ORIGINAL ARTICLE

Contrasted associations between seabirds and marine mammals across four biomes of the southern Indian Ocean

Jean-Baptiste Thiebot · Henri Weimerskirch

Abstract Seabirds associations with marine mammals have been shown to be an efficient way by which the seabirds can detect and access prey patches. However, these associations have been documented locally in the literature and their relevance at the ecosystem level is unknown, mostly because they constitute relatively rare events and therefore few appropriate data exist. In this study, we aimed at quantifying and qualifying these interactions, based on long-term standardised at-sea observations carried out from 1978 to 2005 in the whole southern Indian Ocean. We (1) investigated whether the observed interspecific associations between foraging seabirds and marine mammals could be distinguished from chance using a bootstrap method, and (2) compared their occurrences between four oceanic biomes sampled (tropical, subtropical, subantarctic, Antarctic). Although in our data we could not discriminate active association versus aggregation of species feeding on the same prey patches, our results indicate that, in each biome, 5–10 seabird species were more frequently associated with marine mammals than expected due to chance. Tropical birds appeared to be associated almost exclusively with Delphinidae schools, whereas in the subtropical waters, all the significant associations occurred with marine mammals others than dolphins. In the subantarctic biome, seabirds were mostly associated with Pinnipeds, and the highly productive Antarctic waters provided opportunities for diverse but rare associations. This study suggests that the ecological links between foraging predators can be measured using a randomisation method, and provides conclusive and comparative information on the ecology of apex trophic levels organisms from pelagic communities.

Keywords Foraging strategies · Interspecific interactions · Marine predators · Bootstrap procedure · At-sea observations · Long-term monitoring

Zusammenfassung

Vergleich von Vergesellschaftungen zwischen Seevögeln und Meeressäugern über vier Biome des südlichen Indischen Ozeans hinweg

Vergesellschaftungen von Seevögeln mit Meeressäugern sind eine effiziente Methode für die Seevögel, um Beute zu finden und zu nutzen. Allerdings wurden solche Vergesellschaftungen in der Literatur nur lokal dokumentiert, und ihre Relevanz auf Ökosystemebene ist unbekannt, vor allem, weil sie relativ seltene Vorkommnisse darstellen und es daher nur wenig angemessene Daten gibt. In dieser Untersuchung versuchten wir, diese Interaktionen quantitativ und qualitativ zu beschreiben auf der Basis von standardisierten Langzeit-Beobachtungen auf See, die zwischen 1978 und 2005 im gesamten südlichen Indischen Ozean durchgeführt wurden. Wir (1) untersuchten mit Hilfe einer Bootstrap-Methode, ob sich die beobachteten interspezifischen Vergesellschaftungen zwischen Seevögeln und Meeressäugern von zufälligen Ereignissen unterscheiden ließen und (2) verglichen deren Vorkommen zwischen den

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vier untersuchten ozeanischen Biomen (tropisch, subtropisch, subantarktisch, antarktisch). Obwohl wir in unseren Daten nicht zwischen aktiver Vergesellschaftung und einer Ansammlung von Arten unterscheiden konnten, die zufällig in den selben Beutefeldern jagten, deuten unsere Ergebnisse doch darauf hin, dass in jedem Biom fünf bis zehn Seevogelarten häufiger mit Meeressäugern vergesellschaftet waren als zufällig erwartet. Tropische Vögel schienen fast ausschließlich mit Schulen von Delphinidae vergesellschaftet zu sein, während in subtropischen Gewässern alle wesentlichen Vergesellschaftungen mit anderen Meeressäugern als Delphinen stattfanden. Im subarktischen Biom waren Seevögel meist mit Robben vergesellschaftet, und die hochproduktiven antarktischen Gewässer boten Möglichkeiten zu verschiedenen, aber seltenen, Vergesellschaftungen. Diese Untersuchung legt nahe, dass die ökologischen Verbindungen zwischen jagenden Prädatoren mit Hilfe einer Randomisierungsmethode gemessen werden können und liefert schlüssige und vergleichende Information über die Ökologie von in der Nahrungskette hoch stehenden Organismen aus pelagischen Gemeinschaften.

Introduction

Ecologists have been studying species assemblages for decades. However, concerning marine ecosystems, little is known about the structure of pelagic communities, and as a consequence the underlying mechanisms about how pelagic predators locate prey are still a focus in marine research today (Silverman et al. 2004; Weimerskirch 2007; Nevitt et al. 2008). To investigate these pelagic communities, seabirds are considered as good models because they are relatively easy to monitor at sea among pelagic predators (Ashmole 1971). However, given that they tend to be long-range foragers, studying their behaviour in detail at large enough spatial scales is challenging (e.g. Weimerskirch et al. 1999). At large spatial scales, it has been well documented that, since their prey are not always accessible near the sea surface, most seabirds seem to actively search for physical features, such as upwellings or oceanic frontal zones and shallow areas (Schneider 1991; Hunt et al. 1999; Bost et al. 2009), which enhance accessibility of the targeted species near the surface. Nevertheless, at smaller spatial scales, we still wonder how seabirds can locate and access prey patches that may occur several meters below the surface. The immediate biotic environment (number of individuals foraging together, presence of cooperative and/or competitor species) of the foraging seabirds is expected to be one of the keys that trigger their feeding behaviour

(Nevitt and Veit 1999; Silverman et al. 2004). This type of information is still poorly known, even using the recent technologic advancements which has stimulated much research in this area (Ropert-Coudert and Wilson 2005; but see Sakamoto et al. 2009; Yoda et al. 2011). In particular, many studies have concluded that sub-surface predators may play a crucial role as commensal organisms for seabirds, by making prey patches more easily detectable and accessible to the birds (e.g. Evans 1982; Harrison et al. 1991; Pitman and Ballance 1992; Yamamoto et al. 2010), but few large enough datasets are available to rigorously test the significance of this interaction. In this study, we used a long-term (1978–2005, almost 30 years), standardised dataset of at-sea observations carried out in the southern Indian Ocean along repeated transects to investigate associations between seabirds and marine mammals across a geographic scale spanning four distinct biomes from 11 to 67°S (tropical, subtropical, subantarctic, Antarctic). In this dataset, we examined whether co-occurrence of seabirds and marine mammals were more frequent than expected due to chance, and then compared these associations between the four biomes.

