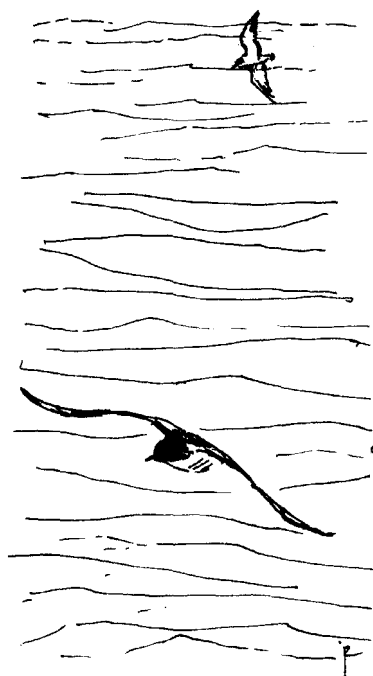


BEHAVIOURAL RESPONSES BY FORAGING PETRELS TO SWARMS OF ANTARCTIC KRILL *EUPHAUSIA SUPERBA*

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Veit R.R. 1999. Behavioural responses by foraging petrels to swarms of Antarctic Krill *Euphausia superba*. *Ardea* 87: 41-50.



Petrels feeding on Antarctic Krill *Euphausia superba* use two basic strategies to locate prey patches. One strategy is area-restricted search, in which individuals interrupt straight-line motion on detecting prey, and then circle about. This increased rate of turning near prey increases the likelihood of detecting additional patches, since patches tend to be clumped in space. A second strategy is local enhancement, in which individuals monitor the behaviour of others, and converge on those individuals that display behaviour indicative of feeding. In this paper, attention is focused on the first strategy, area restricted search, and evidence of increased turning rates in the vicinity of krill patches is sought. The hypotheses tested were first, that six species of krill-feeding petrels engage in area restricted search, and then that the tendency for seabirds to either sit on the water, patter with their feet, or seize prey was correlated with the distance to the nearest krill patch. Seabird abundance and behaviour was paired with krill abundance east of South Georgia (55°S, 35°W) in June 1993. Three species, Cape Petrel *Daption capense*, Northern Giant Petrel *Macronectes halli* and Southern Giant Petrel *M. giganteus*, changed their direction of flight significantly more often when near krill swarms than when in krill-free areas, indicating that they used area restricted search. Cape Petrels were also significantly more likely to sit on the water and to patter along the surface when close to krill swarms.

Key words: *Daption capense* – *Fulmarus glacialis* – *Macronectes giganteus* – *Macronectes halli* – *Pelecanoides urinatrix* – *Halobaena caerulea* – *Euphausia superba* – foraging behaviour – area-restricted search – patchy resources – krill – Antarctic

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INTRODUCTION

Understanding how seabirds in the Antarctic search for prey is an essential link in the study of vertebrate responses to changing distributions or abundance of prey. Attempts to quantify seabird foraging behaviour are scarce, there being only a few previous studies (Dunn 1973; Safina & Burger 1985; Fraser *et al.* 1989; Veit & Prince 1997). Recent modelling efforts have established that micro-scale foraging behaviour of individuals can be meaningfully linked to models of population dynamics (Patlak 1953; Alt 1980; Okubo 1980,

1986; Kareiva & Odell 1987; Othmer *et al.* 1988; Grunbaum 1998). These models all capture the dynamics of individual movement by characterising that movement as a sequence of steps. Thus they require data on turning rates. The purpose of this paper is to demonstrate the feasibility of collecting such data on pelagic seabirds from ships at sea, and to show that the turning rate of birds and step-lengths are statistically related to the presence of the birds' prey. I chose to study Cape Petrel *Daption capense*, Southern Fulmar *Fulmarus glacialis*, Northern Giant Petrel *Macronectes halli*, Southern Giant Petrel *M. giganteus*, Blue

Petrel *Halobaena caerulea*, and Common Diving Petrel *Pelecanoides urinatrix exsul* that feed on Antarctic Krill *Euphausia superba*, because of the relative ease with which the distribution of krill can be quantified using underwater acoustics.

