



Foraging ecology of grey-headed mollymawks at Marion Island, southern Indian Ocean, in relation to longline fishing activity

Deon C. Nel^{a,*}, Jeanne L. Nel^a, Peter G. Ryan^a, Norbert T.W. Klages^b,
Rory P. Wilson^c, Graham Robertson^d

^a*Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa*

^b*Port Elizabeth Museum, PO Box 13147, Humewood 6013, South Africa*

^c*Institut für Meereskunde, Dusternbrooker Weg 20, D-24105 Kiel, Germany*

^d*Australian Antarctic Division, Channel Highway, Kingston 7050, Tasmania, Australia*

Received 30 September 1999; received in revised form 25 April 2000

Abstract

Incidental mortality due to longline fishing has been implicated as the main cause for the global population decline in grey-headed mollymawks (*Thalassarche chrysostoma*). Two of these fisheries, within the potential foraging range of grey-headed mollymawks breeding on Marion Island, have increased drastically over the past 5–10 years. In order to understand the impacts of these fisheries on the grey-headed mollymawk population breeding on Marion Island, we studied their foraging ecology by tracking their foraging trips and sampling their diets. During the incubation stage, birds made long foraging trips, mostly towards the subtropical convergence and sub-Antarctic zones, bringing them into contact with areas of intense southern blue-fin tuna (*Thunnus maccoyii*) longline fishing. Females spent a higher proportion of their time within these areas than males, thus exposing themselves to a higher risk of incidental mortality from this fishery. During the early chick-rearing stage, foraging trips were shorter and to the southwest of the island in the Polar frontal and Antarctic zones, thus avoiding any contact with the southern blue-fin tuna industry. However, short foraging trips (<2 days) were made within the boundary of known Patagonian toothfish (*Dissostichus eleginoides*) longline sets around Marion Island. Males made a higher proportion of short foraging trips and spent more time within the boundaries of the toothfish fishery than females. These differences may account for the male-biased mortality of grey-headed mollymawks observed in the toothfish fishery around Marion Island. Although a decrease in the annual breeding population has not been detected on Marion Island as yet, we warn that the methods used to detect these changes are inaccurate in measuring short term population changes (<10 years) and that the impacts of these fisheries may already have altered the demographic structure of this population. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Grey-headed mollymawks; Foraging ecology; Tracking; Longline fishing; Incidental mortality

1. Introduction

The Prince Edward Islands group (southern Indian Ocean), comprised of Marion and the smaller Prince Edward Island, is one of only seven breeding localities for the grey-headed mollymawk (*Thalassarche chrysostoma*) and collectively support ca. 10% (ca. 9000 pairs) of the global annual breeding population (Gales, 1997; DCN unpubl. data for the Prince Edward Islands). Although the population on Marion Island appears to be stable and recently increasing, populations on South

Georgia (representing 56% of the world population) and Campbell Island have shown long term decreases in numbers, leading to this species being listed as ‘vulnerable’ (Croxall and Gales, 1997). Incidental mortality due to birds being drowned when they attempt to snatch baited hooks deployed by longline fishing vessels, has been implicated as a main cause for the global decline (Gales, 1997).

Initial concern was focused on the pelagic tuna (*Thunnus* spp.) longline fishery (e.g. Brothers, 1991; Murray, et al., 1993). More recently, however, the development of demersal longline fisheries for Patagonian toothfish (*Dissostichus eleginoides*) on the shelf areas surrounding the main breeding localities of the

* Corresponding author. Fax: +27-21-6503295.

E-mail address: dnel@botzoo.uct.ac.za (D.C. Nel).

sub-Antarctic avifauna has raised cause for concern (e.g. Ashford et al., 1995; Cherel et al., 1996; Cherel, Weimer-skirch & Duhamel, 1996; Croxall and Prince, 1996). Sanctioned longline fishing for Patagonian toothfish within the 200 nautical mile Exclusive Economic Zone (EEZ) surrounding the Prince Edward Islands commenced in October 1996. This was after considerable 'poaching' by unsanctioned fishing vessels during the early part of 1996 (Purves, 1997). During the first year of sanctioned fishing large numbers of seabirds were killed (Ryan et al., 1997). This included at least 143 grey-headed mollymawks killed by licensed vessels (16% of total seabird bycatch), but as large scale unsanctioned fishing continued throughout this period, it was estimated that over 900 grey-headed mollymawks could have been killed during this year (Ryan et al.). Examination of carcasses collected by scientific observers aboard sanctioned vessels revealed a strong male bias in all affected species; 89% of the grey-headed mollymawk carcasses were adult males (Ryan and Boix-Hinzen, 1999).

Grey-headed mollymawks are also killed in substantial numbers by pelagic southern blue-fin tuna (SBT) (*Thunnus maccoyii*) longline fisheries south of Africa (Ryan and Boix-Hinzen, 1998) and off western Australia (Gales et al., 1998). SBT longline fishing in the southern Indian Ocean is largely concentrated around the subtropical convergence (Ryan and Boix-Hinzen, 1998). This fishery reached its peak in the southern Indian Ocean during the mid 1980s and decreased to less than half during the early 1990s. Recently, during the mid 1990s, this fishery once again showed a dramatic increase to ca. 80% of the 1985 peak. This was mainly due to increased Korean longline fishing effort (Tuck and Polacheck, 1997).

Albatrosses exhibit an extreme k-selected breeding strategy. They display a low reproductive rate, high adult survival, delayed onset of breeding (up to 10 years) and very strong mate fidelity (Warham, 1996). Increased mortality due to longline fishing will thus have a complex effect on the demographics of a population that may not be immediately noticeable as a change in the number of birds attempting to breed annually (e.g. Weimerskirch et al., 1997; Jouventin et al., 1999). Studies on wandering albatrosses (*Diomedea exulans*) have shown that decreasing adult survival is accompanied by a decrease in the age at first breeding (Croxall et al., 1990; Weimerskirch et al., 1997), which could initially mask the signal. Also, seabird population trends are generally measured by the number of pairs attempting to breed each year. This measure is notoriously inadequate for measuring short term changes (i.e. <10 years) in population size of biennial breeding albatross populations (Moloney et al., 1994; Gales, 1997). However, as albatrosses have such low productivity and recruitment rates, population growth rate will take a very long time to stabilize after a perturbation

(30–50 years in wandering albatrosses) (Moloney et al., 1994). As albatrosses display high site fidelity and breeding sites are limited and often distant from each other, longline fishing effort within the potential foraging ranges of these breeding populations and its resultant impacts may also vary markedly between populations. It is with this in mind that international conservation initiatives strongly urged research into the foraging ranges and ecology of affected albatross populations (e.g. Gales, 1993; Alexander et al., 1997). The main objective of these initiatives is to determine the degree of spatial and temporal overlap of the foraging ranges of albatross populations with known longline fishing grounds and therefore the degree of exposure of these populations to the risk of incidental mortality.

Despite obvious threats from longline fishing operations within the potential foraging range of grey-headed mollymawks breeding at Marion Island, very little is known about their foraging ecology during the breeding season and their potential interaction with these fisheries. Current knowledge is restricted to a study of the diet of grey-headed mollymawks at the Prince Edward Islands during the chick rearing period (Hunter and Klages, 1989) and observations at sea (Abrams, 1985). These studies suggested that most foraging activity was concentrated mainly at the sub-Antarctic front and the polar frontal zone. In this study we: (1) present additional information on the foraging ecology of this population, (2) establish the level of spatial overlap with known fishing grounds while breeding, and (3) ascertain if there are any differences in the foraging behaviour of males and females, that may account for the high male-biased mortality in the local toothfish longline industry.

