



Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago

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ABSTRACT

Aim To delineate biogeographical patterns in Galapagos shallow-water reef fauna at regional scales.

Location Galapagos Islands.

Methods Fishes and macro-invertebrates were quantitatively censused using underwater visual techniques along more than 500 transects at defined depth strata across the Galapagos archipelago. Data were analysed using multivariate techniques to define regional patterns and identify species typical of different regions.

Results Subtidal communities of fishes and macro-invertebrates on shallow reefs differed consistently in species composition across the Galapagos archipelago, with three major biogeographical groupings: (1) the 'far-northern area' containing the islands of Darwin and Wolf, (2) the 'central/south-eastern area', including the east coast of Isabela, and (3) the 'western area', encompassing Fernandina and western Isabela. In addition, the northern islands of Pinta, Marchena and Genovesa form a separate region in the central/south-eastern area, and Bahia Elizabeth and Canal Bolivar separate from other parts of the western area. The far-northern bioregion is characterized by high fish species richness overall, including a high proportion of species of Indo-Pacific origin. However, very few endemic fishes or species with distributions extending south from Ecuador ('Peruvian' species) are present, and the bioregion also possesses relatively low species richness of mobile macro-invertebrate taxa. By contrast, the 'western' bioregion possesses disproportionately high numbers of endemic fish taxa, high numbers of cool-temperate Peruvian fish species, and high invertebrate species richness, but very few species of Indo-Pacific origin. The Bahia Elizabeth/ Canal Bolivar bioregion possesses more endemic species and fewer species with Peruvian affinities than coasts within the western bioregion. The northern bioregion of Pinta, Marchena and Genovesa represents an overlap zone with affinities to both the far-northern and south-eastern islands. The south-eastern bioregion includes species from a variety of different sources, particularly 'Panamic' species with distributions extending north to Central America.

Main conclusions On the basis of congruent divisions for reef fish and macro-invertebrate communities, the Galapagos archipelago can be separated into three major biogeographical areas, two of which can be further subdivided into two regions. Each of these five bioregions possesses communities characterized by a distinctive mix of species derived from Indo-Pacific, Panamic, Peruvian and endemic source areas. The conservation significance of different regions is not reflected in counts of total species richness. The regions with the lowest overall fish species richness possess a temperate rather than tropical climate and highest levels of endemism.

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Keywords

Benthos, Galapagos, fishes, macro-invertebrates, reef, biogeographical region, species richness, endemism, faunal distribution.

INTRODUCTION

The more than 100 volcanic islands and islets of Galapagos possess one of the most interesting biogeographical settings on earth. Galapagos is the only tropical archipelago lying at the intersection of major warm- and cool-water current systems, being located in the path of (1) the warm south-westerly flowing Panama Current, (2) the cool north-westerly flowing Peru current, and (3) the cold eastward-flowing subsurface equatorial undercurrent (Houvenaghel, 1978; Banks, 2002). The latter rises to the surface along western and southern margins of the Galapagos Plateau, generating highly productive upwelling systems (Pak & Zanfield, 1974). As a consequence, oceanographical conditions vary markedly over short spatial scales across the archipelago, with quite extreme environmental differences existing between the cool upwelling region in the west and the warm oligotrophic north. For example, water temperature at 10 m depth at Punta Espinosa on the westernmost island of Fernandina averaged 18 °C compared with 24 °C 180 km north off the island of Wolf between June 1996 and February 1997 (Wellington *et al.*, 2001). Much of this regional variation in ocean climate disappears during El Niño years (Banks, 2002), when water temperatures rise above 25 °C throughout the archipelago for periods that can exceed a year (Wellington *et al.*, 2001).

The anomalous ocean climate surrounding Galapagos translates to distinctive marine ecosystems that occur in close proximity, and a biota that includes elements characteristic of tropical (e.g. manta rays, reef sharks, corals), temperate (sea lions, kelp) and even subantarctic (fur seals, penguins, albatross) seas. A large component of endemic species is present (Bustamante *et al.*, 2000), notably including the marine iguana (*Amblyrhynchus cristatus*), flightless cormorant (*Phalacrocorax harrisi*) and the only tropical laminarian kelp (*Eisenia galapagensis*).

Despite this scientific importance, little has been published on the distribution of marine biodiversity across the region (Bensted-Smith, 2002). The most widely quoted marine regionalization for the archipelago was described more than 30 years ago by Harris (1969). This regionalization was originally physical rather than biological, with water temperature data used as a surrogate for biological data because the latter were largely lacking (Harris, 1969). In the Harris scheme, Galapagos waters were subdivided into five regions (north, west, south, central and central mixing). Jennings *et al.* (1994) provided some support for Harris' (1969) scheme with information on reef fishes; however, only 10 sites were investigated during that study and insufficient data were available to compare variation within as well as between regions. In the sole major archipelago-wide investigation prior

to the present study, Wellington (1975) considered that four major biogeographical regions were clearly defined for Galapagos (western, southern, central and northern).

The present study aimed to clarify broad-scale marine biogeographical patterns across Galapagos. It was initiated partly for scientific interest and partly in response to a management need. All waters extending 40 miles offshore from an imaginary line joining the outer islands are regulated by the Ecuadorian Government for conservation of biodiversity within the Galapagos Marine Reserve (GMR). The GMR is regulated by a Management Plan, which states as a principal aim that biodiversity will be protected in all biogeographical regions. The Management Plan was negotiated by local stakeholders, who recognized that marine plants and animals required protection within 'no-take' sanctuary zones of adequate size in all different bioregions. This aim could only be achieved if biogeographical regions were more accurately defined than currently in the Harris scheme.

