Article

Estimates of sea turtle nesting populations in the southwestern Indian Ocean indicate the importance of Chagos Archipelago

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Abstract Global sea turtle population assessments have highlighted the significance of the southwestern Indian Ocean (SWIO) region, despite data gaps for five islanded atolls (~67 islands; 235 km oceanic coastline) of Chagos Archipelago. Chagos hosts nesting hawksbill *(Eretmochelys imbricata)* and green turtles *(Chelonia mydas)*, heavily exploited for nearly two centuries until protection in 1968-1970. Available nesting habitat and spatial distribution of nesting activity were assessed during rapid-surveys of 90% of the Chagos coastline in 1996, 1999, 2006 and 2016. An estimated 56% (132 km) of coastline provide suitable nesting habitat. Diego Garcia and Peros Banhos atolls account for 90.4% of hawksbill and 70.4% of green turtle nesting. Seasonality and mean annual egg clutch production were quantified from monthly track counts (143 surveys in 76 months between 2006-2018) along a 2.8 km Index Beach on Diego Garcia island also rapid-surveyed in 1996, 1999 and 2006. Hawksbills showed a distinct nesting peak during October-February, while green turtles nested year-round with elevated activity June-October. Estimates of 6300 hawksbill and 20,500 green turtle clutches laid annually in Chagos during 2011-2018 indicate important increases in nesting by both species since 1970, with a higher rate of increase amongst green turtles. Regional estimates indicate green turtles produce ten times more egg clutches than hawksbills, and Chagos accounts for 39-51% of hawksbill and 14-20% of green turtle clutches laid in SWIO. This improved status may reflect >40 years without significant exploitation. Long-term monitoring is needed to capture inter-annual variation in nesting numbers and minimize uncertainty in population estimates.

Keywords Conservation policy, endangered species, global assessments, IUCN Red List, nesting seasonality, Regional Management Unit

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Introduction

To assess conservation status of a species, key biological questions focus on population status, trends and spatio-temporal variability (Sutherland et al., 2013b), knowledge of extinction risk or species loss (Sutherland et al., 2013a), as well as how disturbances are altering species distribution and abundance (Parsons et al., 2014). In order to provide an overarching view of the conservation status of species, the International Union for Conservation of Nature (IUCN) Red List of Threatened species often relies on individual groups to provide systematically collated metrics on population sizes and trends in abundance over time (Barnes et al., 2015). Aspects of the ecology and habitat of a species may make such data hard to collect (González-Suárez et al., 2012).

Population size is usually determined with methods that include direct sampling (e.g. mark and recapture through tagging) and indirect sampling (e.g. track or clutch observations); but such data may be unavailable for species occurring in remote or inaccessible habitats (e.g., trans-boundary migrating birds (Bishop et al., 2015) or trans-equatorial migrating basking sharks (Skomal et al., 2009)). Direct observation of marine species is difficult if they are submerged most of the time, range widely or occur at low densities. For some groups, however, aspects of their life-history provide windows of opportunity to assess their status. Species of seabirds and seals may come ashore and congregate to breed, enabling collection of extended time-series of abundance data (Paleczny et al., 2015; Trillmich et al., 2016; Collins et al., 2016). Sea turtles are another group for which population status is often assessed using annual numbers of nesting females or egg clutch production as an indicator (Balazs & Chaloupka, 2004; SWOT 12, 2017).

In this manner, global and regional populations of all species of sea turtles have been assessed during the last 20 years. IUCN currently lists green turtles, *Chelonia mydas*, as Endangered based on global population declines of 37-61% over the previous three turtle generations (Seminoff, 2004), and hawksbill turtles, *Eretmochelys imbricata*, as Critically Endangered based on a decline of >80% using the same criteria (Mortimer & Donnelly, 2008). Fortunately, sea turtle populations respond well to extended periods (decades) of protection at the nesting beach, and population recovery has been documented at multiple sites for green turtles and hawksbills (Mazaris et al., 2017). On a global scale, the southwestern Indian Ocean (SWIO) which includes Chagos Archipelago, hosts some of the most important national populations of hawksbills (Mortimer & Donnelly, 2008) and green turtles (Seminoff, 2004). Genetic studies of both nesting and foraging hawksbills (Mortimer & Broderick, 1999; Vargas et al., 2016) and nesting green turtles (Bourjea et al., 2015) demonstrate linkages between Chagos and those elsewhere in the SWIO, especially Seychelles.

After almost two centuries of permanent human settlement and associated exploitation and trade in green turtle meat, hawksbill shell, turtle oil and eggs (Mortimer, 2009; Wenban-Smith & Carter, 2016) the Chagos islands have been uninhabited since 1973 (except Diego Garcia, site of a joint UK/USA military base). In 2010, one of the world's largest (640,000 km^2) permanent no-take Marine Protected Areas (MPAs) was created within British Indian Ocean Territory (BIOT) (Koldewey et al., 2010). This presents an opportunity to track the status of remnant sea turtle populations no longer exploited. In 1970, Frazier visited a few of the islands, interviewed the human inhabitants, and concluded only a few hundred hawksbill and green turtles remained (<1000 clutches laid annually by each species) (Frazier, 1975). In 1996, the first systematic, territory-wide snapshot survey of turtle nesting in Chagos was conducted (49 islands over six-weeks) (Mortimer & Day, 1999), estimating 300-700 nesting hawksbills (1200-2800 clutches) annually and 400-800 green turtles (2200-4400 clutches) by using seasonality data from Seychelles (Mortimer & Bresson, 1999; Mortimer 1988) to extrapolate from the 1996 rapid-survey data. Long-term monitoring was recommended to define critical habitats, nesting seasonality and long-term population trends.

The present study examines patterns of spatial and seasonal distribution, and abundance of hawksbill and green turtle nesting activity at Chagos Archipelago during 1996-2018, as evidenced by: a) body pit counts conducted during rapid-surveys of 90% of the islands and 90% of the coastlines (at least once) in 1996, 1999, 2006, and 2016 combined to assess spatial use of nesting habitat; and b) long-term monthly monitoring of a 2.8 km Index Beach on Diego Garcia island to define patterns of seasonality and annual egg clutch production. We then compare our estimates of annual egg clutch production in Chagos to those reported for sites elsewhere in the region. Recently updated estimates of turtle nesting activity in the SWIO are summarized in the SWOT 12 report (2017) but do not include information about Chagos Archipelago.

