

Review

## Marine predators at South Georgia: an overview of recent bio-logging studies

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**Abstract:** There is a unique diversity and density of land-based marine predators breeding at Bird Island, South Georgia, operating at a wide variety of spatial and temporal scales. These provide exceptional opportunities for bio-logging studies, the objectives of which have been to investigate trophic interactions in ecosystem contexts (including applications in fisheries and environmental management and conservation). Associated data from studies on feeding ecology, reproductive performance and population dynamics provide valuable contextual information for bio-logging analyses. An associated ship-based offshore marine science programme also provides vital information about the local and regional biological and physical environment, which is both complex and highly variable. Further developments of our bio-logging studies at South Georgia face a number of important challenges. These include:

- acquiring samples large enough for statistical analysis;
- replicating study sites and/or populations in order to characterize population and species behaviour;
- collecting simultaneous data from multiple sensors or devices in order to interpret foraging behaviour;
- acquiring key collateral data on prey and environment at appropriate spatial and temporal scales to understand foraging dynamics in context.

We illustrate approaches to address some of these challenges from recent studies of the South Georgia marine ecosystem.

**key words:** environment, foraging, free-living, seabirds, marine mammals

### Introduction

Natural environments are not homogeneous and all organisms (at some scale) depend upon the heterogeneity that they find in their environment to survive (Sanderson *et al.*, 2002). For example, organisms generally depend upon temporary concentrations of food resources, which leads to the clustering of their foraging activity. Therefore, to understand how and why organisms modify their foraging behaviour, we have to investigate the levels of environmental heterogeneity that they (and their prey) experience, as well as studying their behavioural responses.

Factors affecting the environment (as sampled by a predator) are numerous and complex and act at a variety of temporal and spatial scales. Some factors may impact directly upon for-

aging (*e.g.* seasonal sea-ice cover), whereas others may act indirectly through lower trophic levels (*e.g.* seasonal levels of primary production). Such variability will not only affect any study animals, but potentially (in the context of our incomplete knowledge) how we perceive the animal's response.

Under most circumstances, it is impossible directly and continuously to observe the activities of a free-living organism. As a consequence there has been a recent and rapid development of miniaturized data loggers that are capable of recording parameters associated with a given activity. When carrying out such bio-logging studies and creating an image of an animal's foraging activity, it is particularly important that we interpret the resulting image in the context of the best available information from the environment.

Some environmental factors have very obvious impacts, others less so. Large-scale processes, such as the Antarctic Circumpolar Wave (White and Peterson, 1996) or the El Niño/Southern Oscillation, have an obvious, albeit complex influence. For example, ENSO influences oceanographic conditions through atmospheric or oceanic teleconnections (Mann *et al.*, 2000). This may have both local and regional impacts, potentially affecting prey availability at a variety of spatial and temporal scales. Thus, links between ENSO and the marine ecosystem in the Scotia Sea have been demonstrated (Croxall, 1992; Trathan and Murphy, 2003) and potentially linked to the abundance of Antarctic krill (*Euphausia superba*) at South Georgia (Trathan *et al.*, 2003). In turn, the biomass of krill in the Scotia Sea is known to affect the foraging efficiency (Mori and Boyd, 2003) and breeding success (Croxall *et al.*, 1988; Boyd and Murray, 2001) of predators at South Georgia. At a smaller scale, local variability in environmental factors such as bottom topography (Takahashi *et al.*, 2003) or resource extraction by commercial fisheries (Prince *et al.*, 1998) can affect the foraging behaviour of species. Thus, knowledge about the levels of variability present in the physical, biological and anthropogenic environment are important when studying the foraging behaviour of marine predators and creating images of their activity from bio-logging studies. Multi-animal, multi-year, and multi-site studies are particularly important in this respect as they enable the scale and pattern of natural variability to be understood and unusual or atypical responses to be detected or identified.

### **Bird Island, a unique site for bio-logging studies**

The British Antarctic Survey study site at Bird Island, South Georgia (Fig. 1) is ideally suited for bio-logging studies of land-based marine predators. The site possesses a number of important attributes for such work. Firstly, the island has a globally important diversity and density of marine predators that forage over a wide range of spatial and temporal scales (Croxall and Prince, 1979). This includes populations of seabirds and seals, many of which are relatively easy to catch and recapture. Secondly, some of the species breeding at Bird Island have been studied since the site was first occupied in 1958, with more studied since consistent occupation in 1971. This research includes studies on feeding ecology, reproductive performance and population dynamics (Croxall and Prince, 1980; Croxall *et al.*, 1988). Thirdly, there is an existing wealth of knowledge about levels of variability in the physical and biological environment around South Georgia, mainly derived from collaborative studies involving an associated BAS offshore marine biological programme currently based on the *RRS James Clark Ross*. In addition, Bird Island has been occupied year round since 1982