Because the benefit for seabirds to forage in association with marine mammals would increase when the probability of encountering prey decreases (Clark and Mangel 1984) or when foraging methods do not allow seabird species to reach prey at depth (Ashmole 1971), we predicted contrasting numbers of significant associations with marine mammals between biomes. For example, fewer associations would occur in Antarctic versus tropical biomes since diving seabird species are dominant in Antarctic waters and absent in the tropics (Ashmole 1971; Au and Pitman 1986; Ballance and Pitman 1999). In line with the different abundances of marine mammals in each region, we also expected a greater number of associations with dolphin species in the tropical biome (Au and Pitman 1986; Jaquemet et al. 2004) versus more associations with baleen whales near Antarctica (Bierman and Voous 1950; Brown and Lockyer 1984).

Materials and methods

Study area

The study was conducted in the southern Indian Ocean, from 11 to 67°S and from 20 to 120°E. This oceanic region shows a very strong latitudinal gradient of sea-surface temperature (SST) and sea-surface productivity, with high levels of productivity found during austral summer at the cold southern waters' surface, while very low levels occur in the large tropical and subtropical gyres (Schneider 1991; Hunt et al. 1999).

Data collection

This study is based on the analysis of at-sea observations of seabirds and marine mammals carried out from the pilot house of the R/V "Marion-Dufresne" (17 m eye height over the sea surface) between 1978 and 2005 by trained observers using a pre-established protocol. Our dataset spans over 27 years of standardised observations along constant track lines: four to five times per year (from November to March, and in August–September), the "Marion-Dufresne" leaves Réunion Island to supply the French Southern Territories (Crozet, Kerguelen, Saint-Paul and Amsterdam Islands). Moreover, this vessel is involved in oceanographic cruises, hence observations could be made near the Antarctic continent and in tropical regions (Fig. 1).

The method consisted of a 10-min scan every hour, from sunrise to sunset whenever possible, to the front and the side of the vessel with best visibility (e.g. least sun glare or wind). This method was chosen to allow sufficient time to conduct an exhaustive census of the predators, while at the same time reducing the risks of repeating counts of the same individuals from one census to the next, and reducing the fatigue of the observer (Tasker et al. 1984; Hyrenbach 2001). With the aim of limiting correlation between two consecutive scans, observations were conducted only once the vessel reached its cruise speed (10–16 knots;

18.5–29.6 km h^{-1}). Doing this reduced both the time of residence of the ship into a region and the opportunity for the birds to stay around the ship from one scan to the next. In addition, observations were not carried out when conditions were considered unsuitable by the observer for sampling (visibility lower than 1 km, waves over 5 m, precipitations, inconstant route, observer fatigue), and while coasts were visible to avoid overabundances of local breeders (Veit et al. 1993). In 2003 and 2004, the method used differed in that the survey was made continuously during transects of hours; in that case, we sub-sampled the first 10 min of each transect and then one 10-min period every subsequent hour to reproduce comparable sampling, with a decreased probability of multiple counting of individuals (Hyrenbach 2001). The effects of observer fatigue and inter-observer variability between years could not be directly taken into account, but were nevertheless reduced (see "Quantifying interspecific associations" below).

Data collected during surveys included seabird and marine mammal observations identified to species (or otherwise to lowest possible taxonomic level), number of individuals and seabirds' behaviour (accompanying ship, following in wake, going past ship, naturally feeding, resting, feeding on ship discards). However, as some identifications are hard to make at sea, the taxonomic level recorded for some taxa could not be the species.

Fig. 1 The southern Indian Ocean showing cruises during which at-sea observations were carried out (each *grey dot* represents a 10-min scan) and 3, 13 and 24 °C summer sea-surface isotherms set as limits of the four biomes (tropical, subtropical, subantarctic, Antarctic from north to south) and averaged over the study period (data extracted from the PO.DAAC Ocean ESIP Tool website)
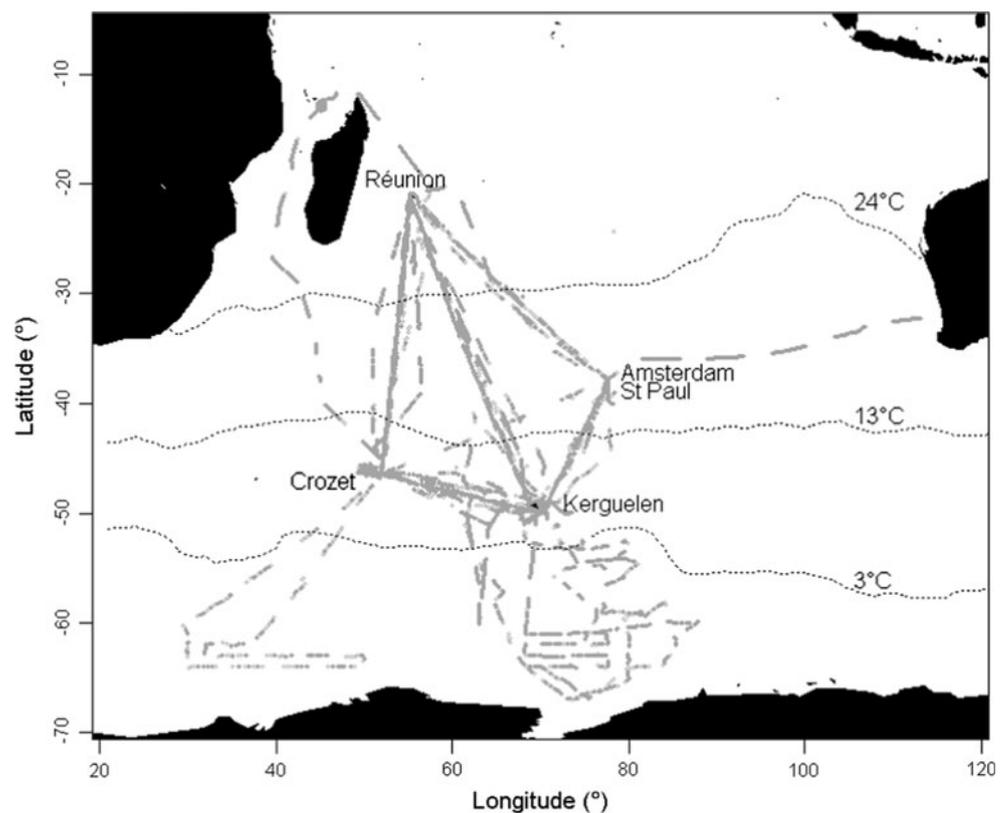
This was mainly the case for marine mammals, but also for seabirds such as the prions (genus *Pachyptila*), the diving-petrels (genus *Pelecanoides*) and the Sooty versus Bridled terns, *Onychoprion fuscata* and *O. anaethetus*, respectively. Each observation is stored in the Chizé database of at-sea observations (1978 until present), and amounted to 11,261 observation scans by 2005.

