Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf

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Overfishing has dramatically depleted sharks and other large predatory fishes worldwide except for a few remote or well-protected areas. The islands of Darwin and Wolf in the far north of the Galápagos Marine Reserve (GMR) are known for their large shark abundance, making them a global scuba diving and conservation hotspot. Here we report quantitative estimates of fish abundance at Darwin and Wolf using stereo-video surveys, which reveal the largest fish biomass ever reported (16 t ha^{-1} on average), consisting largely of sharks. Despite this, the abundance of reef fish around the GMR, such as groupers, has been severely reduced because of unsustainable fishing practices. Although Darwin and Wolf are within the GMR, they are not fully protected from fishing. Stronger protection is required to preserve this ecological hotspot of unique global value.

1 **Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf**

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Abstract

10 Overfishing has dramatically depleted sharks and other large predatory fishes worldwide except
11 for a few remote or well-protected areas. The islands of Darwin and Wolf in the far north of the
12 Galápagos Marine Reserve (GMR) are known for their large shark abundance, making them a
13 global scuba diving and conservation hotspot. Here we report quantitative estimates of fish
14 abundance at Darwin and Wolf using stereo-video surveys, which reveal the largest fish biomass
15 ever reported (16 t ha^{-1} on average), consisting largely of sharks. Despite this, the abundance of
16 reef fish around the GMR, such as groupers, has been severely reduced because of unsustainable
17 fishing practices. Although Darwin and Wolf are within the GMR, they are not fully protected
18 from fishing. Stronger protection is required to preserve this ecological hotspot of unique global
19 value.

Introduction

21 Overfishing has reduced biomass of most sharks and other large predatory fishes worldwide by
22 over 90% (Baum et al., 2003; Myers & Worm, 2003; Ward-Paige et al., 2010), and even remote
23 locations have been severely impacted (Sibaja-Cordero, 2008; Dulvy et al., 2008; Graham,
24 Spalding & Sheppard, 2010; White et al., 2015). One in four species of cartilaginous fishes is
25 now threatened with extinction due primarily to overexploitation and habitat loss (Dulvy et al.,
26 2014). The systematic removal of sharks from marine ecosystems has negative effects that
27 propagate throughout the entire food web (Bascompte, Melián & Sala, 2005; Myers et al., 2007;
28 Heithaus, Wirsing & Dill, 2012). Only a few localities worldwide still maintain large abundances
29 of top predatory fishes due to either being remote and unfished, or having recovered after full
30 protection from fishing (Sandin et al., 2008; Aburto-Oropeza et al., 2011; Graham &
31 McClanahan, 2013; Friedlander et al., 2014a).

32 The Galapagos Islands are known worldwide for its iconic terrestrial fauna and flora, due in large
33 part to a young Charles Darwin who sailed to these islands in 1835 (Darwin, 1839). While
34 Galapagos giant tortoises, Darwin's finches, and mocking birds have received much of the
35 attention since Darwin's visit, the underwater Galapagos remains under-studied and largely
36 unknown. The far northern islands of Darwin and Wolf in the 133,000 km^2 Galapagos Marine
37 Reserve (GMR) represent a unique hotspot for sharks and other pelagic species (Hearn et al.,
38 2010, 2014; Ketchum et al., 2014a; Acuña-Marrero et al., 2014). Most of the studies around this
39 area have focused on the migration of scalloped hammerhead sharks (*Sphyrna lewini*) and other
40 sharks species between Darwin and Wolf and other localities in the Eastern Tropical Pacific
41 (Hearn et al., 2010; Bessudo et al., 2011; Ketchum et al., 2014a). An ecological monitoring
42 program has visited the islands over the past 15 with a strong sampling focus to survey reef fishes
43 and invertebrate communities (Edgar et al., 2011). However, no study to date has examined
44 extensively the density, size, and biomass of sharks and other large predatory fishes around
45 Darwin and Wolf. We conducted an expedition to Darwin and Wolf in August 2014 to establish
46 comprehensive abundance estimates for shark and predatory fish assemblages at Darwin and
47 Wolf.

Materials and Methods

49 This research was approved by the Galapagos National Park Directorate (GNPD) as part of the
50 2014 annual operational plan of the Charles Darwin Foundation (Research permit PC-40-14).

