Quantifying the Trophic Linkages of Antarctic Marine Predators

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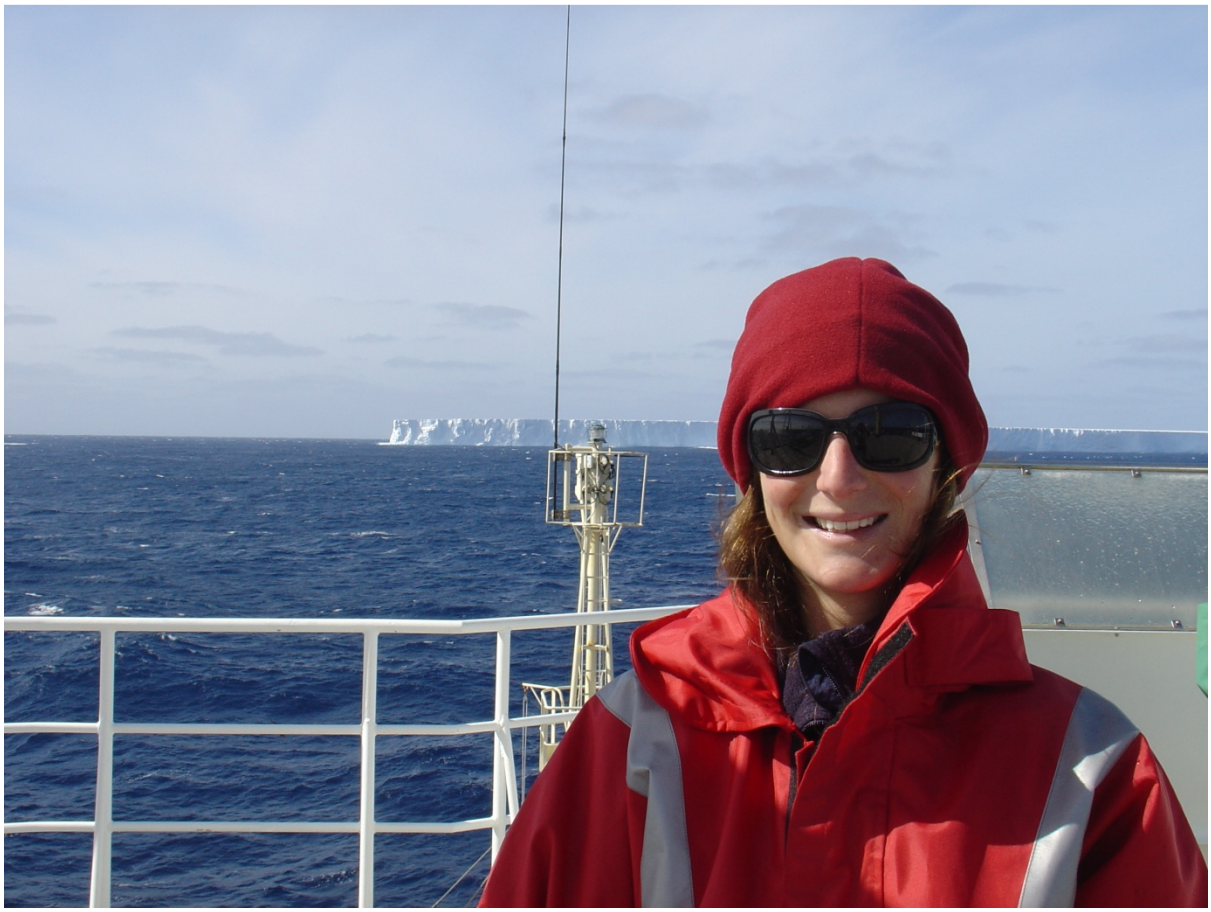

Fieldwork surveying the marine biodiversity of the waters north of Terre Adélie and George V Land in Eastern Antarctica as part of the Collaborative East Antarctic Marine Census (CEAMARC), January-February 2008.

Dedication

To my mum Ruth Walters for always encouraging me to trust my intuition and believe that things will work out.

Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Abstract

Understanding the diet and trophic relationships of animals in space and time, and its implications for population abundance and distributions, is a central problem in ecology. In the marine environment, the dietary study of marine mammal and avian species is impeded by the lack of information on their foraging strategies during the non-breeding period, when individuals migrate from common breeding areas to remote feeding grounds. Moreover, the spatial distribution of males, females and their offspring can differ considerably due to contrasting reproductive requirements and physiological constraints, respectively. Seasonal constraints therefore may influence the spatial distribution of abundant, migratory species, causing the food web structure, energy and nutrient flow within a given system to fluctuate accordingly.

This study is concerned with quantifying the diet and trophic relationships of abundant, widely distributed Antarctic marine predators: the emperor penguin (*Aptenodytes forsteri*), the southern elephant seal (*Mirounga leonina*) and the Antarctic fur seal (*Arctocephalus gazella*). The diet of these predators is assessed in relation to season. The winter diet of highly migratory seals is determined by the integration of stable isotope and telemetry derived sources of information. In this thesis I present isotopic dietary information for:

(1) *Emperor penguins* - using stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for whole blood and isotopic mixing models, the isotopic niche of breeding emperor penguins from the Auster colony, Mawson Coast during winter and chick-rearing in 2008 is defined. Seasonal changes in diet composition between females and males were identified using the stable isotope values of penguin blood and prey. Antarctic krill (*Euphausia superba*) were collected at several sites from open water to over-the-shelf to compare inshore versus offshore isotopic values, which has not been done yet for this important Antarctic prey species. The comparison of isotopic ratios of adults and chicks during late chick–rearing also revealed that adults do not feed on the same prey as those fed to chicks.

(2) *Southern elephant seals* - whisker isotopic techniques and concurrent satellite tracking of seals are successfully used as a non-invasive, complementary tool to identify broad-scale foraging habitat use and dietary preferences of sub-yearlings from Macquarie Island during their first foraging migration. The trophic position of each seal was estimated using $\delta^{13}C$ and

$\delta^{15}N$ values along the length of the whisker, which provided a temporal record of feeding intake.

(3) *Antarctic fur seals* - using a combination of whisker and blood and telemetry techniques we document for the first time the winter foraging habitat and diet of this species. Estimation of whisker growth rates enabled the reconstruction of a time series of isotopic data that could be related to at-sea location during the winter foraging period. Isotopic values reflected the contrasting migratory patterns of adult females from Cape Shirreff, Western Antarctic Peninsula and sub-Antarctic Marion Island, Indian Ocean. Isotopic mixing models indicate a seasonal shift in prey consumption with water mass use.

General discussion - This study has provided important new insights into the trophic ecology of emperor penguins, southern elephant seals and Antarctic fur seals, through the stable isotope analysis of their tissues and prey. Previously undescribed winter diet and habitat use, spanning three ocean sectors, have now been identified for these species through the integration of stable isotope and animal tracking data. This study has two major findings. Firstly, that the trophic niche of predators changes seasonally and secondly, that euphausiids are important to all three species at various stages of the austral winter period. Changes in sea-ice conditions, and the interaction of the Antarctic Circumpolar Current with complex or large bathymetric features appeared to have an important influence on the water masses used, and thus prey types consumed by predators in different regions of the Southern Ocean. Despite differences in reproductive requirements, physiological capabilities and breeding location (Antarctic versus sub-Antarctic), there was a tendency for all three species included in the study to prey on euphausiids (in addition to fish and squid) in ice-associated waters located south of the PF in autumn. During winter however, when maximum sea-ice extent occurs, the trophic position and diet of open water (Antarctic fur seals) and pagophilic (emperor penguins) species diverged, with the latter consuming greater proportions of higher trophic level prey (fish and squid) over Antarctic continental shelf (neritic) waters. The study has demonstrated the utility of stable isotope analysis to provide dietary data that cannot be obtained any other way, as in the case of highly migratory species during the austral winter in the Southern Ocean. Additionally, it has shown how stable isotope analysis can be made even more powerful when linked with other sources of information, such as movement data.

Statement of Publication and Co-authorship

Chapters 2, 3 and 4 comprise manuscripts published or in preparation for submission to peer-reviewed journals. The following publication has been produced from chapter 3 of this thesis:

Walters A, Lea M-A, van den Hoff J, Field I.C., Virtue P, Sokolov S, Pinkerton M.H., Hindell M.A. (2014) Spatially explicit estimates of prey consumption reveal a new krill predator in the Southern Ocean. PLoS ONE 9(1), e86452.

I was the lead author for each of the manuscripts and responsible for the experimental design, some sample collection, laboratory work, data analyses and interpretation, and preparation of manuscripts. The co–authors contributed to either the collection of data from sample sites and logistical support, some data analyses, and played a role in supervision of my PhD and revisions of manuscripts for publication. Contributions of co-authors are outlined below:

- Mark A. Hindell, Mary-Anne Lea and Patti Virtue (Institute for Marine and Antarctic Studies) assisted with guidance and supervision in all aspects of my PhD and in the production of all manuscripts for publication.

- Chapter 2 - Gary Miller (Division of Pathology and Laboratory Medicine, University of Western Australia) undertook fieldwork and provided logistical support for the collection of samples from emperor penguins at the Auster colony, Mawson Coast, Antarctica during winter and spring in 2008. Gary Miller also provided the DNA sex determinations of birds included in the study. Patti Virtue assisted in the identification of age, sex and reproductive classes of Antarctic krill (*Euphausia superba*) specimens. Mark Hindell and Mary-Anne Lea contributed to data interpretation.

- Chapter 3 - John van den Hoff (Australian Antarctic Division) and Iain Field (Department of Environment and Geography, Macquarie University) undertook fieldwork for the deployment of tags and collection of samples from sub-yearling southern elephant seals at Macquarie Island in 1995/1996 and 1999/2000, respectively, and contributed to manuscript preparation. Matt Pinkerton (National Institute of Water and Atmospheric Research) provided isotopic data of fish and squid from the

Northern Ross Sea region and contributed to manuscript preparation. Sergei Sokolov (CSIRO Marine and Atmospheric Research) provided assistance with the spatial analyses of seal tracks in relation to Inter-Frontal Zones (IFZ) of the Antarctic Circumpolar Current (ACC). Mark Hindell and Mary-Anne Lea provided analytical advice and contributed to data interpretation.

- Chapter 4 - Marthan Bester and Chris Oosthuizen (Department of Zoology and Entomology, University of Pretoria) and Mike Goebel (NOAA South West Fisheries Science Centre) undertook fieldwork and provided logistical support for the deployment of tags and collection of samples from adult female Antarctic fur seals at Cape Shirreff, Western Antarctic Peninsula and Marion Island, southern Indian Ocean, respectively. Phil Trathan (British Antarctic Survey) provided collaboration and support and contributed to manuscript preparation. Sergei Sokolov (CSIRO Marine and Atmospheric Research) provided assistance with the spatial analyses of seal tracks in relation to IFZs. Mark Hindell and Mary-Anne Lea provided analytical advice and contributed to data interpretation. Chris Oosthuizen also contributed to manuscript preparation.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above manuscripts published or in preparation for submission to peer-reviewed journals contributing to this thesis:

Mark A. Hindell	Richard Coleman
(Candidate's Supervisor)	(Head of School)

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1. General introduction

An understanding of the diet and trophic interactions of high level predators is essential for evaluating their role within food webs. In the marine environment however, the dietary study of many apex vertebrate predators is impeded by the lack of information on their foraging strategies during the non-breeding period. During this period individuals undertake extensive movements to (i) obtain energy for dependant young, (ii) replenish energy stores diminished during breeding, (iii) limit intra- and inter-specific competition for prey resources or (iv) in response to seasonal changes in local climate, productivity and prey resource availability (Stephens & Krebs 1986; Dingle 1996; Alerstam et al. 2003). Consequently, quantifying dietary variations over the annual migration cycle of animals remains a challenge for ecologists studying the diet and trophic interactions of migratory species. This study is concerned with quantifying the diet and trophic relationships of abundant, widely distributed Southern Ocean marine predators; the emperor penguin (*Aptenodytes forsteri*), the southern elephant seal (*Mirounga leonina*) and the Antarctic fur seal (*Arcocephalus gazella*).

SOUTHERN OCEAN MARINE ECOSYSTEMS

Management and conservation: the importance of food web models

Management and conservation of marine resources and ecosystems is of importance worldwide (Doney et al. 2012). Of particular concern are the polar environments which have undergone faster rates of regional warming than many other regions of the world (Vaughan et al. 2003), and where there are regional effects of climate change and fisheries pressure on species at all trophic levels (Croxall et al. 2002; Vaughan et al. 2003; Trathan et al. 2007; Forcada et al. 2008; Nicol et al. 2008; Kovacs et al. 2011). The use of ecosystem models is an important tool to understand the effects of climate change and other anthropogenic activities across all trophic levels (Constable et al. 2000), however these models are constrained by a lack of spatially explicit quantitative data on diet and tropho-dynamics.

Understanding the diet and trophic interactions of high order predators in space and time is essential for modelling fluxes in energy within the Southern Ocean ecosystem at different times of the year. The magnitude of energy flow from prey to predator, or of predator consumption rates (Brose et al. 2008), and its implications for population abundance and distributions, are central questions to the management of harvested, dependant and competing populations (Agnew 1997; Constable et al. 2000; Parkes 2000). Elucidating predator-prey

relationships in the Southern Ocean is impeded by the lack of information on the diet and foraging ecology of high order predators, such as seals, seabirds and penguins, outside of the breeding season.

During the non-breeding period much less dietary and foraging information is available because individuals often remain at sea, far from their breeding sites. This means that predictions of annual consumption rates of key marine predators, a critical tool in the development of ecosystem-based fisheries management (EBFM; Constable et al. 2000), may be biased because they lack data from other life-cycle phases (*e.g.* Woehler 1995). Acquiring data during the non-breeding period is therefore required to understand the spatial and/or temporal dependencies of predators on their prey, and in turn provide insights into important marine predator habitats which may overlap with fisheries and areas affected by climate change.

Structure and function of ecosystems: the trophic role of top predators

The structure and function of ocean ecosystems generally reflects the spatial and temporal variability in the physical environment and associated biological productivity (Sims et al. 2008). This is particularly true in the Southern Ocean where several important physical, chemical and biological processes interact to produce biologically productive areas. Enhanced primary and secondary production in the water column within these areas attracts crustaceans, fish and squid for higher trophic level predators to feed on (Sydeman et al. 2006).

Southern Ocean ecosystems are broadly structured by the eastward flowing Antarctic Circumpolar Current (ACC; *e.g.* Grant et al. 2006). The flow of the ACC is centred at frontal bands (Orsi et al. 1995; Belkin & Gordon 1996). In the absence of land in the latitudinal band of the Drake Passage, these frontal bands connect the Indian, Pacific and Atlantic Ocean basins (Rintoul et al. 2001). The flow of the ACC concentrates the biomass of primary production and macronutrients in Inter-Frontal Zones (IFZ; Sokolov & Rintoul 2009b; 2009a; see Table 1.1 for definitions). Strong westerly geostrophic winds, in tandem with topographical features, largely dictate the temporal and spatial variability in the flow of the ACC and the position of IFZs (Sokolov & Rintoul 2009a). To the north, the southern branch of the Sub-Tropical Zone (STZ-S) separates the warm sub-tropical waters from the sub-Antarctic waters. Here I refer to the region between the STZ-S and the northern branch of the Sub-Antarctic Front (SAF-N) as the Sub-Antarctic Zone (SAZ), and the region between the

Table 1.1. Inter-Frontal Zones of the Antarctic Circumpolar Current in the Southern Ocean south of the Sub-Tropical Front

Zone	Abbreviation	Location	
Sub-Antarctic Zone	SAZ	Region between the southern branch of the Sub-Tropical Zone to the northern branch of the Sub-Antarctic Front	
Sub-Antarctic Front	SAF	Northern branch of the Sub-Antarctic Front to the southern branch of the Sub-Antarctic Front	
Polar Frontal Zone	PFZ	Region between the southern branch of the Sub-Antarctic Zone to the northern branch of the Polar Front	Permanently Open Ocean Zone (POOZ)
Polar Front	PF	Northern branch of Polar Front to the southern branch of the Polar Front	
Antarctic Zone	AZ	Region between the southern branch of the Polar Front, the northern and southern branches of the southern Antarctic Circumpolar Current Front and the southern Boundary of the Antarctic Circumpolar Current	Seasonal Ice Zone (SIZ)

SAF-N and the southern branch of the SAF (SAF-S) as the SAF. The SAF-S delineates the northern boundary of the three branches of the Polar Front (PF). Here I refer to the region between the SAF-S and the northern branch of the PF as the PF Zone (PFZ), and the region between the northern branch of the PF (PF-N) and the southern branch of the PF (PF-S) as the PF. The PF-S marks the northern boundary of the two branches of the southern ACC Front (SACCF) and the southern Boundary Current (sBdy), which I refer to here as the Antarctic Zone (AZ).

Although phytoplankton abundance is generally low in the Southern Ocean (Arrigo et al. 2008), intense phytoplankton blooms occur in the seasonal sea ice zone, in shallow waters, upwelling zones, near some fronts of the ACC, and in association with large bathymetric features (Moore & Abbott 2000; Sokolov 2008). Seasonal and inter-annual variability in sea-ice extent also affects primary production via the amount of sea-ice algae which can be supported by the sea-ice (Thomas & Dieckmann 2009). These processes combine to produce patchy resource distributions and often zone-specific zooplankton communities and densities in the Southern Ocean (Pakhomov et al. 1994; Hunt & Hosie 2005; Bernard et al. 2007). This in turn, means that the structure and function of different food webs in different regions of the Southern Ocean can vary substantially. Subsequently high order predators can occupy different trophic positions within different regional food webs.

The diversity of marine species in the Southern Ocean is generally low compared to other temperate and tropical oceans, however, it supports an unprecedented biomass of high trophic level predators, including whales, seals, seabirds, penguins and fish (Knox 2007). For air-breathing marine predators breeding along the Antarctic continent, on surrounding Antarctic and sub-Antarctic islands (*e.g.* otariid and phocid seals, penguins and seabirds) or migrating from other areas (*e.g.* baleen whales), the seasonal sea-ice zone is an important foraging area as it is the most productive region in the Southern Ocean (Brierley & Thomas 2002). The zooplankton community associated with sea-ice is dominated by euphausiids, particularly Antarctic krill (*Euphausia superba*; Brierley & Thomas 2002), which forms the main prey for most higher predators in the region (Nicol et al. 2000; Croxall et al. 2002; Fraser & Hofmann 2003; Takahashi et al. 2003). The life history of Antarctic krill is strongly tied to sea-ice (Nicol 2006), which advances and retreats annually under the response of regular climatic variations (e.g. the Southern Oscillation index and Southern Annular Mode; Kwok & Comiso 2002; Trathan et al. 2006; Trathan et al. 2007; Stammerjohn et al. 2008b).

Antarctic krill are a fundamental link in pelagic Antarctic food webs (Boyd & Murray 2001; Reid & Croxall 2001; Nicol 2006), due to their large biomass and reliance on summer phytoplankton blooms in the region for food (Atkinson et al. 2004; Nicol 2006). The main centres of concentrations of Antarctic krill are found over the Antarctic continental shelf slope and around island groups (Nicol 2006). Regionally, the largest concentrations and densities are found in the south Atlantic (Atkinson et al. 2004). The yearly summer standing stock of krill has been broadly linked with the extent of sea-ice in the previous winter (Constable et al. 2003; Atkinson et al. 2004; Smetacek & Nicol 2005). The extent of sea-ice during winter can therefore influence the range and distribution (Burns et al. 2004; Thiele et al. 2004) and reproductive performance (Croxall et al. 1999; Reid & Croxall 2001; Trathan et al. 2007) of higher predators that depend on krill as their main prey.

The distribution of Antarctic krill is limited in its distribution to the north by the PF (Pakhomov et al. 1994; Nicol et al. 2008; Kawaguchi et al. 2010). Higher predators breeding on many sub-Antarctic islands therefore rely on other prey species. In the southern Indian and Pacific Ocean sectors, the PFZ is characterised by discrete, highly productive areas (persistent phytoplankton blooms) centred over large topographical features, such as the Southeast Indian Ridge (SEIR), Kerguelen Plateau (KP) and the Mid-Ocean Ridge (MOR; Sokolov & Rintoul 2007b; Arrigo et al. 2008; Fig. 1.1). Consequently, these regions support a large biomass of predators, such as otariid seals, phocid seals, seabirds and penguins, which breed mainly on islands located within the latitudinal band of the PFZ (Fig. 1.1).

Mesopelagic myctophid fish and squid dominate the mid-trophic levels of the open parts of the Southern Ocean (Collins & Rodhouse 2006; Koubbi et al. 2011; Collins et al. 2012). While myctophid fish and some squid are distributed in Antarctic and sub-Antarctic waters, a more diverse range of species are found closer to the surface and in higher concentrations in the PFZ (Flores et al. 2008; Van de Putte et al. 2010; Koubbi et al. 2011; Collins et al. 2012). The myctophids, a family of diurnally surface migrating mesopelagic fish, are an important trophic link between the meso-zooplankton and higher trophic level predators (seabirds, penguins and marine mammals) and therefore exert considerable control on the transfer of energy within Southern Ocean ecosystems (Pakhomov et al. 1996; Cherel et al. 2010; Koubbi et al. 2011).

In the Indian Ocean sector, species such as Antarctic fur seals and king penguins (*Aptenodytes patagonicus*), breeding on Marion Island, Îles Crozet and Îles Kerguelen, feed almost exclusively on myctophid fish during the summer months (Cherel et al. 1996; Klages & Bester 1998; Lea et al. 2002a). While other smaller or surface feeding predators (other penguin species and seabirds), target crustaceans (mainly euphausiids, calanoid copepods and hyperiid amphipods) in addition to mytophid fish and squid (Pakhomov et al. 1994; Guinet et al. 1996; Bernard et al. 2007). Myctophids are a fatty, high-energy content fish. Together with their high abundance, this makes them an important, easily accessible food resource for predators in summer when their foraging behaviour and distributions are highly constrained by the nutritional status of their partners or offspring (*e.g.* Lea et al. 2002a).

Highly productive foraging areas are also crucial for other higher predators, such as southern elephant seals and Emperor penguins, which fast during the breeding season and annual moult and therefore have highly depleted energy stores (Hindell et al. 1994b; Pütz 1995). Southern elephant seals are numerous, large phocid seals, which breed on subantarctic islands, but migrate to separate non-breeding winter areas to feed for the majority of the year. They travel long distances, often thousands of kilometres, to access prey in highly productive regions of the Southern Ocean, including the PFZ, the Antarctic shelf, the ice edge and the seasonal pack ice (Hindell et al. 1991a; Field et al. 2001; Biuw et al. 2010; Thums et al. 2011). Southern elephant seals therefore spend a considerable amount of their time in the AZ, despite breeding on sub-Antarctic islands (Hindell et al. 2003). Owing to their extraordinary dive capabilities, they can access deep layers of the water column (over 500 m deep; Hindell et al. 1991b; Biuw et al. 2010), which may constitute important over-wintering layers for zooplankton, mesopelagic fish and squid (Flores et al. 2008). Southern elephant seals may therefore occupy a unique trophic niche amongst air-breathing marine predators, feeding on mesopelagic fish and squid deep in the water column that are inaccessible to most air-breathing predators (Cherel et al. 2008; Biuw et al. 2010). They therefore, represent an important top-trophic component of many Southern Ocean ecosystems, particularly during winter when there are low rates of primary production and increased predation pressures from carnivorous macrozooplantkon (*e.g.* copepods, hyperiid amphipods, euphausiids and myctophids, particularly *Electrona antarctica*). These pressures may combine to cause a shift in Antarctic food webs from being bottom-up controlled in summer to top-down controlled in winter (Hunt et al. 2011).

Top-down controls on food webs: ecological implications of climate change

A potential reduction in Antarctic krill in the Western Antarctic Peninsula (WAP) region has been linked to a reduction in sea-ice (Atkinson et al. 2004), mediated through the effects of increased climatic variability in the area (*e.g*. Stammerjohn et al. 2008b). This in turn affects the breeding success of seabird, penguin and marine mammal species that depend on krill as food and may lead to a shift in community structure and associated food webs as higher predators switch from Antarctic krill to other sources of food (Murphy et al. 2007; Trathan et al. 2007). The response of pagophagic predators, such as Adélie (*Pygoscelis adeliae*) and emperor penguins, whose life histories are strongly associated with the sea-ice, is a particular concern (Fraser & Patterson 1997; Jenouvrier et al. 2012). In the WAP, Adélie penguins have exhibited a significant range contraction and are being replaced by other sub-Antarctic open water species, such as gentoo penguins (*P. papua*), by extension of their range southwards (*e.g.* McClintock et al. 2008; McClintock et al. 2010). The projected circumpolar change in winter sea-ice extent and poleward shift of ACC fronts (Stammerjohn et al. 2008a; Sokolov & Rintoul 2009b) is therefore likely to result in other sub-Antarctic open water species migrating further polewards in winter (e.g. king penguins; Thin-billed prion, Pachyptila belcheri; Quillfeldt et al. 2010; Péron et al. 2012).

Knowledge of spatial and temporal variability in the diet and habitat use of Antarctic top predators is required to assess their dependence on lower trophic level resources, particularly krill, and to predict how they may respond to changing environmental conditions. The degree of dietary plasticity of top predators is an important predictor of their resilience to ecosystem change. Of particular importance is information on dietary preferences and habitat use during the non-breeding phase when land-based breeders are unconstrained and no longer behave as central-place foragers (Thiebot et al. 2011). Consequently, their foraging activity or migration strategies are more likely to reflect areas of enhanced prey abundance or accessibility. These areas presumably offer an abundant and predictable source of prey for migratory marine predators (Sydeman et al. 2006) and may therefore constitute critical habitat areas.

Emperor penguins, southern elephant seals and Antarctic fur seals are particularly tractable species for studying these relationships. They are abundant, wide-ranging and important consumers of high biomass species, including krill and several species of fish and squid (Woehler 1995; Guinet et al. 1996; Santos et al. 2001; Hindell et al. 2003). By transferring energy between critical linkages in a trophic system, top predators, such as these, maintain

ecosystem structure and function. Moreover, as wide ranging predators they often move between different water masses during the course of their migrations, enabling nutrient transfer across ecosystem boundaries. Improved knowledge of the spatial and temporal variability in their diet can therefore provide important insights into the structure and function of Southern Ocean ecosystems. Assessment of their diet and habitat use can reveal "biological hotspots" of foraging activity or Areas of Ecological Significance (Hindell et al. 2011). Changes in their foraging behaviour or migration patterns can be a predictor of changes in lower trophic level resources, which are highly susceptible to the effects of climate change and difficult to measure *in situ*.

THE STUDY OF DIET AND HABITAT USE IN SOUTHERN OCEAN MARINE PREDATORS

The development of animal telemetry has greatly improved our understanding of how animals use the Southern Ocean (e.g. Burns et al. 2004; Bailleul et al. 2008; Costa et al. 2010; Friedlaender et al. 2011; Thiebot et al. 2011), but spatially explicit information on diet remains largely unavailable. This is a particular problem for (i) animals that have large foraging ranges (Field et al. 2007b) and (ii) provisioning parents that deliver food to their young, where there may be differences in self provisioning and chick diets (Hodum & Hobson 2000; Cherel 2008; Tierney et al. 2008).

Obtaining direct information on diet in wide ranging, and often deep diving, marine species remains a major challenge (Biuw et al. 2007). Stomach content and faecal analysis have been the primary means for determining the diet and resource partitioning of Southern Ocean marine predators (Hindell et al. 1995; Lea et al. 2002a; Field et al. 2007b). These techniques can yield detailed taxonomic and quantitative data (Slip 1995), but are biased towards the most recent prey intake at the end of foraging trips, and prey hard part structures (or remnants of) that can be visually identified in stomach contents and faeces (Staniland 2002). One alternative is the DNA-based approach, which allows identification of prey species present in samples of stomach contents, vomit and faeces of predators (Jarman et al. 2002). A particular disadvantage of stomach content and faecal analysis, and the DNA-based approach however, is that they are temporally limited to the breeding season, when both study animals and prey items are accessible. Subsequently, these techniques do not provide any indication of dietary variations over the annual migration cycle of animals. It is also difficult to distinguish the diets of provisioning adults and their chicks based on stomach contents, which in some

species may lead to the incorrect assumption that adults feed on the same prey as that fed to chicks.

Stable isotope analysis in protein of tissues

Over the past 20 years, stable isotope ratios of carbon and nitrogen have been increasingly used to trace variation in resource and habitat use of elusive or highly migratory animals, such as marine top predators (Newsome et al. 2012). Their application in dietary studies is based on the fact that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in a predictable manner (Hobson & Clark 1992). Although coarse in taxonomic resolution, the use of naturally occurring ratios of stable isotopes in animal tissues can be a powerful alternative method of dietary analysis. This is because they can yield a data time-series from assimilated, and not just ingested food (Tieszen et al. 1983). Depending on tissue-specific isotopic turnover rates, stable isotope ratios can provide dietary data over days to years and therefore resolve dietary variations at different time-scales (Dalerum & Angerbjörn 2005). Other practical advantages of using stable isotopes are that they do not rely on the recovery of prey hard parts, and so can be sampled easily and non-invasively, with minimal handling time.

Stable isotope ratios of nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) and carbon ($^{13}C/^{12}C$; $\delta^{13}C$) are the main elements used in dietary analyses (see reviews in Peterson & Fry 1987; Gannes et al. 1998; Kelly 2000; Dalerum & Angerbjörn 2005). This is because $\delta^{15}N$ generally exhibits a stepwise and predictable increasewith trophic transfers. Consequently, the $\delta^{15}N$ values in the tissues of consumers tend to be relatively high compared to those of their diets and are therefore used to estimate the diet and trophic position of consumers in a food web (McCutchan et al. 2003; Vanderklift & Ponsard 2003). Stable carbon isotope ratios also increase per trophic transfer, but to a much lesser degree than $\delta^{15}N$ and in the marine environment are mainly used to indicate the foraging habitats of predators (Kelly 2000; McCutchan et al. 2003).

Stable nitrogen and carbon isotope sources (*e.g.* $\delta^{15}N$ and $\delta^{13}C$) at the base of food chains may vary spatially and this is reflected in spatial variability in isotopic composition among food webs (Bearhop et al. 2004). Spatial variability in $\delta^{13}C$ can discriminate between inshore and offshore feeding at a range of spatial scales from oceanic (marine) habitats (Hobson et al. 1994) to lake (freshwater) food webs (Vander Zanden & Rasmussen 1999). Stable carbon values can also differentiate between pelagic and benthic contribution to food intake (Hobson

et al. 1994; Cherel et al. 2011). Inshore/offshore and pelagic/benthic $\delta^{13}C$ gradients have been used as an effective way to investigate the habitats of coastal, neritic and oceanic species of Antarctic fish, with inshore/benthic species having higher $\delta^{13}C$ values than offshore/pelagic species (Cherel et al. 2011). In oceanic waters of the Southern Ocean, there is a latitudinal gradient in particulate organic matter (POM) $\delta^{13}C$ values at the base of the food chain (Rau et al. 1982; Trull & Armand 2001) that is reflected in organisms at higher trophic levels (Cherel & Hobson 2007; Jaeger & Cherel 2011). Geographical $\delta^{13}C$ gradients have therefore been used to investigate the winter foraging areas of Southern Ocean birds and marine mammals (Quillfeldt et al. 2005a; Cherel & Hobson 2007; Jaeger & Cherel 2011).

Stable isotope composition turnover rates vary among tissues, with high rates in tissues such as blood plasma and liver, somewhat lower rates in muscle, and low rates in long-lived tissue such as bone (Tieszen et al. 1983). For otariid, phocid and penguin species, as well as many other avian and mammalian predators, keratinous structures and whole blood are particularly suitable for studying temporal variation in diet. Since keratin is a highly stable structural protein, the $\delta^{13}C$ and $\delta^{15}N$ composition of keratin-based tissues, such as whiskers, remains unchanged after the completion of growth. Thus, whiskers and other keratinous tissues provide a temporal record of feeding dating back several months to years. By comparing the isotope ratios along the length of the whisker with those of suspected prey items, changes in food sources and habitat can be surmised for the temporal span represented by the growth of the whisker. Segmental analysis of whiskers can therefore be applied to study changes in migratory patterns and diet due to environmental change. For example, declining $\delta^{13}C$ values found in the feathers of Thin-billed prions were indicative of a poleward movement, apparently in response to warming sea temperatures (Quillfeldt et al. 2010). Whole blood, on the other hand, provides short- to medium-term dietary signals and can be used to examine diet in discrete temporal windows, including periods outside the limited sampling seasons of traditional dietary methods (Cherel 2008; Tierney et al. 2008).

Interpretation of isotopic data from animals that move between areas of differing isotopic compositions (*e.g.* Schell et al. 1989) however, can be complicated (Hobson 1992), requiring knowledge of a migratory animal's breeding (including haul out sites), wintering and stop over sites. Satellite and archival derived tracking information has been increasingly used in recent (Ambrose & DeNiro 1986)decades to provide such information. The application of

stable isotope techniques to provide spatially explicit dietary information can therefore be greatly enhanced when linked with tracking data (Bentaleb et al. 2011).

The effects of underlying metabolic or physiological variations on isotopic values, in particular the influence of protein balance on $\delta^{15}N$ values, must also be considered when using stable isotopes as dietary tracers (Gannes et al. 1997; Gannes et al. 1998; Rubenstein & Hobson 2004). Protein in the tissues of consumers has a higher $^{15}N/^{14}N$ ratio than dietary protein (Ambrose & DeNiro 1986) due to the preferential excretion of ^{14}N (Gannes et al. 1997). In fasting animals however, the excreted "lighter" nitrogen (^{14}N) is not replaced by dietary nitrogen; therefore, the tissues of fasting animals become progressively ^{15}N enriched as lean body mass decreases (Hobson et al. 1993). For example, fasting for 25 days induced a ^{15}N enrichment in the tissues (blood and feathers) of king penguins thus, leading to an increase in the their apparent trophic level (Cherel et al. 2005a). The effect of fasting on isotopic values of tissues can therefore lead to erroneous interpretations of $\delta^{15}N$ values within the context of feeding ecology. Consideration of an animal's nutritional status must be taken into account when using stable isotopes to elucidate an animal's diet and trophic level.

Study species

Emperor penguins

Distribution and abundance

Emperor penguins are the largest (up to 40 kg) and most abundant penguin species to occur south of the PF in the Southern Ocean (Woehler 1993). They have a circumpolar Antarctic distribution, with recent population estimates of approximately 283 000 breeding pairs, translating to a total population of ~595 000 adult birds among the 46 documented colonies located around the Antarctic coast (Fretwell et al. 2012). The Weddell Sea, Ross Sea and Mawson Coast regions of the Antarctic coast support some of the highest population densities of emperor penguins (Fretwell et al. 2012; Fig. 1.1). The distribution and foraging habits of the species are strongly linked to the fast ice and pack ice (Robertson et al. 1994; Kooyman et al. 2000). Emperor penguins breed on fast ice during the winter, and feed in the surrounding pack ice (Robertson et al. 1994). Individuals travel long distances across the fast ice to feed, often targeting ice-free areas, such as polynyas within the pack ice (Ancel et al. 1992) in outer continental shelf and shelf slope waters (Kirkwood & Robertson 1997a; Wienecke & Robertson 1997; Zimmer et al. 2008). Unlike other penguin species, emperor penguins (and Adélie penguins) do not moult near breeding colonies, because the fast ice on which they

breed starts to break up and disintegrate in summer when breeding adults moult. Instead, birds typically find moult refuges within the pack ice, which affords a stable platform to remain dry for the next 2 to 4 weeks (Kooyman et al. 2000).

Breeding biology

Emperor penguins are unique amongst the community of Southern Ocean seals, penguins and seabirds in that they breed and rear their offspring during the Antarctic winter and spring (Robertson et al. 1994). This ensures that chicks fledge in early December, when weather conditions are most favourable and the fast ice breaks up, making prey more accessible in adjacent coastal areas (Kirkwood & Robertson 1997a). The breeding season begins in early autumn when males and females return to colonies to court, followed by females laying a single egg. In late autumn, females leave the colony to forage at sea for two months, leaving the egg with their partner to incubate over the ensuing winter period. Females return to colonies at the time of egg hatching, which usually takes place in July (Kirkwood & Robertson 1997b). Females then take over chick-rearing duties from their partners which by this time have been fasting for at least four months (Prévost 1961). Emperor penguins have the longest chick-rearing period of any Southern Ocean seabird or penguin (approximately five months), and subsequently, adult emperor penguins spend much of the year in the vicinity of the colonies. During the chick-rearing period (mid-winter to early summer) parents alternate between foraging at sea and provisioning their chicks. Adults must therefore catch sufficient prey to provision their chicks as well as themselves (Robertson et al. 1994; Kirkwood & Robertson 1997b).

Foraging ecology

The dietary preferences and aspects of foraging behaviour of emperor penguins are subject to substantial geographic variation. Overall, the diet of emperor penguins typically comprises varying proportions of crustaceans (mainly Antarctic krill and amphipods), nototheniid fish (mainly *Plueragramma antatrcticum*) and squid (mainly Psychroteuthis glacialis; Kirkwood & Robertson 1997a; Cherel & Kooyman 1998). In Adélie Land, Amanda Bay and the Ross Sea, the diet of emperor penguins is dominated by fish, accounting for 88 to 97% (wet mass) of the diet (Offredo & Ridoux 1986; Gales et al. 1990; Cherel & Kooyman 1998). Fish are also an important component of the diet in the eastern Weddell Sea and on the Mawson Coast (Auster and Taylor Glacier), accounting for 27 to 75% (wet mass) of the food of birds (Klages 1989; Robertson et al. 1994; Pütz 1995; Kirkwood & Robertson 1997a). The

notothenid *P. antarcticum* is the main fish prey in the Ross Sea (Cherel & Kooyman 1998), Amanda Bay (Gales et al. 1990) and the eastern Weddell Sea (Klages 1989), and most likely in Adélie Land (Offredo & Ridoux 1986). *Pleuragramma antarcticum* also predominated in the diet of emperor penguins from the Mawson Coast in winter 1993 (Kirkwood & Robertson 1997a), but birds mainly consumed the larger notothenid *Trematomus eulepidotus* during spring 1988 (Robertson et al. 1994). The proportion of squid in the diet of emperor penguins ranges from 3% (wet mass) in Adélie Land (Offredo & Ridoux 1986) to 69% at Taylor glacier on the Mawson Coast (Klages 1989; Gales et al. 1990; Robertson et al. 1994; Cherel & Kooyman 1998) and 75% in diet samples collected in the Weddell Sea (Ainley et al. 1992). Antarctic krill account for a significant part of the diet (25 to 70% by wet mass) of emperor penguins at the Auster colony in winter and in the Weddell Sea in spring and summer (Klages 1989; Pütz 1995; Kirkwood & Robertson 1997a). Seasonal variability in the diet and foraging behaviour of emperor penguins during winter and spring at Auster and Taylor Glacier colonies was found to be influenced by fluctuating sea-ice conditions, differences in available prey, changes in day -length toward summer and increasing demands of the growing chicks (Kirkwood & Robertson 1997b). During summer, however, when sea-ice limitations diminish and adult birds no longer behave as central-place foragers, their dietary preferences and foraging behaviour are still largely unknown (Pütz 1995).

Southern elephant seals

Distribution and abundance

Southern elephant seals are one of two species of elephant seal, the other found in the Northern Hemisphere (northern elephant seals, *M. angustirostris*; Le Boeuf & Laws 2007). In the Southern Ocean, there are four genetically distinct stocks of southern elephant seals, including the Peninsula Valdés population in Argentina, the South Georgia population in the southern Atlantic Ocean, the Îles Kerguelen population in the southern Indian Ocean and the Macquarie Island population in the southern Pacific Ocean (Slade et al. 1998). The main breeding colonies for these populations are located on Peninsula Valdés, South Georgia Island, Heard Island, Îles Kerguelen, and Macquarie Island, respectively (Fig. 1.1). Southern elephant seals haul out on sub-Antarctic beaches at least twice a year to breed and to moult. When seals are not hauled out, they make long-distance foraging migrations of up to 5000 km, utilising large parts of the Southern Ocean. The foraging range of some individuals can encompass waters north of the PFZ to high Antarctic waters over the continental shelf (Hindell et al. 1991a). Juvenile seals show ontogenetic shifts in habitat use, with younger

seals using a smaller total area and travelling shorter distances than older seals (Field et al. 2005). There is also some sexual segregation in habitat use between adults, with males tending to feed in more southerly waters associated with the Antarctic continental shelf (Hindell et al. 1991a; Campagna et al. 1999; Bailleul et al. 2007; Tosh et al. 2009).

During the 19th century, following the demise of the fur seal industry, southern elephant seals were hunted extensively and their numbers were significantly reduced in the southern Indian and Pacific Ocean sectors (Croxall et al. 1992). Sealing at Macquarie Island ceased in 1919 and by the 1950s the population had recovered, with numbers (183 000) estimated to be over 50% above pre-exploitation levels (Hindell & Burton 1988). Populations in the southern Indian and Pacific Ocean sectors have experienced significant declines since the 1950s and 1960s, whereas populations in the southern Atlantic have remained stable or are increasing (McMahon et al. 2005a). At Macquarie Island, it was estimated that the population had declined by 59% from 1949 to 2001 (76 000; McMahon et al. 2005a and references therein). While the reasons for these declines have been broadly attributed to changes in food supply (Hindell 1991; McMahon et al. 2003), the proximal mechanisms are still not understood (McMahon et al. 2005b; Field et al. 2007b; Newland et al. 2009).

Breeding biology

The annual breeding cycle begins when the largest male southern elephant seals haul out in August. Females then arrive in large numbers and give birth to a single pup 2 to 5 days later. Mothers stay with their offspring throughout the lactation process providing a continuous supply of milk to their offspring. During this time, mothers rely on the energy stores in their blubber to sustain them and provide milk. Southern elephant seal mothers wean their pups after feeding them for about 24 days (Arnbom et al. 1993). During this very short time the pup can quadruple in weight, due to the large fat stores accumulated as blubber (Hindell et al. 1994a). At weaning, mothers depart for remote feeding grounds leaving pups to spend the next 3 to 8 weeks on breeding beaches, before they too depart on their initial foraging migration. During the post-weaning period on beaches, pups do not feed but draw on the fat reserves stored in their blubber for energy.

Foraging ecology

The life history of southern elephant seals is strongly linked to the marine environment where they spend up to 80% of their annual life-cycle. While fish and squid are thought to comprise

an important part of the diet of southern elephant seals (Rodhouse et al. 1992b; Green & Burton 1993; Slip 1995; Daneri & Carlini 2002; Field et al. 2007b), what they feed on during long distance migrations remains largely undocumented due to spatial and temporal separation in feeding and haul out sites. Southern elephant seals are deep diving marine predators, capable of reaching depths in excess of 1400 m (Hindell et al. 1991b) to exploit prey resources deep in the water column, such as large mesopelagic fish and deep-water squid (Rodhouse et al. 1992b).

Southern elephant seals exhibit a range of migration and diving strategies from pelagic dives within the open waters of the ACC to demersal foraging over continental shelves in the east Antarctic and WAP regions (Hindell et al. 1991b; Biuw et al. 2007). Recent studies have demonstrated that the movements and foraging activity of southern elephant seals can be strongly influenced by environmental features such as fronts, eddies, ice distribution and sub-surface hydrographic regimes which act to concentrate prey species (Bornemann et al. 2000b; Field et al. 2001; Campagna et al. 2006; Bailleul et al. 2010a; Biuw et al. 2010). Southern elephant seals are regarded as generalist feeders, with geographical (Green et al. 1998; Daneri et al. 2000), seasonal (Bradshaw et al. 2003) and age-related differences in diet composition between adults and juveniles (Slip 1995; Field et al. 2007; Newland et al. 2011). First-year survival (70-80%) is a key demographic parameter (McMahon et al. 2005b), and habitat and diet of young animals differs considerably from adults (McMahon et al. 2005a). To date however, there has been no study that assesses the diet and foraging locations of young pups concurrently with their crucial first trip to sea.

Antarctic fur seals

Distribution and abundance

Antarctic fur seals are highly abundant Southern Ocean predators breeding mainly on islands south of the Polar Front. The principal breeding sites are in the South Shetland Islands, South Georgia and Bouvetoya in the southern Atlantic Ocean, Marion Island, Îles Crozet, Îles Kerguelen and Heard Island in the Indian Ocean, and at Macquarie Island in the Pacific Ocean (Fig. 1.1). South Georgia supports the largest breeding population, holding more than 95% of the world population (Croxall et al. 1992). During the early 19th century the species was commercially exploited for fur to the point of extinction throughout its geographical range (Bonner & Laws 1964). Recovery of the species started around 1940 at South Georgia

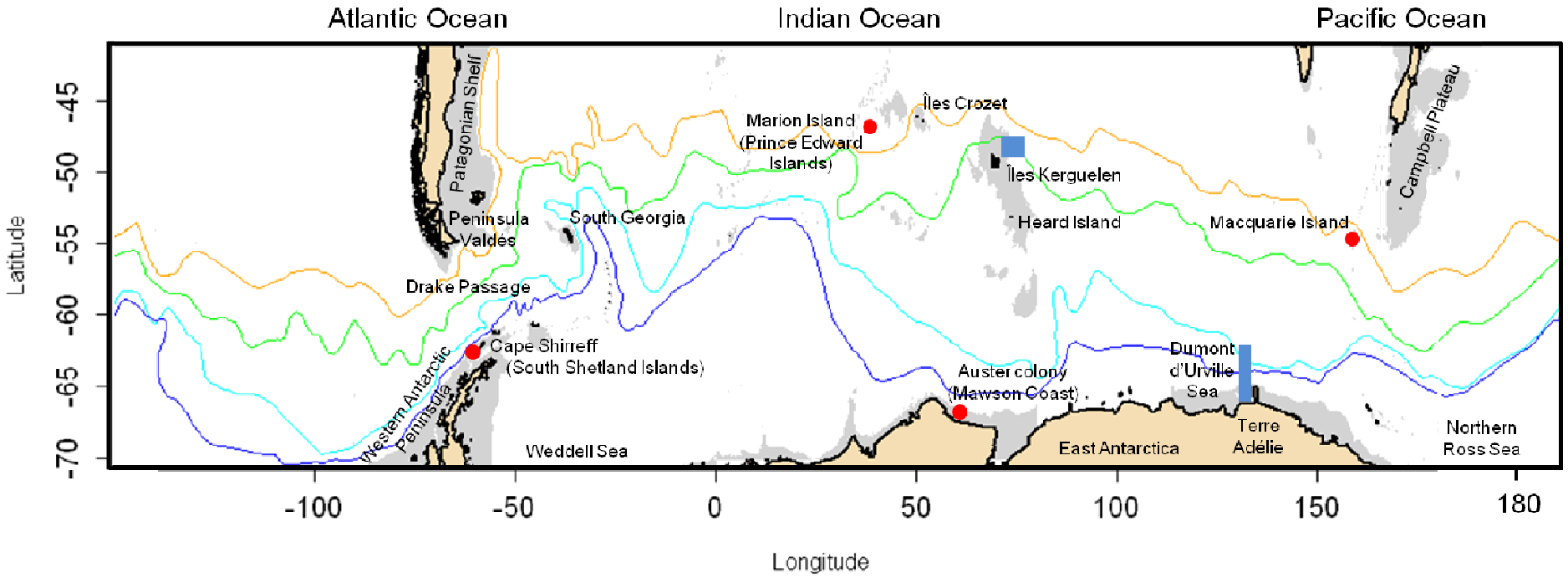

Figure 1.1. Emperor penguin, southern elephant seal and Antarctic fur seal study sites. Emperor penguins: Auster colony on the Mawson Coast, Antarctica, Indian Ocean; southern elephant seals: Macquarie Island in the southern Pacific Ocean; Antarctic fur seals: Marion Island in the Prince Edward Islands in the southern Indian Ocean and Cape Shirreff, Livingston Island in the South Shetland Islands, Western Antarctic Peninsula, southern Atlantic Ocean. Blue shapes: the sampling sites of other Southern Ocean marine organisms, including myctophid fish to the north-east of Îles Kerguelen and crustaceans, fish and squid from north of Terre Adélie to the Dumont d'Urville Sea in the southern Indian Ocean. Coloured lines indicate the location of the Antarctic Circumpolar Current (ACC) fronts. Orange: Sub-Antarctic Front (SAF); green: the Polar Front (PF); light blue: the southern ACC Front (SACCF), and dark blue: southern Boundary of the SACCF (sBdy).

