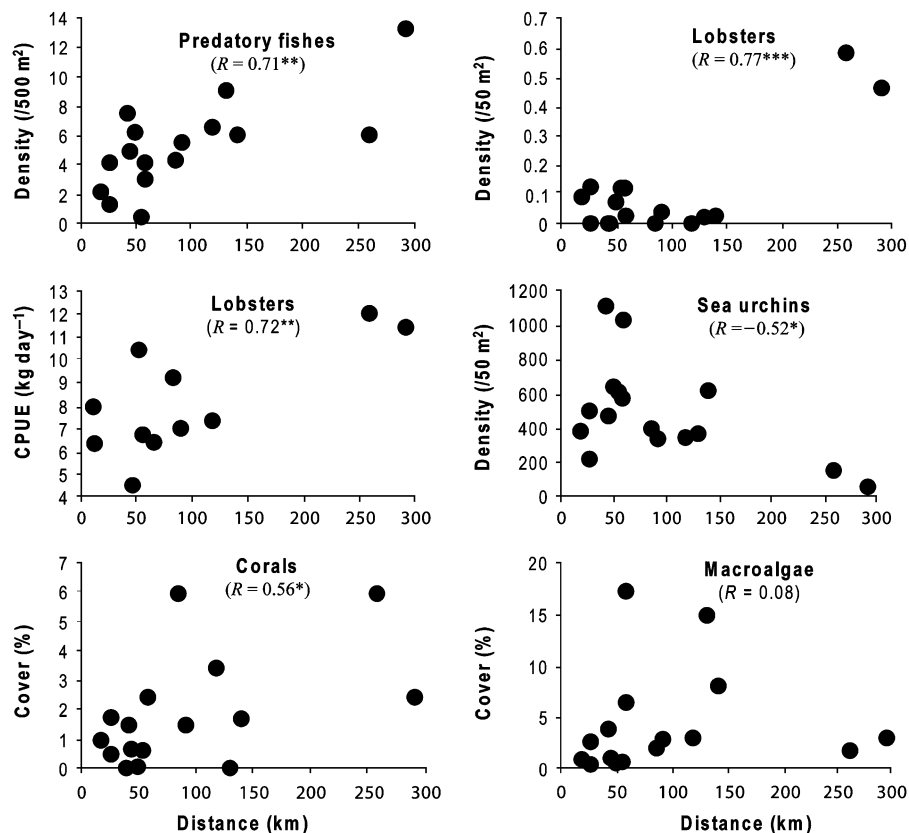


Fig. 6 Scatterplots showing relationships between total densities of large predatory fishes, spiny lobsters, sea urchins, corals and macroalgae and distance from fishing port. Data shown are means for islands where >15 field surveys were undertaken during 2000–2001 GMR baseline surveys. Pearson's correlation coefficients, with associated significance values based on two-tailed tests, are also shown.

present in sufficient numbers to prevent re-establishment of coral and macroalgal habitat, thereby facilitating a regime shift in local benthic habitats. Studies elsewhere indicate that urchin barrens typically develop at sites with urchin densities exceeding about 3 m^{-2} and are maintained at densities $>1\text{ m}^{-2}$ (Tegner & Dayton, 2000; Shears & Babcock, 2003). Densities of urchins are now sufficiently high to preclude regrowth of macroalgae and coral at most sites in Galapagos, with *Eucidaris galapagensis* densities averaging 3.2 m^{-2} (Edgar *et al.*, 2004a), and total urchin densities averaging $>5\text{ m}^{-2}$ across the GMR (Fig. 6). Urchin densities $<1\text{ m}^{-2}$ were consistently recorded only off the far-northern islands of Darwin and Wolf.

Impact of fishing

One possible answer to the pivotal question 'why did the 1982/1983 El Niño generate such catastrophic environmental impacts compared with previous and subsequent events?' is that observed impacts represent naturally recurrent perturbations that are regularly associated with strong El Niño events, but with a cycle

extending longer than our period of study. We consider this unlikely given that the 1982/1983 El Niño destroyed all structural coral reefs in the archipelago, including some that had persisted since at least AD 1600 (Dunbar *et al.*, 1994). Moreover, *Azurina eupalama* and other marine species that presumably frequented Galapagos for tens of thousands of years have apparently now disappeared.

An alternative explanation is that overfishing in recent decades has reduced ecosystem resilience. Specifically, overfishing may have weakened predatory control exerted by lobsters and fishes on populations of urchins, resulting in greatly increased grazing pressure and loss of macroalgae and corals (Sonnenholzner *et al.*, 2009). This hypothesis appears consistent with observations and food web modelling (Bustamante *et al.*, 2008).

