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Are seabirds foraging for unpredictable resources?

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Abstract

It is generally assumed that the extreme life history traits of pelagic seabirds, such as low fecundity or slow growth of chicks, result from the difficulties obtaining energy at sea from unpredictable and patchily distributed resources. However, little information on seabird prey distribution and availability exists to sustain this widely accepted hypothesis. Using tracking studies of 68 sub-populations of flying seabirds, I examine whether it is possible to gain information on the predictability of their marine resources. Because prey are clustered from fine to large scale in nested unities, from swarms to patches and concentrations of patches, it is important to take into account spatial scale. In temperate and polar regions, at large and meso-scales, seabirds appear to have a good knowledge of the location and concentrations of patches and generally use a commuting type of trip to reach foraging zones. Predictability appears to be high at large and meso-scales, with individuals from each sub-population heading in a particular direction from the colony to reach favoured habitats of known enhanced productivity such as shelf edges, frontal zones, upwellings. Within these mesoscale features, the animals use an area-restricted search behaviour to search for patches and swarms at finer scales. Using information on foraging site fidelity of individual birds, I show that differences in predictability at coarse scales are related to the distance and time spent foraging, and in particular to the specific types of foraging habitat. Some habitats appear to be more predictable than others: birds return consistently to the same coarse-scale sectors on shelf edges, whereas predictability is low in oceanic waters, even in frontal zones. Preliminary results on tropical species suggest that the environment here is less predictable in tropic than in temperate or polar zones. This review highlights that patchiness and predictability of marine resources are complex notions: predictability is dependent on the spatial and temporal scale considered, and especially on the marine habitat of foraging interest. I discuss the potential consequences of these results for the breeding success and life history of seabirds.
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1. Introduction

Since Lack's (1968) and Ashmole's (1971) seminal papers, many authors have made an explicit link between the extreme life history of pelagic seabirds and the marine environment (e.g., Ricklefs, 1990; Weimerskirch, 2002). The rational is that, because marine resources are patchy and scattered over large areas, and moreover their locations and availabilities are unpredictable, seabirds have difficulties in finding food, and therefore in provisioning chicks. This constraint has led to a low provisioning rate, a long period of chick growth and therefore to low fecundity that is balanced by high survival rates of adults. At the time of these earlier works, no

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information on the pelagic life of seabirds was available, and therefore these assumptions were derived from land-based studies on breeding phenology, time spent foraging, delivery rates to offspring and diet studies. It is striking to see that since this earlier period, in almost all the hundreds of papers published on pelagic seabirds, authors have invariably based their work, discussions and conclusions on the hypothesis that '*seabirds are relying on patchy and unpredictable resources*'. Although there is evidence that the distribution of seabirds' prey is to some extent patchy, there is little direct evidence to confirm that prey availability and distribution are unpredictable.

Because it is difficult to study the behaviour of marine organisms other than seabirds or seals that return on land to breed, information on the patchy and unpredictable nature of marine resources has remained elusive; it has therefore been suggested that seabirds represent convenient indicators of the distribution and availability of marine resources (Furness and Greenwood, 1993). The influence of prey patchiness and predictability on seabird distribution so far has been extensively investigated through ship-based studies relating seabird distribution patterns to the physical environment and prey distribution patterns (review in Hunt et al., 1999). However, these studies do not tell us how an individual animal copes with the patchiness of prey distribution, and to what extent prey distribution is predictable or not for the individual bird. It is therefore critical to combine studies carried out at sea from ships with land-based studies that allow the tracking of individual behaviour. Indeed, since the early 1990s, with the miniaturisation of electronic, especially satellite-linked transmitters (Jouventin and Weimerskirch, 1990), a logarithmically increasing number of papers have been published on the behaviour of individual seabirds at sea and other pelagic life.

With the development of bio-logging techniques, it is possible now to examine in some detail how central place foragers cope with the patchiness and heterogeneity of marine resources, and whether these resources are predictable. I will address these questions in the first part of this paper, based on the compilation of literature on the foraging behaviour of seabirds, and on unpublished data. In particular, I will focus on the question of predictability of marine resources by examining the degree of foraging site fidelity in seabirds. Since marine productivity, structure and heterogeneity

vary extensively between marine habitats, we can expect that foraging strategies differ in response to these differences. I also will examine whether the structure of the environment influences foraging strategy by comparing populations foraging in contrasting habitats such as tropical and polar regions.