Study area

The Chagos Archipelago comprises some 67 islands and 235 km of oceanic coastline distributed across five atolls (Fig. 1, Supplementary Fig. S1) (Mortimer & Day, 1999). These include four sets of outer-islands (Table 1): Peros Banhos (PB) atoll (36 islands, 80.7 km of coastline), Salomon (Sa) atoll (11 islands, 26.3 km), Great Chagos Bank (GCB) (8 islands, 32.9 km), and Egmont (Eg) atoll (5-8 dynamic sand cay islands, ~22.8 km). The main atoll, Diego Garcia (DG) comprises 4 islands with 72.1 km of coastline (96% on DG island).

The spatial boundaries of the Southwest Indian Ocean (SWIO) regional management units (RMUs) for both *C. mydas* and *E. imbricata* were defined by the IUCN Marine Turtle Specialist

Group (MTSG) (Wallace et al., 2010) based on genetic linkages and documented migratory patterns. They include the territorial waters of mainland countries from southern Somalia to South Africa plus the islands of Comoros, Madagascar, Mauritius, Mayotte, Réunion and its scattered islands, Seychelles, and Chagos Archipelago.

Methods

Data Collection

Habitat assessment. During rapid-surveys of the five islanded atolls in 1996, 1999 and 2006, all stretches of surveyed coastline were scored in terms of suitability for nesting based on accessibility of adequate beach sand platform to turtles. Four features of the shoreline were each rated on a scale of 1 to 4, with 1-2 considered accessible, and 3-4 inaccessible: offshore approach; foreshore; high tide line (erosion cliff and associated barriers); and beach platform (see Supplementary Table S1 for detailed criteria). Where any of the four features were scored as 3 or 4, a turtle was unlikely to either successfully emerge onto the beach or to lay eggs. The amount of "suitable" (i.e., accessible) oceanic coastline was calculated for each island surveyed, including Diego Garcia (Tables 1-2, Fig. 1).

Rapid-Surveys to Determine Spatial Distribution of Nesting Activity Amongst Atolls. Four sets of rapid-surveys were conducted: in 1996, 1999, 2006 and 2016. In February and March of 1996 and 2006 rapid-surveys across the entire archipelago over six-week (10 February to 18 March) and seven-week-long (4 February to 23 March) periods, respectively, were conducted, and in 1999 along the oceanic coastline of DG atoll (27 January to 21 February). Data were collected by walking along the perimeter of each island high on the beach platform and recording the locations and characteristics of all turtle 'tracks' and 'body pits.' A 'track' is defined as the imprint a turtle makes when she crawls on the sand, and a 'body pit' is the large bowl-shaped depression a turtle leaves when she digs a nest (Mortimer & Day, 1999). Tracks can easily be erased during periods of high tide, but body pits, usually dug above the high tide line, can remain visible for weeks and provide a reliable indicator of spatial habitat use, especially when nesting is sparse. All rapid-surveys were conducted outside peak nesting season.

In 1996, 49 islands and 109.2 km of coastline were surveyed (including 60% of the oceanic coastline of the outer-islands); and in 2006, 45 islands and 121.7 km of coastline (including 73% of the outer-island total). See Supplementary Table S2. A sub-sample of the coastline (comprising 34 islands and 80.0 km) was surveyed in both 1996 and 2006 (Mortimer, 2007). In 1999, all 72.1 km of the DG atoll oceanic coastline were surveyed (Mortimer, 2000). During the three rapid-surveys conducted in 1996, 1999, and 2006, 211.8 km (90% of the Chagos oceanic coastline) were surveyed at least once, and >80 km repeatedly. During 21 March to 14 April 2016, 39 islands (105 km) were surveyed by foot and helicopter.

Monthly DG track surveys to assess annual egg clutch production and nesting seasonality. Along the southeast coast of Diego Garcia island, a 2.8 km-long Index Beach (DG-Index) was selected (between S7.41402 E72.45382 and S7.39865 E72.47282) hosting some of the highest densities of nesting activity identified during the 1999 rapid-survey of DG (Mortimer, 2000). Located partially within the Diego Garcia Ramsar Site and adjacent to a paved road, it is easily accessible to survey personnel. Monthly track surveys conducted by Environmental personnel of US Navy Support Facility and US and UK base personnel volunteers were scheduled at two-week intervals towards the end of neap tides when tracks were least likely to be washed away by high tides. Surveys were conducted during the following periods: March 2006 to April 2007 (14 months); April 2011 to May 2013 (26 months); November 2014 to March 2018 (41 months). Survey frequencies per month were the following: 10 months with 3-4 surveys (12.3%); 45 with 2 (55.6%); 21 with 1 (25.9%); and 5 missed months (6.2%). During each survey, all tracks were counted, and their widths measured to confirm the species of turtle: hawksbill tracks typically <95 cm, and green turtles >100 cm wide (Pritchard & Mortimer, 1999), a system used successfully throughout Seychelles since 1997 (Mortimer et al. 2011a). To estimate longevity of turtle tracks on DG-Index, fresh tracks of both species were marked and monitored during 27 November - 9 December 2018.

Data Analysis

Habitat assessment. Using the habitat accessibility data collected during the rapid-surveys of 1996, 1999 and 2006, the amount of available ‘suitable’ habitat for nesting turtles was calculated for each island surveyed, and a mean percent estimate of suitable habitat was calculated for each atoll (Table 1). For atolls where survey coverage was not 100% (i.e. PB and Eg) mean figures for each atoll were used to estimate suitable habitat along the 9% (21 km) of oceanic coastline not surveyed.

Spatial distribution of nesting activity amongst atolls. Indices of nesting density were calculated for each species, by averaging numbers of body pits per km of suitable coastline surveyed at each of the four outer-island atolls (PB, Sal, GCB, Eg), during the 1996 and 2006 surveys which took place on approximately the same dates in both seasons (Table 1). For each atoll, the mean of the 1996 and 2006 indices were then calculated and multiplied by estimated total kms of suitable habitat to produce indices of relative levels of nesting activity (Table 1).

For Diego Garcia atoll, the 1996 and 2006 surveys alone were not adequate to estimate mean total body pits as only 16% and 4%, respectively, of the 72.1 km coastline were surveyed. In 1999, however, the entire DG oceanic coastline was surveyed; and in both 1996 and 2006 the 2.8 km coastline that became DG-Index was surveyed. Assuming relatively constant spatial distribution of nesting activity from year to year, we used 1999 data to extrapolate total body pits at DG atoll in 1996 and 2006 based on body pit counts recorded at DG-Index. Using indices of body pit numbers at all five atolls (Table 1), the percent contribution of each atoll to total nesting activity at Chagos was calculated (Table 1).

