

Monitoring Prey Availability via Data Loggers Deployed on Seabirds: Advances and Present Limitations

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Seabirds constitute a key group of marine top-predators. While foraging seabirds prey mostly on schooling pelagic fish, crustaceans and squids. Because seabirds distribute over a wide spatial range they are sensitive to physical and biotic changes at several temporal scales. In the last 20 years bio-logging science has revolutionized our knowledge of how seabirds can act as monitors of prey stocks. One of the most interesting applications of data loggers on seabirds is determination of the distribution and availability of prey on which we have little knowledge such as mesopelagic fish, squid, and krill. There are now known to be several variables measurable by data loggers which estimate the number of prey caught by free-ranging seabirds. Such data loggers, in combined deployment on seabirds with time-depth or movement loggers (which record acceleration in one or more dimensions) provide data sets representing dependable indices of prey availability. While knowledge of seabird behaviour continues to improve, we still know little about the relationships between seabird behaviour and prey density/availability. Unravelling these relationships is a key step to calibrating the proxies of prey availability recorded by data loggers. Continuing to develop the use of instrumented seabirds as bio-indicators of marine resources is important in the quest to understand marine ecosystems and the conservation of top-predators.

KEYWORDS bio-indicator; data loggers; foraging ecology; monitoring; penguins; seabirds

1. Introduction

The concept of using seabirds as indicators of resource availability and distribution is not new. Fishermen in search of big fish interpret changes in the behaviour of seabirds like boobies and shearwaters, which are attracted to prey chased towards the water surface by species such as tuna (Batty 1989). Seabirds constitute a key group of marine consumers in several ecosystems because of the large amount of biomass they consume (de L. Brooke 2004). Seabirds forage at sea to sustain themselves, reconstitute their body reserves and to obtain food for their young. As marine predators they are dependent on the abundance of secondary and tertiary productivity but plays also a key role in the control of micronektonic species such as in "top-down" or "wasp-waist" ecosystems. The diet of seabirds is composed of combinations of small, schooling, pelagic fish, micro and macrozooplankton, and squids. Between species, diet diversity and foraging behaviours vary considerably. Many seabird species inhabiting high latitudes (auks, auklets) are mostly monophagous (Furness 1978; Cairns 1992; Montevecchi and Myers 1997). Several groups feed in the upper trophic levels and are top-predators (albatrosses, petrels). Some families are highly specialized to search at depth (penguins, cormorans, auks). Among such pursuit divers some are typically benthic foragers (cormorants) and some others feed primarily on pelagic prey (most penguins, diving petrels, auks).

Recently, the importance of seabirds as bio-monitors of the marine ecosystem has begun to be regarded in a new light. The role of seabirds to assess changes in ecosystems at different spatial and temporal scales was highlighted at the International Symposium entitled 'Seabirds as indicators of marine ecosystems' held in 2006 under the auspices of the Pacific Seabird Group (Piatt and Sydeman 2007). Seabirds can distribute

themselves far from their colonies over wide foraging ranges. As a consequence of their dependence on marine resources these predators are, potentially, highly sensitive to environmental change at various temporal scales. Because seabirds are forced to periodically return to their colonies on land they are among the components of marine food webs most accessible for research. Some seabird breeding populations can be easily monitored over periods of up to decades (e.g. Weimerskirch *et al.* 2003). Long-term studies have successfully related changes in demographic parameters to climatic variability that has had an effect on the marine environment (Aebischer *et al.* 1990; Guinet *et al.* 1998; Barbraud and Weimerskirch 2001; Croxall *et al.* 2002). Climate change has been reported to affect seabirds through changes in weather conditions and prey availability (e.g. sea ice and krill, Barbraud and Weimerskirch 2001; sea surface rising in the North Atlantic and decreases in sandeel stocks, Wanless 2006).

Seabird breeding success and population changes are strongly affected by fish stocks and fishery activities (Montevecchi and Myers 1997). Numerous models and empirical studies have shown that seabird and fishery harvests can be in competition (Furness 1978; Croll *et al.* 1998). Decreases in breeding success and population sizes in response to increased fishery activity have been demonstrated through seabird monitoring (e.g. Wanless 2006). Changes in reproductive performance and feeding rates of seabirds have been monitored over several decades to assess variation in food availability (Cairns 1992; Bost and Le Maho 1993; Monaghan 1996; Croxall *et al.* 1999). Some species of seabirds are however, able to buffer breeding success by increasing their foraging effort when prey density declines (Piatt *et al.* 2007).

Given that seabirds travel out to sea in order to feed and presumably strive to forage efficiently so as to maximise their

chances of reproductive success, their foraging behaviours could be effective indicators of short-term prey availability (Cairns 1987; Wilson 1992; Bost and Le Maho 1993). The marine distribution of seabirds is strongly related to increased productivity and prey abundance at physical processes such as frontal areas, shelf slopes and ice edges (Hunt *et al.* 1999; Ainley *et al.* 2005). Until the beginning of the nineties, knowledge of seabird activity and movement at sea was very limited. During the last twenty years the fast development of bio-logging technology (Naito 2004) has revolutionized our vision of seabirds as monitors of the marine environment. Behavioural (diving depth, travel speed, location), energetic (notably heart rate; Green *et al.* 2003; Grémillet *et al.* 2005), environmental (sea temperature, salinity) and biotic parameters (fluorescence, prey catching) can be continuously recorded by instrumented, free-ranging animals thanks to rapid progression towards high-resolution, multi-channel data loggers. These high-tech devices have large memory sizes (several tens of megabytes) and very fast acquisition rates (up to at least 32 Hz; Ropert-Coudert and Wilson 2005).