METHODS

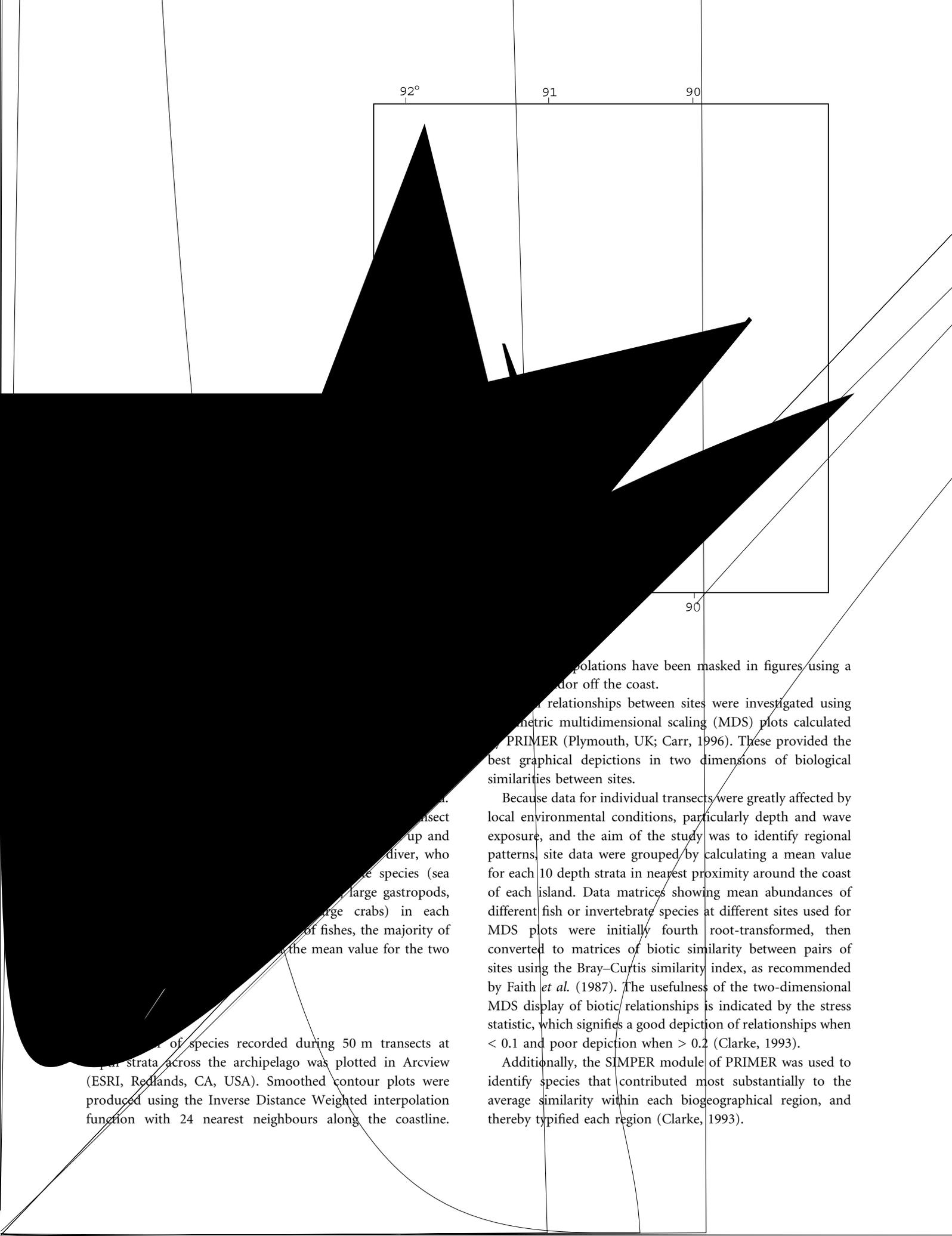
Sites surveyed

Quantitative data were collected between 13 May 2000 and 13 December 2001 during research cruises to define baseline conditions in different management zones within the GMR. The shallow subtidal rocky reef habitat investigated here, and used as the data set for deriving the regionalization, represents the predominant habitat type around the Galapagos coastline (> 95% of shallow habitat, Bustamante *et al.*, 2002). Shallow reefs also comprise the habitat most affected by fishing and other human activity.

Underwater visual censuses along line transects were undertaken during daylight hours at 50 islands and islets distributed across the archipelago (Fig. 1). Generally, two different depth contours were surveyed at a single site. For some sites, the two depth strata surveyed were parallel and immediately adjacent to each other, while in other areas depth strata were offset by up to 300 m when divers were working from different boats. Consequently, the term 'site' is somewhat ambiguous, and the term 'depth strata' preferred, referring to one depth interval at a site. Overall, a total of 579 and 569 depth strata were surveyed for fish and macro-invertebrates, respectively.

Faunal survey protocols

Fish surveys were undertaken by laying a 50 m transect line along a defined depth contour within the range from 2 to 20 m depth. A diver swam beside the transect line at a distance of 2.5 m, recording on a waterproof notepad the abundance of



... interpolations have been masked in figures using a
... or off the coast.

... relationships between sites were investigated using
... metric multidimensional scaling (MDS) plots calculated
... PRIMER (Plymouth, UK; Carr, 1996). These provided the
... best graphical depictions in two dimensions of biological
... similarities between sites.

... Because data for individual transects were greatly affected by
... local environmental conditions, particularly depth and wave
... exposure, and the aim of the study was to identify regional
... patterns, site data were grouped by calculating a mean value
... for each 10 depth strata in nearest proximity around the coast
... of each island. Data matrices showing mean abundances of
... different fish or invertebrate species at different sites used for
... MDS plots were initially fourth root-transformed, then
... converted to matrices of biotic similarity between pairs of
... sites using the Bray-Curtis similarity index, as recommended
... by Faith *et al.* (1987). The usefulness of the two-dimensional
... MDS display of biotic relationships is indicated by the stress
... statistic, which signifies a good depiction of relationships when
... < 0.1 and poor depiction when > 0.2 (Clarke, 1993).

... Additionally, the SIMPER module of PRIMER was used to
... identify species that contributed most substantially to the
... average similarity within each biogeographical region, and
... thereby typified each region (Clarke, 1993).

... of species recorded during 50 m transects at
... 10 m strata across the archipelago was plotted in Arcview
... (ESRI, Redlands, CA, USA). Smoothed contour plots were
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Faunal patterns across the archipelago were also analysed using canonical analysis of principal coordinates (CAP) (Anderson, 2003), a constrained ordination procedure that initially calculates unconstrained principal coordinate axes, followed by canonical discriminant analysis on the principal coordinates to maximize separation between predefined groups (Anderson & Robinson, 2003; Anderson & Willis, 2003). CAP is considered more flexible than

Analysis of the macro-invertebrate data set (Fig. 4) reveals three major groups of sites: (1) Darwin and Wolf, (2) Fernandina and western Isabela, and (3) other islands. Genovesa and Pinta also separate from the main island grouping because of their greater affinity with the fauna of Darwin and Wolf. The fauna of Marchena is quite variable but with a high level of similarity to central and southern islands and north-eastern Isabela. The fauna of Pinzon is distinctive.

The macro-invertebrate fauna also shows a very high degree of variation around Isabela, but is more homogeneous around Fernandina than was seen for the fish fauna (Fig. 5). The invertebrate fauna off the coast of Isabela from Punta Albermarle to Cuatro Hermanos overlaps the fauna of Floreana, Santiago, Santa Fe, Santa Cruz, San Cristobal,

Espanola and Rabida, while the west coast fauna exhibits major differences between Bahia Elizabeth (Islas Marielas) and Caleta Iguana.

Patterns of fish species richness (i.e. the number of fish species observed per 50 m × 10 m transect block) across the archipelago generally reflected clinal trends in communities identified by MDS. Fish species richness was highest around the far-northern islands of Darwin and Wolf and lowest off Fernandina, Santa Cruz, and the Bahia Elizabeth region of western Isabela (Fig. 6). However, the distribution of endemic Galapagos fishes was opposite to that seen for the total fauna, with endemic species present in highest numbers near Islas Marielas in Bahia Elizabeth and also off western Isabela, Fernandina, Santa Fé and south-western Floreana (Fig. 7).

