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Short distance directional migration in the threatened Socotra cormorant: link to primary productivity and implications for conservation

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ABSTRACT: Conservation of threatened seabirds commonly focuses on protection of breeding areas. However, conditions at non-breeding areas also affect population dynamics, calling for a better understanding of seabird migratory ecology. In particular, it is crucial to identify the type of migration and the oceanic conditions determining non-breeding habitat selection. We studied movements of the threatened Socotra cormorant *Phalacrocorax nigrogularis* breeding at Siniya Island, United Arab Emirates (UAE) (35% of the world population), using platform transmitter terminals (PTTs) deployed on adults during the 2013 and 2014 breeding seasons. Concomitantly, we used remotely-sensed chlorophyll *a* concentration data (CHL) of areas visited by birds in the Arabian Gulf and Gulf of Oman regions (2002 to 2016 monthly averages), as an index of primary productivity. The migratory pattern of the Socotra cormorant was non-dispersive, fitting with the gregarious habits and group foraging mode of this forage fish specialist. Birds performed a short westward directional migration to islands off western UAE, then moved eastwards to the Strait of Hormuz before returning to Siniya Island. Birds concentrated at a few localities, which therefore represent areas of high conservation priority. During breeding, CHL around the colony was high. During non-breeding, however, CHL around non-breeding areas was low, even though more productive waters were present within foraging range. The mismatch between the non-breeding phase and CHL could be linked to spatial and temporal lags in responses of secondary and tertiary consumers to primary productivity. Effective conservation will necessitate a better understanding of the ecology and distribution of forage fish within the Gulf.

KEY WORDS: Seabird · PTT · Chlorophyll *a* · Arabian Gulf · Anchovy · Herring · Flying fish · United Arab Emirates

INTRODUCTION

As top predators, seabirds form an abundant and diverse community sustaining marine ecosystem stability through top-down control (Brooke 2004, Frederiksen et al. 2007a). Seabirds are thus regarded as indicators of marine fish stocks and overall marine ecosystem health (Montevecchi 1993, Boyd et al. 2006, Parsons et al. 2008, Mallory et al. 2010). Despite recognition of this important role (e.g. Schreiber & Burger 2002, Barrett et al. 2006), these apex predators continue to face numerous threats, and seabird populations have declined globally by >69% over the last 60 yr (Croxall et al. 2012, Paleczny et al. 2015). Identifying important marine areas that may receive protection has therefore become a matter of

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priority within the scientific community working on seabird conservation (Lascelles et al. 2012). This, however, necessitates adequate knowledge of seabird movements not only during the breeding season, when reproductive success may depend upon local marine resources available within foraging range from the colony (Frederiksen et al. 2005, 2007b), but also during the post-fledging and inter-breeding period. Indeed, juvenile or adult survival is crucial in sustaining population growth, and can be driven by conditions in waters where juveniles disperse, and at non-breeding grounds (Phillips et al. 2005, Sherley et al. 2013).

Most seabirds exhibit annual migratory behaviour between breeding grounds and non-breeding grounds and back (Schreiber & Burger 2002). The duration and distance of migration impose energetic and fitness constraints on seabirds, which in turn affect future reproductive success (Fayet et al. 2016, Shoji et al. 2016). Dispersive migration is different from typical long-distance migration (hereafter named directional migration) in which birds move annually between defined breeding and non-breeding areas (Newton 2008). In dispersive migration, movement can occur in many potential directions from the breeding site, but still involves a return journey. Migrants using a directional, population-level migratory pattern, presumably inherit the migration route genetically or learn it by following conspecifics (Newton 2008, Guilford et al. 2011). Drivers of dispersive migration in seabirds are not well characterized, however, and factors like sex segregation, intra-specific competition, oceanic productivity, prey species composition and prey movement and abundance could collectively drive the dispersive process (Schreiber & Burger 2002, Guilford et al. 2011, Fayet et al. 2016). Year-round tracking of seabirds using miniaturized biologgers or satellite transmitters have greatly improved our understanding of seabird movement (Cooke 2008, Lewison et al. 2012). In particular, migratory behaviour is better quantified, aiding in the identification of areas used for foraging and roosting in the inter-breeding period. For example, non-breeding black-browed albatrosses *Thalassarche melaophrys* may range across a large expanse of open ocean between southern Africa and southeastern South America, selecting areas with high productivity during this period for foraging (Phillips et al. 2005). Black-legged kittiwakes *Rissa tridactyla* in northeastern North America undergo dispersive migration driven by a combination of foraging and numerous oceanic factors, highlighting disjunct areas of conservation significance (McKnight et al. 2011). Hence, it is crucial to gain a clearer understanding of the migratory patterns of seabirds and their associated drivers as inputs for the design of effective conservation strategies. Depending on the type of migration pattern, the type of conservation strategy may vary, with certain types of migration (e.g. dispersive) posing challenges in developing conservation strategies (Guilford et al. 2011, McKnight et al. 2011).

The purpose of this study was to describe the year-round movements of the threatened Socotra cormorant *Phalacrocorax nigrogularis*, and explore what processes (behavioural and oceanic) drive its migratory patterns in order to better inform its conservation. Little information exists on the biology and the ecology of this species (Jennings 2010, Muzaffar et al. 2012, 2013, 2015a, 2015b, Cook et al. 2017) and knowledge on Socotra cormorant movements outside of the breeding season is scarce. In the Arabian Gulf, birds are known to breed from August to January on off-shore islands (Jennings 2010, Muzaffar et al. 2012, 2015a), where they group forage in shallow, coastal waters within 60 km of the colony (Cook et al. 2017). After breeding, however, direction, extent and duration of migration are speculative.

Using state-of-the-art satellite transmitters deployed on birds, we followed the movements of Socotra cormorants over the course of their entire annual cycle. We tested 3 hypotheses: (1) Socotra cormorants stay in the Gulf after breeding. It is assumed that the northern population based in the Gulf is isolated from the southern populations of Oman in the southern Gulf of Oman and north-western Arabian Sea. (Jennings 2010, BirdLife International 2017). (2) The migratory pattern of the Socotra cormorant is dispersive rather than directional (Jennings 2010, Muzaffar et al. 2012). Following a dispersive pattern, we expect birds to visit a wide range of non-breeding grounds, including the Northern Gulf, the islands and coasts of Iran and the Gulf of Oman. (3) Spatial and temporal variations in patterns of marine primary productivity explain choice of breeding and non-breeding grounds in Socotra cormorants. Primary productivity as measured by chlorophyll *a* concentration (CHL) has been linked to areas with high overall fish productivity and concomitant spatial aggregations of seabirds (Suryan et al. 2012, Grecian et al. 2016). Very little knowledge exists on distribution of fish eaten by Socotra cormorants (Muzaffar et al. 2015b), so proxies like CHL could help to establish spatial distribution, especially in the inter-breeding period. Our overall objective was to use CHL data to characterize major -non-breeding habitat to help identify areas of high conservation value.

MATERIALS AND METHODS

Study area: the Gulf

The Arabian Gulf (also called Persian Gulf), hereafter named the Gulf, is a relatively small, shallow, semi-enclosed, hypersaline gulf that has unique properties that make it harsh for aquatic life (John et al. 1990, Nezlin et al. 2007, Grandcourt 2012). With salinities among the highest in the world (typically ranging from 37 to 50 psu, but as high as 59 psu; John et al. 1990), invertebrate and fish assemblages are species-poor compared to the neighbouring Gulf of Oman (Burt et al. 2011, Grandcourt 2012), to which it is connected via the narrow Strait of Hormuz. Productivity is also generally lower in the Gulf compared to the Gulf of Oman. Sea surface temperatures range from 23 to 35°C, with cooler waters occurring away from the coasts towards the central and northwestern regions (John et al. 1990, Nandkeolyar et al. 2013). The absence of thermal stratification in most parts of the Gulf encourages nutrient mixing, and strong northwestern winds during summer and winter create patterns of wind stress that effectively isolate the Gulf from the greater Indian Ocean (John et al. 1990, Nezlin et al. 2007, Riegl & Purkis 2012).