Data preparation

Although some of the birds recorded were non-breeders, we focused on the chick-rearing season for most of the seabird species (i.e., months of January, February and March; see Weimerskirch et al. 1988). During this period, food demand increases and consequently interspecific associations might be particularly useful for finding prey (Bräger 1998). Of the 11,261 10-min scans recorded over the entire 1978–2005 dataset, we extracted 9,630 (>85 %) that were taken during austral summer, amounting to 1,605 h of observation.

Because predators are not always feeding, and prey are likely to try to avoid being eaten, there is much opportunity to observe consumers in the absence of their food; for this reason, a fundamental assumption for this study was that every predator seen at sea was searching for food. We excluded from the analyses all animals which had a noticeable interaction behaviour with the ship (ship followers, accompaniers and feeding on discards) with the aim of limiting the ship attraction effect; we also excluded all bird taxa represented by less than 10 sightings over the entire dataset (rare, vagrant birds or anecdotal records).

In this study, sub-surface predators were limited to marine mammals because these latter are more likely to be detected by trained observers as they come to the surface to breathe, and because they are widely distributed. As marine mammals were far less abundant than seabirds in the dataset and generally harder to identify specifically, we grouped them by taxon as Mysticeti, Delphinidae, Pinnipeds, sperm whales and beaked whales.

The four biomes were defined using the SST boundaries that naturally separate the pelagic communities of this region (Ainley and Boekelheide 1983; Hyrenbach et al. 2007), in order to have reliable unities among years, into which organisms had some chance to co-occur: tropical (SST ≥ 24 °C), subtropical (13 ≤ SST < 24 °C), subantarctic (3 < SST < 13 °C) and Antarctic (SST ≤ 3 °C).

Quantifying interspecific associations

We searched among all the observations within each biome for associations (co-occurrences in our dataset) which could not be expected to be due to chance. To do this, we employed an iterative randomisation procedure (the bootstrap method; Manly 1997); this recent method is now in current use in

ecology to distinguish the occurrence and distribution of specified events from chance (Veit et al. 1993; Silverman et al. 2004). In this work, we considered that, since the investigation of co-occurrences only needs binary presence/absence information from a statistical point of view, we would use this coding in our investigation. No further distinction in the number of individuals in each marine mammal observation was made to avoid working on too small samples of group size classes in the biomes. This data coding also helped to control for inter-observer reliability, observation conditions and differences in the risk of multiple counting between the protocols used. Using only data of animals seen in the vessel's wake would be a good basis for a homogeneous numerical comparison of both datasets, since this part of the observations was kept constant between protocols; however, virtually no marine mammals were seen in the wake during the whole study period. Finally, since no distinction was made during a 10-min scan in the notation of birds whether or not they were foraging with marine mammals, it was not possible to know how many birds were indeed associated with a marine mammal sighting, which would make using the numbers of birds artificial. Practically, we considered that the presence of a species within an entire dataset provides a probability of encountering this species during a scan period, and that this probability allows one to expect a given number of co-occurrences with other species. The estimation of this number of expected co-occurrences is determined using a routine program created with the software R (R Development Core Team 2012). First, a simple index of simultaneous presence was calculated for every possible pair of species over the available scans for each community. We chose the Jaccard index (Jaccard 1908) because it describes well the interference between the distribution of two taxa along a series of presence/absence data. Especially, this index gives proximity to two stations because of the species they share and not by the species they do not share, what is well suited to our case. Secondly, the program generates a new distribution of the surveys of one species for every pair of species analysed, using a random function. This step is realised 10,000 times; for each cycle (iteration), the Jaccard index is calculated from the new distribution, and each index value is saved. The high number of index values constitutes a pool that defines the variation possible for the index concerning each pair of species. We admitted here that chance may explain 95 % of the linkages detected between two species by defining two boundaries (2.5 and 97.5 %) which corresponded to the highest acceptable intervals of negligible variance at both ends of the overall simulated index values distribution. Thus, each pair of species which had an index greater than the 97.5th percentile of the simulated values was considered as significantly associated (i.e. deliberate reliance on marine mammals, or simply aggregation on the same prey patches),

while an index lower than the 2.5th percentile of the simulated values was interpreted as two species significantly independent (i.e. using different habitats in the same biome, or showing avoidance, competitive exclusion).

Results

Seventy-one seabird species occurred in the summer data subset (see Appendix 1), and 30 marine mammal species (see Appendix 2) could be categorised into the five phylogenic groups. We describe here the seabird and mammal communities in each biome, in order to match information on these communities' structure and dynamics with the significant co-occurrences detected.

Seabird communities

The relative composition of the seabird community found within each biome (Fig. 2) showed that, in the tropical biome, terns (mainly Sooty Terns *O. fuscata*) were the birds most frequently seen; other common taxa included petrels (mainly Barau's petrel *Pterodroma baraui*) and shearwaters (mostly the Wedge-tailed and Audubon's shearwaters, *Puffinus pacificus* and *P. lherminieri*, respectively). Several taxa were exclusive to this biome: Phaethontidae, Sulidae, Fregatidae and noddies. Conversely, albatrosses (Diomedeidae), prions and storm-petrels (Oceanitidae) were present in all except the tropical biome. The subtropical biome showed the highest proportion of petrels (mainly the White-chinned *Procellaria aequinoctialis*, Soft-plumaged *Pterodroma mollis* and Great-winged *P. macroptera*) and albatrosses (especially Wandering *Diomedea exulans* and Yellow-nosed *Thalassarche carteri*). Penguins (Sphenisciformes) and diving-petrels (Pelecanoididae) appeared only in the subantarctic and Antarctic biomes, and more coastal birds like gulls (Laridae) and cormorants (Phalacrocoracidae) were observed only in the subantarctic biome, making this the most diversified biome in our study. Taxa showed more balanced frequencies in this biome; however, the Black-browed Albatross *Thalassarche melanophris* and Wilson's Storm-petrel *Oceanites oceanicus* were the most frequently recorded species. Finally, the Antarctic biome, even though dominated by petrels (mainly White-chinned and Blue *Halobaena caerulea*), showed also high diversity of taxa.