The unusually high species richness in the far-northern region was caused by the presence in that area of numerous species with ranges extending westward across the Indo-Pacific (Fig. 8a). Many of these species were coral reef-associated wrasses, butterflyfishes, pufferfishes and jacks. The far-northern islands also possessed a disproportionately high number of species with 'Panamic' ranges that extend north of Ecuador but not south (Fig. 8b); nevertheless, in addition to the virtual absence of endemic Galapagos fishes (Fig. 7), this region included very few species with 'Peruvian' ranges extending south along the South American coast (Fig. 8d).

Southward-ranging Peruvian species were largely restricted to western, northern and southern Fernandina, and south-western and north-western Isabela (Fig. 8d), probably because most of these species associate with seaweed habitats that are largely absent elsewhere in the archipelago. Fish species with wide South American ranges that extended both north and south of Ecuador were widespread throughout the archipelago (Fig. 8c), except for disproportionately low numbers off Bahia Elizabeth, Fernandina (particularly the east coast) and Santa Cruz.

In contrast to the situation with fishes, the number of macro-invertebrate species recorded per 50 m × 2 m transect block varied relatively little across the archipelago, with a general average of 6.0 species per transect (Fig. 9). Nevertheless, 25% fewer species occurred around the far-northern islands of Darwin and Wolf (4.5 species per transect) than elsewhere.

Invertebrate species with Indo-Pacific distributions occurred throughout the archipelago, with lowest species richness in the south-west (Fig. 10a). Species with ranges only to the north of Ecuador were also widely distributed but with no decline apparent in the western region (Fig. 10b). The relatively low species richness of macro-invertebrates around the two northernmost islands was caused by few species with widespread South American distributions occurring in the far-northern area (Fig. 10c). Widespread South American species were, however, disproportionately abundant off western Isabela and Fernandina, and presumably tolerated cooler conditions than the other regional species groups.

No macro-invertebrate species were sighted that possessed a distribution on the South American continent solely south

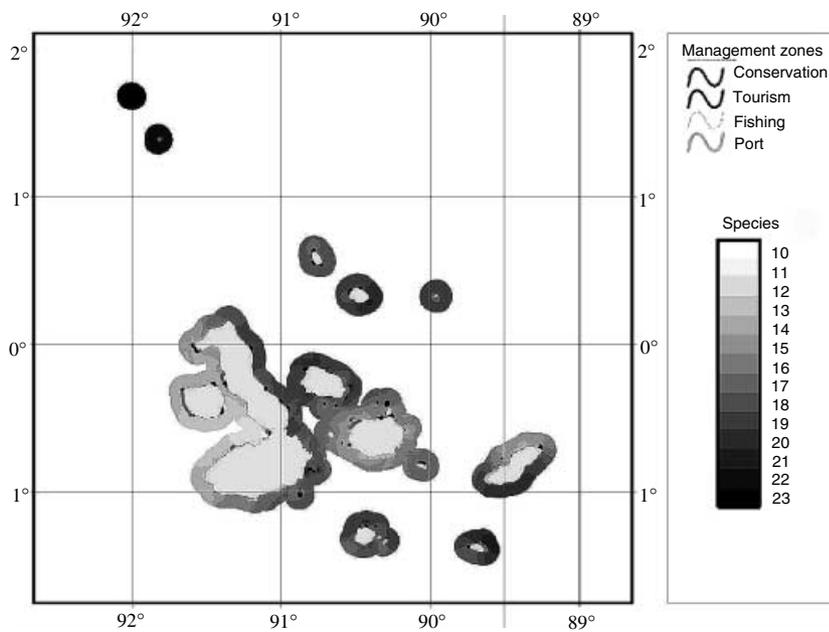


Figure 6 Shaded contour plot showing mean total number of fish species observed per 50 m transect around different coasts of Galapagos. Line width of island outline reflects management zone of that section of coast.

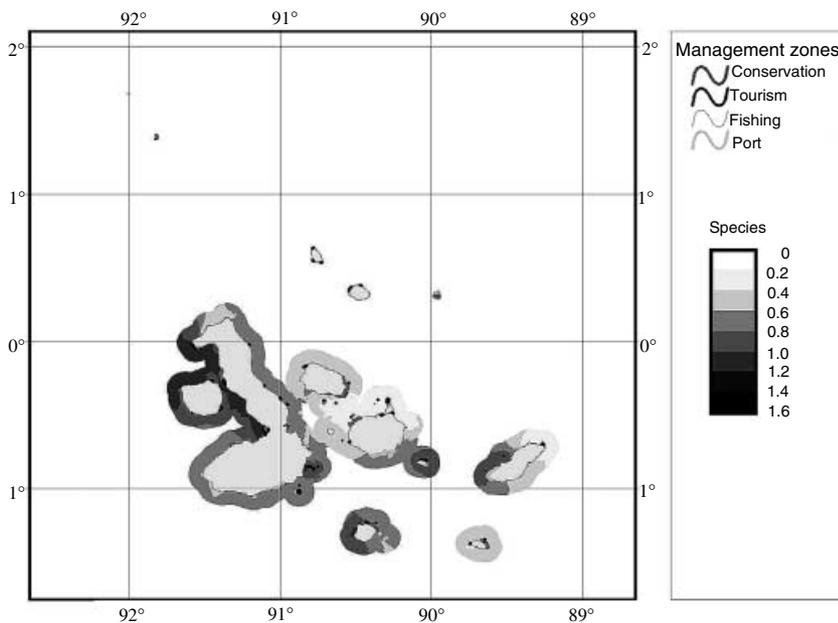


Figure 7 Shaded contour plot showing mean total number of endemic Galapagos fish species per 50 m transect.

from Ecuador. Moreover, only four endemic invertebrate species were recorded in transects – the slipper lobster *Scyllarides astori*, the sea urchin *Eucidaris galapagensis*, the octopus *Octopus oculifer* and the scallop *Nodipecten magnificus*, hence plots of macro-invertebrates comparable with Figs 7 and 8d could not be depicted.

Generally, species richness analyses for fish and invertebrate data sets were consistent with MDS analyses in showing that Galapagos coastal waters are best divided into the five marine biogeographical regions (bioregions) shown in Fig. 11. These bioregions are referred to as ‘far-northern’, ‘northern’, south-eastern’, ‘western’ and ‘Elizabeth’. The name ‘Elizabeth’ has

been used because the core features of that bioregion are most evident within Bahia Elizabeth rather than Canal Bolivar, which possess more overlap with the ‘western’ bioregion. The Elizabeth bioregion extends from Punta Espinosa and the northern point of Tagus Cove in the north to Punta Mangle and just east of Punta Moreno in the south. The western bioregion on Isabela extends from just west of Punta Albermarle to just east of Isla Tortuga.