2. Methods

Approximately 7600 grey-headed mollymawk pairs breed annually in dense colonies on the southern coast of Marion Island (46°54'S, 37°45'E). Adults return to the colonies early in September, and eggs are laid during the middle of October. During the 1997/1998 season, the first chicks hatched between 14 and 21 December 1997 and the first chicks fledged during the last week of April 1998. Adults weigh between 3.0 and 3.7 kg with males being slightly heavier (Marchant and Higgins, 1990)

We investigated the foraging ecology of breeding grey-headed mollymawks at Marion Island by tracking the foraging movements of breeding adults and sampling the diet of chicks.

2.1. Foraging movements

Breeding grey headed mollymawks were tracked for a total of 117 days using two types of tracking devices: (1)

ST10 platform transmitter terminals (PTTs) manufactured by Telonics (USA) and packaged by Sirtrack Limited (New Zealand), and (2) pillbox geo-locating sensors (GLSs) manufactured by Driesen and Kern (Germany).

The PTTs transmitted at 90 s intervals and were monitored using the CLS-ARGOS satellite tracking system. This system uses the NOAA (National Oceanic and Atmospheric Administration, USA) satellites to receive signals from the PTTs. These data are then relayed to CNES (Centre National des Etudes Spatiales) where the location of the device is determined. The average interval between successful locations was ca. 2 h. GLSs determine position by means of measuring light intensity at 60 s intervals. This information is stored on a data logger and downloaded onto a computer once the device has been retrieved. These data were analysed by RPW using algorithms within the programme MULTITRACE (Jensen Software Systems, Germany). Briefly, since daylength is Julian day- and latitude-dependent and local noon is longitude-dependent, the geographic position of the equipped animal can be determined. This procedure gives two positional fixes per 24 h, which are nominally taken to be around mid-night and mid-day. The various procedures used to minimise errors in positional fixes are detailed in Wilson et al. (1998). As GLSs only acquire two positional fixes per day (i.e. at 12 h intervals) and thus cannot resolve the convoluted paths often followed by albatrosses, these data were ignored in any calculations requiring knowledge of total distance covered, or fine scale movements (i.e. < 12 h interval) such as time spent in the toothfish fishing zone (which was typically < 12 h per visit, for PTT-tracked birds).

The PTTs and GLSs weighed < 100 g, and were attached to feathers on the back of the birds (approximately between the wings) by means of adhesive tape. Care was taken to ensure that the light sensor of the GLSs was exposed when the bird's wings were folded in. Devices were deployed on adults of known sex from a demographic study colony. Sex was determined by means of bill measurements (based on data collected by PGR on 94 dead birds caught on sanctioned toothfish longline fishing vessels). Birds with a depth of the bill at the nail > 29 mm were generally deemed to be males, but culmen length and minimum depth were also considered if the separation was not clear on depth at nail alone.

During late incubation (24 November–17 December 1997) two males and two females were tracked for a total of 56 days using PTTs. Birds were captured immediately after they had been relieved of their incubation shift by their mates, and were taken to the side of the colony where the devices were attached. Attachment took 10–15 min. During early chick-rearing stage (20 January–5 February 1998) three males and three

females were tracked for a total of 61 days and 15 complete foraging trips, using two PTTs (on one male and one female) and four GLSs (on two males and two females). Devices were attached to adults immediately after they had completed feeding their chick and were left on for successive foraging trips.

Movement data were plotted and analysed spatially using ARCVIEW GIS Version 3.0a (ESRI 1992). Due to the large scale movements made by these birds and low level accuracy required, all location classes were considered for analysis, unless the location proved to be implausible according to predicted maximum flying speeds by Pennycuik (1982). Distances were calculated using an equidistant azimuthal (south pole) projection. The ratio of total distance covered to maximum range from the colony was calculated to give an indication of the convolutedness of the path. As grey-headed mollymawks dive mostly during the day and are thought mainly to rest on the surface of the water during the night (Huin and Prince, 1997), we considered plots when birds moved at a speed of < 10 km h⁻¹ during daylight hours as indicative of concentrated foraging in an area. This is consistent with theoretical models that predict that high frequency of prey capture leads to an increase in complexity of movement and decreased velocity in order to maximise search effort in profitable areas (Knoppien and Reddingius, 1985; Benhamou and Bovet, 1989).

Bird movements were analysed in relation to monthly remote-sensed sea surface temperature data available from Integrated Global Ocean Services System (IGOSS). The extent of thermal zones was estimated using information from Lutjeharms and Emery (1983), Lutjeharms, Walters and Allanson (1985) and Belkin and Gordon (1996). These authors recognize three major thermal fronts within our area of interest in the South Indian Ocean. These fronts divide the ocean into four major thermal zones: (1) the Antarctic zone (AZ) which covers the area between the Antarctic divergence and the polar front (PF), (2) the polar frontal zone (PFZ) which lies between the PF and the sub-Antarctic front (SAF), (3) the sub-Antarctic zone (SAZ) which lies between the SAF and the sub-tropical convergence (STC), and (4) the sub-tropical convergence zone (STCZ) which is the broader extent of the STC. The PF is not well expressed at the surface but it lies between the 3° and 5°C isotherms. The SAF has a core temperature of 8°C, while the STC has a core temperature of 14°C in the African sector of the South Indian Ocean. In this study we loosely define the AZ as the area south of the 4°C isotherm, the PFZ as the area between the 4 and 8°C isotherms, the SAZ as the area between the 8 and 12°C isotherms, and the STCZ as the area between the 12 and 16°C isotherms. Waters to the north of the 16°C isotherm are referred to as the sub-tropical zone (STZ) (see Fig. 3 for isotherms).

2.2. Diet sampling

Thirty stomach samples were collected at two separate periods during chick rearing: 25 January–5 February (early chick-rearing), 8 March–16 April (late chick-rearing).

Chicks were sampled immediately after they had been fed and their parents had left the colony. They were induced to regurgitate by inverting them over a bucket, while gently squeezing their stomachs and massaging their necks. The total mass of the sample was measured immediately, after which the liquid portion was drained off and the mass of the solid portion determined. The solid portion was then divided into prey categories, which were weighed separately. All items that could assist in the identification of species, were removed and stored appropriately. These were analysed at the Port Elizabeth Museum upon our return.

2.3. Information on longline fishing effort

The most recent data on SBT longline fishing effort in the south Indian Ocean was taken from Polacheck and Tuck (1995). Positions of all lines set by sanctioned Patagonian toothfish longline fishing vessels within the South African EEZ were made available by the South African Department of Marine and Coastal Management (M. Purves, personal communication). We have used the 95% probability contour of a kernel home range analysis (Worton, 1989) of all sets as the boundary of the toothfish fishing zone.

All statistical analyses follow Zar (1984). Statistical significance was assumed at the $P \leq 0.05$ level but, because of the relatively small sample sizes involved in this type of work, all analyses with $P \leq 0.1$ are reported.

3. Results

3.1. Foraging movements

During incubation, four foraging trips were followed using PTTs. One device stopped working after 5 days of an 18-day foraging trip (due to water entering the battery casing) and one device was lost at sea after 18 days of a 26-day trip. It is assumed that the latter bird lost its device at the beginning of its return flight, as it covered the return journey of 3500 km in 8 days at an average speed of 35 km h⁻¹. This would leave little time for detours or extensive foraging activity. The other two trips were tracked to completion. Three of the four birds resumed incubation after successful removal of the device, while one nest failed while the tracked bird was still at sea.

During the early chick-rearing stage, six individuals were tracked for 14 foraging trips using two PTTs and

four GLSs. All the devices functioned for the duration of the study and were recovered successfully.