Site description

52 Darwin and Wolf are the two northernmost islands in the Galapagos Archipelago, a group of 13
53 major islands and 100 islets and rocks located 1000 km west of mainland Ecuador, in the ETP
54 (Snell, Stone & Snell, H. L., 1996); (Fig.1). The Galapagos Archipelago lies at the congruence of
55 three major oceanic currents, which provides a highly dynamic and unique oceanographic setting
56 (Palacios, 2004). Darwin and Wolf represent the far northern biogeographic region of the
57 archipelago and are heavily influenced by the warm Panama current that comes from the
58 Northeast, which supports sub-tropical marine communities to these islands (Edgar et al., 2004;
59 Acuña-Marrero & Salinas-De-León, 2013). Darwin and Wolf are small (approximately 1 and 2
60 km^2, respectively) and represent the tops of eroded, extinct submerged volcanoes, which rose
61 from the surrounding seafloor > 2000 m below (McBirney & Williams, 1969; Peñaherrera-Palma,
62 Harpp & Banks, 2013). Darwin and Wolf are exposed to a predominant north-western water flow
63 that supports a unique pelagic assemblage on the south-eastern portions of these islands (Hearn et

64   al., 2010). In contrast to much of the Galapagos, which is dominated by the cold equatorial
65   counter-current, the waters of Darwin and Wolf range from 22.5 to 29 C throughout the year,
66   peaking during February-March (Banks, 2002).

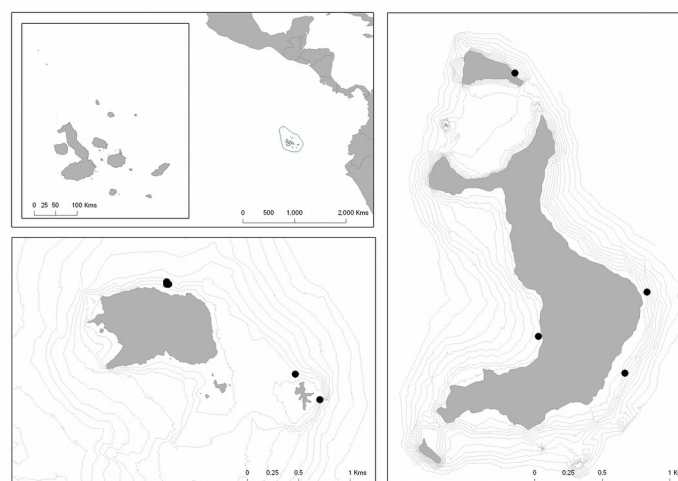
Data collection

67

Underwater census using Diver Operated Stereo-video

68

69   A diver operated stereo-video system (DOV) was used to sample fish assemblages around
70   Darwin and Wolf in August 2014. DOVs use two Canon HFG-25 full high-definition cameras
71   mounted 0.7 m apart on a base bar inwardly converged at seven degrees and are operated by
72   experienced divers using standard open-circuit SCUBA equipment. DOVs can overcome some of
73   the biases associated with Underwater Visual Census (UVC) by eliminating the inter-observer
74   effect and the over/underestimation of sampling area and fish lengths estimations (Harvey &
75   Shortis, 1995, 1998; Shortis et al., 2000; Harvey, Fletcher & Shortis, 2001, 2002; Harvey et al.,
76   2003, 2004; Goetze et al., 2015)

77   Fishes were surveyed at seven sites around Wolf (n = 4) and Darwin (n = 3) islands (Fig. 1)
78   during August 2014. At each site, divers towed a surface buoy equipped with a GPS (Garmin
79   GPSmap 78) to create a detailed track of the area surveyed, with GPS position and exact time
80   recorded using a watch synchronized with the GPS at the beginning and end of each survey
81   (Schories & Niedzwiedz, 2012). Divers followed the 20 m depth contour for a period of 25-30
82   min in order to complete a minimum of ten 50 m long and 5 m wide replicate transects at each
83   site. Dive times were based on preliminary surveys that revealed that swimming at a constant
84   speed, a 2-minute DOVS survey covered approximate 50 m. At some sites, strong currents
85   resulted in longer distances covered by the survey team, resulting in a greater area surveyed at
86   some of the study sites. The diver towing the GPS also conducted standard UVCs to record
87   sharks and large pelagics (50x5x5 m) in parallel to the stereo surveys, therefore the 2 minute
88   surveys were also used to synchronize both sampling methodologies (Supplementary
89   Information).

90   **Figure 1. Survey locations around Darwin and Wolf Islands.**

Calibration and video analysis

Stereo-video cameras were calibrated prior to field deployments using the program CAL (SeaGIS Pty Ltd, Harvey & Shortis 1998). Following the dives, paired videos were viewed on a large monitor and analysed in the program Event Measure (SeaGIS Pty Ltd). Every fish observed was identified to species and measured to the nearest mm (FL). Lengths were converted to biomass (kg) using published length-weight relationships (Froese & Pauly, 2007). For individual fishes that were not measured (e.g. not present in both camera views), we calculated biomass using an average total length for that species from the site where it occurred. Cryptic reef fishes (<8cm) were excluded from our surveys due to the limited ability of the DOVs to detect these species and their lack of importance to the fisheries and overall biomass (Ackerman & Bellwood, 2000). Fishes were classified into four different tropic categories based on published information: Apex predators, lower-level carnivores, planktivores and herbivores (Friedlander & DeMartini, 2002)

For largely abundant schooling fishes, primarily the abundant planktivorous species locally known as *gringo* (*Paranthias colonus),* which form dense schools that are difficult to quantify, we developed a specific methodology in the software Event Measure. For each of the study sites surveyed, we measured to the nearest mm a subsample of 100 individuals across all replicate transects and obtained a specific set of mean individual lengths. Then, transects were divided into blocks of identical length using the GPS tracks and every individual for each 10x5x5 m wide 'cube' was counted. The number of cubes varied according to transect lengths. Total biomass for these sites were obtained by multiplying the total numbers of individuals counted in each cube by the mean individual length for each species at that site.