2. Data used

So far, most studies on seabirds have been carried out on breeding birds, i.e. on birds that are limited in their foraging range because they have to return to their colonies regularly, either to alternate with their partner on the egg, or to ensure regular feeding of the chick. Very few species have been studied outside the breeding season, and these studies generally focus on only a few animals using Argos satellite telemetry. Recently, the extreme miniaturisation of geolocating systems (Weimerskirch and Wilson, 2000) has allowed the deployment of large numbers of loggers for extended periods, particularly during the non-breeding period (Croxall et al., 2005). However, the low precision of these systems precludes detailed analysis of small-scale foraging behaviour. Only two studies have tracked juvenile birds: emperor penguins (Kooyman et al., 1996) and wandering albatrosses (Weimerskirch et al., 2006). Therefore, in view of the data available, I have limited my investigations to breeding seabirds studied by telemetry (mainly Argos satellite transmitters, but also VHF transmitters or GPS data loggers) where information is at least available on foraging trip duration, foraging range and zone. Because of the fundamental differences between flying (albatrosses) and swimming seabirds (penguins) in terms of travelling speed, it is important to separate the two groups (Fig. 1). Here, I will consider only flying seabirds because there is a largest number of studies, and larger spatial scales are covered. I have used data published in the literature as well as data (published or unpublished) from our own database on southern ocean seabirds and on tropical studies carried out on Europa Island, Clipperton Island, and French Guiana (Appendix). When data were available for several populations of the same species, populations have been treated separately. The stages of the breeding cycle (incubation, brooding of chick and chick rearing) were treated separately because the same population can change its foraging strategy (type of movement, area, range) according to the stage of the
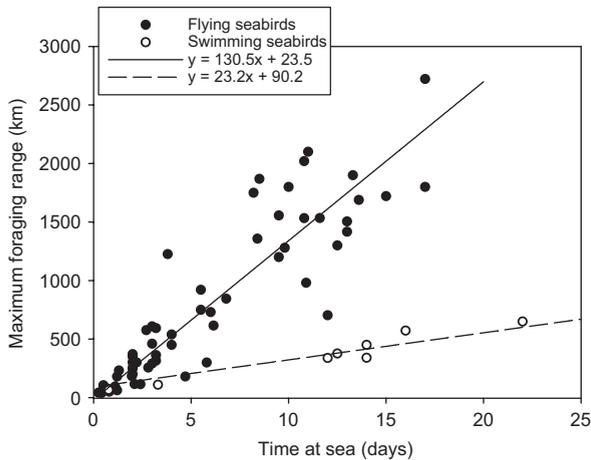
Fig. 1. Relationship between time spent foraging and maximum foraging range during foraging trips in flying ($y = 130.5x + 23.5$, $R^2 = 0.815$, $p < 0.001$) and swimming seabirds ($y = 23.2x + 90.2$, $R^2 = 0.980$, $p < 0.001$).

breeding season (e.g., Weimerskirch et al., 1993; Stahl and Sagar, 2000). Similarly, when parents in a given population used during the chick rearing period a two-fold strategy of alternating short and long trips to provision their chick (Weimerskirch et al., 1994), short and long trips were treated separately. In addition, sexes were grouped.

In total, I have gathered information on 80 categories—which I refer to as sub-populations, including 68 for flying species and 12 for penguins. For flying species, the 68 sub-populations included 29 species of 38 populations, with 58 sub-populations of temperate and polar species, and 10 of tropical species (see Appendix). Ninety-four percent of the studies used the Argos satellite system; the rest used VHF or GPS tracking. Because albatrosses and petrels were the first species to be studied due to their large size and easy handling, they dominate the sample (67% of sub-populations). Tracking the movement of an animal may give a biased view, since the interval between two locations can be long (for example an hour or more with the Argos satellite system), with appropriately long successive step intervals. More recent GPS tracking provides step durations as short as 1 s and with high precision (Weimerskirch et al., 2002). I define foraging site fidelity as the percentage of birds that return to the same site from one trip to the next, the same site being within 10–20 km for oceanic species (tracked by Argos satellite telemetry or GPS), or within a radius of 1 km for offshore species.

3. Marine environment structure and scale dependence

Seabirds forage in a highly heterogeneous environment as clearly illustrated by maps of sea-surface temperatures, chlorophyll concentrations or sea-surface height. Based on regional discontinuities in physical processes and the availability of ecologically significant variables such as light or nutrients, the oceans are conveniently divided into biomes (Longhurst, 1998). These biomes may support distinctive invertebrate and vertebrate communities on which top predators may specialise, becoming convenient indicators of particular biomes (Hunt and Schneider, 1987). Within these large-scale biomes interactions between ocean currents, bathymetry and other physical and biological processes promote growth and retention of plankton, leading to a further spatial heterogeneity in organisms' distribution (Haury et al., 1978). Within these mesoscale zones of higher productivity, seabirds prey are found in patches of various sizes, depending on the process concentrating them and on the behaviour of their prey. Thus, the physical processes and their associated biological components are scale dependent, with scales varying from large (more than 1000 km), to meso (100–1000 km), to coarse (1–100 km) and to fine-scale (less than 1 km) (Haury et al., 1978; Hunt and Schneider, 1987). As a result, fine-scale prey patchiness may be nested within larger-scale patches. This has led to the idea of hierarchical patch structure (Kotliar and Wiens, 1990). With increasing spatial scales, the time scale of processes also increases because in processes operating at slower rates, time lag increases and indirect effects become increasingly important (Wiens, 1989; Fig. 2A).

