

Seasonal changes in the diet and feeding behaviour of a top predator indicate a flexible response to deteriorating oceanographic conditions

J. C. Xavier · M. Louzao · S. E. Thorpe ·
P. Ward · C. Hill · D. Roberts · J. P. Croxall ·
R. A. Phillips

Received: 17 August 2012 / Accepted: 7 March 2013 / Published online: 26 March 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Shifts in the diet of top predators can be linked to changes in environmental conditions. In this study, we tested relationships between environmental variation and seasonal changes in diet of a top predator, the grey-headed albatross *Thalassarche chrysostoma*, breeding at Bird Island, South Georgia in an austral summer of 1999/2000. Oceanographic conditions in that year around South Georgia were abnormal (i.e. anomalously high sea surface temperature to a relative 19-year long-term mean). The diet of grey-headed albatrosses showed high seasonal variation, shifting from cephalopods (42.9 % by mass) in late February to Antarctic krill *Euphausia superba* (58.3 %) in late April, and grey-headed albatrosses breeding performance was low (16.8 %). This study shows these albatrosses did not manage to find sufficient alternative prey and highlight the risk to top predators if there is an increase in the frequency or severity of food shortages in Antarctic waters.

Communicated by S. Garthe.

J. C. Xavier (✉)
Institute of Marine Research, Department of Life Sciences,
University of Coimbra, 3001-401 Coimbra, Portugal
e-mail: JCCX@cantab.net

J. C. Xavier · S. E. Thorpe · P. Ward · C. Hill · D. Roberts ·
J. P. Croxall · R. A. Phillips
British Antarctic Survey, Natural Environment Research
Council, High Cross, Madingley Road,
Cambridge CB3 0ET, UK

M. Louzao
Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934,
79369 Villiers en Bois, France

M. Louzao
Helmholtz Centre for Environmental Research-UFZ,
Permoserstraße 15, 04318 Leipzig, Germany

Introduction

Climate processes have a major impact on the structure and function of ecological systems (Stenseth et al. 2002). A wide range of studies has shown links between fluctuations in climate, and changes in terrestrial, freshwater and marine ecosystems worldwide (Wuethrich 2000; Attrill and Power 2002; Stenseth et al. 2002; Quetin and Ross 2003). In the marine environment, top predators, such as seabirds, have to cope with resources that are patchily distributed and seasonally variable (Brooke 2004; Weimerskirch 2007; Fauchald 2009). For this reason, their ability to adapt to changing environmental constraints has an important influence on their breeding performance and population dynamics (Phillips et al. 1996; Lewis et al. 2006).

Adaptation of seabirds and other marine organisms to environmental conditions may be immediate or show a temporal lag of weeks, seasons, decades or even generations (Reid and Croxall 2001a; Walther et al. 2002; Atkinson et al. 2004). For example, rhinoceros auklets *Cerorhinca monocerata* breeding in Japan responds within days to changes in the food web caused by fluctuations in ocean currents, resulting in a switch in diets from euphausiids to fish (Ito et al. 2009). Other studies have recorded major annual changes in the diets of seabirds in relation to environmental perturbation (Xavier et al. 2003a, b; Ito et al. 2009; Wang et al. 2009). Indeed, growth rates and survival of offspring of many seabirds and other marine predators are frequently related to the quantity or quality of prey consumed (Croxall et al. 1988; Phillips et al. 1996; Boyd et al. 2006).

The Southern Ocean is a highly dynamic marine ecosystem, currently showing signs of unusually rapid environmental change (King 1994; Reid and Croxall 2001a; Atkinson et al. 2004; Meredith and King 2005). Seabirds

are amongst the major consumers in the region (Croxall and Prince 1980). Many species are also threatened by conflict with fisheries (competition for the same stocks of prey or incidental mortality) or predation by introduced mammals (Croxall et al. 1998, 2012; Wood et al. 2000; Xavier et al. 2003b; Phillips et al. 2004b). They are known to feed on a range of prey, including fish, crustaceans and cephalopods in particular (Xavier et al. 2003a, b; Xavier and Croxall 2007). However, no detailed study has ever assessed seasonal variation in their diet.

In 2000, oceanographic conditions were unusually warm close to South Georgia in March and April, with sea surface temperature higher by up to 1 °C compared with the average of the last 19 years in the region (for example, at 40.5°W 54.5°S, the sea surface temperature was 3.92 °C compared with 2.99 °C for the average) (Xavier et al. 2003b). In April 2000, which is the late chick-rearing period for grey-headed albatrosses, 89 % of grey-headed albatrosses fitted with satellite transmitters ($n = 9$) foraged far from the colony in Antarctic waters than recorded in chick rearing in other years (Wood et al. 2000; Xavier et al. 2003b; Catry et al. 2004; Phillips et al. 2004a); grey-headed albatrosses usually forage north of South Georgia, in Antarctic Polar Frontal Zone/sub-Antarctic waters during their chick-rearing period, feeding mostly on the omastrephid squid *Martialia hyadesi*, and on fish, with the consumption of *M. hyadesi* being positively correlated with high breeding success (Rodhouse et al. 1996; Prince et al. 1999; Xavier et al. 2003a, b) and also south-west to the Scotia Sea, South Shetlands and Antarctic peninsula regions but the proportion using each area shows strong annual variation (Wood et al. 2000; Xavier et al. 2003b; Phillips et al. 2004a). In 2000, trip duration was unusually long, averaging 13.3 days (range 5–26 days), compared with a mean of 2–3 days typical of the chick-rearing period in other years (Huin et al. 2000; Phillips and Croxall 2003), which was reflected in a low breeding success (16.8 %; Xavier et al. 2003a), the sixth worst of the 24 years between 1989 and 2012 for which data are available (British Antarctic Survey, unpublished data) for grey-headed albatrosses breeding at Bird Island. In this study, using a unique dataset for the year 2000, we investigate how a top predator, the grey-headed albatross, copes with seasonal changes in oceanographic conditions by analysing changes in diet composition and the implications for breeding performance. Therefore, aims of the study were to (1) describe seasonal changes in the diet of grey-headed albatrosses at fine temporal scale (samples collected every 2 weeks) between February and April 2000 and (2) relate changes in diet to sea surface temperature anomalies in alternative foraging areas to examine relationships with putative changes in distribution.

