At-sea behaviour of three krill predators breeding at Bouvetøya —Antarctic fur seals, macaroni penguins and chinstrap penguins

Marie-Anne Blanchet[1], Martin Biuw[1,3], G. J. Greg Hofmeyr[2,4], P. J. Nico de Bruyn[2], Christian Lydersen[1], Kit M. Kovacs[1,*]

[1]Norwegian Polar Institute, Framsentret, 9296 Tromsø, Norway [2]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, Pretoria, South Africa

[3]*Present address:* Norwegian Institute for Nature Research, Framsentret, 9296 Tromsø, Norway [4]*Present address:* Port Elizabeth Museum at Bayworld, Humewood 6013, Port Elizabeth, South Africa

ABSTRACT: Interspecific competition is an important structuring element in marine ecosystems, especially in the Southern Ocean which offers few prey choices to comparatively large predator populations. We present the first simultaneous observations of at-sea behaviour and attendance patterns of 3 synchronously breeding, central place, krill foragers at Bouvetøya — a small, isolated, sub-Antarctic island in the South Atlantic. Time depth recorders and satellite transmitters were deployed during the austral summer of 2007/2008 on 47 lactating Antarctic fur seals *Arcto-cephalus gazella* (AFS) rearing pups and on 20 macaroni *Eudyptes chrysolophus* (MAC) and 30 chinstrap *Pygoscelis antarctica* penguins (CHIN) rearing chicks. All 3 species showed a strong preference for the west side of the island, and their foraging ranges overlapped markedly. Solar elevation influenced the timing of departures from, and arrivals to, the island with markedly different patterns between the seals and the penguins. Diving patterns also showed significant differences among the 3 species, with the frequency of diving being higher at night for the AFS, while both penguin species dove more frequently during the day. But a common, vertical diel pattern occurred in all 3 species, with shallow diving occurring at night and deep diving during the day, consistent with the vertical migration of krill. MACs targeted 2 depth layers for feeding, including a deep prey layer at ~70 m, which was not exploited by AFSs and CHINs. The results suggest that there is potential for competitive overlap among these 3 krill predators at Bouvetøya, but that it is reduced via both spatial (horizontal and vertical) and temporal partitioning of foraging areas.

KEY WORDS: Competition · Diving behaviour · Foraging ecology · Niche separation · Southern Ocean

INTRODUCTION

If 2 or more species are resource limited, share similar prey types and have substantial spatiotempo-ral overlap in their distribution (Hutchinson 1957, Schoe ner 1974, Alley 1982), there is potential for competition. Competition theory predicts that com-plete overlap of realised niches leads to an unsustainable situation causing the demise of 1 or more of the competing species (Hutchinson 1957, Hardin 1960). Therefore, in order to co-exist species must differ in their realised niches (Trivelpiece et al. 1987, Fried-laender et al. 2009, Miller et al. 2010) and are expected to show partitioning in at least 1 resource

axis (prey, spatial, or temporal) when overlapping in range (Barlow et al. 2002). Potential competitors can reduce the impact of competition by partitioning resources through habitat, dietary, or temporal segregation (Schoener 1974, Alanärä et al. 2001).

Lactating otariids and breeding seabirds share similar foraging constraints, utilise similar marine re -sources and often breed sympatrically and synchronously (Costa 1991, Boyd 1998). This is especially true in the Southern Ocean where there are few islands that can serve as haulout sites for large populations of land-breeding predators, including sea birds, penguins and seals. These animals are central place foragers (Orians & Pearson 1979) during the breeding season; they must return to the colony to deliver food to their land-based offspring (Beauplet et al. 2004, Ichii et al. 2007). Thus, they are constrained in the distance that they can travel by the time between feeding sessions. There is therefore potential for resource competition between such species during the breeding season if they share a common food resource (Boyd et al. 2002, Ballard et al. 2012).

Three krill-predators, Antarctic fur seals *Arcto-cephalus gazella* (AFSs), macaroni penguins *Eudyp -tes chrysolophus* (MACs) and chinstrap penguins *Pygoscelis antarctica* (CHINs) breed synchronously and sympatrically during the austral summer on Bouve tøya in the South Atlantic. The breeding pe -riod spans from mid-November to late March–April for the seals and from late December to late February–early March in the case of the penguins (Krafft et al. 2002). Female fur seals come ashore to give birth to their single pups and then alternate between periods of 1 to 10 d foraging at sea and periods of 1 to 3 d ashore attending their young (Lunn & Boyd 1993, Boyd 1999, Staniland et al. 2004, Biuw et al. 2009) until the pup is weaned after ~16 wk of nursing (Costa 1991, Kovacs & Lavigne 1992). MACs and CHINs typically lay 2 eggs a few days apart (Croxall & Davis 1999, Green et al. 2002). The second egg is always subjected to brood reduction in MACs which raise only 1 offspring per season (Waluda et al. 2010). CHINs raise both chicks when there is sufficient food available (Croxall et al. 1988, Meyer et al. 1997). Young penguin chicks are brooded (and guarded) by one parent, while the other forages for periods of 12 to 24 h, until the chicks are old enough to thermoreg-ulate on their own, at which time they are left in a crèche with other young while both parents often forage, and a few adults guard. Penguin chicks are fed with whole food items, directly via regurgitation of parental stomach contents, which puts special tem-

poral constraints on the adult birds' foraging (see Costa 1991, Croxall & Davis 1999). In MAC pairs the female does most of the chick provisioning, being assisted by the male only during the crèche period (Green et al. 2002). In CHINs both parents tend the chick(s) and both undertake foraging trips (Croxall et al. 1988, 1993, Jansen et al. 1998). Fledging occurs between mid-February and early March for both species, ~60 and 54 d after hatching for MACs and CHINs, respectively (Croxall et al. 1988).

Krill *Euphausia superba* is a key component in the diets of the AFSs, MACs and CHINs throughout much of the sub-Antarctic region (Jansen et al. 1998, Hofmeyr et al. 2010, Waluda et al. 2010), with the exception of the southern Indian Ocean sector (see Lea et al. 2002, de Bruyn et al. 2009), though all 3 species do also feed on fish and squid (Reid et al. 2006, Hofmeyr et al. 2010, Waluda et al. 2010). All 3 species appear to select mature female krill preferentially in most areas, and their reproductive performances are similar in periods of krill fluctuation (Reid et al. 1999, Barlow et al. 2002, Croll et al. 2006, Waluda et al. 2010).

