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The discovery of deep-water seagrass meadows in a pristine Indian Ocean wilderness revealed by tracking green turtles

N. Esteban[a,*], R.K.F. Unsworth[a], J.B.Q. Gourlay[a], G.C. Hays[b]

[a] Swansea University, Seagrass Ecosystem Research Group, Department of Biosciences, Swansea SA2 8PP, UK
[b] Deakin University, Centre for Integrative Ecology, Warrnambool campus, Victoria, Australia

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ABSTRACT

Our understanding of global seagrass ecosystems comes largely from regions characterized by human impacts with limited data from habitats defined as notionally pristine. Seagrass assessments also largely focus on shallow-water coastal habitats with comparatively few studies on offshore deep-water seagrasses. We satellite tracked green turtles (*Chelonia mydas*), which are known to forage on seagrasses, to a remote, pristine deep-water environment in the Western Indian Ocean, the Great Chagos Bank, which lies in the heart of one of the world's largest marine protected areas (MPAs). Subsequently we used in-situ SCUBA and baited video surveys to survey the day-time sites occupied by turtles and discovered extensive monospecific seagrass meadows of *Thalassodendron ciliatum*. At three sites that extended over 128 km, mean seagrass cover was 74% (mean range 67–88% across the 3 sites at depths to 29 m. The mean species richness of fish in seagrass meadows was 11 species per site (mean range 8–14 across the 3 sites). High fish abundance (e.g. *Siganus sutor:* mean MaxN.site^{-1} = 38.0, SD = 53.7, n = 5) and large predatory shark (*Carcharhinus amblyrhynchos*) (mean MaxN.site^{-1} = 1.5, SD = 0.4, n = 5) were recorded at all sites. Such observations of seagrass meadows with large top predators, are limited in the literature. Given that the Great Chagos Bank extends over approximately 12,500 km^2 and many other large deep submerged banks exist across the world's oceans, our results suggest that deep-water seagrass may be far more abundant than previously suspected.

1. Introduction

The importance of seagrasses as structural components of ecosystems is well recognized. Seagrasses are one of the most productive ecosystems on earth (Duarte and Chiscano, 1999). Seagrass/algae beds have been rated the third most valuable ecosystem globally for ecosystem services, after estuaries and swamps/flood plains (Costanza et al., 1997). In the tropical Indo-Pacific, seagrass meadows are key components of marine habitats providing critical and highly valued ecosystem services (Coles et al., 2011; Costanza et al., 2014). The tropical Indo-Pacific bioregion has the highest seagrass diversity in the world with as many as 14 species growing on reef flats as well as in very deep waters (Short et al., 2007). Seagrass ecosystems also play a critical role in trophodynamics, habitat provision, substrate stability and biogeochemical cycling (Green and Short, 2003).

Global seagrass assessments largely focus on shallow-water coastal habitats and comparatively few studies have focused on offshore deep-water seagrasses (Fonseca et al., 2008). Thus the majority of what we know about seagrass ecology comes from studies on inter-tidal or coastal seagrass ecosystems. Unsurprisingly, due to logistical and technological challenges, comparatively few studies have focused on deep-water seagrasses, for example, *Zostera marina* meadows in the Mediterranean (Pergent-Martini et al., 2005), *Halophila decipiens* meadows in the Caribbean (Josselyn et al., 1986; Hammerstrom et al., 2006) and *H. decipiens* and *H. spinulosa* in the Great Barrier Reef (York et al., 2015). Recent evidence suggests that deep-water seagrass meadows are extensive and productive (Rasheed et al., 2008; Coles et al., 2009) and worthy of more extensive research efforts.

Deep-water seagrasses (> 15 m depth) have depth ranges most likely to be controlled by the availability of light for photosynthesis. Seagrass habitats in clear tropical waters can occur to depths of 61 m (Coles et al., 2009) and theoretically it is possible that seagrass can extend to a depth of 90 m (Duarte, 1991), supported by reports of 70 m seagrass from Sudan's transparent Red Sea waters (Jones et al., 1987). Although scarce below 50 m depth, *Halophila stipulacea* was collected from 145 m by dredging activities off Cyprus (Lipkin et al., 2003) and is the deepest seagrass reported worldwide (Short et al., 2007). Deep-water tropical seagrass habitats are often extensive, monospecific

* Corresponding author.
E-mail address: n.esteban@swansea.ac.uk (N. Esteban).