The mean densities of common fish and invertebrate species in different bioregions are listed in Tables 1 and 2. Species disproportionately abundant or rare in each bioregion, as identified using SIMPER analysis (Clarke, 1993), are also

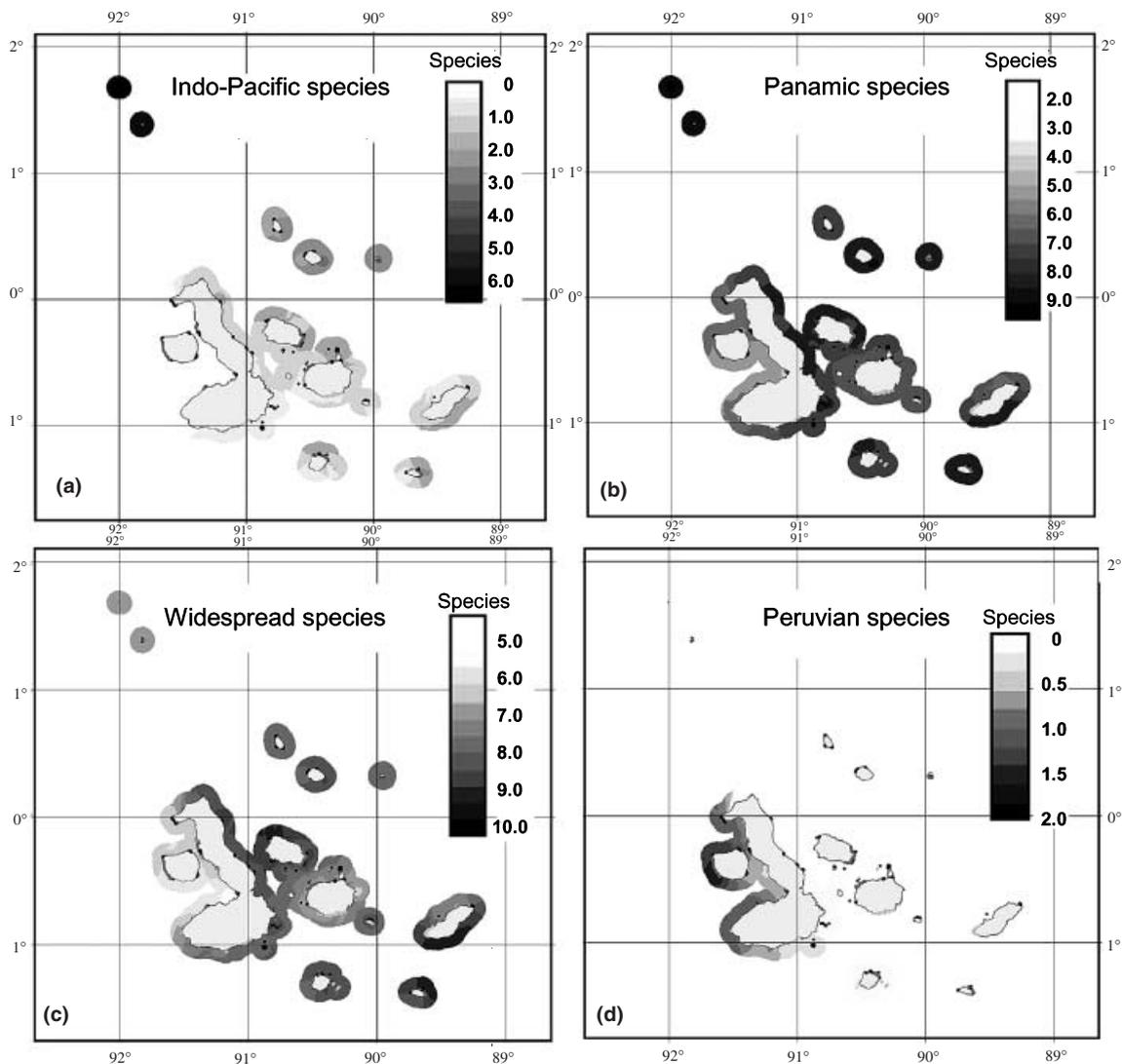


Figure 8 Shaded contour plot showing mean total number of fish species per 50 m transect for species with Panamic (ranges extending northwards along the South American coast but not southwards from Ecuador), Indo-Pacific (ranges extending westwards to at least Hawaii), Peruvian (ranges extending southwards along the South American coast but not northwards from Ecuador) and widespread (ranges extending both northwards and southwards along the South American coast from Ecuador) ranges.

indicated. Note that species showing disproportionately high mean abundances within a bioregion are not necessarily identified by SIMPER analysis as typifying that bioregion. For example, the endemic goby *Lythrypnus gilberti* is most abundant in the south-eastern bioregion but better typifies the Elizabeth bioregion. This fish occurred in extremely high abundance ($> 1 \text{ m}^{-2}$) at a few sites on south-western Isabela in the south-eastern bioregion but was absent from the majority of sites, whereas the species occurred in lower maximal abundance in the Elizabeth bioregion but at a high proportion of sites.

Faunal abundance data for different biogeographical regions exhibited similar patterns to species richness data in that densities of Indo-Pacific species were generally highest in the far-northern bioregion, endemic species were most abundant

in the Elizabeth and western bioregions, and Peruvian species were most abundant in the western bioregion. Nevertheless, a few anomalous distributions existed. For example, the Indo-Pacific pufferfish *Spherooides annulatus* was not recorded in the far-northern islands while the parrotfish *Scarus ghobban* was widely distributed throughout the archipelago rather than being concentrated in the far north. In addition, although the echinoid *Echinometra vanbrunti* and the holothurian *Holothuria difficilis* possess Panamic distributions, these species were not detected in the warm far-northern region of Galapagos.

Faunal data pertaining to different 0.01° latitude and longitude grid cells have been classified in multidimensional space using CAP analysis to maximize differences between the five bioregional groups. The best congruence with the five bioregional groups was found using the first 20 principal

components for fishes and first 10 principal components for macro-invertebrates. Differences between bioregional groups were statistically significant for all pairwise comparisons (permutation test, $P < 0.001$, including Bonferoni correction for 10 pairwise tests).

For both fishes (Fig. 12) and macro-invertebrates (Fig. 13), the first two canonical axes did not separate the western and Elizabeth regions (Figs 12a and 13a); hence the third canonical axes have been included in figures (Figs 12b and 13b). Although these figures indicate a stronger separation between the western and Elizabeth bioregions for fishes than invertebrates, the leave-one-out procedure indicates a stronger separation between these bioregions for the macro-invertebrate data when all canonical axes are considered (Tables 3 and 4).

Data for each grid cell were accurately classified into the appropriate bioregional group in the majority of cases using the leave-one-out procedure, with misclassification primarily occurring between the western and Elizabeth bioregions, and between the northern and south-eastern bioregions. Thus, a primary three-group separation exists between far-northern, northern + south-eastern, and western + Elizabeth bioregions.

Species showing high correlations with the major canonical axes included nearly all species identified by SIMPER analysis as typifying particular regions. A large group of species, including the moray eel *Gymnothorax dovii*, surgeonfishes *Acanthurus nigricans* and *Prionurus laticlavus*, priacanthid *Heteropriacanthus cruentatus*, trumpetfish *Aulostomus chinensis*, Moorish idol *Zanclus cornutus*, pufferfishes *Arothron meleagris* and *Canthigaster punctatissima*, wrasse *Thalassoma lucasanum*, triggerfish *Sufflamen verres*, sea urchin *Diadema mexicanum*, spiny lobster *Panulirus penicillatus* and crab *Percnon gibbesi*, were principally confined to the far-northern islands. The majority of these species possess Indo-Pacific distributions.