Over the last two decades there has also been growing evidence that foraging behaviours of instrumented predators can be used as bio-indicators of available resources (Wilson *et al.* 1994, 2002; Bost *et al.* 1997, 2007; Croll *et al.* 1998; Austin *et al.* 2006; Ropert-Coudert *et al.* 2006; Garthe *et al.* 2007; Grémillet *et al.* 2008). Several species of schooling fish that are of commercial interest are patchily distributed, highly mobile and hard to localize (e.g. Cushing 1988; Davoren *et al.* 2003; Piatt *et al.* 2007). Inter-year changes in their distribution, typical depth in the water column and recruitment are thus difficult to assess. Moreover, few data are available for some fish stocks that are still not commercially exploited. This is the case for some key species of food webs such as Antarctic krill (*Euphausia superba*;

Nicols *et al.* 2000) and pelagic fish (myctophids; Ichii *et al.* 2007). Most seabird prey are difficult to locate by traditional sampling techniques because of their patchy distribution, periodically inaccessibility (e.g. due to sea-ice) and thus the costs of adequate sampling.

The present paper discusses progressions in our understanding of marine resources gained through the instrumentation of seabirds. However, we do not promote the use of seabird derived parameters to detect new unexploited stocks of fish; modern fisheries are highly efficient, employing advanced technologies to locate fish stocks. Instead, we endeavour to show how independent information derived from seabirds at sea can help to 1) better assess changes in prey availability and ecosystems by giving relevant informations of spatial aggregation or presence of preys in unsampled areas or throughout the year, and 2) promote protection of prey stocks and the main foraging areas of seabirds in the context of ecosystem conservation. The majority of the data used in the present paper have been obtained through extensive work conducted over the last 20 years on several top-consumers in the southern oceans such as penguins and albatrosses.

2. Foraging at Sea

Seabirds forage in a heterogeneous environment where the resources are patchily distributed (Ashmole 1971; Weimerskirch 1997). Bio-logging studies have demonstrated that many seabirds exhibit high predictability in their directional movements at macro- and meso-scales. Tracked seabirds from polar and temperate marine regions generally leave their colony quickly and head in a set direction (Weimerskirch 2007). The destination of their trips usually corresponds to particular meso-scale features such as fronts, eddies or shelf breaks (Fig. 1), which hold predictable prey. Flighted birds

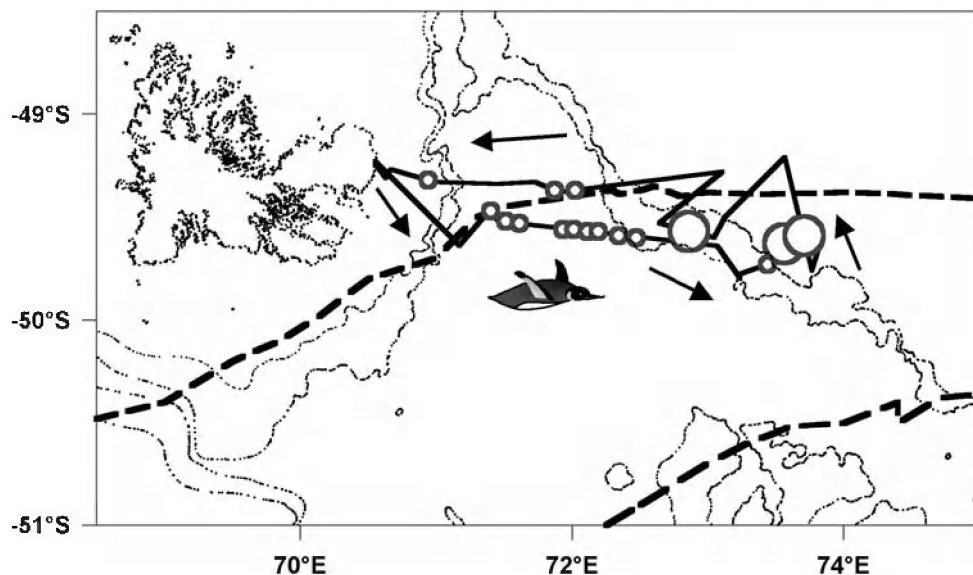


Fig. 1. Example of a foraging trip by a typical pelagic forager (king penguin), which was satellite tracked (Argos) at the polar frontal zone near Kerguelen Island, south Indian Ocean. The bird was instrumented with two loggers: a time-depth recorder and a stomach temperature recorder. The size of the circles corresponds to the amount of foraging activity estimated from the stomach temperature records. The dotted line corresponds to the limit of the polar front. Most of the foraging activity occurs at the limit of the maximal foraging range although significant activity is recorded over the whole trip including the return phase towards the colony.

searching for patchy prey can deviate from a straight line during travelling and decrease flight speed after catching prey. Such searching behaviour is called “area restricted searching” (ARS). Area-restricted searching is as a response to an increase in prey density, i.e. the discovery of a prey-rich area (Kareiva and Odell 1987; Fauchald and Tveraa 2003; Pinaud 2008).

