

Foraging movements of great frigatebirds from Aldabra Island: Relationship with environmental variables and interactions with fisheries

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ABSTRACT

Great Frigatebirds (*Fregata minor*) are large tropical seabirds that rely primarily on sub-surface predators such as tunas or cetaceans to capture their prey. We studied the foraging movements of 14 Great Frigatebirds breeding on Aldabra Island (9.4°S, 46.4°E), the largest colony in the Indian Ocean. This colony is located at more than 500 km from the main fishing grounds of a very important industrial purse-seine fishery targeting surface-dwelling tunas. Despite their slow flight speeds (16 km h⁻¹), frigatebirds are able to forage at more than 1000 km from the colonies when breeding, using 2500–4750 km long foraging loops over oceanic waters. All trips were directed to the north of the island up to the equator. Foraging bouts, indicated by reduced flight speeds, were rare and located throughout the trips. Foraging spots tended to be more frequent on higher surface chlorophyll concentration and in association with some cyclonic vortices. However, mesoscale activity is relatively weak between Aldabra and the equator and the chlorophyll variability is mostly the result of wind-mixing processes during the southwest monsoon. These results suggest that frigatebirds forage for widely distributed resources to the north of Aldabra. The northernmost foraging bouts were located in the vicinity of the purse-seine fishing grounds, but without a significant overlap between frigatebirds and tuna fleets. The results of the study are compared with those from another population at Europa Island (22.3°S, 40.3°E) where birds were foraging on predictable features, the edge of cyclonic eddies that are marked in the Mozambique Channel. We discuss the consequences of the reliance of populations on contrasted oceanographic conditions on foraging strategies and on the evolution of life histories in these long-lived animals in a changing climate, as well as the possible effects of overfishing on frigatebird populations.

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1. Introduction

Zones of high productivity and high prey densities tend to concentrate predators. In the marine environment, these zones are often marked, such as upwelling zones along continents, fronts, or zones of high geostrophic activities in the open oceans (e.g. Bakun, 2006). Marine predators such as seabirds forage over these zones of higher productivity (Hunt et al., 1999). Oceanic tropical waters are less productive overall than temperate and polar areas, and furthermore are less structured (Longhurst and Pauly, 1987). As a result, the distribution of prey concentrations is more unpredictable for predators, and the specific life history traits of tropical predators have been selected accordingly. For example tunas are highly mobile species that can cope for this constraint.

Seabirds are central place foragers during the breeding season, having to commute regularly between colonies and foraging zones during incubation or when they feed their chicks. Many species are

well known to associate with specific oceanographic features such as zones of upwelling, shelf edges, frontal zones or the edge of eddies (Haney, 1987; Hunt et al., 1999; Spear et al., 2001). In the tropical waters, because of the low productivity and patchy and unpredictable distribution of resources, seabirds have evolved specific foraging strategies that reduce flight costs and enhance flight efficiency (Ashmole, 1971; Ainley and Boekelheide, 1983; Flint and Nagy, 1984; Weimerskirch, 2007). Proficient locomotion in these predators allows them to travel over vast oceanic areas (Ballance and Pitman, 1999; Weimerskirch et al., 2004). One other characteristic of the foraging strategy of tropical seabirds is to feed primarily in multispecies flocks in association with sub-surface predators, especially tunas but also other large fishes or dolphins (Au and Pitman, 1986), that bring prey close to the surface in the open ocean.

Frigatebirds are tropical seabirds with extreme life history traits. Although they rely entirely on marine resources, they are the only marine animal that never enters into the marine environment, and does not even sit on the sea surface (Weimerskirch et al., 2003, 2004). They have the lowest wing loading (ratio mass over wing surface) of all birds, allowing them to spend long periods

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gliding and soaring over the sea surface with extremely low energetic costs (Pennycuik, 1987). They stay aloft for days without sitting on the sea surface or on land, at average altitudes of 200 m, but reaching altitudes up to 2800 m (Weimerskirch et al., 2003, 2004). Compared to other seabirds, they have an even more extreme breeding strategy, with extremely low provisioning rate and growth of chicks, and probably very long life span (Weimerskirch, 2002). Like many tropical seabirds, frigatebirds rely to a large extent on association with sub-surface predators, but probably even more than other seabirds because they are unable to dive or rest on the water surface, and are thus specialised in snatching prey just at or near the surface (Ashmole, 1971). It should therefore be expected that frigatebirds should concentrate in areas where sub-surface predators are concentrated.

A previous study has shown that frigatebirds from Europa Island in the Mozambique Channel concentrate foraging effort over specific habitats, the edges of cyclonic eddies (Weimerskirch et al., 2004). Cyclonic eddies are generally assumed to have enhanced production at their edges (Bakun, 2006). The flow in the Mozambique Channel is dominated by an alternation of anti-cyclonic and cyclonic eddies that propagate southward (De Ruijter et al., 2002). These mesoscale features constitute a particular and localised habitat in tropical waters, so that such zones of enhanced production are probably not available in the vicinity of other frigatebird breeding grounds. In particular, the largest frigatebird colonies in the world, in the Galapagos and at Aldabra Island in the Indian Ocean, have no such features in the vicinity of the colonies (Chelton et al., 2007). This suggests that frigatebirds at those sites have either to travel farther away or to adopt different foraging strategies, with possible consequences on their life history traits.

The purpose of this work was first to study the foraging strategy of Great Frigatebirds (*Fregata minor*) breeding on Aldabra Atoll, in the western Indian Ocean, and to characterise the habitat used by this population. The second and central objective of the study was to compare the foraging strategies of two populations of frigatebirds breeding on Europa and Aldabra, i.e. on islands located in two distinctive marine environments. This comparison is used to examine two hypotheses, whether frigatebirds are able to adjust foraging strategies and foraging effort in relation to different environments, or alternatively, less favourable environment may affect foraging efficiency and ultimately breeding success. In addition, because they rely extensively on surface-dwelling tuna for foraging, it is hypothesized that a substantial decrease of tuna biomass due to fishing by industrial fleets would have negative effects on frigatebird populations, but this remains unstudied. Aldabra in particular, is located in the vicinity of a widely spread and active purse-seine and longline tuna fisheries (IOTC, 2008), and we examine here the possible overlap with such fisheries.

2. Methods

The study was carried out on Aldabra Island (9°24'S, 46°20'E) in the western Indian Ocean (Fig. 1) between 5 and 22 October 2006. Aldabra is a raised 35 km long × 13 km wide coralline atoll located 420 km northwest of Madagascar. It comprises four main islands circling a central lagoon, and many islets. Aldabra supports the largest breeding population of frigatebirds in the Indian Ocean, and the second largest in the world, with ca. 6000 pairs of Lesser Frigatebirds (*Fregata ariel*) and 4000 pairs of Great Frigatebirds (Diamond, 1975; Reville, 1983; Burger and Betts, 2001). The study was carried out on the eastern tip of Malabar Island, in the largest colony of frigatebirds, at Middle camp (see Reville, 1983; Burger and Betts, 2001). During our stay we counted 4096 active nests in this colony (2070 Great Frigatebirds nests and 2026 Lesser

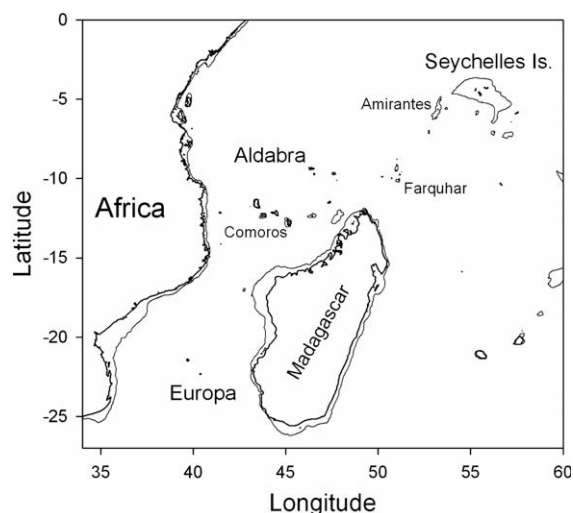


Fig. 1. Map of the south western Indian Ocean showing the –200 m depth contour (dotted line) separating shelf neritic areas from oceanic waters, and the location of Aldabra and the other islands.

