



## SYMPOSIUM

# Approaches to Studying Climatic Change and its Role on the Habitat Selection of Antarctic Pinnipeds

Daniel P. Costa,<sup>1,\*</sup> Luis A. Huckstadt,<sup>\*</sup> Daniel E. Crocker,<sup>†</sup> Birgitte I. McDonald,<sup>\*</sup> Michael E. Goebel<sup>‡</sup> and Michael A. Fedak<sup>§</sup>

<sup>\*</sup>Long Marine Laboratory, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, USA; <sup>†</sup>Department of Biology, Sonoma State University, 1801 East Cotati Avenue, Rohnert Park, CA 94928, USA; <sup>‡</sup>Antarctic Marine Living Resources Program, Southwest Fisheries Science Center, NOAA-NMFS 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA; <sup>§</sup>Sea Mammal Research Unit, University of St. Andrews, Fife KY16 8LB, Scotland

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<sup>1</sup>E-mail: costa@biology.ucsc.edu

**Synopsis** Top predators integrate resources over time and space, and depending on the particular species they represent, different components of the marine environment. The habitat utilization of top predators has been studied using electronic tags to follow their movements and foraging behavior. In addition, these tags provide information on the physical characteristics of the water column (temperature and salinity) at a scale and resolution that is coincident with the animals' behavior. In addition to data on the animals' behavior, these tags provide physical oceanographic data in regions or at times they cannot be collected using other currently available technologies. These data inform us on how these important top predators are likely to respond to climatic change, as well as about how the Southern Ocean is changing.

## Introduction

Marine mammals have evolved diverse life-history patterns that accommodate the extreme fluctuations in the physical and biological environment of the Southern Ocean (Costa and Crocker 1996). Because they are long-lived animals, they must be able to withstand variations in food resources that may occur over large spatial and temporal scales (Costa 1993; Forcada et al. 2008). A basic understanding of the foraging behavior and habitat utilization of pelagic predators requires knowledge of this spatial and temporal variation, coupled with information on how organisms respond to these changes. Our initial understanding of these associations came primarily from studies in which animals' locations were correlated with remotely sensed oceanographic features or, less frequently, with shipboard measurements of physical and biological properties (Ribic et al. 1991; Veit et al. 1993; Bester et al. 1995; Chapman et al. 2004; Tynan et al. 2005; Ribic et al. 2008). Over the

past two decades, advances in satellite telemetry, electronic tags, and methods of remote sensing have significantly increased our ability to examine these linkages across scales of time and space not previously possible (Guinet et al. 1997; Croll et al. 1998, 2005; Lea and Dubroca 2003b; Bailleul et al. 2007; Biuw et al. 2007; Simmons et al. 2007, 2010). Together, these approaches indicate that apex predators forage in areas where oceanographic features such as currents, frontal systems, thermal layers, sea mounts, and the edge of the continental shelf increase the availability of prey (Haney 1986; Hunt et al. 1990; Tynan 1998, 2004; Lea and Dubroca 2003a; Tynan et al. 2005; Simmons et al. 2007, 2010; Bost et al. 2009). Within the Antarctic, additional features, including icebergs, polynyas, eddies, and characteristics of the marginal ice zone, enhance local productivity and influence predators' distributions (Ainley and Jacobs 1981; Ainley et al. 1998; Tynan 1998; Bost et al. 2009). All of these

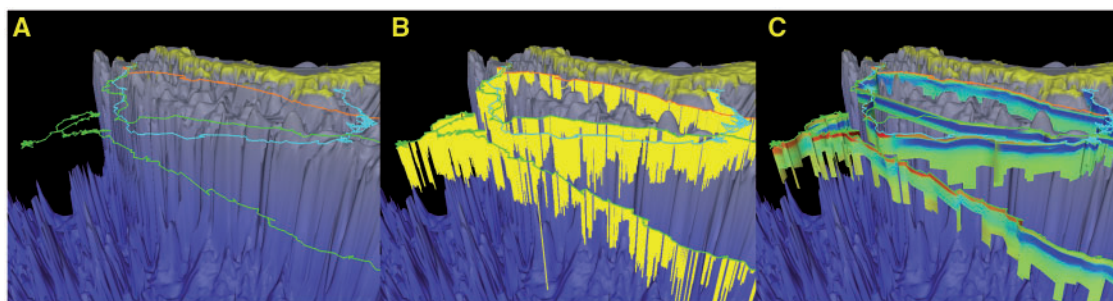
oceanographic features and processes are thought to impact the distributions of marine predators by physically forcing prey to aggregate and, thus, create areas where foraging efficiency can be increased (Ainley and Jacobs 1981; Ribic et al. 1991, 2008; Trathan et al. 1996; Ainley et al. 1998; Chapman et al. 2004; Bost et al. 2009). Indeed, for many marine predators, regions of highly localized productivity may be essential for reproduction and survival (Costa et al. 1989; Fraser et al. 1989; Costa 1991, 1993, 2008; Hunt et al. 1992; Croll et al. 1998, 2005; Lea et al. 2006b). The biophysical coupling associated with these processes is driven by climate (Hofmann et al. 2004, 2008). Therefore, an assessment of the potential impact of climatic change on apex predators requires both an identification of the oceanographic features and the processes on which these predators rely, coupled with knowledge of how these oceanographic processes are likely to change (Barbraud and Weimerskirch 2001a, 2001b, 2006; Weimerskirch et al. 2003; Crocker et al. 2006; Jenouvrier et al. 2006, 2009; Lea et al. 2006a; Barbraud et al. 2008; Simmons et al. 2010).

