

Spatial patterns of distribution and relative abundance of coastal shark species in the Galapagos Marine Reserve

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ABSTRACT: A better understanding of the patterns of distribution and abundance of sharks and their potential biological and environmental drivers is essential to develop and evaluate spatial management plans for conservation and fisheries. Benthic and pelagic baited remote underwater stereo-video systems (stereo-BRUVs) were used to describe spatial and temporal patterns in coastal shark assemblages in the Galapagos Marine Reserve (GMR). From 629 stereo-BRUV deployments, 877 sharks from 10 species were recorded. Shark assemblages displayed high spatial variation, likely in response to the diversity of habitats occurring in the GMR. The relative importance of environmental and biological drivers differed among shark species according to their mobility. Some species were widespread across the Galapagos Archipelago (GA) but occurred primarily only as either juveniles (*Carcharhinus galapagensis*) or adults (*C. limbatus* and *Triaenodon obesus*), while others were more spatially restricted and associated with geographical features (*Sphyrna lewini* and *Galeocerdo cuvier*) or specific habitats (Triakidae spp. and *Heterodontus quoyi*). The highest diversity of sharks was found in the Centre South bioregion of the GA, in areas with heterogeneous habitat and high overall fish diversity (islets and Floreana Island), while the greatest total abundance of sharks was recorded at the northern oceanic islands of Darwin and Wolf. Overall, the GMR harbours a unique coastal shark community that varies in composition across the GA. It is dominated by large semipelagic species but is also characterised by the presence of less mobile benthic species that are not found near other oceanic islands in the Eastern Tropical Pacific region.

KEY WORDS: Shark conservation · Baited remote underwater video · BRUV · Marine protected areas · Environmental drivers · Shark-habitat selection · Elasmobranchs

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INTRODUCTION

Shark numbers are declining globally (Dulvy et al. 2014), mainly as a result of fishing and coastal habitat degradation (Jennings et al. 2008, Davidson et al. 2016). As sharks are widely distributed top predators in the ocean (Ferretti et al. 2010), these significant declines have induced complex changes in marine com-

munities resulting in socio-economic and ecological consequences (Heithaus et al. 2008, Ferretti et al. 2010). Currently, an increasing global demand for tourism based on shark encounters presents a clear incentive for active shark conservation and management (Gallagher & Hammerschlag 2011).

Coastal areas worldwide provide a wide range of habitats that are used by a variety of shark species,

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with greater representation of the families Carcharhinidae and Sphyrnidae in the tropics and Triakidae in temperate environments (Compagno 1984). Two general theoretical models describe the spatial distributions of coastal shark populations (Knip et al. 2010). Under the first model, young sharks are born and remain in shallow coastal habitats (nursery grounds) until they reach sexual maturity. They subsequently join other adult individuals in offshore environments when they reach maturity (Springer 1967). Large, highly mobile Carcharhinidae and Sphyrnidae species, such as *Galeocerdo cuvier* and *Sphyrna lewini*, seem to fit this general model, first inhabiting coastal nursery grounds, then switching to movements between nearshore and open-water areas (Klimley 1987, Lea et al. 2015). Under the second model, sharks remain in coastal environments for their entire life span, with juvenile and adult individuals sharing habitats or showing a variable degree of habitat specificity (Knip et al. 2010). These behaviours are often associated with smaller shark species. Exceptions and variations to these 2 general models occur, with some shark species even exhibiting opposing strategies in different areas of their ranges (Knip et al. 2010).

Few studies have described patterns of distribution and abundance of coastal sharks at local and regional scales. Factors affecting the occurrence and distribution of sharks are not well understood (Simpfendorfer et al. 2011, Espinoza et al. 2014). In the Great Barrier Reef Marine Park (Australia), reef sharks have species-specific preferences for particular habitats, with their spatio-temporal movements being more strongly associated with biological factors (such as prey density, competition, reproduction and dispersal) than with broader environmental patterns (Chin et al. 2012, Heupel & Simpfendorfer 2014). Spatial patterns in semipelagic sharks (following nomenclature from Camhi et al. 2009) are complex to study, as these animals are highly mobile, potentially occurring across a broad spatial extent and making occasional or seasonal long-distance migrations. They can also occupy a variety of habitats and are often segregated by gender and/or size (Klimley 1987, Simpfendorfer 2005).

Marine protected areas (MPAs) can play a crucial role in the conservation of coastal shark populations by protecting critical habitats for reproduction and foraging (Knip et al. 2012, White et al. 2017). Research and conservation efforts have focussed on inshore nursery areas used by neonate and juvenile sharks (Heupel & Simpfendorfer 2005), although all life-history stages should be considered (Kinney & Simpfen-

dorfer 2009). The particular characteristics of the environment, as well as prey availability and the presence or absence of competing species, can exert some influence on the local distributions and habitat uses of shark species in particular areas (Knip et al. 2010). Variations in behaviour and habitat requirements among different age classes, gender and/or species of sharks also have management implications (Espinoza et al. 2014). Thus, it is necessary to document the patterns of distribution and abundance of shark populations in response to both local environmental factors and potential biological drivers, such as the richness, composition and abundance of other fishes or macrofaunal species. Only then can critical habitats for all life stages of sharks be identified or predicted by models that can inform the design or evaluation of effective spatial management for shark conservation (Simpfendorfer et al. 2011, Knip et al. 2012).

The Galapagos Marine Reserve (GMR) is one of the largest MPAs in the world (138 000 km²) and is a biodiversity hotspot of global significance (Heylings et al. 2002). The GMR is also one of the last remaining places where abundant populations of large sharks can still be found (Zárate 2002, Hearn et al. 2014). Indeed, the highest biomass of sharks in the world was recently recorded at its oceanic islands of Darwin and Wolf (Salinas-de-León et al. 2016). The geographical and seasonal variability in the oceanographic conditions in the Galapagos Archipelago (GA) provides a wide range of coastal habitats, from tropical to temperate reefs, supporting a diverse group of sharks (at least 33 species from 10 families; Hearn et al. 2014). The GMR has afforded full legal protection to all sharks since 1989 (Zárate 2002). Yet, observations of the most common species have declined in the GMR (Baum et al. 2007), potentially due to illegal fishing inside the reserve and/or high fishing pressure during long-distance migrations beyond reserve boundaries (Jacquet et al. 2008, Carr et al. 2013).

The present study investigated patterns of distribution and abundance of sharks in the coastal waters of the GMR using benthic and pelagic baited remote underwater stereo-video systems (stereo-BRUVs). Specifically, we aimed to test the following hypotheses: (1) the composition of shark assemblages will vary spatially and temporally across the GA; (2) individual species of sharks will show different levels of association (co-occurrence) with one another; (3) individual species of sharks will differ in their occurrence and relative abundances at different sites and regions across the GA; (4) individual species of shark will be influenced differentially by a variety of potential environmental and biological predictor variables,

a

Costa Rica

Cocos Island National Park

Malpelo Flora and Fauna Sanctuary

Colombia

Ecuador

Galapagos Marine Reserve

0 250 500 Kms

b

Far North

D_W

North

Marchena

M_G

IS_NW

IS_NE

FE_W

C_BLV

Cold West

Isabela

IS_SW

IS_SE

Santiago

SA_N

SA_S

SX_N

SX_E

SX_W

SX_S

Santa Cruz

Center South

FL

Floreana

S_REEF

San Cristóbal

SC_N

SC_S

ESP

0 15 30 Kms

Legend:

- Sphyrna lewini*
- Carcharhinus galapagensis*
- Carcharhinus limbatus*
- Galeocerdo cuvier*
- Triakonodon obesus*
- Triakis maculata*
- Mustelus alpinus*
- Heterodontus quoyi*

Scale: 4, 1, 0.5, 0.1, 0.05

Most of the GA sits over a relatively shallow platform that drops dramatically towards the west and southwest, reaching depths of 3000 m only 10 km from the coastline in certain areas (Banks 2002). The Centre South bioregion covers the largest proportion of this insular platform, all except its western side, which is located in the Cold West bioregion (Fig. 1b). Towards the northeast, this insular shelf fuses with the Coco and Carnegie ridges, with a more gradual

Study site

The Galapagos Islands comprise 13 major islands and over 100 islets situated approximately 1000 km west of continental Ecuador, in the Eastern Tropical Pacific region (Snell et al. 1996; Fig. 1a). The GA is

bathymetric gradient from where the islands of Pinta, Marchena and Genovesa arise, forming the North bioregion (Fig. 1b). The Far North bioregion is at the northern tip of the GA and is comprised of the emergent tops of 2 eroded volcanoes, the oceanic islands of Darwin and Wolf (Fig. 1b).

Variation in the strength of major oceanic currents converging at the GA yields 2 main seasons: a warm season, from January to June, when the Panama Current prevails and the EF moves south; and a cool season, from July to December, when the Humboldt Current increases in intensity and the EF moves north and settles just north of the GA (Palacios 2004). In addition, periodical climatic disturbances, such as El Niño Southern Oscillations (ENSO), significantly affect the marine communities of the GA (Chavez et al. 1999).

Stereo-BRUVS

Stereo-BRUVs are a non-destructive tool able to quantify the spatio-temporal patterns in relative abundances of fishes (Cappo et al. 2003). BRUVs are increasingly being used to sample shark populations, as they are especially adept at detecting piscivorous predators (Santana-Garcon et al. 2014a, Jaiteh et al. 2016).

Stereo-BRUVs were used to estimate diversity, relative abundance and size and gender distributions of shark species. The systems consisted of 2 GoPro HERO4 Black edition high-definition digital cameras mounted 0.7 m apart and converging inwards at 6° onto a stainless steel frame, baited with ca. 800 g of yellow-fin tuna *Thunnus albacares*. Stereo-BRUVs were deployed at each of 2 depths: benthic (depth ca. 25 m) or pelagic (depth ca. 10 m), as described by Cappo et al. (2001) and Santana-Garcon et al. (2014b), respectively.