Statistical tests

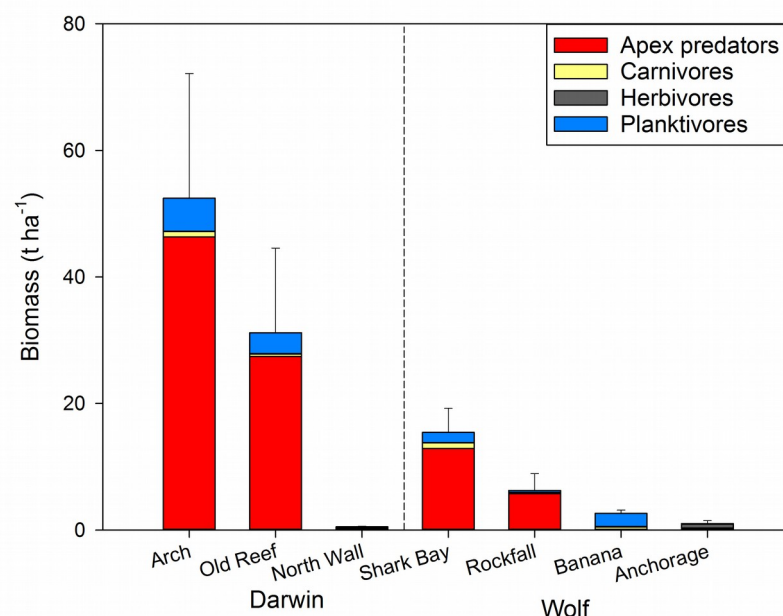
Patterns of fish biomass between islands and exposures were analyzed using generalized linear mixed models (Zuur, 2009) using the R package glmmADMB (Skaug & Fournier, 2004) in the R statistical program version 3.0.2 (R Development Core Team). Due to the skewed nature of our biomass estimates, data were fit with a gamma error structure with an inverse link function that works well for continuous-positive data and has a flexible structure (Crawley, 2011). Location was used as a random effect in the model. Biomass by trophic group was assessed in a similar manner except data were fitted to negative binomial distributions due to the number of zero in these data. Unplanned post hoc multiple comparisons were tested using a Tukey's honestly significant difference (HSD) test.

To describe the pattern of variation in fish trophic structure and their relationship to environmental factors we performed direct gradient analysis (redundancy analysis: RDA) using the ordination program CANOCO for Windows version 4.0 (Ter Braak, 1994). Response data were compositional and had a gradient < 3 SD units long, so linear methods were appropriate. The RDA introduces a series of explanatory (environmental) variables and resembles the model of multivariate multiple regression, allowing us to determine what linear combinations of these environmental variables determine the gradients. The environmental data matrix included island (Darwin, Wolf) and exposure (NW, SE). To rank environmental variables in their importance for being associated with the structure of the assemblages, we used a forward selection where the statistical significance of each variable was judged by a Monte-Carlo permutation test (ter Braak & Verdonschot, 1995). Permutations tests were unrestricted with 499 permutations.

133 Similarity of Percentages (SIMPER) was used to determine the fish species most responsible for
134 the percentage dissimilarities between islands and exposures using Bray-Curtis similarity analysis
135 of hierarchical agglomerative group average clustering (Clarke, 1993).

136 Differences in fish trophic biomass were tested using permutation-based multivariate analysis of
137 variance (PERMANOVA, (Anderson, Gorley & Clarke, 2008)). Data were 4th-root-transformed.
138 Pair-wise tests were conducted between island x exposure combinations.

Results

140 Overall fish biomass averaged 15.9 t ha^{-1} ($\pm$ 33.0 SD), and was 4.5 times larger at Darwin (28.3 $\pm$
141 46.3) than at Wolf (6.3 $\pm$ 8.9 SD); (Fig. 2; Table 1). In addition to this large difference in biomass
142 between islands (z=2.6, p=0.008), biomass was > 20 times higher at the SE exposures (26.2 $\pm$
143 40.0 SD) compared to NW exposures (1.3 $\pm$ 1.5 SD, z=9.7, p<0.001). However, there was a
144 significant interaction, with NW Darwin (0.5 $\pm$ 0.2 SD) differing from all other island x exposure
145 combinations. Total biomass at SE Darwin (40.7 $\pm$ 51.3 SD) did not diff from SE Wolf (10.6 $\pm$
146 10.8 SD), while NW Wolf (1.7 $\pm$ 1.6 SD) and SE Wolf were also similar to one another.

