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FEATURE ARTICLE

Trophic cascades in the western Ross Sea, Antarctica: revisited

David G. Ainley[1],[*], Grant Ballard[2], Randolph M. Jones[3], Dennis Jongsomjit[2], Stephen D. Pierce[4], Walker O. Smith Jr[3], Sam Veloz[2]

[1]**H.T. Harvey & Associates Ecological Consultants, Los Gatos, CA 95032, USA**
[2]**Point Blue Conservation Science, Petaluma, CA 94954, USA**
[3]**Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA 23062, USA**
[4]**College of Earth, Ocean, & Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA**

ABSTRACT: We investigated mesopredator effects on prey availability in the Ross Sea, Antarctica, assessing the reasons why Adélie penguin *Pygoscelis adeliae* foraging trip duration (FTD) increases and diet changes from krill to fish as numbers of foraging penguins and competing cetaceans increase in the penguins' foraging area. To investigate penguins' seasonally changing FTD as a function of foraging-population size—previously investigated indirectly—we used bio-logging to determine the penguins' 3-dimensional foraging volume, while an autonomous glider quantified the depth, abundance, and distribution of potential prey. As numbers of foraging penguins and cetaceans increased, penguins spent more time on foraging trips, traveling farther and deeper, and their diet included more fish, as average maximum depth of krill increased from 45 to 65 m, and that of small fish also deepened, but only from 51 to 57 m. With a need to forage at greater depths for increasingly overlapping prey, the penguins consumed more of the energy-dense fish. Krill depth was negatively correlated with chlorophyll (a proxy for krill food), indicating an uncoupling between the two and the overwhelming importance of predation avoidance by the krill relative to food acquisition. Results support the hypotheses that (1) predators remove the grazers from Ross Sea surface waters, controlling their vertical distributions; and (2) the food web has a 'wasp-waist' structure, in which middle- and upper-trophic levels are controlled top-down, whereas phytoplankton production and accumulation are regulated bottom-up, largely independent of grazer control. Ross Sea models need revision to reflect this food web structure.

[*]Corresponding author: dainley@penguinscience.com
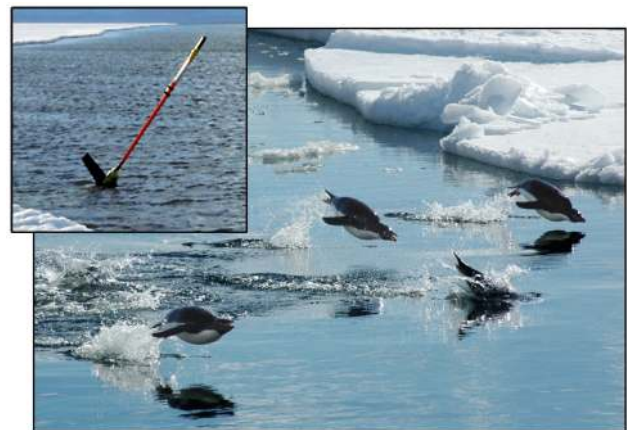
Adélie penguins returning from foraging; and the glider at Cape Crozier, Ross Island—nose down, antenna up—poised to begin quantification of penguin food.

Photos: D. Ainley and W. Smith

KEY WORDS: Adélie penguin · Foraging competition · Ross Sea · Trophic cascade · Wasp-waist food web structure

INTRODUCTION

Despite accumulating evidence (e.g. Sergio et al. 2014, Springer & van Vliet 2014), the importance of top-down processes in structuring marine ecosystems remains under-appreciated (Terborgh & Estes 2010, Estes et al. 2011). In part this is due to the large sizes of marine pelagic systems, which provide few opportunities for 'experiments' with which to eluci-

date the importance of top-down forcing and trophic cascades (e.g. Myers et al. 2007, Heithaus et al. 2008, Wirsing et al. 2008, Estes 2014). As the capacity for top-down forcing declines due to upper-level predator removal (e.g. Jackson et al. 2001, Myers & Worm 2003, Baum & Worm 2009, Estes et al. 2011, Cheung et al. 2013), and as changes associated with climate modification increase (e.g. Thomas et al. 2004, Ainley et al. 2010, Cheung et al. 2013, Smith et al. 2014b), such systems will likely be increasingly difficult to study.

Evidence indicates that top-down forcing is important and measurable in the Ross Sea, Antarctica, among pelagic mesopredators and their prey (Testa et al. 1985, Ainley et al. 2006, Lyver et al. 2014), as well as among benthic communities (Dayton 1989, Pinkerton & Bradford-Grieve 2014). The Ross Sea is the least anthropogenically affected continental shelf on Earth (Halpern et al. 2008); it still has substantial cetacean and other apex and mesopredator populations, and until recently has experienced little fishing (Ainley 2010, Ainley & Pauly 2014). The effects on penguins of changing cetacean populations in decades past have been investigated (Ainley et al. 2007), as has the alteration in penguin foraging behavior in the presence of killer whales *Orcinus orca* and leopard seals *Hydrurga leptonyx* (Ainley & Ballard 2012; see also Ainley et al. 2005). Environmental changes related to changing physical properties have been assessed (reduced salinity, increasing sea ice concentrations, and altered sea-ice season: Jacobs et al. 2002, Jacobs 2006, Stammerjohn et al. 2008, 2012), as have population responses by major mesopredators as exhibited by the penguins (Ainley et al. 2010, Lyver et al. 2014) and seals (Ainley et al. 2015). As a result, the Ross Sea remains an excellent system in which to investigate the relative roles of top-down and bottom-up forcing in a pelagic marine food web.

The Ross Sea is highly productive, supporting a food web having multiple trophic pathways (Smith et al. 2014a). Despite comprising just 2% of the Southern Ocean, the Ross Sea contributes an estimated 28% of its total primary production, as assessed by satellite-based models, and plays a significant role in the carbon budget of the Southern Ocean (Arrigo et al. 1998, 2008, Smith & Comiso 2008). Consistent with this high primary productivity, the populations of the highest trophic levels are immense, e.g. 38% of the world's Adélie penguins *Pygoscelis adeliae*, 25% of emperor penguins *Aptenodytes forsteri*, 30% of Antarctic petrels *Thalassoica antarctica,* and substantial populations of marine mammals (Ballard et al. 2012, Smith et al. 2014a). However, the estimated

standing stocks of middle trophic levels (herbivores such as copepods and krill; secondary consumers such as small fish) are surprisingly low, more than an order of magnitude lower, for example, than in the Scotia Sea (Deibel & Daly 2007).

One hypothesis to explain the high productivity–low grazer biomass enigma is a trophic cascade in which mesopredators reduce the abundance of middle level organisms, resulting in much of the phytoplankton biomass being ungrazed (Arrigo et al. 2003, Ainley 2007, Smith et al. 2007, 2011b). This hypothesis is consistent with the substantial aggregate fluxes (Asper & Smith 2003) and the large vertical fluxes of organic matter that have been found (Asper & Smith 1999, Collier et al. 2000, Smith et al. 2011b); nutrient budgets indicate that vertical flux can be as much as 10% of the annual production (Sweeney et al. 2000, Smith et al. 2011b). Under this scenario, this surplus of ungrazed resources at the base of the trophic web is explained by a depressed abundance of grazers. This hypothesis would be amenable to ecosystem modeling, but without more knowledge of the key elements driving mid-trophic prey availability, the system is too poorly defined for an in-depth modeling approach. These modeling efforts are further complicated by the fact that many Ross Sea mesopredators prey on both crystal krill *Euphausia crystallorophias*, a major grazer of phytoplankton, and silverfish *Pleuragramma antarcticum*, a major predator of crystal krill (Eastman 1985, Ainley et al. 2003a, Ainley 2007, Pinkerton et al. 2013).

Studies of mesopredator foraging can help elucidate the tropic pathways in the absence of knowledge of exact prey distributions. Our research on the foraging of Adélie penguins from Ross Island, using tags that identify geographic position and diving activity (e.g. Lescroël et al. 2010, 2014, Ford et al. 2014), provides evidence supporting predator-driven tropho-dynamics—facilitated by extensive diet overlap among penguins and cetaceans (Ainley et al. 2006, Ballard et al. 2012)—though they likely forage differently (see Discussion). By investigating phytoplankton biomass and penguin prey abundance where penguins do and do not forage, we might better understand the spatial and temporal components of the trophic interactions that occur within the pelagic food web. Adélie penguins forage near some phytoplankton blooms but not others (V. Toniolo unpubl. data). Hence, on one hand, diatom production may lead to a 4-level trophic chain composed of primary, secondary and tertiary consumers (diatoms–krill–fish–penguins). On the other hand, the production of colonial *Phaeocystis antarctica*, which dominates the

phytoplankton during austral spring as well as on an annual basis (Smith et al. 2011b), may lead to a shorter trophic chain having only one known macro-consumer (pteropods), with a large portion of the *Phaeocystis* biomass being microbially remineralized within the water column (Smith et al. 2011a).