3.1.1. Duration of foraging trips and chick provisioning

During incubation, the average foraging trip duration for the four birds carrying PTTs, was 19.3 days (range = 10–26). Although time constraints did not allow us to measure the average foraging trip duration for undisturbed birds, this is considerably longer than the average incubation shift measured on the Crozet Islands (9.2 days, range = 1–19) (Weimerskirch et al., 1985). There was no difference in trip length in relation to sex.

During the early chick-rearing stage, a total of 113 feeding events were observed at 16 nests. On average chicks were fed every 1.64 days. The average duration of 23 individually timed foraging trips (15 from birds carrying devices and eight from undisturbed birds) was 3.45 days. The average for birds carrying devices was 3.66 days, while for undisturbed birds it was 3.05 days. This difference was not significant ($t = 0.64$; $P = 0.54$).

The frequency distribution of the duration of foraging trips during the early chick-rearing phase appeared to be bimodal (Fig. 1), with seven trips (30%) of < 2 days in length (average = 19.1 h) and 16 trips of > 2 days (average = 112.2 h). Males made a higher proportion of very short (≤ 2 days) and very long (≥ 7 days), while females made a higher proportion of medium duration foraging trips (3–6 days). However, this result was not statistically significant ($\chi^2 = 1.97$; $P = 0.16$).

3.1.2. Flight path parameters

During incubation, tracked birds ranged 1053–4060 km from the colony and covered a total distances of 6600–17,870, during a single foraging trip (Table 1). During the early chick-rearing stage foraging trips were significantly shorter in duration ($t = 7.54$; $P < 0.01$), range ($t = 3.3$; $P < 0.01$) and total distance ($t = 4.07$; $P < 0.01$) (Table 1). During this stage birds only moved 70–1812 km from the island and covered total distances of 180–4737 km in a single foraging trip. The ratio of distance/range was also smaller for during chick-rearing ($t = 2.21$; $P = 0.06$), indicating that foraging trips were less convoluted and more directed.

The frequency distribution of maximum foraging ranges (Fig. 2), shows that females made a higher proportion of medium distance foraging trips (400–800 km) ($\chi^2 = 2.8$; $P = 0.09$), while the maximum foraging range of males was more variable than females ($F = 0.306$; $P = 0.09$) (i.e. males more very short and very long foraging trips).

During incubation the average velocity during daylight hours (27 km h⁻¹) was 4.3 times faster than the average velocity during the hours of darkness (6 km h⁻¹). During the night, birds spent 83% of their time moving at < 10 kmh⁻¹, while only 31% of the daytime

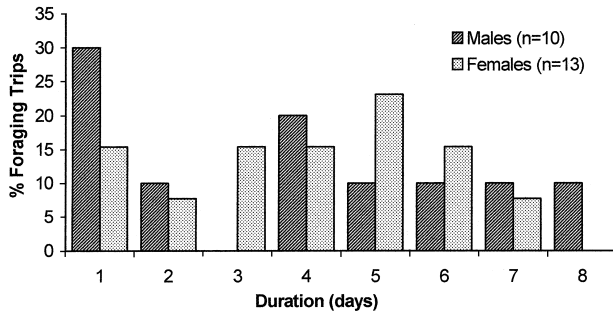


Fig. 1. Frequency distribution of individually timed foraging trips of grey-headed mollymawks breeding on Marion Island during early chick-rearing.

was spent moving at velocities of $< 10 \text{ km h}^{-1}$. A similar pattern occurred during the early chick-rearing stage, when the average daytime velocity (32 km h^{-1}) was 3.7 times faster than average nighttime velocity (8.7 km h^{-1}). During the night 75% of the time was spent moving at velocities of $< 10 \text{ km h}^{-1}$, while only 24% of daytime was spent moving at velocities of $< 10 \text{ km h}^{-1}$.

3.1.3. Foraging movements in relation to thermal fronts

During incubation all four birds initially left the island in a westerly direction. Three birds (two females and one male) then moved northwards and foraged in the warmer waters of the STCZ and SAZ (Fig. 3), while the fourth (a male) foraged mostly in the PFZ and AZ.

The two females moved rapidly in a northwesterly direction before foraging in the SAZ and STCZ south of Africa. Unfortunately the device of the female foraging in the SAZ stopped working after four days in this area. The other female moved 1400 km further westwards before again foraging in the STCZ and SAZ. The first male also moved rapidly northwards to the STCZ where it foraged extensively, before following the 12°C isotherm westwards to Amsterdam Island where it

proceeded to forage for 7 days. Unfortunately, this bird lost its device at this point. The second male displayed very different foraging behaviour to the previous three birds, following a highly erratic flight path confined to waters of the PFZ and AZ, before briefly visiting the STCZ and then returning to the colony.

During the early chick-rearing stage, all 14 tracked foraging trips were confined to the PFZ and AZ in the quadrant to the south west of Marion Island (Fig. 4a and b). Two main types of foraging trips can be identified in Fig. 4a and b: short foraging trips during which birds ranged 80–145 km from the island, and long foraging trips, during which birds ranged 414–1812 km from the island. The PTT-tracked female made two long foraging trips while the male alternated long and short foraging trips (Fig. 4a). Three of the four long satellite-tracked foraging trips showed intensive foraging activity in a very specific area (ca. 53°S and 33°E), ca. 900 km to the south west of the island. On one occasion the PTT-tracked male and female foraged within 100 km of each other on the same day. The male again foraged in this area on its following long foraging trip. One of the males carrying a GLS also foraged in this area. Both satellite-tracked and GLS-tracked males tended to forage farther south than females, during long foraging trips.

During the early chick rearing stage, tracked birds spent significantly more time in the PFZ ($t=3.58$; $P=0.007$), while during incubation stage birds spent more time in the STCZ ($t=1.96$; $P=0.09$) and SAZ ($t=1.84$; $P=0.1$) (Fig. 5).

3.2. Diet

The diet composition is detailed in Table 2. Fish (59%) and cephalopods (32%) were the major constituents of the solid fraction, giving a fish:cephalopod ratio of 1.86. Crustaceans only contributed 3% by drained mass.

Table 1

Flight path parameters of grey-headed mollymawks tracked by means of PTTs and GLSs from Marion Island during the incubation and early chick-rearing stages

Parameter	Incubation mean±S.D. (range)	Early chick-rearing mean±S.D. (range)	<i>t</i> Stat (Incubation vs Chick)	<i>P</i>
No. of individuals	4 (all PTT)	6 (2PTT, 4 GLS)		
No. of foraging trips	4 (all PTT)	14 (6PTT, 8GLS)		
Duration (days)	19.25±6.99 (10–26)	3.88±2.15 (0.5–7.1)	7.54	< 0.01
Range (km)	2182±1408 (1053–4060)	722±538 (70–1812)	3.30	< 0.01
Distance (PTTs only) (km)	12 210±5635 (6600–17870)	2420±1 866 (180–4737)	4.07	< 0.01
Av. speed (PTTs only) (km/h)	19.4±6.8 (12.1–27.7)	22.6±6.1 (13.4–27.7)	−0.79	> 0.1
Distance/range (PTTs only)	5.88±4.15 (2.6–10.5)	2.39±0.28 (2.1–2.8)	2.21	0.062

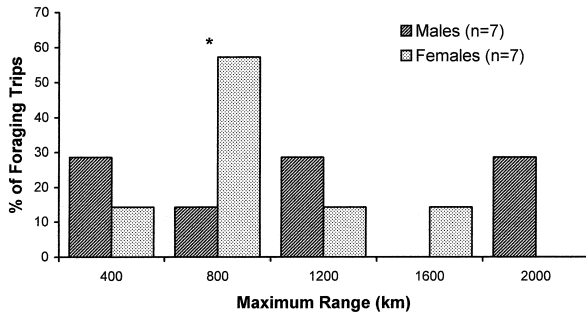


Fig. 2. Frequency distribution of the maximum foraging ranges of male and female grey-headed mollymawks tracked by means of PTTs and GLSs during the early chick-rearing period. * = P (Chi Square) < 0.1.