Materials and methods

Diet sampling

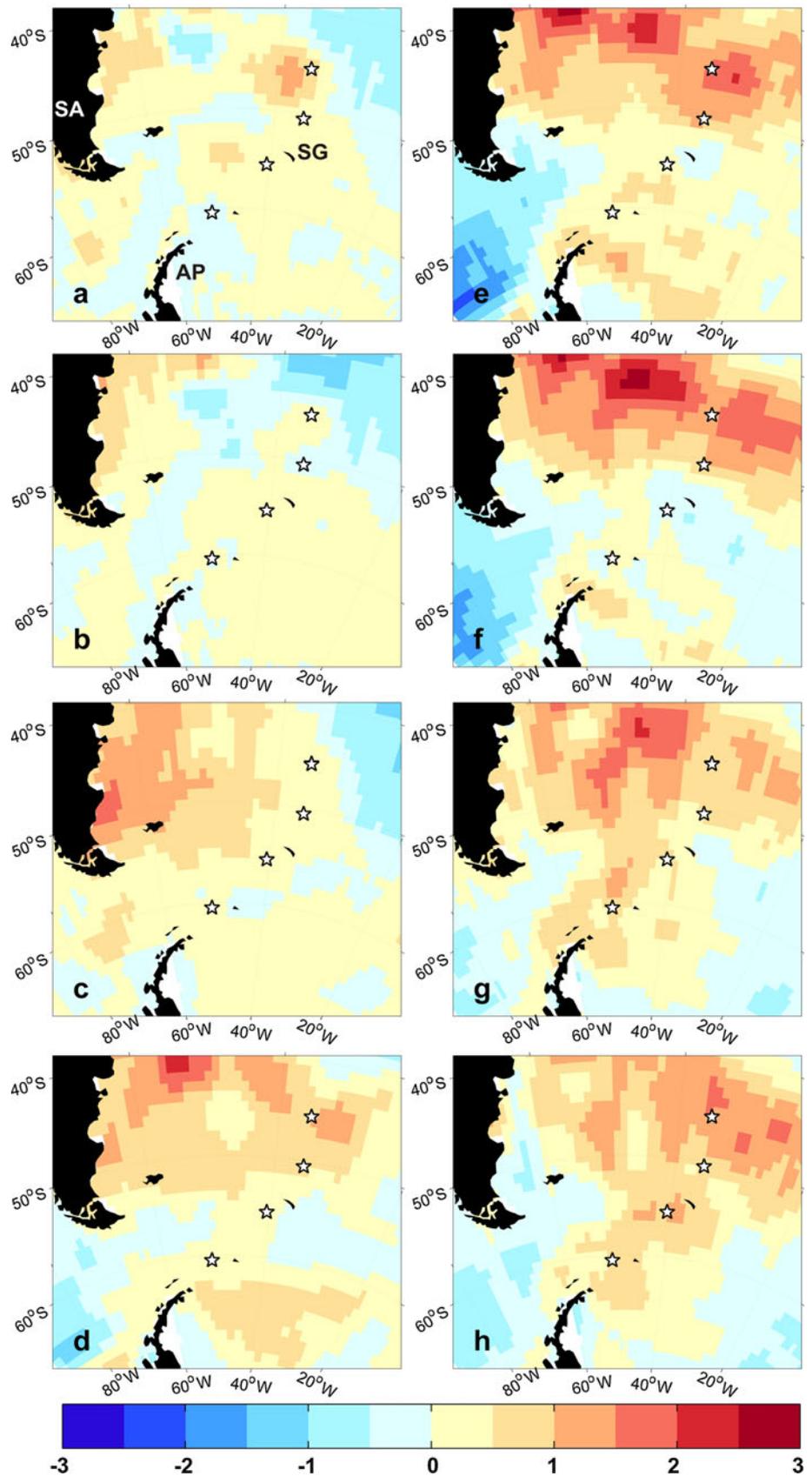
Food samples (stomach contents) were collected from grey-headed albatross chicks at Bird Island, South Georgia every 2 weeks from early February to late April, in 2000. Food sampling was by induced regurgitation after the chick had been fed by the parent and has no effect on chick survival or mass at fledging (Phillips 2006). These samples were analysed on the same day that they were obtained. The samples were weighed, and the overall mass was recorded. All components were sorted into categories (cephalopods, crustaceans, fish and others; the latter comprising carrion, penguin feathers, barnacles and jellyfish), and fresh remains weighed following Cherel et al. (2000) and Xavier et al. (2003a).

Within each component, fresh remains were identified according to Clarke (1986), Boltovskoy (1999), Xavier et al. (2003b) and Xavier and Cherel (2009) and using reference collections held at the British Antarctic Survey (BAS), UK and at the Institute of Marine Research (IMAR), PT. Loose beaks were examined along with those extracted from the other cephalopod remains when determining the species composition and size classes of cephalopods consumed. The diet data were summarised as frequency of occurrence, proportions by number and proportions by mass, following Xavier et al. (2003a).