Advances in electronic tags have made it possible not only to collect data on animals' movements and behavior remotely, but also to obtain information on the physical environment (temperature and/or salinity, chlorophyll profiles) surrounding them (Fig. 1). Marine animals can thus be used as highly cost-effective platforms from which to collect detailed oceanographic data on a scale not possible with conventional methods (Boehlert et al. 2001; Lydersen et al. 2002; Boehme et al. 2008a, 2008b; Charrassin et al. 2008; Costa et al. 2008; Nicholls et al. 2008). These tag-borne oceanographic sensors offer a significant advantage over remotely sensed data in that they acquire oceanographic-quality data at a scale and resolution that matches the animals' behavior (Fig. 1).

## Animals as oceanographers

In addition to increasing our ability to study the movement and foraging behavior of animals that were not otherwise possible, these new electronic tags are providing oceanographic data in areas where traditional shipboard and Argo-float coverage is limited or absent. These data are particularly lacking in the Southern Ocean because ship time is limited there (especially in the winter), the capability of satellite remote-sensing systems is often reduced due to cloud cover, and Argo floats are unable to work in ice and have a propensity to be advected away from the Antarctic Continent. This lack of data has limited our understanding of key features of the Southern Ocean such as the formation of sea ice and of Antarctic Bottom Water, variability in the Antarctic Circumpolar Current (ACC) and associated ocean fronts, and properties of the ocean-mixed layer (Stocker 2001).

The absence of traditional sources for oceanographic data, in combination with a large abundance of marine mammals that are relatively easy to handle, and that cover large areas of the ocean during all seasons of the year, make the Southern Ocean an ideal location to use animals as autonomous ocean profilers. The first commercially available CTD tag that could be deployed on animals was developed by the Sea Mammal Research Unit (SMRU) in 2004 (<http://www.smru.st-andrews.ac.uk/Instrumentation/>). Data on an animal's behavior and environment are collected by the tag, summarized, and transmitted via the ARGOS satellite system in near real time when the animal is at the surface. This tag collects information on depths of dives, speed of swimming, and ocean temperature and conductivity and has enabled studies of animal behavior in relation to characteristics of the water mass (Biuw et al. 2007) and answered oceanographic questions (Boehme et al. 2008a, 2008b; Charrassin et al. 2008;



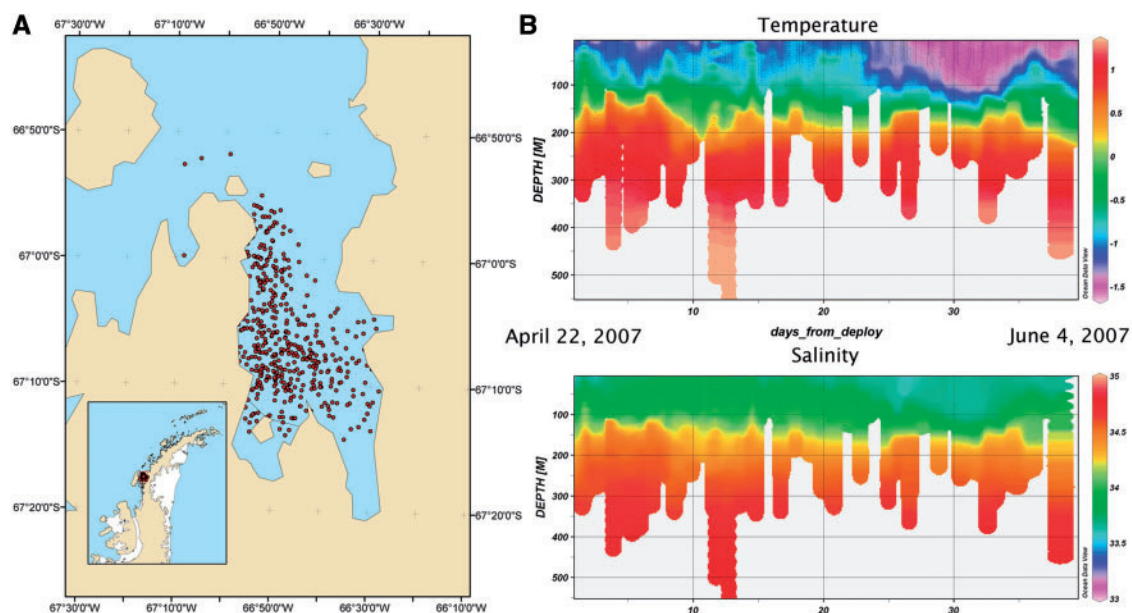
**Fig. 1** Track of southern elephant seals in the Western Antarctic Peninsula obtained using the SMRU CTD-SRDL 9000. (A) Shows just the surface track, (B) shows the surface track along with dives, and (C) shows the temperature and salinity sections that can be obtained to provide data on the physical environment through which the animals are moving.

Meredith et al. 2008; Nicholls et al. 2008). The data are transmitted via the ARGOS satellite system using algorithms where time depth profiles are summarized by four inflection points where the trajectory changes most rapidly (i.e., local maxima of the second derivative of the time-depth function) (Fedak et al. 2002). An example of the kind of temperature/salinity data provided by these tags can be seen in Fig. 2. The temperature/salinity profiles were collected by a Weddell seal in Lallemand Fjord, located on the Western Antarctic Peninsula (WAP) and documents the presence of modified Circumpolar Deep Water (CDW), along with the fall transition from Antarctic Surface Water (AASW) to Winter Water (WW) (22 April to 4 June, 2007). An earlier version of this tag, deployed on crabeater seals during 2002, was used to describe changes in temperature structure, heat content, and heat flux in the upper oceanic waters of the WAP continental shelf (Costa et al. 2008). These seal-derived data documented the fall-to-winter transition of the upper water column and the shelf-wide presence of modified CDW below 150–200 m on the WAP continental shelf (Costa et al. 2008). The seal-derived measurements of ocean temperature provided a broader spatial and temporal resolution than was possible using any other method.