The groupers *Paralabrax albomaculatus* and *Mycteroperca olfax*, goby *Lythrypnus gilberti*, sea cucumber *Stichopus fuscus*, and sea stars *Nidorellia armata* and *Pharia pyramidata* were most highly correlated with the Elizabeth bioregion; the wrasse *Halichoeres dispilus*, weedfish *Labrisomus dendriticus*, and sea urchins *Lytechinus semituberculatus* and *Centrostephanus coronatus* with the western bioregion; and the wrasses *Semicossyphus darwini* and *Bodianus eclancheri*, hornshark *Heterodontus quoyi*, and knifejaw *Oplegnathus insignis* were disproportionately abundant in both these bioregions. Species highly correlated with the south-eastern region included the damselfish *Abudefduf troschelii*, wrasse *Halichoeres nicholsi*, grunt *Haemulon scudderi*, and sea urchin *Tripneustes depressus*. The holothurians *Holothuria atra* and *Holothuria fuscocinerea* were primarily associated with the northern bioregion.

DISCUSSION

Biogeographical patterns

Faunal abundance and species richness data both indicate that Galapagos inshore reef ecosystems [shoi09.shore78406](https://doi.org/10.1111/jbi.12109). <https://doi.org/10.1111/jbi.12109>

Pinta, Marchena and Genovesa possessed a fauna distinctively

Far northern

Centra

differing from the fish fauna, which showed a relatively close affinity to the Indo-Pacific. The patterns were not consistent across the invertebrate data sets. The degree of variation between individual islands was also high. In the invertebrates around the archipelago, we found a high variation between island groups. In the invertebrate data sets, we found a high variation between eastern and southern islands.

The distinctive patterns of unexpected outliers, the degree of affinity, the degree of difference between islands, and the degree of difference between island groups.

The degree of this difference is related to the degree of the GMR (Glynn & Ault, 2002); nearly all images of the GMR are produced by productivity in the Elizabeth Bay region of the archipelago. This high productivity is a key system its distinctive character.

The strong regional divisions in the Galapagos marine fauna probably reflect both local environmental conditions and connectivity of larval propagules with external source regions. Species with Indo-Pacific distributions occur predominantly in the far-northern region of Galapagos, where water temperatures are highest, turbidity is low, coral development is most extensive, and warm currents are likely to first strike the archipelago. Many amongst the diverse far-northern component of species probably maintain gene flow across the East Pacific Barrier, particularly during El Niño years when currents from the north-east and north prevail (Glynn & Ault, 2000). In addition to long-lasting larval stages, Indo-Pacific fishes in Galapagos often penetrate much

has been (Glynn, 1998).

The 1982/83 El Niño clearly had a major impact on Galapagos marine biodiversity, with consequences that persist today (Bensted-Smith, 2002). Macroalgae and invertebrates with cool-temperate affinities appear to have been most affected (also corals: Glynn, 1994), their ranges contracting greatly and populations now being largely confined to localized areas in the west. Thus, patterns of invertebrate biodiversity identified would perhaps have been quite different if our surveys had been conducted in 1980.

The poor recovery of marine invertebrates following El Niño compared with fishes is likely due to limited metapopulation

Table 1 Mean abundance per 500 m² transect in different biogeographical regions of fish species recorded on at least five transects. Fish species identified using SIMPER analysis to be associated with particular bioregions are listed by superscript in rank order of strength of association, with negative numbers indicating negative association

Species	Biogeographical region					Overall
	Far-northern	Northern	South-eastern	Western	Elizabeth	
Endemic species						
<i>Lythrypnus gilberti</i> (Heller & Snodgrass)	0	0	24.6	1.40	17.6 ²	15.2
<i>Xenocys jessiae</i> Jordan & Bollman	0	0.63	6.87	41.0	20.3	12.1
<i>Girella freminvillei</i> (Valenciennes)	0.02	0.60	2.64	2.57	2.01	2.09
<i>Orthopristis forbesi</i> Jordan & Starks	0	0.10	4.38	1.62	1.88	2.80
<i>Lepidonectes corallicola</i> (Kendall & Radcliffe)	0.16	0.26	1.47	4.45	2.51 ⁴	1.77
<i>Acanthemblemaria castroi</i> Stephens & Hobson	0	0	2.20	1.56	0.01	1.41
<i>Mugil rammelsbergi</i> (Ebeling)	0	0.10	0.39	0	8.06	1.06
<i>Paralabrax albomaculatus</i> (Jenyns)	0	0.46	0.15	0.09	1.34 ⁵	0.30
<i>Sphoeroides angusticeps</i> (Jenyns)	0	0.10	0.10	0.02	0.07	0.08
<i>Odontoscion eurymesops</i> (Heller & Snodgrass)	0	0	0	0.35	0	0.05
Panamic species						
<i>Thalassoma lucasanum</i> (Gill)	1027.9	158.8	44.7 ⁻¹	28.0 ⁻³	4.67 ⁻³	123.2
<i>Prionurus laticlavus</i> Valenciennes	123.2	141.5	160.3	24.6 ⁻²	6.58 ⁻²	118.6
<i>Stegastes beebei</i> (Nichols)	21.6 ⁻²	76.5	75.8	118.0	107.7	81.8
<i>Apogon atradorsatus</i> Heller & Snodgrass	0.08	0.08	44.0	2.35 ⁻¹⁰	3.32 ⁻¹⁰	24.3
<i>Stegastes arcifrons</i> (Heller & Snodgrass)	13.9	22.5	7.28	0.21 ⁻¹¹	2.51	8.30
<i>Microspathodon dorsalis</i> (Gill)	0.91	6.61	7.94	7.79	0.22	6.43
<i>Johnrandallia nigrirostris</i> (Gill)	7.41	7.93	7.98	0.67 ⁻⁵	0.32 ⁻⁷	6.03
<i>Haemulon scudderi</i> Gill	0	0	10.5	1.93	1.04	6.00
<i>Mycteroperca olfax</i> (Jenyns)	0.06	1.74	2.20	13.6	4.28	3.92
<i>Lutjanus viridis</i> (Valenciennes)	0.33	1.96	5.82	1	0.01	3.56
<i>Halichoeres nicholsi</i> (Jordan & Gilbert)	0.07	0.69	4.17	1.16 ⁻⁸	0.56 ⁻⁹	2.56
<i>Labrisomus dendriticus</i> (Reid)	0.60	1.22	1.22	9.60	2.30	2.55
<i>Cirrhitus rivulatus</i> Valenciennes	1.41	1.96	1.50	3.03	1.33	1.77
<i>Chromis alta</i> Greenfield & Woods	0.19	0.43	2.28	1.06	0.35	1.49
<i>Lutjanus aratus</i> (Günther)	0	0.63	1.86	0	0	1.08
<i>Scarus compressus</i> (Osborn & Nichols)	0.18	1.31	1.11	0.66	0.66	0.96
<i>Microspathodon bairdii</i> (Gill)	0.95	0.58	0.79	0.82	2.33	0.94
<i>Thalassoma grammaticum</i> Gilbert	1.95	0.20	0.07	2.58	0	0.59
<i>Kyphosus elegans</i> (Peters)	1.50	0.44	0.27	0.29	0.06	0.36
<i>Cephalopholis panamensis</i> (Steindachner)	0.36	0.41	0.41	0.09	0.03	0.32
<i>Dermatolepis dermatolepis</i> (Boulenger)	1.65	0.25	0.23	0.16	0.01	0.30
<i>Canthigaster punctatissima</i> (Günther)	0.74	0.71	0.23	0	0	0.28
<i>Gymnothorax dovii</i> (Günther)	1.90	0.82	0.04	0	0	0.27
<i>Sargocentron suborbitalis</i> (Gill)	0.05	0.25	0.05	0.53	0.85	0.24
<i>Euthynnus lineatus</i> Kishinouye	0	1.06	0.12	0.07	0	0.22
<i>Myripristis leiognathos</i> Valenciennes	0.03	0.39	0.31	0	0	0.22
<i>Lutjanus novemfasciatus</i> (Gill)	0.17	0.18	0.2	0	0	0.14
<i>Dasyatis brevis</i> (Garman)	0	0.02	0.14	0.08	0.03	0.09
<i>Coryphopterus urospilus</i> Ginsburg	0	0.02	0.15	0.07	0	0.09
<i>Synodus lacertinus</i> Gilbert	0.17	0.01	0.08	0.01	0.12	0.07
<i>Scorpaena mystes</i> Jordan & Starks	0.15	0.04	0.06	0.06	0	0.06
<i>Hypsoblennius brevipinnis</i> (Günther)	0	0	0.08	0.07	0	0.05
<i>Hoplopagrus guentheri</i> Gill	0.07	0.01	0.01	0	0	0.01
Peruvian species						
<i>Anisotremus scapularis</i> (Tschudi)	0.12	0.02	1.21	17.1 ⁵	5.52	3.81
<i>Bodianus eclancheri</i> (Valenciennes)	0	0	0.26	9.48 ⁶	0.74	1.65
<i>Sphyræna idiaestes</i> Heller & Snodgrass	0	0	1.72	0.33	0.60	1.03
<i>Oplegnathus insignis</i> (Kner)	0.10	0	0.14	4.01	0.81	0.77
<i>Semicossyphus darwini</i> (Jenyns)	0	0	0.03	2.84	0.49	0.49
<i>Heterodontus quoyi</i> (Fremenville)	0	0	0	0.12	0.15	0.03