Therefore, when considering the foraging behaviour of a predator in such a heterogeneous environment, it is important to consider the spatial scale at which the foraging process takes place. This is particularly true for a fast moving seabird that can cross a large range of spatial scales within hours. Recent developments of theoretical work have been made on the foraging behaviour of predators in such hierarchical patch systems (Fauchald, 1999). Thus, when considering a 'typical' seabird' foraging for a 'typical' type of prey, based on our knowledge of the diet, foraging ecology and biology of prey, we may consider that at the smallest scale, prey are congregated in swarms which are within patches which are grouped in
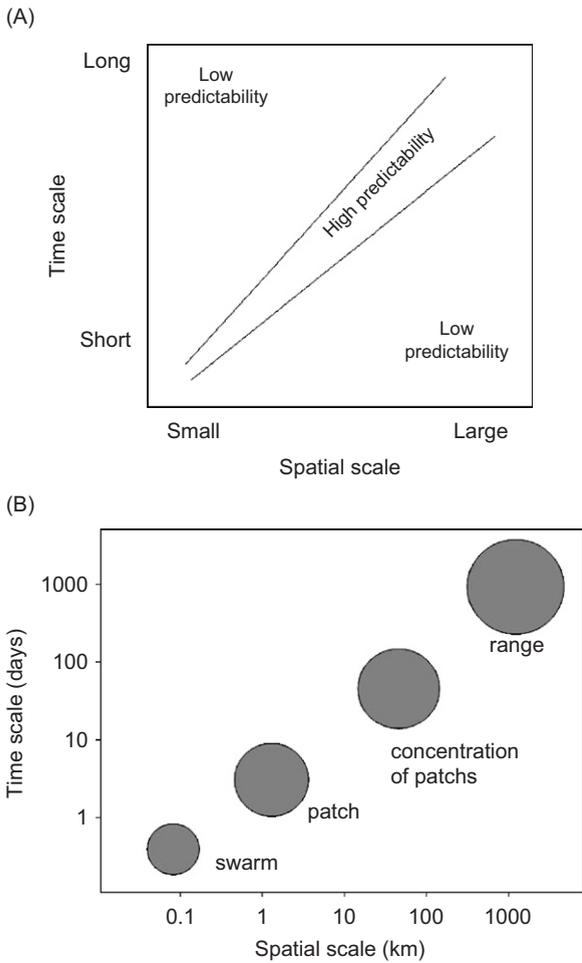
(A)

(B)

Fig. 2. (A) Hypothetical relationship between the time and spatial scales of processes, and predictability (from Wiens, 1989), and (B) the perception of spatial units for prey searching strategies (units of prey for krill, based on Murphy et al., 1988).

concentrations. These concentrations are found in the range of the prey, with corresponding duration of occurrence (Fig. 2B). Because of difficulties inherent in foraging in such a complex environment, it is expected that there has been a strong selection for efficient foraging, and therefore that predators such as seabirds adopt specific movement patterns and behaviours to cope with this situation. Since the environmental heterogeneity is present at several temporal and spatial scales, a scale-dependent approach is required. We therefore expect that adjustments in search effort will vary with scale (Fauchald, 1999).

4. Foraging mode and movement

How should a central place flying seabird search for food in the marine environment? The most distinctive feature of flying seabirds, compared to any other marine predators, is that they can move rapidly—over all the scales considered within a few days. A second feature is that, as a central place forager, the bird has to return to its starting point within a limited period. In this context, typical correlated random walks, where an animal takes successive steps, each in a random direction (Fig. 3), are rarely observed in foraging seabirds. Among the hundreds of tracks examined, only a handful of tracks could be described as such. The typical movement adopted by the majority of populations is composed of numerous short legs interspersed with series of directed longer legs. During the shorter legs, birds increase their turning rate. It has been proposed that such movements may follow a Levy flight pattern (Viswanathan et al., 1996), which may under certain conditions, represent an
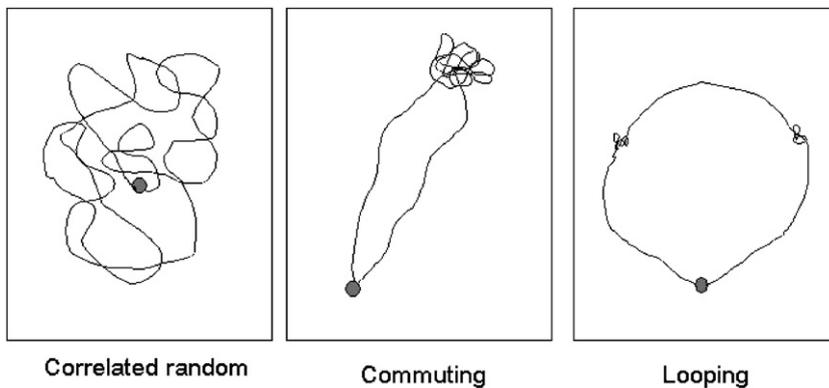

Fig. 3. Type of movements of a central place forager. The grey circle indicates the colony.

optimal way of prey searching. The behaviour during short bouts with numerous turns is typical for what has been described as area-restricted search—ARS (Kareiva and Odell, 1987). ARS is based on the hypothesis that a foraging animal should increase its search effort in areas where resources are plentiful rather than in areas where resources are scarce. An animal should thus increase its turning rate and reduce its speed as a response to increased intake rate.