More recently, elephant seals were used to understand better the hydrography in the vicinity of the Wilkins Ice Shelf (WIS), which experienced several large break-ups in 2008. The maximum depths

recorded for the seals led to the discovery of several deep troughs that extend from the outer to the inner continental shelf near the WIS (T. Bolmer et al., manuscript in preparation). These troughs provide conduits for the across-shelf movement of warm ( $>1^{\circ}\text{C}$ ) Upper Circumpolar Deep Water (UCDW), and for transport of water at all depths across the front of the ice-shelf. These data suggest that the thinning of the WIS during the two decades prior to the 2008 break-up events may be explained by a reduction in the distribution of sea-ice in summer leading to increased solar heating of the upper ocean (Padman et al., manuscript in review). Similarly, temperature and salinity data recovered from an instrumented Weddell seal foraging on the continental shelf of the central southern Weddell Sea documented the poorly known circulation of this region and documented “supercooled” (below  $-2^{\circ}\text{C}$ ) water flowing out from under the shelf (Nicholls et al. 2008). The seal-derived vertical sections of temperature and salinity showed a full depth flow of Modified Warm Deep Water onto the shelf via a sill at the edge of the continental shelf that accounted for most of the water draining from the continental shelf of the Southern Weddell Sea. Such data on the sea-ice in wintertime could not have been collected with any other currently available technology.

Probably the best example of how this work can address oceanographic questions, as well as providing insight into animal behavior, can be seen in the



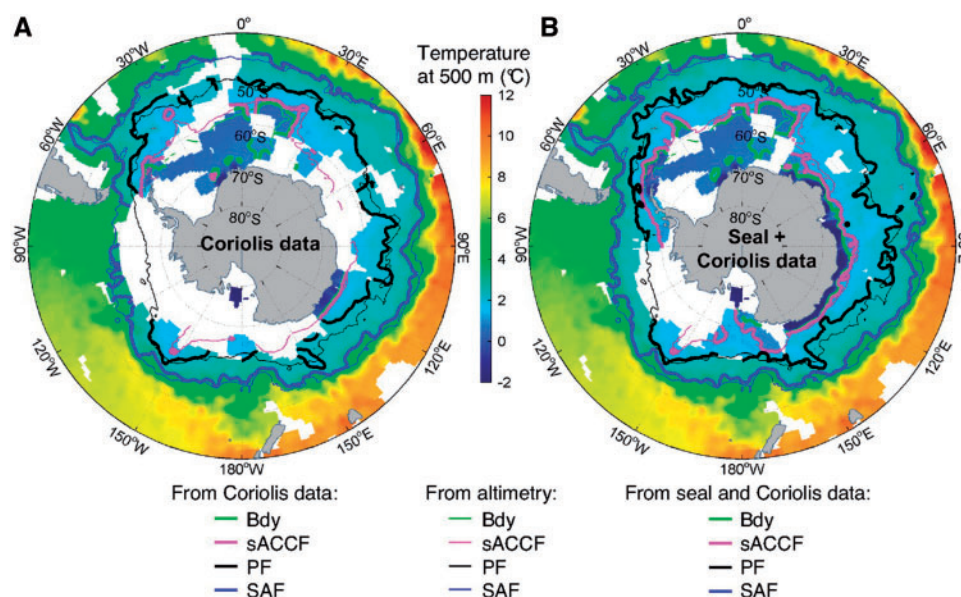
**Fig. 2** (A) Location of Weddell seal when CTDs were taken in the Lallemand Fjord, WAP. (B) smoothed temperature and temperature sections obtained from a single Weddell seal from 22 April to 4 June, 2007. The small inset at lower left shows the location of the Lallemand Fjord just to the east of the northern tip of Adelaide Island.



results of a large-scale international effort called Southern Elephant Seals as Oceanographic Sensors (SEaOS). This program deployed the SMRU CTD tags on 85 elephant seals simultaneously at Kerguelen, South Georgia, Macquarie Island, and the South Shetlands between January 2004 and April 2006 (Biuw et al. 2007). The temperature and salinity profiles collected south of 60°S as part of this effort increased 9-fold the number of profiles collected by traditional methods (Charrassin et al. 2008). The seal-collected data were especially useful at filling gaps in knowledge about regions in the Southern Indian Ocean, along the Antarctic Peninsula and north of the Ross Sea (Fig. 3). These data were used in concert with data collected by traditional methods to extend the maps of the southernmost fronts deep into ice-covered areas. Combined with conventional data, the seals' data offered a quasi synoptic, circumpolar view of high-latitude fronts within the Southern Ocean, therefore increasing our knowledge of this otherwise poorly sampled region (Charrassin et al. 2008). These data also provided information on rates of ice formation in generic pack ice (80% concentration of sea ice) where data are not available due to high cost or to limitations of current technologies.