Frigatebirds). Great Frigatebirds were observed at all stages of breeding, although the majority of nests contained either incubating adults or large chicks; few nests contained brooded chicks. In this colony the two species of frigatebirds nest in the mangrove or on Pemphis shrubs on small coralline islets called ‘champignons’.

From the hut at Passe Hoareau, we accessed the colony using kayaks. The colony was mapped using Google Earth® Image. By day, accessible nests with Great Frigatebirds were mapped, and also located precisely with GPS (Global Positioning System); nests were not approached to avoid disturbance of the colony. Males and females were distinguished using plumage characteristics: males have completely black plumage and a black bill and females have dark plumage with a white belly, bluish beak and pink eye ring. Since frigatebird colonies are very sensitive to disturbance, to avoid desertion or pirating of nest material by non-breeders, birds were handled only at night. We approached nests at night in a kayak in complete darkness, and birds were captured after being temporarily blinded with a powerful spotlight. We captured only birds that were incubating or brooding. Birds were captured by hand and fitted with a transmitter before being returned to their nests. Birds always resumed their breeding duties and using this technique, we had only two desertions immediately following attachment of the equipment. Nests were checked daily with binoculars from a distance of 30–100 m from the kayak. Birds were relieved by their partner and left for the sea. However breeding success in frigatebirds is naturally low (Diamond, 1975; Weimerskirch, personal observations), so the rate of nest desertion is high. Some nests were deserted by the partner, and thus when the bird equipped with a transmitter returned to find an empty nest, the bird returned to sea. Birds deserting the nest after being equipped plus three others that stopped breeding after finding an empty nest, were named failed breeders in the study. This allowed us to compare successive foraging trips of breeding birds followed by trips of the same bird as a failed breeder (i.e. with no constraints of breeding).

We fitted 14 birds (seven males and seven females) with Argos transmitters (PTT 100 with different packaging and batteries; Microwave telemetry, Columbia, MA, USA) weighing 18–20 g (five transmitters) and 30 g (nine transmitters), i.e. 1.2–3% of the mass of adults. Twelve birds were incubating and two rearing small chicks. The transmitters were taped on the back (30 g transmitters) or tail feathers (18–20 g transmitters) using Tesa® tape. Since we

left Aldabra before being able to recover all the PTTs on birds returning to their nest, they continued to transmit information until 15 November 2006. Based on past experience with frigatebird tracking, we expected the PTTs to be lost during moult, ca. 2–4 months after deployment. We obtained a total of 27 foraging trips, from 1 to 5 successive trips by the same birds, with 11 trips of incubating birds, 5 of brooding birds, the rest being trips of failed breeders.

The outward part of the trip was considered to be the section up to the point of maximum range from the colony, and the remainder of the trip considered the return portion. Because individuals were tracked for several successive trips, we avoided pseudoreplication by analysing data on the trip characteristics using mixed-model ANOVAs. Speed, range and distance covered were dependent variables, trip segment (return versus outward trip) and time (day versus night) as fixed factors, and the individual was considered a random factor.

The locations obtained by the Argos system were filtered following Weimerskirch et al. (1993), allowing for a maximum flight speed of 65 km h^{-1} for frigatebirds (Weimerskirch et al., 2003, 2004). Satellite telemetry data provided the location of animals but did not indicate whether birds were transiting between colonies and foraging grounds, or foraging. We therefore used periods with reduced flight speed as an indicator of foraging activity. This method has been validated by the use of transmitter and altimeters that indicate when birds come close to the surface to feed (Weimerskirch et al., 2004, unpublished data). Since frigatebirds come close to the surface to feed during the day only (Weimerskirch et al., 2004), we separated the period of reduced flight speeds into day and night time. In contrast to transit movements, we define a foraging bout as the area where daytime flight speed among at least three Argos locations, all in succession, was lower than 10 km h^{-1} . Very short time intervals between locations can produce erroneous estimates of speed because of the relative inaccuracy of the locations; therefore, we only used pairs of locations at sea separated by more than 30 min.

To quantify the overall foraging areas of the Aldabra frigatebirds, we used kernel estimation techniques to delineate foraging ranges and core habitat areas used by breeding birds fitted with satellite transmitters. We used the fixed kernel method (Worton, 1995) and the least square algorithm (Seaman and Powell, 1996). We estimated contours levels including 10–90% of the locations distribution (Wood et al., 2000; Hyrenbach et al., 2002). To characterise the habitat used by frigatebirds, we used bathymetry, sea level anomalies, and sea surface chlorophyll *a* concentrations. The chlorophyll *a* concentrations (CC), provided by the NOAA/GSFC (<http://oceancolor.gsfc.nasa.gov/SeaWiFS/>) were distributed daily on a $9 \text{ km} \times 9 \text{ km}$ grid. The CC values were log-transformed to handle normally distributed data for statistical analysis. We examined the daily data for October and November 2006 and found them considerably spoiled by cloud cover. We then constructed weekly and monthly composites by averaging the $\text{Log}_e(\text{CC})$ at each pixel. In the study area, there were still 35–60% of cloudy pixels in the weekly composites whereas all pixels had a CC value in the monthly composites. Because of the widespread and persistent cloud cover in the area, it was not possible to calculate correlations between the bird's locations and corresponding CC. Then, we tested the effect of CC on birds' activity by comparing the frequency distributions of available CC for the corresponding month (in the surveyed area), where birds flew (crossed) and where birds foraged.

Unlike the visible remote sensing, the altimetry data were not affected by presence of clouds. Sea-surface height anomalies (SSHA) and geostrophic current strength were available weekly with a spatial resolution of $1/3^\circ$ from MSLA products computed by Ssalto/Duacs and distributed by Aviso, with support from CNES

(<http://www.aviso.oceanobs.com/>). Wind direction and wind speed data were obtained from the “NASA JPL QuikSCAT Daily Level 3 Gridded Ocean Wind Vectors” (data product #109, <http://poet.jpl.nasa.gov>). Data from fisheries were obtained from IOTC (Indian Ocean Tuna Commission, <http://www.iotc.org>).

Summary statistics and nonparametric tests were performed with STATISTICA 6.0 and results are reported as mean \pm one standard deviation. The exploration of functional relationships between environmental variables and foraging activity was undertaken with Generalized Additive Models (GAMs) using R (*mgcv* package). GAMs are nonparametric generalizations of multiple linear regression techniques (Hastie and Tibshirani, 1990; Chambers and Hastie, 1992). We performed binomial GAMs as we tested the effect of the environment on the presence or absence of foraging. The foraging response was studied using a set of mesoscale descriptors (SSHA, vorticity, shear and stretch); however, as some of these descriptors are strongly correlated, we used the model with only SSHA. We prepared a matrix containing foraging locations and SSHA values of the corresponding weeks for the analysis. The model used the form:

$$E(\text{foraging}) = \beta_0 + s(\text{SSHA}) + s(\text{Lon}, \text{Lat}).$$

The SSHA predictor was modelled as a continuous variable. We also considered a spatial interaction effect that was modelled as a bivariate function of longitude and latitude.