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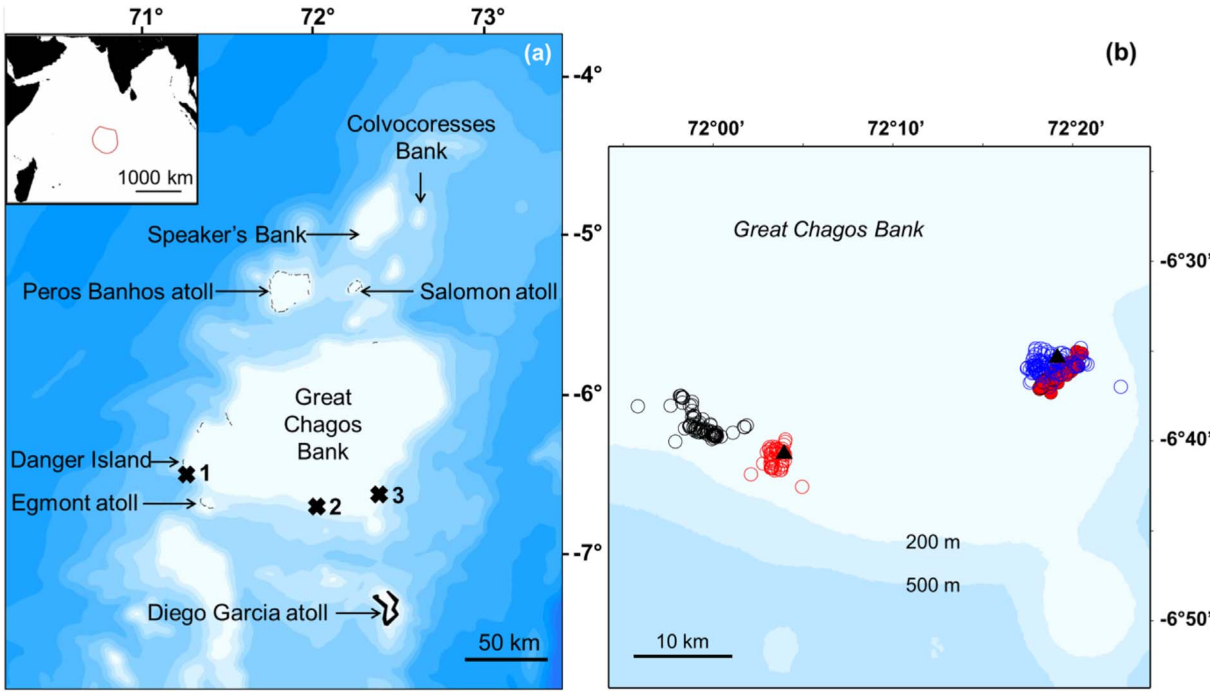

Fig. 1. (a) The seagrass study sites in the Chagos Archipelago in the Western Indian Ocean with the boundary of the British Indian Ocean Territory and Chagos marine protected area shown in red (inset). Bathymetry of the Chagos Archipelago is shown in 500 m contours (source: GEBCO) to highlight atoll locations. Seagrass surveys were carried out at three sites (distance of 128 km between sites 1 and 3) on the Great Chagos Bank (indicated by black crosses). (b) Daytime Fastloc GPS locations obtained from 4 green turtles satellite tracked from their nesting beaches on Diego Garcia to foraging grounds on the Great Chagos Bank. These turtle location data were used to select sites 2 and 3 for seagrass surveys. For clarity, different coloured circles (open red, solid red, open black, open blue) show a random sample of 100 Fastloc-GPS locations for each turtle. Open blue circles overlay many of the solid red circles indicating these two turtles used broadly the same foraging area. Black triangles show sites 2 and 3.

meadows dominated by *Halophila* species (Lee Long et al., 1993). Deep (to 70 m) coastal tropical Indo-Pacific seagrasses are also dominated by the *Halophila* species, particularly *H. stipulacea*, *H. decipiens* and *H. spinulosa* (Short et al., 2007). In East Africa, eastern Indonesia and the Torres Straits sub-tidal meadows dominated by *Thalassodendron ciliatum* are common from 0 to 15 m (Short et al., 2010). *T. ciliatum* is adapted to live in coarser substrates and is often the dominant species on these substrates in deeper waters, forming extensive mono-specific meadows (Den Hartog, 1970).

In attempting to understand the complex ecological interactions present within seagrass meadows globally, effort is largely focused around systems where stressors are present or where management actions have taken place to reverse degradation or loss (Waycott et al., 2009; Short et al., 2011), so that our understanding of seagrass ecosystems comes largely from regions of the world characterized by human impacts (Grech et al., 2012). Unfortunately, limited data exist from habitats defined as notionally pristine and, when examining the status of seagrass ecosystems, it is difficult to present them relative to a suitable baseline. This creates a scenario in which seagrass scientists as well as conservation managers and the general public are subject to the process of a shifting baseline. Data and case studies are required from locations that can be defined as pristine, particularly with respect to associated fauna.