SEaOS data were also used in more regional analysis where hydrographic data provided by elephant seals migrating to and from South Georgia and the South Shetland Islands were used to examine

variability of the upper ocean in the Scotia Sea. The large-scale features of the ACC in the Atlantic part of the Southern Ocean were examined by merging Argos data and data obtained by animal-borne CTD sensors (Boehme et al. 2008a). These merged data fields provided a level of resolution not possible using either data set alone and revealed some novel structures previously not observed. All frontal positions in the years 2004 and 2005 were more variable than previously observed across the Scotia Sea and west of the Mid-Atlantic Ridge on seasonal time scales. These merged data also provided higher resolution of the temporal variability of frontal structure around South Georgia Island than had ever before been available. In addition, they found that the position of the Southern ACC Front (SACCF) was further north than previously thought and the SubAntarctic Front crossed the Mid-Atlantic Ridge 400 km further north than expected. A time series of winter temperatures and salinities were obtained from an elephant seal that foraged for several months close to Signy Island (60°43' S, 45°36' W), located at the northern limit of the seasonal extension of sea-ice (Meredith et al. 2008). The seal-tag data were used to examine the evolution of salinity in the upper layer at this locality, and indicated that it reflects production rates of sea ice occurring at higher latitude in the Weddell Sea, rather than local freezing. Finally, in the Southern Indian Ocean sensors deployed on elephant seals migrating



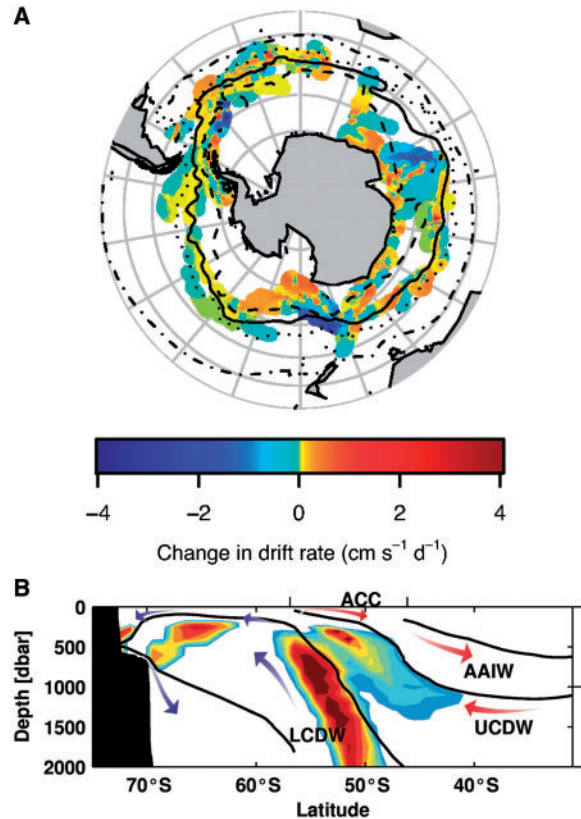
**Fig. 3** Temperature field at 500 m during 2004–2005 from the Coriolis database and from the merged Coriolis and elephant seal databases. Mean front positions during the same period derived from Coriolis (A) or Coriolis and seal temperature field at 500 m (B) (thick lines), and from altimetry (thin lines in A and B). Plotted fronts are Bdy, southern branch of sACCF, and central branches of PF and SAF. Note the increased level of detail in the combined plots. Figure from Charrassin et al. (2008).

from Kerguelen Island provided new information on the ACC transport as part of it is deflected south of Kerguelen Island (Roquet et al. 2009). These data detailed the presence of a strong northeastwardly current flowing across the Fawn Trough (sill depth: 2600 m; 56°S, 78°E). This current transports cold Antarctic waters found mostly south of the Elan Bank, between the Ice Limit (58°S) and the Antarctic Divergence (64°S) in the eastern Enderby Basin, toward the Australian–Antarctic Basin. The Fawn Trough acts a bottleneck channelling the Antarctic Circumpolar flow found south of the Polar Front.

All of these oceanographic data could not have been acquired easily or cost effectively using traditional techniques and yet they are critical for understanding the water transport and heat flux of the ocean and the changes in the strength and location of currents. Many, if not all, of these oceanographic processes are critical for creating habitats for marine organisms and are all likely to change with a changing climate. Thus, the tags deployed on animals can inform us on how the physical and biological oceanography of the Southern Ocean is changing as the earth's climate changes.

### Habitat utilization

An equally important component of the effort of the SEaOS was the ability to examine the foraging behavior of elephant seals throughout much of the Southern Ocean and to define their foraging habitat in terms of physical oceanographic characteristics (Biuw et al. 2007). The instruments were deployed at the end of the annual molt in January and February, allowing us to observe the foraging behavior over the longest foraging trip prior to the autumn breeding season. The elephant seals explored three main habitats: the open ocean in the Polar Frontal Zone (most seals from South Georgia and South Shetland, and some seals from Kerguelen and Macquarie Island); the marginal sea ice zone (most animals from Macquarie Island); and the peri-Antarctic Continent (seals from Kerguelen and Macquarie, diving benthically). Using changes in drift rate measured during dives as a proxy of body condition (fatter seals tend to be more buoyant while leaner seals tend to sink), and CTD profiles obtained from the seals, the most favorable water masses in terms of foraging were identified (Fig. 4). CDW upwelling areas within the ACC, and High-Salinity Shelf Waters or temperature/salinity gradients under the winter pack ice in the Indian and Pacific Ocean Sectors appeared to be the most



**Fig. 4** (A) Circumpolar map of physiological changes during winter migrations of elephant seals. Daily change in drift rate was calculated for 36 individuals during their winter migrations in 2004 and 2005. Blue shading represents a decrease in vertical change in depth during passive drifts, indicating reduced relative lipid content, whereas green–red shading indicates a change to increased vertical depth and increasing relative lipid content. (B) Generalized section of the SO, highlighting areas where southern elephant seals are predicted to alter their relative stores of body fat. The derived potential density values were matched to highlight the main water-mass boundaries between AAIW, UCDW, and Lower Circumpolar Deep Water (LCDW). Colored contours represent the accumulated number of matches between temperature, salinity, and derived values of density obtained from seals, and corresponding values in the schematic hydrographic section. Note the preference for upwelling regions of Circumpolar Deep Water and regions of transformation of water masses adjacent to the Antarctic continent, and the avoidance of regions of AAIW subduction. Figure from Biuw et al. (2007).

profitable for the elephant seals (Fig. 4). South Georgian seals favored relatively close feeding grounds in the Southern Ocean frontal systems, whereas seals from Kerguelen and Macquarie preferred more distant locations close to the Antarctic continental shelf. The stronger dependence on sea ice of the latter group, combined with climatological changes in extent of the ice (that declined in the 1970s), could explain the contrasting trends in

abundance observed in these populations (Boyd et al. 1996; McMahon et al. 2003).