The most frequently occurring fresh prey species was the ommastrephid squid (*Martialia hyadesi*) (occurring in 27% of samples), followed by the decapod shrimp (*Pasiphaea scotiae*) (23%) (Appendix A). Fresh specimens of the fish *Magnisudis prionosa* and the amphipod *Themisto gaudichaudii* occurred in 20% of the samples. Fresh squids were recorded more frequently in samples taken from the late chick-rearing stage compared to those taken during early chick-rearing ($\chi^2=4.7$; $P=0.03$). This was mainly due to the appearance of *M. hyadesi* in 42% of the samples taken during the late chick-rearing stage. This was significantly different from the early chick-rearing stage ($\chi^2=6.3$; $P=0.01$). Amphipods also occurred more frequently during the late chick-rearing period ($\chi^2=2.7$; $P=0.09$).

Only two specimens that could have originated as offal from toothfish longline vessels were found in a single sample. These were two specimens of the family

Macrouridae, which are a major bycatch species in the toothfish industry. No known longline bait species were found. Man-made litter, which included a squid jig and two hard pieces of plastic, were found in 10% of the samples.

3.3. Spatial overlap with known longline fishing grounds

3.3.1. Incubation phase

The extensive use of the STCZ and SAZ during this phase brought these birds into areas of intensive SBT longline fishing (Fig. 3). Both females moved north westwards to forage in the grid square 40–45°S and 25–30°E. This area supported the highest intensity of SBT fishing in the South Indian Ocean during 1991, with > 6 million hooks set in this 5° grid square (Polacheck and Tuck, 1995). One of the tracked males utilised the STCZ further to the east, encountering areas of low to moderate SBT fishing effort (< 1 million hooks annually) between 40°E and 85°E. The second male remained south of the main SBT fishing grounds. On average the four birds spent 36% of their total time at sea within the 5° grid squares which supported > 1 million SBT hooks (Table 3), and 66% of their time within areas which supported any level of SBT fishing activity. During this stage, tracked birds moved rapidly in the close vicinity of the island, spending only 0.7% of their time within the boundary of known Patagonian toothfish longline sets (Table 3).

3.3.2. Early chick-rearing stage

During this stage, all tracked birds ($n=6$) foraged to the southwest of Marion Island, thus avoiding SBT

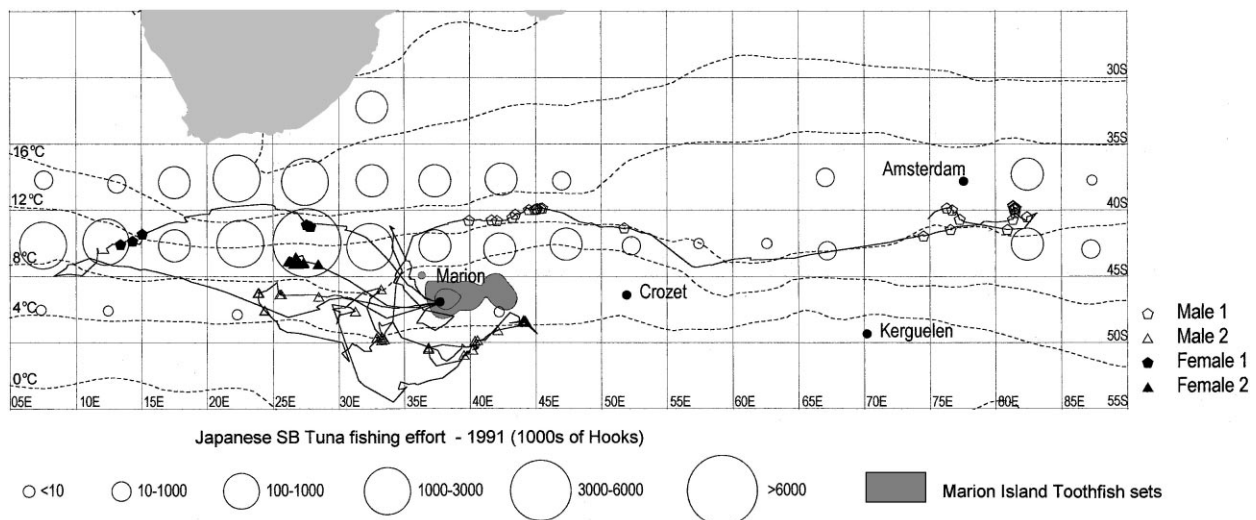


Fig. 3. The foraging tracks of four breeding grey-headed mollymawks (two males and two females) tracked by means of PTTs from Marion Island during the incubation phase. The symbols indicate positions at which the birds were moving at < 10 km h⁻¹ during daylight hours, indicating probable foraging areas. The sea surface isotherms (from average monthly remote-sensed IGOSS images) for the period of the deployment are also shown.

longline fishing areas totally. However, the satellite-tracked birds spent 11% of their total time at sea within the boundary of known Patagonian toothfish longline sets (Table 3). This was significantly higher than during the incubation stage ($t=3.3$; $P=0.03$). Although most toothfish sets were to the north east of the island, some fishing took place to the south, within 200 km of the island. It is in this area that the PTT-tracked male foraged during three of its four foraging trips (Fig. 4a). On two of these occasions the bird was engaged in a short foraging trip (<24 h) while on the

third, the bird foraged here briefly on the outward leg of a longer foraging trip (6 days). No licensed Patagonian toothfish longline vessels were in this area at the time of deployment.

3.3.3. Differences between males and females

During incubation the two tracked females spent 69% of their time at sea within 5° grid squares supporting > 1 million SBT hooks. This was significantly more than the two males, which only spent 2% of their time in these areas ($t=4.8$; $P=0.04$) (Table 3). During