Ainley et al. (2006) presented 2 models based on some natural experiments during 8 yr of study at 3 Ross Island Adélie penguin colonies of varying size, thus having co-varying radii of foraging 'halos' ex-tending out from each (see Elliott et al. 2009, Ford et al. 2014 for a summary of the concept). In the first model, given that krill were replaced by fish in the diet over time during the breeding season, the preva-lence of krill in the penguins' diet was explained by colony, time, and breeding population size (including both between- and within-colony size variation: a measure of intraspecific competition; Lewis et al. 2001). In the second model, penguins' foraging trip duration (FTD) was explained by colony, time, ice cover, and proportion of krill in the diet. When the prevalence of cetaceans was entered into these mod-els, FTD was best explained by colony and the abun-dance of both Antarctic minke whales *Balaenoptera bonaerensis* (mainly a krill feeder) and fish-eating killer whales (ecotype C); prevalence of krill in the penguins' diet was best explained by colony and prevalence of minke whales. Penguin FTD was longer with larger colony sizes and when more whales were present (see also Ballance et al. 2009). On the basis of these results, foraging by penguins and whales appeared to alter the availability of fish and krill to penguins, at least over mesoscale spatial variations in the south-western Ross Sea. In addition, the seasonally increasing FTD was at least partially due to an expansion over time of the foraging area at the large Crozier colony (Ainley et al. 2004, Ford et al. 2014). However, the ques-tion remained as to how these predators were altering prey availability: by inter-ference competition, with whales driving krill deeper than the diving capability of penguins, or by exploitative competition via intra- and interspecific prey depletion.

We tested the opposing hypotheses that (1) predators remove the grazers from Ross Sea surface waters, controlling their vertical distributions and impacts on phytoplankton; versus (2) food availability for middle and up-per trophic levels is regulated by bottom-up processes as a function of phytoplankton availability. To address these questions, we used an autonomous underwater vehicle (glider) equipped to assess both chlorophyll fluorescence and prey abundance (via acoustics), and deployed the glider at the same time and location where penguins were instrumented to elucidate foraging behavior (as in Ford et al. 2014). The study area was adjacent to one of the world's largest Adélie penguin colonies at Cape Crozier, Ross Island (280 000 breeding pairs; Lyver et al. 2014); here penguins and cetaceans forage in the marginal ice zone of the Ross Sea Polynya (Dugger et al. 2014, Lescroël et al. 2014; Fig. 1). The Crozier colony also has a very extensive foraging 'halo,' much larger than the smaller colonies in the re-gion, the size of the halo being a manifestation of the relative amount of prey depletion near to the colony (cf. Ainley et al. 2004, Ballance et al. 2009, Ford et al. 2014). We sought to learn whether increased FTD was due to a wider (farther from colony, longer duration spent foraging) and/or a more intensive (deeper div-ing) search for prey as prey became less available ow-ing to predation pressure through time (Ainley et al. 2004, 2006). We predicted that we would observe longer distance and duration of penguin foraging trips and deeper diving as the penguin breeding sea-son proceeded, and that there would be a correlated deepening of the main penguin prey species, also as-sociated with the number of minke whales and killer whales in the study area. Both whale species are com-mon in the area and can forage significantly deeper than the penguins (reviewed by Ballard et al. 2012).
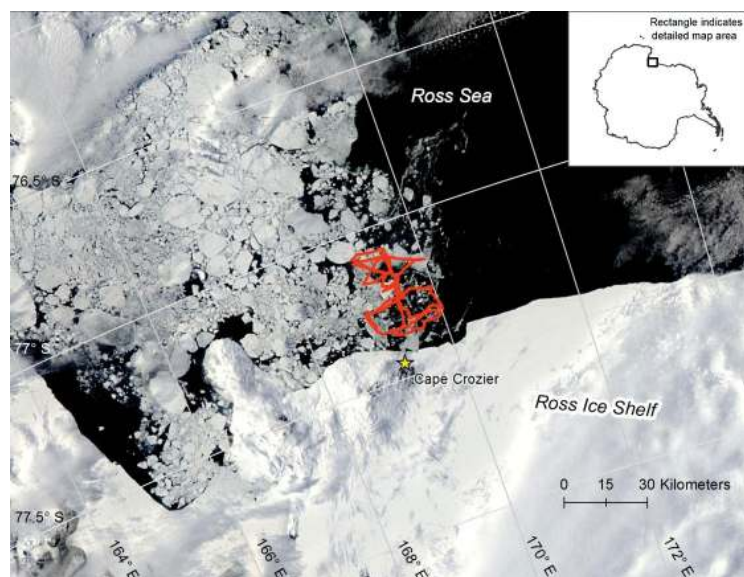

Fig. 1. Location of the glider track lines during the period when Adélie penguins *Pygoscelis adeliae* at the Cape Crozier colony (yellow star) were tagged to record foraging behavior, 10 December 2012 – 4 January 2013. Image depicts ice concentrations on 3 December 2012; courtesy NASA MODIS

MATERIALS AND METHODS

Data acquisition

Glider operations

Gliders are buoyancy-propelled, autonomous underwater vehicles carrying instrumentation to collect physical and biological measurements on 'V-shaped' trajectories between surface and depth (e.g. Kaufman et al. 2014). With a fixed wing and no external moving parts, gliders navigate descending and ascending trajectories by shifting their center of mass on 2 axes and by varying the volume of oil in a buoyancy bladder external to the pressure housing. Vertical movement is typically at a speed of ~25 cm s^{-1}, and the glider typically travels ca. 2.5 km between each surfacing. Satellite communications with a remote base station occur when the glider is at the surface, allowing the glider to determine its position, transmit data to the base station, and obtain modified navigation and/or sampling commands. Our sampling utilized an iRobot 1KA Seaglider™ fitted with a SeaBird CT Sail, Aanderaa Oxygen Optode 4330F, and Wet Labs ECO Puck sensors, as well as an Imagenex 853 echo sounder. The glider was not allowed to move within 5 km of sea ice, as judged from satellite imagery, as gliders cannot surface under sea ice and maintain communication. Thus, the study area moved slightly west, sampling the adjacent open water as the marginal ice zone retreated.

The glider was deployed from the fast ice (77.44° S, 169.75° E; Fig. 1) near Cape Crozier on 22 November 2012 at ~09:25 h UTC. To obtain a full section across the marginal ice zone and its meltwater lens (see Smith & Nelson 1985), the glider initially headed northeast for its first 50 dives before returning close to the point of deployment. For the remainder of the study, the glider followed a radiator pattern (25 × 50 km), completing multiple passes along selected transects and continuously collecting data through 700 m (the mean depth in the study area). The transects were selected to cover the 95% minimum convex polygon of foraging penguins' at-sea locations previously determined using satellite telemetry for Cape Crozier (Ballard et al. 2010, Ford et al. 2014). Data were collected approximately every 5 s; the Wet Labs ECO Puck and Imagenex 853 echo sounder were disabled below 250 m (200 m for the echo sounder after dive 53) to conserve battery power. The glider completed 571 dives

over 78 d and was retrieved at 76.77° S, 167.73° E by the RVIB 'Nathaniel B. Palmer' (Cruise NBP12-10) on 8 February 2013 at ~00:44 h UTC. A conductivity, temperature, and depth (CTD) calibration cast was completed upon recovery, and water samples were collected for chlorophyll and particulate organic carbon/nitrogen determinations. Fluorescence voltages (FL) were converted into chlorophyll concentrations (CHL) using the regression CHL (μg l^{-1}) = 0.00725 × FL + 0.371 (R^2 = 0.71) determined from the calibration cast.