(Croxall et al. 1992), and since this time populations elsewhere have also increased, including in the South Shetland Islands (~19 000 individuals; Bengtson et al. 1990), Îles Kerguelen (Guinet et al. 1996) and Heard Island (Shaughnessy et al. 1988).

Breeding biology

The annual breeding cycle begins when adult males arrive at breeding colonies in late October to early November to establish territories. Females generally arrive at breeding colonies in late November to early December and give birth to a single pup within a few days of arrival (Doidge et al. 1986). Pups are reared over the austral summer, and unlike southern elephant seal mothers which remain with their pups until weaning (up to 24 days), Antarctic fur seal mothers have episodic periods ashore with their offspring between longer periods at sea while they forage (Gentry & Kooyman 1986). Antarctic fur seals therefore rear their single pup during a longer period of approximately four months, with weaning usually taking place by late March to mid-April (Doidge et al. 1986; Robinson et al. 2002). Over the course of the lactation period, Antarctic fur seal mothers spend longer both at sea and ashore (Doidge et al. 1986). They therefore meet the high energetic requirements of their rapidly growing pups by increasing their time at sea feeding and on land to supply milk to their offspring (Doidge et al. 1986; Costa et al. 1989; McCafferty et al. 1998; Robinson et al. 2002).

Foraging ecology

Antarctic fur seals show considerable variability in diet and foraging behaviour throughout their geographical range. In the Atlantic Ocean sector, where the vast majority of the population lives and breeds, the summer diet is dominated by Antarctic krill at South Georgia and Bouvetoya (Doidge & Croxall 1985; Reid 1995; Reid & Arnould 1996), while Antarctic krill, mesopelagic fish (myctophids), nototheniid fish and some squid comprise the diet at South Shetland Islands (Casaux et al. 1998; Osman et al. 2004) and other populations in the WAP region (Daneri 1996; Daneri & Carlini 1999; Casaux et al. 2003a; Casaux et al. 2003b). In the Indian and Pacific Ocean sectors, the diet of sub-Antarctic breeding populations is largely comprised of myctophid fish and squid, including at Marion Island (Condy 1981; Klages & Bester 1998; Makhado et al. 2008), Îles Crozet (Cherel et al. 2007), Îles Kerguelen (Lea et al. 2002a), Heard Island (Green et al. 1989) and Macquarie Island (Goldsworthy et al. 1997).

At South Georgia, the diving activity of seals is shallower at night (up to 30 m) than during the day (40-75 m) in response to the vertical distribution of their main prey, Antarctic krill (Croxall et al. 1985). Seals forage over the Antarctic continental shelf slope and beyond up to 350 km from the colony (Boyd et al. 1998). At Cape Shirreff, South Shetland Islands the foraging range and dive behaviour of seals varies in response to bathymetry and prey type (Goebel et al. 2000). At sites where fish and squid comprise a large part of the diet the foraging ecology of seals is more variable. At sites where the shelf is wide (*e.g.* Heard Island and Îles Kerguelen in the Indian Ocean), benthic prey items, such as nototheniids, appear to be more important in the diet than at localities where the shelf is narrow (*e.g.* Macquarie Island and Marion Island in the Pacific and Indian sectors, respectively) and myctophids dominate the diet (Goldsworthy et al. 1997; Klages & Bester 1998). Fish species generally found closer inshore are largely absent from the diet at Marion Island, suggesting feeding occurs further offshore in deeper, oceanic waters than at other sites (Goldsworthy et al. 1997; Green 1997; Klages & Bester 1998). While the diet and foraging behaviour of seals during summer has been shown to vary geographically and inter-annually in response to changes in prey availability and physical factors (Boyd et al. 1994b; Lea et al. 2002a; Lea & Dubroca 2003), the diet and feeding behaviour of seals during the non-breeding winter period has not been studied.

AIMS

Understanding the effects of climate change on Southern Ocean ecosystems, including changes in marine resources and biodiversity and ecosystem plasticity, requires data on the abundance, distribution and diet of high order predators. The overarching aim of this thesis was to quantify the diet and trophic relationships of key Southern Ocean predator species; the emperor penguin, southern elephant seal and the Antarctic fur seal, during times of year that are often difficult to measure *in situ*. Since these species are abundant, wide-ranging and important consumers of high biomass species (including krill, fish and squid) they are particularly good subjects for examining linkages between diet, season and habitat use.

The following three key objectives were addressed in order to examine the trophic linkages of predators within Southern Ocean marine ecosystems, particularly in relation to krill predation:

1. Can telemetry derived sources of information of far ranging predator species be integrated with isotope data from their tissues to estimate diet and habitat use effectively?

2. Can predator isotopic signals be used to assess temporal and spatial variability in resource partitioning (fish, squid or krill) for a variety of avian and mammalian predators?

3. Can predator isotopic signals be used to quantify differences in the timing and importance of krill consumption amongst predators? The outcome of this objective has important implications for the management of krill stocks and predator populations which depend on them.

THESIS STRUCTURE

The thesis has been written as a series of separate manuscripts and consequently some textual overlap occurs between chapters. The thesis consists of three chapters describing aspects of the foraging ecology of each species, which are brought together and synthesized in a final discussion chapter. The contribution of co--authors is outlined in the Statement of Co-authorship at the start of the thesis. A single bibliography is presented at the end of the thesis using the Journal of Animal Ecology referencing style.

2. Seasonal and inter-specific variation in the diet of breeding emperor penguins as inferred by stable isotopes

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ABSTRACT

Knowledge of spatial and temporal variability in the diet and habitat use of Antarctic top predators is required to assess their dependence on lower trophic level resources, and to predict how they may respond to changing environmental conditions. Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for whole blood and multi-source stable isotope mixing models using SIAR (Stable Isotope Analysis in R) were used to define the trophic position and diet of emperor penguin (*Aptenodytes forsteri*) adults (n=96) and chicks (n=60) from the Auster colony, Mawson Coast (67°23'S, 64°04' E). Penguins were sampled during courtship/egg-laying (May), egg-hatching (August), early (September/October) and late chick-rearing (November) periods in 2008. Stable isotope ratios for blood reflected the use of high Antarctic waters during the non-breeding and breeding periods. Seasonal and inter-specific variation in trophic position and diet were identified using the stable isotope values of penguins and prey. In the winter, when males remain in the colony to incubate eggs, the isotopic signature of females foraging at-sea indicated increased importance of higher trophic level prey (fish and squid) from autumn to winter, concurrent with a shift in $\delta^{15}N$ from 11.2 to 11.8‰. Segregation of isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for male and female adult emperor penguins indicates different feeding ecology during autumn and spring. Stable carbon isotope values suggest spatial variation in foraging habitat between sexes, while sex and season differences in the trophic position and diet of adults can be inferred from variability in $\delta^{15}N$ values. In the spring, when parents alternate feeding their chicks and foraging, segregation of $\delta^{15}N$ signatures between adults and chicks indicates that adults consumed both crustaceans, fish and squid (10.6‰), but also fed higher trophic level prey (fish and squid) to their young (11.4‰). Antarctic krill (*Euphausia superba*) collected at several sites to compare inshore versus offshore isotopic values, were increasingly enriched in ^{13}C from oceanic (-28.1±0.5‰) and shelf slope waters (-27.8±0.6‰,) to outer (-26.9±0.4‰) and medium-shelf waters (-25.8±1.0‰). However, the reverse was true for $\delta^{15}N$ values, with a 3.3‰ increase from oceanic to medium-shelf waters. The results of this study highlight the utility of stable isotope analysis to study changes in diet and habitat use of emperor penguins, particularly during periods when data cannot be acquired any other way.

INTRODUCTION

As a pagophilic marine predator, the emperor penguin (*Aptenodytes forsteri*) uses sea-ice for breeding, foraging and moulting habitat. As such, the species is highly susceptible to climate related changes in sea-ice distribution (Jenouvrier et al. 2009; Jenouvrier et al. 2012). This in turn may also change community food web structure influencing emperor penguin diet (Barbraud & Weimerskirch 2001; Croxall et al. 2002; Ainley et al. 2005; Forcada & Trathan 2009). Understanding the winter diet and trophic relationships of the emperor penguin is therefore critical to interpreting how reduction in the extent and seasonal duration of sea-ice (Stammerjohn et al. 2008a; Massom & Stammerjohn 2010) will influence the range and distribution of the species and their principal prey, namely Antarctic krill (*Euphausia superba*).

The sea-ice environment is an integral part of the Antarctic marine ecosystem (Tynan 1998; Fraser & Hofmann 2003; Atkinson et al. 2004; Arrigo et al. 2008), providing important nursery grounds for zooplankton, and in particular, Antarctic krill. During the winter breeding and spring chick rearing periods, the foraging range of emperor penguins is constrained to sea-ice habitat in high Antarctic waters (Ancel et al. 1992; Kirkwood & Robertson 1997a; Wienecke & Robertson 1997; Rodary et al. 2000; Zimmer et al. 2008). Individuals travel long distances across the fast-ice to feed exclusively at sea. Penguins often target ice-free areas, such as polynas within the pack-ice zone (Ancel et al. 1992) in outer continental shelf and shelf slope waters, located in excess of 100 km from breeding colonies (Kirkwood & Robertson 1997a; Wienecke & Robertson 1997; Zimmer et al. 2008).

In outer continental shelf and shelf slope waters (200-500m deep), Antarctic krill, notothenioid fishes, particularly Antarctic silver fish (*Pleuragramma antarcticum*) and the glacial squid (*Psychroteuthis glacialis*) are important prey sources for foraging penguins (Kirkwood & Robertson 1997b; Kirkwood & Robertson 1997a; Wienecke & Robertson 1997; Cherel 2008). Over the course of the winter breeding and chick rearing periods, changing environmental conditions, *i.e.* advance and retreat of the seasonal sea-ice zone, day-length and ambient temperatures, affects the seasonal availability and abundance of prey species in an individual's foraging range (Kirkwood & Robertson 1997b; Kirkwood & Robertson 1997a; Wienecke & Robertson 1997). Intrinsic factors, such as sex, body condition and reproductive status also shapes the way an individual forages (Kirkwood & Robertson 1997b; Wienecke & Robertson 1997; Rodary et al. 2000; Kooyman et al. 2004; Zimmer et al. 2008).

Consequently, it remains unclear to what extent emperor penguins rely on Antarctic krill in the winter months; information of which is critical to assess the species potential response to changes in krill abundance. At-sea foraging by emperor penguins affords little opportunity for the direct observation of feeding and subsequently indirect sampling methods (*e.g.* stomach content and fecal analysis) are used for the purpose of estimating diet composition. Thus, investigation of feeding habits over long temporal scales (months) is impeded by sampling constraints (*i.e.* temporal mis-match between feeding and sampling, differential digestive rates and the retention of prey hard parts in the stomachs of individuals).

To compare the trophic position and diet of penguins from the same locality between three consecutive seasons (during the same year), we used isotopic ratios in the tissues of birds and of their potential prey, including Antarctic krill collected in shelf, shelf slope and oceanic waters. Isotopic dietary tracers integrate the diet of a consumer over ecologically significant periods of time (for example months; Quillfeldt et al. 2005a; Cherel 2008). Stable isotope ratios of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) are typically used in dietary studies because the $\delta^{13}C$ and $\delta^{15}N$ ratios in the tissues of consumers reflect those of its dietary components assimilated in a reliable and predictable manner (DeNiro & Epstein 1978; DeNiro & Epstein 1981). The abundance of $\delta^{13}C$ does not alter significantly within a food web and reflects the source of carbon at the base of the food chain (DeNiro & Epstein 1978; McCutchan *et al.* 2003), while step-wise ^{15}N enrichment along food chains (Minagawa & Wada 1984; McCutchan et al. 2003) facilitates the use of $\delta^{15}N$ to estimate trophic position (Hobson 1992). Thus, by measuring the abundance differences of ^{15}N or ^{13}C in consumers' tissues, trophic relationships between organisms within an ecosystem may be determined (Gannes et al. 1998). Moreover, there is well defined $\delta^{13}C$ gradient between inshore/neritic and offshore/oceanic Antarctic phytoplankton (Trull & Armand 2001), which is transferred to higher levels within a food web (Cherel et al. 2011). Thus, the isotopic signatures of Antarctic krill collected at several sites from open-water to over-the-shelf in this study can be used to compare inshore versus offshore isotopic values, which has not been done yet for this important Antarctic prey species. The objectives of this study were to: (1) define the trophic position of breeding emperor penguins from the Auster colony, Mawson Coast during breeding and non-breeding periods; and (2) identify seasonal changes in diet composition using the stable isotope values of penguin blood and potential prey to build a series of isotopic mixing models; (3) compare the inshore (over-the-shelf) versus offshore (open water)

isotopic values of Antarctic krill, and (4) compare stable isotope values of adults and chicks during late chick-rearing to investigate if adults fed on the same prey as those fed to chicks.

METHODS

Study site and sample collection

The study was conducted at the Auster colony (67°23'S, 64°04' E), located on the fast sea-ice on the Mawson Coast, Antarctica, during the breeding and chick-rearing period in winter/spring in 2008. Sampling was done during four different stages:

1) *Courtship and egg-laying (females and males, May).* The May sampling period was following a long period of feeding at sea by adult penguins and a short fasting period. The penguins go to sea in early to mid-January after the moult period and spend the next 3-4 months building up fat reserves for the winter. Individuals without eggs were captured and sampled in the second half of May. Birds had been fasting since their arrival at the colony.

2) *Egg hatching (females and males, August).* Prior to the second sampling period in August, male birds had remained at the colony to incubate eggs and were therefore, sampled after their extended winter fast which lasted for at least 62 days (the incubation period). Females on the other hand, had departed the colony in late May to forage at sea for 2 months for self-maintenance and were thus sampled when they returned to take over chick brooding and feeding duties from the males. Females were estimated to have walked approximately 60 km from the nearest open water to the colony and thus had fasted for approximately 2-6 days prior to sampling. Females were sampled before they changed over with their mates.

3) *Early chick-rearing (young chicks, September/October.).* The third sampling period in late September/early October was of early chicks only. All were independent of the parents' feet, but 4-6 weeks old. The first recorded chick in the colony was on 15th July, 6 weeks before sampling began on 28th September.

4) *Late chick-rearing (females, males and older chicks, November).* In the final sampling period, the adults were sampled at random and had either been alternating feeding a chick, or were without a chick and had recently been foraging. At the time of sampling the chicks were approximately 4 weeks before fledging (approx. 8-19 weeks old) and had only received food from their parents directly.

In each sampling period, individuals were caught by hand with the aid of a 'shepherd's crook'. Adults were wrapped in a custom-made restraint and blood samples were obtained from the

ulnar vein in the right flipper. Chicks did not require the wrap. Whole blood samples were immediately frozen and stored at -20°C until isotopic analysis. A second blood sample was allowed to clot for at least 4 hours and then spun down to harvest the serum for another study. The cell portions of those samples were preserved with Queen's Lysis buffer (0.01M Tris pH8.0, 0.01M NaCl, 0.01M EDTA, 2% SDS) for the DNA sex determinations.

Each sampling group was independent, with no paired samples in this study, *i.e.* no chicks and parent or two sequential samples from the same adult in different samples. Due to the temporal integration of whole blood in penguins (27-45 d; Cherel et al. 2007), we considered that the isotopic signature of whole blood represented the isotopic niche of the penguins in the last 1-2 months preceding sampling.

DNA sex determination of emperor penguins

The DNA sex determinations of emperor penguins (adults and older chicks) were carried out using the same PCR method and primers (P2 and P8) as described in Griffiths et al. (1998). Briefly, a subsample of the preserved cell fraction was spotted onto FTA cards (™Whatman Inc.) for analysis. For each sample, a 2 mm punch was treated and washed. The primers P2 and P8 as described in Griffiths et al. (1998) were used as well as the temperature cycle they used for PCR. After completing the PCR cycles, the Lightcycler 480 analyses the PCR products by determining their melting point(s). Males show a single peak of PCR product whereas females give 2 peaks. Each result was inspected to make the final determination of sex from the sample.

Isotopic signatures of potential prey species

A list of the main prey species of emperor penguins from the Auster colony, Mawson coast, including fish, squid and Antarctic krill, was compiled from Robertson et al. (1994), Kirkwood and Robertson (1997b; 1997a) and Wienecke and Robertson (1997) and each species assigned a $\delta^{13}C$ and $\delta^{15}N$ value (Appendix A). The isotopic values for Antarctic krill were obtained from the Japanese TRV *Umitaka maru* using pelagic trawls (International Young Gadoid Pelagic Trawl, IYGPT, and Rectangular Midwater Trawl, RMT) in the Dumont d'Urville Sea as part of the Collaborative East Antarctic Marine Census (CEAMARC) in January/February 2008 (Hosie et al. 2011). Antarctic krill were collected at six stations along a transect from Terre Adélie to the Mertz Glacier tongue, in George V Land (61°45' to 67°30'S, 140° to 143°E) ranging from open water to over-the-shelf to compare offshore versus inshore $\delta^{13}C$ and $\delta^{15}N$ values. Samples

were sorted and identified on deck and stored in 70% ethanol until isotopic analysis. In the laboratory, Antarctic krill samples were measured to the nearest 0.1 mm with calipers (standard length, SL), and the age, sex and condition (*e.g.* gravid or spent females) of individuals determined.

We used published isotopic values for fish (Krahn et al. 2006; Cherel 2008; Cherel et al. 2011; Polito et al. 2011; this study) and squid (Zimmer et al. 2007; Bury et al. 2008; this study). Chitinized squid beaks are impoverished in ^{15}N when compared to protein (Cherel & Hobson 2005; Cherel et al. 2009a). Consequently, beak $\delta^{15}N$ values must be corrected to allow comparison with other organisms. A correction factor of 3.5‰ (Cherel et al. 2009a) was therefore applied to the beak $\delta^{15}N$ values of *Alluroteuthis antarcticus* taken from Zimmer et al. (2007; Appendix A).

Isotopic analysis

For isotopic analysis, we randomly chose 20-40 emperor penguin whole blood samples for each sampling period (n=160). Samples were thawed before been vortexed to fully homogenize samples. Approximately 0.5-1 ml was subsampled into 1.5 ml screw cap vials, weighed, dried in an oven at 60˚C for a minimum of 24 hrs and then re-weighed. Whole specimens of Antarctic krill were freeze dried and ground to a fine powder before lipids and carbonates were removed following the methods in Kojadinovic et al. (2008) and Hobson and Cherel (2006), respectively. Lipids are depleted in ^{13}C relative to protein and carbohydrates (DeNiro & Epstein 1978; Tieszen et al. 1983) thus, the use of delipidated samples allows the comparison of $\delta^{13}C$ signatures among individuals and species of different lipid contents. The low lipid content of whole blood does not usually require the removal of lipids (Cherel et al. 2005b), as verified in this study by the consistently low C:N ratio (<4) of samples (Table 2.1.) which serves as a measure of lipid content in animal tissue (Post et al. 2007). Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass, UK) continuous-flow isotope-ratio mass spectrometer. Results are reported using standard δ notation in parts per thousand (‰) relative to Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric N^2 (Air) for $\delta^{15}N$ as follows:

$$\delta X = [(R_{samples}/R_{standard}) - 1] \times 1000$$

where δX is $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Replicate measurements of internal laboratory standards (Alanine) indicate measurement errors < 0.20‰ and < 0.21‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope analysis was performed by the Environmental Biology Group, Research School of Biological Sciences, Australian National University (ANU), Canberra, Australia.

Statistical analyses

All data were analysed using R (R Development Core Team 2012) and Primer 6 (Clarke & Gorley 2006). To analyse the effects of stage, sex and age on dependant variables ($\delta^{13}C$ and $\delta^{15}N$ concentrations) we used linear models fitted with the *lm* function in R. We first examined data for normality. If the distribution was significantly different to normality, we log transformed the data. For adult penguins, only courtship/egg-laying and late chick-rearing were tested for stage and sex effects, while females sampled in courtship/egg-laying, egg-hatching and late chick-rearing were tested for stage effects. The isotopic values of adults and chicks were compared for the November sample. We used Analysis of Variance (ANOVA) along with Tukey's Honestly Significant Difference (HSD) post-hoc analysis to indicate where response variables differed.

To analyse spatial differences in $\delta^{13}C$ and $\delta^{15}N$ values of Antarctic krill we used linear models. Sampling location (medium- and outer-shelf, shelf slope and oceanic) was a factor and $\delta^{13}C$ and $\delta^{15}N$ values were the dependent variables. We assessed significance for statistical tests at the 0.05 level. Values are presented as mean ±SD.

Isotopic mixing models

To estimate the diet composition of emperor penguins during different stages of the breeding and chick-rearing period we used a multi-source isotopic mixing model in the SIAR (Stable Isotope Analysis in R) package in R by Parnell and Jackson. The SIAR model provides probability distributions for multiple source contributions to a mixture that account for the observed variability in the isotopic signatures for the sources as well as the mixture. The model also accounts for variation in diet-tissue fractionation by allowing the user to specify fractionation values (Parnell et al. 2010). We assumed that the diet-tissue fractionation values between whole blood and lipid-free whole prey were +0.02‰ and +2.72‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and +0.46‰ and +1.86‰ for $\delta^{13}C$ and $\delta^{15}N$ values between whole blood and lipid-free muscle, respectively (Cherel et al. 2005b).

To better characterise the isotopic values of potential prey species included in the models, we applied a Hierarchical Cluster Analysis using the mean and variance for species. Isotopic groupings resulting from the analysis were assigned to ecological groups (benthic, pelagic, etc.). To test if there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between prey groups resulting from the cluster analysis, we used one-way Analysis of Similarities (ANOSIM) tests (Global R) based on a Euclidean distance matrix using 999 permutations (Clarke 1993). The mean and standard deviation for $\delta^{13}C$ and $\delta^{15}N$ values of each of the prey groups identified by the cluster analysis were included in the models.

RESULTS

Isotopic signatures of adult emperor penguins

Carbon ($\delta^{13}C$) values. Stable carbon values were low for all adult penguins sampled during courtship/egg-laying, egg hatching and late chick-rearing (Table 2.1.). Whole blood $\delta^{13}C$ values ranged from -25.1 to -22.4‰, with females having the greatest range of values. Preliminary examination of the data showed the range in $\delta^{13}C$ values for females was driven by a single individual sampled during courtship/egg-laying (-22.4‰; Table 2.1.). We therefore, removed this sample from the data prior to statistical analysis.

Average $\delta^{13}C$ values ranged from -24.3±0.3‰ and -24.0±0.3‰ for females and males in courtship/egg-laying, respectively, and from -24.5±0.3‰ and -24.2±0.5‰ for females and males in late chick-rearing, respectively. A significant difference in $\delta^{13}C$ values was found between sexes (Females: -24.3±0.3‰; Males: -24.1±0.4‰; ANOVA: $F_{1,54} = 8.38$, $P = 0.01$), indicating spatial variability in foraging habitat between sexes (Fig. 2.1.). There was no overall significant difference in $\delta^{13}C$ values among stages and there was no interaction between stage and sex (Stage: $F_{1,54}=1.76$, $P > 0.05$; Stage x Sex: $F_{1,54} = 0.03$, $P > 0.05$).

The $\delta^{13}C$ values of females sampled during egg hatching (Table 2.1.) were significantly different to those of females sampled during courtship/egg-laying and late chick-rearing (ANOVA: $F_{2,56} = 35.64$, $P < 0.0001$; Tukey's HSD post-hoc analyses, both $P < 0.0001$; Table 2.1.), with females during egg hatching relatively 13C enriched (-23.7±0.2‰) compared to females during courtship/egg-laying (-24.2±0.5‰) and late chick-rearing (-24.5±0.3‰; Fig. 2.1.).

Nitrogen ($\delta^{15}N$) values. The nitrogen values of adult penguins encompassed a range of 2.7‰ (Table 2.1.). A difference of ~3‰ in $\delta^{15}N$ values reflects one trophic level of difference between some adult penguins. Average $\delta^{15}N$ values ranged from 11.2±0.7‰ and 10.6±0.5‰ for females and males sampled during courtship/egg-laying, respectively, and from 10.5±0.5‰ and 10.6±0.6‰ during late chick-rearing, respectively. Stage and sex were both significant in explaining variation in $\delta^{15}N$ values of adult penguins (Stage: $F_{1,54} = 7.56$, $P = 0.01$; Sex: $F_{1,54} = 4.54$, $P = 0.04$),

Table 2.1. The $\delta^{13}C$ and $\delta^{15}N$ signatures (means ± standard deviation and range) and C/N ratios of adult and chick emperor penguin whole blood sampled at various stages of the austral winter period at the Auster colony, Mawson Coast, Antarctica in 2008.

Stage	Age	n	Body mass (kg)	Tissue	$\delta^{13}C$ (‰) (range)	$\delta^{15}N$ (‰) (range)	C/N mass ratio
Courtship/egg laying (May)	Adults	39	27.5±3.5	Blood	-24.2±0.4 (-24.4 - -22.4)	11.0±0.6 (9.9 - 11.7)	3.5±0.1
	Females	27	25.6±2.1	Blood	-24.2±0.5 (-25.1 - -22.4)	11.2±0.6 (10.4 - 12.7)	3.5±0.1
	Males	12	31.8±2.1	Blood	-24.0±0.3 (-24.4 - -23.5)	10.6±0.5 (9.9 - 11.7)	3.4±0.0
Egg hatching (August)	Adults	37	26.5±3.3	Blood	-23.8±0.3 (-24.4 - -23.3)	11.8±0.4 (10.7 - 12.8)	3.3±0.0
	Females	23	26.5±3.4	Blood	-23.7±0.2 (-24.4 - -23.2)	11.8±0.3 (11.1 - 12.4)	3.3±0.0
	Males	14	26.5±3.5	Blood	-24.0±0.3 (-24.4 - -23.3)	11.8±0.6 (10.7 - 12.8)	3.3±0.0
Early chick rearing (September/October)	Chicks	40	3.2±0.7	Blood	-23.8±0.4 (-24.6 - -23.0)	11.8±0.4 (11.0 - 12.6)	3.5±0.1
Late chick-rearing (November)	Adults	20	23.5±2.0	Blood	-24.3±0.4 (-24.8 - -23.4)	10.6±0.6 (9.8 - 11.6)	3.3±0.0
	Females	10	22.7±2.0	Blood	-24.5±0.3 (-24.8 - -23.9)	10.5±0.5 (9.9 - 11.4)	3.3±0.0
	Males	10	24.3±1.8	Blood	-24.2±0.5 (-24.7 - -23.4)	10.6±0.6 (9.8 - 11.6)	3.3±0.0
	Older chicks	20	10.0±2.6	Blood	-24.4±0.3 (-24.9 - -23.8)	11.4±0.9 (10.3 - 12.4)	3.4±0.1
	Females	7	10.8±3.4	Blood	-24.3±0.3 (-24.9 - -23.9)	11.4±0.6 (10.6 - 12.4)	3.4±0.0
	Males	13	9.6±2.1	Blood	-24.4±0.3 (-24.8 - -23.8)	11.3±0.4 (10.3 - 12.0)	3.3±0.1

reflecting the more ^{15}N enriched blood of females during courtship/egg-laying (0.6‰ difference; Fig. 2.1.). Moreover, males sampled during late chick-rearing showed substantial variation in their isotopic signatures, with three males showing relatively high values ($\delta^{13}C$: -23.5±0.1; $\delta^{15}N$: 11.4±0.2) compared to other individuals at this time ($\delta^{13}C$: -24.5±0.2; $\delta^{15}N$: 10.2±0.4, n=7). There was no interaction between stage and sex ($F_{1,54}$=3.65, P = 0.06).

Females sampled during egg hatching were segregated by their $\delta^{15}N$ values from females sampled in both courtship/egg-laying and late chick-rearing (ANOVA: $F_{2,56}$ = 28.2, P < 0.0001; Tukey's HSD post-hoc analyses, both P < 0.0001; Fig. 2.1.). The $\delta^{15}N$ values of females during egg hatching (11.8±0.3‰) were relatively high compared to that of females sampled during courtship/egg-laying (11.2±0.6‰) and late chick-rearing (10.5±0.5‰), respectively. It is interesting to note that males sampled during egg hatching after their long winter (incubation) fast showed similar $\delta^{13}C$ signatures to males sampled during courtship/egg-laying (Tukey's HSD post-hoc analyses, P = 0.9), but were significantly ^{15}N enriched by a magnitude of 1.2‰ (P < 0.0001; Table 2.1.) and showed similar $\delta^{15}N$ values to that of females also sampled during egg hatching (ANOVA: $F_{1,35}$ = 0.02, P = 0.9).

Isotopic signatures of adult and chick emperor penguins

As no significant difference in isotopic values of male and female adult penguins sampled during late chick-rearing were found, the data was pooled. The isotopic values of older chicks did not vary significantly with sex (ANOVA: $\delta^{13}C$: $F_{1,18}$ = 0.02, P = 0.9; $\delta^{15}N$: $F_{1,18}$ = 0.02, P = 0.9) and were like-wise pooled.

The $\delta^{13}C$ values of adult and chick penguins encompassed a similar range of values (Table 2.1.) and were not significantly different (ANOVA: $F_{1,38}$ = 0.05, P = 0.8). The $\delta^{15}N$ values of chicks however, were significantly high compared to adults (ANOVA: $F_{1,38}$ = 22.65, P < 0.0001), with average $\delta^{15}N$ values ranging from 10.6±0.6‰ in adults to 11.4±0.5‰ in chicks (0.8‰ difference). Furthermore, no relationship was found between the weight of chicks and their $\delta^{15}N$ values (logarithmic regression model, $\delta^{15}N = 0.0127x + 11.234$, R^2 = 0.0045, P = 0.7, n=20). These results indicate ^{15}N enrichment in chicks was not related to the size of chicks, but to dietary intake.

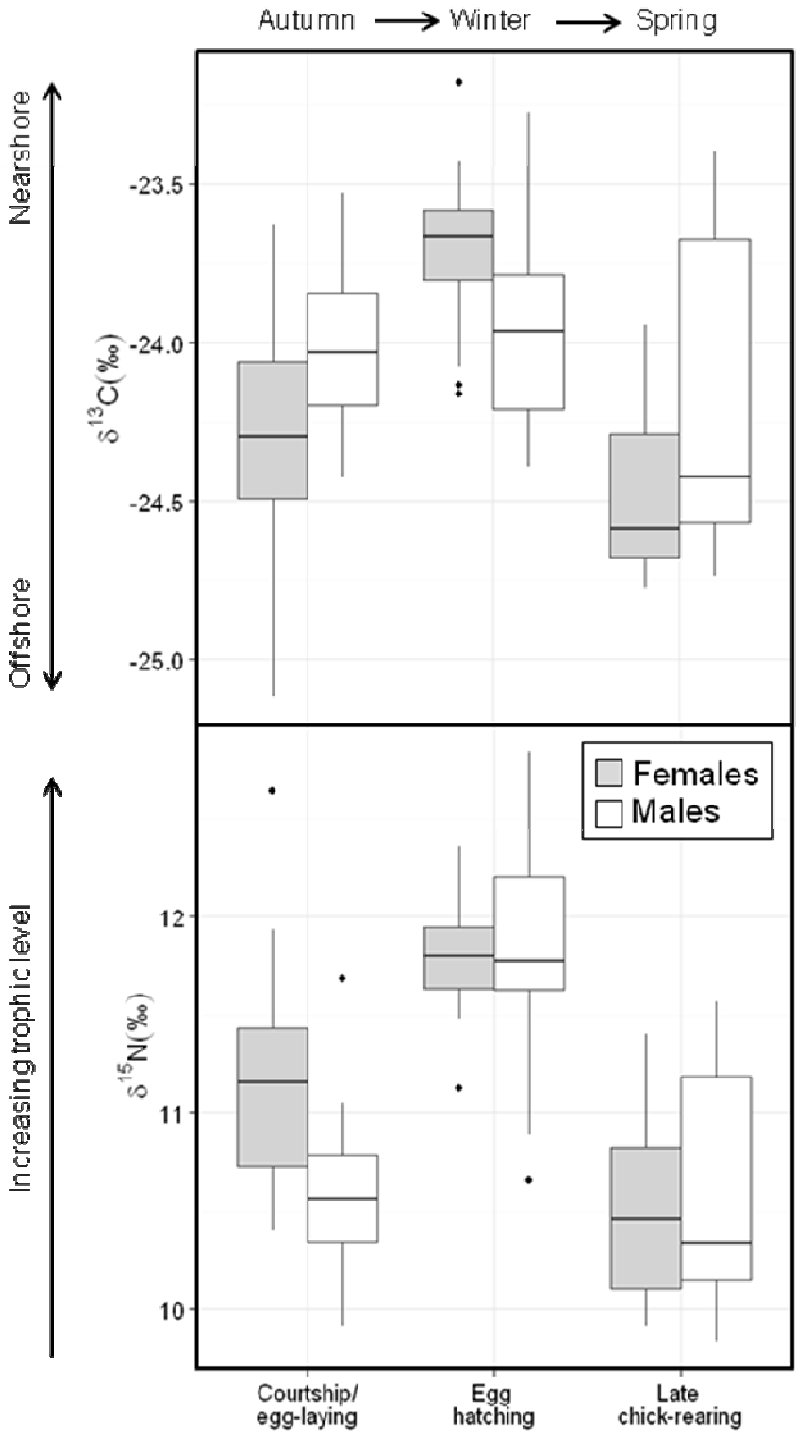

Figure 2.1. A comparison of the $\delta^{13}C$ and $\delta^{15}N$ values of adult female and male emperor penguin whole blood sampled during the courtship/egg laying, egg hatching and late chick-rearing periods at the Auster colony, Mawson Coast, Antarctica in 2008. Females: grey; Males: white. Values are means ± standard deviations (SD).

Furthermore, young chicks sampled during early chick-rearing showed similar $\delta^{15}N$ values to females sampled during egg hatching (Table 2.1.), indicating that the dietary intake of chicks during early chick-rearing was similar to that of their parents.

Isotope values of potential prey

Antarctic krill. The $\delta^{13}C$ values of Antarctic krill ranged widely from -28.7 to -23.7‰. Average $\delta^{13}C$ values ranged from -28.1±0.5‰, -27.8±0.6‰, -26.9±0.4‰ and -25.8±1.0‰ in oceanic, shelf slope, outer- and medium-shelf waters, respectively. Significant differences were found between sampling locations (ANOVA: $F_{3,41} = 29.31$, $P < 0.0001$; Table 2.2.), with multiple comparison tests indicating that individuals sampled in medium-shelf waters were significantly enriched in ^{13}C compared to those in shelf slope and oceanic waters, respectively (Tukey's HSD post-hoc analyses, both $P < 0.0001$). While individuals sampled in outer-shelf waters were ^{13}C enriched relative to those in oceanic waters ($P < 0.0003$). Moreover, there was a negative correlation between standard length (SL, mm) and $\delta^{13}C$ values of krill (regression model, $\delta^{13}C = -0.6961x-24.302$, $R^2 = 0.1619$, $P = 0.006$), with adult (SL: 4.6±0.7mm, n=19) and predominantly juvenile stages (SL: 3.8±0.4mm, n=4) sampled in oceanic and medium-shelf waters the most ^{13}C depleted and enriched, respectively (Table 2.2.; Fig. 2.2.).

The $\delta^{15}N$ values enclosed a 3.3‰ difference, with average $\delta^{15}N$ values ranging from 2.7±0.4‰, 2.6±0.4‰, 2.8±0.4‰ and 3.8±0.7‰ for krill sampled in oceanic, slope, outer- and medium-shelf, waters, respectively (Table 2.2.). A significant difference was found in $\delta^{15}N$ values of krill in relation to sampling location (ANOVA: $F_{3,41} = 9.29$, $P < 0.0001$), with individuals sampled in medium-shelf waters significantly ^{15}N enriched compared to those sampled in outer-shelf (Tukey's HSD post-hoc analysis, $P = 0.01$), slope and oceanic waters (both $P < 0.0001$). There was however, no relationship between $\delta^{15}N$ and SL (logarithmic regression model, $\delta^{15}N = 1.022x + 0.002$, $R^2 < 0.0001$, $P > 0.5$, n=45).

Prey groups. Antarctic krill (*E. superba*) sampled over-the-shelf, shelf slope and in oceanic waters showed relatively low $\delta^{13}C$ and $\delta^{15}N$ values compared to that of fish and squid species (Fig. 2.3.B). Benthic fish species (*Gymnodraco acuticeps* and *Chionodraco hamatus*) were more enriched in ^{13}C and ^{15}N than other prey species

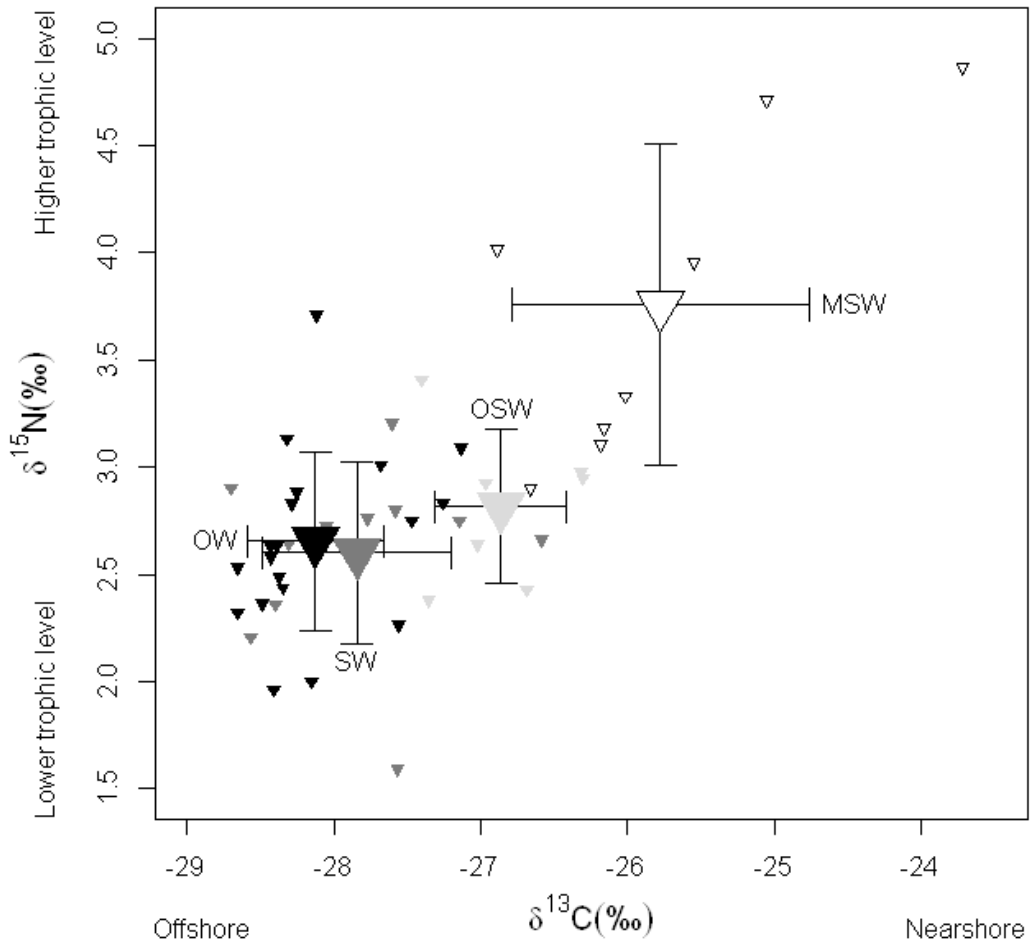

Figure 2.2. The $\delta^{13}C$ and $\delta^{15}N$ values of Antarctic krill (*Euphausia superba*) sampled by the *Umitaka maru* in 2008. The shades indicate individuals sampled in medium-shelf waters (MSW), outer-shelf waters (OSW), slope waters (SW) and oceanic waters (OW). Large symbols indicate the mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ values. Small symbols indicate individual $\delta^{13}C$ and $\delta^{15}N$ values. More depleted $\delta^{13}C$ and $\delta^{15}N$ values indicate foraging offshore.

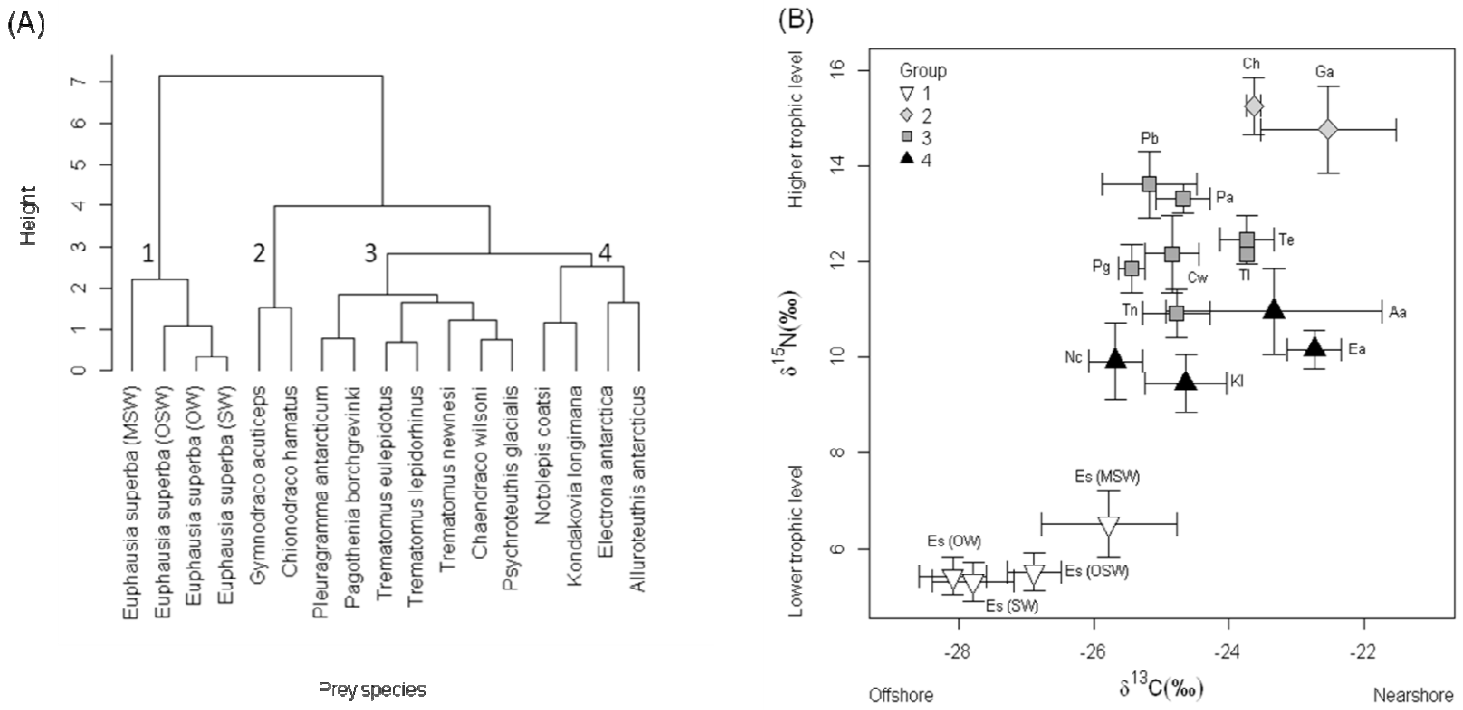

Figure 2.3. Results of the Cluster Analysis on the 14 potential prey species showing (A) the dendrogram indicating the four main groups and (B) plot of the $\delta^{13}C$ and $\delta^{15}N$ values (mean ±SD) for each of the prey species. Isotopic data of prey species are corrected for diet-tissue fractionation between whole blood and lipid-free whole prey by adding +0.02‰ and +2.72‰ to $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and between whole blood and lipid-free muscle by adding +0.46‰ and +1.86‰ to $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Cherel et al. 2005b). The different colours indicate prey groups assigned by the cluster analysis. Aa: *Alluroteuthis antarcticus*; Ch: *Chionodraco hamatus*; Cw: *Chaendraco wilsoni*; Ea: *Electrona antarctica*; Es (OW): *Euphausia superba* (oceanic waters); Es (SW): *E. superba* (slope waters); Es (OSW): *E. superba* (outer-shelf waters); Es (MSW): *E. superba* (medium-shelf waters); Ga: *Gymnodraco acuticeps*; Kl: *Kondakovia longimana*; Nc: *Notolepis coatsi*; Pa: *Pleuragramma antarcticum*; Pb: *Pagothenia borchgrevinki*; Pg: *Psychroteuthis glacialis*; Te: *Trematomus eulepidotus*; Tl: *T. lepidorhinus*; Tn: *T. newnesi.*

Table 2.2. Age, sex, condition and stable isotopic characteristics of Antarctic krill (*Euphausia superba*) sampled by the *Umitaka maru* in 2008. Values are means ± standard deviations (SD).