We conducted a pilot study in November and December 2014 to assess the appropriate number of replicates and length of time for the deployment of stereo-BRUVs to achieve reasonable precision, using pseudo multivariate dissimilarity-based standard error (MultSE), as proposed by Anderson & Santana-Garcon (2015). A minimum of 4 replicates, each with a deployment time of 90 min, was deemed appropriate (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m593p073_supp.pdf). During the pilot study, we found that conventional benthic BRUVs (those with the camera frame settled on the seabed; Cappo et al. 2001) were frequently entangled or dismantled by large sharks biting the bait, which was often removed when using conventional wire mesh

baskets. Thus, the design of the camera sets was altered. First, the bait was contained in a rigid PVC pipe with multiple holes and wire mesh at both ends to allow dispersion of the bait plume. Second, benthic samples used the same setting as pelagic stereo-BRUVs (i.e. a floating camera frame) but cameras were close to the bottom, at ca. 1 m over the seabed (Fig. S2 in the Supplement). These design changes proved to be effective (no entanglements and only 0.8% rate of bait loss).

Both benthic and pelagic stereo-BRUV systems were deployed at 25 m depth, with pelagic sets designed to remain at mid-water at ca. 10 m depth, approximately 15 m above the seabed. The 4 replicates of each type of set were separated by a minimum distance of 500 m to minimise overlap, following Santana-Garcon et al. (2014a). The benthic and pelagic settings were spatially alternated during deployment at each site. Deployments were done during daylight hours, but never within 1 h of sunrise or sunset. Stereo-BRUVs were deployed for minimum bottom time of 100 min, which allowed us to discard the first and last 5 min of footage to minimise potential disturbance to the animals by the boat.

Data collection/video analysis

Date, time, location (latitude and longitude), depth and sea surface temperature (SST, °C) were recorded *in situ* for each deployment. Monthly daytime chlorophyll *a* (chl *a*, mg m⁻³) was obtained from remote-sensing data at a 4 km spatial resolution (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua>). We used the minimum distance from the deployment point to the 1000 m isobaths, obtained from ArcGIS 10.1 software (ESRI) as a proxy for the insular shelf boundaries. The mean fetch of each deployment (i.e. average distance to land in all directions) was calculated using the R package 'waver' (Marchand & Gill 2017) and was used as a surrogate for exposure (following Smith et al. 2013). The distance to the insular shelf boundaries and the degree of exposure can indicate the level of access by sharks to open and/or deeper waters (including potential pelagic prey). Fine-scale habitat was characterised visually during the video analysis for each benthic stereo-BRUV deployment by estimating the seabed composition as the percentage cover of rock vs. sand and assigning an ordinal value from 0 to 3 for each seabed type (i.e. corals, macroalgae, rubble) and slope aspect (Table 1). Our modified stereo-BRUV benthic setting with the floating camera resulted in a field of view that was not

Table 1. Environmental and biological predictor variables included in models of shark relative abundances, using distance-based redundancy analysis (DISTLM, dbRDA) and boosted regression trees (BRTs). BRUV: baited remote underwater video

| Habitat characterisation | Predictor | Type | Range | Mean \pm SD |
|--|--|-------------|---|---------------------|
| Geographic | Distance to 1000 m isobath (m) | Continuous | 316–66 990 | 18 906 \pm 15 653 |
| | Mean fetch (m) | Continuous | 9095–48 323 | 23 552 \pm 7198 |
| Sea surface temperature | SST ($^{\circ}$ C) | Continuous | 18.50–29.90 | 24.91 \pm 2.62 |
| Productivity (chlorophyll a) | Chlo_a (mg m^{-3}) | Continuous | 0.16–1.72 | 0.58 \pm 0.33 |
| Fish and macrofauna assemblages (excluding sharks) | S (species richness) ^a | Continuous | 0–29 | 9.73 \pm 7.83 |
| | Log (N+1) (species abundance) ^a | Continuous | 0–3.05 | 1.99 \pm 2.05 |
| | Gini-Simpson (species evenness) ^a | Continuous | 0–0.94 | 0.48 \pm 0.29 |
| | Fish assemblage groupings (k-R clustering) | Categorical | 3 groups (benthic) and 9 groups (full assemblage) | |
| Benthic habitat (only for benthic stereo-BRUVs) | Bottom inclination | Ordinal | 1 = 0–33 $^{\circ}$; 2 = 33–66 $^{\circ}$; 3 = 66–90 $^{\circ}$ | 1.48 \pm 0.63 |
| | Rock_cover (%) | Ordinal | 0–100 | 60.28 \pm 37.42 |
| | Sand_cover (%) | Ordinal | 1–100 | 39.72 \pm 37.42 |
| | Ahermatypic coral_cover | Ordinal | 0 = nothing; 1 = low; | 0.87 \pm 1.09 |
| | Hermatypic coral_cover | Ordinal | 2 = medium; 3 = high | 0.04 \pm 0.22 |
| | Macroalgae_cover | Ordinal | | 0.89 \pm 1.10 |
| | Rubble_cover | Ordinal | | 0.13 \pm 0.59 |

^aBy 90 min deployment

fixed. Thus, the fine-scale habitat characterisation was conducted using the entire 90 min of video footage for each deployment. Rotation of the camera often allowed for a complete view (360 $^{\circ}$) of the surrounding benthic habitat.

The software EventMeasure (SeaGIS) was used to analyse the 90 min video footage. All fish (except species with maximum total length [TL] <10 cm) and macrofaunal species (reptiles and mammals) were identified to the lowest taxonomic level possible and quantified, using the MaxN index of relative abundance; i.e. the maximum number of individuals of a particular species observed in 1 still video frame, as described by Cappo et al. (2004).

For sharks, measurements of fork length (FL, averaged across 3 measurements of the same individual in different video frames) allowed classification of each individual as either adult or juvenile, using the smallest size of the published range of lengths for sexual maturity for each shark species for demarcation (Froese & Pauly 2015). Individuals that could not be measured were classified as maturity-indeterminate. In the case of the whitemargin smoothhound *Mustelus albigipinnis* and the spotted houndshark *Triakis maculata*, no published sizes for sexual maturity were available, so these were allocated using relevant information from similar species within their respective genus. Finally, the Galapagos bullhead shark *Heterodontus quoyi* does not have a published size at maturity, nor do any other species recorded within its family. All individuals of this species were categorised as maturity-indeterminate.

Gender in sharks was determined based on the presence/absence of claspers in those individuals categorised as adults that provided a clear and close view of their ventral area. Sharks were categorised as male, female or juvenile. Those individuals that could not be sexed were categorised as gender-indeterminate.

To measure relative abundances of coastal sharks from video footage, we modified the approach described by Cappo et al. (2004). First, we recorded the maximum number of individual sharks per species observed in a single still video frame throughout the 90 min deployment (i.e. MaxN; Cappo et al. 2004). Next, we added to this value per species any other individual shark that was uniquely and clearly distinguishable within the deployment and that was not already included in the MaxN calculation. We termed this value a corrected MaxN (cMaxN). Individual sharks could be identified using a combination of several criteria, including: (1) the presence/absence of claspers in adult individuals, (2) unique scars or markings (e.g. dot patterns in *Triaenodon obesus* and *Triakis maculata*); and (3) the total body length (taken as an average of 3 measurements, each from a different video frame) when this differed by more than 50% between individuals.

MaxN was also recorded for a total of 154 fish and marine macrofauna species, excluding sharks, from each stereo-BRUV deployment to study the potential influence of assemblages of other fishes and marine macrofauna on the patterns of distribution and abundance of sharks. We calculated 3 complementary

measures of diversity: namely, log-relative abundance (measured as $\log(\text{MaxN}+1)$), species richness (number of unique species observed during each 90 min deployment), and Gini-Simpson's evenness index (Jost 2006), as potential predictor variables. We also identified groups of samples having similar fish and marine macrofaunal assemblages on the basis of a k -R cluster analysis applied to the Bray-Curtis dissimilarity measure of fourth-root-transformed abundance values (Clarke et al. 2016). We generated results for each of $k = 2$ –10 groupings, then selected the grouping which minimised the multivariate analogue to the small-sample-size-corrected Akaike's information criterion (AICc; Burnham & Anderson 2004, Anderson et al. 2008). This was done on fish and marine macrofaunal assemblages for the full dataset (pelagic + benthic sets combined), as well as for only the benthic stereo-BRUV sets.

Sampling design

Sampling was done following a spatially stratified random design. The perimeter of geographic features (islands, islets and submerged reefs) was re-defined using 20 m isobaths, as stereo-BRUVs were to be deployed at approximately this depth. Single land units larger than 5000 m in perimeter were classed as islands, while groups of nearby islets (i.e. within a range of 4 km from the centre of the group) were pooled together as a single geographic feature and classed as islets. In the case of submerged reefs, only those shallower than 20 m depth were included and classed as submerged reefs. All islets and submerged reefs smaller than 5000 m in perimeter were excluded from the sampling, as they were too small to provide enough independent spatial replication for comparative purposes across geographical strata and sites.

The 20 m depth contour around the full set of features defined above was then divided into 19 geographic strata based on bioregion, orientation, bathymetric gradient (proximity to the 1000 m isobaths) and exposure to the predominant southeasterly currents (Banks 2002). Within each stratum, a set of candidate sites separated by 4 km (the necessary length to deploy 8 units of stereo-BRUVs, i.e. 4 benthic and 4 pelagic, keeping a distance of 500 m between them) was defined by placing a systematic sample of points along the 20 m depth contour of each island. Two sites were then selected randomly from the set of available sites within each stratum, with the exception of the larger stratum at the islands of Pinta,

Marchena and Genovesa (stratum 'M_G' in Fig. 1b), in the North bioregion, where 5 sites were randomly selected to obtain adequate representation. In addition to the randomly selected sites, a total of 9 hot-spots, where the abundance and species richness of sharks was known *a priori* to be potentially high, were also included. In those strata where there was a pre-selected hotspot, only 1 additional site was chosen randomly. The 4 islets and 2 submerged reef sites identified by us were included in the sampling, yielding 2 additional geographic strata (Islets [ISL] and Submerged Reef [S_REEF]), as these habitats are traditionally recognised as areas of high relative abundance of sharks in the Galapagos Islands. The resulting 48 study sites (Fig. 1b) were surveyed using both types of stereo-BRUV settings during each of 2 survey campaigns: one in the warm season (March and April) and another in the cold season (August and September).