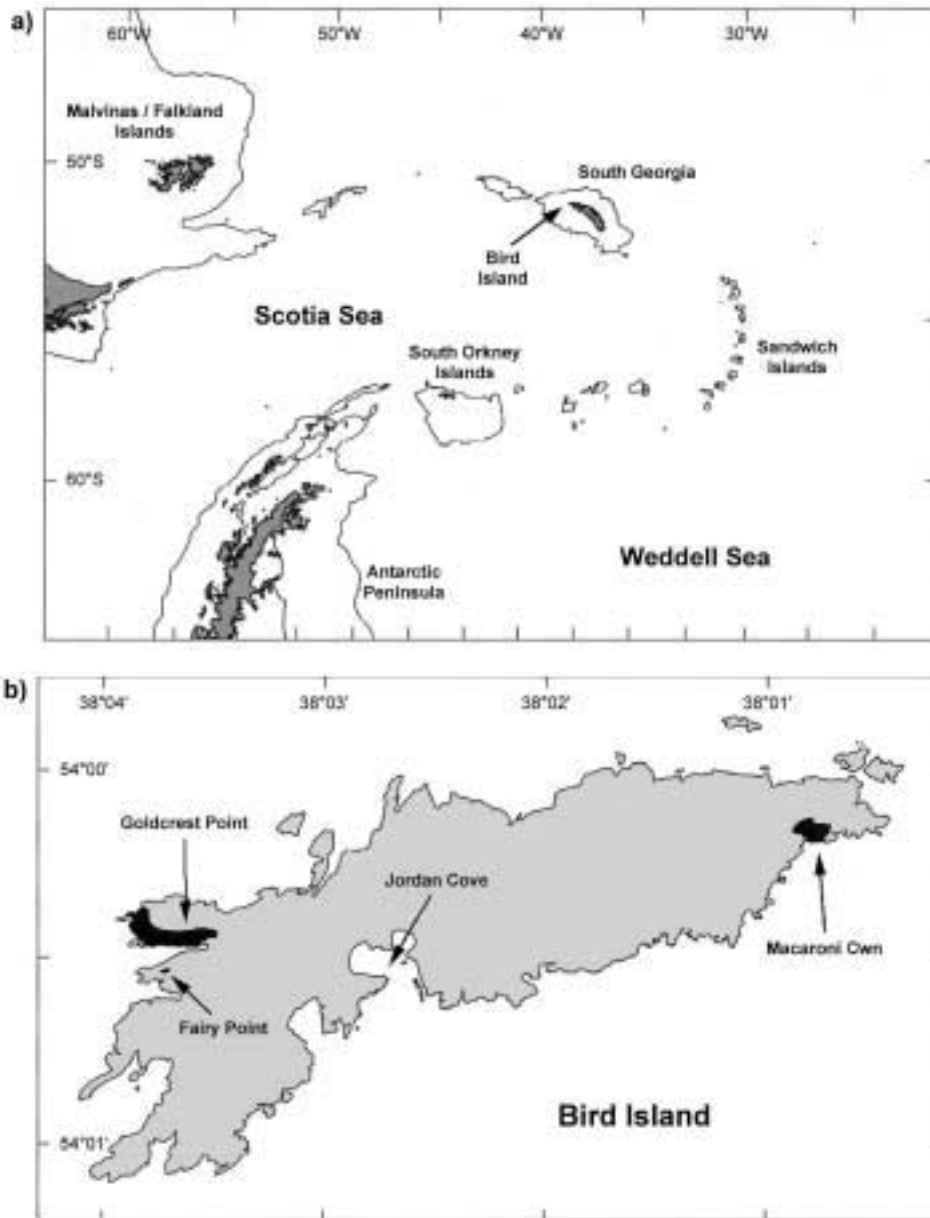


Fig. 1. a) Map of the Scotia Sea showing the location of South Georgia and Bird Island.  
b) Map of Bird Island showing the locations of satellite tracking colonies for macaroni penguins (Fairy Point, Goldcrest Point and Macaroni Cwm) and Antarctic fur seals (Jordan Cove).

and is an important long-term monitoring site contributing to a number of international environmental conservation objectives, including those of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR, <http://www.ccamlr.org/>) Ecosystem Monitoring Programme.

All of these properties contribute to Bird Island being well suited for bio-logging studies. They help provide valuable background information about either the predators themselves, or about the local and regional environment. For example, there is now a detailed understanding about the local (Brandon *et al.*, 1999, 2000) and regional (Trathan *et al.*, 1997, 2000; Trathan and Murphy, 2003) oceanographic structure; about inter-annual variability in oceanographic conditions (Whitehouse *et al.*, 1996; Meredith *et al.*, 2003); about the relatively simple marine food web and in particular about Antarctic krill—the key species that dominates in the Southern Ocean in this region (Everson, 1977; Trathan *et al.*, 1995; Brierley *et al.*, 1997; Murphy *et al.*, 1998). In addition, recent work has provided valuable insights into the environmental interactions that potentially govern the abundance of krill available to marine predators (Murphy, 1995; Trathan *et al.*, 2003) and a detailed understanding of the established and developing commercial fisheries in the region (Everson and Goss, 1991; Murphy *et al.*, 1997; Trathan *et al.*, 1998b; Prince *et al.*, 1998) that interact or potentially compete with marine predators for the same resource.

Many of the parameters measured in the oceans around Bird Island, or from the predators breeding on the island provide valuable context for bio-logging studies. Without such knowledge it is often more difficult to properly interpret the behavioural images derived from bio-logging devices. For example, fluctuations in the abundance of key prey species has a profound consequence for predator foraging behaviour, in that periods of low krill availability can result in predators switching to other prey species that under normal circumstances would be energetically less efficient (*cf.* Everson *et al.*, 1999). This can lead to a change in foraging behaviour (Mori and Boyd, 2003), as well as reduced breeding success or complete breeding failure in some years (Boyd and Murray, 2001).

Foraging behaviour is potentially dependent upon an animal's current status and context; as a result we also need to combine data on foraging with information about annual breeding performance, demographic status and life-history strategy in order to understand how marine predators exploit their environment. Developing bio-logging studies within this broader context will help us achieve a more integrated view of the long-term consequences of foraging behaviour. Long-term study sites such as Bird Island, where there is a wealth of historical data available, are amongst the best sites worldwide for such long-term integrated studies.

### **Bio-logging at Bird Island**

Over the past decades BAS has had many successful national and international collaborations, leading to novel and innovative insights into the foraging behaviour of a variety of species, including seals, penguins, petrels and albatrosses. This work has relied upon the extensive use of a variety of logging devices, including time-depth recorders (TDR) (Kooyman *et al.*, 1986; Croxall *et al.*, 1993; Boyd *et al.*, 1995; Boyd, 1996; McCafferty *et al.*, 1998a, b), heart rate-depth loggers (HRDL) (Bevan *et al.*, 2002; Green *et al.*, 2002, 2003), automatic weighing nests (AN) (Huin *et al.*, 2000), activity recorders (AR) (Prince and Francis, 1984; Afanasyev and Prince, 1993); platform terminal transmitter (PTT) satellite tracking devices (Prince *et al.*, 1992, 1998; Berrow *et al.*, 2000; Barlow and Croxall, 2002; Gonzalez-Solis *et al.*, 2002), light sensitive geo-location devices (GLS) (Afanasyev, 2004; Phillips *et al.*, 2004), underwater cameras (UWC) (Hooker *et al.*, 2002), and conductivity-

temperature recorders (CT) (Hooker and Boyd, 2003).

Current work at South Georgia focuses on the description of the complex foraging behaviour of a number of species, including Antarctic fur seals (*Arctocephalus gazella*), macaroni (*Eudyptes chrysolophus*) and gentoo (*Pygoscelis papua*) penguins, black-browed (*Thalassarche melanophrys*), grey-headed (*T. chrysostoma*) and wandering (*Diomedea exulans*) albatrosses, white-chinned (*Procellaria aequinoctialis*) and giant (*Macronectes halli* and *M. giganteus*) petrels and southern skuas (*Stercorarius skua lonnbergi*). The use of miniaturized data loggers has principally focussed on the behavioural mechanisms and energetic efficiency of foraging. Deployments have been generally short term, and have focussed on the frequency and duration of foraging trips, the spatial distribution of foraging effort, the vertical distribution of effort, and the energetic efficiency of foraging.