Annual egg clutch production and nesting seasonality. Data from monthly track surveys at DG-Index were used to estimate total nesting emergences and egg clutches each month and describe seasonality of nesting activity. For each species, each month, a mean figure was calculated from all track counts that month. For five unsurveyed months we averaged data from the months before and after. Estimated total numbers of nesting emergences (i.e., turtle tracks) were extrapolated for each month using estimates of track longevity calculated in November/December 2018: for hawksbills 2.8 days (mean=2.79; SE=0.2621; range=1-7; n=45) and for green turtles 3.9 days (mean=3.94; SE=0.4950; range=1-9; n=23). To calculate numbers of egg clutches laid each month at DG-Index, we then assumed 55% of total turtle tracks resulted in egg laying, based on data from similar habitats in Seychelles (Mortimer & Bresson, 1999; Mortimer et al. 2011a). Estimated egg clutches laid annually by hawksbills and green turtles at DG-Index were then calculated for each of the following six 12-month (April to March) periods: 2006-2007, 2011-2012, 2012-2013, 2015-2016, 2016-2017, 2017-2018. These were graphed over time along with an estimate of egg clutches laid annually at DG-Index in 1995-1996 based on the mid-points of the bracketed estimates derived in 1996 by Mortimer & Day (1999) and the assumption of consistent spatial distribution of nesting activity over time. Regressions were calculated to provide indications of population trends during 1995-1996 to 2017-2018. As a further indication of population trends, we compared body pit counts at the same time of year in both 1996 and 2006, along an 80 km section of coastline.

We averaged annual egg clutch production recorded at DG-Index during five recent seasons between 2011-2012 and 2017-2018 and extrapolated that mean to the entire DG atoll using 1999 data that indicate 8.6% of hawksbill and 8.5% of green turtle nesting activity occurred at DG-Index (Table 2). Estimated egg clutch production at the other four atolls was then extrapolated from calculations of spatial distribution of body pits (Table 1).

To define seasonality and illustrate intra-annual patterns, the track counts calculated for each month at DG-Index were graphed linearly over each of the six 12-month (April to March) periods along with a graph of the mean of all six seasons combined.

We assessed relative contribution of Chagos egg clutch production to the SWIO region based on information available in the literature including SWOT 12 (2017). We produced a map of SWIO indicating estimated annual egg clutch production at each of the study sites included in the SWIO review. Exclusive Economic Zone (EEZ) boundary, country border and coastline data (Claus et al., 2018) were downloaded and projected on ArcMap version 10.5.1. We grouped the annual clutch data at each site in bins and presented data graphically. Country sources include: for Seychelles (Mortimer, 1998; Mortimer, 2004; Allen et al., 2010; Mortimer et al., 2011a; Mortimer et al., 2011b; Burt et al., 2015; Mortimer, 2017; Alphonse Foundation, Bird Is Lodge, Constance Lémuria Resort, Denis Is Private, Desroches Foundation, Farquhar Foundation, Fregate Is Private, Global Vision International Seychelles, Green Island Foundation, Island Conservation Society, JA Mortimer, Marine Conservation Society Seychelles, North Island, Seychelles Ministry of Environment, Seychelles Islands Foundation, Seychelles National Parks Authority, Silhouette Foundation, & WiseOceans, unpublished data); for Mauritius (Chapman & Swinnerton, 1996; Mangar & Chapman, 1996); for the French Territories (Legall et al., 1986; Legall et al., 1988; Ciccione & Bourjea, 2006; Bourjea et al., 2007; Lauret-Stepler et al. 2007; Ciccione & Bourjea, 2010; Lauret-Stepler et al., 2010; Dalleau et al., 2012; Derville et al., 2015; Jean et al., 2017; Quillard & Ballorain, 2017); for Madagascar (Rakotonirina & Cooke, 1994; Mortimer, 2002; Mortimer & Donnelly, 2008; Bourjea et al., 2006; UNEP-WCMC cited in SWOT 12, 2017); for Comoros (Frazier, 1985; Bourjea et al., 2015); for Somalia (Mortimer, 2002; Mortimer & Donnelly, 2008); for Kenya (Okemwa et al., 2004); for Tanzania (Dunbar, 2011; Joynson Hicks & West, 2017); and for Mozambique (Garnier et al., 2012; Fernandes et al., 2016). For complete literature citations see Supplementary Table S4.

All work was approved by Swansea University Ethics Committee and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office.

Results

Available habitat and spatial distribution of nesting activity. Suitable turtle nesting habitat occurs along 132 km (58%) of 235 km of oceanic coastline, ranging from 51% to 76% per atoll (Table 1). For hawksbills, percent of total nesting activity recorded at each of the five atolls was DG, 48.8%, PB, 41.6%, Eg, 5%, Sa, 2.5%, and GCB, 2%; and for green turtles, PB, 38.8%, DG, 31.6%, GCB, 16.1%, Eg, 10.2%, and Sa, 3.4% (Table 1). Percent of total hawksbill and green turtle nesting activity relative to available habitat at each atoll, shown in Fig. 2, indicates DG and PB are the most important atolls in all respects. The 1999 rapid-survey results show that at DG (Fig. 1c), along the western perimeter (29.1 km), nesting activity was low with only 8.5% (Ei) and 7.8% (Cm) of total DG nesting, compared to 89.2% (Ei) and 88.2% (Cm) along the eastern perimeter (31.7 km) (Table 2). No significant nesting was recorded inside the DG lagoon; and little, 1.3% (Ei) and 3.9% (Cm), at the three small islands.

Annual egg clutch production and population trends. We estimate mean annual egg clutch production in Chagos for the period from 2011-2012 to 2017-2018 at 6308 for hawksbills and 20,487 for green turtles, distributed amongst the five atolls as in Table 1. Estimated nesting activity at DG-Index between 1995-1996 and 2017-2018 shows marked inter-annual variation but also changes over time (Fig. 3). For green turtles there was a marked, and highly significant, increase in the number of green turtle clutches, with an order of magnitude increase (100 to 1000) in the number of clutches per season over the 23-year time-series. This increase was best described by a logarithmic function ($F_{1,5}$=37.2, p <0.01, r^2=0.88). Hawksbill turtles showed an increase, albeit not significant, in numbers of clutches from start to end of the time-series, (e.g. for a linear trend $F_{1,5}$ = 0.70, r^2=0.12, p >>0.05). Another indication of population trends is comparison of body pit counts along the 80 km of coastline rapid-surveyed in both 1996 and 2006 which suggest an increase of 23% for hawksbills (1996, 91 pits; 2006, 112 pits), and 147% for green turtles (1996, 167 pits; 2006, 413 pits) (Mortimer, 2007).