The Chagos Archipelago that forms the British Indian Ocean Territory (BIOT) in the Western Indian Ocean is a potential example of a pristine seagrass ecosystem, lying at the heart of one of the world's largest marine protected areas (MPAs). The remoteness of the Chagos Archipelago, combined with very low levels of anthropogenic disturbance (the only inhabited island since 1970 is Diego Garcia) has resulted in some of the cleanest seas and healthiest reef systems in the world (Everaarts et al., 1999; Sheppard et al., 2012), and is of considerable importance to global biodiversity (Procter and Fleming, 1999).

Open water transparency in the Chagos Archipelago is close to maximum theoretical levels reflecting the nutrient-poor state of the central Indian Ocean. The sublittoral photic zone of the archipelago is as much as 60,000 km^2 (Dumbraveanu and Sheppard, 1999) and it is likely that large areas of this are suitable habitat for seagrass to exploit. As over 95% of the Chagos Archipelago remains unstudied, there remain opportunities to discover extensive new marine habitats (Sheppard et al., 2012). Existing knowledge of seagrass in Chagos is spatially and temporally restricted and associated data is limited (Willis and Gardiner, 1931; Drew, 1980; Sheppard, 1980; Spalding, 2005; JNCC, 2008).

The present study examines the seagrass status and abundance and diversity of associated fish assemblages on the Great Chagos Bank. This seagrass was first reported to exist anecdotally during a 2010 SCUBA based expedition (Sheppard et al., 2012). Subsequently we started to track green turtles (*Chelonia mydas*), known foragers on seagrass, from their nesting beaches on Diego Garcia to foraging sites on the Great Chagos Bank (Hays et al., 2014; Christiansen et al., 2017) which suggests seagrass may exist at multiple sites in the area. Here we report the first in-situ surveys of subtidal seagrass on the Great Chagos Bank and provide information on the importance of seagrass habitats to fish communities in the Chagos Archipelago.

2. Methods

2.1. Selecting sites for in situ seagrass surveys

In October 2012 and July 2015 we equipped 18 nesting green turtles on Diego Garcia (7.428°S, 72.458°E) with Fastloc-GPS Argos tags (SPLASH10-BF, Wildlife Computers, Seattle, Washington (n = 14) and model F4G 291A, Sirtrack, Havelock North, New Zealand (n = 4)). Turtles were located while they were nesting ashore at night and when returning to the sea they were restrained in a large open topped and bottomless wooden box and tags attached with quick setting epoxy (Pure-2 K, Powers Fastening Innovations and Pure 150-PRO, DeWalt) (see Esteban et al., 2017 for more details). We then tracked these turtles as they migrated to their foraging grounds at the end of the nesting season. Fastloc-GPS locations obtained from 4 or more satellites and with residual values of < 35 were examined (see Dujon et al., 2014 for a description of Fastloc-GPS accuracy). Many individuals travelled to very distant sites including the Seychelles and east coast of Africa (see for example Hays et al., 2014). Here we focus on the tracking data for individuals that travelled to the Great Chagos Bank ($n = 4$, mean = 8.6 ± 5.7 months). These tracking data were analysed to identify repeat locations visited during day time (between sunrise +2 h and sunset −2 h). Eight day-time locations used by green turtles were visited by one of us (NE) in March 2016 and benthic substrate noted from the surface. Depths were measured using the vessel echo sounder and validated using dive computers. The shallowest of these day-time locations (sites 2 and 3) were selected for a SCUBA survey. Additionally, one location at a further site (site 1) was surveyed at a shoal south of Danger Island (indicated by the westernmost cross in Fig. 1a) as this was previously reported as a seagrass habitat (Sheppard, pers. comm.). In total we surveyed seagrass at 9 locations across 3 sites.

SCUBA surveys (video transect and quadrat) of the sites 1–3 on the Great Chagos Bank took place in March 2016 (Table 1). Survey duration (40, 22 and 38 mins) and thus numbers of replicate transects and quadrats were affected by varying depths. Mono-BRUV (Baited Remote Underwater Video) surveys (2–3 BRUV replicates as 1 BRUV unit was lost at site 2) were conducted before SCUBA surveys to assess fish diversity and relative abundance at each site (Cappo et al., 2004).

