Ecology of Sharks and Human Attitudes Towards Shark Conservation in the Galapagos Marine Reserve

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Abstract

In this thesis, I used a multi-disciplinary approach to study both the spatial ecology of coastal sharks and human attitudes towards sharks at the Galapagos Marine Reserve (GMR). Benthic and pelagic baited remote underwater stereo-video systems recorded coastal shark assemblages that displayed high spatial variation, with the relative importance of environmental and biological drivers differing among shark species according to their mobility. Telemetry data (both acoustic and satellite) from tagged tiger sharks (*Galeocerdo cuvier*) showed a high degree of philopatry, with movements of adult tiger sharks concentrating at the most important nesting areas for sea turtles at the GMR. Using diver-operated stereo-video systems (DOVs) I demonstrated that non-instantaneous surveys yield estimates of shark densities that can almost double the ones obtained from instantaneous surveys. Furthermore, I proposed a new methodological approach to study attitudes towards sharks that proved to be reliable and informative, showing that attitudes were shaped by a range of psychological factors, such as aesthetics, and also by the socio-economic context of individual respondents. Strong correlations were found between attitudes and behavioural responses, such as tolerance or support for shark protection.

In conclusion, I demonstrated that sharks at the GMR have species-specific and size-specific spatial requirements for particular habitats and food resources. Indeed, the presence of a predictable source of prey and suitable habitats at the GMR might reduce the spatial extent of the potential areas used by large and highly mobile shark species, such as tiger sharks, thereby enhancing the potential effectiveness of the GMR for their protection. I also propose the use of non-instantaneous DOV surveys to provide more accurate estimates of shark densities than underwater visual techniques. In addition, the multivariate methods used here for the first time to study human perspectives on sharks allowed me to identify specific attitudes and associated factors having the greatest influence on human behaviours towards shark conservation. In summary, with mounting anthropogenic pressures on shark populations, this thesis provides timely and critical information for the global objective of identifying effective strategies for the management and conservation of sharks to ensure their long-term survival.

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Table of contents

List of Tables

Table A-1. Performance of the boosted regression tree (BRT) models using the environmental and biological variables (Table 1) to predict total log-abundance and diversity of sharks, and occurrences of individual shark species (oc.), using proportion of the deviance explained assessed by cross-validation (CVDE) and area under the receiver operative characteristic curve (AUC) scores.

Table B-1. Total number of sharks recorded in the study.

List of Figures

Figure 1-1. Map showing the zoning scheme implemented at 2016 at the Galapagos National Park (GNP) and Galapagos Marine Reserve (GMR). The black line indicates the boundary of the GMR and the green polygons are dedicated conservation areas, where all commercial fishing activities are prohibited. Grey dashed lines show bathymetry (100 m isobaths).

Figure 2-1. Maps showing (a) the location of the Galapagos Archipelago in the Eastern Tropical Pacific and (b) the distribution and abundance of coastal sharks recorded by stereo-BRUVs within the Galapagos Marine Reserve (GMR). Black dashed lines in panel (a) indicate the boundaries of the MPAs located at oceanic archipelagos. In panel (b), bold names in grey indicate bioregions with strata delimited by continuous lines in grey scale at the 20 m isobaths of each island and the stratum composed of islets is highlighted by a red-dotted-line square). Black dots show the location of the study sites and grey dashed lines indicate the 100 m isobaths (the 1,000 m isobath is highlighted with thicker grey dashed lines). Presence and relative abundance of coastal sharks is indicated using segmented bubble plots where each shark species is represented by a circle segment corresponding to a given colour (upper right legend) whose size is proportional to its average relative abundance per stratum (# sharks per 90 min, lower left legend).

Figure 2-2. Maps showing the distribution and relative abundances of different sizes and sex categories of the most common coastal shark species (a: *Carcharhinus galapagensis*, b: *Sphyrna lewini*, c: *Carcharhinus limbatus*, d: *Galeocerdo cuvier*, e: *Triaenodon obesus*, f: *Triakis maculata* and *Mustelus albipinnis*) recorded by stereo-BRUVs at the Galapagos Marine Reserve. Black dots show the locations of the study sites and grey dashed lines indicate the 100 m isobaths (1,000 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 (# sharks per 90 min, see the individual legends with a separate scale provided on each map) for each of the different size/sex categories (as different colours).

Figure 2-3. Size distribution of the eight 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. Dashed 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).

Figure 2-4. Non-metric MDS ordination plot of shark assemblages at the GMR, based on a zero-adjusted Bray-Curtis similarity matrix (Clarke et al. 2006) produced from square-root-transformed relative abundances of shark species, averaged by stratum and BRUV type. Labels indicate the different strata (Fig. 2-1b).

Figure 2-5. Non-metric MDS plot showing the inter-specific associations among shark species based on the index of association calculated from square-root transformed relative abundances of shark species (*cMaxN*). Levels of similarity from a hierarchical agglomerative cluster analysis are indicated by a green line (20% similarity) and a blue dashed line (40% similarity). Species belonging to different families are shown by different symbols.

Figure 2-6. Partial dependence plots (following Elith and Leathwick 2016) showing the four most influential variables in the prediction of total shark abundance and diversity and the occurrence of *Carcharhinus galapagensis*, *Galeocerdo cuvier*, *Sphyrna lewini* and *Triaenodon 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.

Figure 2-7. Partial dependence plots (following Elith and Leathwick 2016) showing the four most influential variables in the prediction of the occurrence of the two Triakidae species (*Triakis maculata* and *Mustelus albipinnis*), *Heterodontus quoyi* and adult and juveniles of *Carcharhinus galapagensis* and *Sphyrna lewini*. 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, Diversity_evenness and Abundance refer to the richness, evenness and total log-abundance (*Log (MaxN+1)*) (respectively) of the associated assemblage of non-shark species.

Figure 2-8. Canonical analysis of principal coordinates (CAP) ordination plot showing the relationship between (i) the richness (*S*) and total log-abundance (*log(cMaxN+1)*) of sharks (averaged by stratum) and (ii) the Bray-Curtis dissimilarity matrix of fourth-root-transformed relative abundances (*log(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).

Figure 3-1. Patterns of residency behaviour of satellite tagged tiger sharks. Resident (red circles), transient (yellow circles) and undetermined (orange circles) behaviours associated with each 12-hour estimated position provided by the switching state-space model. Top panel (a) displays the complete tracks of TS2 and TS4 (pink and green dashed lines, respectively) overlaid with the exclusive economic zones (grey line) and marine protected areas (grey dashed line) of Eastern Tropical Pacific countries. Lower panel (b) shows the estimated positions of all tracked sharks within the Galapagos Marine Reserve (black dashed line, top panel), indicating the study sites, the most important turtle-nesting beaches (sea turtle icons) and the 100 m isobaths (blue dashed lines).

Figure 3-2. Kernel density estimates of satellite-tagged tiger shark positions. Sharks are pooled by size classes: (a) large (> 300 cm TL, n = 3), (b) medium (200-300 cm TL, n = 12) and (c) small (< 200 cm TL, n = 1); or by season: (d) sea turtle-nesting season (n = 11) and (e) non-nesting season (n = 7). Red indicates core range areas (50 % percent-volume contour, PVC), yellow represents activity space areas (95 % PVC) and orange indicates the intermediate 75 % PVC. Underlined names of study sites (Isabela-South = I-S, Cerro-Ballena = C-B, Bachas-Salinas = B-S) indicate those locations where sharks were tagged in each case. White sea turtle icons show the turtle-nesting areas and local bathymetry is displayed by 100 m isobaths (blue dashed lines).

Figure 3-3. 12-hourly estimated positions provided by SSM by shark size. Colours indicate three size classes of tiger sharks (large = red, medium = orange, small = white). Black dashed lines indicate the 5 and 10 km buffer areas around the study sites (I-S = Isabela-South, C-B = Cerro Ballena, B-S = Bachas-Salinas) and sea turtle nesting beaches (white sea turtle icon). Local bathymetry is displayed by 100 m isobaths (blue dashed lines). Right panels show zoomed areas of the study sites of I-S (upper) and B-S (lower).

Figure 3-4. Patterns of residency and diel occurrence of acoustic-tagged tiger sharks. Left panels refer to Bachas-Salinas and right panels to Cerro-Ballena. The top panel (a, b) shows residency index (RI, the total number of days a shark was detected divided by the number of days that the shark was monitored by the receivers) for the total monitored time (Total) and per season (Non-nesting and Nesting); the middle panel (c, d) shows Fast Fourier Transformations (FFT) of the number of hourly detections, with peaks indicating periods of dominant cycles; and the lower panel (e, f) shows daily detections of tiger sharks; the circle represents a period of 24 hours and the length of each wedge indicates the number of detections within each hour.

Figure 3-5. Relative abundance of tiger sharks at the three study sites. Number of individual tiger sharks per hour by sex recorded by the stereo-BRUVs in the nesting or the non-nesting season for turtles. The number of camera deployments at each site is reported in parentheses. The average TL ± SE (cm) of the sharks recorded at each site is given at the top of each bar.

Figure 3-6. Total length (TL) of tiger sharks tagged and observed by stereo-BRUVs. Total length is shown as raw data values and as means (black circles) with 95% confidence intervals for males (blue) *vs* females (red) in either the nesting season (circles) or the non-nesting season (triangles), and at each of the three study locations.

Figure 4-1. Schematic diagram of the methodology that can be implemented using DOVs in order to differentiate between instantaneous *vs* non-instantaneous records of sharks. Each shark recorded is categorised as an instantaneous record (*IN*) if it was inside the transect limits (5 m × 5 m) at the time that it was first sighted, or as a non-instantaneous record (*OUT*) if it was outside of the transect limits when first sighted, but then later moved into the transect limits. An instantaneous survey would include only instantaneous records, while a non-instantaneous survey would include both instantaneous and non-instantaneous records. The grey halo shown around each shark indicates where it was when it was first sighted, while dotted lines and arrows show the direction of their movements of sharks over the period of time of the survey.

Figure 4-2. Maps showing the long-length surveys conducted using DOVs ('supertransects') at (a) Darwin and (b) Wolf islands, with (c) inset map showing the locations of these islands at the Galapagos Marine Reserve. The supertransects (conducted along the 20-m isobath perimeters of each island) are each represented by a band (width is not to scale), with the relative density of sharks (count km^{-2}) indicated by a blue colour scale (see legend). A number is assigned to each supertransect for their identification in Table 4-1. Grey dashed lines represent the 10 m isobaths in (a) and (b) and the 100 m isobaths in (c).

Figure 5-1. Diagram showing the conceptual framework used in this study relating attitudes (produced after an evaluating process involving beliefs and emotions) and behaviours (reflected in the tolerance to coexistence situations with wildlife, support for its protection and willingness to increase knowledge about it). Lighter-gray area delimited by dashed line refers to the local social and ecological context.

Figure 5-2. Vectors showing the degree of correlation (i.e., proximity of the arrow heads representing each variable to the unit circle) of the 14 selected factors to the first two principal components (PCs) of the PCA, which together explain 39.3 % of the variation. The first principal component (PC1) is interpreted as an index of overall attitudes towards sharks, based on its loadings. Embedded table shows the loadings for each of the 14 selected factors for the first and second principal components (PC1 and PC2, respectively).

Figure 5-3. Classification and rating of the people experiences with sharks in the wild (frequencies in parentheses) by respondents.

Figure 5-4. Partial dependence plots (following Elith and Leathwick (2016)) showing the eight most influential variables in the prediction of tolerance (a) and support for shark protection (b) from Boosted Regression Trees (BRTs). Individual plots show the fitted value of the response variable (i.e., tolerance in (a) and support for shark protection in (b)) on the Y-axis versus each of the potential predictor variables, integrated across all other variables in the model. Prediction performance was assessed using the area under the curve (AUC; Hosmer and Lemeshow 2000) with the BRT models providing acceptable (AUC = 0.78) and excellent (AUC = 0.85) model predictions, respectively.

Figure A-1. Multivariate pseudo standard error (*MultSE*; Anderson & Santana-Garcon 2015) as a function of the number of replicates (sample size) of a zero-adjusted Bray-Curtis (Clarke et al. 2006) dissimilarities calculated on shark abundance data from the pilot study from (a) benthic and (b) pelagic stereo-BRUVs for four different soak times (upper right legend), with permutation-based means and bias-adjusted bootstrap-based error bars (10,000 resamples).

Figure A-2. Benthic stereo-BRUV design used in the study. The camera frame remains floating at *ca* 1 m over the seabed.

Figure A-3. Video frames showing the shark species recorded by stereo-BRUVs at the Galapagos Marine Reserve (a: *Carcharhinus altimus*, b: *Carcharhinus falciformis*, c: *Carcharhinus galapagensis*, d: *Carcharhinus limbatus*, e: *Galeocerdo cuvier*, f: *Sphyrna lewini*, g: *Triaenodon obesus*, h: *Heterodontus quoyi*, i: *Mustelus albipinnis*, j: *Triakis maculata*).

Figure A-4. Distance–based redundancy analysis (dbRDA) ordinations for the fitted model of the (a) full, (b) semipelagic and (c) benthic shark assemblages based on a zero-adjusted Bray-Curtis similarity matrix (Clarke et al. 2006) produced from square-root-transformed relative abundances of shark species (*cMaxN*) averaged by site and position in the water column (benthic *vs* pelagic). Corresponding bioregions are indicated by coloured icons (upper right legend). Overlying vectors in blue show the environmental and biological predictors fitted by the model.

Figure B-1. Map showing the study sites of (a) Bachas-Salinas, and (b) Isabela-South and Cerro-Ballena. White sea turtle icons indicate the most important nesting beaches for green sea turtles in the area, according to Zárate and Dutton (2002) and Zárate et al. (2009). Black crosses show the locations of SBRUV deployments, and black rectangles show the locations of acoustic receivers.

Figure B-2. Frequency distribution of the time interval (in days) between subsequent detections of satellite locations obtained for tagged sharks.

Figure B-3. Chronology of acoustic detections for each of the acoustic-tagged sharks (TS1-TS20) by site (colour coded).

Figure C-1. Questionnaire for evaluating the attitude towards sharks in residents and visitors to the Galapagos Islands.

Chapter 1. General introduction

1.1 Sharks - Vulnerable top predators

Sharks are the most widely distributed top predators in the ocean (Ferretti et al. 2010). Like most chondrichthyans, sharks have a slow growth rate, late maturity, long gestation periods and low fecundity (Cortés 2000). These life-history traits make populations of sharks very vulnerable to the impacts of fishing and limits their recovery potential (Ferretti et al. 2010, Ward-Paige et al. 2010, Hutchings et al. 2012). Consequently, there is a growing concern about the global decline of shark populations (Dulvy et al. 2014). With an estimated 100 million sharks being captured annually worldwide, many of their populations have undergone serious decline and are threatened with extinction, with 20% of the extant species of shark being listed by the International Union for Conservation of Nature (IUCN) as threatened (Worm et al. 2013, Dulvy et al. 2014).

The presence of sharks is thought to increase the resilience of some ecosystems against major human impacts, such as global warming and overfishing (Friedlander and De Martini 2002, Myers et al. 2007, Heithaus et al. 2008). Moreover, due to their high mobility, sharks play a key role in connecting distant food webs (Musick et al. 2004, Ferretti et al. 2010). Significant decline or loss of shark populations has resulted in complex changes in marine communities, suggesting that these large predators can exert top-down control over some ecosystems (Sandin et al. 2008). The release of mesopredators from shark predation, yielding stronger predatory pressures on other teleost fishes, invertebrates and even primary producers, have been documented and/or predicted by ecosystem models following a decline in abundances of large sharks (Myers et al. 2007, Ferretti et al. 2010).

There is also an increasing global demand for tourism based on shark encounters (Richards et al. 2015). This sustainable activity can generate significant incomes at local and national levels, providing economic incentives for shark conservation (Clua et al. 2011, Gallagher and Hammerschlag 2011, Cisneros-Montemayor et al. 2013). Sharks are also considered to be valuable as so-called umbrella species; efforts to conserve shark populations and their habitat will result in protection of a large number of other marine species (Thompson and Mintzes 2002, Hearn et al. 2010).

Marine protected areas (MPAs) can play a crucial role in the conservation of shark populations by protecting critical habitats for reproduction and feeding. Given the high mobility and wide home-ranges of many shark species, the utility of MPAs for shark conservation needs to be evaluated (Simpfendorfer et al. 2011). Studies assessing the effectiveness of spatial management approaches in the conservation of elasmobranchs have mostly been limited to small MPAs and/or species having relatively small ranges, such as reef sharks (Aburto-Oropeza et al. 2011, Bond et al. 2012, Knip et al. 2012, White et al. 2015). In fact, no study has yet documented the recovery of shark populations in a large MPA (Ward-Paige et al. 2012).

1.2 Spatial ecology of sharks

1.2.1 Patterns of distribution and abundance

Knowledge of the status of shark populations and their spatial ecology is essential to identify those species and populations most at risk (Simpfendorfer et al. 2011), while providing key information for the design and evaluation of spatial management approaches, such as MPAs (Simpfendorfer et al. 2011, Hammerschlag et al. 2011, Knip et al. 2012). To date, studies of the patterns of distribution and abundance of sharks, demographic models and ecological risk assessments have mostly been based on fishery-dependent data (Cortés 1998, Menni et al. 2010). In addition to the potential ethical and political issues attending such data, fishery-dependent data cannot be obtained from no-take MPAs or areas where shark fishing has been banned. Thus, there is a crucial need for quantitative fishery-independent evaluations of the distribution and abundance of sharks using modern non-lethal survey methods (Hammerschlag and Sulikowski 2011). Such data can serve as a baseline of information for future quantitative evaluations of the potential recovery of shark populations. Towards this end, underwater video techniques provide a non-invasive approach to quantify patterns in the relative abundance and distribution of fishes (Mallet and Pelletier 2014). Baited remote underwater video cameras (BRUVs), deployed on either the bottom or in pelagic environments, are increasingly being used to sample fish populations, and they are especially adept at detecting piscivorous predators (Colton and Swearer 2010, Langlois et al. 2010, White et al. 2013, Espinoza et al. 2014, Santana-Garcon et al. 2014a).

There are few published studies describing patterns of distribution and abundance of sharks at local or regional scales. Habitat requirements and environmental and biological factors affecting the occurrence and distribution of sharks are not well understood (Simpfendorfer et al. 2011, Espinoza et al. 2014). In the few studies published thus far, reef sharks have shown species-specific habitat preferences, although their movements and habitat usage have been related to biological factors (such as prey density, competition, reproduction and dispersal) rather than broad-scale environmental variables (Chin et al. 2012, Heupel and Simpfendorfer 2014). Espinoza et al. (2014) showed that the distributions, assemblage structure, and species richness of sharks on the Great Barrier reef were more strongly associated with geographical factors (such as proximity to reefs, latitude, and distance across the shelf) and variables relating to biophysical habitats (complexity of the reef and percentage cover of hard corals) than environmental factors such as Sea Surface Temperature (SST) or concentrations of Chlorophyll-a.

More studies are needed to identify the major drivers of patterns of distribution and abundance of shark populations worldwide. This is especially urgent in areas that might play a critical role for shark conservation, such as large MPAs, known hotspots of shark diversity or areas that harbour endangered populations of sharks.

1.2.2 Movement patterns – a case-study of the tiger shark *Galeocerdo cuvier*

Understanding the patterns of movement and migration of sharks provides the basis for determining the appropriate spatial scales for marine management (Hammerschlag et al. 2011). Fine-scale data may be used to identify specific habitats or locations that are important to a species, while broad-scale data show migratory routes and pathways that could be established as international marine corridors connecting isolated MPAs (Hammerschlag et al. 2011, Simpfendorfer et al. 2011). The tiger shark (*Galeocerdo cuvier*) is a model species for investigating the spatial patterns of habitat usage by a marine top predator, due to its status as the largest predatory fish in coastal areas of tropical seas. Methods used elsewhere include the deployment of satellite tags (SPOT and PAT), accelerometers, passive and active acoustic telemetry, and crittercams (Heithaus et al. 2002, Heithaus et al. 2007, Nakamura et al. 2011).

Previous studies at other locations have shown that tiger sharks display both long-distance and wide-ranging movements along with more resident behaviours in specific areas (Meyer et al. 2009, Lea et al. 2015). Migrations have been recorded in adult males and females, while juveniles tend to migrate less and remain in cooler areas during winter (Papastamatiou et al. 2013, Werry et al. 2014, Lea et al. 2015). Partial migrations have been repeatedly documented in tiger sharks. Individuals can alternate between transient and resident behaviours, yielding seasonal and inter-annual variations in abundance (Fitzpatrick et al. 2012, Papastamatiou et al. 2013, Holmes et al. 2014, Lea et al. 2015). Aggregations of tiger sharks in specific areas have been documented and may be linked to an abundant source of available prey (Meyer et al. 2009), suggesting that individuals of this species learn from experience about the location and timing of foraging events (Meyer et al. 2010). Simpfendorfer et al. (2001) suggested that tiger sharks may especially target air-breathing species, with turtles identified as the most common prey in their diet. Accordingly, tiger sharks may aggregate in nesting areas of sea turtles to take advantage of abundant prey (Heithaus et al. 2008).

Despite a growing number of published studies focused on patterns of movements and habitat usage by tiger sharks (e.g. Werry et al. 2014, Hammerschlag et al. 2015, Lea et al. 2015), no such studies have been conducted in the Eastern Tropical Pacific (ETP) region. This knowledge would result in a better understanding of the ecological roles of tiger sharks in the region and would provide relevant information to managers and authorities, both to enhance shark conservation and to minimise human-shark conflicts.

1.3 Estimating densities of sharks and their implications in conservation

Marine ecosystems were once dominated by large predators (Jackson et al. 2001). With the current global exploitation of sharks by humans, our understanding of their former natural levels of abundance is limited. The composition of unexploited shark assemblages in the absence of human impacts may have been very different to what is seen today (Friedlander et al. 2010). Surveys in uninhabited, remote and protected locations with minimal human disturbance over long periods of time may provide an indication of predators' natural levels of abundance and community composition (Friedlander et al. 2010).

Underwater visual surveys, remote cameras (such as BRUVs), and mark-recapture methods have all been used to estimate shark abundance, but each method has different intrinsic biases (McCauley et al. 2012). Despite providing a high detection probability for sharks, BRUVs do not provide unbiased estimates of absolute density, as it is not possible to know the area sampled; i.e., the distances from which fish are attracted to the bait (Harvey et al. 2007). Mark-recapture methods are limited to those species having physical features that allow identification of individuals, such as distinctive colour patterns (Vanderklift et al. 2014).

Visual surveys at some remote and near-pristine locations have yielded results that suggest the existence of inverted biomass pyramids; i.e., where the biomass of top predators, mainly sharks, is larger than the biomass of their potential prey (Sandin et al. 2008). However, inverted pyramids may be artefacts of an overestimation of absolute shark densities, due to the small spatial extent and non-instantaneous nature of visual transect surveys (Ward-Paige et al. 2010, Nadon et al. 2012). Researchers conducting underwater visual censuses may count fish that enter the survey area from surrounding areas over the period of time that the survey is being done, with simulation studies indicating that such non-instantaneous surveys may yield upwardly-biased density estimates (Ward-Paige et al. 2010).

A recently-developed alternative to traditional visual surveys—namely, Diver-Operated Video systems with stereo-cameras (stereo-DOVs)—can increase the accuracy of the estimation of fish lengths and sampled area, avoid inter-observer variability, and provide a video record that can be validated or re-analysed (Langlois et al. 2010). The DOV method can be taken one step further to address the issues associated with non-instantaneous surveys. Specifically, a posterior comparative analysis of the video record allows data to be recorded instantaneously (i.e., not counting sharks that enter the survey area in front of the observer after the survey has begun) or non-instantaneously (i.e., counting also any sharks that enter the survey area after the survey has begun). Thus, a formal comparison of resulting estimated densities using these two approaches can be achieved.

Continuous tracking of scalloped hammerhead sharks conducted at the oceanic island of Wolf, at the northern tip of the Galapagos Marine Reserve (GMR), showed an intense use of the more exposed southeast corner of the island (Ketchum et al. 2014a). Hearn et al. (2010) reached similar conclusions after tagging several species of sharks and deploying an array of acoustic receivers at the same island. These previous studies did not provide sufficient information, however, regarding the fine-scale spatial distribution of sharks at these oceanic islands, due to limitations in acoustic telemetry methods, limited coverage and small detection ranges of receivers (Hearn et al. 2010).

In summary, stereo-DOVs implemented at near-pristine locations may be useful for collecting accurate information about the abundance, spatial dynamics, structure and function of sharks in marine ecosystems. Quantifying the ecological role of these top predators can in turn be used to inform policies designed to protect sharks (Sandin et al. 2008, Vanderklift et al. 2014).

1.4 Human attitudes towards sharks

A consequence of the current growth rates of human populations worldwide, particularly in coastal areas, is that marine wildlife and humans are increasingly competing for space and resources. Without properly addressing these potential human-wildlife conflicts, the achievement of a sustainable coexistence might fail, with conservation efforts losing stability and progress (Madden 2004). The successful implementation of conservation initiatives not only relies on robust biological information, but also relies on knowledge of human attitudes and behaviour (Decker and Chase 1997, Kooiman and Jentoft 2009).

Public support and positive attitudes towards environmental issues can lead to important shifts in conservation policies (O'Bryhim and Parsons 2015). In contrast, negative attitudes towards large carnivores that are often perceived as dangerous can counteract conservation efforts, aggravating management policies and increasing illegal hunting (Paulson 1999, Thompson and Mintzes 2002, Whatmough et al. 2011). This direct relationship between public attitudes and behaviour and conservation outcomes is especially relevant in the case of sharks, due to their critical conservation status and the generally fearful and negative response of most humans towards them (Thompson and Mintzes 2002, Whatmough et al. 2011). The economic value of sharks has been explored in several studies, but relatively few researchers have studied the attitudes of people towards sharks and their conservation (Simpfendorfer et al. 2011).

Motivation, knowledge, values, experience, culture, educational level, and demographic variables (such as age, gender, income or ethnicity) have been discussed as potential factors that might shape the perception, attitude and behaviour of people towards sharks (Thompson and Mintzes 2002, O'Bryhim and Parsons 2015). Garla et al. (2015) and O'Bryhim and Parsons (2015) found that knowledge of sharks was the most important factor shaping attitudes and willingness to support the conservation of sharks. In contrast, Friedrich et al. (2014) found that personal experience, not knowledge, was the most influential factor motivating engagement in shark conservation. However, attitudes can vary strongly among individuals having different ethnic, cultural and socio-economic backgrounds at a given place and time. For example, local people at the Fernando de Norohna Archipelago (Brasil) were found to have less knowledge and fewer positive attitudes towards sharks than tourists in this tropical archipelago environment (Garla et al. 2015). Thus, studies of attitudes and implications for management and communication with the public must take such factors into account.

The need for social research is particularly relevant in areas where humans and sharks coexist in close proximity. Such locations provide an excellent opportunity to evaluate potential human-wildlife conflict scenarios, as people are more likely to have direct interactions with sharks; such events typically receive extensive international media coverage (Muter et al. 2013, Garla et al. 2015). An increase in our understanding of the human sociology surrounding sharks will improve management, the formation of policies and effective governance (Jentoft et al. 2012, Muter et al. 2012).

1.5 The study system – the Galapagos Marine Reserve

The Galapagos Marine Reserve (GMR) is a hotspot of biodiversity of global significance, and one of the few MPAs in the world where abundant populations of large sharks can still be found (Zárate 2002, Hearn et al. 2010, Salinas-de-León et al. 2016). The Galapagos Archipelago comprises 13 major islands and over 100 islets situated over the equator, at approximately 1,000 km off mainland Ecuador, in the ETP region (Snell et al. 1995). The convergence of three major oceanic current systems, together with the proximity of the Equatorial Front and exposure to upwelling conditions, makes the physical environmental setting of these islands both unique and highly variable (Palacios 2004).

The GMR was granted with a national protected area status in 1998. The Management Plan for the Conservation and Sustainable Uses of the GMR established a provisional multi-use zoning scheme, which was agreed and put into place in 2000 (Heylings et al. 2002). In order to enhance the integration of the marine and terrestrial protected areas and articulate them with the populated areas, a new zoning scheme for the GMR was defined and established in 2016. With the declaration in the same year of a Marine Sanctuary around the oceanic islands of Darwin and Wolf and several seamounts, 33% of the GMR is now a no-take marine reserve. In the rest of the GMR the local artisanal fleet can operate (Fig. 1-1).

Shark finning was initiated in the Galapagos Islands in the 1950s (INP 1964) and then expanded significantly in the late 1980s, when thousands of sharks were caught by industrial vessels for the Asian market (Camhi 1995). While commercial fishing, including shark finning, was banned after the implementation of the GMR, it was not until 2003 that the Ecuadorian Government explicitly prohibited shark fishing, landing and trading within its boundaries. At a national scale, sharks can only be caught and commercially exploited if they arise as incidental by-catch in Ecuadorian waters. However, in 2007 a presidential decree allowed the export of the fins from these 'incidental' captures, which has resulted in a 40% increase in shark catches between 2008 and 2014 according to the Ecuadorian Secretary of Marine Resources. All available evidence indicates that Ecuadorian fishers target sharks and it is suspected that a substantial proportion of the sharks landed in surrounding continental coastal areas has been caught illegally at the GMR (Jacquet et al. 2008, Carr et al. 2013).

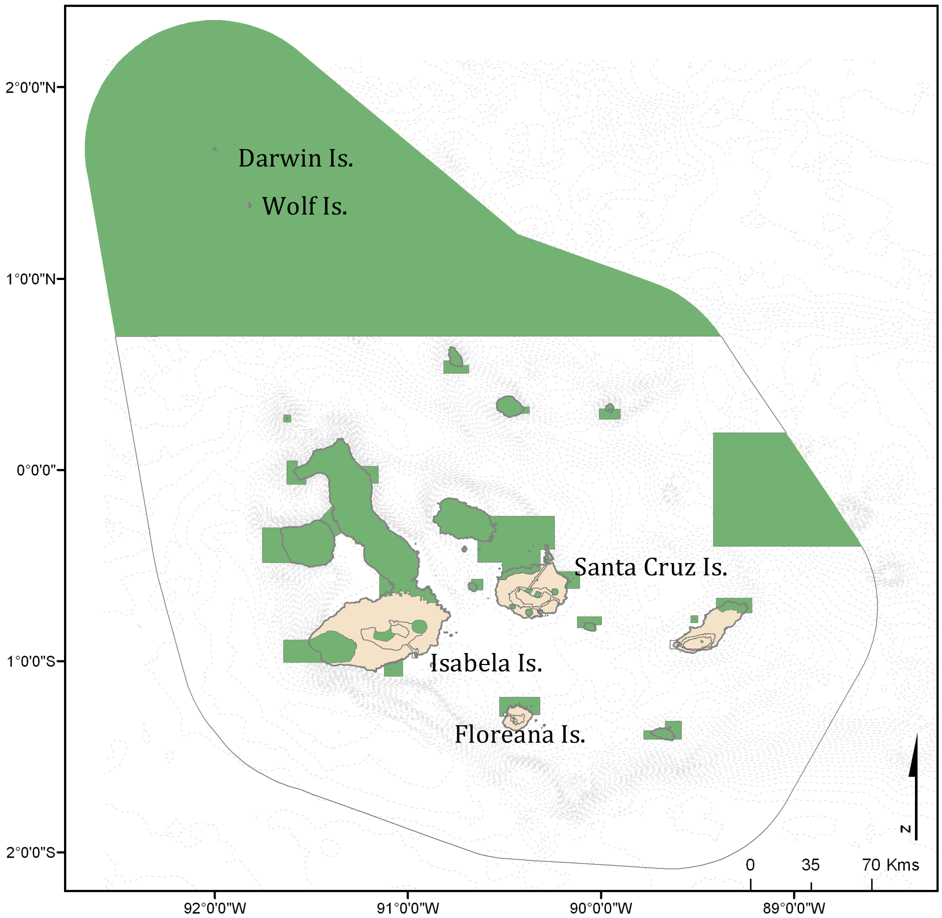

Figure 1-1. Map showing the zoning scheme implemented at 2016 at the Galapagos National Park (GNP) and Galapagos Marine Reserve (GMR). The black line indicates the boundary of the GMR and the green polygons are dedicated conservation areas, where all commercial fishing activities are prohibited. Grey dashed lines show bathymetry (100 m isobaths).

The islands of Darwin and Wolf, at the northern extent of the GMR, comprise the Far North bio-geographical region, which is mostly influenced by tropical conditions provided by the warm Panama Current (Edgar et al. 2002). These oceanic islands receive relatively low human impact, and harbour extraordinarily high densities of multiple species of large sharks and other marine top predators (Hearn et al. 2010, Salinas-de-León et al. 2016). These islands provide a unique opportunity to study shark assemblages in near-pristine conditions.

A severe general decrease in the number of sharks has been noted by observers at the GMR (Baum et al. 2007), potentially due to illegal fishing in the reserve (Carr et al. 2013). Despite the iconic status of the islands and their marine life, there has been no scientific evaluation of the effectiveness of the GMR in protecting shark populations, and the conservation status and spatial ecology of coastal semi-pelagic shark species remain unknown.

From a human perspective, the Galapagos Islands have a unique biological and historical identity, being recognized as a Natural World Heritage Site by UNESCO (UNESCO 2017) and constituting one of the most renowned and iconic environmental sites in the world. The Galapagos Archipelago harbours a resident human population and sees a growing number of visitors year on year. The GMR is governed under a spatial management approach in order to integrate the conservation of its marine resources with the human activities conducted within its boundaries. Wide public interest in the natural history of the Galapagos ensures that key scientific and management outcomes will receive global exposure and can serve as models for sustainable coexistence of humans and wildlife.

1.6 Aims

This thesis was conceived as a broad body of scientific work with a central aim of improving the management and conservation of shark populations at the GMR. The research questions addressed in this thesis where identified and selected by an inter-institutional group of shark researchers through an evaluation of the priorities for shark research and conservation at the GMR, resulting in a technical report presented to the Galapagos National Park Directorate (GNPD) in 2013 (Acuña-Marrero et al. 2013a).

The thesis contains four central chapters, in addition to the introduction and general discussion. The four central chapters have been written as stand-alone articles that have been published in or submitted to peer-reviewed international scientific journals. Specifically, they address the following objectives and associated research hypotheses (H):

- Objective 1: To characterise the distribution and relative abundance of coastal sharks in the Galapagos Marine Reserve.

    H1.1: Sharks have different species-specific habitat requirements (Espinoza et al. 2014); thus, spatial distributions will differ among shark species.

    H1.2: Sharks respond positively to their prey (Hearn et al. 2010, Ketchum et al. 2014a, Klimley 2015); thus, the spatial distribution of sharks will be non-random and will be aggregated in areas of high prey abundances.

    H1.3: Size segregation is widely documented in sharks (Burgess et al. 2014); thus, individual sharks of different sizes will show different non-random patterns of distribution and abundance across the GMR.

    H1.4: A general characteristic of semipelagic sharks is sexual spatial segregation (Klimley 1987); thus, male and female sharks will show different non-random patterns of distribution and abundance across the GMR.

- Objective 2: To describe the habitat usage and patterns of movements of tiger sharks at the GMR.

    H2.1: Tiger sharks show ontogenic differences in their diets and therefore in their patterns of movement and habitat usage (Meyer et al.

2009); thus, sharks of different sizes will show spatial and temporal differences in their activity-spaces at the GMR.