Additional parameters derived from glider data

Several physical and biological parameters were calculated or derived from the core data for various analyses and correlations (Table 1). Distance from the glider to Cape Crozier (77.46° S, 169.25° E) was calculated using a great circle distance. Mixed layer depth (MLD) was computed using a potential density threshold method (Thomson & Fine 2003), which defines the MLD as the minimum depth at which a 0.01 kg m^{-3} increase is observed over the value of σ_θ at 3 m. Fluorescence measurements were processed by calibrating the sensor data with *in situ* bottle data collected at glider retrieval. Samples for chlorophyll *a* concentrations were analyzed by fluorometry using the acid-addition method on a Turner 10-AU fluorometer (JGOFS 1996). Glider measurements of fluorescence were converted to chlorophyll using the regression between fluorescence and extracted chlorophyll (Kaufman et al. 2014). Depth integrations of chlorophyll were calculated using trapezoidal integration.

Acoustic data

The glider-mounted Imagenex 853 echo sounder had a frequency of 120 kHz, 10° beam width, pulse length of 100 μs, a bin interval of 0.5 m, and maximum range of 100 m. The transducer source level was 210 dB μPa at 1 m and receiver sensitivity

Table 1. Mean (SD) values as observed by the glider in the Ross Sea, Antarctica, for the early (10–18 December 2012), middle (19–25 December), and late (26 December – 4 January) periods

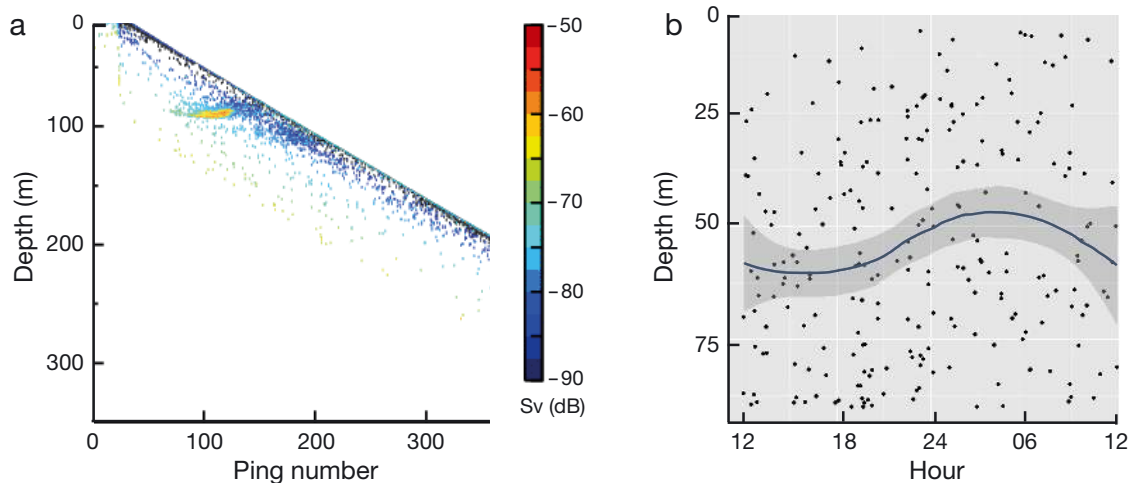|	Early	Middle	Late
Sea surface temperature (°C)	−0.37 (0.62)	−0.22 (0.65)	0.02 (0.46)
Sea surface salinity	34.13 (0.24)	34.08 (0.28)	34.17 (0.22)
Integrated 0–50 m chlorophyll (mg m^{-3})	14.5 (4.0)	11.6 (3.1)	8.4 (1.7)
Mixed layer depth (m)	6 (13)	19 (21)	10 (10)

Fig. 2. (a) Krill swarm at 90 m as detected by the acoustic transducer on the glider. (b) Depth of krill swarms as a function of hour within the upper 90 m of the water column; the line is a smoothing spline ± 95 % CI ($F_{2, 237}$ = 3.081, p = 0.048)

−180 dB V(μPa)$^{-1}$. It was operated in self-logging 'glider mode' with 1 ping every 4 s and a gain of 40 dB. The raw binary format data were translated to ascii columns with the Linux command line program 'octal dump' (od -w256 --format=u1). Subsequent processing used these ascii data. Additional details about using the Imagenex 853 on a seaglider and obtaining volume backscatter from the instrument can be found in Guihen et al. (2014).

We characterized the background acoustic noise present in each echosounder profile and removed this noise prior to applying the time-varying-gain using the method of De Robertis & Higginbottom (2007). The effective echosounder range, where signal was above the noise level, varied from about 50 to 75 m. The echosounder was usually enabled only during downcasts when the glider depth was between 0 and 200 m, so the typical depth range with acoustic data during a dive was 0 to 250 m. The glider would typically move about 375 m horizontally during an acoustic measurement phase. The acoustic bin distances below the transducer were corrected for the effects of glider pitch and roll: these data were subsequently regridded into 1 m vertical ocean depth bins of mean volume backscattering strength (S_v, in dB).

For each glider dive, the gridded S_v values were analyzed for krill aggregations. A krill aggregation was defined as a connected region in the acoustic matrix where all elements have S_v > −70 dB, following Lawson et al. (2008) and Bernard & Steinberg (2013). Data within 5 m of the ocean surface and within 1 m of the acoustic transducer were not included, as these are particularly biased by bubbles and other noise sources. The aggregation-detection method appeared to be effective in identifying krill

swarms (e.g. Fig. 2). The non-krill acoustic signal at these frequencies was considered primarily to be silverfish, and the acoustic/trawling study of silverfish in the Ross Sea by O'Driscoll et al. (2011) suggests that this is a reasonable assumption. Bioacoustic sections were created for each of the 571 glider dives (e.g. Fig. 2). We examined data from the entire 250 m depth range of the glider, and calculated summary data for each dive from 0 to 90 m depth, where 97 % of the acoustic backscatter was found.

Investigation of Adélie penguin foraging/chick provisioning

At the Cape Crozier colony (Figs. 1 & 3), breeding penguins arrive in late October; the females usually lay 2 eggs by mid-November, and chicks are fed from mid-December to early February. During the brooding and guard stages (~10 to ~31 December), one parent remains with the chick(s) while the other forages at sea. Nest reliefs occur every 1 to 3 d. During the crèche stage (1 January to 15 February), chick caloric demands force both parents to forage simultaneously, thus, greatly increasing the foraging population: from about 380 000 penguins foraging on any given day (considering foraging also by non-breeders who re- main for long periods at their nests) to 660 000 as the guard stage transitions to the crèche stage. Crèching in 2012–2013 began on 30 December. Our study period included all of the brood and guard stage and the early part of the crèche stage. We divided the study period into 2 halves for some analyses: 10 to 25 December is the 'early' chick-rearing period (one parent foraging) and 26 December to 4 January is the
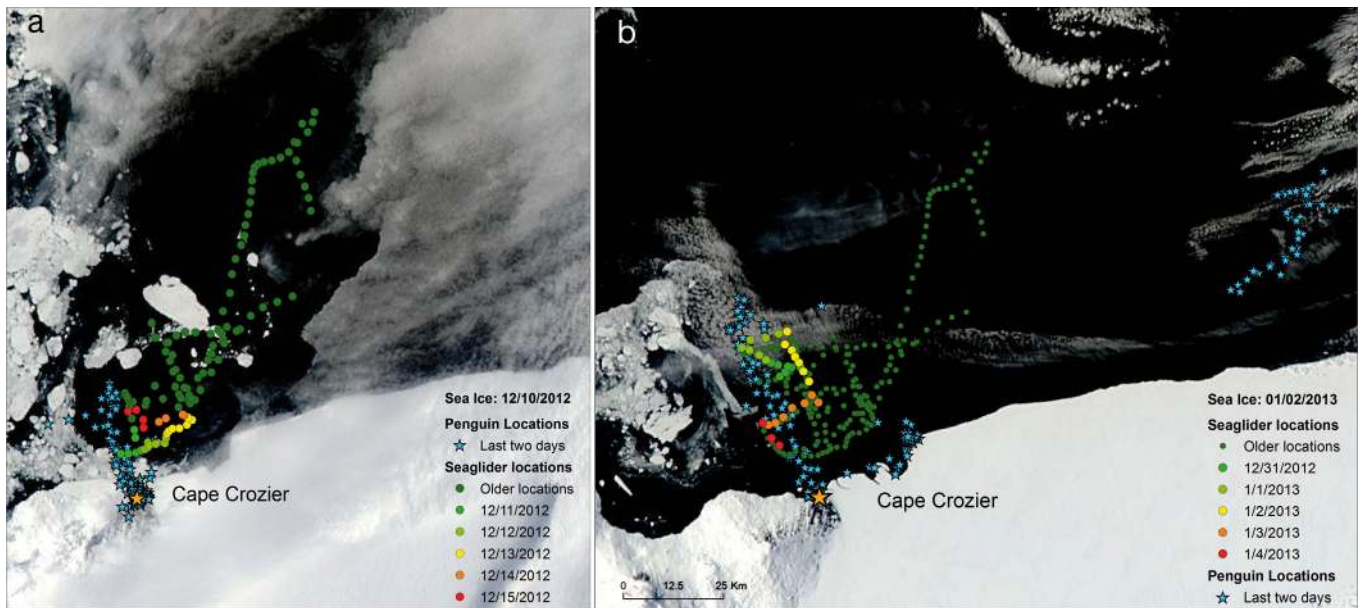
Fig. 3. Glider tracks, Adélie penguin *Pygoscelis adeliae* positions, and sea ice on (a) 10 December 2012, near the start of the early period ('older locations'), compared to (b) 2 January 2013, at the end of the late period. Last two days: (a) 16–17 December, and (b) 5–6 January