Oceanographic data

Sea surface temperature anomalies (SSTa) were obtained from 4 reference locations randomly selected across the study region in known foraging areas of grey-headed albatrosses during chick rearing (Xavier et al. 2003b; Phillips et al. 2004a): north of the Antarctic Polar Front (45.5°S 35.5°W), South Georgia region (50.5°S 35.5°W), mid-Scotia Sea (55.5°S 40.5°W) and at the Antarctic Peninsula region (60.5°S 50.5°W) (Fig. 1). Annual variation was assessed by comparing SSTa between 1982 and 2000. Weekly sea surface temperature anomalies (SSTa, Reynolds et al. 2002) were obtained from http://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCEP/EMC/CMB/GLOBAL/Reyn_SmithOIv2/weekly/. Absolute dynamic height data, provided by Aviso (Archiving, Validation and Interpretation of Satellite Oceanographic data) (Rio and Hernandez 2004), were overlaid with the average position of the major oceanic fronts in the study region (Sub-Antarctic Front, Antarctic Polar Front, Southern Antarctic Circumpolar Current Front, Southern Boundary of the Antarctic Circumpolar Current) in order to identify any substantial changes in the positions of these fronts. Values

Fig. 1 Map of the study region (SA South America, SG South Georgia, AP Antarctic Peninsula), locations of the 4 reference locations (*star symbols*) and oceanographic conditions (monthly mean sea surface temperature anomaly ($^{\circ}\text{C}$) relative to 1971–2000 mean) between September 1999 (a) and April 2000 (h). Anomalies $<0^{\circ}\text{C}$ are indicated by blue colours, anomalies $\geq 0^{\circ}\text{C}$ are indicated by yellow to red colours



for oceanographic parameters were obtained from the closest date to the diet sampling (range 0–2 days).

Statistical analysis

All statistics were carried out using Minitab (Sowers Printing Company, Pennsylvania). We examined relationships between different diet parameters—the frequency of occurrence and estimated mass of cephalopods, crustaceans and fish, and number of each of the main prey species, the ommastrephid squid *Martialia hyadesi*, cranchiid squid *Galiteuthis glacialis*, onychoteuthid squid *Kondakovia longimana*, lamprey *Geotria australis* and Antarctic krill *Euphausia superba* (hereafter referred as krill)—and SSTa obtained from the four reference locations according to the sampling diet dates, by means of Spearman's rank correlation coefficient, r_s . Since multiple tests were performed, we applied the Bonferroni correction (1/number of correlations carried out for each reference location) and interpreted correlation patterns following Hills (1969). General linear models (GLMs) were used to test whether the proportions of the various prey groups in the diet varied significantly across sampling periods. Values are reported as mean \pm standard error (SE) unless stated otherwise.

Results

Seasonal variation in diet composition

A total of 120 food samples were collected from grey-headed albatross chicks between early February and late April 2000 (i.e. 20 samples every 2 weeks). Average weight of food samples changed significantly, from 271 ± 24.6 g in early February to 202 ± 20.7 g in late April (ANOVA, $F_{5,114} = 3.1$, $P = 0.01$), decreasing throughout the sampling periods (Linear regression, $F_{1,118} = 4.86$, $P = 0.03$, $r^2 = 4.0$).

Regarding diet composition, when all samples were combined, grey-headed albatrosses consumed mainly crustaceans (61 % by mass), followed by fish (19 %) and cephalopods (17 %) (Fig. 1; see also Xavier et al. 2003a). However, there were considerable changes between sampling periods (Fig. 2), including significant differences in the frequency of occurrence of the components (crustaceans, fish and cephalopods; $\chi^2_{10} = 32.0$, $P < 0.01$). Results from the GLMs also showed that the proportions by mass of crustaceans ($F_{5,114} = 4.53$, $P < 0.01$) and cephalopods ($F_{5,114} = 4.97$, $P < 0.01$), but not fish ($F_{5,114} = 1.0$, $P = 0.40$), differed significantly between sampling periods. Cephalopods increased from <1 % by mass in early February to 42.9 % (and were the most important prey group) in late February, whereas crustaceans were the

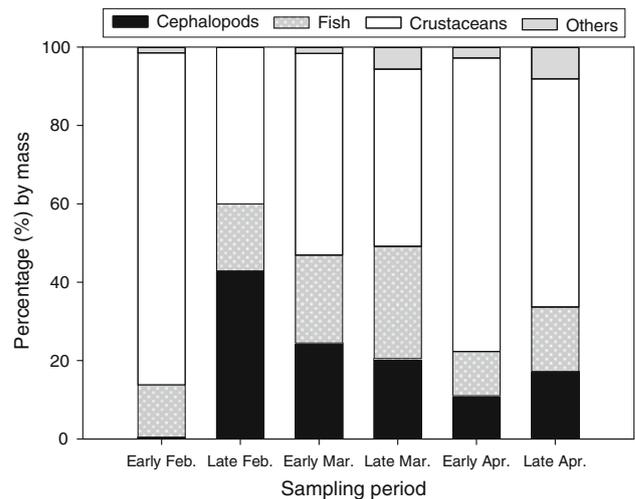


Fig. 2 General composition of the diet of grey-headed albatrosses at Bird Island (South Georgia), between February and April 2000

most consumed prey group in all other periods (Fig. 2). There were also considerable changes in species composition by number: the sub-Antarctic squid *Martialia hyadesi* was the most important cephalopod species in early February, but then declined in importance thereafter, as the proportion of the Antarctic squid species *Galiteuthis glacialis* increased (*K. longimana* was always the most important cephalopod consumed by mass; Fig. 3). Within the fish component, *G. australis* was the most important by number in all sampling periods, but by mass *Magnisudis prionosa* was the most consumed fish prey in early February, and then declined in importance, as the proportion of *G. australis* increased (Fig. 4). Krill dominated the crustacean component, by number ($>$ in all sampling periods) and by mass (>99 %) in all sampling periods (Fig. 2).