In summary, the full sampling design had 5 factors: bioregion (4 levels, fixed), geographic stratum (21 levels, fixed, nested in bioregion), site (48 levels, random, nested in geographic stratum), position in the water column (benthic vs. pelagic, B vs. P; 2 levels, fixed, crossed with all other factors) and season (2 levels, fixed, crossed with all other factors). There were $n = 4$ replicates of each stereo-BRUV position per site, resulting in a total of 752 planned individual deployments.

Data analysis

Spatial variation in the structure of shark assemblages at each spatial scale (bioregions, strata and sites) across the GA was quantified using distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). This analysis was based on a matrix of pairwise 0-adjusted Bray-Curtis similarities (Bray & Curtis 1957, Clarke et al. 2006) of square-root-transformed relative abundances of 10 shark species (cMaxN) on the site averages obtained separately for each position in the water column (i.e. benthic vs. pelagic). Tests of all terms in the full PERMANOVA model were done using Type III SS, and p-values were obtained using 9999 permutations under a reduced model (Freedman & Lane 1983). Statistically significant ($p < 0.05$) interactions were further explored with appropriate post hoc pairwise tests. Patterns of similarities among shark assemblages by stratum and bioregion were visualised using non-metric multidimensional scaling (NMDS) ordination (Kruskal & Wish 1978) of the

Table 2. Summary of shark sightings, abundance and mean size recorded by the stereo-BRUVs at the Galapagos Marine Reserve. cMaxN: corrected MaxN, i.e. maximum number of sharks observed in one still video frame (MaxN) incremented by any other additional uniquely identifiable individuals seen in other frames during the entire 90 min deployment. UN: refers to individuals that could not be identified at the species level

| Family (semipelagic/ benthic) | Species | Total no. indiv. | % total sharks | Highest cMaxN | cMaxN per deployment (mean \pm SD) | | | Fork length, cm (mean \pm SD) |
|-------------------------------------|----------------------------------|---------------------|-------------------|------------------|--------------------------------------|-----------------|-----------------|---------------------------------------|
| Carcharhinidae | | 585 | 66.70 | | | | | |
| Semipelagic | <i>Carcharhinus galapagensis</i> | 334 | 38.08 | 8 | 0.52 \pm 1.13 | 0.76 \pm 1.30 | 0.26 \pm 0.85 | 116.98 \pm 50.43 |
| | <i>Carcharhinus limbatus</i> | 117 | 13.34 | 3 | 0.18 \pm 0.43 | 0.17 \pm 0.41 | 0.19 \pm 0.46 | 156.19 \pm 35.93 |
| | <i>Carcharhinus altimus</i> | 6 | 0.68 | 3 | 0.01 \pm 0.14 | 0.01 \pm 0.16 | 0.01 \pm 0.10 | 173.95 \pm 38.65 |
| | <i>Carcharhinus falciformis</i> | 6 | 0.68 | 2 | 0.01 \pm 0.11 | < 0.01 | 0.16 \pm 0.02 | 142.40 \pm 32.54 |
| | <i>Galeocerdo cuvier</i> | 42 | 4.79 | 6 | 0.07 \pm 0.36 | 0.09 \pm 0.42 | 0.04 \pm 0.26 | 202.72 \pm 71.96 |
| Benthic | <i>Triaenodon obesus</i> | 72 | 8.21 | 4 | 0.11 \pm 0.44 | 0.21 \pm 0.59 | 0.01 \pm 0.10 | 114.54 \pm 16.84 |
| | Carcharhinidae UN | 8 | 0.91 | | – | – | – | – |
| Sphyrnidae | | 207 | 23.60 | | | | | |
| Semipelagic | <i>Sphyrna lewini</i> | 207 | 23.60 | 24 | 0.32 \pm 1.69 | 0.36 \pm 1.76 | 0.29 \pm 1.62 | 160.35 \pm 44.96 |
| Triakidae | | 61 | 6.96 | | | | | |
| Benthic | <i>Mustelus albipinnis</i> | 24 | 2.74 | 3 | 0.04 \pm 0.24 | 0.07 \pm 0.33 | 0 | 101.23 \pm 30.34 |
| | <i>Triakis maculata</i> | 36 | 4.10 | 5 | 0.06 \pm 0.38 | 0.12 \pm 0.51 | 0 | 124.73 \pm 17.36 |
| | Triakidae UN | 1 | 0.11 | | – | – | – | – |
| Heterodontidae | | 24 | 2.74 | | | | | |
| Benthic | <i>Heterodontus quoyi</i> | 24 | 2.74 | 3 | 0.04 \pm 0.23 | 0.07 \pm 0.31 | 0 | 48.06 \pm 7.46 |

stratum-by-position-in-the-water-column centroids. In addition, spatial associations between shark species were visualised using NMDS ordination based on the index of association (Somerfield & Clarke 2013) calculated between each pair of shark species after relative abundances (cMaxN) were square-root-transformed and averaged by site and position in the water column (benthic vs. pelagic). Maps showing the distribution and relative abundances of individual shark species, and also the size and gender categories of common shark species, were produced using segmented bubble plots of proportional relative abundance per stratum (Purcell et al. 2014).

We examined the relationship between shark assemblages and the full set of measured environmental and biological predictor variables (Table 1) using distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999, McArdle & Anderson 2001). Analyses were conducted for data obtained from both the benthic and the pelagic stereo-BRUVs combined, and were also done separately for each of the semipelagic and benthic sub-sets of data (Table 2). We used the distance-based multivariate analogue to AICc (Burnham & Anderson 2004, Anderson et al. 2008) to select an appropriate parsimonious model in each case.

All multivariate analyses and bubble plots for distribution maps were done using PRIMER 7 (Clarke & Gorley 2015) with the add-on package PERM-

ANOVA+ (Anderson et al. 2008). We tested the null hypothesis that the proportions of different species of sharks and the proportions of adults vs. juveniles observed did not differ for benthic vs. pelagic stereo-BRUVs using chi-squared tests. We tested the null hypothesis that either species richness or total abundances of sharks did not differ for benthic vs. pelagic stereo-BRUVs using Mann-Whitney tests.

To identify the most influential environmental and biological drivers (Table 1) of the log-abundance, species richness and occurrence (for individual species and individual size categories) of sharks, we constructed predictive univariate models using boosted regression trees (BRTs; implemented using the R package 'dismo'; Hijmans et al. 2017). This allowed us to examine potential inter-specific and ontogenic differences in habitat use by coastal shark species. Partial dependence plots were produced to illustrate salient patterns and relationships and to identify the most important predictor variables in each case (following Elith et al. 2008). Prediction performance was evaluated using cross-validation (estimated deviance explained for withheld data) in the case of models for continuous distributions (shark abundance and diversity) and the area under the receiver operating characteristic curve (AUC) in models for binary response variables (occurrence of each shark species or size category), following Hosmer & Lemeshow (2000). BRT models with AUC scores below 0.7 were

deemed to have poor predictive performance and were thus discarded.

The potential effects of the community structure of other fishes and macrofauna on the total log-abundance and richness of sharks was examined using canonical analysis of principal coordinates (CAP; Anderson & Willis 2003). More specifically, we first constructed a Bray-Curtis similarity matrix from fourth-root-transformed relative abundances (MaxN) of fishes and marine macrofauna (excluding sharks). This matrix was then related directly to 2 variables calculated from the shark species in a canonical correlation-type of analysis in CAP: namely, richness (S = the total number of shark species) and log-abundance ($\log(N+1)$) of sharks (where N = the total value of cMaxN summed across all shark species). An appropriate number (m) of PCO (Principal Coordinates analysis) axes to use for the CAP analysis was chosen as the value of m that minimised the leave-one-out residual sum of squares (Anderson et al. 2008). A vector overlay on the resulting CAP ordination plot was then used to identify individual non-shark species having strong associations with shark richness and/or abundance. This allowed us to explore potential associations between total richness or abundance of all sharks and non-shark species.

RESULTS

Sampling and summary details

From a total of 629 stereo-BRUV deployments, we sampled 45 sites (330 deployments: 178 benthic and 152 pelagic) during the warm season (March and April 2015); 3 sites were not surveyed due to time/weather constraints. During the cool season (July to September), we surveyed 40 sites with 299 deployments (156 benthic and 143 pelagic); 8 sites were not sampled due to adverse sea conditions.

A total of 62 955 records (59.94% from benthic, 40.06% from pelagic stereo-BRUVs) were obtained from video analysis of all deployments, comprising 164 species of bony fishes (97.10%), elasmobranchs (2.10%), sea reptiles (0.63%) and sea mammals (0.14%) belonging to 4 different classes and 53 families.