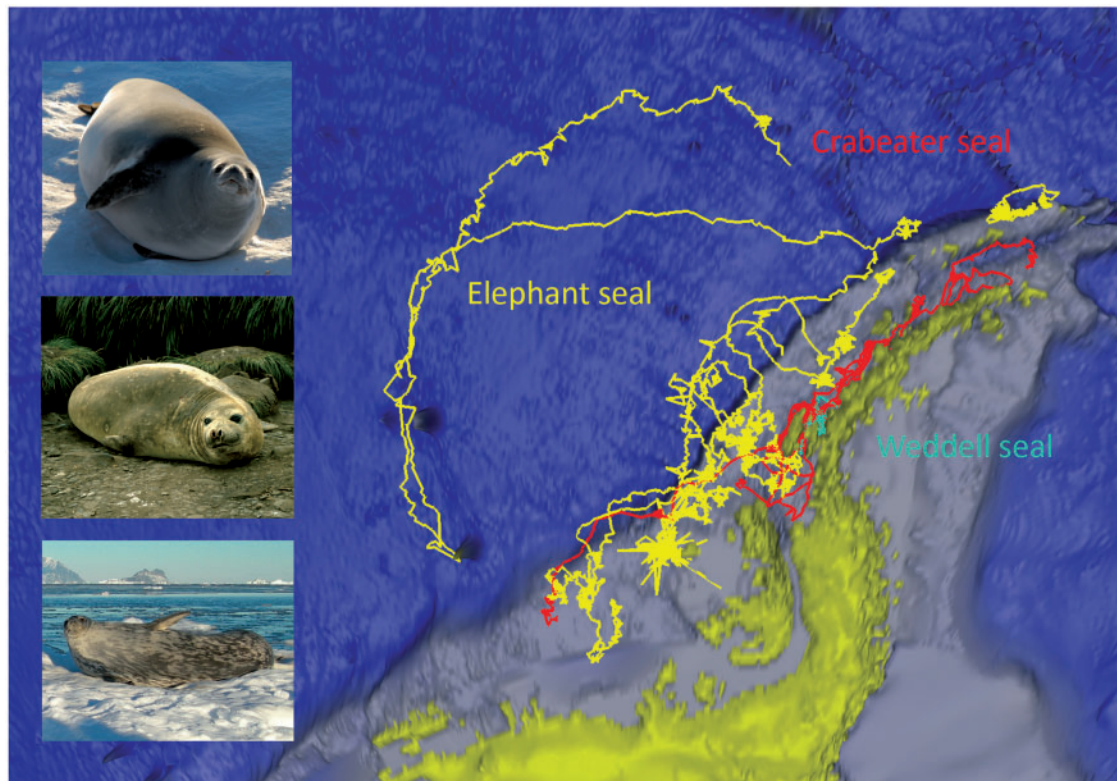
More recently, we examined simultaneously the foraging behavior and habitat utilization of three species of seals with contrasting foraging ecology: southern elephant seals (*Mirounga leonina*), crabeater seals (*Lobodon carcinophaga*), and Weddell seals (*Leptonychotes weddelli*). Although these three species are phylogenetically related (sub-family Monochinae), previous work in different areas or at different times indicates that they use different, but adjacent, habitat types. Southern elephant seals are pelagic, roaming throughout the Southern Ocean (McConnell et al. 1992; Field et al. 2001), occasionally venturing into the seasonal pack-ice whereas crabeater seals range throughout the seasonal pack-ice, venturing occasionally into open water (Burns et al. 2004). However, this earlier work had only been conducted on a single species in different places and at different times. In order to directly examine patterns of habitat utilization and potential niche overlap in these three species, we measured the foraging behavior of the three species in the WAP during 2007. While limited availability of ship-time precluded us from completing multispecies studies in other years, we were able to examine interannual variation in the foraging behavior of southern elephant seals in this region from 2005 to 2009. We were also able to compare our crabeater seal data collected in 2007, with equivalent data collected during 2001 and 2002 (Burns et al. 2004).

In addition to measurements of diving behavior and patterns of movement, the use of SMRU CTD tags allowed us to compare the habitat utilization of these three species with respect to the oceanographic features of the water column. The ability to identify habitat types with respect to different water masses allows us to integrate the foraging behavior of seals with hydrographic models of the WAP. In turn, hydrographic models can be used to forecast how the WAP is likely to change with changing climate, thereby allowing a more refined prediction of how the habitats of these animals are likely to change.

This work was carried out by deploying CTD Tags on elephant seals (57) at the US AMLR Program's summer field camp at Cape Shirreff, Livingston Island (62° 29'S, 60° 47'W) over 5 years (2005, 2006, 2007, 2008 and 2009), and on crabeater (9) and Weddell (2) seals from the ARSV L.M. Gould in the region of Crystal Sound to the northeast of Adelaide Island during 2007. Animals were handled and tags deployed using previously reported methods (Le Boeuf et al. 2000; Burns et al. 2004).