3. Results

3.1. Foraging parameters

Incubating Great Frigatebirds foraged at sea for trips lasting between 8.3 and 11.7 days (mean: 9.8 ± 1.2 days) at a mean maximum range of 944 km from the colony (range: 680–1444 km). The mean total distance covered was 3270 km ranging from 2493 to 4730 km, with daily distances travelled of 332 km d^{-1} (Table 1). The average flight speed was $16.3 \pm 2.1 \text{ km h}^{-1}$ and flight speeds were significantly higher during the day ($17.6 \pm 2.7 \text{ km h}^{-1}$) than at night ($14.7 \pm 2.2 \text{ km h}^{-1}$; Wilcoxon test for paired samples, $Z = 3.2$, $p = 0.001$). There were no significant differences between the foraging parameters of males and females during incubation (Mixed ANOVAs: flight speed $F_{1,9} = 0.01$, $p = 0.967$; duration of trip $F_{1,9} = 0.365$, $p = 0.556$; foraging range $F_{1,10} = 0.208$, $p = 0.665$), so data for both sexes were pooled.

Periods of reduced flight speeds occurred on average 6.7 times per trip, (i.e. 0.67 times daily since the average trip lasts 10 days) and represented 13.3% of the total foraging trip (Table 1). Periods of reduced speed at night were more numerous (0.441 period of reduced speed daily) and longer than those conducted during the day (Table 1). The period of reduced speed during daytime or foraging bouts (see Section 2) were more abundant in the evening, with reduced foraging activity in the morning and at midday (Fig. 2). There was on average 2.5 foraging bouts per trip (0.257 bouts d^{-1}), representing 4.3% of the total foraging trip (Table 1).

In brooding birds, trips were shorter (5.2 ± 3.5 days) and individuals foraged closer to Aldabra (maximum range $325 \pm 227 \text{ km}$) whereas failed breeders had trips of similar duration but more variable (8.4 ± 9.4 days, range: 0.9–20.6 days), with three birds travelling to different islands from where they foraged during short trips.

3.2. Foraging movements of breeding birds

Foraging movements of incubating frigatebirds consisted of long looping tracks (Fig. 3), in a clockwise direction, all directed to the north of Aldabra. When leaving the colony, all birds headed to the north–north west, and the return movement of the birds was

Table 1

Comparison between the foraging parameters of Great Frigatebirds from Aldabra Island and Europa Island. Data reported as mean \pm one standard deviation (sample size) and range. Significant p -values in bold.

	Aldabra	Europa	Mixed ANOVA
Duration of foraging trip (days)	9.8 \pm 1.2 (9) 8.3–11.7	5.8 \pm 1.8 (52) 3–12	$F_{1,12} = 10.9$, $p = 0.0064$
Foraging range (km)	944 \pm 207 (10) 680–1444	349 \pm 173 (10) 72–600	$F_{1,13} = 34.1$, $p < 0.001$
Total distance covered (km)	3270 \pm 619 (9) 2493–4730	1400 \pm 811 (10) 234–3201	$F_{1,17} = 31.2$, $p < 0.001$
Daily distance covered (km d ⁻¹)	332 \pm 42 (9) 266–404	262.3 \pm 52 (10) 152–420	$F_{1,12} = 6.4$, $p = 0.027$
Flight speed (km h ⁻¹) Over entire trip	16.3 \pm 2.1 (10) 12.4–20.2	14.7 \pm 1.4 (10) 10.9–17.2	$F_{1,16} = 3.2$, $p = 0.092$
Daily number of periods of reduced speed	0.672 \pm 0.459 0.107–0.672	1.22 \pm 0.861 (10) 0–2.6	$F_{1,17} = 4.9$, $p = 0.062$
Percentage of foraging time with reduced speed	13.3 \pm 9.0 (9) 0–26.8	22.6 \pm 16.6 (10) 0–45.5	$F_{1,17} = 2.2$, $p = 0.155$
Daily number of foraging bouts	0.257 \pm 0.301 (9) 0–1.04	0.665 \pm 0.503 (10) 0–1.3	$F_{1,17} = 5.4$, $p = 0.032$
Daily number of stops at night	0.421 \pm 0.205 (9) 0.11–0.645	0.599 \pm 0.436 (10) 0–1.37	$F_{1,17} = 1.24$, $p = 0.280$
Percentage of foraging bouts/total trip duration	4.3 \pm 5.6 (9) 0–16.7	12.7 \pm 8.4 (10) 0–24.1	$F_{1,17} = 6.8$, $p = 0.018$
Percentage of time spent at night stopped/total trip duration	9.3 \pm 5.2 (9) 1.4–16.7	11.8 \pm 8.7 (10) 0–23.2	$F_{1,17} = 0.54$, $p = 0.473$
Flight speed by day	17.7 \pm 1.2 (9)	15.3 \pm 1.1 (10)	$F_{1,17} = 4.5$, $p = 0.042$
Flight speed at night	14.5 \pm 1.1 (9)	14.5 \pm 1.5 (10)	$F_{1,17} = 0.07$, $p = 0.933$

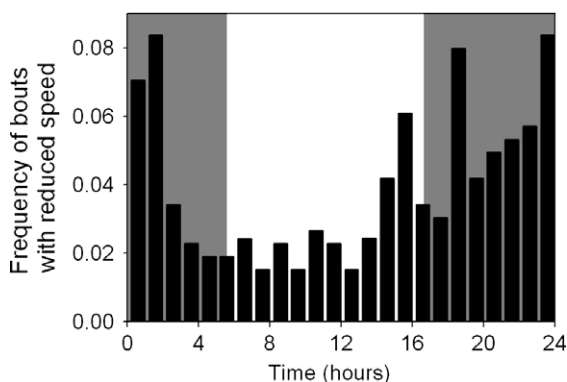


Fig. 2. Distribution of the timing of foraging bouts derived from satellite telemetry data when birds reduced their flight speed under 10 km h⁻¹ (periods of darkness denoted with grey).

mainly to the southwest (Fig. 3). Some individuals reached waters close to the equator located ca. 1000 km north of the colony. Throughout the study period, strong south-easterly winds were occurring. When leaving the colony, all birds had a north–north-west route (Fig. 3), which was probably facilitated by tail winds, whereas the return part was made with head or side winds. The speed of the outward phase of the foraging trip was significantly higher than the return phase (16.8 \pm 18.1 km h⁻¹ and 15.0 \pm 9.8 km h⁻¹, respectively, Mixed ANOVA $F_{1,10} = 8.9$, $p = 0.018$). Foraging bouts were distributed throughout the range, with no particular hotspot.

3.3. Foraging movements of failed breeders

Five birds were tracked after breeding failure on their nest. After returning to the nest and finding it deserted, three birds continued to perform looping foraging trips similar to those of breeding birds

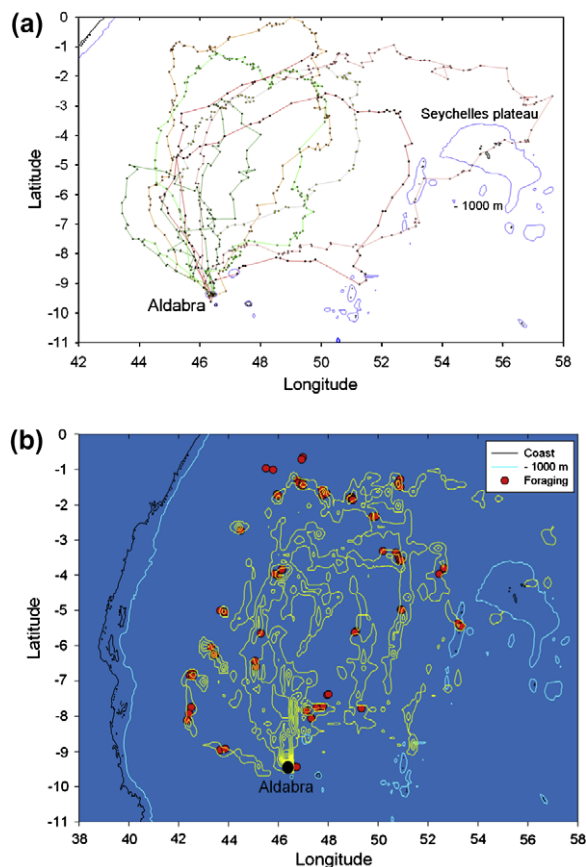


Fig. 3. (a) Foraging trips from Aldabra of six different individuals during incubating and (b) Kernel distribution of all locations of incubating birds.