Seasonality. Mean nesting seasonality documented for Chagos hawksbills indicate 86% occurred October-February, with a peak 28% in December. Green turtle nesting was less predictable occurring year-round with 64% of nesting in June-October, a mean peak of 19% in August, and 3-7% of annual nesting emergences in each of the other months (Fig. 4).

Relative importance of Chagos in the SWIO. Total estimated mean annual reproductive output in the SWIO region, at 20 hawksbill and 26 green turtle sites, are 12,466-16,047 hawksbill and 103,944-143,466 green turtle clutches (Supplementary Table S4). Five sites--in Seychelles (Inner Islands, Amirantes), Madagascar (general), and Chagos (Peros Banhos, Diego Garcia)--each annually produce 1001-5000 hawksbill clutches. Five sites--in Seychelles (Cosmoledo group, Aldabra group), French islands (Europa, Mayotte), and Comoros--each produce >10,000 green turtle clutches annually (Fig. 5). Chagos hosts available nesting habitat (132 km) comparable to that of Seychelles (193 km) (Supplementary Table S4).

Discussion

Current estimates of 6300 hawksbill and 20,500 green turtle clutches laid annually in Chagos represent an increase of 225-525% for hawksbills and 465-930% for green turtles since the surveys performed in 1996 which estimated 1200-2800 and 2200-4400 clutches respectively (Mortimer & Day, 1999). The relatively higher rate of increase for green turtles accords with trends documented at DG-Index during 2006-2018.

Differing patterns of nesting density amongst atolls likely reflect a combination of ecological factors and historical human impact. The Chagos Archipelago was inhabited by some 650-1200 coconut plantation labourers who collected wood and caught fish and turtles, beginning in the years 1776 at DG, 1808 at Eg, and 1813 at PB, Sa and GCB, and ending in 1935 at Eg and GCB, and 1971-1973 at DG, Sa and PB (Wenban-Smith & Carter 2016; Supplementary Table S3.) So current nesting densities may reflect historic human exploitation, with higher nesting densities now reported on atolls whose islands were relatively less accessible.

PB and DG host most of the nesting habitat and the largest populations of nesting turtles in Chagos. Since 1968 and 1970, green turtles and hawksbills (respectively) have been protected by conservation legislation. Since 1973, protection for turtles has been reinforced by several Special Nature Reserves without human habitation or artificial lighting. At PB, topography affords protection whereby abundant habitat occurs on 36 small islands scattered along the rim of the vast (34 km diameter) lagoon. At both PB and GCB, rough seas and primitive sail and oar-driven boats would have limited the efficiency of historic turtle hunts (Wenban-Smith & Carter, 2016). At many GCB islands, high energy beaches, which offer ideal habitat for green turtles and restrict human access, may explain abundant green turtle nesting at GCB. In contrast, Sa atoll with 10.6% of total nesting habitat, today hosts <5% of turtle populations despite reports of abundant turtles in 1786 (Horsburgh 1809, in Mortimer & Day, 1999) and 1813 (Wenban-Smith & Carter, 2016). Sa atoll comprises a nearly closed island-ring enabling human access to all nesting beaches regardless of weather. Egmont atoll, like Sa, has islands easily accessible year-round; but its human population was relatively smaller, habitation ended earlier in 1935, and its beaches (13.1% of total) today host 16.1% of Chagos green turtles and 5.0% of hawksbills.

The inter-annual variability shown by DG monthly surveys typifies nesting populations worldwide (Broderick et al., 2001), driven by varying remigration intervals where non-annual breeding occurs (e.g., Hays, 2000). Individual turtles experience differing environmental conditions year-to-year at their foraging grounds which modulate the time females take to achieve breeding body condition. So, in some years relatively higher proportions of the population may attain this body condition and migrate to breed. Remigration intervals vary between individuals and even over time for the same individual (Miller, 1997).

The turtle populations of Chagos show signs of recovery after two centuries of exploitation. Recovery occurs in two phases. Once protection begins, females that would previously have been killed after only a few nesting attempts now survive the season to produce full complements of clutches and return as re-migrant females in subsequent seasons. This produces an immediate increase in nesting activity and reproductive output even though absolute numbers of adult females have not yet increased (Mortimer, 1985, 1988; Balazs & Chaloupka, 2004). Then, after a lag of some 30-40 years, the time estimated for Indo-Pacific hawksbill (Bell & Pike, 2012) and green turtle (Limpus & Chaloupka, 1997) hatchlings to attain sexual maturity, a second phase of recovery commences once the offspring produced on protected beaches mature and return as reproductive adults (Dutton et al., 2005). In Seychelles, a 40-year recovery pattern has been documented for both hawksbills (Allen et al., 2010) and green turtles (Mortimer et al., 2011b) with up to 800% increase in clutches after four decades of protection. Such recovery is underway in Chagos and we predict will become more evident with continued protection of the MPA (Koldewey et al., 2010) and long-term monitoring (Wallace et al., 2011). The statistically significant upward trend in Chagos green turtles is encouraging; while for hawksbills continued monitoring is needed to determine whether the apparent upward trend is significant or simply reflects inter-annual variability. The need for long time-series to confirm statistical significance of apparent trends in abundance was recently highlighted by Mazaris et al. (2017) who reported that, around the world, many time-series documenting sea turtle abundance remain non-significant because they are too short-term. Another threat to turtle rookeries is the presence of non-native rats that prey on hatchlings (Caut et al., 2008) and embryos (JA Mortimer, unpublished data, DG island, 2006) and disrupt both terrestrial and marine ecosystems (Graham et al., 2018). The ongoing and planned rat eradication in Chagos (Hilton & Cuthbert, 2010) will likely further accelerate turtle recovery.