In contrast to flighted seabirds, diving seabirds exploit the water mass in the three dimensions when searching for food. Highly specialized diving species such as penguins travel towards predictable physical features (Bost *et al.* 1997; Hull *et al.* 1997; Rodary *et al.* 2000; Lescroël and Bost 2005). Penguins are more constrained than flying species in terms of travelling speed and hence foraging distance. When foraging many penguin species rely on three main prey types accord-

ing to prey locality or availability: small crustaceans aggregated in swarms, small pelagic, schooling fish and pelagic squids (Croxall and Lishman 1987). Once penguins have left their colony they quickly find favourable areas by alternating shallow travelling dives with deeper prospecting and feeding dives (Wilson 1995). During the central phase of the foraging trip, travel speed decreases in relation to an increased frequency of deep dives and foraging effort (Bost *et al.* 1997; Cotté *et al.* 2007). Penguins are visual hunters (Wilson *et al.* 1992) and exhibit a diel pattern of diving with respect to light transmission at depth. Deepest dives are thus undertaken during daylight and only relatively shallow dives, if any, at night (Wilson *et al.* 1992; Bost *et al.* 2002). During the return phase, heading back to the colony, penguins increase their horizontal speed (Wilson 1995; Cotté *et al.* 2007).

3. Determining How Seabirds Feed

3.1. Feeding recorders

To date, three different biological variables recordable by data loggers have been determined as reliable proxies of the number of prey caught by free-ranging seabirds. The first of these variables recorded was stomach temperature, used to monitor feeding activity and success in large volant seabirds such as albatrosses (Wilson *et al.* 1992; Weimerskirch *et al.* 1994). Stomach temperature temporarily decreases after ingestion of a prey item (whose body temperature is below that of the predator). In species that ingest large prey (fish, squid), recording stomach temperature enables estimation of the mass of each prey. After the ingestion of such prey, a characteristic temperature drop occurs. It is followed by an approximate exponential rise as the prey is warmed to the bird normal body temperature. The integration of the curve from the timing of ingestion until the beginning of the asymptote allows calculating the mass of big prey (Wilson *et al.* 1992). The location of prey capture can provide new information on the distribution and patchiness of poorly understood species such as squids (Catry *et al.* 2004; Weimerskirch *et al.* 2005, 2007). The data logger is swallowed by the bird prior to a foraging trip and recovered by stomach lavage upon return (Wilson 1984). There is a risk that data are lost due to the bird regurgitating the logger at sea. However this can be circumvented by the addition of a back-mounted receiver that enables the logger to transmit recorded data to remote storage.

For diving predators such as penguins, accurate estimations of prey ingestion and prey size are more complicated. This is due to changes in abdominal temperature during the long periods of submersion associated with their foraging dives (Handrich *et al.* 1997), coupled with the relatively small size of prey caught. However, recording oesopha-

geal temperature (at a high temporal resolution) is more reliable for detecting small prey. In king penguins (*Aptenodytes patagonicus*), temperature drops of $\geq 0.06^{\circ}\text{C s}^{-1}$ in the oesophagus correspond to prey ingestion (Charrassin *et al.* 2001; Bost *et al.* 2007). Thus these temperature recordings have been used for quantifying penguin foraging success (Ancel *et al.* 1997; Charrassin *et al.* 2001; Bost *et al.* 2007). The data logger can either be attached to the back of the bird, with implanted leads linking the logger to the temperature probe in the oesophagus (Ropert-Coudert *et al.* 2000, 2001; Charrassin *et al.* 2001; Bost *et al.* 2007), or the logger can be swallowed by the bird before departure, with the leads suspended in the oesophagus by a thin thread glued to the beak. The third measurement suitable for detecting prey ingestion is beak-opening activity, which can be recorded using a Hall sensor (Fig. 2; Wilson *et al.* 2002a). On one mandible of the beak a Hall sensor is attached to record the magnetic field produced by a magnet attached to the other mandible. When the bird opens its beak (to catch a prey, drink, preen or vocalise), the strength of the magnetic field decreases. This can be calibrated with degree of beak opening. Penguins open their beaks underwater mostly to catch prey. Therefore it is potentially possible from Hall sensor data to know when a penguin has ingested a prey and furthermore, by calibrating beak opening angle with prey size, the size of the food ingested. The associated data logger has been implanted in larger penguins (e.g. *Aptenodytes*) or fitted to the back of smaller penguins (e.g. *Pygoscelis*, *Spheniscus*; Wilson *et al.* 2002a, b). The accuracy and reliability of the second and third proxies of prey ingestion, oesophageal temperature and beak opening angle, have been compared in captive penguins, for which both proxies were recorded simultaneously (Wilson *et al.* 2002a, b). Particularly when feeding rates are high, measuring periods of beak opening detects more ingestions than does measuring changes in oesophageal temperature