Sampling location	n	Standard length (mm)	Age/sex/condition: Adult female	(gravid)	(spent)	Adult male	Juvenile	$\delta^{13}C$ (‰) (range)	$\delta^{15}N$ (‰) (range)	C/N mass ratio
Oceanic (63-64°01')	19	4.6±0.7 (3.7-6.5)	7	3	0	9	0	-28.1±0.5 (-28.7 - -27.1)	2.7±0.4 (2.0 - 3.7)	3.7±0.5
Slope (65°09'-65°45')	11	4.6±0.6 (3.2-5.2)	0	6	2	2	1	-27.8±0.6 (-28.7 - -26.6)	2.6±0.4 (1.6 - 3.2)	3.8±0.6
Outer-shelf (65°74')	7	4.6±0.5 (4.0-5.1)	1	1	1	1	3	-26.9±0.4 (-27.4 - -26.3)	2.8±0.4 (2.4 - 3.4)	4.0±0.1
Medium-shelf (66°36')	8	4.0±0.4 (3.2-4.8)	1	0	0	3	4	-25.8±1.0 (-26.9 - -23.7)	3.8±0.7 (2.9 - 4.9)	3.8±1.0
Total	45	4.5±0.6 (3.2-6.5)	9	10	3	15	8	-27.4±1.1 (-28.7 - 23.7)	2.9±0.9 (1.6 - 4.9)	3.8±0.1

(Fig. 2.3.B). Mesopelagic fish (*Electrona antarctica* and *Notolepis coatsi*) and squid (*Alluroteuthis antarcticus* and *Kondakovia longimana*) occurring in off-shelf (oceanic) waters were depleted in their ^{13}C and ^{15}N values compared to neritic/over-the-shelf fish and squid species (Fig. 2.3.B).

This broad pattern in $\delta^{13}C$ and $\delta^{15}N$ values was reflected in the cluster analysis, with Antarctic krill, benthic fish, neritic/over-the-shelf fish and squid and mesopelagic fish and squid occurring in oceanic waters split into four prey groups (ANOSIM: Global R = 0.911, SSS = 0.1%, NPS < 0 = 0; Fig. 2.3.). The four prey groups were labelled as: (1) pelagic crustaceans (Antarctic krill), (2) benthic fish, (3) neritic/over-the-shelf fish and squid, and (4) oceanic/mesopelagic fish and squid.

Inferred diet of emperor penguins

When we compare the mean isotopic values for the penguins during various stages of the austral winter period to those of the prey species (Fig. 2.4.) the emperor penguin data lay closest to prey groups three (neritic/over-the-shelf fish and squid) and four (oceanic/mesopelagic fish and squid), which themselves lay between groups one (pelagic crustaceans, Antarctic krill) and two (benthic fish).

Isotopic mixing models were run using the four groups of prey identified by the cluster analysis. The models indicated sex and season differences in the diet composition of adult penguins (Fig. 2.5.). Modal estimates showed males fed predominantly on oceanic/mesopelagic fish and squid, which constituted 48% and 42% of their diet in the autumn (courtship/egg-laying) and spring (late chick-rearing), respectively. Neritic/over-the-shelf fish and squid were the least common prey in the diet of males, and made up <10% of their diet in both stages. In contrast, benthic fish and oceanic/mesopelagic fish and squid contributed the greatest proportion to the diet of females, constituting 29 to 41%, and 25 to 40%, respectively. Moreover, the diet of
adult females was most similar during courtship/egg-laying and late chick-rearing, with squid and fish (groups 2, 3 and 4) and Antarctic krill constituting similar proportions of their diet in both stages (~80% and ~20%, respectively; Fig. 2.5.). In the winter (incubation) however, benthic fish and oceanic/mesopelagic fish and squid constituted the greatest proportion of the fish and squid component of their diet (81%) and Antarctic krill constituted 11% of their diet. Interestingly, young chicks sampled

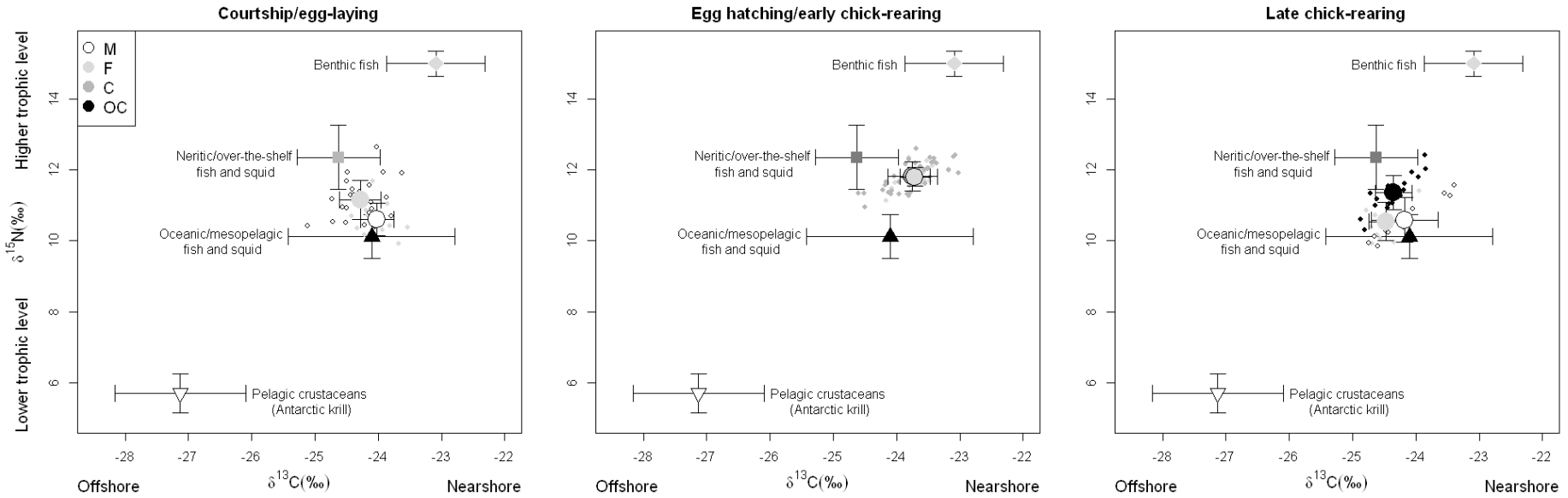

Figure 2.4. Plot of the mean $\delta^{13}C$ and $\delta^{15}N$ values of whole blood of emperor penguins collected in each sampling period and of their potential prey. The different symbols and colours indicate male (M, open circles), female (F, light grey circles), chick (C, dark grey circles) and older chick (OC, black circles) emperor penguins and each prey group assigned by cluster analysis in Fig. 2.3. Isotopic data of prey species are corrected for diet-tissue fractionation (for details see Fig. 2.3.). Isotopic data for adult males sampled during egg hatching are not included due to individuals fasting during the egg incubation period. Isotopic data for male and female older chicks sampled in November are pooled. Values are means ± standard deviations (SD).

during early chick-rearing showed similar proportions of benthic fish, and oceanic/mesopelagic fish and squid (83%) in their diet compared to females sampled during egg hatching, but slightly less krill (7%; Fig. 2.5).

During late chick-rearing, modal estimates indicated different proportions of krill, fish and squid in the diet of adult and older chick penguins (Fig. 2.5.). Krill contributed 24% and 17% to the diet of adults and chicks, respectively, and fish and squid contributed 77% and 81%, respectively, indicating that adults feed on greater proportions of krill than that preferentially fed to their young, while the opposite is true for fish and squid.

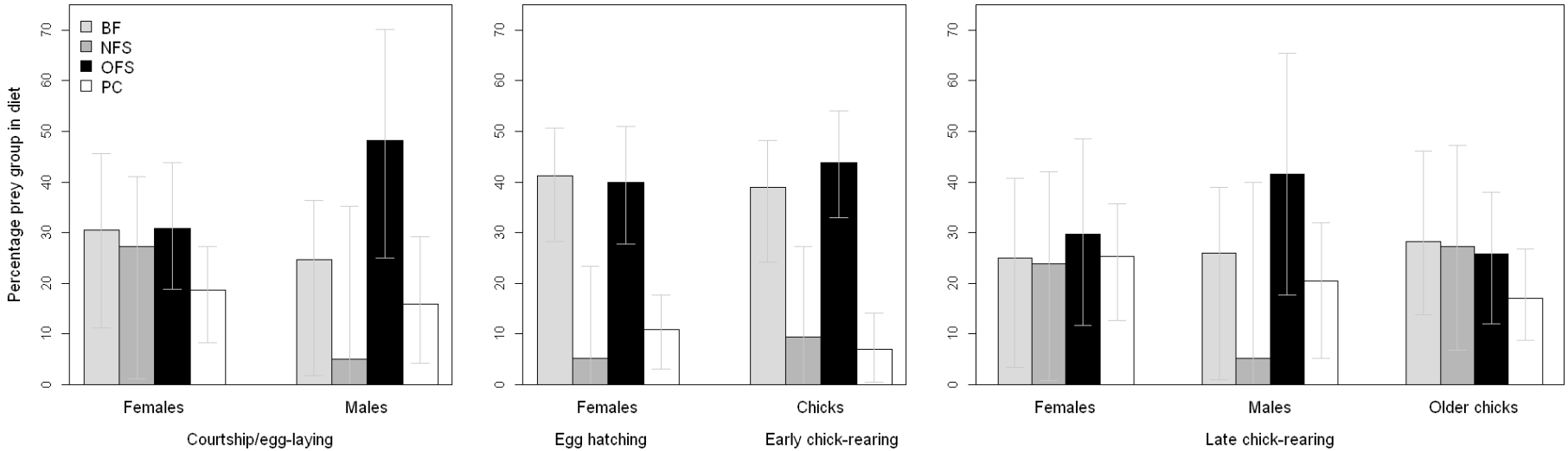

Figure 2.5. Estimated diet composition of emperor penguins for each season/sex/age combination during different stages of the breeding and chick-rearing periods at the Auster colony, Mawson Coast, Antarctica in 2008. From left to right, prey groups are benthic fish (BF), neritic/over-the-shelf fish and squid (NFS), oceanic/mesopelagic fish and squid (OFS) and pelagic crustaceans (Antarctic krill, PC). The modal values and 95% confidence limits resulting from the SIAR in R package are indicated.

DISCUSSION

Knowledge of spatial and temporal variability in diet and foraging behaviour are central to understanding climatic and other environmental influences on marine predator populations, and also important requirements for conservation and fisheries management (Reid et al. 2005a; Trathan et al. 2007). Our ability to assess temporal patterns in resource use by these predators however, is limited by the lack of information on their dietary preferences during the non-breeding period.

In this study, we used stable isotope analysis to compare the trophic position and diet of adult and chick emperor penguins and to evaluate intra-annual variations in diet and foraging ecology. Stable isotope analysis provided dietary data corresponding to autumn (pre-breeding), winter (incubation) and spring (chick-rearing). Our isotopic data provided two new and important insights into the foraging ecology of emperor penguins. Firstly, that the diets of adult emperor penguins varied intra-annually, with stable isotope data suggesting that for autumn, oceanic/mesopelagic fish and squid (OFS) are dominant for males, whereas benthic fish (BF), neritic/over-the-shelf fish and squid (NFS), and OFS are equally important for females. In the winter, when males remain in the colony to incubate eggs, females do not consume NFS, but prefer BF and OFS. In spring, OFS are again dominant for males, wheres BF, NFS, OFS and pelagic crustaceans (Antarctic krill; PC) are equally important for females. Secondly, that adults do not feed on the same prey as those fed to chicks, but preferentially feed higher trophic level, energy rich prey (fish and squid) to their young. The results of this study highlight the utility of stable isotope analysis to monitor changes in diet and habitat use of emperor penguins, particularly during periods when data cannot be acquired any other way (Quillfeldt et al. 2005a). The finding that adults may selectively provision their chicks with higher trophic level prey has important implications for dietary studies that use stomach samples from chick-provisioning adults to infer adult diet. The results of such studies may only reflect chick diet and may thus, underestimate the importance of prey species, such as krill, to the diet of adults (Hodum & Hobson 2000).

Trophic ecology of prey

The isotopic prey groups showed a continuum of increasingly enriched isotopic values from offshore (pelagic) waters (*i.e.* Antarctic krill, offshore/mesopelagic fish and squid) to nearshore (neritic) waters (*i.e.* neritic/over-the-shelf fish and squid, benthic fish *Gymnodraco acuticeps* and *Chionodraco hamatus*). These data agree with the isotopic gradient in $\delta^{13}C$

values between offshore/oceanic and inshore/neritic Antarctic waters in other components of the food web (Trull & Armand 2001; Cherel et al. 2011).

Antarctic krill (*E. superba*) is a major link in the transfer of energy from low to high trophic levels in the pelagic zone of the Antarctic ecosystem (Weber & El-Sayed 1985; Veit et al. 1993). Stable nitrogen values showed an average difference of less than one trophic level (~1.1‰) between oceanic (2.7±0.4‰) and medium-shelf waters (3.8±0.7‰). We found no relationship between $\delta^{15}N$ and the standard length of individuals, suggesting that both juvenile and adult stages feed on a range of food sources as indicated in previous studies (Atkinson et al. 2002).

Trophic ecology of emperor penguins in relation to season

Traditional dietary techniques, such as stomach content analysis, can yield detailed taxonomic and quantitative data, but are temporally limited to the breeding season (Robertson et al. 1994). Consequently, what is known about the diet of emperor penguins comes largely from studies during the breeding season (Table 2.3.). These studies indicate that the overall diet of emperor penguins consists of varying proportions of fish (mainly nototheniids, particularly *P. antarcticum*), crustaceans (mainly *E. superba* and amphipods), and squid (mainly *P. glacialis*) across their geographical range (Table 2.3.).

Our results indicated a significant influence of season on both $\delta^{13}C$ and $\delta^{15}N$ in whole blood of adult females sampled during courtship/egg laying (May), egg hatching (August) and late chick-rearing (November). Isotope ratios in whole blood represent an integration period of 27 to 45 days (Cherel et al. 2007) and thus, provided dietary information corresponding to the autumn (pre-breeding), winter (incubation) and spring (chick-rearing) periods. Whole blood $\delta^{15}N$ values defined two trophic niches, with adult penguins occupying similar trophic levels during autumn and spring, while the more ^{15}N enriched blood of adult females in winter (when adult males remained in the colony to incubate eggs) indicated a shift to a higher trophic level.

Stable isotope results and multi-source stable isotope mixing model estimates suggest a higher proportion of Antarctic krill in the diet of adult emperor penguins in autumn and spring (contributing 19 and 25% to the diets of females in autumn and spring, respectively, and 16 and 20% to the diets of males, respectively) than in the diet of females in winter

(contributing11% to the diet; Fig. 2.5.). Moreover, mixing model estimates indicated a higher proportion of benthic fish in the diet of females in winter than in the diets of adults in autumn and spring (contributing 41% to the diets of females in winter, but less than 30% to the diets of adults in autumn and spring). Taking into account the isotopic gradient from offshore or pelagic (oceanic) habitats to coastal/neritic and benthic food webs (Cherel et al. 2011), the ^{13}C and ^{15}N enriched blood of adult female emperor penguins in winter may reflect considerable feeding on higher trophic level (fish and squid) prey in neritic/benthic waters over the Antarctic continental shelf. This is corroborated by tracking studies that show that the foraging areas of female penguins during this time rarely exceeds to deeper waters over the shelf slope, with the movements of animals constricted by pack-ice (Kirkwood & Robertson 1997a; Wienecke & Robertson 1997; Zimmer et al. 2008). Additionally, mixing model estimates of the diet composition of females in winter (Antarctic krill, fish and squid contributing 11 and 86% to the diets of females, respectively) are in good agreement with the winter dietary trends previously described by Wienecke and Robertson (1997) for Auster females in winter (Antarctic krill, fish and squid contributing 12, 72 and 16% by mass to the diets females, respectively; Table 2.3.).

There is little information on the diet of emperor penguins during the period between the adult moult and the new breeding season, with only a single study in Adélie Land providing information on the food of penguins during the post-moult period (Table 2.3.). This is a critical stage in the annual-cycle as it is when they spend three to four months feeding at-sea to generate energy reserves for the up-coming breeding season. This foraging period is particularly important for male birds which fast for up to four months during courtship/egg laying and incubation (Prévost 1961). At this time, the relatively low $\delta^{13}C$ values of female and male adult penguins suggest feeding further offshore in oceanic waters and is consistent with adults, unconstrained by breeding, travelling greater distances to access deeper waters over the Antarctic shelf slope (Zimmer et al. 2008). The corresponding $\delta^{15}N$ values of birds indicates they were likely consuming resources over more than one trophic level, which the stable isotope

Table 2.3. The diet composition of emperor penguins at various breeding colonies around Antarctica.

Location	Stage	Frequency of Occurrence (%)			Number (%)			Mass (%)			Source
		Fish	Squid	Crustaceans	Fish	Squid	Crustaceans	Fish	Squid	Crustaceans	
Adélie Land											
Point Géologie	Spring	100	93	<82	65	1	34	95	3	2	Offredo and Ridoux (1986)
Princess Elizabeth Land											
Auster	Winter/Spring	74	58	82	52	48	?	55	45	?	Robertson et al. (1994)
Auster	Winter	100	41	88	4	<1	96	27	3	70	Kirkwood and Robertson (1997)
Auster	Winter	?	?	?	20	11	69	72	16	12	Wienecke and Robertson (1997)
Amanda Bay	Winter/Spring	86	36	<41	83	4	13	97	3	<1	Gales et al. (1990)
Taylor Glacier	Winter/Spring	29	55	87	27	73	?	31	69	?	Robertson et al. (1994)
Ross Sea											
Cape Roget	Spring	100	100	25	99	1	<1	93	7	<1	Cherel and Kooyman (1998)
Cape Washington	Spring	100	0	100	38	0	62	89-95	0	5-11	Cherel and Kooyman (1998)
Coulman Island	Spring	100	86	86	94	3	3	88	12	<1	Cherel and Kooyman (1998)
Weddell Sea											
Drescher Inlet	Spring	73	80	93	17	3	80	38	10	52	Klages (1989)
Drescher Inlet	Summer	93	0	93	17	0	83	~75	0	~25	Pütz (1995)

? = Not quantified

mixing model predicted to be Antarctic krill, fish and squid (Fig. 2.5.). Antarctic krill and glacier squid (*P. glacialis*) are at their greatest abundances in the vicinity of the shelf slope (Kawaguchi et al. 2010; Van de Putte et al. 2010). Antarctic krill (in addition to fish and squid) may therefore provide an abundant, easily accessible energy source for emperor penguins prior to the new breeding season, at a time when they must accumulate large fat stores for the energetically costly incubation and chick-rearing periods (Kooyman et al. 2004).

Adult penguins during spring showed similar $\delta^{13}C$ signatures to adults during the autumn suggesting penguins used common foraging areas at these times. However, tracking data from Auster (Kirkwood & Robertson 1997b; Wienecke & Robertson 1997) and other colonies (Rodary et al. 2000; Zimmer et al. 2008) confirms that adults in spring forage over the Antarctic shelf (and in similar areas as winter foraging birds), due to time constraints imposed by having to return to the colony to feed chicks. It is, therefore, unlikely that the relatively low $\delta^{13}C$ values of adults during spring are due to feeding further offshore in oceanic waters. The chick-rearing period coincides with the spring ice break-up, and the onset of phytoplankton blooms. This gives the birds greater access to open water, where enhanced biological productivity in the upper limits of the water column attracts fish, crustaceans, particularly Antarctic krill, and squid for penguins to feed on (Kirkwood & Robertson 1997b). It therefore follows that the $\delta^{13}C$ signatures of chick-provisioning adults in spring is due to increased pelagic feeding over shelf waters, where polynyas provide the closest open water to the colonies (Kirkwood & Robertson 1997b).

The physiological state of an animal can also affect the isotopic ratios in its tissues (Hobson et al. 1993). During incubation, adult males undergo extensive fasting (> 60 days duration). Their apparent increase in trophic level at this time, and similar to that of foraging females (Fig. 2.1.), is likely due to fasting rather than dietary in nature. Avian studies have shown that fasting and nutritional stress induce ^{15}N enrichment in the tissues, mainly due to recycling of endogenous amino acids (Hobson et al. 1993; Cherel et al. 2005a). Thus, penguins, which essentially "feed on themselves" during extended periods of fasting, show an increase in their apparent trophic level compared to non-fasting birds (Cherel et al. 2005a).

Trophic segregation of male and female emperor penguins

Male and female adult emperor penguins differed in both their $\delta^{13}C$ and $\delta^{15}N$ values indicating different feeding ecology during autumn and spring (excluding the incubation

period when males are not foraging). Taking into account the isotopic gradient from offshore or pelagic (oceanic) habitats to coastal/neritic and benthic food webs (Cherel et al. 2011), the significantly ^{13}C enriched blood of male emperor penguins during autumn and spring suggests a tendency to feed in more southerly waters than females. This is corroborated by satellite tracking of Auster adults which showed that males foraged in more southerly waters over the shelf in August/September than did females from late May to July (Wienecke & Robertson 1997). Males also foraged for longer, dived deeper (>300m) and more frequently than females (Wienecke & Robertson 1997).

The significantly ^{15}N enriched blood of females in the autumn indicated that females consumed a higher proportion of fish and squid than did males. Conversely, the relatively ^{15}N depleted blood of males suggested a higher proportion of lower trophic level prey (Antarctic krill) in their diets. Indeed, stomach content data shows that the diet of Auster females comprises more fish and squid (72% and 16% by mass, respectively) than krill (12% by mass), while the contribution of krill to the diet of males is much higher (krill, fish and squid contributed 43%, 53% and 2% by mass, respectively; Wienecke & Robertson 1997). Multi-source stable isotope mixing models however, had difficulty estimating the contribution of fish and squid species (which occupy similar trophic levels) to the diet of male and female emperor penguins. These results reflect the low taxonomic resolution afforded by the stable isotope approach. This in turn emphasises the need to integrate traditional dietary techniques (Tierney et al. 2008; Dale et al. 2011; Polito et al. 2011) in future isotopic dietary studies to resolve biogeochemical variation in the diet of migrating predators.

Despite sexual segregation in feeding ecology, males and females showed substantial individual variability in their isotopic signatures indicating that adult emperor penguins use a range of foraging strategies. Males in particular showed substantial individual variability in $\delta^{13}C$ values in the spring, indicating greater plasticity in forage range at this time. A difference of ~3‰ in $\delta^{15}N$ values among individuals indicates that some individuals fed at one trophic level lower than others. Emperor penguins are the deepest diving seabird species in the world, with maximum dive depths in excess of 500 m (Kooyman & Kooyman 1995). They perform both pelagic and benthic dives to exploit their main prey, including pelagic crustaceans and fish and bentho-pelagic/mesopelagic fish and squid (Rodary et al. 2000; Zimmer et al. 2008). Their large size and deep diving capabilities allow them to access deep layers of the water column where mesopelagic prey, such as the nototheniid *Notolepis coatsi*

and the glacial squid *P. glacialis* occur in high densities (Wilson et al. 1993; Piatkowski & Pütz 1994; Kooyman & Kooyman 1995; Moteki et al. 2009). During winter and spring, fast-ice covers much of the continental shelf waters along the Mawson Coast. This fast-ice largely excludes emperor penguins from Auster (and Taylor Glacier) from potential foraging areas, forcing them to feed in either areas of open water (polynyas) over the continental shelf or in pack-ice regions further offshore (Kirkwood & Robertson 1997b; Wienecke & Robertson 1997). In order to survive through the winter and catch sufficient prey to provision themselves as well as their chicks, emperor penguins therefore employ a range foraging styles to maximise their foraging capabilities within these constraints.

Chick-provisioning in emperor penguins

The food of emperor penguin chicks is primarily composed of fish (mainly *T. eulepidotus*), squid (mainly *P. glacialis* and *A. antarcticus*) and crustaceans at the Auster colony (Robertson et al. 1994). The larger, bentho-pelagic nototheniid fish *T. eulepidotus* (14% by number and 31% by mass) was by far the commonest prey at Auster in the 1988 chick-rearing period, with *P. antarcticum* being a minor item (13% by number and 5.2% by mass; Robertson et al. 1994). The squid *A. antarcticus* (42% by number and 20% by mass) and *P. glacialis* (27% by number and 13% by mass) formed the remainder of the food of chicks at Auster (Robertson et al. 1994). Crustaceans were also identified in the diet (occurred in 82% of stomach samples of adult birds), but were heavily digested and not quantified.

The diet-tissue fractionation value of 2.7‰ between penguin food and blood (Cherel et al. 2005b), suggests that the theoretical $\delta^{15}N$ value of chick diet was about 8.7‰. This value is higher than that of Antarctic krill. The high nitrogen values from late chick-rearing chicks is in agreement with nototheniid fish being their main food item and is consistent with the food and isotopic signature of emperor penguin chicks previously studied in Adélie Land by Cherel (2008). A striking difference in the findings of this study and that of Cherel (2008) however, was that chick-rearing adults had higher $\delta^{15}N$ values than chicks. This indicates that, unlike emperor penguins in Adélie Land, emperor penguins at Auster fed on crustaceans (Antarctic krill), fish and squid, but delivered higher trophic level prey to chicks. The multi-source stable isotope mixing model also estimated that Auster adult and chick diets consisted of different proportions of krill, and fish and squid. Kooyman and Kooyman (1995) suggested that shallow pelagic diving by adults over the Antarctic shelf on the last days of a foraging trip were foraging dives to capture different prey for chicks. In contrast, chicks

during early chick-rearing had identical isotopic signatures as female adults during winter. This suggests that adults feed on the same prey as that fed to chicks during early chick development in the absence of Antarctic krill in the winter months (Nicol 2006) and consistent with females feeding on bentho- and pelagic fish and squid in neritic/over-the-shelf waters at this time.

A fish (*e.g. P. antarcticum*, 22 kJ g^{-1}; Van de Putte et al. 2010) and squid based diet (*e.g. Moroteuthis ingens*, 24 kJ g-1; Cherel & Ridoijx 1992) rather than a krill based diet (4.5-4.8 kJ g^{-1}; Chapman et al. 2010) ensures chicks receive prey of high energy density during this critical stage of growth. Indeed, Robertson et al. (1994) found the energy density of chick food to increase substantially prior to fledging when maximum growth occurs. Moreover, the food ration of chicks at Auster accounted for about 9.5% of adult maintenance during the same period (Robertson & Newgrain 1996). This indicates that chick-provisioning adults maximise their limited time at-sea for self-maintenance feeding by capturing energy rich prey for chicks on the final days of foraging. Such a provisioning strategy has been previously shown in Antarctic procellariiforms (Hodum & Hobson 2000) and Adélie penguins in Adélie Land (Cherel 2008), while Tierney et al. (2008) suggested Adélie penguins on the Mawson Coast may also use a similar strategy.

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APPENDICES

Appendix A. Stable isotope signatures and C/N ratios of potential prey of emperor penguin

Species	n	Tissue	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C/N mass ratio	Source
Crustaceans						
Euphausiacea						
Euphausia superba						
Oceanic waters (63-64°01')	19	Whole body	-28.1±0.5	2.7±0.4	3.7±0.5	This study
Slope waters (65°09'-65°45')	11	Whole body	-27.8±0.6	2.6±0.4	3.8±0.6	This study
Outer-shelf waters (65°74')	7	Whole body	-26.9±0.4	2.8±0.4	4.0±0.1	This study
Medium-shelf waters (66°36')	8	Whole body	-25.8±1.0	3.8±0.7	3.8±1.0	This study
	45	Whole body	-27.4±1.1	2.9±0.9	3.8±0.1	This study
Fish						
Bathydraconidae						
Gymnodraco acuticeps	8	White muscle	-23.0±1.0	12.9±0.9	3.1±0.0	Cherel et al. (2011)
Channichthyidae						
Chaendraco wilsoni	11	White muscle	-25.3±0.4	10.3±0.8	3.4±0.1	Cherel et al. (2011)
Chionodraco hamatus	7	White muscle	-24.1±0.1	13.4±0.6	3.2±0.0	Cherel et al. (2011)
Myctophidae						
Electrona antarctica	9	White muscle	-23.2±0.4	8.3±0.4	3.3±0.0	This study
Nototheniidae						
Pagothenia borchgrevinki	2	Whole body	-25.2±0.7	10.9±0.7	–	Krahn et al. (2006)
Pleuragramma antarcticum	5	Stomach contents	-24.7±0.4	10.6±0.3	3.8±0.2	Cherel (2008)
Trematomus eulepidotus	5	White muscle	-24.2±0.4	10.6±0.5	3.2±0.0	Cherel et al. (2011)
T. lepidorhinus	1	White muscle	-24.2	10.3	3.1	Cherel et al. (2011)
T. newnesi	10	Whole body	-24.8±0.5	8.2±0.5	3.3±0.1	Polito et al. (2011)
Paralepididae						
Notolepis coatsi	3	Whole body	-25.7±0.4	7.2±0.8	3.2±0.1	Polito et al. (2011)
Squid						
Alluroteuthis antarcticus	4	Beaks corrected	-23.8±1.6	9.1±0.9	–	Zimmer et al. (2007)
Kondakovia longimana	20	Mantle	-25.1±0.6	7.6±0.6	3.2±0.1	Bury et al. (2008)
Psychroteuthis glacialis	3	Mantle	-25.9±0.2	10.0±0.5	3.5±0.3	This study

*A correction factor of 3.5‰ was applied to the beak $\delta^{15}N$ value (mean ±SD) of *Alluroteuthis antarcticus* taken from Zimmer et al. (2007) to correct for ^{15}N depletion due to chitin following Cherel et al. (2009a). Values are means ± standard deviations (SD).

3. Spatially explicit estimates of prey consumption reveal a new krill predator in the Southern Ocean

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ABSTRACT

Development in foraging behaviour and dietary intake of many vertebrates are age-structured. Differences in feeding ecology may correlate with ontogenetic shifts in dispersal patterns, and therefore affect foraging habitat and resource utilization. Such life-history traits have important implications in interpreting tropho-dynamic linkages. Stable isotope ratios in the whiskers of sub-yearling southern elephant seals (*Mirounga leonina*; n = 12) were used, in conjunction with satellite telemetry and environmental data, to examine their foraging habitat and diet during their first foraging migration. The trophic position of seals from Macquarie Island (54°30′S, 158°57′E) was estimated using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) ratios along the length of the whisker, which provided a temporal record of prey intake. Satellite-relayed data loggers provided details on seal movement patterns, which were related to isotopic concentrations along the whisker. Animals fed in waters south of the Polar Front (>60°S) or within Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Subareas 88.1 and 88.2, as indicated by both their depleted $\delta^{13}C$ (<−20‰) values, and tracking data. They predominantly exploited varying proportions of mesopelagic fish and squid, and crustaceans, such as euphausiids, which have not been reported as a prey item for this species. Comparison of isotopic data between sub-yearlings, and 1, 2 and 3 yr olds indicated that sub-yearlings, limited by their size, dive capabilities and prey capture skills to feeding higher in the water column, fed at a lower trophic level than older seals. This is consistent with the consumption of euphausiids and most probably, Antarctic krill (*Euphausia superba*), which constitute an abundant, easily accessible source of prey in water masses used by this age class of seals. Isotopic assessment and concurrent tracking of seals are successfully used here to identify ontogenetic shifts in broad-scale foraging habitat use and diet preferences in a highly migratory predator.

INTRODUCTION

The interplay between the physical and biological regimes of the Southern Ocean (Constable et al. 2003) dictates the dispersal, foraging habitats and diet of higher order predators (Bost et al. 2009a). Information on diet is fundamental to better understand the diversity of linkages within Southern Ocean marine ecosystems and the response of higher order predators to large-scale ecosystem change and other anthropogenic activities such as commercial fishing (Reid & Croxall 2001). Due to their marine existence, the dietary study of marine mammals is one of the most challenging of any vertebrate taxon (Iverson et al. 1997). Moreover, marine mammal species often exhibit ontogenetic shifts in dispersal patterns, foraging habitat and resource utilisation (Field et al. 2007b). Such life-history traits have important individual and population level implications and must be taken into account when assessing the diet and trophic interactions of a species within an ecosystem.

Natal dispersal is a fundamental, but poorly understood, demographic parameter (Lindström 1999), particularly amongst vertebrate marine predators (Alerstam et al. 2003). The mechanism which governs this phenomenon is largely unknown (Paradis et al. 1998), although intra-specific competition for resources (*e.g.* food, space and mates) is one of the main hypothesises advanced to explain natal dispersal in the life history of most species (Breed et al. 2011).

The southern elephant seal (*Mirounga leonina*) is such an example of a polar species which exhibits an extreme natal dispersal strategy (McConnell et al. 2002). At weaning, adult female seals depart for remote feeding grounds, leaving pups to spend another three to eight weeks ashore before they too depart natal colonies (Arnbom et al. 1993; Arnbom et al. 1997). The lack of maternal input into dispersal strategies means the likelihood of these young animals foraging successfully, in an unfamiliar ocean environment, is largely dependent on chance. Consequently, this may contribute to the relatively high first year mortality in this species (McMahon et al. 2005a).

Surviving seals disperse over many thousands of kilometres (Field et al. 2005) to access different prey communities (Bradshaw et al. 2003), and seem to develop site fidelity to areas known to previously provide good feeding (Bradshaw et al. 2004). This behaviour is also noted for their northern counterpart, the northern elephant seal (*M. angustirostris*, Robinson et al. 2012). Dispersal patterns may correlate with increased intra-specific competition for resources, physiological capabilities (*e.g.* related to size, sex, diving capacity), familiarity with habitat,

temporal shifts in haul-out behaviour and reduced mortality risks of extensive movement (Field et al. 2005; Field et al. 2007a; Field et al. 2007b). Adult females from Macquarie Island, constrained by breeding requirements, make directed movements south of the major Antarctic Circumpolar Current (ACC) fronts to feed over the East Antarctic continental shelf before the winter sea ice makes this habitat inaccessible (Thums et al. 2011). In contrast, younger seals, constrained by physiological capabilities (Irvine et al. 2000), make less directed travel, predominantly north of the southern limits of the ACC, closer to their natal island (McConnell et al. 2002; van den Hoff et al. 2002; Field et al. 2005).

What is known about the diet of this species stems largely from studies of stomach contents and faecal analysis (van den Hoff et al. 2003; van den Hoff 2004; Field et al. 2007b), but interpretation is impeded by the wide separation between feeding and haul-out sites (Field et al. 2001). Stable isotope analysis, which assesses ratios of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) isotopes in various body tissues, is being increasingly used to study the foraging habitat and trophic position of highly migratory animals (Koch et al. 1995; Best & Schell 1996; Bearhop et al. 1999; Hobson 1999; Rubenstein & Hobson 2004) as it can yield a data time-series derived from assimilated, and not just ingested food (Hobson et al. 1996).

Carbon isotope ratios change by only ~0.8 to 2‰ per trophic level, and thus closely track differences in carbon isotope composition at the base of the food chain (Fry & Sherr 1984; Peterson & Fry 1987) and are therefore used to reflect a consumer's foraging habitat. Nitrogen isotope ratios in tissues of consumers typically increase at ~3‰ per trophic level (Minagawa & Wada 1984; McCutchan et al. 2003) and are used to estimate trophic position (Hobson 1992). As whiskers are keratin-based tissues, which are metabolically inert after synthesis (Rubenstein & Hobson 2004), they approximate a time-line of stable isotope values derived from food sources, with the tip of the whisker representing the oldest growth, and the root the most recent growth.

In this study, stable isotope and satellite telemetry for consumers and corresponding environmental data are combined to quantify the feeding habits and trophic position of sub-yearling elephant seals in relation to habitat during their first feeding migration from Macquarie Island. The specific aims of this study were to determine: 1) the growth rates of whiskers of sub-yearlings in the six months after weaning, and 2) the trophic position (*i.e.* $\delta^{13}C$ and $\delta^{15}N$) of seals in relation to foraging location, water mass type and seal age.

MATERIALS AND METHODS

Data collection

Seal whiskers

Facial vibrissae (whiskers) were collected from southern elephant seal pups equipped with Satellite Relayed Data Loggers (SRDLs, Sea Mammal Research Unit, St Andrews, UK), which consisted of a data logger interfaced to a 0.5-W Argos radio frequency unit (Fedak et al. 1996). Satellite Relayed Data Loggers were fitted to pups during their post-weaning fast at Macquarie Island (54˚30'S, 158˚57'E) in December 1995 (n=6) and 1999 (n=6). A six hour record was summarized and transmitted. One whisker was collected from each individual at SRDL deployment (pre-trip whisker; 1995 only, n=5) and a second whisker was collected when the SRDL was retrieved approximately 4 to 7 months later (post-trip whisker; n=12; Table 3.1.). All animals were sampled within 7 days of their return (mean=3.1±2.5 days, n=12). Whiskers were not plucked but cut as close to the face as possible from the same location on the left hand side of the muzzle (C.R. McMahon, Personal communication). Details of the capture, handling and attachment of telemetry devices to study animals are provided elsewhere (Fedak et al. 1983; Baker et al. 1990; Hindell et al. 1999).

Prey specimens

In the absence of available prey stable isotope data for this region of the Southern Ocean we used published and unpublished values corresponding to latitudinal ranges similar to this population of juvenile southern elephant seals, although outside the current foraging range. We have assumed that despite the geographic disparity, the prey isotope values will be broadly consistent with those within the seals foraging areas. Mid-latitude (<55°S) specimens of fish (*Protomyctophum tenisoni*, n=8; *Electrona antarctica*, n=10; *Gymnoscopelus piabilis*, n=2; *G. nicholsi*, n=10 and *G. fraseri*, n=8) were collected by the RV *La Curieuse* during bathypelagic trawls, to the northeast of the Kerguelen Archipelago (49°07’S, 70°45’E) in June 1998 (see Lea et al. 2002b). The samples were collected at night using an IYGPT net (International Young Gadoid Pelagic Trawl net; opening: 12 x 7 m) with a 10 mm mesh size in the cod end (Duhamel et al. 2000), and were sorted on deck and frozen. Lower beaks of two squid species (*Martialia hyadesi*, n=66 and *Histioteuthis eltaninae*, n=71) were obtained from the stomach contents of juvenile southern elephants seals (one, two and three year olds) during their annual haul-out periods as they returned ashore at Macquarie Island (54º30’S, 158º57’E), from November 1997 and December 2000 (Hughes, A.R. unpubl. data). Details of the capture, handling and stomach

Table 3.1. Morphometric, tag deployment and tracking details for 12 weaned southern elephant seals from Macquarie Island, including the number of days (mean ±SD) spent in transit and Area Restricted Search (ARS) by seals.

Seal ID No.	Sex	Weaning Mass (Kg)	Deployment Mass (Kg)	Transit duration (days)	ARS duration (days)	Total duration (days)
1995/1996						
J226	F	78.0	62.0	47.0	70.0	126.0
J263	M	143.0	107.0	45.0	86.0	149.0
J373	F	92.0	73.0	56.0	66.0	130.0
J375	F	89.0	68.0	12.0	62.0	146.0
J492	F	88.0	62.0	50.0	72.0	148.0
J503	M	92.0	66.0	46.0	81.0	137.0
Mean		97.0±23.1	73.0±17.2	42.7±15.5	72.8±9.0	139.3±9.8
1999/2000						
T719	F	195.0	123.0	42.0	108.0	178.0
T825	F	104.0	96.0	57.0	105.0	182.0
T839	F	101.0	71.0	56.0	79.0	139.0
T867	F	90.0	62.0	50.0	95.0	179.0
T875	F	85.0	60.0	76.0	62.0	155.0
T887	F	93.0	70.0	63.0	94.0	169.0
Mean		111.3±41.6	80.3±24.5	57.3±11.6	90.5±17.3	167.0±16.9
Overall mean		104.2±32.9	76.7±20.5	50.0±15.1	81.7±16.1	153.2±19.5

lavaging of study animals are provided elsewhere (McMahon et al. 2000; Field et al. 2002; Field et al. 2007b). The filtered stomach contents were stored in 70% ethanol.

High latitude (>60°S) specimens of fish (*E. antarctica*, n=10), euphausiids (*Euphausia triacantha*, n=10), hyperiid amphipods (*Themisto gaudichaudii*, n=7) and squid (*Bathyteuthis abysicola*, n=2 and *Psychroteuthis glacialis*, n=3) were collected by the Japanese TRV *Umitaka Maru* using pelagic trawls in the Dumont d'Urville Sea, ranging from Terre Adélie to the Mertz Glacier tongue, in George V Land (61°45' to 67°30'S, 140° to 143°E) as part of the Collaborative East Antarctic Marine Census (CEAMARC) in January/February 2008 (Hosie et al. 2011; Moteki et al. 2011). Samples were collected at night and day using an IYGPT net (opening: 5.5 x 12 m) with a mesh of 100 mm in the front, then tapering through 80 mm to 40 mm to 20 mm to 10 mm mesh in the cod end and were sorted on deck and frozen. Samples were stored at -80°C until analysis.

Foraging habitat

We fitted a first-difference correlated random walk switching (DCRWS) model (Jonsen et al. 2005) incorporating Argos error to elephant seal satellite location data originating and terminating at Macquarie Island (n=14). Using 360 minute time step intervals, the model indexed movement parameters (differences in latitude and longitude between consecutive positions along the track) according to two behavioural modes (Morales et al. 2004); transit and Area Restricted Search (ARS) modes. Area Restricted Search corresponded to periods of reduced travel speed and increased turning rate (parameter estimates between 1.8 and 2.0), which are more likely to be associated with foraging movements as opposed to transit movement (parameter estimates between 1.0 and 1.2; Morales et al. 2004). Locations which did not fit these criteria (*i.e.* parameter estimates between 1.2 and 1.8; 14.2% of all locations at sea) were discarded. The methodology used to fit the model to elephant seal location data is described in detail in Jonsen et al. (2013).

Using the ARS locations, we calculated the proportion (%) of time spent by the seals in defined ACC Inter-Frontal Zones (IFZs). To map the position of ACC fronts, we used 19 years (1992 to 2011) of weekly sea surface height (SSH) gradients. The approach used to identify fronts in SSH data is described in detail by Sokolv and Rintoul (2007a; 2009b; 2009a) and summarized briefly here.

To map fronts in the Southern Ocean, twelve SSH contours were used, as in Sokolov and Rintoul (2009a). Of these, nine contours are associated with the ACC itself and three contours correspond to elevated SSH gradients associated with subtropical western boundary currents and their extension along the northern edge of the Southern Ocean. The ACC front positions inferred from satellite SSH maps were validated using independent data from Argo floats and high resolution hydrographic sections as described in detail in Sokolov and Rintoul (2009b; 2009a).

Each elephant seal satellite location was ascribed to an IFZ (Sokolov & Rintoul 2007b; Sokolov & Rintoul 2009b; Sokolov & Rintoul 2009a) defined as: (1) south of sBdy, (2) sBdy to SACCF-S, (3) SACCF-S to SACCF-N, (4) SACCF-N to PF-S, (5) PF-S to PF, (6) PF to PF-N, (7) PF-N to SAF-S, (8) SAF-S to SAF, (9) SAF to SAF-N, (10) SAF-N to SAZ, (11) SAZ to STZ-S, (12) STZ-S to STZ-N and (13) N STZ-N, where sBdy: southern Boundary Current; ACC: Antarctic Circumpolar Current; N: north; S: south; PF: Polar Front; SAF: sub-Antarctic Front; SAZ: sub-Antarctic Zone and STZ: sub-Tropical Zone.

These IFZs were summarised into seven distinct zones as follows: 1. S of SACCF-S (IFZ 1,2); 2. ACC to PF-S (IFZ 3,4); 3. PF (IFZ 5,6); 4. PF to SAF (IFZ 7); 5. SAF (IFZ 8,9); 6. SAF-N to SAZ (IFZ 10), and 7. SAZ to STZ-S (IFZ 11). Numbers in brackets correspond to IFZs above.

Sample preparation and stable isotope analysis

Seal whiskers

The whiskers were cleaned with successive rinses in a 2:1 chloroform:methanol solution, and then dried in an oven at 60˚C for 72 hours. The twelve post-trip whiskers were weighed and sectioned into approximately 2 mm sections. The sections from each whisker were numbered sequentially, starting from the base, in order to track the temporal integration of isotope values along the length of the whisker.

Prey specimens

Isotopic analysis was performed on the white muscle of fish, the mantle and lower beaks of squid, and whole specimens of amphipods and euphausiids. Muscle tissues (fish and squid) and whole specimens were freeze dried and ground to fine powder before lipids were removed from all samples (Kojadinovic et al. 2008), and carbonates were removed from amphipod and euphausiid samples (Hobson & Cherel 2006). Different ratios of chitin (a ^{15}N-depleted molecule) to protein are found in undarkened, darkening and darkened parts of squid beaks, with much

more chitin in undarkened than in darkened parts (Miserez et al. 2007; Cherel et al. 2009a). Consequently, the darkened wings of lower beaks are less impoverished in ^{15}N relative to diet and were therefore used for stable isotope analysis. The lower beaks of squid were cleaned with successive rinses of distilled water, before the wing parts of beaks were cut away using scissors. Wings of lower beaks were then dried in oven at 60˚C for a minimum of 16 hours and ground to fine powder. Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass, UK) continuous-flow isotope-ratio mass spectrometer. Results are reported using standard δ notation in parts per thousand (‰) relative to Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric N^2 (Air) for $\delta^{15}N$ as follows:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where δX is $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$

Replicate measurements of internal laboratory standards (Alanine) indicate measurement errors < 0.20 ‰ and < 0.21 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope analysis was performed by the Environmental Biology Group, Research School of Biological Sciences, Australian National University (ANU), Canberra, Australia.

Whisker growth dynamics and isotopic values of sub-yearlings

Southern elephant seals undergo a 24 day lactation period (McMahon & Bradshaw 2004) in which post-partum pup growth is fuelled exclusively by energy from stored reserves in fasting mothers (Arnbom et al. 1997). Isotope values along the length of a pre-trip whisker are therefore derived from *in-utero* development and post-partum, while isotopic values in the post-trip whisker reflect a shift from maternal investment to independent foraging. As pups mature, the process of weaning leads to a change in isotopic signal when the assimilation of carbon and nitrogen shifts to sources other than mother's milk, such as free-ranging prey (Hobson et al. 1993; Hirons 2001; Stegall et al. 2008a) and/or energy stores (fasting) post-weaning and pre-departure (Arnbom et al. 1993). Thus, weaning essentially represents a change in trophic level from mother's milk (higher trophic level) to free ranging prey (lower trophic level).

To identify which part of the post-trip whisker reflected independent foraging at sea, we therefore compared $\delta^{15}N$ values along the length of the post-trip whisker to the basal section of the pre-trip whisker (containing the isotopic signal of *in-utero* development and post-partum; red symbol, Fig. 3.1.). The horizontal solid line indicates where the pre-trip basal segment intercepts

the $\delta^{15}N$ values along the length of the post-trip whisker (10.8‰). Note that the point of interception occurs during the drop of 3.9‰ in $\delta^{15}N$ from 12.4 to 8.5‰, which we interpret as a trophic level shift from mother's milk and/or fasting to independent foraging at sea. Once the lowest $\delta^{15}N$ is reached (*i.e.* the transition is complete), we consider this and all subsequent samples to represent amino acids derived from independent foraging. The proportion (mm) of post-trip whisker that represents $\delta^{15}N$ values incorporated during independent foraging at sea is 14 mm (Fig. 3.1.).