Specific richness varied significantly between biomes (ANOVA, $F_{1, 9,626} = 2{,}557$; $p < 0.0001$) and revealed a dichotomy between biomes with low (tropical and subtropical) versus high (subantarctic and Antarctic) mean specific richness (Fig. 3a). The frequency of birds seen feeding also varied significantly between biomes (ANOVA, $F_{1, 9,626} = 4.5$; $p = 0.01$), and the dichotomy previously highlighted
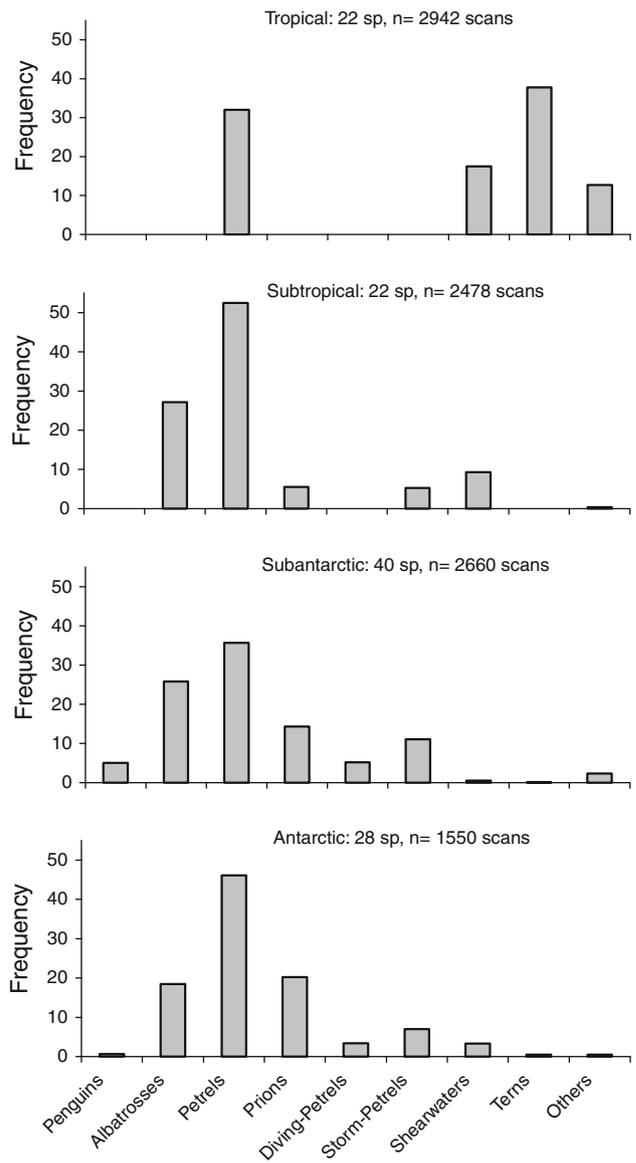
Fig. 2 Occurrence frequency of seabird taxa among the observations carried out into each biome

was also conspicuous here (Fig. 3b). Finally, the mean number of species recorded in a scan during which at least one species was feeding (Fig. 3c) was strikingly different among biomes (ANOVA, $F_{1, 9,626} = 13.1$; $p < 0.0001$). Thus, the fewer opportunities to feed in the tropical biome (Fig. 3b) seemed to cause large species aggregations at these scarce events, while in the other biomes the mean number of species feeding together was relatively low.
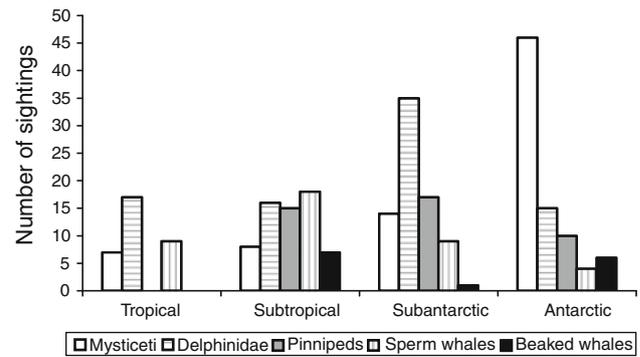
Marine mammal observations

A total number of 254 marine mammal sightings were available in the survey. Phylogenic groups showed contrasted distributions among biomes (Fig. 4). Mysticeti were
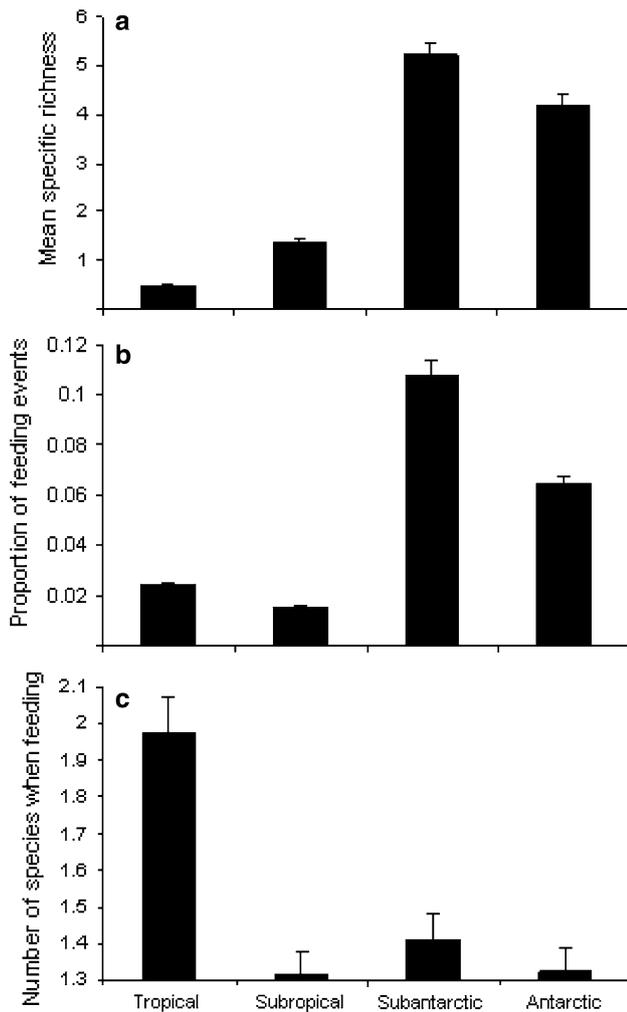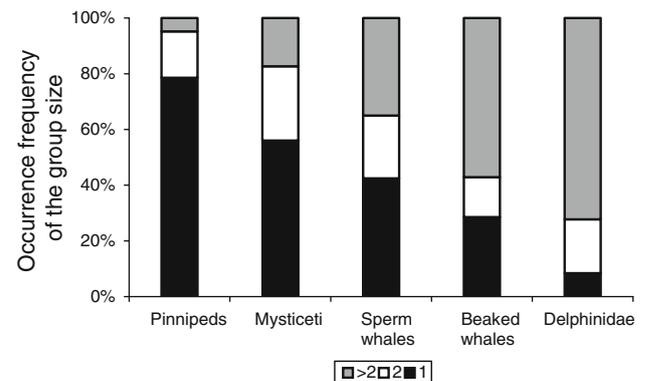
Fig. 3 a Mean number of seabird species recorded during a 10-min period into each biome (*error bars* 95 % confidence interval; sample size for each biome as in Fig. 2); b mean feeding behaviour frequency for one species in each biome; c mean number of seabird species recorded during an observation period in which at least one was feeding, for each biome