147 **Figure 2. Fish trophic biomass (t ha^{-1}) by island and sampling site.** Error bars are standard
148 error of the mean.

149 **Table 1. Comparisons of fish trophic biomass by island and exposure.** Results of generalized
150 linear mixed models fit with a gamma error structure and an inverse link function. Unplanned
151 post hoc multiple comparisons tested using a Tukey's honestly significant difference (HSD) test.
152 Only significant multiple comparisons are shown.

	Estimate	Std. Error	z	P
Island	1.22	0.46	2.6	0.008
Exposure	4.39	0.45	9.7	<0.001
Island x Exposure	2.58	0.58	4.4	<0.001
Darwin SE (40.7 ± 51.3) Wolf SE (10.6 ± 10.8) Wolf NW (1.7 ± 1.6) Darwin NW (0.5 ± 0.2)				

153 Hammerhead sharks (*Sphyna lewini*) dominated the fish assemblage, accounting for 68% of the
154 overall biomass. This was followed by Galapagos sharks, *Carcharhinus galapagensis* (11% of
155 total biomass), gringos *Paranthias colonus* (11%), and bluefin trevally *Caranx melampygus*
156 *(*4%). Hammerheads were recorded at 71% of the survey sites but were most abundant at the
157 Arch at Darwin, with a mean biomass of 43.0 t ha^{-1} (± 63.0 SD). Galapagos sharks were most
158 abundant at Shark Point (Wolf) with a mean biomass of 8.4 t ha^{-1} (± 12.1 SD). Gringos were most
159 abundant at the Arch (Darwin) with a mean biomass of 5.1 t ha^{-1} (± 4.3 SD).

160 The average dissimilarity between islands, based on species biomass, was 77% with hammerhead
161 sharks accounting for 36% of the dissimilarity, followed by gringos (23%) and Galapagos sharks
162 (12%); (Table 2). The average dissimilarity between exposures was 91%, with the same species
163 assemblage accounting for this dissimilarity (Table S1).

164 **Table 2.** Fish species most responsible for the dissimilarity between Darwin and Wolf islands
165 based on Similarity of Percentages (SIMPER) analysis. Values for islands are biomass (t ha^{-1}).
166 Diss. – average dissimilarity. SD – Standard deviation. Contrib% – percent contribution to
167 dissimilarity. Cum. % – Cumulative dissimilarity.

Species	Darwin	Wolf	Diss. (±SD)	Contrib. %	Cum.%
Sphyrna lewini	21.98	2.21	27.19 (0.88)	35.55	35.55
Paranthias colonus	2.79	0.92	17.83 (0.89)	23.31	58.86
Carcharhinus galapagensis	1.12	2.37	9.15 (0.59)	11.96	70.82
Caranx melampygus	1.43	0	4.03 (0.4)	5.27	76.09
Prionurus laticlavius	0.06	0.06	2.11 (0.46)	2.75	78.84
Taeniura meyeni	0	0.11	2.07 (0.2)	2.71	81.55
Scarus ghobban	0.02	0.02	1.74 (0.33)	2.28	83.83
Holacanthus passer	0.05	0.04	1.74 (0.38)	2.27	86.11
Kyphosus analogus	0	0.11	1.72 (0.17)	2.24	88.35
Melichthys niger	0.04	0.01	1.05 (0.43)	1.37	89.72
Caranx sexfasciatus	0.2	0	0.65 (0.24)	0.85	90.57

168 Apex predators (primarily hammerhead and Galapagos sharks) accounted for 84.9% of the total
169 biomass on transects, followed by planktivores (11.3%), lower level carnivores (2.8%), and
170 herbivores (1.0%); (Fig. 1). Trophic structure, based on biomass, was not significantly different
171 between islands, but differed between exposures, as well as the interaction between islands and
172 exposures, with all island x exposure pairwise comparisons different from one another except for
173 NW Darwin and NW Wolf (Table 3).

174 **Table 3**. **Differences in fish trophic biomass by island and exposure**. Results of permutation-
175 based multivariate analysis of variance (PERMANOVA) followed by pair-wise tests are shown.
176 Data were 4th-root-transformed.

