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RESEARCH ARTICLE

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Foraging habitats of the seabird community of Europa Island (Mozambique Channel)

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Abstract We investigated the foraging habitats of the winter breeding community of tropical seabirds from Europa Island (Mozambique Channel) in September 2003. We focused our study on the dominant species of this austral community, the sooty tern (*Sterna fuscata*), the red-footed booby (*Sula sula*), and the frigatebirds, including the great (*Fregata minor*) and the lesser frigatebirds (*F. ariel*). We considered the at-sea distribution and abundance of these species in relation to chlorophyll concentration, sea-surface temperatures, sea-surface height anomalies, depth of the thermocline, distance to the colony, and presence of surface marine predators, flying fishes and other seabirds. Although the marine environment where seabirds foraged was oligotrophic, it presents the best feeding opportunities for seabirds for the area in winter. Our study demonstrates that the winter-breeding seabird species of Europa Island tend to forage in productive waters in association with other marine predators when possible. Sooty terns and frigatebirds were widely distributed in the whole study area, whereas red-footed boobies were not found farther than 160 km from their colonies and were associated with relatively productive waters. Sooty terns and red-footed boobies were aggregated where flying fishes were abundant. The presence of other marine predators was associated with larger multispecies feeding flocks than when no association occurred. Sooty terns, which are numerically dominant at Europa and adopted network foraging, seem to be catalysts of feeding events, and represented a good target for the other foraging species, especially frigatebirds. However, when possible, frigatebirds favour association with flocks of red-footed boobies.

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Introduction

Oceanic seabirds have to cope with major constraints when breeding, which are spatial and temporal changes in prey distribution, and the necessity to commute from feeding to breeding areas (Ricklefs 1983). These constraints are probably especially severe in tropical waters where the primary production is low (Longhurst and Pauly 1987), often resulting in low prey density (Ashmole 1971).

Physical factors like thermal gradients, frontal zones, or upwellings may locally increase primary production (Schneider 1990), and thereby affect availability and predictability of prey to seabirds. These factors have been shown to influence seabird distribution at polar (Hunt 1990; Hunt et al. 1999), temperate (Hoefer 2000; Hyrenbach et al. 2002), and tropical latitudes (Spear et al. 2001). Since surface productivity is low in the tropics, however, numerous tropical species depend on other marine predators such as tuna and mammals to drive prey to the surface, and therefore distribution of tropical seabird flocks is to a certain extent determined by the distribution of tuna and other predators (Au and Pitman 1986; Ballance and Pitman 1999; Jaquemet et al. 2004). Some species are even regarded as near-obligate commensals of surface tunas (Au and Pitman 1986). However tunas and cetaceans are very mobile predators that are themselves searching for unpredictable and scarce patches of prey. A way to compensate for this scarcity of prey for seabirds has been to increase their foraging efficiency. Some species particularly, like sooty terns and frigatebirds, have flying abilities based on energy saving which allow them to cover large oceanic areas at low costs (Flint and Nagy 1984; Ballance 1995;

Ballance et al. 1997; Weimerskirch et al. 2003); others, like boobies, tend to forage in zones of relative higher productivity where competition may be higher (Ballance et al. 1997).

Although they rely on less productive environments than their temperate or polar counterparts, tropical seabirds may constitute colonies of thousands or even millions of breeding pairs consuming tons of oceanic biomass daily. This is illustrated by the seabird community of Europa Island (Mozambique Channel), which is a breeding site with more than one million pairs of eight species (Le Corre and Jouventin 1997). Furthermore, most of the species breed simultaneously during the austral winter (Le Corre 2001), increasing the overall food requirements for the community as a whole, and raising the question of how so many birds find so much food in a supposedly impoverished marine environment within their foraging range imposed by breeding.

Here, we study the at-sea distribution and abundance of the seabird species that breed during the austral winter on Europa Island in relation to physical and biological factors. We tested how the different species distributed themselves within their foraging range and whether specific locations aggregate foraging seabirds. We also examine the foraging strategies adopted by each species, particularly the importance of local enhancement on the feeding activity of the seabirds.

Materials and methods

Study area

At-sea surveys of seabirds and marine mammals were carried out during the ECOTEM 9 oceanic cruise (7–21 September 2003), aboard the long-liner "Cap Morgane". The survey area extends from 20°S to 23°5′S and from 39°E to 41°40′E (Fig. 1). It includes the Europa and Bassas da India Islands, the Hall Bank, and the Jaguar Seamount, which reaches within 200 m of the surface. The water circulation is shaped by both bathymetry and large coastal anticyclonic and cyclonic eddies that occur along the African and Malagasy coasts, respectively (Quartly and Srokosz 2004). Oceanic islands and seamounts restrict the route taken by the eddies along the African coast and generate upwelling that favours primary production in the central part of the channel (Quartly and Srokosz 2004) in the vicinity of the Bassas da India system particularly. During winter, the subtropical and temperate waters flow into the southern part of the Mozambique Channel. These cold upwelled waters probably favour primary production since satellite measurements (SeaWIFS data) show that the surface chlorophyll concentration increases in July in the southern part of the channel (Quartly and Srokosz 2004). This overall increase of biological production leads, hence, to an increase of the food availability for marine top predators like pelagic fish (Stequert and Marsac 1986), seabirds (Le Corre 2001), and marine mammals.