Fig. 4 Distribution of marine mammals observations in the four biomes

Fig. 5 Frequency of group sizes (a single animal, two, more than two) for each type of marine mammal

particularly well represented in the Antarctic waters with abundant records of minke whale *Balaenoptera acutorostrata*, while in the tropical and subantarctic biomes, the Delphinidae were the most frequent marine mammals seen, specifically striped *Stenella coeruleoalba* and hourglass *Lagenorhynchus cruciger* dolphins, respectively. Pinnipeds were not recorded in the tropical waters, but fur seals (genus *Arctocephalus*) were abundant around the subtropical and subantarctic islands where they breed, and so were Phocid seals near the Antarctic. The sperm whale *Physeter macrocephalus* was recorded in every biome, and most often in the subtropical region; other species in this group (genus *Kogia*) were much less often recorded. The sightings of beaked whales were scarce events, occurring mostly in open waters (subtropical and Antarctic regions); the

species recorded most often was the southern bottlenose whale *Hyperoodon planifrons*.

Lastly, the marine mammal groups also differed in the mean number of individuals per sighting (Fig. 5): a gradient appeared between the Delphinidae, which were most frequently recorded in groups, and the Pinnipeds, which were most often recorded as solitary individuals (Kruskal–Wallis rank sum test, $H_{4, 254} = 100.2$; $p < 0.0001$).

Interspecific associations

Tropical biome

In the tropical biome, five seabird species among the 22 observed showed a significant link with marine mammals (Table 1). These five species were all associated with Delphinidae; in addition, one species (Audubon's Shearwater) was also linked to Mysticeti, mostly represented in this sector by the minke whale.

Subtropical biome

In the subtropical biome, 10 of the 22 seabird species were significantly associated with marine mammals (Table 2).

Table 1 Taxa showing significant associations in the tropical biome; no Pinnipeds or beaked whales were recorded in this biome

	Mysticeti n = 7	Delphinidae n = 17	Sperm whales n = 9
Wedge-tailed Shearwater	0.0075	**0.0360**	0
n = 127	(0–0.0145)	(0–0.0203)	(0–0.0152)
Audubon's Shearwater	**0.0163**	0.0227	0
n = 118	(0–0.0150)	(0–0.0205)	(0–0.0159)
White-tailed Tropicbird	0.0133	**0.0361**	0
n = 69	(0–0.0152)	(0–0.0244)	(0–0.0154)
Sooty/Bridled Terns[a]	0	**0.0353**	0
n = 388	(0–0.0149)	(0–0.0238)	(0–0.0152)
Brown Noddy	0	**0.0411**	0
n = 59	(0–0.0175)	(0–0.0263)	(0–0.0175)

Jaccard indices from the simulated values boundaries, meaning a significant association between the two taxa, shown in bold; the 2.5 and 97.5 % values of the maximum Jaccard index from simulations are in parentheses

n in first column, number of scans during which the taxa was seen in this sector

[a] Sooty/Bridled Terns are undistinguishable at sea

Here, no association was found with Delphinidae, but significant links were detected with every other group of marine mammals.

Subantarctic biome

Since there was only a single sighting of a beaked whale recorded in the subantarctic biome, we did not consider this mammal group in the analyses. Ten of the 40 seabird species identified showed significant associations with marine mammals (Table 3). Seven out of ten species showed a significant link with the land-breeder Pinnipeds. It is noteworthy that in this biome, a significant independence in habitat use in space and/or time was detected between Mysticeti and the Northern giant petrel *Macronectes halli*.

Antarctic biome

In the Antarctic biome, 5 among 28 species identified were significantly associated with marine mammals (Table 4), with two of these linked to Mysticeti. Prions seemed not to be associated with any mammal group. Furthermore, Antarctic seabirds were not found to be associated as frequently with Pinnipeds as in the subantarctic biome, but interestingly the two bird species that did associate with them (i.e., Black-browed albatross and Wilson's stormpetrel) were also detected as being linked to these mammals in the subantarctic biome.

Discussion

The results of the present study suggest that, in the four biomes from the tropics to Antarctica, several seabird species were seen concomitantly with a given marine mammal group, more often than expected due to chance. Such relationships seem to vary extensively according to the biome under consideration. These results also show that the mammal group most frequently seen in a biome (see Fig. 4) was not necessarily the group that co-occurred with seabirds most frequently in that biome. For instance, few associations were found with the sperm whale, while it was the mammal species most often recorded in our study. Beyond these general remarks, we can draw contrasting global functioning schemes for the four communities, with respect to the method's strengths and limitations.