In the following paragraphs we describe one, particularly well studied, species to exemplify the bio-logging approaches used to characterise foraging and one, more recently studied species, to indicate new approaches and considerations of how to address interactions between species and the environment. The species described are Antarctic fur seal, for which foraging is perhaps best understood at Bird Island, and macaroni penguins, for which relatively little is still known. Even for Antarctic fur seals, however, there are still important gaps in our understanding; for example, though the dive cycle is well understood (Boyd, 1996), less is known about how animals locate and capture their prey.

### **Antarctic fur seals, a detailed bio-logging study**

Antarctic fur seals have been studied at Bird Island since 1958; bio-logging devices have been part of this study for approximately 30 years, since 1983 (Kooyman *et al.*, 1986; Boyd and Croxall, 1992; Boyd *et al.*, 1994; Boyd, 1996). During this period, a large number of animals have been instrumented with a variety of bio-logging devices. TDRs deployments, and more recently, combined TDR/PTT deployments account for the majority of these studies. As a consequence, knowledge about fur seal diving behaviour has increased rapidly and ever more detailed questions about foraging behaviour have been investigated. These include: characterising foraging trip duration in relation to offspring requirements and prey/environmental conditions; assessing activity budgets during foraging trips, including aspects of timing and duration of diving and relationships between surface/dive partitioning; defining the structure of sub-surface activities (for example, swimming speeds, dive durations and metabolic rates); gaining information about the prey field; and, it has also been possible to gain some understanding of inter-individual and inter-site variation.

Thus, dive characteristics and bout characteristics have been comprehensively described (*e.g.* Kooyman *et al.*, 1986; Boyd, 1996; Mori and Boyd, 2003). Fur seals spend most time diving in bouts with only occasional exploratory dives (Boyd, 1996). These dive bouts are thought to occur mainly in the vicinity of elevated prey concentrations (Boyd, 1996). Swimming speeds vary during each dive with mean speeds of between 1.32 to 1.99 m/s (Boyd *et al.*, 1995) and are fastest during the descent and ascent phases, with a reduction in speed near the bottom of the dive. The swimming speeds recorded during a dive cycle represent only part of the broader range of speeds recorded from animals swimming at the surface.

Boyd *et al.* (1995) showed that metabolic rates are greatest during the foraging phase of dives, and suggested that fur seals maximize the time spent within the foraging zone, balanc-

ing their supply of, and demand for, oxygen. The effort spent in foraging varies according to conditions; for example, during periods of low prey abundance female fur seals invest a significantly greater effort in foraging, both increasing the time spent foraging, and increasing activity during foraging. This increase in effort potentially represents an increase in costs of 30–50% during years of low food abundance (Boyd *et al.*, 1994).

The relationship between foraging behaviour and energy expenditure is complicated by other factors; for example, female fur seals regularly undertake foraging trips of different duration, spending between 3 and 9 days away from their pup (Boyd, 1999; Staniland and Boyd, 2003; Staniland *et al.*, 2003). Females undertaking long trips have higher metabolic rates; however, the energetic efficiency with which females gain mass is independent of the time they spend at sea (Arnould *et al.*, 1996). As such, within the range of conditions observed at South Georgia, there is no apparent energetic advantage to females in undertaking foraging trips of any particular duration. To understand why foraging trips are of different duration requires knowledge of the prey field and the ecological interactions that an animal experiences.

When animals forage they potentially optimise their foraging behaviour in relation to their prey availability (Stephens and Krebs, 1986). Past experience is potentially an important element in this optimisation process; experience gained over the current trip and over other recent trips will also be important, as will ‘knowledge’ gained throughout the life of the animal (Staniland *et al.*, 2003).

### Macaroni penguins, a developing bio-logging study

Different species are likely to optimise their foraging behaviour in different ways, even though they may actually target the same prey resource. Both intrinsic and extrinsic factors may be important. For example, a predator's innate diving ability, or cueing and knowledge of prey availability, or competitive exclusion by other predator species may affect foraging patterns. Both Antarctic fur seals and macaroni penguins feed on Antarctic krill. On average, the dive characteristics of both species are very similar, at least in terms of their dive duration, maximum dive depth and surface interval (Table 1).

Table 1. Comparison between dives made by Antarctic fur seals and macaroni penguins.

Species and study period	Parameter	No. animals	No. days	No. dives	Q1	Median	Q3
Antarctic fur seal 1998–1999	Previous surface interval (s)	51	295.29	104179	18.0	32.0	56.0
	Dive duration (s)	51	295.29	97920	10.0	62.0	95.0
	Maximum dive depth (m)	51	295.29	104178	5.0	19.0	40.0
Macaroni penguin 2000–2001	Previous surface interval (s)	24	224.91	101570	18.0	26.0	38.0
	Dive duration (s)	24	224.91	101570	38.0	70.0	100.0
	Maximum dive depth (m)	24	224.91	101570	7.5	18.0	39.5

Table 2. Comparison between dives made by macaroni penguins during different periods within a single breeding season.

Macaroni penguin 2000–2001	Parameter	No. animals	No. days	No. dives	Q1	Median	Q3
Incubation	Previous surface interval (s)	4	50.33	26161	18.0	24.0	34.0
	Dive duration (s)	4	50.33	26161	40.0	70.0	96.0
	Maximum dive depth (m)	4	50.33	26161	6.5	15.5	34.0
Broodguard	Previous surface interval (s)	5	19.75	5525	24.0	32.0	42.0
	Dive duration (s)	5	19.75	5525	58.0	96.0	114.0
	Maximum dive depth (m)	5	19.75	5525	15.5	39.0	57.0
Crèche	Previous surface interval (s)	10	45.98	24024	18.0	26.0	38.0
	Dive duration (s)	10	45.98	24024	32.0	70.0	102.0
	Maximum dive depth (m)	10	45.98	24024	8.0	19.5	41.5
Premoult	Previous surface interval (s)	5	108.85	45860	20.0	28.0	38.0
	Dive duration (s)	5	108.85	45860	38.0	66.0	98.0
	Maximum dive depth (m)	5	108.85	45860	8.0	17.0	38.5

Antarctic fur seals dive mainly at night (Croxall *et al.*, 1985; Boyd, 1996), whereas macaroni penguins dive mainly during the hours of daylight (Croxall *et al.*, 1993; Trathan *et al.*, unpublished data). Fur seal dives can be separated into bouts using sequential difference analysis of the preceding surface interval (Mori and Boyd, 2003); however, for macaroni penguins the preceding surface interval is not, by itself, an adequate criterion to separate bouts. An additional descriptor is required to generate bouts that have an internally consistent diving pattern. For macaroni penguins, the start of a new bout can best be determined by using sequential difference analysis of both the preceding surface interval and the difference in maximum depth (*cf.* Mori *et al.*, 2002). Such analysis helps determine when birds move to different prey patches by separating dives into groups that are internally consistent, thereby providing a more realistic description of dive behaviour.