Although many studies on krill predators have been conducted in the past 30 yr, they have been focused to a large extent on areas around South Georgia and the Antarctic Peninsula (e.g. Croxall et al. 1985, Boyd et al. 1991, Jansen et al. 1998, Trivel-piece et al. 2007, Goldsworthy et al. 2010, Waluda et al. 2010). Little information is available from the ocean sector surrounding Bouvetøya, although some data are available regarding fur seal foraging from this area (Biuw et al. 2009, Hofmeyr et al. 2010). In recent years, a significant decline in MAC and CHIN numbers has taken place at the Nyrøsa breeding colonies on Bouvetøya (Huyser 2001, Krafft et al. 2002). It is therefore important to acquire a better understanding of the underlying ecological processes driving the interactions among the 3 krill predators, particularly in light of the fact that increased krill harvesting is taking place in the Southern Ocean (Tou et al. 2007, Krafft et al. 2010, Nicol et al. 2012). This paper explores the at-sea-dis-tribution and diving behaviour of the 3 krill-depen-dant predators (AFSs, MACs, CHINs) at Bouvetøya during their common breeding season in 2007–2008.

MATERIALS AND METHODS

This study took place at Nyrøysa (54.41° S, 03.29° E) on the west coast of Bouvetøya, between 12 December 2007 and 12 February 2008. We captured

47 mother–pup AFS pairs (Table 1). The mothers were manually restrained with a large cone-shaped hoop net (1.5 m long × 1 m Ø) attached to an aluminium frame and handle (see David et al. 1990). Body mass was measured to the nearest 0.1 kg using a 100 kg Salter scale prior to instrument attachment and upon recovery (Table 1). Three instruments were simultaneously deployed on each adult female to obtain data on her movement patterns and diving behaviour: a 0.5 W Sirtrack Kiwisat 101 platform terminal transmitter (PTT, Sirtrack), a Wildlife Computers Mk9 time-depth re corder (TDR, Wildlife Computers) and a Sirtrack VHF radio transmitter (to facilitate recapture). The instruments were glued to the fur of the mid-dorsal region with 2-component industrial grade epoxy (Huntsman AW2101/HW2951, Inter -tronics or 5-Cure, Industrial Formulator Inc.). The PTTs had a repetition rate of 40 s (with no duty cycling). The TDRs were programmed to record depth, at a resolution of 0.5 m, and light level every second, both when wet and dry in order to record attendance patterns precisely. The VHF radio transmitter had an individual frequency ranging from 151.200 to 151.540 MHz (in steps of 10 KHz, 60 pulses min^{-1}, no duty cycling). In air, the PTT weighed 100 g (120 × 56 × 17 mm). It had a cross-sectional area of 9.5 cm^2. The TDR and the VHF transmitter weighed 30 g (67 × 17 × 17 mm) and 35 g (60 × 25 × 15 mm) with cross-sectional surface areas of 2.9 and 3.7 cm^2, respectively. The combined weight of the instruments represented 0.4% of the animal's average body weight in the air, and the instruments'

cross-sectional areas represented 1.9, 0.6 and 0.7% of the animals' frontal cross-sectional area for the PTT, TDR and VHF, respectively (assuming an average front cross-sectional area surface for a female AFS of 490 cm^2, see Biuw et al. 2009). Instruments were left attached for 1 to 5 foraging trips. We captured a total of 20 female MACs and 31 CHINs of unknown sex on their nests during the brood-guard period and weighed using a 10 mm (thickness) rope noose passed under the wings, suspended from a 10 kg Salter scale (accurate to within 50 g) (Table 1). Two types of instruments were simultaneously attached to each penguin, a 0.5 W Sirtrack Kiwisat 202 PTT (Sirtrack Inc.) and a Wildlife Computers Mk9 TDR identical to the one used on the AFSs. Both instruments were glued to the dorsal feathers using Loctite 323 rapid-setting glue. The penguin PTTs weighed 100 g in air (90 × 34 × 25 mm) and had a cross-sectional surface area of 8.5 cm^2, which repre-sented 5.6% of the penguins' frontal cross-sectional area (assuming ~150 cm^2 for both species Croll et al. 1991), while the TDRs represented 1.9% of the penguins' cross-sectional area surface. The combined weight of the instruments represented 2.9 and 3.1% of the body weight for the MACs and the CHINs, respectively. Instruments were left attached for 1 to 15 trips. Upon recapture the penguins were re -weighed. Seven animals of each species were purposely left with the PTT at tached to monitor at-sea movements after the breeding season (to be published elsewhere, see also Biuw et al. 2010a); data are presented herein up until 15 February, when the

Table 1. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica.* Summary statistics per species (AFS: Antarctic fur seal; MAC: macaroni penguins; CHIN: chinstrap penguins), instrumented at Bouvetøya. Means ± SD, range in (). PTT: platform terminal transmitter; TDR: time depth recorder

Variable	AFS	MAC	CHIN
Individuals instrumented (n)	47	20	31
Body mass at deployment (kg)	38.9 ± 10 (29.0–51.0)	4.4 ± 0.4 (3.6–5.3)	4.1 ± 0.4 (3.4–5.5)
Body mass at recovery (kg)	37.7 ± 4 (25.0–49.0)	4.2 ± 0.4 (3.6–5.2)	4.2 ± 0.4 (3.4–5)
PTTs (n)	45	20	24
TDRs (n)	43	16	26
PTT + TDR (n)	41	16	21
Tagging period (PTT + TDR)	19 Dec–7 Feb	14 Jan–11 Feb	3 Jan–8 Feb
Track duration (d)	9 ± 4 (3–20)	9 ± 6 (4–24)	7 ± 4 (2–18)
No. of trips per individual	1.9 ± 1.1 (1–5)	4.2 ± 2.6 (2–11)	6.6 ± 4.2 (1–15)
Total number of trips	77	67	172
Trip duration (h)	65 ± 34 (5–160)	28 ± 30 (1–204)	9 ± 7 (1–49)
Haul-out duration (h)	36 ± 20 (4–79)	14 ± 4 (8–33)	17 ± 6 (2–44)
Mean max. distance (km)	54 ± 34 (2–134)	48 ± 46 (2–284)	10 ± 12 (1–57)
Total number of dives (>4 m)	48212	33346	43382
Dive duration (s)	59 ± 34 (7–290)	85 ± 36 (9–246)	62 ± 25 (8–238)
Max. depth (m)	20 ± 17 (4–133)	32 ± 26 (4–133)	20 ± 14 (4–99)
Percent time at sea spent diving	16 ± 6	47 ± 9	52 ± 9

field crew departed; all tagged animals were known to still be caring for young at this time.