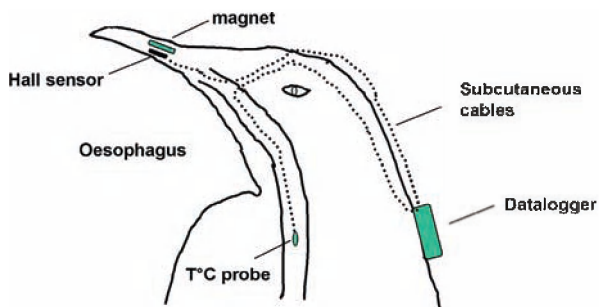


Fig. 2. View of a king penguin fitted with two kinds of feeding data loggers: a beak-opening recorder (Hall sensor) and an oesophagus temperature recorder. The leads connecting the Hall and temperature sensors to the data logger (attached to the back) were either implanted under the skin or attached to the feathers.

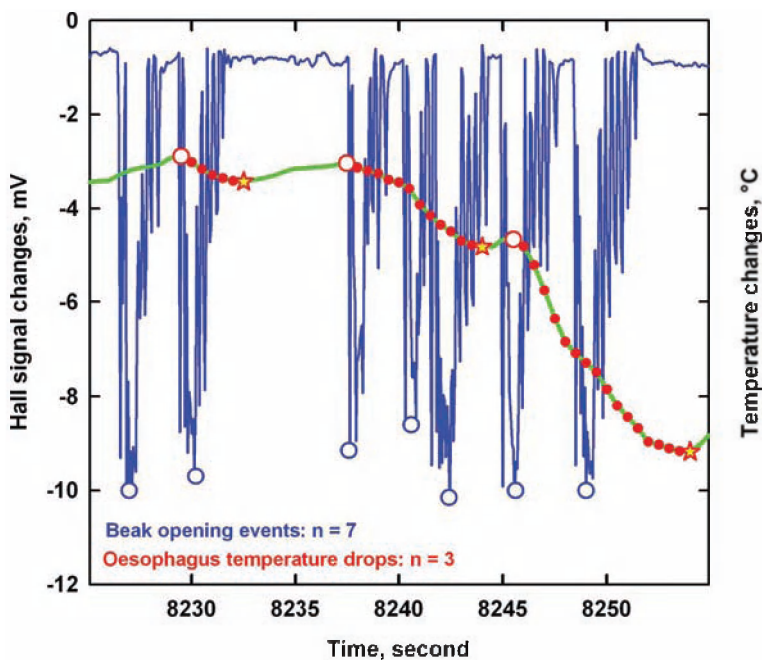


Fig. 3. Differences in response time of an oesophagus temperature sensor and a beak opening sensor (Hall sensor) on the same instrumented king penguin (this study). The blue circles correspond to the feeding events detected by the Hall sensor method. The red circles correspond to the feeding events detected by the oesophagus temperature method. The stars indicate the end of the ingestions events following Charrassin *et al.* (2001) criteria.

(Fig. 3). Recordings of beak-opening are reliable when applied to species feeding on small, aggregated prey such as pelagic fish

or euphausiids (Wilson *et al.* 2002a, b; Hanuise, Handrich and Bost, in prep.). Until now these two systems have mostly been

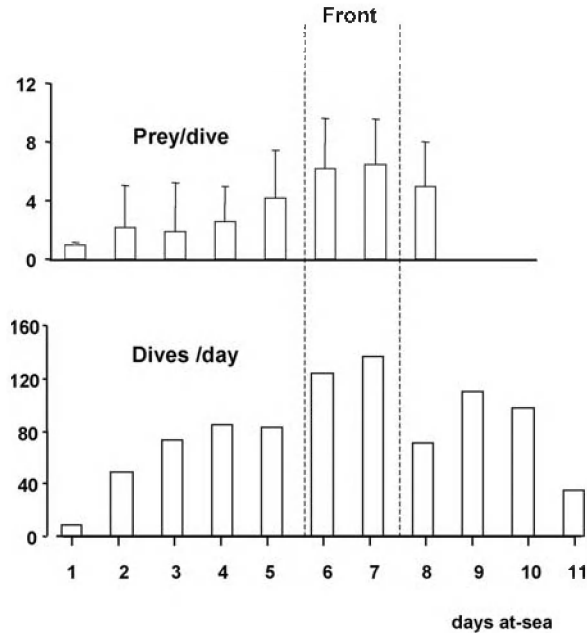


Fig. 4. Changes in feeding success per dive and diving frequency per day of a king penguin while travelling towards the polar front (Crozet Island, South Indian Ocean).

applied to penguins (Wilson *et al.* 2002a, b; Takahashi *et al.* 2004b; Bost *et al.* 2007). Deployed in conjunctions with an activity recorder (TDR Time-Depth-Recorder) such feeding recorders have allowed scientists to accurately monitor the change in penguins feeding activity. In turn these data have been used to assess the distribution and availability of mesopelagic fish (Fig. 4), whose distribution from conventional surveys are still very poorly known (Lancraft *et al.* 1989; Pakhomov *et al.* 1996).