Antarctic krill is the principal food of many species of pelagic birds that winter at sea near South Georgia (Prince & Morgan 1987; pers. obs.). Krill form swarms ranging in size from a few meters up to a few kilometres across (Miller & Hampton 1989). The primary function of this swarming behaviour is not known, but swarms tend to be located near hydrographic fronts and over slopes and sea-mounts (Miller & Hampton 1989), and at South Georgia, swarms tend to form much more frequently during summer than during winter (Everson & Goss 1991). It is not clear whether birds search directly, for swarms, or use physical cues such as hydrographic fronts to direct them towards krill (Hunt & Schneider 1987; Hunt 1990). To locate swarms of krill, either directly or indirectly through detection of associated physical cues, seabirds must employ a search strategy comprising two components. The first of these is the sensory detection of swarms, for which seabirds use both vision (Hoffman *et al.* 1981) and olfaction (Nevitt *et al.* 1995). The second component of the search for swarms is what is often referred to as a foraging 'strategy'; that is, a sequence of decisions about how to move about the environment in such a way as to heighten the probability of encountering swarms. I focus on this second component.

Area-restricted search is the focusing of one's searching effort in the vicinity of resource patches. If resource patches are statistically likely to have other patches nearby, then foragers will enhance the probability that they will encounter patches by circling rather than continuing straight-line movement. Since krill swarms are clustered in space (Mangel & Adler 1994) and vary considerably in size (Miller & Hampton 1989), birds could use area restricted search to identify local maxima in prey abundance, that is to find the most suitable patch within a cluster. If

foraging birds respond in this way to krill swarms, then turning rates of foraging birds will be related to probabilities of swarm encounter at any particular place.

Although statistical associations between seabird abundance and prey abundance has been repeatedly documented (e.g. Veit *et al.* 1993), associations between behavioural actions by birds and abundance of their prey have been rare (Veit & Prince 1997). In addition to searching for evidence of area restricted search, I quantify some other behaviours indicative of feeding to see if they are statistically associated with krill swarms detected acoustically. The behaviours I analyse are turning rates, and the tendency to alight upon the water, 'patter' or commence feeding.

METHODS

Data were collected at South Georgia (54°S, 35°W) during winter, when krill-feeding seabirds are probably especially challenged to find krill owing to the relative scarcity of swarms, compared to the summer (Miller & Hampton 1989). This study was conducted during the austral winter, when seabird populations are at their annual minimum, and krill swarms are least likely to form near the surface. Winter bird populations have not been thoroughly censused, but due to the absence of several species, we know that fewer than 500 000 birds remain for the months May to October. The only species to increase in numbers during winter are Southern Fulmar and perhaps Snow Petrel. Diets of these birds at South Georgia during winter are poorly known, except that those species that eat krill during summer seem to also eat krill during winter whenever it is available (Williams 1991; pers. obs.).

Data on the presence and abundance of krill were collected along two 65 nm (nautical miles) transects off the eastern end of South Georgia that were surveyed three times each (Figure 1). The survey dates were 2, 3, 11, 12, 19 and 20 June 1993. Hull-mounted acoustic transducers were operated continuously at 38 and 120 kHz during

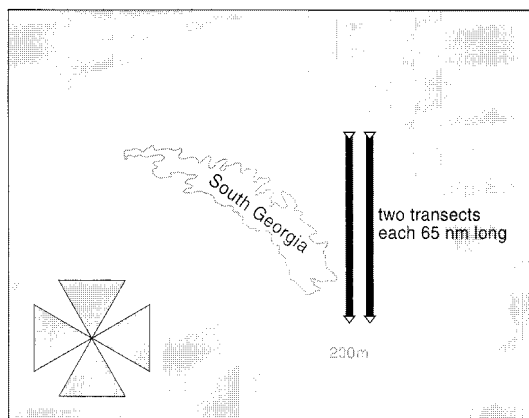


Fig. 1. Location of transects off eastern end of South Georgia and configuration of cloverleaf search pattern (inset).