Field data collection

Seabirds and marine mammals were surveyed by 1 observer with 10*50 binoculars, along the route of the ship during 21 daylight linear transects (Fig. 1), totalling 50 h of observation and 780 km^2 surveyed. The mean length (±standard error) of the transects was 37±2.9 km (range 13–63 km). The first four transects were performed by an observer and all the others by a second observer, both of whom were familiar with tropical Indian Ocean seabird species. A transect was defined as a continuous survey period, with a constant boat speed averaging 10 knots, following the standard strip transect method (Tasker et al. 1984). At the beginning and end of each transect, the GPS position and sea-surface temperature were noted. Every seabird or marine mammal observed during each transect, within a band of 500 m width on both sides of the ship, was included in the data set. Distance from the boat was estimated using the radar of the boat. In addition to species identification and individual count, the behaviour of the birds (flying, sitting on water or feeding) and whether they were associated with schools of surface dwelling predators, were recorded. From the 4th transect, we also attributed to each one a flying fish abundance index according to the following scale: 1 no flying fish, 2 low numbers of flying fishes with a scattered distribution, 3 low numbers but continuous observations, 4 high numbers and continuous observations. We considered transects eastward and westward from Europa to analyse the relative abundance of flying fish. For transects that were overlapping the limit, we pooled them in the category where the main part of the transect was performed. During the cruise, 14 hydrographic stations were carried out in different sectors around Europa Island (Fig. 1) to determine, in particular, the depth of the thermocline using a CTD profiler.

Satellite data

We used average weekly Sea Surface Temperatures (SST) and Chlorophyll Concentration (CC), obtained from the International Research Institute for Climate Prediction (http://ingrid.ldgo.columbia.edu/) and from the Sea-viewing Wide Field-of-view Sensor (SeaWIFS, http://seawifs.gsfc.nasa.gov/SEAWIFS.html) data collections, respectively. Chlorophyll concentrations were derived from SeaWiFS 8-day composites and daily images, with a spatial resolution of 9 km. Within the range of 0.05–50 mg.m^{-3}, SeaWiFS estimates are within 35% of in-situ chlorophyll *a* concentrations (Hooker and McClain 2000), with the greatest discrepancies in

