

1 **A review of a decade of lessons from one of the world's largest MPAs:**  
2 **conservation gains and key challenges**

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76 **Abstract**

77 Given the recent trend towards establishing very large marine protected areas (MPAs) and the high  
78 potential of these to contribute to global conservation targets, we review outcomes of the last decade  
79 of marine conservation research in the British Indian Ocean Territory (BIOT), one of the largest  
80 MPAs in the world. The BIOT MPA consists of the atolls of the Chagos Archipelago, interspersed  
81 with and surrounded by deep oceanic waters. Islands around the atoll rims serve as nesting grounds  
82 for sea birds. Extensive and diverse shallow and mesophotic reef habitats provide essential habitat  
83 and feeding grounds for all marine life, and the absence of local human impacts may improve  
84 recovery after coral bleaching events. Census data have shown recent increases in the abundance of  
85 sea turtles, high numbers of nesting seabirds and high fish abundance, at least some of which is  
86 linked to the lack of recent harvesting. For example, across the archipelago the annual number of  
87 green turtle nests (*Chelonia mydas*) is ~20,500 and increasing and the number of seabirds is ~1  
88 million. Animal tracking studies have shown that some taxa breed and/or forage consistently within  
89 the MPA (e.g. some reef fishes, elasmobranchs and seabirds), suggesting the MPA has the potential  
90 to provide long-term protection. In contrast, post-nesting green turtles travel up to 4000 km to distant  
91 foraging sites, so the protected beaches in the Chagos Archipelago provide a nesting sanctuary for  
92 individuals that forage across an ocean basin and several geopolitical borders. Surveys using divers  
93 and underwater video systems show high habitat diversity and abundant marine life on all trophic  
94 levels. For example, coral cover can be as high as 40-50%. Ecological studies are shedding light on  
95 how remote ecosystems function, connect to each other and respond to climate-driven stressors  
96 compared to other locations that are more locally impacted. However, important threats to this MPA  
97 have been identified, particularly global heating events, and Illegal, Unreported and Unregulated  
98 (IUU) fishing activity, which considerably impact both reef and pelagic fishes.

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Keywords: VLMPA, biologging, conservation, marine megafauna, shark, coral reefs, Aichi targets, seamounts

## Introduction

The growing recognition that marine ecosystems are threatened by biodiversity declines and habitat degradation (McCauley et al. 2015) has led to international calls for protecting the world's ocean, including within Marine Protected Areas (MPAs) (Convention on Biological Diversity's Aichi Target 11 <https://www.cbd.int/sp/targets/>; Woodley et al. 2019). Negotiations at the United Nations are also ongoing to establish a new international treaty within which MPAs would be established in Areas Beyond National Jurisdiction (ABNJs) (O'Leary et al. 2020). A large body of research spanning over 50 years demonstrates that in general, MPAs lead to increases in biodiversity, abundance, size and biomass (e.g. Ballantine 2014; Lester et al. 2009). Importantly, there is also clear evidence of fisheries benefits (Goñi et al. 2010; Harrison et al. 2012), well-being and social benefits (Ban et al. 2019), and resilience afforded by protection in the face of climate change (Mellin et al. 2016; Roberts et al. 2017). While there are recognised limitations (Devillers et al. 2015; Edgar et al. 2014; Giakoumi et al. 2018), impacts of protection are largely positive in coastal ecosystems.

Very Large Marine Protected Areas (VLMPAs), areas > 100,000 km<sup>2</sup>, are fundamental to halting and reversing ocean health declines and to meeting global targets. The Aichi Target calls for a minimum of 10% of the world's ocean to be protected by 2020, a target that will not be met with currently only 2.5% of the ocean's surface in highly protected MPAs (<http://www.mpatlas.org/>; Sala et al. 2018). Additionally, the 30x30 initiative, supported by the analysis of O'Leary et al. (2016), suggests that a minimum of 30% of the ocean should be in highly protected MPAs. Positive conservation outcomes from large-scale protection are also expected to generate positive social, economic and equity outcomes with respect to food security and resource access (Sumaila et al. 2015). However, the benefits of VLMPAs remain debated and empirical studies evaluating their effectiveness are essential. These studies have been limited due to the relatively young age of VLMPAs; the first VLMPA to be established was the Pacific Remote Islands National Marine Monument in 2009 (MPA Atlas, <http://mpatlas.org/mpa/sites/7704395/>). Significant challenge also exists in delivering conservation research in remote regions and on large spatial scales that include offshore pelagic environments.

The British Indian Ocean Territory (BIOT) MPA was proclaimed by the UK Government in April 2010. It is classified as a VLMPA at 640,000 km<sup>2</sup> and as an IUCN management category 1a strict nature reserve (Day et al. 2019), with effectively no permitted fishing. At the time of its designation, it was the largest contiguous highly protected MPA. The MPA includes a range of habitats with deep oceanic areas surrounding the shallow reef environments and reef islands of the Chagos Archipelago. Its recognition as an important site for conservation (reviewed previously by Sheppard et al. 2012) has helped drive a concerted programme of ongoing studies to understand the outcomes of the MPA's creation and its importance for the species and ecosystems it hosts. At the same time, the legality of this MPA has been challenged (Appleby 2015; United Nations 2019). Given both the ongoing challenges to the BIOT MPA and the wealth of recent studies, here we assess the knowledge gains over the past decade regarding this MPA's conservation value. We also discuss the ongoing conservation challenges facing the BIOT MPA that continue to require new and innovative approaches and consider the implications of the lessons learnt for marine conservation planning and management more broadly across the globe.

150 **Materials and methods**

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152 **Identifying Case Studies**

153 Marine research in BIOT extends back to the 1970s but has increased rapidly in the last 15 years.  
154 Recently, much of the research within the BIOT MPA has been coordinated through the Bertarelli  
155 Programme in Marine Science (BPMS). At the annual BPMS meeting in London (18-20 September  
156 2019), programme-supported scientists were asked to describe their key recent findings that highlight  
157 either the conservation value or the challenges facing the MPA. Experts who attended this meeting  
158 were also asked to identify other individuals from around the world who should be invited to  
159 participate in writing a review summarizing the last decade of research on the BIOT MPA. The  
160 assembled authors were able to provide comprehensive coverage of the breadth of recent work that  
161 has taken place concerning the BIOT MPA, including work on a range of habitats including shallow  
162 coral reefs and pelagic realms as well as a range of taxa including fishes, seabirds and turtles. Case  
163 studies were identified by taxonomic group, by habitat, or by ecological question and then experts in  
164 each area prepared text describing their recent discoveries, which are synthesised below.

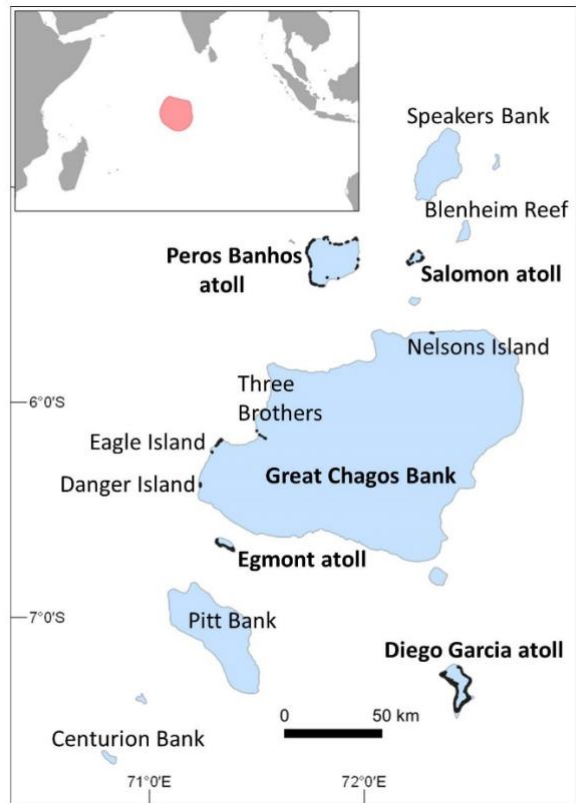
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167 **Background and overview of recent scientific work**

168 Of the 640,000 km<sup>2</sup> of the BIOT MPA, 19,120 km<sup>2</sup> is shallower than 100 m and the remainder is  
169 deep oceanic water with maximum depths of >5,000 m. The Chagos Archipelago consists of discrete  
170 atolls with around 58 associated islands, submerged banks, and an estimated 86 seamounts. The  
171 Great Chagos Bank is described as the world's largest atoll structure, covering an area of 12,642 km<sup>2</sup>  
172 and water depths down to about 90 m (Fig. 1). The land area of the islands within the archipelago  
173 totals only 56 km<sup>2</sup>. These islands are surrounded by shallow fringing coral reefs and encompass  
174 lagoons with sheltered reefs, patch reefs, coral outcrops and seagrass meadows. The BIOT MPA  
175 covers the entire Economic Exclusion Zone (EEZ) with the exception of Diego Garcia atoll and a  
176 three-nautical mile buffer around it, noting that large parts of this atoll and waters receive separate  
177 protection under multiple legal and other regulatory controls (<https://biot.gov.io/>). From the 18<sup>th</sup>  
178 century until the 1970s, the archipelago was managed as a coconut oil plantation. When the final  
179 plantations closed, the archipelago was declared a military exclusion area, and the remaining  
180 population was relocated (Wenban-Smith and Carter 2017). Since then, commercial fishing -  
181 comprising licensed pelagic longline and purse seine fisheries and a relatively small-scale demersal  
182 fishery - was allowed up until 2010 at which point all legal commercial fishing ceased. Local human  
183 impacts on the reefs within the MPA have generally been minimal, but were significant on the  
184 islands when previously settled. Approximately half of Diego Garcia, which has the only current  
185 human settlement in the archipelago, has been extensively altered for the creation of a large military  
186 facility, with buildings and infrastructure, including coastal modification, ports and anchorages.