Within a season, macaroni penguins show differences in diving behaviour. During the brood-guard period, when males are guarding and females are provisioning their chick (Williams and Croxall, 1991), foraging dives were both deeper and longer (Table 2). During this period, female birds are more constrained than at any other time (Barlow and Croxall, 2002; Barlow *et al.*, 2002), and potentially rely upon prey resources that are sub-optimal in terms of foraging efficiency. Interpreting this observation will require detailed information from the environment about prey availability, distribution and abundance.

### Competition between species

At South Georgia, Antarctic fur seals and macaroni penguins depend heavily upon Antarctic krill and are, respectively, the main land-based mammalian and avian consumers of krill. Both species have very large breeding populations, with more than 3 million female fur seals (Boyd, 1993) and possibly as many as 2.5 million pairs of macaroni penguins (Trathan *et al.*, 1998a). The population of fur seals has increased, particularly since the late 1950s (Payne, 1977), following recovery from exploitation in the early nineteenth century. In con-

trast, the population of macaroni penguins has declined, especially over the past 25 years (Trathan *et al.*, 1998a; Barlow *et al.*, 2002). Both species breed at approximately the same time of year, feed on krill of similar size ranges, dive to similar depths and are restricted in their foraging range at least while provisioning their offspring. They therefore may be assumed to compete directly for resources. Recent bio-logging studies highlight the potential for this overlap (Barlow *et al.*, 2002).

Understanding the mechanics of this potential competitive interaction will require fine definition bio-logging studies, and simultaneous information from the environment about prey availability, distribution and abundance.

### How representative are single study colonies

Most bio-logger deployments have been carried out from a small number of sites and relatively little is known about the behaviour of animals away from their main study colonies. For a few species, deployments have been carried out at different sites; however, in most such studies, site differences may be confounded by seasonal or annual differences. For some parameters, the differences between colonies may not be important but for others, inter-colony differences may be critical to our understanding of the behaviour of the target species, particularly if valid generalisations are to be drawn for the wider local or regional population.

Studies on chinstrap penguins breeding at the BAS study site on Signy Island in the South Orkney Islands highlight the value of using alternative study sites for bio-logging studies. During the 2001–2002 breeding season foraging chinstrap penguins showed unique diving patterns in their foraging behaviour that had not been recorded previously (Takahashi *et al.*, 2003). Individual penguins were found diving deeper (179 m) than previously reported (*cf.* Bengtson *et al.*, 1993; Wilson and Peters, 1999) and feeding benthically. Though these findings could be the consequence of using smaller, more sophisticated devices, it is more probable that they represent behavioural adaptations to the local foraging environment. Feeding at the sea floor under the circumstances of this study appeared to be an efficient way of foraging compared to pelagic feeding.

Studies on macaroni penguins breeding at Bird Island, South Georgia also highlight the value of using alternative study sites. Satellite tracking of penguins from Bird Island has been carried out during each breeding season since 1999. During the brood-guard stage of chick rearing parental duties are divided; males guard the chick whilst females provision the chick (Williams and Croxall, 1991). The female penguins leave the study colony (located at Fairy Point on the north coast of the island) and forage predominantly in the area to the north of the island, over the continental shelf and towards the shelf-break (Barlow and Croxall, 2002). Foraging during this period is more constrained than at any other time of the breeding season. Based on the evidence from the Fairy Point study colony (Fig. 2a), birds foraging from the other macaroni penguin colonies located on Bird Island may be expected to forage in an analogous manner, leaving the colony and foraging directly offshore over the continental shelf. However, satellite tracking from 2 other colonies during January 2003, suggests that structure in the local ecosystem is critical to the direction that birds follow. As expected, birds from the Goldcrest Point colony (also located on the north coast of the island) foraged towards the north of the colony (Fig. 2b). In contrast, birds from the Macaroni Cwm colony (located on the south coast of the island) also foraged over the northern shelf (Trathan *et al.*,



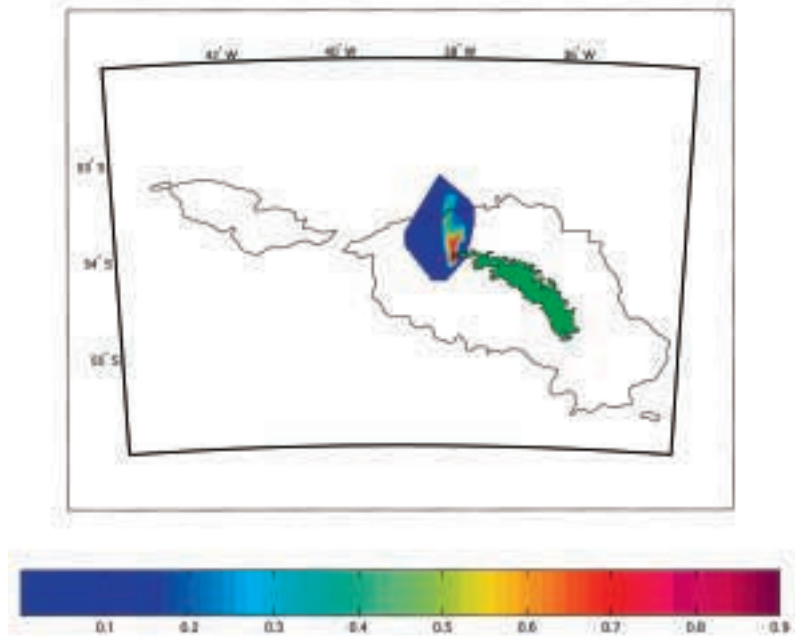


Fig. 2a. Relative utilisation by foraging time for macaroni penguins satellite tracked from Fairy Point (January 2003).