2.2. Field-based in situ seagrass surveys

2.2.1. Seagrass species composition

Observers swam along 4–7 transects at each site (determined by bottom time limits), each 30 m long and 30 m apart (estimated using fin kicks), using a compass for direction (Table 1). The observer swam at a constant depth of 2 m above the seabed and took a video (Go Pro Hero 3) with the camera angled 45° forwards to allow seagrass species composition and cover to be assessed across the wider site (see Supplementary Video 1). Water clarity was estimated during transects simply by looking at the second diver at the other end of the 30 m transect. Seagrass cover was assessed visually as % cover based on ten random time frames within the video footage for each transect site. The video was paused at each of the ten random time frames selected then advanced to the nearest point on the transect where the bottom was visible. From this frame, an observer recorded an estimated percent cover of seagrass and species composition (following Seagrass-Watch subtidal percent cover standards, McKenzie et al., 2007). To standardise percent cover estimates a 0.25 m^2 quadrat, scaled to the video camera lens used in the field, was superimposed at the bottom centre of the screen.

2.2.2. Communities associated with seagrass habitats

To extend results from the seagrass species composition video analysis, quadrat assessments were conducted at intervals of at least 10 m apart (estimated using fin kicks), 5–9 quadrats (0.25 m^2) were placed to assess seagrass % cover, relative cover of broad benthic groups (seagrass, macro-algae, epiphytes, sand, coralline rubble), and species composition. Care was taken to search under the seagrass canopy for any additional species.

2.3. Fish abundance

Sampling used 2-3 mono Baited Remote Underwater Video systems (BRUVS) (see Table 1) deployed during full daylight hours (1030–1700 h) to prevent any concerns with respect to diel influences recorded on fish assemblages in seagrass meadows (Unsworth et al., 2007). The mono-BRUV systems were placed on natural seabed and deployed simultaneously (within 5 mins of each other) at least 100 m apart. A distance of 100 m between samples was considered to provide a minimum point of independence from each other (Ellis and DeMartini, 1995). The deployment duration for each drop (a sample) was 30 mins. All deployments were in water depths of between 13.0 and 27.3 m (Table 1). The BRUV systems were a modified version of the mono-BRUV system described in Cappo et al. (2004). The systems used Hero 3 GoPro video cameras mounted at a fixed position on a galvanised steel tripod frame with a 90 cm bait pole. Bait was comprised of tuna and grouper (Site 1) and squid (Site 2–3) causing a potential bias. Squid was not available at Site 1.

Video footage was assessed to determine the MaxN of each individual fish species in each video sample. MaxN is a metric commonly used for the quantification of the relative abundance of fish observed on underwater video (Cappo et al., 2004; Unsworth et al., 2014a). It counts the maximum number of fish recorded at any one time (single video frame) and therefore removes the concerns associated with potentially double counting individual fish (Priede et al., 1994). Due to the high abundance of predatory fish the shortest duration of bait availability (i.e., before the bait box was emptied) was 20 min. Results are therefore only presented for the first 20 min of each drop. One of the bait boxes at Site 1 was emptied during deployment and therefore the video image was not analysed. A small number of individuals could not be identified to species level and were grouped by Family.

All footage was analysed at Swansea University using the specialised SeaGIS software EventMeasure (Version 4) (www.seagis.com.au). This software allows for the footage to be labelled with fish species identifications leading to simple calculation of MaxN. In order to analyse the footage, the MaxN of each species was determined every frame throughout the 20 min of footage and an overall MaxN then calculated at the end of each 20 min. All summary data is presented as means ± standard deviation. One-way ANOVA tests were conducted to test for variance between sites after data were tested for normality using the Shapiro-Wilk test of normality.

Table 1
Characteristics of three study sites surveyed by SCUBA and Baited Remote Underwater Video (BRUV) on the 12,500 km^2 Great Chagos Bank. Maximum distances between sites were 128 km, site locations are indicated on Fig. 1(a). Surveys were conducted at each site with number of SCUBA surveys depending on depth.

Site name	Depth (m)	Date (2016)	Latitude longitude	Closest land km, bearing, name	Visibility (m)	Number of video transects (SCUBA) (n)	Number of quadrats (SCUBA) (n)	Number of BRUV frames (n)
1. Danger Island shoal								
	13.0	29Mar	−6.4583°S 71.2405°E	6.9 N Danger Island	> 30	5	9	2
2. Chagos Bank SE (W)								
	27.3	30Mar	−6.6786°S 72.0658°E	73.4 SSE Diego Garcia	> 30	4	5	2
3. Chagos Bank SE (E)								
	23.2	30Mar	−6.5895°S 72.3191°E	75.0 S Diego Garcia	> 30	7	5	2

All survey work in the Chagos Archipelago was approved by the British Indian Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office.

3. Results

We conducted seagrass surveys at 9 locations in 3 distinct sites spread across a distance of 130 km of the Great Chagos Bank.