4. Changes in Foraging Behaviour as Proxies of Feeding Success

Data loggers measuring proxies of prey ingestion are now used to assess 'catch per unit effort' (CPUE) in seabirds. However some ethical issues concerning instrumentation of the birds still exist and technical problems in data acquisition often occur. Birds need

to be immobilized or anaesthetized in order to be instrumented and the recovery of ingested loggers upon the return of the bird can be complicated. To recover an ingested logger a magnet embedded in silicone tubing is introduced via the oesophagus (Wilson and Kierspel 1998). In fact, methods of data logger recovery involve minimal stress so long as the logger and sensors remain intact and the fieldworker has experience in bird handling. Even with the logger attached to the back the feeding data recovered may often cover only part of the foraging trip if, for example, the leads break part way through deployment. This is because in diving birds, the mechanical stresses placed on the oesophagus temperature or beak opening sensors and leads are high. As a consequence the leads connecting the sensor to the logger are sometimes broken before the end of the foraging trip. An attractive alternative to the aforementioned proxies of prey ingestion is

the measurement of a behavioural variable that requires less invasive instrumentation. Data loggers that record feeding success are indeed mostly deployed on the same birds instrumented with loggers recording fine-scale movement in the 3 dimensions of the marine environment and hence foraging behaviour (e.g. GPS, accelerometers, TDR).

4.1. Volant seabirds

New insights into the foraging behaviours of wandering albatross (*Diomedea exulans*) were obtained through the combined deployment of GPS loggers and stomach temperature loggers (Weimerskirch *et al.* 2002, 2007). Multiple logger deployment on individual birds allowed an examination of whether albatrosses adapt their foraging behaviour after they have detected and hunted prey. Albatrosses are long-distance foragers that travel by gliding and soaring, dispersing over long distances to find prey, typically squid. Wandering albatross searching for such patchy prey should exhibit ARS behaviour after catching prey. Biologging studies have shown most albatross food consumption occurs during two modes of feeding (Weimerskirch *et al.* 2007): foraging during flight over a generally straight travel path over long distances (up to 3000 km per foraging trip during breeding; Weimerskirch 1997). Secondly prey catching occurs while sitting on the water. However, wandering albatrosses do not catch more prey in areas where travel sinuosity is increased. At a small spatial scale, albatrosses can increase their foraging effort in response to the capture of prey but this behaviour is temporally limited. The ARS behaviour is only exhibited by wandering albatrosses when they are present around specific oceanographic features such as shelf breaks (Weimerskirch *et al.* 2007). Extrapolating information about prey capture and hence feeding success from changes in travelling sinuosity is thus complicate in species such as wandering albatross that forage over very large areas.

4.2. Diving birds

Accurate records of diving depths in relation to time (dive profiles) can be obtained relatively straightforwardly using high frequency (1 s to 4 ms) and high resolution (up to 22 bit) TDRs. Special attention must be provided to instrument diving predators with data loggers. This concerns especially penguins which are highly streamlined diving birds (Bannasch *et al.* 1994). Externally attached loggers can have deleterious effects on their behaviour and increase the energetic cost of movements, decreasing foraging efficiency (Wilson *et al.* 1986). Continuous advances in the development of miniaturized TDRs and accelerometers provide however reliable behavioural data that further elucidate the diving behaviour of predators (Ropert-Coudert and Wilson 2005). Diving behaviour has been classified from the temporal scale of a 'wiggle' within a dive to the scale of a foraging bout (a discrete series of foraging dives; Halsey *et al.* 2007). At the bottom of a foraging dive (bottom phase) a diving bird will search for, and attempt to capture, prey before ascending to the surface. During ascent, swimming angle and speed are constant, at least until close to the surface. However, foraging dive profiles can include a number of complexities. For example, maximum depth can vary considerably, while the periods of descent and ascent can include phases of horizontal travel, which create plateaus in the dive profile (Halsey *et al.* 2007). Several proxies of rate of prey capture have, however, been developed from details of diving behaviour (Ropert-Coudert *et al.* 2006; Bost *et al.* 2007; Sato *et al.* 2007).

4.3. Parameters at depth

4.3.1. Bottom duration

Model predictions have estimated the optimal duration spent in the bottom phase of a foraging dive in terms of overall prey capture