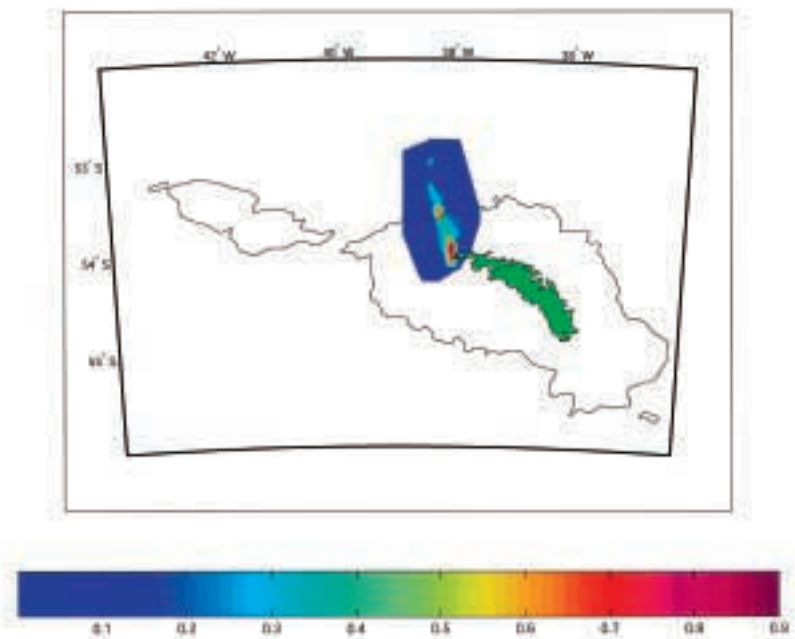


Fig. 2b. Relative utilisation by foraging time for macaroni penguins satellite tracked from Goldcrest Point (January 2003).

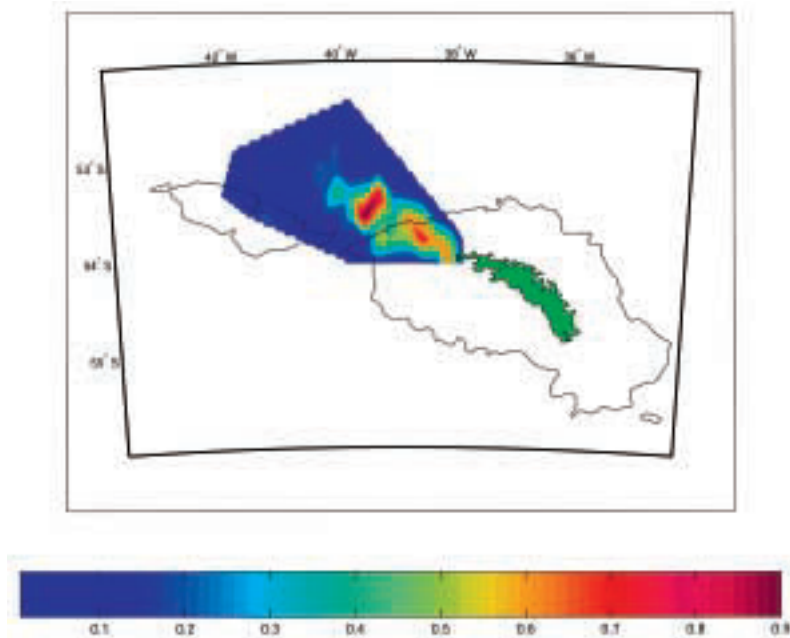


Fig. 2c. Relative utilisation by foraging time for Antarctic fur seals satellite tracked from Jordan Cove (January 2002).

unpublished data). This suggests that aspects of the northern shelf system are potentially of critical importance to birds at this time of the breeding season.

Satellite tracking studies of female Antarctic fur seals foraging from Bird Island to provision their pups has been carried out since 1996. The study colony of fur seals at Bird Island is located on the south of the island at Jordan Cove; however, studies have shown that female fur seals feed predominantly over the northern shelf (Fig. 2c) (Boyd *et al.*, 1998, 2002; Staniland *et al.*, 2003), again suggesting that aspects of the northern shelf are potentially of critical importance for foraging predators.

### Environmental data from associated studies

The foraging areas that both macaroni penguins and Antarctic fur seals target are within a region where a westerly flow of water occurs along the northern edge of the shelf at South Georgia. This shelf-break front results from water density differences between shelf waters and deeper oceanic waters (Brandon *et al.*, 1999, 2000). The front is also influenced by the regional oceanography, being affected by the Southern Antarctic Circumpolar Current Front, one of the fast moving jets of the Antarctic Circumpolar Current (see Trathan *et al.*, 1997; Thorpe *et al.*, 2002).

The relationship between foraging and oceanography suggests a strong preference for feeding along the main axis of the westward flow, either because prey are more abundant, more reliable, or more detectable in the flow than they are elsewhere. Certainly the fast moving water at the edge of the shelf appears to be a major factor structuring the foraging effort

of predators breeding at the northwest of the island. The combined information available from the three macaroni penguin colonies and from Antarctic fur seals, improve our understanding of this ecosystem and of the factors structuring ecosystem interactions.

### **Comparison with other Southern Ocean locations**

At South Georgia, the diet of both Antarctic fur seals and macaroni penguins is dominated by Antarctic krill (Croxall *et al.*, 1985, 1988, 1993; Boyd, 2002, and references therein). Elsewhere in the Southern Ocean, fish (particularly myctophid fish) are known to dominate in the diet of both species. Various myctophid fish species are present at South Georgia, but they are of lesser importance in the diet of both species than they are elsewhere. For example, at the Iles Kerguelen, Antarctic fur seals feed primarily on fish with 25 species being taken and myctophid fish accounting for an average of 94% by number of all fish consumed (Lea *et al.*, 2002). Likewise, at Macquarie Island, fish dominate fur seal diets with myctophid fish representing the main prey item (93.9%) (Robinson *et al.*, 2002). In contrast, on the Danco Coast, Antarctic krill are important, though fish represent an important component in some years with channichthyids representing the most important taxon eaten (Casaux *et al.*, 2003). Similarly, macaroni penguins at the Prince Edward Islands feed mainly on pelagic fish, with myctophids being the most important prey item (70% of total prey biomass) (Adams *et al.*, 1993). Thus, elsewhere in the Southern Ocean, differences in the principal prey may potentially result in differences in dive behaviour, particularly with respect to dive depth and location. For example, analysis of prey and foraging behaviour of Antarctic fur seals at South Georgia suggests prey related differences occur in both dive depth and distance from colony; dives categorised as oceanic and far oceanic (*cf.* shelf and shelf-break), included a higher proportion of fish (Staniland and Boyd, 2003; Staniland *et al.*, 2003). Thus, local availability of prey and local conditions may influence behaviour.