(similar range and speed; Fig. 4), with one bird ending on the Farquhar Islands, 600 km to the east of Aldabra (Fig. 1). Two birds

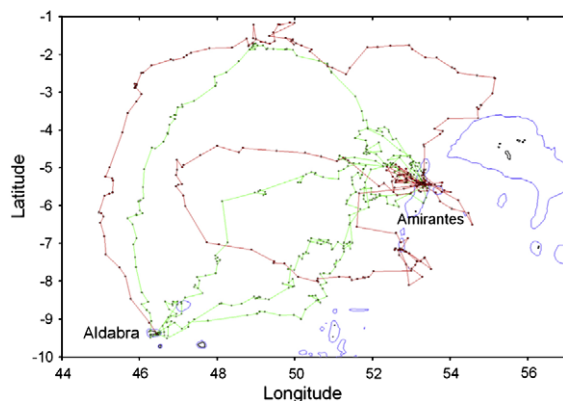


Fig. 4. Foraging movements of two failed breeders from Aldabra, and later from the Amirantes Islands.

moved to the Amirantes and foraged from D'Arros Island, performing short foraging trips (1–3 days, range 120 km) with stays of 2–5 days on the island (Fig. 4).

3.4. Foraging habitat

The foraging zone of incubating Aldabra Great Frigatebirds ranged strictly over oceanic waters north of the breeding island, up to the equator (Fig. 3). At the time of the study the average Chlorophyll Concentration (CC) of the foraging zone was $0.20 \pm 0.05 \text{ mg m}^{-3}$ and $0.13 \pm 0.03 \text{ mg m}^{-3}$ in October and November, respectively. These concentrations were slightly below the 2000–2005 average but they remain within the standard deviation about the mean. In October 2006, CC were higher in the west part (42°E – 50°E) of the study area except a ridge of relatively higher values

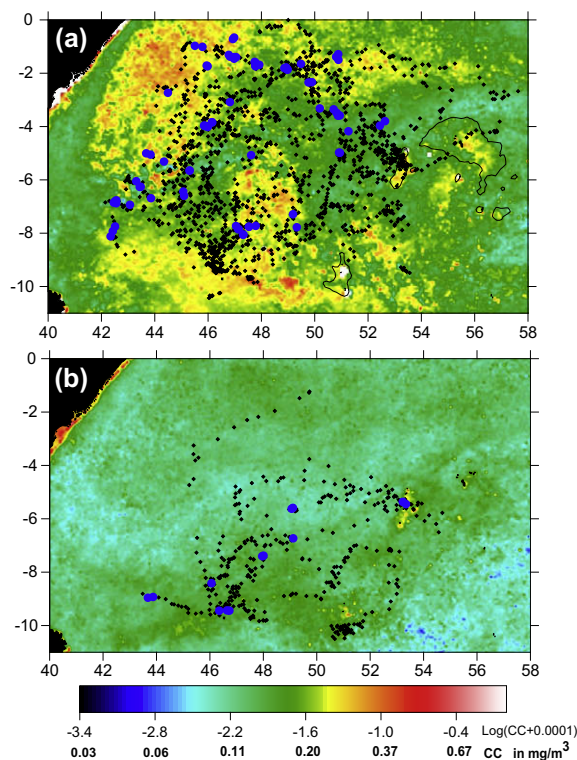


Fig. 5. Chlorophyll concentrations (CC) observed by Sea WIFS for: (a) October and (b) November 2006. Locations of birds are in black dots and foraging spots in blue dots.

along 2°S at all longitudes (Fig. 5a). In November 2006, CC decreased significantly and higher values were mostly found in the southern area (8 – 10°S) and in the vicinity of Amirantes Islands (Fig. 5b). Foraging bouts appear more frequently in the west region in October and in the south region in November. Crossed and foraged distributions were similar ($\chi^2_1 = 9.9$, $p = 0.827$) whereas they both differed significantly from the distribution of available CC ($\chi^2_2 = 69.5$, $p < 0.0001$) indicating that birds tended to concentrate their search in the most productive areas (Fig. 6).

During the study period, there was a trough in the sea-surface height between 4°S and 8°S , that developed gradually to the west (Fig. 7). There were more negative SSHA than positive ones; the strongest SSHA gradients occurred during the second part of the tracking experiment (26 October–8 November). Most of the flight and foraging spots are restricted to negative SSHA. There are also some occurrences in close association with SSHA gradients and cyclonic eddies, such as during the first, third and fourth week of the tracking experiment (Figs. 7a, c, and d). The GAM model explained 18.5% of the deviance (Table 2). The shape of the response (Fig. 8) reflects a positive effect of cyclonic vortices on foraging. The positive trend appearing for SSHA larger than $+5 \text{ cm}$ should not be considered because of the large 95% confidence interval.

3.5. Location of fisheries

The distribution of catches by the purse-seine fishery between 1991 and 2006 shows that fishing occurs generally within the range of the Aldabra frigatebirds breeding population (Figs. 9a and 10a). During the study period, the purse-seine fishery was

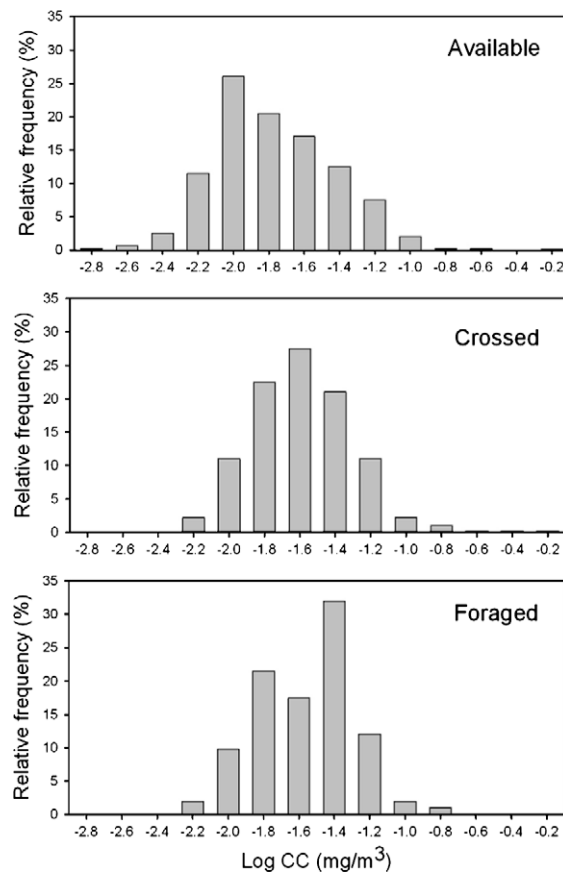


Fig. 6. Frequency distributions of CC present in the study area (upper panel), present in the area over which birds flew (middle panel) and present in areas where birds forages (lower panel). CC values are expressed in $\text{Log}_e(\text{CC} + 0.0001) \text{ mg m}^{-3}$.