A state-space model, based on a Kalman filtering algorithm (Patterson et al. 2008, 2010), was applied to the tracks to obtain the best possible representation of the real path followed by the animals. The TDR records were correlated with the PTT records, based on time, in order to calculate a geographic position for each dive. Start and end times of trips were de-fined based on conductivity switch records from the TDRs, or distance from the island for animals with only PTT records available. Diel periods were de-fined according to the sun angle as follows: night was defined as a solar elevation below -12° (McCafferty et al. 1998; nautical twilight, US Naval Oceanography Portal 2011); day was defined as a solar elevation >0°; and dusk and dawn were defined as the periods with a solar elevation between -12° and 0°. Dawn and dusk were analysed as 1 period in analyses using solar elevation. These time periods were only usable in analyses for records where both PTT and TDR data were available, because solar elevations were calculated from positions and local time. When data was explored based on time of day (GMT), all of the TDR records were included. A depth of 4 m was set as a minimum for classification of a dive to avoid including surface travelling or resting as diving (Waluda et al. 2010, Staniland et al. 2011). Sea-surface temperature (SST) was taken as the temperature recorded by the TDR at the beginning of each dive. Each position was linked to the closest bathymetry value in the GEBCO gridded data (1 min resolution dataset— http://neo.sci.gsfc.nasa. gov/ Search.html; j session id = A1DD 800CF1E2DAD6A 31AA64948C134AE?group = 28).

All statistical analyses were conducted using R, Version 2.12.1 (R Development Core Team 2009) unless otherwise specified. Analyses of the animals' behaviour were performed either at the dive, location, foraging trip, or individual level. Filtered positions were interpolated every kilometre to avoid biases due to the number of locations depending on satellite coverage. The circular mean bearings were calculated for each trip based on interpolated po-sitions. Circular statistics were used on the mean bearings to see if the travel direction was random (Kuiper's test). cANOVA was performed to examine the consistency of the mean bearing of each individual trip between the 3 species. These analyses were done using the Circstats and circular packages (Jam-malamadaka & SenGupta 2001). Trip duration, haul-out duration, maximum distance from the island per trip (log transformed to correct for non-normal distri-

bution), proportion of time spent diving per trip and mean maximum depth per diel period (night, dusk or dawn, day) were compared between the 3 species using linear mixed effect models (nlme package; Pinheiro et al. 2012). These models were fitted with species as a fixed effect and animal identification (ID) as a random effect, to take into account individual variability and multiple trips performed by some indi viduals. All models were fitted using maximum likelihood so that they were comparable. Model fitting was based on the examination of the residuals, and Kolmogorov-Smirnov tests were used to assess whether or not they were normally distributed. Models were compared using small-sample-corrected Akaike's information criterion (AICc; Akaike 1974) and the relative weight of each candidate model (Burnham & Anderson 2002). When no significant differences between 2 models were found, the simplest was chosen following the principle of parsimony. Post hoc multiple comparison tests were performed using Tukey's pairwise comparisons (mult comp package; Bretz et al. 2010) to assess the significance of the differences between factors and the interactions among factors. All distances from the colony refer to great circle distances (Meeus 1991), and the maximum corresponds to the most distant point reached within a trip.

Distribution of the timing of departures and arri-vals from or to the island in relation to the time of day were compared within and between species with a 2-sample Kolmogorov-Smirnov test. Frequency and maximum dive depths were also examined in relation to the time of day and solar elevation. Kernel densities were fitted to the distributions using local polynomial kernel smoothers available in the Kern -Smooth library (Wand & Ripley 2005). The number of dives per hour was calculated for each trip for each individual. Generalised additive mixed effects models (GAMM) were fitted for each species to account for the non-linear relationship between the response and the explanatory variables. Animal ID was used as a random effect, with an Order 1 auto regressive term (correlation = corAR1[form = ~1|ID]) to account for the lack of independence between observations from the same individual. A quasi- Poisson error structure was used because the data were over dispersed. The smoothed terms were fitted using thin-plate-penalised regression (Woods 2006). The explanatory variables tested in these models were distance to the colony (DIST), solar elevation, water depth (as a factor, shelf = 0 to 1000 m, oceanic > 1000 m) and SST. Analyses were performed using the mgcv (Woods 2006) and MuMIn packages (Barton 2012). Model
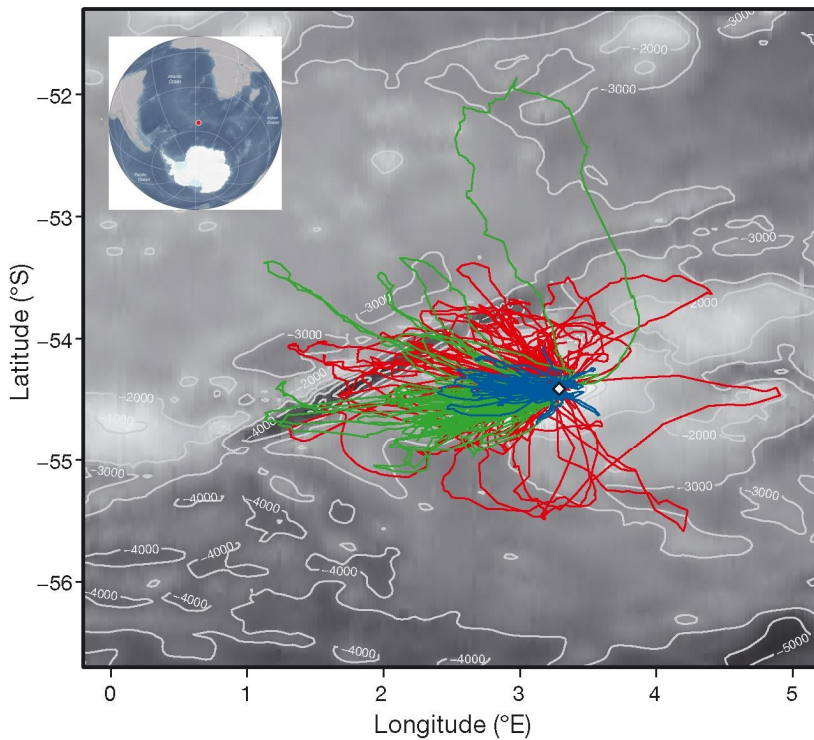
Fig. 1. *Arctocephalus gazella*, *Eudyptes chrysolophus*, *Pygoscelis antarctica*. Tracks of all Antarctic fur seals (red, n = 45), macaroni penguins (green, n = 20) and chinstrap penguins (blue, n = 24) between 19 December 2007 and 15 February 2008, instrumented at Bouvetøya. The tracks have been filtered through a state–space model. White lines represent depth contours of 100, 500, 1000, 2000, 3000, 4000 and 5000 m

selection was based on information criteria (Burnham & Anderson 2002) using QAIC because the data were over-dispersed.