Oceanographic conditions within the foraging area of breeding grey-headed albatrosses

Oceanographic conditions between the north of the Antarctic Polar Front (APF) and the Antarctic Peninsula were unusually warm during some months: SSTa north of the APF was warmer (i.e. positive SSTa), for most of the breeding cycle (late incubation to late chick rearing) of grey-headed albatrosses (December 1999, January–February 2000 and April–May 2000; Figs. 1, 5), than the mean long-term average in the previous 19 years (1982–2000; Fig. 5). Further south, around South Georgia, high SSTa values were observed slightly later, between January 2000 and April 2000 (Fig. 5). In the mid-Scotia Sea, abnormal SSTa was only apparent in April 2000 (Fig. 5), and at the Antarctic Peninsula, SSTa was higher from March 2000 to July 2000 (Fig. 5), which corresponds to the late chick-rearing period of grey-headed albatross. Examination of

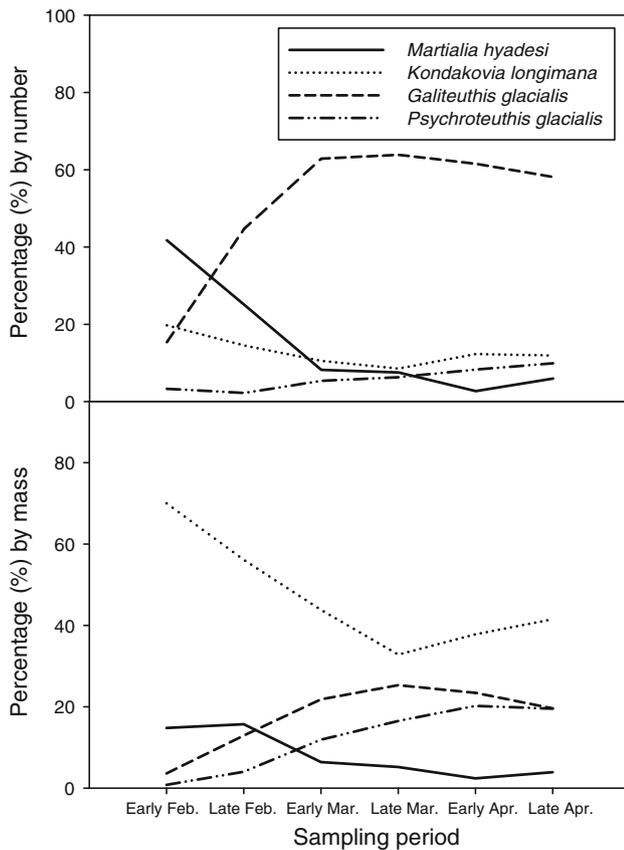


Fig. 3 Seasonal changes of the most important cephalopod species, by number and by mass, in the diet of grey-headed albatrosses between February and April 2000

absolute dynamic height data showed that this was due to widespread warming of surface waters rather than shifts in the position of the fronts of the Antarctic Circumpolar Current (ACC). Large-scale surface warming in this region has previously been recorded, most recently in 2009 (Venables et al. 2012).

Relationships between prey availability and SSTa

There were 2 significant correlations between values for the main diet parameters (i.e. frequency of occurrence and mass of crustaceans, cephalopod and fish; number of items of the most important prey: krill, *Martialia hyadesi*, *Galiteuthis glacialis*, *Kondakovia longimana* and lamprey) and SSTa at each reference location: the number of *G. australis* was positively correlated with SSTa in the South Georgia region (Spearman's rank correlation; $r_s = 0.943$; $P = 0.05$), and the mass of *M. hyadesi* was positively correlated with SSTa in the mid-Scotia Sea (Spearman's rank correlation; $r_s = -0.943$; $P = 0.05$). No other significant relationships or other obvious patterns were evident.

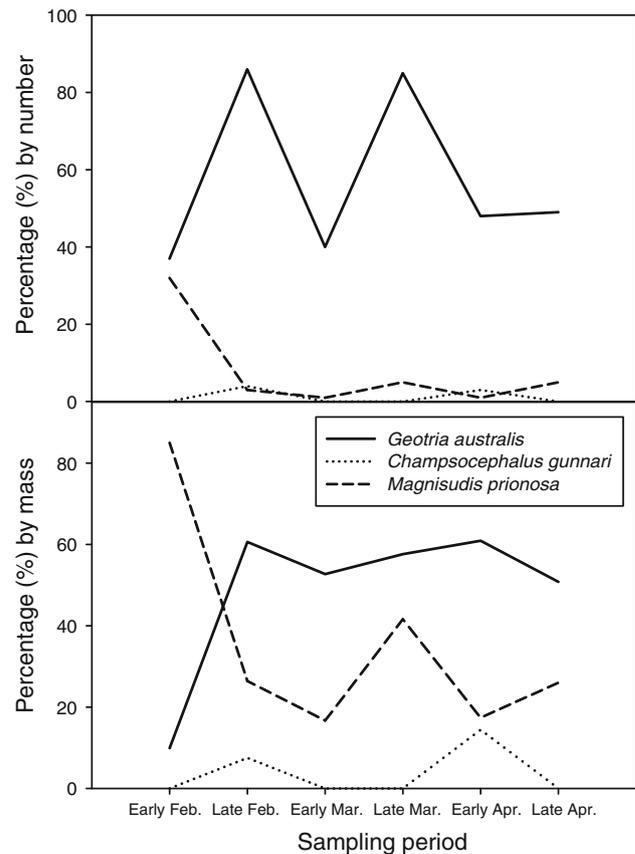


Fig. 4 Seasonal changes of the most important fish species, by number and by mass, in the diet of grey-headed albatrosses between February and April 2000

Discussion

Our study identified significant seasonal changes in the diet of grey-headed albatrosses at South Georgia when confronted by unusual environmental conditions. Based on prey biogeography, the reduction in *Martialia hyadesi* and lamprey and increase in krill and *Galiteuthis glacialis* in the diet represent shifts from feeding in the Antarctic Polar Frontal Zone (APFZ) to waters at much higher latitudes. Despite this, breeding success in 2000 was poor (16.8 %; Xavier et al. 2003a). In our study, the oceanographic conditions were unusually warm close to South Georgia between January and April 2000, with sea surface temperature warmer by up to 1 °C in comparison with annual data between 1982 and 2000 (see “Results”).