For this particular situation of central place foraging seabirds, two broad types of movements have been described (Weimerskirch, 1997). The 'commuting' type movement is where the bird leaves the colony with a particular bearing, and keeps this bearing while flying rapidly until it reaches a particular area where it increases its turning rate, and eventually decreases its flight speed. After a certain time, the bird returns in a direct flight path to the breeding colony (Fig. 3). The bird can search several areas with an ARS during the same trip. The outward and return phases of the commuting trip are generally straight, but can also be curvilinear, or broken. The return path, however, generally follows the outward route. The second broad type is a looping trip, where the bird does not return to the colony from the same direction as the outward phase. The typical shape is that of a loop, but it can be a figure eight. A bird can stop moving for some time in one or several areas where ARS occurs (Fig. 3). Commuting is much more common than looping (93% of sub-populations). The two types of movements can be used by the same species, often during the different stages of the breeding cycle or even within the same stage as an alternate strategy by the same individual, or as individual specific strategies. For example, wandering albatrosses do commuting trips to the Crozet shelf edge when brooding the chick, looping trips to oceanic waters during incubation, and alternate the two types when rearing large chicks (Weimerskirch et al., 1993). The fundamental difference between the two types is probably related to the spatial predictability of the location of foraging zones. Commuting trips suggest that the bird 'knows' where to find food, probably from previous experience, whereas the looping course suggests that the bird is searching continuously, and stopping only when it encounters a foraging opportunity.

In a heterogeneous, patchy environment like the ocean, scale-dependent adjustments of movement are found in foraging seabirds (Fauchald and Tveraa, 2003; Fritz et al., 2003; Viswanathan et al., 1996; Pinaud and Weimerskirch, 2005). This has been demonstrated in wandering albatrosses tracked with GPS at a sampling rate of one location per second (Fritz et al., 2003). This study showed that individuals use scale-dependent adjustments of movement patterns to cope with the features of the environment. Fine-scale zigzagging movements are used to take advantage of wind conditions, while large-scale linear—curvilinear movements are used to commute between patches. At coarse scales, birds use an ARS behaviour probably for prey searching (Fig. 4). In another study on the same species at the same site, using stomach temperature sensors and satellite tracking, only 21% of prey caught are clustered (within 1 km), with an average distance between prey of 56 km (Weimerskirch et al., 2005). The two results obtained on the same species are complementary (Fig. 4) and suggest that birds rarely catch several prey in the same swarm or patch, but rather move between patches where they use an ARS behaviour. At each spatial scale, a specific type of movement is used to cope with the different constraints of the environment, such as the need for economical flight at small scale and resulting use of zigzag flight, or the distribution of prey patches at coarse scale.

Different species can exploit the same environment using different foraging strategies and we can expect these differences to be reflected in
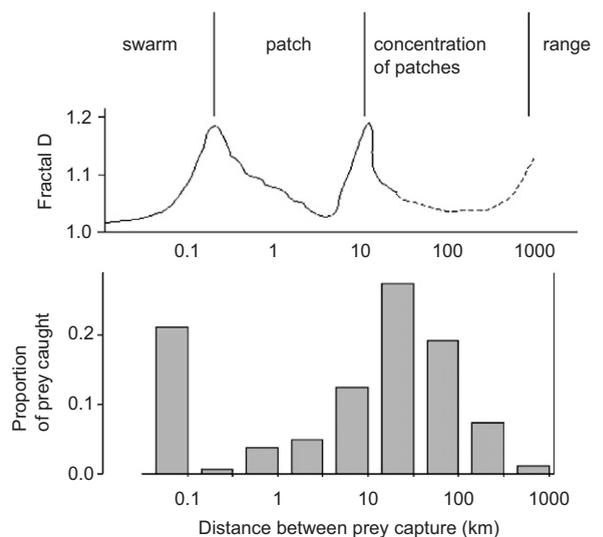

Fig. 4. Scale-dependent fractal dimension for the movement of foraging wandering albatrosses, and scale-dependent distribution of distance between prey capture.

species-typical movement patterns that will vary with environmental conditions (Fritz et al., 2003). In oceans, the heterogeneity of the physical environment leads to an irregular distribution in biological production (Haury et al., 1978), meaning that some habitats are more profitable for predators than others. For example, Fauchald (1999) showed in a model that a predator should adjust its search radius according to its prey encounter rate, which, in turn, is related to the prey density and the spatial scale of the patch.

5. Scale-dependent predictability

To what extend are the location and availability of resources predictable? Predictability is time- and scale-dependent, and predictions have been made on how temporal and spatial scales might be related (e.g., Wiens, 1989, Fig. 2A). Because information on prey distribution, availability, predictability and variability is sparse in general apart for some species such as Antarctic krill, one way to examine this question in marine predators such as seabirds is to study foraging site fidelity. The hypothesis is that foraging site fidelity should be strongest when prey availability is predictable. This hypothesis can be tested at several spatial and temporal scales by examining whether an individual returns to the same site from one trip to the next, or from one breeding season to the next. Information on the latter case, i.e. fidelity of an individual to the same site from 1 year to the next, is generally not available.