Positions of dives were grouped into 0.1 × 0.06 de -gree spatial cells to calculate the percentage of overlap between the 3 species' foraging areas. So, for each species the number of cells containing at least 1 foraging dive was obtained. The percentage of cells containing dives from >1 species was then calculated.

RESULTS

Tracking data for AFSs commenced in mid-December and extended into early February. Because of the later start of the bree ding season of the MAC and CHIN penguins the avian records commen ced in early January and extended until early February. The average duration of the tracking periods per individual were similar among the 3 species (ANOVA p = 0.35) (Table 1). The failure of some instruments resulted in the length of PTT and TDR records differing for some individuals and the number of PTT and TDR records not being equal (Table 1).

At-sea movements

All trips made by individuals of the 3 species during our defined study period are shown in Fig. 1. A preference for the western sector was evident for all species but most notably for the penguins. The AFSs' tracks were more dispersed than those of the penguins, with a few trips directed to -

wards the south- southeast of the island. The western orientation was even more evident when considering the interpolated location bearings plotted as a circular diagram (Fig. 2). The preference for a particular direction was statistically significant; the circular mean bearings per trip were not uniformly distributed for the 3 species (Kuiper test D_{AFS} = 50.9, D_{MAC} = 73.7, D_{CHIN} = 28.3; p < 0.01), and the individual variation in mean bearing was smaller than the difference
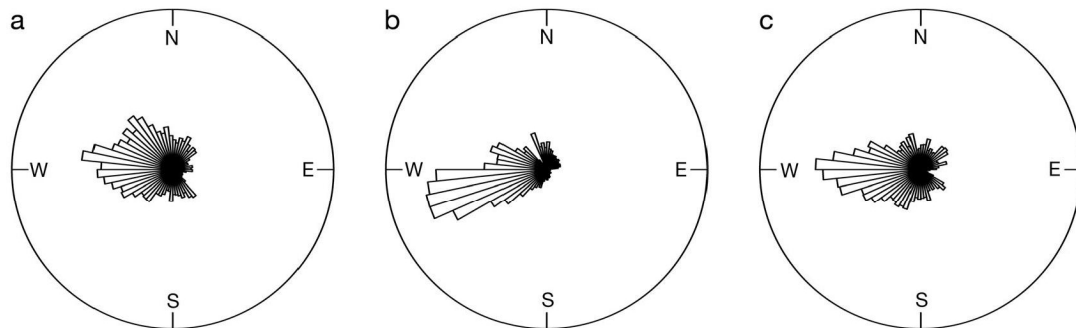

Fig. 2. *Arctocephalus gazella*, *Eudyptes chrysolophus*, *Pygoscelis antarctica*. Circular diagram of interpolated location bearings for (a) Antarctic fur seals, (b) macaroni penguins and (c) chinstrap penguins tracked from Bouvetøya

ob served between species (cANOVA: $F_{2,89} = 12.34$, p < 0.001). AFSs showed a degree of preference for the northwestern sector despite individual variability. MACs' tracks were clustered in the west-southwest direction, while most CHINs' tracks were due west.

Attendance patterns and trip durations

Mean foraging trip duration differed among species (lme trip duration ~ species: $F_{2,75} = 136.3$, p < 0.001), and all pairwise comparisons between spe -cies were also significantly different $(z_{AFS-MAC} = 6.49$, p < 0.001, $z_{AFS-CHIN} = -16.55$, p < 0.001, $z_{MAC-CHIN} = -7.37$, p < 0.001). Trip duration was longer for the AFSs than for the MACs which in turn were longer than for the CHINs. Trip duration was correlated with the maximum distance reached during the trip ($R^2_{AFS} = 0.78$, $R^2_{MAC} = 0.93$, $R^2_{CHIN} = 0.81$; p < 0.001; also see Fig. 3). A pattern of short (MAC < 20 h; CHIN < 10 h) and long trips (MAC > 20 h; CHIN > 10 h) was ob ser ved for both penguin species, which corresponded to day trips and over night trips; though it must be noted that day trips were most common for both species (Fig. 3). The bimodal patterns for MACs and CHINs were not the result of individual strategies, as almost all individuals performed at least 1 over -

night trip at some point in their data record. By contrast, no particular patterns in trip duration or maximum distance from the island were observed for the AFSs.

Maximum distance from the island per trip was sig-nificantly different between the 3 species (lme max. distance ~ species: $F_{2,75} = 81.20$, p < 0.001). Pairwise comparisons showed that the difference between AFSs and MACs was not significant $(z_{AFS-MAC} = 0.630$, p = 0.8), whereas the differences between AFSs and CHINs and between MACs and CHINs were significant $(z_{AFS-CHIN} = -10.59$, p < 0.001, $z_{MAC-CHIN} = -8.43$, p < 0.001). CHINs stayed significantly closer to the island than either MACs or AFSs (Table 1). Mean time spent ashore (haul-out duration) also differed on a species-specific basis (lme haulout ~ species: $F_{1,56} =$
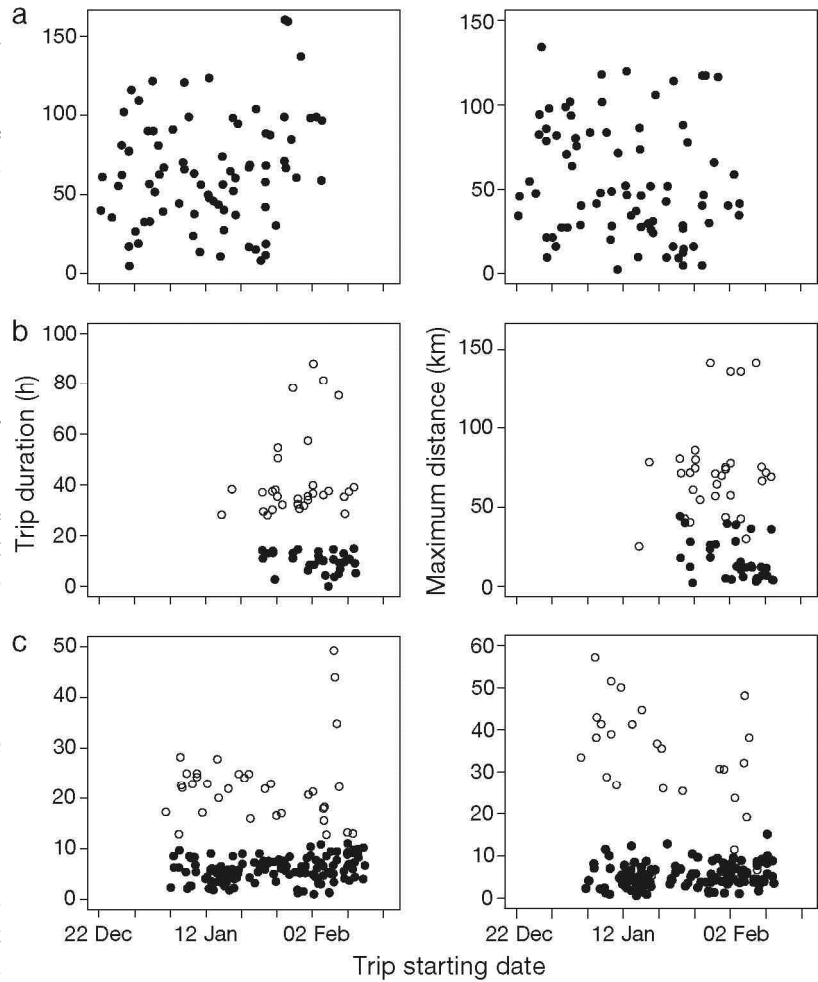