Source	df	MS	Pseudo-F	P (perm)
Island	1	466.8	1.02	0.354
Exposure	1	22371.0	48.84	0.001
Island x Exposure	1	3610.9	7.88	0.001
Residual	62	458		
Total	65			

Pair-wise comparison	t	Perm (p)
SE Darwin – SE Wolf	2.98	0.002
NW Darwin – NW Wolf	1.01	0.345
SE Darwin – NW Darwin	8.72	0.001
SE Wolf – NW Wolf	3.13	0.002

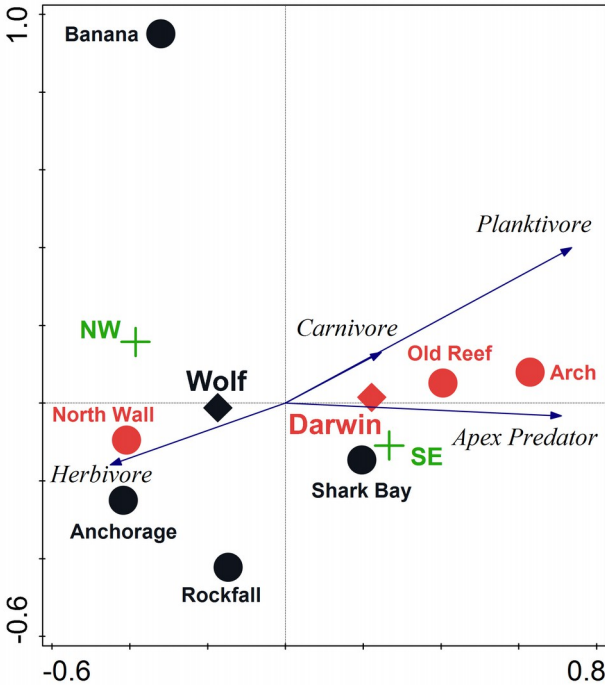
183 Differences in biomass of apex predators among locations were dramatic, with mean biomass at
184 the SE locations around Darwin (35.9 ± 52.5), nearly 4 times higher than SE Wolf (9.1 ± 10.5).
185 Biomass of sharks was trivial at NW Wolf (0.05 ± 0.14), with no sharks present at NW Darwin,
186 thus precluding statistical comparisons. Biomass of planktivores was 3.7 times greater at the SE
187 sites (Arch and Old Reef at Darwin; Shark Point and Rockfall at Wolf) compared to the NW sites
188 (North Wall at Darwin; Anchorage and Banana at Wolf) (Table 3a). Similarly, lower-level
189 carnivores were twice more abundant in the SE compared with the NW (Table 3b). In contrast,
190 herbivore biomass was > 6 times larger at the NW locations compared to the SE (Table 3c).

191 **Table 3. Comparisons of fish trophic biomass by island and exposure.** Results of generalized
192 linear mixed models fit with negative binomial error structure. Unplanned post hoc multiple
193 comparisons tested using a Tukey's honestly significant difference (HSD) test. Only significant
194 multiple comparisons are shown. A. Planktivores, B. Herbivores, and C. Lower-level carnivores.

A. Planktivores	Estimate	Std. Error	z	P
Island	1.06	1.179	0.9	0.369
Exposure	3.332	1.177	2.83	0.005
Island x Exposure	-2.849	1.519	-1.88	0.061
SE (2.6 ± 2.8) > NW (0.7 ± 1.1)				

B. Herbivores	Estimate	Std. Error	z	P
Island	0.564	0.546	1.03	0.302
Exposure	-1.33	0.544	-2.44	0.015
Island x Exposure	-0.772	0.706	-1.09	0.274
NW (0.32 ± 0.76) > SE (0.05 ± 0.07)				

C. Carnivores	Estimate	Std. Error	z	P
Island	0.902	0.693	1.3	0.193
Exposure	1.424	0.686	2.08	0.038
Island x Exposure	-1.295	0.898	-1.44	0.149
SE (0.60 ± 1.03) > NW (0.28 ± 0.48)				

195 The SE locations at Darwin (Arch and Old Reef) were distinct in ordination space from the other
196 locations. This distinction was driven largely by apex predators and planktivores (Fig. 3). Banana
197 at Wolf Island was well separated from the other locations. Exposure to the prevailing current
198 explained most of the variation among locations, accounting for > 67% of the total (Table 3).

199 **Figure 3. Biplot of results of redundancy analysis of fish trophic biomass with location and**
200 **wave exposure.** Black circles are locations around Wolf and red circles are locations around
201 Darwin. Crosses are wave exposures. Diamonds are centroids of Darwin and Wolf. Vectors are
202 magnitude and directional effects of each trophic group on orientation of locations in ordination
203 space.

204 **Table 3.** A. Results of redundancy analysis (RDA) on square root transformed fish trophic
205 biomass with environmental variables (e.g., island, wave exposure). B. Conditional effects of
206 Monte-Carlo permutation results on the redundancy analysis (RDA).