'late' chick-rearing period. In one subcolony, where foraging trip duration was measured using a weigh-bridge as described below, among 22 monitored nests (almost all members with radio frequency ID [RFID] tags), there were no chicks in the crèche stage on 10, 15, 20, and 25 December, but by 31 December, 5 January, and 10 January, respectively, 5, 28, and 86% of nests had chicks in crèches.

Adélie penguins forage by diving, mostly at depths ≤50 m but to a maximum of ~175 m (Whitehead 1989, Watanuki et al. 1997, Ainley & Ballard 2011). During the study period, we equipped 46 adult birds, each having at least one chick, with 'Splash' tags (Wildlife Computers) that measure diving behavior as well as location. The first tag was applied on 10 December and the last one was removed on 4 January. The tags recorded depth, irradiance, and temperature every second; they weighed 62 g (1.6% of a 4 kg Adélie penguin) and had a cross-sectional area of 3.2×10^{-4} m^2 (1.0 to 1.6% of a penguin's cross-sectional area). One foraging trip was recorded for each equipped individual (46 trips, 35642 dives total). Attachment procedures are described by Ballard et al. (2001). Diving data were processed using the program Divesum (v.7.5.5; G. Ballard unpublished software). Divesum classified dives into 3 types: foraging, exploratory, and other by parameterizing several components of each dive (Chappell et al. 1993, Schreer et al. 2001, Lescroël et al. 2010, Ford et al. 2014): (1) dive duration (s); (2) maximum depth (m);

(3) depth change rate (m s^{-1}; calculated as a running average for each 5 s block of the dive duration) in 2 categories: slow, i.e. < 1 m s^{-1}, or fast, i.e. > 1.5 m s^{-1} (dives for which depth change rates ≥4 m s^{-1} were recorded were excluded because of likely instrument error); (4) rate of ascent and descent (m s^{-1}; sustained rate of depth change in same direction from surface to bottom and from bottom to surface; bottom is any depth within 60% of the maximum depth reached on the dive); (5) bottom time (s) – the amount of time spent within 60% of the maximum depth and with no change in depth exceeding 0.5 m s^{-1}; and (6) number of undulations. Foraging and exploratory dives both were at least 10 m. Foraging dives had ≥4 undulations and either had ≥15 s bottom time, 30% of the dive duration spent in slow depth change rate and 30% with fast depth change rate, or ≥6 undulations and rapid (≥1 m s^{-1}) ascent/descent phases. Exploratory dives had <4 undulations or had <15 s bottom time and fewer than 6 undulations. All other dives were categorized as 'other' and are thought to be primarily traveling dives (see also Ford et al. 2014).

All satellite transmissions were processed within the Argos system (CLS Corporation). Satellite positions were filtered using the 'Argosfilter' package for R (Freitas 2012), which first removes all records with invalid locations (class Z), then all locations that require unrealistic swimming speeds (maximum 2.3 m s^{-1}), and finally removes all spikes with angles <15 and 25° if their extension is higher than 2500 and

5000 m, respectively (Freitas et al. 2008). Because raw Argos positions are biased by satellite orbital parameters and the penguins' latitudinal positions (Georges et al. 1997), we used a linear interpolation algorithm (Tremblay et al. 2006) to create a temporally uniform distribution of locations every 15 min along each foraging track.

Because of the differences in temporal resolution between the dive (1 s) and location data (15 min, after interpolation), we used temporal proximity to assign an approximate geographic location to each dive. We assumed that the farther interpolated positions were in space and time from a known position (TKP), the greater was their positional error. Thus, we removed highly interpolated positions (>30 min TKP), which allowed more dives to be included in the analysis while reducing the locational errors.

Using a weighbridge (WB) across which penguins had to travel going to and from foraging trips (Ballard et al. 2010), we also measured FTD (h) of 40 breeding penguins with RFID tags from the start of Splash tag deployment until 20 January. Splash-tagged birds did not have RFID tags. We used the WB data for these (instead of the Splash data) for 2 reasons: (1) WB provided an independent estimate of FTD from a relatively large number of penguins per day, enabling a more complete basis for inferring colony-wide patterns (e.g. Ballard et al. 2010, Lescröel et al. 2010, 2014); and (2) WB data were of higher temporal resolution because sampling was continuous, whereas Splash tag satellite positions are only available when Argos positions are available (on the order of every 1 to 6 h). During this period, we also assessed the chicks' diet by observing the color and consistency of food boluses; pink paste was considered to be krill, and gray, more granular food was determined to be fish (Ainley et al. 2006, Whitehead et al. 2015). Diet observations were summarized to provide average proportion of krill vs. fish fed to chicks per day. We also logged the number of whales in the foraging area as described by Ainley et al. (2006) – i.e. binocular/telescope-aided observations made for 1 h twice per day from a coastal hill, 400 m a.s.l., effectively enabling a scan of ~7 km out to sea.

Data analysis

2-dimensional kernel utilization distribution

To examine the 2-dimensional (2-D) space use of penguins, we developed 2-D utilization distributions (UDs) with only foraging locations as described above and a fixed-kernel density estimation (Worton 1989) using the 'adehabitatHR' package (Calenge 2006) in R. The UD is the probability density that an individual is found at a given location. To visualize the UDs, we created 50, 75, and 95% UDs for the early (10–25 December) and late (26 December – 4 January) periods for all individuals combined. Kernels were smoothed using the default 'href' method (Worton 1989).

3-D kernel UD

While satellite positional data allows us to track the horizontal space use of the penguins, dive data allow us to examine their 3-D space use and relate their positions to the 3-D (i.e. latitude, longitude, depth) distributions of phytoplankton and prey species as detected by the glider. To do this, we developed both 50 and 95% 3-D penguin UDs. We included only foraging locations for all individuals combined and a 3-D kernel estimator using the 'ks' package (Duong 2013) in R. Kernels were smoothed using the default bandwidth selector (Gitzen et al. 2006, Duong 2007).

Following Simpfendorfer et al. (2012), we accounted for the uncertainty in our positional data by multiplying our smoothing factor by a value >1. To determine this multiplier, we calculated the 50 and 95% UD and multiplied the smoothing factor by values from 1 to 10. We then determined the amount of change in the ratios between the 50 and 95% UDs for each multiplier value. The multiplier closest to the one with the smallest change was used (in this case, 3). We overlaid the glider-based krill and fish signals onto the penguin 3-D foraging plots for both the early and late periods.

Statistical modeling

We used linear regression to evaluate factors correlated with penguin foraging distance and depth. First, we used a mixed-effects generalized linear model to assess the effect of time in season (day of year) on FTD from the WB data, controlling for penguin identity as a random effect and sex as a fixed effect (males make shorter duration trips than females; Ballard et al. 2001, 2010).

Similar to the FTD analysis described above, we evaluated the effect of study day (10 December – 4 January) on penguin maximum foraging distance (MFDi, km; distance to farthest foraging location from Cape Crozier) as determined from the Splash

tags, controlling for penguin identity as a random effect. MFDi was square-root transformed prior to the analysis to ensure normality of residuals. We were unable to directly assess the distance of prey from Cape Crozier as an explanatory variable in the FTD and MFDi models because the glider did not have sufficient location sampling frequency at the range of distances required to match the penguin behavior.