Study species: the Socotra cormorant

The Socotra cormorant *Phalacrocorax nigrogularis*, an endemic to the Arabian Peninsula (Jennings 2010), is one of the most abundant seabirds in the Gulf (Aspinall 2010, Jennings 2010, BirdLife International 2017). The global population is in the order of 110 000 pairs, or about 750 000 individuals (Jennings 2010, BirdLife International 2017), the bulk of which (~90 %) make up the northern population that resides and breeds within the Gulf. Despite these apparently large numbers, the species is undergoing catastrophic declines within its restricted range and its relatively small area of occupancy (Jennings 2010, EAD 2014, BirdLife International 2017). Identified primary threats include disturbance at, or destruction of, the limited number of small breeding colonies, mainly through radical transformations of islands and coastlines by man (Sheppard et al. 2010).

Currently, 14 colonies of Socotra cormorants are known within the Gulf. At least 7 colonies have already been abandoned due to oil exploitation activities (BirdLife International 2017). In the Gulf of Salwa, west of Qatar, 4 colonies (3 colonies in Saudi Arabia, with collectively about 27 000 pairs and 1 colony in Bahrain with about 30 000 to 40 000 pairs) constitute possibly the largest concentration of the species in the world (Jennings 2010, BirdLife International 2017, although see Muzaffar et al. 2017). East of Qatar, most of the 9 colonies of the UAE are small, hosting a few thousand pairs, with the exception of one large colony, Siniya Island, that hosts 28 000 to 41 000 pairs breeding between the months of August and January (Muzaffar et al. 2012, 2017). Breeding Socotra cormorants on Siniya feed on 11 000 to 18 000 t of small pelagic fish every year (Muzaffar et al. 2015b), suggesting that the species plays a major role in the Gulf ecosystem.

Conservation of the species is a contentious matter, since fishermen may perceive them to be a threat to fisheries (Muzaffar 2015b). However, the only published study on Socotra cormorant diet has shown that there is minimal overlap between the diet of the birds when breeding (composed of small pelagic fish) and the fish species targeted by local fisheries in the eastern Gulf (Muzaffar et al. 2015b). Additionally, Socotra cormorants are suspected of carrying *Coxiella burnetii*, a tick borne pathogenic bacterium that could infect people to cause Q-fever (Sonnevend et al. 2011). However, a recent study from the largest colony in the United Arab Emirates (UAE) only found non-pathogenic *Coxiella* endosymbionts that are widespread in the region (Al-Deeb et al. 2016). The species is globally Vulnerable (BirdLife International 2017) and is listed in Appendix II of the Convention on Migratory Species, which promotes the conservation of migratory species through international agreements (CMS 2015). In the UAE, the species is protected under a federal law prohibiting hunting of wild animals, although enforcement is limited (EAD 2014).

Study colony and logger deployments

We deployed portable transmitter terminals (PTTs) on adults breeding at the Siniya colony (25° 37′ N, 55° 37′ E). PTTs were previously deployed successfully on the larger double-crested cormorant *Phalacrocorax auritus* using a harness attachment technique (Guillaumet et al. 2011, King et al. 2012). To our knowledge, this is the first time that PTTs have been deployed on an average-sized, entirely marine species of cormorant. Socotra cormorant study birds were randomly chosen within the study colony, and captured on their nest by the foot using a noose triggered remotely. Birds were only captured during the late incubation-hatchling phase, and not during the

later chick-rearing phase, when medium to large chicks may be accidentally snared by the capturing device and injured. In November 2013 and November to December 2014, 8 and 10 birds, respectively, were equipped with Kiwisat PTTs (Model K3H 174A, Sirtrack), using a harness built with 14 mm wide Teflon ribbons attached in a back-pack harness similar to Miller et al. (2005) and modified according to Muzaffar et al. (2008).

Before deployment, birds were checked to ensure they were in good condition; no measurements were made, in order to reduce time of manipulation. Average (± SD) adult body mass of Socotra cormorants is 1.5 ± 0.1 kg (Cook et al. 2017). Each PTT weighed 36.5 g, thus representing 2.4 ± 0.2% of the body mass of birds, below the 3% recommended for a payload deployed on flying birds (Phillips et al. 2003). Cormorants were immediately released as soon as the harness was secure. Total time between bird capture and release was ≤20 min. Study nests were monitored for a few days after capturing sessions and all study birds returned to their nests following release.

PTT recordings and data analyses

PTTs recorded between 00:00 and 05:00 h daily to optimize battery life and satellite costs. In 2013–2014, locations were recorded during the months of November and December 2013 and May and June 2014 (80 d of recording). The January to April gap in recordings was caused by a technical failure of the ARGOS system, which ceased to record PTT signals. In 2014–2015, locations were recorded from November 2014 to August 2015 (264 d of recording). A total of 2331 and 16 976 locations from 8 and 10 birds were recorded in 2013–2014 and 2014–2015, respectively. Location data with specified levels of accuracy (location classes) were obtained from www.argos-system.org. Low quality positions (locations classes 0, A, B, or Z) were excluded. These usable location data formed 44.2 and 51.6% of locations in 2013–2014 and 2014–2015, respectively. Aberrant locations (far inland or on another continent or ocean) were then excluded manually (n = 8 and 59 in 2013–2014 and 2014–2015, respectively). In the end, a total of 1219 and 7960 usable locations from 8 and 10 birds were recorded in 2013–2014 and 2014–2015, respectively (Table 1). The number of useful locations recorded daily per PTT varied between 0 and 36 and 0 and 24 in 2013–2014 and 2014–2015, respectively.

We analysed the density distribution of Socotra cormorant positions on a monthly basis using kernel analyses performed in R 3.0.3 (R Core Team 2017) with ks (Duong 2007), a kernel smoothing package which implements diagonal and unconstrained data-driven bandwidth matrices (smoothing parameters) for kernel density estimation. We also calculated the linear distance between the breeding colony (Siniya Island) and every roosting location. For roost locations in the Gulf of Oman, distance to colony was calculated by adding the linear distance between the colony and the northernmost point of Musandam Peninsula on the Strait of Hormuz (26° 24′ N, 56° 30′ E) to the linear distance between the latter point and roost location. This 2-step calculation was done because Socotra cormorants do not cross large land masses while migrating, but mostly follow the coastline (Orta 1992). All maps were drawn in ArcGIS 10.2.0 for Desktop (Esri® ArcMap™).

Table 1. Summary of monthly tracking data on Socotra cormorants *Phalacrocorax nigrogularis* in the Arabian Gulf following breeding on Siniya Island in 2013 and 2014, showing the number of platform transmitter terminals (PTTs) recording and number of night locations recorded in each month after filtering of raw data

Year	Month	PTTs	No. of locations
2013	Nov	8	323
2013	Dec	8	360
2014	May	2	387
2014	Jun	1	149
2014	Nov	8	679
2014	Dec	9	1177
2015	Jan	9	924
2015	Feb	8	1072
2015	Mar	8	1063
2015	Apr	4	832
2015	May	4	630
2015	Jun	4	880
2015	Jul	4	634
2015	Aug	2	72

Primary productivity around roosting areas

We estimated primary productivity in areas visited by Socotra cormorants using CHL data. CHL is widely used as an index of phytoplankton biomass and, as such, is a key input to primary productivity models (Monticelli et al. 2007). Data were recorded by the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument aboard NASA's Aqua satellite. MODIS measures CHL every day over the entire planet. We used imageries produced by the Earth Observatory Group) with CHL at a pixel reso-

lution of 0.1°. Maps covering the period 2013–2015 lack significant data due to cloud cover. Hence, we worked with maps averaging monthly data over the entire time series of the Aqua-MODIS dataset, i.e. 2002 to 2016. This is appropriate, as timing of phytoplankton blooms in the region are predictable according to season and locality (Nezlin et al. 2007). We imported these average monthly data maps in ArcGIS and calculated the mean CHL inside the most important areas used by cormorants, i.e. which were visited by at least 75% of birds. Sampling was performed inside circles with a 60 km radius, the approximate maximum foraging range of Socotra cormorants (Cook et al. 2017).