Fig. 3. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica.* Trip duration (left panels) and maximum distance to Bouvetøya (right panels) for (a) Antarctic fur seals, (b) macaroni penguins and (c) chinstrap penguins as a function of the trip starting date. For both penguin species: ○ = overnight trips, ● = day trips. The x-axis is the same for each plot, while the y-axis has a different scale to encompass the different ranges for each species

19.30, p < 0.001), though MACs and CHINs did not differ from each other $(z_{MAC-CHIN} = -1.78$, p = 0.24). The mean haul-out duration for the AFSs was longer than that for the MACs $(z_{AFS-MAC} = -6.47$, p < 0.001) or CHINs $(z_{AFS-CHIN} = -5.67$, p < 0.001).

Arrivals to and departures from the island did not occur randomly throughout the day for any of the 3 species (Fig. 4) (Kolmogorov-Smirnov tests, arrivals-departures: $D_{AFS} = 0.29$, $D_{MAC} = 0.78$, $D_{CHIN} = 0.39$; p < 0.001), and there were significant differences among the species (Kolmogorov-Smirnov tests, de -partures: $D_{AFS-MAC} = 0.69$, $D_{AFS-CHIN} = 0.37$, $D_{MAC-CHIN} = 0.42$; p < 0.001; arrivals: $D_{AFS-MAC} = 0.45$, p < 0.001, $D_{AFS-CHIN} = 0.28$, p < 0.001, $D_{MAC-CHIN} = 0.21$, p < 0.05). AFSs left the island mostly around mid-day and in the evening, with a peak right after sunset (Fig. 4).
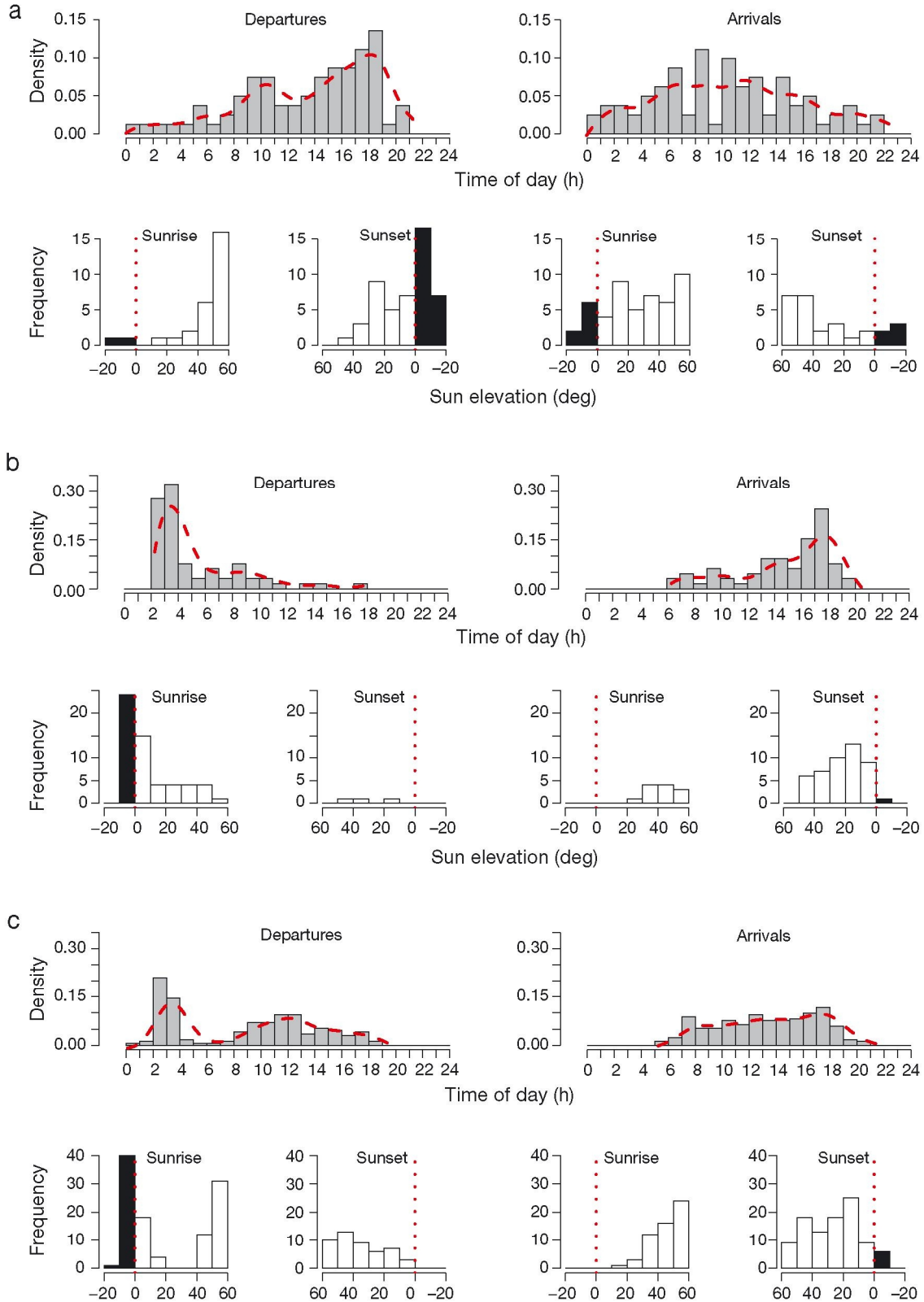
Fig. 4. *Arctocephalus gazella*, *Eudyptes chrysolophus*, *Pygoscelis antarctica*. Density (upper panels) and frequency (lower panels) of departures from and arrivals to Bouvetøya for (a) Antarctic fur seals, (b) macaroni penguins and (c) chinstrap penguins, as a function of the time of day (upper panels) or of the solar elevation (lower panels). Fitted dashed red line = local polynomial kernel smoothers with a bandwidth of 1 h. Vertical dotted red line = solar elevations of 0°, sunrise and sunset in the dawn and dusk histograms, respectively. The histogram bars are shaded according to the period of the day (black = before sunrise or after sunset; white = day). Histograms for dawn periods: solar elevations increasing from left to right (−20 to 60°); histograms for dusk periods: solar elevations decreasing from left to right (60 to −20°)
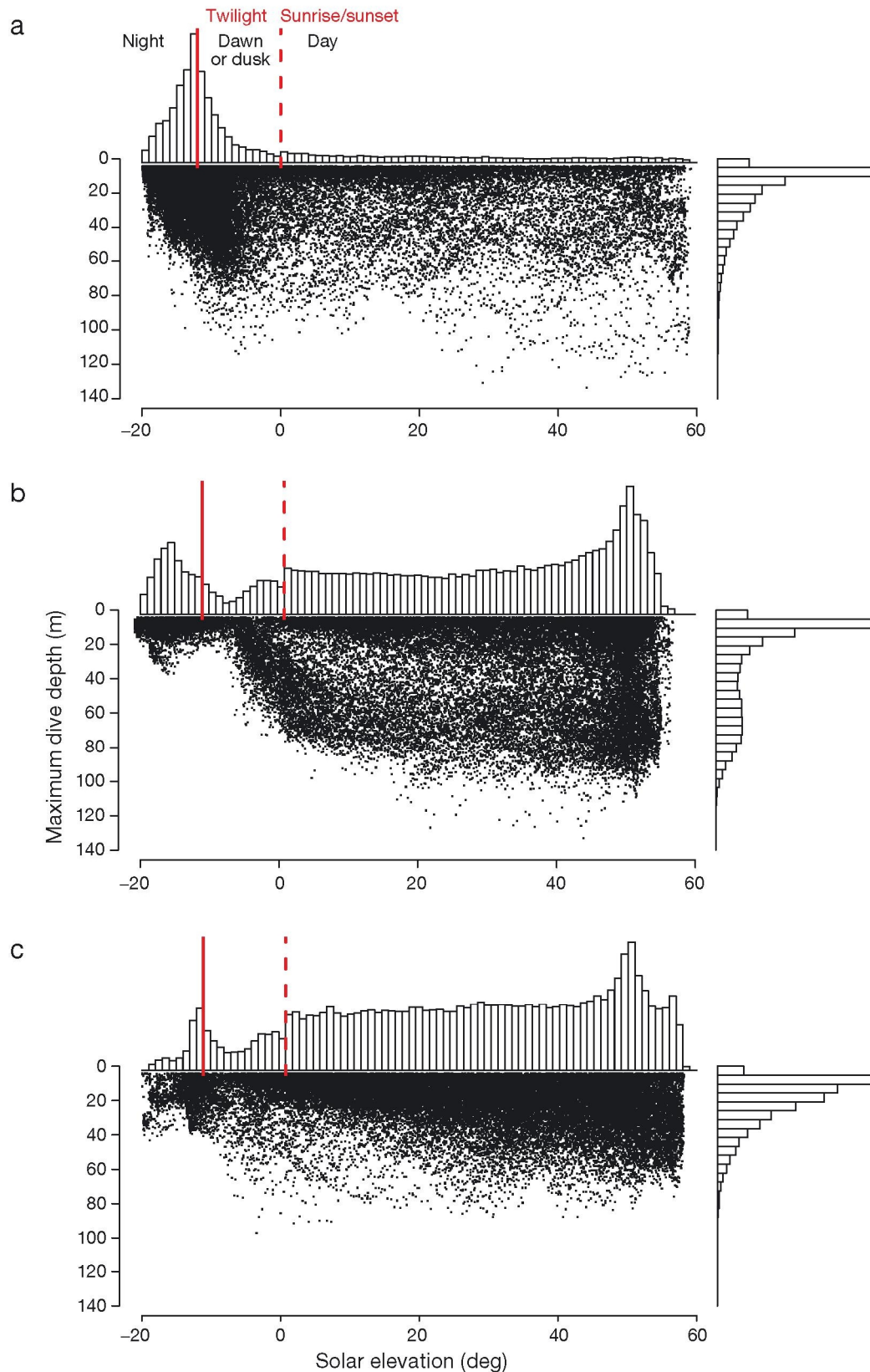