We also assessed factors influencing the maximum depth of foraging by penguins, including the half-day (12 h) mean depth of prey (krill and fish; see below), chlorophyll concentration, and study day, predicting that the foraging depth of the penguins would correlate with the mean prey depth, and that as the season progressed and prey were depleted, this correlation would grow stronger (i.e. the inter-action between study day and depth of prey would be significant because prey would be increasingly less available). We included a factor for 'day' (04:00 to 21:00 h local time) and 'night' (22:00 to 03:00 h local time) among predictors in the model, as forag-ing behavior of penguins can be sensitive to irradi-ance levels in the water column (Ainley & Ballard 2012). Note that photoperiods were 24 h during the entire study, but local light levels varied by time of day, with lowest levels during the 'night' period described above (sun level lowest, and behind the high mountains of Ross Island; G. Ballard & D. Ainley pers. obs.). As above, we included a random effect for individuals in the analysis to account for the repeated sampling of each penguin during each foraging trip. We used day/night means in this analysis because this was the highest temporal resolution for which we could achieve a good match between sampling efforts of the glider and the penguins and also evalu-ate effect of light level associated with time of day in the model.

We used the 'lmer' function in the 'lme4' package (Bates et al. 2014) in R to conduct the mixed-effect model analyses and a Type III Wald F-test with Ken-ward-Roger degrees of freedom to test the statistical significance of the fixed effects of the depth model using the ANOVA function in the 'car' package (Fox & Weisberg 2011) in R, and the goodness of fit was assessed with the marginal R^2GLMM 'R2GLMM(m)' of the model and the conditional R^2GLMM of the model 'R2GLMM(c)' (Nakagawa & Schielzeth 2013). All continuous explanatory variables in the penguin depth model were standardized to mean and unit variance prior to the analysis.

We evaluated factors affecting krill and fish depth as determined by the glider (described above) using linear models with a stepwise AIC reduction ap-proach, considering the effects of study day, concen-trations of chlorophyll in the upper 50 m of the water column, and distance of the glider from the Crozier colony. In the case of the fish depth model, we also tested krill depth as an explanatory variable (be-cause the fish also eat the krill).

RESULTS

Seasonal changes in bio-physical aspects of the study area

Typical of the southwestern Ross Sea, ice concen-trations decreased during the study period (Gloersen et al. 1992, Smith et al. 2014a), with spring concentra-tions being extensive immediately north of Ross Island and Cape Crozier but reduced to the east in the Ross Sea Polynya (Fig. 1). Ice concentrations decreased through summer, and sea ice largely dis-appeared north of Ross Island except for what re-mained directly to the north. Throughout, however, the marginal ice zone of the polynya existed within the study area extent.

Mixed-layer chlorophyll concentrations were max-imal during mid-December and approached 20 mg m^{-3}, but decreased rapidly in early January (Table 1, Fig. 4). Spatial variability was observed, but this was far less than the temporal variability found over the entire spring–summer season. Sea-surface tempera-ture was higher towards the end of the penguin instrument deployment period, perhaps owing to fewer wind and mixing events in that time and
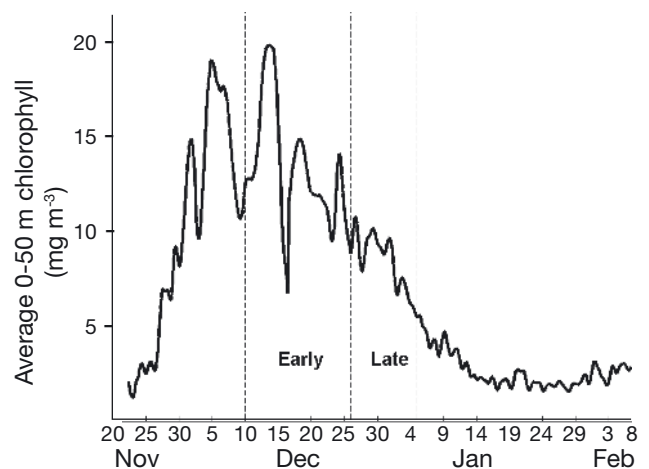

Fig. 4. Chlorophyll concentrations in the study area, 22 November 2012 to 8 February 2013: average chlorophyll (mg m^{-3}) in the upper 50 m

increased solar heating of the mixed layer. Surface salinity and MLD showed only modest changes, indicating our success in keeping the glider at the same position relative to proximity to sea ice in the marginal ice zone throughout the penguin instrument deployment period.

Seasonally changing penguin foraging behavior

FTD as determined by the WB remained relatively constant during the early period, but began to increase thereafter. Within the entire study period, FTD increased at about 1% d^{-1} ($\beta = 0.01 \pm 0.003$, p < 0.001; Fig. 5a) after controlling for significant effects of sex (FTD of males was 16% shorter than that of females; $\beta = 0.16 \pm 0.07$, p = 0.02). MFDi also increased throughout the study ($\beta = 5.80 \pm 0.96$, p < 0.0001, $R^2 = 0.46$; Fig. 5b). On 11 December, observed and predicted MFDi was <25 km from the colony. Observed MFDi peaked at 146 km on 2 January (when the mean was 53.8 km), while predicted mean MFDi increased to 63 km by 3 January.

Penguin chick diet at Cape Crozier was composed almost entirely of krill during the early period, but with the start of the late period, fish began to be eaten (Fig. 6). During the late period, fish contributed a third or more of the diet, similar to patterns described previously (Ainley et al. 2003a, 2006). The numbers of whales reached a maximum at the end of the early period and remained high into the late period (Fig. 7). However, since only about 6% of the penguin forag-
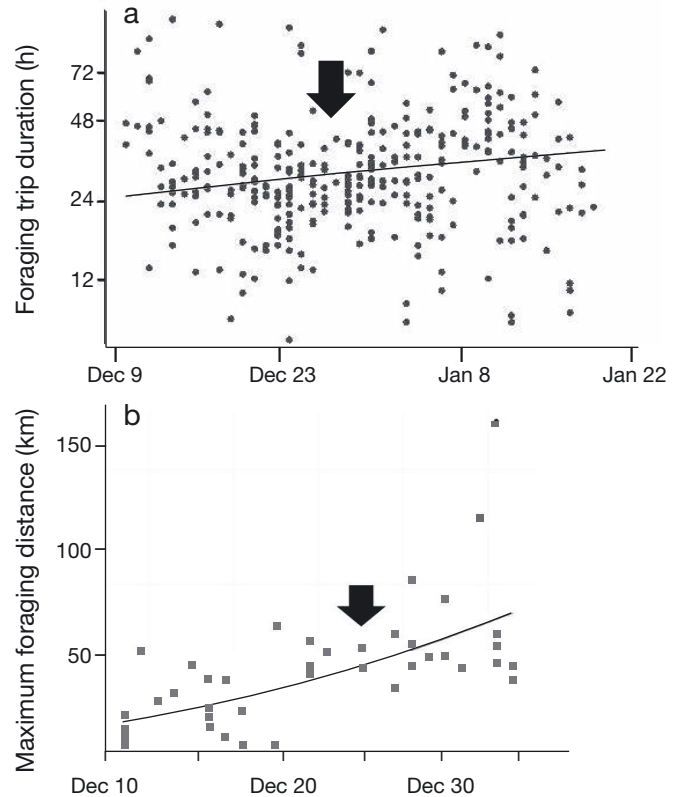