H2.2: Tiger sharks show a high degree of residency and site fidelity in specific areas where sea turtles aggregate in high numbers during their nesting season (Heithaus et al. 2008, Meyer et al. 2009, Fitzpatrick et al. 2012); thus, movements of tiger sharks will be spatially and temporally correlated with the most important nesting events of sea turtles at the GMR.

H2.3: Patterns of movements of tiger sharks at the population level are characterised by partial migration (Papastamatiou et al. 2013, Holmes et al. 2014); thus, only a sub-set of tiger sharks will conduct broad-scale regional movements while others will remain as year-round residents in the GMR.

- Objective 3: To provide an accurate estimation of biomass and fine-scale spatial distributions of sharks at the oceanic islands of Darwin and Wolf.

H3.1: Estimates of individual and biomass densities of sharks based on non-instantaneous records will be consistently positively biased (Ward-Paige et al. 2010, Nadon et al. 2012); thus, estimates of individual and biomass densities of sharks from non-instantaneous records will result in higher estimates when compared to using instantaneous records.

H3.2: In offshore islands of the GMR, sharks are not randomly distributed spatially, but tend to aggregate in areas exposed to oceanic currents (Hearn et al. 2010, Ketchum et al. 2014a); thus, sharks at Darwin and Wolf islands will show a non-random spatial distribution characterised by higher relative abundance in areas exposed to oceanic currents.

- Objective 4: To characterise the attitudes of people in the local community and visitors to the Galapagos Islands towards sharks and their conservation.

  H4.1: Knowledge, values, personal experiences and demographic variables can influence the attitudes and behaviour of people towards sharks (Friedrich et al. 2014, O'Bryhim and Parsons 2015); thus, attitudes held and behaviours exerted towards sharks by people at the Galapagos Islands will be correlated with their personal experiences, values and knowledge of sharks.

  H4.2: Visitors (tourists) are more likely to engage and cooperate with management actions aimed at shark conservation than residents (Garla et al. 2015); thus, visitors to the Galapagos Islands will have more positive attitudes towards sharks than locals.

A diverse group of methods were used to achieve the proposed objectives of this thesis. The patterns of distribution and abundance of sharks were evaluated by deploying benthic and pelagic baited remote underwater stereo-video systems (stereo-BRUVs) around the coastal areas of the GMR across the two oceanographic seasons occurring at the Archipelago. The same methodology was implemented at specific areas where tiger sharks aggregate to shed light on the habitats used by this apex predator; this was supplemented by the use of acoustic and satellite tags to study their movement and migratory patterns. Belt transects using stereo-DOVs in combination with towed GPS units were conducted around Darwin and Wolf islands to compare estimates of density and biomass obtained using non-instantaneous *vs* instantaneous surveys, and also to provide fine-scale distributional maps of the target species. Finally, interviews using closed-ended questions were conducted to canvas locals and visitors to the Galapagos Islands to quantify the influence of different emotions and beliefs, together with demographic and socio-economic factors, that might shape the attitudes and behavioural responses of people towards sharks.

In the General Discussion (chapter 6) results are discussed, articulating their implications as well as the major novel and unique contributions of this thesis. An overall assessment of the potential performance of the GMR in shark conservation is also considered, based on these results, including recommendations to managers and proposing directions for further research.

Chapter 2. Spatial and temporal distributions of coastal shark populations at the Galapagos Marine Reserve

2.1 Abstract

A better understanding of the patterns of distribution and abundance of sharks and their biological and environmental drivers is essential to establish baselines and 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 seasonal patterns in coastal shark assemblages at the Galapagos Marine Reserve (GMR). From 629 stereo-BRUV deployments, 877 sharks from 10 species were recorded over two seasons. Shark assemblages displayed high spatial variation, likely in response to the diversity of habitats occurring at the GMR. The relative importance of environmental and biological drivers differed among shark species according to their mobility. Semipelagic shark occurrence were mostly influenced by exposure to open and deep waters, sea surface temperature and richness of the associated assemblage, whereas occurrences of benthic sharks were primarily related to the type of seabed cover. Some species displayed widespread distributions across the Archipelago, but showed a size range mostly limited to juvenile (*Carcharhinus galapagensis*) or adult individuals (*C. limbatus* and *Triaenodon obesus*), while others displayed spatial restrictions in their distributions due to geographical features (*Sphyrna lewini* and *Galeocerdo cuvier*) or habitat type (Triakidae species and *Heterodontus quoyi*). The highest diversity of sharks was found in the center-south of the Archipelago, in areas of heterogeneous habitats and high fish diversity (islets and Floreana Island), while the northern oceanic islands (Darwin and Wolf) harboured the highest recorded total abundances of sharks. Our results show a unique coastal shark

community with a high spatial variability across the Archipelago, which is dominated by large semipelagic species, but with the particularity of the presence of less-mobile benthic species that are absent from any other oceanic island at the Eastern Tropical Pacific region.

2.2 Introduction

There is a global decline in populations of sharks (Dulvy et al. 2014), mainly caused by 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 communities 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 and Hammerschlag 2011).

Worldwide coastal areas provide a wide range of habitats that are used by a variety of shark species, with greater representation of the Carcharhinidae and Sphyrnidae families in the tropics and of the Triakidae family 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 two general models occur with some shark species even exhibiting opposing strategies in different areas of their ranges (Knip et al. 2010).

There are few studies describing 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). At 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 and 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 sex 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 been focused on inshore nursery areas used by neonate and juvenile sharks (Heupel and Simpfendorfer 2005), although all aspects and stages should be taken into consideration (Kinney and Simpfendorfer 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, sex 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 related to the associated marine macrofaunal assemblage. 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 km^2) and 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 at the Archipelago 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 stereo-BRUVs to establish a first comprehensive baseline. Specifically, we aimed to: (i) determine which spatial and seasonal factors were associated with variation in shark assemblages, (ii) explore potential inter-specific associations between shark species, (iii) provide distribution and abundance maps for coastal sharks assemblages and for the different size and sex categories within each species and size/sex levels, (iv) identify the most influential environmental and biological drivers of the occurrence of each shark species, and (v) examine potential associations between sharks and non-shark species from the fish and marine macrofaunal assemblage.

2.3 Materials and methods

Study site

The Galapagos Islands comprise 13 major islands and over 100 islets situated approximately 1,000 km west of continental Ecuador, in the Eastern Tropical Pacific region (Snell et al. 1996; Fig. 2-1a). The Galapagos Archipelago is characterized by unique and highly variable oceanographic conditions due to the confluence of three major oceanic currents, its proximity to the Equatorial Front (EF), and strong, periodic upwellings (Palacios 2004). Consequently, four major bioregions have been identified according to subtidal reef communities (Edgar et al. 2004; Fig. 2-1b), which cover a wide range of habitats, but are primarily composed of rocky reefs interspersed with areas of soft sediment (Bustamante et al. 2002).

Most of the Archipelago sits over a relatively shallow platform that drops dramatically towards the west and southwest, reaching depths of 3,000 m only 10 km from the coastline in certain areas (Banks 2002). The Center-South bioregion covers a larger proportion of this insular platform, all except its western side, which is located in the Cold-West bioregion (Fig. 2-1b). Towards the northeast, this insular shelf fuses with the Coco and Carnegie ridges, with a more gradual bathymetric gradient from where the

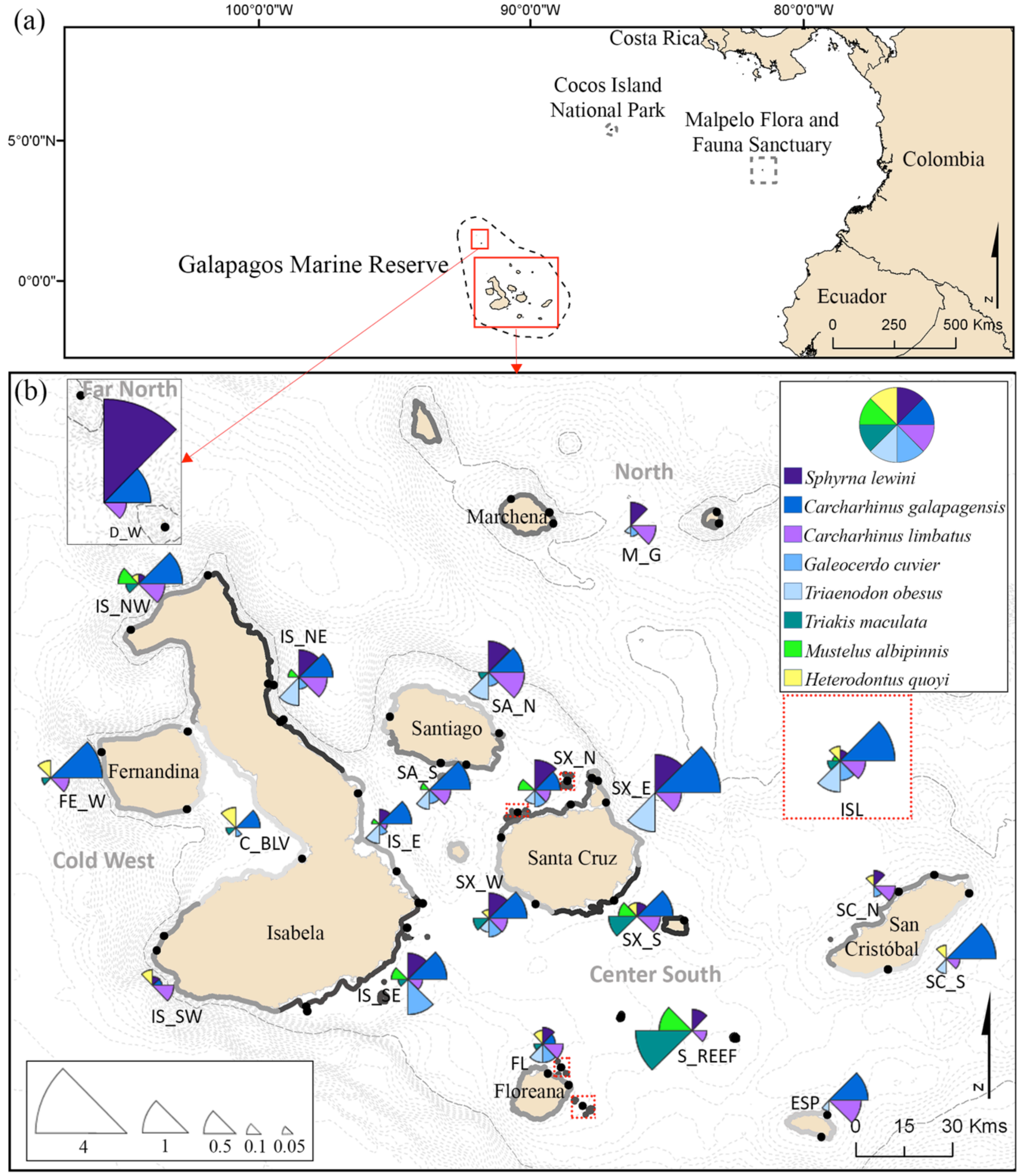

Figure 2-1. Maps showing (a) the location of the Galapagos Archipelago in the Eastern Tropical Pacific and (b) the distribution and abundance of coastal sharks recorded by stereo-BRUVs within the Galapagos Marine Reserve (GMR). Black dashed lines in panel (a) indicate the boundaries of the MPAs located at oceanic archipelagos. In panel (b), bold names in grey indicate bioregions with strata delimited by continuous lines in grey scale at the 20 m isobaths of each island and the stratum composed of islets is highlighted by a red-dotted-line square). Black dots show the location of the study sites and grey dashed lines indicate the 100 m isobaths (the 1,000 m isobath is highlighted with thicker grey dashed lines). Presence and relative abundance of coastal sharks is indicated using segmented bubble plots where each shark species is represented by a circle segment corresponding to a given colour (upper right legend) whose size is proportional to its average relative abundance per stratum (# sharks per 90 min, lower left legend).

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

Variation in the strength of major oceanic currents converging at the Archipelago yields two 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 Archipelago (Palacios 2004). In addition, periodical climatic disturbances, such El Niño Southern Oscillations (ENSO), significantly affect the marine communities of the Galapagos Archipelago (Chávez et al. 1999).

Stereo-BRUVS

Baited remote underwater stereo-video systems (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, size- and sex-distribution of shark species. The systems consisted of two GoPro HERO4 Black edition high-definition digital cameras (GoPro, Inc., California, USA) 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 two 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 Nov-Dec 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 and Santana-Garcon (2015). A minimum of four replicates, each with a deployment time of 90 min was deemed appropriate (App. A, Fig. A-1). 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 (App. A, Fig. A-2). 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 four replicates of each type of set were separated by a minimum distance of 500 m to minimize 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 one hour 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* (chlo-*a*, mg m^{-3}) was obtained from remote-sensing data at a 4 km spatial resolution (NASA 2016). We used the distance from the deployment point to the 1,000 m isobaths, obtained from ArcGIS 10.1 software (ESRI, Redlands, California, USA) 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 and Gill 2017) and was used as a surrogate for exposure (following Smith et al. 2013). Information about both, the distance to the insular shelf boundaries and the exposure, can inform about the degree of access to open and/or deeper waters and pelagic prey by the recorded sharks. Fine-scale habitat was characterized visually during the video analysis for each benthic stereo-BRUV 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 2-1). Our modified stereo-BRUV benthic setting with the floating camera resulted in a field of view that was not fixed. Thus, the fine-scale habitat characterisation was conducted using the entire 90 minutes of video footage for each deployment. Rotation of the camera often allowed for a complete view (360º) of the surrounding benthic habitat.

The software EventMeasure (SeaGIS Pty Ltd.) was used to analyse the 90 min video footage. All fish (excepting those species with maximum total length TL <10 cm) and macrofaunal species (sea 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 one still video frame, as described by Cappo et al. (2004).

Table 2-1. Environmental and biological predictor variables included in models of shark relative abundances, using distance–based redundancy analysis (DISTLM, dbRDA) and boosted regression trees (BRTs).

Habitat characterization	Predictor	Type	Range	Mean ± SD
Geographic	Distance to 1000m isobath (m)	continuous	316 – 66,990	18,906 ± 15,653
	Mean fetch (m)	continuous	9,095 – 48,323	23,552 ± 7,198
Sea Surface Temperature	SST (°C)	continuous	18.50 – 29.90	24.91 ± 2.62
Productivity	Chlo_a (mg m^{-3})	continuous	0.16 – 1.72	0.58 ± 0.33
Fish and macrofauna assemblages (excluding sharks)	S (species richness)*	continuous	0 – 29	9.73 ± 7.83
	Log (N+1) (species abundance)*	continuous	0 – 3.05	1.99 ± 2.05
	Gini-Simpson (species evenness)*	continuous	0 – 0.94	0.48 ± 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°; 2=33°–66°; 3=66°–90°	1.48 ± 0.63
	Rock_cover (%)	ordinal	0 – 100	60.28 ± 37.42
	Sand_cover (%)	ordinal	1 – 100	39.72 ± 37.42
	Ahermatypic corals_cover	ordinal	0=nothing; 1=low; 2=medium; 3=high	0.87 ± 1.09
	Hermatypic corals_cover	ordinal		0.04 ± 0.22
	Macroalgaes_cover	ordinal		0.89 ± 1.10
	Rubbles_cover	ordinal		0.13 ± 0.59

*by 90-min deployment

For sharks, measurements of fork length (FL, averaged across three 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 and Pauly 2015). Individuals that could not be measured were classified as *maturity-indeterminate*. In the case of the whitemargin smoothhound (*Mustelus albipinnis*) and the spotted houndshark (*Triakis maculata*), there were no published sizes for sexual maturity, 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.

Sex 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 *sex-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-minute 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 *T. maculata*); and (3) the total body length (taken as an average of three measurements, each from a different video frame) when this differed by more than 50 % between individuals.

MaxN was also recorded on a total of 154 fish and marine macrofaunal 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 three complementary measures of diversity: namely, log-relative abundance (measured as log(*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 AIC criterion (AICc; Burnham and 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 5,000 m in perimeter were classed as *islands* while groups of nearby islets (i.e., within a range of 4 km from the center 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 5,000 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 1,000 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–four benthic and four 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 (M_G), in the northern bioregion, where five sites were randomly selected to obtain adequate representation. In addition to the randomly selected sites, a total of nine hotspots, 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 one additional site was chosen randomly. The four islets and two submerged reef sites identified by us were included in the sampling, yielding two additional geographic strata (islets (ISL) and submerged reef (S_REEF)), as these habitats are traditionally recognized as areas of high relative abundance of sharks in the Galapagos Islands. The resulting 48 study sites (Fig. 2-1b) were surveyed using both types of stereo-BRUV settings during each of two survey campaigns: one in the warm season (Mar-Apr) and another in the cold season (Aug-Sep).

In summary, the full sampling design had five 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; two levels, fixed, crossed with all other factors) and season (two 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

In order to analyse for spatial variation in the structure of shark assemblages we used distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on a matrix of pairwise zero-adjusted Bray-Curtis similarities (Bray and Curtis 1957, Clarke et al. 2006) of square-root-transformed relative abundances of 10 shark species (*cMaxN*), averaged by site and position in the water column (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 and Lane 1983). Statistically significant (i.e., $p < 0.05$) interactions were further explored with appropriate *post hoc* pair-wise tests. Patterns of similarities among shark assemblages by stratum and bioregion were visualised using non-metric multidimensional scaling (nMDS) ordination (Kruskal and Wish, 1978) of the stratum-by-position-in-the-water-column centroids. In addition, inter-specific associations were visualised using nMDS ordination based on the index of association (Somerfield and 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 sex 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 2-1) using distance–based redundancy analysis (dbRDA; Legendre and Anderson 1999, McArdle and 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 2-2). We used the distance-based multivariate analogue to AICc (Burnham and 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 and Gorley 2015) with the add-on package PERMANOVA+ (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-square 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.

In order to identify the most influential environmental and biological drivers (Table 2-1) of the log abundance, species richness and occurrence (for individual species and individual size categories) of sharks at replicate level 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 the coastal shark species. Partial dependence plots were produced to illustrate salient patterns and relationships in these models and to identify the most important predictor variables in each case (following

Table 2-2. Summary of shark sightings, abundance and mean size recorded by the stereo-BRUVs at the GMR.

Family (semipelagic/benthic)	Species	total # indiv.	% total sharks	Highest *cMaxN*	*cMaxN* per deployment (mean ± SD) total	benthic	pelagic	Fork length (FL) (mean ± SD)
Carcharhinidae		585	66.70					
semipelagic	*Carcharhinus galapagensis*	334	38.08	8	0.52 ± 1.13	0.76 ± 1.30	0.26 ± 0.85	116.98 ± 50.43
	Carcharhinus limbatus	117	13.34	3	0.18 ± 0.43	0.17 ± 0.41	0.19 ± 0.46	156.19 ± 35.93
	Carcharhinus altimus	6	0.68	3	0.01 ± 0.14	0.01 ± 0.16	0.01 ± 0.10	173.95 ± 38.65
	Carcharhinus falciformis	6	0.68	2	0.01 ± 0.11	< 0.01	0.16 ± 0.02	142.40 ± 32.54
	Galeocerdo cuvier	42	4.79	6	0.07 ± 0.36	0.09 ± 0.42	0.04 ± 0.26	202.72 ± 71.96
benthic	*Triaenodon obesus*	72	8.21	4	0.11 ± 0.44	0.21 ± 0.59	0.01 ± 0.10	114.54 ± 16.84
	Carcharhinidae UN	8	0.91		—	—	—	—
Sphyrnidae		207	23.60					
semipelagic	*Sphyrna lewini*	207	23.60	24	0.32 ± 1.69	0.36 ± 1.76	0.29 ± 1.62	160.35 ± 44.96
Triakidae		61	6.96					
benthic	*Mustelus albipinnis*	24	2.74	3	0.04 ± 0.24	0.07 ± 0.33	0	101.23 ± 30.34
	Triakis maculata	36	4.10	5	0.06 ± 0.38	0.12 ± 0.51	0	124.73 ± 17.36
	Triakidae UN	1	0.11		—	—	—	—
Heterodontidae		24	2.74					
benthic	*Heterodontus quoyi*	24	2.74	3	0.04 ± 0.23	0.07 ± 0.31	0	48.06 ± 7.46

**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.

**Carcharhinidae and Triakidae UN refer to individuals belonging to these families that could not be identified at species level.

Elith and Leathwick 2016). Prediction performance was evaluated using cross-validation (estimated deviance explained) and the area under the Receiver Operating Characteristic curve (AUC; Hosmer and Lemeshow 2000). Accordingly, BRT models with AUC scores below 0.7 were deemed to have poor predictive performance and were thus discarded.

Finally, we examined the relationship between: (i) 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) and (ii) the assemblage of non-shark species (i.e., other fishes and macrofauna) conducting a canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) in a canonical-correlation-type analysis. Doing so, we explored potential associations between sharks and non-shark species, such as predator-prey relationships or cleaning interactions. The CAP analysis was based on a Bray-Curtis similarity matrix constructed from fourth-root-transformed relative abundances (*MaxN*) of fishes and marine macrofauna (excluding sharks). An appropriate number (m) of PCO axes to use for the CAP analysis was chosen as the value of m that minimised the leave-one-out residual sum of squares. A vector overlay on the resulting CAP ordination plot was used to help identify non-shark species having strong associations with shark richness and abundance.

2.4 Results

Sampling and summary details

We sampled a total of 45 sites with 330 stereo-BRUV deployments (178 benthic and 152 pelagic) during the warm season (Mar-Apr 2015); three sites were not surveyed due to time/weather constraints. During the cool season (Jul-Sep), we surveyed 40 sites with 299 deployments (156 benthic and 143 pelagic); eight 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 four different classes and 53 families.

A total of 10 shark species from four families were recorded, consisting of 877 individual sharks (1.39 % of all records; Table 2-2 and App. A, Fig A-3). FL measurements, and therefore size categorization, could be done on 68.19 % of these individuals, and sex 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 ± SD), and species richness varied between 0 and 4 (0.79 ± 0.93), with at least one 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 two sites located at Wolf and Darwin islands recorded the highest total numbers of sharks (107 and 54, respectively). However, they were not among the nine 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. 2-1b). The highest total numbers of sharks were recorded at Darwin and Wolf (D_G), the Islets (ISL) and Santa Cruz East (SX_E) strata, which together accounted for 40% of all records. While Darwin and Wolf (D_G) and Santa Cruz East (SX_E) were among the strata with lowest species richness, islets (ISL) harboured the richest shark assemblage, with 8 species, only equalled by the stratum at Floreana (FL; Fig. 2-1b).

Spatial patterns for individual shark species

Carcharhinus galapagensis

The Galapagos shark (*C. galapagensis*) was the most abundant species recorded (Table 2-2), being also relatively widespread, observed in 16 out of 21 strata (Figs. 2-1b and 2-2a). The majority of the sightings of this species (66 % overall) were juvenile individuals (Figs. 2-2a and 2-3a). 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 adult males of this species were recorded (Fig. 2-2a).

Sphyrna lewini

The scalloped hammerhead shark (*S. lewini*), the second most abundant species (Table 2-2), had 59 % of its records in the Darwin and Wolf (D_G) stratum (Figs. 2-1a and 2-2b) and, in contrast with *C. galapagensis*, was rarely observed in the Cold-West bioregion (Fig. 2-2b). For *S. lewini*, the relative abundance recorded for adults of both sex was similar to the relative abundance of juveniles (Fig. 2-3b).

Carcharhinus limbatus

The blacktip shark (*C. limbatus*) had the broadest spatial distribution of all shark species, being absent in only one of the 21 strata (Canal Bolívar, C_BLV; Figs. 2-1a and 2-2c). Most of the recorded individuals of this species were adults, and predominantly female (Figs. 2-2a and 2-3c).

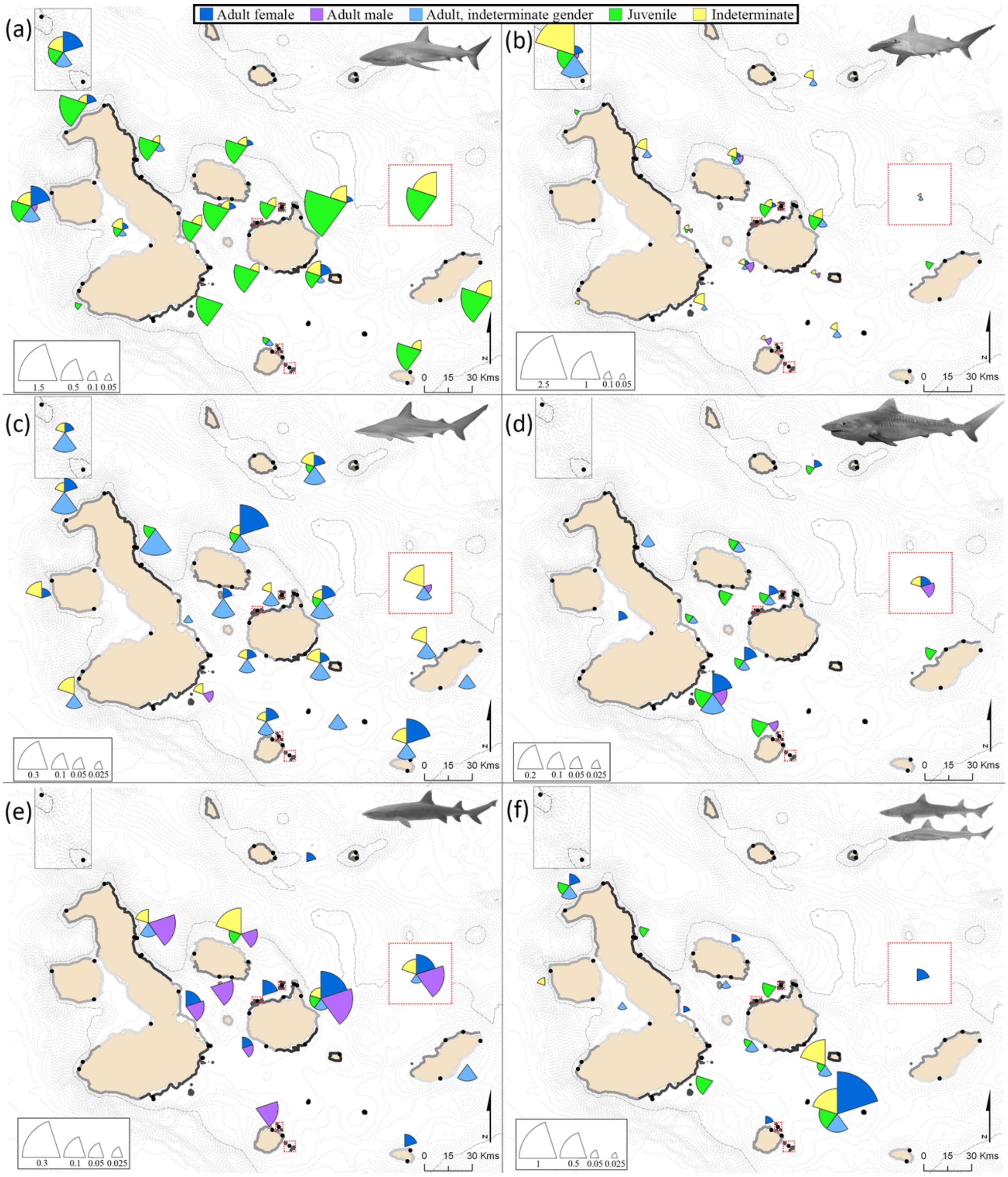

Figure 2-2. Maps showing the distribution and relative abundances of different sizes and sex categories of the most common coastal shark species (a: *Carcharhinus galapagensis*, b: *Sphyrna lewini*, c: *Carcharhinus limbatus*, d: *Galeocerdo cuvier*, e: *Triaenodon obesus*, f: *Triakis maculata* and *Mustelus albipinnis*) recorded by stereo-BRUVs at the Galapagos Marine Reserve. Black dots show the locations of the study sites and grey dashed lines indicate the 100 m isobaths (1,000 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 (# sharks per 90 min, see the individual legends with a separate scale provided on each map) for each of the different size/sex categories (as different colours).

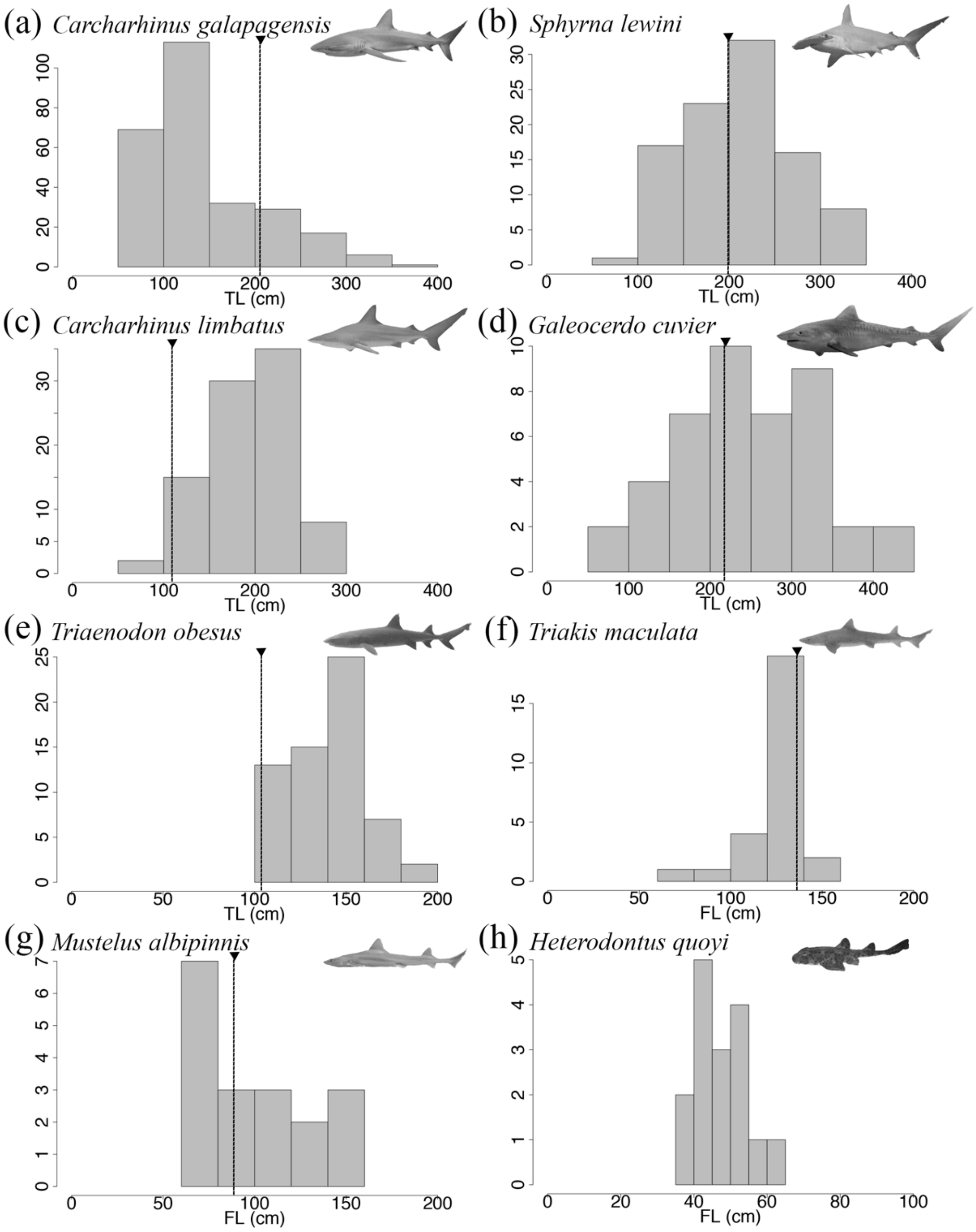

Figure 2-3. Size distribution of the eight most common shark species recorded by the stereo-BRUVs at the Galapagos Marine Reserve. Y-axes indicate the number of recorded individual sharks per species. Dashed lines indicate the smallest size of the published range of lengths for sexual maturity for each 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).

Galeocerdo cuvier

The largest shark species recorded, the tiger shark (*G. cuvier*), was mostly sighted at the center-south of the Archipelago, with the majority of records occurring in the strata of Isabela Southeast (IS_SE), islets (ISL) and Floreana (FL) (Figs. 2-1a and 2-2d). For tiger sharks, the proportion of males *vs* females and adults *vs* juveniles were similar (Figs. 2-2d and 2-3d).

Triaenodon obesus

The whitetip reef shark (*T. obesus*) was also mostly sighted in the center-south of the Archipelago (Fig. 2-2e). Records of juveniles were almost absent for this species, with adult males and females usually recorded together (Fig. 2-3e).

Triakidae species

The spotted hound shark (*Triakis maculata*) and the white-margin fin smooth-hound shark (*Mustelus albipinnis*) were located mostly in the southern part of the Archipelago (Fig. 2-1b). These two species were the most abundant in the Submerged reef (S_REEF) stratum (Figs. 2-1a and 2-2f). In the case of *T. maculata*, most recorded individuals were close to the size of sexual maturity (Fig. 2-3f), while *M. albipinnis* provided records of both juveniles and adults (Fig. 2-3g). No males were recorded for either *T. maculata* or *M. albipinnis*.

Heterodontus quoyi

The Galapagos bullhead shark (*H. quoyi*) was observed in the southern and western parts of the Archipelago (Fig. 2-1b). Sizes of individuals were mostly limited to 40-60 cm FL (Fig. 2-3h).

Carcharhinus falciformis and *C. altimus*

The other two 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 2-2); *C. falciformis* was observed at Darwin and Floreana Islands, and *C. altimus* was observed at Darwin, Isabela, and San Cristóbal Islands.

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 2-3). The Far-North, North and Cold-West bioregions were shown in the nMDS plot to have distinct assemblages, with strata within the Center-South bioregion showing high variability relative to other bioregions (Fig. 2-4). Differences between shark assemblages recorded by the benthic and pelagic stereo-BRUVs were apparent for the Center-South and Cold-West bioregions (Table 2-3, pair-wise tests). Benthic assemblages were generally more variable than pelagic assemblages (Fig. 2-4).

The two positions in the water column (benthic *vs* pelagic stereo-BRUVs) recorded significantly different proportions of different shark species and different size distributions (juveniles *vs* adults) of sharks ($\chi^2_{[3]} = 19.04$, $p < 0.001$ and $\chi^2_{[1]} = 6.04$, $p = 0.014$, respectively). In addition, both the species 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 four species were absent from pelagic stereo-BRUV footage. These four species were categorised as *benthic* sharks, and the

Table 2-3. PERMANOVA partitioning using Type III SS based on adjusted Bray-Curtis dissimilarities of spatial variation in the structure of the shark assemblages (using square-root-transformed values of *cMaxN*) in response to the full 5-factor experimental design; p-values were obtained using 9,999 permutations of residuals under a reduced model. Bold numbers indicate statistical significance (P < 0.05).