We recorded 10 shark species from 4 families, consisting of 877 individual sharks (1.39% of all records; Fig. 2, Table 2). FL measurements, and therefore size categorisation, could be done on 68.19% of these individuals, and gender could be determined for 56.91% of the sharks categorised as

adults. The number of sharks recorded per deployment varied between 0 and 26 (1.37 ± 2.40 , mean \pm SD), and species richness varied between 0 and 4 (0.79 ± 0.93), with at least 1 shark recorded in 53.42% of deployments (66.77% benthic, 38.31% pelagic). At the site level, the total number of individual sharks and shark species richness ranged from 0 to 107 (18.23 ± 18.78) and 0 to 6 (3.73 ± 1.55), respectively, with sharks recorded at all sites except one (MA3 at Marchena Island). The 2 sites located at Wolf and Darwin islands recorded the highest total numbers of sharks (107 and 54, respectively). However, they were not among the 9 sites that recorded the highest species richness. These sites were located at the islands of Floreana, Isabela and Santa Cruz, and the islets of Daphne (north of Santa Cruz Island). At the level of whole strata, the total number of sharks varied between 9 and 161 (41.67 ± 36.16), while species richness ranged from 3 to 8 (5.38 ± 1.40 ; Fig. 1b). The highest total numbers of sharks were recorded at Darwin and Wolf (D_W), the Islets (ISL) and Santa Cruz East (SX_E) strata, which together accounted for 40% of all records. While Darwin and Wolf (D_W) and Santa Cruz East (SX_E) were among the strata with the lowest species richness, Islets (ISL) harboured the richest shark assemblage, with 8 species, only equalled by the stratum at Floreana (FL; Fig. 1b).

Shark assemblage structure and inter-specific associations

The bioregion, stratum and site factors, together with the position in the water column (benthic vs. pelagic), all had significant effects on shark assemblage structure (Table 3). The Far North, North and Cold West bioregions were shown in the NMDS plot to have distinct assemblages, with strata within the Centre South bioregion showing high variability relative to other bioregions (Fig. 3). Differences between shark assemblages recorded by the benthic and pelagic stereo-BRUVs were apparent for the Centre South and Cold West bioregions (Table 3, pairwise tests). Benthic assemblages were generally more variable than pelagic assemblages (Fig. 3).

The 2 positions in the water column (benthic vs. pelagic stereo-BRUVs) recorded proportions of sharks that did not differ between juveniles vs. adults and males vs. females ($\chi^2_{[1]} = 0.179$, $p = 0.6717$ and $\chi^2_{[1]} = 0.10$, $p = 0.749$, respectively), but were significantly different for the different shark species ($\chi^2_{[1]} = 19.04$, $p < 0.001$). In addition, both the species



Fig. 2. Video frames showing the shark species recorded by stereo-BRUVs at the Galapagos Marine Reserve. (a) *Carcharhinus altimus*, (b) *C. falciformis*, (c) *C. galapagensis*, (d) *C. limbatus*, (e) *Galeocerdo cuvier*, (f) *Sphyrna lewini*, (g) *Triaenodon obesus*, (h) *Heterodontus quoyi*, (i) *Mustelus albipinnis*, (j) *Triakis maculata*

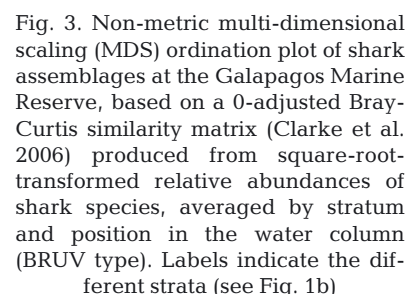
richness (1.87 ± 2.61 vs. 0.83 ± 2.01) and the average total number of sharks recorded (1.08 ± 1.01 vs. 0.47 ± 0.70) were significantly higher in benthic vs. pelagic stereo-BRUVs (Mann-Whitney $W = 68501$, $p < 0.001$ and $W = 68362$, $p < 0.001$,

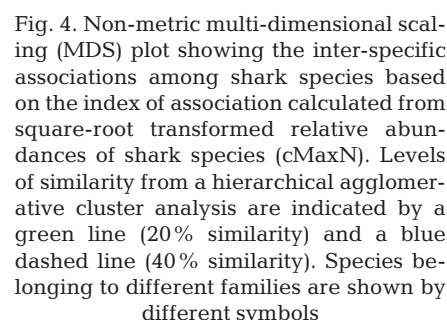
respectively). All shark species sighted in this study were recorded by benthic stereo-BRUVs, but 4 species were absent from pelagic stereo-BRUV footage. These 4 species were categorised as benthic sharks, and the other 6 as semipelagic sharks for subse-

Environmental and biological drivers

The 4 most common shark species (*Carcharhinus galapagensis*, *Sphyrna lewini*, *C. limbatus* and *Triaenodon obesus*, together accounting for 83% of shark records) showed the highest degree of interspecific spatial association (Fig. 4). Other species did not show any strong spatial associations, with the exception of the 2 Triakidae species, whose spatial occurrences were >20% similar (Fig. 4).

BRT models indicated that both the total relative abundance of sharks and shark species richness were well explained by similar sets of variables, although the percentage of deviance explained was much higher for species richness (33 vs. 92 %, respectively; Fig. 5 and see Table S2 in the Supplement). The strongest predictor of the total relative abundance and species richness of sharks was the species richness of the associated assemblage of non-shark species (approx. 30 % of predictive power), while the





BRTs were also used to predict the occurrence of each shark species, with the exception of *C. limbatus*, where the model was deemed to be poor ($AUC < 0.7$). For the remaining 3 semipelagic species (*C. galapagensis*, *Galeocerdo cuvier* and *S. lewini*), the distance

to the insular shelf (distance to the nearest 1000 m isobath) was the best predictor of occurrence, although the relationship was very different among the 3 species (Fig. 5). While sightings of *S. lewini* were more likely to occur at the border of the insular shelf (<2 km to 1000 m isobaths), *G. cuvier* showed an increasing probability of occurrence towards the interior shallow waters of the GA (>55 km to 1000 m isobaths); finally, *C. galapagensis* were more likely to occur at either of the extreme ends of this gradient (<2 km and >50 km distance to 1000 m isobaths). A higher species evenness of the accompanying assemblage (non-shark species) (>0.6 or 0.7 Gini-Simpson),

| | Full shark assemblage | | Semipelagic shark assemblage | | Benthic shark assemblage | |
|--|---|----------------|---|----------------|---|----------------|
| | % ^a | % ^b | % ^a | % ^b | % ^a | % ^b |
| dbRDA axis | | | | | | |
| 1 | 70.04 | 17.16 | 76.81 | 17.24 | 72.84 | 19.18 |
| 2 | 88.48 | 21.67 | 97.39 | 21.87 | 96.91 | 25.52 |
| 3 | 96.29 | 23.59 | 99.25 | 22.28 | 100 | 26.34 |
| 4 | 100 | 24.5 | 100 | 22.45 | – | – |
| Selected predictors | Distance to 1000 m isobath (m) Mean fetch (m) SST (°C) <i>S</i> (species richness) | | Distance to 1000 m isobath (m) Mean fetch (m) SST (°C) <i>S</i> (species richness) | | Ahermatypic coral cover Macroalgal cover Rubble cover | |
| AICc score | 587.4 | | 559.54 | | 260.6 | |
| ^a % cumulative explained variation out of the fitted model | | | | | | |
| ^b % cumulative explained variation out of the total (unconstrained) variation | | | | | | |

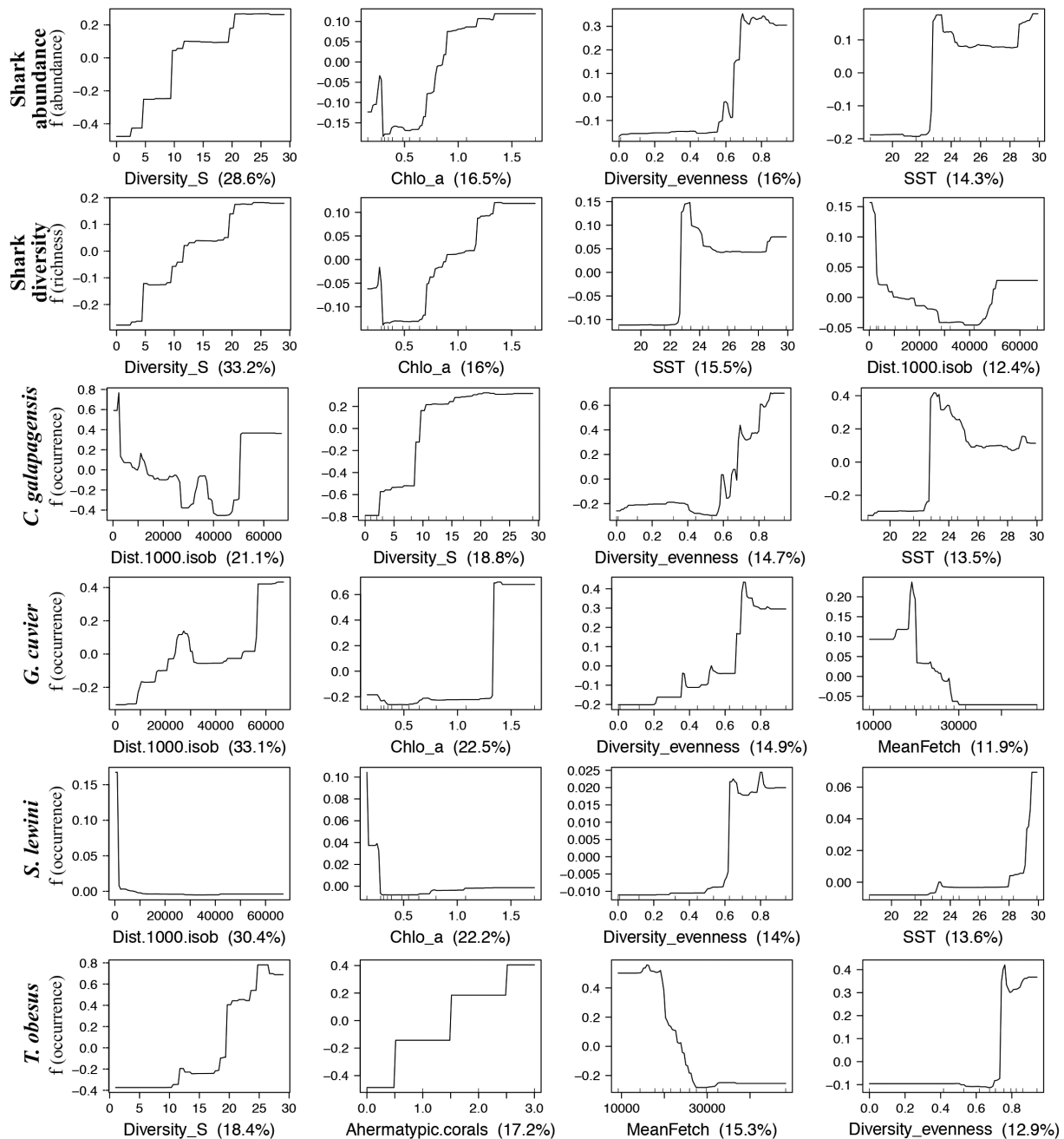


Fig. 5. Partial dependence plots (following Elith et al. 2008) showing the 4 most influential variables in the prediction of total shark abundance and diversity and the occurrence of *Carcharhinus galapagensis*, *Galeocerdo cuvier*, *Sphyrna lewini* and *Trienodon obesus*. Individual plots show the fitted value of the response variable on the y-axis versus each of the potential predictor variables, integrated across all other variables in the model (see Table 1). Diversity_S and Diversity_evenness refer to the richness and evenness (respectively) of the associated assemblage of non-shark species