Table 1 continued

Species	Biogeographical region					
	Far-northern	Northern	South-eastern	Western	Elizabeth	Overall
Indo-Pacific species						
<i>Scarus ghobban</i> Forsskal	0.58	8.12	5.20	1.84 ⁻⁷	2.29	4.47
<i>Cirrhichthys oxycephalus</i> (Bleeker)	5.61 ⁶	1.22	1.51	0.77	0.08	1.50
<i>Acanthurus nigricans</i> Linnaeus	19.0 ³	0.47	0.17	0	0	1.49
<i>Sphaeroides annulatus</i> (Jenyns)	0	0.01	2.47	0.16	0.26	1.37
<i>Zanclus cornutus</i> (Linnaeus)	2.86 ⁹	3.80 ⁶	0.80	0.02	0	1.16
<i>Scarus rubroviolaceus</i> Bleeker	1.24	0.72	0.63	0.02	0.19	0.55
<i>Aulostomus chinensis</i> Lacepede	4.79 ⁷	0.42	0.08	0	0	0.44
<i>Seriola rivoliana</i> Valenciennes	0.76	1.61	0.27	0	0.01	0.42
<i>Arothron meleagris</i> (Bloch & Schneider)	1.37	1.45	0.16	0.01	0	0.39
<i>Melichthys niger</i> (Bloch)	3.08	0.26	0.17	0	0	0.34
<i>Elagatis bipinnulata</i> (Quor & Gaimard)	0.33	0.40	0.27	0	0	0.23
<i>Fistularia commersonii</i> Rüppell	0.36	0.75	0.10	0.03	0	0.19
<i>Chilomycterus affinis</i> Günther	0	0.01	0.14	0	0.15	0.09
<i>Taeniura meyeri</i> (Müller & Henle)	0.01	0.03	0.10	0.09	0.03	0.07
<i>Sphyrna lewini</i> (Griffith & Smith)	0.79	0.01	0.02	0	0	0.07
<i>Acanthurus xanthopterus</i> Valenciennes	0.02	0.01	0.10	0.02	0.02	0.06
<i>Diodon hystrix</i> Linnaeus	0	0.02	0.07	0.02	0.02	0.05
<i>Heteropriacanthus cruentatus</i> (Lacepede)	0.60	0.08	0	0	0	0.05
<i>Triacodon obesus</i> (Rüppell)	0.02	0	0.07	0	0	0.04
<i>Muraena lentiginosa</i> Jenyns	0	0.02	0.04	0.03	0.09	0.04
<i>Diodon holocanthus</i> Linnaeus	0	0	0.06	0.04	0.03	0.04
<i>Novaculichthys taeniourus</i> (Lacepede)	0.18	0.04	0.03	0.02	0	0.04
<i>Aetobatus narinari</i> (Euphrasen)	0.05	0	0.02	0.01	0	0.02
<i>Myripristis berndti</i> Jordan & Evermann	0.02	0.02	0.02	0	0	0.02
<i>Ostracion meleagris</i> Shaw	0	0	0.02	0	0	0.01
<i>Bothus leopardinus</i> (Günther)	0.04	0.02	0.01	0	0	0.01
<i>Acanthocybium solandri</i> (Cuvier)	0	0	0.02	0	0	0.01
<i>Carcharhinus galapagensis</i> (Snodgrass & Heller)	0.05	0	0.02	0	0	0.01
<i>Arothron hispidus</i> (Linnaeus)	0	0.02	0	0	0	0.01
<i>Thalassoma purpuraceum</i> (Forsskal)	0.06	0	0	0	0	0.01
<i>Pseudobalistes naufragium</i> (Jordan & Starks)	0	0	0.01	0.01	0	0.01
Widespread species						
<i>Paranthias colonus</i> (Günther)	1033.4 ²	452.6	604.0	234.3 ⁻¹	164.5 ⁻¹	511.6
<i>Halichoeres dispilus</i> (Gill)	0.90 ⁻¹	36.5	38.4 ⁻²	90.7	40.2 ⁶	43.6
<i>Ophioblennius steindachneri</i> Jordan & Evermann	72.8 ⁴	33.2	20.7	21.0	4.39 ⁻⁴	24.4
<i>Bodianus diplotaenia</i> (Gill)	11.9	15.9	19.3	18.9	21.1 ⁻⁶	18.4
<i>Holacanthus passer</i> Valenciennes	7.77 ⁻³	16.0	16.8 ³	7.23 ⁻⁴	2.92 ⁻⁵	13.2
<i>Abudefduf troschelii</i> (Gill)	0.01	2.00 ⁻²	21.6 ⁴	0.83	3.99 ⁻⁸	12.4
<i>Anisotremus interruptus</i> (Gill)	0.1	15.9 ⁵	16.9	1.30 ⁻⁹	0.05	11.5
<i>Plagiotremus azaleus</i> (Jordan & Evermann)	20.0 ¹⁰	6.96 ⁻¹	9.28	11.9	17.8 ¹	11.0
<i>Epinephelus labriformis</i> (Jenyns)	1.91	5.42	6.31	2.77 ⁻⁶	14.1	6.15
<i>Mulloidichthys dentatus</i> (Gill)	0.5	7.45	6.26	8.42	0.51	5.75
<i>Chromis atrilobata</i> Gill	0.03	3.62	6.5	4.52	4.96	5.19
<i>Serranus psittacinus</i> Valenciennes	0.07	5.57 ³	2.61	1.4	1.82	2.58
<i>Trachinotus stilbe</i> (Jordan & Macgregor)	5	0.1	2.11	0	0	1.49
<i>Sufflamen verres</i> (Gilbert & Starks)	4.78 ⁸	2.74 ⁴	1.17	0.09	0.28 ⁻¹¹	1.39
<i>Orthopristis chalceus</i> (Günther)	0	0.05	2.28	0.34	0.87	1.37
<i>Chaetodon humeralis</i> Günther	0	0.05	1.38	0.27	0.4	0.83
<i>Scarus perrico</i> Jordan & Gilbert	0.08	0.15	1.05	0.58	0.05	0.68
<i>Lutjanus argentiventris</i> (Peters)	0	0.1	0.69	0.27	0.11	0.44
<i>Nicholsina denticulata</i> (Evermann & Radcliffe)	0	0.1	0.08	1.92	0.12	0.36
<i>Kyphosus analogus</i> (Gill)	3.3	0.2	0.05	0.01	0	0.29
<i>Apogon pacificus</i> Herre	0	0	0.21	0	0.81	0.20