5.1. Large scale

Each species or population forages preferentially in a specific biome. For example, within southern albatrosses, yellow-nosed albatrosses are typically sub-tropical foragers, whereas grey-headed albatrosses are sub-Antarctic. Because of their ability to move rapidly over large distances, a species colony may be in a different biome from where it forages. For example, Crozet or Kerguelen yellow-nosed albatrosses breed on sub-Antarctic islands, but move to sub-tropical waters to feed. Time spent in sub-Antarctic waters is mainly for commuting. Laysan albatrosses breed on tropical Hawaiian islands but forage mainly in temperate-polar waters of the north Pacific (Hyrenbach et al., 2002). Whether the location of feeding grounds is unpredictable we might expect that individuals

would leave the colony from all directions, either by looping movements or by commuting flights. This is very rarely the case in the seabird species studied so far. Among the 58 sub-populations available, only in six populations (including wandering albatrosses and white chinned petrels at Crozet during incubation) were birds heading in all directions from the colony. In the rest of cases, at the level of the population or colony, the large majority of birds headed in the same direction.

5.2. Mesoscale

The fact that the majority of seabird populations depart from a colony in specific directions implies that the mesoscale availability of prey is predictable in both time and space. Eighty-seven percent of sub-populations have a directed, commuting type flight, of which 13% have a looping course with ARS in several domains. These data suggest that birds probably commute to reach predictable productive zones. In the majority of the cases where commuting flight is used, individuals head to a particular mesoscale feature, such as frontal area (e.g. polar front, sub-tropical frontal zones), zones of eddies (e.g. Agulhas Return Current), shelf edges, upwelling zones or the ice edge (Fig. 5). As many as 91% of birds return consistently to the same mesoscale feature, at the same reproductive stage, suggesting that the location of mesoscale concentrations of patches is again predictable. These mesoscale features are well known for concentrating prey because of enhanced productivity, or physical forcing. This is certainly the case for fronts and shelf edges for which there is an abundant literature
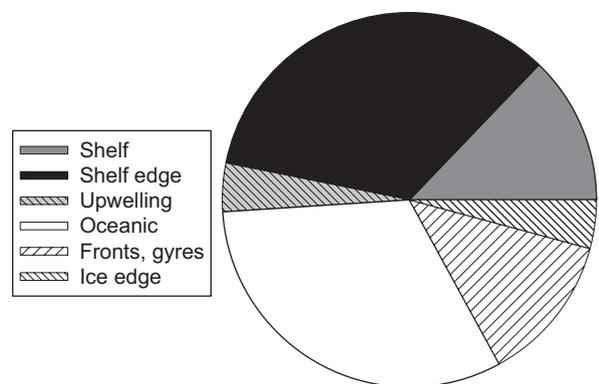

Fig. 5. Mesoscale habitats used by 68 sub-populations of 29 seabird species.

on their role for concentrating prey and their predators (e.g., Hunt et al., 1999).

5.3. Coarse scale

Patches are likely to be scattered within these mesoscale features. The degree of site fidelity to patches at coarse scales (1–100 sq km) varies by both species and stage of the breeding season. According to species, 0–88% of individuals return to the same patch in successive foraging trips. The distance to the foraging site appears to be an important factor determining site fidelity in that birds are less faithful to distant foraging sites (Fig. 6). One factor that may explain this trend is that foraging range is directly related to the duration of the foraging trip (Fig. 1). For distant foraging zones, returning to the same site takes more time, increasing the probability that the resources have either been depleted, or moved actively or passively. Therefore, predictability at a small spatial scale is likely to become low with increasing time elapsed (Fig. 2A). However, it is remarkable to see that there is still a certain degree of fidelity in some long ranging species (Fig. 6). This is the case for species such as wandering albatrosses or black-footed albatrosses that during long foraging trips forage either over oceanic waters, or over distant shelf edges. Whereas they show no site fidelity to the same oceanic sector from one trip to the next, they return to exactly the same sector over shelf edges located at 1000s of kilometres from the colony. The value for long trips in these species is an average over oceanic trips with

no site fidelity, and trips to distant shelf edges with high site fidelity. Thus, site fidelity is largely influenced by the type of mesoscale habitat visited. Birds rarely return to the same coarse scale sites over oceanic waters, including frontal areas (average site fidelity 4.6% ± one S.D. = 12.1 for 12 sub-populations), but are faithful to zones of coarse scale size over shelf edges (50.8 ± 18.8 for 8 sub-populations). Over shelves, fidelity is, on average, high (51.2 ± 32.6%), but extremely variable (range 0–88.2%) according to local conditions. High fidelity occurs in zones with strong physical forcing, such as tidal fronts (88.2% in kittiwakes; Irons, 1998) or shelf edges (e.g., Crozet wandering albatrosses during short trips, 55–75% according to the reproductive stage). An exception is for fulmars, where no site fidelity occurs in foraging for short trips over the large homogeneous shelf of the Barents Sea, suggesting that the shelf itself does not provide predictable zones, except if strong physical processes occur. These results stress that site fidelity, and therefore the predictability of marine resources, is not only dependent on the time scale and thus distance to feeding grounds, but also on the habitat visited. Predictability of marine resources appears variably between species, sites and stage of the breeding cycle.

5.4. Fine scale

The study of fine-scale movements (over <1 s km) is only possible with high accuracy GPS data loggers. Indeed the use of the Argos satellite system for detecting small-scale ARS movements is not appropriate and may even generate biases. Locations from a fixed Argos transmitter show a pattern of ARS behaviour—only because of the inaccuracy of the locations (Pinaud and Weimerskirch, in prep.).