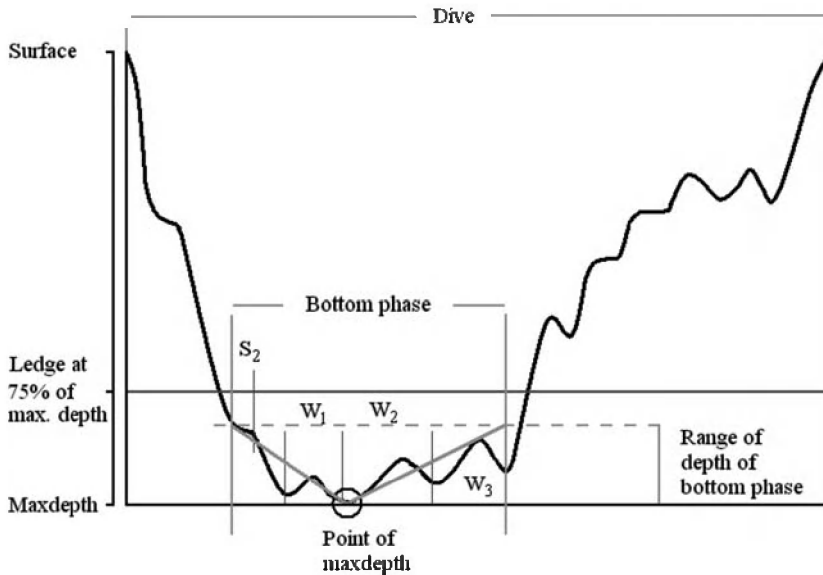


Fig. 5. Typical feeding dive of a king penguin. The different parameters of the dive are indicated as follows: S, step; W, wiggle. The ledge is a specific threshold corresponding to a percentage of maximum depth below which wiggles and steps are used to define the bottom phase of the dive (see Halsey *et al.* 2007).

rates (e.g. Houston and Carbon 1992; Mori *et al.* 2002). Diving predators should stay longer at depth when patch quality/density is higher. Preliminary results from the combined use of beak-opening records and oesophagus temperature records indicate that penguins stay longer at the bottom phase of dives when feeding success is high (Hanuise, Handrich and Bost, in prep.).

4.3.2. Number of wiggles in depth profiles

Wiggles correspond to short periods in the dive profile that are concave in shape (Halsey *et al.* 2007; Fig. 5). The exact definition of a wiggle, a period within a dive profile during which at three points the vertical speed passes below 0 m s^{-1} (Halsey *et al.* 2007), enables the exact number of wiggles within a dive to be counted, and for this process to be automated. Among penguins the number of ingestions recorded per dive is linearly related to the number of wiggles occurring

during the bottom phase and the ascent phase of the dives (king penguins and Adélie penguins, *Pygoscelis adeliae*; Bost *et al.* 2007; chinstrap penguins, *Pygoscelis Antarctica*; Takahashi *et al.* 2004b). Hence high resolution TDRs can be used to accurately assess the number of prey caught per dive, especially in divers feeding on small pelagic fish such as myctophids. King penguin wiggles correspond to prey ingestion events in the majority of dives by individuals (range 50–70%), determined from data sets including dive profiles and one or more proxies of prey ingestion (Bost *et al.* 2007; Hanuise, Handrich and Bost, in prep.)

4.3.3. Change in acceleration

Accelerometers can provide accurate information to monitor the fine-scale behaviour of divers at depth, potentially in three dimensions (Sato *et al.* 2002; Ropert-Coudert *et al.* 2006). A proxy of CPUE can be developed from the number of prey pursuits per

unit time submerged. Prey pursuits are indicated by clear changes in frequency and amplitude of wing or flipper beats during dives. The use of these data as proxies of prey (fish) capture assumes that an encounter with any potential prey will induce pursuit behaviour through an increased rate of flipper beating (Ropert-Coudert *et al.* 2006) and that the pursuit is successful. For instance in the little penguin (*Eudyptula minor*), which feeds on small schooling fish such as sprat, pilchard, garfish and anchovy in western Australia, 'pursuit phases' occur principally during the bottom periods of dives near the seabed. Plotting CPUE against time of day indicated a peak at midday with 90% limits between 05–06h and 18–19h. The higher rate of prey encounter during the middle of the day may be the consequence of greater light at depth, increasing the probability of prey detection by the predator (Ropert-Coudert *et al.* 2006).

Recently the deployment of accelerometers on cormorants, which dive for prey and continuously flap their wings during flight, have allowed finer-scale quantification of the number of prey caught. Furthermore, variation in the body mass of cormorants has been determined from accurate changes in wing stroke frequency after a series of dives (Sato *et al.* 2007).

5. Seabird-Derived Estimates of Prey Availability Compared to Survey Estimates

5.1. Comparison with conventional sampling

To validate the use of behaviours at sea as proxies of prey availability, independent data from extensive simultaneous surveys using relevant sampling methods are needed. Very few studies, however, have tackled the validity of estimates derived from seabird foraging and feeding data (Grémillet *et al.* 2004). This is because it remains difficult to combine effective monitoring of foraging

success with simultaneous and unbiased sampling of prey (Guinet *et al.* 2001; Bost *et al.* 2002). Recently Ichii *et al.* (2007) provided one of the first detailed reports on the distribution of Antarctic marine predators while simultaneously assessing the abundance of their prey (krill and myctophid fish) within their foraging areas. Brooding chinstrap penguins must return frequently to their chick to feed it and thus forage in shelf areas where high krill concentrations are found. Incubating chinstrap penguins are less time constrained and forage in more distant slope and oceanic areas. They have to spend more time foraging due to lower krill abundance. However, this is somewhat counter-balanced by the fact that the krill have a higher energy content (Ichii *et al.* 2007).