Variation in habitat and trophic position ($\delta^{13}C$ and $\delta^{15}N$) of seals with the location of foraging

Within the Southern Ocean, there is a well defined geographical $\delta^{13}C$ gradient in particulate organic matter (POM) surface waters, ranging from high $\delta^{13}C$ values in warm subtropical waters in the north, to depleted values in cold Antarctic waters in the south (Rau et al. 1982; Rau et al. 1989; Goericke & Fry 1994; Popp et al. 1999; Trull & Armand 2001). This is subsequently transferred to higher levels within the food chain (Cherel et al. 2006; Cherel & Hobson 2007). In order to relate isotopic signatures to foraging habitat we therefore took into account the latitudinal gradient in tissue $\delta^{13}C$ values of top predators in the Southern Ocean (Cherel et al. 2006; Cherel & Hobson 2007) and the location of the major oceanographic frontal zones, *e.g.* SAF, PF and sBdy (Sokolov & Rintoul 2007b) of the Southern Ocean.

The greatest proportion of seal ARS locations occurring in a particular IFZ defined their habitat use. Isotopic signatures of elephant seals were then grouped according to habitat.

Inferred prey consumption during the first six months

We used $\delta^{13}C$ and $\delta^{15}N$ values of marine organisms from mid- and high latitude Southern Ocean waters to infer the diet of elephant seals in relation to foraging habitat (Schmidt et al. 2004; Bury et al. 2008; Cherel 2008; Cherel et al. 2008; this study; Table S1.). For mid-latitude waters, we used a combination of pelagic fish (myctophids), squid and euphausiids from waters located around the PF in the Indian and Atlantic Ocean sectors of the Southern Ocean.

The beaks of two species of squid (*M. hyadesi* and *H. eltaniane*) contained in stomach lavage samples of returning juvenile Macquarie Island southern elephant seals were also examined (Hughes, A.R. unpubl. data). Cephalopod beak structure is species specific (Rodhouse 1989) and the lower beak rostral length (LRL) can be used to estimate mantle length and mass of

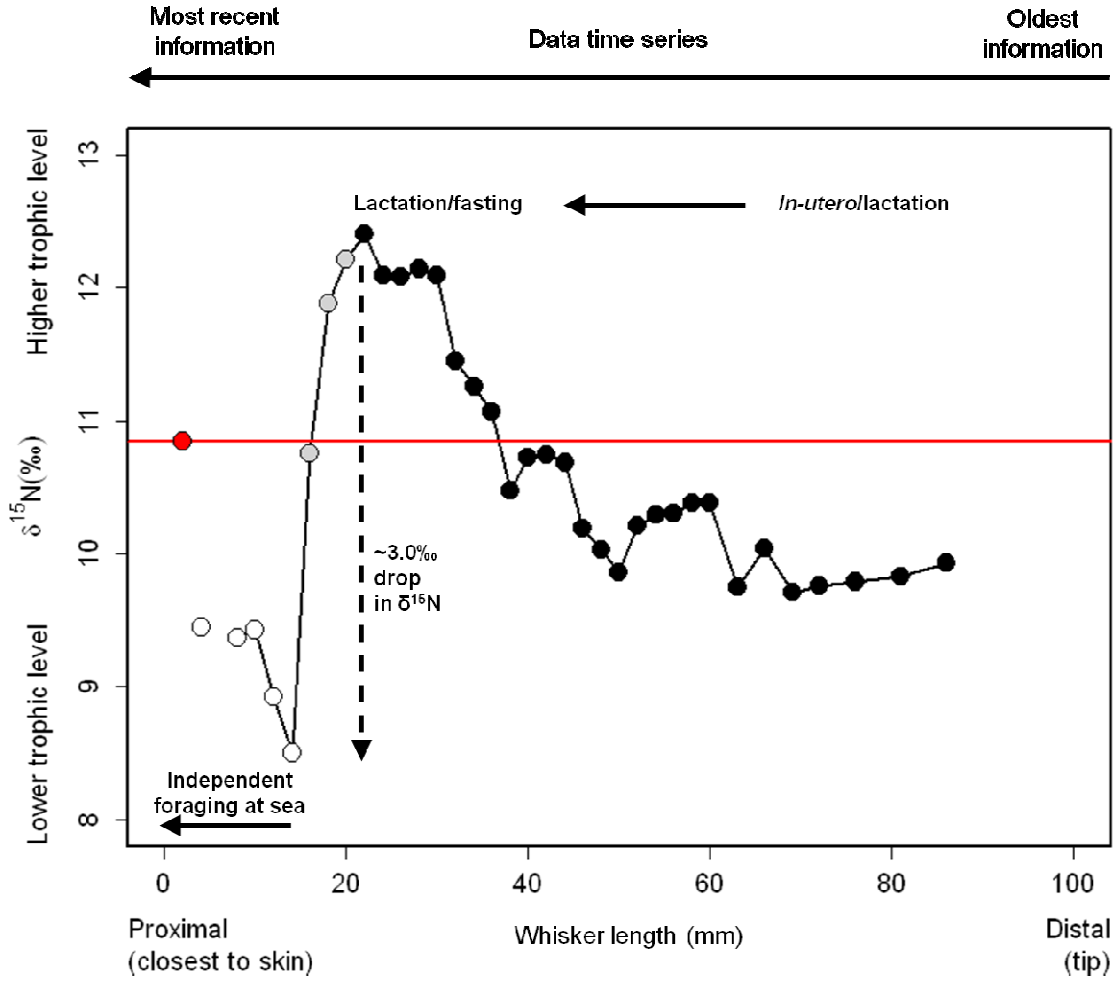

Figure 3.1. A schematic plot used to determine the shift to independent foraging along the post-trip whisker. We used stable nitrogen isotope values incorporated along the temporal span of the whisker as represented by the growth of the whisker from the distal (tip; oldest isotopic information) to proximal region (closest to the skin; most recent isotopic information). The red line indicates where the pre-trip basal segment (red symbol) intercepts $\delta^{15}N$ values along the length of whisker. Solid arrows indicate the shift in food source along the temporal span from *in utero*/lactation to lactation/fasting (black symbols) to independent foraging at sea (open symbols). Dashed arrow indicates 3.9‰ drop in $\delta^{15}N$ (equivalent to one trophic level ~3.0‰; grey symbols). The first 14 mm of whisker represents independent foraging at sea.

squid from allometric data (Clarke 1986). To assess the size of squid consumed by sub-yearlings we therefore used mean $\delta^{13}C$ and $\delta^{15}N$ values of small, medium and large LRL sized beaks according to species (for details see Table S1.).

From high latitude waters (>60°S) north of Adélie and George V Land in the Indian Ocean sector, we used myctophids (*Electrona antarctica*), euphausiids (*Euphausia triacantha*) and amphipods (*Themisto gaudichaudii*) sampled in pelagic waters at depths of <500 m (62 to 65°30'S, 140 to 143°E); the deep-sea squid *Bathyteuthis abysicola*, sampled at depths of <1000 m (63°S, 140°E), and the glacial squid *Psychroteuthis glacialis*, sampled at depths of <200 m in high latitude waters (65°30'S, 140°E). Values of Antarctic krill (*Euphausia superba*) sorted from emperor penguin (*Aptenodytes forsteri*) regurgitates from Adélie Land (Cherel 2008), and of pelagic squid from the northern Ross Sea area in the Pacific Ocean sector, were also used (Bury et al. 2008).

We used whisker-specific isotopic fractionation values for $\delta^{13}C$ and $\delta^{15}N$ of 3.2‰ and 2.8‰, respectively, as obtained from a study of captive pinnipeds (Hobson et al. 1996), since studies reporting the isotopic fractionation for $\delta^{13}C$ and $\delta^{15}N$ between diet and whiskers for wild populations of elephant seals or other pinniped species are absent. Correction factors of 3.2‰ and 2.8‰ were therefore applied to $\delta^{13}C$ and $\delta^{15}N$ values, respectively, when comparing seal values to the isotopic values of marine organisms. Cephalopod beaks are depleted in ^{15}N, due to the presence of chitin (a ^{15}N depleted molecule) and accordingly, contain lower $\delta^{15}N$ values compared to the mantle (~3.5‰) and buccal mass (~2.6‰) soft tissue of cephalopods (Cherel et al. 2009a). A correction factor of 3.5‰ was therefore applied to the $\delta^{15}N$ values of *H. eltaninae* and *M. hyadesi* beaks prior to isotopic comparison with elephant seals and other marine organisms.

Variation in habitat and trophic position ($\delta^{13}C$ and $\delta^{15}N$) of seals with age

To assess age-related shifts in trophic level and diet structure we compared the isotopic signatures in whiskers of sub-yearlings (n=12; this study) to that of one (n=5), two (n=40) and three (n=27) year old elephant seals sampled between 1999 and 2000 from Macquarie Island (Newland et al. 2011). Isotopic signatures of one, two and three year old seals were derived from a single, randomly selected 2 mm section from each whisker.

Statistical analyses

We performed all statistical analysis using R version 2.15.0 (R Development Core Team 2012). To determine if the stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of migratory, sub-yearling elephant seal whiskers were influenced by sampling year or the location of foraging (as inferred by the proportion of ARS locations occurring in IFZs) we used multivariate analyses of variance (MANOVA) fitted with the MANOVA function in R. To determine if $\delta^{13}C$ or $\delta^{15}N$ values were influenced by sampling year or the location of foraging separately, we used a linear model fitted with the lm function in R, with whisker $\delta^{13}C$ or $\delta^{15}N$ values as the dependent variables, year and foraging location as factors and the two way interaction term. We used Analysis of Variance (ANOVA) along with Tukey's Honestly Significant Difference (HSD) post-hoc analysis to indicate where response variables differed. Proportional data were arcsine transformed prior to statistical analysis.

Linear mixed-effects models were used to examine the effects of age class and sex on variation of stable isotope values. The dependent variable was either $\delta^{13}C$ or $\delta^{15}N$, with sampling year as a random factor, and age and sex as fixed factors. If the distribution was significantly different from normality, the data were log-transformed and normality verified. Interactions between sampling year and dependent variables were examined. Effects of age and sex were, likewise, tested systematically in all analyses. We further assessed qualitative patterns of variation in habitat and trophic position through graphical examination of $\delta^{13}C$ and $\delta^{15}N$ values, respectively. We assessed significance for statistical tests at the 0.05 level. Mean values are given ± standard deviation (SD).

RESULTS

Whisker growth dynamics and isotopic values of sub-yearlings

Post-trip whiskers ranged in length from 42 to 144 mm (mean=113.7±19.2 mm; n=12; Table 3.2.) with the number of segments per whisker ranging from 17 to 55 (mean=33±9.4). Overall, a total of 551 sections were cut and analysed.

Isotopic values of whisker segments ranged from -22.9 to -16.6‰ (a difference of 6.3‰) for $\delta^{13}C$, and from 7.9 to 13.9 (a difference of 6‰) for $\delta^{15}N$ (Fig. 3.2.). From the distal to proximal regions of the whiskers, $\delta^{13}C$ values showed an initial rise and then plateau in ^{13}C abundance, before starting to fall again (Fig. 3.2.). The number of segments and fall in ^{13}C abundance varied among individuals. This pattern was even more pronounced in $\delta^{15}N$ values, with seven seals showing a distinct peak and ~4.0‰ drop in ^{15}N abundance (range=3.8 to 4.8‰). A difference of ~4.0‰ in $\delta^{15}N$ values reflects more than one trophic level of difference (~3.0‰). The decline in $\delta^{15}N$ values (grey symbols, Fig. 3.2.) coincided with the point of interception with the pre-trip basal segment (red symbol and line, Fig. 3.2.; n=5), indicating a shift in food source from maternal milk and/or fasting (black symbols, Fig. 3.2.) to independent prey acquisition (open symbols, Fig. 3.2.).

Other seals (J373, T719, T825, T839 and T887) showed only an initial increase in ^{15}N abundance along the temporal span (Fig. 3.2.), with whiskers on average 21.4 mm shorter than that of other seals (101.2±20.9 mm, n=5 versus 122.6±12.7 mm, n=7; Table 3.3.). For the latter group of seals, this indicates that the portion of whisker that contains the subsequent decline in ^{15}N abundance (Fig. 3.1.) was still beneath the skin, and thus not sampled.

The portion of post-trip whisker grown during *in-utero*/lactation/fasting ranged in length from 85 to 102 mm (mean=93.4±6.9 mm; 77.2±5.7% of total whisker length; n=8; Table 3.3.) with the number of segments per whisker ranging from 24 to 31 (mean=26.8±2.3), while the portion of post-trip whisker grown during independent foraging at sea ranged in length from 4 to 30 mm (mean=11.7±9.5 mm; 9.1±6.4% of total whisker length; n=7; Table 3.3.) with the number of segments per whisker ranging from 2 to 9 (mean=4.4±2.5).

Foraging habitat

The number of days that the sub-yearling elephant seals spent at sea ranged from 126 to 182 days (mean=153.2±19.5d; Table 3.1.). The time spent in transit mode ranged from 12 to 76

Table 3.2. Proportion of time spent (percentage) in Area Restricted Search (ARS) by seals in Inter-Frontal Zones (IFZs), including the Antarctic zone south of the southern Antarctic Circumpolar Current front-Southern Branch (S of SACCF-S), the ACC to Polar Front-Southern Branch (ACC to PF-S), the Polar Front (PF), the Polar Front to sub-Antarctic Front (PF to SAF) and the sub-Antarctic Front (SAF).

Seal ID	Sex	Proportion of ARS locations occurring in IFZs (%)						Habitat group	
No.		S of SACCF-S	ACC to PF-S	PF	PF to SAF	SAF	Total	IFZ	Latitude (°S)
1995/1996									
J226	F	0.0	0.0	47.8	5.7	2.0	55.5 (Dec-Apr)	PF	62°41'
J263	M	0.0	28.6	23.1	6.0	0.0	57.7 (Dec-Mar)	ACC to PF-S	64°60'
J373	F	0.0	0.0	46.3	4.4	0.0	50.7 (Dec-Feb)	PF	62°97'
J375	F	0.0	3.1	19.8	19.1	0.0	42.0 (Dec-Mar)	PF	63°19'
J492	F	0.0	13.9	24.2	10.3	0.0	48.4 (Dec-Mar)	PF	62°98'
J503	M	0.0	0.0	40.7	18.7	0.0	59.5 (Dec-Mar)	PF	62°84'
Mean		0.0	7.6±11.6	33.6±12.7	10.7±6.7	0.3±0.8	52.2±6.6		63°17'±0°75'
1999/2000									
T719	F	0.0	0.0	49.3	7.8	3.4	60.5 (Jan-May)	PF	56°46'
T825	F	34.6	22.8	0.0	0.0	0.0	57.4 (Feb-May)	S of SACCF-S	61°64'
T839	F	0.0	56.5	0.0	0.0	0.0	56.5 (Jan-Mar)	ACC to PF-S	64°57'
T867	F	11.3	29.6	9.9	2.2	0.0	53.0 (Jan-Apr)	ACC to PF-S	64°80'
T875	F	0.0	24.6	14.6	1.0	0.0	40.1 (Jan-Apr)	ACC to PF-S	59°43'
T887	F	0.0	36.3	18.7	0.4	0.0	55.5 (Jan-May)	ACC to PF-S	62°43'
Mean		7.6±13.9	28.3±18.5	15.4±18.3	1.9±3.0	0.6±1.4	53.9±6.5		61°55'±3°19'
Overall mean		3.8±10.2	18.0±18.3	24.5±17.8	6.3±6.7	0.4±1.1	53.1±6.3		62°36'±2°36'

The greatest proportion of seal ARS locations occurring in a particular IFZ defined their habitat group.

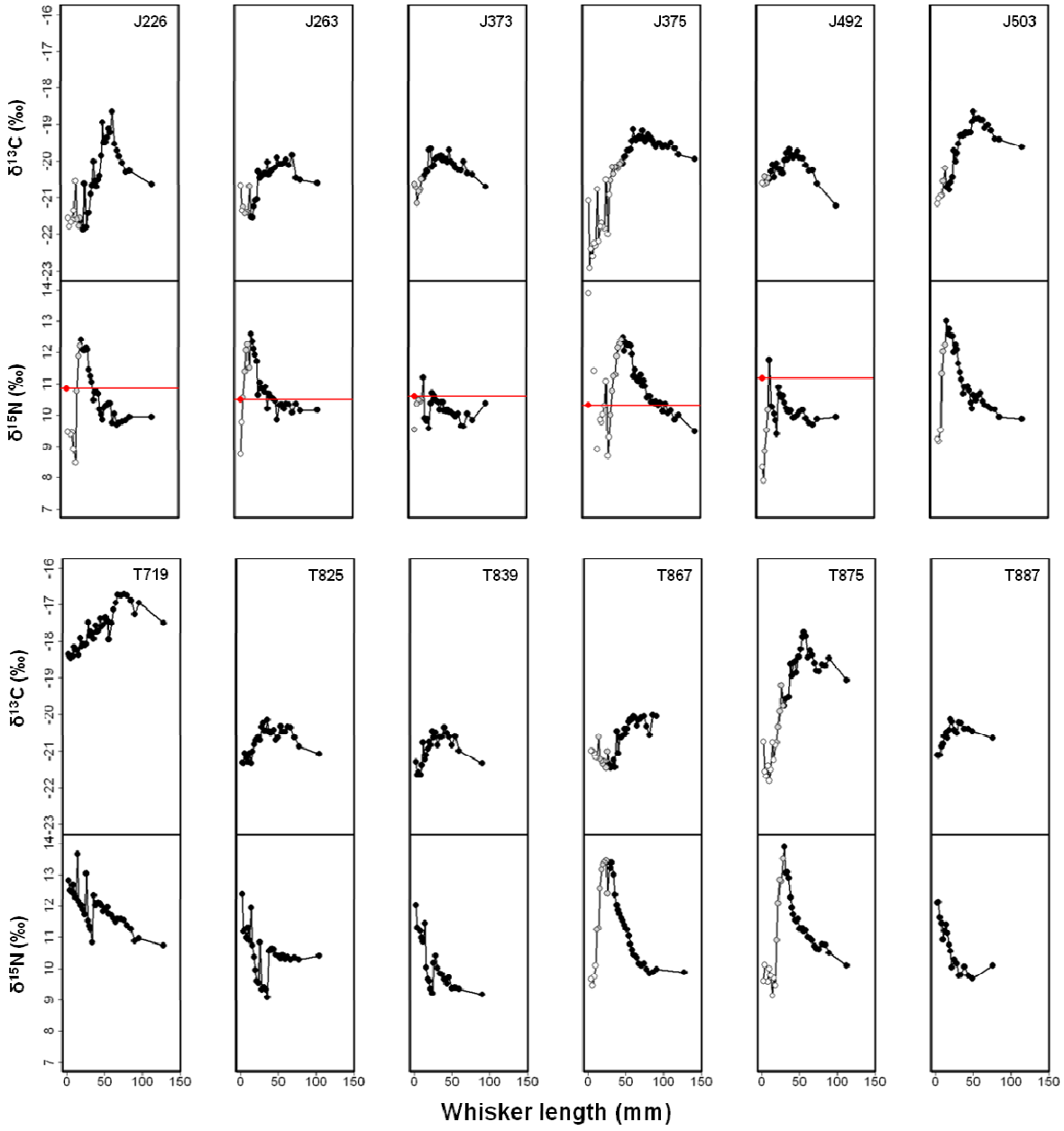

Figure 3.2. Schematic plots of $\delta^{13}C$ and $\delta^{15}N$ values along the post-trip whiskers of 12 sub-yearling southern elephant seals. We used stable carbon and nitrogen isotope values incorporated along the length of the whisker (mm). Values are colour-coded according to shift in food source along the temporal span of whisker presented in Fig. 3.1. Black symbols: *in-utero*/lactation/fasting; grey symbols: diet shift from mother's milk and/or fasting to other food sources; open symbols: independent foraging at sea.

Table 3.3. Stable isotopic characteristics of post-trip whiskers for each sub-yearling elephant seal (n=12).

Seal ID No.	Sex	Whisker length (mm)	Pre-trip basal segment		Post-trip whisker stable isotopic characteristics									Habitat group
					Overall			*In-utero*/lactation/fasting			Independent foraging at sea			
			$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰) (range)	$\delta^{15}N$ (‰) (range)	C:N ratio	Length (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Length (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	
1995/1996														
J226	F	121.0	-20.0	10.8	-20.5±1.0 (-21.9 – -18.7)	10.5±1.0 (8.5 – 12.4)	2.9±0.1	95.0 (27)	-20.2±0.9	10.6±0.9	12.0 (60)	-21.4±0.5	9.1±0.4	PF
J263	M	112.0	-20.3	10.5	-20.6±0.5 (-21.5 – -19.8)	10.9±0.8 (9.8 – 12.6)	3.0±0.1	90.0 (26)	-20.4±0.5	10.8±0.7	4.0 (2)	-21.0±0.5	9.3±0.7	ACC to PF-S
J373	F	105.0	-19.9	10.6	-20.2±0.4 (-21.1 – -19.7)	10.2±0.4 (9.6 – 11.2)	3.0±0.1	85.0 (27)	-20.1±0.3	10.2±0.4	-	-	-	PF
J375	F	148.0	-19.6	10.3	-20.2±1.1 (-22.9 – -19.1)	10.9±0.9 (8.7 – 12.5)	3.0±0.0	98.0 (31)	-19.5±0.2	10.9±0.8	30.0 (5)	-21.8±0.7	10.3±1.5	PF
J492	F	112.0	-20.4	11.2	-20.2±0.3 (-20.6 – -19.7)	10.0±0.7 (7.9 – 11.8)	2.9±0.1	90.0 (24)	-20.1±0.3	10.2±0.5	4.0 (2)	-20.6±0.0	8.1±0.3	PF
J503	M	116.0	-	-	-19.7±0.8 (-21.2 – -18.6)	11.1±1.0 (9.2 – 13.0)	3.0±0.1	102.0 (28)	-19.5±0.6	11.1±0.9	6.0 (3)	-21.1±0.1	9.3±0.2	PF
Mean		119.0±15.2	-20.0±0.3	10.7±0.3	-20.2±0.8 (-22.9 – -18.6)	10.6±0.9 (7.9 – 13.0)		93.3±6.2 (27.2±2.3)	-20.0±0.6	10.7±0.8	11.2±11.0 (3.6±1.8)	-21.5±0.7	9.6±1.3	
1999/2000														
T719	F	132.0	-	-	-17.6±0.5 (-18.5 – -16.7)	11.9±0.6 (10.8 – 13.7)	2.9±0.1	129.0 (39)*	-17.7±0.5	11.9±0.6	-	-	-	PF
T825	F	104.0	-	-	-20.7±0.3 (-21.3 – -20.1)	10.4±0.7 (9.1 – 11.9)	2.9±0.1	104.0 (32)*	-20.7±0.4	10.4±0.7	-	-	-	S of SACCF-S
T839	F	89.0	-	-	-20.9±0.4 (-21.6 – -20.4)	10.1±0.7 (9.2 – 11.4)	2.8±0.1	90.0 (24)*	-20.9±0.4	10.1±0.8	-	-	-	ACC to PF-S
T867	F	129.0	-	-	-20.7±0.5 (-21.5 – -20.0)	11.4±1.3 (9.4 – 13.4)	2.9±0.1	102.0 (27)	-20.5±0.5	11.2±1.1	8.0 (4)	-21.1±0.1	9.7±0.3	ACC to PF-S
T875	F	120.0	-	-	-19.4±1.3 (-21.8 – -17.8)	11.3±1.2 (9.1 – 13.9)	2.9±0.0	85.0 (24)	-18.6±0.5	11.5±0.9	18.0 (9)	-21.3±0.4	9.7±0.3	ACC to PF-S
T887	F	76.0	-	-	-20.5±0.3 (-21.1 – -20.1)	10.6±0.8 (9.7 – 12.1)	2.8±0.1	76.0 (19)*	-20.6±0.3	10.7±0.8	-	-	-	ACC to PF-S
Mean		108.3±22.6	-	-	-19.8±1.4 (-21.8 – -16.7)	11.1±1.1 (9.1 – 13.9)		93.5±12.0 (25.5±2.1)	-19.6±1.1	11.3±1.0	13.0±7.1 (6.5±3.5)	-21.4±0.4	9.7±1.0	
Overall mean		113.7±19.2	-20.0±0.3	10.7±0.3	-20.0±1.1 (-22.9 – -16.7)	10.8±1.0 (7.9 – 13.9)		93.4±6.9 (26.8±2.3)	-19.9±0.8	10.8±0.9	11.7±9.5 (9.1±6.4)	-21.4±0.6	9.6±1.0	

*Seals showed incomplete whisker growth (mm) during *in-utero*/lactation/fasting. Results for these animals are not included in the mean and overall mean (± standard deviation).

days (mean=50.0±15.1d; 32.4% of all locations at sea), while the time spent in ARS mode ranged from 62 to 108 days (mean=81.7±16.1d; 53.2% of all locations at sea).

Area Restricted Search locations for sub-yearlings in the 1995/1996 deployment occurred between December 1995 and April 1996, and between January and May 2000 in the 1999/2000 deployment (Table 3.2.). Area Restricted Search locations occurred primarily at the distal portion of tracks (Fig. 3.3.A; see Fig. S1. for individual tracks). The highest proportion of sub-yearlings (1995/1996: n=6; 1999/2000: n=2) utilized waters southeast of Macquarie Island, parallel with the Mid-Ocean ridge (MOR), ranging from 55ºS to 66ºS and 160ºE to 170ºW (Fig. 3.3.A). In 1999/2000, three individuals utilized waters further to the southeast ranging from 59ºS to 64ºS and 160ºE to 160ºW, while one individual (T719) utilized waters southwest of Macquarie Island, associated with the Southeast Indian Ridge (SEIR), ranging from 53ºS to 58ºS and 130ºE to 160ºE (Fig. 3.3.A). The majority of ARS locations of seals occurred within Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Subareas 58.4.1, to the southwest of Macquarie Island, and 88.1 and 88.2 to the southeast (Fig. 3.3.A).

Of the seven summarised IFZs utilised by sub-yearlings during migration from Macquarie Island (Fig. 3.3.B), five were used by young seals while in ARS mode (Table 3.2.). Of these, the PF was the most commonly used, with 24.5±17.8% of all ARS locations occurring in this zone, followed by the ACC to PF-S (18.0±18.3%), the PF to SAF (6.3±6.7%), the S of SACCF-S (3.8±10.2%) and lastly, the SAF (0.4±1.1%). Between deployment years, the PF was the most commonly used zone in 1995/1996 (n=5), while the ACC to PF-S was the most commonly used zone in 1999/2000 (n=5). A single individual in 1999/2000 however, predominantly utilized waters south of the SACCF-S, with 34.6% of all search locations occurring in this zone (Table 3.2.). The mean latitude of ARS locations occurring in each zone ranged from 56º5'S to 63º2'S in the PF, from 59º4'S to 64º6'S in the ACC to PF-S, and 61º6'S in the S of SACCF-S. We therefore identified two main habitat groups, the 'ACC to PF-S' (n=5) and the 'PF' (n=6; Table 3.2.). The small sample size of seals utilizing the region south of the SACCF-S (n=1) however, precluded further statistical comparison of this IFZ.

Variation in habitat and trophic position ($\delta^{13}C$ and $\delta^{15}N$) of seals with the location of foraging

There was considerable overlap in $\delta^{13}C$ and $\delta^{15}N$ whisker values between individuals, with no significant differences in isotopic means and variances between years or IFZs detected in multivariate (MANOVA, Wilk's λ: Year: $F_{1,2}$=1.150, P=0.426; Zone: $F_{1,2}$=0.499, P=0.650) and in uni-variate analysis (ANOVA: $\delta^{13}C$: all $P > 0.688$; $\delta^{15}N$: all $P > 0.514$). Mean isotopic values of sub-yearling elephant seal whiskers foraging in both the ACC to PF-S and PF were -21.2±0.4‰ (range=-21.8 to -20.6‰; a difference of 1.2‰) for $\delta^{13}C$, and 9.4±0.7‰ (range=8.1 to 10.3‰; a difference of 2.2‰) for $\delta^{15}N$ (Table 3.3.; Fig. 3.4.A).

As latitude is central in relating isotopic signatures in the tissues of consumers to foraging habitat in the Southern Ocean, we looked at the potential relationships between isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of elephant seal whiskers and the mean latitude of their foraging locations (*i.e.* habitat group, Table 3.2.). No significant relationship between whisker isotopic values and mean latitude of foraging was detected (ANOVA: $\delta^{13}C$: $F_{1,5}$=0.263, P=0.630; $\delta^{15}N$: $F_{1,5}$=0.004, P=0.950), with considerable overlap in both $\delta^{13}C$ and $\delta^{15}N$ values and mean latitude of foraging location among seals (Fig. 3.4.). Foraging locations of sub-yearlings encompassed a narrow latitudinal band (~60 to 65°S), with mean latitude of locations ranging from 62°42' to 63°19'S for seals foraging in the PF zone (n=4), and from 59°43' to 64°80'S for seals foraging in the ACC to PF-S zone (n=3; Fig. 3.4.B).

Inferred prey consumption during the first 6 months

Mean $\delta^{13}C$ and $\delta^{15}N$ values for seal whiskers (corrected for trophic discrimination) and potential prey items were plotted together (Fig. 3.5.; Table S1.). Seals foraging in the two IFZs showed similar isotope values to a mixture of intermediate trophic level mesopelagic fish, such as *E. antarctica* ($\delta^{13}C$: -23.2‰ and $\delta^{15}N$: 8.3‰), *G. fraseri* ($\delta^{13}C$: -22.5‰ and $\delta^{15}N$ value: 8.0‰), *Krefftichthys anderssoni* ($\delta^{13}C$: -22.3‰ and $\delta^{15}N$: 7.6‰), and the squids *Kondakovia longimana* ($\delta^{13}C$: -25.1‰ and $\delta^{15}N$: 7.6‰) and *Galiteuthis glacialis* ($\delta^{13}C$: -24.7‰ and $\delta^{15}N$: 8.1‰), and lower trophic level mesopelgic fish, such as *P. tensioni* ($\delta^{13}C$: -22.1‰ and $\delta^{15}N$ value: 6.4‰), and the squid *M. hyadesi* ($\delta^{13}C$: -21.6‰ and $\delta^{15}N$ value: 6.6‰).

The $\delta^{13}C$ and $\delta^{15}N$ values recorded in the seals (as shown in Fig. 3.5.) strongly suggest that crustaceans, such as euphausiids, are consumed. This is because the isotopic values of seals are (to varying degrees) intermediate between crustaceans, such as *E. triacantha* ($\delta^{13}C$: -23.6‰

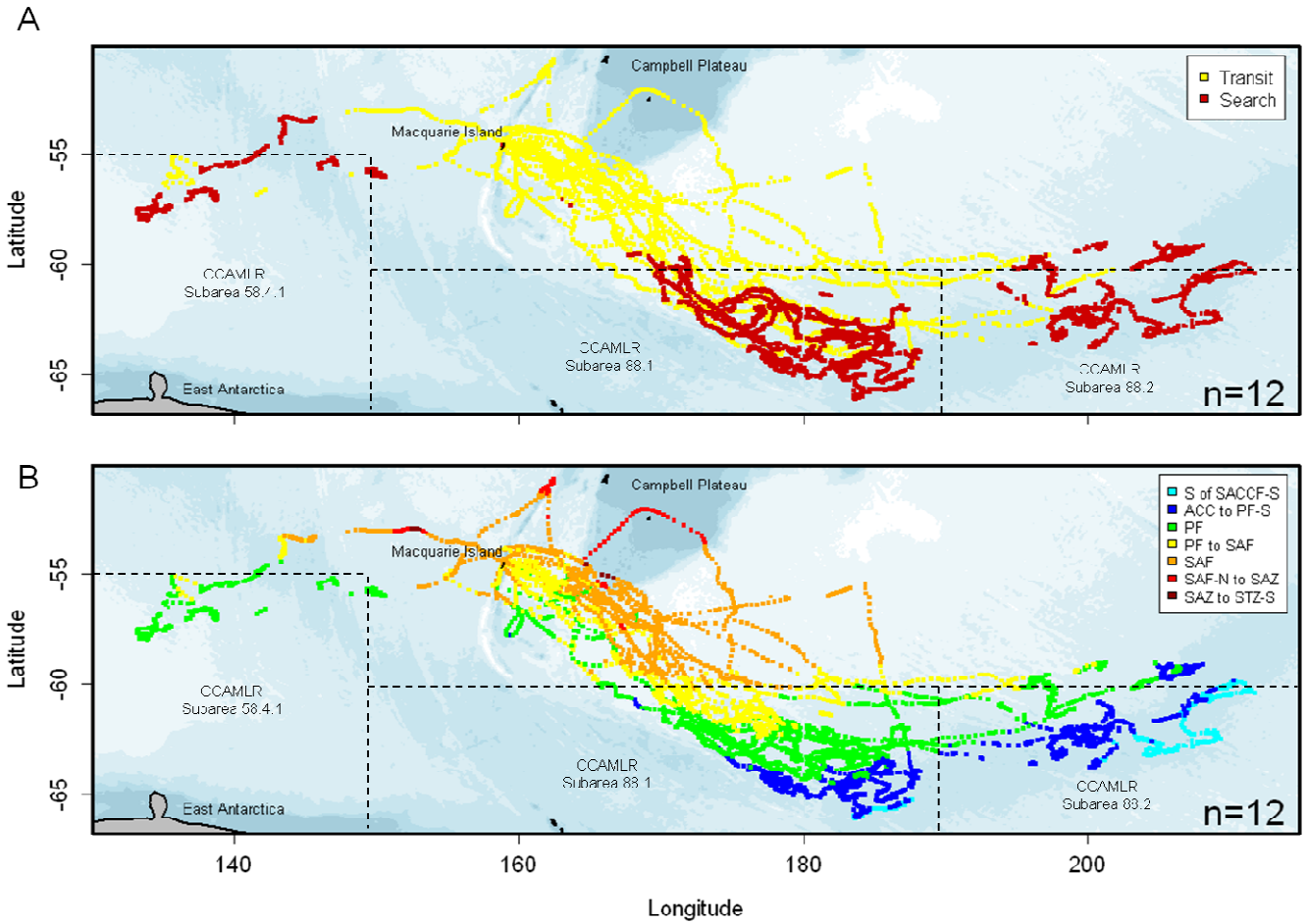

Figure 3.3. Tracks of 12 weaned southern elephant seals during their first migration from Macquarie Island. Tracks are colour-coded according to (A) behavioural state estimates from the two-state first-difference correlated random walk switching (DCRWS) model overlaid in yellow (Transit) and red (Area Restricted Search) and (B) Inter-Frontal Zones (IFZs). From south to north, IFZs included the Antarctic zone south of the southern Antarctic Circumpolar Current Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to sub-Antarctic Front (PF to SAF), the SAF, and the SAF-Northern branch to sub-Antarctic Zone (SAF-N to SAZ). Dashed lines indicate the boundaries of CCAMLR Statistical Subareas 58.4.1, 88.1 and 88.2. All seal tracks originated and terminated at Macquarie Island, located in the South-West Pacific Ocean sector of the Southern Ocean.

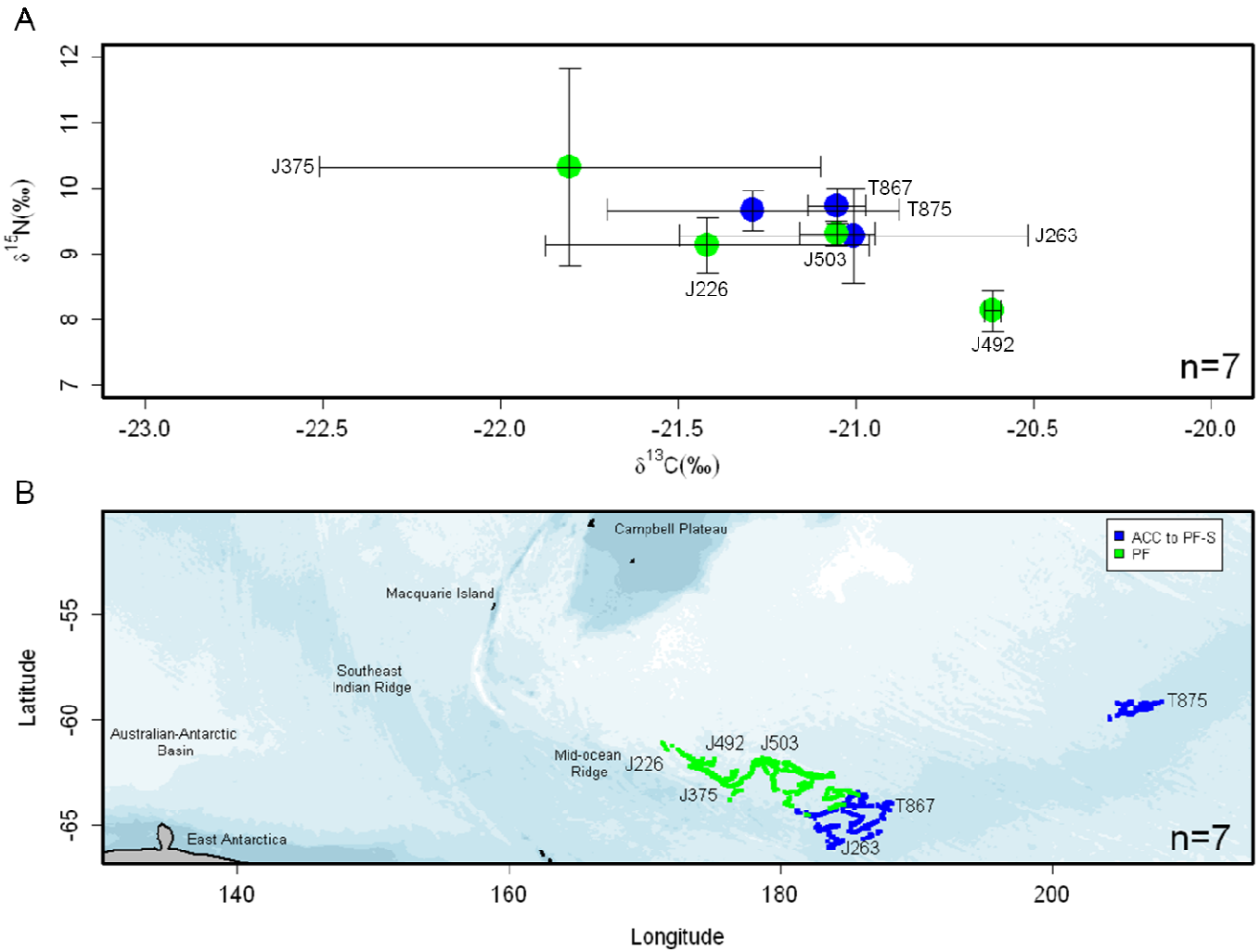

Figure 3.4. Area Restricted Search locations and whisker $\delta^{13}C$ and $\delta^{15}N$ values reflecting independent foraging at sea. (A) Mean $\delta^{13}C$ and $\delta^{15}N$ whisker values and (B) Area Restricted Search locations for 7 sub-yearling elephant seals during their first migration from Macquarie Island are colour-coded according to foraging location (Inter-Frontal Zones, IFZs, presented in Fig. 3.2.). Bathymetric features including the Southeast Indian Ridge, Australian-Antarctic Basin and Mid-Ocean Ridge are indicated in (B). Values are mean ± SD.

and δ^{15}N value: 6.3‰), *E. superba* (δ^{13}C: -25.8‰ and δ^{15}N value: 5.5‰) and *T. gaudichaudii* (δ^{13}C: -26.0‰ and δ^{15}N value: 5.4‰), and higher trophic level fish and squid (Fig. 3.5.). In at least four individuals (J263, J226, J503 and J492) they appear to have had some euphausiids in their diets. The interpretation of the other three individuals (J375, T867 and T875) is more ambiguous as their position on the plot could be due to either a mixture of squid, such as *P. glacialis* (δ^{13}C: -25.3‰ and δ^{15}N value: 7.9‰) and *M. hyadesi* or euphausiids and squid, such as *E. frigida* (δ^{13}C: -24.3‰ and δ^{15}N value: 4.9‰) and *P. glacialis* or even a combination of fish, squid and crustaceans.

Variation in habitat and trophic position (δ^{13}C and δ^{15}N) of seals with age

Stable carbon values in whiskers showed significant variation with age (mixed-effects ANOVA: $F_{3,126}$=10.116, P = 0.001), reflecting spatial variability in foraging habitat between age classes. Mean δ^{13}C values ranged from -21.4±0.6‰ (range=-21.9 to -20.5‰) for sub-yearlings, compared to -20.2±0.9‰ (range=-21.7 to -17.7‰), -20.2±1.0‰ (range=-22.3 to -18.2‰) and -20.7±0.9‰ (range=-23.0 to -19.1‰) for one, two and three year olds, respectively (Fig. 3.6.). Post-hoc analysis indicated sub-yearlings were significantly depleted in δ^{13}C compared to one and two year olds (Tukey's HSD post-hoc difference tests, both $P < 0.0001$). Sub-yearlings also appeared depleted in δ^{13}C compared to three olds, however no significant variation was detected (P=0.06).

Stable nitrogen isotopic values in whiskers showed significant variation with age (mixed-effects ANOVA: $F_{3,126}$=8.720, $P < 0.0001$). Mean δ^{15}N values ranged from 9.6±1.0‰ (range=7.9 to 13.9.0‰) for sub-yearlings, compared to 11.0±1.3‰ (range=8.8 to 13.3‰), 11.2±1.4‰ (range=8.7 to 13.8‰), and 10.7±1.1‰ (range=9.4 to 13.2‰) for one, two and three year old age classes, respectively (Fig. 3.6.). Post-hoc analysis indicated sub-yearlings were significantly depleted in δ^{15}N compared to one, two and three year old seals (Tukey's HSD post-hoc difference tests, all $P < 0.01$). Some one and two year old seals however, showed similar depleted δ^{13}C and δ^{15}N values as sub-yearlings, indicating overlap in both foraging habitat and trophic position.

DISCUSSION

The foraging range and prey intake of air-breathing marine predators is largely dictated by their physiological capabilities, most often related to body size (Schreer & Kovacs 1997; Burns 1999; Weise et al. 2010). The diet of young, independent offspring during their first foraging migration may therefore, differ substantially from that of older and larger conspecifics. This is particularly true for species where physiological and behavioural attributes can take several years to reach adult capacity. In southern elephant seals the dive durations and depth of newly weaned seals are known to be limited by their body size (Hindell et al. 1999; Irvine et al. 2000).

Using a combination of tracking and stable isotope data, we found the diet of sub-yearling southern elephant seals from Macquarie Island, foraging predominantly in waters at or south of the PF (~60°S) and within CCAMLR Statistical Subareas 88.1 and 88.2, to be consistent with the consumption of mesopelagic fish and squid, and crustaceans. The predominance of mesopelagic fish and squid in the diet of older juvenile and adult seals has been well documented (Daneri & Coria 1992; Green & Burton 1993; Slip 1995; Daneri et al. 2000; Daneri & Carlini 2002; Field et al. 2007b) however, the likely importance of crustaceans, such as euphausiids, in the diet of young seals feeding inside the CCAMLR management zone, is a significant, new finding for this species. Comparison of whisker isotopic values of sub-yearlings and older juvenile age classes (one, two and three year olds; Newland et al. 2011; this study), showed sub-yearlings to be relatively depleted in both $\delta^{13}C$ and $\delta^{15}N$. This is indicative of younger seals (constrained by their size, dive capabilities and prey capture skills) unable to access larger, higher trophic level prey deep in the water column (> 300 m), feeding closer to the surface where lower trophic level crustaceans, such as euphausiids, offer an abundant source of prey in addition to fish and squid.

Precaution must be taken in interpreting dietary trends inferred from isotopic results, as the combination of prey types using this technique can never be accurately quantified (Quillfeldt et al. 2005b; Tierney et al. 2008; Polito et al. 2011). The most plausible explanation for the low mean $\delta^{13}C$ and $\delta^{15}N$ values of sub-yearlings however is the consumption of euphausiids (and copepods and amphipods). Moreover, tracking data confirms that the foraging range of sub-yearlings at this time of year overlaps with the maximum sea-ice extent and known distribution of euphausiids in this region of east Antarctica (Worby et al. 1998; Nicol et al. 2000; Hunt & Hosie 2005). Further, the known dive depth and diurnal migrations of sub-yearlings

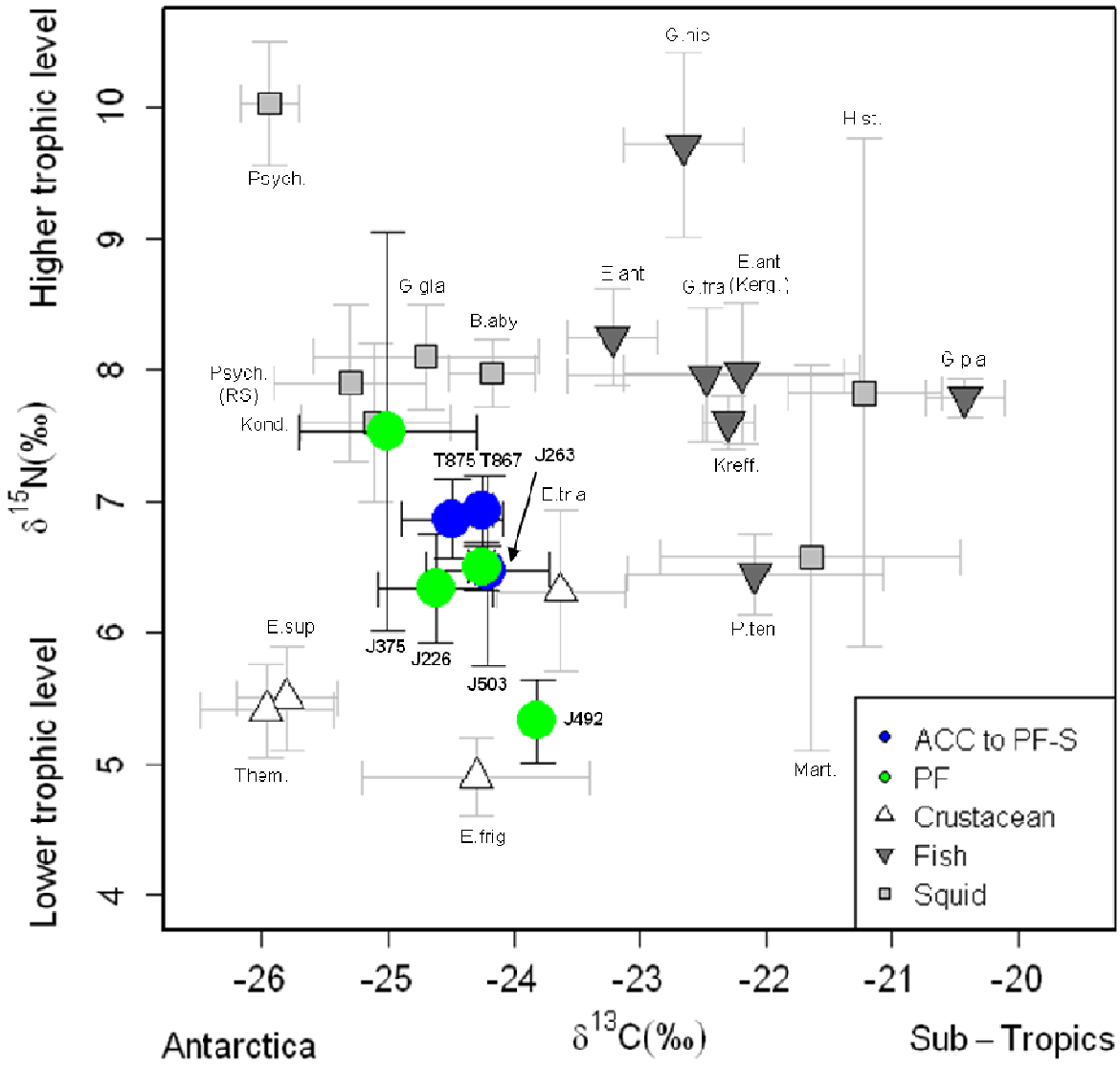

Figure 3.5. Mean $\delta^{13}C$ and $\delta^{15}N$ values of sub-yearling elephant seals and other Southern Ocean marine organisms. Mean $\delta^{13}C$ and $\delta^{15}N$ values in the whiskers of individual sub-yearlings foraging in ACC to PF-S (blue symbols) and PF (green symbols) zones, corrected for trophic discrimination by subtracting 3.2‰ and 2.8‰ from $\delta^{13}C$ and $\delta^{15}N$ values in Fig. 3.4.B, respectively. Mean $\delta^{13}C$ and $\delta^{15}N$ values in the tissues of other Southern Ocean marine organisms ((Schmidt et al. 2004; Bury et al. 2008; Cherel 2008; Cherel et al. 2008), this study) were grouped into crustacean, fish and squid taxa (white, dark grey and grey symbols, respectively). E.frig: *Euphausia frigida*; E.sup: *E. superba*; E.tria: *E. triacantha*; Them: *Themisto gaudichaudii*; E.ant: *Electrona antarctica*; E.ant (Kerg.): *Electrona antarctica* (Kerguelen); G.fra: *Gymnoscopelus fraseri*; G.nic: *G. nicholsi*; G.pia: *G. piablis*; Kreff.: *Krefftichthys anderssoni*; P.ten: *Protomyctophum tenisoni*; B.aby: *Bathyteuthis abysicola*; Hist.: *Histioteuthis eltaninae*; Kond.: *Kondakovia longimana*; Psych.: *Psychroteuthis glacialis*; Psych. (RS): *Psychroteuthis glacialis* (Ross Sea); G.gla: *Galiteuthis glacialis*; Mart.: *Martialia hyadesi*. Squid beak values were corrected for the reduced ^{15}N enrichment due to chitin. Values are mean ± SD.