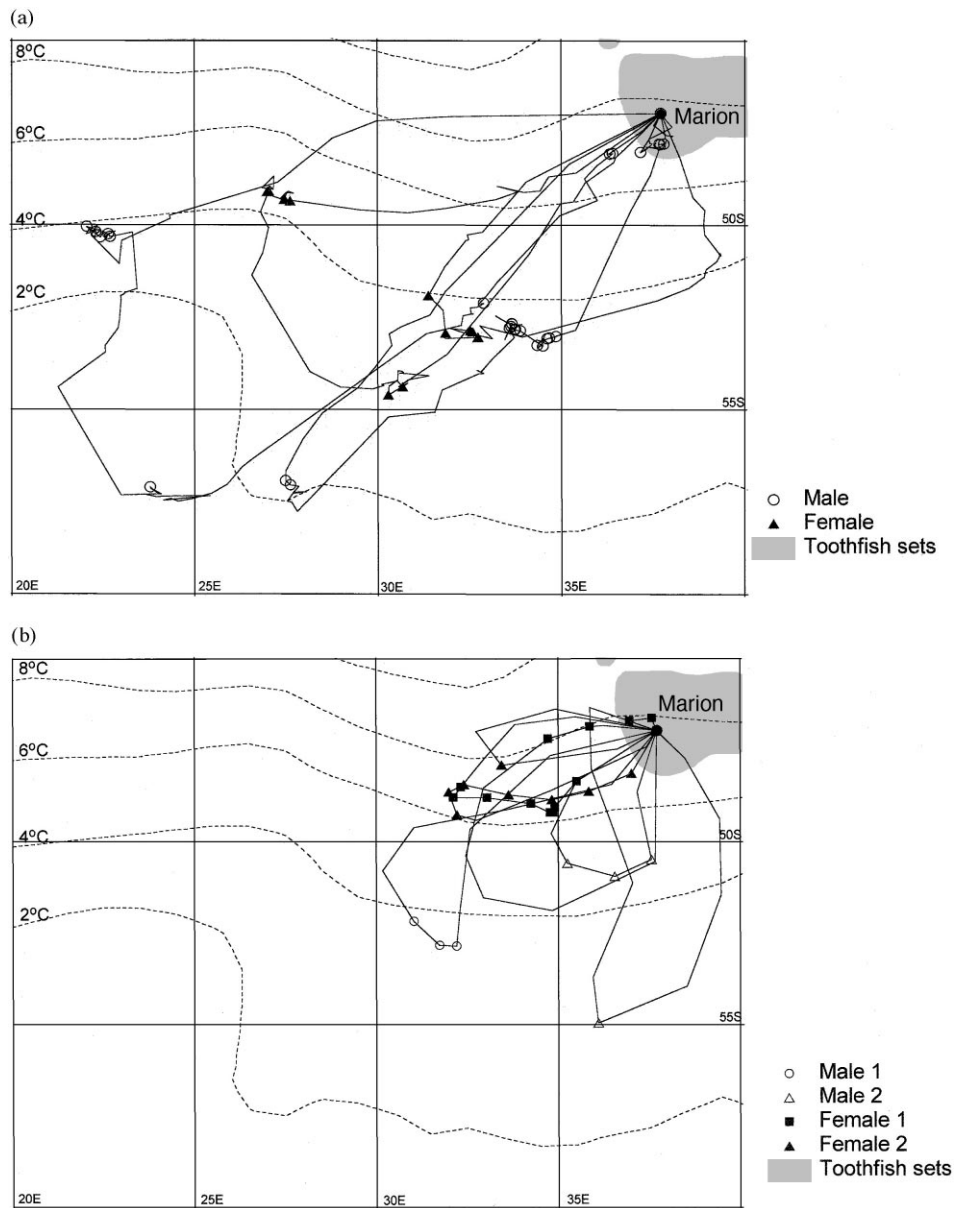


Fig. 4. Foraging tracks of grey-headed mollymawks breeding at Marion Island, during the early post guard phase: (a) six tracks obtained from two individuals (one male and one female) carrying PTTs and (b) nine tracks from four individuals (two males and females) carrying GLSs. The position of the symbols indicate probable foraging areas and were taken for (a) as being positions at which birds moved at speeds of 10 km h^{-1} during daylight hours and for (b) as being positions at which birds moved 120 km h^{-1} during a 12 h daylight period. The sea surface isotherms (from average monthly remote-sensed IGOSS images) for the period of the deployment are also shown.

the early chick-rearing stage the PTT-tracked male spent 17% of its total time at sea within the boundary of toothfish longline sets, while the female only spent 6% of its time in this area (Table 3). This was due to the male foraging within the toothfish fishing zone during its two short foraging trips and on the outward leg of one of its long foraging trips (Fig. 4a).

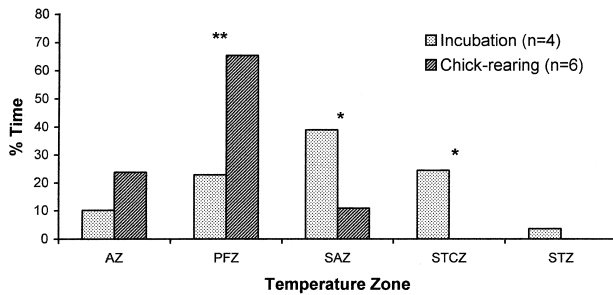


Fig. 5. The average % time spent in various sea surface temperature zones by grey-headed mollymawks tracked from Marion Island. AZ = Antarctic zone, PFZ = polar frontal zone, SAZ = sub-antarctic zone, STCZ = sub-tropical convergence zone, STZ = sub-tropical zone. * = $P(t \text{ test}) \leq 0.1$ and ** = $P(t \text{ test}) \leq 0.05$.

Table 2
Composition of grey-headed mollymawk diet samples collected at Marion Island, January–March 1998

Parameter	Mean±S.D. (g)	Range (g)	% of Total mass
<i>Summary data</i>			
Total mass	722±294	302–1432	
Liquids	353±244	0–934	49
Solids	368±155	123–692	51
% of Solid fraction			
<i>Prey categories</i>			
Fish	220.1±210.2	0–680	59
Squid	114±109.5	0–409	32
Crustacean	6.3±11.6	0–59	2
Other	25.1±74.2	0–328	7

Table 3
The % time spent within known SB tuna and toothfish longline fishing grounds by grey-headed mollymawks tracked from Marion Island^a

	Incubation				Early chick-rearing			
	Males (2 PTTs)	Females (2 PTTs)	All (4 PTTs)	M vs F (<i>t</i> test)	Males (1 PTT, 2 GLSs)	Females (1 PTT, 2 GLSs)	All (2 PTTs, 4 GLSs)	Incubation vs chick-rearing (<i>t</i> test)
SB Tuna ^a (PTT's and GLSs)	1.86	69.4	35.7	$P=0.04$	0	0	0	$P=0.06$
Toothfish (PTTs only)	0.61	0.87	0.74	$P=0.8$	16.7	6.2	11.4	$P=0.03$

^a SB tuna grounds are represented by 5° grid squares in which more than 1 million hooks in 1991 (Polacheck and Tuck, 1995), while toothfish fishing grounds are represented by the 95% probability boundary of a Kemal Home Range analysis of all lines set during 1996–1998.

4. Discussion

The results of this study have added greatly to our understanding of the foraging ecology of grey-headed mollymawks breeding at Marion Island. This in turn has allowed us to gain an understanding of both the nature and scale of interactions with longline fishing operations within their potential foraging range. Furthermore, a preliminary understanding of gender differences in the foraging strategy that could contribute towards sex-biased mortality in longline fishing operations was also developed.

4.1. Foraging movements and ecology

The foraging movements of grey-headed mollymawks during the incubation and early chick-rearing stage showed substantial differences. Trips made during the early chick-rearing stage were shorter (in duration, range, and total distance), and more directed (lower ratio of total distance:maximum range) than during incubation. These differences are expected as foraging behaviour during the incubation phase is primarily aimed at the adult regaining its body condition for the next incubation (and thus starvation) period, whereas foraging behaviour during chick rearing is a constant compromise between provisioning the chick and maintaining the body condition of the parent (Weimerskirch et al., 1994). Time constraints imposed by the need to feed the chick at regular intervals, also preclude parents from being more selective of foraging sites during early chick rearing. The mean foraging range during incubation (2182 km) recorded in this study (although from only three complete tracks) is only slightly shorter than among incubating white-chinned petrels, which have the longest mean foraging range reported for any seabird (2390 km; Weimerskirch et al., 1999). The bimodal distribution of foraging trip duration recorded during early chick-rearing, has also been noted for grey-headed mollymawks at Campbell Island (Waugh et al., 1999), as well as several other procellariiforms (e.g. Weimerskirch et al., 1994, 1997).

These differences in foraging ranges between incubation and early chick-rearing led to substantial differences in the utilization of the various oceanographic thermal zones. During incubation the STCZ and SAZ was preferred, while during the early chick-rearing period the PFZ and AZ were utilized exclusively. The use of the PFZ by grey-headed mollymawks during the chick-rearing period is consistent with other studies on grey-headed mollymawks, conducted at South Georgia (Prince et al., 1997) and Campbell Island (Waugh et al., 1999). However, our results present the first foraging tracks of incubating birds, and show a markedly different foraging strategy during this stage. This preference for warmer subtropical waters during incubation, and colder Antarctic waters to the south during chick-rearing, is similar to that recorded for white-chinned petrels (*Procellaria aequinoctialis*) at the nearby Crozet islands (Weimerskirch et al., 1999), which have a similar breeding season and are also killed in large numbers by longline fishing operations.