### **Application to fisheries and environmental management and conservation**

Predators at South Georgia potentially interact with commercial fisheries operating in the area. Information from bio-logging has therefore been used to help with regional fisheries management objectives and global conservation goals. Two examples serve to illustrate the insights from such studies.

Even though the current harvest is only about 1% of the total stock, the commercial fishery for Antarctic krill is one of the largest single-species crustacean fisheries in the world. Each year the harvest is taken from a number of traditional fishing grounds that are also the same areas where krill-dependent penguins and seals forage to feed their young (Everson and Goss, 1991; Murphy *et al.*, 1997; Trathan *et al.*, 1998b). To assess potential competition between these dependent species and the krill fishery (Trathan *et al.*, 1998a), the regional management authority responsible for the fishery (the Commission for the Conservation of Antarctic Marine Living Resources - CCAMLR) has used satellite-tracking data from seals and penguins to model areas of possible overlap. Satellite-tracking data from individual study colonies has been extrapolated to other areas where there is no such information, but where the potential for overlap is also high. The resulting 'small-scale management units' generated from the integration of fisheries catch data, predator foraging data and colony loca-

tion data, have now been adopted by CCAMLR (CCAMLR, 2002).

Bio-logging studies at Bird Island, particularly satellite tracking and geo-locator studies, have also highlighted the impact of long-line fisheries on the populations of albatross and petrel species (Ashford *et al.*, 1995; Croxall and Prince, 1996; Prince *et al.*, 1998; Croxall and Gales, 1998; Croxall *et al.*, 1998; Berrow *et al.*, 2000; Gonzalez-Solis *et al.*, 2002). Long-line fisheries set lines that may be many kilometres long. Each line has attached tens of thousands of baited hooks. These lines are set to catch high value fish that may be either bottom dwelling (*e.g.* Patagonian toothfish, *Dissostichus eleginoides*) or pelagic (*e.g.* tuna species). As the lines are set and the hooks sink, the baits attract large numbers of seabirds. Though many birds manage to steal the bait and escape, many are hooked and drowned as the lines sink. Such incidental mortality has been associated with the critical population declines recorded in a number of albatross populations (Croxall *et al.*, 1998; Croxall and Gales, 1998).

In the CCAMLR Convention area of the Southern Ocean, long-line fisheries are now regulated to reduce seabird by-catch and levels in the licensed fishery have been reduced to levels that have negligible population effects (CCAMLR, 2001, 2002). However substantial mortality still occurs, chiefly from unlicensed and unregulated pirate operations both within and outside the CCAMLR area. Recent evidence from grey-headed albatrosses, tracked outside their breeding season (Croxall *et al.*, unpublished data), show that these species are even more vulnerable at other times of year than when breeding. Such circumpolar migrations mean that albatross species are threatened by various long-line fisheries located at numerous locations elsewhere in the Southern Ocean, including outside the CCAMLR area.

### Conclusion

Studies at South Georgia include a number of elements that help increase the value of bio-logging data to explore foraging activity. They highlight the value of multi-individual, multi-year studies that enable more robust conclusions to be drawn; they emphasize the value of multi-site, multi-species, multi-year comparisons to help improve our understanding of ecosystem interactions; and they show how the availability of contextual environmental data from satellites, from associated ship-based marine programmes, from other land-based studies, and from modelling exercises, can extend our understanding of ecosystem structure.

The integrated studies carried out at Bird Island, highlight the value of combining bio-logging studies with other methods of data capture. They also indicate the advantage of using spatial data mapping tools, such as Geographical Information Systems, that allow complex spatial analyses of foraging within a multi-dimensional system.

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## References

- Adams, N.J., Moloney, C. and Navarro, R. (1993): Estimated food consumption by penguins at the Prince Edward Islands. *Antarct. Sci.*, **5**, 245–252.
- Afanasyev, V. (2004): A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem. Natl Inst. Polar Res., Spec. Issue*, **58**, 227–233.
- Afanasyev, V. and Prince, P.A. (1993): A miniature storing activity recorder for seabird species. *Ornis Scandinavica*, **24**, 243–246.
- Arnould, J.P.Y., Boyd, I.L. and Speakman, J.R. (1996): The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J. Zool., London*, **239**, 769–782.
- Ashford, J.R., Croxall, J.P., Rubilar, P.S. and Moreno, C.A. (1995): Seabird interactions with long-lining operations for *Dissostichus eleginoides* around South Georgia, April to May 1994. *CCAMLR Sci.*, **2**, 111–122.
- Barlow, K.E. and Croxall J.P. (2002): Provisioning behaviour of macaroni penguins *Eudyptes chrysolophus*. *Ibis*, **144**, 248–258.
- Barlow, K.E., Boyd, I.L., Croxall, J.P., Reid, K., Staniland, I.J. and Brierley, A.S. (2002): Are penguins and seals in competition for Antarctic krill at South Georgia? *Mar. Biol.*, **140**, 205–213.
- Bengston, J.L., Croll, D.A. and Goebel, M.E. (1993): Diving behavior of chinstrap penguins at Seal Island. *Antarct. Sci.*, **5**, 9–15.
- Berrow, S.D., Wood, A.G. and Prince, P.A. (2000): Foraging location and range of white-chinned petrels *Procellaria aequinoctialis* breeding in the South Atlantic. *J. Avian Biol.*, **31**, 303–311.
- Bevan, R.M., Butler, P.J., Woakes, A.J. and Boyd, I.L. (2002): The energetics of gentoo penguins, *Pygoscelis papua*, during the breeding season. *Funct. Ecol.*, **16**, 175–190.
- Boyd, I.L. (1993): Pup production and distribution of breeding Antarctic fur seals *Arctocephalus gazella* at South Georgia. *Antarct. Sci.*, **5**, 17–24.
- Boyd, I.L. (1996): Temporal scales of foraging in a marine predator. *Ecology*, **77**, 426–434.
- Boyd, I.L. (1999): Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behav. Ecol.*, **10**, 198–208.
- Boyd, I.L. (2002): Inmate food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J. Anim. Ecol.*, **39**, 103–119.
- Boyd, I.L. and Croxall, J.P. (1992): Diving behaviour of lactating Antarctic fur seals. *Can. J. Zool.*, **70**, 919–928.
- Boyd, I.L. and Murray, A.W.A. (2001): Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.*, **70**, 747–760.
- Boyd, I.L., Arnould, J.P.Y., Barton, T. and Croxall, J.P. (1994): Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J. Anim. Ecol.*, **63**, 703–713.
- Boyd, I.L., Reid, K. and Bevan, R.M. (1995): Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Anim. Behav.*, **50**, 769–784.
- Boyd, I.L., McCafferty, D.J., Reid, K., Taylor, R. and Walker, T.R. (1998): Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can. J. Fish. Aquat. Sci.*, **55**, 845–852.
- Boyd I.L., Staniland, I.J. and Martin, A.R. (2002): Distribution of foraging by female Antarctic fur seals. *Mar. Ecol. Prog. Ser.*, **242**, 285–294.
- Brandon, M.A., Murphy, E.J., Whitehouse, M.J., Trathan, P.N., Murray, A.W.A., Bone, D.G. and Priddle, J. (1999): The shelf break front to the east of the sub-Antarctic island of South Georgia. *Cont. Shelf Res.*, **19**, 799–819.
- Brandon, M.A., Murphy, E.J., Trathan, P.N. and Bone, D.G. (2000): Physical oceanographic conditions to the north-west of the sub-Antarctic Island of South Georgia. *J. Geophys. Res.*, **105**, 23983–23996.
- Brierley, A.S., Watkins, J.L. and Murray, A.W.A. (1997): Interannual variability in krill abundance at South Georgia. *Mar. Ecol. Prog. Ser.*, **150**, 87–98.
- Casaux, R., Baroni, A. and Ramon, A. (2003): Diet of antarctic fur seals *Arctocephalus gazella* at the Danco Coast, Antarctic Peninsula. *Polar Biol.*, **26**, 49–54.
- CCAMLR (2001): Report of the Twentieth Meeting of the Commission. CCAMLR, Hobart, Tasmania.
- CCAMLR (2002): Report of the Twenty-first Meeting of the Commission. CCAMLR, Hobart, Tasmania.
- Croxall, J.P. (1992): Southern ocean environmental changes—effects on seabird, seal and whale populations. *Philos. Trans. R. Soc. London, Ser. B*, **338**, 319–328.
- Croxall, J.P. and Gales, R. (1998): Assessment of the conservation status of albatrosses. *Albatross Biology and*