3.1. Green turtle satellite tracking

Four green turtles were tracked to the Great Chagos Bank, where transmitters continued to provide Fastloc-GPS locations for many months. For these four turtles the length of tracking on the foraging grounds, and in brackets the number of Fastloc-GPS locations, were 265 d (814), 232 d (703), 105 d (301) and 279 d (1582). These tracking data were analysed to identify repeat locations visited during daytime. Eight day-time locations used by green turtles at sites 2 and 3 (Table 1) were visited by one of us (NE) in March 2016 and benthic substrate noted from the surface. To make sure that the locations corresponded to actual daytime and nighttime hours, we only included positions recorded outside of 2 h of sunrise and sunset. Daytime locations and the location of sites 2 and 3 are shown in Fig. 1b.

3.2. Seagrass surveys

Surveys of the 9 locations spread across 3 sites (Fig. 1) indicated the presence of healthy monospecific seagrass meadows of *Thalassodendron ciliatum*. Seagrass *T. ciliatum* was observed at all the locations surveyed, growing at a range of depths: 12–13 m on a shoal south of Danger Island (site 1) and 23–29 m at eight locations identified as green turtle foraging grounds (mean = 26.08 m, SD = 1.99).

Seagrass composition was 100% *Thalassodendron ciliatum* at all sites. Based on SCUBA video transects the mean seagrass percent cover at the 3 sites was 74% (site 1, mean cover = 67%; site 2 mean cover = 67%; site 3, mean cover = 88%) (Fig. 2(a)).

Analysis of SCUBA quadrat survey data supports the SCUBA transect estimates of seagrass cover with mean percent cover recorded of 71% (90% (SD = 13.23) at site 1, 60% (SD = 12.25) at site 2 and 63% (SD = 10.95) at site 3). The shallower Danger Island shoal (site 1) had a higher percent cover of seagrass (mean = 90%) than the deeper South East GCB sites (sites 2 and 3; 60% and 63%). An ANOVA comparing SCUBA quadrat seagrass cover revealed that sites are significantly different ($p < 0.001$). All substrata were coralline rubble. Percent cover of macroalgae was typically very low (< 6%) and epiphyte cover was low (< 5%). Shoot length and canopy height varied across all sites: mean shoot length was 9.1 cm (mean range 8.5–10.2 cm, SD = 0.92, $n = 57$) and mean canopy height (vertical rhizomes + shoot length) was 33.47 cm (32.0–34.7, SD = 1.34, $n = 57$) (Fig. 2d). An ANOVA comparing shoot length and canopy height across sites revealed that sites are significantly different ($p < 0.001$ for both metrics).

3.3. Fish abundance estimation

High fish abundance was recorded at all sites and we observed a maximum number of 351 individuals (MaxN), representing 25 different species from 10 families (Table 2, Fig. 2e–f). The mean species richness of fish was 11 species per site (mean range 8–14 species across the 3 sites, $n = 5$). The most numerically abundant species was the African whitespotted rabbitfish (*Siganus sutor*) observed only at site 3 (mean MaxN.drop^{-1} = 114, $n = 2$) followed by the red snapper (*Lutjanus argentimaculatus*) observed on 60% of surveys. The most frequently occurring species was the smalltooth emperor (*Lethrinus microdon,* mean MaxN.drop^{-1} at 3 sites = 6.0, SD = 5.0, $n = 5$) and the longbarbel goatfish (*Parupeneus macronemus,* mean MaxN.drop^{-1} at 3 sites = 3.0, SD = 1.6, $n = 3$). Both were observed in 100% of surveys and sites. High relative fish abundance was recorded across the 3 sites (Table 2, e.g. Red Snapper, *Lutjanus argentimaculatus:* mean MaxN.drop^{-1} = 3.7, SD = 3.9, n = 5). Four species observed have not been previously recorded in the Chagos Archipelago (Table 2). Large predatory grey reef shark (*Carcharhinus amblyrhynchos*) were observed in all surveys (MaxN ≥ 2 in 80% of surveys, mean MaxN.site^{-1} = 1.6, SD = 0.8) (Table 2; see Supplementary Video 2). An ANOVA comparing mean relative fish abundance (MaxN.drop^{-1}) across sites showed that sites are not significantly different ($F_{2,75}$, = 1.12, $p = 0.33$).