and also diversity (>10 spp.) in the case of *C. galapagensis*, generally resulted in a higher probability of occurrence of these 3 shark species (Fig. 5). However, while sightings of *G. cuvier* were more likely at locations with high chl *a* (>1.3 mg m⁻³) and low wave exposure (mean fetch <30 km), the probability of

occurrence of *S. lewini* was higher in areas having warmer waters (>28°C) and low chl *a* (<0.25 mg m⁻³) (Fig. 5). Finally, *C. galapagensis* was more likely to occur when SST ranged between 23 and 24°C.

The influence of the associated assemblage of non-shark species varied substantially among the 4 ben-

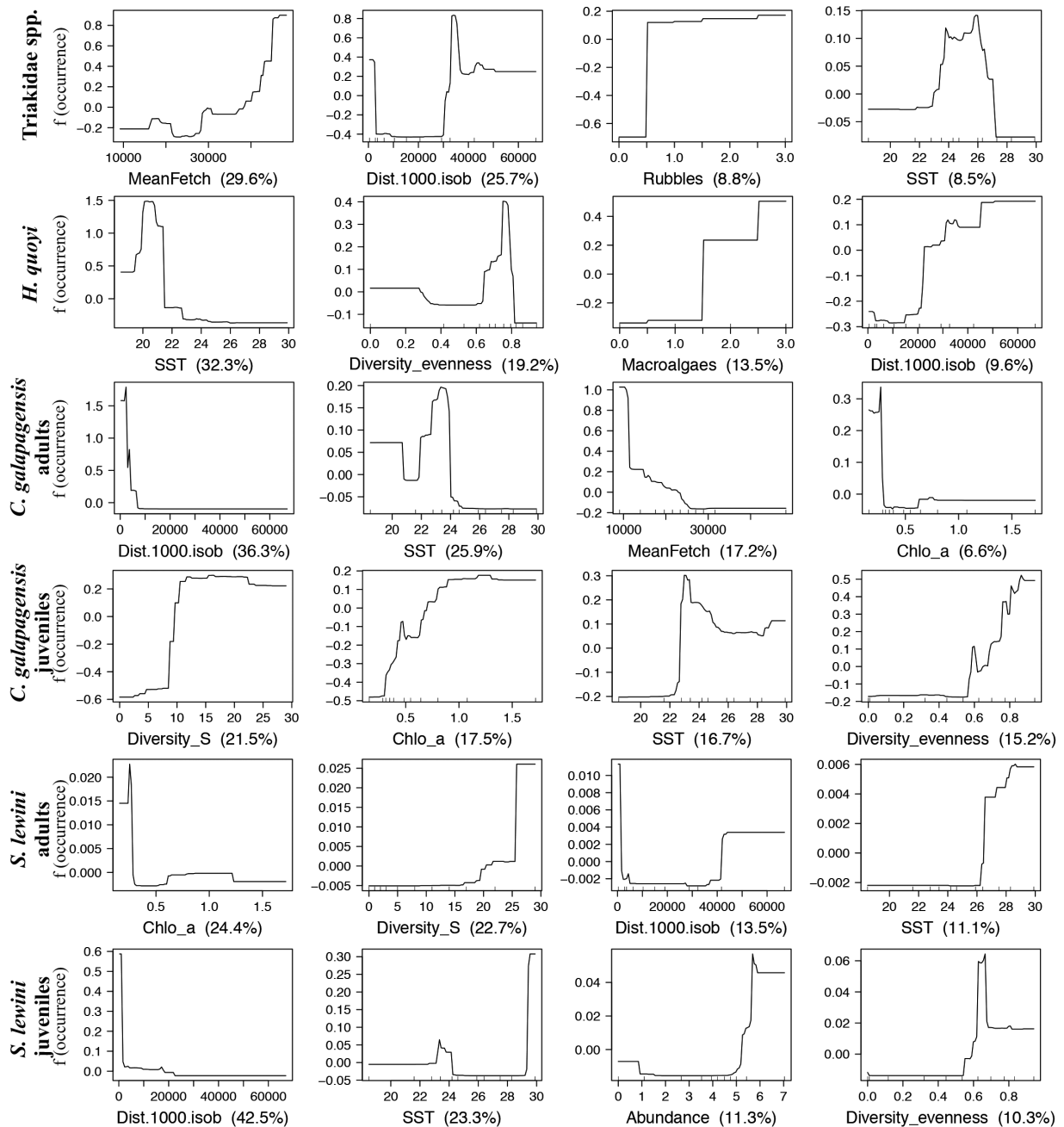


Fig. 6. Partial dependence plots (following Elith et al. 2008) showing the 4 most influential variables in the prediction of the occurrence of the 2 Triakidae species (*Triakis maculata* and *Mustelus albipinnis*), *Heterodontus quoyi* and adult and juveniles of *Carcharhinus galapagensis* and *Sphyrna lewini*. Abundance refers to the total log-abundance ($\text{Log}(\text{MaxN}+1)$) of the associated assemblage of non-shark species; other details as in Fig. 5

this shark species (Fig. 5). Sightings of *T. obesus* increased in probability in locations with high diversity (>20 spp.) and species evenness (>0.75 Gini-Simpson), while the 2 Triakidae species were more influenced by the relative abundance of accompanying species ($\text{log}(\text{MaxN}+1) > 4$), and *Heterodontus quoyi* was more likely to occur with high levels of

species evenness ($0.65 > \text{Gini-Simpson} < 0.8$; Fig. 6). Sightings of *T. obesus* increased gradually in probability in less exposed locations (mean fetch <27 km) having higher cover of ahermatypic corals; in contrast, the Triakidae species were more likely to occur at very exposed locations (mean fetch >30 km) where rubble had at least a low cover on the seabed (Fig. 6).

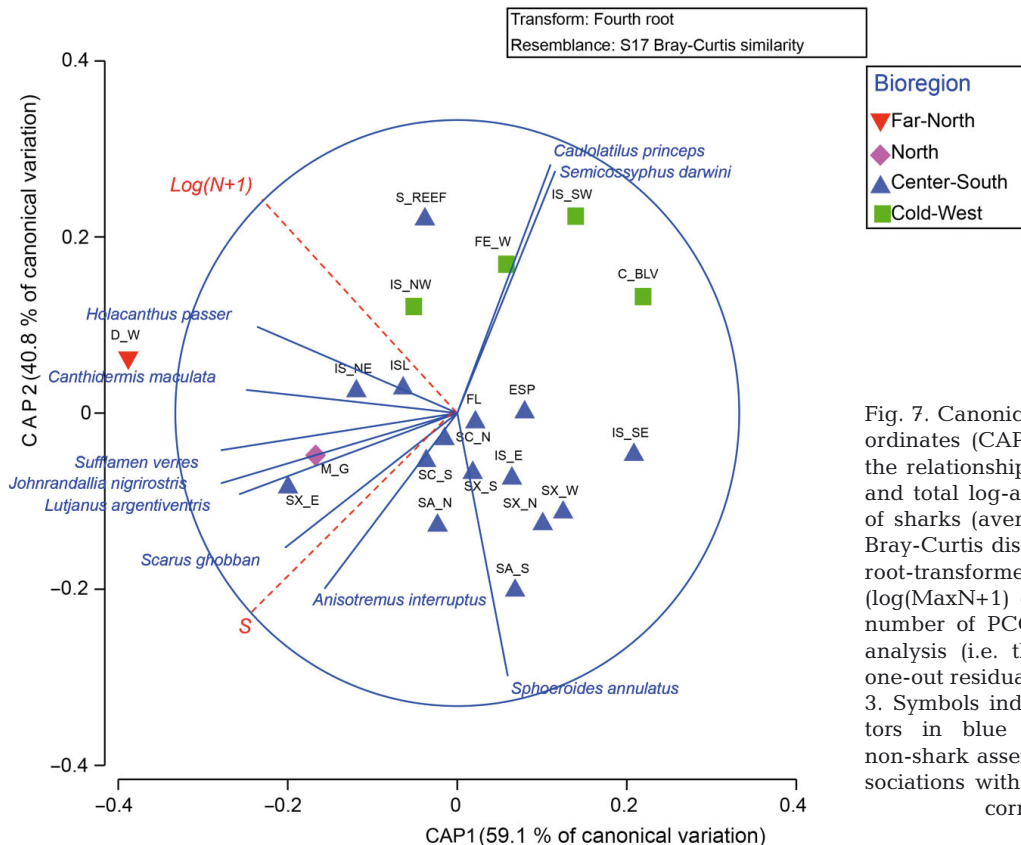


Fig. 7. Canonical analysis of principal coordinates (CAP) ordination plot showing the relationship between the richness (S) and total log-abundance ($\log(c\text{MaxN}+1)$) of sharks (averaged by stratum) and the Bray-Curtis dissimilarity matrix of fourth-root-transformed relative abundances ($\log(\text{MaxN}+1)$) of non-shark species. The number of PCO axes used for the CAP analysis (i.e. that minimised the leave-one-out residual sum-of-squares) was $m = 3$. Symbols indicate the bioregions. Vectors in blue indicate species in the non-shark assemblages having strong associations with the first 2 CAP axes (i.e. correlations > 0.75)

In the case of *H. quoyi*, SST was the most influential predictor, with a higher probability of occurrence in waters below 22°C , in locations with macroalgae ($>$ medium cover) and far from the edge of the insular shelf (> 20 km to 1000 m isobaths; Fig. 6).