Review of the method employed

Our analyses were based on a unique, consequent dataset of at-sea observations of seabirds and marine mammals, enabling us to work with satisfying sample sizes in the four marine biomes for almost all categories of predators defined. Amongst the 9,630 10-min surveys analysed and the 476 possible combinations, the randomisation method we employed allowed us to distinguish from chance 38 positive and 1 negative interactions between seabird species and phylogenic groups of marine mammals. These results show that the co-occurrences that were seen at sea are not anecdotal but conversely are relevant at the scale of the biome.

Nevertheless, we must be careful in over-interpreting the associations highlighted in this study since we cannot tell if these interactions are foraging associations or if the interacting species exploit the same habitat and areas for feeding, creating dense co-occurrences during at-sea observations. In any event, the results presented here are compelling in that they document variation in the specific assemblages of foraging predators in the pelagic communities over a broad geographic range.

Our results may not be accurate for some species. Indeed, the probability of seeing some animals like shy marine mammals or small, cryptic seabirds is still low in any weather conditions (Barbraud and Thiebot 2009; Southwell and Low 2009). Moreover, for some seabirds, the presence/absence data coding was not optimal for the analyses. For example, prions were observed in up to 85 % of the scans made in the Antarctic sector. In this case, the abundance of observations might have induced all random redistributions to be similar, and therefore it was unlikely to discriminate from chance the co-occurrences with marine mammals, even if these co-occurrences were numerous. This method thus requires the taxa to be well represented

Table 2 Taxa showing significant associations in the subtropical biome (see legend and footnotes in Table 1)

	Mysticeti $n = 8$	Delphinidae $n = 16$	Pinnipeds $n = 15$	Sperm whales $n = 18$	Beaked whales $n = 7$
Wandering Albatross	0.0084	0.0062	0.0062	0.0124	**0.0084**
$n = 472$	(0–0.0085)	(0–0.0130)	(0–0.0126)	(0.0019–0.0144)	(0–0.0080)
Yellow-nosed Albatross	0.0034	0.0066	**0.0374**	0.0065	0.0034
$n = 290$	(0–0.0103)	(0–0.0158)	(0–0.0153)	(0–0.0166)	(0–0.0100)
Sooty Albatross	0.0090	0.0084	**0.0531**	0.0167	0
$n = 104$	(0–0.0179)	(0–0.0224)	(0–0.0208)	(0–0.0242)	(0–0.0165)
Soft-plumaged Petrel	**0.0092**	0.0045	0.0068	0.0135	0.0046
$n = 432$	(0–0.0089)	(0–0.0136)	(0–0.0132)	(0–0.0147)	(0–0.0074)
Barau's Petrel	0	0	0	**0.0357**	0
$n = 40$	(0–0.0238)	(0–0.0317)	(0–0.0256)	(0–0.0323)	(0–0.0238)
Prions[a]	**0.0158**	0	0	0.0050	0
$n = 185$	(0–0.0117)	(0–0.0183)	(0–0.0164)	(0–0.0199)	(0–0.0111)
White-chinned Petrel	**0.0084**	0.0084	0.0036	**0.0132**	**0.00601**
$n = 829$	(0–0.0063)	(0.0023–0.0109)	(0.0023–0.0106)	(0.0024–0.0120)	(0–0.00598)
Flesh-footed Shearwater	0	0	**0.0355**	0	0
$n = 131$	(0–0.0150)	(0–0.0210)	(0–0.0205)	(0–0.0216)	(0–0.0146)
Great Shearwater	0	0	0	**0.0667**	**0.0500**
$n = 14$	(0–0.0455)	(0–0.0370)	(0–0.0370)	(0–0.0345)	(0–0.0455)
Little Shearwater	**0.0426**	0	0	0	0
$n = 41$	(0–0.0238)	(0–0.0303)	(0–0.0233)	(0–0.0323)	(0–0.0238)

[a] Prion species indistinguishable at sea

Table 3 Taxa showing significant associations in the subantarctic biome (see legend and footnotes in Table 1); the single record of beaked whale in this biome was omitted from the analyses

	Mysticeti $n = 14$	Delphinidae $n = 35$	Pinnipeds $n = 17$	Sperm whales $n = 9$
Wandering Albatross	0.0030	**0.0220**	0.0040	0.0040
$n = 990$	(0.0020–0.0089)	(0.0077–0.0186)	(0.0029–0.0103)	(0.0010–0.0061)
Black-browed Albatross	0.0028	0.0111	**0.0122**	**0.0066**
$n = 1,062$	(0.0019–0.0086)	(0.0078–0.0182)	(0.0028–0.0102)	(0.0009–0.0063)
Sooty Albatross	0.0091	0.0167	0	**0.0140**
$n = 208$	(0–0.0148)	(0–0.0256)	(0–0.0175)	(0–0.0130)
Northern Giant Petrel	**0**	0.0185	0.0072	0.0058
$n = 683$	(0.0014–0.0102)	(0.0057–0.0202)	(0.0014–0.0117)	(0–0.0074)
Cape Petrel	0.0077	0.0035	**0.0350**	0.0039
$n = 249$	(0–0.0148)	(0–0.0253)	(0–0.0159)	(0–0.0118)
White-headed Petrel	0	0.0154	**0.0216**	0
$n = 361$	(0–0.0130)	(0.0026–0.0231)	(0–0.0141)	(0–0.0088)
White-chinned Petrel	0.0057	**0.0177**	**0.0083**	0.0031
$n = 1,921$	(0.0036–0.0068)	(0.0103–0.0157)	(0.0046–0.0082)	(0.0021–0.0047)
Wilson's Storm-petrel	0.0039	0.0167	**0.0144**	0.0053
$n = 756$	(0.0013–0.0095)	(0.0063–0.0196)	(0.0024–0.0113)	(0–0.0069)
Diving-petrels	0.0041	0.0163	**0.0125**	0.0056
$n = 716$	(0.0013–0.0099)	(0.0063–0.0200)	(0.0014–0.0114)	(0–0.0071)
Kerguelen Shag	0.0115	**0.0381**	**0.0341**	0
$n = 74$	(0–0.0235)	(0–0.0303)	(0–0.0238)	(0–0.0154)

[a] Diving-petrel species indistinguishable at sea

Table 4 Taxa showing significant associations in the Antarctic biome (legend as in Table 1)