Fig. 5. *Arctocephalus gazella*, *Eudyptes chrysolophus*, *Pygoscelis antarctica*. Scatterplots of maximum dive depths and histograms of dive frequencies (top) as a function of solar elevation combined with histograms of maximum dive depth (right side) for (a) Antarctic fur seals, (b) macaroni penguins and (c) chinstrap penguins tracked from Bouvetøya. Solid line red: nautical twilight (−12°); broken red line: sunrise or sunset (0°). The period on the left of the solid line is night, between the 2 red lines is dusk or dawn, and on the right of the broken red line (indicating sunset or sunrise) is day

Their returns were diffusely spread, with only a slight preference for mid-morning. MACs showed a very distinct peak during the dawn and early mor-ning for departures (with very few birds leaving during the day). This peak was even more evident when departures were expressed as a function of solar elevation, with the majority of departures occurring just before sunrise (Fig. 4). Arrivals were also clustered, peaking just before sunset. CHINs showed 2 departure peaks, one just before sunrise and the other around mid-day. CHINs arrived back to the island throughout the day, with only a slight preference for the late afternoon. Arrivals after sunset were not common for any of the 3 species.

Diving behaviour

Dive summary statistics are presented in Table 1. The proportion of time spent diving during a foraging trip differed significantly between the 3 species (lme $F_{2,231} = 364.8$, $p < 0.001$), with the penguins spending ~50% of their time diving, while AFSs spent only 16% of their time diving. The frequency of diving varied as a function of solar elevation (Fig. 5) for all 3 species. Most AFS diving occurred at night (42%) or at dusk or dawn (31%), with a peak around twilight. Both penguin species did most of their diving during the day (MAC: 79%, CHIN: 87%), with a peak around mid-day. Both penguin species dove very little during the dusk or dawn periods (9%) or during the night (MACs: 12%, CHINs: 4%). The temporal distri bution of diving was significantly dif fe rent between all pair-wise com pari sons among the 3 species (Kol mo gorov-Smirnov test: $D_{AFS-MAC} = 0.29$, $D_{AFS-CHIN} = 0.32$, $D_{MAC-CHIN} = 0.07$; $p < 0.001$).