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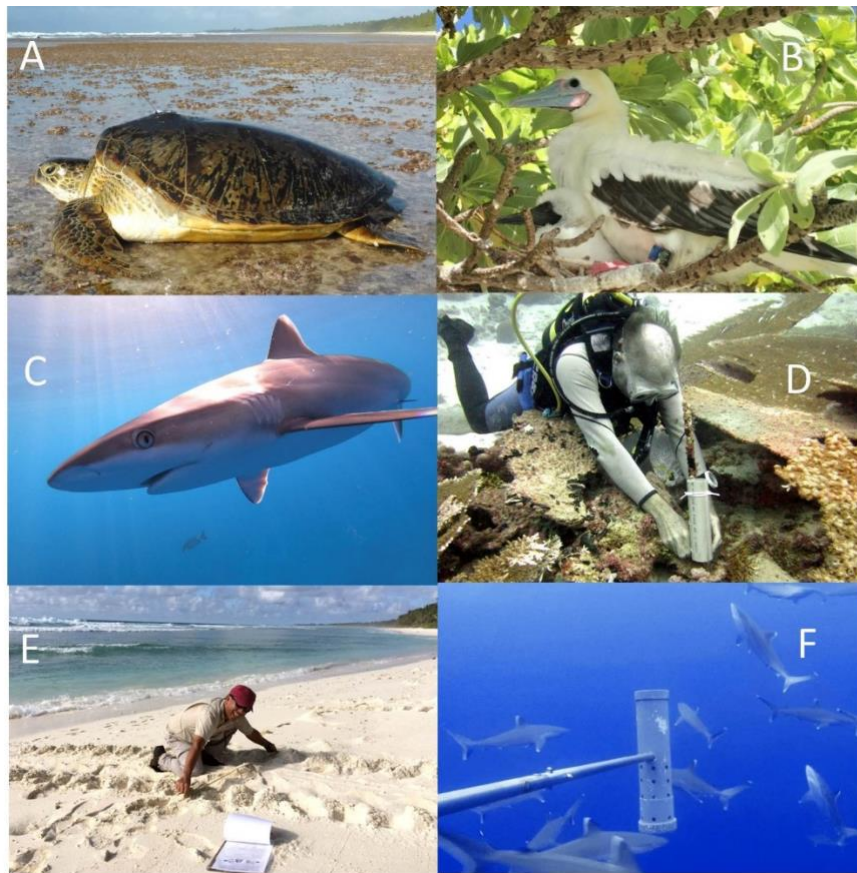
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190 **Fig. 1 The Chagos Archipelago.** Inset shows the general location within the Indian Ocean and the  
 191 MPA boundary (red). Main map shows the archipelago which lies at the heart of the MPA. The five  
 192 atolls with land are in bold, versus selected submerged reefs and atolls not in bold. Islands on the  
 193 Great Chagos Bank include Danger Island, Eagle Island, Three Brothers islands and Nelsons Island.  
 194 Blue shading indicates water shallower than approximately 100 m.

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196 The isolated and protected nature of the Chagos Archipelago means that many human influences are  
 197 minimal. This limited human presence and remote setting of the BIOT MPA provides a baseline to  
 198 other systems more impacted by anthropogenic pressures. All else being equal, it might be expected  
 199 that the MPA would result in positive species and habitat conservation outcomes. There have been  
 200 considerable recent efforts, documented below, to quantify species abundances for comparison with  
 201 other areas in the Indian Ocean, as well as assessing long-term changes within the archipelago. This  
 202 work has shown the value of the MPA for sea turtles, pelagic and reef-associated fishes, seabirds,  
 203 invertebrates and key habitats, such as coral reefs and seagrass beds (Fig. 2). To assess patterns of  
 204 movement in relation to the MPA, a range of turtles, fishes and seabirds have been tracked using  
 205 satellite (Argos and GPS), acoustic telemetry and archival biologging packages. Coral reef surveys  
 206 have been conducted for four decades, thus informing research on how climate change impacts these  
 207 ecosystems. Fish surveys on reefs and in pelagic areas with stereo Baited Remote Underwater Video  
 208 Systems (BRUVS) have been used to describe species assemblages and relative abundance. More  
 209 recently, detailed oceanographic studies have been undertaken to better understand the drivers  
 210 behind the biotic patterns and behaviours observed, while remotely operated vehicles (ROVs) have  
 211 been employed to study the health and diversity of mesophotic reefs and how they may act as refuges  
 212 for shallow reefs. The temporal, spatial and bathymetric extent of data is thus now significant and  
 213 increasing rapidly. In addition to these studies on abundance, trends and movements, the MPA has  
 214 allowed a range of questions to be addressed on ecosystem functioning, movement ecology and  
 215 animal behaviour in an environment relatively free of most human influences. At the same time,

216 patrols of the MPA provide indications of the extent of Illegal, Unreported and Unregulated (IUU)  
217 fishing activity.  
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222 **Fig. 2 The breadth of recent studies in the BIOT MPA.** Recent work in the BIOT MPA has used  
223 electronic tags to track the movements of sea turtles, seabirds and fish. Pictured with tags attached **a**  
224 a green turtle (*Chelonia mydas*) with a Fastloc-GPS Argos tag on the carapace, **b** a red-footed booby  
225 (*Sula sula*) with a light-based geolocator tag on its leg, **c** a silvertip shark (*Carcharhinus*  
226 *albimarginatus*) prior to being fitted with a long-term, internal acoustic transmitter. **d** Habitat  
227 surveys using SCUBA and deployed instruments have shown long-term changes in reef  
228 environments and water temperature. **e** Counting tracks on beaches has revealed long-term increases  
229 in sea turtle nesting numbers. **f** Marine surveys have been extended using technology such as Baited  
230 Remote Underwater Video Systems (BRUVS) deployed in the open ocean or in shallow coastal  
231 areas. Pictured in (f) silvertip sharks. Images courtesy (a,e) Nicole Esteban and Graeme Hays, (b)  
232 Hannah Wood, (c) David Curnick, (d) Charles Sheppard, (f) Jessica Meeuwig.

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235 **Review structure**

236 We begin by examining the importance of the BIOT MPA for coral reefs and coral reef research. We  
237 then consider work with taxa that has included tracking individuals and/or census surveys including  
238 coral reef fish, turtles, seabirds and pelagic fish. We then consider recent knowledge gains regarding  
239 invertebrate fauna and mesophotic reefs. We examine how the MPA has provided an environment  
240 for seminal work on natural behaviours and ecological relationships in the absence of anthropogenic  
241 influences and we consider the physical oceanography of the region may influence its ecological

242 value. Finally, we highlight the key threats the MPA faces, particularly climate warming impacts on  
243 coral reefs and IUU fishing impacts on fish stocks.

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## 246 **Results**

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### 248 **Importance of the BIOT MPA for coral reefs and coral reef research**

249 The BIOT MPA represents a valuable reference site for understanding coral community resilience in  
250 an ocean where most reefs have undergone significant and continuing declines in health. Although  
251 reefs in the Chagos Archipelago have not been spared from the effects of large climate driven  
252 stressors (i.e. temperature driven coral bleaching), the MPA has afforded protection from many of  
253 the local threats that reefs face in other parts of the world such as destructive fishing practices, local  
254 pollution, or sedimentation and eutrophication from anthropogenic land-based sources.

255 Data collected following the major coral bleaching event of 1998 showed that despite its  
256 geographically isolated position, the Chagos Archipelago was not immune from widespread coral  
257 mortality, which extended to depths of > 40 m in some locations (Sheppard et al. 2012). However,  
258 most of the reefs recovered quickly and by 2012 coral cover on reefs in the BIOT MPA averaged 40-  
259 50% (Fig. 3a,d), with juvenile coral densities of 20-60 colonies m<sup>-2</sup> (Fig. 3b) (Sheppard et al. 2017;  
260 Sheppard and Sheppard 2019). Thus, the reefs had largely regained coral cover levels consistent with  
261 those documented prior to 1998 and coral recruitment was clearly prolific. This high coral cover and  
262 return of dominant branching and tabular species on many fore reef sites supported high net positive  
263 carbonate budgets, an important metric influencing reef growth potential and the maintenance of  
264 habitat complexity (Perry et al. 2015). Resultant estimates of average vertical reef accretion rates on  
265 *Acropora* dominated reefs ( $4.4 \pm 1.0$  mm yr<sup>-1</sup>) were high in a global context, indicating that many of  
266 the reefs would have the capacity to track projected future sea level rise (Perry et al. 2018). For  
267 context it is important to note that not all reefs in the wider region recovered as well or as fast after  
268 the 1997-1998 bleaching event. For example, shallow reefs in the Maldives recovered to pre-  
269 bleaching states by 2013-2014, albeit comparatively slowly and displaying subtle changes in  
270 community composition (e.g. Morri et al. 2015), whilst in the Seychelles reefs followed more  
271 divergent recovery trajectories. Some sites recovered well, while others regime-shifted to macroalgal  
272 or rubble dominated states with coral cover <10% (e.g. Chong-Seng et al. 2014; Harris et al. 2014,  
273 Graham et al. 2015). Regime-shifted sites had negative carbonate budgets and reef accretion rates  
274 (Perry et al. 2018).

275 It is clear that the absence of local impacts, provided by the remoteness of the Chagos  
276 Archipelago and the presence of the MPA, aided relatively rapid recovery of many reefs compared to  
277 other Indian Ocean sites (Sheppard and Sheppard 2019). In particular, water quality is emerging as  
278 an important factor shaping the response of corals and reefs to heat stress (Wooldridge and Done  
279 2009; D'Angelo and Wiedenmann 2014; MacNeil et al. 2019; Lapointe et al. 2019; Donovan et al.  
280 2020). Specifically, an increase in nitrogen (especially nitrate) coupled with phosphorous limitation,  
281 which are typical of land-based pollution, exacerbate the effects of heat stress and prolongs recovery  
282 time following bleaching events (Wiedenmann et al. 2013; Ezzat et al. 2016; Burkepile et al. 2020).  
283 The absence of such stressors within the Chagos Archipelago is likely a key contributor to the rapid  
284 recovery observed on these reefs compared to other reefs within the region and within other MPAs  
285 (e.g., the Florida Keys National Marine Sanctuary and the Great Barrier Reef Marine Park) (MacNeil  
286 et al. 2019; Lapointe et al. 2019).