the transects. We integrated back-scattering strength over the depth range 15–250 m, and over 0.1 nm horizontal segments (Hewitt & Demer 1994). Using these continuous data we were able to pinpoint the location of krill swarms and to apportion their biomass among 10 m depth bins. To check our supposition that acoustic echoes were krill, we traversed the same transects during the following night, and conducted net hauls at 15 nm intervals along the transect lines. At each station, we performed two net hauls. The first was an oblique tow, during which a one m Isaacs-Kidd Mid-water trawl was lowered to a depth of 200 m (or to within 10 m of the bottom) and then raised at 20 m min⁻¹. The second was a surface tow, in which a one m circular frame with a 505 μ mesh was lowered to the surface and towed at about 1.5 knots for 15 minutes. We counted, measured and identified to species all euphausiids, fishes and squids from the samples.

We quantified bird movement behaviour by following individual birds chosen at random with binoculars while steaming along transects and ‘cloverleaf’ search patterns (described later). Two people worked together to record these behavioural data. One person followed birds with binoculars, and the second person recorded data on a microcomputer. To select birds for study, one of four

sectors (0–90°, 90–180°, 180–270° or 270–360°) was chosen at random and the first bird detected in that sector was then followed. Birds closer than 100 m to the ship, or ones that were obviously circling or following the ship, were ignored. By ignoring such individuals, it is likely that the turning behaviour that we observed did not represent response to the presence of the ship.

Once the observer chose a bird, the recorder started entering data following a ‘buffer’ period of ten seconds. We used this buffer period to reduce the bias that might arise from accumulating data on birds that could only be followed for a few seconds (e.g. birds flying rapidly downwind or in the opposite direction from the ship’s course). The observer then called out whenever the bird’s behaviour changed. We defined a ‘change in behaviour’ as one of the following

- For flying birds, a change of >90° in the bird’s direction of flight. Additional increments of 90° were considered to be additional turns, so that a direction change of 270° was recorded as three consecutive turns. Flight directions and turning angles were estimated using the ship’s gyroscopic compass repeaters.
- A change from flying to sitting, or from sitting to flying.
- Initiation of feeding. A bird was recorded as ‘feeding’ if it was seen to capture prey.
- Initiation of milling. Birds occasionally flew in tight circles or ‘milled’. When they did this, they changed their direction of flight too quickly for us to record individual turns, so we created this additional behavioural category.
- Initiation of pattering. Cape Petrels and storm-petrels often fly at close to stalling speed while springing off the surface of the water using their feet.

The observations were recorded on a hand-held microcomputer that recorded the time to the nearest 1/100th of a minute. I later extracted the time elapsed between each change in behaviour. I defined ‘step-length’ as the time elapsed between successive 90° turns.

We also used survey data collected simultaneously along the transects. The survey data consisted of strip transects, in which the strip was 100 m wide and centred 100 m directly ahead of the ship (Veit *et al.* 1994). Each bird recorded on the surveys was assigned a behavioural code (either flying, sitting, milling, pattering, ship-following or feeding), so the distribution of 'feeding' or 'milling' birds relative to the distribution of krill swarms along transects could be mapped. These survey data were analysed using cross-correlation analysis.

All data were collected at a spatial scale large enough to assure sampling a number of krill swarms, yet small enough to record behavioural observations on a number of birds at each swarm. To sample the behaviour of foraging birds in relation to the distribution of the birds' prey, an area was covered that approximated the area over which an individual bird might travel in a day (Croxall *et al.* 1984). For these large scale studies, three transects that were each 65 nm (120.4 km) long were sampled. Transect length was determined by the day length at South Georgia during winter (6.5 h) and the average speed of the ship (10 knots). The position of the transects, off the eastern end of South Georgia, was determined by our finding of numerous krill swarms in that area during June 1985 and June 1991 (Veit *et al.* 1991).