4. Discussion

Our study is the most extensive attempt to date to document seagrass meadows on the Great Chagos Bank, the world's largest contiguous undamaged reef area (12,642 km^2) (Sheppard et al., 2012). Extensive seagrass meadows have rarely been previously reported elsewhere in the Chagos Archipelago (Spalding, 2005; Drew, 1980; Den Hartog, 1970). Willis and Gardiner (1931) reported a few plants at Peros Banhos at a depth of 0.5 m; Drew (1980) reported extensive patches at 2 m and low water levels in the lagoon in Diego Garcia, extensive sublittoral patches at Colvoccoresses Bank and Speakers Bank and small patches in the Salomon Islands; and Spalding (2005) reported extensive patches at depths to 20 m in Speakers Bank. So our observation that *T. ciliatum* can form such extensive and dense deep-water meadows is noteworthy. Our seagrass measurements (low algal cover, leaf blade length in the typical range recorded for *T. ciliatum* (Sartoni, 1995); high seagrass cover) together with an abundant fish community dominated by large predators and containing key herbivores indicate a healthy and resilient seagrass ecosystem (Unsworth et al., 2014b). Unlike the deep-water monospecific meadow of *T. ciliatum* growing on a hard substrate of coralline rubble reported in our study, seagrass records in the Tropical Indo-Pacific bioregion report deep-water seagrass habitat dominated by *Halophila* (Short et al., 2007; Rasheed et al., 2008). These deep Halophila communities tend to occur on soft bottoms and so are fundamentally different in structure to the *T. ciliatum* seagrass meadows we observed.

This is the first documented study, to our knowledge, to record density, canopy height and shoot length of deep-sea *T. ciliatum*. These variables are important bio-indicators of the environmental health of a seagrass meadow (Jones and Unsworth, 2016). Shoot density and above-ground biomass of a seagrass meadow are recognized as key bio-indicators of light availability (McMahon et al., 2013). The values for bio-indicators (seagrass density, canopy height and shoot length) varied significantly at the 3 sites across the Great Chagos Bank. This variability may be indicative of changes in light availability (perhaps due to 14 m depth range of study sites) and broad environmental drivers (e.g., nutrient and water quality (Hemminga and Duarte, 2000)) across the surveyed area of 130 km of this 12,500 km^2 coral atoll. Excessive growth of epiphytic algae contributes to seagrass degradation by smothering and decreasing light absorption (Lavery and Vanderklift, 2002). We report very low occurrence of epiphytic algae on seagrass meadows which further indicates the healthy status of the *T. ciliatum* on the Great Chagos Bank.

It is well known that coral reef fish biomass estimates for Chagos (Graham et al., 2010) far exceed values from both fished and protected reefs elsewhere in the Western Indian region, such as Kenya, Seychelles, Madagascar and the Maldives (McClanahan et al., 2009; Graham et al., 2010; McClanahan, 2011). Yet the relative importance of seagrass meadows at Chagos as fish habitats is far less well characterized. Data on seagrass fish assemblages in the Indo-Pacific is mostly limited to a few centres of research and the majority of this relates to nearshore and very shallow seagrass communities (Unsworth et al., 2015). There are very limited data on nearshore subtidal seagrass and next to no data on fish species, abundance and biomass of fish in deep-water seagrass meadows. Our study provides the first assessment of fish assemblage in seagrass meadows in the largely unexploited Chagos Archipelago and