The three species of seals showed quite distinct differences in their habitat utilization. While the two Weddell seals remained within the immediate vicinity of the site at which they were tagged, the crabeater and elephant seals moved quite extensively (Fig. 5; Table 1). The movement pattern of crabeater seals in 2007 was quite similar to that previously reported (Burns et al. 2004). As in 2001 and 2002, they foraged along the continental shelf and remained deep within the pack ice throughout the winter, remaining closer to shore than did elephant seals. Some moved considerable distances (664 km to northeast, 1147 km to southwest), but most remained within 300 km of the location where they were tagged (Fig. 5). However, the southern elephant seals not only moved along the outer margins of the continental shelf (86% of the elephant seals), they moved considerable distances offshore into pelagic waters (14% of the elephant seals). Further, there were substantial differences between years. Some elephant seals remained in WAP and foraged along the continental slope in all years with some of these remaining in the pack ice as it formed during the winter. In all years except 2007, at least one individual foraged well into the Amundsen and Bellingshausen seas, the furthest reaching 5400 km to the west (Fig. 6). In contrast, during 2007 all elephant seals remained in the WAP region or in the Drake Passage. It is interesting that even though the crabeater seals did not cover as much distance as did the elephant seals, they still averaged the same mean speed of travel (Fig. 6; Table 1). This suggests that although they did not cover as great a distance, they were still traveling a similar amount but within a smaller area. Given the small area covered, the lower daily travel speed of Weddell seals was expected. Just as there were differences in patterns of movement, there were striking differences in the way the seals used the water column. Crabeater seals made dives to an average depth of 61 m that lasted 3.8 min. In contrast Weddell seals made dives to 91 m that lasted 11.5 min (deepest 455 m, longest 27.5 min) and elephant seal dove on average 345 m deeper (single deepest dive 2388 m), and 24.3 min longer. In summary, Weddell seals remained inshore in the fjord, diving to intermediate depths, and remaining quite resident; crabeater seals dived to shallower depths, but moved extensively along the inner continental shelf region. Finally, elephant seals traveled extensively along the outer margin of the continental shelf, foraging to the bottom, and/or foraging offshore into the mesopelagic zone and making very deep, long dives (Fig. 7).





**Fig. 5** Comparison of the tracks of crabeater (red), elephant (yellow), and Weddell (green) seals (images of species on left in order from top to bottom) foraging along the WAP. Data are from 26 April to 30 July, 2007—the period of time when the tags from all animals-species were transmitting.

**Table 1** The length of time that the tag transmitted, the maximum range covered, total distance traveled, and mean speed of travel for three species of Antarctic seals that were captured and tagged in the WAP. The mean is given followed by the range in parenthesis.

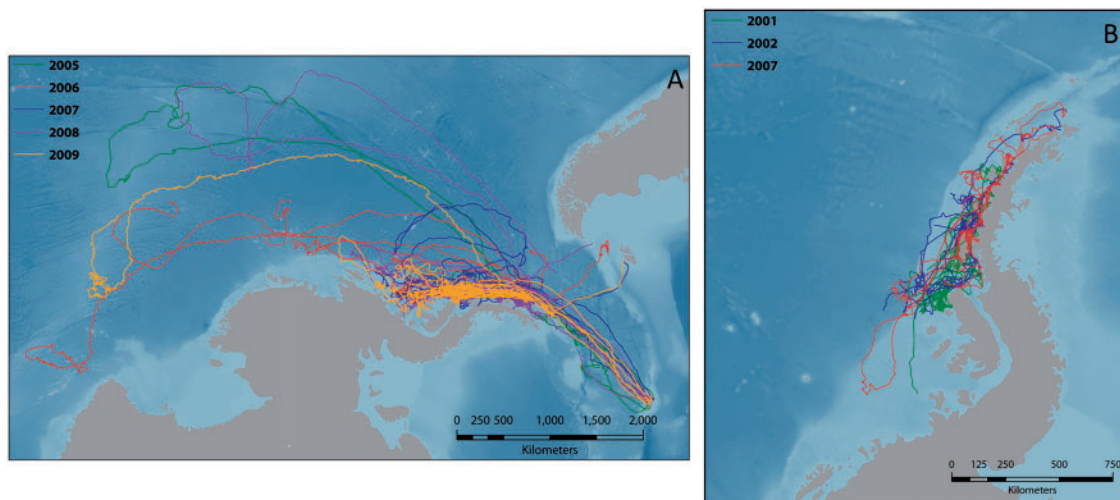
	Days transmitting	Max range (km)	Total distance (km)	Travel speed (km/day)
Elephant seal, $n = 12$	220 (93–301)	1024 (355–1703)	4890 (2343–16771)	22.2
Crabeater seal, $n = 9$	92 (27–168)	367 (68–867)	2046 (640–5724)	22.2
Weddell seal, $n = 2$	180 (154–204)	94 (63–125)	2005 (1980–2031)	11.2

Data on crabeater, Weddell and elephant seals are from the 2007 study reported here.  $n$  = sample size.