287 However, it is also relevant to note that these reefs have not been immune from repeated  
288 disturbances over the last decade. Localised outbreaks of crown-of-thorns starfish (*Acanthaster*  
289 *planci*) were observed in 2013, causing high mortality of branching *Acropora* spp. and White  
290 Syndrome disease was prevalent on many reefs in 2014 and 2015, causing widespread mortality of  
291 tabular *Acropora* colonies (Wright 2016; Sheppard et al. 2017). Most significantly, however, the

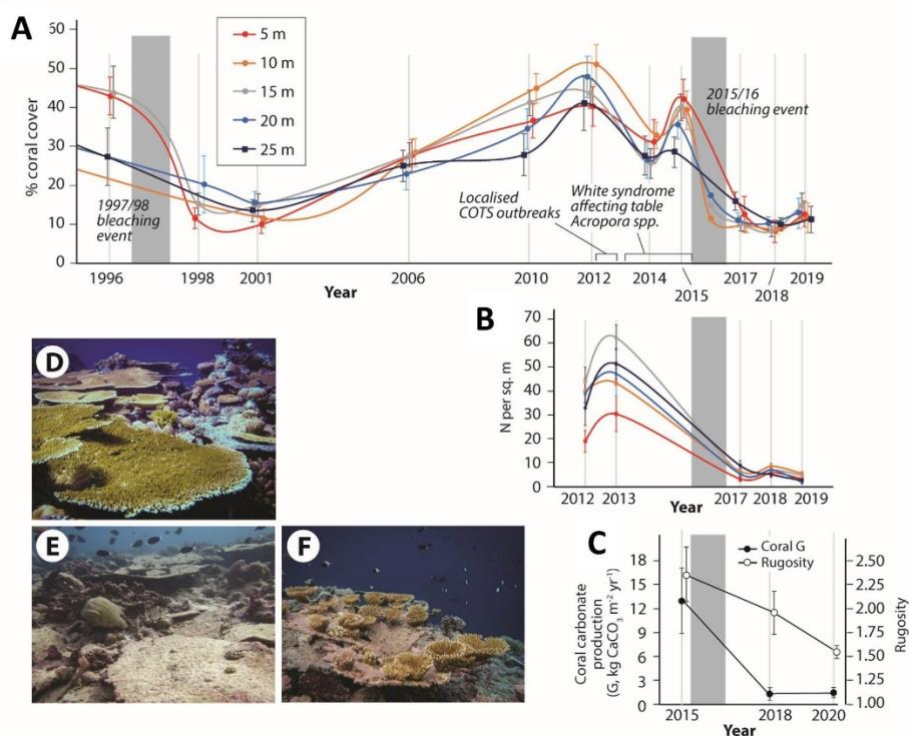
292 reefs were again heavily impacted by the recent global heat stress event, which caused back-to-back  
293 coral bleaching and mortality in 2015 and 2016. Intensive research efforts in BIOT over the last five  
294 years are providing detailed insights into subsequent ecological changes across a wide range of  
295 depths and habitats.

296 As after the 1998 event, widespread coral mortality reduced average coral cover to around  
297 10% in 2017, mainly affecting reefs to a depth of 15 m (Fig. 3a,e) (Sheppard et al. 2017; Head et al.  
298 2019). This decline in coral cover was driven primarily by a ~90% decline in *Acropora* spp. cover in  
299 shallow and mid depths, shifting community composition from competitive to stress-tolerant taxa  
300 and leaving *Porites* spp. as the dominant coral genus post-bleaching (Head et al. 2019; Lange and  
301 Perry 2019). In deeper water (20 m+), the largest losses were of foliaceous forms. No evidence of  
302 coral acclimation following 1998 can thus be inferred. Soft corals have also been lost, especially on  
303 shallow reefs and seaward facing exposed reefs, and now occupy less than 4% in the 15-25 m depth  
304 range. Sponges showed an initial increase in 2018, especially in deep waters, but have declined to  
305 about 12% cover in 2019 (Sannassy Pilly et al. unpubl. data). Despite the decrease in coral cover,  
306 fleshy macroalgae are very rare, which may be attributed to absent nutrient stress from fertilizer and  
307 sewage runoff that negatively affect reefs in most coastal areas (Fabricius 2005; Lapointe et al.  
308 2019). The only life form to show a mean increase across reefs are calcifying algae (especially  
309 *Halimeda* spp.), which have increased from negligible values to 12% in shallow waters and to 15-  
310 16% in deeper waters. Crustose coralline algae cover has increased from 8% to around 25% in  
311 shallow water and to around 20% in deeper waters in 2019 (Benkwitt et al. 2019; Sannassy Pilly et  
312 al. unpubl. data). From a geo-ecological perspective, the main consequence of the above community  
313 changes has been a major decline in carbonate production rates, which have dropped by an average  
314 of 77% (Fig. 3c). At the same time, mean reef rugosity declined by 16% (Fig. 3c) and rubble cover  
315 doubled between 2015 and 2018 (Lange and Perry 2019).

316 Critical questions at present are whether the reefs will follow the same recovery trajectories  
317 as after 1998, or whether more divergent trajectories will occur in different sites and locations (see  
318 section below on Key Ongoing Threats). The presence of the BIOT MPA guarantees that recovery  
319 trajectories will not be impeded by local stressors such as anthropogenically-derived nitrogen  
320 enrichment and altered nutrient ratios, which can exacerbate coral disease and bleaching and has led  
321 to reef degradation in other protected areas, e.g. the Florida Keys National Marine Sanctuary  
322 (Lapointe et al. 2019). Still, recovery potential will ultimately depend on recurrence intervals and  
323 magnitudes of future heat stress events.

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**Fig. 3 Metrics of reef health on ocean-facing coral reefs across the Chagos Archipelago. a** Live coral cover (%) at different depths 1995-2019; **b** Juvenile coral densities (individuals m<sup>-2</sup>) at different depths 2012-2019; **c** Coral carbonate production rate (kg m<sup>-2</sup> yr<sup>-1</sup>) and rugosity at 8-10 m depth 2015-2019. All values are means ± SD. Shaded areas represent major coral bleaching events. Photographs show reef states in **d** 2015, **e** 2018 and **F**) an example of young *Acropora* spp. growing on a dead table coral in 2019. Note that 2020 data in **c** are based on a subset of survey locations. Photographs: (d) Chris Perry, (e,f) Ines Lange.

### Coral reef fishes are much more abundant than in other Indian Ocean locations

The first underwater visual surveys of fish biomass and community structure in the Chagos Archipelago were conducted on the outer reef slopes of the atolls in 2010, the year the MPA was established. The archipelago had also been a *de facto* MPA for reef fishes, with very limited reef fishing since the 1970s (Koldewey et al. 2010). Fish biomass on these reefs was six times greater than even the best-protected smaller MPAs surveyed across eight other countries in the WIO (Graham and McClanahan 2013). Much of this biomass was made up of species targeted by fishing elsewhere in the region, higher trophic level species and larger body-sized fishes (Graham et al. 2013). These species often have large home ranges (Green et al. 2015), making them vulnerable to fishing pressures outside smaller MPAs. The trophic structure of fish communities across the Indian Ocean changes dramatically with fishing pressure (Barley et al. 2017; Barley et al. 2020) and in the Chagos Archipelago forms a concave shape, with biomass accumulating at the top and bottom of the trophic structure, allowing for efficient energy transfer through the food-web (Graham et al. 2017). The semi-pristine fish community allowed for baselines in a range of community-level life history and functional metrics, including maximum length, length at maturity and abundance of top predators and grazers, to be benchmarked across the region (McClanahan and Graham 2015; McClanahan et al. 2015), and regional-level management priorities to be set (McClanahan et al. 2016).

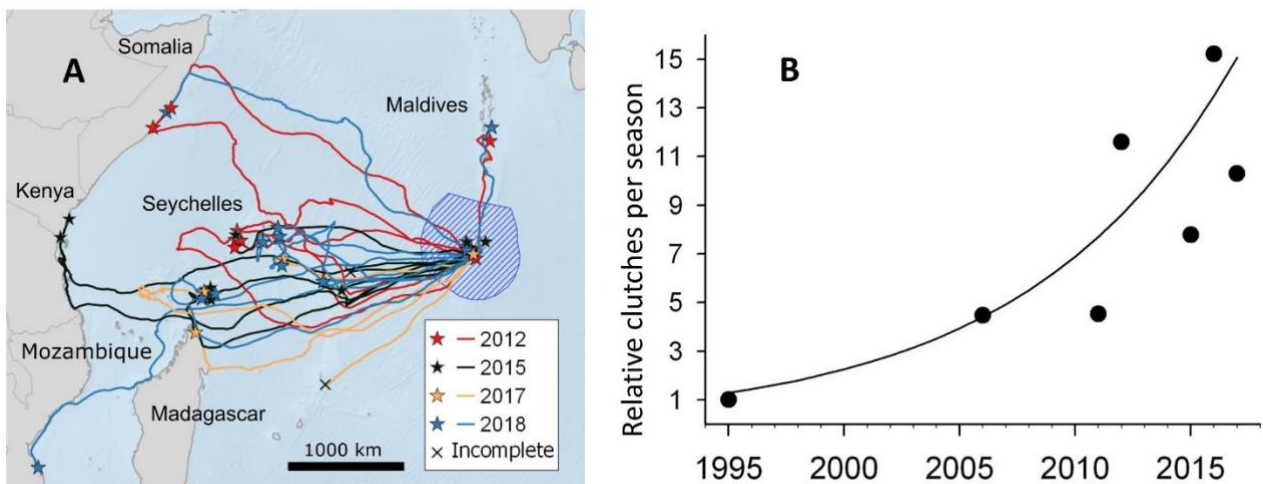
354 The high biomass values and relatively intact community structure have also been  
355 informative to global fish ecology and fisheries studies. Along with some remote locations in the  
356 Pacific, fish biomass and structure in the Chagos Archipelago enabled estimates of unfished biomass  
357 for coral reefs globally (MacNeil et al. 2015) and the functional structure of semi-pristine fish  
358 communities to be established (D'Agata et al. 2016). Globally, the reef fish biomass in the Chagos  
359 Archipelago stands out as a 'bright spot', being greater than would be expected based on the human  
360 and environmental conditions experienced alone (Cinner et al. 2016), with indications that deep-  
361 water refuges and the natural flow of nutrients may contribute to this high biomass (Graham et al.  
362 2018). Further, the biomass and proportion of reefs with top predators helped identify the key role of  
363 distance to markets as a driver of resource condition inside and out of MPAs (Cinner et al. 2018), as  
364 has been also observed for pelagic species (Letessier et al. 2019). Reef fish otolith studies in the  
365 region have revealed the effects of fishing pressure on life spans and patterns of mortality of fishes in  
366 other locations across the Indo-Pacific (Taylor et al. 2019). Biochronological reconstructions of  
367 growth histories of fish species have furthermore helped to refine ecological feedback loops between  
368 parrotfishes and habitat disturbance (Taylor et al. 2020a) as well as decadal growth responses to  
369 oceanographic conditions (Taylor et al. 2020b).