To explore ontogenic differences in habitat associations within the same species, separate BRTs were conducted to predict the occurrence of adults vs. juveniles for each of *C. galapagensis* and *S. lewini*. For *C. galapagensis*, sightings of adults were more likely to occur in locations very close to the insular shelf (< 5 km to the 1000 m isobaths), with lower SST ($< 25^{\circ}\text{C}$), low exposure to waves (mean fetch < 25 km) and high exposure to currents (Fig. 6). However, occurrence of juveniles of *C. galapagensis* was mostly influenced by the richness and evenness of the accompanying assemblage (> 10 spp. and > 0.6 Gini-Simpson, respectively), and juveniles were more likely to occur in locations with high productivity ($> 0.5 \text{ mg m}^{-3}$) and SST close to 23°C (Fig. 6). A higher probability of occurrence of adult *S. lewini* was related to areas having low productivity ($< 0.25 \text{ mg m}^{-3}$), high SST ($> 26^{\circ}\text{C}$) and greater diversity in the accompanying assemblage (> 25 spp.), as well as at locations that were either very close to the edge of the insular shelf or well within the interior of the GA

(< 5 km or > 40 km to the 1000 m isobaths; Fig. 6). Juveniles of *S. lewini* showed increasing probability of occurrence at the boundaries of the insular shelf (< 5 km to the 1000 m isobaths), where SST was either below 24°C or above 29°C , and where there was a high log-abundance of species in the accompanying assemblage ($\log(\text{MaxN}+1) > 5.5$; Fig. 6).

The CAP revealed that several species from the accompanying assemblage of non-shark fishes and other macrofauna were strongly associated with shark log-abundance and richness (Fig. 7). The king angelfish *Holocanthus passer* had a positive association, while the bullseye puffer *Sphaeroides annulatus* had a negative association with the log-abundance of sharks (Fig. 7). Shark species richness had a strong positive association with the blue-barred parrotfish *Scarus ghoban* and the burrito grunt *Anisotremus interruptus*, and a strong negative association with the Galapagos sheephead wrasse *Semioscopus darwini* and the ocean whitefish *Caulolatilus princeps* (Fig. 7).

Spatial patterns for individual shark species

***Carcharhinus galapagensis*.** The Galapagos shark was the most abundant species recorded (Table 2)

and was also relatively widespread, having been observed in 16 out of 21 strata (Figs. 1b & 7a). The majority of the sightings of this species (66 % overall) were juvenile individuals (Figs. 7a & 8a). Records of adult Galapagos sharks were concentrated at D_W and the west side of Fernandina (FE_W stratum), the latter being the only place where males of this species were recorded (Fig. 8a).

***Sphyrna lewini*.** The scalloped hammerhead shark, the second most abundant species (Table 2), had 59 % of its records in the Darwin and Wolf (D_W) stratum (Figs. 1a & 7b) and, in contrast with *C. galapagensis*, was rarely observed in the Cold West bioregion (Fig. 8b). For *S. lewini*, the relative abundance recorded for adults of both genders was similar to the relative abundance of juveniles (Fig. 9b).

***Carcharhinus limbatus*.** The blacktip shark had the broadest spatial distribution of all shark species, being absent in only 1 of the 21 strata (Canal Bolívar, C_BLV; Figs. 1b & 7c). Most of the recorded individuals of this species were adults, and predominantly female (Figs. 7a & 8c).

***Galeocerdo cuvier*.** The tiger shark, the largest shark species recorded, was mostly sighted at the Centre South of the GA, with the majority of records occurring in the strata of Isabela Southeast (IS_SE), Islets (ISL) and Floreana (FL) (Figs. 1b & 7d). For tiger sharks, the proportion of males vs. females and adults vs. juveniles were similar (Figs. 7d & 8d).

***Triaenodon obesus*.** The whitetip reef shark was also mostly sighted in the Centre South of the GA (Fig. 8e). Records of juveniles were almost absent for this species, with adult males and females usually recorded together (Fig. 9e).

Triakidae spp. The spotted houndshark *Triakis maculata* and the whitemargin smoothhound shark *Mustelus albipinnis* were located mostly in the southern part of the GA (Fig. 1b). These 2 species were the most abundant in the Submerged Reef (S_REEF) stratum (Figs. 1a & 7f). In the case of *T. maculata*, most recorded individuals were close to the size of sexual maturity (Fig. 9f), while *M. albipinnis* provided records of both juveniles and adults (Fig. 9g). No males of either species were recorded.

***Heterodontus quoyi*.** The Galapagos bullhead shark was observed in the southern and western parts of the GA (Fig. 1b). Sizes of individuals were mostly limited to 40–60 cm FL (Fig. 9h).

***Carcharhinus falciformis* and *C. altimus*.** The other 2 shark species sighted in this study, the silky shark *C. falciformis* and the bignose shark *C. altimus*, were limited to 6 records in each case (Table 2); *C.*

falciformis was observed at Darwin and Floreana Islands, and *C. altimus* was observed at Darwin, Isabela and San Cristóbal Islands.

DISCUSSION

Here we have described the salient patterns of distribution and abundance for 10 coastal shark species across the GA, highlighting the potential importance of the GMR in the overall maintenance of shark biodiversity across the region. Variation in the structure of shark assemblages and the diversity of spatial distributions observed for different individual shark species found in our study indicate that the GMR harbours a broad range of suitable shark habitat, performing multiple ecological functions for shark populations. These could include, but may not be limited to, the provision of prey, nursery habitats, refuge from predation and cleaning services.

Spatial and temporal variation in shark assemblages

Spatial variation in the structure of shark assemblages found in our study is likely the result of habitat heterogeneity across the GMR. At higher latitudes, the tropical oceanic islands of Darwin and Wolf harboured distinct shark assemblages, characterised by high abundances of large and highly mobile species and a low diversity of sharks (Fig. 1b). Conversely, the central and western part of the GA harboured more diverse and variable shark assemblages, where benthic species were regularly present (Fig. 1b).

In general terms, the shark assemblages found in the GMR are characterised by the dominance of large and highly mobile semipelagic shark species with broad distributions, similar to Cocos and Malpelo, the 2 closest islands in the Eastern Tropical Pacific (Bessudo-Lion & Álvarez-León 2014, White et al. 2015; Fig. 1a). However, 3 species that we observed in the GMR, namely *Triakis maculata*, *Mustelus albipinnis* and *Heterodontus quoyi*, have never been recorded at either of these other 2 oceanic islands. These are reef-associated species that are mostly limited to the continental shelf of western Central and South America. The greater diversity of habitats (including temperate reefs) available at the GA might provide favourable conditions for the settlement of species with less mobility and specific habitat requirements that cannot be found in small tropi-