Although our tracking during chick rearing was restricted to the early part, diet samples taken during the early and late-chick-rearing stages confirmed that the SAZ and PFZ were the predominant foraging zones throughout this period. The most frequently recorded fresh prey species during the late chick-rearing stage, the ommastrephid squid (*Martialia hyadesi*), is strongly associated with the Antarctic polar front (Rodhouse et al., 1992). Although little is known about the biology and distribution of the most abundant and frequently occurring fish species, *Magnisudis prionosa* (Gon and Heemstra, 1990), it is commonly found in the diets of other sub-Antarctic seabirds and seals, which are known to make extensive use of the PFZ (e.g. Hindell, 1988; Cherel et al., 1996; Reid et al., 1996; Klages and Bester, 1998). The importance of *M. hyadesi* in grey-headed mollymawks breeding at Marion Island is of conservation significance, as this species has major potential for commercial exploitation (Rodhouse, 1997). *M. hyadesi* is the dominant squid prey (85% by mass) of grey-headed mollymawk populations breeding at South Georgia (Rodhouse et al., 1990) and Campbell Island (Waugh et al., 1999), which also make extensive use of the PFZ during chick-rearing.

An increase in man-made litter during the past decade was also detected in the diet our samples. Litter items were found in 10% of our samples, compared to Hunter and Klages (1989) who found no litter items in 88 samples taken in 1985 and 1987. This trend is consistent with global increases in man-made marine litter (e.g. Ryan and Moloney, 1993). Albatross chicks are prone to the accumulation of large amounts of man-made litter within the proventriculus when litter items are repeatedly fed to them by their parents (Nel and Nel, 1999). This can lead to a decrease in body condition (Ryan, 1987) and possibly even starvation (Nel and Nel, 1999).

4.2. Exposure to the risk of incidental mortality by longline fishing industries

The extensive use of the STCZ and SAZ during incubation (November/December) recorded in this study, brings these birds into close contact with the band of intense SBT longline fishing activity situated between 40 and 45°S (Fig. 3). This interaction was especially intense in the grid square 40–45°S and 25–30°E, where the Agulhas retroflection current regularly joins the STC and increases its intensity and productivity (Lutjeharms and Emery, 1983). Data on the seasonal variation in SBT longline effort is only available for the Japanese fleet (Polacheck and Tuck, 1995). During 1996, 21.5% of the effort took place during the first and fourth quarters of the year (i.e. October–March), which coincides with the main part of the grey-headed mollymawk breeding season. However, prior to 1976, ca. 50% of effort took place during these months. This decrease in effort during the austral summer months is largely due to the imposition of catch quotas. The Japanese quota year begins in April (Tuck and Polacheck, 1997) and many vessels will thus have filled their quotas by the time summer arrives. However, the decrease in Japanese SBT fishing effort in the summer months, results largely in a spatial contraction, with the most intensely fished areas (i.e. > 1 million hooks per annum; as used for analyses in this study), still being fished during the austral summer months. These seasonal trends also do not apply to the growing Korean and Taiwanese longline fleets, which during 1996 landed 48% of the catches of SBT in the Western Indian Ocean (FAO database-<http://apps.fao.org>).

Due to a limited observer program on SBT vessels in international waters, little is known about rates of seabird bycatch in this area. However, Japanese observers reported 84 grey-headed mollymawks killed during fishing operations south of Africa between 1992–1996 (at a rate of 0.045 birds per 1000 hooks) (Ryan and Boix-Hinzen, 1998). Our data indicate that grey-headed mollymawks breeding at Marion Island show a high degree of spatial overlap with this fishery during the incubation stage and are thus at high risk of incidental mortality during this stage. Recent dramatic increases in Korean longline fishing effort in the Southern Indian Ocean could thus have a severe impact on the Marion Island population.

During the early chick-rearing stage, our tracked birds moved south of the island, thus avoiding SBT longline fishing grounds. However, PTT-tracked birds spent significantly more time within the boundaries of the local Patagonian toothfish longline sets during this stage, thus placing themselves at higher risk of incidental mortality by this fishery. The potential for interaction with this fishery was clearly demonstrated with foraging activity recorded within the boundaries of

this fishery during two short foraging trips (<2 days) and on the outward leg of a long foraging trip (Fig. 4a). Individually timed foraging trips also showed that these short trips (<2 days) were a common feature (30% of all trips) of the foraging strategy during the early chick-rearing stage.

These data are consistent with the actual mortality rates of grey-headed mollymawks recorded by licensed vessels during 1996/1997. Lowest catch rates were recorded during the incubation period (0.041 birds/1000 hooks), while the catch rate during chick-rearing period was more than double this (0.109 birds/1000 hooks) (PGR unpublished data). No seasonal variation in fishing effort exists in the Marion Island toothfish industry (Ryan and Watkins, 1999). Although Ashford et al. (1995) and Prince et al. (1997) both report grey-headed mollymawks at South Georgia as being shy of toothfish vessels, and therefore, at low risk from this fishery, Boix-Hinzen (personal communication) reports grey-headed mollymawks as being present at all daylight sets around Marion Island during May 1997, and as being the most active scavenging species. Cherel et al., (1996) also reports grey-headed mollymawks successfully competing for toothfish longline baits in Kerguelen waters.

The absence of toothfish bait species in our diet samples was initially surprising, given the high level of mortality of grey-headed mollymawks recorded on licensed toothfish vessels during their first season. However, the reasons for this are twofold. First, after initially setting lines both at day and at night during the first season, licensed vessels have been restricted to setting lines exclusively during the hours of darkness since the second season (the time of this study). This mitigation measure has reduced the bycatch of albatrosses and mollymawks drastically (Ryan and Watkins, 1999). Our results also indicate that grey-headed mollymawks are far less active during the night (spending ca 75% of the night virtually stationary) and thus support this mitigation measure. Secondly, far fewer unsanctioned fishing vessels (which set lines by day or night) were sighted within the South African EEZ during the year of this study (personal observation and Purves, 1997). This was presumably due to the declining resource becoming economically less lucrative rather than any disincentive by South African authorities. Due to logistical constraints, no real attempt was made to patrol these waters (personal observation).

Grey-headed mollymawks breeding on Marion Island are thus at higher risk of incidental mortality in the local toothfish industry during the early chick-rearing stage than during incubation. This risk is mainly during short foraging trips (<2 days) and can be virtually eliminated if lines are set exclusively during the hours of darkness. However, illegal longline fishing operators show scant regard for these regulations and could, therefore, have a severe impact on the Marion Island

grey-headed mollymawk population, should it become economically viable for these operations to resume.

Decreased adult survival due to incidental mortality by longline fishing leads to complex effects on the demographics and productivity of albatross populations (e.g. Croxall et al., 1990; Weimerskirch et al., 1997), and may not be immediately noticeable as a change in the number of breeding birds. This study has demonstrated the vulnerability of the breeding population of grey-headed mollymawks on Marion Island to incidental mortality by two different and spatially disjunct longline fisheries, during incubation and chick-rearing. Although the effect of this has not yet been detected in annual counts of the breeding population, we caution that these methods are inadequate for assessing short term changes (<10 years) in biennial breeding albatross populations. Increased adult mortality due to a recent increase the SBT longline effort in the Southern Indian Ocean and the development of a Patagonian toothfish longline industry in the close vicinity of the island, may have already led to complex effects on the demography of this population. This in turn may lead to a decline in the annual breeding population in the future, which once detected, could take a long time to stabilise (>30 years).