Our study is the first to document nesting seasonality at Chagos following records of snapshot surveys (Frazier, 1975; Mortimer & Day, 1999; Mortimer, 2000, 2007). The clear October-February nesting peak exhibited by DG hawksbills corresponds to that in Seychelles where 94%

and 98% of annual nesting occurs in October-February in the inner islands (Mortimer & Bresson, 1999) and Amirantes (Mortimer et al., 2011a), respectively. At each site peak hawksbill season concurs with high northwest monsoon precipitation (Mortimer & Bresson, 1999). Green turtles typically nest year-round throughout the SWIO (Dalleau et al., 2012) with patterns of high intra- and interannual variation (Mortimer et al., 2011a, Mortimer 2012). The June-October (austral winter) nesting peak at DG accords with comparative data from the SWIO suggesting a tendency for lower latitude nesting to peak in the austral autumn and winter, and at higher latitudes in the austral summer, a pattern indicating temperature may be moderating seasonality (Mortimer, 2012; Dalleau et al., 2012). Across species and ocean basins, Mazaris et al. (2013) noted slope of the relationship between temperature and date of first breeding is steeper at higher latitudes. Variations in environmental parameters (e.g. sea surface temperature) that form part of global climate change (IPCC, 2014) have been associated with shifts in timing of seasonal events for a broad range of organisms (Ramp et al., 2015; Walther et al., 2002), including earlier onset of nesting in loggerhead turtles, *Caretta caretta* (Hawkes et al., 2007). Further investigation of seasonality in Chagos may also reveal variation in peak nesting amongst the five atolls.

Our review of mean annual egg clutch production in the SWIO indicates that Chagos accounts for 39-51% of hawksbill and 14-20% of green turtle reproduction in the SWIO. The IUCN Red List assessment criteria focus on annual numbers of nesting females, but we suggest egg clutch production is a more meaningful statistic given lack of consensus amongst turtle researchers regarding within-season clutch frequency. IUCN's published estimates of 3-5 clutches for hawksbills (Mortimer & Donnelly, 2008) accords with data from Seychelles (Mortimer & Bresson, 1999); while its 3 clutches for green turtles (Seminoff, 2004) is likely an underestimate. Esteban et al. (2017) recorded a minimum mean of 6.0 clutches per turtle by satellite tracking internesting female green turtles at Diego Garcia. It follows that although green turtle populations in the SWIO produce almost ten times more egg clutches than hawksbill populations, there may be only five times as many female green turtles as hawksbills nesting annually. Genetic studies by Vargas et al. (2016) identified the Seychelles-Chagos hawksbill populations as a separate RMU, which accounts for 97% of known hawksbill nesting in the SWIO. The Chagos/SWIO linkage is also supported by the migrations of most satellite-tracked post-nesting Chagos green turtles to Seychelles, Madagascar, and eastern Africa (Hays et al., 2014). Chagos is, however, situated at the interface of the SWIO and the IUCN/MTSG-designated Northwest Indian Ocean (NWIO) RMU (Wallace et al. 2010); so, evidence of Chagos/NWIO linkage is expected. In fact, three post-nesting Chagos green turtles migrated to the NWIO sites of Maldives and northern Somalia (Hays et al., 2014); and the possibility that some immature hawksbills foraging in Chagos have genetic links with the Arabian Peninsula (Mortimer & Broderick, 1999) warrants further investigation. Our understanding of sea turtle populations in the WIO region constantly improves, and conservation managers need to use these findings to work across international boundaries to protect sea turtles at nesting habitats and foraging sites. Our findings demonstrate the importance of the Chagos Archipelago to nesting turtles on both a regional and global scale. The MPA can be expected to help assure long-term protection of these resources.

Author contributions Study design: JAM, NE and GCH. Rapid-survey fieldwork: JAM in 1996, 1999 and 2006; NE in 2016. Monthly surveys: design and inception, JAM; fieldwork implementation, ANG. Data compilation, analysis, and manuscript writing: led by JAM and NE, with contributions from all authors.

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Conflicts of interest None.

Ethical standards The research was non-intrusive, and all necessary permits were obtained for conducting research in BIOT.

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TABLE 1 Physical features of each of the five islanded atolls of the Chagos Archipelago (see maps, Fig. 1, SI Fig. 1) including: numbers of islands, total oceanic coastline (km), and oceanic coastline suitable for nesting (expressed in km and as a percentage of the total). Indices of nesting density represent mean numbers of body pits counted per km of suitable coastline surveyed in 1996 and 2006. Percentages of total egg clutch production contributed per atoll are calculated by averaging the 1996 and 2006 indices for each atoll and using 1999 survey data to extrapolate to total suitable coastline. The mean estimated numbers of egg clutches produced annually at DG atoll were calculated from monthly track surveys of the DG Index Beach conducted during the 2011-2012 to 2017-2018 nesting seasons. Estimated egg clutch production by each species at each of the four outer island atolls were extrapolated based on relative levels of nesting activity.

			Oceanic Coastline Suitable for Nesting		Hawksbills						Green Turtles					
					Index of Nesting Density			Relative Levels of Nesting Activity			Index of Nesting Density			Relative Levels of Nesting Activity		
Atoll	**# of Islands**	**Total Oceanic Coast-line (km)**	**km**	**% of Total**	**1996**	**2006**	**Mean (1996, 2006)**	**Est. Mean Total Body Pits**	**% of Total for Chagos**	**Est. Mean Egg Clutches Laid Annually**	**1996**	**2006**	**Mean (1996, 2006)**	**Est. Mean Total Body Pits**	**% of Total for Chagos**	**Est. Mean Egg Clutches Laid Annually**
PB	36	80.7	41.2	51%	9.0	5.9	7.5	307	41.6%	2627	5.8	12.8	9.3	383	38.8%	7941
Sa	11	26.3	13.9	53%	1.2	1.5	1.4	19	2.5%	158	0.1	4.7	2.4	33	3.4%	696
GCB	8	32.9	18.8	57%	1.0	0.6	0.8	15	2.0%	126	4.5	12.4	8.5	159	16.1%	3295
Eg	8	22.8	17.3	76%	1.3	3.0	2.2	37	5.0%	316	6.9	4.8	5.9	101	10.2%	2088
Total Outer Islands	63	162.7	91.2	56%												
DG	4	72.1	40.5	56%	6.6	11.2	8.9	360	48.8%	3081	6.7	8.7	7.7	312	31.6%	6467
Total Chagos	67	234.8	131.7	56%				738	100%	6308				988	100%	20,487

TABLE 2 Distribution of suitable nesting habitat and levels of turtle nesting activity recorded during the 1999 rapid survey of 72.1 km of oceanic coastline at Diego Garcia atoll. Sections of coastline included: 29.1 km along the outer west coast (AB, BC); 31.8 km along the outer east coast (CD, DE, EF) (including the 2.8 km DG Index Beach within CD); 8.2 km inside the east coast of the lagoon (FG); and the coastlines of the three small islands at the mouth of the lagoon (see Fig. 1). The spatial distributions of hawksbill and green turtle nesting activity recorded in each section of coastline (based on numbers of body pits) are presented as percentages of total nesting activity at Diego Garcia atoll.