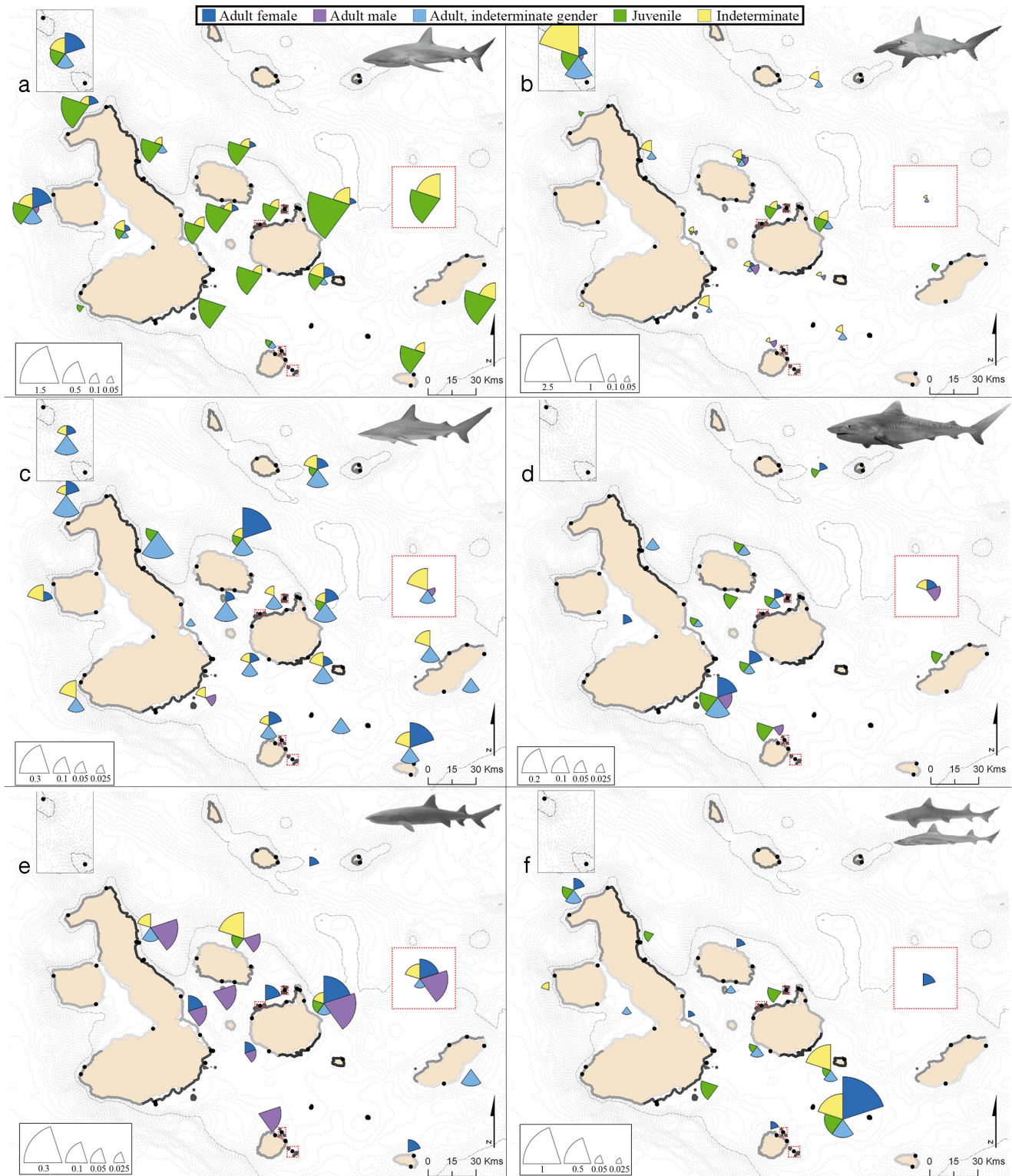


Fig. 8. Distributions and relative abundances of different sizes and gender categories of the most common coastal shark species recorded by stereo-BRUVs at the Galapagos Marine Reserve. (a) *Carcharhinus galapagensis*, (b) *Sphyrna lewini*, (c) *Carcharhinus limbatus*, (d) *Galeocerdo cuvier*, (e) *Triaenodon obesus*, (f) *Triakis maculata* and *Mustelus albipinnis*. Black dots show the locations of the study sites and grey dashed lines indicate the 100 m isobaths (1000 m isobath shown with thicker grey dashed lines). Segmented bubble plots show segments whose sizes are directly proportional to the average relative abundance per stratum (no. sharks per 90 min deployment, see the individual legends with a separate scale provided on each map) for each of the different size/gender categories (as different colours)

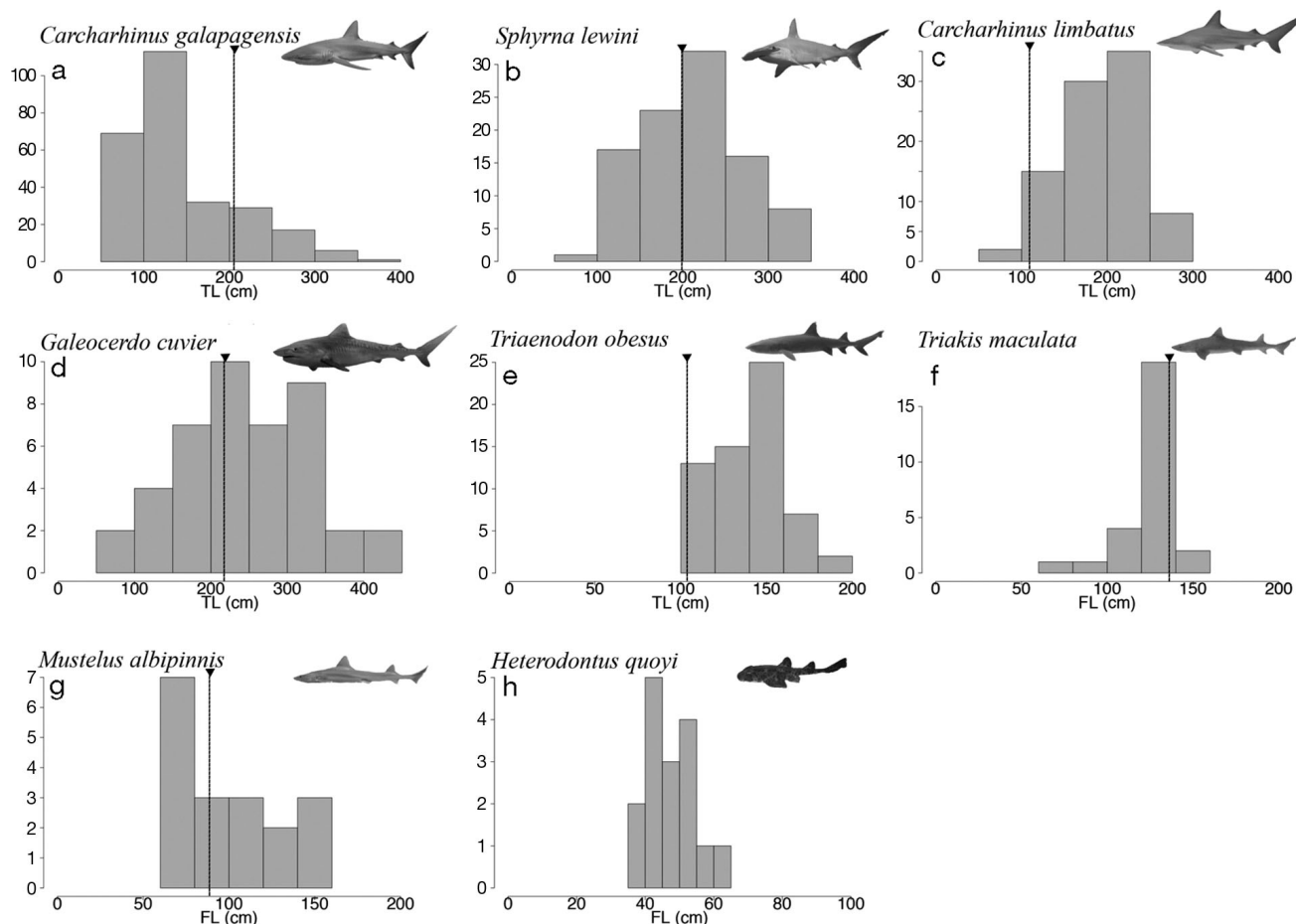


Fig. 9. Size distribution of the 8 most common shark species recorded by the stereo-BRUVs at the Galapagos Marine Reserve. Y-axes indicate the number of recorded individual sharks per species. Vertical lines indicate the smallest size of the published range of lengths for sexual maturity for each shark species (in the case of *T. maculata* and *M. albipinnis*, the size for sexual maturity was obtained from similar species in their respective genus). Length for sexual maturity has not been published for *H. quoyi* or any other species within this genus. TL: total length, FL: fork length

cal oceanic islands lacking an insular shelf, such as Cocos and Malpelo.

The groups of islets and Floreana Island were the areas that showed the highest species richness of sharks (2 of the 4 surveyed islet sites also happened to be close to Floreana Island; Fig. 1b). Despite its small size, Floreana offers a great variety of habitats and oceanographic conditions, with upwelling areas and temperate reefs covered by macroalgae along its western side, and more tropical conditions, including coral reefs, and several islets on its eastern side (Feingold & Glynn 2014). This variability in habitats also yields highly diverse assemblages of other non-shark fishes (Edgar et al. 2004), which has been identified in our study as being strongly associated with increased shark diversity. Finally, low diversity and abundance of sharks was observed in the Cold West bioregion, likely in response to lower fish diversity (Edgar et al. 2004) and particular environmental con-

ditions (lower water temperature) that might restrict the presence of species with more tropical affinities (e.g. *Sphyrna lewini*, *Galeocerdo cuvier* or *Trienodon obesus*).

Sharks make seasonal movements and switch between habitats in response to changes in water temperature and other abiotic variables (Schlaff et al. 2014). However (and contrary to what was expected), our results showed a lack of any significant temporal variation in shark assemblages across seasons. This may be due to the occurrence of an ENSO event during our study, which produced anomalies in SST at the GMR ranging from +0.7 to +2.0°C between February and October 2015 (www.cpc.ncep.noaa.gov). During El Niño years, seasonal differences are reduced, with both an increase and a homogenization of SST across the GA (Banks 1999). Future studies of shark assemblages at the GMR should evaluate the potential effects of ENSO.

Environmental and biological drivers

We found considerable differences in the environmental and biological drivers of potential importance to semipelagic vs. benthic sharks, which could be explained by their different movement capacities and foraging behaviours. Semipelagic sharks aggregate at structurally complex sites that are exposed to currents, such as islets, seamounts and reef edges (Hearn et al. 2010, Ketchum et al. 2014). Although we did not measure current flow here, associations with geographically derived variables, such as proximity to the insular shelf edge and the degree of wave exposure (main fetch), suggested that exposure to main currents and access to pelagic prey are likely to be important requirements for pelagic species (Dudley & Cliff 1993, Wetherbee et al. 1996). Conversely, the assemblage of reef-associated sharks was more influenced by fine-scale benthic habitat variables; the effect of seabed cover by ahermatypic corals, macroalgae and rubble was particularly strong, as recorded for other reef shark species at the Great Barrier Reef (Espinoza et al. 2014).

Biotic factors, such as the availability and distribution of prey, exert a strong influence on the spatial ecology of sharks (Torres et al. 2006). Both the species richness and evenness of other fishes and marine macrofauna showed a positive correlation with shark diversity, abundance and occurrence. Thus, sharks not only showed a higher affinity for habitats with more diverse assemblages of other species, but also assemblages where individuals are more evenly distributed across fish and other marine macrofaunal species (i.e. high evenness). This would seem consistent with analyses of stomach contents of mesopredatory and apex sharks, which generally show a broad range of prey species that might reflect low prey specialization (Compagno 2001). The relationships between sharks and assemblages of other fishes and marine macrofauna are not restricted, however, to predator–prey associations, e.g. 2 of the reef fish species showing strong positive correlations with the log-abundance and richness of sharks (*Johnrandallia nigrirostris* and *Holocanthus passer*) have cleaning interactions with some of the abundant sharks recorded at the GMR (Quimbayo et al. 2017).