Maximum dive depth varied as a function of solar elevation (Fig. 5) in a similar manner for the 3 species. Shallower dives typically occurred at night, while deeper dives occurred during the day, and diving to intermediate depths took place during the dusk or dawn period (lme $F_{2,532} = 148$, $p < 0.0001$). The interaction between species and diel period was significant (lme $F_{4,532} = 30$, $p < 0.0001$), but there were no clear interspecific differences (lme $F_{2,77} = 0.5$, $p = 0.6$). Dur-

ing the day MACs dove deeper (~35 m) than AFSs and CHINs (~20 m) $(z_{AFS-MAC} = 4.06$, $p < 0.001$, $z_{AFS-CHIN} = -0.56$, $p = 0.99$, $z_{MAC-CHIN} = 4.63$, $p < 0.001$), during the dusk or dawn period AFSs remained at the same depth as during the day, but the MACs and CHINs did not dive as deeply (~15 m) $(z_{AFS-MAC} = -4.43$, $p < 0.001$, $z_{AFS-CHIN} = -7.35$, $p < 0.001$, $z_{MAC-CHIN} = 1.95$, $p = 0.55$). During the night, the MACs dove less deeply (~8 m) than the AFSs and CHINs (~15 m) $(z_{AFS-MAC} = -4.73$, $p < 0.001$, $z_{AFS-CHIN} = 0.2$, $p = 1$, $z_{MAC-CHIN} = -4.07$, $p < 0.001$). The distrib-ution of the maximum dive depths for the MACs was bi modal, especially during the day, with a peak at ~10 m and another at ~70 m (Fig. 5), whereas it was unimodal for both the AFSs and the CHINs.

Areas of high diving intensity

The most important covariates describing where the animals tended to dive differed according to species. Solar elevation and temperature were present in the top-ranked models for the AFS, temperature and water depth for the MACs and distance from the island and solar elevation for the CHINs (Table 2). Considering all dives throughout a 24 h period, the density of diving was highest in the vicinity of the island (Fig. 6) (20 to 80 km for AFS, 30 to 40 km for MAC, ~10 km for CHIN) for each of the 3 species.

Table 2. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica*. Sets of candidate generalised additive mixed effects models used to explore the variability in the number of dives per hour for each species, instrumented at Bouvetøya. Only models with weights >0.00 are presented, with QAIC and ΔQAIC models. Water depth is introduced in the model as a factor. DIST: the distance to the colony; sunangle: the solar elevation; SST: sea-surface temperature. ×: variable is included in the model

| Model	Inter-cept	DIST	Sun angle	SST	Water depth	df	QAIC	ΔQAIC	Weight
Antarctic fur seals (AFS)									
1.1	0.6651		×	×		8	4087.70	0.00	0.64
1.2	0.6624		×	×	×	9	4088.90	1.24	0.34
1.3	0.6421	×	×	×	×	11	4095.50	7.76	0.01
Macaroni penguins (MAC)									
2.1	1.005			×		6	644.90	0.00	0.67
2.2	1.018			×	×	7	647.20	2.32	0.21
2.3	1.018	×		×	×	9	651.40	6.53	0.03
2.4	1.017				×	5	652.10	7.20	0.02
Chinstrap penguins (CHIN)									
3.1	1.138	×	×			8	24.10	0.00	0.62
3.2	1.125	×	×		×	9	25.90	1.75	0.26
3.3	1.138	×	×	×		10	28.00	3.84	0.09
3.4	1.125	×	×	×	×	11	29.70	5.61	0.04
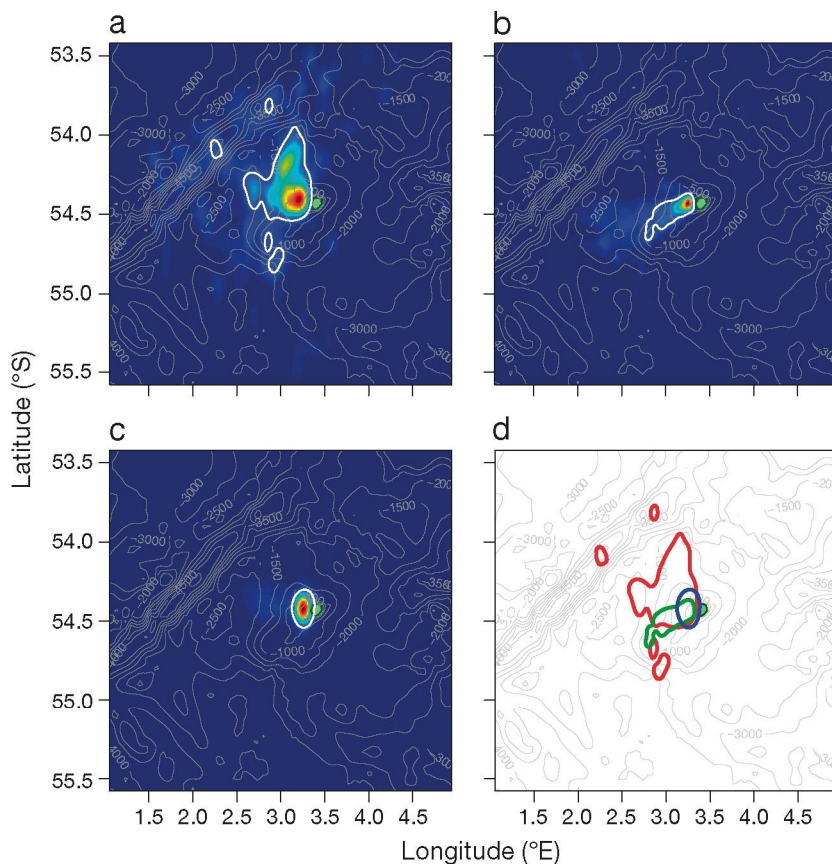
Fig. 6. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica.* Density plots based on the total number of dives performed by (a) Antarctic fur seals, (b) macaroni penguins and (c) chinstrap penguins, instrumented on Bouvetøya. Warm colours: high densities; cold colours: low densities. (d) Areas of high diving intensity for the 3 species (red: Antarctic fur seals; green: macaroni penguins; blue; chinstrap penguins) overlaid on bathymetry

AFSs and MACs concentrated their diving over gentle slopes, where depth of the water ranged broadly from 100 to 1000 m. AFSs showed high densities of dives in more distant areas, above deep oceanic waters. CHINs dove mainly over depths of <500 m. All 3 species showed a peak of diving intensity in water masses that were at temperatures between 0.5 and 1.5°C, with a decrease in diving frequency as the temperature increased (Fig. 7).