RESULTS

Distribution range

During both years, Socotra cormorants breeding on Siniya Island spent their entire annual cycle on the coast and islands along the southern coastline of the Gulf, between Qatar (51° 30′ E) and the Strait of Hormuz (56° 30′ E) (Fig. 1). Birds used a variety of coastal roosts and visited many different offshore islands (Table S1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m575p181_supp.pdf). Birds ignored all islands north or west of Denna Island (24° 58′ N, 52° 24′ E). The one exception was Alia Island (25° 24′ N, 51° 34′ E), which was visited during 1 wk by 2 birds in March 2015. Alia Island corresponded also to the maximum migration distance from Siniya Island (409 km). Birds did not move east and south into the Gulf of Oman, except for 1 bird, which used an unidentified roost between January and March 2015 along the coast of Fujairah (UAE), 130 km south of the Strait of Hormuz.

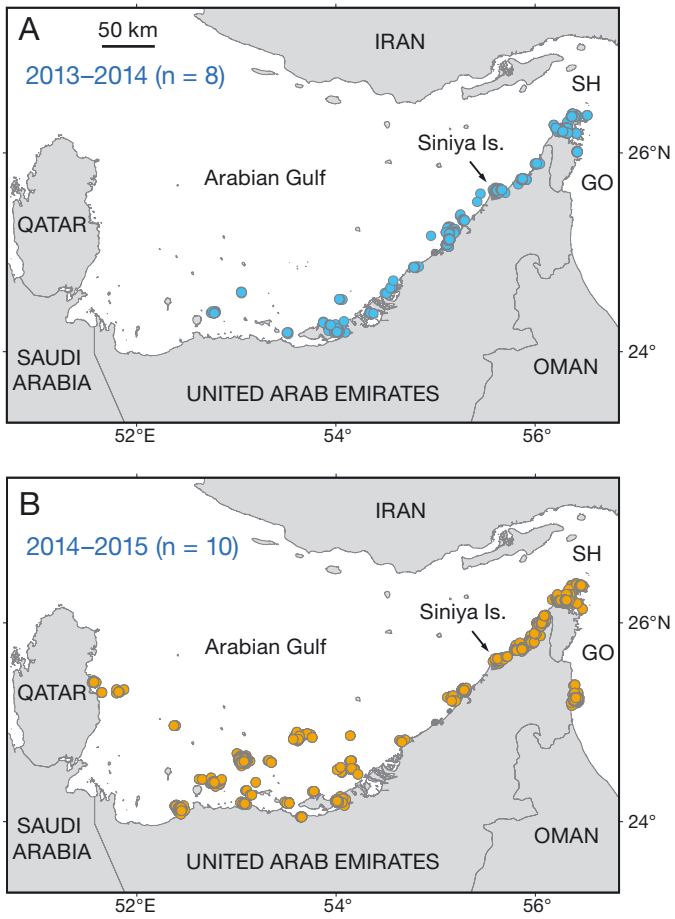


Fig. 1. Night locations (filtered data) of Socotra cormorants in the Arabian Gulf during (A) 2013–2014 (n = 1219 locations) and (B) 2014–2015 (n = 7960 locations). Birds were captured and equipped with platform transmitter terminals (PTTs) while breeding on Siniya Island. The numbers in parenthesis following the date ranges refer to the number of PTTs (i.e. individual birds) which contributed to the dataset. Data were recorded for 80 and 264 d in 2013–2014 and 2014–2015, respectively. SH: Strait of Hormuz, GO: Gulf of Oman

Non-breeding grounds and timing of movements

Post-breeding migration away from Siniya Island started in late November. The average monthly distance from the colony followed 3 phases: (1) an increase during December to January, (2) a stabilisation at around ca. 300 km during February to April and (3) a rapid decrease in May followed by a stabilisation around ca. 150 km during May to July (Fig. 2).

The first phase of this pattern corresponded to 89% of birds moving southwest down the coast of the UAE in December. By the end of January, 87% of birds were roosting on islands off the western coast of the UAE. This behaviour was consistent in both years, birds occupying the same portions of coast and islands (Figs. 3 & 4). The second phase corresponded to a 4 month non-breeding period (January to April), with 87% of birds roosting off western UAE. Birds used various strategies during this phase. A minority (12%) barely moved, roosting on Shuwayhat Island almost throughout the entire period (Figs. 4, & S1). The majority, however, moved regularly between islands, with a centre over Umm Jassar Island and Bu Tinah Shoals, 2 island groups separated by 40 km (Figs. 4 & S1). Cormorants roosted for one or several consecutive nights on one island, moved to another island and then returned. They were rarely present all at once on

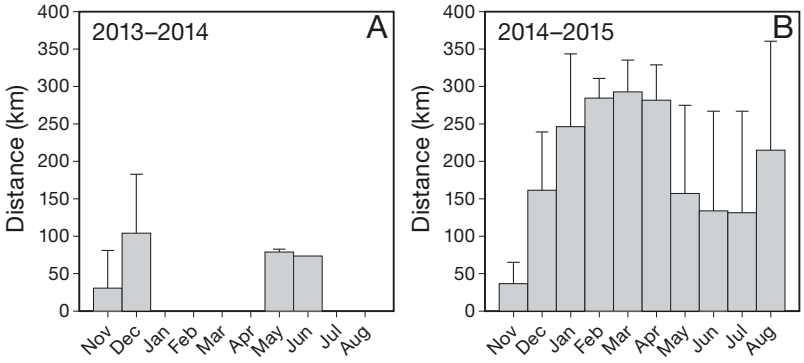


Fig. 2. Monthly average distance (average of individual averages; error bars: SD) of night locations of Socotra cormorants from the breeding colony on Siniya Island in (A) 2013–2014 and (B) 2014–2015

one island, due to birds splitting into at least 2 or 3 groups. Cormorants also moved regularly from one group to another (Table 2). The third phase corresponded to most birds leaving this region in May for other non-breeding grounds located in the easternmost part of the Gulf. These waters were reached by cormorants following the coastline up to the area of the Strait of Hormuz (Figs. 3 & 4). There, birds roosted in the cliffs of the fjords of Musandam Peninsula (Oman) during May to June (Figs. 3, 4 & S1G). During July to August, Socotra cormorants were found all along the coast of Ras al Khaimah, from Musandam Peninsula, to the north, to Siniya Island, to the south (Fig. 4). The annual cycle of Socotra cormorants breeding on Siniya Island is summarised in Fig. 5.

Primary productivity at breeding and non-breeding grounds

Mean monthly CHL composites were obtained at 5 locations corresponding to the distribution range and main roosting localities of Socotra cormorants as determined from PTT data (Fig. 6A). During May to October, CHL was relatively low (1 to 2 mg m^{-3}) throughout the range of cormorants which breed on Siniya Island. CHL increased substantially after October in the eastern part of the range (Area 2 in Fig. 6A), reaching a maximum during February to March (~4 mg m^{-3}) and decreasing again in April (Figs. 6B & S2). However, productivity was locally higher, for example around Siniya during September to February (Fig. 6C). Waters around Siniya Island also had a higher CHL than around Musandam