Source	Shark assemblage structure				
	df	MS	Pseudo-F	P(perm)	ECV
B*vs*P	1	1,059.1	3.8126	**0.0105**	41.9
Bioregion	3	3,037.8	5.7067	**0.0004**	164.6
Stratum(Bi)	17	828.9	1.5808	**0.0191**	72.6
B*vs*PxBi	3	582.9	2.0982	**0.0256**	39.6
Site(St(Bi))	27	527.1	1.8976	**0.0002**	127.0
B*vs*PxSt(Bi)	Pooled term				
Residual/Pooled	42	277.8			277.8
Pairwise test			**t**	**P**	
Far North	B*vs*P		1.0866	0.2519	
North	B*vs*P		0.8190	0.5134	
Center-South	B*vs*P		4.7286	**0.0001**	
Cold-West	B*vs*P		2.8248	**0.0080**	

df, degrees of freedom
MS, mean square
ECV, estimated component of variation

other six as *semipelagic* sharks for subsequent analyses of potential environmental and biological drivers (see Table 2-2).

The four 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. 2-5). Other species did not show any strong spatial associations, with the exception of the two Triakidae species, whose spatial occurrences were >20 % similar (Fig. 2-5).

Environmental and biological drivers

Variation in either the structure of assemblages including all sharks (benthic and semipelagic sharks combined), or semipelagic sharks alone were best explained by a

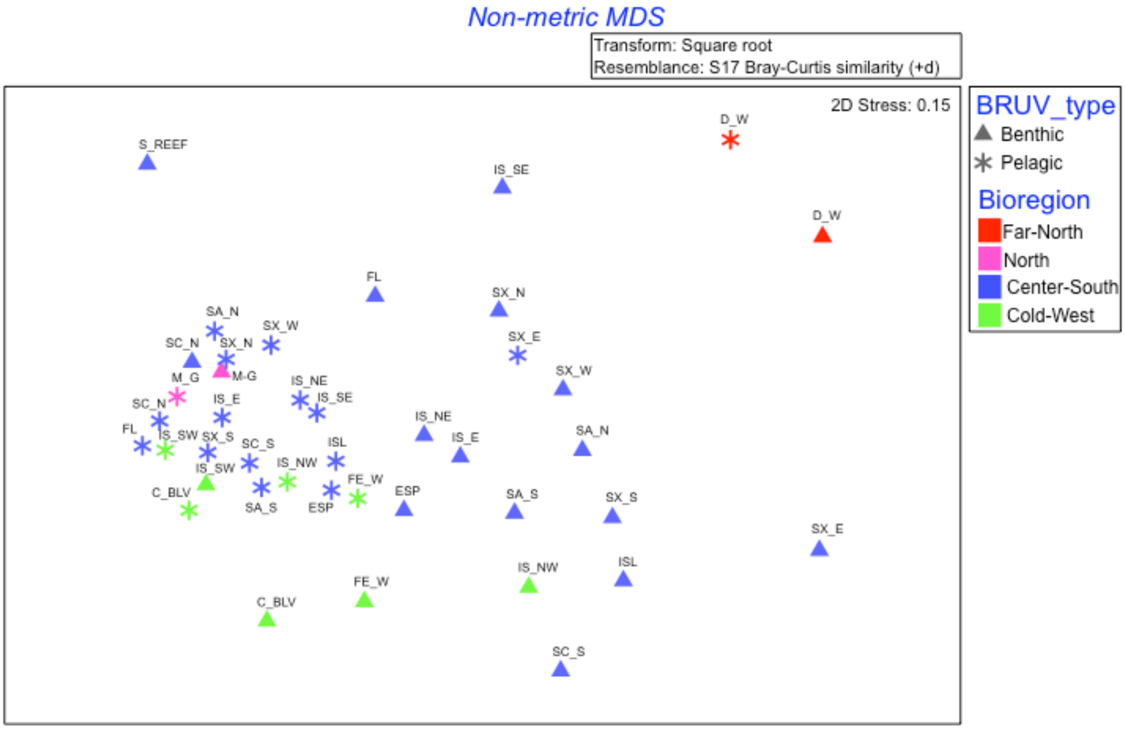

Figure 2-4. Non-metric MDS ordination plot of shark assemblages at the GMR, based on a zero-adjusted Bray-Curtis similarity matrix (Clarke et al. 2006) produced from square-root-transformed relative abundances of shark species, averaged by stratum and BRUV type. Labels indicate the different strata (Fig. 2-1b).

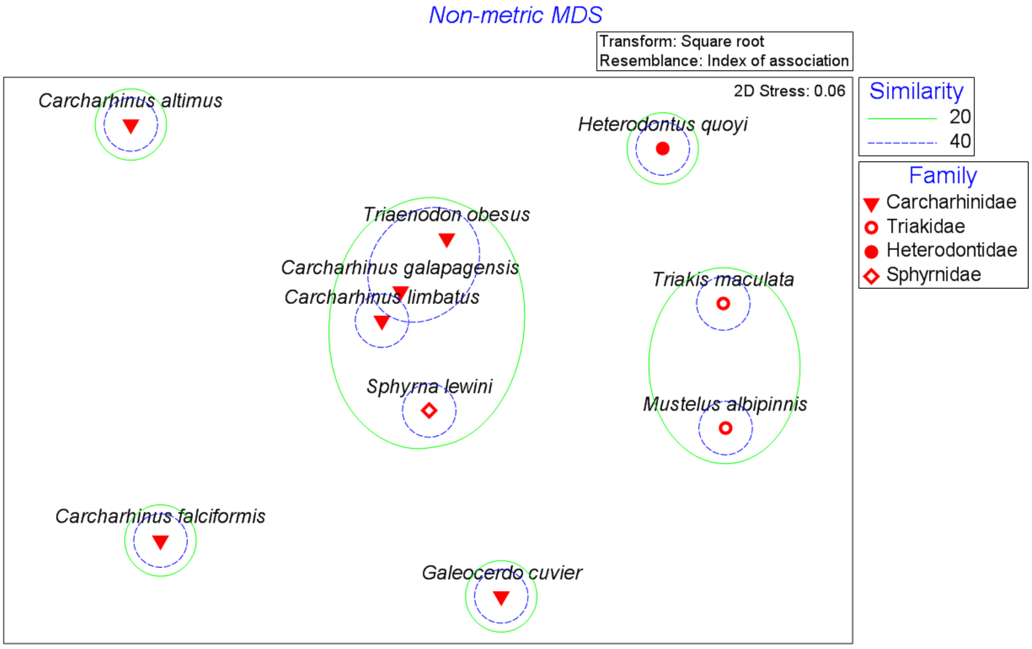

Figure 2-5. Non-metric MDS plot showing the inter-specific associations among shark species based on the index of association calculated from square-root transformed relative abundances of shark species (*cMaxN*). Levels of similarity from a hierarchical agglomerative cluster analysis are indicated by a green line (20% similarity) and a blue dashed line (40% similarity). Species belonging to different families are shown by different symbols.

common sub-set of predictor variables, which included geographical variables (distance from 1,000 m isobaths and mean fetch), environmental variables (*SST*) and biological variables (richness of the associated community, *S*) (Table 2-4, App. A, Fig A-4). Conversely, the best model to explain variation in benthic shark assemblages (excluding semipelagic sharks) included variables describing the benthic habitat, specifically the nature of the seabed (i.e., the amount of cover of ahermatypic corals, macroalgae and rubble; Table 2-4, App. A, Fig A-4).

Boosted regression tree models (BRTs) 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. 2-6 and App. A, Table A-1). 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 evenness of the associated community had a greater influence on shark diversity than on shark abundance (Fig. 2-6). Both shark richness and abundance showed a positive (partial) association with productivity (Chlo_a). Shark richness and abundance were both high at SST values around 23 ºC and greater than 29 ºC, with the latter peak particularly strong for species richness (Fig. 2-6).

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 three semipelagic species (*C. galapagensis*, *Galeocerdo cuvier* and *S. lewini*), the distance to the insular shelf (distance to the nearest 1,000 m isobath) was the best predictor of occurrence, although the relationship was very different among the three species (Fig. 2-6). While sightings of *S. lewini* were more likely to occur at the border of the insular shelf (< 2 km to 1,000 m isobaths), *G. cuvier* showed an increasing

Table 2-4. Results of the distance–based redundancy analysis (dbRDA) showing the selected environmental and biological predictors that best explain variation in shark assemblages (using the multivariate analogue of AICc) based on the adjusted Bray-Curtis resemblances calculated from square-root-transformed *cMaxN* values.

	Full shark assemblage		Semipelagic shark assemblage		Benthic shark assemblage	
dbRDA axis	%[a]	%[b]	%[a]	%[b]	%[a]	%[b]
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 1,000 m isobath (m) Mean fetch (m) SST (ºC) S (species richness)		Distance to 1,000 m isobath (m) Mean fetch (m) SST (ºC) S (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

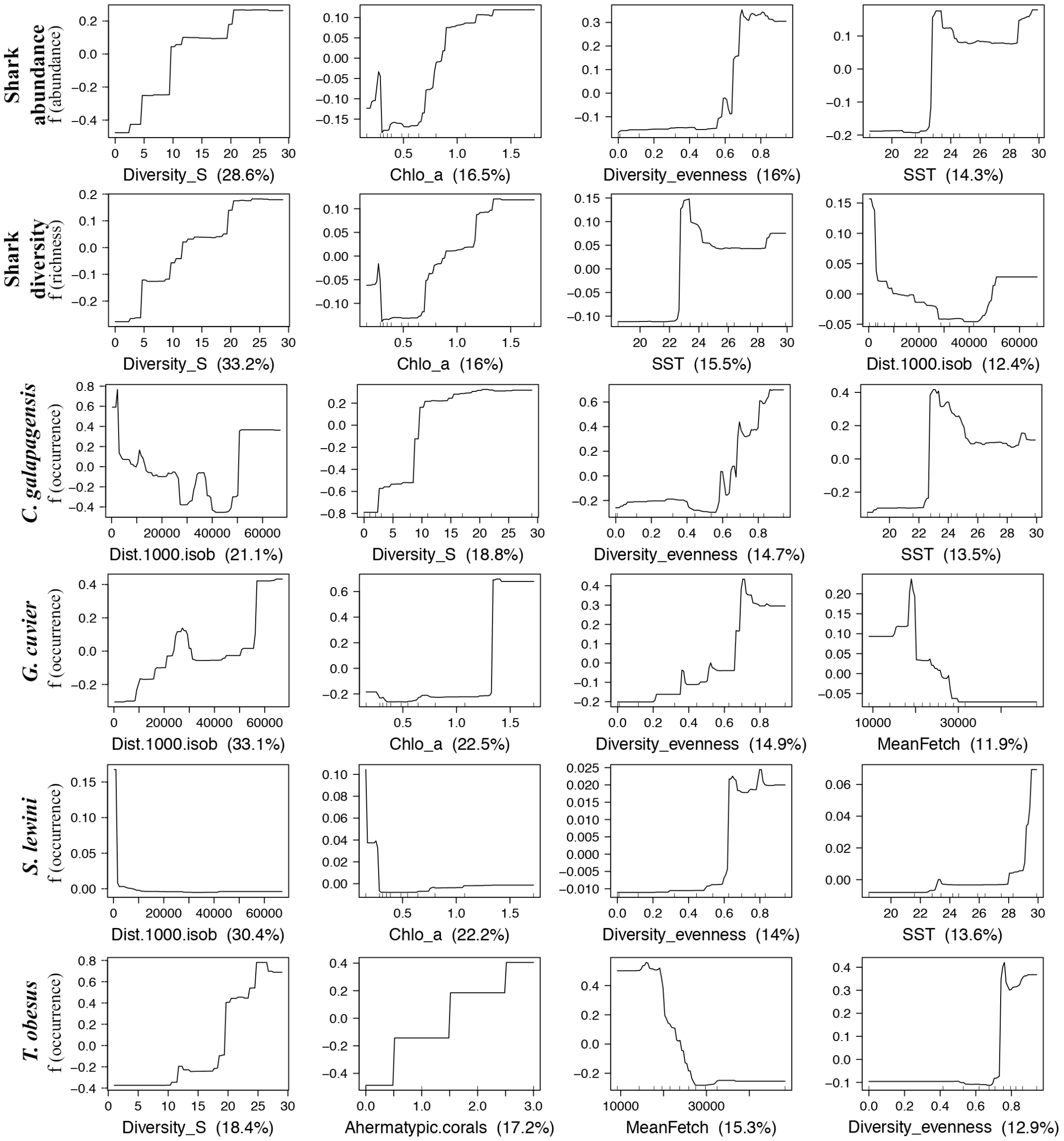

Figure 2-6. Partial dependence plots (following Elith and Leathwick 2016) showing the four most influential variables in the prediction of total shark abundance and diversity and the occurrence of *Carcharhinus galapagensis*, *Galeocerdo cuvier*, *Sphyrna lewini* and *Triaenodon obesus*. Individual plots 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.

probability of occurrence towards the interior shallow waters of the Archipelago (> 55 km to 1,000 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 1,000 m isobaths). A higher species evenness of the accompanying assemblage (non-shark species) (> 0.6 or 0.7 Gini-Simpson), and also diversity (> 10 spp) in the case of *C. galapagensis*, resulted generally in a higher probability of occurrence of these three shark species (Fig. 2-6). However, while sightings of *G. cuvier* were more likely at locations with high cholorophyll-*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 ºC) and low chlorophyll-*a* (< 0.25 mg m^{-3}) (Fig. 2-6). Finally, *C. galapagensis* was more likely to occur when SST ranged between 23-24 ºC.

The influence of the associated assemblage of non-shark species varied substantially among the four benthic shark species (Fig. 2-6). Sightings of *T. obesus* increased in probability in locations with high diversity (> 20 spp) and species evenness (> 0.75 Gini-Simpson), while the two Triakidae species were more influenced by the relative abundance of accompanying species (log (*MaxN*+1) > 4) and *Heterodontus quoyi* was more likely to occur with high levels of species evenness (0.65 > Gini-Simpson < 0.8; Fig. 2-7). 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. 2-7). In the case of *H. quoyi*, SST was the most influential predictor, with a higher probability of occurrence in waters below 22 ºC, in locations with macroalgae (> medium cover) and far from the edge of the insular shelf (> 20 km to 1,000 m isobaths; Fig. 2-7).

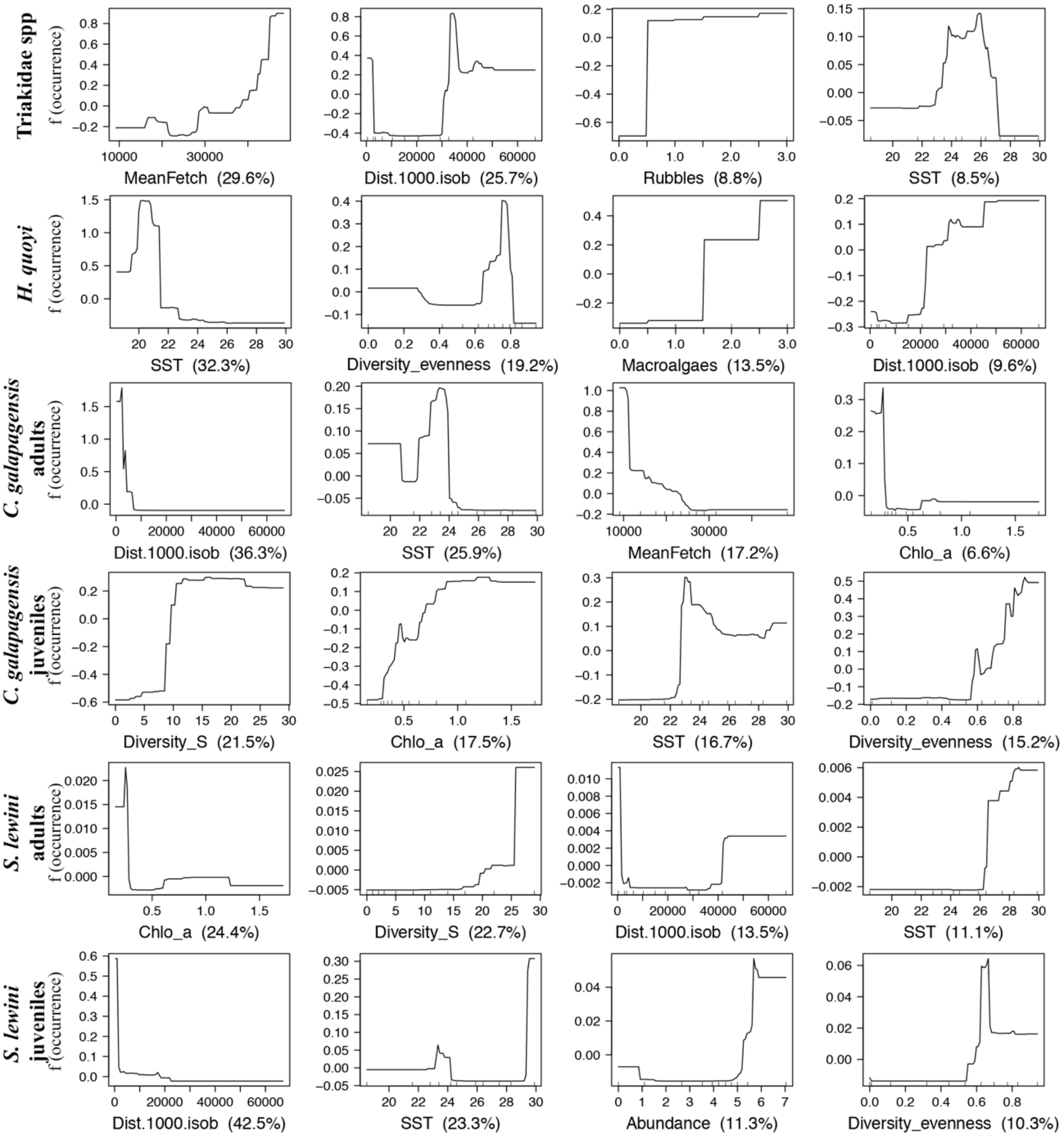

Figure 2-7. Partial dependence plots (following Elith and Leathwick 2016) showing the four most influential variables in the prediction of the occurrence of the two Triakidae species (*Triakis maculata* and *Mustelus albipinnis*), *Heterodontus quoyi* and adult and juveniles of *Carcharhinus galapagensis* and *Sphyrna lewini*. 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, Diversity_evenness and Abundance refer to the richness, evenness and total log-abundance (*Log (MaxN+1)*) (respectively) of the associated assemblage of non-shark species.

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 1,000 m isobaths), with lower SST (< 25 ºC), low exposure to waves (mean fetch < 25 km) and high exposure to currents (Fig. 2-7). However, occurrence of juveniles of *C. galapagensis* were mostly influenced by the richness and evenness of the accompanying assemblage (> 10 spp and > 0.6 Gini-Simpson, respectively), and were more likely to occur in locations with high productivity (> 0.5 mg m^{-3}) and a SST close to 23 ºC (Fig. 2-7). A higher probability of occurrence of adult *S. lewini* was related to areas having low productivity (< 0.25 mg m^{-3}), high SST (> 26 ºC) 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 Archipelago (< 5 km or > 40 km to the 1,000 m isobaths; Fig. 2-7). Juveniles of *S. lewini* showed increasing probability of occurrence at the boundaries of the insular shelf (< 5 km to the 1,000 m isobaths), where SST was either below 24 ºC or above 29 ºC, and where there was a high log-abundance of species in the accompanying assemblage (log (*MaxN*+1) > 5.5; Fig. 2-7).

The canonical analysis of principal coordinates (CAP) revealed that several species from the accompanying assemblage were strongly associated with shark log-abundance and richness (Fig. 2-8). The king angelfish (*Holocanthus passer*) had a positive association, while the bullseye puffer (*Sphoeroides annulatus*) had a negative association with the log-abundance of sharks (Fig. 2-8). Shark species richness had a strong positive association with the blue-barred parrotfish (*Scarus ghoban*) and the burrito grunt (*Anisotremus interruptus*), and strong negative associations with the

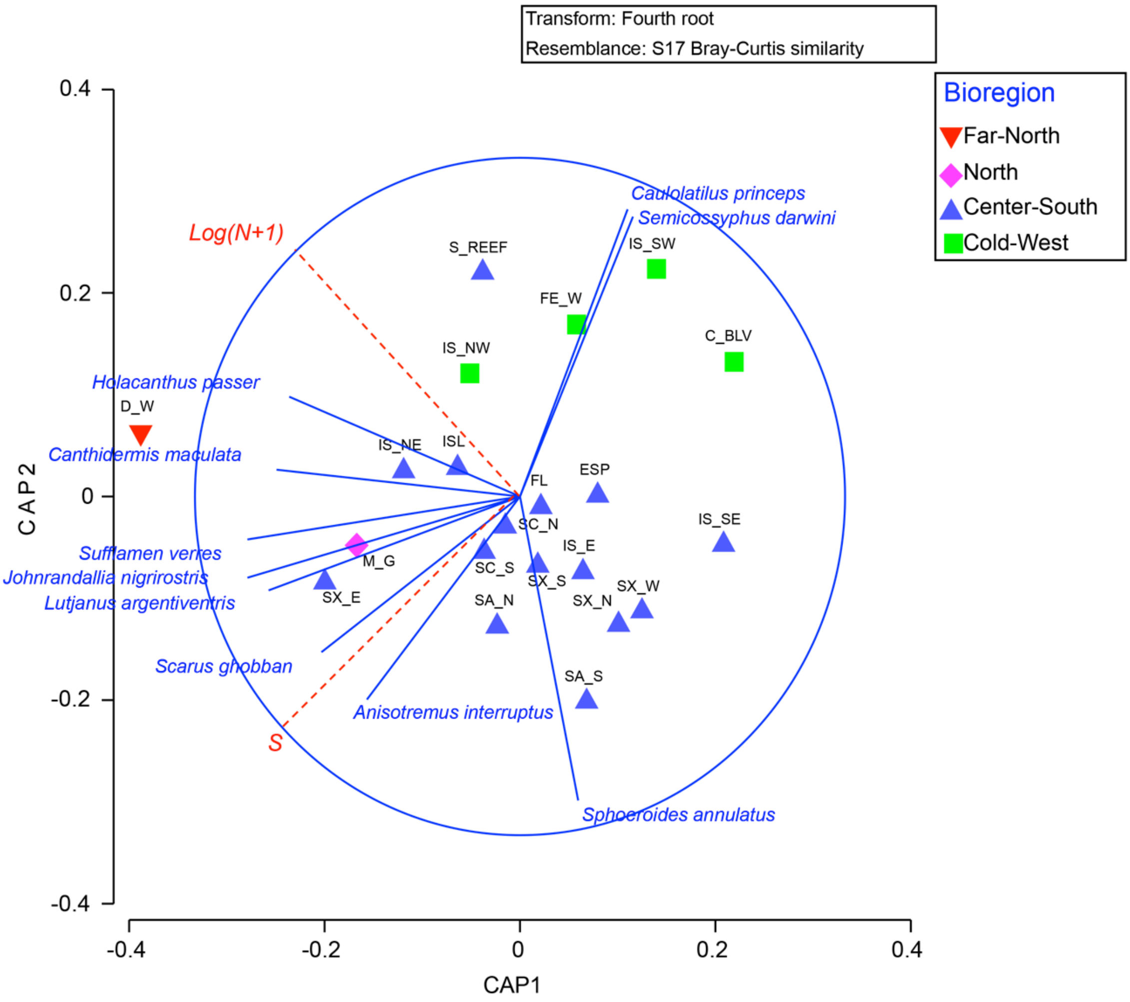

Figure 2-8. Canonical analysis of principal coordinates (CAP) ordination plot showing the relationship between (i) the richness (*S*) and total log-abundance (*log(cMaxN+1)*) of sharks (averaged by stratum) and (ii) the Bray-Curtis dissimilarity matrix of fourth-root-transformed relative abundances (*log(MaxN+1)* 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).

Galapagos sheephead wrasse (*Semiccossyphus darwini*) and the ocean whitefish (*Caulolatilus princeps*; Fig. 2-8).

2.5 Discussion

This study has clarified the spatial distributions and usage patterns of several shark species at the GMR, highlighting its potential role in the ecological maintenance of shark biodiversity across the region. Variability in shark assemblage composition and the diversity of spatial distribution for different shark species found in our study indicates that the GMR harbours a broad range of suitable habitats that perform multiple ecological functions for shark populations. These might include the provision of prey sources, nursery habitats, refuge from predation, and cleaning services.

Spatial patterns of individual shark species

Carcharhinus galapagensis

C. galapagensis was the most abundant shark species recorded in our study, as it has been reported in other oceanic islands in the South Pacific (e.g., Lord Howe (Heagney et al. 2007) and the Kermadec Islands (Duffy and 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. 2-2a). 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 utilise 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. 2-2a). 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 is a species that aggregate in large numbers at islets and seamounts (Hearn et al. 2010, Ketchum et al. 2014a), using shallow protected bays as nursery areas. However, the presence of suitable nursery grounds for this species at 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 (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 100-200 cm TL) and adults at the GMR. Sex could not be determined for the majority of adult individuals, 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. 2-1b and 2-2c), 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 at the GMR, where records from adults 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 two 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 six young-of-the-year individuals (< 150 cm TL, Meyer et al. 2014; Figs. 2-2d and 2-3d), 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 at the GMR, which could play an increasingly important role for this species at a regional scale by providing both nursery and feeding grounds.

Triaenodon obesus

The most commonly recorded benthic shark in our study, *T. obesus*, is known to prey 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, a species common around walls and caves at the GMR (Calvopiña et al. 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 at 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 Galapagos Archipelago (Fig. 2-2e).

Triakidae species

Despite the wide distribution and relatively common occurrence of *T. maculata* and *M. albipinnis*, these two Triakidae species had only been previously recorded on very few occasions at the GMR since their first registered sightings there in 1980 (Grove and Lavenberg 1997) and 2013 (Acuña-Marrero et al. 2013b), respectively. Very little is known about the biology of these two 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 two 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. albipinnis* (Pérez-Jiménez et al. 2005).

Heterodontus quoyi

We found that *H. quoyi* has a broader distribution range at 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 two distinctive subpopulations could be two 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 (App. A, Fig. A-2). 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.

Spatial and seasonal variation of the shark assemblage

The high spatial variability of the shark assemblage found in our study is likely the result of the heterogeneity in habitats provided by the GMR. At higher latitudes, the tropical environment of the 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. 2-1b). Conversely, the central and western part of the Archipelago harboured more diverse and variable shark assemblages, where benthic species were regularly present (Fig. 2-1b).

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

The groups of islets and Floreana Island were the areas that showed highest species richness of sharks (two of the four surveyed islet sites also happened to be close to Floreana Island; Fig. 2-1b). Despite its small size, Floreana Island offers a great variety of habitats and oceanographic conditions, with upwelling areas and temperate reefs covered by macroalgae in its western side, and more tropical conditions, including coral reefs, and several islets on its eastern side (Feingold and 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 conditions (lower water temperature) that might restrict the presence of species with more tropical affinities (e.g., *S. lewini*, *G. cuvier* or *T. 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 seasonal variation in the shark assemblages. This may be due to the occurrence of an El Niño Southern Oscillation (ENSO) event during our study, which produced anomalies in SST at the GMR ranging from + 0.7 to +2.0 ºC between February and October 2015 (NOAA 2016). During El Niño years, seasonal differences are reduced, with both an increase and a homogenization of SST across the Archipelago (Banks 1999). Future studies of shark assemblages in the GMR should evaluate the effect of ENSO.

Environmental and biological drivers

Our results suggest considerable differences in the environmental and biological drivers of 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. 2014a). 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 important requirements for pelagic species (Dudley and 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., two 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).

Stereo-BRUV performance

The 10 shark species recorded in our study comprise approximately 60 % of the coastal shark species that have ever been reported at the GMR (Hearn et al. 2014). Four of the seven coastal sharks not sighted in this study (*Carcharhinus albimarginatus*, *C. plumbeus*, *Mustelus mento* and *Nasolamia velox*) are considered uncommon or very rare in the Archipelago, and records of the other three species (*Carcharodon carcharias*, *Sphyrna mokarran* and *S. tiburo*) are yet to be confirmed (Grove and Lavenberg 1997, McCosker and Rosenblatt 2010). Prior to our study, two multi-year (2001-2012) scuba-based visual surveys of reef and pelagic fishes were conducted at the GMR. Despite their length and high spatial coverture, none of these studies recorded three shark species sighted in our study, with two of them (*Triakis maculata* and *Mustelus albipinnis*) showing a wide distribution and relatively common presence around the Archipelago (Fig. 2-1b). It is very likely that these Triakidae sharks avoid divers, as they were recorded by the stereo-BRUVs in some areas that were 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 2-2). 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 using BRUVs might use only benthic deployments when working at similar depths to the ones used at our study.

Limitations of this study

First, we only sampled at two distinct times; greater temporal replication would allow seasonal and inter-annual variation to be estimated more rigorously, providing also 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. 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 (App. A, Fig. A-2) might affect the detectability of small or cryptic species with low mobility, although only *H. quoyi* has those characteristics among the sharks recorded. This species was, however, repeatedly identified in our study even in areas out of its previously described distributional range and generally displayed inquisitive behaviour towards the stereo-BRUVs. Fifth, sex could only be determined in a limited number of individuals, which reduced our ability to assess potential sex 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 indicates that sharks have species-specific, sex-specific, and size-specific spatial requirements for particular habitats, food resources, protection from predators or avoidance of competitors. Spatial patterns in distributions are also likely to change and evolve through time at large 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 implies that sophisticated spatial modelling will be needed to understand and guide management for conservation purposes, in order to achieve successful outcomes for sharks overall into the future.

Chapter 3. Residency and movement patterns of an apex predatory shark (*Galeocerdo cuvier*) at the Galapagos Marine Reserve

This chapter was published as

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3.1 Abstract

The potential effectiveness of marine protected areas (MPAs) as a conservation tool for large sharks has been questioned due to the limited spatial extent of most MPAs in contrast to the complex life history and high mobility of many sharks. Here we evaluated the movement dynamics of a highly migratory apex predatory shark (tiger shark *Galeocerdo cuvier*) at the Galapagos Marine Reserve (GMR). Using data from satellite tracking, passive acoustic telemetry, and stereo baited remote underwater video, we estimated residency, activity spaces, site fidelity, distributional abundances and migration patterns from the GMR and in relation to nesting beaches of green sea turtles (*Chelonia mydas*), a seasonally abundant and predictable prey source for large tiger sharks. Tiger sharks exhibited a high degree of philopatry, with 93% of the total satellite-tracked time across all individuals occurring within the GMR. Large sharks (> 200 cm TL) concentrated their movements in front of the two most important green sea turtle-nesting beaches in the GMR, visiting them on a daily basis during nocturnal hours. In contrast, small sharks (< 200 cm TL) rarely visited turtle-nesting areas and displayed diurnal presence at a third location where only immature sharks were found. Small and some large individuals remained in the three study areas even outside of the turtle-nesting season. Only two sharks were satellite-tracked outside of the GMR, and following long-distance migrations, both individuals returned to turtle-nesting beaches at the subsequent turtle-nesting season. The spatial patterns of residency and site fidelity of tiger sharks suggest that the presence of a predictable source of prey and suitable habitats might reduce the spatial extent of this large shark that is highly migratory in other parts of its range. This highly philopatric behaviour enhances the potential effectiveness of the GMR for their protection.

3.2 Introduction

Effective conservation strategies are urgently required to mitigate and reverse the current global declines exhibited by many populations of large sharks (Lucifora et al. 2011, Worm et al. 2013, Dulvy et al. 2014). Marine protected areas (MPAs) could play a crucial role in the conservation of shark populations by protecting critical habitats for reproduction and feeding (Norse 2010, Escalle et al. 2015). However, given the complex life history, high mobility, and broad spatial ranges of most large sharks, the effectiveness of MPAs for these species remains questionable and in need of critical evaluation, especially given that most MPAs are relatively small and were established to protect highly resident teleosts (Mora et al. 2006, Simpfendorfer et al. 2011, Graham et al. 2016).

A scheme called ‘triangle migrations’ was proposed by Chapman et al. (2015) to describe the spatial structure of coastal shark populations, based on the movements of sharks between nursery grounds and habitats occupied by adults of different sexes, which tend to display spatial segregation for most of the year (Springer 1967). The distances between the habitats used during different life stages, together with the tendency of individuals either to stay for long periods (residency) or repeatedly return (site fidelity) to their home areas (i.e., "philopatry"), can therefore structure populations at identifiable spatial scales (Chapman et al. 2015). Philopatric behaviour is common in sharks (Mayr 1963, Hueter et al. 2005), potentially reducing the spatial distributions of shark populations and allowing MPAs to be effective at smaller scales than previously supposed (Hueter et al. 2005). Overall, the benefits of MPAs for sharks will depend on the time individuals spend within their boundaries, which can vary by species, life stage, sex, size, and physiological state as well as the level of protection and enforcement afforded in the protected area (Speed et al. 2010, Escalle et al. 2015, Graham et al. 2016).

The Galapagos Islands, a Marine Natural World Heritage Site, has been described as one of the richest marine ecosystems in the world (UNESCO, http://whc.unesco.org/en/list/1). The Galapagos Marine Reserve (GMR; established in 1998) is among the world's largest MPAs, spanning 138,000 km^2 (Heylings et al. 2002; Fig. 3-1a). The GMR harbours abundant populations of marine megafauna, such as large sharks (Zárate 2002, Hearn et al. 2014), with the highest known biomass of sharks in the world in its northern islands of Darwin and Wolf (Salinas-de-León et al. 2016). However, it remains unknown to what extent the spatial ranges of different shark species occur within the GMR.