		Suitable Coastline for Nesting		% of Total Nesting Activity at DG Atoll	
Section of Coastline	**Total Oceanic Coastline (km)**	**km**	**% of Total**	**Hawksbill**	**Green Turtles**
Diego Garcia Island:					
AB: NW coast	16.0	9.2	58%	2.4%	3.9%
BC: SW coast	13.1	3.0	23%	6.1%	3.9%
CD: South Pt. to Horsburgh Pt.	9.8	9.4	95%	44.5%	41.2%
DE: Horsburgh Pt. to Cust Pt.	12.8	8.6	67%	27.0%	41.8%
EF: Cust Pt. to Barton Pt.	9.1	5.9	65%	17.7%	5.2%
FG: Inside lagoon: Barton to Cust Pt.	8.2	4.1	50%	0.9%	0.0%
DG Island Totals	69.1	40.2	58%	98.6%	96.1%
3 Small Islands:					
West, Middle, East	3.0	0.3	9%	1.3%	3.9%
DG Index Beach (within CD)	2.8	2.8	100%	8.566%	8.497%

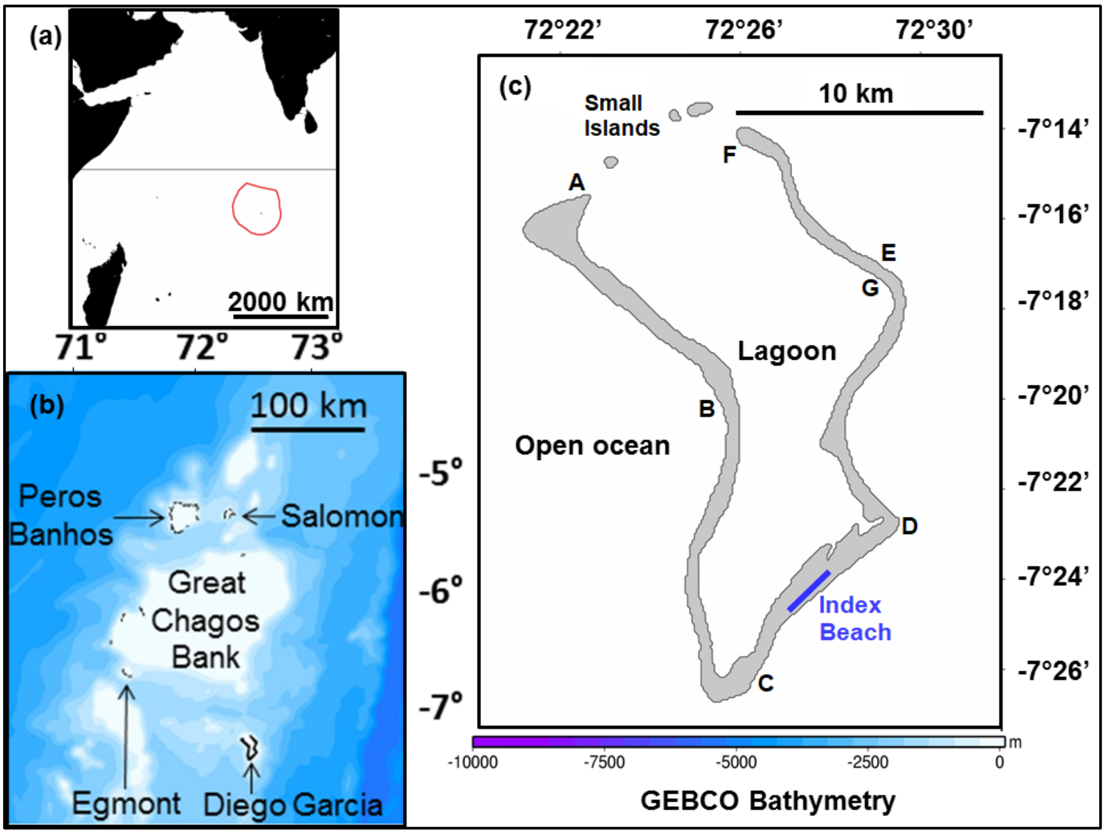

FIG. 1 (a) Location of study site, Chagos Archipelago in the Western Indian Ocean with boundaries of British Indian Ocean Territory (BIOT) shown in red. Hawksbills and green turtles nest across 67 islands at five atolls. (b) Bathymetry is shown in 100 m contours (source: GEBCO) indicating delineation of atolls separated by deep water. (c) Location of 2.8 km Index Beach and three small islands at Diego Garcia atoll. Six sections of coastline (AB, BC, CD, DE, EF, FG) were each surveyed to assess suitable nesting habitat and relative percent nesting activity by species (Table 2).