4.3. Differences between males and females

Although our limited data should be treated with caution, the differences in the foraging behaviour of males and females that we recorded could contribute towards sex-biased mortality of grey-headed mollymawks in longline fisheries. During the incubation phase satellite-tracked females spent significantly more time in the intense SBT longline fishing areas south of Africa, than males. This will result in a higher level of exposure to the risk of incidental mortality for females. No data on the gender composition of grey-headed mollymawks killed by the SBT longline fishery in pelagic waters south of Africa are available. However, female adult wandering albatrosses from the Crozet Islands have a lower survival rate than their male counterparts. A higher degree of exposure to the risk of incidental mortality by SBT longline fisheries has been implicated as the main reason for this (Weimerskirch and Jouventin, 1987).

During the chick-rearing stage the PTT-tracked male spent more time foraging within the boundaries of the local toothfish longline sets than the female. This was largely due to the male making two short foraging trips (<2 days), within these boundaries. Individually timed foraging trips of a larger sample of birds, showed that males made a higher proportion of these short foraging trips (<2 days). The frequency distribution of maximum ranges of all tracked birds also showed that females made a higher proportion of medium distance foraging trips (400–800 km range), while male foraging

range was more variable (i.e. males made more very short or very long foraging trips). This is consistent with studies on wandering albatrosses on Marion Island (DCN, unpublished data) and on the nearby Crozet Islands (Weimerskirch et al., 1997), which showed that males spent a higher proportion of their time on short foraging trips than females. It is thus possible that these subtle differences in foraging strategy in combination with physical attributes such as aggression when competing for baits, can account for the male biased mortality observed in the Prince Edward Island Patagonian toothfish industry during the first season.

As grey-headed mollymawks are largely monogamous (96% breed with the same mate in successive attempts; Prince et al., 1994), sex-biased mortality of breeding adults will obviously have added costs to the population, other than the direct cost of decreasing the number of breeding birds. Jouventin et al. (1999) showed that remating for the monogamous wandering albatross exerts an average reproductive cost of 15% of the lifetime reproductive success. Sex-biased mortality will thus also decrease the fecundity of the population, and may not be detected as an immediate decline in the annual breeding population.

Gender differences in foraging strategy and incidental mortality by longline fishing vessels should thus be closely monitored and researched, and the added cost of sex-biased incidental mortality should be taken into account when assessing the detrimental effects on these populations.

Acknowledgements

Financial and logistical support was received from the Department of Environmental Affairs and Tourism through the South African National Antarctic Programme, the Foundation for Research Development, the World Wide Fund for Nature- South Africa, the Charl van der Merwe Foundation, and the University of Cape Town. Thanks also to Michelle Greyling for helping with deployments and John McLinden for downloading and relaying positions of birds to us, while we were in the field. Martin Purves (Department of Marine and Coastal Management, South Africa), kindly supplied valuable information and insight into the South African Patagonian toothfish industry. Thanks also to Dr. Brian Davis and two anonymous referees for their valuable comments on earlier drafts of this paper.

Appendix A

The frequency of occurrence of fresh prey items identified in grey-headed mollymawk diet samples taken

during early (January 1998) and late (March and April 1998) chick-rearing, from Marion Island

Taxa	Early chick-rearing	Late chick-rearing	Total	Early vs late	
	(N=11) % (n)	(N=19) % (n)	(N=30) % (n)	χ^2	P
Fish	63.6 (7)	63.2 (12)	63.3 (19)		
Family Macrouridae					
<i>Cynomacurus piriei</i>	9.1 (1)		3.3 (1)		
Family Myctopidae	18.2 (2)	5.3 (1)	10.0 (3)		
<i>Electrona subaspera</i>	9.1 (1)		3.3 (1)		
<i>Gymnoscopelus piabilis</i>	9.1 (1)		3.3 (1)		
Unid. <i>Myctophidae</i>		5.3 (1)	3.3 (1)		
Family Paralepididae					
<i>Magnisudis prionosa</i>	18.2 (2)	21.1 (4)	20.0 (6)		
Family Photichthyidae					
<i>Photichthys argenteus</i>		10.5 (2)	6.7 (2)		
Unidentified fish	27.3 (3)	36.8 (7)	33.3 (10)		
Squid	27.3 (3)	68.4 (13)	53.3 (16)	4.7	0.03
Family Chiroteuthidae					
<i>Chiroteuthis</i> sp.	18.2 (2)		6.7 (2)	3.7	0.05
Family Histioteuthidae					
<i>Histioteuthis eltaninae</i>		5.3 (1)	3.3 (1)		
Family Neoteuthidae					
<i>Alluroteuthis antarctica</i>		5.3 (1)	3.3 (1)		
Family Ommastrephidae					
<i>Martialia hyadesi</i>		42.1 (8)	26.7 (8)	6.3	0.01
Family Onychoteuthidae					
<i>Kondakovia longimana</i>		15.8 (3)	10.0 (3)		
Unidentified squid	9.1 (1)	10.5 (2)	10.0 (3)		
Crustaceans	72.7 (8)	68.4 (13)	70.0 (21)		
Amphipoda	9.1 (1)	36.8 (7)	26.7 (8)	2.7	0.09
<i>Themisto gaudichaudii</i>	9.1 (1)	26.3 (5)	20.0 (6)		
Unidentified amphipods		10.5 (2)	6.7 (2)		
Decapoda	54.6 (6)	31.6 (6)			
<i>Austropandalus grayi</i>	9.1 (1)	5.3 (1)	6.7 (2)		
<i>Pasiphaea scotiae</i>	36.4 (4)	15.8 (3)	23.3 (7)		
Unidentified decapods	9.1 (1)	10.5 (2)	10.0 (3)		
Euphausiacea	9.1 (1)	21.1 (4)	16.7 (5)		
<i>Euphausia superba</i>	9.1 (1)		3.3 (1)		
Unidentified Euphausiid		21.1 (4)	13.3 (4)		
Other		10.5 (2)	6.7 (2)		
Goosebarnacles		5.3 (1)	3.3 (1)		
Jelly fish		10.1 (2)	6.7 (2)		
Mammal lung		5.3 (1)	3.3 (1)		

References

- Abrams, R.W., 1985. Energy and food requirements of pelagic aerial seabirds in the different regions of the African sector of the Southern Ocean. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin, pp. 466–472.