Spatial patterns of individual shark species

***Carcharhinus galapagensis*.** *C. galapagensis* was the most abundant shark species recorded in our study, similar to what has been reported in other

oceanic islands in the South Pacific (e.g. Lord Howe Island, Heagney et al. 2007; Kermadec Islands, Duffy & Francis 2010). We did find ontogenic differences in habitat associations for this species, however, with juveniles occurring in higher abundances and being more widely distributed spatially than adults (Fig. 8a). Our results indicate that *C. galapagensis* is using a broad range of coastal areas of the GMR as nursery grounds, where juveniles may find abundant prey and refuge from predation. Adults might use deeper habitats (Wetherbee et al. 1996) or may embark on seasonal migrations out of the coastal areas of the GMR (Meyer et al. 2010, Hearn et al. 2014). Adults were observed predominantly at oceanic islands (Darwin and Wolf) and locations near the edge of the insular shelf (Fig. 8a). Most recorded adults were females, with very few records of males, which could indicate some degree of sexual segregation, as reported for this species elsewhere (Wetherbee et al. 1996).

***Sphyrna lewini*.** Despite showing a broad spatial distribution around the GMR, records of *S. lewini* were clearly concentrated at Darwin and Wolf Islands. This species aggregates in large numbers at islets and seamounts (Hearn et al. 2010, Ketchum et al. 2014), using shallow protected bays as nursery areas. However, the presence of suitable nursery grounds for this species in the GMR is considered very unlikely (Hearn et al. 2014), as previous surveys using gill nets at shallow bays around the GMR have resulted in very few records of *S. lewini* (Jaenig 2010, Llerena et al. 2010). Thus, most adults recorded at the Galapagos Islands likely migrate to continental nursery grounds for breeding (Salinas-de-León et al. 2017), such as those found in the gulfs of Ecuador (P. Salinas-de-León unpubl. data), Costa Rica (Zanella et al. 2009), Colombia (Quintanilla et al. 2015) and Panama (Rodríguez 2011). Our study recorded similar numbers of juveniles (mostly between 100 and 200 cm TL) and adults in the GMR. Gender could not be determined for the majority of adults, so although sexual spatial segregation has been documented for this species elsewhere (Klimley 1987), it could not be evaluated in our study.

***Carcharhinus limbatus*.** *C. limbatus* showed the broadest and most spatially even distribution of all shark species (Figs. 1b & 7c), which may be explained by its adaptability to a great variety of habitats (Compagno et al. 2005). Records of this species in our study were mostly restricted to adult individuals. However, there is clear evidence that this species breeds in high numbers at the GMR, with nursery grounds located in shallow sheltered bays (Jaenig

2010, Llerena et al. 2010). The near lack of recordings of juveniles of *C. limbatus* in our study may indicate that they remain in these shallow habitats until they are close to sexual maturity. Most records of adult *C. limbatus* were females. Sexual segregation has been reported for this species, where females display a higher degree of philopatry than males and remain closer to nursery areas (Sims 2005).

***Galeocerdo cuvier*.** The largest species recorded in our study, *G. cuvier*, showed a centralised distribution in the GMR, where records from adults of both genders were mostly concentrated between the southeast of Isabela Island and the north of Santa Cruz Island. Telemetry studies using satellite and acoustic devices have shown that adults of this species tend to aggregate seasonally in these 2 areas of the GMR, likely in response to high densities of potential prey, such as nesting aggregations of the Pacific green sea turtle *Chelonia mydas* (Acuña-Marrero et al. 2017). Juveniles displayed a broader distribution around the GMR. The recorded size range included at least 6 young-of-the-year individuals (<150 cm TL, Meyer et al. 2014; Figs. 7d & 8d), suggesting that the GMR supports a nursery ground for this species. *G. cuvier* has been considered rare in the GMR until recently (Hearn et al. 2014). However, our results and those published by Acuña-Marrero et al. (2017) indicate that *G. cuvier* is well established in the GMR, which could play an increasingly important role for this species at a regional scale by providing both nursery and feeding grounds.

***Triacodon obesus*.** The most commonly recorded benthic shark in our study, *T. obesus*, preys on a large range of benthic species, using reef edges, caves and crevices to rest between foraging excursions and to avoid predation from larger sharks (Randall 1977). This behaviour might explain its higher occurrence in areas with greater fish diversity and presence of black corals, which are common around walls and caves in the GMR (Calvopiña 2002). Similar to *C. limbatus*, records of *T. obesus* were mostly restricted to adult individuals, although this species is also known to use shallow bays as nursery grounds in the GMR (Jaenig 2010, Llerena et al. 2010). Our findings are consistent with previous studies that have found no evidence of sexual segregation in *T. obesus*, as adult males and females were repeatedly sighted together across different areas of the GA (Fig. 8e).

Triakidae spp. Despite the wide distribution and relatively common occurrence of *Triakis maculata* and *Mustelus albiguttatus*, these 2 Triakidae species had only been previously recorded on very few occa-

sions in the GMR since their first registered sightings there in 1980 (Grove & Lavenberg 1997) and 2013 (Acuña-Marrero et al. 2013), respectively. Very little is known about the biology of these 2 sharks (Castro-Aguirre et al. 2005), and to our knowledge, the present study might be providing the first video footage of these sharks in the wild. These 2 species showed a high affinity for relatively flat areas covered by rubble on submerged reefs. Only juveniles and females were recorded for either species, which might indicate that males are spatially segregated to deeper areas. These species have a deeper depth range in continental areas, especially in the case of *M. albiguttatus* (Pérez-Jiménez et al. 2005).

***Heterodontus quoyi*.** We found that *H. quoyi* has a broader distribution range in the GMR than previously described (i.e. extending beyond the Cold West bioregion and the west side of Floreana Island; Kyne et al. 2004). *H. quoyi* is a poorly known, small-sized reef shark endemic to the coast and offshore islands of Peru and the Galapagos Islands, although some have suggested that individuals of these 2 distinctive subpopulations could be 2 different species (Kyne et al. 2004). *H. quoyi* has a reported maximum length of 105 cm TL, with records of sexual maturity at 48 cm TL (Compagno 2001). Most individuals recorded in our study were ca. 50 cm FL, indicating that a high proportion of them could be sexually mature. The absence of juveniles of this species in our study, which have a small size (reported hatching size 17 cm TL) and display cryptic behaviour (Compagno 2001), might be due to a lack of detectability (Fig. S2). It is also likely, however, that there are ontogenic differences in habitat selection, with juveniles of *H. quoyi* potentially using a different depth range than adults.

Stereo-BRUV performance

The 10 shark species recorded in our study comprise approximately 60% of the coastal shark species that have ever been reported in the GMR (Hearn et al. 2014). Four of the 7 coastal sharks not sighted in this study (*Carcharhinus albimarginatus*, *C. plumbeus*, *Mustelus mento* and *Nasolamia velox*) are considered uncommon or very rare in the GA, and records of the other 3 species (*Carcharodon carcharias*, *Sphyrna mokarran* and *S. tiburo*) are yet to be confirmed (Grove & Lavenberg 1997, McCosker & Rosenblatt 2010). Prior to our study, 2 multi-year (2001–2012) scuba-based visual surveys of reef and pelagic fishes were conducted in the GMR. Despite

their length and large spatial coverage, none of these studies recorded 3 shark species that were sighted in our study, with 2 of these (*Triakis maculata* and *M. albipinnis*) being relatively common and showing a broad distribution around the GA (Fig. 1b). It is very likely that these Triakidae sharks avoid divers, as they were recorded by the stereo-BRUVs in some areas that have been regularly visited in previous visual surveys (Edgar et al. 2004). Consequently, we consider stereo-BRUVs to be the most reliable non-extractive method for surveying sharks in the GMR on a regular basis.

To our knowledge, this is the first published study that combines the use of benthic and pelagic stereo-BRUVs to survey coastal shark populations. Although there were significant differences in the shark assemblages recorded by benthic vs. pelagic stereo-BRUVs, the benthic deployments recorded all shark species found in this study in either similar or higher numbers than the pelagic units (Table 2). Conversely, benthic shark species showed a more restricted vertical behaviour, as none of them was recorded by the pelagic stereo-BRUVs. Thus, future studies of shark assemblages at coastal areas might preferably deploy only benthic BRUVs for studies conducted at similar depths to those examined here.

Limitations of this study

First, we only sampled at 2 distinct times; greater temporal replication would allow seasonal and inter-annual variation to be estimated rigorously, also providing the capacity to assess the potential influence of periodic broad-scale climate-driven events, such as ENSO, on shark assemblages. Second, our study may be biased against species with a high degree of nocturnal activity (e.g. *T. obesus*), as we only deployed stereo-BRUVs during daylight hours. Third, the use of MaxN calculated from stereo-BRUVs will yield conservative estimates of abundance, especially in high-density areas (Cappo et al. 2003). This bias may be somewhat ameliorated by the use of cMaxN, albeit to varying degrees across individual species; species with elusive behaviours or that lack unique identifiable features will have a lower probability of being individually identified in the video analysis. Fourth, our modifications to conventional benthic stereo-BRUVs (Fig. S2) might affect the detectability of small or cryptic species with low mobility, although only *H. quoyi* has those characteristics among the sharks recorded. However, this species was repeatedly identified in our study even in areas outside

of its previously described distributional range and generally displayed inquisitive behaviour towards the stereo-BRUVs. Fifth, gender could only be determined in a limited number of individuals, which reduced our ability to assess potential gender differences in habitat use. Although bait generally attracted sharks, some species showed elusive behaviours or remained in positions where their ventral surface was not visible.

Summary

Our study has demonstrated that sharks have species-specific and size-specific spatial distributions in the GMR. These patterns are highly likely to be driven by differential requirements for particular habitats, food resources, protection from predators and/or avoidance of competitors. Spatial patterns in distributions are also likely to change and evolve through time at large and intermediate scales due to human-mediated and climate-driven impacts. The complexity of distributional patterns and responses of shark assemblages as a whole to a variety of biological and environmental factors imply that sophisticated spatial modelling will be needed to guide management towards successful outcomes for sharks overall into the future.

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