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373 **A climate resilient nesting sanctuary for turtles from across the Western Indian Ocean (WIO)**  
374 Green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles nest in the Chagos  
375 Archipelago with both species heavily exploited for two centuries prior to protection being  
376 introduced in 1968-1970, with the creation of the MPA further reinforcing this protection (Mortimer  
377 et al. 2020). Ongoing census data have highlighted both regionally important nesting populations as  
378 well as upwards trends in abundance. For example, estimates of the annual number of clutches across  
379 the archipelago for the period 2011-2018 are 6,300 and 20,500 for hawksbill and green turtles  
380 respectively, increasing 2-5 times for hawksbills and 4-9 times for green turtles since 1996  
381 (Mortimer et al. 2020). These upward trends in nesting for both species presumably reflect, at least in  
382 part, the fact that there has been no known human exploitation of eggs or adults in the Chagos  
383 Archipelago for ~50 years. Regional estimates indicate that the Chagos Archipelago accounts for 39-  
384 51% of hawksbill and 14-20% of green turtle clutches laid across the entire south-western Indian  
385 Ocean (Mortimer et al. 2020).

386 Satellite tracking of nesting green turtles in the Chagos Archipelago has shown that they  
387 disperse widely across the WIO at the end of their nesting season, which peaks during June to  
388 October (Fig. 4) (Hays et al. 2020; Mortimer et al. 2020). While some individuals travel to foraging  
389 grounds around 80 km away on the Great Chagos Bank, others travel to foraging grounds 1,000s of  
390 km away, for example, in the Seychelles, Maldives and mainland Africa. The Chagos Archipelago  
391 thus provides a key nesting sanctuary for adult green turtles foraging across much of an ocean basin.  
392 Ongoing work is assessing migration patterns in adult hawksbill turtles after their nesting season,  
393 which peaks during October to February (Mortimer et al. 2020). These green and hawksbill turtle  
394 tracking data are being used to inform marine spatial planning broadly across the WIO, helping, for  
395 example, to determine boundaries of protected areas in the Seychelles. Investigation of foraging  
396 grounds within the MPA have led to discoveries of extensive, deep-water seagrass meadows across  
397 the south-east Great Chagos Bank (Esteban et al. 2018). Little is known about these newly  
398 discovered habitats, but they appear to support abundant and diverse fish communities (Esteban et al.  
399 2018). As marine mega-herbivores can act as indicators of the presence of seagrass meadows (Hays  
400 et al. 2018), future tracking of green turtles in BIOT may increase knowledge of the distribution of  
401 these important habitats broadly across the entire WIO. In addition, immature hawksbill and green  
402 turtles foraging at Diego Garcia are also being satellite tracked to assess their patterns of space use.

403 Sand temperature monitoring has shown that the nesting beaches at Diego Garcia are  
 404 particularly climate resilient with regard to incubation temperatures (Esteban et al. 2016). The sex of  
 405 sea turtle hatchlings is determined by the temperature in the nest in the middle third of incubation.  
 406 Around the world there is concern that, with a warming climate, populations are becoming  
 407 increasingly feminised, as females are produced at warmer temperatures. A lack of male hatchlings  
 408 may ultimately lead to population extinction. At many sites globally, hatchling production is already  
 409 heavily female skewed (Hays et al. 2014). However, at Diego Garcia, the sand at nest depths is  
 410 relatively cool, most likely because of a combination of heavy rainfall and shading provided by  
 411 vegetation behind the nesting beaches. As a consequence of these cool incubation temperatures, it is  
 412 estimated that hatchling sex ratios are currently balanced (Esteban et al. 2016). Hence, in scenarios  
 413 of climate warming, excessive feminisation of hatchlings will be much less likely to occur in the  
 414 Chagos Archipelago than at most other nesting sites around the world. The Chagos Archipelago also  
 415 supports immature foraging green and hawksbill turtles and ongoing work with drone surveys is  
 416 estimating the size of these populations and their regional importance (Schofield et al. 2019).  
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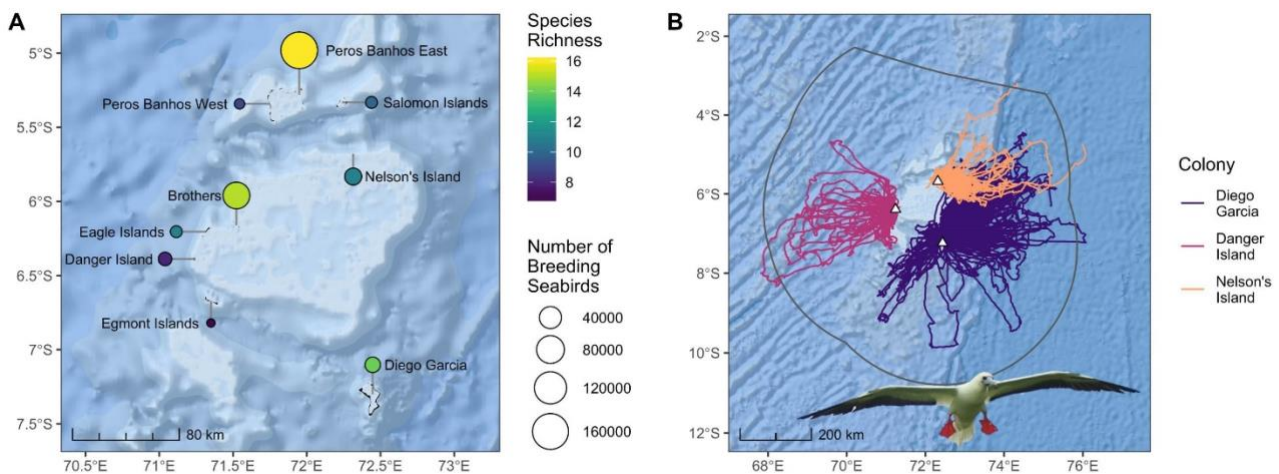
419  
 420 **Fig. 4 The value of the Chagos Archipelago for sea turtles.** **a** The archipelago provides a nesting  
 421 sanctuary for green turtles that forage at distant sites throughout the Western Indian Ocean. Tracks of  
 422 35 adult female green turtles are shown, with individuals equipped with tags on nesting beaches on  
 423 Diego Garcia and then dispersing widely at the end of the nesting season. The extent of the MPA is  
 424 indicated by the blue hatched area. Stars denote the foraging locations of turtles, i.e. the end-point of  
 425 migrations where turtles remained for many months before tags failed (modified from Hays et al.  
 426 2020). **b** The significant positive trend ( $p < 0.01$ ,  $r^2 = 0.88$ ) in the estimated number of green turtle  
 427 clutches laid throughout the Chagos Archipelago. Numbers are scaled relative to those estimated in  
 428 1995, i.e. abundance in 1995 appears as one, to highlight the extent of the increase (modified from  
 429 Mortimer et al. 2020). Between 2001-2018, the estimated mean number of clutches per year  
 430 throughout the archipelago was 20,500 (Mortimer et al. 2020).

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 433 **The BIOT MPA protects globally significant seabird populations**

434 Research in the Chagos Archipelago has reinforced the important role seabirds play in tropical  
 435 marine ecosystems. The WIO has been estimated to support ~19 million seabirds of 30 species, with  
 436 the Chagos Archipelago supporting ~1 million (or 5% of the WIO total) individuals (Danckwerts et  
 437 al. 2014). However, their status and distribution required updating, and until recently virtually

438 nothing was known about their at-sea distribution. A recent synthesis of seabird status and breeding  
 439 distribution across the Chagos Archipelago based on visits to all 55 islands, estimated 281,596  
 440 breeding pairs of 18 species (Fig. 5a). Of these, 96% comprised three species, the sooty tern  
 441 (*Onychoprion fuscatus* 70%), lesser noddy (*Anous tenuirostris* 18%) and red-footed booby (*Sula sula*  
 442 8%) (Carr et al. 2020). Assuming 50% breeding success, 281,596 breeding pairs (563,192  
 443 individuals) will produce 140,798 offspring, equating to ~704,000 breeding adults and immatures, or  
 444 ~4% of the regional total (Dankwerts et al. 2014). Current estimates are considerably lower than  
 445 those proposed by Dankwerts et al. (2014), and there is strong evidence from early visiting  
 446 naturalists (Bourne 1886) and guano mining records (Edis 2004, Wenban-Smith and Carter 2017) to  
 447 suggest this is a fraction of the historic breeding seabird populations. Yet, it is unclear whether trends  
 448 observed in BIOT are representative of the WIO. Therefore, updated estimates from across the WIO  
 449 are now needed to reassess the status of breeding seabirds for this region.

450 At-sea behaviour and distribution of one of the most widely distributed and abundant species  
 451 in the archipelago, the red-footed booby, is being revealed through the deployment of GPS loggers  
 452 on breeding adults. Tracking reveals adults commute long-distances over relatively straight paths to  
 453 feed in deeper waters beyond the Great Chagos Bank (Fig. 5b) and suggests at-sea segregation as  
 454 seen elsewhere with seabirds from different colonies (Wakefield et al. 2013). As the vast majority of  
 455 individuals remained within the MPA (Fig. 5b), the lack of commercial fishing within the MPA may  
 456 help ensure high availability of forage fish and reduce threats from fisheries bycatch. The restriction  
 457 of suitable breeding habitat due to the persistence of introduced rats and associated abandoned  
 458 coconut plantations across 95% of the terrestrial landmass, remains a constraint to seabird recovery  
 459 and the MPA delivering its full potential as a seabird sanctuary, although a feasibility study for  
 460 eradicating rats across the archipelago has recently been completed.  
 461



462 **Fig. 5 Seabird abundance and movements.** **a** Seabird species richness and abundance varies across  
 463 the Chagos Archipelago. Data are from breeding seabird counts on all 55 islands 2008-2018 (Carr et  
 464 al. 2020). **b** Centrally placed red-footed boobies breeding on the Chagos Archipelago largely forage  
 465 within the MPA and show evidence of colony-specific at-sea segregation. Data are from 192  
 466 individuals at three colonies (DG: Diego Garcia, 2016-18, n=99; DI: Danger island, 2019 n=30; NI:  
 467 Nelson's Island, 2018-19, n=63). Study colony locations are marked with triangles and the grey line  
 468 delineates the MPA.  
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 472 **The large no-take MPA encompasses important pelagic wildlife**

473 The relatively recent establishment of very VLMPAs, combined with the logistical and  
 474 methodological challenges of sampling remote, expansive regions means that empirical data on the

475 effectiveness of these MPAs for pelagic species are currently limited and conclusions are sometimes  
476 conflicting. Some studies suggest that MPAs are beneficial for mobile species, with the benefits of  
477 MPAs increasing with size, remoteness and age (Edgar et al. 2014). The BIOT MPA therefore  
478 represents an excellent reference site for such studies.