Table 1 continued

Species	Biogeographical region					
	Far-northern	Northern	South-eastern	Western	Elizabeth	Overall
<i>Balistes polylepis</i> Steindachner	0.36	0.3	0.2	0.03	0	0.18
<i>Rypticus bicolor</i> Valenciennes	0.05	0.07	0.25	0.06	0	0.16
<i>Malacoctenus tetranemus</i> (Cope)	0.02	0	0.16	0.06	0.05	0.10
<i>Caulolatilus princeps</i> (Jenyns)	0	0	0.02	0.14	0.65	0.10
<i>Scomberomorus sierra</i> Jordan & Starks	0.01	0	0.13	0.02	0.03	0.08
<i>Alphestes immaculatus</i> Breder	0	0.04	0.09	0.02	0.12	0.07
<i>Rypticus nigripinnis</i> Gill	0	0.02	0.11	0	0	0.06
<i>Hippocampus ingens</i> Girard	0	0	0.02	0.04	0.09	0.03
<i>Stegastes acapulcoensis</i> (Fowler)	0	0.01	0.01	0	0.06	0.01

Table 2 Mean abundance per 100 m² transect in different biogeographical regions of macro-invertebrate species recorded on at least two transects. Species identified using SIMPER analysis to be associated with particular bioregions are listed by superscript in rank order of strength of association, with negative numbers indicating negative association. Taxonomic groups are: E, echinoid; A, asteroid; H, holothurian; C, crustacean; M, mollusc

Species	Taxon	Biogeographical region					
		Far-northern	Northern	South-eastern	Western	Elizabeth	Overall
Endemic species							
<i>Euclidaris galapagensis</i> (Valenciennes)	E	54.5 ⁻¹	264.4	392.9	252.7	280.0	316.8
<i>Octopus oculifer</i> Hoyle	M	0	0.02	0.07	0.22	0.18	0.09
<i>Scyllarides astori</i> Holthuis	C	0	0	0.06	0.44	0	0.09
Panamic species							
<i>Tripneustes depressus</i> (Agassiz)	E	0.65 ⁻³	45.2	49.1 ¹	29.2	2.40 ⁻²	37.6
<i>Echinometra vanbrunti</i> (Agassiz)	E	0 ⁻⁸	0.66 ⁻⁶	0.79 ⁻⁴	63.2 ⁴	230.2 ³	30.2
<i>Diadema mexicanum</i> (Agassiz)	E	65.4 ¹	2.98 ⁻³	5.65 ⁻³	2.67 ⁻³	0.70 ⁻⁴	8.88
<i>Toxopneustes roseus</i> (Agassiz)	E	0.07	0.24	0.28	0	0	0.19
<i>Aniculus elegans</i> Stimpson	C	0	0.18	0.27	0	0	0.17
<i>Holothuria difficilis</i> Semper	H	0	0	0	0.16	0.09	0.03
<i>Holothuria imitans</i> (Ludwig)	H	0	0	0.01	0	0	0.01
<i>Trizopagurus magnificus</i> (Bouvier)	C	0	0.01	0.01	0	0	0.01
<i>Holothuria impatiens</i> (Forsk.)	H	0.02	0	0	0	0	0
<i>Luidia foliata</i>	A	0	0	0	0	0.04	0
Indo-Pacific species							
<i>Holothuria kefersteini</i> (Selenka)	H	1.22	2.95	3.87 ⁴	0.68 ⁻⁴	2.75	2.96
<i>Holothuria atra</i> (Jaeger)	H	0.23 ⁻⁷	3.09 ¹	2.34 ⁵	0.02 ⁻⁵	0.03 ⁻⁵	1.75
<i>Stichopus horrens</i> Selenka	H	0.3	0.08	0.72	0.02	0.03	0.43
<i>Holothuria fuscocinerea</i> (Jaeger)	H	0.14	0.80 ²	0.38	0	0	0.34
<i>Mithrodia bradleyi</i> Verrill	A	0	0.05	0.26	0	0	0.15
<i>Asteropsis carinifera</i> (Lamarck)	A	0.02	0.14	0.07	0	0.02	0.06
<i>Panulirus penicillatus</i> (Olivier)	C	0.55	0.01	0.02	0	0	0.06
Widespread species							
<i>Lytechinus semituberculatus</i> (Agassiz)	E	0 ⁻²	40.7 ⁻¹	103.6	369.3 ¹	44.3 ⁻¹	120.6
<i>Stichopus fuscus</i> (Ludwig)	H	0.19 ⁻⁴	0.96 ⁻²	1.46 ⁻¹	30.4 ²	32.5 ¹	8.33
<i>Hexaplex princeps</i> (Broderip)	M	6.45	7.82	9.56 ²	5.91 ⁻¹	3.32 ⁻³	7.96
<i>Pentacaster cumingi</i> (Gray)	A	0 ⁻⁶	4.27	4.83 ³	1.04 ⁻²	3.71	3.71
<i>Nidorellia armata</i> (Gray)	A	0 ⁻⁵	0.43 ⁻⁴	1.61 ⁻²	11.2 ³	11.5 ²	3.60
<i>Centrostephanus coronatus</i> (Verrill)	E	0 ⁻⁹	1.25 ⁻⁵	0.46 ⁻⁵	9.35 ⁵	15.3 ⁵	3.18
<i>Phataria unifascialis</i> (Gray)	A	0	0.08 ⁻⁷	0.21 ⁻⁶	2.21 ⁶	1.71 ⁴	0.61
<i>Pharia pyramidata</i> (Gray)	A	0	0.02	0.05	0.66 ⁷	1.74 ⁶	0.28
<i>Linckia columbiae</i> Gray	A	0.02	0	0.03	1.41	0.40	0.26
<i>Percnon gibbesi</i> (H. Milne Edwards)	C	2.19 ²	0.10	0	0.01	0	0.18
<i>Plouroploca princeps</i> Sowerby	M	0	0.02	0.05	0.07	0.10	0.05