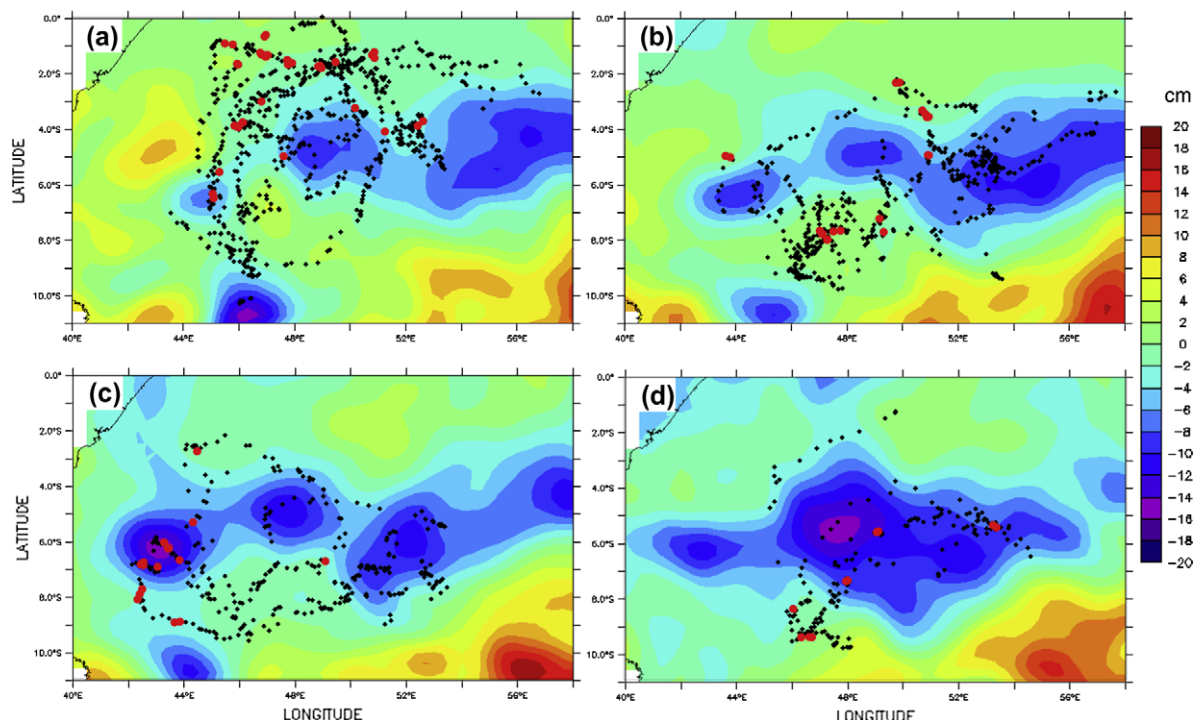


Fig. 7. Locations (black dots) and foraging spots (red circles) of Great Frigatebirds overlaid onto weekly composites of sea-surface height anomalies (SSHA) in the western Indian Ocean for: (a) 12–18 October, (b) 10–25 October, (c) 26 October–2 November, (d) 3–8 November. Positive SSHA denote anti-cyclonic eddies (yellow and red), negative SSHA cyclonic eddies (blue and purple). All units are in centimeters (source of altimetry data: SSALTO/DUACS, NRT MSLA).

Table 2

Analysis of deviance of the GAM relating foraging activity of Aldabra's frigatebirds to SSHA. Δ UBRE score represents the change in the UBRE score (a statistic for judging the relative appropriateness of binomial models).

Predictor variable	df	χ^2	Δ UBRE score	p-Value	Cumulative deviance explained (%)
SHHA	5.03	28.12	−0.25	9.1×10^{-4}	1.17
(Long, Lat)	19.14	79.66	−0.08	3.61×10^{-8}	18.5

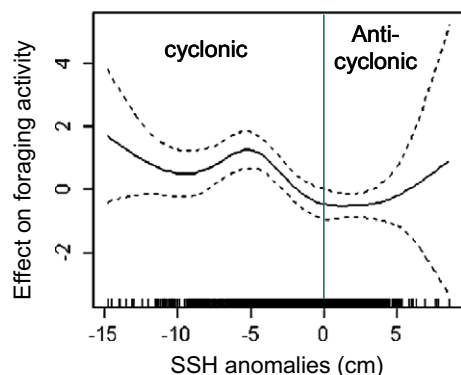


Fig. 8. GAM-derived effect of SSH anomalies on foraging activity of Aldabra's Great Frigatebirds.

operating to the extreme north of the range of the Aldabra breeding population (Figs. 9b and 10b). During this season, purse seiners are mostly fishing on schools associated with fish aggregating devices (FADs) north of the equator. A greater proportion of sets made on free schools occurs in the surroundings of the Seychelles banks. In October 2006, we do not find any overlap between the area surveyed by the breeding frigatebirds and the purse-seine, but this was a rather unusual situation compared to the average distribution of catch for the period 1991–2006 (Fig. 9a). Indeed,

with the catch being very successful in the northern region (as far as 10°N), this tended to concentrate the fishing effort beyond the area covered by the Aldabra population. In November 2006, the fleets moved southward progressively (Fig. 10b), as also occurs in the average situation (Fig. 10a), but the overlap with the range of breeding Great Frigatebirds remained limited. The only area where purse seiners and tracked birds overlapped was in the surroundings of Amirantes Islands. There, purse seiners were fishing on free-swimming schools (Fig. 10b).

3.6. Comparison between Europa and Aldabra Great Frigatebirds

Birds from Aldabra had longer durations of foraging trips and had a longer range from the colony than birds from Europa, during incubation (Table 1). The daily distances covered were higher for Aldabra birds, as well as flight speeds, but only during the daytime (Table 1). The daily number of periods with reduced speed was higher at Europa, as well as the percentage of the total trip at sea (Table 1); the birds from Aldabra had fewer daily foraging bouts as well as shorter times foraging (Table 1). There was no difference between birds from each site, in the number and percentage of time spent in stopovers at night (Table 1).

Foraging habitats were very different between the two populations. A striking difference was observed in the mesoscale eddies activity. The equatorial environment (extending from Aldabra to the equator) is more homogeneous than in the Mozambique Channel where the Great Frigatebird breeding population of Europa

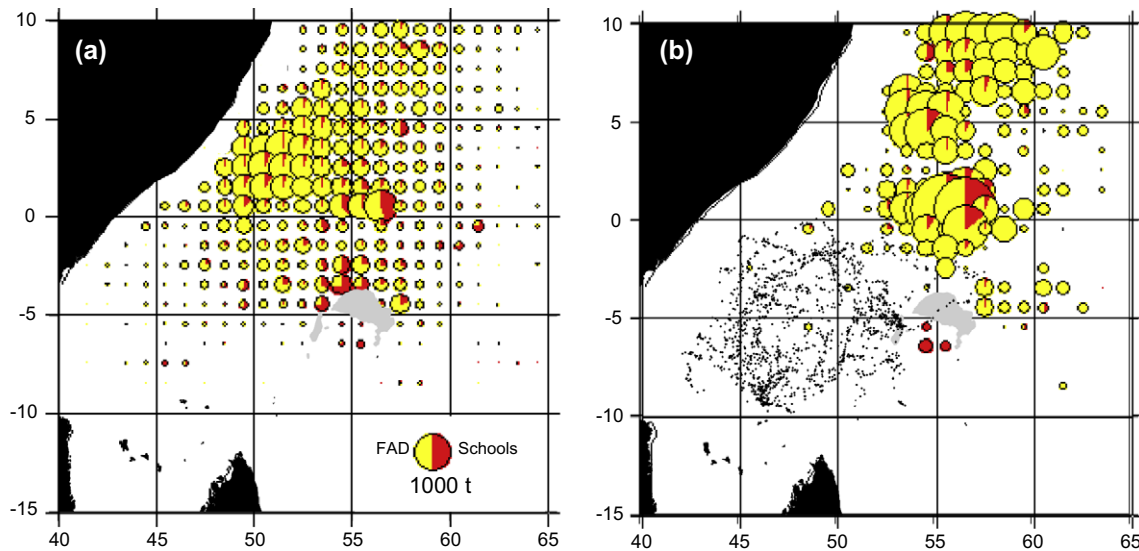


Fig. 9. Maps of purse-seine catches: (a) average 1991–2006 for October and (b) situation in October 2006. The color in the circles denotes the relative proportion of catches made on fish aggregating devices (FADs) and on free-swimming schools (data source: IOTC).