479 Since the establishment of the MPA, electronic tagging studies have reported, albeit with  
480 relatively low numbers and limited durations, higher than expected residency of pelagic fish species,  
481 such as silky sharks (*Carcharhinus falciformis*), sailfish (*Istiophorus platypterus*) and yellowfin tuna  
482 (*Thunnus albacares*) (Carlisle et al. 2019). The historical fishing record shows that large yellowfin  
483 tuna have also been reported to occur in the archipelago year-round (Curnick et al. 2020). Further,  
484 activity spaces of all pelagic species tagged around the Chagos Archipelago were significantly  
485 smaller than the extent of the MPA, suggesting it may be large enough to provide a refuge for  
486 extended periods of time (Carlisle et al. 2019).

487 Increased understanding of large pelagic species around the Chagos Archipelago has also  
488 been informed through the use of fisheries independent mid-water stereo-BRUVS (Fig. 2f).  
489 Assessments of pelagic richness and biomass using mid-water stereo-BRUVs (in 2012, 2015 and  
490 2016) showed variation among pelagic habitats associated with atolls, seamounts and a deep-sea  
491 trench (Meeuwig unpubl. data). This is consistent with historical fisheries data that show high spatial  
492 heterogeneity in the distributions of species such as yellowfin tuna (Dunn and Curnick 2019).  
493 Pelagic richness and biomass around the Chagos Archipelago are also relatively high compared to  
494 global averages (Letessier et al. 2019).

495 The BIOT MPA was established for biodiversity conservation and not as a fisheries  
496 management tool. Studies elsewhere have shown benefits to adjacent tuna fisheries by VLMMPA  
497 establishment (Boerder et al. 2017) and residency behaviour in yellowfin tuna to remote locations  
498 (Richardson et al. 2018). Yet a recent study of commercial catch data found no direct evidence that  
499 indices of yellowfin tuna abundance have improved in the areas immediately surrounding the MPA  
500 (Curnick et al. 2020). However, since the MPA's establishment, mismanagement of the yellowfin  
501 tuna fishery and a failure to adhere to catch reduction measures (Andriamahefazafy et al. 2020) has  
502 resulted in the stock being downgraded to "overfished and subject to overfishing" since 2015 (IOTC-  
503 SC21, 2018). It is therefore not surprising that a single MPA one twelfth of the size of the fished  
504 region would be sufficient to turn around such declines, arguing the need for greater regional  
505 protection.

506 All pelagic shark species evaluated by the Indian Ocean Tuna Commission (IOTC) – with the  
507 exception of the blue shark (*Prionace glauca*) – have no or uncertain stock assessments (IOTC-  
508 SC21 2018). Tracking studies have shown that pelagic sharks may travel across the Indian Ocean to  
509 the BIOT MPA, providing further evidence that the MPA may provide an important sanctuary for  
510 this group (Queiroz et al. 2019). So, while tracking data confirm sometimes protracted residence of  
511 pelagic species within the BIOT MPA (Carlisle et al. 2019) and BRUVs data show high pelagic  
512 species richness (Letessier et al. 2019), benefits may also be partly negated by overfishing in the  
513 surrounding region (IOTC-SC21, 2018, Curnick et al. 2020) and/or the ongoing IUU fishing activity  
514 (see below). Combined, these initial studies suggest that the BIOT MPA and its habitats could have  
515 considerable benefits for pelagic wildlife, particularly in the context of high fishing pressure in the  
516 region (Kroodsma et al. 2018).

## 517 518 519 520 **The BIOT MPA hosts exceptionally high cryptofauna diversity**

521 First estimates of the decapods in the Chagos Archipelago, one of the most speciose cryptofauna  
522 groups on coral reef microhabitats (Stella et al. 2011), recorded 1,868 individuals across 164 nominal  
523 species on 54 dead coral colony microhabitats (Head et al. 2018). This number of species is  
524 exceptionally high relative to similar studies in other locations (e.g. Preston and Doherty 1990;

525 Plaisance et al. 2009; Enochs and Moanzello 2012; Head et al. 2018) and community structure is  
526 unusual due to a prevalence of obligate coral-dwelling decapods, such as Trapezia crabs (Head et al.  
527 2015). Studies are now being undertaken across the archipelago to identify the most important  
528 environmental drivers of cryptofauna communities.

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532 **The BIOT MPA protects diverse mesophotic coral ecosystems**

533 Mesophotic coral ecosystems (MCEs) are typically found at depths of 30m to >150m (Turner et al.  
534 2017). Much of our knowledge of MCEs in BIOT is based on diver surveys from the 1970s  
535 (Sheppard 1980) and a small number of brief ROV surveys in 2016 (Andradi-Brown 2019). Building  
536 on these studies, in late 2019, high-resolution multibeam and a sophisticated ROV fitted with a HD  
537 camera were used to conduct extensive surveys of both upper and lower mesophotic communities  
538 from 30-150 m at seven sites around Egmont Atoll and Sandes Seamount. Preliminary analysis has  
539 revealed diverse and abundant MCEs at all locations surveyed, hosting communities of  
540 zooxanthellate scleractinian corals, soft corals, sea fans and sponges. A number of scleractinian coral  
541 specimens were also sampled at multiple sites and depths during the surveys. Using molecular  
542 techniques, work is ongoing to identify the species of corals sampled and to assess genetic  
543 connectivity among shallow and mesophotic reefs. Preliminary observations indicate that the MCEs  
544 of BIOT offer huge potential in the level of diversity they encompass and the extension of the  
545 shallow-water reefs into deeper waters, which is especially pertinent given recent bleaching events in  
546 the region (Head et al. 2019). Thus, the BIOT MPA has significant value in protecting extensive  
547 areas of diverse mesophotic coral ecosystems, which have the potential to support both local and  
548 regional shallow-water reefs in the face of climate change.

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551 **Long-term protection preserves habitat connectivity, natural behaviours and ecological**  
552 **relationships**

553 Remote areas like the BIOT MPA can act as natural laboratories that deepen our ecological  
554 understanding of reef ecosystems. The BIOT MPA is home to numerous species of seabirds and  
555 mobile teleost and elasmobranch fishes that play an important role in connecting discrete habitats.  
556 Due to their proximity to deeper waters, the atoll ecosystems are spatially heterogeneous and  
557 temporally dynamic with resource availability continually shifting under the influence of diel and  
558 seasonal cycles, as well as oceanographic processes. Quantifying connectivity across these seascapes  
559 is important for understanding the degree to which populations should be treated and managed as  
560 distinct units (Jacoby and Freeman 2016) and to uncover the functional role that mobile species play  
561 in nutrient transfer (Williams et al. 2018a), predation pressure (Heupel et al. 2014) or local measures  
562 of biodiversity (Benkwitt et al. 2020).

563 Seabirds in the Chagos Archipelago forage in the open ocean, far from the islands on which  
564 they roost and breed (Fig. 5). In doing so, they transfer large quantities of nutrients from pelagic food  
565 webs to terrestrial systems. This pathway of nutrient flow from seabird guano to coral reefs is  
566 illustrated by elevated nitrogen signatures in terrestrial soils and plants, benthic marine organisms,  
567 such as sponges and algae, and marine consumers, including herbivorous damselfish (Graham et al.  
568 2018). These nutrient subsidies, in turn, bolster the growth rates of individual coral-reef fishes, and  
569 lead to enhanced biomass and ecosystem functioning (including secondary productivity, grazing and  
570 bioerosion rates) of entire fish assemblages (Graham et al. 2018; Benkwitt et al. 2020). Contrary to  
571 anthropogenically-derived nutrient inputs, which negatively affect coral physiology and increase  
572 susceptibility to bleaching (Wooldridge and Done 2009; Wiedenmann et al. 2013; D'Angelo and  
573 Wiedenmann 2014; MacNeil et al. 2019; Donovan et al. 2020), naturally-derived nutrients provide  
574 nitrogen and phosphorous in optimal ratios and can thus increase coral growth (Shantz and Burkepile

575 2014; Savage 2019) and may reduce susceptibility to heat stress (Ezzat et al. 2016). Indeed, nutrient  
576 inputs from seabirds can also alter the response of coral reefs to marine heatwaves, as demonstrated  
577 in part by the proliferation of calcifying algae (e.g., crustose coralline algae) around islands with  
578 abundant seabirds following the 2015/2016 mass coral bleaching event in the Chagos Archipelago  
579 (Benkwitt et al. 2019) (Fig. 6).

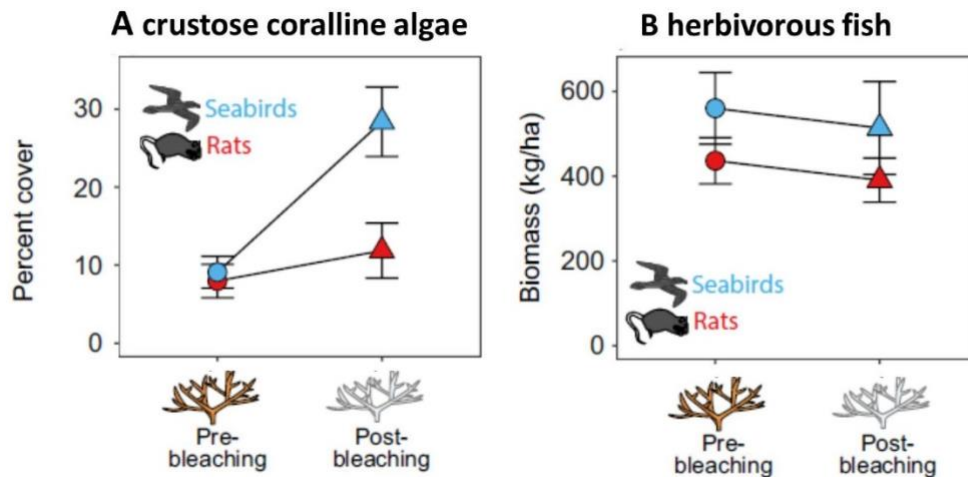
580 Since 2013, a large network of acoustic receivers installed across the archipelago, and annual  
581 deployments of both acoustic and satellite tags, are beginning to reveal the extent to which large  
582 mobile fishes utilise and link different areas across atoll archipelagos (Carlisle et al. 2019; Jacoby et  
583 al. 2020). Acoustic tracking of grey reef and silvertip sharks, both of which are a principal target of  
584 IUU fishing activity in the BIOT MPA, has revealed a few key locations where connectivity is  
585 unexpectedly high (Jacoby et al. 2020). A closer look at the reef shark assemblage, using network  
586 analyses of the telemetry data, reveals how these species play different roles in connectivity across  
587 the MPA, with grey reef sharks exhibiting more residential/site-attached behaviour, while silvertip  
588 sharks have considerably more dynamic movements (Carlisle et al. 2019; Jacoby et al. 2020).  
589 Interestingly, the movement patterns, and thus connectivity of these sympatric species, vary both  
590 diurnally and seasonally suggesting both spatial and temporal segregation within the reef shark  
591 assemblage, corroborating patterns observed through stable isotope analyses in BIOT (Curnick et al.  
592 2019).