Grey-headed albatrosses tracked in April 2000 foraged predominantly in Antarctic waters, mainly on the shelf or shelf-slope waters of the South Orkneys and South Shetlands and at the Antarctic Peninsula north of Adelaide Island feeding on krill (Xavier et al. 2003a). In contrast, earlier in the season, the diet consisted predominantly by number of the subantarctic squid *Martialia hyadesi*, which

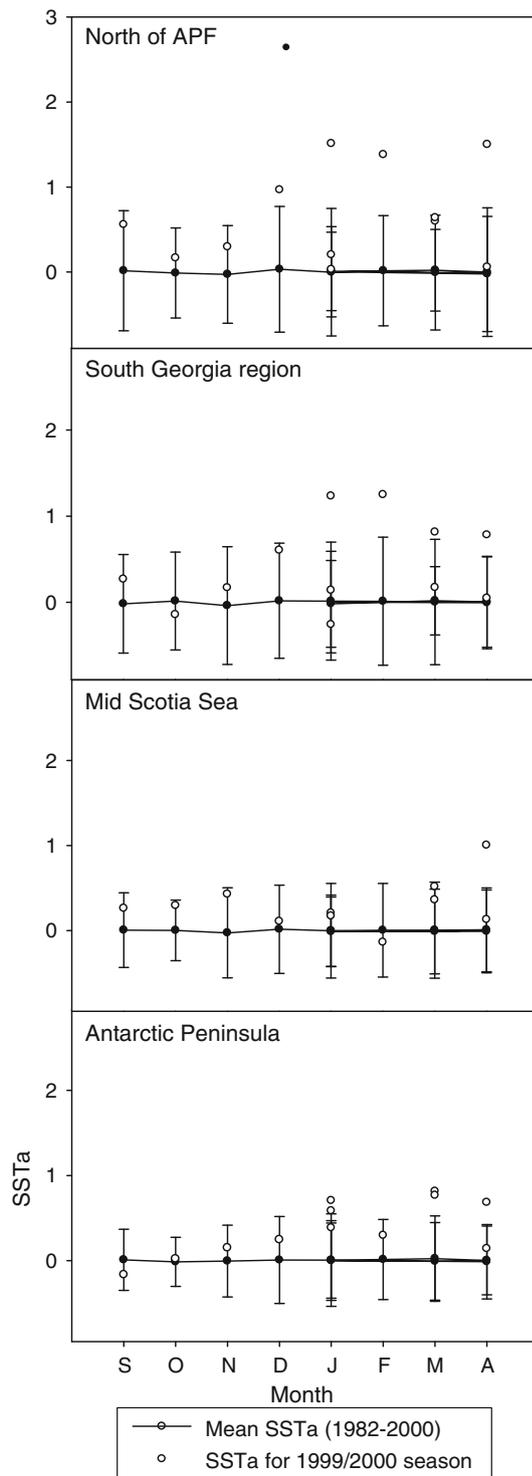


Fig. 5 Mean monthly sea surface temperatures anomalies (SSTa) between 1982 and 2000 at 4 randomly selected reference locations (black symbols) in the study area: north of the Antarctic Polar Front (45.5°S 35.5°W), South Georgia region (50.5°S 35.5°W), mid-Scotia Sea (55.5°S 40.5°W) and Antarctic Peninsula (60.5°S 50.5°W). White symbols are values for the 1999/2000 season. The values are given mean \pm SD

is obtained mainly at the APFZ (Rodhouse et al. 1996). The switch to long trips carries an increased risk that the chick will die of starvation in the interim, and hence, breeding success in 2000 was ultimately poor. Previous studies at South Georgia suggest that breeding failure in grey-headed albatrosses is associated with some years in which krill (Croxall et al. 1999) or *M. hyadesi* (Xavier et al. 2003a) is scarce. This was the case in 1994, even though grey-headed albatrosses continued to forage north of South Georgia but fed more on fish and less on squid than usual (Rodhouse et al. 1996; Prince et al. 1999). Together, these results suggest that the key determinant of successful breeding in grey-headed albatrosses is the availability of *M. hyadesi*, hence the significant positive correlation between the proportion of this squid in the diet and breeding success (Xavier et al. 2003a) and SSTa (this study). Feeding only on krill at the Antarctic Peninsula seems not to be a viable alternative, presumably because it is not sufficiently available/abundant in some years and often requires much longer foraging trips to Antarctic Peninsula, which reduces overall provisioning rates.