A. Statistic	Axis 1	Axis 2	Axis 3
Eigenvalues	0.49	0.01	0.001
Pseudo-canonical correlation	0.74	0.39	0.35

Explained variation (cumulative)	49.51	50.73	50.87
Explained fitted variation (cumulative)	97.14	99.54	100.00
B. Variable	Pseudo-F	p	% explained
SE	32.7	0.002	33.8
NW	32.7	0.002	33.8
Rockfall	13.4	0.004	11.6
Arch	3.8	0.042	3.1

Discussion

The first quantitative fish surveys using the stereo-video approach around Darwin and Wolf islands revealed the largest fish biomass reported to date worldwide (Fig. 4). This extraordinary biomass, which consists mostly of sharks, is considerably larger than the next largest fish biomasses reported at Cocos Island National Park (Friedlander et al., 2012) and the Chagos Marine Reserve (Graham et al., 2013). Our results add to the growing body of literature that demonstrates that nearly pristine areas are dominated by top predatory fishes, mainly sharks (Friedlander & DeMartini, 2002; Sandin et al., 2008; Graham et al., 2013; Friedlander et al., 2013, 2014a). At Darwin and Wolf, top predators account for an astonishing 85% of the fish biomass, a percentage found previously only at the pristine Kingman Reef on the Line Islands (Sandin et al., 2008). Inverted biomass pyramids had been unreported until recent surveys of pristine coral reefs (Sala, 2015), and they can be maintained when the top levels of the food web have a much lower turnover rate (slower growth rate per biomass unit) than their prey (Sandin & Zgliczynski, 2015). In the case of Darwin and Wolf, these high levels of predatory fish biomass are supported not only by the high abundance of lower trophic levels fish on the reefs but also the very productive surrounding pelagic waters

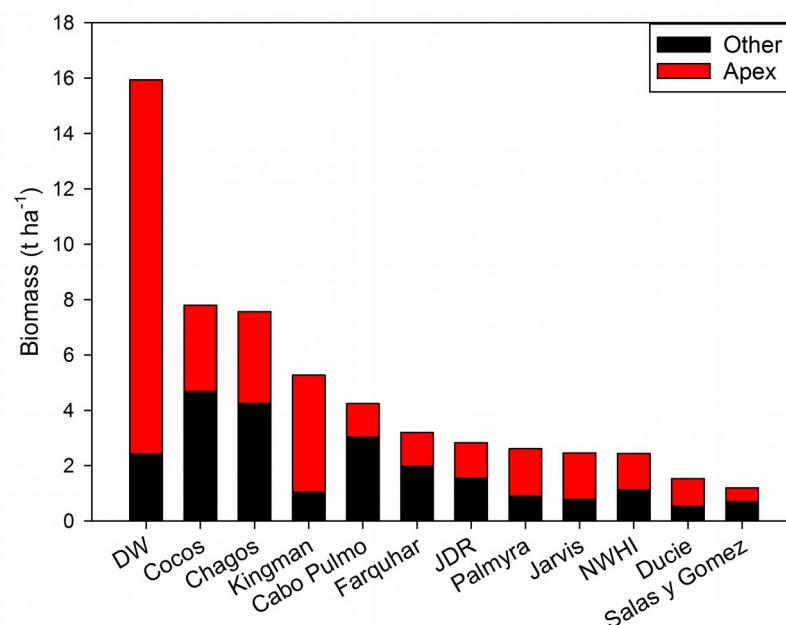
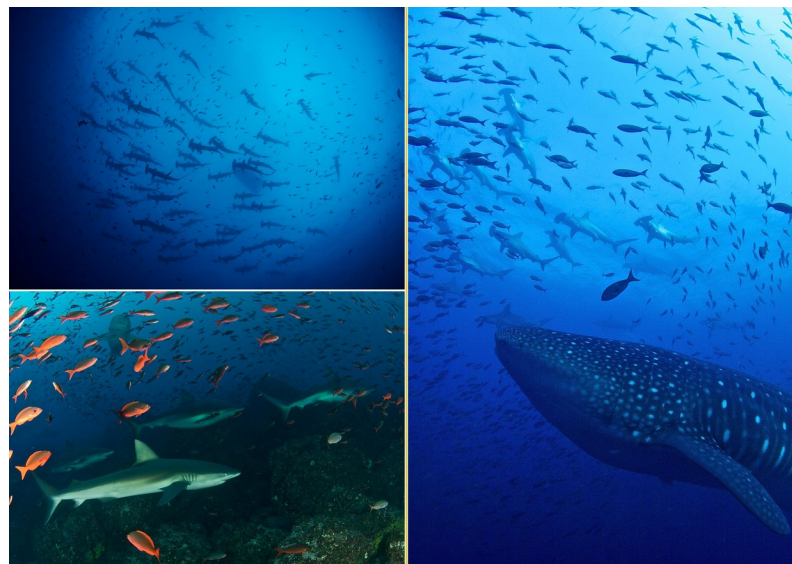



Figure 4 Biomass at Darwin and Wolf compared to other remote pristine locations and MPAs around the world. Data from (Sandin et al., 2008; DeMartini et al., 2008; Aburto-Oropeza et al., 2011; Friedlander et al., 2012, 2013, 2014a,b; Graham et al., 2013).