The tiger shark *Galeocerdo cuvier* is a large (up to 381-550 cm total length, TL; see Whitney and Crow (2007)) apex predator, globally distributed in coastal and epipelagic waters of temperate and tropical seas (Compagno

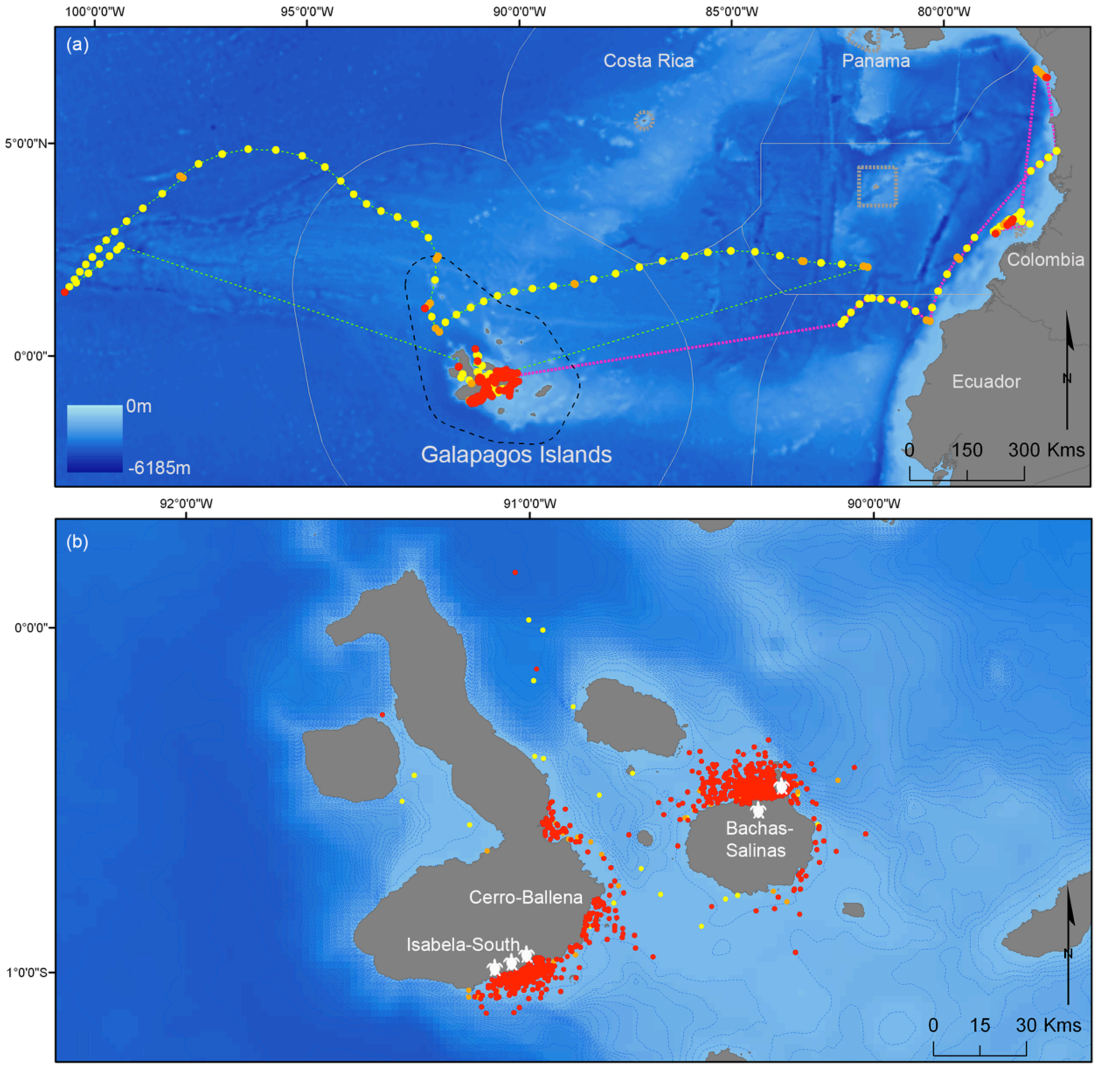


Figure 3-1. Patterns of residency behaviour of satellite tagged tiger sharks. Resident (red circles), transient (yellow circles) and undetermined (orange circles) behaviours associated with each 12-hour estimated position provided by the switching state-space model. Top panel (a) displays the complete tracks of TS2 and TS4 (pink and green dashed lines, respectively) overlaid with the exclusive economic zones (grey line) and marine protected areas (grey dashed line) of Eastern Tropical Pacific countries. Lower panel (b) shows the estimated positions of all tracked sharks within the Galapagos Marine Reserve (black dashed line, top panel), indicating the study sites, the most important turtle-nesting beaches (sea turtle icons) and the 100 m isobaths (blue dashed lines).

et al. 2005). Despite tiger sharks having been observed at the Galapagos Islands since 1924 (Beebe 1924), formal records of tiger shark have been rare at the GMR (Zárate

2002, Hearn et al. 2014). Tiger sharks display both wide-ranging and resident behaviours, the latter occurring in specific areas with abundant sources of prey (Meyer et al. 2009, Hammerschlag et al. 2012, Werry et al. 2014). It has been suggested that individual tiger sharks learn from experience about the location and timing of such foraging opportunities and may have a mental map allowing them to time their migrations to take advantage of seasonal food pulses (Meyer et al. 2010). Ontogenetic dietary shifts occur in tiger shark, as young individuals are nocturnal bottom feeders while larger sharks feed on larger prey such as mammals, elasmobranchs and sea turtles (Lowe et al. 1996). Sea turtles, in particular, have been identified as the most common prey in their diet in some areas of its distribution (Simpferdorfer et al. 2001), and large tiger sharks may concentrate their movements around turtle-nesting beaches to take advantage of this seasonally predictable and abundant food source (Fitzpatrick et al. 2012, Hammerschlag et al. 2015, 2016).

The GMR is one of the most important nesting and resident sites for the green sea turtle (*Chelonia mydas*) in the Eastern Pacific, supporting more than 40% of their total population in this region (Seminoff et al. 2008, Zárate 2009). Close to 2,000 nesting events are recorded annually at the GMR, mostly during the warm season (Dec-May), with peak nesting activities occurring during February and March (Zárate 2009, Zárate et al. 2013, Parra et al. 2015).

The present study investigated the spatial ecology of tiger sharks at the GMR, with a particular focus on residency patterns in relation to green sea turtle nesting beaches given their potential importance as an abundant prey item. We employed a combination of field methods, including satellite and acoustic telemetry to record spatial and temporal use of the GMR by tiger sharks as well as baited remote underwater stereo-video systems (stereo-BRUVs) to explore differences in the size and relative abundance of tiger sharks at green turtle nesting sites. Specific study objectives were to: (1) describe movement patterns in and around the GMR, (2) quantify degree of philopatric behaviour, including patterns of residency and site fidelity at the study sites, (3) explore ontogenic differences in habitat usage, and (4) test for seasonal differences in relative abundances and size distributions of tiger sharks at the study sites. Based on previous studies (Fitzpatrick et al. 2012, Hammerschlag et al. 2015, 2016), we hypothesized that tiger sharks would exhibit a high degree of residency and site fidelity to the turtle-nesting areas, and that patterns in the spatial distributions of tiger sharks would also display seasonal, gender-specific and ontogenic variation (following Meyer et al. (2010) and Fitzpatrick et al. (2012)). We then discuss the implications of our results for the effectiveness of the protection provided by the Galapagos Marine Reserve World Heritage Site to the tiger sharks.

3.3 Materials and methods

Ethics statement

This research was approved by the Galapagos National Park Directorate (GNPD) as part of the research permit granted to Dr Alex Hearn (GNPD permit #PC-01-14) and Dr. Pelayo Salinas de León of the Charles Darwin Foundation (GNPD permits #PC-40-14 & #PC-17-15), with the methods described here reviewed and approved by a Galapagos National Park Directorate's committee that assesses animal care in research activities.

Study site

The Galapagos Archipelago is composed of 13 major islands and over 100 islets located on the equator, approximately 1,000 km west of continental Ecuador, in the Eastern Tropical Pacific (ETP; Snell et al. 1996; Fig. 3-1a). Two distinctive seasons occur at the Archipelago, driven by oscillations in the strength of predominant currents: a warm rainy season runs from December to May, driven by the northeastern Panama Current; and a cool dry season runs from June to November, due to the Humboldt Current, arising from the southeast (Banks 2002). Green turtles nest during the warm season. We gathered data within each of the two distinct climatic seasons, each identifiable by referent to the green turtle-nesting activities: namely, a 'nesting season' from December to May (warm period) and a 'non-nesting season' from June to November (cool period).

We conducted our study within 2014 and 2015, with sampling focused on three locations in the GMR (Isabela-South, Bachas-Salinas and Cerro-Ballena; Fig. 3-1b). Two locations, Isabela-South and Bachas-Salinas, were selected because they are the two largest nesting areas for green turtles within the GMR (Zárate et al. 2013). Isabela-South contains several consecutive nesting beaches west of Puerto Villamil, the most important being Quinta Playa, while Bachas-Salinas, located between Santa Cruz and Baltra islands, includes the nesting beaches of Las Bachas and Las Salinas (Zárate and Dutton 2002, Zárate et al. 2013; App. B, Fig. B-1). Both Isabela-South and Bachas-Salinas have similar seabed composition and depth profiles, with predominance of sandy bottoms, sparse rocky reefs, and gentle slopes. However, Isabela-South is exposed to the predominant southern wind and swell, while Bachas-Salinas has more sheltered conditions. The third location, Cerro Ballena, was selected based on the reported incidental catches of juvenile tiger sharks during scientific fishing surveys (Pazmiño pers. comm.). Cerro Ballena is located at the southeastern tip of Isabela Island (App. B, Fig. B-1), though it is more sheltered than Isabela-South and has no sandy beaches. We focused our sampling efforts throughout the year, encompassing both the green turtle 'nesting season' from December to May (warm period) and the 'non-nesting season' from June to November (cool period).

Movement patterns and habitat usage

Capture and tagging

Tiger sharks were captured at each of the three study locations (Fig. 3-1b). Sharks were attracted to boats using fish burley and captured using handlines baited with wahoo (*Acanthocybium solandri*) or yellow-fin tuna (*Thunnus albacares*). Following Heithaus et al. (2002), captured sharks were secured alongside the vessel and inverted to induce tonic immobility (Holland et al. 1999), except sharks TS1-4 (Table 3-1), which were drawn onto a submerged platform attached to a mother vessel (MV Ocearch) that was then raised above the water level. Each shark was sexed and measured, then classified into one of three size classes: small (< 200 cm TL), medium (200–300 cm TL) or large (> 300 cm TL) following Lowe et al. (1996).

Two types of tagging device were deployed on most of the captured sharks: a satellite SPOT tag was attached to the first dorsal fin (Smart Position or Temperature Transmitting; SPOT5, Wildlife Computers Ltd., Washington, USA; Hammerschlag et al. 2011)), and an acoustic transmitter was surgically implanted into the intraperitoneal cavity (V16-6x, VEMCO Ltd., Nova Scotia, Canada; see Meyer et al. (2009)). Using two tagging approaches provided distinct and complementary information on the movements of tiger sharks at different spatial scales (Werry et al. 2014).

Residency, site fidelity and broad movements from the GMR

The SPOT satellite tags provided geolocations of sharks derived from Doppler-shift calculations made by the Argos Data Collection and Location Service (www.argos-system.org; for a detailed description of the functioning of satellite tags see Hammerschlag et al. (2011)). Given the irregularity of positions from SPOT-derived data, spatial analyses were conducted using a Bayesian state-space model (SSM; Jonsen et al. 2005) implemented with the R package 'bsam' (Jonsen et al. 2013). As outlined in Jonsen et al. (2003), SSMs are "time-series models that allow unobservable, true states to be inferred from observed data by accounting for errors arising from imprecise observations and from stochasticity in the process being studied". Specifically, SSMs combine a statistical observation model that deals with Argos satellite telemetry precision, with a specified process model of the movement dynamics related to the animal behaviour and environment (Patterson et al. 2008). This modelling approach offers multiple advantages, particularly when working with diving animals that surface briefly and irregularly; such animals generally yield poor-quality, intermittent tracking data (Jonsen et al. 2007). Analysis by SSMs provides regular estimated positions assuming a correlated random walk on the differences in subsequent locations, rather than on the locations themselves (Jonsen et al. 2007). SSMs also account for the mean turning angle and autocorrelation in speed and direction of the animal, as well as the location error due to the quality of the transmission (modelling the Argos position errors–6 quality classes– with appropriate independent *t*-distributions) (Jonsen et al. 2005, 2007).

To ensure our analyses were as robust as possible, we took several data-preparation steps prior to fitting the model. The data were checked for obvious errors, removing duplicate data points from the same track with the same time and/or position. In addition, tracks with gaps exceeding one week were split into separate

Table 3-1. Summary of acoustic and satellite tag deployments on tiger sharks at the three tagging locations within the Galapagos Marine Reserve in 2014-15.

				Satellite		Acoustic			
Shark ID	Tagging date	TL (cm)	Sex	Days transmitting	% residency time*	Days monitored **	Days transmitting	No. detections	RI*** (per tagging site)
Bachas-Salinas									
TS1	30-Jan-2014	274	F	116	90.48	307	152	761	0.50
TS2	30-Jan-2014	251	F	210	74.83	79	19	150	0.24
TS3	30-Jan-2014	248	F	127	99.02	-	-	-	-
TS4	30-Jan-2014	383	F	333	82.78	262	111	438	0.42
TS5	11-Jun-2015	225	F	-	-	104	71	482	0.68
TS6	11-Jun-2015	240	F	67	98.48	104	47	185	0.45
Average TL ± SE = 270.17 ± 23.49									
Cerro Ballena									
TS7	23-Jul-2014	140	F	-	-	180	41	140	0.23
TS8	23-Jul-2014	224	M	25	87.50	303	68	510	0.22
TS9	24-Jul-2014	234	F	26	100.00	271	16	82	0.06
TS10	24-Jul-2014	171	F	21	100.00	286	45	399	0.16
TS11	24-Jul-2014	260	F	115	100.00	-	-	-	-
TS12	7-Oct-2014	180	M	-	-	113	23	376	0.20
TS13	7-Oct-2014	180	M	-	-	195	93	1183	0.48
TS14	21-Feb-2015	206	F	58	78.12	74	10	23	0.14
TS15	21-Feb-2015	202	M	84	98.30	177	16	99	0.09
Average TL ± SE = 199.67 ± 12.14									
Isabela-South									
TS16	22-Feb-2015	378	F	128	100.00	-	-	-	-

TS17	22-Feb-2015	282	F	14	100.00	58	1	1	-
TS18	22-Feb-2015	324	M	45	100.00	118	2	2	-
TS19	23-Feb-2015	286	M	66	95.61	-	-	-	-
TS20	23-Feb-2015	242	M	37	100.00	68	1	1	-
	Average TL ± SE = 302.40 ± 22.93								

*% residency time refers to the percent of time spent in resident behaviour within the GMR, as determined by the SSM model.

**Days monitored refers to the number of days that the shark could be detected by the acoustic receivers (note that acoustic receivers were deployed after the sharks were tagged).

***RI= residency index per site (i.e., total number of days a shark was detected divided by the number of days that the shark was monitored by the receivers).

segments and recombined after fitting the model (as recommended by Jonsen pers. com.).

We used a hierarchical, first-difference, correlated, random-walk, switching SSM (hDCRWS; Jonsen et al. 2013). This model allows for estimate parameters jointly across multiple individual tracks. The model provided a set of estimated positions for each shark at regular 12-h time intervals. An interval of 12 h was chosen (following Lea et al. (2015)) because the majority (82.2%) of gaps between input points were less than 12 h apart (App. B, Fig. B-2). Points estimated to be on land were discarded, as were those points that were estimated over intervals lacking data for longer than 3 days (Jonsen pers. com.). The SSM allows for individuals to switch between two behavioural states: an area-restricted search or “resident” state, and a migratory or “transient” state. The behavioural state is inferred based on the simplifying assumption that animals travel in a straight line between regularly spaced unobserved locations and that the spatial autocorrelation among pairs of points is higher when the animal is in a resident state, while turning angles should be closer to 0 in transient states (Jonsen et al. 2007). The behavioural state (b_t) is either 1 (resident) or 2 (transient) for each animal at each time point (t). Uncertainty in the value of b_t was quantified with a Markov Chain Monte Carlo (MCMC) algorithm. The mean value of b_t across MCMC draws for each animal at each time point was used to classify the state as being either predominantly transient (mean b_t<1.25) or predominantly resident (mean b_t>1.75; Jonsen et al. 2007, Fitzpatrick et al. 2012), with the remaining (5.75%) middle values omitted for the spatial analyses. The relative frequencies of the two behavioural states were then used to evaluate the prevalence of resident *vs* transient states in tiger sharks inside and outside the GMR.

Core ranges and activity space

We identified high-use areas for tiger sharks by applying spatial kernel density estimation (KDE; Hammerschlag et al. 2012, Graham et al. 2016) to the estimated positions provided by the SSM, pooled across individuals. KDE was conducted in ArcGIS 10.3.3. (ESRI 2016), and was based on the quadratic kernel function described by Silverman (1986). We calculated percent-volume contours (PVCs) using the “isoline” tool available from the Geospatial Modelling Environment add-on to ArcGIS (Beyer 2012). We defined “core range” (CR) and "activity space” (AS) as the area within the 50% and 95% PVCs, respectively and independently of a track’s duration. Following Hammerschlag et al. (2015) we also reported intermediate PVCs (75%). The individual CR and AS data were right-skewed in their distributions so further analyses were based on log-transformed values. Log-transformed CRs and ASs each showed a marginally significant positive linear relationship with the log-transformed number of positions (log-N, where N is the number of positions) from which they were calculated (regression on log-N; coefficient for log-HR: $\hat{\beta} = 0.924 \pm 0.41$ SE, $t_{14} = 2.24$, $p = 0.042$; and for log-CR: $\hat{\beta} = 0.744 \pm 0.350$, $t_{14} = 2.13$, $p = 0.052$). Hence, log-N was included as a predictor in subsequent linear models to account for the length of time over which the individual was observed. Multi-way ANOVA was used to test for variation in AS and CR based on the factors of season and size, with differences in variances evaluated using Levene’s Tests.

Habitat usage at study sites

To test for potential ontogenic differences in the associations between tiger shark positions and sea turtle-nesting sites, we conducted chi-square tests on the proportions of the estimated shark positions provided by the SSM of different size ranges that fell within 5 and 10 km of the sea turtle-nesting beaches. In previous studies, a proportion of the sea turtles remained resident within a 10 km range of the beach after nesting (Seminoff et al. 2008, Parra et al. 2015). The smaller buffer of 5 km was included to explore hierarchical spatial uses of the nesting areas by the different size classes of sharks.

Four acoustic receivers (VR2W, Vemco Ltd., Nova Scotia, Canada) were deployed at the green turtle-nesting beaches (App. B, Fig. B-1) to measure patterns of residency and site fidelity from acoustically tagged sharks at high spatiotemporal resolution (for a detailed description of passive acoustic tracking see Meyer et al. (2009)). One receiver was deployed at each of Isabela-South and Cerro-Ballena from October 2014 to August 2015. One receiver was deployed at each of Las Salinas and Las Bachas from November 2014 to September 2015. Due to the close proximity of Las Salinas and Las Bachas, the data from these two receivers were pooled and analysed as one location (Bachas-Salinas).

Data obtained from the four acoustic receivers were pre-processed, removing single detections potentially caused by signal collisions or noise (following Bond et al. (2012)). A Residency Index (RI) was defined, for each shark, as the proportion of the total number of monitored days that the shark was detected (and thus near the nesting beach). This proportion was calculated separately for each season and location (Cerro-Ballena and Bachas-Salinas). Diel patterns of usage were examined by classifying the detections at each location into hourly bins and analysing the counts per bin using a Fast Fourier Transformation (FFT, periodogram function, R package TSA (Meyer et al. 2007, Papastamatiou et al. 2009, Peñaherrera et al. 2012)). While we did not conduct range testing of receivers, we assumed them to be up to 300 m, based on previous detection ranges obtained in telemetry studies at the GMR (Hearn et al. 2010).

Size structure and relative abundance at study sites

Data on the presence, relative abundance, size- and sex-distribution of tiger sharks were collected using stereo-BRUVs between March and September 2015. The systems consisted of two GoPro HERO4 digital cameras (GoPro, Inc., California, USA) mounted 0.7 m apart and converging inwards at a 6° angle on stainless steel frames, baited with *ca* 800 g of yellow-fin tuna (*Thunnus albacares*). Replicate stereo-BRUV deployments were conducted at each of the three locations (App. B, Fig. B-1) at *ca* 25 m and at each of two depths: ‘benthic’ sets were deployed 1.5 m above the sea bed (Watson et al. 2005), and ‘pelagic’ sets were deployed in mid-water at *ca* 10 m depth (Santana-Garcon et al. 2014b). Four benthic deployments were made at Cerro-Ballena, four benthic and four pelagic deployments at Isabela-South, and eight benthic and eight pelagic deployments at Bachas-Salinas during each season (App. B, Fig. B-1).

Stereo-BRUVs were deployed along the *ca* 25 m depth contour separated by a minimum distance of 500 m (following Santana-Garcon et al. (2014a)), alternating between benthic and pelagic deployments. All deployments were made during daylight hours and never within 1 hour of sunrise or sunset. Stereo-BRUVs were set for at least 100 min, with initial and final 5 min periods discarded to minimise the influence of the boat. The remaining 90 min of footage were analysed using the software EventMeasure (SeaGIS Pty Ltd., Victoria, Australia). To evaluate relative abundance of tiger sharks from stereo-BRUVS, we employed an approach modified from Cappo et al. (2004). First, we recorded the maximum number of individual tiger sharks observed in a single still video frame throughout the 90-minute deployment (i.e., MaxN; Cappo et al. 2004). Next, we added to this value any other tiger shark clearly distinguishable within the deployment that was not already included in the MaxN calculation (i.e. MaxN *plus* number of different tiger sharks identified in deployment). We termed this value corrected MaxN (cMaxN). Different tiger sharks could be distinguished in BRUVS using a combination of several criteria: (1) the presense/absence of claspers in adult individuals, (2) presense/absence and location of scars or markings; and (3) body total length (taken as an average of three measurements of TL, each from a different video frame). Multi-way ANOVA was used to test for variation in lengths based on the factors of sex, season, and location. Seasonal or gender differences in spatial patterns of occurrence were tested using Fisher's exact tests.

3.4 Results

Movement patterns and habitat usage

Of the 20 sharks captured (13 females, 7 males; Table 3-1), 16 were double tagged with both satellite and acoustic transmitters, two were tagged with only a satellite transmitter, and two were tagged with only an acoustic transmitter. All tagged sharks provided at least one type of data (either acoustic or satellite) for a minimum of 14 days after being released, so there was no indication of mortality caused by the tagging process. Two satellite tags (TS12 and TS13) provided no signal, but the acoustic tags of these two sharks provided data for 113 and 195 days, respectively. Two sharks (TS3 and TS19) were never recorded by any of the acoustic receivers. The satellite track of TS19 did not pass close to any of our receivers, but TS3 provided satellite positions for more than 100 days around her tagging site (where the acoustic receivers were deployed), pointing to a likely failure of TS3's acoustic transmitter.

Residency, site fidelity and broad movements from the GMR

When pooled across the 16 sharks for which we received data from satellite tags between January 2014 and July 2015, 1,339 (92.6%) of the 1,446 SSM-estimated positions were located within the GMR. The behavioural state was classified for a total of 1,347 positions, the majority of which (80.6%) were classified as resident. For positions located within the GMR, resident behaviour was also dominant (86.4%). In contrast, 71.0% of positions estimated to be outside the GMR were classified as having transient behaviour, with only 8.4% showing resident behaviour (based on two sharks, TS2 and TS4; see Table 3-1).

Two satellite-tagged sharks left the GMR during the study period, both of which were female. The first (TS2; 251 cm TL) headed east towards the continental coast of South America in April 2014, exhibiting a mixture of resident and transient behavioural states along the coast of continental Ecuador and Colombia during the following 3 months (Fig. 3-1a). This shark was then detected again at her tagging site by the acoustic receivers at Bachas-Salinas at the beginning of the subsequent turtle-nesting season (App. B, Fig. B-3). The second shark to leave the GMR was the largest tagged in this study (TS4; 383 cm TL); after transmitting from within the GMR from January–July 2014, her signal was lost, resuming 2 months later in the Pacific Ocean *ca* 1,000 km west of her original tagging site (Fig. 3-1a). TS4 then headed eastward, passing through the GMR and continuing on to continental South America, when transmissions again stopped in mid-October 2014. One month later, at the beginning of the subsequent turtle-nesting season, TS4 returned to her original tagging site in the GMR at the turtle-nesting beach of Bachas-Salinas (Figs. 3-1a and App. B, B-3).

Core ranges and activity space

Core range (CR) areas for individual sharks ranged from 2.3–292.5 km^2, with a median of 73.8 km^2. Activity space (AS) areas ranged from 11.1–4,976 km^2, with a median of 174 km^2.

At the individual level, neither log-AS nor log-CR was significantly related to either season (log-AS: $F_{1,11} = 0.67, p = 0.431$; log-CR: $F_{1,11} = 0.03, p = 0.872$) or TL (log-AS: $F_{1,11} = 0.43, p = 0.523$; log-CR: $F_{1,11} = 0.01, p = 0.942$). There was significantly greater variability in log-AS values during the nesting season (median: 455 km^2; min–max: 11–4,976 km^2) *vs* the non-nesting season (median: 118 km^2; min–max: 81–168 km^2; Levene's Test, $F_{1,14} = 4.78, p = 0.05$). There was no such seasonal difference in the variance of log-CR (Levene's Test, $F_{1,14} = 0.23, p = 0.64$). When points were pooled across individuals within size classes, the collective AS area of medium sharks was approximately double that of large sharks, while the collective CR areas for these two size classes were almost the same (Table 3-2; Fig. 3-2). When pooled within seasons, different patterns were apparent for AS and CR; the AS was 41% lower in the non-nesting *vs* the nesting season, whereas the CR was 66% greater (Table 3-2; Fig. 3-2).

Table 3-2. Collective activity space (95 % PVC) and core range (50 % PVC) areas (pooled across individual satellite-tagged tiger sharks) within the Galapagos Marine Reserve.

		Number of sharks	Activity space (km^2)	Core range (km^2)
Season	Nesting	11	6,500	356
	Non-nesting	6	3,827	1,046
Size range	Large (>300 cm TL)	3	3,324	422
	Medium (200-300 cm TL)	10	7,088	406
	Small (<200 cm TL)	1	782	179

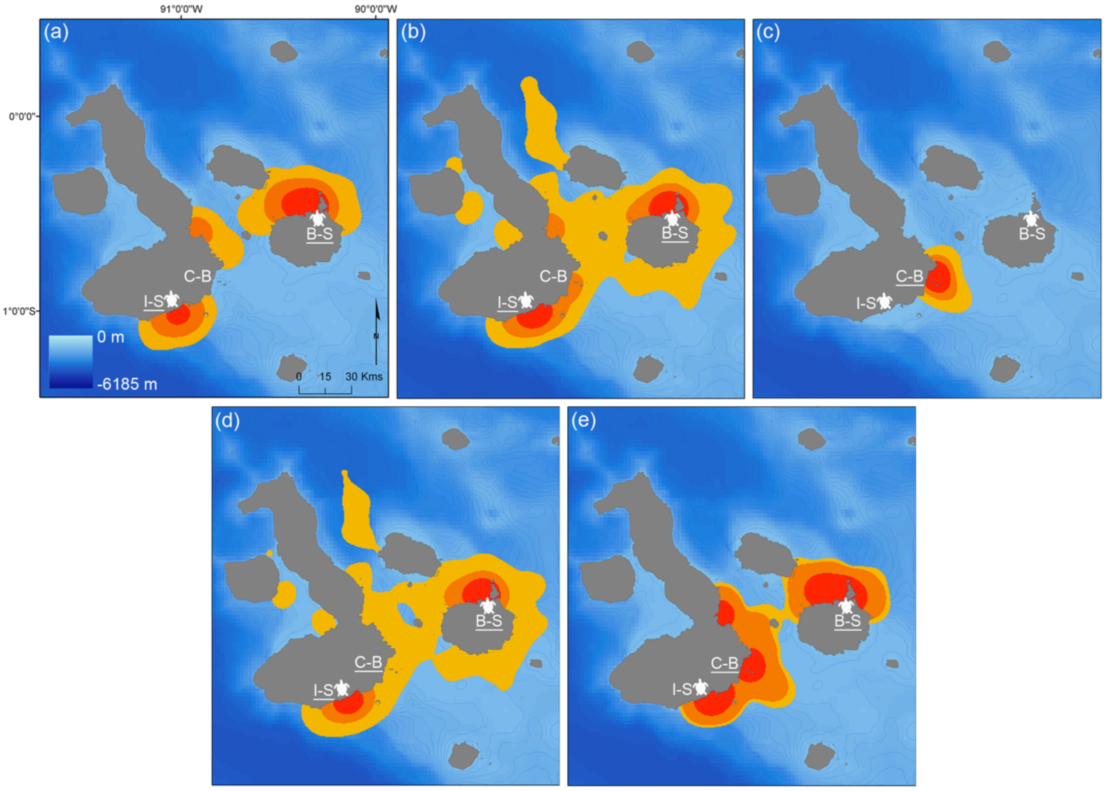


Figure 3-2. Kernel density estimates of satellite-tagged tiger shark positions. Sharks are pooled by size classes: (a) large (> 300 cm TL, n = 3), (b) medium (200-300 cm TL, n = 12) and (c) small (< 200 cm TL, n = 1); or by season: (d) sea turtle-nesting season (n = 11) and (e) non-nesting season (n = 7). Red indicates core range areas (50 % percent-volume contour, PVC), yellow represents activity space areas (95 % PVC) and orange indicates the intermediate 75 % PVC. Underlined names of study sites (Isabela-South = I-S, Cerro-Ballena = C-B, Bachas-Salinas = B-S) indicate those locations where sharks were tagged in each case. White sea turtle icons show the turtle-nesting areas and local bathymetry is displayed by 100 m isobaths (blue dashed lines).

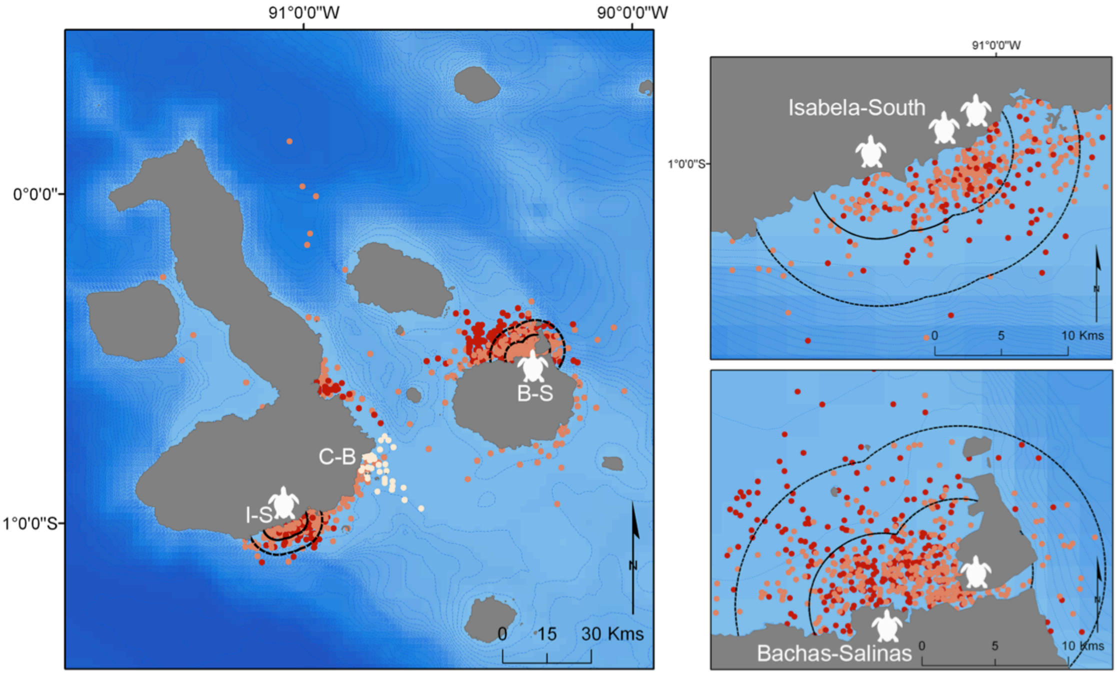


Figure 3-3. 12-hourly estimated positions provided by SSM by shark size. Colours indicate three size classes of tiger sharks (large = red, medium = orange, small = white). Black dashed lines indicate the 5 and 10 km buffer areas around the study sites (I-S = Isabela-South, C-B = Cerro Ballena, B-S = Bachas-Salinas) and sea turtle nesting beaches (white sea turtle icon). Local bathymetry is displayed by 100 m isobaths (blue dashed lines). Right panels show zoomed areas of the study sites of I-S (upper) and B-S (lower).

Habitat usage at study sites

Of the total time that medium and large sharks were tracked within the GMR, 80% of the time was spent within 10 km, and around half of the time within 5 km, of the sea turtle-nesting beaches (Fig. 3-3). Almost all (99.33%) of the time spent within the GMR corresponded with resident behaviour. In contrast, the only small shark that provided a satellite track did not approach the nesting locations, and remained in the vicinity of the third study site, Cerro-Ballena, where it had been tagged (Figs. 3-2c and 3-3). There were no significant differences, however, between medium and large sharks in the proportion of time spent within 5 or 10 km of nesting beaches ($\chi^2_{[2]} = 1.93$, $p = 0.38$).

None of the sharks tagged at Bachas-Salinas were ever detected by acoustic receivers at either of the other two locations, but two sharks (TS9 and TS13) tagged at Cerro-Ballena were detected briefly at Bachas-Salinas (App. B, Fig. B-3). The residency index (RI) was not correlated with the TL of the sharks ($r^2 = 0.11021$, $p = 0.27$). At both locations, the RI was very similar between seasons (Figs. 3-4a and 3-4b). Spectral analysis (FFT) revealed a strong diel cycle of use (Figs. 3-4c and 3-4d), with highly differentiated proportions of day *vs* night detections in the two locations ($\chi^2_{[1]} = 1685.2$, $p < 0.001$). Detections of sharks at Bachas-Salinas occurred almost exclusively at night, while those in Cerro-Ballena were mostly restricted to daylight hours (Figs. 3-4e and 3-4f).

Size structure and relative abundance at study sites

Twenty tiger sharks (13 females, 7 males) were captured and tagged (Table 3-1) and another 22 sharks (8 female, 6 male, 8 undetermined) were recorded by stereo-BRUVs (Fig. 3-5; App. B, Table B-1). The cMaxN counts of tiger sharks in the stereo-BRUVs depended on the season and the location. The seasonal pattern of counts differed significantly among locations (Fisher's exact test, $p = 0.01$); specifically, more tiger sharks were recorded in the nesting season than in the non-nesting season at Bachas-Salinas and Isabela-South (none were detected at Isabela-South during the non-nesting season), whereas the reverse was true for Cerro-Ballena (Fig. 3-5; App. B, Table B-1). There was no evidence for any differences in sex ratios among locations (Fisher's exact test, $p = 0.67$; App. B, Table B-1).

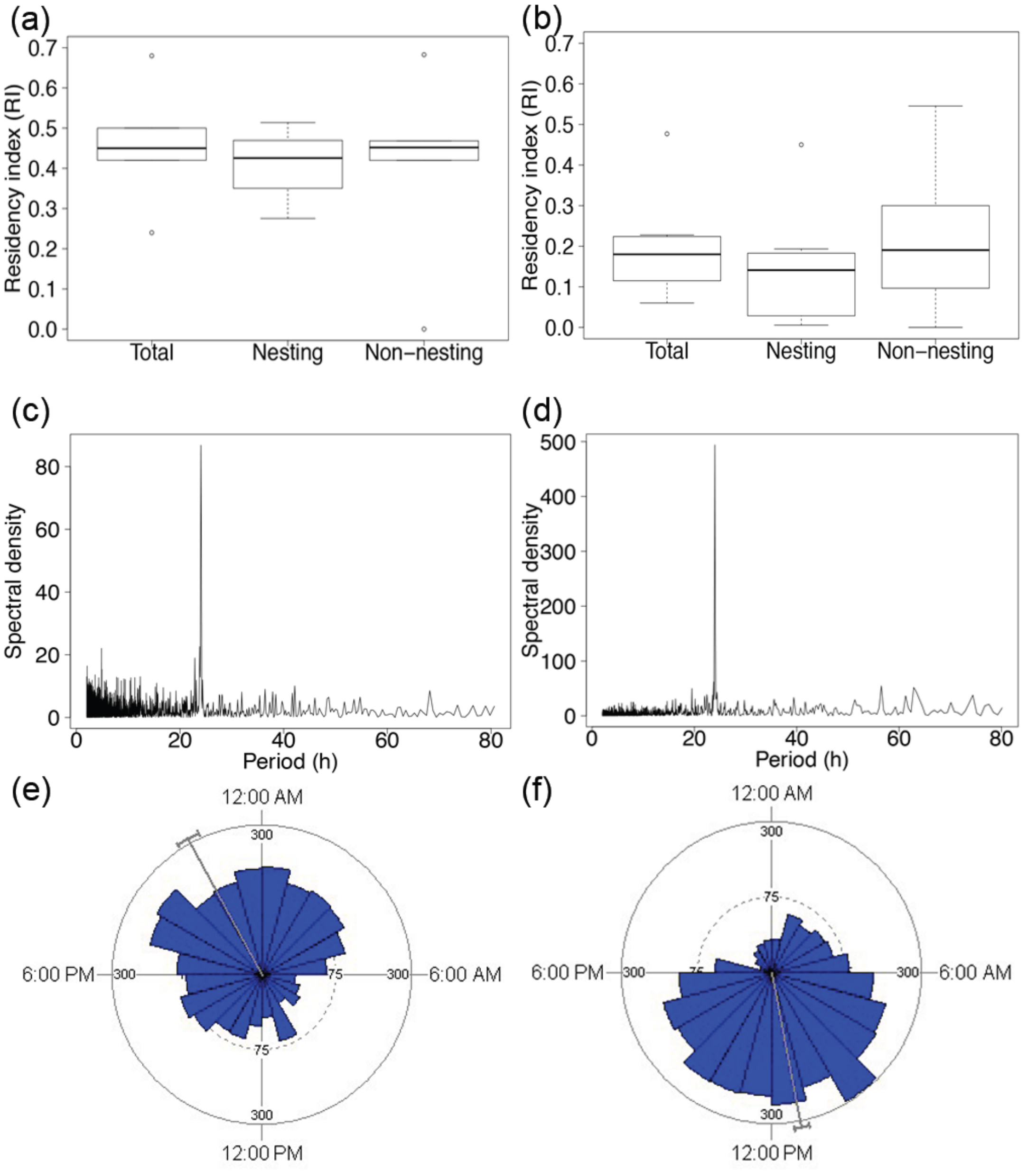


Figure 3-4. Patterns of residency and diel occurrence of acoustic-tagged tiger sharks. Left panels refer to Bachas-Salinas and right panels to Cerro-Ballena. The top panel (a, b) shows residency index (RI, the total number of days a shark was detected divided by the number of days that the shark was monitored by the receivers) for the total monitored time (Total) and per season (Non-nesting and Nesting); the middle panel (c, d) shows Fast Fourier Transformations (FFT) of the number of hourly detections, with peaks indicating periods of dominant cycles; and the lower panel (e, f) shows daily detections of tiger sharks; the circle represents a period of 24 hours and the length of each wedge indicates the number of detections within each hour.