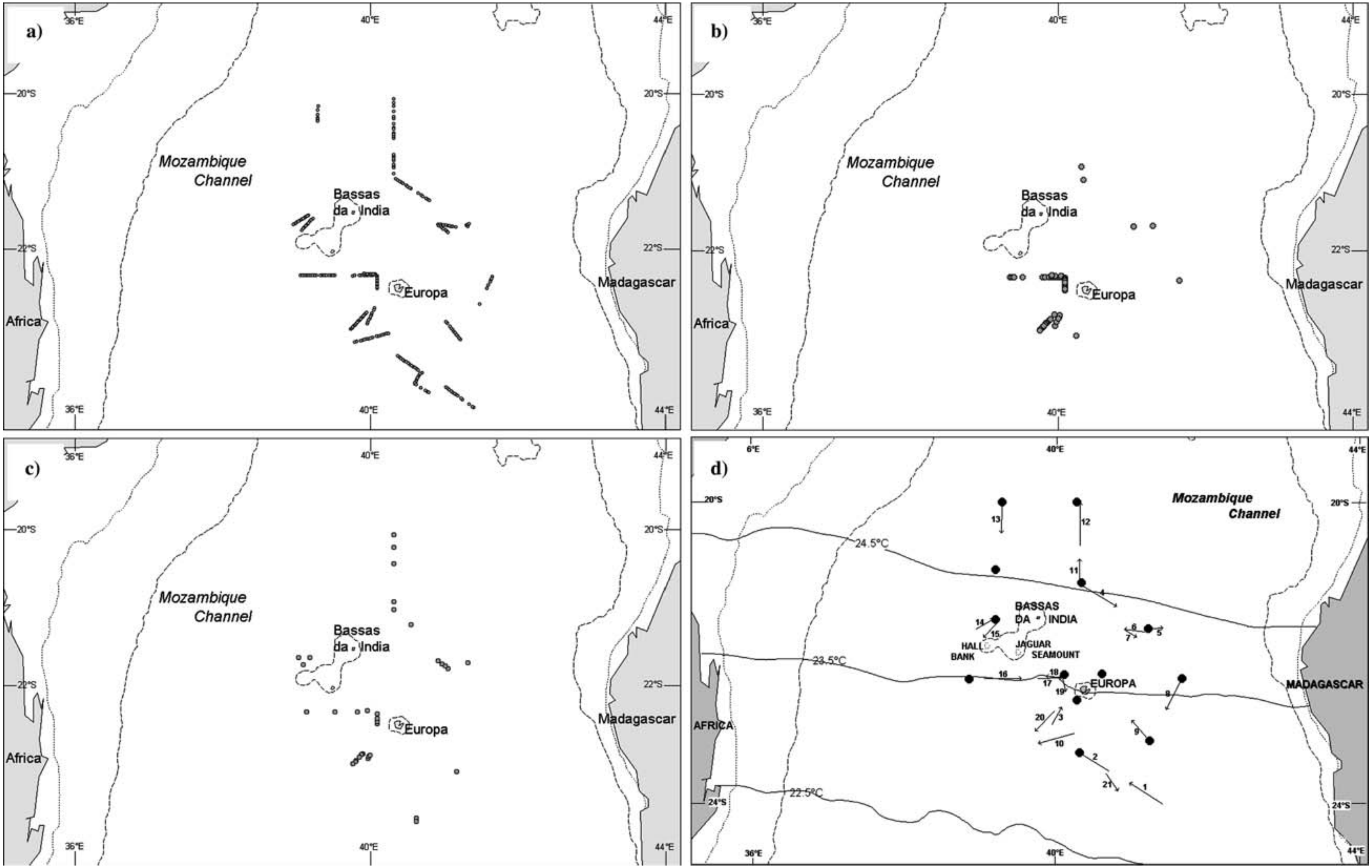

Fig. 1 Observations of sooty terns (**a**), red-footed boobies (**b**), frigatebirds (**c**), and map of the study area (**d**) with the 200-m (...) and 2,000-m (– – –) isobaths, the average Sea Surface Temperatures, transects (→) and hydrological stations (●)

waters between 1 and 10 mg.m^{-3} (Kahru and Mitchell 1999). Following Hooker and McClain (2000) for this analysis, high chlorophyll *a* concentrations beyond the range of SeaWiFS validation (>50 mg.m^{-3}) were excluded. We used Sea Surface Height anomalies (SSHa) from the AVISO data base of the CLS Physical Oceanography Division (http://www.aviso.oceanobs.com/), with each point as a 4-day mean datum. Indeed, areas between positive and negative anomalies of the sea level are often productive, and are important foraging habitats of seabirds, as recently demonstrated for the frigatebirds from Europa (Weimerskirch et al. 2004). Each satellite data set was gridded with an approximate resolution of 9*9 km.

Data analyses

All observations of seabirds made during the transects were pooled in 10-min periods (Tasker et al. 1984), and this allowed us to calculate occurrence of the species by 10 min of observations. All the satellite data were interpolated afterwards with the kriging method using Surfer 8.01 software (Golden Software, Colo.) in order to assign a value of CC, SST and SSHa to each 10 min period box. The shortest distance between every observation pooled in 10-min periods and the different measures of thermocline were calculated to attribute the nearest value of the thermocline to each observation. We used Generalised Linear Models (GLMs) on the abundance of birds per 10-min periods to determine whether the oceanic habitats used by birds varied significantly across species. This comparison included only the winter breeding species of Europa for which the number of observations was sufficient ($n>30$). Analyses of variance (ANOVA) were performed on abundance of birds per 10-min periods to assess the impact of marine predatory schools and the presence of a particular seabird species on the other. Data of abundance were previously transformed in (log+1) to accord with necessary conditions of application of the ANOVA. Statistical analyses were performed with Statistica 6.0 (Statsoft, Tulsa, Okla.).

Results

The marine environment

In the study area, the marine environment was spatially structured with a northward increase of the SST (from 21.8°C at 24°S to 25.1°C at 20°S, Fig. 1). Moreover, SST were positively correlated with SSHa (Spearman rank test, $R_s=0.37$, $P<0.01$) and negatively correlated with CC (Spearman rank test, $R_s=-0.31$, $P<0.01$). A local enrichment with higher CC occurred westward of Europa and around Bassas da India and was associated with low SSHa. The flying fish index, which was positively correlated with the CC (Spearman rank test, $R_s=0.02$, $P<0.01$), was significantly higher westward (2.5 ± 1) of Europa than eastward (1.5 ± 0.7) (Mann-Whitney test $U=22$, $P<0.05$), reflecting the fact that flying fishes were more abundant westward of Europa. Finally, average CC in the area increased significantly from 0.07 ± 1.98 mg.m^{-3} during the 1st week to 0.104 ± 1.98 mg.m^{-3} during the 2nd week (Wilcoxon $Z=17.72$, $P<0.01$) as the consequence of enrichment westward of Europa Island (Fig. 2).