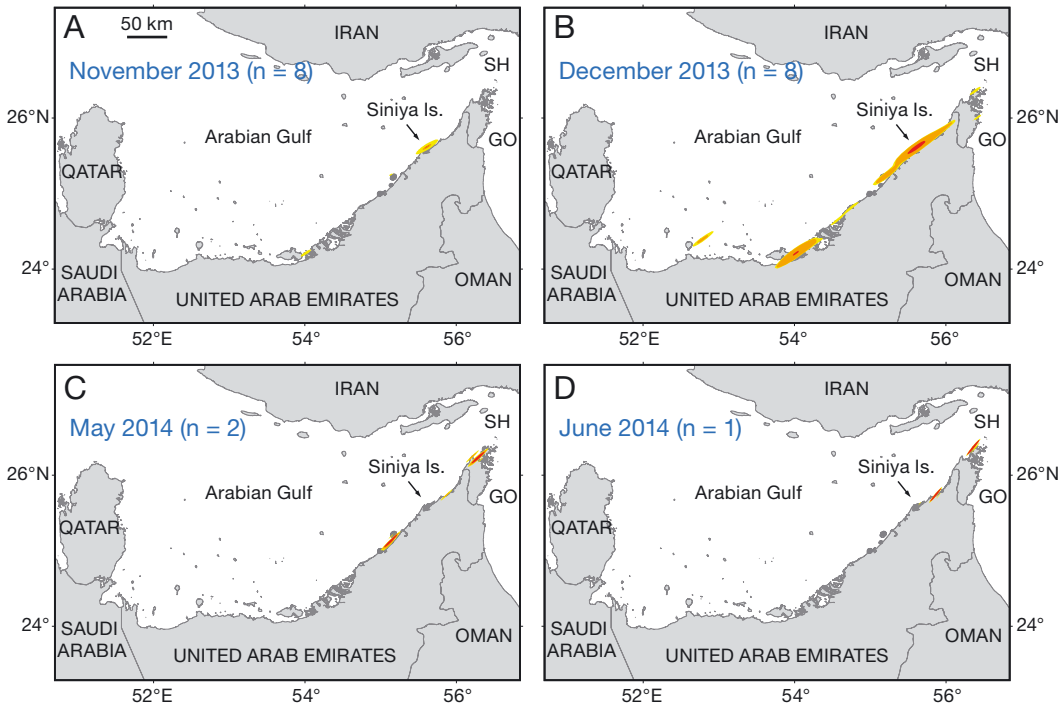


Fig. 3. Kernel density plots of night locations of Socotra cormorants tracked in 2013–2014 for (A) November 2013, (B) December 2013, (C) May 2014 and (D) June 2014. Birds were equipped with PTTs in November 2013 while breeding on Siniya Island. Parentheses: number of PTTs recording (i.e. individual birds tracked) during each month. SH: Strait of Hormuz, GO: Gulf of Oman. Red, orange and yellow hues: 50, 75 and 90% utilisation distribution contours

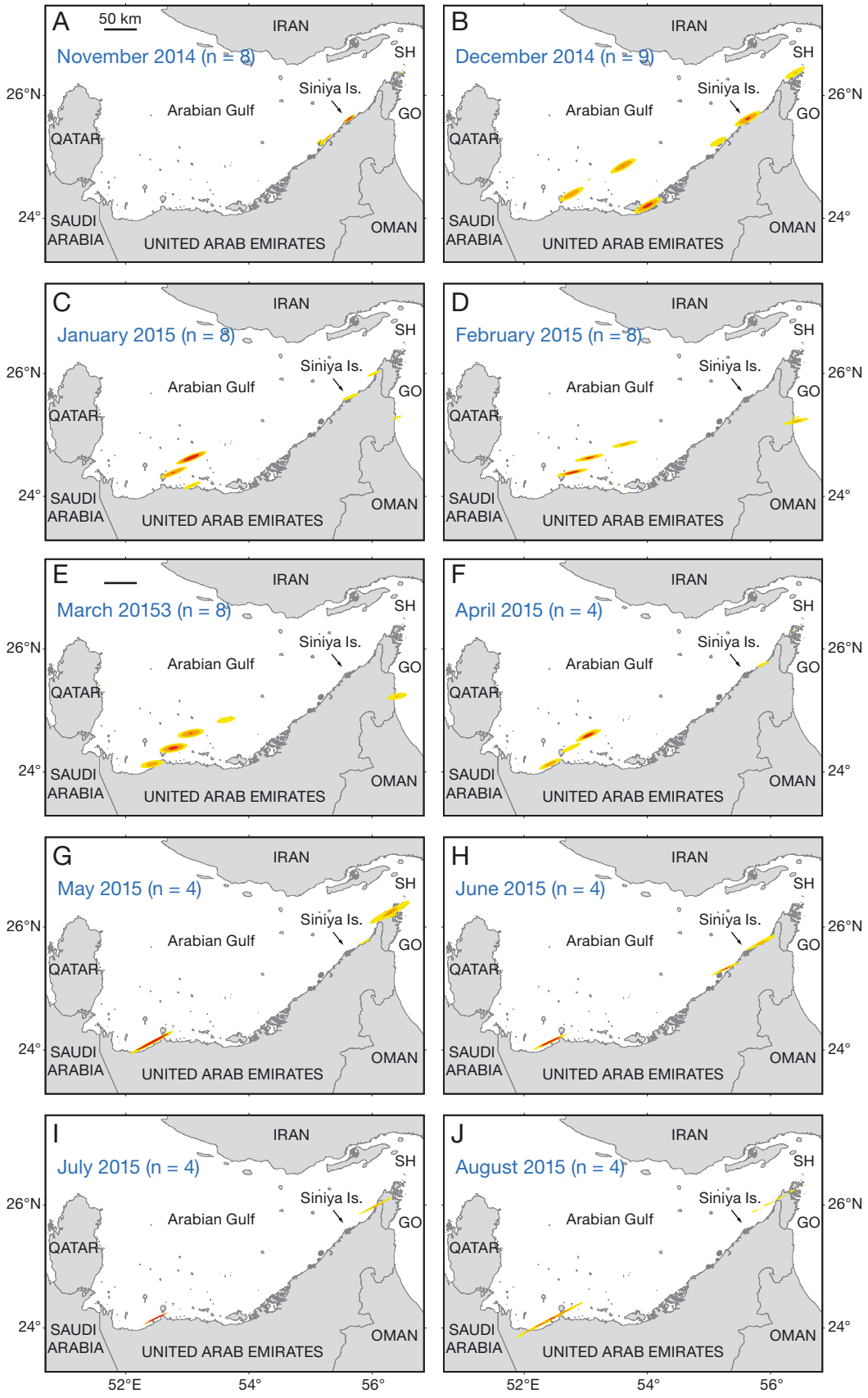
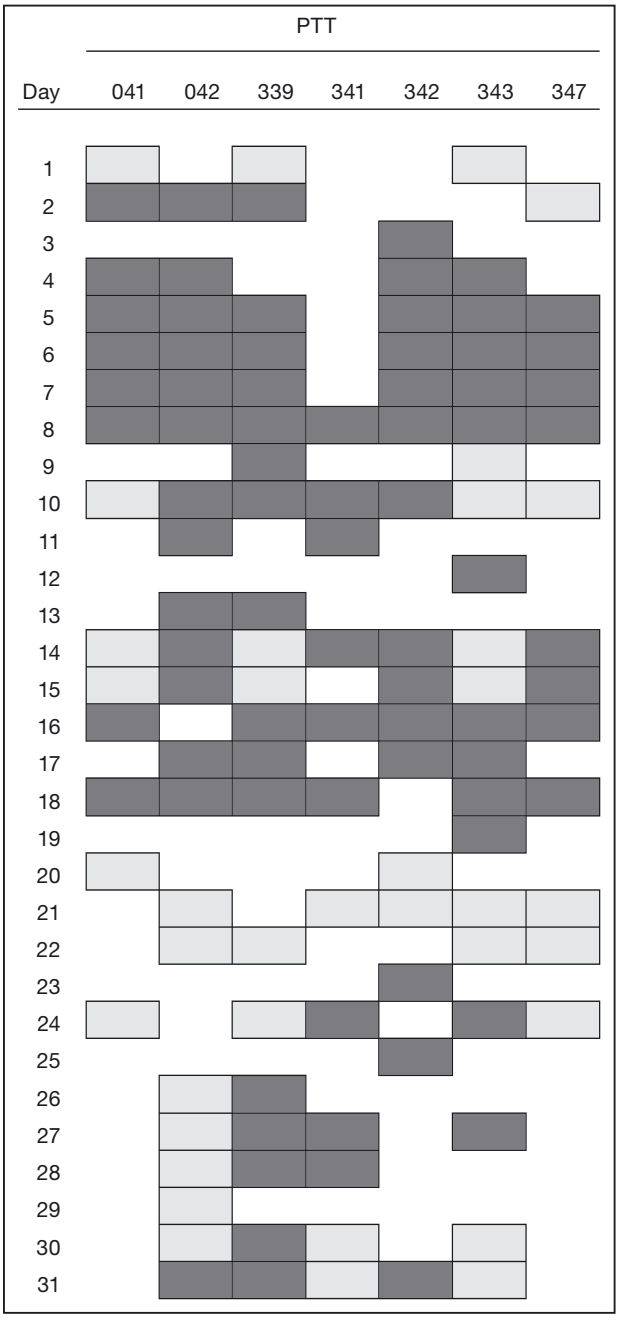


Fig. 4. Kernel density plots of night locations of Socotra cormorants in 2014–2015. Panels (A–J) show monthly data from November 2014 to August 2015. Birds were equipped with PTTs in November and December 2014 while breeding on Siniya Island. The numbers in parenthesis refer to the number of PTTs recording (i.e. individual birds tracked) during each month. SH: Strait of Hormuz, GO: Gulf of Oman. Red, orange and yellow hues: 50, 75 and 90% utilisation distribution contours