Fig. 5. (a) Foraging trip duration in hours (note scale of y-axis) of 40 breeding Adélie penguins *Pygoscelis adeliae* making 263 foraging trips at Cape Crozier, December 2012 to January 2013 (weighbridge data). Line shows predicted duration by date accounting for a fixed effect of sex and random effect of penguin identity. (b) Maximum foraging distance as determined from splash data. Arrows demarcate the end of the early and start of the late study period
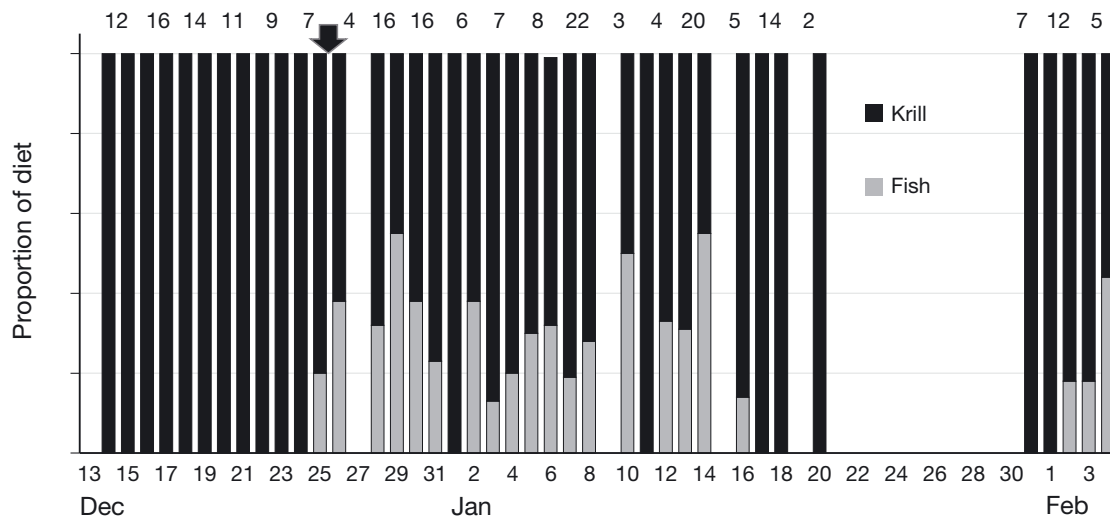

Fig. 6. Proportion of krill and fish in the diet of Adélie penguin *Pygoscelis adeliae* chicks at Cape Crozier, 14 December 2012 to 4 February 2013, based on methods of Ainley et al. (2006). The arrow demarcates the end of the early (26 December) and the beginning of the late period, which extended to 4 January. Numbers along top are 2 d sample sizes
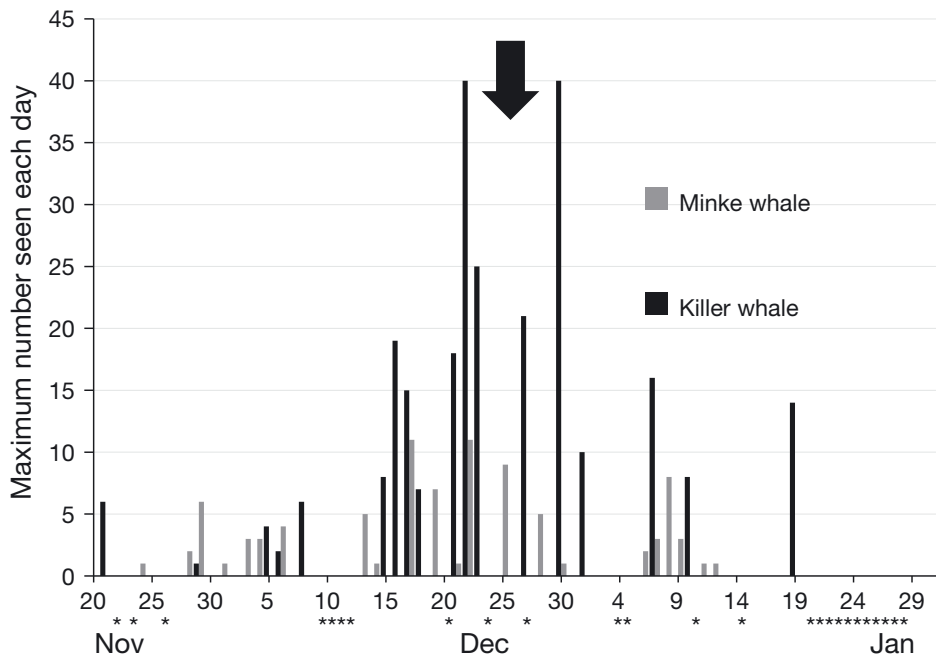
Fig. 7. Maximum number of minke *Balaenoptera bonaerensis* and killer whales *Orcinus orca* seen in waters offshore of the Cape Crozier Adélie penguin *Pygoscelis adeliae* colony; observations made twice daily from a coastal hill 400 m above sea level (Ainley et al. 2006). The arrow demarcates the end of the early (26 December) and the beginning of the late observation period, which extended to 4 January. Asterisks along the date line indicate dates on which no observations were made, usually owing to poor visibility

ing area could be seen from the whale observation point at Crozier (Ainley et al. 2006), it was not possible to know whether there was a decrease in number of whales foraging in the area or just that we could not see them as presumably, like the penguins, they moved to areas farther away and out of sight from Crozier. Therefore, we did not use whale numbers in the modeling.

Penguin foraging behavior relative to prey availability

Krill depth increased with study day, from ~45 to ~65 m, and fish depth also increased with study day (from ~51 to ~57 m; Fig. 8). The 46 Splash-tagged penguins made 35 642 dives between 10 December and 4 January, of which 16 675 (46.8%) were classified as foraging. Both the 2-D UD maps (Fig. 9) and 3-D UD maps (Fig. 10) indicate that penguins had an expanded foraging area and volume in the late study period compared to the early period. Higher-abundance prey detections tended to be, but were not exclusively, farther from the colony in the late period (Fig. 9).

During the early period, penguin diving depths ranged from near the surface to about 80 m, completely overlapping the depth distribution of krill, but with fish near the bottom of the penguin foraging dives (Fig. 10a,c). During the late period, maximum krill abundance was near 70 m, slightly deeper than

the depths where fish occurred (Fig. 10b,d). This is reflected in the higher proportion of fish in the late period (see Fig. 6).

We found a significant increase in penguin foraging depth over time (Table 2, Fig. 10). All of the fixed effects in our model were significant predictors of foraging depth (marginal R^2GLMM of the model = 0.338 and the conditional R^2GLMM = 0.640). Study day (positive) and chlorophyll concentration (negative) had the strongest effect on penguin foraging depth. The effect of fish depth on penguin foraging depth varied through the study period; the effect of study day on penguin foraging depth was stronger when fish were at shallower depths than when fish were at deeper depths. Maximum penguin foraging depth was positively correlated to krill depth, and increasingly so later in the study (Table 2).

DISCUSSION

Our results showed that the change in diet and the increase in penguin FTD, as the intensity of predation pressure increased (more penguins foraging as more chicks entered the crèche phase, arrival of foraging whales), i.e. the importance of study day in the modeling, corresponded with an expansion of the foraging area (foraging farther from the colony; MTDi) and deeper diving. That is, the foraging volume increased over time. These changes were best explained as a response to reduction and deepening