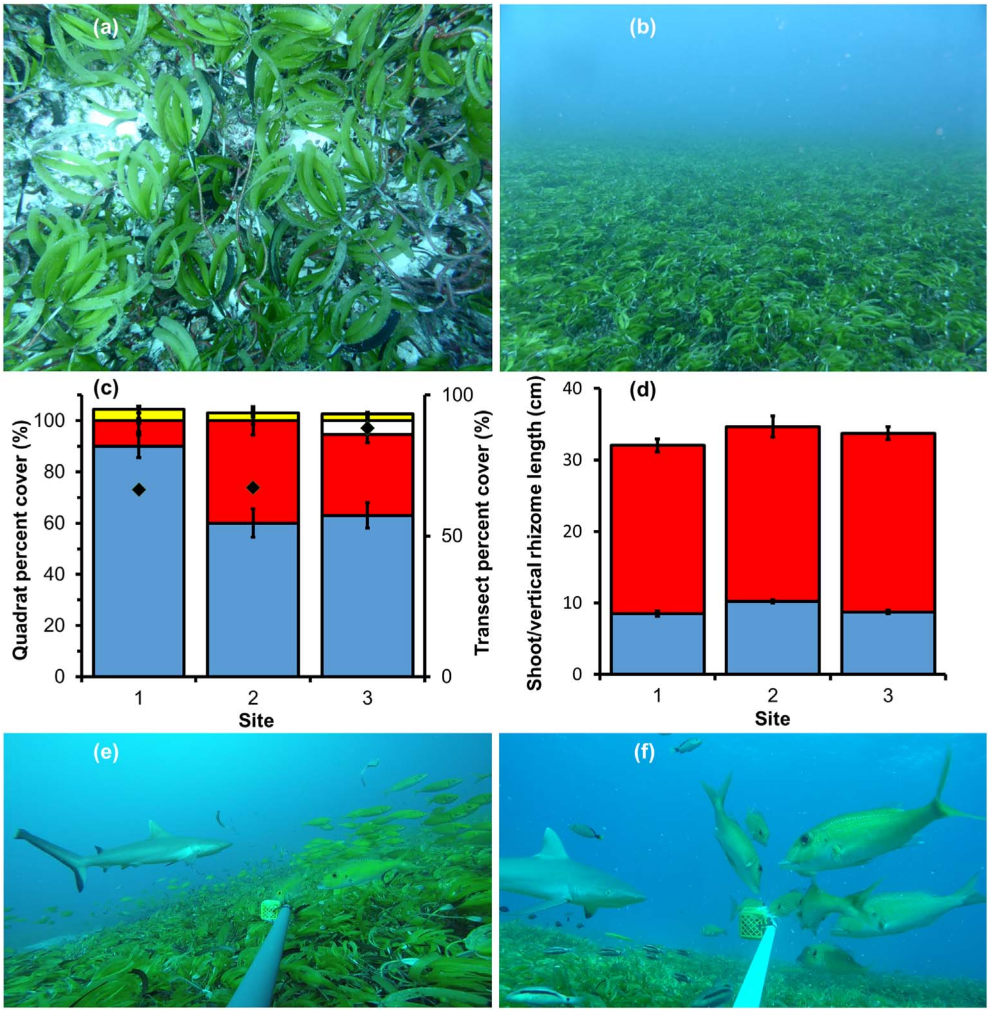

Fig. 2. Relative abundance of benthic habitat and indicators of seagrass status at three sites on the Great Chagos Bank. (a and b) SCUBA quadrat and video transect frame shows dense cover by seagrass *Thalassodendron ciliatum*. (c) Benthic habitat categories are presented as mean percent cover from all quadrats at each site. Benthos is composed of seagrass (blue), coralline rubble (red), macro-algae (white) and epiphyte cover on seagrass (yellow). The first three categories amount to 100% cover. The diamonds represent the mean percent cover of seagrass in video transects (secondary y axis). (d) Seagrass habitat provides a canopy height of at least 30 cm. Mean shoot length (blue) and mean vertical rhizome length (red) of monospecific seagrass meadow of *Thalassodendron ciliatum*. Error bars indicate standard error. (e–f) Mixed-species assemblages of Lethrinidae, Lutjanidae and Mullidae with predatory Grey Reef Shark in background (BRUVS screen shots at Sites 1 and 2).

Table 2
Relative abundance of fish observed in seagrass meadows on the Great Chagos Bank. Fish observed in baited remote underwater video surveys at 3 sites on the Great Chagos Bank (site 1, $n = 1$; site 2, $n = 2$, site 3, $n = 3$). MaxN is an estimator of fish abundance generated using the single highest count of a given fish species observed at a single point in a video recording. Occurrence is the percentage of surveys in which a given fish species was observed. Known range sources: IUCN, 2016; Froese and Pauly, 2017, Spalding, 2005.

Family	Species	Known range	MaxN (all sites)	Mean MaxN (SD)	Occurrence (% sites)
Balistidae		n/a	1	0.3 (0.5)	20
Carangidae	*Carangoides plagiotaenia*	Yes	2	0.3 (0.5)	20
Carcharhinidae	*Carcharhinus amblyrhynchos*	Yes	2	1.5 (0.4)	100
Labridae	*Halichoeres* sp.	n/a	1	0.3 (0.5)	20
	Cheilio inermis	Yes	1	0.3 (0.5)	20
Lethrinidae	*Lethrinus* sp.	n/a	1	0.2 (0.2)	20
	Lethrinus lentjan	Yes	2	0.8 (0.6)	60
	Lethrinus microdon	Yes	13	6.0 (5.0)	100
	Lethrinus obsoletus	Yes	2	0.7 (0.9)	20
	Lethrinus ornatus	No	2	0.3 (0.5)	20
	Lethrinus rubrioperculatus	Yes	6	1.0 (1.4)	20
	Lethrinus variegatus	Yes	1	0.2 (0.2)	20
Lutjanidae	*Lutjanus argentimaculatus*	No	10	3.7 (3.9)	60
	Lutjanus lemniscatus	No	1	0.2 (0.2)	20
	Lutjanus lutjanus	No	1	0.2 (0.2)	20
	Macolor macularis	Yes	1	0.3 (0.5)	20
	Aprion virescens	Yes	2	0.8 (0.6)	60
Mullidae	*Parupeneus cyclostomus*	Yes	3	1.0 (1.4)	20
	Parupeneus indicus	Yes	2	0.7 (0.9)	20
	Parupeneus macronemus	Yes	6	3.0 (1.6)	100
	Parupeneus pleurostigma	Yes	1	0.3 (0.5)	20
Nemipteridae	*Scolopsis* sp.	n/a	6	1.8 (1.3)	60
Scaridae	*Hipposcarid harid*	Yes	1	0.3 (0.5)	20
	Chlorurus capistratoides	Yes	1	0.3 (0.2)	40
	Scarus sp.	n/a	3	1.3 (1.2)	60
Siganidae	*Siganus sutor*	Yes	165	38.0 (53.7)	40