Using the methods just described, we could best approximate distances between krill and birds as the distance separating them along the transect. Furthermore, since krill swarms are usually <1 km across, the ship would ordinarily steam over a swarm in <3 minutes. Therefore, using only data collected on transects we could not collect sufficient samples over krill swarms, because most time would have been spent steaming over water devoid of swarms. To increase the data set from over krill swarms, we approximated a two-dimensional mapping of krill and bird distribution by steering the ship in a 'cloverleaf' or 'iron cross' search pattern (Fig. 1). Three such cloverleaf searches were begun by positioning the ship directly over a swarm of krill detected by echo-sounder, and then steering a cloverleaf pat-

tern achieved by making a series of 60° turns at the vertices of each of the four 'leaves' of the cloverleaf. Thus each leaf was an equilateral triangle with sides measuring 2.5 nm. Cloverleaf searches were conducted on days other than those on which we sampled the 65 nm transects described above.

For determining distances between birds and krill swarms, a swarm was defined as any contiguous group of 0.1 nm segments of transect in which estimated krill biomass exceeded 100 g m⁻³ within 50 m of the surface. Krill swarms yield a distinctively shaped pattern on the chart record; by setting the threshold at 100 g m⁻³, ascertaining that all swarms were included. Krill deeper than 50 m is not likely to be available to foraging birds (aside from penguins). The linear distance along the transect line between the bird and the swarm was measured. Rank correlation analysis was used to relate frequency of bird behaviour to distance from krill.

Cross-correlation analysis (Wilkinson 1988) was used to assess whether milling behaviour is a good predictor of krill availability. This analysis was performed on a transect-by-transect basis, and included only these transects on 2, 12 and 19 June on which more than eight milling petrels were observed. Each of the transects was subdivided into approximately 650 segments of length 0.1 nm, and each of these segments was assigned a value for krill abundance and number of milling petrels. This resulted into two parallel series for each transect, one for milling petrels and the other for krill. To assess spatial association between milling petrels and krill, correlation coefficients were calculated between the two series at a sequence of different spatial lags. The lags were in units of 0.1 nm, and were achieved by 'sliding' one series relative to the other. Correlation was calculated at 15 spatial lags, from +0.7 nm to -0.7 nm, for each transect.

RESULTS

During June 1993 we encountered between zero

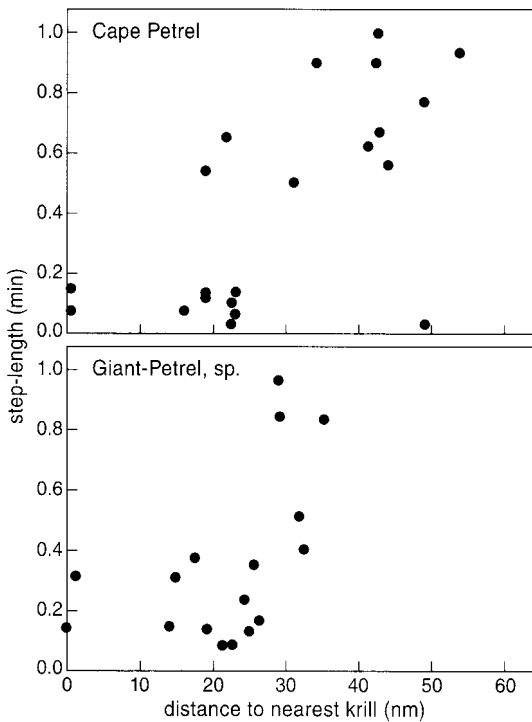


Fig. 2. Step-length by Cape Petrels (top diagram) in relation to distance from the nearest available krill patch ('available' means within 50 m of the surface) on the 2 June 1993 transect ($r_s = 0.50$, $P = 0.02$, $n = 22$ birds), and step-length by giant-petrels (bottom diagram) in relation to distance from nearest krill swarm on the 2 June 1993 transect ($r_s = 0.62$, $n = 17$ birds, $P < 0.005$).

and two krill swarms per 65 nm of transect. The mean krill density for the surveys (averaged over all six transects) was 60.9 g m^{-3} , and the median was 9 g m^{-3} . The densest swarm, seen on 2 June, was $40\,000 \text{ g m}^{-3}$, five times denser than the next most dense, seen on 11 June. The swarms we found tended to be located consistently in the same places over the shallowest part of the transects. These swarms were all smaller than 500 m in chord length. They tended to descend to the ocean floor during the day and then ascend to the surface at night (Demer & Hewitt 1995).