- Conservation, ed. by G. Robertson and R. Gales. Chipping Norton, Surrey Beatty, 46–65.
- Croxall, J.P. and Prince, P.A. (1979): Antarctic seabird and seal monitoring studies. *Polar Rec.*, **19**, 573–595.
- Croxall, J.P. and Prince, P.A. (1980): Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol. J. Linnean Soc.*, **14**, 103–131.
- Croxall, J.P. and Prince, P.A. (1996): Potential interactions between wandering albatrosses and longline fisheries for Patagonian toothfish at South Georgia. *CCAMLR Sci.*, **3**, 101–110.
- Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C. and Davis, R.W. (1985): Fur seal diving behaviour in relation to vertical distribution of krill. *J. Anim. Ecol.*, **54**, 1–8.
- Croxall, J.P., McCann, T.S., Prince, P.A. and Rothery, P. (1988): Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. *Antarctic Ocean and Resources Variability*, ed. by D. Sahrhage. Berlin, Springer, 261–285.
- Croxall, J.P., Briggs, D.R., Kato, A., Naito, Y., Watanuki, Y. and Williams, T.D. (1993): Diving patterns and performance in the macaroni penguin *Eudyptes chrysolophus*. *J. Zool.*, London, **230**, 31–47.
- Croxall, J.P., Prince, P.A., Rothery, P. and Wood, A.G. (1998): Population changes in albatrosses at South Georgia. *Albatross Biology and Conservation*, ed. by G. Robertson and R. Gales. Chipping Norton, Surrey Beatty, 68–83.
- Everson, I. (1977): The living resources of the Southern Ocean. Southern Ocean fisheries Survey Programme. FAO Report GLO/SO/77/1, 156 p.
- Everson, I. and Goss, C. (1991): Krill fishing activity in the southwest Atlantic. *Antarct. Sci.*, **3**, 351–358.
- Everson, I., Parkes, G., Kock, K.-H. and Boyd, I.L. (1999): Variation in standing stock of the mackerel icefish *Champocephalus gunnari* at South Georgia. *J. App. Ecol.*, **36**, 591–603.
- Gonzalez-Solis, J., Croxall, J.P. and Briggs, D.R. (2002): Activity patterns of giant petrels *Macronektes* spp., using different foraging strategies. *Mar. Biol.*, **140**, 197–204.
- Green, J.A., Butler, P.J., Woakes, A.J. and Boyd, I.L. (2002): Energy requirements of female macaroni penguins breeding at South Georgia. *Funct. Ecol.*, **16**, 671–681.
- Green, J.A., Butler, P.J., Woakes, A.J. and Boyd, I.L. (2003): Energetics of diving in macaroni penguins. *J. Exp. Biol.*, **206**, 43–57.
- Hooker, S.K. and Boyd, I.L. (2003): Salinity sensors on seals: use of marine predators to carry CTD data loggers. *Deep-Sea Res., Part I*, **50**, 927–939.
- Hooker, S.K., Boyd, I.L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P.L. and Bengtson, J.L. (2002): Monitoring the prey-field of marine predators: Combining digital imaging with datalogging tags. *Mar. Mam. Sci.*, **18**, 680–697.
- Huin, N., Prince, P.A. and Briggs, D.R. (2000): Chick provisioning rates and growth in black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis*, **142**, 550–565.
- Kooyman, G.L., Davis, R.W. and Croxall, J.P. (1986): Diving behaviour of the Antarctic fur seal *Arctocephalus gazella*. *Fur Seals: Maternal Strategies on Land and at Sea*, ed. by R.L. Gentry and G.L. Kooyman. Princeton, Princeton Univ. Press, 115–125.
- Lea, M.A., Cherel, Y., Guinet, C. and Nichols, P.D. (2002): Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. *Mar. Ecol. Prog. Ser.*, **245**, 281–297.
- Mann, M.E., Bradley, R.S. and Hughes, M.K. (2000): Long-term variability in the El Niño/Southern Oscillation and associated teleconnections. *El Niño and the Southern Oscillation: Multiscale Variability and Global and Regional Impacts*, ed. by H.F. Diaz and V. Markgraf. Cambridge, Cambridge Univ. Press, 357–412.
- McCafferty, D.J., Boyd, I.L. and Taylor, R.I. (1998a): Diving behaviour of Antarctic fur seal (*Arctocephalus gazella*) pups. *Can. J. Zool.*, **76**, 513–520.
- McCafferty, D.J., Boyd, I.L., Walker, T.R. and Taylor, R.I. (1998b): Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar. Ecol. Prog. Ser.*, **166**, 285–299.
- Meredith, M.P., Brandon, M.A., Trathan, P.N., Murphy, E.J. and Bone, D.G. (2003): Variability in oceanographic conditions to the east and northwest of South Georgia, 1996–2001. submitted to *Prog. Oceanogr.*
- Mori, Y. and Boyd, I.L. (2003): The behavioural basis for non-linear functional responses: the case of the Antarctic fur seal. submitted to *Ecol. App.*
- Mori, Y., Takahashi, A., Mehlum, F. and Watanuki, Y. (2002): An application of optimal diving models to diving behaviour of Brunnich's guillemots. *Anim. Behav.*, **64**, 739–745.