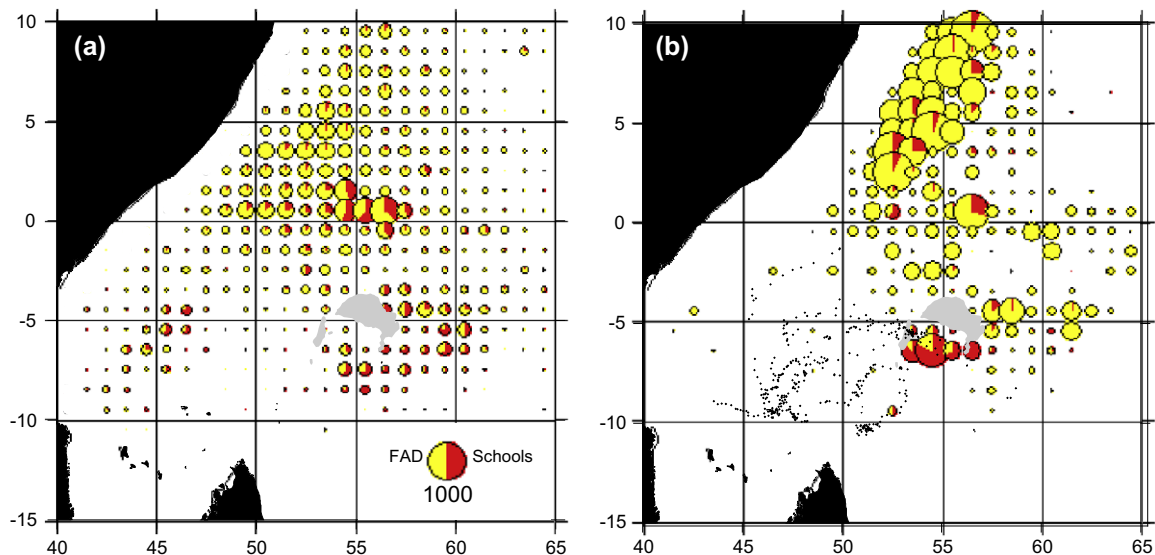


Fig. 10. Maps of purse-seine catches: (a) average 1991–2006 for November and (b) situation in November 2006. The color in the circles denotes the relative proportion of catches made on fish aggregating devices (FADs) and on free-swimming schools (data source: IOTC).

forages (Fig. 11). A summary of the main mesoscale descriptors allows a comparison between both regions (Table 3). North of Aldabra, the SSHA range is less (−10 cm to +15 cm) than in Europa (−30 cm to +30 cm). Vorticity, which describes the rotation of the water mass, and shear and stretch which are metrics of eddy deformation and formation of filaments (Testor and Gascard, 2005) differ by an order of magnitude between the two regions. Such differences are not restricted to the study period but are also found throughout the year. In order to compare the functional responses of foraging between the two environments, we used the tracking data of the Europa experiment (Weimerskirch et al., 2004) and tested GAMs with several mesoscale descriptors. The complete analysis of these descriptors and their effects on foraging can be found in Tew Kai and Marsac (this issue). SSHA and its associated gradient are strongly correlated ($r_s = -0.49$, $n = 318$), as for the Aldabra population (Fig. 8). We only considered SSHA gradient as it best depicts the transition between eddies of opposite sign,

notably in the Mozambique Channel where mesoscale eddies are well formed and propagate in close interaction (Schouten et al., 2003). SSHA gradient itself explains 2.4% of the deviance. There is a positive response of foraging activity as SSHA gradient increases (Fig. 12) indicating that foraging hotspots are distributed at the edge of eddies of opposite sign.

4. Discussion

4.1. Foraging strategy of *Aldabra frigatebirds* and its relation with environment

Aldabra frigatebirds forage strictly over oceanic waters in an extensive zone north of the breeding island with no movements observed to the south. The climatological CC field in October (not shown) points out a clear limit along 11°S between higher CC to

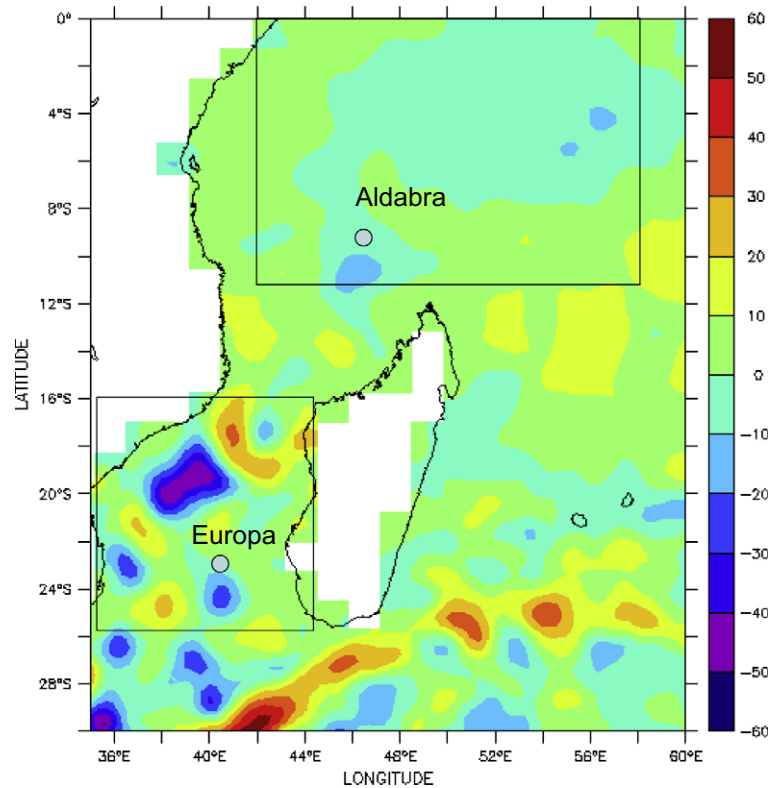


Fig. 11. SSH anomalies in the southwest Indian Ocean (dated 15 October 2006) showing the drastic difference in mesoscale activity between the equatorial region and the Mozambique Channel. The foraging range of Great Frigatebirds breeding populations of Europa and Aldabra are represented by the frames (data source: SSALTO/DUACS, NRT MSLA).

Table 3

Comparison of mesoscale descriptors at the time of the tracking experiments in Aldabra (October–November 2006) and Europa (August–September 2003).

	North Aldabra (42°E–58°E/0°–11°S)		Europa (35°E–45°E/16°S–26°S)	
SSHA	–15	10	–30	30
Vorticity	–1.70E+07	9.00E+06	–2.30E+07	2.10E+07
Shear	–9.00E+06	8.20E+06	–2.00E+07	1.30E+07
Stretch	–9.80E+06	7.80E+06	–1.80E+07	1.70E+07

the North and chlorophyll-depleted waters to the south. This may be a reason why frigatebirds exhibited directed movements to the north and thus could be interpreted as habitat selection. For a sea-bird moving at such a slow speed, the foraging range was quite extensive. The slow horizontal speed of frigatebirds is due to their extensive vertical movements; birds climb by soaring, and then glide over long distances horizontally, staying at average altitudes of 200 m above sea level (Weimerskirch et al., 2003, 2004). Periods of further speed reduction were observed during daytime, but especially at night. Since frigatebirds are feeding solely during the day (Weimerskirch et al., 2004), reduced speed at night could be due to bird resting or sleeping at night in flight. Indeed since frigatebirds never land on the sea surface, during foraging trips lasting 10 days, they should obligatorily sleep aloft (Rattenborg, 2006). Periods of daytime reduction in flight speed are attributed to foraging bouts, when birds come close to the sea surface (Weimerskirch et al., 2004). Periods of foraging activity of Aldabra birds were extremely rare suggesting that resources were scarce and widely dispersed in the area.