Adequate behavioural data (more than 15 individuals followed) were obtained only for Cape

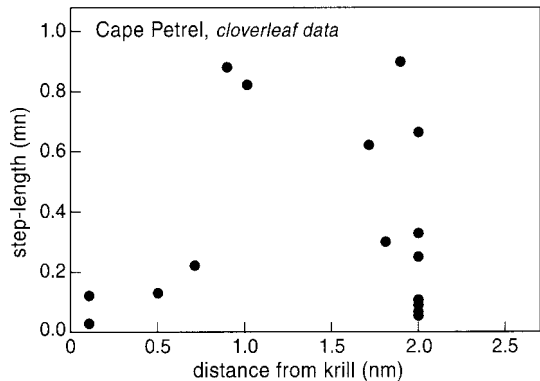


Fig. 3. Step-lengths of Cape Petrels in relation to distance from the centre of the cloverleaf search centred on a krill swarm. Step-lengths closer than 0.7 nm from the krill patch are significantly shorter than those farther away (Mann Whitney- U test; $U = 52$, $n = 17$ birds, $P = 0.002$).

petrel, giant petrels, Common Diving Petrel and Blue Petrel. There was no relationship between step-length and distance to krill swarms for Blue Petrels or Common Diving Petrels. Cape Petrels and giant petrels, however, turned more frequently when close to swarms on one (2 June) of six transects (Fig. 2). On the cloverleaf search pattern, we were able to follow enough Cape Petrels (17) to quantify step-length with respect to distance from swarms (Fig. 3). For Cape Petrels, step-lengths further than 0.7 nm from the krill swarm were variable, whereas step-lengths closer to the swarm were consistently short, and comparable in length to those measured near krill swarms on the transects. Four of the shortest step-lengths recorded, at distances of two nm from the centre (Fig. 3), were from birds milling over a pod of Killer Whales *Orcinus orca* at the outer edge of the cloverleaf.

The results from Cape Petrels for each survey were clear. Along the six transects, more than 50% of Cape Petrels within five nm of a krill swarm were sitting on the water, and this proportion declined with increasing distance (Fig. 4a). In contrast, the other two species studied, Blue Petrels and Common Diving Petrels did not alter

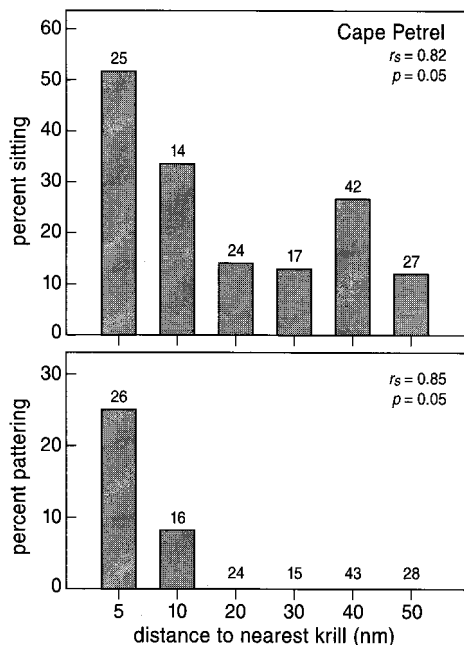


Fig. 4. Incidence of behaviour indicative of feeding by Cape Petrels with increasing distance from a krill patch, from transect data. The numbers over the columns are sample sizes, in numbers of birds. Top diagram: proportion of birds sitting ($n = 149$ birds), bottom diagram: proportion of birds pattering ($n = 152$ birds).

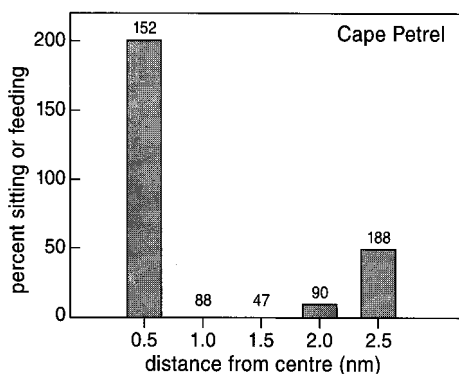


Fig. 5. Proportion of Cape Petrels seen either sitting or feeding during a cloverleaf search pattern north of Bird Island, 21 June 1993 ($n = 565$ birds).