The lengths of captured tiger sharks ranged from 140–383 cm TL and those observed by stereo-BRUVs ranged from 102–416 cm TL. The mean TL of captured sharks was 247 cm, and that of sharks observed by stereo-BRUVs was 291 cm; although these means were not significantly different ($t_{40} = 1.93$, $p = 0.06$).

There was weak evidence for an interactive effect of sex and season on the average lengths of sharks observed in the stereo-BRUVs ($F_{1,\,28} = 3.74$, $p = 0.06$); females recorded were 53 cm longer on average in the nesting *vs* non-nesting season ($F_{1,\,28} = 4.56$, $p = 0.08$), whereas the average lengths of males did not differ significantly between the two seasons ($F_{1,\,28} = 0.68$, $p = 0.42$; Fig. 3-6). A greater range of lengths was observed among the 21 females (140–416 cm TL) than the 13 males (180–342 cm TL), though there was no significant difference in variances between sexes (Levene's test $F_{1,\,28} = 2.28$, $p = 0.37$; Fig. 3-6).

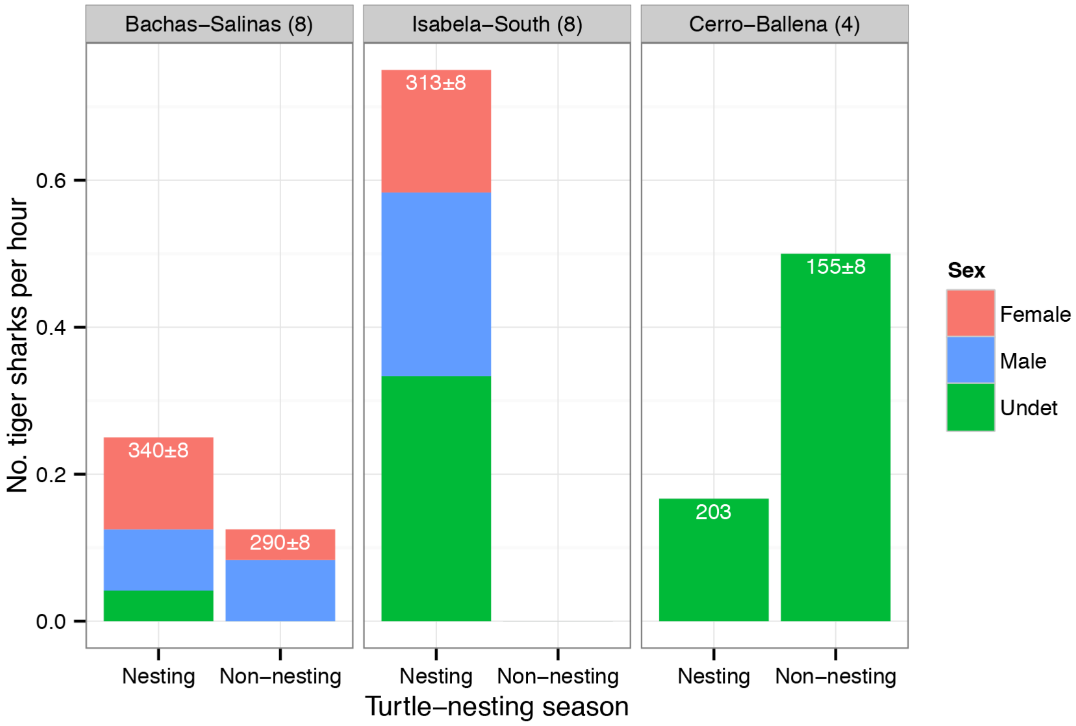


Figure 3-5. Relative abundance of tiger sharks at the three study sites. Number of individual tiger sharks per hour by sex recorded by the stereo-BRUVs in the nesting or the non-nesting season for turtles. The number of camera deployments at each site

is reported in parentheses. The average TL ± SE (cm) of the sharks recorded at each site is given at the top of each bar.

All but one shark either captured or recorded by stereo-BRUVs at Bachas-Salinas and Isabela-South were of medium or large size, whereas only small- and medium-sized sharks were observed at Cerro-Ballena (App. B, Table B-1). Accordingly, the mean lengths of sharks differed significantly among locations ($F_{2, 35} = 9.43$, $p = 0.0007$; Fig. 3-6). There was no significant difference in mean lengths between the two nesting locations (ANOVA contrast of Bachas-Salinas *vs* Isabela-South, $F_{1, 28} = 1.05$, $p = 0.31$) but sharks observed at the non-nesting location of Cerro-Ballena were on average smaller (mean TL ± SE: 196.6 ± 15.4 cm) than those observed at the two nesting locations (308.25 ± 10.8 cm), and this contrast was significant ($F_{1, 28} = 19.6$, $p < 0.001$; estimated difference in means of 111.7 cm, 95% CI 70.6–152.7; Fig. 3-6).

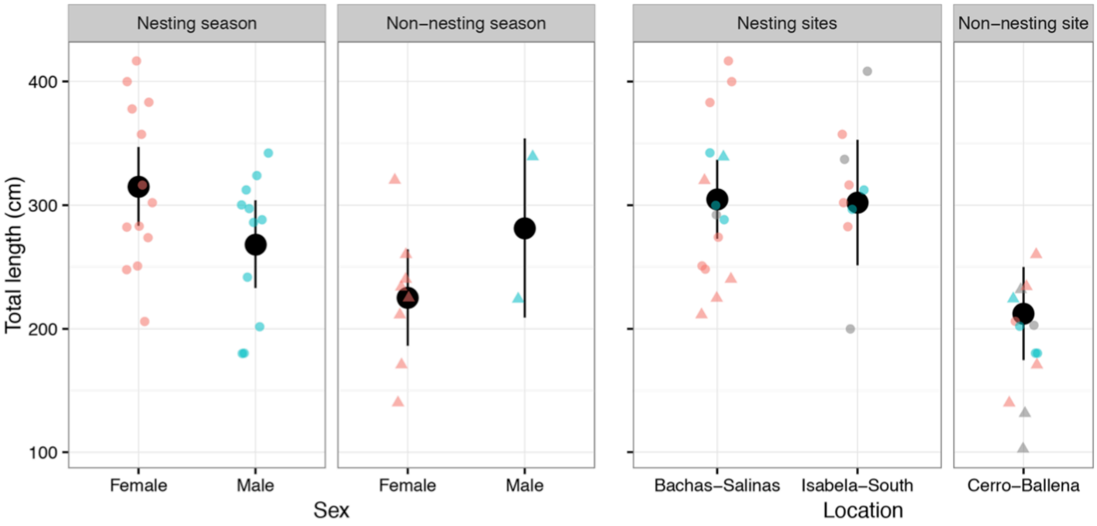


Figure 3-6. Total length (TL) of tiger sharks tagged and observed by stereo-BRUVs. Total length is shown as raw data values and as means (black circles) with 95% confidence intervals for males (blue) *vs* females (red) in either the nesting season (circles) or the non-nesting season (triangles), and at each of the three study locations.

3.5 Discussion

Tiger sharks tagged displayed strong philopatric behaviour, with intense use of specific areas associated with green turtle-nesting beaches that could provide year-round reliable food sources. Overall, tagged tiger sharks spent a remarkable 93% of their total tracked time within the protected waters of the GMR (Fig. 3-1). The high availability of prey (i.e., the presence of a large population of nesting and resident sea turtles) and a potential provision of suitable habitats for all life stages, supported by the wide range of sizes recorded, might explain this high residency. Additionally, only two individuals exhibited long-distance round-trip movements. These two sharks showed strong site fidelity to the turtle-nesting sites at which they were tagged, both returning at the beginning of the subsequent turtle-nesting season. We consider that the remoteness of the GMR and the habitats that it provides, which include reliable and predictable food sources for adult tiger sharks, may structure the population into a smaller spatial extent than might be expected due to the potential mobility of this species (Chapman et al. 2015). Similarly, Heupel and Simpfendorfer (2014) suggested that high levels of isolation, particularly in large and productive reefs, might result in an increase in the residency of sharks at the Great Barrier Reef (GBR). This high residency may enhance the effectiveness of the GMR to protect tiger sharks, suggesting that the inclusion of healthy ecological communities that ensure high prey availability can improve the efficacy of protected areas in the conservation of highly mobile top predators. Indeed, spatially restricted populations of reef sharks (e.g., due to small-scale 'triangle migrations', *sensu* Chapman et al. (2015)) elsewhere have been successfully protected by properly enforced MPAs, even when nearby areas are heavily fished (Speed et al. 2010, White et al. 2017).

We found strong evidence that medium and large tiger sharks are using turtle-nesting sites as feeding grounds, as has been documented in other tropical locations (Fitzpatrick et al. 2012, Hammerschlag et al. 2015, 2016). Here, this inference is supported by two key results. Firstly, the movements of medium and large tiger sharks at the GMR were closely associated with the turtle-nesting sites, even outside of the turtle-nesting season (Fig. 3-2e). Seminoff et al. (2008) and Parra et al. (2015) found that some of the nesting sea turtles at the GMR remained in the vicinity of their nesting areas once the nesting season had ended. We speculate that the reduced occurrence of large sharks at this time of year might enhance predation opportunities for remaining individuals on resident sea turtles. Extended residency by tiger sharks would allow them to avoid long migratory movements with high energetic costs. Secondly, we observed daily visits by sharks to the turtle-nesting sites almost exclusively at night, when turtles would be most available and vulnerable (Fig. 3-4e), as green sea turtles are nocturnal nesters (Witherington 1992). Similarly, great white sharks (*Carcharodon carcharias*) have been found to target cape fur seals (*Arctocephalus pusillus pusillus*) at their island entry and exit points during times of low light (Martin et al. 2005, Hammerschlag et al. 2006).

Our observations of high residency and fidelity of tiger sharks to areas of high prey availability, with some individuals conducting broad round-trip migrations, are consistent with results obtained in other studies done in areas having similar characteristics. In Raine Island (Australia), Fitzpatrick et al. (2012) and Hammerschlag et al. (2016) found year-round residency at an important sea turtle-nesting area for the majority of observed tiger sharks. A similar pattern was observed at the French Frigate Shoals (Hawaii Islands, USA), where some individual tiger sharks were residents while others just visited the atoll during the season with higher availability of bird prey (Meyer et al. 2010).

The availability of breeding sites at the GMR is another potential reason for mature female tiger sharks to remain resident there. If we assume that tiger sharks grow *ca* 100 cm year^{-1} (following Afonso et al. (2012) and Meyer et al. (2014)), then at least six of the 42 individuals recorded in our study were young-of-the-year, although a high degree of variation on growth rates has been reported for this species (Meyer et al. 2014). There are at least three other recent records of newborn (< 100 cm TL) tiger sharks at the GMR (Schuhbauer and Pazmiño pers. comm.), indicating that tiger sharks actively breed and pup at the GMR.

Tagged juvenile tiger sharks (< 200 cm TL) displayed spatial segregation from larger individuals, although two juveniles were detected for short periods of time at the sea turtle-nesting sites. While we only recorded one satellite track within this size range to support this, most of our records of juvenile individuals (from acoustic receivers, tagging activities and stereo-BRUVs) occurred in an area with no turtle-nesting beaches (Cerro-Ballena, Table 3-1; Figs. 3-2 and 3-5). The pattern of use at this site, with daily daytime visits, suggests that this area might be used to forage by juveniles on diurnal prey that differs from that of adults (given ontogenetic diet expansion in tiger sharks (Lowe et al. 1996, Simpferdorfer et al. 2001)). Juvenile tiger sharks may also be competitively excluded by larger conspecifics, and/or may actively avoid areas with larger tiger sharks to limit their exposure to potential cannibalism (Meyer et al. 2009). Juvenile tiger sharks might use Cerro-Ballena as a daytime refuge from which to conduct foraging excursions at nearby nocturnal feeding grounds (e.g., Cuatro Hermanos islets or the various adjacent seamounts). Patterns of spatial segregation of size classes have been reported in other large sharks in feeding areas elsewhere, such as white sharks at seal-colony hunting grounds (Klimley et al. 2001, Martin et al. 2009). Juveniles possibly remain resident in the GMR year-round, as limitations on broader movements for juvenile tiger sharks have been previously documented elsewhere (Werry et al. 2014, Lea et al. 2015).

Our study had relatively small sample sizes, particularly in the case of the number of stereo-BRUVs deployed and the number and duration of the satellite tracks obtained for small tiger sharks. The resulting number of recorded sharks (44 sharks seen on video or tagged), together with the recorded relatively short tracking durations (median = 66.5 days), necessarily limits the extent of our inferences and ecological interpretations of the patterns observed. Moreover, we focused our sampling efforts at discrete locations where tiger sharks had previously been reported to occur, thus the data collected is not representative of the entire tiger shark population of the GMR. Clearly, it is desirable that additional stereo-BRUVs surveys and tagging efforts be implemented throughout the GMR to more extensively document spatial patterns in population structure and relative abundances of tiger sharks. It is also worth noting that tagging location may have an impact on habitat use results (i.e., high residency to sea-turtle beaches may be an artefact of tagging sharks near these areas, and not related to food availability for the sharks). However, our results suggest that tagging location was not the driver of habitat use patterns. In fact, of the six tiger sharks tagged at non-nesting sites, the majority (4/6) were not detected again at the tagging site, but was instead subsequently detected at the turtle nesting beaches. Indeed, all of our results indicate that the GMR is a high-use area for tiger sharks across all life-stages and for both sexes.

It is remarkable that the local abundances of such a large predator at this highly visited World Heritage Site have gone unnoticed until recently (Hearn et al.

2014). This may reflect a recent recovery of the tiger shark population in the GMR, perhaps following the arrival of migrant individuals that then remained because of the suitable environmental conditions, year-round predictable and abundant food sources, and low levels of fishing. A similar case, albeit at a much smaller scale than the GMR, has been described at Cocos Island, Costa Rica, where tiger sharks apparently arrived in 2007 and since became year-round residents (White et al. 2015). The long-term residency of tiger sharks in specific areas may exert strong structuring effects on local communities and ecosystem dynamics (Ferreira et al. 2015), so our findings may provide relevant insights for the understanding of the ecosystem functioning of the GMR.

This is the first published study on patterns of movement and habitat usage of tiger sharks in the Galapagos Islands and Eastern Pacific. The isolation and unique nature of the GMR indicate that the patterns observed may differ to those exhibited by tiger sharks elsewhere. We acknowledge that further studies are needed, especially to identify the evolving status of the population at the GMR, to establish its size-sex structure and spatial relative abundances, and to evaluate the importance of this area as a nursery ground, along with any inter-annual variations. Collectively, our findings suggest that the establishment of properly enforced MPAs that protect suitable habitats and predictable food resources for both juvenile and adult marine apex predators, even at relatively small spatial scales, might play a key role in the conservation of their populations.

Chapter 4. Improving the accuracy of density estimations for mobile marine predators using instantaneous records from diver-operated stereo-video

4.1 Abstract

Our understanding of sharks and other top predators in marine ecosystems relies on accurate estimates of their densities. Some widely used transect-based methods are subject to a potential bias due to the transect being surveyed over a non-instantaneous period of time, during which individual animals may enter the transect and be recorded. Here, we used diver-operated stereo-video systems (DOVs) applied in belt transects to compare estimates of individual and biomass densities from instantaneous *vs* non-instantaneous methods of recording sharks at Darwin and Wolf Islands at Galapagos Archipelago. Using DOVs in combination with synchronised towed GPS units we produced fine-scale distributional maps of sharks at the studied locations. Estimates based on non-instantaneous surveys (i.e., including both instantaneous and non-instantaneous records) of sharks from DOV transects resulted in individual and biomass densities of sharks that almost doubled estimations based on instantaneous records. The areas with the highest densities of sharks were located at the south-eastern side of both islands, which had strong hydrodynamic variability. Due to its capacity to differentiate between instantaneous and non-instantaneous records during data analysis, DOVs can provide more accurate estimates of shark densities than classical underwater visual census methods, especially in locations having high abundance of the target species. By obtaining better estimates of shark populations and their fine-scale distributions, we can

improve our understanding of the ecology and conservation status of these threatened apex predators.

4.2 Introduction

Sharks are the most widely distributed top predators in the ocean (Ferretti et al. 2010). However, overfishing and habitat degradation have dramatically reduced shark populations worldwide (Worm et al. 2013, Dulvy et al. 2014), leading to cascading effects in some marine communities (Myers et al. 2007, Ferretti et al. 2010). Achieving accurate estimations of shark densities is essential to identify temporal trends and especially declines in shark populations so that appropriate management responses and policies can be implemented (McCauley et al. 2012). Additionally, at remote protected areas that retain near-pristine conditions, estimates of shark densities can provide ecological baselines for expected natural abundances of apex predators and the structure and functioning of the associated marine ecosystems (Sandin et al. 2008, Friedlander et al. 2010).

Developing an accurate and standardised method to estimate shark densities has proved challenging (Thompson 2013, Vanderklift et al. 2014). In most exploited coastal environments, sharks are often rare and elusive in their behaviour, so baited remote video cameras are increasingly being used to survey shark populations (Langlois et al. 2010, White et al. 2013, Espinoza et al. 2014, Santana-Garcon et al, 2014a). However, remote video camera systems cannot be used to estimate absolute density, but rather yield a relative index of density that is generally conservative, especially in areas having high densities (Cappo et al. 2003). Traditionally, densities have been estimated from underwater visual censuses (UVC) conducted by divers using belt transects, stationary-point counts, or towed-diver surveys (McCauley et al. 2012, Nadon et al. 2012).

However, these three methods have been shown to provide different estimates of shark densities for the same locations, creating uncertainty about their reliability and the influence of particular biases associated with each method (McCauley et al. 2012, Nadon et al. 2012, Rizzari et al. 2014, Vanderklift et al. 2014).

The presence of divers is the most frequently identified source of bias when human observers are in the water, as sharks can be either attracted to or actively avoid divers (Watson and Harvey 2007). In the case of towed-diver surveys, this bias could be aggravated by the proximity of motorised boats, as this method has consistently provided lower estimates of densities than any other UVC method (Nadon et al. 2012, Rizzari et al. 2014). For belt transects and stationary-point counts, some studies conducted at protected locations with high abundances of sharks have shown that the presence of divers does not influence the results of the survey or explain the differences found between the different survey methods (McCauley et al. 2012, Rizzari et al. 2014).

Furthermore, methods based on belt transects or point counts can suffer from other potential sources of bias and variance, such as (i) the use of different observers (Thompson and Mapstone 1997), who may vary in their swim speed and skills of observation, identification, recording (Sale and Sharp 1983), fish length measurement (Harvey et al. 2001, Salinas-de-León et al. 2016), and estimation of the surveyed area (Harvey et al. 2004); (ii) variation in fish behaviour (Watson et al. 1995); (iii) insufficient size of the sampled area relative to the scale of fish movements (Nadon et al. 2012); and (iv) difficulties in conducting a truly instantaneous ('snapshot') census, particularly for highly mobile species (Ward-Paige et al. 2010).

Here, we focus primarily on the bias associated with non-instantaneous surveys (*sensu* Ward-Paige et al. 2010). This bias results from the common practice in UVC of recording fish in a sampling unit (e.g., a transect) over the entire period of time that it takes the observer to traverse the sampling unit. Non-instantaneous surveys accumulate information over time across the area/volume being surveyed, whereas instantaneous surveys take only a ‘snapshot’ in time at any particular position in space (Fig. 4-1). Non-instantaneous methods will therefore over-estimate counts of individuals (Ward-Paige et al. 2010) because organisms that move into the sampled area at any time during the survey are counted. Models conducted by Ward-Paige et al. (2010) identified the speed at which fish move as the main factor influencing the degree of overestimation of non-instantaneous UVC fish counts; biases for highly mobile (~ 1 m s^{-1}) species, such as sharks, could reach one order of magnitude.

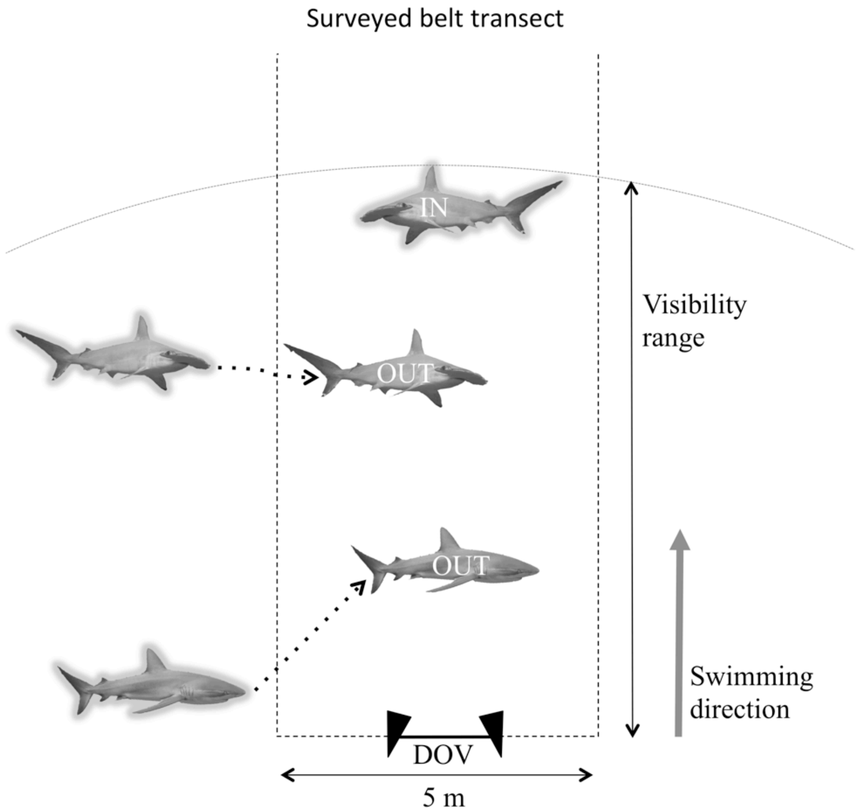


Figure 4-1. Schematic diagram of the methodology that can be implemented using DOVs in order to differentiate between instantaneous *vs* non-instantaneous records of sharks. Each shark recorded is categorised as an instantaneous record (*IN*) if it was inside the transect limits (5 m × 5 m) at the time that it was first sighted, or as a non-instantaneous record (*OUT*) if it was outside of the transect limits when first sighted, but then later moved into the transect limits. An instantaneous survey would include only instantaneous records, while a non-instantaneous survey would include both instantaneous and non-instantaneous records. The grey halo shown around each shark

indicates where it was when it was first sighted, while dotted lines and arrows show the direction of their movements of sharks over the period of time of the survey.

The present study used a diver-operated stereo-video system (DOV; Watson et al. 2010) to empirically quantify differences in estimates of individual and biomass densities of sharks obtained using instantaneous *vs* non-instantaneous belt transect surveys. DOVs allow careful identification, counting and measuring of each individual shark to be done in posterior video analysis, rather than *in situ* by divers underwater. By using DOVs, researchers can effectively eliminate the majority of the biases (specifically, biases (i), (iii), and (iv) listed above) that are inherent in the use of UVC. Importantly, DOVs allow instantaneous and non-instantaneous counts of organisms to be recorded separately. Furthermore, by using DOVs in combination with a synchronised towed GPS, one can obtain a detailed track (time and position every second) of the surveyed area.

Our study was done at Darwin and Wolf, two oceanic islands in the Galapagos Marine Reserve (GMR) where the largest shark biomass ever recorded worldwide has been recently reported (Salinas-de-León et al. 2016). We compared mean counts and biomass estimates of sharks taken from DOV surveys using instantaneous records only *vs* using both instantaneous and non-instantaneous records, to determine the magnitude of the bias associated with including non-instantaneous records. Additionally, we used DOVs in combination with towed GPS units in order to geo-reference individual shark sightings and hence to produce fine-scale distributional maps of the target species at the study sites.

4.3 Materials and methods

Study site

Darwin and Wolf are two isolated oceanic islands located at the northern tip of the Galapagos Archipelago, 1,000 km west of continental Ecuador. Both islands, which are 38 km apart, are the emergent tops of two eroded submerged volcanoes, with sharp surrounding depth gradients down to over 2,000 m (Fig. 4-2).

Darwin and Wolf Islands harbour a unique subtropical fish community and the last remaining coral reefs of the Galapagos Archipelago (Banks et al. 2009), constituting a distinctive biogeographic region within the GMR (Edgar et al. 2004). These two oceanic islands are considered important stopovers within the migratory pathways used by marine apex predators at the Eastern Tropical Pacific (ETP; Hearn et al. 2010, Bessudo et al. 2011, Ketchum et al. 2014b). In 2016, the Ecuadorian government extended the protection framework of Darwin and Wolf islands, establishing a no-take Marine Sanctuary of 38,000 km^2, which represents 28 % of the total surface of the GMR.

Data collection

Sharks were surveyed in August 2015 using DOVs consisting of two GoPro HERO4 Black edition high-definition digital cameras (GoPro, Inc., California, USA) mounted onto a stainless steel frame 0.7 m apart and converging inwards at a 6° angle.

Divers operating the DOV towed a buoy with an attached GPS unit (Garmin GPSMAP 78, Garmin Ltd., Switzerland), which recorded the position every second. The DOV and GPS units were synchronised in time, enabling a geo-location (i.e., latitude/longitude coordinates) and a specific time-point to be associated with each initial sighting of a shark during a given video recording.

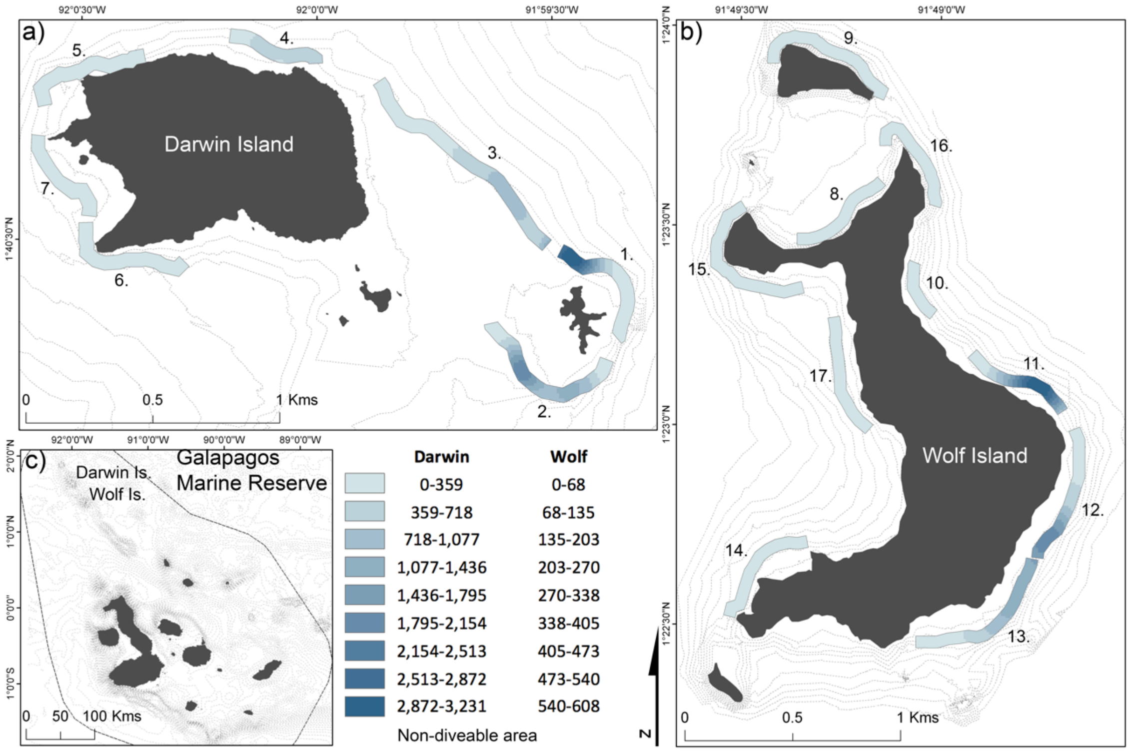


Figure 4-2. Maps showing the long-length surveys conducted using DOVs ('supertransects') at (a) Darwin and (b) Wolf islands, with (c) inset map showing the locations of these islands at the Galapagos Marine Reserve. The supertransects (conducted along the 20 m isobath perimeters of each island) are each represented by a band (width is not to scale), with the relative density of sharks (count km^{-2}) indicated by a blue colour scale (see legend). A number is assigned to each supertransect for their identification in Table 4-1. Grey dashed lines represent the 10 m isobaths in (a) and (b) and the 100 m isobaths in (c).

DOVs were used in belt transects along most of the 20 m isobaths around Darwin and Wolf Islands, with the exception of their southern areas, which are not suitable for diving in regular conditions due to strong waves and currents (Figs. 4-2a and 4-2b). Divers aimed to maintain a constant swimming speed of approximately 25-30 m min^{-1}, although whenever possible transects were conducted so that divers were swimming in a similar direction to the prevailing current to increase their speed and the distance covered during the survey. The swimming speed was estimated for each time- or distance-replicate using the data obtained from the GPS track.

Video analysis

Video footage obtained from the DOV were analysed using the software Event Measure (SeaGIS Pty Ltd., Australia), which allows specification of a standardised width and height of the video frame to be surveyed. A 5 × 5 m square was selected, and the area surveyed (m^2) in each replicate transect was calculated. For each replicate transect, all sharks observed within the 5 m × 5 m square were recorded, identified to species level and measured to the nearest mm (fork length, FL). Mean FL obtained within the same replicate transect was imputed for individual sharks that could not be measured due to an obstruction of the camera view by other fish (following Salinas-de-León et al. 2016). The biomass (weight in tonnes) for each recorded shark was estimated using published length-weight relationships specific to each species (Froese and Pauly 2017).

The lengths of the entire DOV transects ('supertransects') ranged from 500.2 to 1122.6 m. Following McCauley et al. (2012) these supertransects were divided into replicates of one-minute duration, separated by a five-second buffer. The distances covered by each replicate were obtained from the GPS tracks.

Instantaneous *vs* non-instantaneous surveys

The DOV method allows the separation of non-instantaneous and instantaneous records of sharks. Each shark observed on video was assigned a '3D point'—the three-dimensional spatial position relative to the observer at the moment it was first sighted. A shark that was inside the survey area when it was first sighted (i.e., ≤ 2.5 m left/right and higher/lower than the DOV) was categorised as an instantaneous record, while a shark that was outside of the survey area when it was first sighted, but subsequently moved inside the survey area, categorised as a non-instantaneous record (Fig. 4-1). Our analyses excluded any records of sharks that did not enter the survey area at any time, or swam in the same direction as the diver and overtook them before subsequently entering the survey area (Fig. 4-1).

Statistical Analysis

Following O'Hara and Kotze (2010), we estimated the mean density of individuals (N km^{-2}) and of biomass (tonnes ha^{-1}) of sharks on the basis of one-minute replicates using generalised linear models (GLMs) fit using the glmmTMB package for R (Magnusson et al. 2017). The numbers of individuals were assumed to come from a negative binomial distribution, and biomass from a tweedie distribution, both with a log link function. The models for estimating overall means were fit only with an intercept term and the log of the area units as an offset, so that the exponential of the intercept could be interpreted as the overall mean density.

We also fit glmmTMB models, using the same distributions and link function, to estimate the factor by which including the non-instantaneous records inflated the densities. For this analysis, we used a dataset with two lines of data for each replicate: one line for the instantaneous-survey counts (or biomass) and one for the non-instantaneous survey counts (or biomass). A binary predictor variable indicated non-instantaneous counts with a '1' and instantaneous counts with a '0'; the effect of non-instantaneous records was then given by the exponential of the coefficient for this binary variable. A replicate-level random effect was also fitted. Any replicates with no sharks were excluded for this analysis.

Fine-scale spatial distribution of sharks

We applied spatial kernel density estimation (KDE; Worton 1989) to the geo-referenced positions of each shark recorded to characterise the fine-scale spatial distribution of sharks and to identify areas of high usage by sharks around Darwin and Wolf islands. KDE was done using ArcGIS 10.1.1. (ESRI 2016), with the quadratic kernel function described by Silverman (1986).

4.4 Results

A total of 17 DOV supertransect surveys were done at Darwin and Wolf islands in August 2015 (Table 4-1), covering 5,419.4 and 7,952.6 m along their 20m-isobath contours, respectively (Figs. 4-2a and 4-2b). This corresponds to 73.7 % (Darwin) and 80.0 % (Wolf) of the total 20m-isobath contour surrounding these islands; if non-diveable areas are excluded (see Figs. 4-2a and 4-2b), these percentages are 87.3 % and 86.2 %, respectively.

A total of 368 sharks were recorded, belonging to two different species: the scalloped hammerhead shark *Sphyrna lewini* (349 records; 255.85 ± 21.89 cm TL total length, mean ± SE) and the Galapagos shark *Carcharhinus galapagensis* (19 records; 256.82 ± 123.63 cm TL).

Instantaneous *vs* non-instantaneous surveys

Combining instantaneous and non-instantaneous records (i.e., non-instantaneous surveys) yielded an estimate of the overall mean density of 4,712 individuals km^{-2} (95% confidence interval = 3,291-6,747). Using only instantaneous records, the overall mean was estimated at 2,448 individuals km^{-2} (1,684-3,557). Including the non-instantaneous records was estimated to increase the estimate of the mean individual density by a factor

Table 4-1. Summary of long-length surveys ('supertransects') conducted using DOVs at Darwin and Wolf islands from 23-26 August 2015.