It is important to note that breeding birds foraged strictly over oceanic waters, and never stopped on other islands, even though

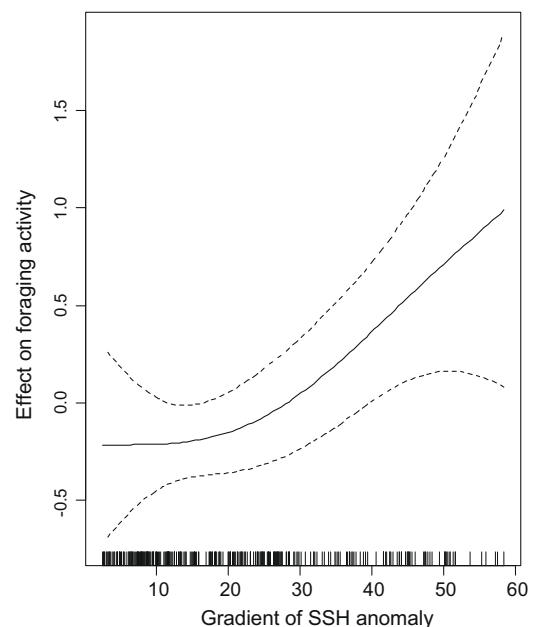


Fig. 12. GAM-derived effect of gradient of SSH anomalies on foraging activity of Europa's Great Frigatebirds.

several birds were passing close to the central Seychelles or Amirantes Islands. This is in contrast with failed breeders. Two of these failed breeders moved immediately to the Amirantes and foraged from D'Arros Island and neighbouring St. Joseph Atoll. These islands are known to host a very large roost of frigatebirds with more than 1000 birds roosting (Bristol, 2003). Similarly, one failed

breeder continued several trips from Aldabra, and then moved to Farquhar where it stayed several days, making short foraging trips from this location. Farquhar is also known to host a roost of frigatebirds (Rocamora and Skerrett, 2001). Although they are well known for their habit of parasitizing other seabirds near their breeding grounds, this technique represents only a minor proportion of the food source (Vickery and Brooke, 1994; LeCorre and Jouventin, 1997) and concerns only nonbreeding birds, since breeding birds remain in oceanic waters. The size of the nonbreeding portion of the Aldabra population is probably extensive since it comprises young immature birds, which constitute more than half of the total population of these long-lived animals, and also failed breeders. It is this nonbreeding part of the frigatebird population that explains the extensive number of birds roosting in various sites in the western Indian Ocean, whereas the main breeding site of the region is restricted to Aldabra.

4.2. Comparison between Europa and Aldabra

At Europa Island, foraging bouts of Great Frigatebirds during incubation were located at the edge of mesoscale cyclonic eddies (Weimerskirch et al., 2004) where it is likely that production is concentrated as the result of the advection of surface waters (Bakun, 2006). The positive response of strong gradients at the periphery of eddies is also supported by the GAM in this study (Fig. 12). Tew Kai and Marsac (this issue) also demonstrate the coupling that exists between those gradients, CC enhancement, and higher probability of foraging for predators such as tunas. These eddies slowly move southward off the Mozambique continental shelf in the Mozambique Channel (De Ruijter et al., 2002; Schouten et al., 2003). There is evidence of tongues of enriched-CC waters extruding from the coast under the action of eddies (Quartly and Srokosz, 2004). For the frigatebird population breeding on Europa, the location of these mesoscale features is relatively predictable since they always pass to the west of the island. At short temporal and spatial scales, the southward movement of eddies is slow. Thus, locating the edge of eddies becomes less predictable. Consequently, birds do not return from one foraging trip to the next in the same sector (Weimerskirch et al., 2004).

Aldabra birds appear to rely on even less predictable and patchier resources than Europa birds. The mesoscale activity is less intense north of Aldabra compared to the Mozambique Channel; gradients are weak and there is no large continental shelf in the neighbourhood where elevated CC could originate and be transported to the open sea by passing eddies. The annual cycle of CC is strongly related to SST variability (Fig. 5c): higher CC is associated with the colder winter temperatures. The austral winter that occurs during the southwest monsoon is characterized by strong and sustained winds (Schott and McCreary, 2001) resulting in enhanced vertical mixing. Therefore the CC variability in the north Aldabra region is more controlled by seasonal variability than by mesoscale forcing. However, some foraging spots were detected along the edge or in the core of cyclonic vortices, suggesting local prey enrichment associated with these features (Figs. 7 and 8). The sea-surface height anomalies can explain some part of the foraging activity but the associated pattern is not as clear as that observed for frigatebirds in the Mozambique Channel.

Probably as result of these regional differences in oceanography, overall, foraging bouts of the Aldabra's birds are rare compared to the Europa's birds (Table 1). Foraging trips are two times longer, and foraging range and distance covered are three times longer: the difference in ratio between trip duration and distance covered and range is made possible by the faster flight speeds and the reduced proportion of time foraging. This difference in foraging strategy at Aldabra is probably an adaptation to more patchy and scattered feeding opportunities and less predictable food

resources. Yet at Aldabra, birds forage on flying fishes similar to birds at Europa (Diamond, 1971, 1975; Lecorre, pers. obs.).

4.3. Implications for the evolution of life histories and the impact of climate change

The more patchy resources on which Aldabra birds rely have major consequences for the life history of Aldabra birds. Long foraging trips during incubation, and probably during chick rearing (although our sample size is reduced) result in a higher probability of nest failure during incubation, and reduced provisioning to the chick. Breeding success at Aldabra is extremely low (Diamond, 1975; Reville, 1983) and probably less than at Europa (Weimerskirch, pers. obs.). The foraging range of Aldabra breeding frigatebirds is located in the corridor of an anomalous SSH ridge that develops and propagates westward between 0° and 10°S during the positive ENSO events, as described by Webster et al. (1999) for the 1997/1998 El Niño. The biological effect of such a dynamic feature forced by Rossby waves is an overall reduction of the CC west of 60°E (see Fig. 13 in Murtugudde et al., 2004). Positive ENSO in the west are also accompanied by weakened trade winds that limit the vertical mixing and nutrient input in the euphotic layer. If speculations on increased frequency of ENSOs with future greenhouse warming (Timmermann et al., 1999) are confirmed by on-going climate observations, then we can suspect that Aldabra's frigatebirds may face harsher conditions in the forthcoming decades that may influence their survival.

4.4. Relationship with fisheries

During the course of our study in October–November 2006, there was no direct overlap between foraging frigatebirds and the purse-seine fishery that was located north of the equator where the success rate of sets is maximised by the abundance of floatsam and artificial FADs. However the fishery progressively moved southward in November and December, but there was still little overlapping with the foraging zone of the Aldabra population of frigatebirds. The 16-year average of purse-seine catches in the region also confirm that direct overlap is limited between October and November, indicating that birds forage independently of the purse-seine fishery. Thus, frigatebirds are not necessarily associated with fishing boats, but rather are searching independently for surface feeding tunas or dolphins that provide feeding opportunities for them (Au and Pitman, 1986). Indeed, tuna skippers try to detect bird flocks while searching tuna schools since the ratio of schools seen in association with seabirds is high, estimated to 70% from ship surveys (Marsac, 1992). The absence of purse-seine vessels in operation north of Aldabra does not mean that tuna are not present or even abundant in this region. Longliners operated by Asian countries do obtain significant catches in the area. The average 1991–2005 catch for October and November are 1200 t and 1800 t, respectively, in the area 40°E–60°E/0°–10°S (IOTC database www.iotc.org; IOTC, 2008). However, the absence of the purse-seine fishery suggests that tunas are not found near the surface. Therefore frigatebirds are not relying heavily on surface school, but on some other mechanism that force prey to the surface. For example, tunas targeted by longliners occur at intermediate depths (50–350 m) but those fish can also congregate in surface-dwelling schools during the day and for transient chasing events and thus make sub-surface prey available to frigatebirds.