226 Sharks, mainly hammerhead and Galapagos sharks, dominated the fish assemblage, but other
227 predators like the bluefin trevally, black jack (*Caranx lugubris*) and bigeye jack (*C. sexfasciatus*)
228 were also common at several of the sites surveyed (Fig.5a-c). Our results revealed a marked
229 concentration of sharks and planktivorous fish biomass at the southeast corners of Darwin (Arch
230 and Old Reef sites) and Wolf (Rockfall and Shark Point). The higher abundance at these SE
231 locations may be related to local oceanographic features, dominated by a unidirectional current
232 from the southeast to the northwest that collides with the southeast corner of both islands (Hearn
233 et al. 2010). This may enhance productivity that supports rich benthic and planktivorous fishes,
234 mainly gringos, which may serve as a food source for sharks and other fishes around these islands
235 (Hamner et al., 1988). It is important to consider that these results likely represent maximum
236 annual shark biomass because the surveys were carried out during the cold season, when
237 hammerhead sharks are most abundant (Palacios, 2004; Hearn et al., 2014). Seasonal changes in
238 fish assemblages and biomass are likely since hammerheads are known to migrate from these
239 islands between February and June (Ketchum et al., 2014b). Future studies should focus on
240 seasonal trends and depth gradients (Lindfield, McIlwain & Harvey, 2014) in shark abundance
241 and distribution.

242 **Figure 5 Common encounters around Darwin and Wolf Islands.** A large school of
243 hammerhead sharks (*Sphyrna lewini*, B. A group of Galapagos sharks (*Carcharhinus*
244 *galapagensis*), including a couple of heavily pregnant females, C. A large female whale shark
245 (*Rhincodon typus*) swims among a school of hammerhead sharks. All photos by Pelayo Salinas-
246 de-León.

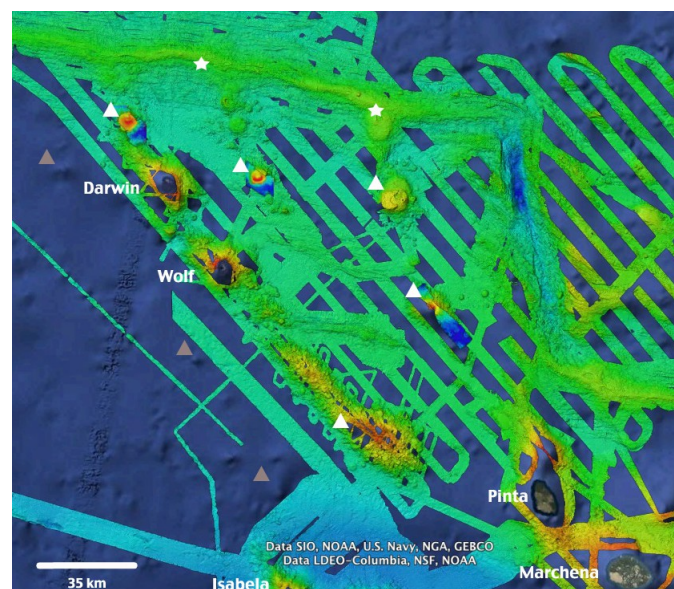
247 A total ban on the capture, transport, and trade of sharks within the GMR was established in 2000
248 (AIM, 2000). However, illegal fishing within GMR boundaries (Jacquet et al., 2008; Carr et al.,
249 2013) and recent efforts by local artisanal fishermen to expand longline fishing, a practice banned
250 since 2005 due to extremely large by-catch [35-36], threaten shark populations. While veteran
251 divers report larger abundance of sharks at Darwin and Wolf over the past 30 years (Peñaherrera-
252 Palma et al., 2015), the absence of long-term quantitative studies to monitor shark and large
253 pelagic fish on a systematic basis and with enough replication does not allow an accurate

254 assessment of the magnitude of decline of shark populations at Darwin and Wolf. By comparison,
255 the recent analysis of a 21-year monitoring program for sharks and large pelagic fishes at Cocos
256 Island National Park in Costa Rica revealed a sharp decline in 8 of the 12 elasmobranch species
257 monitored, including the endangered hammerhead shark and the giant manta ray (*Manta*
258 *birostris*) (White et al., 2015).