	Long-length DOV surveys				
Island	Name (numerical code from Fig. 4-2)	Total length (m)	Overall time elapsed (min)	Average speed (m min-1)	No. 1-minute replicate transects
Darwin	Darwin's Arch north (1)	697.6	30	23.25	18
Darwin	Darwin's Arch south (2)	823.4	22	37.43	21
Darwin	Old reef (3)	1122.6	26	43.18	25
Darwin	Darwin anchorage (4)	550.8	17	32.40	17
Darwin	Northern wall (5)	783.3	25	31.33	24
Darwin	Southern wall (6)	941.5	21	44.83	20
Darwin	Hidden reef (7)	500.2	21	23.82	16
Wolf	North bay (8)	680.6	19	35.82	18
Wolf	Banana (9)	766.4	20	38.32	20
Wolf	Corals north (10)	689.4	17	40.55	18
Wolf	Corals south (11)	825.6	21	39.31	22
Wolf	Landslide north (12)	849.7	18	47.21	17
Wolf	Landslide south (13)	1018.7	23	44.29	22
Wolf	Elephant (14)	692.5	23	30.11	21
Wolf	Northwestern wall (15)	986.7	24	41.11	24
Wolf	Pinnacle (16)	633.1	15	42.21	17
Wolf	Wolf anchorage (17)	809.9	26	31.15	24
	Mean ± SE	*786.59 ± 40.09*	*21.65 ± 0.94*	*36.84 ± 1.74*	*20.23 ± 0.71*

of 1.95 (1.57-2.41). Similarly, the estimated overall mean biomass density for non-instantaneous surveys was 4.54 t ha^{-1} (3.35-6.17) and, for instantaneous surveys, was 2.52 t ha^{-1} (1.81-3.51). The effect of including non-instantaneous records increased the biomass estimate by a factor of 1.84 (1.52-2.23).

Fine-scale distribution of sharks

The estimated number of sharks per km^2 obtained from the kernel density estimations ranged from 0 to 3,231 at Darwin Island and from 0 to 608 at Wolf Island (Fig. 4-2). The highest estimated densities of sharks occurred in the south-eastern corner of Darwin Island (i.e., 'Darwin's Arch north' and 'Darwin's Arch south'), and at the east and south-eastern sides of Wolf Island (i.e., ‘Corals south’ and ‘Landslide north’) (Fig. 4-2).

4.5 Discussion

This is the first study to demonstrate empirically that non-instantaneous surveys from belt-transect surveys can cause overestimation of the density of individuals and biomass of sharks. Estimates obtained when including non-instantaneous records were almost double than those obtained from using only the instantaneous records. The bias observed here was considerably lower than the order-of-magnitude scale predicted by Ward-Paige et al. (2010). In the models developed by Ward-Paige et al. (2010), swimming speeds were much slower (1 to 7 m min^{-1}) than the speeds recorded in our study (> 30 m min^{-1}), which could explain the difference between their predicted effect size and our results. Covering the belt transect at faster speeds reduces the chances of sharks outside the survey area moving into it over the period of observation (Figs. 4-1; Ward-Paige et al. 2010). Other factors might also influence the magnitude of this over-estimation, such as species-specific swimming behaviours (e.g., swimming speed, horizontal *vs* vertical movements and potential schooling behaviour), hydrodynamics (e.g., exposure to currents) and topography of the surveyed area (e.g., reef slope and complexity).

Sightings of sharks were not distributed randomly around Darwin and Wolf islands, but were concentrated along their south-eastern coastlines (Figs. 4-2a and 4-2b). This is consistent with results from previous acoustic telemetry studies at these locations, which indicated greater usage by sharks of areas corresponding to the sides of these oceanic islands more exposed to currents (Hearn et al. 2010, Ketchum et al. 2014a). A similar spatial distribution of sharks in relation to dominant currents has been reported at Malpelo Island, Colombia, another oceanic island of the ETP (Bessudo et al. 2011). Hearn et al. (2010) suggested that a continuous provision of plankton along the sides of the islands exposed to currents support abundant populations of planktivorous pelagic and reef fishes, which in turn provide a food source for meso- and top predators.

DOVs *vs* UVC for estimating individual and biomass densities of sharks

The use of DOVs provides significant benefits compared to visual observers (UVC) when conducting density estimations of highly mobile fishes in belt transects. For UVC, the observer needs to estimate the size of the surveyed area (width and height), provide taxonomic identifications, counts and length estimates of moving individuals of the target species. This task becomes even more complicated if the target species are highly mobile and are present in high numbers (Watson et al. 1995, Harvey et al. 2004, Colton and Swearer 2010). Under these circumstances, it seems unlikely that a visual observer would be able to accurately determine, moment by moment, whether each individual recorded was initially sighted within the surveyed area or not in order to avoid a non-instantaneous survey and its consequent overestimation of densities. In addition, underwater visual observers will likely need to reduce their swimming speed to under 10 m min^{-1} in order to be able to complete so many tasks (Ward-Paige et al. 2010), which would both reduce the total area surveyed and, more importantly, could increase the likelihood of overestimation.

Conversely, when using DOVs, data are obtained during video analysis in a laboratory, ensuring greater accuracy for taxonomic identifications (potentially by including consultation with other experts) and counting (Shortis et al. 2007). The use of a stereo-video setting also provides accurate and reliable measurements of the surveyed area and the lengths of fish (Harvey et al. 2004). For example, Salinas-de-León et al.

(2016) reported the tendency of underwater visual observers to underestimate the TL of large sharks. Indeed, our recorded mean size for *S. lewini* (2.6 ± 0.2 m TL) using DOVs clearly exceeded the size range published by Ketchum et al. (2014b) (1.8 to 2 m TL), which was based on visual underwater estimates of 134 individual sharks by free-divers at Darwin and Wolf islands. Importantly, unlike UVC, the use of DOVs allows instantaneous ('snapshot') surveys of shark occurrences within a belt transect. The video-analyser can stop the video footage every time a shark is seen and accurately determine if it is inside or outside the limits of the transect being surveyed, and hence whether or not it should be counted. Finally, by not having to collect data *in situ*, divers using DOVs can increase their swimming speed considerably (> 30 m min^{-1} of mean speed in our study). This means the total area surveyed can be larger, optimising the time spent underwater.

Further benefits accrue when DOVs are used in combination with a towed synchronised GPS unit. The most important feature is that all shark records can be geo-referenced (Kuch et al. 2012), providing information about the fine-scale spatial distribution of the target species (Lynch et al. 2015). Of course, there will be limitations on the spatial accuracy and precision of georeferencing obtained *via* towed GPS; e.g., there will be slight differences in the position of the towed buoy and the diver (Schories and Niedzwiedz 2012). Nevertheless, spatial data can provide relevant information about the behaviour and ecology of the target species and can be a useful tool to identify priority areas for conservation and fisheries management. Another benefit of using this system is that a single supertransect can be divided into replicates after conducting the survey, which provides the opportunity to conduct comparisons with results of other studies that may have used replicates of varying sizes. Finally, this system reduces potential biases associated with species-specific responses of fish to divers' activities underwater, as divers do not need to unreel tapes to measure lengths of replicate transects nor estimate time or space intervals between them (Dickens et al. 2011).

Our results support the findings of Ward-Paige et al. (2010), who predicted that non-instantaneous surveys would fail to provide reliable estimates of densities of highly mobile species. Overestimation of densities could have serious consequences for endangered species, such as sharks, as they could lead to management decisions that could negatively impact their conservation. In summary, the use of DOVs combined with towed GPS units for the estimation of densities of individuals and biomass of sharks provides a significant improvement over UVC in terms of accuracy, efficiency, and optimization of time spent by divers underwater. DOVs allow the elimination of potential biases associated with the use of non-instantaneous records, and can provide both individual length measurements and fine-scale spatial distributional maps of the target species. Consequently, we encourage the use of DOVs for future surveys of sharks and other large mobile marine species.

Chapter 5. Understanding human attitudes towards sharks to promote sustainable coexistence

5.1. Abstract

Better understanding of human attitudes towards sharks is essential to foster support for shark conservation. Here, a quantitative multivariate approach was used to analyse data from questionnaire-based surveys of public attitudes towards sharks in the Galapagos Marine Reserve to identify some of the most influential socio-economic factors, emotions and beliefs that shape those attitudes. The aesthetic value of sharks, their environmental role, and their perceived dangerousness had the greatest influence on attitudes. However, attitudes also varied according to the gender, occupation, and residency status of respondents. Knowledge and experience with sharks had a moderate influence on attitudes, while behavioural responses, such as tolerance and support for the protection of sharks, showed strong correlations with attitudes. Therefore, it is recommended that efforts to promote positive attitudes and behaviours towards sharks should use strategies that encourage support for shark conservation policies by targeting the most influential emotions and beliefs held by the public.

5.2 Introduction

Public support for environmental issues can lead to important shifts in conservation policies (O'Bryhim and Parsons 2015). Conversely, negative attitudes towards wildlife can reduce support for conservation efforts and allow detrimental activities such as illegal hunting (Thompson and Mintzes 2002). Therefore, communication strategies aimed at inducing positive changes in attitudes and behaviours are essential tools in nature conservation. Yet, an estimated 50% of these initiatives fail (van der Ploeg et al. 2011), likely due to poor understanding of the drivers of public attitudes towards conservation issues and how these might affect behaviour (Kollmuss and Agyeman 2002, Mosler and Martens 2008).

The concept of ’attitude’ is central to behavioural science (Thomas and Znaniecki 1918). An attitude is broadly defined as "a psychological tendency that is expressed by evaluating a particular entity with some degree of favour or disfavour" (Eagly and Chaiken 1993, p.1). It is generally accepted that attitudes comprise a cognitive component (i.e., beliefs) and an affective component (i.e., emotions and feelings; Verplanken et al. 1998, Glikman et al. 2012; Fig. 5-1). Attitudes are thought to be strongly influenced by experiences of the particular entity and highly predictive of future behaviours towards that entity (see also Fazio & Zanna (1978), Kraus (1995); Fig. 5-1).

Studies of public attitudes towards conservation initiatives have led to some important insights (Kideghesho et al. 2007). In particular, attitudes influence important behavioural responses such as ‘tolerance’ of a species (i.e., the degree of acceptance of living in coexistence with a wild population (Bruskotter and Wilson 2014)), support for protection, and willingness to increase knowledge about a species (Monroe 2003; Fig. 5-1). Public tolerance of and attitudes towards sharks are particularly contentious (Simpfendorfer et al. 2011). Large animals that can physically harm humans generally suffer from negative attitudes and low tolerance (Crossley et al. 2014), though these may be offset by perceived economic benefits derived from wild populations (Bruskotter and Wilson 2014). Indeed, negative attitudes towards sharks are thought to be driven primarily by fear, negatively impacting management policies around the world (Achen and Bartels 2004), but they persist despite the potential of sharks to

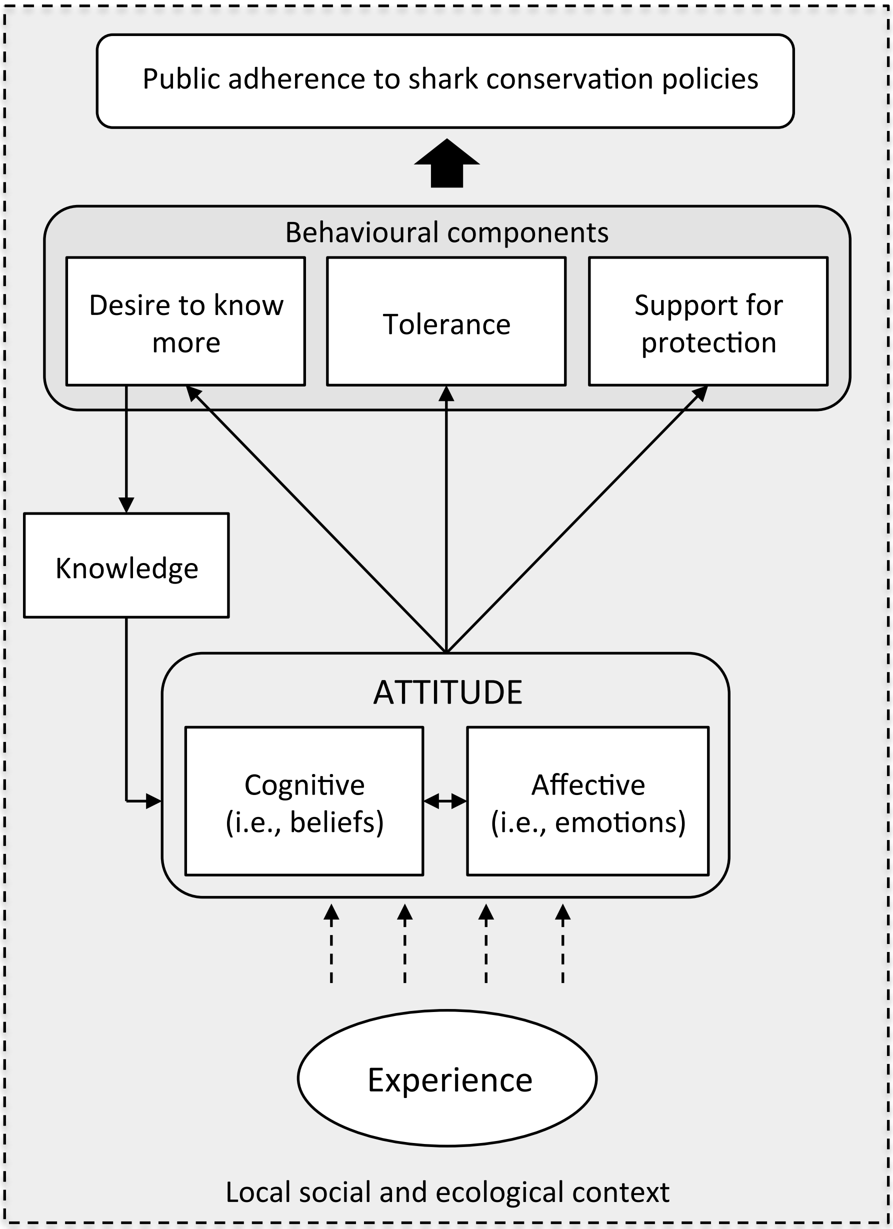


Figure 5-1. Diagram showing the conceptual framework used in this study relating attitudes (produced after an evaluating process involving beliefs and emotions) and behaviours (reflected in the tolerance to coexistence situations with wildlife, support for its protection and willingness to increase knowledge about it). Lighter-gray area delimited by dashed line refers to the local social and ecological context.

provide considerable economic benefits *via* ecotourism (Vianna et al. 2012, Cisneros-Montemayor et al. 2013). Given the critical status of many shark populations worldwide

(Dulvy et al. 2014), a better understanding of public attitudes and behaviours towards sharks is urgently required to foster support for conservation initiatives.

Questionnaire-based surveys are a key tool in the study of attitudes but they pose some important methodological challenges. Attitudes expressed directly by respondents are context-dependent, varying according to the circumstances of the survey and the format or wording of the questions (Schuman and Presser 1981). Instead, a deeper understanding of attitudes can be achieved through questions that target the various judgmental processes—the cognitive and emotional variables—that comprise attitudes (Bohner and Schwarz 2001). The few questionnaire-based studies of humans' attitudes towards sharks are limited to relating responses to direct questions about attitudes to differences in demography, knowledge and experience (Friedrich et al. 2014, Garla et al. 2015, O'Bryhim and Parsons 2015). Remarkably, in only one study (O'Bryhim and Parsons 2015) was the test of attitude assessed for its reliability (e.g., using the standard method developed by Cronbach (1951)), and a poor reliability coefficient score resulted in attitude being excluded from the analysis. In addition, to date, there has been no study of the underlying cognitive and affective components that comprise attitudes towards sharks, or attempt to identify relationships between attitudes and their willingness to tolerate coexisting with sharks.

This study introduces a new methodological approach to understanding and quantifying public attitudes towards sharks. Following literature on attitudes (Fazio and Zanna 1978, Verplanken et al. 1998, Glikman et al. 2012) we used a conceptual framework where attitudes comprise cognitive and emotional components, are able to predict behavioural responses and can be influenced by previous experiences (Fig. 5-1). Using the Galapagos Islands as a case study, questionnaire-based interviews were used to collect data on the cognitive and affective variables, and behavioural responses associated with attitudes, which were then analysed using a multivariate statistical approach. This study aimed, firstly, to quantify the relative contributions of a set of proposed variables in the formation of overall attitudes. Negative emotional variables (e.g., the fear of sharks) were expected to have a strong negative influence on attitudes, whereas some cognitive components (e.g., perceptions of ecological and economic benefits, and endangered populations) were expected to be positively associated with attitudes. Secondly, differences were tested in the construction of attitudes among various demographic groups, such as males *vs* females and residents *vs* visitors to the islands. Thirdly, it was examined how attitudes influenced behavioural responses, such as tolerance of living near sharks, willingness to increase knowledge of sharks, and support for conservation measures. Finally, it was discussed how these results may be used constructively in the design of more effective communication strategies to foster support for shark conservation policies.

5.3 Materials and methods

Study population and survey design

The Galapagos Archipelago (Ecuador) is a UNESCO Natural World Heritage Site (UNESCO 2017) located on the equator *ca* 1,000 km west of continental South America. The Archipelago harbours a resident population of *ca* 25,000 and receives over 200,000 visitors per year (Granda and Salazar 2013). The Galapagos Marine Reserve (GMR) provides full protection to sharks, and is one of the few places in the world where abundant populations of these top predators can still be found (Hearn et al. 2014, Salinas-de-León et al. 2016). Sharks are an important attraction for a growing nature-focused tourism industry, which is the base of the local economy (Epler 2007).

Artisanal fishing, research, maritime transport and tourism are all permitted in the GMR under a co-management system (Barragán-Paladines and Chuenpagdee 2015).

The study population comprised adult (> 15 yrs) residents and visitors to the Galapagos Islands in October-November 2015. Residents were approached in a haphazard manner at Puerto Ayora (Santa Cruz Island), the most populated town of the Archipelago (Granda and Salazar 2013), while visitors were approached at the Charles Darwin Research Station, which is visited by most tourists. After conducting a pilot study to ensure the comprehension of questions by respondents and to evaluate the most appropriate method of administration (i.e., self-administered *vs* interview-based), the questionnaire was filled out by researchers during an interview with each respondent. Questionnaires contained close-ended questions structured into sections: demography, previous experience, affective and cognitive variables, knowledge and behavioural responses to sharks (questionnaire provided in App. C, C-1). Within the demographic section, the occupation of the respondent was classified into the sectors of Tourism, Science-Conservation, Fishing, Other, Retired, or Student and also whether they had a relation in the Tourism or Fishing sectors. It was expected that people connected with fishing *vs* tourism sectors would have opposing attitudes and economic interests, as these sectors correspond to extractive *vs* non-extractive uses, respectively.

Rather than asking direct questions about attitudes, this survey was designed to quantify separately affective and cognitive responses towards sharks. This allowed to examine the underlying construction of attitude on the basis of these separate components, using a multivariate approach. Each respondent provided scores for each of 14 variables considered to be associated with either the affective (including two positive and two negative emotions) or cognitive (including five pairs of opposing beliefs) components of attitude, based on our review of relevant literature (Table 5-1).

Scores were recorded on a four-point ordinal scale (from 1 to 4, where 1 = ‘nothing’, to 4 = ‘high’; see questionnaire in App. C, C-1). Self-perceived knowledge about sharks, and previous experiences with sharks in the wild, were also evaluated and ranked (on scales of 1 to 4 and -2 to +2, respectively). Behavioural responses to sharks were assessed by asking respondents’ willingness to coexist with sharks (i.e., tolerance), to support their conservation or to increase knowledge about them, and were evaluated through positive/neutral/negative categorizations.

Data analysis

The multivariate reliability and consistency among the 14 affective and cognitive variables associated with attitude were supported by a Cronbach’s α (Cronbach 1951) score of 0.77. Principal component analysis (PCA, implemented with the R package ‘FactomineR’; Lê 2008) was then used on the 14 variables. Based on its loadings, the first PCA axis, PC1, was interpreted as an index of overall attitude and the relative contributions of the 14 variables were examined. Permutation-based multivariate analysis of variance (PERMANOVA (Anderson 2001), implemented using the add-on package PERMANOVA+ to PRIMER 7 (Anderson et al. 2008, Clarke and Gorley 2015)) was used to test for differences in attitudes (based on pair-wise Euclidean distances calculated from the 14 attitude variables) in response to demographic factors, levels of knowledge, experiences with sharks, and behavioural responses. All factors were treated as fixed.

Linear discriminant analyses (LDA, R package ‘MASS’ (Venables and Ripley 2002)) were used to determine which of the 14 attitude variables best discriminated among demographic categories (specifically, gender and residency). This allowed to identify differences in the attitudes of males *vs* females and residents *vs* visitors.

Table 5-1. Variables (emotions and beliefs) involved in the construction of the attitude towards sharks.

Component	Attitude variables	PC1 eigenvector weights[a]					LDA[b]	
		Total	Females	Males	Residents	Visitors	Gender	Residency
Affective (emotions)	Curiosity	0.49	0.48	0.52	0.50	0.53	-0.05	0.36
	Excitement	0.63	0.57	0.68	0.67	0.57	0.11	0.2
	Fear	-0.27	-0.40	-0.16	-0.21	-0.37	-0.73	0.32
	Repulsion	-0.44	-0.41	-0.48	-0.44	-0.47	0.17	0.09
Cognitive (beliefs)	Threatened	0.46	0.38	0.53	0.46	0.46	0.01	-0.06
	Abundant	-0.22	-0.06	-0.39	-0.28	-0.14	0.56	-0.27
	Vulnerable	0.47	0.39	0.55	0.50	0.44	-0.25	0.12
	Dangerous	-0.58	-0.62	-0.55	-0.56	-0.60	-0.35	0.44
	Economy pos.	0.49	0.49	0.48	0.50	0.51	-0.03	-0.48
	Economy neg.	-0.5	-0.49	-0.49	-0.58	-0.37	0.04	0.24
	Ecology pos.	0.67	0.58	0.76	0.77	0.56	0.34	0.08
	Ecology neg.	-0.57	-0.52	-0.60	-0.66	-0.46	0.17	0.65
	Aesthetic pos.	0.71	0.73	0.71	0.73	0.69	-0.12	0.42
	Aesthetic neg.	-0.63	-0.63	-0.64	-0.66	-0.53	0.22	-0.1

[a] Relative importance of the individual components for all respondents and by gender and residency categories, with positive values along PC1 corresponding to overall positive attitudes.

[b] Loadings for the linear discriminant analysis (LDA), indicating which variables best discriminate between males *vs* females (positive *vs* negative LDA, respectively) and between residents *vs* visitors (negative *vs* positive LDA, respectively).

Differences in fear and tolerance to sharks between residents and visitors were tested using Mann-Whitney and chi-square tests, respectively.

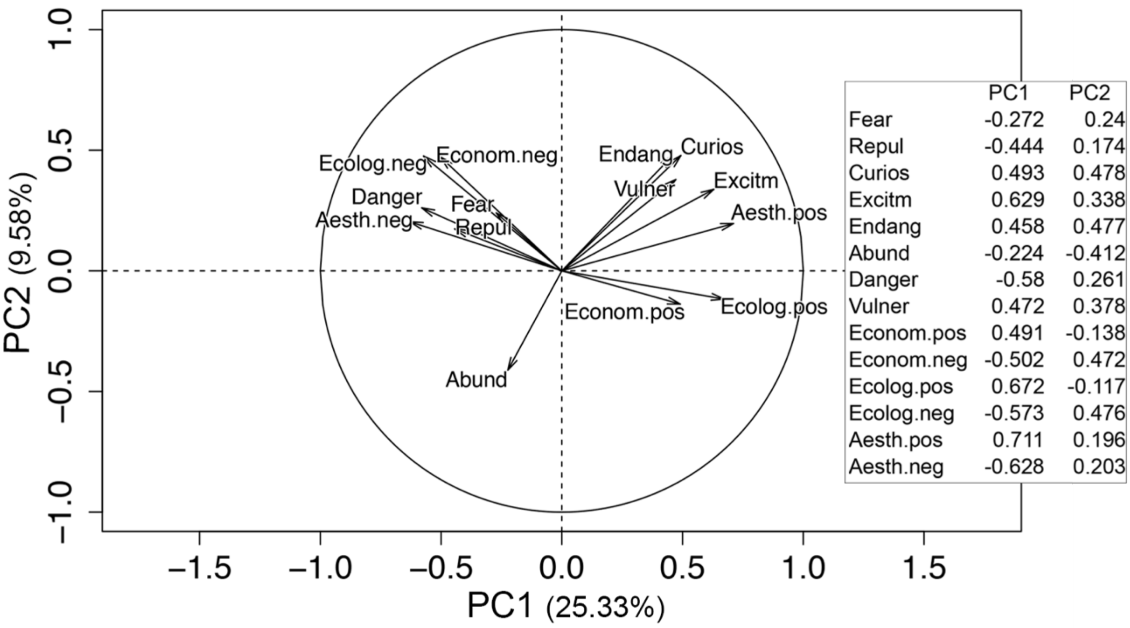
Boosted regression trees (BRTs; implemented using the R package 'dismo' (Hijmans et al. 2017)) were used to build predictive models of behaviours towards sharks (i.e., willingness to tolerate sharks or support shark conservation) using the variables provided by the surveys. The ability of the models to discriminate these binary variables was assessed using the area under the receiver-operating curve statistic (AUC); only models with acceptable (AUC>0.7) or excellent (AUC>0.8) scores were selected (Hosmer and Lemeshow 2000).

5.4 Results

A total of 455 respondents were interviewed (51% females, 49% males), ranging from 16 to 95 years old, with an average of 37 years. Fourteen percent were students and 4% were retired. From the 247 local respondents, a majority (75%) were long-term residents (>10 years), and were employed in the local tourism sector (27%), commercial fishing sector (11%), science-conservation sector (9%), or other occupations (37%). Ten percent of the 208 respondents that were visitors to the Galapagos worked in science-conservation.

Attitude

The first axis (PC1) of the PCA explained 28 % of the total variance (Fig. 5-2). The signs of the loadings of variables on PC1 were consistent with its interpretation as an index of overall attitudes towards sharks, from negative to positive. The greatest loadings of individual variables on PC1 were associated with aesthetic variables (having positive loadings with PC1), followed by belief in the importance of sharks for the environment (positive loadings), and then the belief that sharks are dangerous (negative loadings; Table 5-1). Respondents declared a low-to-moderate fear of sharks (Table 5-1), which was higher on average in visitors than in residents (Mann-Whitney W = 21758, $p = 0.002$). Age showed a weak, negative correlation with PC1 ($r = -0.19$, $p < 0.001$). The subsequent principal component axes were not analysed any further because they were not easily interpretable and explained less than 10 % of the variance (Fig. 5-2).



	PC1	PC2
Fear	-0.272	0.24
Repul	-0.444	0.174
Curios	0.493	0.478
Excitm	0.629	0.338
Endang	0.458	0.477
Abund	-0.224	-0.412
Danger	-0.58	0.261
Vulner	0.472	0.378
Econom.pos	0.491	-0.138
Econom.neg	-0.502	0.472
Ecolog.pos	0.672	-0.117
Ecolog.neg	-0.573	0.476
Aesth.pos	0.711	0.196
Aesth.neg	-0.628	0.203

Figure 5-2. Vectors showing the degree of correlation (i.e., proximity of the arrow heads representing each variable to the unit circle) of the 14 selected factors to the first two principal components (PCs) of the PCA, which together explain 39.3 % of the variation. The first principal component (PC1) is interpreted as an index of overall attitudes towards sharks, based on its loadings. Embedded table shows the loadings for each of the 14 selected factors for the first and second principal components (PC1 and PC2, respectively).

PERMANOVA identified significant effects of gender, occupation, and residency on the attitudes towards sharks, based on the full 14-variable multivariate space (Table 5-2). Leave-one-out allocation of individuals to groups yielded miss-classification rates of 37 % and 36 % for the gender and resident/visitor status in the LDA models, respectively, which identified the components of attitude that differed most between genders. In the case of females, negative attitudes were associated with greater fear, whereas, in males, they were driven more by the perception that sharks are abundant (Table 5-1). With regards to residency status, visitors believed more strongly that sharks have a negative impact on the environment, while residents believed them to have a positive impact on the economy (Table 5-1).

Table 5-2. Results of the PERMANOVA analysis indicating the degrees of freedom (df), mean sum of squares (MS) and p-values (P) based on 9,999 permutations for each evaluated factor.

Source	df	MS	P(perm)
Gender	1	29.3	0.0017
Age group	3	8.81	0.4756
Occupation	5	28.56	0.0001
Relation Fisher/Tourism	3	9.88	0.325
Residency	1	26.52	0.0039
Experience	1	69.16	0.0001
Experience rate	1	296.63	0.0001
Knowledge	4	45.88	0.0001
Tolerance	3	97.83	0.0001
Support for protection	3	47.9	0.0001
Increase knowledge	2	32.56	0.0002

Positive attitudes (i.e., high PC1 scores) were significantly related to self-perceived knowledge (mean ± SE, on a scale of 1 to 4: 2.36 ± 0.04), having had experiences with sharks (which was the case for 83% of residents and 64% of visitors), and also with how positively these experiences were rated (1.26 ± 0.05). Knowledge and experience-ratings showed moderate positive correlations with attitude (r = 0.31 $p < 0.001$ and r = 0.43, $p < 0.001$, respectively). Watching sharks from the beach or from boats was the most common experience, followed by activities such as snorkelling or scuba diving (Fig. 5-3). All types of experiences with sharks in the wild were mostly rated positively, except for those that occurred while respondents were either surfing or fishing, in which case the positive *vs* negative experiences were roughly equal (Fig. 5-3).

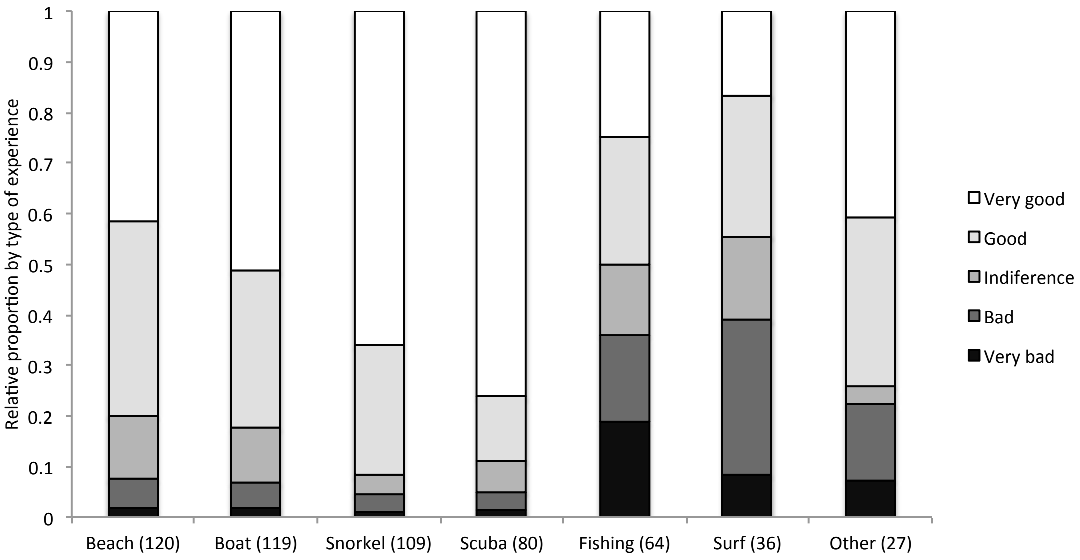


Figure 5-3. Classification and rating of the people experiences with sharks in the wild (frequencies in parentheses) by respondents.

On average younger respondents and people who themselves or their close relatives worked in science-conservation or tourism sectors tended to have positive attitudes, while older respondents and those either retired or working in fisheries (or having close relatives doing so) exhibited negative attitudes (Table 5-3). Other demographic categories showed neither significantly positive nor negative attitudes, on average (Table 5-3).

Tolerance and support for protection

The three behavioural components (i.e., tolerance, support for protection, and wishing to increase knowledge of sharks) were all positively correlated with attitudes (Table 5-2). Tolerance was significantly different between residents (61 % acceptance) and visitors (38 % acceptance; $\chi^2_{[2]}=33.34$, $p = 5.76\text{e-}08$). The most influential predictor variables for tolerance of sharks were occupation (with the conservation and tourism sectors being associated with higher tolerance) and the perception of danger (with the

Table 5-3. Relationships between PC1 (principal component 1, i.e., overall attitude) and individuals levels of each qualitative factor.

Qualitative factor	Categories[a]	PC1 coordinate	cos2	V-test[b]
Gender	Female	-0.036	0.009	-0.393
	Male	0.037	0.009	0.393
Age group	15-29 yrs.*	0.378	0.834	3.055
	30-44 yrs.	-0.023	0.013	-0.191
	45-59 yrs.	-0.37	0.643	-1.714
	> 60 yrs†	-0.674	0.568	-2.526
Occupation	Conservation	0.847	0.794	2.989
	Fishing†	-2.51	0.575	-6.8
	Other	-0.077	0.051	-0.845
	Retired†	-1.669	0.71	-3.653
	Student	0.172	0.191	0.748
	Tourism*	0.938	0.738	4.237
Relation Fisher/Tourism	Both	-0.441	0.12	-1.17
	Fishing†	-1.638	0.61	-4.778
	None	0.022	0.007	0.346
	Tourism*	0.596	0.7	3.254
Residency	Resident	0.102	0.056	1.199
	Visitor	-0.12	0.056	-1.199
Residency index	< 1 yrs.	0.664	0.387	1.536
	> 10 yrs.	0.004	0	0.034
	1-5 yrs.*	1.022	0.743	2.425
	5-10 yrs.	-0.65	0.261	-1.339
	Visitor	-0.12	0.056	-1.199
Experience w sharks	None†	-0.525	0.438	-3.307
	Yes*	0.178	0.438	3.307
Tolerance	Indifference	-0.189	0.361	-1.251
	No†	-1.525	0.871	-8.501
	Yes*	0.8	0.904	8.582
Support for protection	Agree*	0.187	0.881	6.938
	Disagree†	-5.499	0.895	-8.892
	Indifference†	-1.836	0.799	-3.781
Increase knowledge	No†	-3.456	0.951	-7.993
	Yes*	0.165	0.91	6.885

[a] V-test values higher than 2 in absolute value indicate either a positive (*) or negative (†) attitude.

[b] V-tests indicate if the projection of the barycenter of individuals belonging to that category along the PC1 axis was significantly different from zero (Lê et al. 2008).

perception of greater danger being associated with lower tolerance) (Fig. 5-4a). To predict the level of support for the protection of sharks, the most important variables were the perception that shark populations are vulnerable and that they are important to the environment (Fig. 5-4b).