(dive depth ~100m; Hindell et al. 1999) is consistent with the vertical distribution of krill in the Western Antarctic Peninsula during winter (Croxall et al. 1985; Lascara et al. 1999).

From a conservation and management viewpoint, our findings have important implications. We provide evidence of a new crustacean (krill) predator, the southern elephant seal, within waters managed under CCAMLR. Our findings show that regions associated with the Ross Sea constitute important foraging grounds for southern elephant seals during their critical, first year of life in which they transition to independent foraging.

Whisker growth dynamics

Bio-logging and natural biochemical tracers are increasingly being used to provide spatially explicit dietary information for highly migratory marine predators (Bailleul et al. 2010b; Bentaleb et al. 2011; Thiebot et al. 2011; Zbinden et al. 2011). Whiskers, collected from animals tracked by satellite, contain a time-series of stable isotope ratios of carbon and nitrogen which can potentially be related to individual telemetry tracks, establishing a means to link diet to remote feeding grounds. To interpret this dietary information in a spatio-temporal context however requires knowledge of the growth history of the whisker (Hirons et al. 2001; Greaves et al. 2004; Zhao & Schell 2004).

Accounting for the growth dynamics of whiskers enables the correct interpretation of the time-series of diet information incorporated along the length of the whisker (Hirons et al. 2001). In all sub-yearling elephant seals we found a similar pattern in isotopic enrichment along the temporal span of the whisker, *i.e.* from the distal to proximal region. However, this pattern was more pronounced in $\delta^{15}N$ values, with an initial rise and distinct peak in ^{15}N abundance indicative of the shift in food source from *in-utero* development to mother's milk during lactation. Nursing offspring essentially feed at a higher trophic level than their mothers do as has been shown in several species, including pinnipeds (Polischuk et al. 2001; Stegall et al. 2008b; Habran et al. 2010). In northern elephant seals, Habran et al. (2010) found young pups to be increasingly enriched in ^{15}N compared to that of their mothers from early (+0.6‰, day 5) to late lactation (+1.3‰, day 22), while in Steller sea lions (*Eumetopias jubatus*), Stegall et al. (2008b) recorded the root of the whisker (representing current growth) of young pups to be ^{15}N enriched (+2.0‰) over their diet (ingested mother's milk) during lactation.

Of the twelve sub-yearlings with concurrent isotopic and tracking data, seven seals showed a subsequent fall in $\delta^{15}N$ values, equivalent to more than one trophic level of a difference (~3‰) and indicative of a diet shift from mother's milk and/or fasting to free ranging prey. We suggest that the reason we do not see this decline in $\delta^{15}N$ values in the other five seals is that slower whisker growth meant that the new material, synthesized after weaning, never appeared above the skin and was therefore not sampled. The portion of whisker grown during independent foraging at sea accounted for 11.7±9.5 mm or 9.1±6.4% of total growth, indicating that an average of 12 mm of growth is contained under the skin for the latter group of seals. In contrast, the portion of post-trip whisker grown during *in-utero*/lactation/fasting accounted for 93.4±6.9 mm or 77.2±5.7% of total whisker growth (n=8). In elephant seals, whiskers are established early during *in-utero* development with foetal whiskers growing as much as 27 mm in length, and are not shed during their annual pelage moult but randomly after seals are at least two years of age (Ling 1966). Moreover, whisker growth rates (0.87 mm per day) of new born, nursing bearded seals (*Erignathus barbatus*) suggest periods of rapid, somatic growth may be reflected in the growth of the whiskers (Hindell et al. 2012). These results therefore suggest that like other phocid species, the rapid accumulation of energy reserves as blubber by nursing elephant seals (Arnbom et al. 1993; Hindell et al. 1994a), may be reflected in the growth of the whiskers.

In summary, we found whiskers to be extremely useful tools for accessing time integrated diet information of elephant seals during their first year of life as we can trace the origin of the signature incorporated along the length of the whisker, *i.e.* from maternal investment to independent foraging. A significant finding of this study was that whiskers collected after the first foraging trip were predominantly still composed of *in-utero* and pre-weaning material as a result of relatively slow whisker growth rates during the 3 to 4 month foraging trip. The results of this study also highlight the need to sample plucked and not cut whiskers for future isotopic dietary analysis in order to capture the most recent isotopic information contained in the root of the whisker under the skin.

Foraging habitat

The foraging behaviour of a predator can change in response to the distribution of prey resources in a large heterogeneous environment. Identifying changes in the movement behaviour of a predator can therefore be informative as to the distribution and consumption of prey resources at a range of temporal scales. Over a period of 4 to 6 months satellite tracking data showed that sub-yearling elephant seals dispersed, in some cases thousands of kilometres, to the

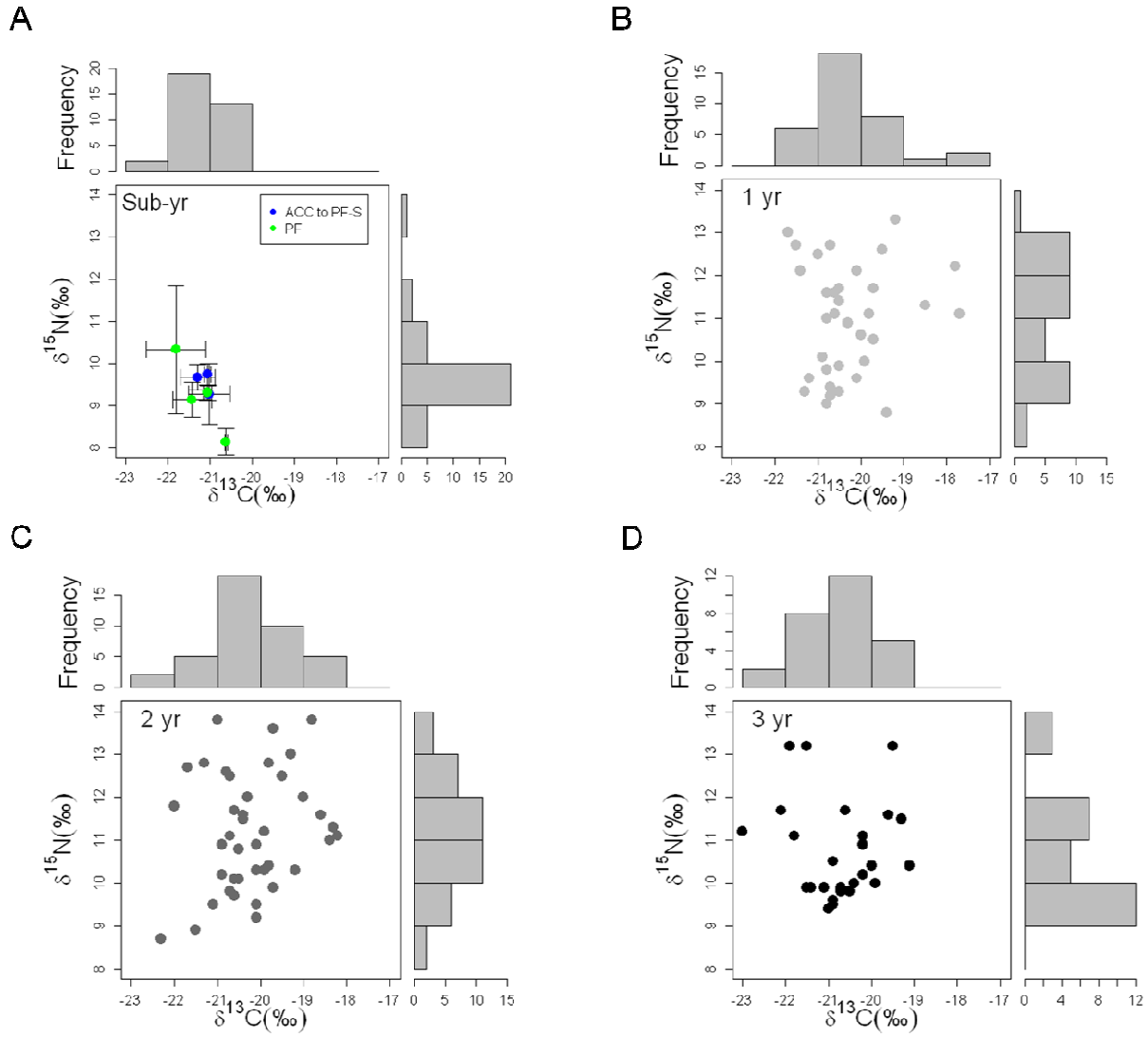

Figure 3.6. Whisker $\delta^{13}C$ and $\delta^{15}N$ values of juvenile southern elephant seals from Macquarie Island. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values from a randomly selected 2 mm section of whisker from (A) sub-yearling (n=7; colour coded by foraging locations (IFZs) presented in Fig. 3.4.), (B) one year (n=35; light grey symbols), (C) two year (n=40; dark grey symbols) and (D) three year old (n=27; black symbols) age classes of elephant seals from Macquarie Island ((Newland et al. 2011), this study). Also shown are marginal frequency distributions for the $\delta^{13}C$ and $\delta^{15}N$ values for each age class.

southeast of Macquarie Island (Hindell et al. 1999; McConnell et al. 2002; this study), apart from one individual which travelled to the southwest of Macquarie Island. Area Restricted Search locations, used as a proxy for foraging areas of sub-yearling elephant seals, occurred at the distal portion of tracks.

Foraging locations in the southeast group were primarily associated with ACC frontal branches of the PF (PF-S to PF-N, summarised as the PF; n=5) and the SACCF (SACCF-S to PF-S, summarised as the ACC to PF-S; n=6) and bathymetric features such as the MOR. The foraging locations of the single seal which travelled to the southwest of Macquarie Island were primarily associated with frontal branches of the PF and the SEIR. In this study, the foraging locations of only one seal were primarily associated with waters to the south of the sBdy (south of sBdy to SACCF-S, summarised as S of SACCF-S).

The movement and foraging behaviour of sub-yearling elephant seals from this site has been previously investigated (Hindell et al. 1999; Bornemann et al. 2000a; McConnell et al. 2002; van den Hoff et al. 2002). Two studies in particular, detail the movement, foraging areas (Hindell et al. 1999; McConnell et al. 2002) and dive behaviour (Hindell et al. 1999) of seals, including animals from this study. In this study, we separated travel into two phases, transit and ARS. Area Restricted Search behaviour is thought to occur in response to the patchy distribution of resources in an environment (Kareiva & Odell 1987). This behaviour corresponds with periods of reduced travel speed and increased turning rate, which are more likely to be associated with movements associated with feeding as opposed to transit (Morales et al. 2004). McConnell et al. (2002) and Hindell et al. (1999) separated travel into three phases (initial outbound transit, intermediate movement and final return transit) based upon daily travel rates for a large number of sub-yearlings (n=30 for both studies). Intermediate tracks, presumed to represent feeding, corresponded to slower and less directed travel, interrupted by occasional bouts of increased travel (Hindell et al. 1999; McConnell et al. 2002). The dive behaviour of seals during this time consisted of relatively shallow and short dives (117±48 m and 5.9±1.4 min, respectively; Hindell et al. 1999). Concentrated activity (locations of feeding) was centred on localised patches up to 1900 km from Macquarie Island, with the southern boundary of tracks in the southeast group aligned with the SACCF (Hindell et al. 1999; McConnell et al. 2002). These foraging areas (mean duration 67 days) matched well with the ARS areas (mean duration 81 days) of the sub-yearlings in this study.

Variation in habitat ($\delta^{13}C$) of seals with the location of foraging

We found that the most depleted $\delta^{13}C$ values incorporated along the temporal span of the whisker (as represented by the growth of the whisker) were contained in the portion of whisker grown during independent foraging at sea (-21.4±0.6‰, n=7; Fig. 3.2.), while the most enriched $\delta^{13}C$ values were contained in the portion of whisker grown during *in-utero*/lactation/fasting (-19.8±1.1‰, n=12; Table 3.2.). In oceanic waters of the Southern Ocean, the POM $\delta^{13}C$ values become more depleted with increasing latitudes, and these latitudinal changes are subsequently transferred to higher levels within the food chain (Cherel et al. 2006; Cherel & Hobson 2007). The decline in $\delta^{13}C$ values towards the proximal region of the whisker is therefore consistent with the southward migration of seals (outward transit tracks) to high latitude foraging areas (ARS tracks) located at or south of the PF (~60°S) to the southeast of Macquarie Island (Fig. 3.4.B; Fig. S1.).

It remains unclear to what degree young seals feed on the outward transit leg of their foraging trips (Thums et al. 2011) however it is most likely that sub-yearlings are in a state of transition from mother's milk and/or fasting to free ranging prey, as indicated by the concurrent ~3‰ drop in $\delta^{15}N$ and reduced whisker growth (~10 mm), at this time (Fig. 3.3.). However, $\delta^{13}C$ values related to independent foraging appear to stabilise at ~-21.0‰, presumably after seals have reached their main foraging grounds. We are therefore fairly certain the $\delta^{13}C$ values contained in the portion of whisker grown during independent foraging at sea are representative of core foraging habitat use, namely waters of the PF and ACC to PF-S.

There was considerable overlap in the $\delta^{13}C$ signatures of sub-yearlings related to independent foraging, both between years and foraging locations (IFZs: PF=-21.5±0.5‰, n=4; ACC to PF-S =-21.2±0.4‰, n=3), indicating that even though seals were using similar latitudes (62°89'±1°77'; n=7), they were in fact in different water masses, and there was no difference in $\delta^{13}C$ between those water masses. The structure and flow of the ACC is complex, consisting of multiple frontal filaments or branches that are strongly influenced by bathymetry (Sokolov & Rintoul 2007a). The PF marks the southern boundary of the PF to SAF zone and the beginning of the ACC to PF-S zone, while the sBdy delimits the southern boundary of the ACC to PF-S and the beginning of the S of SACCF-S zone. In the southwest Pacific sector, the frontal branches of the PF and SACCF merge to form a single frontal zone on the northern slope of the MOR near 170°E or where diverted to the south by obstacles like the Campbell Plateau. Frontal branches however, are clearly separated over deep ocean basins, such as the Australian –

Antarctic Basin to the southwest of Macquarie Island (Sokolov & Rintoul 2007a). As a consequence, the magnitude of the latitudinal variation in the boundaries of the PF and SACCF is much greater to the southwest of Macquarie Island than to the southeast of Macquarie Island (Sokolov & Rintoul 2007b; Sokolov & Rintoul 2007a; Sokolov 2008; Sokolov & Rintoul 2009b; Sokolov & Rintoul 2009a). This indicates that $\delta^{13}C$ signatures are not adequate to resolve habitat (water mass) at this scale and consequently, seals located to the southeast of Macquarie Island and predominantly associated with frontal branches of the PF and SACCF (*i.e.* PF and ACC to PF-S zones, respectively) and the MOR show similar $\delta^{13}C$ values.

Inferred prey consumption during the first six months

Very little is known about the diet of southern elephant seals during the course of their migrations, particularly in relation to core foraging areas. Lavaged stomachs of both juvenile and adult seals returning to colonies, which represent the most recent prey intake at the end of foraging trips, consist largely of mesopelagic fish and squid at Macquarie Island (Green & Burton 1993; Hindell et al. 2003; van den Hoff 2004; Field et al. 2007b), and other populations across the Southern Ocean (Rodhouse et al. 1992a; Boyd et al. 1994a; Slip 1995; Daneri et al. 2000; Daneri & Carlini 2002; van den Hoff et al. 2003), while an increasing amount of inferential data from biochemical tracers, such as stable isotopes and fatty acids augment the dietary trends identified by stomach content analysis (Bradshaw et al. 2003; Cherel et al. 2008; Newland et al. 2009; Newland et al. 2011). There is however, very little information available on the diet of elephant seals during their first foraging migration (Slip 1995). The whisker isotopic signatures of sub-yearlings provided dietary information corresponding to at least the first half of their foraging trips. Stable nitrogen values spanned more than one trophic level, with considerable overlap in $\delta^{15}N$ values of seals both between years and foraging locations (IFZs) suggesting that all seals fed at a similar trophic level irrespective of foraging habitat. However, there was considerable individual variability in their diet. Pronounced individual variability has also been described in diving behaviour within water masses for this species (Field et al. 2001). Individual specialisation in diet increases the niche breadth for a population and may offer some buffering against a changing resources base (Hindell et al. 2012).

The trophic position of seals, which foraged to the southeast of Macquarie Island in waters at or south of the PF and within CCAMLR Subareas 88.1 and 88.2 (> 60°S; Fig. 3.3.) were consistent with the consumption of a mixture of intermediate trophic level mesopelagic fish and squid ($\delta^{15}N$: ~8‰, such as *E. antarctica, G. fraseri*, *K. anderssoni, G. glacialis*, *K. longimana* and *P.*

glacialis), lower trophic level mesopelagic fish and squid (δ^{15}N: ~5-7‰, such as *M. hyadesi* and *P. tenisoni*) and lower trophic level crustaceans (δ^{15}N: <6‰, such as euphausiids, copepods and amphipods) characteristic of that sampled within colder, high latitude eastern Antarctic waters (Hunt & Hosie 2005). The consumption of mesopelagic fish and squid is consistent with the dietary trends of elephant seals determined in previous studies. However, sub-yearlings showed lower mean δ^{15}N signatures compared to older juvenile (Fig. 3.6; Newland et al. 2011) and adult seals (Cherel et al. 2008). When we compare the isotopic signatures of sub-yearlings and potential prey, the most parsimonious explanation is the consumption of lower trophic level crustaceans, such as euphausiids, in addition to fish and squid. In addition, stable isotope data provided dietary information relating to the first half of foraging trips, with the most recent isotopic values contained in the root of the whisker under the skin. Therefore, this may only be a conservative estimate of the level of crustacean consumption by seals in this study and requires further investigation.

Caution must be taken however, in over-interpretation of these observed dietary trends as prey data (other than squid beak data for *H. eltaninae* and *M. hyadesi*) are taken from outside the foraging range of juvenile elephant seals from this site (van den Hoff et al. 2002; Field et al. 2005) and therefore, requires further examination. Moreover, isotopic fractionation values for keratinous tissues vary among species and studies (Newsome et al. 2010) thus, factors determined for captive pinnipeds (as applied in this study) may not accurately represent wild populations. Nevertheless, the presence of myctophid fish, such as *Electrona* and *Gymnoscopelus* spp. (Slip 1995; Field et al. 2007b) and of squid, such as *P. glacialis* and *H. eltaninae* in the stomach contents of older juveniles from Macquarie Island (van den Hoff 2004) and Heard Island (Slip 1995), confirms the consumption of mesopelagic prey by sub-yearlings. Moreover, similarities in foraging behaviour (Hindell et al. 1999) and trophic level among seals and one of the most specialised consumers of myctophids and squid, the king penguin (*Aptenodytes patagonicus*; Adams & Klages 1987; Cherel et al. 2002; Cherel et al. 2007), which forages in similar regions of the PF south of Macquarie Island (Wienecke & Robertson 2006), also provides evidence that sub-yearlings fed at depths where similar mesopelagic fish and squid prey were accessible.

Crustaceans have been reported in the diet of elephant seals (Green & Burton 1993; Slip 1995; van den Hoff et al. 2003; Field et al. 2007b), however, this has usually been attributed to incidental or secondary consumption. Nevertheless, stomach content analysis revealed higher

proportions of crustaceans in the diet of one and two year-old seals compared to that of three year-olds (Field et al. 2007b), and were reported as primary prey of elephant seals by Green and Burton (1993). *Euphausia triacantha* generally occurs in waters between 50°S and 65°S, with vertical distribution between 250 to 750 m during the day and above 250 m at night (Roper 1969). *Euphausia superba* is predominantly herbivorous (Mayzuad et al. 1985; Hopkins & Torres 1989), while more northern species, such as *E. triacantha*, are carnivorous (Phleger et al. 2002), which explains its higher trophic position relative to *E. superba*. Due to the diurnal changes in the abundance and distribution of euphausiids (Pakhomov et al. 1994; Croxall et al. 1999), sub-yearlings, which are smaller and cannot dive as deep or for as long as larger seals (Hindell et al. 1999; Irvine et al. 2000), may encounter euphuasiid species at densities sufficiently large at shallower depths to make these important prey items.

Moreover, the southern boundary of foraging areas of sub-yearlings aligned with the sBdy (~65°S; Fig. 3.3.), coinciding with the maximum sea-ice extent (Worby et al. 1998) and known distribution of Antarctic krill (*E. superba*) in east Antarctic waters during late summer/early winter (Nicol et al. 2000; Hunt & Hosie 2005). Collectively, these results indicate that lower trophic level crustaceans, namely euphausiids, may form an important part of the diet for young seals. Consequently, sub-yearlings may be an important krill predator that should be taken into account within the CCAMLR management zone. These areas are important to elephant seals during the transition to independent foraging, and other marine predators of Macquarie Island, which exploit similar areas to the south of Macquarie Island (*e.g.* king penguins and royal penguins, *Eudyptes schlegeli*; Hull et al. 1997; Wienecke & Robertson 2002).

Variation in habitat and trophic position ($\delta^{13}C$ and $\delta^{15}N$) of seals with age

Ontogenetic changes in movement patterns, foraging habitat use and diet have been reported for older juvenile southern elephant seals from Macquarie Island (van den Hoff et al. 2002; van den Hoff 2004; Field et al. 2007a; Field et al. 2007b; Newland et al. 2011), other populations (Green & Burton 1993; Slip 1995) and in their northern counterpart, the northern elephant seal (Le Boeuf et al. 1996). Sub-yearlings showed more depleted $\delta^{13}C$ and $\delta^{15}N$ values than older juvenile seals, indicating ontogenetic segregation in both foraging range and trophic position, respectively. These observed isotopic differences are in good agreement with sub-yearlings feeding at a lower trophic level than older seals, since their size, dive capabilities and predation skills are limited (Hindell et al. 1999; Irvine et al. 2000). The increased diving capabilities of elephant seals with increasing age are well documented (Slip et al. 1994), and may give older

juveniles and adults a substantial advantage in capturing prey found at greater depths. Indeed, higher trophic level cephalopod prey of elephant seals, such as *P. glacialis* and *Alluroteuthis antarcticus* (Green & Burton 1993; van den Hoff 2004), occur at high densities deep in the water column (500 to 1000 m). Sub-yearling elephant seals, limited to some extent by their physiological capabilities, are restricted to the upper 300 m of the water column (mostly 100 to 200 m depth; Hindell et al. 1999). Lower trophic level pelagic prey, such as smaller-sized myctophid fish and crustaceans, which occur in high densities in the upper limits of the water column, may therefore provide an abundant and easily accessible source of prey for smaller seals. Crustaceans may, therefore, form a significant part of the diet of some sub-yearlings.

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APPENDICES

Table S1. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values of various marine organisms from the Southern Ocean.

Species	Location	Tissue	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
Mid latitude waters (<55°S)						
Euphausiids						
Euphausia frigida	Weddell Sea (49˚S, 20˚E)	Whole individuals	4	-24.3 ± 0.9	4.9 ± 0.3	Schmidt et al. (2004)
Fish						
Krefftichthys anderssoni	Kerguelen (49°21'S, 70°18'E)	White muscle	12	-22.3 ± 0.2	7.6 ± 0.2	Cherel et al. (2008)
Electrona antarctica	Kerguelen (49°21'S, 70°18'E)	White muscle	10	-22.2 ± 0.9	8.0 ± 0.5	This study
Gymnoscopelus fraseri	Kerguelen (49°21'S, 70°18'E)	White muscle	7	-22.5 ± 1.1	8.0 ± 0.5	This study
Gymnoscopelus nicholsi	Kerguelen (49°21'S, 70°18'E)	White muscle	10	-22.7 ± 0.5	9.7 ± 0.7	This study
Protomyctophum tenisoni	Kerguelen (49°21'S, 70°18'E)	White muscle	5	-22.1 ± 1.0	6.4 ± 0.3	This study
Gymnoscopelus piablis	Kerguelen (49°21'S, 70°18'E)	White muscle	2	-20.4 ± 0.3	7.8 ± 0.1	This study
Squid						
Histioteuthis eltaninae (LRL: 2.2±0.2 mm)	Macquarie Island (54˚30'S, 158˚57'E)	Beaks (corrected)	26	-21.2 ± 0.6	7.8 ± 1.9	Hughes (unpubl. data)
Martialia hyadesi (LRL: 6.5± 0.3 mm)	Macquarie Island (54˚30'S, 158˚57'E)	Beaks (corrected)	17	-21.6 ± 1.2	6.6 ± 1.5	Hughes (unpubl. data)
High latitude waters (>60°S)						
Amphipod						
Themisto gaudichaudii	Dumont d'Urville Sea (65°30'S, 143°E)	Whole individuals	7	-26.0 ± 0.5	5.4 ± 0.4	This study
Euphausiids						
Euphausia superba	Adélie Land (66°S, 136°E)	Whole individuals	12	-25.8 ± 0.4	5.5 ± 0.4	Cherel (2008)
Euphausia triacantha	Dumont d'Urville Sea (63°S, 140°E)	Whole individuals	10	-23.6 ± 0.5	6.3 ± 0.6	This study
Fish						
Electrona antarctica	Dumont d'Urville Sea (62°S, 140°E)	White muscle	9	-23.2 ± 0.4	8.3 ± 0.4	This study
Squid						
Psychrotheuthis glacialis	Northern Ross Sea (65°S, 180°E)	Mantle	20	-25.3 ± 0.6	7.9 ± 0.6	Bury et al.(2008)
Galiteuthis glacialis	Northern Ross Sea (65°S, 180°E)	Mantle	3	-24.7 ± 0.9	8.1 ± 0.4	Bury et al.(2008)
Kondakovia longimana	Northern Ross Sea (65°S, 180°E)	Mantle	20	-25.1 ± 0.6	7.6 ± 0.6	Bury et al.(2008)
Bathyteuthis abysicola	Dumont d'Urville Sea (63°S, 140°E)	Mantle	2	-24.2 ± 0.3	8.0 ± 0.3	This study
Psychrotheuthis glacialis	Dumont d'Urville Sea (65°30'S, 140°E)	Mantle	3	-25.9 ± 0.2	10.0 ± 0.5	This study

Beaks (corrected) = Squid beak isotopic values presented are corrected for reduced $\delta^{15}N$ enrichment due to chitin. See Materials and Methods for details.
LRL = Lower Rostral Length of squid beaks.

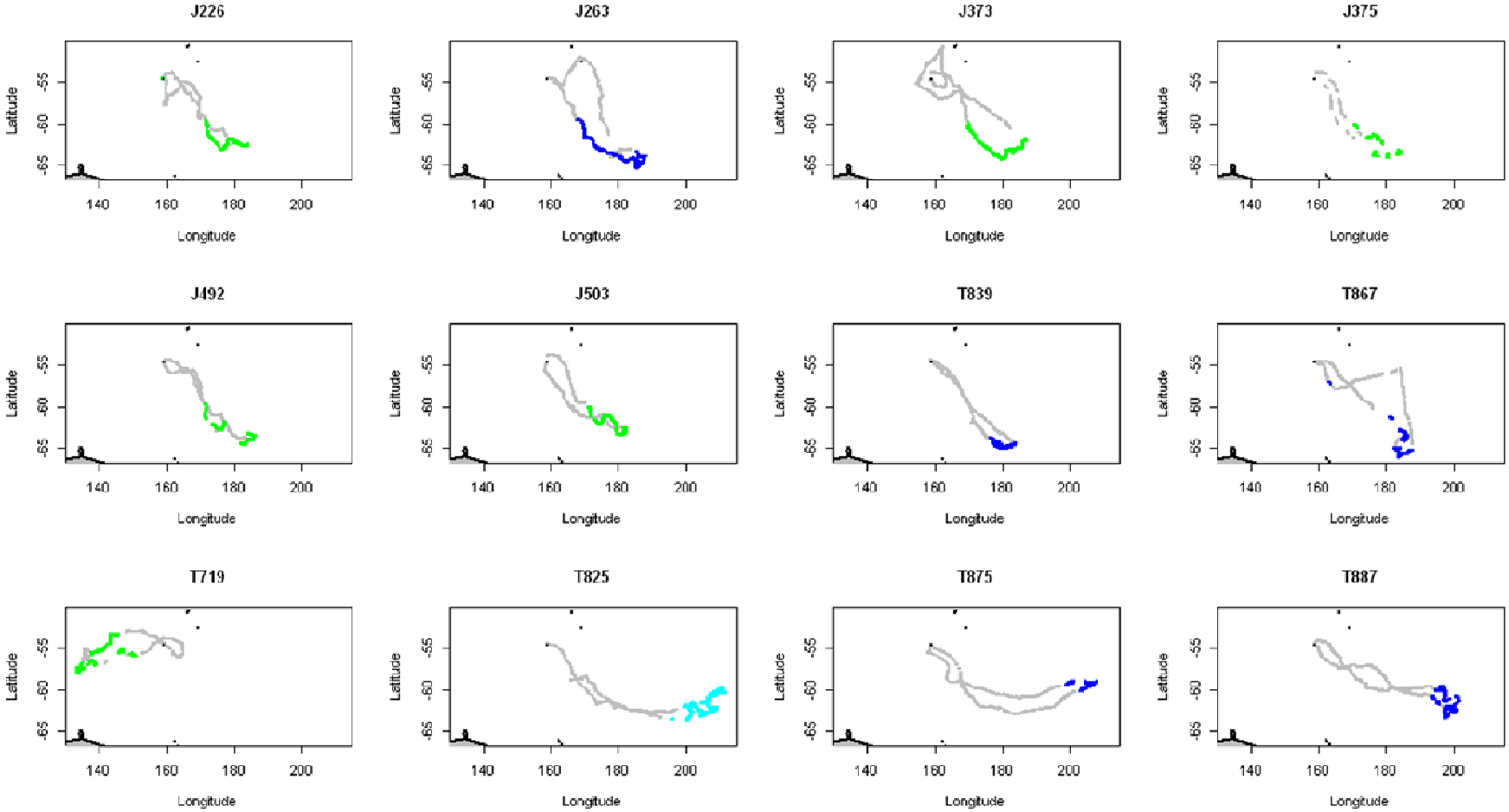

Figure S1. Tracks overlaid with state estimates from the two-state first-difference correlated random walk switching (DCRWS) model. Tracks of 12 weaned southern elephant seals during their first foraging migration from Macquarie Island, colour coded by state estimates. Grey: transit locations; light blue, blue and green: Area Restricted Search (ARS) locations for S of SACCF-S, ACC to PF-S and PF zones, respectively.

4. Finding food in the freezer: The winter diet of migratory adult female Antarctic fur seals inferred from stable isotopes

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ABSTRACT

1. There is a strong relationship between annual winter sea ice extent and the population parameters of several Antarctic marine predators. Understanding the trophic linkages for Southern Ocean marine predators in the non-breeding period is critical to interpreting winter ecosystem dynamics, particularly in light of projected changes in winter sea ice extent and front location. The Antarctic fur seal (*Arctocephalus gazella*) is one of the best-studied Southern Ocean predators, however little is known of their foraging habitat and feeding preferences during the non-breeding winter migration period. By combining stable isotopes in whiskers and blood and telemetry techniques, we documented variation in winter foraging habitat and diet of seals from Cape Shirreff (Antarctic Peninsula, southern Atlantic Ocean, n=24) and subantarctic Marion Island (southern Indian Ocean, n=19) in 2008 and 2009.
2. Whisker growth rates (0.10±0.04 mm d^{-1}) were estimated using the re-growth of whiskers, which were cut on the initial geolocation logger deployment. Stable isotope analysis of consecutive sections of whisker (~27 to ~30 days worth of dietary information per 3 mm section) and whole blood enabled the reconstruction of a time series of stable isotope data that could be related to at-sea location during the winter foraging period.
3. Stable isotope values reflected the contrasting winter migratory patterns of seals breeding on opposite sides of the Polar Front (PF) and the marked regional difference in front location. Breeding site, foraging period and location all explained significant variation in seal stable carbon isotope ($\delta^{13}C$) values during winter migration, while the stable nitrogen isotope ($\delta^{15}N$) values of seal tissues varied significantly with foraging period and location.
4. Seasonal shifts in prey consumption in relation to water mass use were identified by SIAR (Stable Isotope Analysis in R) Bayesian mixing models. In the Atlantic sector, seals migrated north of the PF to feed predominantly on mesopelagic fish and squid (contributing 82.1% to the diets of seals) in productive foraging areas in off-shelf/oceanic waters along the coast of Chile and the Patagonian shelf. Seals in the Indian Ocean sector showed different feeding strategies in winter. Seals underwent longitudinal or northward movement in Subantarctic Front (SAF) waters or migrated south to feed on Antarctic krill (22.4%) in ice-associated habitat in winter, in addition to mesopelagic fish and squid (50.9%) in PF and SAF waters. Later in the season, seals shifted to a diet of energy rich, high trophic level prey, such as myctophid fish (*Electrona antarctica*) and squid (78.0%) in PF and SAF waters.

5. At the population level, our data suggest that seals feed on krill, fish and squid during winter, but shift to a diet dominated by energy rich mesopelagic resources (fish and squid) in spring, prior to the energetically demanding breeding period (October-December) in predictable, high resource areas.

INTRODUCTION

The Southern Ocean is a dynamic, semi-closed system, characterized by distinct oceanographic frontal zones (Gordon et al. 1978; Orsi et al. 1995; Belkin & Gordon 1996) concentrating the biomass of primary producers and consumers, which are then exploited by higher order predators (Tynan 1998; Nicol et al. 2000). The concentration of biota within these zones often translates to patchily distributed resources and often zone-specific prey communities and densities (Pakhomov et al. 1994; Tynan 1998; Nicol et al. 2000; Hunt & Hosie 2005). Additionally, very low phytoplankton concentrations in autumn and winter (O'Brien et al. 2011), and inter-annual variation in overall primary productivity (Constable et al. 2003; Blain et al. 2007; Boyce et al. 2010; Cassar et al. 2011) means that the availability of resources changes at a range of temporal scales.

In a seasonal environment, resources (*e.g.* food, mates and habitat) are often limited (Fretwell 1972). In order to survive, reproduce and maintain population equilibrium (Slobodkin 1955), many species share a common breeding area, but migrate to separate non-breeding areas to feed (Griswold et al. 2010). Moreover, in many species the spatial distribution of males and females during the non-breeding season can differ considerably due to contrasting reproductive requirements (Loretto & Vieira 2005). Seasonal constraints therefore may dictate the spatial distribution of migratory species, causing the food web structure, energy and nutrient flow within a given ecosystem to fluctuate accordingly (Baker 1978).

Understanding of the winter foraging habitat and diet of abundant, wide-ranging marine predators is therefore an important step in gaining a greater understanding of the dynamics of Antarctic food webs. Such information can then be used to predict how changing climate-related factors such as sea ice patterns (Nicol et al. 2008; Massom & Stammerjohn 2010) and southwards movement of fronts (Sokolov & Rintoul 2009b) will influence Antarctic marine predator communities in general (Péron et al. 2012). For less numerous, cryptic or migratory species feeding far from where they breed, retrospective dietary techniques, such as stable isotope analysis, are useful for discerning habitat use and prey consumption (Ambrose & DeNiro 1986; Hilderbrand et al. 1996; Cryan et al. 2012; Pauli et al. 2012). In the marine environment, tracking devices provide information on an animal's at-sea movements (*e.g.* longitude and latitude position), and behaviour, such as overall time spent at-sea (days), dive depth (m) and duration (min/h), which can then be associated with oceanographic conditions (*e.g.* sea surface temperature, bathymetry, salinity, sea surface height). By integrating

isotopic signatures of animal tissues with animal location and associated environmental parameters, changes in diet, habitat use and environmental variability can be concurrently assessed at both local and broad spatial and temporal scales (Guinet et al. 2001; Bradshaw et al. 2003; Lea & Dubroca 2003; Cotte´ et al. 2011).

Predator diet can be inferred from biochemical tracers over different time scales depending on the tissue sampled (Dalerum & Angerbjörn 2005). Metabolically active tissues, such as whole blood, represent relatively short-term dietary tracers, providing up to twelve weeks worth of time-integrated information (Halley et al. 2010). Alternatively, whiskers, a keratin-based tissue, provide a time-series of longer-term (seasonal) dietary information (Kernaléguen et al. 2012), making them particularly useful for tracing temporal variation. Stable isotope values of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$), which reflect a consumer's foraging habitat (Fry & Sherr 1984; Peterson & Fry 1987) and trophic position (Minagawa & Wada 1984; Hobson 1992; McCutchan et al. 2003), respectively, are incorporated into the keratin structure providing a time-series of information from assimilated, not only ingested food (Hobson et al. 1996).

The Antarctic fur seal (*Arctocephalus gazella*) is a highly abundant Southern Ocean predator breeding mainly on islands south of the Polar Front (PF). The summer diet of this species consists primarily of Antarctic krill (*Euphausia superba*) and fish in the southern Atlantic Ocean sector (Doidge & Croxall 1985; Daneri 1996; Reid & Arnould 1996; Kirkman et al. 2000; Casaux et al. 2003b), and predominantly mesopelagic fish (myctophids) and squid in the Indian Ocean sector where Antarctic krill does not occur (Klages & Bester 1998; Lea et al. 2002a; Makhado et al. 2008).

Surprisingly, the winter dietary preferences of adult female seals, which migrate to remote foraging areas during the non-breeding winter period (Lea et al. in review), are still unknown. The specific objectives of this study were to: (1) Quantify whisker growth rates of adult female Antarctic fur seals during the non-breeding season to assist interpretation of the time-series of stable isotope information in a spatial context, (2) Determine how habitat ($\delta^{13}C$) and trophic position ($\delta^{15}N$) of females varies with the location of foraging as inferred from telemetry across the winter migration period, and (3) Measure the temporal changes in fur seal diet composition across the winter migration period.

METHODS

Study sites and oceanographic context

The diet and foraging habitat of two Antarctic fur seal sub-populations, one Antarctic (Cape Shirreff, Antarctic Peninsula) and one subantarctic (Marion Island) were examined in summer and winter during 2008 and 2009. Marion Island (46°54'S, 37°45'E), part of the Prince Edward Archipelago, is situated within the eastward-flowing Antarctic Circumpolar Current (ACC), located in the western part of the Indian Ocean sector. Cape Shirreff (62º28'S, 60º48'W) is located towards the western end of the ice-free north coast of Livingston Island, South Shetland Islands, Western Antarctic Peninsula (WAP).

Sampling protocols

On average, female seals arrive at their respective breeding colonies in late November (for details see Lea et al. in review) and usually give birth to a single pup, which they then suckle until weaning in late March/early April (Bonner 1981). Geolocation loggers were attached to a customised flipper tag and deployed on females in February/March/April, prior to the winter migration period. Females breeding at Marion Island undertake one long, or up to nine short overwintering trips, compared to females breeding at Cape Shirreff which undertake one long overwintering foraging trip (Lea et al. in review). Whiskers and whole blood were collected from adult females equipped with geolocation loggers (GLS; BASTrak, British Antarctic Survey).

Summer

Whiskers, cut at the skin surface, and whole blood were sampled from each animal during the deployment of GLS tags in March/April in 2008 and 2009. A sub-sample of whiskers (Marion Island: n=10; Cape Shirreff: n=10) was isotopically analysed for stable carbon and nitrogen abundance. Whole blood was not collected from Cape Shirreff animals during deployment in 2008 and 2009, but during the following deployment (2010). These samples were subsequently used to establish the summer isotopic signal for the Cape Shirreff breeding site. A sub-sample of plucked whiskers collected from three females at Cape Shirreff during the 2008 deployment also provided an estimate of the extent of whisker present under the fur/skin (see Appendix A).

Winter

Whiskers and blood samples were also collected when the GLS tag was retrieved in November/December 2008 and 2009 at both breeding sites (Appendix B). To capture the fine-scale winter diet information for Marion Island animals undertaking one, or several short trips, re-growth of the whisker collected at deployment (*i.e.* during May/April) and whole blood were sampled after each short foraging trip, or at the end of the last trip (*i.e.* November/December). Females were generally sampled on the day of return (20% and 5.3% of animals at Cape Shirreff and Marion Island, respectively) or up to three weeks post-resight. One individual from Marion Island was sampled 33 days after return to the island. Samples were stored at -20ºC until isotopic analysis.

Winter whisker growth rates

Whisker growth rates (mm d^{-1}) were calculated for each individual using the re-growth (mm) of the deployment whisker for Marion Island (n=16) and Cape Shirreff (n=11) seals, and the corresponding number of days between deployment and sampling date (Table 4.1.).

We then used the mean whisker growth rate (mm d^{-1}) to relate $\delta^{13}C$ and $\delta^{15}N$ values along the length of the whisker to seal foraging locations grouped bi-monthly (*i.e.* March/April, May/June, July/August, September/October and November/December). Whisker segments (approximately 3 mm length) were numbered sequentially from the base (region closest to the skin surface) to the tip (distal region) of the whisker.

Whole blood

Whole blood represents relatively short-term dietary signals, providing up to twelve weeks worth of integrated information (Halley et al. 2010). The isotopic signature of whole blood, sampled at the end of the non-breeding period (late November/early December) therefore, provided dietary information during spring and the pre-breeding period (October-December) following Cherel et al. (2007). Samples collected more than ten days after the female's return to the island were not included in this analysis.

Habitat ($\delta^{13}C$) and trophic position ($\delta^{15}N$) corresponding to winter non-breeding

The time-series of corresponding seal locations have been assigned to Inter-Frontal Zones (IFZs) as per Lea et al. (in review) using definitions of Sokolov and Rintoul (2009b; 2009a).

Table 4.1. Tissue sampling, whisker growth and tracking details for female Antarctic fur seals from Cape Shirreff, Livingston Island, Western Antarctic Peninsula, southern Atlantic Ocean and Marion Island, southern Indian Ocean, during the winter migration period in 2008 and 2009.

	GLS deployment (days)		Whisker growth (mm)							Whole blood (N) (short-trips)
						Over winter growth rate (mm d^{-1})		Over winter growth		
Site/ Year	Overall (N)	Short-trips (N)	Full whisker (N)	Re-growth Overall (N)	Short-trips (N)	Overall (range) (N)	Short-trips (range) (N)	Skin surface to tip (short-trips)	Root to tip (short-trips)	
Cape Shirreff										
2008	254.1±24.7 (13)	–	71.6±27.0 (13)	–	–	0.10±0.04 (0.05-0.18) (13)	–	4.1±2.9	26.2±2.6	10
2009	246.7±10.1 (11)	–	75.8±12.8 (11)	26.3±7.1 (11)	–	0.11±0.03 (0.07-0.14) (11)	–	2.2±1.9	26.3±1.1	10
	245.8±19.1 (24)	–	**73.6±21.3 (24)**	**26.3±7.1 (11)**	–	**0.11±0.04 (0.05-0.18) (24)**	–	**3.2±2.6**	**26.2±2.0**	**20**
Marion Island										
2008	233.9±8.7 (14)	75.9±11.4 (2)	111.1±65.1 (2)	19.0±5.9 (12)	10.0±3.6 (2)	0.08±0.03 (0.05-0.14) (12)	0.13±0.5 (0.09-0.19) (2)	8.2±2.5 (8.5±2.1)	23.5±0.8 (8.5±2.1)	13 (2)
2009	255.5±13.6 (6)	95.0 (1)	89.1±40.9 (7)	30.0±14.9 (4)	9 (1)	0.11±0.05 (0.04-0.18) (4)	0.09 (1)	9.2±2.8 (3.0)	25.7±1.5 (9.5)	7 (2)
	240.4±14.3 (20)	**78.6±12.7 (3)**	**94.1±43.4 (9)**	**21.7±9.7 (16)**	**9.8±3.2 (3)**	**0.09±0.04 (0.04-0.18) (16)**	**0.12±0.5 (0.09-0.19) (3)**	**8.4±2.4 (7.6±2.9)**	**24.1±1.4 (8.1±1.2)**	**20 (4)**
						10.0±0.04 (0.04-0.19) (19)				

From south to north, IFZs included the Antarctic zone south of the southern ACC Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to Subantarctic Front (PF-SAF), the SAF, the SAF-Northern branch to Subantarctic Zone (SAF-N-SAZ), and the SAZ to Subtropical Zone-Southern branch (SAZ-STZ-S). We aggregated GLS locations into bi-monthly groups to better facilitate comparisons with whisker and whole blood samples.