593 For large-bodied, wide-ranging planktivores like reef manta rays (*Mobula alfredi*), habitat  
594 selection is strongly influenced by prey availability (Stewart et al. 2018). Telemetry and biologging  
595 approaches are beginning to show that the reef manta rays found in the BIOT MPA frequently utilise  
596 atoll ecosystems, sometimes with long-term site fidelity and aggregation sites, such as at Egmont and  
597 Salomon atolls (Carlisle et al. 2019; Harris 2019; Andrzejaczek et al. 2020). Connectivity is greatly  
598 facilitated by dynamic reef manta movements over frequent short-distances (<10 km) and infrequent  
599 long-distance (>200 km) horizontal movements as well as dives recorded as deep as 500 m  
600 (Andrzejaczek et al. 2020). Characterising the portion of the population that is highly mobile will  
601 enable us to better understand drivers of connectivity across the archipelago.

602 A range of unusual or rarely observed behaviours have been studied in the Chagos  
603 Archipelago, which are likely linked to its isolation. Examples include moray eels (*Gymnothorax*  
604 *pictus*) diurnally hunting shore crabs on land (Graham et al. 2009), day octopus (*Octopus cyanea*)  
605 hunting cooperatively with fishes (Bayley and Rose 2020) and coconut crabs (*Birgus latro*) preying  
606 on adult seabirds (Laidre 2017). All such behaviours are rarely seen, if at all, in highly human-  
607 impacted systems elsewhere (Graham and McClanahan 2013). Furthermore, parrotfish and  
608 surgeonfish in the archipelago exhibit reduced ‘flight’ behaviour compared to fished areas, showing  
609 either an inherited or learned effect of wariness in response to fishing pressure (Januchowski-Hartley  
610 et al. 2015). Protected or wilderness areas can therefore provide a valuable window into the natural  
611 ecological interactions and behaviours, which have otherwise disappeared or been modified.

612 In remote systems such as the Chagos Archipelago, characterised by high consumer biomass  
613 (Graham and McClanahan 2013), general ecological theories can be tested about relationships and  
614 behaviours. Such locations are ideal for investigating what mechanisms maintain trophic structure,  
615 drive variation in structure and complexity, and what the implications are for individual behaviours,  
616 species interactions, or food web stability and productivity (McCauley et al. 2012, 2018; Woodson et  
617 al. 2018). Current work in the Chagos Archipelago has just begun to test such broader ecological  
618 theories, for example, the biodiversity-ecosystem function relationship (Benkwitt et al. 2020). Thus,  
619 not only can remote MPAs like the Chagos Archipelago inform conservation, but also contribute to  
620 broader basic ecology research.

621



622 **Fig. 6 Benefits of rat-free islands to coral reefs.** On rat-free islands in the Chagos Archipelago, seabird guano supplies nutrients to the adjacent coral reefs. These nutrient subsidies, in turn, bolster the growth rates of individual coral-reef fishes, leading to enhanced biomass and ecosystem functioning. Additionally, these nutrient inputs from seabirds can also alter the response of coral reefs to marine heatwaves, as demonstrated by responses to the 2015/2016 mass coral bleaching event. Even though seabird nutrients did not enhance community-wide resistance to bleaching, they may still promote recovery of these reefs through their positive influence on **a** calcifying algae (e.g., crustose coralline algae) and **b** herbivorous fishes (modified after Benkwitt et al. 2019).

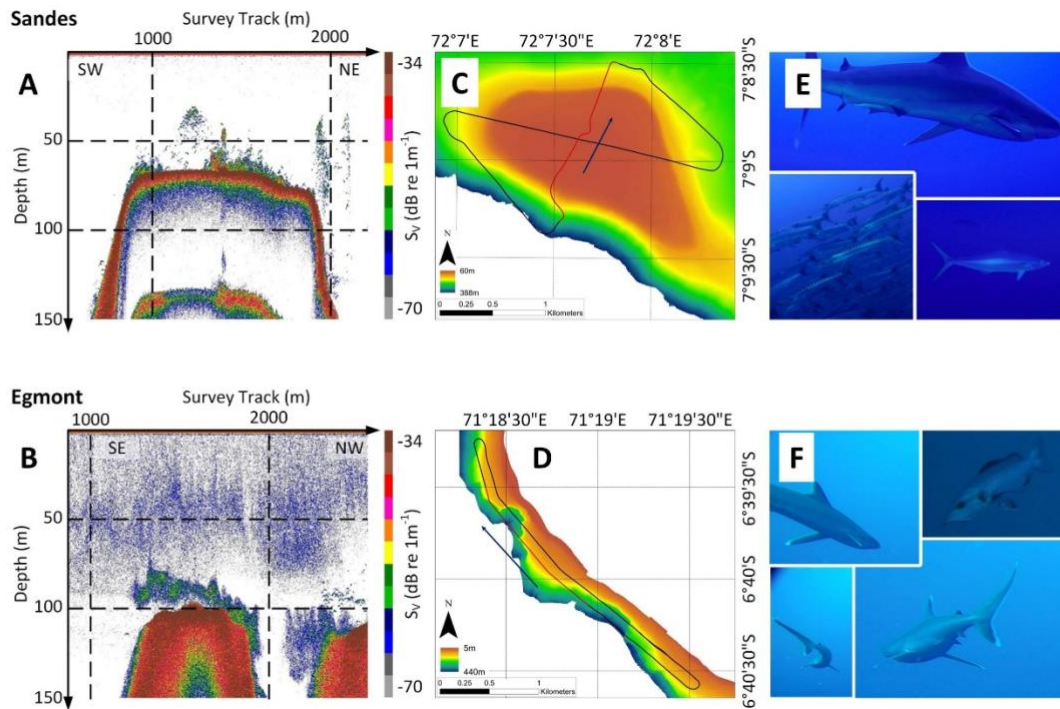
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### 633 Understanding the physical oceanography driving biodiversity across the archipelago

634 Deep oceanic flushing of cold water into the atolls across the Chagos archipelago drives plankton distributions and ecosystem functioning within the sheltered lagoons (Sheehan et al. 2019).  
635 Seamounds are also particularly important features within BIOT and include relatively shallow features such as the Sandes and Swartz seamounds west of Diego Garcia. Their biological significance has been suggested from acoustic surveys during which backscatter indicated 100x  
636 higher biomass in close proximity to seamounds and a “halo” influence of the seamount of approximately 1.8 km (Letessier et al. 2016). Recognised as a hotspot for pelagic sharks (Tickler et al. 2017), studied seamounds exhibit internal lee waves that flush the summits with nutrient rich, cool water (Hosegood et al. 2019). The steep and narrow seamounds found throughout the archipelago, however, prohibit the formation of Taylor Columns that are frequently cited as the mechanism causing the local retention of nutrients and the subsequent primary production over seamounds (Genin, 2004). Instead, the local generation of turbulent and energetic currents associated with the lee waves are proposed to encourage schooling behaviour of lower trophic levels upon which sharks prey and thereby explain the corresponding acoustic signature in biomass over the drop-off where the internal wave impacts are most pronounced. Acoustic surveys during 2019 over the slopes surrounding Egmont Island, further confirmed that the intensification of biomass is not limited to seamounds but extends to the steep slopes surrounding islands and atolls throughout the archipelago (Fig. 7).

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656 **Fig. 7 Use of sonar and cameras to reveal mid-water fauna.** 38 kHz raw Sv echograms of  
657 submerged banks at **a** Sandes and **b** Egmont (lower). Dense dark red echogram returns show the  
658 seabed and second echo at Sandes, with aggregations of biomass (fish and zooplankton) in shallower  
659 water, confirmed opportunistically using camera drops. **c** and **d** cruise tracks showing seabed depth  
660 (with red showing echogram portion. **e** and **f** camera validation of targets (Hosegood, Williamson &  
661 Embling, unpublished data, 2019).

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664 **Key ongoing threats**

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666 **Illegal fishing poses a major threat to vulnerable habitats and species in the BIOT MPA**

667 IUU fishing activity is a considerable challenge inside the BIOT MPA. Historically, IUU occurred  
668 alongside a licensed tuna fishery and it has persisted since the fishery closure in 2010 (Fig. 8). From  
669 2002 to 2018, the majority (78%) of vessels have originated from Sri Lanka, although vessels from  
670 south-west India are also active (12% of sightings). The Sri Lankan vessels are medium-sized (10-15  
671 m) operating both gill-net and long-line gears, often using illegal wire trace to target sharks (MRAG,  
672 2015) (Fig. 8).

673 Enforcement occurs primarily through use of the BIOT Patrol Vessel, which is responsible  
674 for the detection and apprehension of IUU fishing vessels within the MPA. Ferretti et al. (2018)  
675 estimated that 20 to 120 boats enter the area annually. However, determining the actual level of IUU  
676 threat is complicated by temporal and spatial variation in patrolling effort. Although patrolling has  
677 occurred since 1996, patrol effort data have only been logged consistently since December 2013.  
678 That notwithstanding, trends in IUU vessel encounters suggest that the MPA's implementation has  
679 had little discernible impact on the IUU activity (Fig. 8). Spatial and temporal analyses of all vessel  
680 encounters suggest that suspected IUU is focused on the shallow reefs and northern sectors (Fig. 8)  
681 with peaks in activity in the months of May-June and December (MRAG, unpublished data).