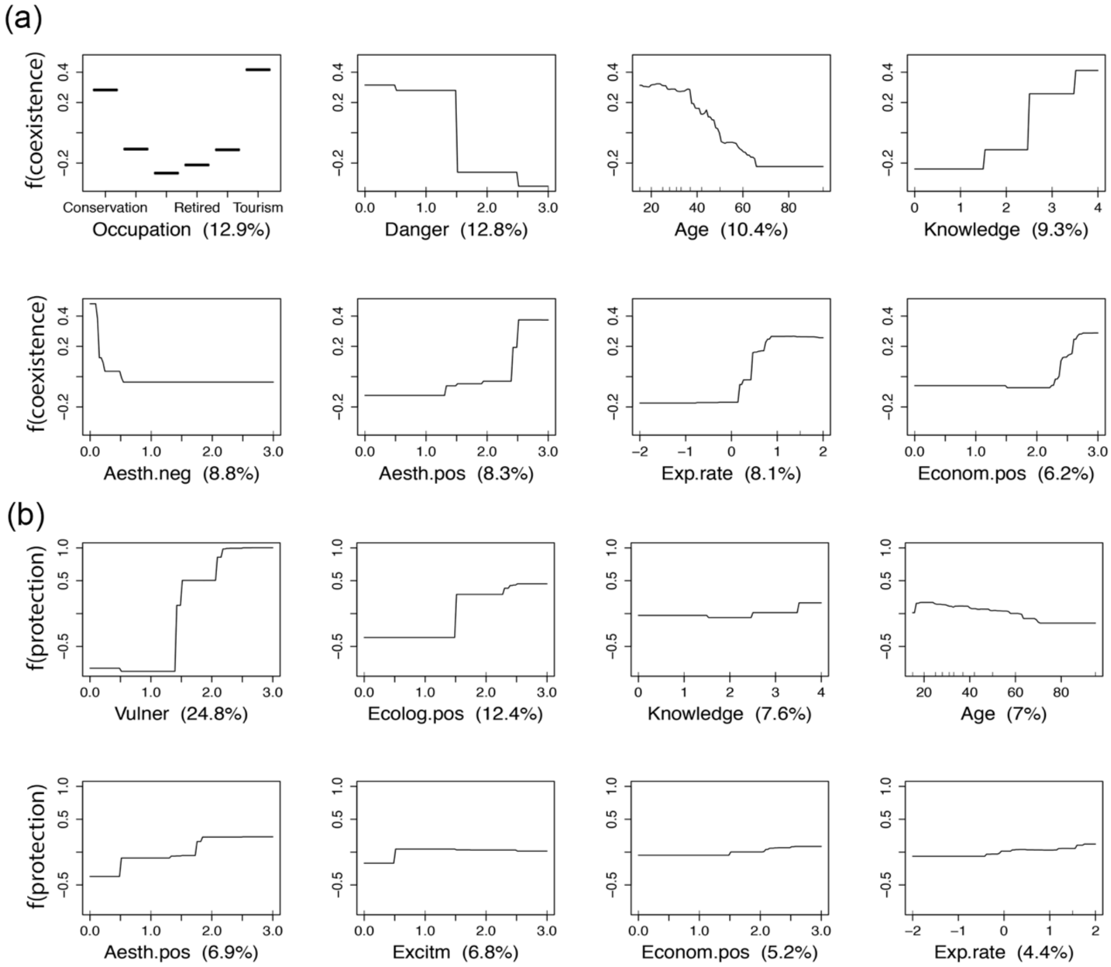


Figure 5-4. Partial dependence plots (following Elith and Leathwick (2016)) showing the eight most influential variables in the prediction of tolerance (a) and support for shark protection (b) from Boosted Regression Trees (BRTs). Individual plots show the fitted value of the response variable (i.e., tolerance in (a) and support for shark protection in (b)) on the Y-axis versus each of the potential predictor variables, integrated across all other variables in the model. Prediction performance was assessed using the area under the curve (AUC; Hosmer and Lemeshow 2000) with the BRT models providing acceptable (AUC = 0.78) and excellent (AUC = 0.85) model predictions, respectively.

5.5 Discussion

This novel approach of constructing multivariate models of attitudes, based on 14 comprising variables, revealed that attitudes towards sharks among survey respondents at the Galapagos Islands were complex and heterogeneous. Attitudes were shaped by a range of psychological factors, such as aesthetics, and also by the socio-economic context of individual respondents. Strong correlations were found between attitudes and behavioural responses, such as tolerance or support for shark protection. These results strongly support the critical role played by demographic, socio-economic and contextual factors in structuring both cognitive and affective components of attitudes that, in turn, provide the underlying basis and development of behavioural tendencies in humans. Thus, to positively change public behaviour towards wildlife populations, such as fostering higher tolerance and support for their protection, it is necessary to find creative ways to target the emotional and rational apparatuses that shape public attitudes.

Although attitudes were similar across genders and residency statuses in term of the overall scale from negative to positive attitudes (Table 5-3), these groups nevertheless differed in terms of the relative importance of particular emotions and beliefs underlying the construction of these attitudes (Table 5-1). Consequently, when designing communications or experiences aimed at improving attitudes, different approaches might be used according to the target population. For example, women could be approached with messages aimed at moderating the fear of sharks, whereas men might be given more information about the current declines in shark populations.

Perhaps unexpectedly, aesthetic values had the greatest influence on attitudes towards sharks, surpassing variables such as fear and perceived danger. Yet, this is consistent with studies of other taxa, which identified physical appearance as one of the most important qualities in the appeal of animals to humans (Kellert 1996) and in predicting attitudes (de Pinho et al. 2014) and the level of support for species protection (Knight 2008). Accordingly, the way sharks are visually represented likely plays a major role in shaping public attitudes and attitudes might be lifted by representing sharks as beautiful, majestic and magnificent animals, rather than through menacing music (Nosal et al. 2016) and threatening images representing them as voracious predators (Myrick and Evans 2014).

Negative attitudes were more strongly associated with the belief that sharks are dangerous, than with the emotional variable of fear (Table 5-1), which was contrary to previous expectations. On average, residents were less fearful of sharks than were visitors, perhaps because residents live in closer proximity to abundant populations of sharks, leading to more experiences and better understanding of sharks (Neff and Yang 2013). Negative emotions, such as fear, interfere with reasoning, so cognitive changes might best be achieved by providing factual information (Pham 2007). Environmental agencies and managers at the Galapagos Islands are encouraged to inform the public about the genuinely low probability and risk of being attacked by sharks within the Archipelago (Acuña-Marrero and Peñaherrera-Palma 2011).

There was a moderately positive association between respondents' attitudes towards sharks and having had previous experiences and knowledge of them. Observing sharks in their environment (snorkelling and scuba diving) generally provided good experiences, despite being potentially vulnerable to attacks (Fig. 5-3). Accordingly, shark-based eco-tourism not only provides economic incentives for the local population to conserve sharks, but may also be important for promoting of positive attitudes and behavioural responses towards sharks more broadly. In contrast, encounters while surfing provided a higher proportion of bad experiences, likely because surfers make up a high proportion of shark-attack victims (Last and Stevens 2009).

The results of this study confirm the strong associations between attitudes and behaviours. Positive attitudes were strongly predictive of tolerance and support for efforts to conserve shark populations. The primary predictor of tolerance was having an occupation in sectors that derive potential economic benefit from sharks and their protection, such as tourism and science-conservation. Notably, even a moderate belief of sharks as dangerous animals does not preclude a willingness to coexist with them, particularly when there are economic benefits of doing so (Fig. 5-4a). This highlights the importance of informing the local community of the benefits provided by sharks to the economy and emphasizing the genuinely low risk of danger in order to increase tolerance. Finally, helping the public to understand the vulnerability of sharks to overfishing and their important ecological roles is clearly important for fostering support for shark protection (Fig. 5-4b). All of these specific messages should be highlighted in educational programs and communications with the local population and visitors.

The new methodological approach introduced here proved to be reliable and informative, allowing to (1) construct multivariate models of attitudes towards sharks based on a set of comprising affective (emotions) and cognitive (beliefs) variables, (2) articulate differences in the construction of attitudes among various demographic categories, and (3) create predictive models to identify which aspects of attitudes had the greatest influence on behaviours related to shark conservation. In the local context, these results provided clear guidelines for those wishing to promote support for conservation policies through public communication and education programs. More broadly, it is clear that attitudes are complex and heterogeneous, both within and among populations. It is considered that, by using a similar multivariate approach, researchers aiming to understand and enhance public attitudes and maturity in environmental policy formation for management of wildlife populations can formulate useful scientific advice on how to directly influence positive behaviours towards conservation. Effective tailor-made communication and awareness strategies can then be designed to gain support for and to ensure adherence to environmental policies that ensure the long-term conservation of threatened wildlife populations.

Chapter 6. General discussion

The central aim of this thesis was to make a meaningful contribution to shark conservation at the Galapagos Marine Reserve (GMR) and the Eastern Tropical Pacific (ETP) region. In this final chapter, I first provide an overview of each chapter, highlighting the main contributions and implications for shark conservation in the GMR and beyond. I then broadly discuss the current performance of the GMR in conserving sharks, in light of my research, and make recommendations for how such efforts may be improved. Directions for further research at both local and broader scale are discussed throughout.

6.1 Overview of research contributions

This thesis highlights the utility of a multi-disciplinary approach to conservation research, specifically by integrating the study of the spatial ecology of sharks at the GMR with the human context of this UNESCO World Heritage Site (UNESCO 2017). To achieve the best outcomes for shark conservation in a multi-use Marine Protected Area (MPA), such as the GMR, it is essential that the management authorities have detailed information about the spatial distribution and movement range of shark populations. This information provides the basis for identifying priority areas for shark conservation where avoid potential conflicts with human uses (e.g., the use of gillnets in shark nursery areas), or areas that may provide opportunities for profitable sustainable activities (e.g., shark eco-tourism in areas of high shark density). However, we acknowledge that governance of the GMR also faces challenges that arise due to the interests and behaviour of local people, rather than a lack of biological or ecological knowledge (Barragán-Paladines and Chuenpagdee 2015). Any negative public attitudes towards wildlife can reduce support for conservation efforts and motivate detrimental activities such as illegal hunting (Thompson and Mintzes 2002). In the case of the Galapagos Islands, sharks have played an important historical socio-economic role as a resource for fishing (extractive) and for tourism (non-extractive) activities; yet, sharks may also be perceived negatively by local people due to occasional incidents with humans (Acuña-Marrero and Peñaherrera 2011, Carr et al. 2013). As the GMR is governed under a participative management model, public support and positive attitudes towards marine organisms, such as sharks, are essential to achieve conservation goals. Human-shark interactions at the Galapagos Islands had not yet been studied from a social perspective. This thesis aimed to fill this gap, complementing the research about the spatial ecology of sharks with a social study that aimed to identify the factors that shape the attitudes of locals and visitors towards these threatened predators. This provides the management authorities of the GMR with the necessary knowledge and tools to not only develop efficient environmental policies for the long-term conservation of shark populations but also to bolster public support for their implementation.

6.1.1 Patterns of distribution and abundance of coastal sharks at the GMR (Chapter 2)

The study of the spatial and temporal distributions of coastal shark populations at the GMR is the first of its kind in the ETP region, despite it being a recognised global shark hotspot (Klimley 2015). This study provides the first comprehensive baseline of abundance and distribution of coastal sharks at the GMR. This information is essential to inform and evaluate the suitability of the zoning scheme implemented at the GMR for shark conservation. It also lays the foundation for future assessments that allow establishing population trends and detects variability in shark assemblages according to changes in management or impacts of climatic events, such as El Niño/ENSO or global warming. In addition, this work identifies associations between the distribution and abundance of several shark species and a range of environmental and biological variables, yielding interesting hypotheses about the drivers of the spatial patterns of shark populations, and providing the opportunity to develop predictive models that could be applied in similar environments where empirical data are lacking.

The lack of seasonal variability of the shark assemblages found in our study was likely caused by an El Niño/ENSO event occurring at the Galapagos Archipelago during the year of the study (2015). To clarify this and provide a longer temporal data set, a second BRUV survey was conducted in 2016 at the GMR, visiting most of the same study sites. At the time of submitting this thesis, the data from this second survey are being analysed. However, we expect the second survey to also be somewhat anomalous relative to regular years, as the El Niño/ENSO event was considered to have continued until the first half of 2016, and it was succeeded by a La Niña event which brings atypically low sea temperatures to the Archipelago (Banks 2002). Thus, we recommend further replication of this survey in both the short and long terms, in order to get a better understanding of potential inter-annual variations in the shark assemblages and the impact of climatic events in shark populations. In the current scenario of global warming, this data may be essential to inform the management of shark populations worldwide.

6.1.2 Movement patterns – a case-study of the tiger shark *Galeocerdo cuvier* (Chapter 3)

The movement patterns of large predatory sharks have been well studied in a few regions (Hammerschlag et al. 2011). Telemetry techniques (acoustic and satellite) have been extensively used to determine residency, migratory patterns and activity space of most of the largest coastal predatory sharks, including the tiger shark (*Galeocerdo cuvier*). Chapter 3 presents the first study of the spatial ecology and movements of tiger sharks at the ETP, despite its wide distribution and likely important trophic role in this region (White et al. 2015, Ketchum unpublish. data).

Tiger sharks are highly mobile, potentially migratory top predators (Lea et al. 2015); yet, our study points to tiger sharks having a reduced spatial extent at the GMR due to the provision of a predictable source of prey and suitable habitats. These findings have important conservation implications, as this highly philopatric behaviour potentially enhances the effectiveness of MPAs in the protection of this species. We consider that including healthy ecological communities that ensure high prey availability in MPAs can improve the efficacy of protected areas in the conservation of highly mobile marine top predators. This finding has important implications in the current context of debate about the efficacy of MPA in the protection of large sharks due to a limitation in the size of the protected areas in comparison with their high movement capacity (Chapman et al. 2015, Mee et al. 2016). Our results suggest that, when designing a MPA to protect large sharks, it is important to consider the ecological 'quality' (i.e., provision of prey and suitable habitats for the target species) as well as the overall size of areas set aside for protection.

The tiger shark is considered potentially dangerous to humans (ISAF, https://www.floridamuseum.ufl.edu), but it is also an attraction to divers in eco-tourism activities (Hammerschlag et al. 2012). While this species was recorded sparsely in the BRUV deployments throughout the majority of the GMR, there were two specific areas where adult individuals of this species aggregate during the warm season (Jan-May; Fig. 3-2). The reason for these aggregations is likely the feeding opportunities provided by the nesting activities of sea turtles. The predictability in space and time of these aggregations provides an opportunity to the management authorities of the GMR to help mitigate dangerous encounters between sharks and humans through the regulation of human activities in these locations during aggregation events. Humans engaging in surfing, snorkelling, or underwater fishing with harpoons (e.g., local lobster fishery) may be at severe risk of shark attack during these feeding aggregations. At the same time, the high density of this charismatic species may create opportunities for sustainable and profitable shark encounter activities, if these are conducted properly (Clua et al. 2011, Hammerschlag et al. 2012).

This first study of tiger sharks at the GMR revealed important insights into the spatial ecology of tiger sharks, but several unanswered questions remain. Further monitoring of this species at the GMR with BRUV and tagging methods is recommended. BRUV surveys could provide the necessary data for estimating the size of the local population, based on mark-recapture analyses of the occurrences of identified individual sharks. Continuation of this study could be used to study the population trends through time and test whether it is indeed recovering as we suspect. We also recommend increasing the survey effort in those areas where juveniles were found in higher numbers (south-east of Isabela Island; Fig. 3-2), to establish the use of the GMR as a nursery ground by this species. The continuation of the satellite and acoustic tagging studies is required to more fully evaluate the limited movement range and long-distance migrations of this species at the GMR, and their fidelity to the sea turtle nesting sites, as suggested by our results. Finally, diet analysis could be used to confirm the predation of sea turtles by tiger sharks. A comparison of diet between the sea turtle nesting and non-nesting seasons allow predictions of the overall trophic implications of a growing and highly resident population of this apex predator in the marine ecosystems of the GMR.

6.1.3 Estimating densities of sharks with Diver-Operated Video (Chapter 4)

We provide an empirical demonstration of the overestimation of density and biomass of sharks incurred when using non-instantaneous surveys with belt transects, with important implications for studies of highly mobile marine animals worldwide. For example, overestimating population sizes of endangered species, such as sharks, could lead to incorrect evaluations of their conservation status and management decisions that negatively impact conservation outcomes. This sampling bias can also interfere with our understanding of the ecological baselines of abundance and trophic interactions of apex predators in marine ecosystems (Ward-Paige et al. 2010). Our results suggest that previous estimates of shark densities based on sampling methods that cannot ensure the instantaneous nature of their records should be reviewed and updated using instantaneous sampling. We propose the use of instantaneous diver-operated stereo-video (stereo-DOV) surveys to ensure more accurate estimates of shark densities, especially in areas of high shark abundance. This method could also be applied to survey other highly mobile species on reefs.

Our study also highlighted that the combination of DOV with towed GPS units can provide valuable information about the fine-scale spatial distribution of target species, which can be useful to identify priority areas for conservation or fishing closure. In the case of our study sites, Darwin and Wolf islands, it would be informative to repeat our surveys across seasons and years to assess the temporal variability of shark densities and their fine-scale distribution around these hotspots. The three-dimensional information provided by DOV can be also used to study the schooling behaviour of sharks at the reef or the location and structure of potential inter-specific spatial associations, such as cleaning stations used by sharks.

6.1.4 Human attitudes towards sharks (Chapter 5)

Our study of public attitudes towards sharks at the GMR introduced a new multivariate approach to understanding public attitudes towards wildlife. Our method allowed us to assess the attitudes of the respondents and identify the most influential socio-economic factors, emotions and beliefs that shape them. A range of psychological factors shaped attitudes, with a dominance of aesthetics, and by the socio-economic context of each respondent. Attitudes and behavioural responses, such as tolerance or support for shark protection, showed strong correlations. Therefore, our results provided clear guidelines for those wishing to promote support for conservation policies for sharks through public communication and education programs. While the specific results obtained in our study are currently only applicable to sharks within the context of the GMR, our methods may be used elsewhere with any wildlife species in potential conflict with a human population. Such studies can provide the basis for effective, tailor-made communication and awareness strategies that target specific emotions and beliefs to bolster public support for environmental policies that ensure the long-term conservation of threatened wildlife populations.

The survey and analysis method used here could also be used to test for changes in attitudes before and after communication and awareness campaigns. It would also be desirable to extend the assessment of attitudes towards sharks at the Galapagos Islands to other age ranges, such as kids and teenagers, as our study was focused on the adult population.

6.2 Assessing the performance of the GMR in shark conservation

Our results highlight the diversity of coastal shark species inhabiting GMR, and the broad range of suitable habitats that provide multiple ecological functions for shark populations. The full legal protection offered to sharks, together with the provision of nursery habitats, abundant and predictable prey sources, refuge habitats from predation, and cleaning stations, make the 138,000 km^2 area of the GMR one of the most important shark sanctuaries in the world. While the shark assemblages recorded at the GMR are dominated by large semipelagic species, this great diversity of habitats, including temperate reefs, favours the presence of several less-mobile benthic shark species, which have not been recorded in any other island or archipelago at the ETP. This variety of habitats, and the high fishing pressure in neighbouring unprotected open water and coastal continental areas, highlights the important role of the GMR in maintaining the ecological diversity of sharks in this region.

6.2.1 Main threats for shark populations at the GMR

The two main threats to shark populations at the GMR are (i) fisheries within the GMR, either from incidental by-catch by the local artisanal fleet or from illegal shark fishing activities from both local and external fishers, and (ii) shark fisheries outside the reserve, during shark movements out of the boundaries of the protected area.

6.2.1.1 Shark by-catch in local artisanal fisheries

While commercial fishing for sharks is banned in the GMR, artisanal fisheries of other species are allowed. Artisanal fisheries are relatively small scale and limited in the types of gear, so they likely have only limited impact on shark populations, although more information is needed in order to conduct a proper assessment. This could change dramatically the GMR allowed the use of longlines, as requested by local fishers. Bellow there is a short assessment of the fisheries conducted at the GMR that are susceptible of resulting in shark by-catches and their potential impacts on shark populations.

Gillnets

Local fishers use gillnets at the GMR to catch baitfish and mullets (fam. Mugilidae) in shallow protected bays and mangrove areas. While these shallow habitats were not subject of survey and study in this thesis, it is well known that they are used as nurseries by some shark species at the GMR, especially the blacktip shark (*Carcharhinus limbatus*; Jaenig 2010, Llerena et al. 2010, Llerena et al. 2012). The impact of this fishery in these nursery habitats is still pending on evaluation. However, sightings of juvenile blacktip sharks are becoming more frequent and abundant in shallow coastal areas of the Archipelago (Authors pers. observ.).

Hook and lines

All coastal shark species recorded in our study are susceptible of being captured as by-catch by hook and lines, with perhaps the exception of the Galapagos bullhead shark (*Heterodontus quoyi*), as this benthic shark reaches a small size, has low mobility and nocturnal habits, and feeds primarily on crustaceans (Kyne et al. 2004). The most common fishing gear used at the GMR to catch reef and pelagic fishes are handlines armed with one to several hooks or a fishing lure. This gear can be used in different ways (trawling or stationary) and be deployed at different depths or heights in the water column. Unlike the other methods, handlines are continuously attended by the fisher, rather than being set and checked later. Thus, when a shark is caught incidentally, it is quickly released by the fisher cutting the line. This usually results in a relatively short period of fight and stress for the shark compared with drumlines or longlines, likely resulting in a lower at-gear or post-release mortality rate. However, most sharks are released with the hook attached, which may cause physical damage such as severe lesions, with potential lethal consequences for the sharks. The morbidity and mortality associated with retained hooks still need to be properly assessed (Borucinska et al. 2002, Donaldson et al. 2008, Bansemer and Bennet 2010).

Longlines

The artisanal fishers at the GMR have repeatedly requested that the GMR be opened to the use of longlines to capture more efficiently tunas and billfishes. In response, up to five pilot programs (1997-2013) have assessed the rate of by-catch of the longline fishery at the GMR using different numbers and types of hooks and deployment depths (Reyes et al. 2014). Percent by number of bycatch species in these pilot programs have ranged from 11 to 77%, with sharks being the most common bycatch species captured in all the programs (Reyes et al. 2014). Concerns regarding the validity of the pilot program (2012-13), which produced the lowest estimated percent of by-catch species (11%) has prompted requests for the study to be repeated (Reyes et al. 2014). With regards to sharks, when hooks are deployed at mid water, only semi-pelagic species that enter the water column are susceptible of been caught. Accordingly, up to 14 species of sharks have been identified in the incidental captures of longline studies, including the six semipelagic species recorded in our BRUV deployments (Reyes et al. 2014).

The soak time and duration of handling in longlines are likely factors that influence the at-gear and post-release mortality rates of bycaught sharks (Mandelman and Skomal 2009, Marshall et al. 2012). Importantly, post-release mortality can be caused by high levels of stress incurred when a shark is entangled by a longlines, (up to 26%; Donaldson et al. 2008, Heberer et al. 2010), which would dramatically increase estimates of mortality based on only on 'on-board' mortality events. The impact of catch-and-release procedures in the rate of survivorship varies greatly among shark species (Mandelman and Skomal 2009, Marshall et al. 2012, Gallagher et al. 2014). For the species recorded in our study, the scalloped hammerhead shark (*Sphyrna lewini*) and the blacktip shark have shown some of the highest stress responses to capture and handling, making them very vulnerable to fishing (Young et al. 2002, Mandelman and Skomal 2009). Importantly, these two species were among those most often recorded in our study at the GMR (along with the Galapagos shark, *C. galapagensis*), and the scalloped hammerhead shark is listed as 'Endangered' by the IUCN. In contrast, the tiger shark has shown a high resiliency to capture and handling in longlines and drumlines (Mandelman and Skomal 2009, Marshall et al. 2012, Gallagher et al. 2014). Longline pilot programs conducted at the GMR found generally high mortality rates for bycaught sharks, from 31% in the case of hammerhead sharks (*Sphyrna spp*), and between 5 and 33% for *Carcharhinus* species (Reyes et al. 2014).

The permission of longline fishing at the GMR would likely cause much greater incidence of stress and mortality for sharks, due to their longer soak time and much greater potential fishing capacity (# hooks per fishers) than the currently allowed handline method. Due to the high inter-specific variability in stress levels and associated mortality rate, longlines may disproportionately impact less resilient species, thereby altering the structure and diversity of the shark assemblages and their ecological roles. Furthermore, the high spatial variability of the shark assemblages at the coastal areas of the GMR, the high mobility of the majority of shark species, and high diversity of habitats and areas that are critical to their various life-history stages, suggest that longlines could not be used in any area of the GMR without putting the conservation of its shark populations at extremely high risk. The current proposed zoning scheme provides only provides full protection to some of the areas with high relative density and diversity of sharks, such as Darwin and Wolf Islands and most of the northern part of Santa Cruz Island (Fig. 1-1). However, it allows fishing at several other important areas, such as the east and southeast of Isabela Island and the south of Santa Cruz and Floreana Islands (Fig. 2-1). Shark populations in these areas are particularly vulnerable to longlining because they are dominated by semipelagic species (Fig. 2-1).

6.2.1.2 Illegal fishing inside the GMR

The great extent (138,000 km^2) and high proportion of offshore zones in the GMR makes it difficult to enforce fisheries regulations and control illegal shark fishing activities. The Galapagos National Park Directorate (GNPD) monitors the industrial fishing fleet that operates outside the GMR using the automatic identification system (AIS), which provides real time positions of fishing vessels. However, the Ecuadorian fishery for large pelagic species employs mother ships (‘*nodriza*’) that tow small, fast, outboard-powered, fiber-glass boats (‘*fibras*’), which operate the longlines (Martínez-Ortiz et al. 2015). While the *nodriza* boats are tracked by the AIS and normally remain at the border of the GMR, the *fibras* cannot be tracked and may conduct incursions into the marine reserve. This activity has been repeatedly witnessed and reported by the tourist and scientific boats that regularly visit Darwin and Wolf Islands (Acuña-Marrero pers. observ.). When sea conditions are optimal, the *fibras* can easily cover the 40 miles that separate these oceanic islands from the border of the protected area, deploy and recover the longlines during the night, and leave the area before sunrise. As proof of this activity, the authors have reported several times to the GNPD the discovery of entangled longlines (Acuña-Marrero et al. 2012) and discarded bodies of sharks with their fins removed in the waters around Darwin and Wolf Islands (Fig. 6-1, Acuña-Marrero et al. 2013c).

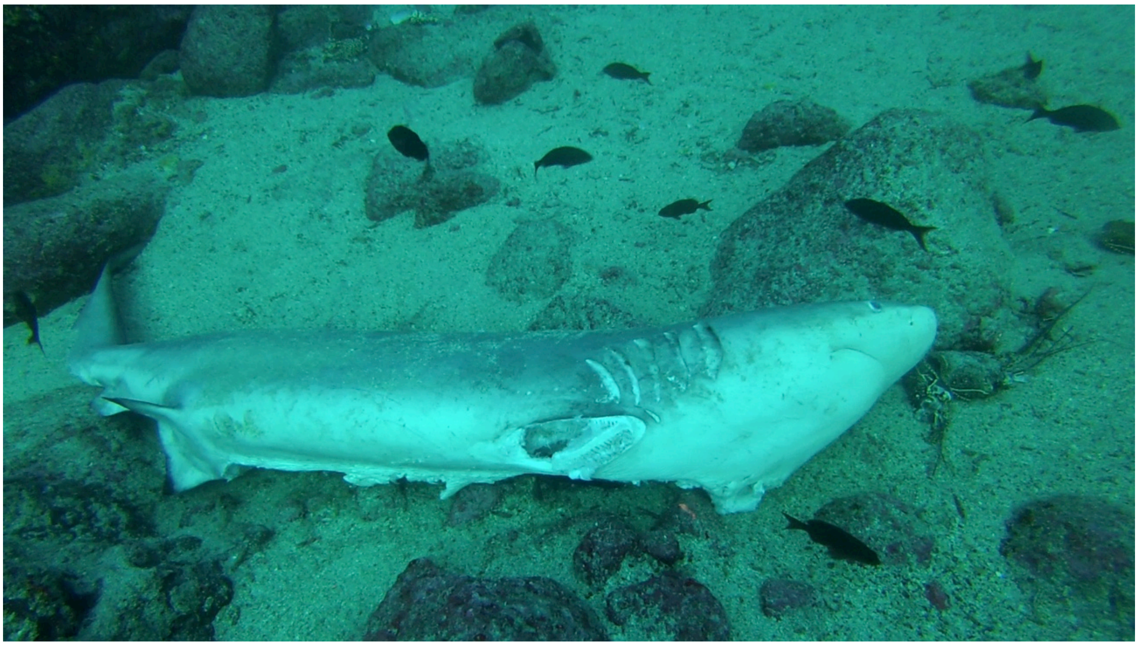


Figure 6-1. One of several dead Galapagos sharks (*Carcharhinus galapagensis*) with its fins removed, found at the anchorage of Wolf Island in November 2013 (photo: David Acuña-Marrero).

Illegal fisheries at these world-renowned shark hotspots can have a considerable negative impact. Studies presented in chapters 2 and 4, and Salinas-de-León et al. (2016), show that Darwin and Wolf Islands harbour not only the highest abundance of sharks at the GMR, but also the largest biomass of sharks ever recorded worldwide. Moreover, the largest proportion of this high shark biomass comprises large schools of scalloped hammerhead sharks, a species especially vulnerable to fishing and the most endangered shark at the GMR together with the whale shark (*Rhincodon typus*). We therefore recommend that a permanent surveillance base of the GNPD, with adequate resourcing, be re-established at Darwin and Wolf Islands to ensure that the rules of the GMR are properly enforced at these unique islands.

Finally, illegal shark fishing by local fishers has been reported, particularly following the collapse of the sea cucumber fishery in the late 1990s (Watts and Wu 2005). Although Ecuadorian authorities have seized illegally finned sharks in some local fishing vessels (Jacquet et al. 2008), the extent and frequency of illegal activity by local fishers remains unknown. The local artisanal fleet is likely to have only a minimal impact on shark populations at present because it is relatively small-scale and there is regular surveillance of the landing ports at the GMR. However, the impact of the local fleet could increase dramatically if it was allowed to use longlines, as more sharks would be captured as by-catch. The risks to sharks could then be exacerbated by the economic incentive for fishers to illegally trade sharks rather than releasing them.

6.2.1.3 Shark migrations and movements out of the GMR

Leaving aside illegal shark fishing within the GMR, an individual shark's risk of being caught will be correlated with the amount of time it spends outside the boundaries of the protected area of the GMR. This has been illustrated using a 'triangle migrations' scheme (*sensu* Chapman et al. 2015), which describes the movement of coastal sharks between nursery grounds and habitats occupied by adults of different sexes. The distances between these habitats, together with the tendency for philopatric behaviour, will structure the spatial movements of sharks. Thus, sharks that regularly exit the GMR to find suitable habitats for particular life stages will be more vulnerable to the impact of fishing out of the marine reserve.

The six semipelagic shark species recorded in our study at the GMR have the capacity to make long migrations through open waters (Compagno et al. 2005), which potentially limits the protection provided by this marine reserve. Accordingly, five of the semipelagic species that were tagged at the GMR have been tracked (satellite tags) or detected (acoustic tags) out the reserve, showing movements that transcend its boundaries (Hearn et al. 2014, Acuña-Marrero et al. 2017).

The high mobility of semipelagic shark species surely limits the effectiveness of the GMR and other MPAs at oceanic islands of the ETP in protecting shark populations. The unprotected open waters used by migratory sharks in this region comprise the economic exclusive zones of several countries and international waters, which are fished heavily by an international industrial fleet. Thus, a significant increase in the area covered by protected areas, particularly at oceanic islands and continental coasts that include important nursery grounds for sharks, and the establishment of marine corridors based on international agreements along their main migratory routes, are required to ensure the long-term conservation of shark populations in the ETP.

6.2.2 Effects of the GMR on the populations and assemblage structure of coastal sharks

The cessation of industrial fishing and large-scale shark finning activity at the Galapagos Islands after the establishment of the GMR likely had a strongly positive impact on shark populations. A lack of baseline data on the distribution and abundance of sharks at the GMR, since its implementation in 1998, has thus far precluded any proper assessment of temporal trends in populations and assemblage structure of sharks.

However, and based on our results and other published studies, it is possible to make some hypotheses about the effects of the full protection of the GMR on coastal shark species.

We expect any effects of the GMR on sharks to be highly species-specific. Differences in the spatial extent of migrations, philopatric behaviour, and the availability of major nursery grounds within the GMR will determine the amount of time and periodicity that each species will spend outside of the protected zone and, therefore, their vulnerability to fishing. In addition, the degree of overlap in the use of habitats by the various species and size classes of sharks within the GMR will likely influence assemblage structure via predator-prey interactions, resource partitioning, and/or competitive exclusion.

The location of nursery grounds within the GMR seems to play a major role in the effects of the reserve on shark populations. The scalloped hammerhead shark is the only coastal semipelagic species commonly found at the GMR that is not known to reproduce extensively within the reserve (Hearn et al. 2014, Salinas-de-León et al. 2017). Nursery grounds for the scalloped hammerhead shark at the ETP are located at the heavily-fished, continental, coastal areas of Central and South America, while adults tend to aggregate at oceanic islands, most of which offer some level of protection (Salinas-de-León et al. 2017). The large spatial extent of the migration triangle for scalloped hammerhead sharks, together with their high vulnerability to fishing (Young et al. 2002), may be causing severe declines in the populations of this species at the ETP (Baum et al. 2007, Bessudo et al. 2011, White et al. 2015).

Most of the blacktip sharks recorded by our coastal BRUV deployments in the GMR were adult females (Fig. 2-2); this is unsurprising as juveniles are known to remain at shallow protected bays of the GMR (Llerena et al. 2010, Llerena et al. 2012), and adult males tend to use open water habitats to prey on pelagic species, and neither of these habitats were sampled herein. Adult females are known to display philopatric behaviour, remaining closer to nursery areas (Sims 2005, Keeney and Heist 2006). Thus, males are likely to have much greater exposure to fishing than female blacktip sharks. Yet, the suitable habitats for nurseries found within the GMR, and philopatric behaviour showed by adult females, seem to favour this species; sightings of blacktip sharks at dive sites have increased in the last decade, supporting the idea that the population of this species in the GMR is growing (Hearn et al. 2014).

Recent studies using genomic data from Galapagos sharks (*C. galapagensis*) at the southern islands of the Galapagos Archipelago indicated an elevated risk of extinction due to a genetic bottleneck (Pazmiño et al. 2017). Yet, Galapagos sharks were the most abundant and widespread of all species in our stereo-BRUV surveys of the GMR. The majority of recorded individual Galapagos sharks were juveniles; records from adults were restricted to a few specific locations, such as Darwin and Wolf Islands and the northwest coast of Fernandina Island (Fig. 2-2). The high abundance and seasonality of records of adults at these two locations, together with their close proximity to deep and open waters, suggest that this species migrates beyond the reserve boundaries. If so, Galapagos sharks may actively breed in coastal areas inside the GMR but leave the GMR during adult stages, at least on a seasonal basis—the very opposite strategy to scalloped hammerhead sharks. However, the strategies of both species imply regular movements to open waters that likely take them out of the protection framework of the GMR. Accordingly, genetic studies of these populations indicate that the conservation status of both species is of concern (Nance et al. 2011, Pazmiño et al. 2017).