Fig. 8. Mean half-day depth of krill and fish within the upper 90 m of the water column vs. study day. The lines represent the regression predictions holding all other factors in the regressions at their mean value; the shaded areas indicate ±1 SE. The arrows demarcate the end of the early (26 December) period, which began 10 December, and the beginning of the late observation period, which extended to 4 January
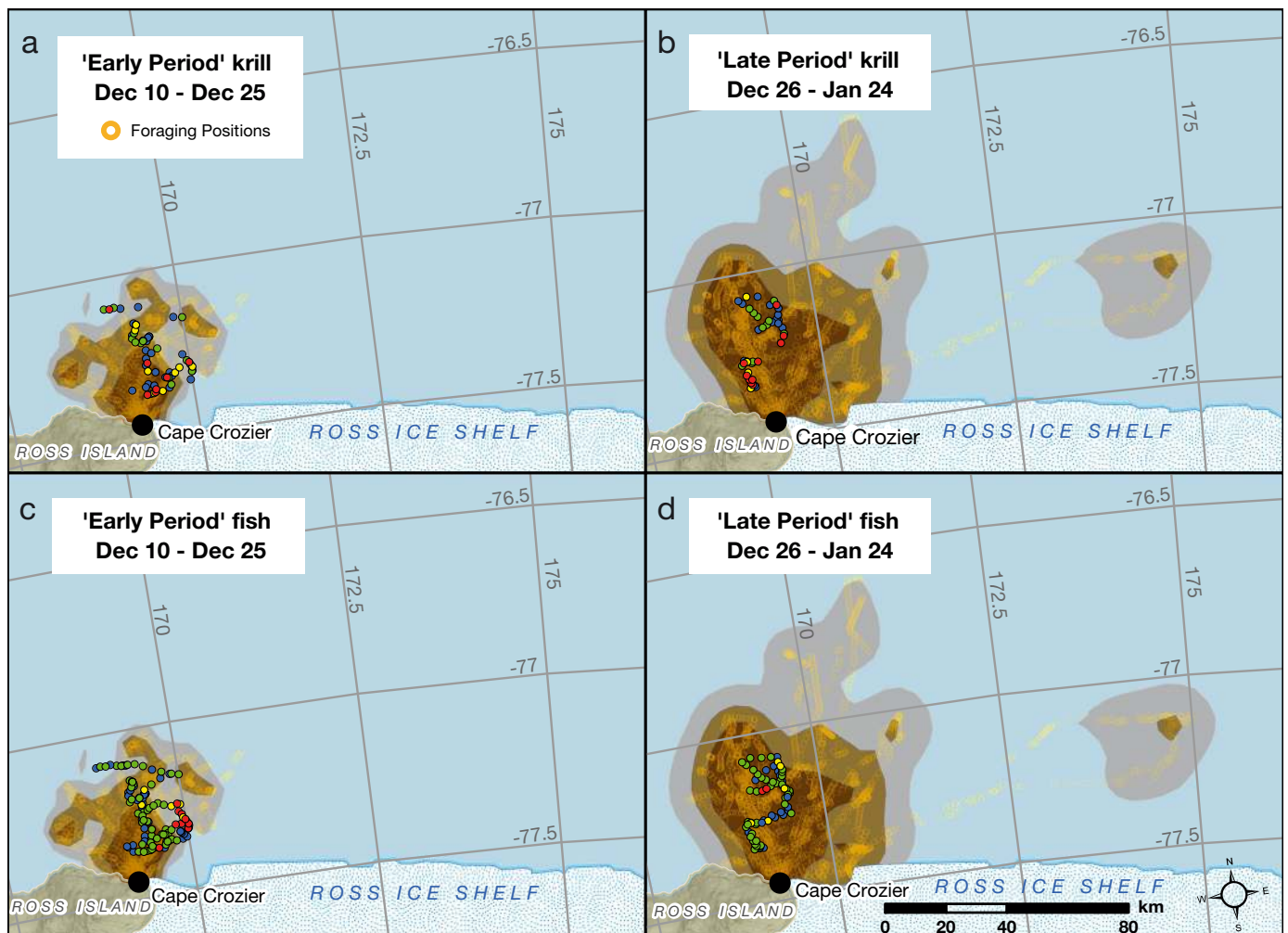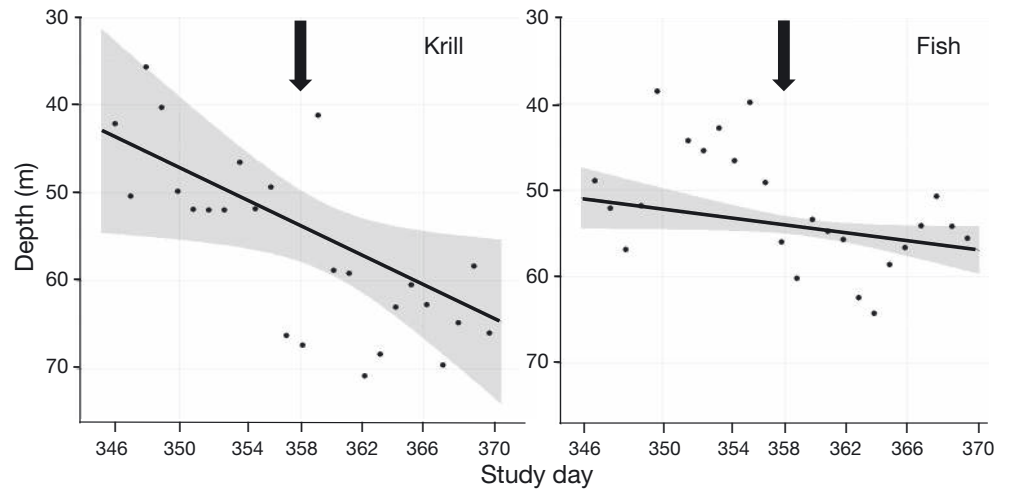

Fig. 9. Two-dimensional kernel utilization densities based on Adélie penguin *Pygoscelis adeliae* foraging locations (yellow circles); (a, c) early period and (b, d) late period together with krill (a, b) and fish (c, d) locations. Within the outer boundary of the foraging areas, intensity of penguin foraging density is depicted by color; dark brown: high (50 % utilization distribution), light brown: intermediate (75 % utilization distribution), gray: low (95 % utilization distribution). Colored points indicate volume backscattering strength (S_v) of krill or fish (blue: low; green: intermediate; yellow: intermediate/high; red: high abundance)
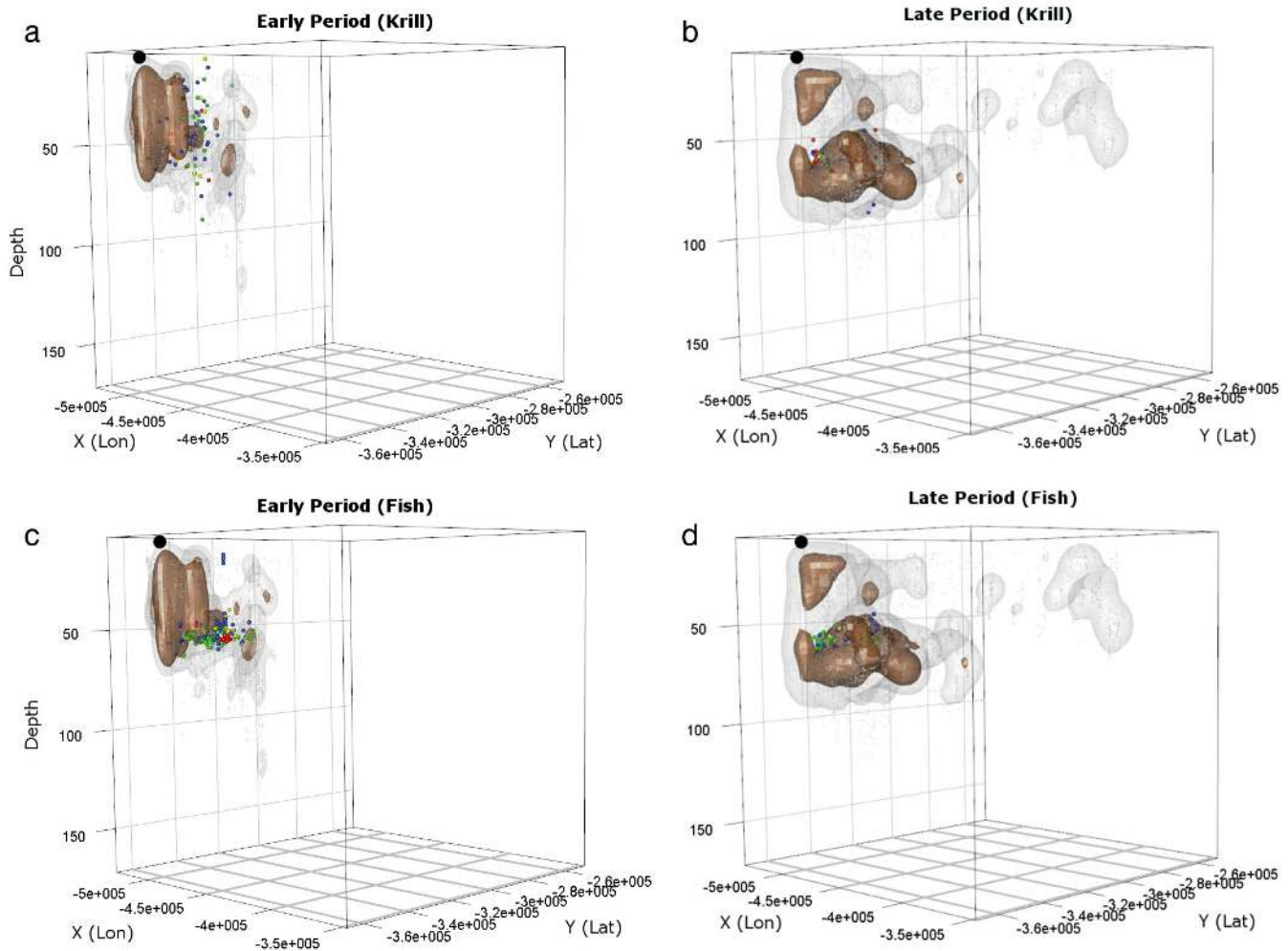
Fig. 10. Underwater side views (looking northwest) of the Adélie penguin *Pygoscelis adeliae* 3-dimensional utilization distributions together with (a, b) krill and (c, d) fish locations during the early (a, c) and late (b, d) periods. Depth axis (*z*) in m; longitudinal axis (*x*) extends ~150 km, latitudinal axis (*y*) 100 km (cf. Fig. 1). Thicker grid lines are parallel to the depth plane; thinner gray lines are along the western-most plane. Colored points indicate volume backscattering strength (*S*$_v$) of krill or fish (blue: low, green: intermediate, yellow: intermediate/high, red: high abundance). Brown areas indicate higher penguin foraging density (50% utilization distribution); gray areas indicate lower penguin density (95% utilization distribution). The large black dot indicates the location of the Cape Crozier penguin colony