ARS is present in both looping and commuting trip movement patterns, and is generally expected to result from prey encounter. But recent data from the simultaneous use of GPS and stomach sensors (Fig. 7) depart from theoretical predictions about ARS. Indeed results on wandering albatrosses indicate that birds engage in an ARS not as a result of prey encounter and capture but rather more likely increase sinuosity when they enter a particular environment or sector such as the shelf edge. For example, a bird may start ARS when entering a particular oceanic sector known to be productive from a previous visit, as implied by data collected at larger scales showing that seabirds have a good
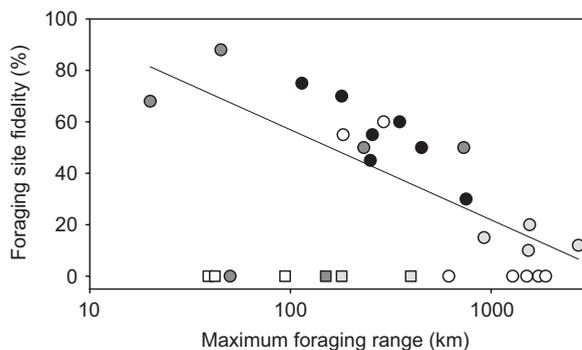
Fig. 6. Relationship between maximum foraging range and site fidelity ($y = -35x + 127$, $R^2 = 0.475$) for temperate and polar species. Circles indicate the temperate and polar sub-populations for which the foraging zones were in oceanic waters (white circles), over continental shelf (dark grey), shelf edges (black) and in a combination of oceanic and shelf edges (light grey). Squares are for tropical species, with same fillings as for temperate species.
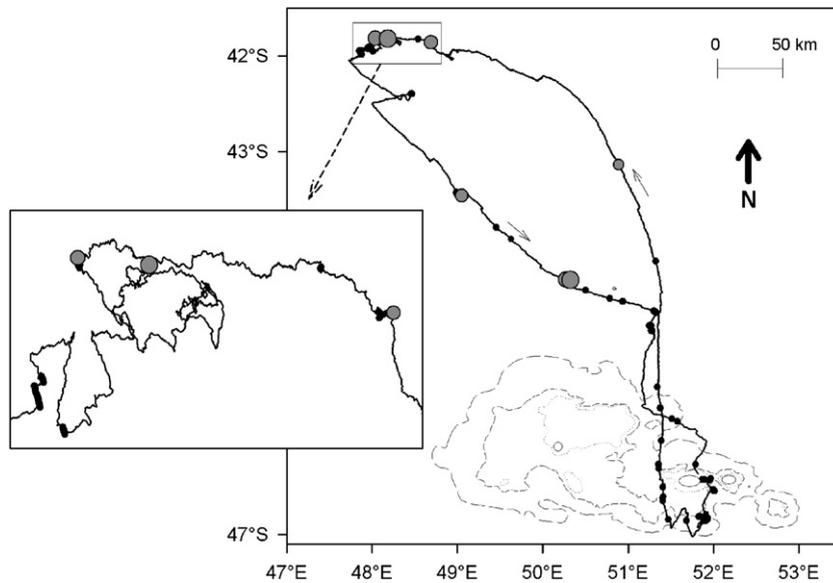
Fig. 7. GPS track of a wandering albatross foraging from the Crozet Islands. The bird was fitted with a stomach temperature sensor. Grey circles indicate prey capture locations and small black circles indicate landings.

knowledge of their environment, and impressive navigating abilities. But they also may be able to recognise water masses such as shelf edges, seamounts or frontal zones from physical characteristics such as the colour of the sea or scent, and increase sinuosity when they enter a zone of known potential higher profitability. In the case of procellariforms that show olfaction abilities to locate prey at a fine scale (Nevitt et al., 1995; Nevitt, 1999), birds may use smell to detect the presence of potential prey before they locate them visually. Finally, the presence of congeners or of other species is likely to be used as indicators of the presence of potential food resources. Seabirds probably monitor the presence and behaviour of other seabirds, a tactic known as local enhancement (Haney et al., 1992). To reach feeding zones seabirds also may follow or monitor the movements of other congeners, using a network foraging (Wittenburger and Hunt, 1985).

5.5. Tropical waters

So far, I have considered seabirds studied in temperate and polar regions. Tropical waters are less productive, less structured, with probably a more patchy distribution of resources, and furthermore the food web structure is much different, with a larger number of large predatory fishes compared to other waters (Longhurst and Pauly, 1987).

We can expect selection for contrasting foraging strategies between temperate-polar regions and tropical waters. Surprisingly, whereas studies in temperate and polar regions are numerous, those on tropical species are extremely rare, and very recent. Although preliminary, the first results carried out in tropical waters indicate that seabird foraging strategies differ markedly from those of temperate and polar species. The first evidence comes from foraging site fidelity. In tropical waters, for the five sub-populations where site fidelity has been studied (two frigatebird species and two booby species in three sites), there was no foraging site fidelity although foraging range was limited (average range 40–300 km) compared to temperate-polar species (Fig. 6). Second, the examination of fine-scale foraging tracks of tropical species studied by using GPS data loggers suggests that typical ARS behaviour is less frequently used and looping courses are much more common. Commuting trips occur, but with no or limited time spent in ARS.