The onychoteuthid squid *Kondakovia longimana* was consistently the most important cephalopod consumed by grey-headed albatrosses by mass in all sampling periods (Fig. 2). The biology and distribution of *K. longimana* is still poorly known, although it is known to occur in Antarctic (circumpolar) and APFZ waters (Cherel and Weimerskirch 1999; Xavier et al. 1999), potentially mating/spawning on shelf areas (Cherel and Weimerskirch 1999) and be available in the upper strata of the water column (Lu and Williams 1994) potentially accessible live to grey-headed albatrosses throughout their foraging range breeding while breeding in South Georgia (Croxall and Prince 1994; Phillips et al. 2004a; Xavier and Croxall 2007). Despite this squid species occur regularly in the diets of grey-headed albatrosses (Xavier et al. 2003a; Xavier and Cherel 2009), its availability is likely not to be in high numbers as *K. longimana* is the main cephalopod prey by mass in poor breeding success years (Xavier et al. 2003a; this study).

Galiteuthis glacialis was the most important cephalopod species in most sampling periods by number (Fig. 3). *G. glacialis* is a typical Antarctic species, being caught all around the Southern Ocean (Xavier et al. 1999) and found in numerous Antarctic predators (Xavier and Cherel 2009). Like *K. longimana*, *G. glacialis* is more abundant in the diet of grey-headed albatrosses by number in poor breeding success years (Xavier et al. 2003a; this study).

The lamprey *G. australis* was the main prey in the fish component in grey-headed albatrosses by number in all sampling periods (and by mass, except in early February, in which *M. prionosa* was the most important; Fig. 3) and was

related to SSTa in the South Georgia region. This agrees with previous studies, in which *G. australis* dominated the diet of grey-headed albatrosses (Xavier et al. 2003a). Unlike *K. longimana*, *G. australis* had been the most important fish species in both good and bad breeding years of grey-headed albatrosses (Xavier et al. 2003a), suggesting that *G. australis*, known to occur in APFZ waters, is a prey regularly and consistently available to this predator (Xavier et al. 2003a).

Our study showed correlations between SSTa and *G. australis* and *M. hyadesi* from the diets of grey-headed albatrosses during chick rearing, suggesting that changes in SSTa may influence albatrosses foraging distribution. This high flexibility in feeding strategies is also apparent in changes typical of the transition between different breeding stages. For example, grey-headed albatrosses breeding at Marion Island are known to forage north of this island during incubation and south-west during chick rearing (Nel et al. 2001). Similarly, black-browed albatrosses breeding at Bird Island foraged predominantly around and to the north-west of Bird Island during incubation, stayed on the shelf around South Georgia and Shag Rocks during brood-guard, and tended to switch to more southerly Antarctic waters in chick rearing (Phillips et al. 2004a). Female grey-headed albatrosses from South Georgia forage in the APFZ, and males in the APFZ and also far to the south-west and south-east in Antarctic waters during incubation, and both sexes mainly in the APFZ in brood-guard (Phillips et al. 2004a, b). During chick rearing, both sexes travel to the APFZ and also south-west to the Scotia Sea, South Shetlands and Antarctic peninsula regions but the proportion using each area shows strong annual variation (Wood et al. 2000; Xavier et al. 2003a; Phillips et al. 2004a, b; BAS unpublished data). In addition, individual birds that travel first to the APFZ will, if they experience poor feeding success, switch immediately to Antarctic waters without returning to the colony (Catry et al. 2004). It would therefore appear that during chick rearing, grey-headed albatrosses favour waters around or to the north of South Georgia in the APFZ when environmental conditions are favourable (i.e. SSTa conditions are normal), but, as our seasonal trends in diet indicate, will gradually change their foraging patterns if confronted by challenging environmental conditions, as occurred in 2000.

We show that oceanographic conditions were atypically warm across the Scotia Sea (including South Georgia) from September 1999 to May 2000 (Figs. 1, 5). Warming anomalies were first observed north of the APF at the end of the austral winter in September 1999. Then, warming conditions extended further south, first around the intermediate reference locations and eventually at the Antarctic Peninsula in late May. Typically, in years in terms of both normal oceanographic conditions and good breeding

performance (Xavier et al. 2003a), grey-headed albatrosses forage at the APF, usually returning with the sub-Antarctic squid *M. hyadesi* (Xavier et al. 2003a; Catry et al. 2004). Although *M. hyadesi* was still present in the diet in March and April 2000, numbers were low (see “Results”). Indeed, another predator of *M. hyadesi*, the Patagonian toothfish *Dissostichus eleginoides* that, unlike grey-headed albatrosses forage deep in the water column, also barely fed on *M. hyadesi* in 2000, indicating that abundance of the latter was uncharacteristically low (Pilling et al. 2001; Xavier et al. 2002). This ties in with the shift between late February and March to other squid, *Galiteuthis glacialis* and *Kondakovia longimana*, which are typically Antarctic species (Xavier et al. 1999), and to krill. Lamprey, which is a typically sub-Antarctic species, was regularly present in the diet of grey-headed albatrosses throughout the whole breeding season (see “Results”), probably consumed during the small proportion of trips to the APFZ (Xavier et al. 2003a). Lamprey distribution may also extend further south in warm years, but this, and indeed many other aspects of the life cycle of oceanic lamprey, including their host and how they become available to albatrosses at South Georgia, are unknown (Potter et al. 1979).

Changes in the diet of grey-headed albatrosses in this study were highly correlated with environmental conditions. The proportions of crustaceans and fish by mass, as well as the number of several squid species, were significantly related to SSTa. Temperature anomalies in the South Pacific sector of the Southern Ocean are propagated via the ACC into the South Atlantic on time scales of more than 1 year, whereas atmospheric processes related to ENSO and the Southern Annular Mode have a direct influence on shorter time scales (<6 months) (Murphy et al. 2007a). These changes in SSTa across the South Atlantic sector are related to the recruitment and dispersal of krill (Murphy et al. 2007a). The density and distribution of krill have exhibited dramatic spatial and temporal fluctuations in the south-west Atlantic, where >50 % of krill in the Southern Ocean are concentrated and have declined since the 1970s (Atkinson et al. 2004). This oceanographically driven variation in krill population dynamics and abundance has affected dependent predators, including some seabirds and marine mammal predators (Croxall et al. 1999; Reid and Croxall 2001b). In our study, we demonstrate that there was a shift in the diet of grey-headed albatrosses, which may be related to a functional link between the oceanographic conditions and abundance/availability of krill, fish and squid, that affected the breeding performance of albatrosses, reducing their chick survival. Such propagating anomalies, mediated through physical and trophic interactions, are likely to be an increasingly important component of variation in ocean ecosystems in the light of predicted anthropogenic climatic change.