- Murphy, E.J. (1995): Spatial structure of the southern-ocean ecosystem - predator- prey linkages in southern-ocean food webs. *J. Anim. Ecol.*, **64**, 333–347.
- Murphy, E.J., Trathan, P.N., Everson, I., Daunt, F.H.J. and Parkes, G. (1997): Krill fishing distribution around South Georgia. *CCAMLR Sci.*, **4**, 1–18.
- Murphy, E.J., Watkins, J.L., Reid, K., Trathan, P.N., Everson, I., Croxall, J.P., Priddle, J.P., Brandon, M.A., Brierley, A.S. and Hofmann, E.H. (1998): Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish. Oceanogr.*, **7**, 381–390.
- Payne, M.R. (1977): Growth of a fur seal population. *Philos. Trans. R. Soc. London, Ser. B*, **279**, 67–79.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. and Briggs, D.R. (2004): Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.*, **266**, 265–272.
- Prince, P.A. and Francis, M. (1984): Activity budgets of foraging grey-headed albatrosses. *Condor*, **86**, 297–300.
- Prince, P.A., Wood, A.G., Barton, T.R. and Croxall, J.P. (1992): Satellite-tracking wandering albatrosses *Diomedea exulans* in the South Atlantic. *Antarct. Sci.*, **4**, 31–36.
- Prince, P.A., Croxall, J.P., Trathan, P.N. and Wood, A.G. (1998): The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. *Albatross Biology and Conservation*, ed. by G. Robertson and R. Gales. Chipping Norton, Surrey Beatty, 137–167.
- Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. and Hindell, M.A. (2002): The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Mar. Freshwater Res.*, **53**, 1071–1082.
- Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B. and Ward, S.E. (2002): A conceptual model for conservation planning based on landscape species requirements. *Landscape Urban Plann.*, **58**, 41–56.
- Staniland, I.J. and Boyd, I.L. (2003): Variation in the foraging location of Antarctic fur seals (*Arctocephalus gazella*) and the effects on diving behaviour. *Mar. Mam. Sci.*, **19**, 83–95.
- Staniland, I.J., Reid, K. and Boyd, I.L. (2003): Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals. submitted to *Mar. Ecol. Prog. Ser.*
- Stephens, D.W. and Krebs, J.R. (1986): *Foraging Theory*. Princeton, Princeton Univ. Press, 264 p.
- Takahashi, A., Dunn, M.J., Trathan, P.N., Sato, K., Naito, Y. and Croxall, J.P. (2003): Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Mar. Ecol. Prog. Ser.*, **250**, 279–289.
- Thorpe, S.E., Heywood, K.J., Brandon, M.A. and Stevens, D.P. (2002): Variability of the southern Antarctic Circumpolar Current front north of South Georgia. *J. Mar. Syst.*, **37**, 87–105.
- Trathan, P.N. and Murphy, E.J. (2003): Sea surface temperature anomalies near South Georgia: relationship with the Pacific El Niño regions. *J. Geophys. Res.*, **108**(C4), 8075, doi:10.1029/2000JC000299.
- Trathan, P.N., Everson, I., Miller, D.G., Watkins, J.L. and Murphy, E.J. (1995): Krill biomass in the Atlantic. *Nature*, **367**, 201–202.
- Trathan, P.N., Brandon, M.A. and Murphy, E.J. (1997): Characterisation of the Antarctic Polar Frontal Zone to the north of South Georgia in summer 1994. *J. Geophys. Res.*, **102** (C5), 10483–10497.
- Trathan, P.N., Croxall, J.P., Murphy, E.J. and Everson, I. (1998a): Use of at-sea distribution data to derive potential foraging ranges of macaroni penguins during the breeding season. *Mar. Ecol. Prog. Ser.*, **169**, 263–275.
- Trathan, P.N., Everson, I., Murphy, E.J. and Parkes, G. (1998b): Analysis of haul data from the South Georgia krill fishery. *CCAMLR Sci.*, **5**, 9–30.
- Trathan, P.N., Brandon, M.A., Murphy, E.J. and Thorpe, S.E. (2000): Transport and structure within the Antarctic Circumpolar Current to the north of South Georgia. *Geophys. Res. Lett.*, **27**, 1727–1730.
- Trathan, P.N., Brierley, A.S., Brandon, M.A., Bone, D.G., Goss, C., Grant, S.G., Murphy, E.J. and Watkins, J.L. (2003): Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. *Fish. Oceanogr.*, **12**, 569–583.
- White, W.B. and Peterson, R.G. (1996): An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature*, **380**, 699–702.
- Whitehouse, M.J., Priddle, J.P. and Symon, C. (1996): Seasonal and annual change in seawater temperature, salinity, nutrient and chlorophyll a distributions around South Georgia, South Atlantic. *Deep-Sea Res., Part I*, **43**, 425–443.
- Williams, T.D. and Croxall, J.P. (1991): Annual variation in breeding biology of macaroni penguins *Eudyptes chrysolophus* at Bird Island, South Georgia. *J. Zool. London*, **223**, 189–202.
- Wilson, R.P. and Peters, G. (1999): Foraging behaviour of the chinstrap penguin *Pygoscelis antarctica* at Ardley Island, Antarctica. *Mar. Ornithol.*, **27**, 85–95.