Although preliminary, these two series of observations suggest that tropical seabird foraging strategies are probably much different from those of temperate or polar species, and probably because they are preying less on predictable resources. Based on shipboard observations, Ballance and Pitman

(1999) stressed that the most important foraging strategy of tropical seabirds is to feed in multi-species flocks associated with sub-surface predators, primarily tunas. This food resource brought to the surface by foraging tunas is probably much less predictable in location, as suggested by the difficulties of tuna fisheries to locate free-ranging tuna schools, compared to fisheries operating over shelf edges of shelves in temperate waters.

6. Conclusions

In a study on kittiwake foraging near colonies, Irons (1998) predicted that future studies will demonstrate that foraging area fidelity occurs in other seabirds, and that the extent of area faithfulness should vary among species and among regions. From my preliminary review based on a wide range of species, it seems logical to conclude that the predictability and patchiness of resources for seabirds are scale and habitat dependent. Whereas the location of resources at large and meso-scales appears fairly predictable for seabirds over long time lags, at coarse and fine scales, this is no more the case in most habitats such as oceanic waters or frontal areas. However, some zones, such as shelf edges and possibly others such as up welling (few data are available yet), appear to provide predictable food resources at coarse scale over long periods. Such differences should have important consequences for individual and population strategies.

At the individual level, behavioural differences exist, but knowing the location of profitable and predictable foraging zones should represent an advantage and increase individual fitness. At the population level, in general most individuals visit the same mesoscale feature, with each individual having either a preferred zone, or no preferred zone. To what extent does predictability of resources affect foraging success, and ultimately breeding success and survival, are central questions when trying to understand the influence of the marine environment on life history traits. Earlier assumptions that prey availability is unpredictable come from observations that, in pelagic seabirds food delivery is infrequent, and thus results in slow growth, and low fecundity. However, the unpredictability of a resource is probably best measured by the variance than by the mean of fecundity. The comparison between several species of southern albatrosses, whose demography and foraging ecology are well known, gives some clues to this aspect. Wandering albatrosses have high average breeding success that varies little from 1 year to the next, whereas it is generally assumed and demonstrated that they forage for widely dispersed and supposedly unpredictable resources in oceanic waters (Weimerskirch et al., 1993). Most birds rely on oceanic waters during long foraging trips, and show no foraging site fidelity. It is likely that the dispersal of prey is indeed unpredictable, but the foraging strategy based on long looping movements with reduced energy expenditure allows for a predictable yield (Weimerskirch et al., 2005). Black-browed albatrosses from Kerguelen are specialised shelf-brake foragers visiting the same foraging sites not only throughout the breeding season, but also year after year (Weimerskirch et al., 1997). Moreover, individuals visit the same sites from one trip to the next, suggesting a spatially and highly predictable resource. Availability probably varies moderately since breeding success is high, and varies only moderately. Species relying on frontal zones, such as Campbell Island black browed albatrosses or South Georgia grey-headed albatrosses show a lower breeding success with higher variance (Croxall et al., 1997; Prince et al., 1997; Waugh et al., 1999a, b). South Georgia black-browed albatrosses rely on Antarctic krill whose availability varies extremely from 1 year to the next, and probably from one trip to the next, and breeding success is extremely variable, and on average low (Croxall et al., 1997; Prince et al., 1997). These results suggest that there is a link between marine resource predictability and the variance of the breeding success, and therefore that the specialisation of populations, or individuals for a particular habitat may lead to the evolution of a particular life history strategy. Interestingly, Kerguelen black-browed albatrosses relying on a predictable resource at the shelf edge are shorter lived than South Georgian and Campbell populations (Weimerskirch, 2002). Of course, further studies are necessary to confirm this trend. Since individual differences exist within populations, another aspect of major interest is the link between individual foraging tactics (e.g., use of predictable habitats and fidelity to foraging zone) and individual quality.

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Appendix A

For study sites, reproductive stages, and data available on foraging for seabirds, see Table A1.