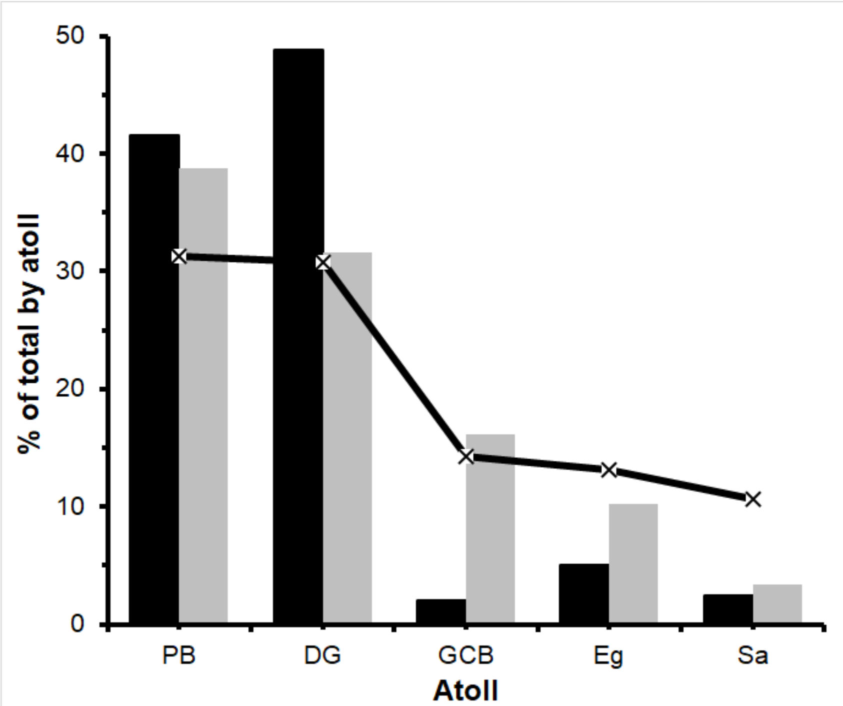

FIG. 2 Percent of total hawksbill (black bars) and green turtle (grey bars) nesting activity relative to percent of total suitable nesting habitat (132 km, line graph) distributed across the five islanded atolls of Chagos. Nesting activity was calculated from mean body pit counts in 1996, 1999 and 2006 (Table 1).

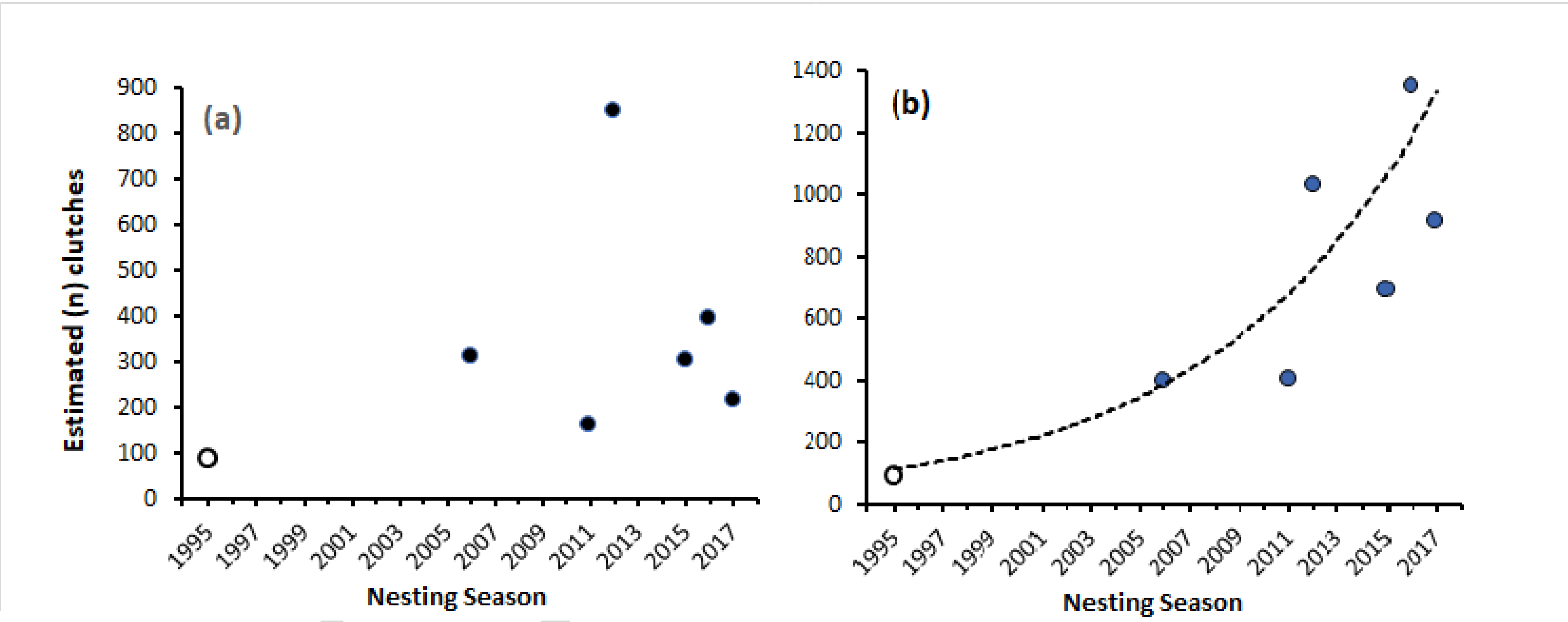

FIG. 3 Estimated annual clutch numbers laid by: (a) hawksbills and (b) green turtles at the 2.8 km Diego Garcia Index Beach between 1995 and 2017. Closed circles represent estimated clutch numbers derived from monthly track surveys conducted in April to March of six seasons: 2006-2007, 2011-2012, 2012-2013, 2015-2016, 2016-2017 and 2017-2018. Open circles are derived from midpoints of bracketed estimates of annual clutches laid during 1995-1996 (Mortimer & Day, 1999). Data show marked inter-annual variation.