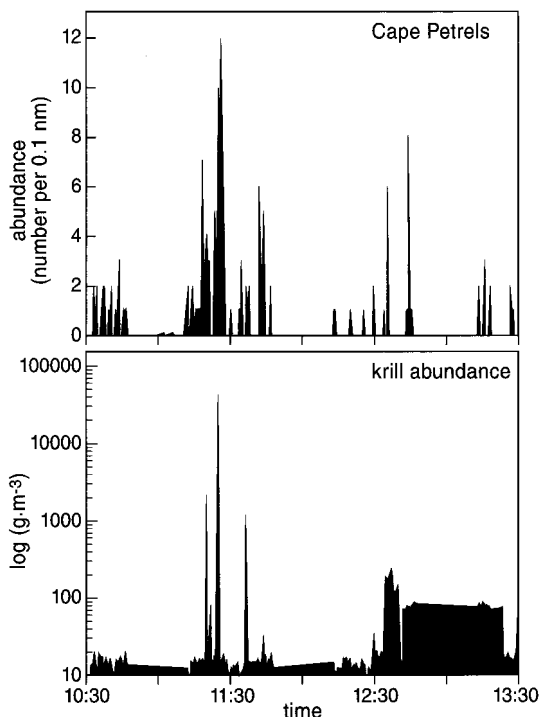


Fig. 6. Distribution of Cape Petrels and krill along southern half of transect run on 2 June (distance represented is 32 nm).

their behaviour when near krill. On the cloverleaf search pattern, the association between sitting behaviour and the presence of prey was evident at a finer spatial scale (Fig. 5). To obtain an adequate sample, all birds displaying evidence of feeding (capturing prey, sitting on the water, or pattering) were grouped. Twenty percent of the Cape Petrels were sitting, feeding or pattering within 0.5 nm of the swarm. None were feeding between 0.5 and 2.0 nm from the swarm. The relatively large proportion (10%) seen feeding or sitting at the outer edge of the cloverleaf pattern was associated with a large pod of killer whales. The ship did not pass directly through the killer whale pod, so krill were not acoustically detected there, but it is possible that the whales had located a swarm of krill and associated predatory fishes or squids. More than 25% of those petrels seen within five nm of swarms on the transects were pattering, and this

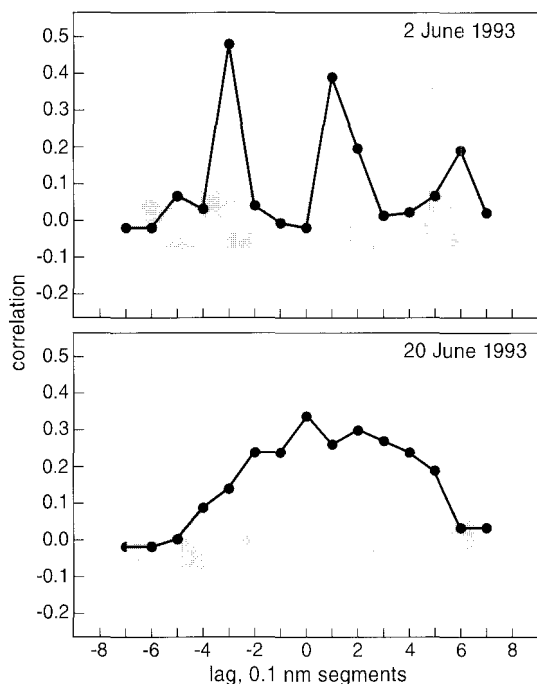


Fig. 7. Cross-correlation between Cape Petrels and krill on the (2 June 1993) transect shown in Fig. 6 (top diagram), and cross-correlation between Cape Petrels and krill on the 20 June transect (bottom diagram).

proportion quickly declined to zero at more than ten nm away from krill (Fig. 4b).