The hypothesis is also largely consistent with outcomes of our analysis of relationships between ecosystem metrics and distance from fishing port. As fishing pressure increases, the density of predatory fishes and lobsters significantly decreases, the density of sea urchins increases and the density of coral decreases (Fig. 6).

In the case of corals, the relationship between cover and fishing pressure is likely affected by a lack of coral growth in the cool upwelling western archipelago, whereas the distribution of macroalgae is greatly enhanced by nutrient upwelling in the west. Thus, patterns of density of corals and macroalgae probably reflect both environmental and anthropogenic drivers, the latter including fishing pressure and its correlate analysed here.

An overfishing hypothesis that includes the premise that predators, particularly lobsters, mediate community interactions involving urchins in Galapagos is supported by field studies across the eastern tropical Pacific. Significantly lower densities of *Eucidaris* urchins are present in marine-protected areas compared with fished reference sites, both for the oceanic region that encompasses Galapagos, Isla del Coco and Malpelo, and for the continental coast extending from Panama to Ecuador (G. Edgar, S. Banks, S. Bessudo, J. Cortés, H. Guzman, F. Rivera, G. Soler, F. Zapata, unpublished results). A keystone predator/urchin relationship in Galapagos is also consistent with studies in South Africa, New Zealand and United States, where lobsters have been found to control invertebrate prey populations, particularly urchins (Tegner & Levin, 1983; Barkai & Branch, 1988; Tegner & Dayton, 2000; Shears & Babcock, 2002). In Galapagos, lobsters were directly observed feeding on urchins at night, and high abundances of lobster were found in our 2001 surveys only around the northern islands of Darwin and Wolf (Fig. 6), where urchins were few, and corals relatively abundant. No clear relationship between distance from port and lobster density is evident in Fig. 6 when Darwin and Wolf are excluded from the plot, an indication that lobster overfishing is probably pervasive other than off the northern islands.

A predator control hypothesis is additionally consistent with the timeline of the development of the Galapagos lobster and reef fish fisheries. The number of registered Galapagos fishers increased from about 100 in 1971 to about 240 in 1985 and to about 1000 in 2001 (Bustamante *et al.*, 2002). The semi-industrial lobster fishery developed rapidly in the 1970s following the introduction of compressed air surface supply diving equipment to the islands (Bustamante *et al.*, 2000b). Predatory fish populations also have been over-exploited, including *Mycteroperca olfax*, the most heavily targeted reef species and biomass dominant amongst the predatory fishes. This Vulnerable species of grouper has been characterized as functionally extinct in the central region of Galapagos (Ruttenberg, 2001; Okey *et al.*, 2004).

The next major El Niño will provide an unwelcome test for a predator control hypothesis, given that the

Galapagos lobster fishery has recently expanded to the northern islands, where spiny lobster numbers were an order of magnitude higher than elsewhere in Galapagos in 2001 (Fig. 6). We predict that unless new conservation strategies are enacted to protect northern populations of lobsters within sanctuary zones, coral habitat will diminish and urchin barrens will become more prevalent in the north. Macroalgal beds are also predicted to decline further unless exploitation of lobsters and predatory fishes is controlled more effectively.

Results of this Galapagos study strengthen the growing contention that marine ecosystems are far from isolated from threatening processes and the risk of species extinction (Roberts & Hawkins, 1999; Dulvy *et al.*, 2003). Lack of distributional and population information, ignorance about genetically distinct sibling species, lack of IUCN Species Survival Commission Specialist Groups to undertake formal Red List assessments, few biodiversity inventories, and failure to review scattered historical data, have presumably contributed to the small number of marine species worldwide currently recognized as extinct or threatened. While major declines in terrestrial plant communities can be directly observed, the Galapagos situation indicates that marine habitats can transform over large areas virtually without notice or documentation. Such oversights are illustrated by a 'low' threat ranking for Galapagos in the global analysis of threats to coral reefs (Bryant *et al.*, 1998). A Global Marine Species Assessment has now been initiated by IUCN to begin to address these issues (<http://www.sci.odu.edu/gmsa/>).

For future studies, the GMR possesses a near ideal environment for quantifying effects of oceanographic anomalies and fisheries on marine biodiversity, and for modelling future impacts of climate change. It also possesses a natural resource management framework well suited to the design of scientific studies, and one that should generate positive conservation outcomes, with subdivision of the coastal environment into interspersed conservation, tourism and fishing zones. Unfortunately, neither field monitoring data nor observations of the distribution of fishing effort indicate that the 'no-fishing' conservation zones are well respected by local fishers (Danulat & Edgar, 2002). If these zones were to be effectively enforced, and new conservation zones added to safeguard sites with populations of threatened species (Edgar *et al.*, 2008), then the GMR should provide invaluable insights into interactive human effects on marine ecosystems associated with climate change.

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