259 Despite the large shark biomass at Darwin and Wolf, our surveys also revealed a low overall
260 biomass of predatory reef fishes such as the leatherbass (*Dermatolepis dermatolepis*) and the
261 sailfin grouper (*Mycteroperca olfax*), both endemic to the Eastern Tropical Pacific (ETP) (Grove
262 & Lavenberg, 1997). These species are highly prized by Galapagos artisanal fishermen, but their
263 life histories (e.g., long lives, slow growing) make them extremely vulnerable to overfishing
264 (Aburto-Oropeza & Hull, 2008; Usseglio et al., 2015). Leatherbass biomass reported for Darwin
265 and Wolf (0.008 t ha^{-1}± 0.05 SD) is 14 times lower than at the unfished Cocos Island (0.1 t ha^{-1})
266 (Friedlander et al., 2012). Artisanal fishermen are known to directly target the only reported
267 spawning aggregation for *M. olfax* in the GMR (Salinas-de-León, Rastoin & Acuña-Marrero,
268 2015), an unsustainable fishing practice known to deplete reefs fish stocks at an alarming rate
269 (Sala, Ballesteros & Starr, 2001; Sadovy & Domeier, 2005; Erisman et al., 2011; Hamilton et al.,
270 2012). The low biomass estimates for groupers reported here are likely caused by the unregulated
271 artisanal fishery for demersal fishes in the GMR that directly targets over 50 coastal fish species
272 and has been shown to have a negative impact on coastal resources of the GMR (Ruttenberg,
273 2001; Molina et al., 2004; Burbano et al., 2014; Schiller et al., 2014).

274 Our results also add to the growing body of literature that supports the use of the stereo video
275 methodology as a complement to traditional visual census, as this technique improves the
276 accuracy and precision of fish length estimates (Harvey, Fletcher & Shortis, 2001, 2002),
277 produces more accurate estimates of area surveyed (Harvey et al., 2004), and eliminates the inter-
278 observer bias associated with species identification (Mallet & Pelletier, 2014). Our study, one of
279 the few to evaluate the use of DOVs with large and highly mobile species such as sharks,
280 confirmed that even experienced divers tend to underestimate the individual length of large fishes
281 (Supplementary material).

Conservation implications

283 This study adds to the growing body of literature that highlights the ecological uniqueness and
284 the global irreplaceable value of Darwin and Wolf. These islands not only harbour the largest
285 shark biomass reported to date, but also represent a unique tropical bioregion within the GMR
286 (Edgar et al., 2004). In addition, they are home to the last true coral reefs in the GMR (Banks,
287 Vera & Chiriboga, 2009; Glynn et al., 2009). These islands also represent essential stepping
288 stones for endangered and highly migratory species, such as hammerhead sharks (Hearn et al.,
289 2010; Bessudo et al., 2011; Ketchum et al., 2014a). They are key waypoints for a recently
290 documented migration probably related to reproductive purposes for the largest fish species on
291 the planet, the whale shark *Rhincodon typus* (Acuña-Marrero et al., 2014) (Fig. 5d), and are home
292 to the only known reproductive aggregation for the regionally endemic sailfin grouper (Salinas-
293 de-León, Rastoin & Acuña-Marrero, 2015). These islands are visited by deep-water species such
294 as the smalltooth sandtiger shark *Odontaspis ferox* (Acuña-Marrero et al., 2013), and are
295 surrounded by numerous seamounts and active hydrothermal vents that harbour unique biological
296 communities (Salinas-de-León, *unpublished data*) (Fig. 6).

297 **Figure 6. High-resolution bathymetry around Darwin and Wolf Islands.** Recent multi-beam
298 echo sounder surveys around D&W have revealed the presence of a number of seamounts (white
299 triangles) and active hydrothermal vents and black smokers (white stars) that support unique
300 biological communities. Additional inferred seamounts (grey triangles) are likely to be
301 discovered to the West of the Islands. Source: (Dennis et al., 2012), Ocean Exploration Trust
302 NA-064 2015.

303 The economic benefits of ecotourism from sharks are far greater than shark fishing (Clua et al.,
304 2011; Gallagher & Hammerschlag, 2011; Cisneros-Montemayor et al., 2013). For instance, the
305 net present value of the average hammerhead shark at Cocos Island National Park was estimated
306 at $1.6 million, compared to the ~$200 that a fisherman obtains by selling a dead shark
307 (Friedlander et al., 2012). In Galápagos, the net present value of a shark to the tourism industry is
308 an astonishing $5.4 million (Lynham et al., 2015). The value of a shark to the tourism industry is
309 ~ $360,000 per year, compared to $158 obtained from a dead shark (Lynham et al., 2015). That
310 makes sharks alive in Galápagos the most valuable on Earth. Despite their high economic value
311 and iconic importance, only about 50 km^2 of the waters around Darwin and Wolf (representing an
312 insignificant 0.04% of the total GMR area) are fully protected from fishing.

313 Given the large-scale migrations reported for several shark species around Wolf and Darwin
314 (Bessudo et al., 2011; Ketchum et al., 2014a), and the night foraging excursions by scalloped
315 hammerhead sharks of up to ~30 km from shore (Ketchum et al., 2014a), present levels of
316 protection are clearly insufficient. Expanding levels of protection around Darwin and Wolf,
317 including the establishment of a large no-take zone that includes some of the numerous
318 seamounts located around these islands (Fig. 6) (similarly to other fully-protected areas in the
319 region such as Isla del Coco in Costa Rica or Malpelo in Colombia) is critical to ensure the
320 recovery and long-term preservation of one of the most extraordinary marine ecosystems on the
321 planet – and an economic engine for Ecuador.

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