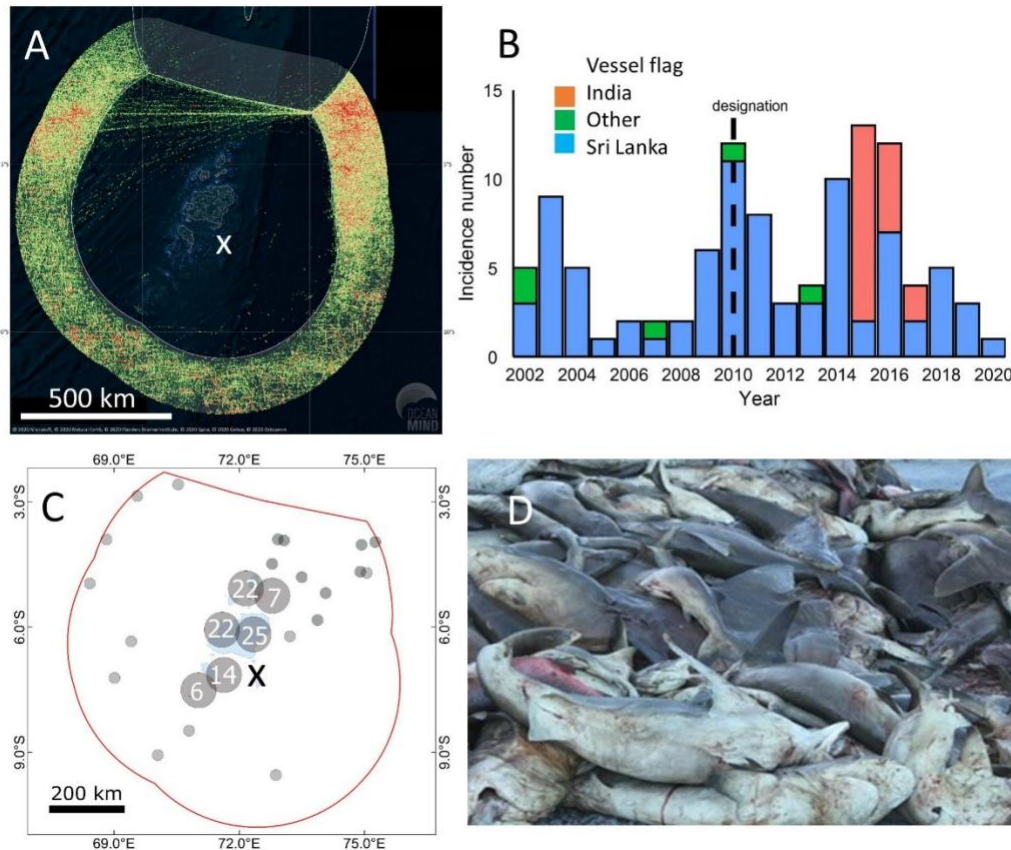
682 IUU fishing appears to have driven declines in some shark populations within the MPA  
683 (Ferretti et al. 2018; Tickler et al. 2019) and so may impair the MPA's function as a refuge for these  
684 species (Letessier et al. 2019). From the catch data, Ferretti et al. (2018) estimated that between

685 1,745 and 23,195 sharks were caught between 1996 and 2015 within the MPA. The number of sharks  
686 seen per scientific dive in the archipelago reduced from ~4 in the 1970s to ~1 since the mid-1990s  
687 (Graham et al. 2010). Recent re-surveys (2018-2019) of the reef fish community structure and  
688 biomass on the outer reef slopes at the same sites, using the same methods, and by the same  
689 observer, have indicated substantial declines in biomass (Graham et al. unpubl. data) that have also  
690 been linked to a reported increase in reef fish within confiscated catches (MRAG, 2015).

691 Similar to the temporal surveys on the outer reef slopes, substantial declines in reef fish and  
692 sharks were observed in BRUVS surveys within the atoll lagoons between 2012 and 2016 (Meeuwig  
693 unpubl. data). Important exploited families, such as serranids and lethrinids, decreased by 74% and  
694 53%, while coral feeding groups, such as chaetodontids, declined by 37% (Meeuwig unpubl. data).  
695 Among the shark species, whitetip reef sharks (*Triaenodon obesus*) declined by 81% and 60% in  
696 relative abundance and size, respectively. The grey reef shark declined by 76% in relative abundance  
697 and by 4% in size. The tawny nurse shark (*Nebrius ferrugineus*) reduced in relative abundance and  
698 size by 37% and 60% (Meeuwig unpubl. data). These declines in relative abundance and size were  
699 coincident with recorded poaching incidents (MRAG 2015).

700 Currently, the BIOT Patrol Vessel has to balance patrol activities, border protection,  
701 scientific research support, as well as refuelling and crew changes outside the territory. As such,  
702 there have been recent efforts to improve enforcement capacity through the trialling of additional  
703 technologies within the MPA through the UK's Blue Belt Programme with a Technology Roadmap  
704 under development. Importantly, the continued threat from IUU fishing highlights the need to  
705 improve monitoring and understanding of the human dimensions (e.g. socio-economic drivers of  
706 illegal fishing) of large MPAs which, although remote, are interconnected within wider socio-  
707 ecological systems (Gruby et al. 2015). Concerns have also been raised about the adequacy and  
708 effectiveness of punitive measures, whereby risks of capture combined with low costs associated  
709 with any arrest may still leave IUU fishing as a viable option for some fishers.

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**Fig. 8 The threat of Illegal, Unreported and Unregulated fishing.** **a** Heat-map of AIS activity from fishing fleets operating in the British Indian Ocean Territory area of interest (BIOT AOI) between 1 January 2014 and 31 December 2019. Fishing vessel identities were confirmed and the activity shown is restricted to AIS transmissions associated with speeds between 0.5-5 knots, speeds typically associated with fishing operations and fishing activity at sea. The extension and level of fishing activity is represented by positional densities that vary from: black = no activity, transparent-green = lower activity (low positional densities) to red/higher activity (hotspots). Legal activity within 3 nautical miles of Diego Garcia (white cross) and slow transits to and from port are not shown. The activity in the northern MPA is produced by small scale commercial fishing vessels (fleet) transiting regularly at slow speed and shaping these lanes between the northeast and northwest boundaries. However, these vessels very frequently deploy fishing gears inside the MPA while on transit and need to be accounted for within the overall fishing activity. Overall, fishing activity is high and widespread through the adjacent high seas. The east and west boundaries of the MPA show high risk due to fishing activity encroaching and entering the marine protected area, with short and repetitive incursions. Additionally, low positional densities inside the southwest MPA are produced from infrequent longer incursions. **b** Vessels suspected of IUU activity that were either detained by authorities or escaped capture from 2002-2020. The dashed line indicates MPA implementation (2010). Flag of origin indicated in legend, other = Indonesia, Mauritius, Japan, Taiwan. Source: MRAG, unpublished data, 2020. **c** Location of detained or escaped vessels suspected of IUU from 2002-2020. Numbers represent the number of vessels from that same site. The cross indicates the location of Diego Garcia. Source: MRAG, unpublished data, 2020. **d** An example of a confiscated catch in the BIOT MPA (photo Tom B Letessier).

739 **Coral reefs in the Chagos Archipelago are not immune to bleaching events**  
740 Reefs in the Chagos Archipelago have repeatedly been impacted by global coral bleaching events,  
741 and the current ecological condition of the reefs suggests they are presently at a critical recovery  
742 stage. While coral cover is starting to increase, structural complexity changes are likely to continue  
743 for several years, as the remaining reef continues to degrade due to intense external and internal bio-  
744 physical erosion. Shallow reefs are increasingly covered by the bioeroding sponge *Cliona* spp.,  
745 decreasing the area suitable for new coral settlement. Additionally, an outbreak of coralline fungal  
746 disease has been observed in 2018, potentially impacting coral recruitment further (Williams et al.  
747 2018b). Indeed, data from 2017 indicates that the density of newly settled coral recruits (<1 year-old)  
748 has reduced by approximately 90% since 2013 (Fig. 3b). Larger young corals (>1 year) are present in  
749 greater numbers, though most are located on unstable dead table corals or mobile rubble (Fig. 3f),  
750 and therefore are likely to experience high mortality rates (Sheppard et al. 2017). Measured growth  
751 rates for several coral species were also comparatively low in 2018-2019, suggesting prolonged  
752 effects of heat stress on coral physiology (Lange & Perry 2020). Since the late 1970s, several coral  
753 species and key species assemblages in the Chagos Archipelago have gone regionally or functionally  
754 extinct. Although species diversity remains high at present, local extinctions may increase in the  
755 future, following a spiral of positive feedback through low recruitment and lack of suitable  
756 settlement substrate (Sheppard et al. 2020).

757 Importantly, the remote and protected nature of the BIOT MPA has previously supported  
758 rapid coral community recovery following widespread mortality in 1997-1998, giving hope for  
759 future recovery (Sheppard et al. 2008). However, it is unclear whether all reefs will restructure in the  
760 same way that they did after 1998, whether recovery will be as fast at all sites, or whether some sites  
761 may regime-shift to other states. The return of *Acropora* spp. dominated communities will be crucial  
762 to restore the key geo-ecological functions of habitat complexity and carbonate production that local  
763 reefs delivered pre-bleaching (Lange & Perry 2019). Ultimately, the primary control on coral reef  
764 recovery in the Chagos Archipelago will be the recurrence intervals and magnitudes of future heat  
765 stress events. Unfortunately, BIOT is predicted to see a large increase in the frequency of annual  
766 severe bleaching events in the coming decades, even under conservative emission scenarios (van  
767 Hooidek et al. 2016). Additionally, atmospheric nitrogen deposition is projected to increase in the  
768 future, negatively affecting even remote coral reefs (Chen et al. 2019).