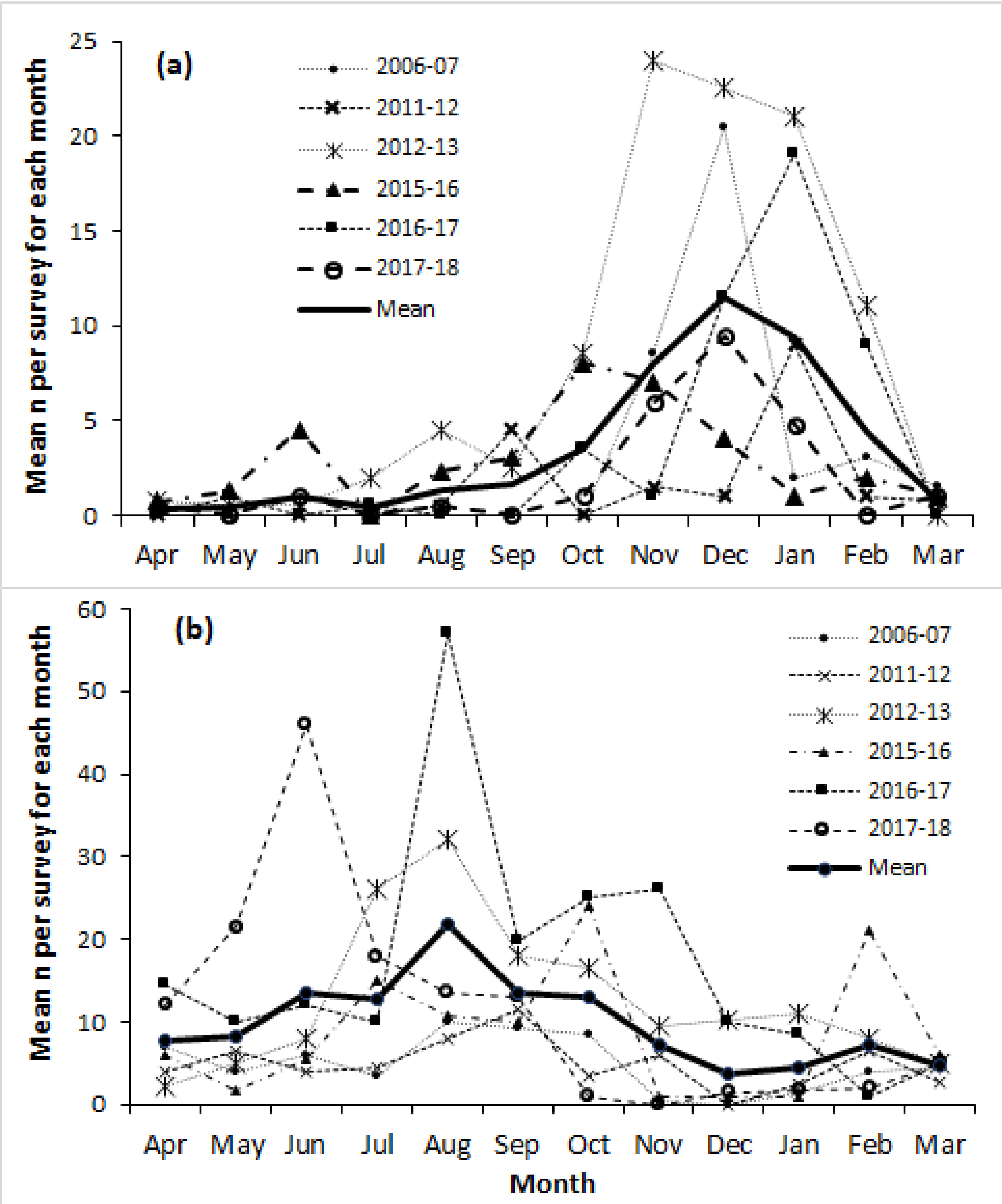

FIG. 4 Monthly distribution of track counts along the 2.8 km Diego Garcia Index Beach. Hatched lines indicate individual seasons, and solid lines mean figures for all seasons combined. (a) Hawksbill nesting peaked in October-February. (b) Green turtles nest year-round with a peak during June-October.

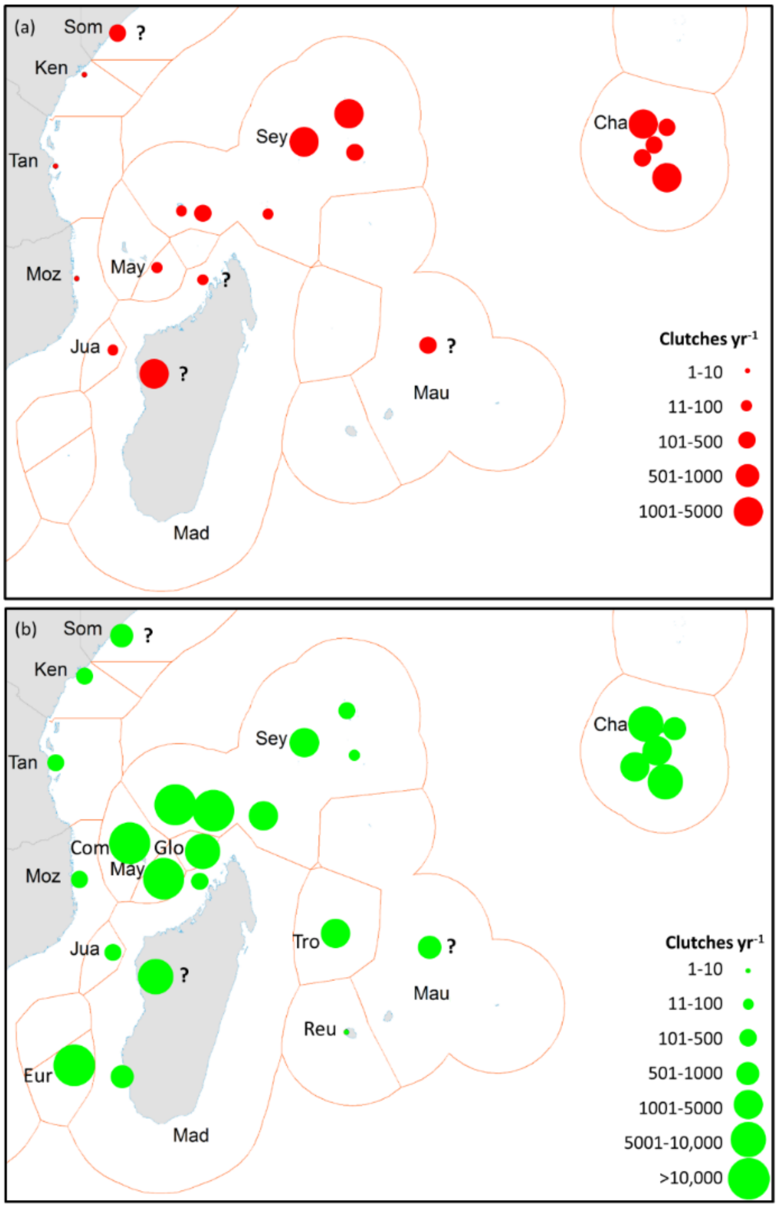

FIG. 5 Important turtle nesting populations in Southwest Indian Ocean region for: (a) hawksbills (red circles) and (b) green turtles (green circles). Circle sizes indicate estimated mean annual egg clutch production. ? indicates poorly surveyed sites. Abbreviations: Cha, Chagos Archipelago; Com, Comores; Eur, Europa; Glo, Glorieuse; Jua, Juan de Nova; Ken, Kenya; Mad, Madagascar; Mau, Mauritius; May, Mayotte; Moz, Mozambique; Reu, Réunion; Sey, Seychelles; Som, Somalia; Tan, Tanzania; Tro, Tromelin. Source data: Supplementary Table S4. Projection: Mercator, map boundaries: 1.5°N to 30°S, 38°W to 78°W. Baseline map source: Claus et al. (2018).