Table A1

Order[a]	Scientific name	Common name	Zone	Locality	Reproductive Stage[b]	ST/LT[c]	Data available[d]	Foraging zone	References[e]
Larif.	*Rissa trydactila*	Black legged kittiwake	Temp	Alaska	C	No	*R, T, F*	Shelf	Ainley et al. (2003), Irons (1998)
	Uria lomvia	Thick-billed murre	Temp	Iceland	I	No	*R, T, F*		Benvenuti et al. (1998)
Pelec.	*Morus bassanus*	Northern Gannet	Temp	Great Britain	I	No	*R, T, F*	Shelf	Hamer et al. (2001)
	Morus capensis	Cape gannet	Temp	South Africa	I	No	*R, T*	Up-welling	Grémillet et al. (2004)
	Sula sula	Red-footed booby	Trop	Europa	I, B, C	No	*R, T, F*	Oceanic	Weimerskirch
	Sula dactylatra	Masked booby	Trop	Clipperton	I, B, C	No	*R, T, F*	Oceanic	Weimerskirch
	Fregetta magnificens	Magnificent frigatebird	Trop	French Guiana	I, B, C	No	*R, T, F*	Shelf	Weimerskirch
	Fregetta minor	Great frigatebird	Trop	Europa	I, B, C	No	*R, T, F*	Oceanic, eddies	Weimerskirch
	Phlacrocorax atriceps	Imperial cormorant	Temp	Argentina	I	No	*R, T, F*	Shelf	Sapoznikow and Quintana (2003)
Procell.	*Diomedea amsterdamensis*	Amsterdam albatross	Temp	Amsterdam	I	No	*R, T*	Oceanic	Weimerskirch
	Diomedea exulans	Wandering albatross	Temp	Crozet, South Georgia	I, B, C	Yes	*R, T, F*	Oceanic, shelf edge	Weimerskirch [3]
	Diomedea antipodensis	Antipodes albatross	Temp	Auckland	I, B	?	*R, T*	Oceanic, shelf edge	Walker et al. (1995)
	Thalassarche melanophris	Black-browed albatross	Temp	Kerguelen, South Georgia, Campbell, Falklands	I, B, C	No, No, Yes, ?	*R, T, F*	Shelf edge, oceanic, shelf	Huin (2002), Weimerskirch et al. (1997), Waugh et al. (1999a, b), Weimerskirch
	Thalassarche chrysostoma	Grey-headed albatross	Temp	South Georgia, Campbell	I, B, C	Yes, No	*R, T, F*	Shelf, oceanic, fronts	Waugh et al. (1999a, b)
	Thalassarche bulleri	Buller's albatross	Temp	Sanres, Solander	I, B, C	Yes	*R, T, F*	Shelf edge, oceanic, shelf	Stahl and Sagar (2000a, b)
	Thalassarche carteri	Indian Ocean albatross	Temp	Amsterdam	I, B, C	Yes	*R, T, F*	Oceanic, eddies	Weimerskirch
	Phoebastria immutabilis	Laysan albatross	Temp	Hawaii	I, B, C	Yes	*R, T, F*	Shelf edge, oceanic	Fernandez et al. (2001), Hyrenbach et al. (2002)
	Phoebastria nigripes	Black-footed albatross	Temp	Hawaii	I, B, C	Yes	*R, T, F*	Shelf edge, oceanic	Fernandez et al. (2001), Hyrenbach et al. (2002)
	Phoebastria irrorata	Waved albatross	Trop	Galapagos	I, B, C,	No	*R, T*	Up-welling	Fernandez et al. (2001)
	Phoebetria fusca	Sooty albatross	Temp	Crozet	I, B	No	*R, T*	Oceanic	Weimerskirch

Table A1 (*continued*)

Order[a]	Scientific name	Common name	Zone	Locality	Reproductive Stage[b]	ST/LT[c]	Data available[d]	Foraging zone	References[e]
	Phoebetria palpebrata	Light-mantled sooty albatross	Temp	Crozet	I, B	No	*R, T*	Oceanic	Weimerskirch
	Macronectes halli	Northern giant petrel	Temp	South Georgia	I, B, C	No	*R, T*	Coastal, oceanic, shelf	Gonzales-Solis et al. (2000a, b)
	Macronectes giganteus	Southern Giant petrel	Temp	South Georgia	I, B, C	No	*R, T*	Coastal, oceanic, shelf	Gonzales-Solis et al. (2000a, b)
	Fulmarus glacialis	Northern fulmar	Polar	Bornoya	B, C	No	*R, T, F*	Shelf	Weimerskirch et al. (2001)
	Fulmarus glacialoides	Southern fulmar	Polar	Adélie Land	B, C	No	*R, T, F*	Ice edge	Weimerskirch
	Procellaria aequinoctialis	White-chinned petrel	Temp	Crozet	I, B, C	Yes	*R, T, F*	Oceanic, shelf edge, fronts	Weimerskirch
Sphenic.	*Aptenodytes patagonicus*	King penguin	Temp	Crozet	I, B, C	No	*R, T, F*	Oceanic, front	Charrassin et al. (1998), Charrassin and Bost (2001), Bost, C.A., Unpubl.
	Aptenodytes forsteri	Emperor penguin	Polar	Adélie Land	I, B, C	No	*R, T*	Polynies	Ancel et al. (1992)
	Pygoscelis adeliae	Adélie penguin	Polar	Ross Sea	I, B, C	No	*R, T*	Ice edge	Ainley et al. (2004)
	Eudyptes chrysolophus	Macaroni penguin	Temp	South Georgia	I, B, C	No	*R, T*	Shelf, fronts	Barlow and Croxall (2002)
	Eudyptes schlegeli	Royal penguin	Temp	Macquarie	I, C	No	*R, T*	Oceanic, fronts	Hull et al. (1997)

[a]Lariformes, Pelecaniformes, Procellariiformes, Sphenisciformes.
[b]B = brooding, I = Incubation, C = chick rearing, chick alone on nest.
[c]ST/LT: use of alternate strategies: yes/no.
[d]Date available: *R*: foraging range, *T*: foraging time, *F*: foraging site fidelity.
[e]Weimerskirch for H. Weimerskirch, Unpubl. data.

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