Seabird abundance at sea

We observed 4,472 birds of 10 species in 700 observations (Table 1); 5 species were Europa breeders and the other 5 were not. The density of birds was the highest for sooty terns but was, however, low for all species. The five breeding species of Europa observed were the sooty tern (83.2% of the birds observed), the red-footed booby (13.6%), the frigatebirds (10.9%, including great and lesser frigatebirds), the white-tailed tropicbird (0.2%) and the Audubon's shearwater (<0.1%). Rare species were removed from the analysis and, hence, we focused the study on sooty terns, red-footed boobies and frigatebirds. The ratio of the number of individuals observed at sea on the number of breeders is the lowest for sooty

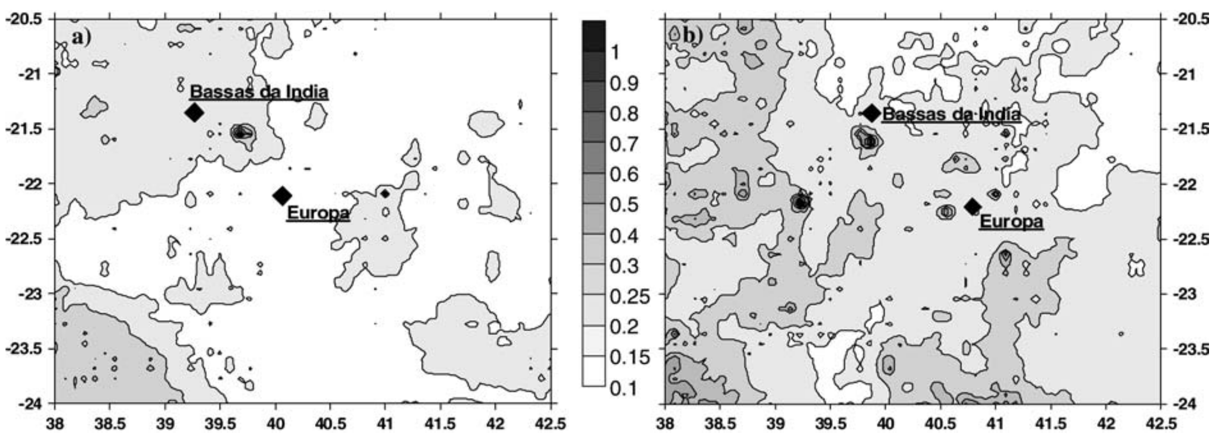

Fig. 2 Average chlorophyll concentration (mg.m^{-3}) in the study area 5–12 September 2003 (**a**) and 12–20 September 2003 (**b**)

Table 1 At-sea observations of seabirds and population size for Europa breeders **in bold** (SD standard deviation)

Species	Observations		Individuals		Occurrence	Density ± SD	Breeding pairs[a]	Ratio indiv
	n	%	*n*	%	%	Indiv/km^2		at sea/breeders
Sooty tern (*Sterna fuscata*)	607	77.9	3696	86.7	83.2	4.7 ± 13	760,000	0.002
Red-footed booby (*Sula sula*)	70	9	626	10	13.6	0.8 ± 11.8	3,000	0.104
Frigatebird species (*Fregata*sp.)	41	5.3	72	1.6	10.9	0.09 ± 0.4	2,300	0.016
White-tailed tropicbird (*Phaethon lepturus*)	7	0.9	8	1	0.2	0.01 ± 0.4	1,000	0.004
Audubon's shearwater (*Puffinus lherminieri*)	3	0.3	3	0.4	0.07	0.004 ± 0.03	50	0.03
Soft-plumage petrel (*Pterodroma mollis*)	22	2.8	36	3.1	0.8	0.04 ± 0.6	-	
Cape petrel (*Daption capense*)	15	1.9	17	2.1	0.4	0.02 ± 0.2	-	
Flesh-footed Shearwater (*Puffinus carneipes*)	3	0.4	3	0.4	0.07	0.004 ± 0.03	-	
Swinhoe's storm-petrel (*Oceanodroma monorhis*)	8	1	8	1.1	0.2	0.01 ± 0.06	-	
White-bellied storm-petrel (*Fregetta grallaria*)	3	0.4	3	0.4	0.07	0.004 ± 0.03	-	

[a]Le Corre and Jaquemet (2005)

terns, the most abundant breeding species, and the highest for red-footed boobies (Table 1).

Sooty terns and frigatebirds were observed in the whole study area (Fig. 1) and even at the furthest distance from Europa that we surveyed (Fig. 3), whereas red-footed boobies were not observed farther than 160 km from Europa (max. 156 km, one observation, Fig. 3), mainly westward of Europa and southward of Bassas da India (Fig. 1). Frigatebirds were distributed in the whole area but were significantly more abundant at less than 100 km from Europa than farther (Kruskall-Wallis test, $H_{3,\ 322} = 16.29$, $P < 0.01$).

Foraging habitats

GLM results, performed on satellite parameters and thermocline depth, supported the notion that sooty terns foraged over all water masses, since the abundance of the species is not significantly influenced by any parameters (Table 2). Conversely, the test revealed significant influences of the SST and the thermocline on the abundance of red-footed boobies and frigatebirds. Moreover, the two species seemed to forage in similar habitats where SST is < 23.5°C and thermocline depth between 110 m and 130 m although their abundance did not peak significantly in such habitats (Kruskall-Wallis test, all $P > 0.05$).