Tuna catches in the western Indian Ocean have considerably increased in the last 20 years, passing from 0.4 to 1.2 million tons from 1985 to 2005. Record catches were recorded, notably from 2003 to 2006, and thus has raised questions about the sustainability of tuna populations in the future (IOTC, 2008). Should tuna stocks become overfished, feeding opportunities for frigatebirds

would become more rare which would also compound the effects of unfavourable climatic events. Since Aldabra birds appear to rely on very patchy resources, a further reduction of feeding opportunities would put the population in serious jeopardy.

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References

- Ainley, D.G., Boekelheide, R.J., 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *Studies in Avian Biology* 8, 2–23.
- Ashmole, N.P., 1971. Seabird Ecology and the Marine Environment. In: Farner, D.S., King, J.R. (Eds.), *Avian Biology*, vol. 1. Academic Press, New York, pp. 223–286.
- Au, D.W.K., Pitman, R.L., 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88, 304–317.
- Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina* 70 (S2), 105–122.
- Ballance, L.T., Pitman, R.L., 1999. Foraging ecology of tropical seabirds. In: Adams, N.J., Slotow, R.H. (Eds.), *Proceeding of the 22nd International Congress*, Durban. BirdLife South Africa, Johannesburg, pp. 2057–2071.
- Bristol, R., 2003. Seabirds noted on d'Arros Island and neighbouring St. Joseph Atoll, November 2002. *Seabird News* 3, 6.
- Burger, A.E., Betts, M., 2001. Monitoring populations of Red-footed Boobies *Sula sula* and frigatebirds *Fregata spp.* breeding on Aldabra Atoll, Indian Ocean. *Bulletin of the British Ornithological Club* 121, 236–246.
- Chambers, J.M., Hastie, T.J., 1992. *Statistical Models*. S. Wadsworth and Brooks/Cole, Pacific Grove, CA, USA.
- Chelton, D.B., Schlax, M.G., Samelson, R.M., de Szoeke, R.A., 2007. Global observations large oceanic eddies. *Geophysical Research Letters* 34, L15606.
- De Ruijter, W.P.M., Ridderinkhof, H., Lutjeharms, J.R.E., Schouten, M.W., Veth, C., 2002. Observations of the flow in the Mozambique Channel. *Geophysical Research Letters* 29, 1502. doi:10.1029/2001GL013714.
- Diamond, A.W., 1975. Biology and behaviour of frigatebirds *Fregata spp.* on Aldabra Atoll. *Ibis* 117, 302–323.
- Flint, E.N., Nagy, K.A., 1984. Flight energetics of free-living Sooty Terns. *Auk* 101, 288–294.
- Haney, J.C., 1987. Ocean internal waves as sources of small-scale patchiness in the seabird distribution on the Blake Plateau. *Auk* 104, 62–70.
- Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. Chapman and Hall, New York.
- Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., Becker, P.H., 1999. Physical processes, prey abundance and the foraging ecology of seabirds. In: Adams, N.J., Slotow, R.H. (Eds.), *Proceedings of the 22nd International Ornithology Congress*. BirdLife South Africa, Johannesburg, pp. 2040–2056.
- Hyrenbach, K.D., Fernandez, P., Anderson, D.J., 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233, 283–301.
- IOTC, 2008. Report of the Ninth Session of the Scientific Committee. Victoria, Seychelles, 5–9 November 2007. IOTC-2007-SC-R[E], pp. 133.
- LeCorre, M., Jouventin, P., 1997. Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the Red-footed Booby. *Condor* 99, 162–168.
- Longhurst, A.R., Pauly, D., 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego, CA.
- Marsac, F., 1992. Etude des relations entre l'hydroclimat et la pêche thonière hauturière tropicale dans l'océan Indien occidental. Thèse de Doctorat, Univ. de Bretagne Occidentale, pp. 353.
- Murtugudde, R., Wang, L., Hackert, E., Beauchamps, J., Christian, J., Busalacchi, A.J., 2004. Remote sensing of the Indo-Pacific region: ocean colour, sea level, winds and sea surface temperatures. *International Journal of Remote Sensing* 25, 1423–1435.
- Pennycuik, C.J., 1987. Flight of seabirds. In: Croxall, J.P. (Ed.), *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University press, Cambridge, pp. 43–62.
- Quartly, G.D., Srokosz, M.A., 2004. Eddies in the southern Mozambique Channel. *Deep Sea Research II* 51, 69–83.
- Rattenborg, N.C., 2006. Do birds sleep in flight? *Naturwissenschaften* 93, 413–425.
- Reville, B.J., 1983. Numbers of nesting frigatebirds *Fregeta minor* and *F. ariel* on Aldabra Atoll Nature Reserve, Seychelles. *Biological Conservation* 27, 59–76.
- Rocamora, G., Skerrett, A., 2001. Seychelles. In: Fishpool, L.D.C., Evans, M. (Eds.), *Important Birds Areas in Africa and Associated Islands: Priorities for Sites Conservation*. Bird Life Conservation Series No. 11. Newbury and Cambridge, UK, pp. 751–768.
- Schott, F.A., McCreary, J.P., 2001. The monsoon circulation of the Indian Ocean. *Progress in Oceanography* 51, 1–123.
- Schouten, M.W., de Ruijter, P.M., van Leeuwen, P.J., Ridderinkhof, H., 2003. Eddies and variability in the Mozambique Channel. *Deep-Sea Research II* 50, 1987–2003.
- Seaman, D.E., Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77, 2075–2085.
- Spear, L.B., Balance, L.T., Ainley, D.G., 2001. Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus equatorial front. *Marine Ecology Progress Series* 219, 275–289.
- Testor, P., Gascard, J.-C., 2005. Large scale flow separation and mesoscale eddy formation in the Algerian basin. *Progress in Oceanography* 66, 211–230.
- Tew Kai, E., Marsac, F., this issue. Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Progress in Oceanography*.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., Roeckner, E., 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398, 694–697.
- Vickery, J.A., Brooke, M. deL., 1994. The kleptoparasitic interactions between Great Frigatebirds and Masked Boobies on Henderson Island, South Pacific. *Condor* 96, 331–340.
- Webster, P.J., Moore, A.M., Loschnigg, J.P., Leben, R.R., 1999. Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997–1998. *Nature* 401, 356–359.
- Weimerskirch, H., 2002. The demography of seabirds and its relationship with the marine environment. In: Schreiber, E.A., Burger, J. (Eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, FL, pp. 115–135.
- Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Research II* 54, 211–223.
- Weimerskirch, H., Chastel, O., Barbraud, C., Tostain, O., 2003. Frigatebirds ride high on thermals. *Nature* 421, 333–334.
- Weimerskirch, H., Le Corre, M., Jacquemet, S., Potier, M., Marsac, F., 2004. Foraging strategy of a top predator in tropical waters: Great Frigatebirds in the Mozambique Channel. *Marine Ecology Progress Series* 275, 297–308.
- Weimerskirch, H., Salamolard, M., Sarrazin, F., Jouventin, P., 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110, 325–342.
- Wood, A.G., Naef-Daenzer, P., Prince, P.A., Croxall, J.P., 2000. Quantifying habitat use in satellite tracked pelagic seabirds: application of the kernel estimation to albatross locations. *Journal of Avian Biology* 31, 278–286.
- Worton, B.J., 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59, 794–800.