Table 2. Roosting areas of tracked Socotra cormorants from the breeding colony on Siniya Island during January 2015. Columns show movements of individual birds, identified by platform transmitter terminal (PTT) numbers, between Bu Tinah Shoals (dark grey) and Umm Jassar Island (light grey); blank cells correspond to days when birds roosted on other islands in the area. Between January and April 2015, Bu Tinah and Umm Jassar were visited by 87% of birds equipped with PTTs, and in January 2015, 54% of the roosts of these birds were at these locations. Other islands where birds roosted included Al Bazim al Gharbi, Bu Khurayj, Mubarraz, Salahah and an unnamed island (Unnamed Island 1). For locations of roosting areas see Table S1 and Fig. S1C,D in the Supplement



Peninsula, except in March, when waters in the Strait of Hormuz had the highest CHL in the region (5.3 mg m^{-3}). Birds left Siniya Island just before productivity became maximal there, and in the nearby Strait of Hormuz, and moved west towards waters with low CHL (1 mg m^{-3}). Later, birds moved east again towards the non-breeding grounds of the Strait of Hormuz, but only after April, when CHL had declined to 0.5 to 1 mg m^{-3} there (Figs. 6C & S2).

DISCUSSION

Directional migration pathways and non-breeding locations

Socotra cormorant movements consistently followed defined pathways during 2 consecutive years, contrary to the hypothesis of a dispersive pattern (Jennings 2010). After breeding, most birds moved westwards from Siniya Island and spent 4 mo on islands off the coast of the western UAE. Amongst the multitude of possible islands, birds consistently chose to roost in an area centred over Bu Tinah Shoals and Umm Jassar Island. In May, birds moved eastwards and spent 2 mo roosting in the cliffs of Musandam Peninsula, on the Strait of Hormuz. From July onwards, birds moved gradually down the coast towards Siniya Island (Fig. 5).

A minority of post-breeding birds migrated to the shoreline of Fujairah, in the Gulf of Oman. They did not migrate south of this point, giving support to the hypothesis that the northern population of Socotra cormorants is primarily restricted to the Gulf (Jennings 2010), with limited mixing with the southern population living along the Omani coastline in the southern Gulf of Oman and north-western Arabian Sea. If it is confirmed that this southern population does not move into the Gulf and mix with the northern population during the non-breeding season, these 2 isolated populations must be treated as evolutionarily significant units with potentially separate conservation strategies based on local environmental conditions and threats (Hällfors et al. 2016).

While Socotra cormorants breeding at Siniya Island did not penetrate far into the Gulf of Oman, they also did not migrate westwards beyond Qatar. Hence, their distribution range is quite restricted and their directional migration short. Interestingly, waters just west of Qatar host a large concentration of breeding Socotra cormorants (Fig. S2). The Qatari Peninsula could represent a barrier isolating the 2 subpopulations, and further studies are needed to determine if

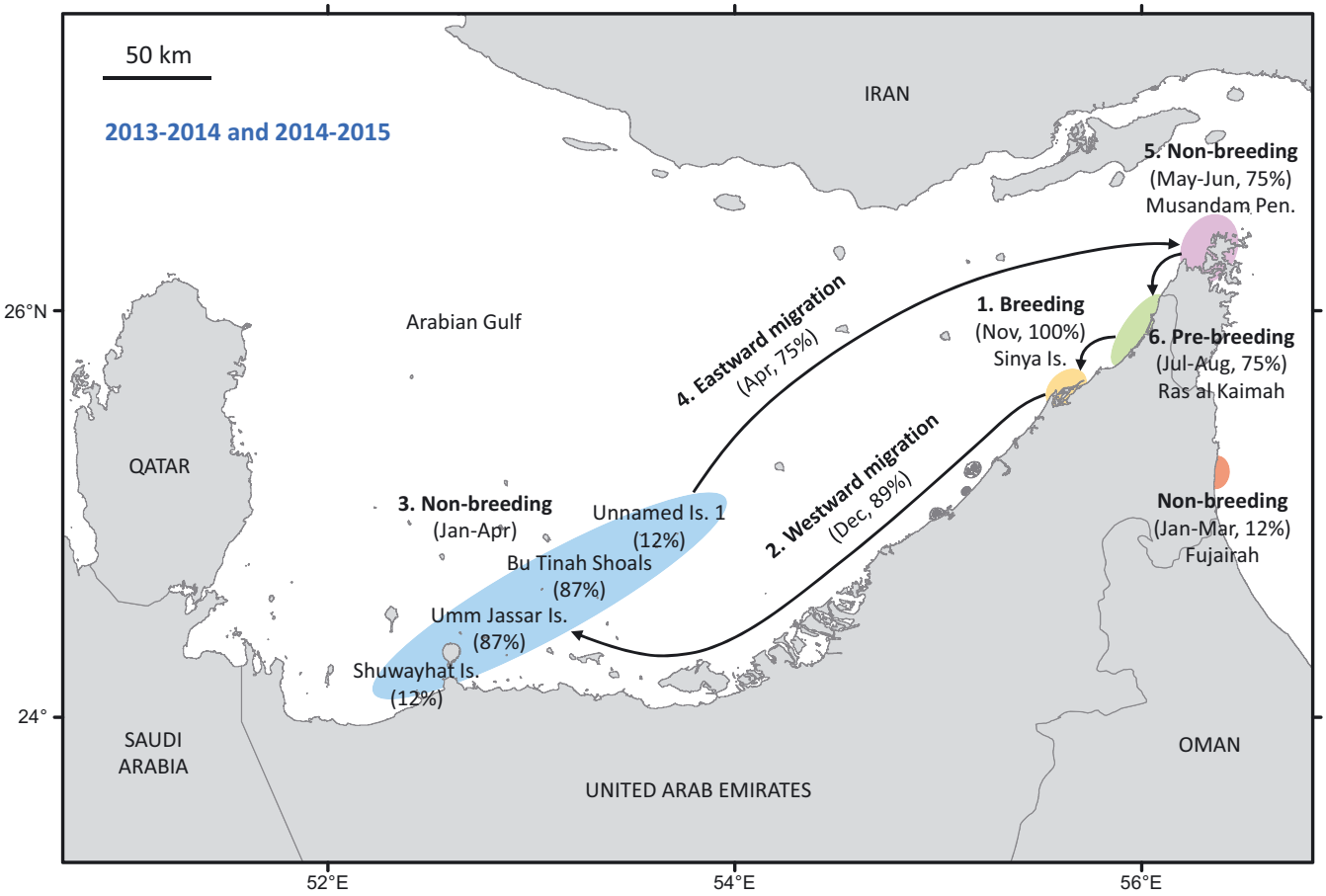
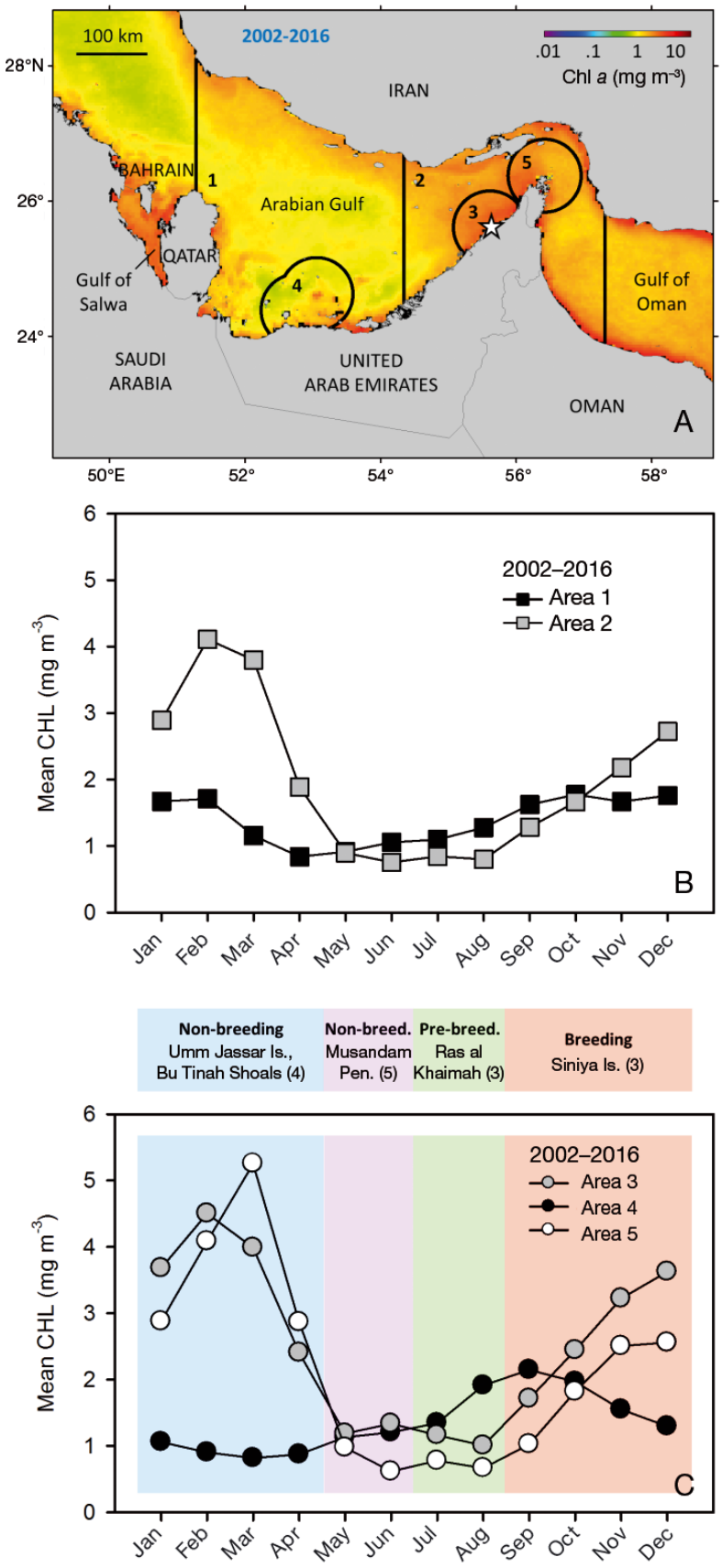