Aggregations of Cape Petrels associated with krill swarms were especially evident on 2 June (Fig. 6a,b) and over a much smaller, deeper swarm on 20 June (Fig. 6c). The degree of association (correlation of 0.5) evident on 2 June is high

relative to other quantifications of seabird-krill association (e.g. Hunt *et al.* 1992, Veit *et al.* 1993).

DISCUSSION

Cape Petrels were the most strongly affected, out of all species studied, by distance from krill (Table 1). They changed direction more often, milled, pattered and sat on the water all in response to the presence of krill. The relationship between turning rate and krill abundance was most pronounced on the 2 June transect. This association was probably strong because the 2 June transect had by far the densest krill swarm ($40\,000\text{ g m}^{-3}$) encountered. It may be that clear-cut behavioural responses only occur for such krill patches larger than a certain threshold (Piatt 1990). Giant petrels also increased their turning rate in response to krill, but otherwise did not behave in a predictable fashion in response to krill swarms. The difference between giant petrels and Cape Petrels with respect to their response to krill swarms may reflect the stronger tendency of giant-petrels to scavenge. Southern Giant Petrel in particular seems to devote more effort to scavenging offal rather than capturing live prey (Croxall & Prince 1980).

Krill at South Georgia in winter migrate vertically on a diurnal pattern, resting near the bottom during daylight hours and ascending to the surface at night (Croxall *et al.* 1985; Fraser *et al.* 1989; Everson & Goss 1991; Demer & Hewitt 1995). In June 1993 we repeatedly observed krill swarms

Table 1. Summary of behavioural results from transect data. Statistically significant relationships between behaviour and distance from krill are indicated with an asterisk (*). Data from the cloverleaf search yielded positive results for Cape Petrels sitting on the water. Data were inadequate to support or refute other behaviours.

Species	turning rate	sitting	pattering
giant petrels <i>Macronectes</i> spp.	*	n.s.	n.s.
Cape Petrel <i>Daption capense</i>	*	*	*
Antarctic Fulmar <i>Fulmarus glacialisoides</i>	n.s.	n.s.	n.s.
Blue Petrel <i>Halobaena caerulea</i>	n.s.	n.s.	n.s.
Common Diving Petrel <i>Pelecanoides urinatrix</i>	n.s.	n.s.	n.s.

ascending to the surface in the late afternoon and sinking again in the early morning. Therefore, it is likely that the behavioural patterns we found were influenced by the greater accessibility of swarms during the early morning hours. The densest, shallow swarm on 2 June was found less than one hour after sunrise. By contrast, the next two densest swarms we encountered were found in the late afternoon of 11 June, and these late afternoon swarms were not accompanied by milling Cape Petrels. This suggests that feeding (and therefore searching) activity had transpired earlier in the day so that we didn't record spatial association of short step-lengths with krill. The two other early morning swarms, those on 19 and 20 June, were both accompanied by milling (searching) Cape Petrels.

Neither Blue Petrels nor Common Diving Petrels changed their behaviour in response to krill. These two species differ significantly from Cape Petrels in several behavioural characteristics. Unlike Cape Petrels, Blue Petrels feed primarily at night (Prince & Morgan 1987) on species such as myctofiid fish, which are vertical migrators and are thus only accessible at the surface after dusk. Giant petrels, more than any other species we studied, scavenge offal. During the winter at South Georgia they were especially apt to feed at moribund jellyfish that we often encountered. So although giant petrels do feed on live krill (Prince & Morgan 1987), they frequently intersperse searching for krill patches with bouts of scavenging. Common Diving Petrels appear to perform most of their 'searching' under the water and therefore may simply drop to the water when first detecting krill rather than circling in the manner of Cape Petrels.

One aspect of the search for krill that our analysis leaves ambiguous is what cues the birds use to first detect prey. Area-restricted search could work both for olfactory and visual cues. One cue that we certainly observed being used was the visual detection of marine mammals, both cetaceans and fur seals. Cape Petrels mill about in response to the presence of Southern Right Whales, and such behaviour may well enable them to detect

patches of krill in the vicinity of the whales. We also noticed birds circling over flocks of fur seals that were feeding on a krill swarm. Herds of fur seals that are feeding, as opposed to porpoising or resting, have a distinctive appearance that birds searching for krill could use to their advantage as a cue. Since fur seals are likely better equipped to find krill swarms than flying birds by virtue of the greater depths they can achieve, and they do track krill density more closely than do birds (Veit *et al.* 1993), so it makes sense for foraging birds to use the feeding activities of seals as a cue to the presence of food.