(a)

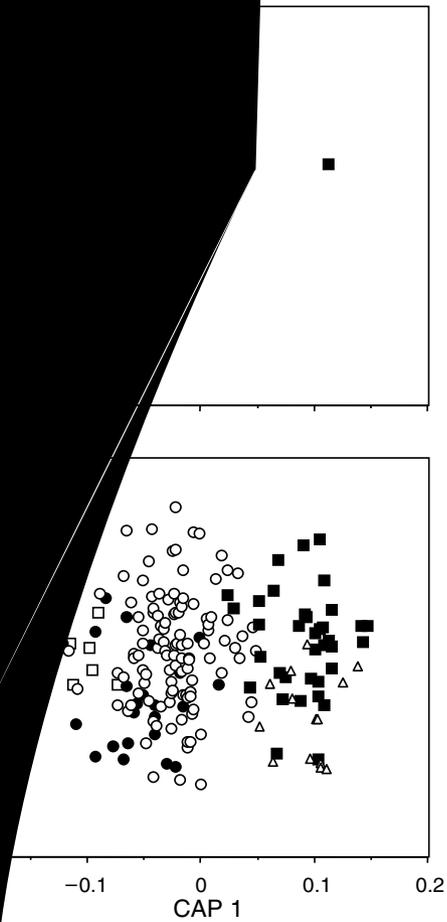
(b)

Figure 12 Results of CAP analysis maximizing differences in fish data between five bioregions, showing distribution of $0.01^\circ \times 0.01^\circ$ grid cells with CAP axes 1 and 2 (a) and axes 1 and 3 (b). Correlations of species abundance with the three CAP axes are also shown for species with $r > 0.4$ (c, d). Species showing high correlations with both CAP axes 2 and 3 are depicted on the graph showing strongest correlation.

Implications for conservation management

Governments worldwide are increasingly recognizing that conservation of marine biodiversity requires *inter alia* a network of wildlife refuges such as marine protected areas (MPAs) that are distributed across all biogeographical regions within their jurisdiction (Australian and New Zealand Environment and Conservation Council Task Force on Marine Protected Areas, 1999; Roff & Taylor, 2000; Roff & Evans,

in the estuarine faunal zonalizations used for management targets. It is shown to be important to understand the ecological processes that maintain the zonalizations. The most heavily



data
to five
leave-
analysis of

Region	Far-northern	Northern	South-eastern	Western	Elizabeth	Total	Correct (%)
Far-northern	5	1	0	0	0	6	0.83
Northern	0	15	8	0	0	23	0.65
South-eastern	1	28	77	4	2	112	0.69
Western	0	0	1	26	9	36	0.72
Elizabeth	0	0	0	3	11	14	0.79

captured by divers provided > 80% of the total
income of fishers over the past 5 years (Murillo,
2012).

Conservation of marine biodiversity in Galapagos would be
assisted by a change in the GMR Management Plan from
recognition of the Harris biogeographical regions to the five

Table 5 Area (km²) included in different management zones for the five biogeographical regions defined in this study

Biogeographical region	Management zone, km ² (%)			
	Conservation	Tourism	Fishing	Total
Far-northern	0.78 (4.6)	3.78 (22.2)	12.46 (73.2)	17.02
Northern	6.23 (5.5)	18.25 (16.0)	89.46 (78.5)	113.94
South-eastern	68.88 (7.7)	98.92 (11.0)	731.49 (81.3)	899.29
Western	36.61 (11.2)	26.37 (8.1)	262.93 (80.7)	325.91
Elizabeth	7.68 (4.8)	16.80 (10.6)	134.64 (84.6)	159.12
Total	120.17	164.12	1230.98	1515.27

biogeographical regions outlined here. During consensual discussions in 2000, stakeholders of the GMR agreed on preliminary 'no-take' conservation zones to protect coastal ecosystems within each of the five Harris zones; however, disproportionately low levels of protection have consequently been afforded to the small distinctive ecosystems in the far-northern and Elizabeth bioregions.

The far-northern region has very high conservation significance due to its distinctive biota with anomalously high species richness of fishes and corals. The area reserved for conservation purposes within this bioregion is very small (0.78 km², Table 5), in part because the bioregion itself is so small, comprising two islands only.

The Elizabeth bioregion includes the smallest percentage of coast zoned for conservation amongst the five Galapagos biogeographical regions described here (Table 5), with only a single small area around Islas Marielas fully protected. A notable feature of this bioregion is a disproportionately high number of endemic Galapagos species, making it the core area for much of the endemic Galapagos inshore marine fauna and possibly an important refuge for local Galapagos species during periods of adverse environmental conditions such as El Niño. Thus, despite its low overall species richness, the Elizabeth bioregion should be considered an area with exceptional conservation significance.

The inverse relationship evident at regional scales in Galapagos between the richness of the total fish fauna and the richness of endemic fish species has broad management implications. In the terrestrial environment, several authors have suggested that conservation areas should be prioritized spatially in terms of 'hotspots' of biodiversity (Meyers *et al.*, 2000). Roberts *et al.* (2002) extended this concept to the marine realm, arguing that centres of marine endemism in the Pacific are congruent with hotspots of species richness (but for alternate view see Hughes *et al.*, 2002). A hotspot strategy for Galapagos, in the absence of gap analysis, would indicate a low conservation rating for western Galapagos and Elizabeth ecosystems, whereas on a global scale these areas possess highest conservation significance. The western upwelling region provides core habitat for virtually all endemic Galapagos marine taxa, including many charismatic species not included in the present study, such as the flightless cormorant

(Valle, 1995), Galapagos penguin (Boersma, 1998) and Galapagos fur seal (Trillmich & Limberger, 1985).

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BIOSKETCHES

Graham Edgar recently returned to Tasmania after 2 years as Head of Marine Science at the Charles Darwin Research Station, Galapagos. He has investigated a variety of ecological interactions in the marine environment, primarily those involving human impacts.

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