To assign whisker segments to IFZs, we calculated the proportion (%) of time spent by the seals in an IFZ during each bi-monthly period. The greatest proportion of seal locations occurring in a particular IFZ in each period defined their habitat use during that period. We then used the mean whisker growth rate (mm d^{-1}) to relate the $\delta^{13}C$ and $\delta^{15}N$ values of each segment along the temporal span of the whisker, as represented by the growth of the whisker (mm) from the distal region (oldest growth) to the root (most recent growth), to seal habitat use.

Inferred prey consumption during winter

We used $\delta^{13}C$ and $\delta^{15}N$ values of 36 potential prey species, including benthic, meso- and pelagic fish, meso- and bathypelagic squid and euphausiids (Appendix C) assigned to groups of similar $\delta^{13}C$ and $\delta^{15}N$ values prior to analysis, to assess variation in diet among foraging locations. To estimate the diet composition of fur seals among foraging locations we used a multi-source isotopic mixing model using the SIAR package in R by Parnell and Jackson. The SIAR model provides probability distributions for multiple source contributions to a mixture, accounting for the observed variability in the isotopic signatures for the sources as well as the mixture. The model also accounts for variation in diet-tissue fractionation by allowing the user to specify fractionation values (Parnell et al. 2010). We used published diet-tissue fractionation values for pinnipeds of 3.2 and 2.8‰ for whisker $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and 1.7‰ for whole blood $\delta^{13}C$ and $\delta^{15}N$ values (Hobson et al. 1996).

Isotope analyses

The whiskers were cleaned with successive rinses in a 2:1 chloroform:methanol solution, and then oven-dried at 60˚C for 72 h. The summer and winter whiskers (n=95) were weighed, sectioned into approximately 3 mm sections and loaded into tin cups. Whole blood samples (n=99) were thawed before been vortexed to fully homogenize samples. Approximately 0.5 to

1.0 ml was sub-sampled into 1.5 ml screw cap vials, weighed, oven-dried at 60˚C for a minimum of 24 h and then re-weighed.

Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass, UK) continuous-flow isotope-ratio mass spectrometer. Results are reported using standard δ notation in parts per thousand (‰) relative to Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric N^2 (Air) for $\delta^{15}N$ as follows:

$\delta X = [(R_{samples}/R_{standard}) - 1] \times 1000$
where δX is $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Replicate measurements of internal laboratory standards (Alanine) indicate measurement errors < 0.20‰ and < 0.21‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope analysis was performed by the Environmental Biology Group, Research School of Biological Sciences, Australian National University (ANU), Canberra, Australia.

Statistical analyses

All data were statistically analysed using R (R Development Core Team 2012) and Primer 6 (Clarke & Gorley 2006). To determine if whisker growth was influenced by either breeding site or year, linear mixed models (LMMs) were fitted with the `lme` function in R. This function allows for the inclusion of individual as a random effect to control for the non-independence of data due to repeated measurements. Analysis of Variance (ANOVA) was applied to indicate where response variables differed.

We used LMMs to determine if the stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of seal whiskers and whole blood during the winter migration period were influenced by breeding site, bi-monthly foraging period and the location of foraging, as inferred by the proportion of GLS locations occurring in IFZs in each bi-monthly foraging period. We parameterized the full LMMs as follows: whisker and whole blood (corrected) $\delta^{13}C$ or $\delta^{15}N$ as the dependent variables, breeding site, bi-monthly period and foraging location (IFZs) as independent variables and two-way interaction terms. We included bi-monthly foraging period as a slope term to describe variation in $\delta^{13}C$ values and an autocorrelation term to describe within group correlation of $\delta^{15}N$ values. We used Analysis of Variance (ANOVA) along with Tukey's Honestly Significant Difference (HSD) post-hoc analysis to indicate where response variables

differed across bi-monthly foraging periods. Due to the relatively small sample sizes, IFZ and stable isotope results for females at both sites in 2008 and 2009 years were pooled and thus, the influence of year could not be examined in this study. We examined data for normality and equal variance and assessed significance for statistical tests at the 0.05 level.

To combine the potential prey into groups with similar $\delta^{13}C$ and $\delta^{15}N$ values we applied a hierarchical cluster analysis to isotopic values of each species using the `hclust` function in R based on a dissimilarity matrix produced from Euclidean distances and average linkage as the agglomeration method. Mean isotopic values ($\delta^{13}C$ and $\delta^{15}N$) defined prey groups. In oceanic waters of the Southern Ocean, there is a well defined geographical $\delta^{13}C$ gradient in particulate organic matter (POM) surface waters, ranging from enriched $\delta^{13}C$ values in warm subtropical waters in the north, to depleted values in cold Antarctic waters in the south (Rau et al. 1982; Goericke & Fry 1994; Popp et al. 1999; Trull & Armand 2001). These latitudinal changes are subsequently transferred to higher levels within the food chain (Cherel et al. 2006; Cherel & Hobson 2007). Hence, these variables should be sufficient to distinguish the provenance ($\delta^{13}C$; *e.g.* Antarctic versus subantarctic) and trophic position ($\delta^{15}N$; *e.g.* upper trophic level fish/squid versus lower trophic level macrozooplankton, such as euphausiids) of the prey groups. To test if there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between prey groups resulting from the cluster analysis, we used one-way Analysis of Similarities (ANOSIM) tests (Global R) based on a Euclidean distance matrix using 999 permutations (Clarke 1993).

In the mixing model program SIAR (Stable Isotope Analysis in R) we applied the mean ± SD of the $\delta^{13}C$ and $\delta^{15}N$ values of each of the prey groups identified by the cluster analysis. We ran 200,000 iterations, thinned by 15 and a burn in of 50,000. The SIAR output gives proportional contributions of each prey group that is a Dirichlet distribution. We plotted the estimated modal contribution of each prey source to the diet of fur seals, overlaid with high and low 95% confidence intervals, for each bi-monthly period.

Latitude is important for relating isotopic signatures in the tissues of consumers to foraging habitat in the Southern Ocean. We therefore used linear models to analyse the potential relationships between $\delta^{13}C$ values of seal whisker segments and whole blood (corrected) and the mean latitude of corresponding seal locations (the greatest proportion of seal locations occurring in a particular IFZ in each period defined their habitat use during that period).

Whisker segment and whole blood $\delta^{13}C$ values were the dependent variables and the mean latitude of seal locations was the independent variable.

RESULTS

The length of full whiskers collected from both Cape Shirreff (CS) and Marion Island (MAR) seals ranged widely from 18.0 to 276.0 mm at deployment (CS: n=20; MAR: n=20), and from 21.0 to 153.3 mm at retrieval (CS: n=24; MAR: n=9; Appendix A and B). The length of whisker re-growth collected at retrieval was considerably shorter (CS: 17.0 to 35.0 mm, n=11; MAR: 11.0 to 45.0 mm, n=16) and after each short winter foraging trip (MAR: 6.0 to 14.5 mm, n=3; Table 4.1.). A total of 1,174 segments of whisker were cut and analysed for the 2008 and 2009 sampling periods.

Growth rate of whiskers

Winter re-growth (from the surface of the skin to the distal region of the whisker) ranged in length from 0.0 to 10.0 mm (3.2±2.6 mm; n=24) for females from Cape Shirreff, and from 4.0 to 13.3 mm (8.4±2.4 mm; n=16) for females from Marion Island, respectively (Table 4.1.). For three Marion Island females (GLS 4272, 4323, 4843) sampled after short-foraging trips, growth ranged in length from 14.5 mm (GLS 4272: 0.19 mm d^{-1}), 6.0 to 11.0 mm (GSL 4323: 0.11±0.03 mm d^{-1}), and 9.0 mm (GLS 4843: 0.09 mm d^{-1}).

A mean whisker growth rate of 0.11±0.04 mm d^{-1} (range: 0.05 to 0.18 mm d^{-1}; n=24) and 0.10±0.04 mm d^{-1} (range: 0.04 to 0.19 mm d^{-1}; n=19) was calculated for females from Cape Shirreff and Marion Island, respectively (2008 and 2009 combined; Table 4.1.), indicating growth was similar across breeding sites (ANOVA: $F_{1,41} = 0.2326$, $P = 0.63$). Consequently, each 3 mm whisker section provides ~27 to ~30 d of dietary information at each breeding site. Overall, this provided < 4 months (March-June) worth of time-integrated information for seals from Cape Shirreff, and < 6 months (March-August) for seals from Marion Island during the winter migration period. Plucked whiskers from three females at Cape Shirreff during 2008 deployment (total length: 81.0, 90.0 and 96.0 mm, respectively) indicated that 10.0, 14.0 and 8.0 mm (10.7±3.1 mm; 12.3%, 15.5% and 8.3% of total whisker length, respectively) of the shaft of the whisker was left under the plane of the skin surface when cutting (see Appendix A). Based on these results < 90 to 100 days of the most recent isotopic information corresponding to the September-December period was missing from the cut whiskers. We therefore used whole blood samples, collected at deployment retrieval (CS: n=19; MAR: n=13; 2008 and 2009 combined) to provide the most recent dietary information (October-December foraging period). To account for variation in isotopic fractionation

between tissues (Hobson et al. 1996) we added 1.5 and 1.1‰ to $\delta^{13}C$ and $\delta^{15}N$ whole blood values, respectively.

Tissue isotopic values for Antarctic fur seals

Whole blood collected at deployment (summer sampling season) and retrieval (winter sampling season) showed seals had a much broader range in their $\delta^{13}C$ values during the non-breeding winter period than during the summer. This range was skewed towards more ^{15}N enriched values for females from Cape Shirreff compared to that of females from Marion Island (Table 4.2.). Females from Marion Island showed relatively high $\delta^{15}N$ values compared to that of females from Cape Shirreff during the summer, but females from both populations exhibited a similar, wide range of values during the winter (Table 4.2.). Whole blood collected at deployment (summer sampling season) therefore, reflected the more subantarctic summer foraging of seals breeding at Marion Island, compared to the more Antarctic summer foraging of females breeding south of the ACC at Cape Shirreff in the WAP region (Table 4.2.).

Whiskers collected from seals in both summer and winter sampling periods showed a similar range in $\delta^{13}C$ and $\delta^{15}N$ values, ranging from relatively low Antarctic values (*e.g.* $\delta^{13}C$: < -24‰; $\delta^{15}N$: < 7‰) to relatively high subantarctic and sub-tropical values (*e.g.* $\delta^{13}C$: < -15‰; $\delta^{15}N$: < 15‰; Table 4.2.; for details see Appendix D). The magnitude of the difference in whisker isotopic values was more than twice that in whole blood in summer ($\delta^{13}C$: 10.0‰ versus 2.6‰; $\delta^{15}N$: 6.4‰ versus 2.2‰) and winter ($\delta^{13}C$: 8.7‰ versus 3.7‰; $\delta^{15}N$: 8.3‰ versus 3.4‰) sampling seasons, respectively. These data therefore clearly indicate that whiskers contain both summer and winter isotopic signals (*i.e.* annual migration foraging patterns), compared to whole blood, which contain only summer or winter foraging patterns (Table 4.2.).

Habitat ($\delta^{13}C$) and trophic position ($\delta^{15}N$) corresponding to winter non-breeding

The number of days that females spent at sea ranged from 218 to 261 d (235.8±11.3 d; n=23) for Cape Shirreff, and from 208 to 282 d (233.6±15.0 d; n=20) for Marion Island (2008, 2009 combined; Table 4.1.). Short-foraging trips for females from Marion Island ranged from 60 to 95 d (78.6±12.7 d; n=3). For bi-monthly periods where concurrent isotopic information was available, results showed that females from Cape Shirreff and Marion Island breeding sites utilised six IFZs (2008 and 2009 combined; Table 4.3.).

Table 4.2. Whole blood and whisker $\delta^{13}C$ and $\delta^{15}N$ values collected from female Antarctic fur seals according to breeding site and sampling season (2008 and 2009 data combined).

				Tissue isotopic values				
Breeding site	Season	N	Tissue	$\delta^{13}C$ (‰)	Range $\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Range $\delta^{15}N$ (‰)	C:N ratio
Cape Shirreff	Summer	17	Whole blood	-23.4±0.5	-24.5 - -22.6	8.8±0.6	8.2 - 10.4	3.4±0.0
(62°28'S, 60°48'W)	Summer	20	Whisker	-20.3±1.7	-25.4 - -15.4	9.4±1.0	5.7 - 11.9	3.0±0.3
	Winter	20	Whole blood	-21.4±0.9	-23.3 - -19.9	10.0±1.0	8.4 - 11.8	3.3±0.0
	Winter	23	Whisker	-20.1±1.7	-24.2 - -15.5	9.7±1.0	6.6 - 14.9	2.8±0.5
Marion Island	Summer	35	Whole blood	-21.7±0.5	-23.4 - -20.8	11.2±0.3	10.3 - 11.8	3.4±0.0
(46°54'S, 37°45'E)	Summer	20	Whisker	-19.4±1.4	-24.9 - -15.7	10.3±1.0	6.9 - 13.3	2.9±0.2
	Winter	27	Whole blood	-22.8±1.2	-25.0 - -21.3	10.3±0.8	8.4 - 11.6	3.4±0.1
	Winter	26	Whisker	-19.6±1.3	-23.7 - -16.9	10.0±1.0	6.4 - 13.6	2.9±0.5

Table 4.3. The number of individual female Antarctic fur seals occurring in Inter-Frontal Zones (IFZs), and source of dietary information (tissue) by breeding site and bi-monthly period in 2008 and 2009. From south to north, IFZs included the Antarctic zone south of the southern Antarctic Circumpolar Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to Sub-Antarctic Front (PF to SAF), the SAF, and the SAF-Northern branch to Sub-Antarctic Zone (SAF-N to SAZ).

Bi-monthly period (season)	Year	Tissue	IFZ					
			S of SACCF-S	ACC to PF-S	PF	PF to SAF	SAF	SAF-N to SAZ
March/April (autumn)								
CS	2008	Whisker	0	6	3	0	1	0
	2009	Whisker	0	5	1	0	0	0
MAR	2008	Whisker	0	1	10	1	1	0
	2009	Whisker	0	0	0	1	2	0
May/June (early winter)								
CS	2008	Whisker	0	3	1	0	2	2
	2009	Whisker	0	1	0	0	0	0
MAR	2008	Whisker	2	2	6	2	1	0
	2009	Whisker	0	0	1	0	3	0
July/August (late winter)								
CS	2008	Whisker	-	-	-	-	-	-
	2009	Whisker	-	-	-	-	-	-
MAR	2008	Whisker	0	2	0	0	1	0
	2009	Whisker	0	0	0	0	0	0
October-December (spring-early summer)								
CS	2008	Blood corrected	0	0	0	0	6	3
	2009	Blood corrected	0	0	0	0	3	7
MAR	2008	Blood corrected	0	0	7	0	6	0
	2009	Blood corrected	0	0	0	0	0	0
Overall								
CS	2008		0	7	4	0	8	4
	2009		0	6	1	0	2	7
MAR	2008		2	2	13	2	6	0
	2009		0	0	1	1	3	0
			2	**15**	**19**	**3**	**19**	**11**

N.B.The greatest proportion of seal locations occurring in an IFZ in each bi–monthly period defined a seals habitat use

*Overall number of seals occurring in IFZs does not include the July/August period

*CS: Cape Shirreff, Western Antarctic Peninsula; MAR: Marion Island, southern Indian Ocean

The interaction between breeding site and bi-monthly foraging period was statistically significant in explaining variation in $\delta^{13}C$ values of seal tissues (Site x Period: $F_{2,40} = 3.66$, $P = 0.03$; Table 4.4.). The $\delta^{13}C$ values of whiskers of females from Marion Island were relatively high compared to that of whiskers of Cape Shirreff females early in the season (*e.g.* March/April and May/June). However, the inverse appears to occur later in the season, with corrected whole blood samples for Marion Island females having relatively low $\delta^{13}C$ values compared to that of whole blood (corrected) of Cape Shirreff females during October-December (Fig. 4.1.; for details see Appendix E). The $\delta^{13}C$ values differed with the location of foraging (Foraging location: $F_{5,40} = 27.10$, $P < 0.0001$; Table 4.4.). Post-hoc analysis indicates tissue samples of females foraging in Antarctic waters (IFZs: S of SACCF-S and ACC to PF-S) were significantly ^{13}C enriched relative to samples of females foraging north of the PF (IFZs: PF to SAF, SAF and SAF-N to SAZ; Tukey's HSD post-hoc difference tests, $P < 0.04$). Moreover, tissues of females foraging in the mid-latitude PF zone were significantly ^{13}C depleted and enriched relative to samples of females foraging in the most northerly (SAF-N to SAZ) and southerly occurring zones (ACC to PF-S), respectively (Fig. 4.1.; Tukey's HSD post-hoc difference tests, $P < 0.0002$). While foraging period and breeding site were included in the model, these factors were not statistically significant in explaining variation in $\delta^{13}C$ values of seal tissues (Period: $F_{2,40} = 1.81$, $P = 0.18$; Site: $F_{1,39} = 1.77$, $P = 0.19$; Table 4.4.).

The $\delta^{15}N$ values of seal tissues varied significantly with the foraging period and the location of foraging (Period: $F_{2,40} = 91.67$, $P < 0.0001$; Foraging location: $F_{5,40} = 2.54$, $P = 0.04$; Fig. 4.1.). Post-hoc analysis indicated that tissue samples of seals foraging in the ACC to PF-S zone were significantly ^{15}N depleted relative to tissues of seals foraging in the more northerly PF zone (Table 4.4.; Tukey's HSD post-hoc difference tests, $P = 0.05$). The $\delta^{15}N$ values were relatively high in October-December (Fig. 4.1., Tukey's HSD post-hoc difference tests, $P < 0.0001$). These results indicate that $\delta^{15}N$ values in whole blood of females from Cape Shirreff, which utilised three distinct areas of SAF and SAF-N to SAZ zones: (1) Open waters to the west of Chile, (2) Off-shelf waters along the Chilean coast, and (3) Off-shelf waters east of the Patagonian shelf, were similar to $\delta^{15}N$ values in whole blood of females from Marion Island which utilised PF and SAF zones (October-December; Fig. 4.1.). Breeding site and the interaction between breeding site and bi-monthly foraging period were not statistically significant in explaining variation in $\delta^{15}N$ values (Site: $F_{1,39} = 0.02$, $P = 0.89$; Site x Period: $F_{2,40} = 0.38$, $P = 0.69$).

Table 4.4. Analysis of Variance (ANOVA) results of linear mixed-effects models for the isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of whole blood corrected for fractionation between tissues (Hobson et al. 1996) and whiskers for adult female Antarctic fur seals from Cape Shirreff, Livingston Island, Western Antarctic Peninsula, southern Atlantic Ocean and Marion Island, Prince Edward Islands, southern Indian Ocean during winter in 2008 and 2009 (data combined). Abbreviations: DF = degrees of freedom, F = variance ratio, P = probability.

	ANOVA table		
Model	DF	F	P
$\delta^{13}C$ in relation to			
Breeding site	1,39	1.77	0.1912
Bi-monthly period	2,40	1.81	0.1772
Foraging location	5,40	27.10	<0.0001
*Breeding site*Bi-monthly period*	2,40	3.66	0.0346
$\delta^{15}N$ in relation to			
Breeding site	1,39	0.02	0.8904
Bi-monthly period	2,40	91.67	<0.0001
Foraging location	5,40	2.54	0.0434
*Breeding Site*Bi-monthly period*	2,40	0.38	0.6853

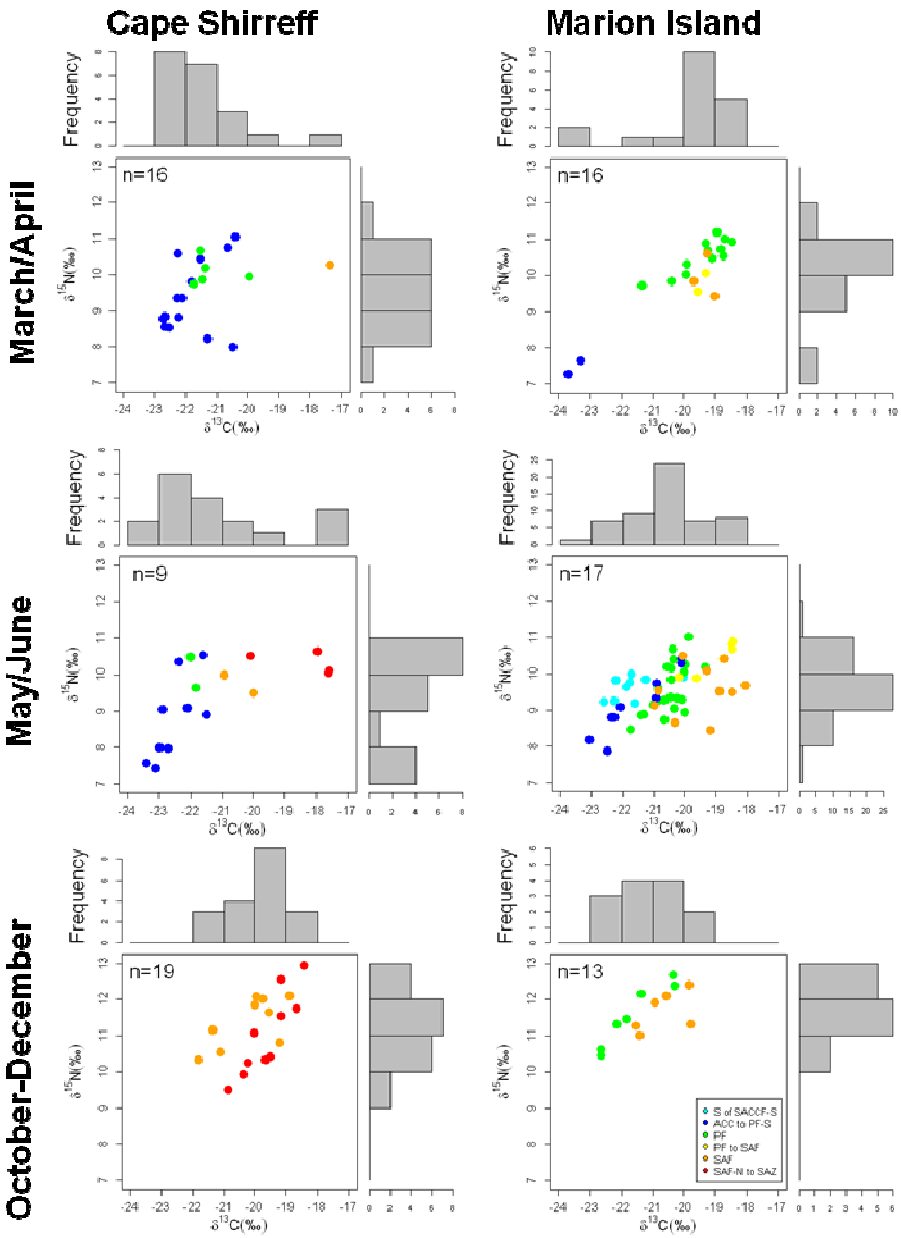

Figure 4.1. The isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of tissues of female Antarctic fur seals according to breeding site (Cape Shirreff, Livingston Island, Western Antarctic Peninsula; Marion Island, southern Indian Ocean) and bi-monthly foraging periods (March/April, May/June and October-December; 2008 and 2009 data combined). Whisker isotopic values represent dietary information incorporated during the March/April and May/June periods. Whole blood isotopic values corrected for variation in fractionation between whole blood and whiskers in pinnipeds (Hobson et al. 1996) represent dietary information incorporated during the October-December period. Also shown are marginal frequency distributions for the $\delta^{13}C$ and $\delta^{15}N$ values for each winter migration period. The isotopic values of whisker segments and whole blood are colour-coded according to foraging location (Inter-Frontal Zones; IFZs). From south to north, IFZs included the Antarctic zone south of the southern Antarctic Circumpolar Current Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to Sub-Antarctic Front (PF to SAF), the SAF, and the SAF-Northern branch to Sub-Antarctic Zone (SAF-N to SAZ).

Inferred prey consumption during winter

Five clusters were identified in the potential prey species (ANOSIM: Global R = 0.85, SSS = 0.1%, NPS ≤ 0 = 0; Fig. 4.2.). These were: (1) Antarctic krill (*Euphausia superba*), (2) other *Euphausiid* spp. including *E. crystallorophias, frigida and triacantha* (3) the benthic Blackgin icefish (*Chaenocephalus aceratus*), the mesopelagic myctophid fish *Electrona antarctica*, the pelagic Antarctic silverfish (*Pleuragramma antarcticum*), and the meso-bathypelagic glacial squid (*Psychroteuthis glacialis*), and (4) lower and (5) higher trophic level fish and squid, as inferred by their relatively depleted and enriched $\delta^{15}N$ values, respectively, predominated by mesopelagic (myctophid) and squid species. The five prey groups were numbered 1, 2, 3, 4 and 5 accordingly (Appendix C). Groups 1, 2 and 3 were characterised by ^{13}C depleted tissues (< -24‰) relative to groups 4 and 5 (> -23‰), indicating high latitude (*e.g.* Antarctic zone) and mid-latitude (*e.g.* subantarctic zone) provenance of prey groups, respectively.

When we compared the mean isotopic signature of seals grouped according to foraging location (IFZ) in each foraging period to those of the prey groups (Fig. 4.3.), the Cape Shirreff seal data lay closest to groups 2 and 4 in March/April and May/June, but closer to groups 4 and 5 in October-December In contrast, data for the Marion Island seals lay closest to groups 1 and 4 in March/April, groups 2 and 4 in May/June and group 3 in October-December For both breeding sites, we found a seasonal shift in prey over the non-breeding foraging periods (Fig. 4.3.). For Cape Shirreff females, tissue (corrected for diet-tissue fractionation) and prey group stable isotope values (mean ± SD) for each foraging period indicated a shift from high to mid-latitude prey from early (March/April) to late in the season (October-December), while the reverse appears to be the case for seals from Marion Island. Estimates of Cape Shirreff seal diet composition for each foraging period (SIAR, Fig. 4.4.), indicated consumption of krill (prey groups 1 and 2) and benthic, meso- and pelagic fish and meso-bathypelagic squid (prey group 3) earlier in the season (March/April: contributing a combined ~77% of the diet) in which most females utilised ACC to PF-S habitat (Fig. 4.3.A). Estimates indicated increased consumption of mesopelagic fish and squid (prey groups 4 and 5) later in the season (October-December: contributing ~58% of the diet) in which most females utilised SAF and SAF-N to SAZ habitat (Fig. 4.3.C).

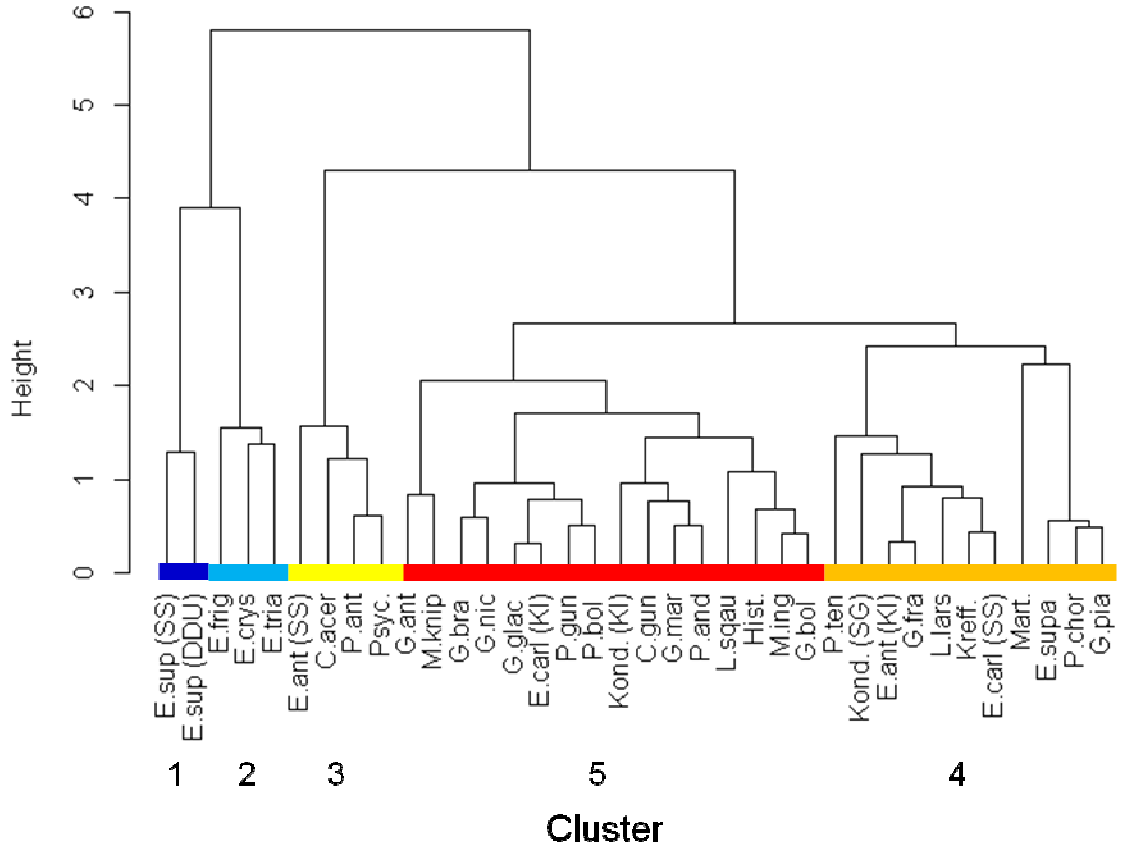

Figure 4.2. Cluster analysis of the Euclidean distance between $\delta^{13}C$ and $\delta^{15}N$ values of Southern Ocean marine organisms showig clusters identified by the hclust function in R (for details see Appendix C).

For females breeding at Marion Island, modal estimates indicated a shift from mesopelagic fish and squid (prey groups 4 and 5) during March/April (contributing a combined ~58% of the diet) in which most females utilised PF habitat (Fig. 4.3.A) to benthic, meso- and pelagic fish and meso-bathypelagic squid (prey group 3; contributing ~56% of the diet), and to a lesser extent mesopelagic fish and squid (prey groups 4 and 5; contributing ~22% of the diet) later in the season (October-December) in which the majority of females from Marion Island utilised PF and SAF habitat (Fig. 4.3.C).

The proportional contribution of krill (prey groups 1 and 2) to the diet of females from both breeding sites was most similar during the May/June period (CS: combined ~47% of the diet; MAR: combined ~45% of the diet; Fig. 4.4.) in which most females from Cape Shirreff and Marion Island in this study utilised habitat at or south of the PF (Fig. 4.3.B).

Tissue isotopic values versus latitude

For both breeding sites, the $\delta^{13}C$ values of seal tissues was linearly correlated with the mean latitude of seal location (CS: linear model, $\delta^{13}C = 0.1918x - 9.3924$, $R^2 = 0.5329$, $P < 0.0001$, n=23; MAR: $\delta^{13}C = 0.1495x - 12.8084$, $R^2 = 0.157$, $P < 0.0001$, n=18), reflecting the winter movement behaviour of seals at both sites and the marked regional difference in front location (Fig. 4.5.). Seals from Cape Shirreff showed a distinct pattern of increasingly ^{13}C enriched tissues with decreasing latitude of foraging location (IFZ), reflecting the northward migration of seals from south (> 60°S; $\delta^{13}C$: -22.0±0.8 and -21.5±0.9‰ for ACC to PF-S and PF zones, respectively) to north of the PF (< 60°S; $\delta^{13}C$ = -19.9±1.2 and -19.2±1.1‰ for SAF and SAF-N-SAZ, respectively) in the southern Atlantic Ocean sector. Seals from Marion Island showed a similar pattern in $\delta^{13}C$ values (S of SACCF-S: -21.5±0.7‰ < ACC to PF-S: -21.3±1.5‰ < PF: -20.5±1.2‰ < PF to SAF: -20.0±1.6‰< SAF: -19.9±1.2‰) however, the relationship with mean latitude of foraging location was less defined (S of SACCF-S: -57.7±1.3 < ACC to PF-S: -54.8±3.1 < PF: -52.3±1.7 < PF to SAF: -49.4±1.0 < SAF: -47.6±1.6; Fig. 4.5.A), reflecting the close proximity and juxtaposition of fronts in the southern Indian Ocean sector (Fig. 4.5.B).

Moreover, tissue $\delta^{13}C$ values indicated the more northerly occurrence of the ACC to PF-S (CS: 64°8'±1.9; MAR: 54°8±3°1') and PF zones (CS: 63°0'±2°6'; MAR: 52°3'±1°7') in the Indian Ocean sector (Fig. 4.5.B), with $\delta^{13}C$ values ranging from -22.0±0.8 and -21.3±1.5‰ (a 0.7‰ difference), and from -21.5±0.9 and -20.5±1.2‰ (a 1.0‰ difference) for Cape Shirref

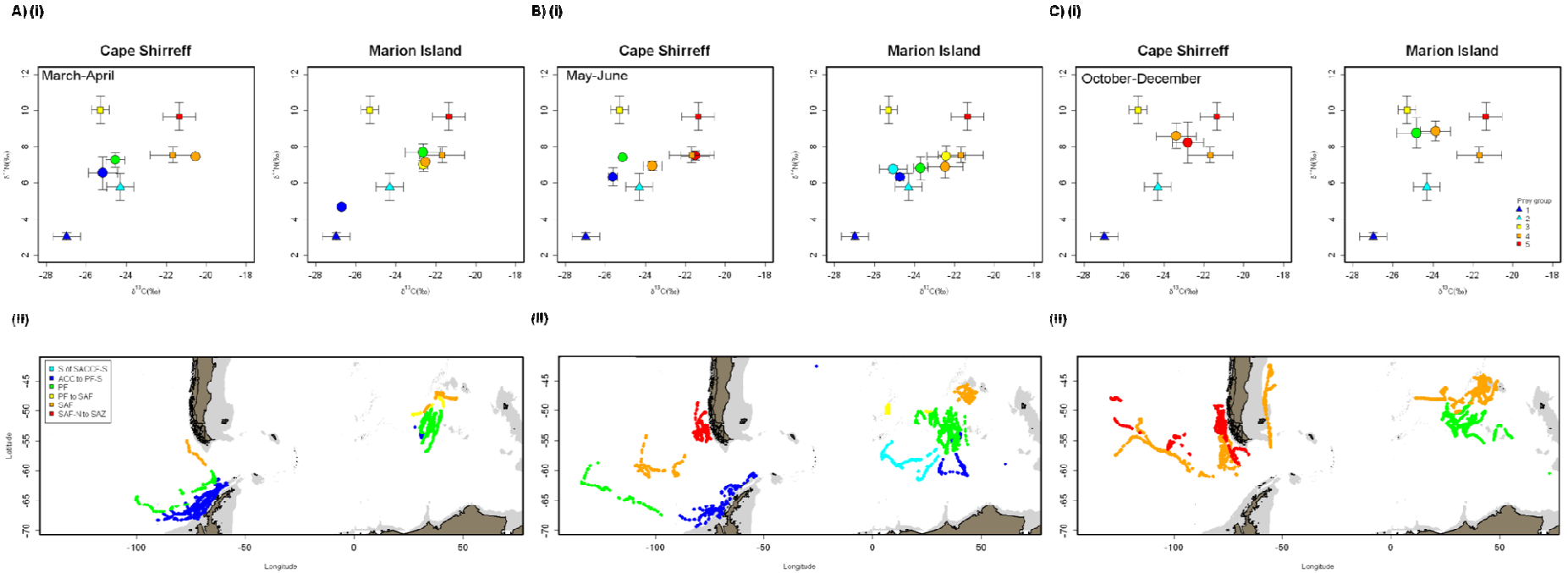

Figure 4.3. The mean $\delta^{13}C$ and $\delta^{15}N$ values of female Antarctic fur seals (AFS; corrected for diet-tissue fractionation following Hobson et al. 1996) according to breeding site and foraging location (Inter-Frontal Zones; IFZs) in bi-monthly periods (March/April, May/June and October-December; A, B and C, respectively) and of the five prey groups identified by cluster analysis in Fig. 4.2. Prey groups: 1. Antarctic krill (*Euphausia superba*); 2. other euphausiids; 3. high latitude fish and squid; 4. mid-latitude lower trophic level fish and squid, and 5. mid-latitude higher trophic level fish and squid. Whisker stable isotope values represent dietary information incorporated during the March/April and May/June periods. Whole blood isotope values represent dietary information incorporated during the October-December period. (i) Isotope values (circle symbols) and (ii) geolocation data for AFS are colour-coded according to foraging location (IFZs). From south to north, IFZs included the Antarctic zone south of the southern Antarctic Circumpolar Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to Sub-Antarctic Front (PF to SAF), the SAF, and the SAF-Northern branch to Sub-Antarctic Zone (SAF-N to SAZ).

and Marion Island seals feeding in ACC to PF-S and PF zones, respectively (Fig. 4.5.A). Seals feeding in the SAF zone however, showed similar $\delta^{13}C$ values (-19.9±1.2‰ for both breeding sites; Fig. 4.5.A) despite regional variation in seal location (CS: 55°2'±4°2'; MAR: 47°6'±1°6'; Fig. 4.5.B), with the exception of two seals from Cape Shirreff which fed in SAF waters off the Patagonian shelf (GLS 4278: 45°7'±3°9'; GLS 4293: 48°7'±3°; Fig. 4.5.B).

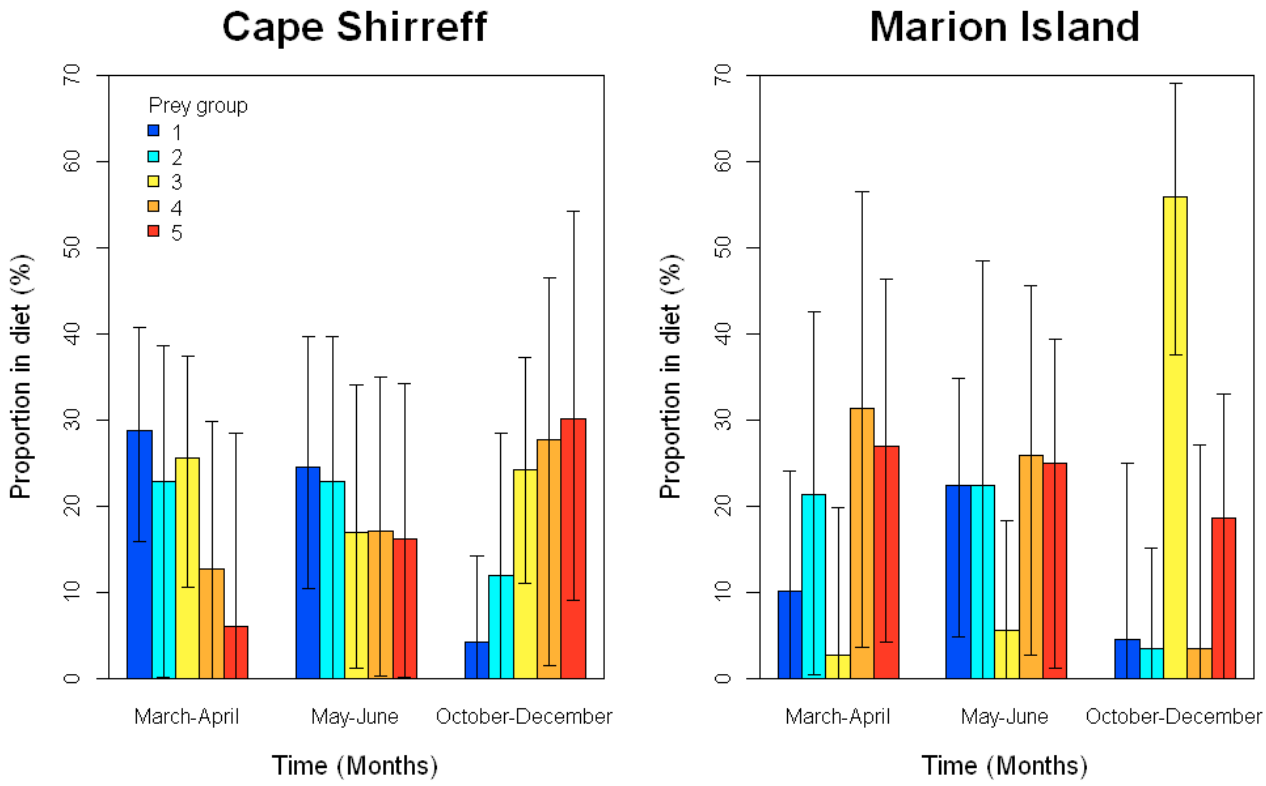

Figure 4.4. Proportional contribution of five prey groups: 1. Antarctic krill (*Euphausia superba*); 2. other euphausiids; 3. high latitude fish and squid; 4. mid-latitude lower trophic level fish and squid and 5. mid-latitude higher trophic level fish and squid to the diet of adult female Antarctic fur seals according to breeding site and bi-monthly period (2008 and 2009 data combined). Prey groups were defined by cluster analysis presented in Fig. 4.2. and color-coded accordingly. Proportional contributions are modal values (bars) overlaid with lower and upper 95% posterior intervals (error bars) of Stable Isotope Analysis in R (SIAR) mixing model output of Antarctic fur seal diet.

DISCUSSION

Many pelagic animals rely on predictable, high food source areas outside the breeding period in order to meet the requirements of the energetically demanding breeding season (Shaffer et al. 2006; Bost et al. 2009b; Breed et al. 2009; Thums et al. 2011). In the Antarctic marine environment the availability, distribution and abundance of important prey species (such as Antarctic krill, mesopelagic fish and squid), for higher predators varies substantially with season and location (Nicol 2006; Van de Putte et al. 2010; Hunt et al. 2011; Koubbi et al. 2011). This is driven by temporal constraints (Pakhomov et al. 1994), variation in sea ice cover (Massom & Stammerjohn 2010), regional-specific climatic variations such as the Southern Annular Mode and Southern Oscillation indices (Kwok & Comiso 2002; Trathan et al. 2006; Murphy et al. 2007; Trathan et al. 2007), changes in primary productivity (Constable et al. 2003) and the location of oceanographic frontal zones, eddies and bathymetry (Sokolov & Rintoul 2007b; Sokolov & Rintoul 2009b; Sokolov & Rintoul 2009a; Durgadoo et al. 2010). The winter diet composition of Antarctic marine predators may therefore, differ substantially from that currently documented in summer.

Through the combination of tracking (Lea et al. in review) and stable isotope data we provide the first insight into the winter dietary preferences of female Antarctic fur seals during the protracted migration period. This study highlights the influence of water mass and season on the prey types consumed by female seals during winter and prior to the energetically demanding breeding period. A key finding of our study was the consumption of lower trophic level macrozooplankton prey (Antarctic krill) by seals in both regions during the winter months, when feeding in ice-associated habitat at, or south of the PF (Lea et al. in review). However, seals shifted to a diet dominated by mesopelagic resources (fish and squid) concomitant with a shift in season from winter to spring, which corresponded to the most intense period of Area Restricted Search by seals in both regions (Lea et al. in review). While isotopic results indicated seals occupied a similar trophic niche during this time, Bayesian mixing models using SIAR indicated regional differences in the relative proportions of fish (and squid) prey consumed, most likely influenced by water mass use.

These results emphasize the importance of integrating information on the movements of animals (Bost et al. 2009b; Revill et al. 2009; Thiebot et al. 2011; Walters et al. 2014; this study) and the use of Bayesian statistics (Semmens et al. 2009; Parnell et al. 2010; Jackson et

al. 2011; Ramos & González-Solís 2012) to interpret isotopic results in an ecologically explicit manner.

Stable isotopes alone cannot discern important differences in the diet composition of highly migratory predators, such as prey type (*e.g.* fish or squid), family (*e.g.* channichthyidae, myctophidae or nototheniidae fish) or species (*e.g.* myctophids). This finding has important implications for future isotopic dietary studies of higher predators, such as Antarctic fur seals and other Antarctic marine predators, which show significant seasonal and/or regional differences in foraging habitat and diet composition.

Growth rate of Antarctic fur seal whiskers

Stable isotopes in tissues of progressive growth, such as whiskers, are increasingly being used to trace the dietary habits of highly migratory marine predators (Hirons 2001; Hückstädt et al. 2007; Cherel et al. 2009b; Newland et al. 2011). There are however several requirements for applying this approach. The first being accurate growth rates to interpret the time-series of isotopic information, which may span months (Hirons et al. 2001; Newland et al. 2011) to several years (Kernaléguen et al. 2012) worth of time integrated information. Using re-growth of whiskers cut on the initial GLS deployment, we quantified whisker growth in female Antarctic fur seals (0.10±0.04 mm d^{-1}) during the non-breeding winter migration period, providing ~27 to ~30 d worth of time-integrated dietary information per 3 mm section of growth. This average growth rate was comparable to those estimated for Antarctic fur seals from Crozet Archipelago (~21 to ~37 d for male and females, respectively; Kernaléguen et al. 2012), and other otariid seals, such as Steller sea lions *Eumetopias jubatus* (~25.0 to ~27.3 d; Hirons et al. 2001), but substantially slower to that estimated in phocid seals, including pre-weaning bearded seals *Erignathus barbatus* (3.5 d; Hindell et al. 2012) and captive gray seals *Halichoerus grypus* (12.5 d; Greaves et al. 2004).

Few studies have documented whisker growth dynamics in pinnipeds (Hirons et al. 2001; Greaves et al. 2004; Zhao & Schell 2004; Hindell et al. 2012; Kernaléguen et al. 2012), but growth characteristics in otariid and phocid species do seem to be remarkably different. These differences are most likely linked to differences in the functionality of the structure in the respective pinniped suborders (Williams & Kramer 2010; Miersch et al. 2011). Growth rates in phocid species indicate irregular growth patterns and short-term retention times, with some species shedding whiskers on an annual basis, *e.g.* harbor seals(Zhao & Schell 2004)

and others randomly, *e.g.* southern elephant seals *Mirounga leonina* (Ling 1966; Newland et al. 2011) and gray seals (Greaves et al. 2004). In contrast, otariid species appear to exhibit more consistent growth and year-to-year retention of their whiskers, *e.g.* Steller sea lions (Hirons et al. 2001) and Antarctic fur seals (Kernaléguen et al. 2012; this study).

Phocid species therefore show a general pattern of accelerated growth, *e.g.* pre-weaning bearded seals (0.85 mm d^{-1}, Hindell et al. 2012), captive gray seals (0.24 mm d^{-1}, Greaves et al. 2004) ensuring that at no time would a seal be without most of its whiskers while at sea. Otariid species, which appear to retain their whiskers from year to year, show a pattern of slower growth, *e.g.* wild sub-adult and adult Steller sea lions (0.10-0.14 mm d^{-1}, Hirons et al. 2001), male and female Antarctic fur seals from Crozet Archipelago (0.14 and 0.08 mm d^{-1}, respectively, Kernaléguen et al. 2012) and female Antarctic fur seals from Cape Shirreff and Marion Island (0.10 mm d^{-1}, this study).