The abundance of sooty terns was high for several values of CC and was the highest when CC was the highest (Fig. 4). Red-footed boobies were almost exclusively present in areas where CC averages 0.17 mg.m^{-3}. Frigatebirds were significantly more abundant in such areas (KW test, $H_{3,\ 322} = 14.29$, $pP < 0.01$; Fig. 4), although individuals were sighted over all CC.

Results of the ANOVA revealed that the abundance of sooty terns was significantly correlated with both the presence of marine predators like tuna or mammals, and/or the presence of red-footed boobies or frigatebirds (Table 3). The abundance of red-footed boobies peaked significantly with the presence of frigatebirds. The

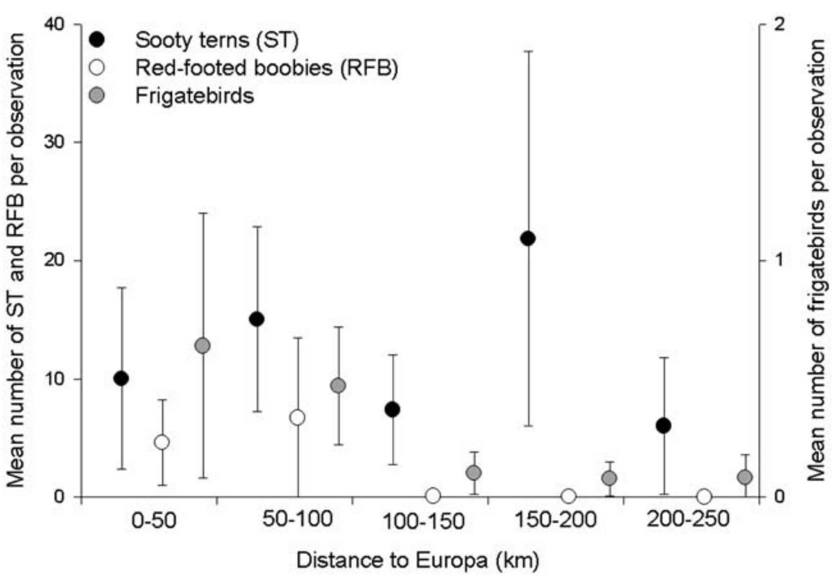

Fig. 3 Mean number (± SD) of sooty terns, red-footed boobies and frigatebirds per 10-min period (observation) in relation to the distance to Europa Island

Table 2 Results of the generalised linear model testing the influence of oceanic factors on the distribution and abundance of the three main winter-breeding species of Europa Island (*df* degree of freedom, * interaction terms). See Table 1 for scientific names of the species. **Bold** denotes significant results

	Sooty terns			Red-footed boobies			Frigatebird spp.		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Chlorophyll	1	0.04	0.827	1	0.29	0.589	1	0.16	0.685
SST	1	1.00	0.317	**1**	**7.57**	**0.006**	**1**	**8.84**	**0.003**
SSHa	1	1.43	0.232	1	1.49	0.222	1	1.73	0.189
Thermocline	1	1.69	0.194	**1**	**10.16**	**0.001**	**1**	**10.95**	**0.001**
Chlorophyll*SST	1	0.09	0.766	1	0.28	0.594	1	0.22	0.637
Chlorophyll*SSHa	1	2.97	0.086	1	0.87	0.350	1	1.55	0.213
Chlorophyll*Thermocline	1	0.52	0.471	1	0.003	0.952	1	0.18	0.667
SST*SSHa	1	1.27	0.259	1	1.93	0.165	1	2.28	0.131
SST*Thermocline	1	1.62	0.203	**1**	**10.26**	**0.001**	**1**	**10.93**	**0.001**
SSHa*Thermocline	1	0.01	0.972	1	1.27	0.261	1	1.39	0.239

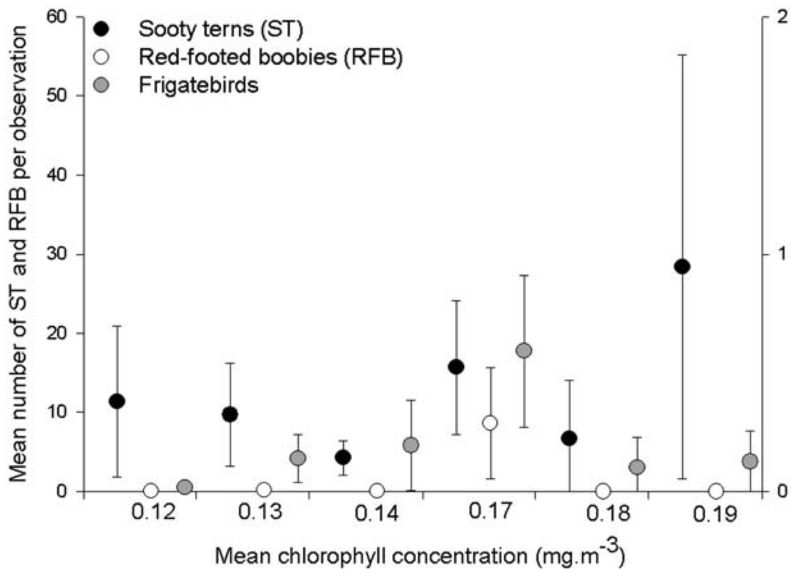

Fig. 4 Mean number (± SD) of sooty terns, red-footed boobies and frigatebirds per 10-min period (observation) in relation to the mean chlorophyll concentration (mg.m^{-3})

abundance of frigatebirds, similarly, was correlated with the presence of red-footed boobies (Table 3).