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## 772 **Discussion**

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### 774 **Future research directions for large MPA science**

775 Here, we have shown how recent research in the BIOT MPA has helped to identify not only its  
776 conservation benefits, such as increased abundance of various species, habitat diversity and  
777 resilience, but also the physical and ecological processes that drive these benefits. Fundamental to  
778 these findings has been the multi-year monitoring that has identified important conservation  
779 successes, such as the increase in nesting turtle numbers, the recovery of coral reefs following  
780 bleaching and mortality, or the preservation of natural processes such as seabird subsidies improving  
781 reef vigour. Global climate change remains a huge threat to coral reefs, both within the BIOT MPA  
782 and elsewhere (e.g. Bates et al. 2019), with the frequency of temperature anomalies and extent of  
783 ocean acidification likely to play key roles in dictating the type of shallow reefs that survive into the  
784 future. Such monitoring needs to be continued and expanded. Long-term monitoring of mesophotic  
785 reefs will help identify if they are more resilient than shallow reefs to global heat waves and if these  
786 deep reefs help the recovery of bleached areas. It will also identify if the encouraging trends of  
787 increased sea turtle nesting continue in the future as well as the impact of potential threats to sea  
788 turtle and seabird nesting posed by rising sea levels. Finally, long-term monitoring of pelagic species

789 at BIOT will also demonstrate the degree to which the MPA generates conservation benefits for  
790 mobile exploited species that contribute to regional fisheries.

791 The BIOT MPA houses regionally significant fish assemblages that play an important role in  
792 the resilience of its coral reefs to climate threats but that continue to be impacted by IUU fishing.  
793 Future research should focus on improving the understanding of the scale and nature of IUU fishing  
794 in the MPA, as well as its drivers to assist with improved enforcement and compliance. Targeted  
795 research is also needed to develop efficient mechanisms to combat IUU fishing given the huge area  
796 of the BIOT MPA poses significant logistical challenges. Innovative methods to combat IUU fishing  
797 have started to be implemented, often with methods tailored to target the specific IUU fishery (e.g.  
798 Tickler et al. 2020) and need expanding.

799 It is important to assess the extent of animal movements in relation to MPAs so that threats to  
800 mobile species can be identified and benefits of different sized protected areas can be objectively  
801 assessed (Dwyer et al. 2020). Given that many marine species may travel many thousands of km  
802 (Hays and Scott 2013), even the largest protected areas, such as the BIOT MPA, may sometimes not  
803 encompass the full extent of marine animal movements. While a number of species have been  
804 tracked (e.g. green turtles and red-footed boobies) important knowledge gaps remain. For seabirds,  
805 their movements outside the breeding season remain unknown. Initial studies suggest that the BIOT  
806 MPA and its habitats could have considerable benefits for pelagic fish. Yet, a challenge remains to  
807 humanely capture and equip a large enough number of individuals to assess the overall patterns of  
808 movement for pelagic fish species. Interestingly, some pelagic sharks equipped with tags 1000s of  
809 km away off southern Africa, have travelled across the Indian Ocean to the BIOT MPA (Queiroz et  
810 al. 2019). So, for some taxa, tagging studies conducted within the BIOT MPA might usefully be  
811 blended with studies being conducted elsewhere to assess patterns of space use across the Indian  
812 Ocean and more broadly (Barkely et al. 2019). The huge value of such data-sharing in animal  
813 tracking studies has recently been emphasised (Sequeira et al. 2019). In some areas, such as marine  
814 animal tracking, routes by which data can drive conservation outcomes have been identified (Hays et  
815 al. 2019) and the tracks of turtles equipped in the Chagos Archipelago that migrate broadly are  
816 already being used to help direct marine spatial planning both in BIOT and the Seychelles.

817 Little is known about some important habitats in the BIOT MPA. While coral reefs have been  
818 a focal habitat for concerted research for some time, a depth limit of 25 m is placed on diving  
819 activities to minimise the risks in such a remote location. Yet most of the Great Chagos Bank, the  
820 world largest atoll structure, is between 25 to 100 m deep. Deeper areas are only starting to be  
821 explored with, for example, the use of drop-down cameras and ROVs (remotely operated vehicles).  
822 Furthermore, research in the BIOT MPA to date has also been focussed on returning to sites  
823 previously surveyed, in order to build a robust, long-term time-series. Yet this has resulted in the  
824 majority of the archipelago remaining unexplored and under-studied, such as the seagrass beds on  
825 the Great Chagos Bank. Here, there may be a very useful synergy between animal tracking studies  
826 and habitat surveys, with hot-spots of space use identified in tracking studies, being used to direct in-  
827 situ habitat surveys, i.e. tracking animals helps identify areas of particular interest (Jacoby et al.  
828 2020). An example here is the use of green turtles to identify the location of seagrass beds on the  
829 Great Chagos Bank that were hitherto unknown (Esteban et al. 2018).

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### 831 **Lessons learned of relevance to other VLMPAs**

832 While the number of MPAs across the world is increasing, their benefits continue to be debated  
833 (Edgar et al. 2014, Bruno et al. 2019). Set against this backdrop, case studies showing the value of  
834 MPAs are important (Murray and Hee 2019). One feature that is evident from much of the recent  
835 research is the importance of long-term monitoring throughout the system. It is well established how  
836 the value of ecological time-series grows as the time-series lengthen (e.g. see Edwards et al. 2010),  
837 allowing the drivers of long-term changes and inter-annual variability to be more clearly identified. It  
838 is therefore important for long-term monitoring to occur in VLMPAs and that it embraces new

839 technology. Such monitoring allows assessment of the success of conservation actions and  
840 identification of emerging threats. For instance, in the Florida Keys National Marine Sanctuary,  
841 whilst highly protected zones have benefited fishes relative to partially protected zones, this high  
842 level of protection has had no impact on the rate of coral decline (Toth et al. 2014) which is driven  
843 both by large scale factors such as poor water quality and climate-related storms and bleaching.

844 That the BIOT MPA, despite its extreme remoteness, remains subject to incursions of IUU  
845 fishing with a demonstrable impact on biodiversity demonstrates the need for more efficient  
846 mechanisms to combat IUU fishing. This may be a common issue with remote MPAs and  
847 necessitates the need for innovative methods to combat IUU fishing (Park et al. 2020). For example,  
848 in the territorial waters around French Islands in the Southern Ocean, radar detecting tags carried by  
849 albatrosses are being used to detect large ships operating illegally (Weimerskirch et al. 2020).  
850 Further, interactions between large static MPAs and mobile fishing gears, such as fish aggregation  
851 devices (FADS) (Bucaram et al. 2018) and industrial fishing fleets around their perimeters  
852 (Kroodsma et al. 2018; Curnick et al. 2020) need to be better understood. Given the huge fishing  
853 pressures in unregulated high seas fisheries outside protected areas, the importance of large MPAs  
854 for pelagic species protection has been stressed (Queiroz et al. 2019). Yet, we emphasise that large  
855 protected areas, such as the BIOT MPA, should not be considered as a silver bullet, but rather in  
856 conjunction with wider sustainable and effective fishery management regulations to provide the  
857 urgent conservation and management benefits needed for pelagic predators. The recent developments  
858 to expand the UN Convention on the Law of the Sea (UNCLOS) to include a new legally binding  
859 instrument on the conservation and sustainable use of marine life in Areas Beyond National  
860 Jurisdiction (General Assembly resolution 72/249) are therefore encouraging.

861 In addition to studying a range of marine habitats within MPAs, another important research  
862 direction is to better quantify the connections between terrestrial and marine environments.  
863 Although this research will take different forms in the BIOT MPA and other remote VLMPAs  
864 compared to smaller MPAs located closer to human population centres, prioritizing research and  
865 encouraging management across land-sea boundaries applies to all MPAs. Specifically, land-based  
866 nutrient pollution plays a large role in declining coral health, especially when coupled with  
867 increasing warming events (Wooldridge and Done 2009; Donovan et al. 2020). As a result, there  
868 have been recent calls to better regulate run-off from land adjacent to MPAs to mitigate continuing  
869 coral loss and enhance recovery following bleaching events (Lapointe et al. 2019; MacNeil et al.  
870 2019). In contrast to these human-derived nutrients, natural nutrient subsidies, such as those provided  
871 by seabirds nesting on islands, may benefit coral reefs and enhance their resilience to global heat  
872 waves (Graham et al. 2018; Benkwitt et al. 2019). Thus, while one research and management priority  
873 within BIOT is the restoration of such natural nutrients (e.g., by eradicating invasive rats and  
874 restoring seabird populations), less remote MPAs will likely need to simultaneously reduce human-  
875 derived nutrient run-off to have similar benefits for coral reefs. Still, jointly managing terrestrial  
876 systems in conjunction with MPAs may be broadly applicable, and may increase the effectiveness of  
877 MPAs at conserving coral reefs and other nearshore habitats.

878 Cutting across all the marine science work in the BIOT MPA, an important goal is to  
879 maximise the translation of the accumulated data into positive conservation outcomes, a theme that  
880 pervades across MPAs more broadly (Lubchenco and Grorud-Colvert 2015). The BIOT MPA was  
881 one of the early wave of no-take VLMPAs implemented from 2006-2010 (with Papahānaumokuākea  
882 Marine National Monument, USA and Phoenix Islands Protected Area, Kiribati) as countries worked  
883 to meet Aichi Target 11 of 10% ocean protection by 2020 under the United Nations' (UN)  
884 Convention on Biological Diversity (CBD), later endorsed under Sustainable Development Goal 14.  
885 Today, only 5.3% of the world's ocean is protected with 2.5% highly protected in no-take MPAs  
886 (<http://mpatlas.org/>, accessed 26 May 2020). However, the UK government is leading the 30-by-30  
887 initiative, pushing for at least 30% of the global ocean to be protected by 2030 with the hope that this  
888 goal will be ratified at the 2020 CBD Conference of the Parties, now rescheduled for 2021. Research

889 from the BIOT MPA therefore provides important insights to inform policy commitments around  
890 ocean protection, including the need for greater regional protection, as part of the actions identified  
891 to rebuild ocean life (Duarte et al. 2020). Mechanisms to effectively achieve this science to policy  
892 interface will be aided by the UN Decade of Ocean Science for Sustainable Development (2021-  
893 2030). The wealth of new information from ongoing work in the BIOT MPA promises to help drive  
894 marine conservation both within the MPA and more broadly, which is, perhaps the most important  
895 legacy this work can leave.

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### Author contributions

900 This manuscript was conceived by GCH and ideas discussed and modified at a workshop led by HK  
901 and DC and held in London during September 2019. GCH, DC, IDL, CTP, DMPJ, HK, JJM, NG,  
902 NE, NLF and CEIH led the writing with all authors contributing. GCH and DC assembled the text  
903 and led the initial editing and all authors contributed to the final manuscript editing.

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