At Dumont D'Urville (Eastern Antarctica), 'real-time' sampling of euphausiids was carried out with net hauls in the same areas visited by tracked Adélie penguins (Jaeger, Koubbi and Bost, in prep.). When the penguins returned to their colonies, individuals were carefully stomach pumped to reconstitute their diet composition. In 2005, euphausiids comprised 80% of the penguin diet by number. Krill (*Euphausia superba*) was the modal prey, representing 69% of prey eaten in terms of reconstituted biomass. However, no krill were found in net hauls at the 'hot spot' of the tracked penguins. Overall data on prey sampling did not match the preferred foraging areas of the penguin (Fig. 6). The highest levels of krill biomass were not detected in the areas where the penguins concentrated their foraging effort. Such a lack of correspondence between penguin diet and net hauls has been reported previously (Bost *et al.* 1994; Hill *et al.* 1996) and may be a result of the inadequacy of some sampling methods, and the aggregative behaviour and mobility of prey swarms. Euphausiids are indeed difficult to sample with conventional methods using net hauls (Everson 2000; Siegel 2005). The difficult nature of sampling euphausiids highlights the

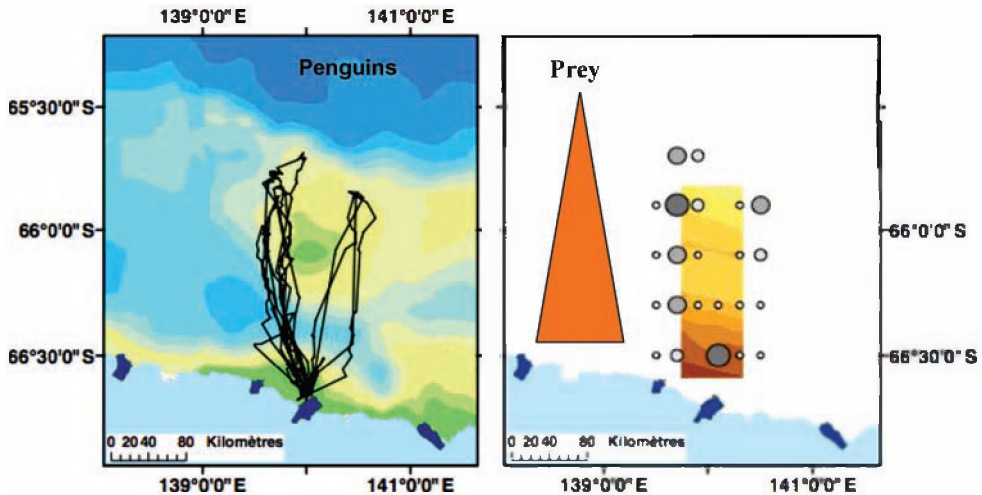


Fig. 6. **Left:** Foraging trips of 10 Adélie penguin satellite tracked at Dumont D'Urville, Antarctica (January 2005). Most of the birds performed extended trips toward the north (mean foraging range: 70 km). **Right:** Comparison of Adélie penguins foraging effort in terms of time spent by sector with the densities of adults euphausiids [range: from 0 (light yellow) to 40 individuals (dark brown). 100 m⁻³]. The densities have been estimated from net haul data (Bongo net, diameter 0.61 m, mesh size: 500 µm).

need to use other sampling techniques such as multi-frequency echo-sounders (Everson 2000; Ichii *et al.* 2007) or wide-opening net hauls such as RMTs (Rectangular Mid-water Trawls), MOCNESS (Multiple Opening and Closing Nets, with an Environmental Sensing System), BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System) or KYMT nets (*Kaiyo Maru* Midwater Trawl) (Herman 1988; Green *et al.* 1998; Wiebe and Benfield 2003) coupled with powerful random sampling designs. Technical limitations in euphausiid sampling, however, do not always explain the mismatch between seabird foraging activity and prey abundance. This is especially so because conventional sampling does not estimate prey abundance in the same conditions as those experienced by predators (Ainley *et al.* 2005). Furthermore, prey densities may need to reach certain levels before seabirds aggregate (Schneider 1990; Piatt *et al.* 2007). Such aggregative response

of seabirds to their main prey can be also scale-dependant. Transects at sea have shown a clear response by seabirds to increased indices of prey abundance at the meso-scale (Hunt *et al.* 1999; Fauchald and Erikstad 2002; Ainley *et al.* 2005). However, at finer scales, seabird distributions have been directly related to prey biomass with only limited success (van Franeker *et al.* 2002; Fauchald and Erikstad 2002). A close relationship between the aggregative response of murre (*Uria* sp.), capelin abundance and patchiness has been found (Fauchald and Erikstad 2002). At the large scale, the overlap between capelin and murre increased with increasing capelin density. Such large-scale concordance between seabirds and capelins could indicate the profitability of this prey relative to other prey items. On the other hand, within the large-scale structures of capelin, the small-scale concordance observed between murre and capelin might reflect the search efficiency of murre

relative to the escape abilities of their main prey. A reduction of patchiness and abundance might reduce the search efficiency of seabirds foraging in a stochastic hierarchical patch system (Fauchald and Erickstadt 2002).

6. Discussion

Over the last twenty years, our knowledge of seabird foraging and feeding behaviour at sea has greatly advanced. We can now reconstruct movement and foraging success of an instrumented bird in the three dimensions of the ocean. Bio-logging studies have shown in detail how pelagic seabirds utilise specific oceanic features. Furthermore, seabird species have been found to adapt their foraging movements and effort over the course of a year (Charrassin *et al.* 2002). The number of prey ingested per unit of foraging time can now also be estimated for seabird predators.