The availability of habitats for nurseries could also be limited by competitive exclusion between shark species. Occasional sightings of newborn scalloped hammerhead sharks have been reported at the GMR (Jaenig 2010, Llerena et al. 2010, Llerena et al. 2012) and Cocos Island (Zanella et al. 2016), indicating that some pregnant females of this species may be giving birth at these oceanic islands. The small extent of coastal habitats and, thus, nursery areas at Cocos Island would likely limit the sustainability of a local population of scalloped hammerhead sharks. In contrast, the GMR has numerous large protected bays that apparently offer similar conditions to those reported at other major nurseries for this species at the ETP (Zanella et al. 2009, Rodríguez 2011, Quintanilla et al. 2015). Young individuals of scalloped hammerhead sharks are seldom seen even in protected bays at the GMR; on the other hand, blacktip sharks uses these habitats extensively (Jaenig 2010, Llerena et al. 2010, Llerena et al. 2012). Thus, it is likely that blacktip sharks, being a more aggressive and adaptable species (Compagno et al. 2005), displace the scalloped hammerhead sharks in the use of nursery areas at the GMR, either by a potential competitive interaction in juvenile phase or by direct predation. Adult blacktips have been seen hunting in these shallow bays and even preying on juveniles of scalloped hammerheads (Albear pers. observ.). Thus, the establishment of the GMR could provide an advantage to more aggressive and adaptable species, such as the blacktip shark, which could be displacing scalloped hammerhead sharks into more exposed and fished nursery grounds at continental areas.

Another potential benefit of the GMR to shark populations is the availability of healthy and productive habitats that provide prey and other ecological functions, such as cleaning services. Shark species that are more adaptable in their movement behaviour may exhibit greater phylopatry and potentially make fewer migrations out of the GMR. This seems to be the case for the largest predatory shark recorded at the GMR, the tiger shark. Our results indicate that the population of tiger sharks at the GMR is generally less migratory than those studied elsewhere (Fig. 3-1; Hammerschlag et al. 2012, Lea et al. 2015), likely due to the abundant habitats for nurseries and feeding grounds found within the GMR. It is likely that this species is benefiting from the implementation of the GMR and its population could be expected to be growing.

It is unknown if the bignose shark (*C. altimus*) and the silky shark (*C. falciformis*) reproduce at the GMR. Both these species have circumglobal distributions and are known to conduct long migrations (Kohler et al. 1998), which may also expose Galapagos populations to fishing outside the GMR. Indeed, the silky shark is the most commonly caught shark by tune purse seine vessels in the ETP region (Watson et al. 2009). The few occurrences of these two species in our coastal BRUV deployments can be explained by a higher preference for deeper (bignose shark) or more open-water habitats (silky shark).

Finally, we emphasise the dearth of information on the distribution and abundance of benthic coastal shark species at the GMR prior to this study. For example, our study is the first to provide information about the abundance and distribution of the Triakid sharks—namely, the spotted houndshark (*Triakis maculata*) and the whitemargin smoothhound (*Mustelus albipinnis*)—at the GMR, other than a few opportunistic records (Grove and Lavenberg 1997, Acuña-Marrero et al. 2013b). We recommend further research effort into these two species and the Galapagos bullhead shark, which could potentially be endemic to the GMR (Kyne et al. 2004), to understand their population structure and connectivity with the continental areas.

It could be expected that the GMR offers the greatest benefits to sharks with small home ranges and low mobility (i.e., benthic sharks) *vs* those with larger movement ranges that can take them out of the protected area (i.e., semipelagic sharks).

However, across all the GMR, coastal shark assemblages recorded by the benthic stereo-BRUV deployments were consistently dominated by semipelagic species (Fig. 2-1). This could be explained by a greater availability of suitable habitats for semipelagic species at the GMR, including a 40-mile-wide band of open water surrounding the coast, compared to the limited extent of the insular shelf used for benthic species (Fig. 2-1). Biotic interactions such as avoidance behaviour or predation could also explain the dominance of larger semipelagic species over smaller benthic sharks.

In summary, the establishment of a full protection framework has likely resulted in a shift in the structure of the coastal shark communities at the GMR. Species that are more aggressive and/or adaptable and plastic in their movement patterns, such as blacktip and tiger sharks, may displace more submissive species and those that are exposed to fishing due to regular movements outside of the protected waters of the GMR, such as the scalloped hammerhead and/or the Galapagos shark. Yet, specific areas of the GMR, such as the oceanic islands of Darwin and Wolf, are dominated by the scalloped hammerhead shark, where their extraordinary seasonal abundance produced the largest estimated biomass densities of sharks ever reported worldwide (Salinas-de-León et al. 2016). The GMR could potentially have indirect, negative effects on smaller shark species *via* predation by apex species, such as the tiger shark, that benefit from protection. Finally, we highlight the potentially important contribution of recovering shark communities at the GMR to the broader ETP region. Three of the most common coastal shark species that reproduce actively at the GMR—namely, the Galapagos, blacktip and tiger sharks—are reportedly increasing in abundance at the neighbouring MPA of Cocos Islands (White et al. 2015), potentially due to a spillover effect from the GMR.

6.2.3 Human dimension of shark conservation at the GMR

The social component of the governing system of the GMR has received very little attention (Barragán-Paladines and Chuenpagdee 2015). In particular, the human element of the management and conservation of sharks at the GMR had only been briefly addressed by researchers in preliminary economic assessments of the value of sharks for the eco-tourism activity. The attitudes of the general public and visitors to the GMR towards sharks remained largely unknown.

From an economic perspective, the preservation of populations of sharks at the GMR yields greater potential benefits to the local economy than shark fisheries (Peñaherrera et al. 2013; Lynham et al. 2015). Accordingly, our study showed that the majority of the human population had a generally positive or neutral view of the protection of sharks by the GMR. Yet, a small proportion of the local population (mostly fishers or people related to them) and visitors (especially retired) harboured very negative attitudes towards sharks (Table 5-2).

Negative attitudes, and consequent behavioural responses (lack of tolerance of sharks and lack of support for their conservation), held by local community of fishers may exert a strong influence on other residents, as fisheries are still perceived by marine reserve users as an important, traditional livelihood at the GMR (Barragán-Paladines 2015). In contrast, respondents involved in the tourism sector, which is the base of the Archipelago's economy (Epler 2007), clearly showed a positive attitude and behavioural responses towards sharks (Table 5-2, Fig. 5-4), as sharks are attracting visitors to the islands and providing significant economic benefits (Peñaherrera et al. 2013, Lynham et al. 2015). Thus, attitudes and behaviours appear to be largely driven by economic interests. Local fishers do not hold positive attitudes towards sharks because, unlike those in the tourism sector, they do not directly benefit economically from the conservation of sharks. Fishers may even see sharks as economically harmful, as by-catch of sharks is the main reason for the prohibition of longlining at the GMR, which is a potentially very profitable but damaging fishery method.

The opposition to shark conservation by this influential social sector is likely the greatest obstacle to broad-scale local support for the GMR and shark conservation. Despite several educational awareness campaigns about the ecological and economic importance of sharks at the GMR, the attitudes of the local fishers remain negative (Vilema pers. comm.). However, after the collapse of two of the most profitable fisheries at the GMR, local fishers are increasingly seeking alternative trades in the tourism sector (Schuhbauer and Koch 2013). Our results suggest that greater involvement of local fishers in shark-based tourism activities would foster more positive attitudes and behaviours towards sharks and their conservation. Thus, we recommend that management authorities facilitate and incentivise local fishers to convert to eco-tourism activities at the GMR, particularly those involving sharks.

Another potential driver of negative attitudes is the belief that sharks are dangerous. Here, there seem to be two potential lines of action to mitigate this negative influence on attitudes. First, perhaps unexpectedly, living in proximity to abundant populations of sharks appears to reduce the perceived risk of shark attack, as this perception was lower in residents than in visitors to the Galapagos Islands. Locals generally had a greater number of experiences with sharks in the wild, which is positively associated with attitudes (Table 5-3). Therefore, we recommend increasing the opportunities for both locals and visitors to experience sharks in the wild through well-managed eco-tourism activities, which will also provide economic incentives to preserve shark populations. Secondly, we support the continuation of education campaigns about sharks. Shark attacks are usually miss-represented by the media, which emphasise the false stereotype of sharks as human-eaters (Morey 2002, Thompson and Mintzes 2002). The public (residents and visitors) should be informed about the actual level of risk of being attacked by sharks at the Galapagos Islands, which, in reality, is very low, based on the inventory of shark-related incidents at the GMR (Acuña-Marrero and Peñaherrera 2011). Making this information more widely available would allow public opinion to be driven more by facts rather than by rumours or inaccurate representations by the local media (Fig. 6-2).

6 El Colono

Prevenga ataques de tiburones

Para muchos turistas admirar y observar a los tiburones de Galápagos es una experiencia increíble, y es la supervivencia de los tiburones la que está ligada a la supervivencia humana. En los últimas semanas se dio un nuevo ataque de tiburón en las islas, lo que preocupó a la comunidad en general. En esta ocasión un residente de Puerto Ayora fue mordido en la playa de la Estación Darwin, al que le ocasionó heridas en el pecho por lo que le tuvieron que coger varios puntos.

Figure 6-2. Example of media misrepresentation of a shark attack. This article showing a fake photo (right) was published by a local newspaper at the Galapagos Islands in 2012, a day after a local swimmer was slightly injured (left corner) by a small-medium shark.

Since 2010, several educational campaigns have been conducted by local NGOs and institutions (Sea Shepherd, the Charles Darwin Foundation and the GNPD) to promote shark conservation at the Galapagos Islands. Most of these campaigns have aimed to increase the knowledge about sharks and highlight their importance for the

Galapagos Islands using different communication strategies directed to the local community, with special focus on kids and schools. These campaigns have generally produced positive results, but their long-term impact on local attitudes and behaviours may be limited by the haphazard and occasional basis on which they occur. Better results may be achieved by integrating this conservation educational material into the official curricula taught at local schools, and improved training of local teachers. This would ensure that future generations of decision makers have sound knowledge and awareness about the ecological and economic importance of the marine ecosystems in general, and sharks in particular, for the Galapagos Islands.

6.3 Final conclusion

This thesis has aimed to contribute to shark conservation at the GMR by following a holistic approach that not only focused on filling a recognised gap in our current knowledge regarding their ecology, but also took into consideration the important role that humans must play in any framework designed to enhance shark conservation. Clarifying the spatial distributions and usage patterns of coastal shark species, evaluating the reserve’s effectiveness in the protection of an apex predatory shark and mitigating biases of survey methods to provide better estimates of shark populations, will all provide environmental authorities of the GMR with essential tools to develop effective management policies for shark conservation. Identifying better strategies to promote positive attitudes and behaviours towards sharks by locals and visitors will also favour successful implementation of conservation policies. It is only through a holistic approach that the conservation of shark populations at the Galapagos Islands and the status of this unique place as a shark sanctuary can be ensured in the long-term. Importantly, the iconic status of the Archipelago and the potential success of its conservation frameworks may serve as a model in a large number of other contexts, where there are significant ecological, social and economic challenges occurring at human-wildlife interfaces worldwide.

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Appendix A Supplementary Material for Chapter 2

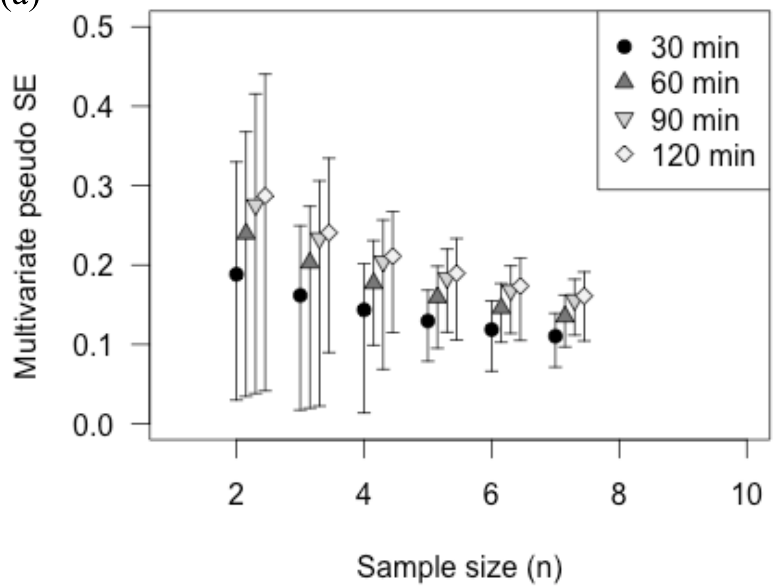
A.1 Performance of the boosted regression tree models to predict occurrences of individual shark species

Table A-1. Performance of the boosted regression tree (BRT) models using the environmental and biological variables (Table 1) to predict total log-abundance and diversity of sharks, and occurrences of individual shark species (oc.), using proportion of the deviance explained assessed by cross-validation (CVDE) and area under the receiver operative characteristic curve (AUC) scores.

BRT model	CVDE	AUC
Shark abundance	0.331	—
Shark diversity	0.923	—
Carcharhinus galapagensis (oc.)	—	0.794
adult	—	0.857
juvenile	—	0.770
Galeocerdo cuvier (oc.)	—	0.704
Sphyrna lewini (oc.)	—	0.701
adult	—	0.765
juvenile	—	0.774
Triaenodon obesus (oc.)	—	0.824
Triakidae species (oc.)		0.761
Heterodontus. quoyi (oc.)	—	0.700

A.2 Multivariate pseudo standard error from pilot study

(a)



(b)

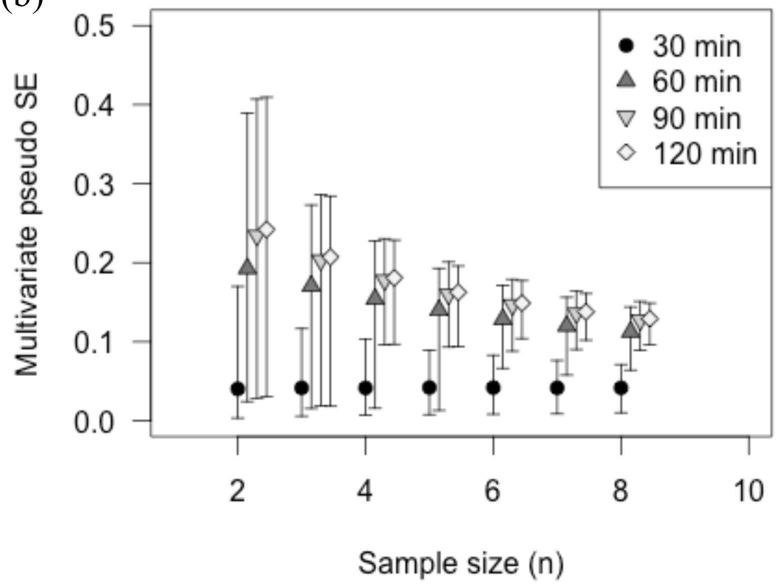


Figure A-1. Multivariate pseudo standard error (*MultSE*; Anderson & Santana-Garcon 2015) as a function of the number of replicates (sample size) of a zero-adjusted Bray-Curtis (Clarke et al. 2006) dissimilarities calculated on shark abundance data from the pilot study from (a) benthic and (b) pelagic stereo-BRUVs for four different soak times (upper right legend), with permutation-based means and bias-adjusted bootstrap-based error bars (10,000 resamples).

A.3 Benthic stereo-BRUV design

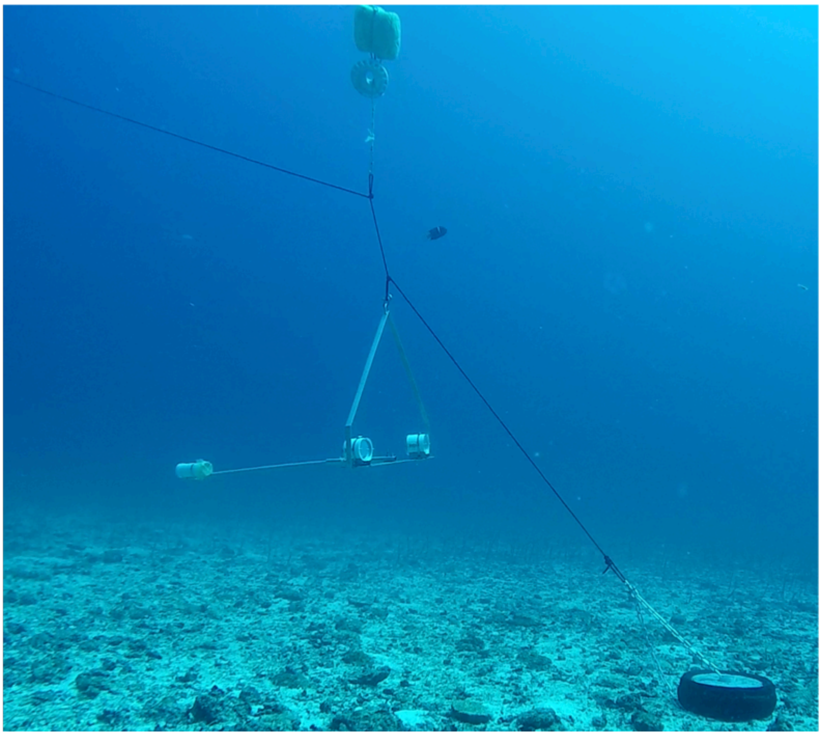


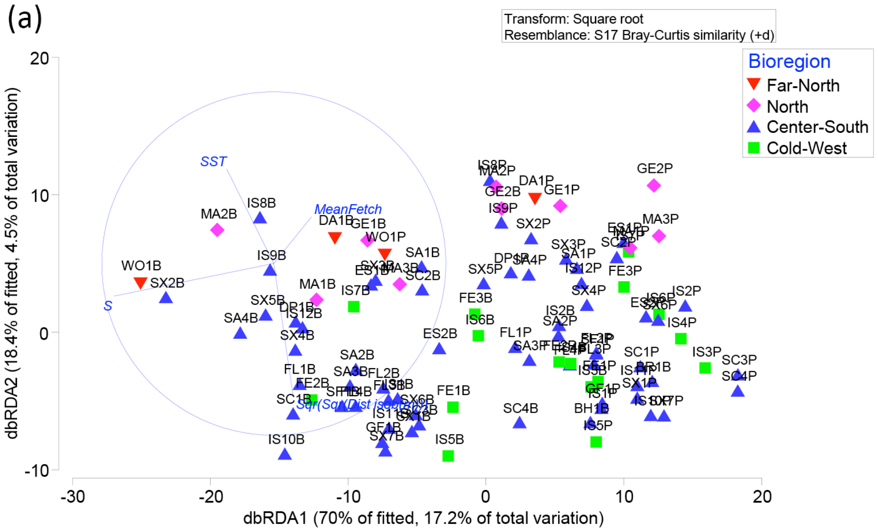
Figure A-2. Benthic stereo-BRUV design used in the study. The camera frame remains floating at *ca* 1 m over the seabed.

A.4 Shark species recorded by stereo-BRUV

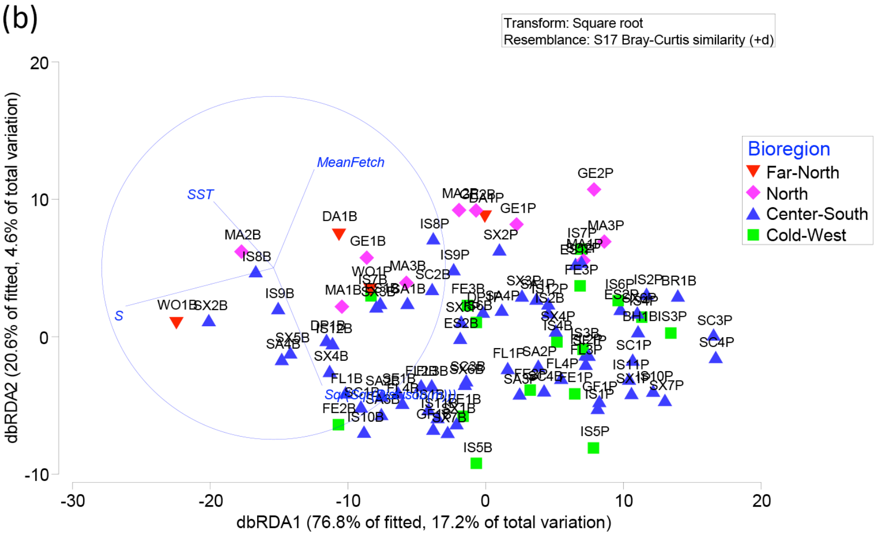
Figure A-3. Video frames showing the shark species recorded by stereo-BRUVs at the Galapagos Marine Reserve (a: *Carcharhinus altimus*, b: *Carcharhinus falciformis*, c: *Carcharhinus galapagensis*, d: *Carcharhinus limbatus*, e: *Galeocerdo cuvier*, f: *Sphyrna lewini*, g: *Triaenodon obesus*, h: *Heterodontus quoyi*, i: *Mustelus albipinnis*, j: *Triakis maculata*).

A.5 Distance–based redundancy analyses for shark assemblages

(a)



(b)



(c)

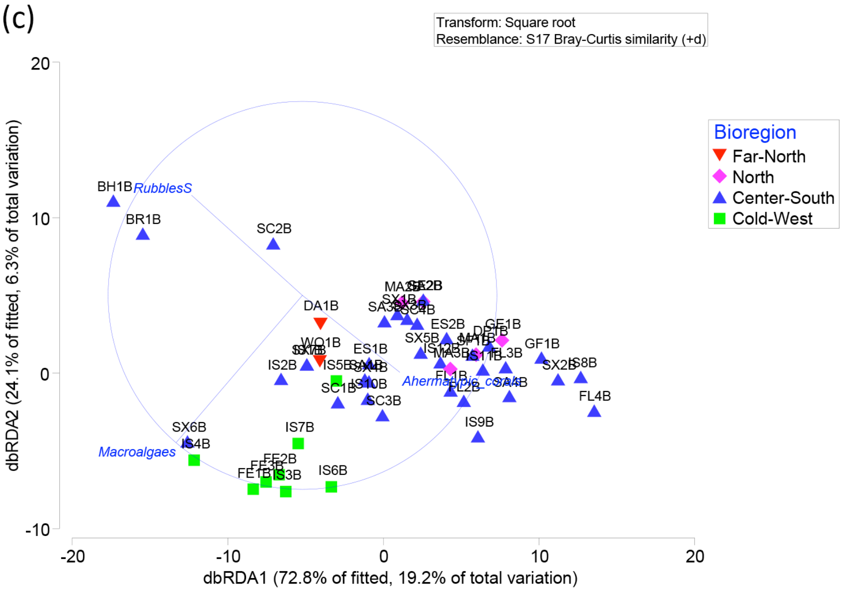


Figure A-4. Distance–based redundancy analysis (dbRDA) ordinations for the fitted model of the (a) full, (b) semipelagic and (c) benthic shark assemblages based on a zero-adjusted Bray-Curtis similarity matrix (Clarke et al. 2006) produced from square-root-transformed relative abundances of shark species (*cMaxN*) averaged by site and position in the water column (benthic *vs* pelagic). Corresponding bioregions are indicated by coloured icons (upper right legend). Overlying vectors in blue show the environmental and biological predictors fitted by the model.

Appendix B Supplementary Material for Chapter 3

B.1 Total number of sharks recorded in the study

Table B-1. Sharks observed in each season, of each size class, and of each sex, at each location (the numbers observed by SBRUVs and by capture are given in parentheses, respectively). Sampling effort was not quantified for captures. For SBRUVs, effort varied among locations but was equal between seasons within each location; the number of SBRUV deployments in each season is given in parentheses for each location.

	Location		
	Bachas-Salinas (16)	Isabela-South (8)	Cerro-Ballena (4)
Season: nesting	10 (6, 4)	14 (9, 5)	5 (1, 4)
Season: non-nesting	5 (3, 2)	0	8 (3, 5)
Sex: female	10 (4, 6)	6 (4, 2)	5 (0, 5)
Sex: male	4 (4, 0)	5 (2, 3)	4 (0, 4)
Size: large	7 (6, 1)	8 (6, 2)	0
Size: medium	8 (3, 5)	5 (2, 3)	7 (2, 5)
Size: small	0	1 (1, 0)	6 (2, 4)
TOTAL	15 (9, 6)	14 (9, 5)	13 (4, 9)

B.2 Study sites for tiger sharks

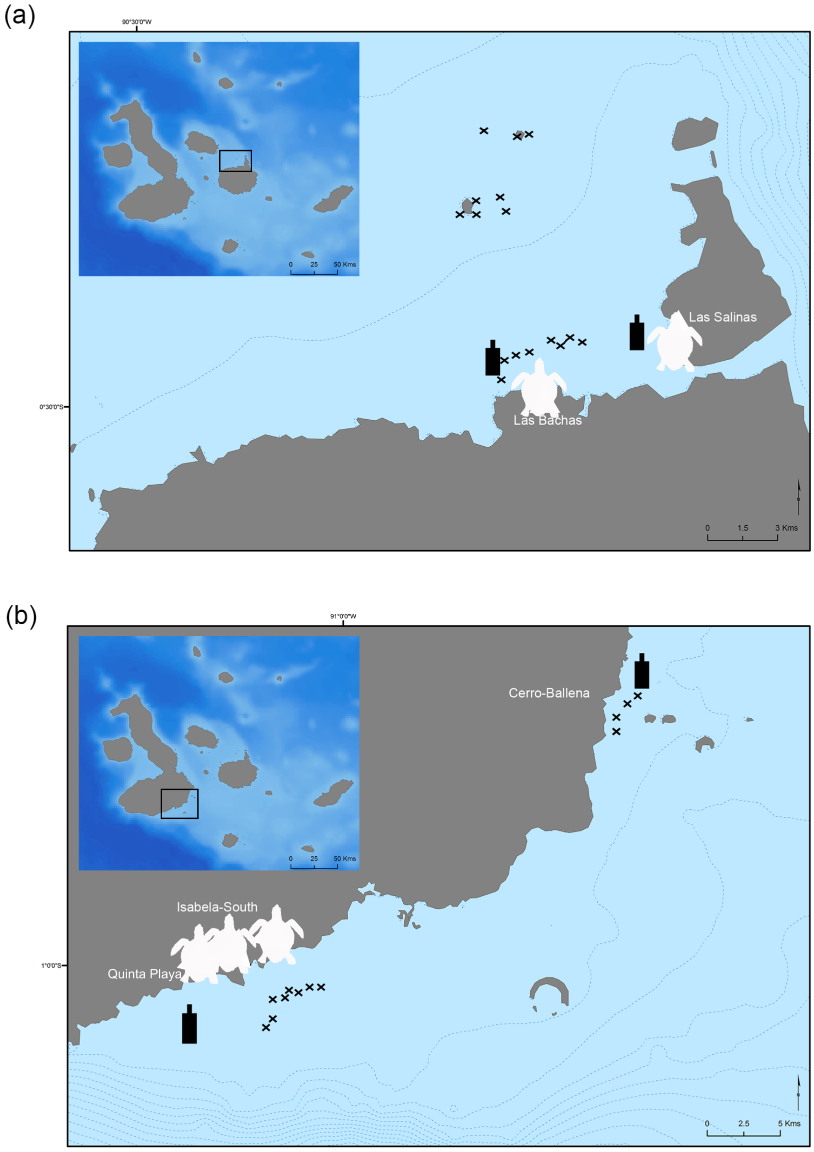


Figure B-1. Map showing the study sites of (a) Bachas-Salinas, and (b) Isabela-South and Cerro-Ballena. White sea turtle icons indicate the most important nesting beaches for green sea turtles in the area, according to Zárate and Dutton (2002) and Zárate et al. (2013). Black crosses show the locations of SBRUV deployments, and black rectangles show the locations of acoustic receivers.

B.3 Frequency distribution of intervals between satellite detections

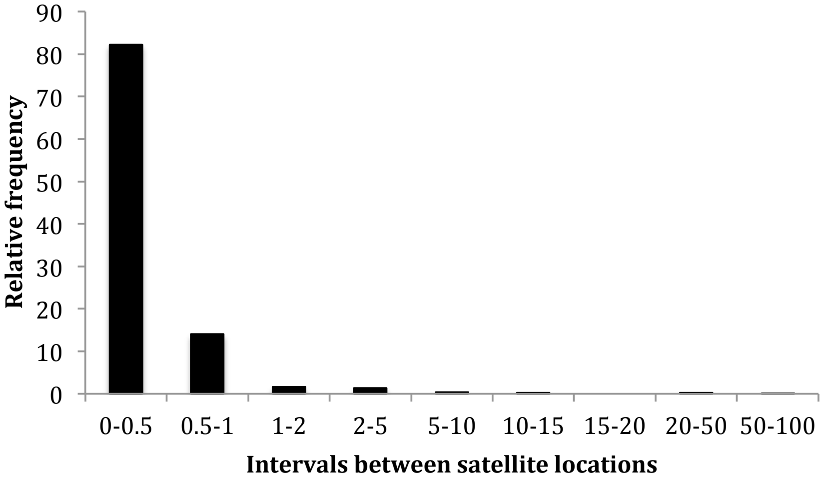


Figure B-2. Frequency distribution of the time interval (in days) between subsequent detections of satellite locations obtained for tagged sharks.

B.4 Chronology of acoustic detections

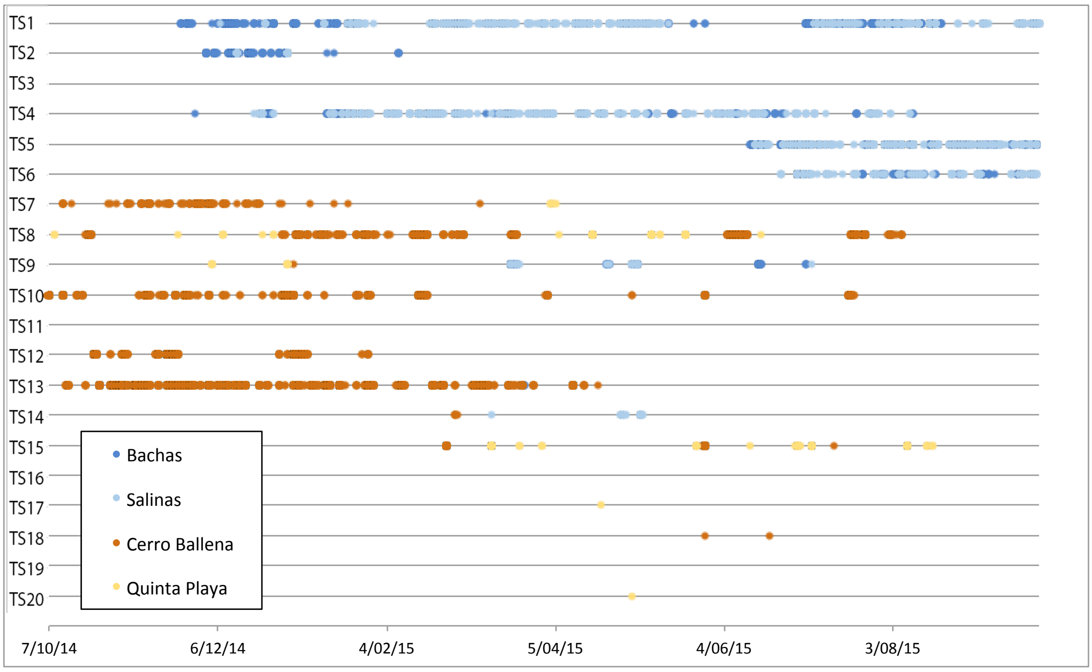


Figure B-3. Chronology of acoustic detections for each of the acoustic-tagged sharks (TS1-TS20) by site (colour coded).

Appendix C Supplementary Material for Chapter 5

C.1 Questionnaire for evaluating attitudes

1. Choose one option: ☐ Male ☐ Female **2.** Age:_______
3. What is your main professional occupation/job?: ________________________________
3.a Do you have a close relative working in ☐ tourism ☐ fisheries, at the Galapagos Islands?
4. (Residents only) Were you born at the Galapagos Islands? ☐ YES ☐ NO
If you answered NO: 4.a How long have you been living at the Galapagos Islands?:__________
5. Have you ever seen a shark in the wild? ☐ YES ☐ NO
If your answer was YES: 5.a How did you encounter the shark and how was your experience? (select all that apply)

	Very bad	Bad	Good	Very good	I didn´t care
5.a Swimming/at the beach					
5.b Scuba diving					
5.c Surfing					
5.d Snorkeling					
5.e From a boat					
5.f Fishing					
5.g Others (¿please, specify?):____________________________					

6. How would you rate your feelings towards sharks? (please place an X in the box for each row)

	Nothing	Low	Medium	High
6.a Fear				
6.b Repulsion				
6.c Curiosity				
6.d Excitement				

7. Do you think sharks are…? (please place an X in the box for each row)

	Nothing	Low	Medium	High
7.a … endangered				
7.b … abundant				
7.c … dangerous				
7.d … vulnerable				
7.e … important for the Galapagos Islands' economy				
7.f … negative for the Galapagos Islands' economy				
7.g … ecologically important				
7.h … ecologically damaging				
7.i … beautiful				
7.j … disgusting and horrible				

8. How would you rate your knowledge about sharks (where they live, what they eat, reproduction, etc.)? ☐ High ☐ Moderate ☐ Low ☐ Nothing ☐ I'm not interested
9. Would you like to live in a place with sharks? ☐ YES ☐ NO ☐ I don't care
10. Do you think sharks should be protected in the Galapagos Islands? (choose one option)
☐ YES ☐ NO ☐ I don´t have an opinion about this

11. Would you like to have more information available about sharks and their management and conservation plans in the Galapagos Islands? ☐ YES ☐ NO

Figure C-1. Questionnaire for evaluating the attitude towards sharks in residents and visitors to the Galapagos Islands.

Appendix D Statement of contribution to doctoral thesis containing publications

DRC 16

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: DAVID ACUÑA MARRERO

Name/Title of Principal Supervisor: Prof. Marti J. Anderson

Name of Published Research Output and full reference:

Acuña-Marrero D, Smith ANH, Salinas-de-León P, Harvey ES, Pawley MDM, Anderson MJ. Spatial and temporal distributions of coastal shark populations at the Galapagos Marine Reserve
Submitted on the 22nd of September 2017 to Marine Ecology Progress Series journal

In which Chapter is the Published Work: Chapter 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate80%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Candidate conceived the experiment and the experimental design, conducted field work, data processing, video analysis and data analysis and wrote the manuscript.

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01/01/2018

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Principal Supervisor's signature

01/01/2018

Date

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: DAVID ACUÑA MARRERO

Name/Title of Principal Supervisor: Prof. Marti J. Anderson

Name of Published Research Output and full reference:

Acuña-Marrero D, Smith AN, Hammerschlag N, Hearn A, Anderson MJ, Calich H, Pawley M, Fischer C, Salinas-de-León P. 2017. Residency and movement patterns of an apex predatory shark (Galeocerdo cuvier) at the Galapagos Marine Reserve. PLOS ONE 12 (8): e0183669.

In which Chapter is the Published Work: 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate 80%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Candidate conceived the experiment, conducted field work, data processing and analysis and wrote the manuscript.

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STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: DAVID ACUÑA MARRERO

Name/Title of Principal Supervisor: Prof. Marti J. Anderson

Name of Published Research Output and full reference:

Acuña-Marrero D, de-La-Cruz-Modino R, Smith ANH, Salinas-de-León P, Pawley MDM, Anderson MJ. Understanding human attitudes towards sharks to promote a sustainable coexistence
Submitted on the 9th of May 2017 to Marine Policy journal

In which Chapter is the Published Work: Chapter 5

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate80%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Candidate conceived the experiment, conducted field work (interviews), data processing and analysis and wrote the manuscript.

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