Table 3 Results of the ANOVA testing the influence of the association with marine predators (tunas and mammals) or another seabird species on the abundance of a particular one (*RFB* red-footed booby, *FREG* frigatebirds, *ST* sooty tern).**Bold** denotes significant results

	df	*F*	*P*
Sooty tern			
Ass. marine predators	**2**	**41.649**	**< 0.001**
RFB	**1**	**5.693**	**0.018**
FREG	**1**	**34.503**	**< 0.001**
Red-footed booby			
Ass. marine predators	2	0.403	0.669
ST	1	1.138	0.287
FREG	**1**	**10.618**	**0.001**
Frigatebird			
Ass. marine predators	2	1.588	0.206
ST	1	2.406	0.122
RFB	**1**	**38.424**	**< 0.001**

Sooty terns and red-footed boobies were more abundant where flying fish were more abundant (Fig. 5) but this relation was significant for sooty terns only (KW test, $H_{3,\ 274} = 14.21$, $P < 0.01$). The number of frigatebirds, finally, was always low even when flying fishes were abundant.

Feeding flocks

Monospecific and multispecific flocks of each species were feeding unassociated with marine predators although monospecific flocks of sooty terns were feeding in association (Fig. 6). Multispecific flocks, which included breeding and non-breeding species of Europa, were always larger than monospecific one. The size of both types of flocks were, however, highly variable as indicated by the high standard deviation (Fig. 6).

Sooty terns were present in more than 81% of the feeding flocks and the species was numerically dominant in all the flocks where it occurred. Frigatebirds were

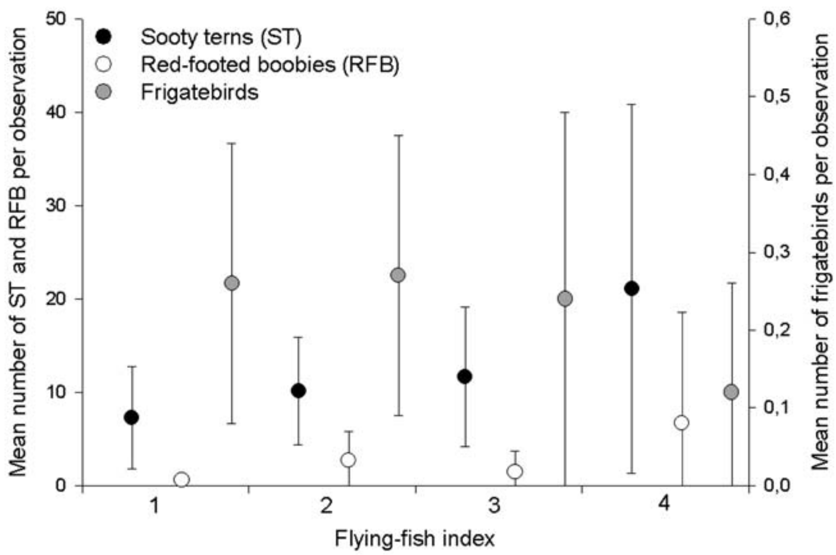

Fig. 5 Mean number (±SD) of sooty terns, red-footed boobies and frigatebirds per 10-min period (observation) in relation to the flying-fish index (see Materials and methods for explanation)

observed feeding alone or in pairs (47% and 21%, respectively, $n=19$), but were in 88% of the feeding flocks with sooty terns and 50% with boobies. In all cases, their numbers never exceeded five individuals, but they were always more abundant in flocks where the two other species occurred. The 3 species occurred together in 11.5% of all the feeding flocks observed ($n=44$).

A total of 17 groups of surface-dwelling predators were encountered during the survey: 5 schools of tuna, which were all out of the foraging range of the red-footed boobies, and 12 pods of cetaceans, mainly false killer whales *Pseudorca crassidens*. Only 47% of observations of tuna or cetacean groups were associated with feeding seabirds. Sooty-tern abundance peaked mostly with the presence of tuna schools, but they were also attracted by cetacean pods (KW test, $H_{3,\ 322}=18.28$, $P<0.01$). Those pods, which occurred westward of Europa, aggregated the three species. Although they were often in associated feeding flocks, the abundance of frigatebirds did not peak significantly during feeding events when associated (Fig. 6). Finally, red-footed boobies were associated only with marine mammals, and these associations represented 50% ($n=10$) of the overall feeding events of the species.