Fig. 5. Main migratory routes and non-breeding grounds of Socotra cormorants as determined from PTTs deployed on birds breeding at Siniya Island. Percentages correspond to the proportion of tracked individuals (i.e. number of PTTs recording during the corresponding time period). Following breeding (1), 89 % of birds with PTTs recording in December performed a westward migration from Siniya Island, closely following the coastline of the United Arab Emirates (2), while the remaining 12 % migrated east into the Gulf of Oman to the coast of Fujairah. Between January and April, Bu Tinah Shoals and Umm Jassar Island were the most important non-breeding locations (3); 87 % of individuals with PTTs recording at that time visited both localities. In April birds migrated eastward (4) to the non-breeding grounds of Musandam Peninsula (Oman) (5). The return migration used the same flyway as the outward migration, but for clarity it is shown farther north on the map. During pre-breeding (6), birds moved progressively south-westwards down the coastline towards Siniya Island. Breeding on Siniya Island occurs from September to December with a peak in November. The arrow linking the pre-breeding period (6) to the breeding period corresponds to a gap in PTT data during September to October, but is supported by observations at the colony (Muzaffar et al. 2017)

individuals from the Gulf of Salwa (south of Bahrain) venture out into the northern and central parts of the Gulf during post-breeding migration, thus potentially mixing with birds from Siniya at their non-breeding grounds off the western UAE. Seabird spatial segregation between conspecifics belonging to different nearby colonies has been reported during the breeding season, and is considered to result from density-dependent competition (Wakefield et al. 2013). It is not clear, however, how widespread such a spatial segregation might be during the non-breeding season, or what mechanisms drive bird behaviour during this stage (Thiebot et al. 2012, Ratcliffe et al. 2014).

Link between bird movements, primary productivity and fish migration

Socotra cormorant distribution patterns did not match consistently with CHL (Figs. 5, 6 & S2). The Gulf and the Gulf of Oman have predictable temporal patterns of primary productivity (Fig. S2; Nezlin et al. 2007). High phytoplankton growth begins in October within the Gulf of Salwa, in the coastal areas near Siniya Island and around the Strait of Hormuz and expands through much of the northern Gulf (Fig. S2; John et al. 1990, Nezlin et al. 2007, Al Rashidi et al. 2009, Nandkeolyar et al. 2013). These



blooms correspond with the peak breeding period at Siniya Island (Muzaffar et al. 2017) and presumably also in the Gulf of Salwa colonies (Jennings 2010). A massive bloom also develops in October within the Gulf of Oman which peaks in March (Fig. S2; Nezlin et al. 2007). Socotra cormorants nesting on Siniya Island are therefore surrounded by areas with high primary productivity during these months. Following March, phytoplankton blooms disperse abruptly and, aside from the Gulf of Salwa (which was not used by cormorants from Siniya Island), primary productivity becomes low, both in the open waters of the Gulf and in the Gulf of Oman. In summary, there is a temporal and spatial match between primary productivity and breeding cormorant distribution, but not between primary productivity and non-breeding cormorant distribution.

The match–mismatch hypothesis predicts that marine top predators like seabirds should breed more successfully when their breeding season overlaps with the seasonal peak in prey availability (Cushing 1990, Durant et al. 2007, Ramírez et al. 2016). Expanding on this notion,

Fig. 6. Mean monthly chlorophyll *a* concentration (CHL) over the period 2002–2016 within the annual distribution range of Socotra cormorants which breed on Siniya Island. (A) Distribution map of average daily CHL from 2002 to 2016 and areas for which CHL data was calculated. Areas 1 and 2, separated by vertical lines on the map, were defined to provide information on regional trends within the range of the population considered in this study. Areas 3, 4 and 5 include main roosting areas of birds throughout the year, i.e. those which were visited by 75 to 100% of tracked birds (see Fig. 5). Area 3: breeding grounds centred on Siniya Island (white star); Area 4: non-breeding grounds centred on Umm Jassar Island and Bu Tinah Shoals; Area 5: non-breeding grounds in the Strait of Hormuz centred on Musandam Peninsula. The radius of circles is 60 km, corresponding to the maximum foraging range of Socotra cormorants. (B) Mean monthly CHL in Areas 1 and 2. (C) Mean monthly CHL in Areas 3, 4 and 5, with stages, locations and associated area numbers of birds over the course of the year indicated by vertical coloured shading'

Socotra cormorants are expected to adjust the phenology of the different phases of their biological cycle to those of their main prey throughout the year. This year-round correlation is found in other migratory seabird species, such as in the sooty shearwater *Puffinus griseus* (Shaffer et al. 2006) or in the Arctic tern *Sterna paradisaea* (McKnight et al. 2013). Breeding Socotra cormorants feed on anchovy *Encrasicholina* spp., bluestripe herring *Herklotsichthys quadrimaculatus* and African sailfin flying fish *Parexocoetus mento* (Muzaffar et al. 2015b). Although these shoaling, phyto- and zooplanktivorous fish should benefit from areas of high primary productivity, the mismatch between primary productivity and Socotra cormorants at their non-breeding grounds suggests that this is not always the case in the southern Gulf.

Patterns of fish movement could help explain the observed patterns of Socotra cormorant movement. We are not aware of any published study documenting the movements of small pelagic fish within the Gulf. Anchovy and sardine *Sardinella* spp. are however believed to migrate westwards along the UAE shoreline or north-westwards in late December to early January (Ministry of Climate Change and Environment pers. comm.), precisely when Socotra cormorants from Siniya Island are moving westwards to their non-breeding grounds off the western coast of the UAE. Off nearby coastal Iran, Salarpour et al. (2008) showed that the diet of the buccaneer anchovy *E. punctifer* consisted primarily of copepods, copepod eggs, *Nauplius* larvae and a range of diatoms, dinoflagellates and other phytoplankton. Temporal variation was evident in their diet, with stomach fullness indices being highest in winter, which is consistent with the high CHL and low sea surface temperature in the central part of the Gulf during that period (Nezlin et al. 2007). Once sea surface temperature starts to increase and blooms begin to disperse after February, buccaneer anchovy presumably migrate northwestwards, where sea surface temperature is cooler than in the southern Gulf during the summer (John et al. 1990, Nezlin et al. 2007).