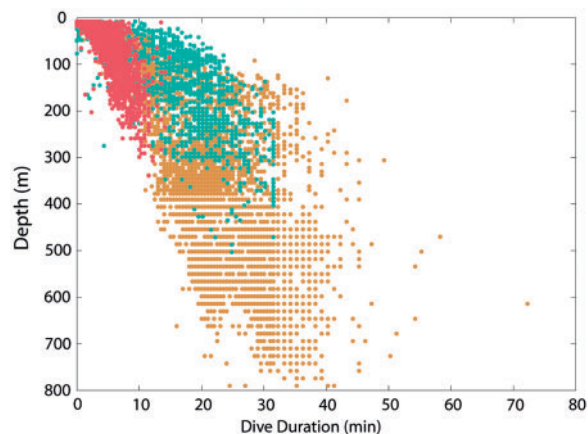
The CTD data provided by these tags also provide an opportunity to see whether the different species utilize different masses of water. To this end, we compared the temperature/salinity values recorded at the bottom of dives thus showing in Fig. 8 that elephant seals utilize the CDW. CDW is typically found along the outer regions of the continental shelf, especially in deep troughs where it has a tendency to well up onto the shelf (Dinniman and Klinck 2004). In contrast, crabeater seals forage in water masses with a lower range of temperature and salinity that are typically found on the inner shelf.

A Regional Ocean Model System (ROMS) model has been developed for the WAP (Hofmann and

Klinck 1998; Dinniman and Klinck 2004). This model not only allows estimation of current flow and of movement of water masses movements under present conditions, but also allows projections of different future scenarios (Dinniman et al., manuscript in review). For example, the model shows considerable intrusions of CDW onto the continental shelf, particularly in the regions where there are deep troughs at the entrances to Marguerite Bay and Crystal Sound. These intrusions bring salty warm water onto the shelf and form ideal habitat for the prey of elephant seals. This warm salty water also helps to maintain regions of open water throughout the year in both Marguerite Bay and Crystal Sound. These areas of open water are important for a variety



**Fig. 6** ARGOS tracks of southern elephant seals (**A**) and crabeater seals (**B**) obtained using the SMRU CTD tags over a 5-year period for elephant seals and during 2007 for crabeater seals. Crabeater seal data for 2001 and 2002 are from Burns et al. 2004. The different colors correspond to the tracks of all seals for each year.



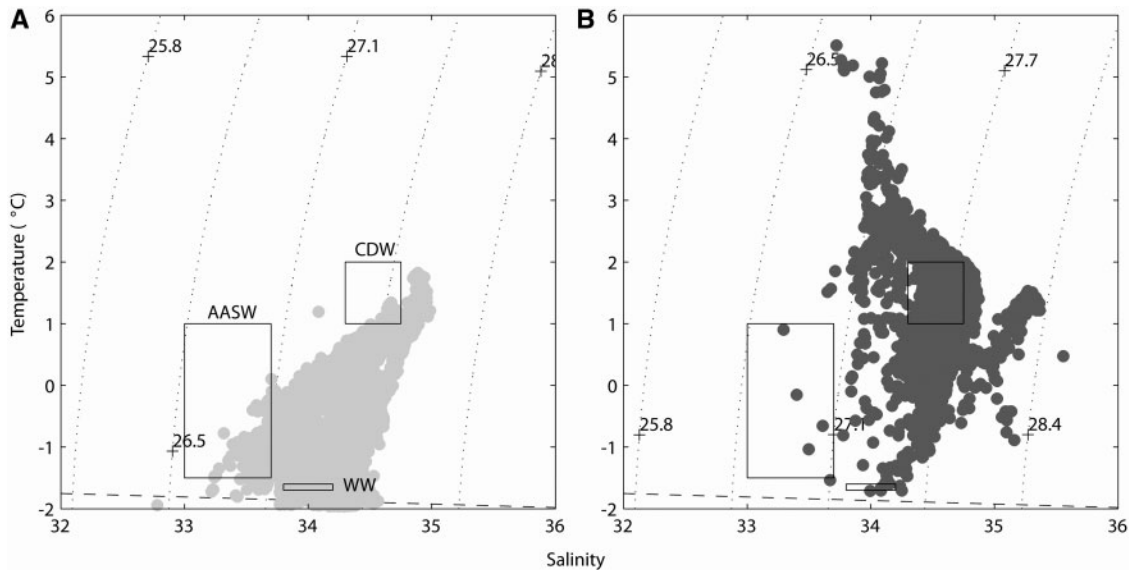
**Fig. 7** The maximum depths and durations of dives by three species of Antarctic seals. Each point represents the maximum depth for that dive and its corresponding duration. The lightest dots are crabeater seals, the dark dots are Weddell seals and the grey dots with the longest and deepest dives are elephant seals.

of marine mammals and seabirds because it provides them with access to open water and may also maintain input of nutrients onto the shelf (Ribic et al. 2008). However, one of the IPCC predictions for this region is an increase in westerly winds. In fact, since the 1970s there has been a poleward intensification of the westerly winds over the Southern Ocean (Hurrell and Vanloon 1994; Thompson and Solomon 2002; Gillett et al. 2003). Running the ROMS model with an increase in the westerlies resulted in an increase in the intrusion of CDW onto the WAP continental shelf as well as a decrease in the extent of sea ice, both in summer and in winter

(Dinneman et al. in press). The intensification of the westerlies has already resulted in a decrease in ice cover by  $\sim 4\text{--}10\%$  per decade (Liu et al. 2004) and a decrease in the ice season by  $\sim 20$  days (Stammerjohn et al. 2008); this trend will likely persist in response to a continued increase in greenhouse gasses.