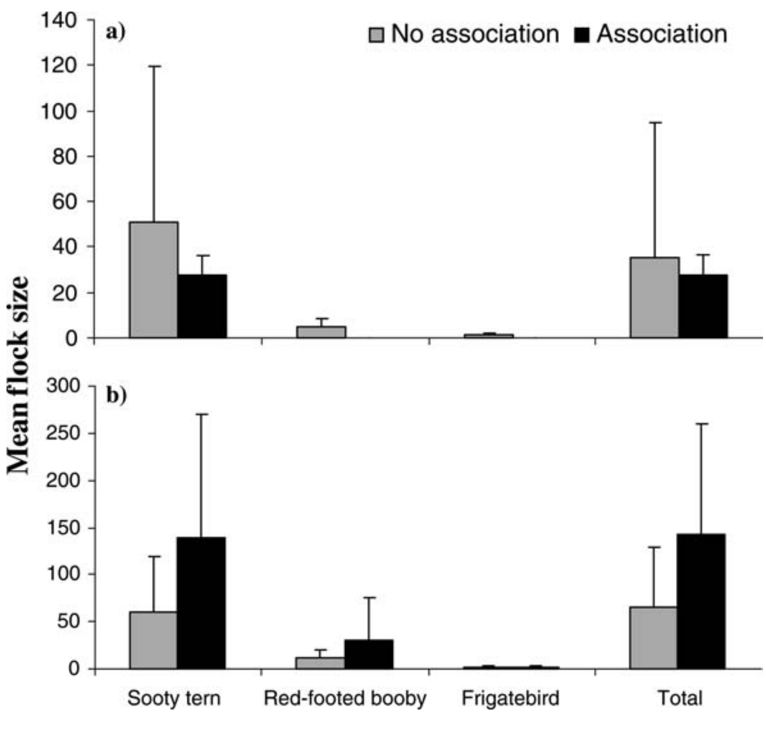

Fig. 6 Characteristics of feeding flocks: mean number of individuals ± standard deviation of monospecific (**a**) and multispecific (**b**) flocks

Discussion

We demonstrate that the winter-breeding seabirds of Europa Island do not forage in the same oceanic habitats. First, sooty terns were widely distributed in the whole survey area and in all water types; however, red-footed boobies, and frigatebirds to a lesser extent, were distributed at less than 160 km from the colonies in water with SSTTable 1; Le Corre and Jaquemet 2005) were rarely sighted at sea, and only solitarily, as previously indicated (Pocklington 1979; Pitman and Ballance 1992; Jaquemet et al. 2004). Finally, the low frequency of Audubon's shearwater observations is in accord with the small size of the population on Europa (Le Corre 2001), and this could indicate that only individuals from Europa were sighted.

The marine environment

The low CC values compared to temperate and polar surface oceanic waters and the deep thermoclines (>85 m) indicate an oligotrophic situation in the Mozambique Channel that is characteristic of tropical waters (Longhurst and Pauly 1987). During austral winter, however, the primary production in the south of the channel is the highest compared to other seasons (Quartly and Srokosz 2004). This overall enrichment of chlorophyll probably leads to a high abundance of patches of prey for the area. Indeed, phytoplankton, zooplankton and flying fish exhibit the same spatial trends but these diminish over the trophic levels. This results in a relatively heterogeneous field of predators (flying fish) on more uniformly distributed fields of prey (plankton) (Piontkovski and Williams 1995). Moreover tunas, which greatly favour access to prey for numerous tropical seabirds (Au and Pitman 1986; Jaquemet et al. 2004), are more abundant in the vicinity of Europa during austral winter (Le Corre 2001).

Although the marine environment in the south of the channel presents few permanent structures that favour biological production (Saetre and Jorge da Silva 1984), geostrophic currents, associated with low SSHa, were stronger and CC higher westward of Europa, and south of Bassas da India. This enrichment may be the consequence of the advection of waters in the central part of the channel by the anticyclonic eddies, which propagate poleward along the Mozambican coasts (Quartly and Srokosz 2004), and on the topographic constraints of the Bassas da India and associated seamounts system. This could explain why flying fishes were more abundant in these areas than eastward of Europa, and such a situation probably produces more feeding opportunities for seabirds.

Thus, in austral winter, it appears that oceanic conditions in the south of the Mozambique Channel, even if they present a quick turnover, seem to be relatively favourable and predictable at mesoscale (100 s km) sufficient to sustain a large top predator community, including seabirds breeding in Europa.

Foraging habitats

Sooty terns were present in all water types, even at the farthest distance from Europa that we surveyed (~250 km). Frigatebirds were also widely distributed but tended to be more abundant in the first 100 km from the colonies, a distance consistent with that found for brooding individuals (Weimerskirch et al. 2004). Red-footed boobies were observed no farther than 160 km from Europa, as recently demonstrated by Weimerskirch et al. (2005) using telemetry instruments. Moreover, the red-footed booby was the species with the highest ratio of "number of birds observed at sea/population size", suggesting that our observations included a larger part of the population of Europa than for other species. Such a result reinforces the idea that the foraging range of this species is more limited than that of the other species. This ratio was lower for sooty terns and frigatebirds suggesting, similarly, that a significant proportion of the population forages beyond the limits of our study area. These results are consistent with the maximal foraging range of 500 km estimated in the Pacific for sooty terns (Flint 1991), as well as that obtained by satellite telemetry for great frigatebirds of Europa (maximal foraging range: 600 km, Weimerskirch et al. 2004).