indicates the importance of seagrass habitat for juvenile fish, for example dusky rabbitfish (*Siganus fuscescens),* as well as for the predatory grey reef shark (*Carcharhinus amblyrhynchos*). Whilst most of the fish are known to occur in the Western Indian Ocean, a number of the species are documented in this region for the first time, such as spotfin wrasse (*Coris dorsomacula*) and ornate emperor (*Lethrinus ornatus*). Previous records are limited to species lists or semi-quantitative abundance estimates at sample sites, for example the wrasse (*Coris caudimacula*) and parrotfish (*Calotomus carolinus*) were observed over *T. ciliatum* in Speakers Bank (Spalding, 2005). Fish species recorded in seagrass meadows in another Chagos atoll (Diego Garcia) have not been reported elsewhere in the archipelago (JNCC, 2008).

The presence of grey reef sharks at every survey site provides an indication of the pristine nature of the seagrass ecosystem and it is likely sharks are fully protected by the size of the Chagos MPA (White et al., 2017). Due to the isolation, limited anthropogenic impacts and full protection of the Chagos MPA, it is likely that the fish biomass found in the *T. ciliatum* seagrass meadows on the Great Chagos Bank is at near-pristine levels and may serve as a reference baseline for both future studies in the Chagos archipelago as well as elsewhere. Clearly our sample sizes for seagrass sampling were limited, but we have shown how the location of foraging green turtles may be used effectively to direct future in situ surveys of other shallow and deep water habitats.

Seagrass research activities have unsurprisingly been focused on shallow, coastal and estuarine seagrass ecosystems (York et al., 2015). In an era of global climate change and reports of decline of seagrass (Waycott et al., 2009), the discovery of extensive deep-water seagrass meadows of *T. ciliatum* on the Great Chagos Bank provides an example of optimism that vast areas of seagrass meadows remain unknown and will assist in providing resilience to future climate change and sea level rise. Various estimates of the extent of mapped seagrass around the world currently exist (e.g., 177,000 km^2 (Waycott et al., 2009)), but a series of authors have speculated that the global extent may actually exceed 600,000 km^2 (Duarte et al., 2010). The evidence presented here suggests that there may still be large areas of extensive seagrass around the world that remain unknown, indicating that these speculative figures may have some basis.

Seagrass productivity is usually limited by nutrient availability, yet the characteristics of *T. ciliatum* on the Great Chagos Bank (> 70 km from nearest population) suggest that this may be an example of an extensive and healthy seagrass meadow in a nutrient-poor environment. Seagrasses require low levels of nitrogen and phosphates compared with other aquatic primary producers (e.g., macro algae) and can often flourish in nutrient-poor environments (Duarte, 1995; Brodersen et al., 2017). There was very low presence of sand on the Great Chagos Bank consistent with the observation that *T. ciliatum* is one of the few species that colonises rocky substrate (Short et al., 2010). It is also possible that the seagrass meadows on the Great Chagos Bank extend much deeper than the maximum survey depth of 29 m. Previous records for *T. ciliatum* extend to depths of 33 m in Seychelles (Short et al., 2010) and theoretical calculations allow for seagrass growth to depths of 90 m (Duarte, 1991).

The discovery of extensive seagrass meadows on the Great Chagos Bank was realized through the first satellite tracking studies of green turtles breeding in the Chagos Archipelago (Hays et al., 2014). Tracking of grazing marine megafauna may play a useful role to identify other seagrass habitats (Hays et al., 2018). We acknowledge the preliminary nature of our sampling and given that there are extensive relatively shallow banks, such as Speaker's Bank and Colvocoresses Bank, throughout the Chagos Archipelago, we might expect further extensive seagrass meadows will be identified in the coming years. Clearly a greater number of seagrass sampling sites on the Great Chagos Bank will help reveal the full extent of seagrass meadows in this area. Furthermore ground biomass assessments will be useful and will help to reveal the ecosystem roles of these seagrass meadows. Encouragingly the creation of the no-take Chagos Archipelago MPA helps assure long-term protection of this extensive seagrass habitat.

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Author contributions

N.E., R.K.F.U. and G.C.H. conceived the study. N.E. carried out field surveys in Chagos in 2016. J.G. analysed fish abundance using BRUV survey data with support from R.K.F.U. N.E. analysed all other data. N.E. and GCH wrote the manuscript with contributions from all authors.

Competing interests

The authors declare no conflict of interest.

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