	Mysticeti $n = 46$	Delphinidae $n = 15$	Pinnipeds $n = 10$	Sperm whales $n = 4$	Beaked whales $n = 6$
Black-browed Albatross	0	0	**0.0280**	0	0
$n = 100$	(0–0.0467)	(0–0.0283)	(0–0.0220)	(0–0.0122)	(0–0.0194)
Blue Petrel	**0.0460**	0.0107	0.0054	**0.0082**	0.0054
$n = 363$	(0.0134–0.0419)	(0.0025–0.0188)	(0–0.0139)	(0–0.0081)	(0–0.0106)
White-chinned Petrel	**0.0333**	0.0109	0.0078	0.0031	0.0039
$n = 1,289$	(0.0253–0.0332)	(0.0071–0.0117)	(0.0046–0.0078)	(0.0015–0.0032)	(0.0023–0.0047)
Sooty Shearwater	0.0210	0.0192	0.0049	0	**0.0150**
$n = 197$	(0.0081–0.0457)	(0–0.0229)	(0–0.0185)	(0–0.0105)	(0–0.0142)
Wilson's Storm-petrel	0.0256	**0.0200**	**0.0176**	0.0076	0.0050
$n = 394$	(0.0141–0.0416)	(0.0024–0.0184)	(0–0.0132)	(0–0.0076)	(0–0.0100)

within the dataset, but preferably with balanced frequencies of presence versus absence data (Manly 1997).

The next step to this approach would be to measure the strength of the associations detected since the number of individuals involved was not taken into account here. We believe that some species of whales, or some sizes of groups, are more attractive to foraging birds than others, but due to our sample sizes we could not (1) base our work on a specific approach regarding marine mammals, or (2) test the importance of group size on the interaction for most of them.

The tropical biome

The results obtained for the tropical biome confirm the existence of a previously reported association between tropical seabirds and Delphinidae schools (Au and Pitman 1986; Pitman and Ballance 1992; Ballance and Pitman 1999). More specifically, the five bird species that were significantly associated with the Delphinidae in our study have already been described as frequently seen foraging with tropical sub-surface predator schools in the Indian Ocean (Jaquemet et al. 2004). Two of these also showed significant association with sub-surface predators in the tropical Pacific (Hebshi et al. 2008). Interestingly, these five species were among the most frequent in this biome, which confirms that a positive correlation seems to exist between the abundance of a seabird species and the strength of an association with a sub-surface predator (Ballance and Pitman 1999). Such an association is indeed considered as almost obligate for feeding by the most abundant species, such as Sooty Tern (Ballance et al. 1997), even if a key player in this scenario may be predatory schools of fish such as tuna (Au and Pitman 1986; Ballance and Pitman 1999), a variable we could not consider in the present study. The foraging behaviour of the sub-surface predators is assumed to allow the birds to feed

near the sea surface on concentrated prey schools (mainly fish and squid) which are prevented from escaping to deeper water, or are disoriented or injured (Ashmole 1971; Ballance and Pitman 1999; Clua and Grosvalet 2001). This ecological interaction is undoubtedly of considerable benefit for the birds of this region, that are characterised by having poor diving abilities in return for the low-cost flight developed to forage in this region with scarce prey-patches (Ballance et al. 1997; Weimerskirch et al. 2005, Yamamoto et al. 2010). Finally, these associations depict well the group strategy of the tropical predators involved, i.e. flock-feeding birds (Fig. 3c) and Delphinidae (Fig. 5), reflecting an adaptation to the low probability of encountering a prey-patch in this environment (Clark and Mangel 1984; Ballance and Pitman 1999).

The subtropical biome

Almost 50 % of the subtropical bird species were found associated with mammals, which is very interesting regarding the low levels of local sea-surface productivity. No association with the Delphinidae was detected in this biome, but was with every other mammal group. Unlike in the tropical biome, here the most abundant locally breeding seabirds associated with Pinnipeds (Duriez et al. 2005). However, since (1) few species breed on St Paul and Amsterdam subtropical islands (Duriez et al. 2005), meaning that many of the pelagic birds seen in the subtropical biome breed elsewhere (tropical and subantarctic islands), and (2) we showed that very few feeding events and species feeding were recorded in this region (Fig. 3), the subtropical biome appears paradoxical. This region provides very few feeding opportunities for the birds, while causing them to travel great distances to forage in this area (Weimerskirch et al. 1999). An explanation is that the feeding events in this region may not have been recorded during our surveys as the birds may feed at night, or at

dawn/dusk, when prey may come closer to the sea surface (Harper 1987). This latter hypothesis is supported by recent studies benefiting from technological advances (Péron et al. 2010), and would explain why, during daylight in this biome, (1) so many seabird species were recorded, (2) very few birds were seen feeding, and (3) numerous associations with deep-foraging marine mammals were found. This is a marked peculiarity of the subtropical biome, as nocturnal feeding is probably not significant in the tropics, due to the dependence of the birds on diurnally feeding sub-surface predators (Ballance and Pitman 1999), nor in polar regions, as suggested by the desertion of the birds from these areas during the winter night (Van Dam and Kooyman 2004).

The subantarctic biome

The results obtained for the subantarctic biome emphasise the previously suggested role of the Pinnipeds in relation to the birds (Harrison et al. 1991; Silverman and Veit 2001). These marine mammals would be very efficient helpers for prey accession, because in comparison to other abundant sub-surface subantarctic predators, such as the penguins, they move quickly from one prey-patch to another, dive more frequently and have a higher food intake, with bigger prey (Costa 1991). This behaviour may force aggregated pelagic or demersal prey to come near to the surface, as well as producing macerated prey or wastes potentially beneficial to the birds (Harrison et al. 1991; Cherel et al. 2000), especially with the bigger prey that they have to consume on the surface. Interestingly, and in contrast to the tropical biome, in the highly productive subantarctic waters, the predators involved in the detected associations reflect a more solitary foraging strategy: rarely flocking bird species (Fig. 3c) and Pinnipeds (Fig. 5). The significant independence found between the Northern Giant Petrel and Mysticeti reflects the fact that these taxa never co-occurred in our dataset while they were likely to do so by chance (see Table 3). Records of these taxa overlapped along the transects in this biome, thus indicating a more probable segregation in time rather than in space between these predators. In other respects, no positive association with the Mysticeti was detected in this biome; this may indicate that both Mysticeti and krill-eating sub-antarctic seabirds migrate southward during the austral summer to feed intensively in the Antarctic region (see Brown and Lockyer 1984; Ridoux 1994; Péron et al. 2010), as krill is found only south of 59°S in our study region (Miquel 1991).