Red-footed boobies were almost exclusively observed during the 2nd week, westward of Europa and south of Bassas da India where the CC was relatively high for the period and the area. Moreover pods of cetaceans also occurred and flying fishes were abundant, suggesting that the species searches mostly for productive waters to forage in, as shown in the Pacific (Ballance et al. 1997). Although sooty terns and frigatebirds are less constrained by long foraging trips, due to low costs of flight (Flint and Nagy 1984; Weimerskirch et al. 2003) and their abilities to stay at sea at night (Flint 1991; Weimerskirch et al. 2004), they also tend to forage in productive waters to increase their encounter rate with prey patches. Frigatebirds especially, which are more abundant when red-footed boobies are present, were often observed westward of Europa in more productive waters.

Feeding opportunities for sooty terns were favoured by the presence of surface-feeding groups of marine predators, especially tuna, as in other tropical waters (Au and Pitman 1986; Ballance et al. 1997; Jaquemet et al. 2004). Frigatebirds associated with any predatory groups, but their abundance did not peak significantly whatever the nature of the association. Red-footed boobies were never observed in close association with tuna when feeding, but no tuna school was observed within the range of boobies. They foraged in areas where cetaceans also foraged, particularly false killer whales which are not known to aggregate fast-moving groups of seabirds like boobies and terns in the Pacific (Pitman and Ballance 1992).

Foraging strategies

The long foraging range and wide distribution of sooty terns in all water types around the breeding grounds is probably the cause of the large number of sooty terns breeding at Europa. Individuals leave colonies grouped, and progressively spin a net of foragers that scan large oceanic areas for feeding opportunities, as already demonstrated for other species, and know as network foraging (Wittenberger and Hunt 1985). Consequently, they are present in almost all the feeding flocks and are often the only species. Feeding flocks are often similar to flock type I observed off Alaska (Hoffman et al. 1981). They are relatively small (< 500 individuals) and transient (often a few minutes) aggregations that form over fish schools. They form after the discovery of a school at the surface and end when the fish descend below contact with birds. Typically, the initiation of the flocks is due to a single or a small group of foraging birds that detect a fish school and begin feeding. The initiators of such feeding flocks are often species that are highly visible and that collaborate in their foraging activity, and are named catalyst species (Hoffman et al. 1981). Since sooty terns are near-obligate feeders of surface tuna (Au and Pitman 1986) and can feed in large flocks (Schreiber et al. 2002), they represent a good target for other species like frigatebirds and red-footed boobies to indirectly detect availability of prey, a process called local enhancement, which may be widely used by seabirds (see, for example, Nevitt and Veit 1999). It appears, thus, that sooty terns could be considered as a catalyst species of the feeding events, as previously demonstrated in tropical waters for other species (Mills 1998; Jaquemet et al. 2004), and already suspected for the sooty tern (Schreiber et al. 2002). Frigatebirds, which were frequently observed in sooty-tern feeding flocks in all water types, seem to be adapted to take advantage of the numerous sooty terns to detect feeding opportunities, but also of red-footed boobies flocks. It may even be foreseen that frigatebirds, which forage at high altitude (Weimerskirch et al. 2004), not only search for prey patches but also for feeding flocks, as suggested for albatrosses from the Southern Ocean that search for penguins (Nevitt and Veit 1999). Red-footed boobies, which are limited in their foraging range, are less dependent on sooty terns but can occasionally also take advantage of their presence to detect feeding opportunities. Finally, the higher number of frigatebirds in red-footed booby feeding flocks compared to sooty terns, suggests that individuals take more advantage of association with the former species. These results may be explained by the fact that boobies prey on larger prey than sooty terns (M. Le Corre and S. Jaquemet, unpublished data), which would be energetically advantageous.

In conclusion, our results demonstrate that the winter-breeding seabird community of Europa Island tends to forage in areas of enhanced productivity to increase its encounter rate with schools of surface marine predators. Although in austral winter, productivity of the waters is the highest for the area, constraints due to foraging from a central location lead to low feeding opportunities. To compensate for this situation, the numerous sooty terns forage over large oceanic areas all around their colonies in a network to increase feeding opportunities. Red-footed boobies, which are limited in their foraging range, tend to forage in more productive waters, where competition may be higher, as already observed in the Pacific (Ballance et al. 1997). Frigatebirds, finally, seem to be the most opportunistic species since they feed in association with any seabird species and any marine predators in all water types, although they favour the presence of feeding flocks of boobies. Future studies will help to increase our knowledge of the at-sea ecology of tropical seabirds and, particularly, favoured habitats and the importance of local enhancement on the feeding efficiency of these species.

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