The study of the migratory cycle of large predatory fish feeding on forage fish seem to correspond to the migratory pattern of forage fish. The Indo-Pacific sailfish *Istiophorus platypterus*, a resident of the Gulf, undergoes regional migratory movements (Hoolihan et al. 2004, Hoolihan 2006, Hoolihan & Luo 2007). Satellite telemetry of sailfish showed a northwestward migration across the Gulf beginning in March (Hoolihan & Luo 2007), presumably consistent with the migratory route taken by small pelagic fish in winter. We propose that the northwestward migratory pathway of small forage fish from the eastern to the northern Gulf drives the post breeding movement of Socotra cormorants from Siniya Island to their non-breeding area off the western UAE. It is not clear, however, what drives the second migratory phase of cormorants to their non-breeding grounds in the Strait of Hormuz and further studies examining small pelagic fish migration inside the Gulf should shed further light on some of the drivers of Socotra cormorant movements.

Conservation implications

This is the first study attempting to quantify the migratory ecology of Socotra cormorants. The importance of a wide portion of the southern Gulf in sustaining populations of this species is highlighted. Socotra cormorants consistently used the same non-breeding areas during 2 consecutive years, pointing to specific islands (e.g. Bu Tinah Shoals and Umm Jassar Island; Fig. S1D) or cliffs (e.g. Ash Sham and Ghubb 'Ali Fjords on Musandam Peninsula; Fig. S1G) and their surrounding waters as areas of high conservation priority. Islands are an important breeding and roosting habitat for seabirds, as they generally host fewer predators than the mainland, and are closer to foraging grounds (Schreiber & Burger 2002). In the Gulf, radical human island transformation (Sheppard et al. 2010) has wiped out several breeding colonies (Jennings 2010, EAD 2014, BirdLife International 2017) and is presumably also preventing non-breeding birds from using many transformed islands for roosting. Thus, current bird numbers and active breeding and roosting localities likely reflect habitat selection by populations that have been disturbed by humans in the recent past or are currently under disturbance.

Socotra cormorants exhibited a directional, albeit short, migration, which is most likely a consequence of their highly gregarious behaviour linked to their dependence on group foraging to secure their prey (Cook et al. 2017). The use of CHL as a proxy of forage fish concentration did not provide convincing results for predicting non-breeding grounds of cormorants. Inferring consumer productivity from primary productivity has produced mixed results in the marine environment (e.g. Suryan et al. 2012, Grémillet et al. 2008, Sherley et al. 2017) and this is presumably the consequence of several processes, including spatial and temporal lags in the responses of secondary and tertiary consumers to primary productivity (Sur-

yan et al. 2012). Assuming non-breeding grounds off the western UAE host most birds from Siniya Island from January to April, cormorants extract from these waters up to 70 t of fish per day (Muzaffar et al. 2015b, Cook et al. 2017) during that period. This is likely an underestimate since it does not account for birds that were breeding at other colonies in the area and that might also use those same waters during non-breeding. Such a high biomass of prey could correspond to forage fish migrating through the area at this time of year, as suggested above. Fish might also concentrate locally under the effect of high primary productivity in a zone that was not part of our sampling area, but still close nearby. Indeed, a small cell of high CHL is present all year round south of Salahah Island (Figs. S1C & S2), just outside the foraging range of cormorants roosting on Umm Jassar Island or Bu Tinah Shoals (Fig. 6A). Further west, the Gulf of Bahrain and the Gulf of Salwa, which also have high productivity all year long and unique water chemistry, presumably retain some of the fish stocks throughout the year (Nezlin et al. 2007). In summary, the major colonies of Siniya Island and in the Gulf of Salwa benefit from high and predictable local primary productivity during the breeding season, which has important consequences for conservation. Islands available to breeding birds are limited, and cormorants would face difficulty in relocating to alternative areas of high productivity if these colonies were threatened by human development. Outside of the breeding season, roosts are also chosen because they are free of human disturbance and close to foraging areas with high fish density.

The conservation of the Socotra cormorant faces political challenges. Socotra cormorants breeding on Siniya Island span over 3 different jurisdictions (in at least 2 different countries) during the course of their annual migratory cycle. The vast majority of cormorants migrate towards waters in the southern part of the Gulf, under the jurisdiction of Abu Dhabi Emirate, one of the 7 emirates of the UAE, although some birds visited the nearby Qatari waters. Cormorants then migrate to the Musandam area, which falls under the jurisdiction of the Sultanate of Oman. During breeding, the Siniya Island population converges under the jurisdiction of Umm Al Quwain, another emirate of the UAE. The Abu Dhabi Emirate has an active environmental agenda promoting conservation of biodiversity with a separate mandate for marine conservation, overseen by the Federal Environment Agency of Abu Dhabi (EAD 2014). The Umm Al Quwain Emirate has its own management under the auspices of the Ministry of Climate Change and Environment, with an emphasis on the protection of marine fish resources. In the Sultanate of Oman, the Ministry of Environment and Climate Affairs oversees environmental protection and pollution control. The Federal Law of the UAE prohibits egg collection, hunting of adults or chicks or destruction of habitat of Socotra cormorants (United Arab Emirates Federal Law No. (24) of 1999 for protection and development of the environment) (Muzaffar et al. 2017). However, current protection measures are clearly not sufficient. The importance of Siniya Island as an Important Bird Area (Evans 1994) and the single largest breeding concentration of the species in the eastern Gulf (ca. 35% of the world breeding population) is already recognized (Muzaffar et al. 2017). It is now essential to develop a conservation plan under which all 3 jurisdictions collaborate to define the best approach to monitor the status of this threatened species and promote conservation actions for its long-term sustainability.

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LITERATURE CITED

Al-Deeb MA, Frangoulidis D, Walter MC, Kömpf D, Fischer SF, Petney T, Muzaffar SB (2016) Coxiella-like endosymbiont in argasid ticks (*Ornithodoros muesebecki*) from a Socotra Cormorant colony in Umm Al Quwain, United Arab Emirates. Ticks Tick Borne Dis 7:166–171

Al Rashidi T, El Gamily H, Amos C, Rakha K (2009) Sea surface temperature trends in Kuwait Bay, Arabian Gulf. Nat Hazards 50:73–82

Aspinall SJ (2010) Breeding birds of the United Arab Emirates. Environmental Agency, Abu Dhabi

Barrett RT, Chapdelaine G, Anker-Nilssen T, Mosbech A, Montevecchi WA, Reid JB, Veit RR (2006) Seabird numbers and prey consumption in the North Atlantic. ICES J Mar Sci 63:1145–1158

BirdLife International (2017) *Phalacrocorax nigrogularis* (amended version published in 2016). The IUCN Red List of Threatened Species 2017: e.T22696802A112380428. www.iucnredlist.org (accessed 12 Jan 2017)

Boyd I, Wanless S, Camphuysen CJ (2006) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge

Brooke M de L (2004) The food consumption of the world's seabirds. Proc Biol Sci 271:S246–S248

Burt J, Feary D, Bauman A, Usseflio P, Cavalcante G, Sale P (2011) Biogeographic patterns of reef fish community