Tracking instrumented seabird predators to get information on prey abundance offers several advantages. Firstly, bio-logging studies can provide a considerable amount of additive information on the distribution and availability of prey. Bio-logging studies can be routinely performed year round (although data collection during winter still remains more difficult). The cost of bio-logging studies is also moderate with respect to conventional surveys (Cairns 1992; Piatt *et al.* 2007). However, inter-individual variation (Weimerskirch *et al.* 2007) requires a number of birds to be instrumented to guarantee a representative sample of the foraging and feeding behaviour of a particular population. Further, attachment of relatively large instrument can have deleterious effect on seabird foraging energetics (Wilson *et al.* 1986) especially during extensive deployment periods or during periods of resource scarcity.

6.1. Applications to conservation

The use of instrumented seabirds as bio-indicators of marine resources is relevant when applying ecosystem management that fo-

cuses on conserving marine predators. Tagged seabirds can be used to determine a feeding 'hotspot' for a population during a particular year, which could be made off-limits to fisheries. Yearly monitoring of seabird foraging behaviour can also provide important information about changes in ecosystem functioning and structure (Hooker and Gerber 2004).

6.2. Can we estimate prey availability from the monitoring of instrumented predators at sea?

While understanding of the foraging patterns of seabird predators is rapidly improving, little work has been done on the validation of proxies derived from instrumented seabirds. We still know very little about the relationships between foraging behaviour at sea and the density/availability of prey (Ropert-Coudert and Wilson 2005; Enstipp *et al.* 2007). To our knowledge no study has however succeeded in quantitatively relating CPUE in seabirds of known origin and breeding status with valid, simultaneous measurements of prey density. The logistic constraints of surveys at sea are indeed considerable, especially in the Southern and Arctic ocean because of the remoteness of the areas and the difficult sea conditions (rough waters, wind, ice).

In captivity, recent experiments into the effects of prey-density and size on foraging behaviour have been performed using double-crested cormorants *Phalacrocorax auritus*, a benthic forager, in a large dive tank (Enstipp *et al.* 2007). This study has shown a linear relationship between the CPUE of a bird and prey density. Feeding success was highly dependent on fish density, with cormorants being less successful and diving longer when targeting schooling fish. However at low fish densities the birds had a disproportionately low CPUE (Enstipp *et al.* 2007). Future experimental studies on prey capture rates should increase our knowledge about seabird-prey interactions at a fine

scale, allowing refinement of predator-prey models.

Future studies should also address whether seabird foraging effort is related to prey abundance. As pointed out by Montevecchi (1993), the significance of prey availability is highly correlated to prey abundance (in term of biomass). Physical factors can induce increased prey availability at the meso-scale. Thus pursuit-diving marine birds such penguins and auks are dependent on the depth of the thermocline that favours much higher accessibility to their preferential prey (Charrassin and Bost 2001).

6.3. Next steps

An important endeavour is to scale up individual records of CPUE and location of prey capture from instrumented birds to estimations of the entire prey base of an ecosystem. This long-term objective requires the use of bio-logging technologies on a large number of individual seabirds in several colonies or populations to develop a standard, international monitoring program. Monitoring of a large number of birds will allow integration of the possible effects of breeding experience and bird quality on the monitoring data.

Filling in the gaps between records of CPUE by individual seabirds during the course of a foraging trip and simultaneous, independent prey estimations should be a priority as it is an essential step towards utilising seabird distributions at sea as accurate proxies of prey abundance. This requires the use of integrated multidisciplinary prey surveys at sea, conducted at several spatial scales. One possible way to collect data on density/distribution of prey that are difficult to sample would be the use of seabird-borne miniaturized digital cameras. Such technology has been one of the most exciting recent advances for obtaining new insights into the social behaviour of seabirds at sea (Takahashi *et al.* 2004a) and can be compared with underwater video profiler or

Visual Plankton Recorder. However, recording video footage at great depths, where light conditions are low, is still a challenge (Watanuki *et al.* 2008).

Quantification of the rate of energy acquisition from behavioural data is also needed (Butler 2000). Measurements of the energetic costs of foraging throughout the annual cycle, and relating this to changes in determined levels of prey density is particularly relevant. The use of heart rate, to estimate energy expenditure have already been recorded in seabirds for an entire year (Green *et al.* 2002; Grémillet *et al.* 2001). This is of particular significance since metabolic rate is likely to differ with level of activity, through the year at each phase of the breeding cycle and as food availability varies (Nagy *et al.* 2001; Grémillet *et al.* 2005). Accurate knowledge of adult field metabolic rate and chick energetic needs (Halsey, Handrich, Butler, Bost, submitted) will allow estimation of the energy gain and the foraging time needed per trip for a given individual whose energetic balance is in equilibrium (Cairns 1992). Finally, research is still required to accurately determine the relationships between seabird foraging parameters and temporal/spatial changes in prey abundance. The usefulness of seabirds as bio-indicators should be enhanced in forthcoming years, especially given the ever growing pressures on marine resources and ecosystems.

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