Table 2. Fixed effects results from a linear mixed model of Adélie penguin *Pygoscelis adeliae* foraging depth including individual penguin identity as a random effect. The values in parentheses in the estimate column are in the original units of the explanatory variables. The marginal R^2GLMM = 0.338 and the conditional R^2GLMM = 0.640

Fixed effect	Estimate	SE	F	df	p(>F)
Krill depth	−1.286 (−0.072)	0.271	22.594	1	<0.001
Fish depth	2.488 (0.806)	0.264	88.740	1	<0.001
Study day	6.735 (1.01)	1.092	37.276	1	<0.001
Mean chlorophyll 0–50 m	−7.821 (−2.477)	0.398	385.729	1	<0.001
Day/night (night)	0.3514	0.351	101.962	1	<0.001
Fish depth × study day	−0.512 (−0.025)	0.228	5.041	1	0.025
Krill depth × study day	2.404 (0.150)	0.306	61.496	1	<0.001

of prey close to the colony. They are consistent with seasonal changes reported by Ainley et al. (2006) and confirmed those of Ford et al. (2014), who found that for penguins from the large Crozier colony, highest quality prey patches, as measured by penguin foraging intensity (increased density and frequency of diving), occurred farther from the colony over time.

Like surface-feeding seabirds (Lewis et al. 2001, Ainley et al. 2003b), intensive and deepening penguin foraging (i.e. subsurface diving birds) is correlated

with reductions in prey availability at shallower depths. During chick-guarding (early period, 10–25 December; one parent foraging at a time), krill occurred in the upper water column. However, as predation pressure increased (both parents foraging, plus whales), the depth of the krill biomass maximum deepened significantly, as did that of silverfish, though only slightly. We suggest that once penguins began to forage at those greater depths, they began to encounter and take the deeper-dwelling fish that are a larger prey packet of significantly higher energy density than krill (5.2 vs. 4.6 kcal g^{-1}; Ainley et al. 2003a), at least in part to compensate for greater energy expenditure during foraging (Ballance et al. 2009).

Unfortunately, we did not have bio-loggers on whales to learn how their foraging contributed to that of the penguins in altering the availability of prey within the penguin foraging area. One problem with bio-logging is that it assesses individual animals (e.g. Watanabe & Takahashi 2013), although penguins forage in flocks of varying size often in synchrony (D. Ainley & G. Ballard pers. obs. of penguins foraging in wide leads in McMurdo Sound and near the fast ice edge at Cape Crozier). Thus, the capacity of penguins to alter prey behavior/availability is not that of a single individual. How a penguin flock 'attacks' a prey school, especially in a possible coordinated way, remains unknown. More is known about the foraging tactics and prey response of Antarctic minke whales, which forage as individuals but have the capacity, owing to mouth size, to have a similar effect as a flock of penguins (e.g. Friedlaender et al. 2014). The depth of minke whale foraging is certainly affected by the depth of their prey and appeared to average well within our prey sampling zone to 90 m (Friedlaender et al. 2014), even if the depth at which prey (krill) aggregate in the presence of whales becomes deeper (Friedlaender et al. 2009). Unfortunately, the low density of the glider tracks precluded our ability to assess how mesopredator foraging might have altered the size and shape of prey schools/swarms.

All this is further evidence that within the Ross Sea food web, upper-level predators change the availability, if not the abundance, of grazers in surface waters during summer. While the total phytoplankton in the upper levels of the water column, including both the colonial haptophyte *Phaeocystis* as well as single-celled diatoms, showed a marked decrease over time, their concentration and consequent depth within the euphotic zone showed little change other than extreme episodic variations (likely induced by

storm passages). Owing to the position of our study area at the open-ocean edge of the Ross Sea Polynya, as well as the time of season, most of the phytoplankton biomass was likely provided by *Phaeocystis*, which appears to be largely ungrazed by crystal krill, unlike diatoms (Smith et al. 2014a). Much of *Phaeocystis* sinks and sustains the Ross Sea benthic communities (Barry et al. 2003) or is remineralized within the water column (Smith et al. 2014a). Furthermore, the expected compositional changes in phytoplankton reflect a change from *Phaeocystis* dominance to diatom dominance after the abrupt decrease in *Phaeocystis* in late December (Smith et al. 2014a), as well as the overall decrease in biomass of all phytoplankton. The multiple simultaneous impacts of numerous trophic levels make the assessment of grazer impacts on diatoms difficult.

Our results, in conjunction with those of Ainley et al. (2006), show a close coupling between mesopredators and their prey in the marginal ice zone. The fact that krill depth increased as phytoplankton biomass decreased (suggesting an uncoupling between krill food and vertical distribution), along with the observation that penguins dove deeper presumably as they (and whales) drove krill deeper, further indicates an overwhelming importance of penguin (and other mesopredator) foraging in regulating krill distribution. Both penguin foraging depth and chlorophyll concentrations were strongly correlated to study day, which in our model is a proxy for changing predation pressure (seasonal increases in penguin foraging density and cetacean populations; see also Ainley et al. 2006). It is unlikely that the krill descended to feed on microzooplankton as phytoplankton standing stocks decreased, as going deeper puts them within the vertical distribution range of silverfish, a major crystal krill predator (Eastman 1985, Pinkerton et al. 2013); as the season progresses into autumn, the silverfish become cannibalistic, feeding on their own larvae (Eastman 1985), suggesting that this feeding response may result from krill becoming seasonally less available. We believe our results are one step closer to confirming the trophic cascade hypothesis; that is, predation pressure by mesopredators on appropriately-sized prey regulates their vertical distribution and abundance, which in turn uncouples the prey's impacts on their food items.

Together, the evidence we collected indicates that a 'wasp-waist' food web structure occurs in the Ross Sea, in which on the one hand top-down controls are most important to the upper and middle trophic levels of the pelagic communities (as opposed to the benthic; Barry et al. 2003, Pinkerton & Bradford-

Grieve 2014), but which are largely uncoupled from the immense bottom-up resource that the Ross Sea's phytoplankton provide. On the other hand, bottom-up control of primary production is driven by both irradiance and micronutrients (Smith et al. 2014a) and is largely uncoupled from grazing. The apparent uncoupling of phytoplankton–mesozooplankton distributions, as well as the relative biomass levels, strongly suggest a lack of grazer control on primary production; however, a detailed assessment of the seasonal changes in all zooplankton and their relationship to phytoplankton is needed to fully test this relationship. These conclusions about food web structure are consistent with those of Frank et al. (2007), who found that 'wasp-waist' food webs predominate in more simple, cold-water continental-shelf ecosystems. Our results suggest that Ross Sea food web models based primarily on bottom-up processes, particularly when dominated by the *Phaeocystis*-based primary production (Pinkerton et al. 2010, Smith et al. 2011b), may not adequately capture the most important ecological interactions that have a major structural impact on the upper levels of the food web. Uncoupling between pelagic meso-predators and phytoplankton/primary production was also indicated by Dugger et al. (2014), who found no correlation between the substantial inter-annual variations in Ross Sea primary productivity (Arrigo et al. 2008, Smith & Comiso 2008) and the productivity and breeding population size of penguins on Ross Island over the past 2 decades. Further research on the diatom- vs. *Phaeocystis*-based pelagic food webs and the top-down controls of middle trophic levels by mesopredators is warranted to better understand trophic cascades and food web structure in the Ross Sea (Smith et al. 2014a).

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