The Antarctic biome

Antarctic krill (*Euphausia superba*) is one of the most highly-aggregated prey types (Hamner et al. 1983) and an essential resource among others for numerous predators in this region (Ridoux 1994). As these patches tend to occur several meters below the surface (Harrison et al. 1991), it has been previously suggested that flying birds would rely on large foraging cetaceans to gain access to this resource (Bierman and Voous 1950). Otherwise, flying birds may also benefit from upward currents close to the pack-ice in order to access prey more easily, not only by direct advection of prey but also because this hydrological activity tends to increase ice melting, causing ice algae to be released into the water column, which in turn induces area-intensive foraging behaviour in the krill (see Plötz et al. 1991 and references therein). In our study, few bird species were found to be significantly associated with mammals in Antarctic waters, and no clear dominance of associations with the abundant Mysticeti was noticed. According to the observers, a segregation in space or time seemed to exist between the high density prey-patches exploited by the birds and those exploited by the mammals. This suggests that the biological richness of this region during the austral summer leads to a decrease in the benefit of an association with another predator, a result which conforms nicely with theories surrounding group-feeding strategies in seabirds (Clark and Mangel 1984). According to this "Information Sharing Model", the time a bird has to spend searching for food itself is one of the main explanations for joining a flock: in the case of the Antarctic seabirds, a short time spent finding food would explain the lower benefit from an association with marine mammals. Accordingly, this model would predict that the optimal group size of seabirds should be lower in the rich Antarctic waters than in the tropics, which was indeed the case in our study (Fig. 3), though this deserves more numerical emphasis.

A taxonomic segregation?

Most (48 out of 71) of the seabird species examined in this study did not show a significant association with marine mammals. Conversely, some taxa with proficient long distance flying capability but poor diving ability, particularly the albatrosses, terns and petrels (Ballance et al. 1997; Weimerskirch et al. 1999, 2000), were often found associated with them. This low-cost locomotion may indeed drive their ability to exploit the behaviour of other species which results in a surface-feeding resource (Ridoux 1987), creating the feeding flocks observed for these birds (Harrison et al. 1991; Nevitt and Veit 1999; Ballance and Pitman 1999). Other flock-feeding birds very often found associated with mammals were the shearwaters, including both the abundant and less common species in our dataset. Although these species have a less proficient flight style, they can nevertheless dominate the end part of the flocks as they are able to consume the prey that are escaping to

depths, thanks to their diving capabilities (Harrison et al. 1991).

Interestingly, seabird species which are typically recorded as solitary individuals (Ridoux 1994) were not or far less often detected as significantly linked to marine mammals. These species were most of the gadfly petrels (genera *Pterodroma* and *Lugensa*), as well as the Grey Petrel *Procellaria cinerea*, and the Light-mantled Sooty *Phoebetria palpebrata* and Shy *Thalassarche cauta* Albatrosses. All of them are known to avoid at-sea interactions with the powerful and aggressive species (such as the White-chinned Petrel, the giant petrels and most of the albatrosses), which generally exclude them from the feeding flocks (Ridoux 1994). It is noteworthy that the Great-winged and the Grey Petrels are both winter breeders; this feature might result in a less intense food search in summer than the other species and therefore make them avoid the aggressive interactions inherent in the flock-feeding assemblages (see Harrison et al. 1991; Ridoux 1994). Other bird taxa that showed no significant association with marine mammals were often predators with particular feeding habits. In the tropical biome, the Red-footed Booby *Sula sula* was the Sulidae species most frequently recorded; amongst all the tropical species, this large bird is known to forage in the locally highest productivity areas (Ballance et al. 1997), using a peculiar aerial capture-feeding technique on marine flying prey (Ballance and Pitman 1999). It was considered as being frequently associated with sub-surface predators (Ballance et al. 1997), and mainly tuna in the Indian Ocean (Weimerskirch et al. 2005), but Hebshi et al. (2008) showed that in the tropical Pacific this species did not associate with any sub-surface predator in greater proportion than what would be expected by chance. In the other biomes, the skuas and jaegers (Stercorariidae), as well as the gulls (Laridae) and the giant petrels, although widely and frequently recorded offshore, were never found associated with mammals in any biome. The scavenging feeding habits of giant petrels show that, even if sub-surface predators may be of occasional benefit when feeding close to the shore (Ridoux 1987), they can obtain the bulk of their food on land, especially during the hatching and pupping periods of targeted species (Ridoux 1994).

Are these associations commensalisms?

In this study, the four biomes considered appear to be different regarding the group of marine mammals with which the seabirds were frequently seen to co-occur. Considering each biome separately, marine mammals could be seen as commensals for seabirds by the way these predators may interact when foraging at sea. However, many widespread bird species were found to be associated with a marine mammal in one sector and not in the others,

while everywhere they still have to access prey that typically occur at depth; this argues against a true commensalisms relationship between the studied predators. In the same way, our results show that one bird species can be associated with different groups of mammals, both within and between biomes, as found for the White-chinned Petrel and the Wandering Albatross, which seems to reflect highly opportunistic behaviour for these species, illustrated by different foraging techniques between the regions (Weimerskirch et al. 1999; Péron et al. 2010), due to different prey types (Ridoux 1994). Finally, the at-sea observations analysed here give a picture of how organisms were spatially or temporally associated in each biome. Since the mechanisms driving these associations and the chronology of their formation are still unknown, these links should not be seen as true commensalisms but rather as "opportunistic" commensalisms. In order to specifically study the question of true commensalisms, it would be necessary to carefully monitor the formation of feeding aggregations at sea, a task that is very difficult in oceanic waters, but equally fruitful (see Harrison et al. 1991; Clua and Grosvalet 2001; Silverman and Veit 2001). This perspective may also help clarify the relationship between Northern Giant Petrels and Mysticeti along a temporal approach of the flocks. Nevertheless, the approach of our work confirms that direct observations at sea remain necessary and highly valuable to understand and complement the knowledge of the seabirds foraging strategies recently gained from telemetry methods, and to interpret them at a number of ecological scales: the individual species biology, the community structure and dynamics, and the pelagic ecosystem (Ballance 2007). Emphasising the great value of long-term surveys to study the pelagic communities from a descriptive to a functioning approach, this study gives a quantified basis to take into account the assumed seabirds foraging association with marine mammals.

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