- Alexander, K., Robertson, G., Gales, R., 1997. The Incidental Mortality of Albatrosses in Longline Fisheries. Australian Antarctic Division, Tasmania.
- Ashford, J.R., Croxall, J.P., Rubilar, P.S., Moreno, C.A., 1995. Seabird interactions with longlining operations for *Dissostichus eleginoides* around South Georgia, April–May 1994. CCAMLR Science 2, 111–121.
- Belkin, I.M., Gordon, A.L., 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. Journal of Geophysical Research 101, 3675–3696.
- Brothers, N., 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. Biological Conservation 55, 255–268.
- Benhamou, S., Bovet, P., 1989. How animals use their environment: a new look at kinesis. Animal Behaviour 38, 375–383.
- Cherel, Y., Weimerskirch, H., Duhamel, G., 1996. Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. Biological Conservation 75, 63–70.
- Cherel, Y., Ridoux, V., Rodhouse, P.G., 1996. Fish and squid in the diet of king penguins *Aptenodytes patagonicus*, during the winter at sub-Antarctic Crozet Islands. Marine Biology 126, 556–570.
- Croxall, J.P., Rothery, P., Pickering, S.P.C., Prince, P.A., 1990. Reproductive performance, recruitment and survival of wandering albatrosses *Diomedea exulans* at Bird Island, South Georgia. Journal of Animal Ecology 59, 775–796.
- Croxall, J.P., Prince, P.A., 1996. Potential interaction between wandering albatrosses and longline fisheries for patagonian toothfish at South Georgia. CCAMLR Science 3, 101–110.
- Croxall, J.P., Gales, R., 1997. An assessment of the conservation status of albatrosses. In: Robertson, G., Gales, R. (Eds.), Albatross Biology and Conservation. Surrey Beatty and Sons, Chipping Norton, pp. 46–65.
- Gales, R., 1993. Co-operative Mechanisms for the Conservation of Albatrosses. Australian Nature Conservation, Hobart.
- Gales, R., 1997. Albatross populations: status and threats. In: Robertson, G., Gales, R. (Eds.), Albatross Biology and Conservation. Surrey Beatty and Sons, Chipping Norton, pp. 20–45.
- Gales, R., Brothers, N., Reid, T., 1998. Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. Biological Conservation 86, 37–56.
- Gon, O., Heemstra, P.C., 1990. Fishes of the Southern Ocean. JLB Institute, Grahamstown.
- Hindell, M.A., 1988. The diet of king penguins *Aptenodytes patagonicus* at Macquarie Island. Ibis 130, 193–203.
- Hunter, S., Klages, N.T.W., 1989. The diet of the grey-headed albatross *Diomedea chrysostoma* at the Prince Edward Islands. South African Journal of Antarctic Research 19, 31–33.
- Huin, N., Prince, P.A., 1997. Diving behaviour of the grey-headed albatross. Antarctic Science 9, 243–249.
- Jouventin, P., Lequette, B., Dobson, F.S., 1999. Age related mate choice in the wandering albatross. Animal Behaviour 57, 1099–1106.
- Klages, N.T.W., Bester, M.N., 1998. Fish prey of fur seals *Arctocephalus* spp. at Sub-Antarctic Marion Island. Marine Biology 131, 559–566.
- Knoppin, P., Reddingius, J., 1985. Predators with two modes of searching: a mathematical model. Journal of Theoretical Biology 114, 273–301.
- Lutjeharms, J.R.E., Emery, E.J., 1983. The detailed thermal structure of the upper ocean layers between Cape Town and Antarctica during the period January–February 1978. South African Journal of Antarctic Research 13, 3–14.
- Lutjeharms, J.R.E., Walters, N.M., Allanson, B.R., 1985. Oceanic frontal systems and biological enhancement. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.) Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.
- Marchant, S., Higgins, P.J., 1990. Handbook of Australian, New Zealand and Antarctic Birds. Royal Australasian Ornithologists Union, Melbourne.
- Moloney, C.L., Cooper, J., Ryan, P.G., Siegfried, W.R., 1994. Use of a population model to assess the impact of longline fishing on wandering albatross *Diomedea exulans* populations. Biological Conservation 70, 195–204.
- Murray, T.E., Bartle, J.A., Kalish, S.R., Taylor, P.R., 1993. Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988–1992. Bird Conservation International 3, 181–210.
- Nel, D.C., Nel, J.L., 1999. Marine debris and fishing gear associated with seabirds at sub-Antarctic Marion Island, 1996/97 and 1997/98: in relation to longline fishing activity. CCAMLR Science 6, 85–96.
- Pennycook, C.J., 1982. The flight of petrels and albatrosses (Procellariiformes) observed on South Georgia and its vicinity. Philosophical Transactions of the Royal Society London 300, 75–106.
- Polacheck, T., Tuck, G., 1995. Trends in tuna longline fisheries in the Southern Ocean and implications for seabird by-catch. Document CCSBT-ERS/95. Division of Fisheries, CSIRO, Hobart, Australia.
- Prince, P.A., Rothery, P., Croxall, J.P., Wood, A.G., 1994. Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 136, 50–71.
- Purves, M.G., 1997. Catch rates and length composition data of the longline fishery for *Dissostichus eleginoides* at the Prince Edward Islands: 1996–1997. Document SC-CAMLR-XVI/BG/28. CCAMLR, Hobart, Australia.
- Prince, P.A., Croxall, J.P., Trathan, P.N., Wood, A.G., 1997. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In: Robertson, G., Gales, R. (Eds.), Albatross Biology and Conservation. Surrey Beatty and Sons, Chipping Norton, pp. 137–167.
- Reid, K., Croxall, J.P., Prince, P.A., 1996. The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at South Georgia. Polar Biology 16, 469–477.
- Rodhouse, P.G., 1997. Precautionary measures for a new fishery on *Martialia hyadesi* (Cephalopoda, Ommastrephidae) in the Scotia Sea: An ecological approach. CCAMLR Science 4, 125–139.
- Rodhouse, P.G., Prince, P.A., Clarke, M.R., Murray, A.W.A., 1990. Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. Marine Biology 104, 353–362.
- Rodhouse, P.G., White, M.G., Jones, M.R.R., 1992. Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. Marine Biology 114, 415–421.
- Ryan, P.G., 1987. The effects of ingested plastic on seabirds: correlations between plastic load and body condition. Environmental Pollution 46, 119–125.
- Ryan, P.G., Moloney, C.L., 1993. Marine litter keeps increasing. Nature 361, 23.
- Ryan, P.G., Boix-Hinzen, C., Enticott, J.W., Nel, D.C., Wanless, R., Purves, M., 1997. Seabird mortality in the longline fishery for patagonian toothfish at the Prince Edward Islands: 1996–97. Document CCAMLR-WG-FSA 97/51. CCAMLR, Hobart, Australia.
- Ryan, P.G., Boix-Hinzen, C., 1998. Tuna longline fisheries off southern Africa: the need to limit seabird bycatch. South African Journal of Science 94, 179–182.
- Ryan, P.G., Boix-Hinzen, C., 1999. Consistent male-biased seabird mortality in the Patagonian Toothfish long-line fishery. Auk 116, 851–854.
- Ryan, P.G., Watkins, B.P., 1999. Seabird bycatch in the Patagonian toothfish longline fishery at the Prince Edward Islands: 1998–1999. Document CCAMLR-WG-FSA 99/22. CCAMLR, Hobart, Australia.
- Tuck, G., Polacheck, T., 1997. Trends in tuna longline fisheries in the Southern Oceans and implications for seabird by-catch: 1997 update. Document CCSBT-ERS/95. Division of Fisheries, CSIRO, Hobart, Australia.

- Warham, J., 1996. *The Behaviour, population Biology and Physiology of the Petrels*. Academic Press Limited, London.
- Waugh, S., Weimerskirch, H., Cherel, Y., Shankar, U., Prince, P.A., Sagar, P., 1999. The exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Marine Ecological Progress Series* 177, 243–254.
- Weimerskirch, H., Jouventin, P., Stahl, J.C., 1985. Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128, 195–213.
- Weimerskirch, H., Jouventin, P., 1987. Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Island: causes and consequences of the population decline. *Oikos* 49, 315–322.
- Weimerskirch, H., Chatsel, O., Chaurand, T., Ackerman, L., Hindermeyer, X., Judas, J., 1994. Alternative long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47, 472–476.
- Weimerskirch, H., Brothers, N., Jouventin, P., 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: Conservation Implications. *Conservation Biology* 79, 257–270.
- Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F., Ridoux, V., 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78, 2051–2063.
- Weimerskirch, H., Catrard, A., Prince, P.A., Cherel, Y., Croxall, J.P., 1999. Foraging white-chinned petrels *Procellaria aequinoctialis* at risk: from the tropics to Antarctica. *Biological Conservation* 87, 273–275.
- Wilson, R.P., Rees, G., Lage, J., Putz, K., Kierspel, M.A.M., Cooper, J. et al., 1998. Determination of animal position at sea using changes in diel light intensity. *Proceedings of the Fifth European Conference on Wildlife Telemetry*.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice Hall, New Jersey.