Table 1 Seasonal variation in the diet of grey-headed albatrosses from Bird Island, South Georgia in 2000

Species	Early February	Late February	Early March	Late March	Early April	Late April	Overall		
	(n = 20) F (%)	F (%)	N (%)	M (%)					
Cephalopods									17 ± 3
<i>Alluroteuthis antarcticus</i>	5	30	20	50	40	40	31	(58) 3	5.2
<i>Galiteuthis glacialis</i>	35	100	95	85	85	60	77	(1,218) 57	19.4
<i>Kondakovia longimana</i>	40	90	85	65	80	55	69	(256) 12	44.5
<i>Martialia hyadesi</i>	25	80	45	60	30	20	43	(251) 12	7.7
<i>Psychroteuthis glacialis</i>	15	25	45	40	45	45	36	(129) 6	12.9
<i>Gonatus antarcticus</i>	15	70	50	45	20	25	38	(82) 4	3.3
<i>Moroteuthis knipovitchi</i>	5	35	25	20	15	15	19	(129) 2	4.0
Fish									19 ± 3
<i>Geotria australis</i>	15	75	70	65	60	35	47	(403) 62	49.3
<i>Champsocephalus gunnari</i>	0	5	0	0	10	0	3	(10) 2	3.7
<i>Magnisudis prionosa</i>	20	15	5	15	5	5	11	(27) 4	36.7
Crustaceans									61 ± 4
<i>Euphausia superba</i>	100	70	100	85	95	80	89	>99	99.6
Others									3 ± 1

Only prey that represented $\geq 5\%$ by mass in the diet were included

n Number of samples, F (%) frequency of occurrence, N (%) percentage of number of individuals (in parentheses there are the raw values), M (%) percentage of the proportion by mass)

The close examination of the diet of grey-headed albatrosses provided a good insight into seasonal variation (Table 1). Although there was little change in the species composition of the crustacean components, and krill tended to dominate, the fish and cephalopod components of the diet changed significantly (Table 1). Furthermore, within these components, the importance of particular species changed considerably, with *G. glacialis* (by number) and *G. australis* (by mass) increasing over time (Figs. 3, 4). These changes would not have been identified if only looking at the overall diet (i.e. if all samples had been pooled). Overall, this study clearly demonstrates how top predators may respond in years when environmental conditions are unfavourable. Despite this flexibility, breeding success was poor, which from a conservation perspective is of particular concern for the study species, the grey-headed albatross, given that the South Georgia population is the largest in the world, and breeds in a hotspot of environmental variability (Murphy et al. 2007b, c).

Acknowledgments We thank Bird Island staff especially Simon Berrow, Richard Humpidge, Nik Aspey and Mark Jessop for help in collecting the samples, Simon Berrow and Robert Taylor for useful discussions on the field protocol, Rachael Shreeve for valuable advice on crustacean identification and Filipe Ceia, Jaime Ramos and Vitor Paiva for statistical discussions. We are particularly grateful to Paul

Rodhouse and Phil Trathan for their advice through the project. This research was initially evaluated by an ethical committee, and it was supported by the Ministry of Science and Technology, Portugal (Fundação para a Ciência e a Tecnologia; FCT) and by the British Antarctic Survey, UK. J.X. was funded by FCT, and M.L. was funded by a Marie Curie Individual Fellowship (PIEF-GA-2008-220063) and *Juan de la Cierva* postdoctoral programme (JCI-2010-07639, *Ministerio de Ciencia e Innovación*). The altimeter products were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>).

References

- Atkinson A, Siegel V, Pakhomov EA, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Attrill MJ, Power M (2002) Climatic influence on a marine fish assemblage. *Nature* 417:275–278
- Boltovskoy D (1999) South Atlantic zooplankton. Backhuys Publishers, Leiden, Netherlands
- Boyd IL, Wanless S, Camphusysen CJ (2006) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge
- Brooke ML (2004) Albatrosses and petrels across the world. Oxford University Press, New York
- Catry P, Phillips RA, Phalan B, Silk JRD, Croxall JP (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar Ecol Prog Ser* 280:261–273