These current and predicted changes will have important impacts on the ecosystem. The WAP shelf is considered one of the most biologically productive areas of the Southern Ocean, with reported chlorophyll values of up to  $40 \text{ mg m}^{-3}$  (Prezelin et al. 2000). Inshore and shelf-break waters are more productive than are offshore waters, and chlorophyll values consistently are higher in the southern part of the WAP (Marrari et al. 2008). The mid-trophic levels of the pelagic ecosystem of the WAP are dominated by euphausiids and copepods, although they can be outnumbered by salps in some years (Knox 1994). In particular, the WAP is characterized as an area of unusually high production of Antarctic krill (Atkinson et al. 2004; Howard et al. 2004; Moline et al. 2004), considered to be the dominant grazer in the Antarctic ecosystem and therefore a major player in the biogeochemistry of the Southern Ocean (Hofmann and Husrevoglu 2003). These mid-trophic levels shape the dynamics of the entire ecosystem, forming two very distinctive trophic webs. Copepods, along with mesopelagic fish and squid, occupy the mid-trophic positions of the food web of the northern slope and oceanic waters along the WAP, while Antarctic krill is the dominant mid-trophic level species of the southern food web in the zone of pack ice (Kock and Shimadzu 1994).





**Fig. 8** Temperature–salinity plots from the deepest points of dives, showing water masses utilized by (A) crabeater seals and (B) elephant seals. The boxes indicate the core values for water masses present in the WAP: CDW, Antarctic Surface Water (AASW), and WW.

The high levels of primary productivity are related to the dynamics of sea ice; therefore, the change in the timing and extent of formation of sea ice will impact timing and location of blooms (Vernet et al. 2008), ultimately impacting recruitment and dynamics of krill. Recruitment of krill is greatest in years when the ice covers a large area and the cover of ice is of long duration (Siegel et al. 1997; Atkinson et al. 2004). The relationships between krill and ice are likely a result of krill's dependence on the blooms for food, and because larvae depend on the ice cover and its associated microbial community for survival over winter (Quetin and Ross 2003). The change in timing and location in phytoplankton blooms may result in a trophic mismatch.

The large and persistent biomass of krill and other mid-trophic species in this region of the Southern Ocean sustains large biomasses of endothermic top predators (Costa and Crocker 1996; Ducklow et al. 2007), possibly the most important community of endothermic top predators in the world in terms of energy flux (Croxall 1992). However, climatic change will impact the predators in different ways. Current trends and future projections suggest an environment that is changing in favor of elephant seals, with their preference for foraging in CDW water and their independence from sea ice. Similarly, we might expect the changing habitat to favor Antarctic fur seals (*Arctocephalus gazella*) as well, given that they breed on land on the South Shetland Islands in the northern reaches of the WAP and are seen on sea ice outside of the breeding season. However,

an increase in available breeding habitat may be offset by a reduction in krill, the primary prey of Antarctic fur seals in the South Shetland Islands (Osman et al. 2004). The decrease in the amount and extent of sea ice will certainly limit the available breeding and foraging habitat for crabeater seals and will likely impact Weddell seals as well. A recent review of the effects of climatic change on Antarctic seals suggests that many of these changes are already taking place (Siniiff et al. 2008). For example, censuses of seals in the Anvers Island area from 1974 to 2004 indicate an increase in both elephant seals and nonbreeding fur seals while Weddell seal numbers have declined (Siniiff et al. 2008). These changes correspond to an overall decline in the extent of sea ice in this region (Ducklow et al. 2007). Unfortunately, no data exist on population trends for the other species of seals; leopard, Ross (*Ommatophoca rossii*) and crabeater seals are quite difficult to survey in a consistent and routine manner because of their choice of pack ice as a habitat. These changes are quite analogous to the replacement of Adelie Penguins by chinstrap penguins along the WAP (Ducklow et al. 2007). Adelie Penguins are more tolerant of ice and are reliant on winter sea-ice while chinstrap penguins are not (Fraser and Trivelpiece 1996).

Harder to interpret is how the changing habitat and associated reductions in sea ice will affect the trophic ecology of this region. While a strong link between the extent of sea ice and the abundance and recruitment of krill has been clearly identified

(Atkinson et al. 2004), the possible alternate states, in which krill is not the principle component of the food web, are less clear (Murphy et al. 2007). Moreover, our understanding of the trophic ecology of mesopelagic communities that elephant seals consume is extremely limited anywhere in the world. However, we do know that elephant seals and fur seals prey on a wide variety of species and show considerable plasticity in their diets. Elephant seals feed on a variety of mesopelagic squids and fishes throughout the southern ocean (Daneri et al. 2000; Piatkowski et al. 2002; van den Hoff et al. 2003; Cherel et al. 2008). While fur seals feed on krill where it is abundant in places like South Georgia Island and the South Shetland Islands (Reid and Arnould 1996; Osman et al. 2004), they feed primarily on fish in other areas such as at Kerguelen Island where krill is less available (Lea et al. 2002). Thus as sea ice and with it, krill decline, fur seals might be able to switch to squid and fish if the altered food web supports sufficient populations of these prey.

## Conclusions

Top predators forage in regions where physical forcing enhances the availability of prey. Our understanding of the specific oceanographic features responsible for increased availability of prey and for the specific foraging patterns of top predators has increased with the advent of electronic tags. In addition to being able to study the behavior of birds and mammals, these tags are providing information on oceanic habitats. Such information is increasing our ability to study regions of the southern ocean that have been out of reach of traditional sampling methods and are providing greater insights into the specific oceanographic features these animals are utilizing. CTD tags deployed on crabeater, elephant and Weddell seals in the WAP have shown that these three species occupy very different types of habitat within this region. In particular, elephant seals primarily forage in CDW on the outer continental shelf, while crabeater seals forage on the inner shelf within a narrower range of temperature and salinity profiles typical of that region. A ROMS hydrographic model shows a trend for increasing intrusions of CDW water onto the continental shelf, which will result in a continued decline in sea ice and associated habitat for crabeater seals. In contrast, these changes are likely to be beneficial for elephant seals and possibly for fur seals, depending on the food web dynamics resulting from changes in the sea ice environment.

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