These results are encouraging because they suggest that area restricted search is a plausible strategy for at least some krill-feeding seabirds, and also because they show the feasibility of quantifying the behaviour of krill predators from shipboard in the Antarctic ocean. Quantification of the linkage between krill and its predators in the Antarctic will become increasingly important as commercial exploitation of krill becomes imminent. If large-scale climatic shifts impact populations of Antarctic krill, it will be especially useful to know how changes in krill abundance translate to changes in bird reproductive success through the essential intermediate link of foraging behaviour of birds.

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SAMENVATTING

Om te kunnen begrijpen hoe de verspreiding van zeevogels op zee samenhangt met het voedselaanbod, is een goede kennis van de (soortspecifieke) foerageerstrategieën belangrijk. Tot dusverre zijn er nog maar weinig pogingen gedaan om het foerageergedrag van vogels op open zee gedetailleerd te bestuderen, en daardoor is onze kennis op dit vlak nog uitermate beperkt. Weinig onderzoekers zijn in staat geweest om de verspreiding van zeevogels en het voedselaanbod van de vogels tegelijkertijd te meten en vervolgens succesvol met elkaar in verband te brengen. Onvoldoende kennis van het menu van zeevogels, vooral de voedselkeuze buiten de broedtijd, en problemen bij de interpretatie van gegevens, zoals de vertaling van 'aanwezige biomassa' naar 'beschikbare voedselvoorkomens' staan heldere resultaten dikwijls in de weg. In dit artikel wordt getracht het foerageergedrag van zes stormvogelachtigen, de Kaapse Duif *Daption capense*, Grijze Stormvogel *Fulmarus glacialisoides*, Noordelijke Reuzenstormvogel *Macronectes halli*, Zuidelijke Reuzenstormvogel *M. giganteus*, Blauwe Stormvogel *Halobastur caerulea*, en het Gewone Duikstormvogeltje *Pelecanoides urinatrix exsul*, die alle krill *Euphausia superba* als belangrijke component in hun menu hebben, in verband te brengen met de aanwezigheid van krillzwermen rond South Georgia (zuidelijke Atlantische Oceaan). Verondersteld wordt dat deze vogels hun ge-

drag aanpassen wanneer zij voedsel ontdekken. Aanvankelijk zullen de zich in rechte lijn verplaatsende zeevogels hooguit afbuigen naar of gaan cirkelen boven plekken met potentieel geschikte voedselzwermen ('area restricted search'). Omdat krillzwermen vaak dicht bijeen voorkomen, hebben cirkelende vogels na het ontdekken van een eerste krillzwerm, ook al is die ongeschikt als voedselbron, een verhoogde kans op het vinden van meer zwermen. Een tweede veronderstelling is dat zeevogels in de omgeving van geschikte prooi voorkomens veel vaker zwemmend, watertrappend of duikend voorkomen. Dergelijke gedragsveranderingen zouden dus aanwijzingen kunnen geven over het voedselaanbod in de onmiddellijke omgeving. De gedragsveranderingen van foeragerende stormvogels werden gemeten door individuele vogels te volgen. Bij drie soorten, de Kaapse Duif en de beide reuzenstormvogels, werd een duidelijk verband gevonden tussen krillvoorkomens en het voorkomen van veelvuldig van koers veranderende vogels. De Kaapse Duif werd in de omgeving van krillzwermen ook veel meer zwemmend en watertrappend waargenomen dan op grote afstand ervan. Een systematische registratie van het gedrag van zeevogels tijdens zeevogeltellingen vanaf schepen zou dus belangrijke, zij het indirecte, informatie over de voedselbeschikbaarheid kunnen verschaffen. Niet alleen wanneer tijdens dergelijke surveys het voedselaanbod niet tegelijkertijd gemeten kan worden, maar ook tijdens tellingen waarbij dat wel gebeurt, is dergelijke informatie van belang.

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