Foraging locations ($\delta^{13}C$) of female Antarctic fur seals

By combining stable isotope and tracking data we have been able to validate that $\delta^{13}C$ values in the tissues of seals change in a logical and consistent way as the seals move through different water masses over time. Indeed, we show that tissue $\delta^{13}C$ values correspond well with mean latitude of foraging location (*i.e.* $\delta^{13}C$ decreases with increasing latitude; Rau et al. 1982; Goericke & Fry 1994; Popp et al. 1999; Trull & Armand 2001) and in turn, reflect the marked regional difference in front location in the southern Atlantic and Indian Ocean sectors (Fig. 4.5.). Thus, $\delta^{13}C$ serves as a good proxy of core habitat use for these seals over the winter migration period.

Taking into account the keratinous effect in seal whiskers (2.8‰ ^{13}C enriched over their diet in pinnipeds, Hobson et al. 1996), the isotopic location of the PF and SAF for fur seal tissues were estimated at approximately -21 and -20‰ in the southern Atlantic Ocean sector, respectively, and at -20‰ for both frontal zones in the southern Indian Ocean sector. The isotopic location of the PF in the Atlantic sector was in good agreement with that estimated for southern elephant seal whiskers in the Pacific sector (PF: 62°9'S, $\delta^{13}C$ = -21‰; Chapter 3). These results highlight the use of isotopic tracers in the tissues of high trophic level consumers to map regional differences in meso-scale features, such as the location of marine fronts. Such information can be used to assess the relative importance of the different frontal zones to apex predators in terms of both spatial distribution and carbon flux, particularly in

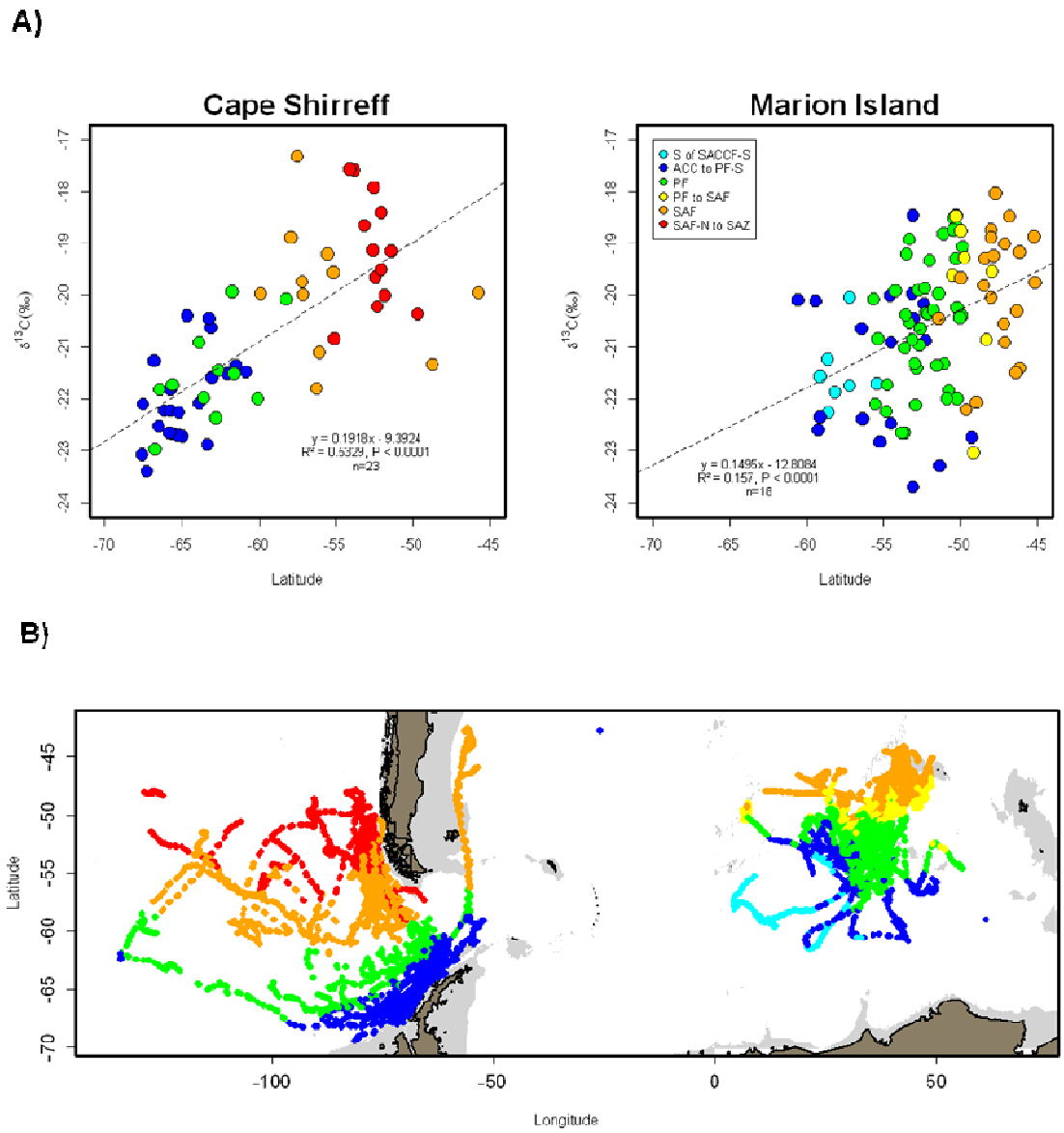

Figure 4.5. (A) Linear models of Antarctic fur seal $\delta^{13}C$ values versus mean latitude of corresponding seal location. Whisker segments (~3 mm length) represent ~27 to ~30 days of dietary information incorporated during the March/June period. Whole blood represents dietary information incorporated during the October-December period. Whole blood isotopic values are corrected for variation in fractionation between whole blood and whiskers in pinnipeds (Hobson et al. 1996). (B) Plot of the corresponding geolocation data of Antarctic fur seals from Cape Shirreff, Western Antarctic Peninsula, southern Atlantic Ocean and sub-Antarctic Marion Island, southern Indian Ocean. Stable isotope values and geolocation data are colour-coded according to foraging location (Inter-Frontal Zones; IFZs). From south to north, IFZs included the Antarctic zone south of the southern Antarctic Circumpolar Front-Southern branch (S of SACCF-S), the ACC to Polar Front-Southern branch (ACC to PF-S), the PF, the PF to Sub-Antarctic Front (PF to SAF), the SAF, and the SAF-Northern branch to Sub-Antarctic Zone (SAF-N to SAZ).

light of projected changes in winter sea ice extent and front location in relation to climate change.

Breeding site, foraging period and the location of foraging all explained significant variation in seal isotopic values during winter migration periods. Seals from Marion Island had more enriched whisker $\delta^{13}C$ values than females from Cape Shireff earlier in the season (*e.g.* March/April and May/June), while the opposite occurred later in the season (October-December) with whole blood $\delta^{13}C$ values for Marion Island females depleted in $\delta^{13}C$ relative to that of Cape Shirreff females. These $\delta^{13}C$ results reflect the contrasting winter migratory patterns for the two sub-populations (Lea et al. in review).

Moreover, offshore or pelagic (oceanic) habitats have depleted food web $\delta^{13}C$ and $\delta^{15}N$ values compared to coastal/inshore and benthic food webs (Clementz & Koch 2001; Cherel & Hobson 2007; Cherel et al. 2011). Hence, females from Cape Shirreff, which targeted off-shelf waters along the Chilean coast and Patagonian shelf showed more depleted $\delta^{13}C$ values, consistent with oceanic feeding (identified by tracking data; (Lea et al. in review), relative to that shown for other neritic foragers along the coast of Chile (*e.g.* southern sea lion *Otaria flavescens*; Hückstädt et al. 2007) and on the Patagonian shelf (e.g. southern elephant seal; Lewis et al. 2006; Eder et al. 2010).

In the Southern Ocean, the flow of the ACC is concentrated at frontal bands (Orsi et al. 1995) and to the north the Subtropical Front (STF) separates the warm waters of the subtropical zone from the subantarctic zone (Durgadoo et al. 2010). The SAF marks the southern boundary of the SAZ and the beginning of the Polar Front Zone (PFZ). The PF marks the southern boundary of the PFZ and the beginning of the Antarctic Zone (AZ). The interplay between bottom topography features and prevailing westerly winds play a major role in the flow of the ACC (Sokolov & Rintoul 2007b).

In the southern Indian Ocean sector, the structure and function of the SAF and PF are subject to spatial and temporal variation downstream of the South-West Indian Ridge (Pollard & Read 2001; Kostianoy et al. 2004; Sokolov & Rintoul 2009b; Sokolov & Rintoul 2009a; Durgadoo et al. 2010) and in the vicinity of the Andrew Bain Fracture Zone (Ansorge & Lutjeharms 2003). Other important topographic features in this region include the Del Cano Rise and Conrad Rise (Durgadoo et al. 2010). To the south of South Africa, the structure of

the PF is complex, breaking into multiple fragments downstream of the SWIR (Sokolov & Rintoul 2009b; Sokolov & Rintoul 2009a; Durgadoo et al. 2010). Meandering of the PF in this region has been attributed to cold eddy formation in the vicinity of the Prince Edward Islands (Durgadoo et al. 2010), resulting in convergence of the PF with the SAF. The isotopic signal for females foraging in the vicinity of the PF and SAF in this region of the Indian Ocean (Lea et al. in review) is therefore mixed.

Inferred diet composition

Summer

Establishing a link between isotopic dietary studies and actual prey consumption is paramount to the correct interpretation of isotopic data (Quillfeldt et al. 2005a). The summer diet of Antarctic fur seals is typically comprised of myctophid fish and squid at Marion Island (Condy 1981; Klages & Bester 1998; Makhado et al. 2008) and other subantarctic islands, including Îles Crozet (Cherel et al. 2007), Heard (Green et al. 1989), Îles Kerguelen (Lea et al. 2002a) and Macquarie Island (Goldsworthy et al. 1997). While Antarctic krill, myctophid fish and squid predominate in the diet of seals at Cape Shirreff (Osman et al. 2004) and other sites in the WAP region (Daneri 1996; Casaux et al. 1998; Daneri & Carlini 1999; Casaux et al. 2003a; Casaux et al. 2003b). The comparison of whole blood and prey isotopic signatures permits assessment of summer dietary patterns (Cherel et al. 2007). The isotopic signatures of fish and squid are enriched in $\delta^{15}N$ relative to Antarctic krill (Appendix C). Thus, the whole blood summer isotopic signatures of females in this study are in good agreement with dietary trends determined in previous studies, from both stable isotope (Cherel et al. 2007; Polito & Goebel 2010) and scat analysis (Klages & Bester 1998; Osman et al. 2004; Cherel et al. 2007; Makhado et al. 2008).

Winter

Very little information exists on the winter diet composition of Antarctic fur seals (Green et al. 1991; Reid 1995; North 1996; Makhado et al. 2008) and there is no information for migrating female seals. The whisker isotopic signatures of seals provided dietary information corresponding to March/April and May/June periods, and whole blood provided information corresponding to October-December. Whisker and whole blood $\delta^{15}N$ values defined two trophic niches, with seals from both regions occupying a similar trophic level during March/April and May/June, while the more enriched $\delta^{15}N$ values in whole blood of females from both regions later in the season (October-December) indicated a shift to a higher trophic

level in spring/early summer. Bayesian mixing models using SIAR identified differences in the diet composition of seals in relation to the water masses used over the course of the migration period.

In agreement with tracking and $\delta^{13}C$ data, we found that Cape Shirreff seals, which predominately utilised sea ice habitat (~65°01'S, ACC to PF-S; Appendix E) along the WAP early in the season (March/April) had more depleted $\delta^{15}N$ values (~9.4‰) than females in the Indian sector foraging in the more northerly PF zone (~51°03'S, $\delta^{15}N$: ~10.5‰; Appendix E). Stable Isotope Analysis in R modal estimates indicates Cape Shirreff seals were preying upon Antarctic krill, squid and fish (contributing 28.7% and 25.6% to the diets of seals, respectively) and Marion Island seals feeding mainly on mesopelagic fish (myctophids) and squid (58.3%), consistent with prey determination of fur seal scats.

In the Atlantic sector of the Southern Ocean, Lea et al. (in review) found that sea ice and winter conditions affect the breeding areas and residence times of seals. Thus, we found that as sea ice advanced and seals moved further off-shore and northwards to deeper, oceanic waters (IFZs: SAF and SAF-N to SAZ), which are dominated by mesopelagic fish (myctophids) and squid (Van de Putte et al. 2010; Koubbi et al. 2011; Collins et al. 2012), the relative proportion and the diversity of fish and squid prey consumed by seals increased from areas close to the WAP in March/April (44.2%) to May/June (50.2%) to October-December (82.1%) in warmer, productive subantarctic waters off the Chilean coast and Patagonian shelf where Antarctic krill does not occur (< 54°04'S; Appendix E).

Oceanic areas adjacent to the coast of Chile and Patagonia are areas of high biological production due to large-scale processes, such as eddies, marine fronts, coastal currents and upwelling, which transport production offshore (Acha et al. 2004; Thiel et al. 2007). These areas promote primary and secondary production in the water column attracting crustaceans, fish and squid for higher predators to feed on. Over the course of migration, Cape Shirreff seals showed maximum foraging effort in these areas, indicative of core foraging habitat (Lea et al. in review). Thus, seals breeding in the WAP region faced with diminished winter productivity (Constable et al. 2003), appear to seek out biologically productive, high food source areas located north of the SAF in spring and prior to the energetically demanding breeding period, as hypothesized in previous studies (Polito & Goebel 2010). When we compared the enriched $\delta^{15}N$ values of Cape Shirreff seals to the dietary habitats and isotopic

signatures of seals in summer, the most parsimonious explanation is that in October-December, seals occupy a different trophic level consistent with a seasonal shift in diet composition from krill, fish and squid to mesopelagic fish and squid as estimated using SIAR.

These results confirm that increased consumption of mesopelagic fish (and squid) in the diets of female seals at Cape Shirreff is due to a change in foraging location, as hypothesised in previous studies (*e.g.* Ichii et al. 2007; Polito & Goebel 2010). Recent studies have shown that seasonal movements of the PF and other oceanographic features influence the spatial distribution of mesopelagic fish and squid (Hunt et al. 2011; Koubbi et al. 2011; Collins et al. 2012). Temporal constraints limit fish diversity in cold Antarctic waters and subsequently there is a decrease in the diversity of species south of the PF (Koubbi et al. 2011). In the Scotia Sea, Collins et al. (2012) found the fish fauna of the Antarctic zone to be dominated by myctophid fish; *E. antarctica*, *Gymnoscopelus braueri* and *Bathylagus antarcticus*, while further north diversity increased with the addition of species such as *Krefftichthys anderssoni*, *Protomyctophum bolini* and *Electrona carlsbergi*. Thus, the spatial distribution and diversity of fish and squid in the pelagic zone, in addition to the availability of Antarctic krill, explains highly seasonal patterns in the consumption of prey by female seals in the Atlantic sector, driven largely by temporal effects.

Seals in the Indian Ocean sector show a different pattern of resource use. Females undertake one or several large-scale central place foraging trips; undergoing longitudinal or northward movement in SAF waters or migrating south of Marion Island to feed predominantly in PF waters during the non-breeding period (Lea et al. in review). Modal estimates suggest that a small proportion of individuals (21%), such as female 4272, which travelled longer distances (~56°07'S, S of SACCF-S; Appendix E) when the ice edge was further south (~56°S, Turner et al. 2004), consumed lower trophic level macrozooplankton prey namely Antarctic krill (22.4%), in addition to mesopelagic fish and squid, which constituted the bulk of the diet (50.9%) for most seals feeding at or north of the PF (< 52°09'S; Appendix E) during May/June.

During July/August when maximum winter sea ice extent occurred at ~55°S at 15°E and ~60°S at 60°E (Lea et al. in review), females 4323 and 4350 from Marion Island showed some of the most depleted whisker isotopic values in this study (δ^{15}N: 7.1 to 8.0‰ and 7.7 to 7.9‰, respectively; Appendix D), similar to that in the whiskers of a highly specialised

predator of Antarctic krill the crabeater seal *Lobodon carcinophaga* (5.4 to 7.9‰; Hückstädt et al. 2012). Concurrent dive behaviour collected for Marion Island seal 4272 by Lea et al. (in review) shows an abrupt change in dive depth from ~52 to 58°S from deeper (< 80 m) to shallower dives (< 20 m) during July/August. Night-time foraging and shallower diving by Antarctic fur seals are indicative of a switch from mesopelagic distributed prey to diurnally migrating crustaceans, *i.e*. krill. This is consistent with the winter foraging ecology of specialised krill eating marine predators from this region (macaroni penguins, *Eudyptes chrysolophus*) which also feed in the vicinity of the PF (Thiebot et al. 2011). Thus, our findings suggest that a significant percentage of seals (n=5 seals in this study) foraging in sea ice habitat (31% of seals, Lea et al. in review) do target krill over the winter period. Previous studies have shown similar depleted isotopic values in the whiskers of male Antarctic fur seals at Crozet Island, with minimum $\delta^{15}N$ values of 7.1‰ (Kernaléguen et al. 2012) and 7.3‰ (Cherel et al. 2009b), indicating other subantarctic breeding populations may also feed on krill during the winter non-breeding period.

During spring and prior to the breeding season (October-December), Marion Island seals showed a marked shift in diet composition to fish and squid (71.6%). During this time seals remained near to sea ice in the PF (~52°03'S), or shifted north to feed in the SAF (~46°07'S; Appendix E). Comparison of the dietary habits and isotopic signatures of seals in summer indicates that seals occupied a similar trophic level in summer and spring (and prior to breeding), consistent with the diet of seals foraging in the PF zone (*e.g.* myctophids and squid, Lea et al. 2002a). However, SIAR estimates indicated increased consumption of more southerly (Antarctic) occurring species, such as *E. antarctica* (56.9%), relative to warm-water species (*e.g. G. piablis, E. electrona, G. nicholsi and G. fraseri*; 22.1%; Hulley 1981; Collins et al. 2012), as indicated by their typically depleted (~ -25‰) and enriched ^{13}C values (> -23‰), respectively (Rau et al. 1982; Cherel et al. 2010). The latter group form an important part of the summer diet of seals at Marion (Klages & Bester 1998; Makhado et al. 2008), Crozet (Cherel et al. 2007), Kerguelen (Lea et al. 2002a) and Macquarie Islands (Goldsworthy et al. 1997), while the former appear to be less important or absent in scat samples.

In the Lazearev Sea, Hunt et al. (2011) recently showed that there was a distinctive seasonal change in the macrozooplankton assemblage structure. Of note amongst these was a shift within the euphausiids from a dominance of *Thysanoessa macrura* in summer to that of *E.*

superba in autumn and winter, and a winter increase in the abundance of the myctophid fish *E. antarctica*, which preferentially feed on the latter. *Electrona antarctica* are one of the most common myctophids occurring in more southerly waters of the Southern Ocean (Flores et al. 2008; Van de Putte et al. 2010; Koubbi et al. 2011; Collins et al. 2012) and are particularly oily (15% wet mass), energy rich prey sources (34.3±2.6 kJ g^{-1}, Lea et al. 2002b) for higher predators. It therefore follows, that female seals unconstrained by breeding cover greater distances to remote ice-associated foraging areas to access abundant, energy rich sources of prey, such as *E. antarctica* at a time when biological productivity is low.

Stable isotope mixing models

The choice of the level of complexity for a stable isotope mixing model is critical; essentially the fewer species included in the model, the lower the likelihood of incorrect inferences regarding possible trophic relationships within a system being made (Bond & Diamond 2010). On the other hand, too few species included in the model will potentially underestimate the importance of some species. Fish represent an important food source for Antarctic fur seals, in addition to krill, and to a lesser extent squid, during the winter migration period in the pelagic food web systems of the Antarctic and subantarctic regions of the Southern Ocean. It was therefore considered important to represent the fish diversity as realistically as possible in the models. Using isotopic derived prey sources, it is difficult to separate fish and squid based on their $\delta^{15}N$ abundance as this can overlap substantially (Quillfeldt et al. 2005a; Polito & Goebel 2010; this study, chapter 3). Our analysis showed that we could not separate squid from fish based on their $\delta^{13}C$ and $\delta^{15}N$ values. However, since POM $\delta^{13}C$ values vary with latitude, the spatial distribution of marine organisms influences their $\delta^{13}C$ signatures. Hence, $\delta^{13}C$ values allow differentiation between species of Antarctic (Antarctic krill, other euphausiids, fish and squid) and subantarctic (mesopelagic fish and squid) provenance (Rau et al. 1982).

Moreover, given the little winter diet information available for Antarctic fur seals, the level of squid predation exhibited by this species remains inconclusive. Several studies have hypothesised that cephalopod prey are taken opportunistically (*e.g.* Hofmeyr et al. 2010). Male seals have been observed preying upon large octopods at Marion Island during winter (Reisinger et al. 2010). Cephalopod beaks are present in seal scats, but occur in low numbers when compared to fish prey remains (Lea et al. 2002a; Makhado et al. 2008). However, large items such as cephalopod beaks are unlikely to appear in scats if digested (Staniland 2002)

and instead retained in the stomach and may be regurgitated at sea during long migration trips (Lea et al. in review).

CONCLUSION

We have demonstrated how the winter, non-breeding feeding ecology of a highly migratory predator, the female Antarctic fur seal, can be elucidated using a combination of stable isotope ratios, tracking data and Bayesian mixing models.

The first key finding of this study was that $\delta^{13}C$ in the tissues of seals reflected their winter migratory patterns and regional variation in front location as validated by tracking data. This is an important finding as it means in the absence of tracking data, $\delta^{13}C$ can be used as a proxy for core winter foraging areas. A second key finding was the consumption of lower trophic level macrozooplankton prey (namely Antarctic krill) by seals in the Indian Ocean sector. While predation of krill by this species in the Atlantic sector is well documented and dominates the diet of seals at South Georgia (*e.g.* Doidge & Croxall 1985; Reid 1995; Reid & Arnould 1996) and Bouvetoya (Kirkman et al. 2000), consumption of krill elsewhere has not been reported. In addition, the proportional contribution of krill to the diet of females from Atlantic and Indian sectors was most similar during winter (May/June) in relation to sea ice habitat.

At the population level, our data suggest that seals feed on krill, fish and squid during winter, but shift to a diet dominated by energy rich mesopelagic resources (fish and squid) in predictable, high resource areas prior to and during the energetically demanding breeding period. This study provides substantial information on the winter foraging ecology of female fur seals, and indeed fur seals overall, and raises important questions about the winter biology of seals in the Indian Ocean sector of the Southern Ocean.

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APPENDICES

Appendix A. Tissue sampling details for adult female Antarctic fur seals from Cape Shirreff, Livingston Island, Western Antarctic Peninsula (WAP), southern Atlantic Ocean and Marion Island, Prince Edward Islands, southern Indian Ocean during the summer breeding period in 2008 and 2009.

Seal GLS No.	Tissue sampling date	Whiskers		Whole blood
		Sampling protocol	Total length (mm) (Root length)	
Cape Shirreff, Livingston Island, WAP, Atlantic Ocean				
4231	30-Jan-08	plucked/full	90.0 (14.0)	X
4274	27-Jan-08	cut/full	132.0	X
4275	22-Jan-08	cut/full	132.0	X
4282	24-Jan-08	cut/full	108.0	X
4283	24-Jan-08	cut/full	108.0	X
4287	24-Jan-08	cut/full	96.0	X
4289	25-Jan-08	plucked/full	96.0 (8.0)	X
4292	25-Jan-08	cut/full	111.0	X
4293	27-Jan-08	plucked/full	81.0 (10.0)	X
4353	3-Feb-08	cut/full	90.0	X
Mean			**104.4±17.3 (10.7±3.1)**	
4789	21-Jan-09	cut/full	54.0	X
4797	15-Jan-09	cut/full	87.0	X
4816	16-Jan-09	cut/full	69.0	X
4817	24-Jan-09	cut/full	48.0	X
4819	17-Jan-09	cut/full	57.0	X
4822	18-Jan-09	cut/full	60.0	X
4826	24-Jan-09	cut/full	45.0	X
4832	19-Jan-09	cut/full	69.0	X
4842	21-Jan-09	cut/full	60.0	X
4847	14-Jan-09	cut/full	51.0	X
Mean			**60.0±12.4**	

Appendix A. (cont.)

Seal GLS No.	Tissue sampling date	Whiskers		Whole blood
		Sampling protocol	Total length (mm) (Root length)	
Marion Island, Prince Edward Islands, southern Indian Ocean				
4272	14-Mar-08	cut/full	51.0	✓
4273	14-Mar-08	cut/full	48.0	✓
4280	14-Mar-08	cut/full	63.0	✓
4284	18-Mar-08	cut/full	120.0	✓
4317	21-Mar-08	cut/full	168.0	✓
4318	20-Mar-08	cut/full	135.0	✓
4323	14-Mar-08	cut/full	51.0	✓
4329	21-Mar-08	cut/full	150.0	✓
4356	3-Apr-08	cut/full	276.0	✓
4823	1-Apr-08	cut/full	108.0	x
Mean			**117.0±71.3**	
4229	21-Mar-09	cut/full	18.0	✓
4268	3-Apr-09	cut/full	132.0	x
4271	15-Mar-09	cut/full	84.0	x
4804	15-Mar-09	cut/full	57.0	x
4805	25-Mar-09	cut/full	18.0	x
4824	24-Mar-09	cut/full	69.0	✓
4836	21-Mar-09	cut/full	48.0	x
4838	23-Mar-09	cut/full	141.0	x
4843	15-Mar-09	cut/full	75.0	x
4846	15-Mar-09	cut/full	63.0	✓
Mean			**70.5±41.1**	□

Whole blood sampled from female Antarctic fur seals at Cape Shirreff during the summer breeding period in 2010.

Appendix B. Tissue sampling details for female Antarctic fur seals from Cape Shirreff, Livingston Island, Western Antarctic Peninsula (WAP), southern Atlantic Ocean and Marion Island, Prince Edward Islands, southern Indian Ocean during the winter non-breeding period in 2008 and 2009.

Seal GLS/ tag no.	Tissue sampling date	Whiskers		Whole blood	GLS deployment (No. of days)		
		Sampling protocol	Total length (mm) (Re-growth)		At-sea	Ashore	Total
Cape Shirreff, Livingston, WAP, southern Atlantic Ocean							
4224	18-Dec-08	cut /full	64.0	✓	229.2 (11 Apr-26 Nov)	21.8 (26 Nov-18 Dec)	251.0
4269	8-Dec-08	cut /full	93.0	✓	225.7 (22 Apr-3 Dec)	5 (3-8 Dec)	230.7
4274	10-Dec-08	cut /full	55.0	✓	224.1 (18 Apr-28 Nov)	12.0 (28 Nov-10 Dec)	236.1
4275	6-Dec-08	cut /full	56.0	✓	233.6 (13 Apr-2 Dec)	4.0 (2-6 Dec)	237.6
4276	10-Dec-08	cut /full	50.0	✓	319.0 (22 Jan-8 Dec)	2.0 (8-10 Dec)	321.0
4277	7-Dec-08	cut /full	108.0	X	239.7 (8 Apr-4 Dec)	3.0 (4-7 Dec)	242.7
4278	5-Dec-08	cut /full	106.0	✓	247.6 (25 Mar-28 Nov)	7.0 (28 Nov-5 Dec)	254.6
4283	4-Dec-08	cut /full	85.0	✓	231.9 (15 Apr-3 Dec)	1.0 (3-4 Dec)	232.9
4287	8-Dec-08	cut /full	54.0	✓	218.6 (28 Apr-3 Dec)	5.0 (3-8 Dec)	223.6
4289	8-Dec-08	cut /full	52.0	X	220.6 (24 Apr-30 Nov)	8.0 (30 Nov-8 Dec)	228.6
4293	18-Dec-08	cut /full	33.0	✓	231.5 (10 Apr-28 Nov)	20.0 (28 Nov-18 Dec)	251.5
4305	5-Dec-08	cut /full	57.3	X	240.3 (6 Apr-2 Dec)	3.0 (2-5 Dec)	243.3
4353	5-Dec-08	cut /full	118.0	✓	230.6 (16 Apr-3 Dec)	2.0 (3-5 Dec)	232.6
Mean			**71.6±27.0**		**237.9±25.7**	**7.2±6.8**	**254.1±24.7**
4789	6-Dec-09	cut /full	69.0 (18.0)	✓	239.7 (8 Apr-4 Dec)	2.0 (4-6 Dec)	241.7
4797	7-Dec-09	cut /full	75.0 (18.0)	✓	257.3 (23 Mar-6 Dec)	1.0 (6-7 Dec)	258.3
4816	9-Dec-09	cut /full	54.0 (24.0)	X	261.1 (19 Mar-6 Dec)	3.0 (6-9 Dec)	264.1
4817	14-Dec-09	cut /full	63.0 (33.0)	✓	227.7 (28 Apr-11 Dec)	3.0 (11-14 Dec)	230.7
4819	4-Dec-09	cut /full	81.0 (17.0)	✓	236.0 (10 Apr-2 Dec)	2.0 (2-4 Dec)	238.0
4822	13-Dec-09	cut /full	81.0 (23.0)	✓	250 (6 Apr-12 Dec)	1.0 (12-13 Dec)	251.0
4826	13-Dec-09	cut /full	69.0 (23.0)	✓	234 (17 Apr-7 Dec)	6.0 (7-13 Dec)	240.0

Appendix B. (cont.)

Seal GLS/ tag no.	Tissue sampling date	Whiskers		Whole blood	GLS deployment (No. of days)		
		Sampling protocol	Total length (mm) (Re-growth)		At-sea	Ashore	Total
4832	4-Dec-09	cut /full	93.0 (35.0)	✓	226 (4 Apr-16 Nov)	18.0 (16 Nov-4 Dec)	244.0
4837	30-Dec-09	cut /full	99.0 (32.0)	✓	228 (20 Apr-4 Dec)	26.0 (4-30 Dec)	254.0
4842	8-Dec-09	cut /full	72.0 (31.0)	✓	238 (13 Apr-7 Dec)	1.0 (7-8 Dec)	239.0
4847	13-Dec-09	cut /full	78.0 (35.0)	✓	251 (4 Apr-11 Dec)	2.0 (11-13 Dec)	253.0
Mean			**75.8±12.8 (26.3±7.1)**		**240.8±12.3**	**6.2±8.7**	**246.7±10.1**
Marion Island, Prince Edward Islands, southern Indian Ocean							
4223	5-Dec-08	cut/re-growth	32.0	✓	228.9 (19 Apr-4 Dec)	1.0 (4-5 Dec)	229.9
4229	5-Dec-08	cut/re-growth	21.0	✓	229.5 (14 Apr-30 Nov)	5.0 (30 Nov-5 Dec)	234.5
4232	5-Dec-08	cut/re-growth	17.0	✓	238.6 (4 Apr-29 Nov)	6.0 (29 Nov-5 Dec)	244.6
4271	10-Dec-08	cut/re-growth	22.0	x	234.2 (20 Apr-10 Dec)	-	234.2
4272	23-Jun-08	cut /full	157.3	✓	60.9 (20 Apr-20 Jun)	3.0 (20-23 Jun)	63.9
4272	12-Sep-08	cut /full	65.2	✓	76.6 (25 Jun-10 Sep)	2.0 (10-12 Sep)	78.6
4272	5-Dec-08	cut/re-growth	14.5	✓	70.6 (20 Sep-30 Nov)	5.0 (30 Nov-5 Dec)	75.6
Total					208.1 (20 Apr-30 Nov)	-	218.1
4273	5-Dec-08	cut/re-growth	16.5	✓	233.7 (15 Apr-5 Dec)	-	233.7
4280	10-Dec-08	cut/re-growth	17.0	✓	241.6 (5 Apr-3 Dec)	7.0 (3-10 Dec)	248.6
4284	5-Dec-08	cut/re-growth	16.0	✓	234.6 (12 Apr-3 Dec)	2.0 (3-5 Dec)	236.6
4317	26-Nov-08	cut/re-growth	11.0	✓	214.3 (20 Apr-21 Nov)	5.0 (21-26 Nov)	219.3
4318	26-Nov-08	cut/re-growth	11.0	✓	231.4 (7 Apr-24 Nov)	2.0 (24-26 Nov)	233.4
4323	15-Jul-08	cut/re-growth	8.5	✓	96 (10 Apr-15 Jul)	-	96.0
4323	29-Sep-08	cut/re-growth	11.0	✓	75 (16 Jul-29 Sep)	-	75.0
4323	5-Dec-08	cut/re-growth	6.0	✓	66 (30 Sep-5 Dec)	-	66.0
Total					239 (10 Apr-5 Dec)	-	237.0

Appendix B. (cont.)

Seal GLS/ tag no.	Tissue sampling date	Whiskers		Whole blood	GLS deployment (No. of days)		
		Sampling protocol	Total length (mm) (Re-growth)		At-sea	Ashore	Total
4329	5-Dec-08	cut/re-growth	17.0	✓	241.9 (5 Apr-3 Dec)	2.0 (3-5 Dec)	243.9
4350	5-Dec-08	cut/re-growth	24.0	✓	231.2 (15 Apr-2 Dec)	3.0 (2-5 Dec)	234.2
4356	28-Nov-08	cut/re-growth	23.0	✓	227.8 (15 Apr-29 Nov)	-	226.8
Mean			**111.1±65.1 (18.6±5.9)**		**231.1±9.6**	**3.6±1.9**	**233.9±8.7**
4270	31-Dec-09	cut /full	90.0	✓	210.1 (17 Apr-29 Nov)	32.5 (29 Nov-31 Dec)	242.6
4782	27-Dec-09	-	-	✓	235.9 (20 Apr-12 Dec)	15 (12-27 Dec)	250.9
4804	26-Dec-09	cut/re-growth	45.0	✓	241.6 (15 Apr-13 Dec)	13 (13-26 Dec)	254.6
4821	22-May-09	-	-	✓	22 Mar-No return	-	-
4824	31-Dec-09	cut/re-growth	12.0	x	282.0 (24 Mar-31 Dec)	-	282.0
4827	15-Oct-09	-	-	✓	8 Jan-No return	-	-
4836	31-Dec-09	cut/re-growth	39.0	✓	234.1 (24 Apr-14 Dec)	17 (14-31 Dec)	251.1
4843	18-Jun-09	cut/re-growth	9.0	✓	15 Mar-No return	-	95.0
4846	31-Dec-09	cut/re-growth	24.0	✓	234.0 (23 Apr-13 Dec)	18 (13-31 Dec)	252.0
4890	22-Aug-09	cut/re-growth	21.0	✓	3 Apr-No return	-	141.0
2PP477	26-Dec-09	cut /full	60.0	✓	-	-	-
B001	5-Dec-09	cut /full	123.0	x	-	-	-
B002	5-Dec-09	cut /full	147.0	x	-	-	-
B003	5-Dec-09	cut /full	87.0	x	-	-	-
B005	4-Dec-09	cut /full	96.0	x	-	-	-
PP496	27-Dec-09	cut /full	21.0	x	-	-	-
Mean			**89.1±40.9 (28.2±13.52)**		**239.6±23.4**	**19.1±7.7**	**255.5±13.6**

GLS: geolocation logger

Appendix C. The $\delta^{13}C$ and $\delta^{15}N$ values of Southern Ocean marine organisms grouped according to five clusters identified by hierarchical cluster analysis in Fig. 4.2.

ID	Species name	N	Family	Taxa	Tissue	Location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
Prey group 1									
E.sup (DDU)	*Euphausia superba*	55	Euphausiidae	Crustacean	Whole	DDU	-27.47±1.07	2.89±0.81	This study
E.sup (SS)	*Euphausia superba*	10	Euphausiidae	Crustacean	Whole	SS	-26.50±0.40	3.20±0.40	Polito and Goebel (2010)
Prey group 2									
E.crys	*Euphausia crystallorophius*	30	Euphausiidae	Crustacean	Whole	DDU	-24.99±0.67	6.10±0.67	This study
E.frig	*Euphausia frigida*	4	Euphausiidae	Crustacean	Whole	WS	-24.30±0.90	4.90±0.30	Schmidt et al. (2004)
E.tria	*Euphausia triacantha*	10	Euphausiidae	Crustacean	Whole	DDU	-23.63±0.51	6.31±0.61	This study
Prey group 3									
C.acer	*Chaenocephalus aceratus*	4	Channichthyidae	Fish	Muscle	AP	-24.90±0.10	11.00±0.60	Dunton et al. (2001)
E.ant (SS)	*Electrona antarctica*	6	Myctophidae	Fish	Muscle	SS	-25.10±0.90	9.10±0.60	Polito and Goebel (2010)
P.ant	*Pleuragramma antarcticum*	76	Nototheniidae	Fish	Muscle	DDU	-25.30±0.20	10.10±0.40	Giraldo et al. (2011)
Psyc.	*Psychroteuthis glacialis*	3	Psychroteuthidae	Squid	Muscle	DDU	-25.90±0.20	10.00±0.50	This study
Prey group 4									
E.ant (KI)	*Electrona antarctica*	10	Myctophidae	Fish	Muscle	KI	-22.20±0.93	7.98±0.54	This study
E.carl (SS)	*Electrona carlsbergi*	6	Myctophidae	Fish	Muscle	SS	-22.60±0.50	7.60±0.30	Polito and Goebel (2010)
E.supa	*Electrona supaspera*	14	Myctophidae	Fish	Muscle	KI	-20.20±0.40	7.30±0.30	Cherel et al. (2010)
G.fra	*Gymnoscopelus fraseri*	7	Myctophidae	Fish	Muscle	KI	-22.48±1.10	7.96±0.51	This study
G.pia	*Gymnoscopelus piablis*	2	Myctophidae	Fish	Muscle	KI	-20.42±0.32	7.79±0.14	This study
Kreff.	*Krefftichthys anderssoni*	12	Myctophidae	Fish	Muscle	KI	-22.30±0.20	7.60±0.20	Cherel et al. (2000)
L.lars	*Lepidonotothen larseni*	5	Nototheniidae	Fish	Muscle	MAR	-22.10±0.40	7.20±0.80	Bushula et al. (2005)
P.chor	*Protomyctophum choriodon*	12	Myctophidae	Fish	Muscle	KI	-20.00±0.50	7.80±0.30	Cherel et al. (2010)
P.ten	*Protomyctophum tenisoni*	5	Myctophidae	Fish	Muscle	KI	-22.09±1.02	6.45±0.30	This study
Kond. (SG)	*Kondakovia longimana*	2	Onychoteuthidae	Squid	Muscle	SG	-23.30±0.83	7.51±1.08	Anderson et al. (2009)
Mart.	*Martialia hyadesi*	12	Ommastrephidae	Squid	Beaks corrected	MI	-20.80±1.36	7.83±2.15	Hughes (unpubl. data)

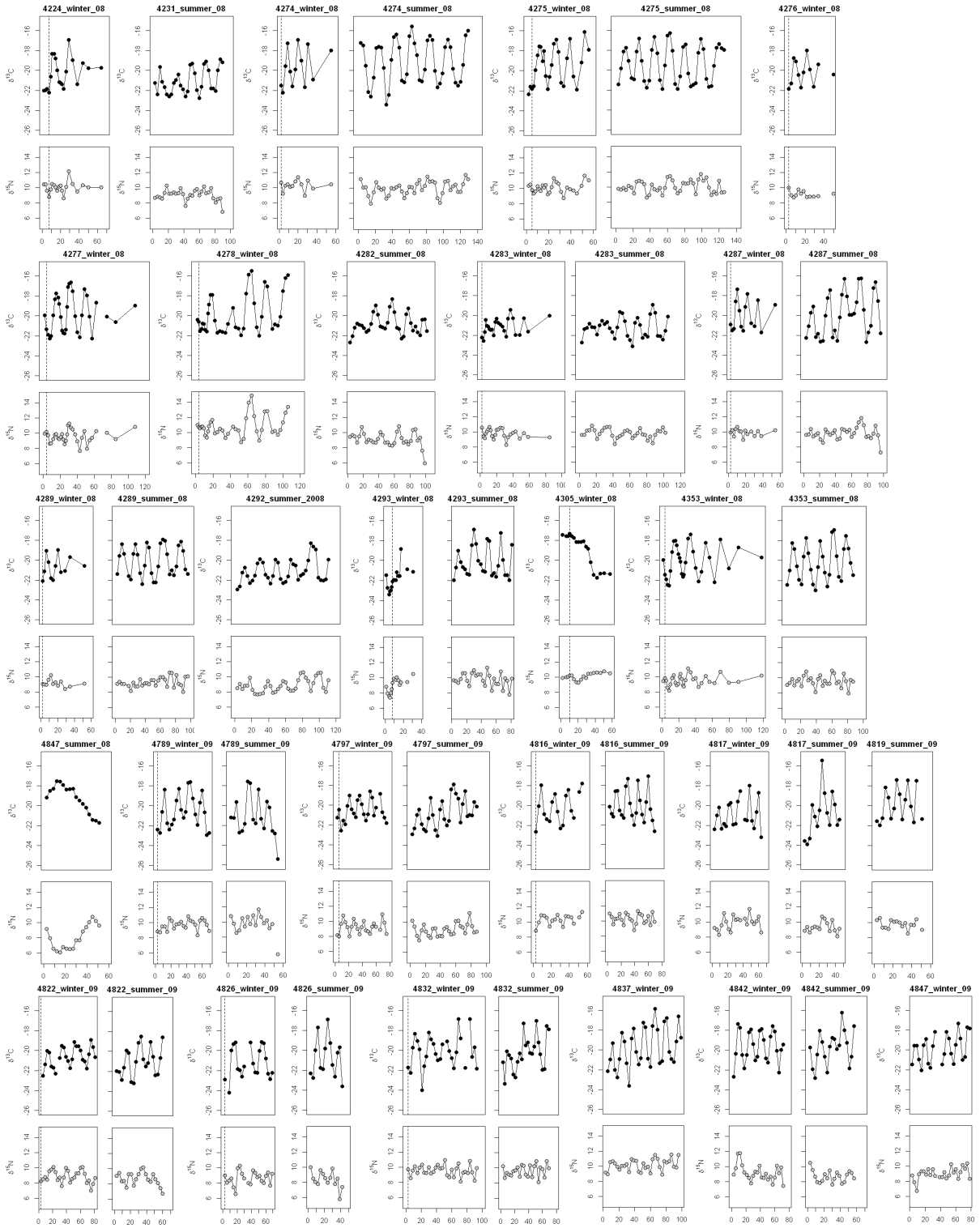
AP: Antarctic Peninsula; DDU: Dumont d'Durville Sea; KI: Kerguelen Islands; MAR: Marion Island; MI: Macquarie Island; SG: South Georgia; SS: South Shetland Islands; WS: Weddell Sea. Values are mean ± standard deviation (SD).

Appendix C. (cont.)

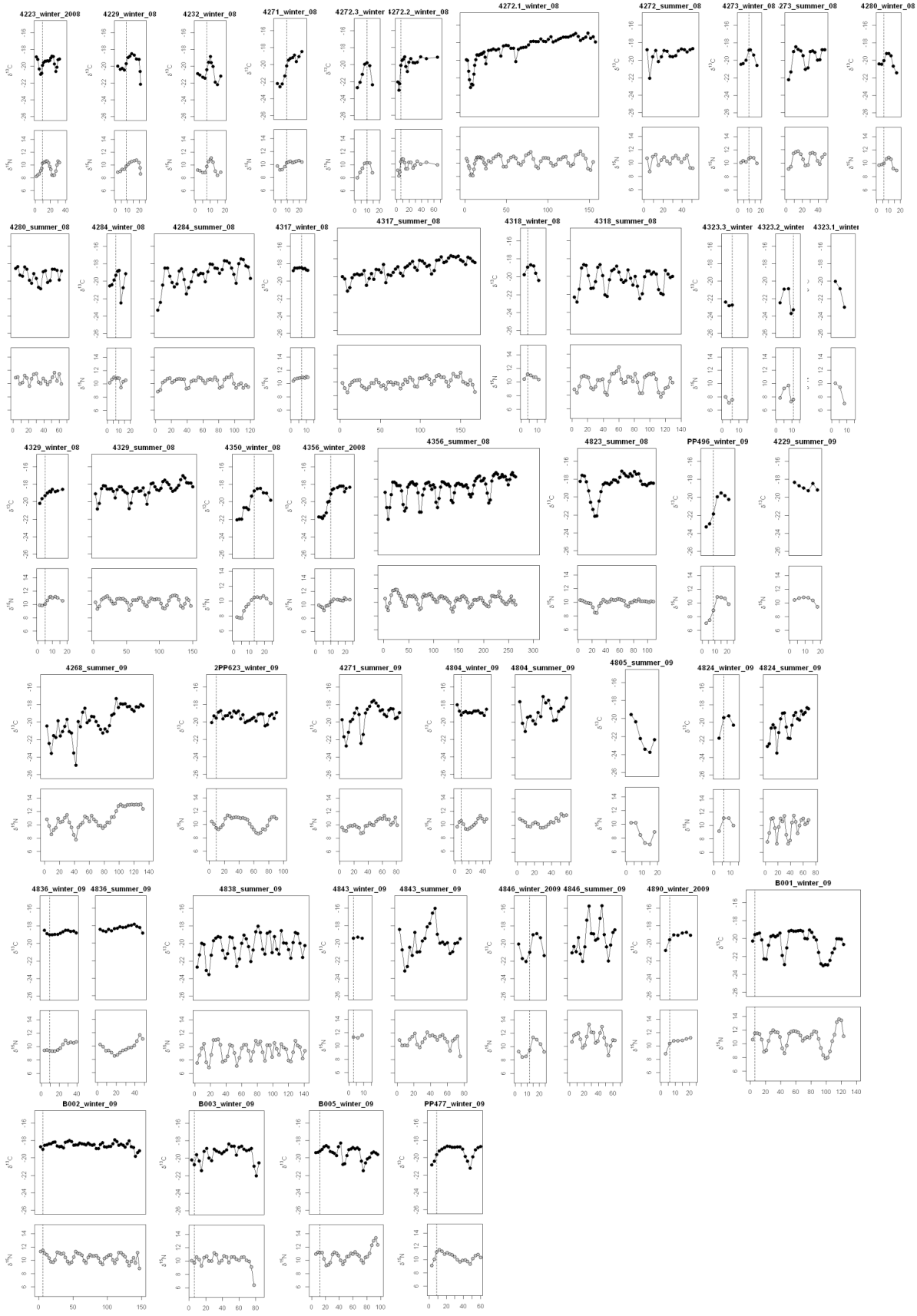
ID	Species name	N	Family	Taxa	Tissue	Location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
Prey group 5									
C.gun	*Champsocephalus gunnari*	16	Channichthyidae	Fish	Muscle	SG	-20.65±0.49	9.28±0.25	Anderson et al. (2009)
E.carl (KI)	*Electrona carlsbergi*	12	Myctophidae	Fish	Muscle	KI	-21.60±0.40	9.50±0.20	Cherel et al. (2008)
G.mar	*Gobionotothen marionensis*	5	Nototheniidae	Fish	Muscle	MAR	-20.60±0.60	8.50±0.60	Bushula et al. (2005)
G.bol	*Gymnoscopelus bolini*	12	Myctophidae	Fish	Muscle	KI	-20.50±0.40	9.90±0.50	Cherel et al. (2010)
G.bra	*Gymnoscopelus braueri*	12	Myctophidae	Fish	Muscle	KI	-22.30±0.70	9.80±0.30	Cherel et al. (2010)
G.nic	*Gymnoscopelus nicholsi*	10	Myctophidae	Fish	Muscle	KI	-22.66±0.48	9.72±0.71	This study
L.squa	*Lepidonotothen squamifrons*	5	Nototheniidae	Fish	Muscle	KI	-20.50±0.90	10.30±1.40	Cherel et al. (2008)
P.gun	*Patagonotothen guntheri*	8	Nototheniidae	Fish	Muscle	SG	-21.97±0.55	8.97±0.31	Anderson et al. (2009)
P.and	*Protomyctophum andriashevi*	7	Myctophidae	Fish	Muscle	KI	-20.90±0.30	8.70±0.40	Cherel et al. (2010)
P.bol	*Protomyctophum bolini*	12	Myctophidae	Fish	Muscle	KI	-22.40±0.60	9.20±0.40	Cherel et al. (2010)
G.gla	*Galiteuthis glacialis*	3	Cranchidae	Squid	Muscle	SG	-21.46±0.49	9.25±0.29	Anderson et al. (2009)
G.ant	*Gonatus antarcticus*	2	Gonatidae	Squid	Muscle	SG	-22.36±0.56	11.36±0.78	Anderson et al. (2009)
Hist.	*Histioteuthis eltaninae*	10	Histioteuthidae	Squid	Beaks corrected	KI	-20.70±0.40	10.40±0.70	Cherel and Hobson (2005)
Kond. (KI)	*Kondakovia longimana*	3	Onychoteuthidae	Squid	Beaks corrected	KI	-21.10±0.50	9.20±1.10	Cherel and Hobson (2005)
M.ing	*Moroteuthis ingens*	10	Onychoteuthidae	Squid	Mantle	KI	-20.10±0.40	10.00±0.40	Cherel et al. (2008)
M.knip	*Moroteuthis knipovitchi*	4	Onychoteuthidae	Squid	Muscle	KI	-21.84±0.61	10.79±0.48	Anderson et al. (2009)

Appendix D. Schematic plots of $\delta^{13}C$ and $\delta^{15}N$ values along the whiskers of female Antarctic fur seals during the summer and winter sampling periods in 2008 and 2009 at A) Cape Shirreff, Livingston Island, Western Antarctic Peninsula (WAP), southern Atlantic Ocean and B) Marion Island, Prince Edward Islands, southern Indian Ocean. Dashed lines indicate the portion of whisker (mm) grown during the winter (non-breeding) migration period in 2008 and 2009.