- Cherel Y, Weimerskirch H (1999) Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. *Mar Ecol Prog Ser* 188:93–104
- Cherel Y, Weimerskirch H, Trouve C (2000) Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Mar Ecol Prog Ser* 207:183–199
- Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford
- Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. *Birdlife Conserv Int* 22:1–34
- Croxall JP, McCann TS, Prince PA, 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. In: Sahrhage D (ed) *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin, pp 261–285
- Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131
- Croxall JP, Prince PA (1994) Dead or alive, night or day: how do albatrosses catch squid? *Antarct Sci* 6:155–162
- Croxall JP, Prince PA, Rothery P, Wood AG (1998) Population changes in albatrosses at South Georgia. In: Robertson G, Gales R (eds) *Albatross biology and conservation*. Surrey Beatty & Sons, Chipping Norton, pp 69–83
- Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177:115–131
- Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. *Mar Ecol Prog Ser* 391:139–151
- Hills M (1969) On looking at large correlation matrices. *Biometrika* 56:249–253
- Huin N, Prince PA, Briggs DR (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
- Ito M, Minami H, Tanaka Y, Watanuki Y (2009) Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird. *Mar Ecol Prog Ser* 393:273–284
- King JC (1994) Recent climate variability in the vicinity of the Antarctic Peninsula. *Int J Climatol* 14:357–369
- Lewis S, Grémillet D, Daunt F, Ryan P, Crawford RJM, Wanless S (2006) Using behavioural variables to identify proximate causes of population change in a seabird. *Oecologia* 147:606–614
- Lu CC, Williams R (1994) *Kondakovia longimana* Filippova, 1972 (Cephalopoda: Onychoteuthidae) from the Indian Ocean sector of the Southern Ocean. *Antarct Sci* 6:231–234
- Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys Res Lett* 32:L19604
- Murphy EJ, Trathan PN, Watkins JL, Reid K, Meredith MP, Forcada J, Thorpe SE, Johnston NM, Rothery P (2007a) Climatically driven fluctuations in Southern Ocean ecosystems. *Proc R Soc B* 274:3057–3067
- Murphy EJ, Trathan PN, Watkins JL, Reid K, Meredith MP, Forcada J, Thorpe SE, Johnston NM, Rothery P (2007b) Climatically driven fluctuations in Southern Ocean ecosystems. *Proc R Soc B* 274:3057–3067
- Murphy EJ, Watkins JL, Trathan PN, Reid K, Meredith MP, Thorpe SE, Johnston NM, Clarke A, Tarling GA, Collins MA, Forcada J, Shreeve RS, Atkinson A, Korb R, Whitehouse MJ, Ward P, Rodhouse PG, Enderlein P, Hirst AG, Martin AR, Hill SL, Staniland IJ, Pond DW, Briggs DR, Cunningham NJ, Fleming AH (2007c) Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Phil Trans R Soc B* 362:113–148
- Nel DC, Lutjeharms JRE, Pakhomov EA, Anson IJ, Ryan PG, Klages NTW (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Mar Ecol Prog Ser* 217:15–26
- Phillips RA (2006) Efficacy and effects of diet sampling of albatross chicks. *Emu* 106:305–308
- Phillips RA, Caldow RWG, Furness RW (1996) The influence of food availability on the breeding effort and reproductive success of Arctic skuas *Stercorarius parasiticus*. *Ibis* 138:410–419
- Phillips RA, Croxall JP (2003) Control of provisioning in grey-headed albatrosses: do adults respond to chick condition? *Can J Zool* 81:111–116
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004a) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc R Soc Lond B* 271:1283–1291
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004b) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc R Soc Lond B* 271:1283–1291
- Pilling GM, Purves MG, Daw TM, Agnew DA, Xavier JC (2001) The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *J Fish Biol* 59:1370–1384
- Potter IC, Prince PA, Croxall JP (1979) Data on the adult marine and migratory phases in the life cycle of the southern hemisphere lamprey, *Geotria australis* Gray. *Env Biol Fish* 4:65–69
- Prince PA, Weimerskirch H, Wood AG, Croxall JP (1999) Areas and scales of interactions between albatrosses and the marine environment: species, populations and sexes. In: Adams NJ, Slotow RH (eds) *Proceedings of 22nd Ornithological Congress*, Durban, August 1998. BirdLife South Africa, Johannesburg, pp 2001–2020
- Quetin LB, Ross RM (2003) Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. *Mar Ecol Prog Ser* 259:185–200
- Reid K, Croxall JP (2001a) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc Roy Soc Lond B* 268:377–384
- Reid K, Croxall JP (2001b) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc R Soc Lond B Biol Sci* 268:377–384
- Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An improved in situ and satellite SST analysis for climate. *J Clim* 15:1609–1625
- Rio M-H, Hernandez F (2004) A mean dynamic topography computed over the world ocean from altimetry, in situ measurements, and a geoid model. *J Geophys Res* 109:12032
- Rodhouse PG, Prince PA, Trathan PN, Hatfield EMC, Watkins JL, Bone DG, Murphy EJ, White MG (1996) Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. *Mar Ecol Prog Ser* 136:37–50
- Stenseth NC, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Venables H, Meredith MP, Atkinson A, Ward P (2012) Fronts and habitat zones in the Scotia sea. *Deep-Sea Res II* 59–60:14–24
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Guddberg OH, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Wang SW, Iverson SJ, Springer AM, Hatch SA (2009) Spatial and temporal diet segregation in northern fulmars *Fulmarus glacialis*

- breeding in Alaska: insights from fatty acid signatures. *Mar Ecol Prog Ser* 377:299–307
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep-Sea Res II* 54:211–223
- Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J Avian Biol* 31:278–286
- Wuethrich B (2000) How climate change alters rhythms of the wild. *Science* 287:793–795
- Xavier JC, Cherel Y (2009) Cephalopod beak guide for the Southern Ocean. British Antarctic Survey, Cambridge
- Xavier JC, Croxall JP (2007) Predator-prey interactions: why do larger albatrosses feed on bigger squid? *J Zool Lond* 271:408–417
- Xavier JC, Croxall JP, Reid K (2003a) Inter-annual variation in the diet of two albatross species breeding at South Georgia: implications for breeding performance. *Ibis* 145:593–610
- Xavier JC, Croxall JP, Trathan PN, Wood AG (2003b) Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Mar Biol* 143:221–232
- Xavier JC, Rodhouse PG, Purves MG, Daw TM, Arata J, Pilling GM (2002) Distribution of cephalopods recorded in the diet of Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar Biol* 25:323–330
- Xavier JC, Rodhouse PG, Trathan PN, Wood AG (1999) A Geographical Information System (GIS) atlas of cephalopod distribution in the Southern Ocean. *Antarct Sci* 11:61–62