structure in the northeastern Arabian Peninsula. ICES J Mar Sci 68:1875–1883
CMS (Conservation of Migratory Species of Wild Animals) (2015) Appendix I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), as amended by the Conference of the Parties in 1985, 1988, 1991, 1994, 1997, 1999, 2002, 2005, 2008, 2011 and 2014. www.cms.int/en/page/appendix-i-ii-cms (accessed 12 Jan 2017)
Cook TR, Gubiani R, Ryan PG, Muzaffar SB (2017) Group foraging in Socotra cormorants: a bio-logging approach to the study of a complex behaviour. Ecol Evol 7: 2025–2038
Cooke SJ (2008) Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endang Species Res 4:165–185
Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34
Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Blaxter JHS, Southward AJ (eds) Advances in marine biology. Academic Press, San Diego, CA, p 250–313
Duong T (2007) ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. J Stat Softw 21:1–16
Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283
EAD (Environment Agency – Abu Dhabi) (2014) Biodiversity annual report 2014: status of key breeding birds in Abu Dhabi. Environment Agency – Abu Dhabi, Abu Dhabi
Evans M (1994) Important bird areas in the Middle East, Vol. 2. Birdlife International, Cambridge
Fayet AL, Freeman R, Shoji A, Boyle D and others (2016) Drivers and fitness consequences of dispersive migration in a pelagic seabird. Behav Ecol 27:1061–1072
Frederiksen M, Wright PJ, Harris MP, Mavor RA, Heubeck M, Wanless S (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. Mar Ecol Prog Ser 300:201–211
Frederiksen M, Furness RW, Wanless S (2007a) Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. Mar Ecol Prog Ser 337:279–286
Frederiksen M, Edwards M, Mavor RA, Wanless S (2007b) Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. Mar Ecol Prog Ser 350:137–143
Grandcourt E (2012) Reef fish and fisheries in the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, London, p 127–162
Grecian WJ, Witt MJ, Attrill MJ, Bearhop S and others (2016) Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biol Lett 12:20160024
Grémillet D, Lewis S, Drapeau L, van Der Lingen CD and others (2008) Spatial match–mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? J Appl Ecol 45:610–621
Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic puffin and its implications for migratory navigation. PLOS ONE 6:e21336
Guillaumet A, Dorr BS, Wang G, Taylor JD and others (2011) Determinants of local and migratory movements of Great Lakes double-crested cormorants. Behav Ecol 22:1096–1103
Hällfors MH, Liao J, Dzurisin J, Grundel R and others (2016) Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecol Appl 26:1154–1169
Hoolihan JP (2006) Age and growth of Indo-Pacific sailfish, *Istiophorus platypterus*, from the Arabian Gulf. Fish Res 78:218–226
Hoolihan JP, Luo J (2007) Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf. ICES J Mar Sci 64: 1791–1799
Hoolihan JP, Premanandh J, D'Aloia-Palmieri MA, Benzie JAH (2004) Intraspecific phylogeographic isolation of Arabian Gulf sailfish *Istiophorus platypterus* inferred from mitochondrial DNA. Mar Biol 145:465–475
Jennings MC (2010) Atlas of the breeding birds of Arabia. Fauna Arab 25:216–221
John VC, Coles SL, Abozed AI (1990) Seasonal cycles of temperature, salinity and water masses of the Western Arabian Gulf. Oceanol Acta 13:273–281
King TD, Strickland BK, Radomski AA (2012) Winter and summer home ranges and core use areas of double-crested cormorants captured near aquaculture facilities in the southeastern United States. Waterbirds 35:124–131
Lascelles BG, Langham GM, Ronconi RA, Reid JB (2012) From hotspots to site protection: identifying Marine Protected Areas for seabirds around the globe. Biol Conserv 156:5–14
Lewison R, Oro D, Godley B, Underhill L and others (2012) Research priorities for seabirds: improving conservation and management in the 21st century. Endang Species Res 17:93–121
Mallory ML, Robinson SA, Hebert CE, Forbes MR (2010) Seabirds as indicators of aquatic ecosystem conditions: a case for gathering multiple proxies of seabird health. Mar Pollut Bull 60:7–12
McKnight A, Irons DB, Allyn AJ, Sullivan KM, Suryan RM (2011) Winter dispersal and activity patterns of post-breeding black-legged kittiwakes *Rissa tridactyla* from Prince William Sound, Alaska. Mar Ecol Prog Ser 442: 241–253
McKnight A, Allyn AJ, Duffy DC, Irons DB (2013) 'Stepping stone' pattern in Pacific Arctic tern migration reveals the importance of upwelling areas. Mar Ecol Prog Ser 491: 253–264
Miller MR, Takekawa JY, Fleskes JP, Orthmeyer DL, Casazza LM, Haukos DA, Perry WM (2005) Flight speeds of northern pintails during migration determined using satellite telemetry. Wilson Bull 117:364–374
Montevecchi WA (1993) Birds as indicators of change in prey stocks. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266
Monticelli D, Ramos JA, Quartly GD (2007) Effects of annual changes in primary productivity and ocean indices on breeding performance of tropical roseate terns in the western Indian Ocean. Mar Ecol Prog Ser 351:273–286

Muzaffar SB, Takekawa JY, Prosser DJ, Douglas DC and others (2008) Seasonal movements and migration of Pallas's gulls *Larus ichthyaetus* from Qinghai Lake, China. Forktail 24:100–107

Muzaffar SB, Gubiani R, Benjamin S (2012) Reproductive performance of the Socotra cormorant (*Phalacrocorax nigrogularis*) on Siniya Island, United Arab Emirates: planted trees increase hatching success. Waterbirds 35: 626–630

Muzaffar SB, Gubiani R, Benjamin S (2013) The impact of fox and feral cat predation on breeding Socotra cormorants. Mar Ornithol 41:171–177

Muzaffar SB, Gubiani R, Benjamin S (2015a) Nest-site location influences hatching success in the Socotra cormorant. Wildl Res 42:13–18

Muzaffar SB, Gubiani R, Benjamin S, Alshihi R, Al Romithi A, Al Kaabi F (2015b) Food consumption patterns of Socotra cormorants (*Phalacrocorax nigrogularis*) indicate minimal overlap with fisheries in the eastern Arabian Gulf. Oryx 51:115–123

Muzaffar SB, Whelan R, Clarke C, Gubiani R, Benjamin S (2017) Breeding population biology in Socotra cormorants (*Phalacrocorax nigrogularis*) in the United Arab Emirates. Waterbirds 40:1–10

Nandkeolyar N, Raman M, Kiran GS, Ajai (2013) Comparative analysis of sea surface temperature pattern in the eastern and western gulfs of Arabian Sea and the Red Sea in recent past using satellite data. Int J Oceanogr 2013:501602

Newton I (2008) The migration ecology of birds. Academic Press, London

Nezlin NP, Polikarpov IG, Al-Yamani F (2007) Chlorophyll distribution in the Arabian Gulf: spatial, seasonal and inter-annual variability. Int J Oceanogr 21:139–156

Orta J (1992) Family Phalacrocoracidae (Cormorants). In: Del Hoyo AE, Sargatal J (eds) Handbook of the birds of the world, Vol 1. Lynx Edicions, Barcelona, p 326–353

Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. PLOS ONE 10:e0129342

Parsons M, Mitchell I, Butler A, Ratcliffe N, Frederiksen M, Foster S, Reid JB (2008) Seabirds as indicators of the marine environment. ICES J Mar Sci 65:1520–1526

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120: 1082–1090

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 86:2386–2396

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramírez F, Afán I, Tavecchia G, Catalán IA, Oro D, Sanz-Aguilar A (2016) Oceanographic drivers and mistiming processes shape breeding success in a seabird. Proc Biol Sci 283:20152287

Ratcliffe N, Crofts S, Brown R, Baylis AMM and others (2014) Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. J Biogeogr 41: 1183–1192

Riegl B, Purkis S (2012) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht

Salarpour A, Darvishi M, Behzadi S, Seraji F (2008) Reproduction and feeding of buccaneer anchovy (*Encrasicholina punctifer*) from coastal waters of Qeshm Island, the Persian Gulf. Iran Sci Fish J 17:45–54

Schreiber EA, Burger J (2002) Seabirds in the marine environment. CRC Press, Boca Raton, FL

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Natl Acad Sci USA 103:12799–12802

Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F and others (2010) The Gulf: a young sea in decline. Mar Pollut Bull 60:13–38

Sherley RB, Ludynia K, Lamont T, Roux JP, Crawford RJM, Underhill LG (2013) The initial journey of an endangered penguin: implications for seabird conservation. Endang Species Res 21:89–95

Sherley RB, Ludynia K, Dyer BM, Lamont T and others (2017) Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. Curr Biol 27: 563–568

Shoji A, Aris-Brosou S, Owen E, Bolton M and others (2016) Foraging flexibility and search patterns are unlinked during breeding in a free-ranging seabird. Mar Biol 163:72

Sonnevend A, Nowotny N, Kolodzjiejek J, Howarth B, Pal T (2011) *Coxiella burnettii* carriage by ticks collected from Socotra cormorants in the Arabian Gulf. Trop Med Int Health 16:73

Suryan RM, Santora JA, Sydeman WJ (2012) New approach for using remotely sensed chlorophyll *a* to identify seabird hotspots. Mar Ecol Prog Ser 451:213–225

Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. Ecology 93:122–130

Wakefield ED, Bodey TW, Bearhop S, Blackburn J and others (2013) Space partitioning without territoriality in gannets. Science 341:68–70

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