A)



B)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4272.3_winter
4272.2_winter_08
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4272_summer_08
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273_summer_08
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4284_summer_08
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4268_summer_09
2PP623_winter_09
4271_summer_09
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4836_summer_09
4838_summer_09
4843_winter_09
4843_summer_09
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4846_summer_09
4890_winter_2009
B001_winter_09
B002_winter_09
B003_winter_09
B005_winter_09
PP477_winter_09

Appendix E. Tissue $\delta^{13}C$ and $\delta^{15}N$ values of female Antarctic fur seals according to breeding site, bi-monthly period (March/April, May/June, July/August and October-December) and foraging location (Inter-Frontal Zones, IFZs; 2008 and 2009 data combined). Whisker isotopic values represent dietary information incorporated during the March/April and May/June periods. Whole blood isotopic values corrected for variation in fractionation between whole blood and whiskers in pinnipeds (Hobson et al. 1996) represent dietary information incorporated during the October-December period.

IFZ	Tissue	Cape Shirreff					Marion Island				
		N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Whisker length (mm)	Latitude (°S)	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Whisker length (mm)	Latitude (°S)
MARCH-APRIL											
S of SACCF-S	Whisker	-	-	-	-	-	-	-	-	-	-
ACC to PF-S	Whisker	11	-22.0±0.7	9.4±0.9	3.0±1.6	-65.1 (1.9)	-	-	-	-	-
PF	Whisker	4	-21.3±0.5	10.1±0.4	2.8±1.0	-63.5 (2.1)	10	-19.4±0.7	10.5±0.4	2.8±2.4	-52.6 (1.6)
PF to SAF	Whisker	-	-	-	-	-	2	-19.6±0.1	9.7±0.3	4.0±1.4	-49.6 (1.2)
SAF	Whisker	1	-17.3	10.3	2.0	-57.1 (1.2)	3	-19.3±0.3	10.0±0.6	2.5±0.9	-47.7 (0.8)
SAF-N to SAZ	Whisker	-	-	-	-	-	-	-	-	-	-
Overall		**16**	**-21.5±1.3**	**9.6±0.9**	**2.9±1.4**	**-64.6 (2.4)**	**15**	**-19.7±1.1**	**10.1±0.8**	**2.9±2.0**	**-51.2 (2.4)**
MAY-JUNE											
S of SACCF-S	Whisker	-	-	-	-	-	2	-21.7±0.5	9.6±0.2	8.0	-58.6 (1.4)
ACC to PF-S	Whisker	5	-22.4±0.4	9.1±0.9	3.5±1.5	-66.0 (2.3)	1	-21.7	9.3	11.0	-59.7 (0.9)
PF	Whisker	1	-21.9	10.2	5.5	-63.6 (2.0)	5	-20.7±0.6	9.7±0.7	6.3±0.5	-53.7 (1.6)
PF to SAF	Whisker	-	-	-	-	-	1	-18.6	10.7	5.5	-49.9 (0.4)
SAF	Whisker	2	-20.4±0.7	9.7±0.4	1.8±0.4	-59.7 (1.2)	4	-19.2±0.8	9.7±0.7	6.6±1.3	-47.4 (0.8)
SAF-N to SAZ	Whisker	2	-18.3±1.0	10.3±0.4	4.3±2.5	-53.1 (1.2)	-	-	-	-	-
Overall		**10**	**-21.1±1.8**	**9.6±0.8**	**3.5±1.7**	**-61.1 (5.7)**	**13**	**-20.4±1.2**	**9.7±0.6**	**7.0±1.5**	**-52.3 (4.5)**

Appendix E. (cont.)

IFZ	Tissue	Cape Shirreff					Marion Island				
		N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Whisker length (mm)	Latitude (°S)	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Whisker length (mm)	Latitude (°S)
JULY-AUGUST											
S of SACCF-S	Whisker	-	-	-	-	-	-	-	-	-	-
ACC to PF-S	Whisker	-	-	-	-	-	1	-22.0	7.8	5.0	-56.6 (0.9)
PF	Whisker	-	-	-	-	-	2	-21.0±0.2	9.1±0.4	8.0±2.8	-54.5 (1.6)
PF to SAF	Whisker	-	-	-	-	-	-	-	-	-	-
SAF	Whisker	-	-	-	-	-	-	-	-	-	-
SAF-N to SAZ	Whisker	-	-	-	-	-	-	-	-	-	-
Overall		**-**	-	-	-	-	**3**	**-21.7±0.8**	**8.4±0.9**	**6.8±2.2**	**-55.1 (1.7)**
OCTOBER-DECEMBER											
S of SACCF-S	Blood corrected	-	-	-	-	-	-	-	-	-	-
ACC to PF-S	Blood corrected	-	-	-	-	-	-	-	-	-	-
PF	Blood corrected	-	-	-	-	-	6	-21.4±1.0	11.8±0.8	-	-52.2 (1.2)
PF to SAF	Blood corrected	-	-	-	-	-	-			-	
SAF	Blood corrected	9	-20.2±1.0	11.4±0.7	-	-54.4 (4.7)	6	-20.7±0.8	11.7±0.5	-	-46.5 (1.4)
SAF-N to SAZ	Blood corrected	10	-19.6±0.8	11.0±1.1	-	-52.2 (1.6)	-	-	-	-	-
Overall		**19**	**-19.9±0.9**	**11.2±0.9**	-	**-53.3 (3.7)**	**12**	**-21.2±1.0**	**11.6±0.7**	-	**-48.9 (3.1)**

5. General discussion

This thesis aimed to provide new information on the diet and trophic relationships of high order Antarctic marine predators, and to describe diet in relation to habitat use. The study has provided insights into the trophic ecology of emperor penguins, southern elephant seals and Antarctic fur seals, through the stable isotope analysis of their tissues and prey. Previously undescribed winter diet and habitat use, spanning three ocean sectors, have now been identified for these species through the integration of stable isotope and animal tracking data.

The study has also demonstrated the utility of stable isotope analysis to provide dietary data that cannot be obtained any other way, as in the case of highly migratory species during the austral winter in the Southern Ocean. Additionally, it has shown how stable isotope analysis can be made even more powerful when linked with other sources of information, such as movement data. This discussion will provide an overview and synthesis of the main findings in the broader ecological context of trophic niches of predators within Southern Ocean marine ecosystems.

TROPHIC NICHES OF PREDATORS WITHIN SOUTHERN OCEAN MARINE ECOSYSTEMS

Biochemical tracers in ecosystems

Information on temporal variation in diet, either as a seasonal variation or as a long-term effect over many years, is required to assess the response of species to anthropogenic influences, such as climate change and commercial fisheries (e.g. Reid et al. 2005b; Forcada et al. 2006; Murphy et al. 2007). As in other marine ecosystems, the vast majority of dietary studies on Southern Ocean birds and marine mammals are limited to the breeding season. During this period, many predators, such as otariid, seabird and penguin species, are central-place foragers (Orians & Pearson 1979), undertaking foraging trips to local feeding areas but consistently returning to a central place, in response to the nutritional status of their mates or offspring (Ropert–Coudert et al. 2004). Between breeding periods however, most animals no longer behave as central-place foragers and often remain at sea, many thousands of kilometres from their breeding sites (*e.g.* sooty shearwaters, *Puffinus griseus*; Shaffer et al. 2006). Consequently, our ability to assess temporal patterns in resource use by these predators is impeded by the lack of information on their dietary preferences during the non-breeding period.

Acquiring data during the non-breeding period has become a priority within the Antarctic research community (Agnew 1997; Constable et al. 2000; Reid et al. 2005a). However, obtaining the required longitudinal dietary records by traditional observational techniques is difficult due to the long periods of time, high costs and logistical challenges of accessing remote, often ice-bound areas of the Southern Ocean by research vessels. Dietary proxies, such as stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), are therefore increasingly being used as an alternative way to address some of the more intractable problems associated with studying the trophic ecology of migratory marine predators (e.g. cetaceans, pinnipeds, seabirds, fish and turtles; Cherel et al. 2007; Phillips et al. 2009; Dempson et al. 2010; Bentaleb et al. 2011; Allen et al. 2013). As stable isotopes are naturally occurring biochemical tracers, already present and circulating in ecosystems, they are ideally suited for estimating the trophic position of and carbon flow to consumers in food webs (Peterson & Fry 1987; Post 2002). Isotopic variance of consumer tissues is increasingly being used by animal ecologists to infer characteristics of community structure and niche width of individuals (Bearhop et al. 2004; Newsome et al. 2009; Jackson et al. 2011). Depending on tissue-specific isotopic turnover, stable isotope tracers can provide a powerful tool to study changes in diet and habitat use of elusive or highly migratory animals, such as marine top predators.

For the stable isotope approach to provide a meaningful measure of niche width at the individual and/or population level, there are two important factors that need to be considered: (i) prey species/taxa must be isotopically distinct and (ii) the tissues analysed must reflect the period at which niche width is expressed (Bearhop et al. 2004). In this study, the isotopic composition of whiskers, which integrate diet over long temporal scales (that cover the period of trophic variation) were used to elucidate the trophic niche width of highly migratory seals that remain at sea for most of the austral (non-breeding) winter period. While whole blood, which integrates over shorter temporal scales, was used to assess niche width in discrete temporal windows for seals (*i.e.* prior to and during the summer breeding period) and penguins (*i.e.* during courtship, incubation and chick-rearing phases).

This study has two major findings. Firstly, that the trophic niche of predators changes seasonally and secondly, that euphausiids are important to all three species at various stages of the austral winter period. Prior to this study there was no information available on the diet

and feeding behaviour of adult female Antarctic fur seals during the winter period and little information available for sub-yearling southern elephant seals during their first foraging migration (Slip 1995). The diet of emperor penguins during the period between adult moult and the new breeding season is also largely undescribed (Pütz 1995). By measuring the isotopic variance of consumer tissues and that of their prey, and through the integration of isotope and tracking data of individuals, this study has provided important new insights into the non-breeding biology of key Southern Ocean predator species, which in the absence of longitudinal data on individuals would otherwise be impossible to acquire.

Linking diet and habitat use in migratory predators

Spatially explicit data on diet and foraging behaviour are central to understanding climatic and other environmental influences on marine predator populations, and also important requirements for conservation and management (Reid et al. 2005a; Trathan et al. 2007; Hofmann et al. 2008; Cotte´ et al. 2011). While considerable advances in the development of satellite tagging and archival loggers have revealed remarkable insights into the movement and foraging capabilities of a range of migratory species (e.g. turtles, sharks, pinnipeds and whales; James et al. 2005; Biuw et al. 2007; Andrews et al. 2008; Hammerschlag et al. 2011), they do not directly address feeding. The $\delta^{13}C$ composition of consumer tissues varies with sea surface temperature (Schell et al. 1989; Cherel & Hobson 2007; Graham et al. 2010). Subsequently, patterns of prey consumption can potentially be linked with regions where prey were actually consumed by matching the time-series of carbon and nitrogen isotopes in the tissues of predators to sea surface temperature records.

In this study, a unique combination of tracking data and stable isotope analysis of pinniped whiskers and blood was used to: (1) validate the relationship between isotope signatures and water mass in two highly migratory species; (2) identify the predominant non-breeding habitats of these species, and (3) determine the extent of individual variation in distribution and trophic level of these predators. In the Southern Ocean, the latitudinal gradient in $\delta^{13}C$ values of POM at the base of food chains within the Southern Ocean is reflected in organisms at higher trophic levels (Cherel & Hobson 2007; Jaeger & Cherel 2011). Continually growing whiskers, which contain a temporal signal, can potentially be related to individual telemetry tracks, establishing a means to link diet to remote feeding grounds.

The pathways and meso-scale variability of the ACC fronts are strongly influenced by large-scale bottom topography and are deflected where the flow interacts with topography (Sokolov & Rintoul 2009a). The ACC fronts also tend to converge near large bathymetric features (*e.g.* Crozet Plateau, downstream of the Kerguelen Plateau and near the Southeast Indian Ridge) and become more widely spaced over the abyssal plains (e.g. the Enderby, Australian-Antarctic, and Southeast Pacific Basins; Sokolov & Rintoul 2009a). As a result, their locations vary annually and even in the same year. Therefore, although isotopic baselines may well be stratified by latitude, the location and width of the strata are highly variable, both spatially and temporally. In addition, even at similar latitudes, $\delta^{13}C$ values in consumer tissue are very variable (Quillfeldt et al. 2005a). Thus, in order to account for latitudinal variability in water masses, SSH data were used in this study to map the mean location of ACC fronts across the Southern Ocean (Sokolov & Rintoul 2009a; Sokolov & Rintoul 2009b). This approach accounts for the spatial and temporal variability in the position of ACC fronts and therefore, addresses the geographic disparity in isotopic baselines in relation to water mass.

The patterns in $\delta^{13}C$ signatures observed in this study varied in a consistent way as the seals moved through different water masses. A number of other studies, which have integrated tracking and isotope data, have also validated the use of stable isotopes to depict the movements and foraging habitat of migratory marine animals at different spatial scales and in a diverse range of environments. These include critically endangered leatherback turtles (*Dermochelys coriacea*) across the northern Pacific Ocean (Seminoff et al. 2012), Mediterranean fin whales (*Meganyctiphanes norvegica*) in the northwestern Mediterranean Sea (Bentaleb et al. 2011), and Atlantic salmon (*Salmo salar*) in freshwater lake systems in Canada (Cunjak et al. 2005). In this study, $\delta^{13}C$ values provided a proxy for the broad-scale latitudinal shift in foraging habitat and diet from breeding to non-breeding foraging areas and reflected the regional variation in front location as validated by tracking data. The results indicate a temporal shift in diet of predators with foraging location (Fig. 5.1.). Consumption of krill occurred in ice-associated waters (S of SACCF-S, ACC to PF-S and PF; $\delta^{15}N$: < 9‰; Fig. 5.1.), with a shift to higher trophic level prey (mesopelagic fish and squid) in warmer sub-Antarctic waters (SAF, SAF-N to SAZ and SAZ to STZ-S; $\delta^{15}N$: > 10‰). The patterns in $\delta^{15}N$ signatures observed in this study with respect to water mass have considerable utility as a representative spatio-temporal map of nitrogen for top marine predators for the southern Atlantic, Indian and Pacific Oceans. To characterise the entire Antarctic food web in this manner, was well outside the scope of this study. Rather, this study had the more specific

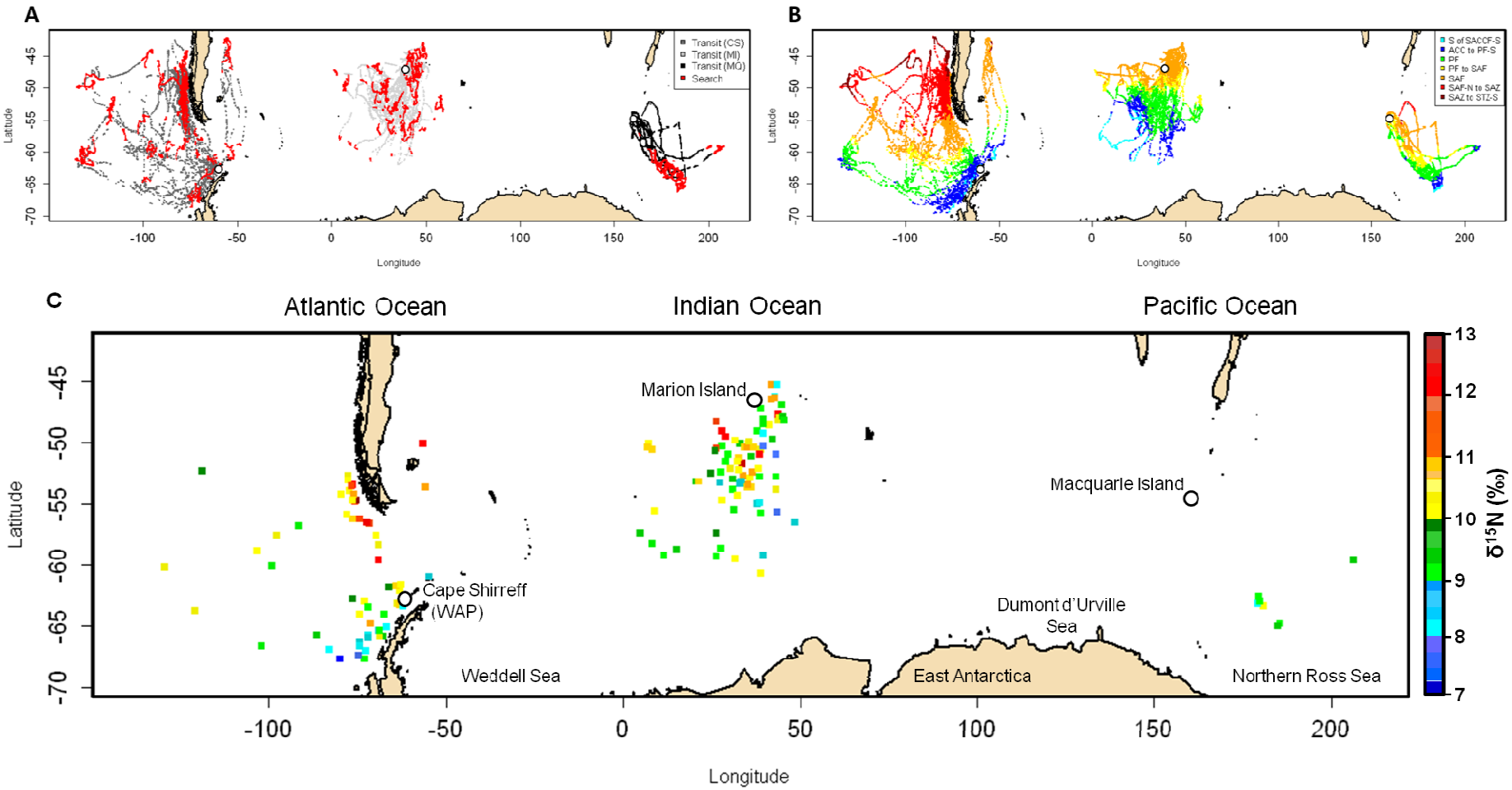

Fig. 5.1. Stable nitrogen isotope values of Antarctic fur seals and southern elephant seals according to at-sea location. Tracks are colour-coded according to (A) behavioural state estimates from the two-state first-difference correlated random walk switching (DCRWS) model overlaid in red (Area Restricted Search) and dark grey, grey and black (transit) for adult female Antarctic fur seals from Cape Shirreff, Western Antarctic Peninsula (WAP) and Marion Island, southern Indian Ocean, and sub-yearling southern elephant seals from Macquarie Island, southern Pacific Ocean. (C) Estimated growth rate of Antarctic fur seals whiskers (0.11 mm d^{-1}) were used to match the time series of stable nitrogen isotope values to corresponding seal locations. Mean stable nitrogen isotope values from the portion of whisker estimated to have been grown at sea are plotted for sub-yearling southern elephant seals. Isotopic values of southern elephant seals are mapped according to the greatest proportion of time spent in defined Inter-Frontal Zones shown in (B).

objective of focusing on three top predators and their prey. Hence, this study has formed the first step in creating a broader-based study, as other trophic components (*e.g*. crabeater seals, *Lobodon carcinophagus*, Weddell seals, *Leptonychotes weddellii*, and other penguin species) can be added subsequently.

Despite the lower spatial resolution afforded by $\delta^{13}C$ values in comparison to that provided by tracking data, *e.g.* lack of a difference in the $\delta^{13}C$ values of sub-yearling southern elephant seals feeding at similar latitudes, but utilising distinct water masses (PF and ACC to PF-S) in the Pacific Ocean sector of the Southern Ocean (Chapter 3) and in leatherback turtles foraging in the eastern and western regions of the northern Pacific Ocean (Seminoff et al. 2012), stable isotope tracers provide a cost-effective and non-invasive tool to identify spatial patterns in habitat and resource use across vast areas for migratory marine species. The results of this study highlight the use of isotopic tracers to determine spatial affinities for a large number of high trophic level predators and map regional differences in meso-scale features, such as the location of oceanographic frontal zones.

The role of sea ice, productivity and frontal zones in the distribution, feeding areas and diet of marine predators

The structure and diversity of food webs in different regions of the Southern Ocean vary substantially, driven largely by the annual advance-retreat cycle of sea-ice, seasonal primary production and distinct oceanographic frontal zones. These processes combine to concentrate the biomass of primary producers and consumers, which are then exploited by higher order predators (Tynan 1998; Nicol et al. 2000). This often translates to patchy resource distributions, with different regions of the Southern Ocean supporting different prey communities and densities (Pakhomov et al. 1994; Hunt & Hosie 2005; Knox 2007). Regions that are utilised by multiple predator species (Bost et al. 2009a; Friedlaender et al. 2011; Hindell et al. 2011; Ribic et al. 2011) are indicative of areas where physical forcing enhances primary and/or secondary productivity (Constable et al. 2003).

Our ability to trace seasonal differences in the trophic position, diet and foraging habitat of predators using stable isotope tracers relies on the fact that their diets consist of isotopically distinct components (Quillfeldt et al. 2005a). Isotopic variance in birds and marine mammal tissue (*e.g.* blood and whiskers, respectively) is determined by the relative proportion of isotopically distinct dietary component

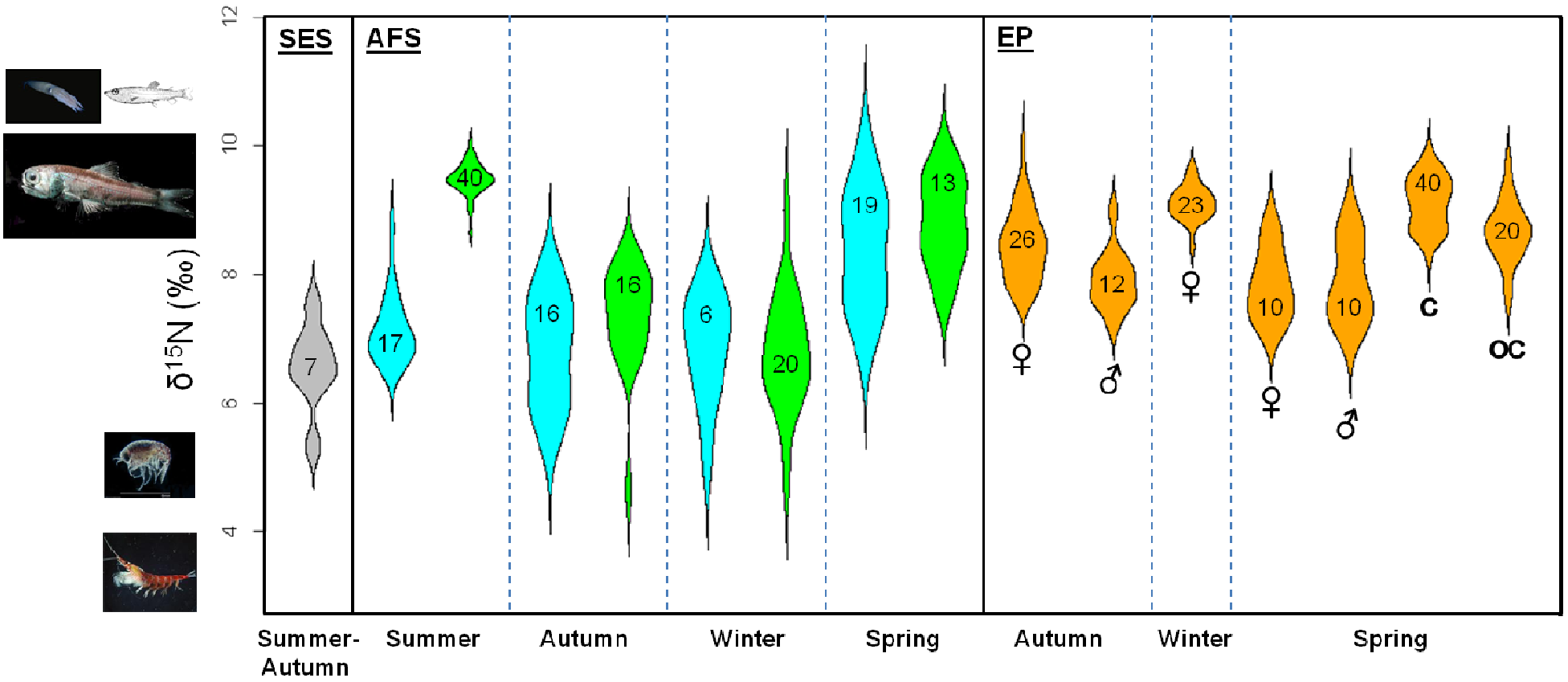

Fig. 5.2. Stable nitrogen isotope values of southern elephant seals, Antarctic fur seals and emperor penguins according to region, season, sex and age. Shapes represent the distribution densities of seals and penguins in each combination of season, sex and age and are colour-coded according to breeding site. Numbers inside shapes indicate the number of animals for each group (species, region, season, sex and age) membership. Grey: sub-yearling southern elephant seals from Macquarie Island, southern Pacific Ocean; Blue: adult female Antarctic fur seals from Cape Shirreff, Antarctic Peninsula, southern Atlantic Ocean; Green: adult female Antarctic fur seals from Marion Island, southern Indian Ocean; Orange: female (♀), male (♂), chick (C) and older chick (OC) emperor penguins from the Auster colony, Mawson Coast, Antarctica, southern Indian Ocean. Data are corrected for diet-tissue fractionation by subtracting 2.8‰ and 1.7% from whisker (SES: summer-autumn; AFS: autumn, winter) and blood (AFS: summer, spring) isotopic values of seals, respectively, and 2.7‰ from blood of penguins.

(Hobson 1992; Hobson et al. 1996; Quillfeldt et al. 2005a; Newsome et al. 2009). In this study, stable isotope results and Bayesian stable isotope mixing models (Stable Isotope Analysis in R, SIAR) identified intra-annual and regionally specific (water mass) differences in the trophic position (Fig. 5.2.) and diet of predators (Table 5.1.; Fig. 5.3.). Multi-source stable isotope mixing models could separate Antarctic krill from most other dietary sources based on their $\delta^{15}N$ values, but not from amphipods due to substantial overlap in $\delta^{15}N$ (and $\delta^{13}C$), and thus trophic levels (Chapter 3). Likewise, the models could not separate higher trophic level fish and squid occupying similar trophic levels (Fig. 5.3.). The latter results are in good agreement with previous studies which have demonstrated that isotopic mixing models (two-source or multi-source) have difficulty in estimating the dietary contribution of high trophic level prey (fish and squid) occupying similar trophic levels without refinement using stomach content analysis data (Tierney et al. 2008; Polito et al. 2011).

Despite the lack of taxonomic detail given by the stable isotope approach, the latitudinal gradient in $\delta^{13}C$ values of marine organisms (Quillfeldt et al. 2005a; Cherel et al. 2007) allowed characterisation of the seasonal change in prey consumption by predators. This ranged from the ice-associated feeding areas of Antarctic fur seals and southern elephant seals (located at or south of the PF) in summer, autumn and winter (Fig. 5.3.) to the warmer sub-Antarctic foraging zones of Antarctic fur seals (to the north of the SAF) in spring. The isotopic gradient from offshore or pelagic (oceanic) habitats to coastal/neritic and benthic food webs (Cherel et al. 2011) also allowed inferences to be made about the seasonal variation in foraging habitat and prey consumption of emperor penguins, feeding in more southerly waters associated with the Antarctic continental shelf (Fig. 5.3.).

Summer trophic niches

The accessibility of study species and their prey during summer (when most land-based predators breed) means that there is much information on the summer diet, foraging behaviour and habitat use of Antarctic marine predators. Comparison of the summer isotopic signatures of predators and their prey thus creates a basis for the interpretation of the isotopic signatures of predators in winter (Cherel et al. 2007).

The range of $\delta^{15}N$ values for adult female Antarctic fur seals in summer indicated a strong trophic segregation between the two sub-populations breeding in the Antarctic (Cape Shirreff, Western Antarctic Peninsula) and sub-Antarctic (Marion Island) regions of the southern

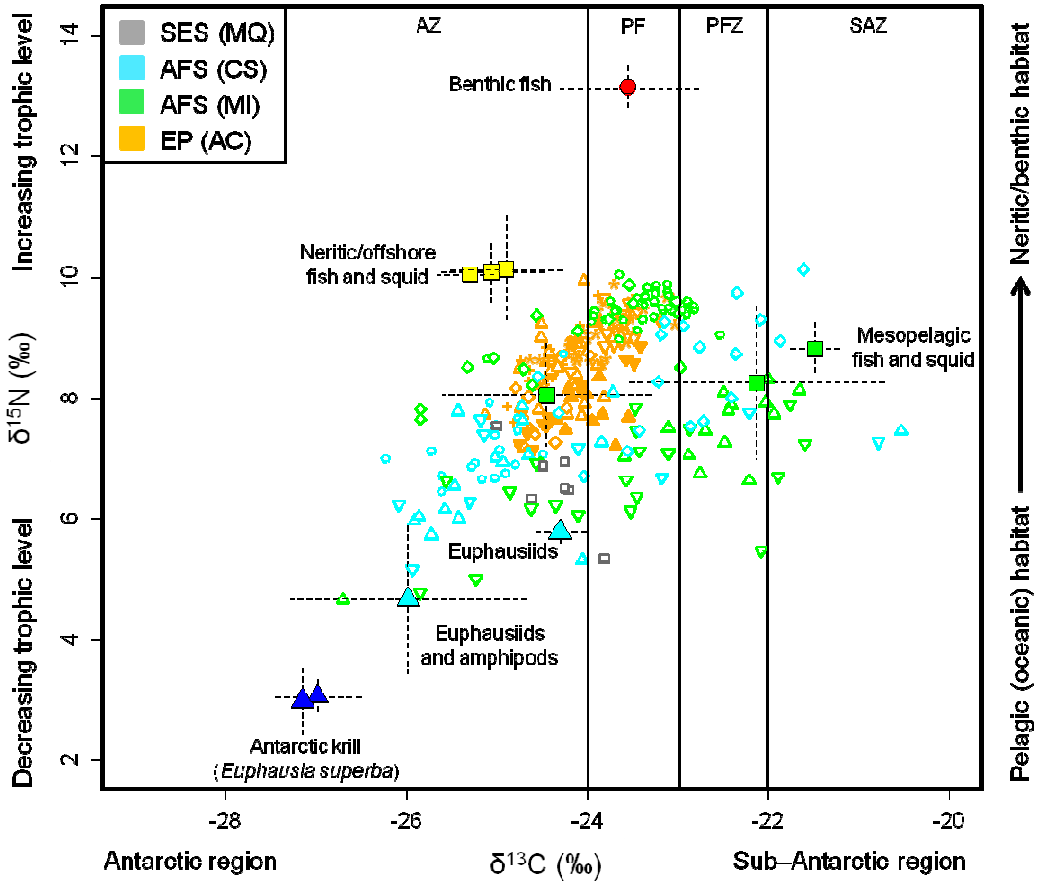

Figure 5.3. Stable isotope inputs to the multi-source mixing models for Southern Ocean marine predators. Data are derived from three predators from four regions of the Southern ocean, including: (1) sub-yearling southern elephant seals from Macquarie Island (SES, MQ) in the southern Pacific Ocean, (2) adult female Antarctic fur seals from Cape Shirreff (AFS, CS) in the Western Antarctic Peninsula, southern Atlantic Ocean and (3) Marion Island (AFS, MI) in the Prince Edward Islands, southern Indian Ocean, and (4) emperor penguins from the Auster colony (EP, AC) on the Mawson Coast, Antarctica, southern Indian Ocean. Prey items from each region have unique means (solid symbols) and standard deviations (dashed lines). For predators (SES: n=7; AFS, CS: n=40; AFS, MI: n=43; EP: n=141), symbols are used to depict group (species, region, season, sex and age) membership. SES (MQ) in summer-autumn: grey open squares; AFS (CS) in summer, autumn, winter and spring: light blue open circles, triangles, inverted triangles and diamonds, respectively; AFS (MI) in summer, autumn, winter and spring: green open circles, triangles, inverted triangles and diamonds, respectively; EP (AC): orange open and closed triangles for females and males in autumn, respectively; orange open inverted triangles for females in winter; orange open and closed diamonds for females and males in spring, respectively, and orange star and cross symbols for chicks and older chicks in spring, respectively. Data are corrected for diet-tissue fractionation as in Fig. 5.2. Horizontal solid lines indicate the isotopic location of the Polar Front (PF) and Sub-Antarctic Front (SAF) for AFS and SES whiskers. AZ: Antarctic Zone; PFZ: Polar Frontal Zone; SAZ: Sub-Antarctic Zone.

Table 5.1. Posterior estimates of diet proportions by region, season, sex and age for three Southern Ocean marine predator species. The modal estimates of each prey group are given along with 95% posterior intervals.

Predator species	Prey group					
	Antarctic krill (*Euphausia superba*)	Other Euphausiids	Euphausiids and Amphipods	Benthic fish	Neritic/offshore fish and squid	Mesopelagic fish and squid
Sub-yearling SES, MQ (n=7)						
Summer-autumn (whisker)	-	-	0.49 (0.35-0.61)	-	0.17 (0.01-0.33)	0.35 (0.18-0.52)
Adult female AFS, CS (n=40)						
Summer (blood, n=17)	0.32 (0.17-0.40)	0.05 (0.00-0.36)	-	-	0.40 (0.32-0.47)	0.04 (0.00-0.35)
Autumn (whisker, n=16)	0.28 (0.15-0.41)	0.24 (0.00-0.40)	-	-	0.25 (0.11-0.38)	0.14 (0.00-0.58)
Winter (whisker, n=9)	0.26 (0.10-0.39)	0.23 (0.00-0.40)	-	-	0.21 (0.01-0.33)	0.36 (0.00-0.71)
Spring (blood, n=19)	0.02 (0.00-0.11)	0.05 (0.00-0.23)	-	-	0.13 (0.01-0.26)	0.71 (0.29-1.00)
Adult female AFS, MI (n=43)						
Summer (blood, n=40)	0.01 (0.00-0.04)	0.01 (0.00-0.08)	-	-	0.46 (0.41-0.51)	0.49 (0.30-0.68)
Autumn (whisker, n=16)	0.11 (0.00-0.25)	0.23 (0.00-0.42)	-	-	0.04 (0.00-0.19)	0.55 (0.08-1.00)
Winter (whisker, n=20)	0.21 (0.06-0.36)	0.24 (0.00-0.46)	-	-	0.10 (0.00-0.22)	0.50 (0.03-0.82)
Spring (blood, n=13)	0.01 (0.00-0.11)	0.04 (0.00-0.25)	-	-	0.43 (0.28-0.60)	0.28 (0.05-0.79)
EP, AC (blood, n=141)						
Autumn (n=38)						
Females (n=26)	0.19 (0.08-0.27)	-	-	0.30 (0.11-0.46)	0.27 (0.01-0.41)	0.31 (0.19-0.44)
Males (n=12)	0.16 (0.04-0.29)	-	-	0.25 (0.02-0.36)	0.05 (0.00-0.35)	0.48 (0.25-0.70)
Winter (n=23)						
Females	0.11 (0.03-0.18)	-	-	0.41 (0.28-0.51)	0.05 (0.00-0.23)	0.40 (0.28-0.51)
Spring (n=80)						
Females (n=10)	0.25 (0.13-0.36)	-	-	0.25 (0.03-0.41)	0.24 (0.00-0.42)	0.30 (0.12-0.49)
Males (n=10)	0.20 (0.05-0.32)	-	-	0.26 (0.00-0.39)	0.18 (0.00-0.40)	0.42 (0.18-0.65)
Chicks (n=40)	0.07 (0.00-0.14)	-	-	0.39 (0.24-0.48)	0.09 (0.00-0.27)	0.44 (0.33-0.54)
Older chicks (n=20)	0.17 (0.09-0.27)	-	-	0.28 (0.14-0.46)	0.27 (0.07-0.47)	0.26 (0.12-0.38)

SES, MQ: Southern elephant seals, Macquarie Island, southern Pacific Ocean; AFS, CS and MI: Antarctic fur seals, Cape Shirreff, Western Antarctic Peninsula, southern Atlantic Ocean and Marion Island, Prince Edward Islands, southern Indian Ocean; EP, AC: Emperor penguins, Mawson Coast, Antarctica, southern Indian Ocean. All summary statistics are generated from Fig. 5.3

Atlantic and Indian Ocean sectors, respectively (Fig. 5.2.). Blood $\delta^{13}C$ and $\delta^{15}N$ values defined two foraging areas and two trophic levels, respectively, and thus two distinct non-overlapping trophic niches (Fig. 5.3.). Cape Shirreff and Marion Island seals forage in distinct zones (Antarctic and sub-Antarctic regions, respectively) due to the central-place foraging requirements of individuals over the summer breeding months, which limit the length of foraging trips and therefore distances travelled from respective breeding sites (Costa et al. 1989; Kirkman et al. 2003).

The prey species of Cape Shirreff and Marion Island seals show typical step-wise trophic enrichment of ^{15}N from Antarctic krill to fish and squid (Cherel et al. 2007; Polito & Goebel 2010; Figure 5.3.). Cape Shirreff seals, which typically consume prey over more than one trophic level (krill, fish and squid), show more isotopic variation than seals from Marion Island, which are known to feed on prey species drawn from a similar trophic level (mesopelagic fish and squid; Fig. 5.2. and 5.3.). Multi-source stable isotope mixing model estimates of the diet composition of Cape Shirreff (Antarctic krill and neritic/offshore fish and squid contributing 32% and 40% to the diets of seals, respectively) and Marion Island seals (fish and squid contributing 95% to the diets of seals; Table 5.1.) are therefore in good agreement with the summer dietary trends previously described for these two sub-populations (Klages & Bester 1998; Osman et al. 2004; Cherel et al. 2007; Polito & Goebel 2010).

Austral winter trophic niches

The $\delta^{15}N$ values of the three predator species included in the study varied in relation to region, season, sex and age (Fig. 5.2.). Adult female Antarctic fur seal $\delta^{15}N$ values exhibited a much larger range (4 to 11‰) than that of the other two species, spanning more than two trophic levels (Fig. 5.2.). The considerable variation in Antarctic fur seal whisker and blood $\delta^{13}C$ and $\delta^{15}N$ values reflected the diversity of oceanic habitats (from the high Antarctic waters to the southern extent of the Sub-Tropical Zone; Fig. 5.1.) and prey (from krill to mesopelagic fish and squid; Fig. 5.3.), respectively, utilised by individuals throughout the austral winter period. At that time, adult female Antarctic fur seals are no longer central-place foragers constrained by their land-based breeding activities in Antarctic (Cape Shirreff seals) and sub-Antarctic (Marion Island seals) regions of the Southern Ocean, and thus are dispersed over wide oceanic areas. This challenges the view that Antarctic fur seals are predominantly krill-eating predators, even in the southern Atlantic Ocean where they are known to feed on krill (South Georgia and in the South Shetland Islands; e.g. Doidge &

Croxall 1985; Reid 1995; Reid & Arnould 1996). Conversely, this highlights the importance of higher trophic level prey (fish and squid) to the diets of these predators in warmer, sub-Antarctic feeding areas where they spend a large proportion of their annual migration cycle.

In contrast to Antarctic fur seal values, the range of $\delta^{15}N$ (and $\delta^{13}C$) for sub-yearling southern elephant seals was narrow (5 to 8‰), and spanned one trophic level (Fig. 5.2.). Isotopic variation of southern elephant seal whiskers reflected the southward migration of seals to regions associated with the Northern Ross Sea (encompassing a narrow latitudinal band; ACC to PF-S and PF; Fig. 5.1.). Southern elephant seal $\delta^{15}N$ values clearly fall between those of Antarctic fur seals breeding at Cape Shirreff in summer, and Antarctic fur seals from both sub-populations in autumn and winter (Fig. 5.2.). Such overlap implies that trophic positions and food resources are commonly shared. This is corroborated by concurrent tracking data and multi-source stable isotope mixing model estimates, which show considerable overlap in broad-scale foraging areas (ACC frontal branches of the SACCF and PF) and diet (euphausiids, fish and squid) of seals in all three regions of the Southern Ocean in autumn and winter (Table 5.1.; Fig. 5.1.).

The range of $\delta^{15}N$ values for emperor penguins (6 to 10‰) indicated that they maintained a relatively high trophic level throughout the austral winter period compared to Antarctic fur seals (Fig. 5.2.). Emperor penguin $\delta^{15}N$ values fall between those of Antarctic fur seals breeding at Marion Island in summer, and Antarctic fur seals from both sub-populations in spring. Such overlap again implies that they share very similar trophic levels, and suggests a high proportion of fish and squid in the diet of emperor penguins (Fig. 5.3.). Stable isotope values for blood reflected the use of high Antarctic waters throughout the austral winter period by emperor penguins. Breeding emperor penguins are pagophilic in their distributions, being associated with sea-ice or its proximity during the incubation and chick-rearing phases (Wienecke & Robertson 1997).

Changes in sea-ice conditions, and the interaction of the ACC with complex or large bathymetric features appeared to have an important influence on the water masses used, and thus prey types consumed by predators in different regions of the Southern Ocean. Despite differences in reproductive requirements, physiological capabilities and breeding location (Antarctic versus sub-Antarctic), there was a tendency for all three species included in the study to prey on euphausiids (in addition to fish and squid) in ice-associated waters located

south of the PF in autumn (Table 5.1.). During winter however, when maximum sea-ice extent occurs, the trophic position and diet of open water (Antarctic fur seals) and pagophilic (emperor penguins) species diverged, with the latter consuming greater proportions of higher trophic level prey (fish and squid) over Antarctic continental shelf (neritic) waters (fish and squid contributed 57, 60 and 86% to the diet of Cape Shirreff Antarctic fur seals, Marion Island Antarctic fur seals and emperor penguins, respectively, in winter; Table 5.1.).

Conversely, the importance of krill to the diet of Antarctic fur seals from Marion Island increased from summer to winter (contributing 0, 11 and 21% in summer, autumn and winter, respectively; Table 5.1.), consistent with the southward migration of seals from sub-Antarctic foraging areas in summer (where Antarctic krill does not occur) to ice-associated Antarctic feeding areas in winter (Fig. 5.1.). While the consumption of krill by Antarctic fur seals from Cape Shirreff decreased from summer to winter (contributing 32, 28 and 26% in summer, autumn and winter, respectively; Table 5.1.), consistent with the northward movement of seals from the Western Antarctic Peninsula region in summer to deeper oceanic waters in winter.

During the austral winter, reduced rates of primary production, increased ice cover and altered hydrographic regimes can influence local prey availability and abundance (Burns et al. 2004). In order to survive through the winter, predators have various strategies to find and exploit the best resources within these constraints. Strategies include migration to separate non-breeding areas to feed, a wider than normal range of foraging strategies, and breeding phases that are adapted to seasonal fluctuations in prey availability for their young (Battaglia et al. 1997). The high latitude position of the Auster colony on the Mawson Coast, Antarctica means that primary production is highly seasonal, driven by the formation and decay of the seasonal sea-ice zone and the annual light/dark cycle (Arrigo et al. 2008; Massom & Stammerjohn 2010). These factors influence local prey availability and abundance, and thus the range and distribution of emperor penguins.

Krill consumption

Antarctic krill is the primary food source for many top predator species in the Southern Ocean (marine mammals, birds and fish), particularly during the austral summer (when most land-based predators breed) and in the Antarctic and sub-Antarctic (South Georgia) regions of the southern Atlantic Ocean (Croxall et al. 1999). The species has been the subject of an

active krill fishery since the late 1960s. The potential for over harvesting of this key marine resource is a concern of CCAMLR (Agnew 1997), particularly in light of climate change effects and increased interest by several nations in krill harvesting in the Southern Ocean. The commission is responsible for managing fisheries in the Antarctic region and it attempts to do so using an ecosystem-based management framework, by maintaining the ecological relationships between harvested, dependent and competing populations (Agnew 1997; Constable et al. 2000; Parkes 2000). The commission is in the process of formulating a new management system for the krill fishery to spatially subdivide the krill catch so that it does not adversely affect marine predators which feed on krill (Australia 2001). The finding that euphausiids are more important in the diet of Antarctic fur seals, southern elephant seals and emperor penguins than previously thought has important implications for the management of krill stocks and for the species that feed on them.

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