There was substantial spatial overlap between the 3 species' core diving areas, with 43, 63 and 99% of the AFS, MAC and CHIN dives, respectively, overlapping with at least 1 other species (Table 3). AFSs covered a larger area than the penguins and had distinct foraging areas at greater distances from the island. CHINs were almost completely encompassed within the AFSs' core areas and also overlapped considerably with MACs. MACs were intermediate in overlapping with the other 2 species. However, when

considering the 3 diel periods, the percentage of overlap between the 3 species decreased dramatically (Table 3), particularly at night. Interestingly diving intensity in core areas differed according to diel period for both penguin species, but this was not the case for the AFSs (Fig. 8). The penguins' night dives were more focussed within oceanic and slope waters at greater distances from the island, compared to daytime diving, particularly for the MACs. During the day, the penguins dove mainly in areas close to the island.

DISCUSSION

All 3 predator species focussed much of their foraging effort on krill; both AFS scats and MAC and CHIN gastric lavage analyses from Bou-vetøya have shown that krill is a key component in the diet at this location, with *Euphausia superba* occurring in > 80 % of the samples for all 3 species. The diet of AFSs and MACs at Bou-vetøya appears to be somewhat more diverse than that of CHINs in this region, with a greater proportion of the samples from the AFSs and MACs containing fish (mainly mycto -phids) and cephalopods (Krafft et al. 2002, Hofmeyr et al. 2010, Norwegian Polar Institute unpubl. data). These results are similar to what has been found in other sub-Antarctic areas such as the Antarctic Peninsula and South Georgia where AFSs (Croxall et al. 1985, Daneri et al. 2008), MACs (Barlow et al. 2002, Hart et al. 2010) and CHINs (Ichii et al. 2007, Miller & Trivelpiece 2008) feed primarily on Antarctic krill (of similar size, ~50 mm), but also prey on the krill-associated fish community (e.g. Van de Putte et al. 2010). It has recently been shown that krill concentrate around isolated islands in the South Atlantic (Atkinson et al. 2008) and, specifically, that high concentrations of krill are found in waters around Bouvetøya compared to nearby, deep oceanic waters (Krafft et al. 2010). Krill recruitment mechanisms in the Bouvetøya area are not well understood, but likely involve a mixture of local recruitment and horizontal advection. Ocean circulation simulation studies suggest that the eastward flow of the Antarc-
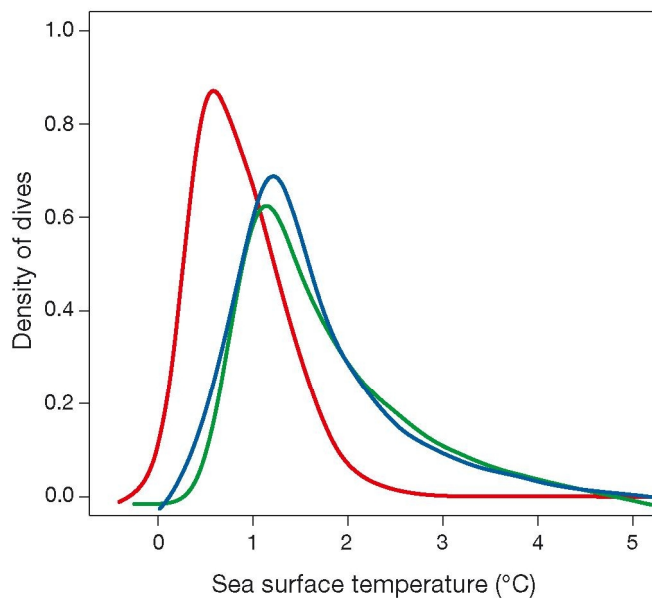
Fig. 7. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica*. Density of dives as a function of the sea-surface temperature for Antarctic fur seals (red), macaroni penguins (green) and chinstrap penguins (blue), instrumented on Bouvetøya. The density function is the result of a local polynomial kernel smoother with a bandwidth of 0.2°C

tic Circumpolar Current (ACC) and the Weddell Gyre could be driving krill advection from the Antarctic Peninsula to the Bouvetøya region (Thorpe et al. 2007, Atkinson et al. 2008, Krafft et al. 2010). This would be consistent with the marked preference of the 3 predator species for waters to the west of the island, with the AFSs and the penguins targeting krill as it first enters the zone accessible to them. Some additional oceanographic connections could also play a role in this regional high prey availability to the west, but the paucity of fine-scale oceano-graphic data from around Bouvet limits the value of further speculation. The tendency to forage on the west side of Bouvetøya has previously been documented for AFSs (Biuw et al. 2009), but is novel in -formation regarding the behaviour of MACs and CHINs, which show extreme clustering in mean bearing of their foraging trips' in this direction.

Antarctic krill is mainly found in cold water and experiences maximum growth rates between 0.5 and 1°C (Atkinson et al. 2006), which is very consistent with the temperature favoured for diving by the predators in our study (~1°C). The normal northern limit of *Euphau sia superba* is the Ant arctic Polar Front (APF) (Atkinson et al. 2008, Krafft et al. 2010). In the Bouvetøya region this occurs at ~52° S, which was also the northern limit of the species tracked in

this study (also see Biuw et al. 2009). The slight difference in the temperatures experienced by the AFSs and the penguins is likely due to the fact that some of the AFSs travelled to the south and southeast of Bou-vetøya, where colder Antarctic water masses occur (see Biuw et al. 2010b). It is important to note that the temperature data in our study are based on the re -cords of the TDRs' temperature sensor. The re sponse time of this sensor is long, which could mean that the temperature taken at the beginning of a dive is in fact air temperature. However, the air temperature at sea level and SST is not likely to differ greatly. Lea & Dubroca (2003) have shown that there is a significant positive correlation between weekly averaged temperatures measured from satellite data and the logged SST from TDRs carried by AFSs at small spatial scales.

Antarctic krill undertake vertical diel migrations triggered by light cycles (Tomo 1983, Godlewska & Klusek 1987, O'Brien 1987, Zhou & Dorland 2004). They tend to form dense schools at greater depths, often just above the thermocline, during the day and occur in more dispersed swarms in shallow waters at night, when their own feeding behaviour makes them more vulnerable to predators because they do not display coordinated swimming behaviour (God -

Table 3. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica*. Percent overlap of the foraging areas of the 3 predator species (AFS: Antarctic fur seal; MAC: macaroni penguins; CHIN: chinstrap penguins), instrumented at Bouvetøya, according to diel period

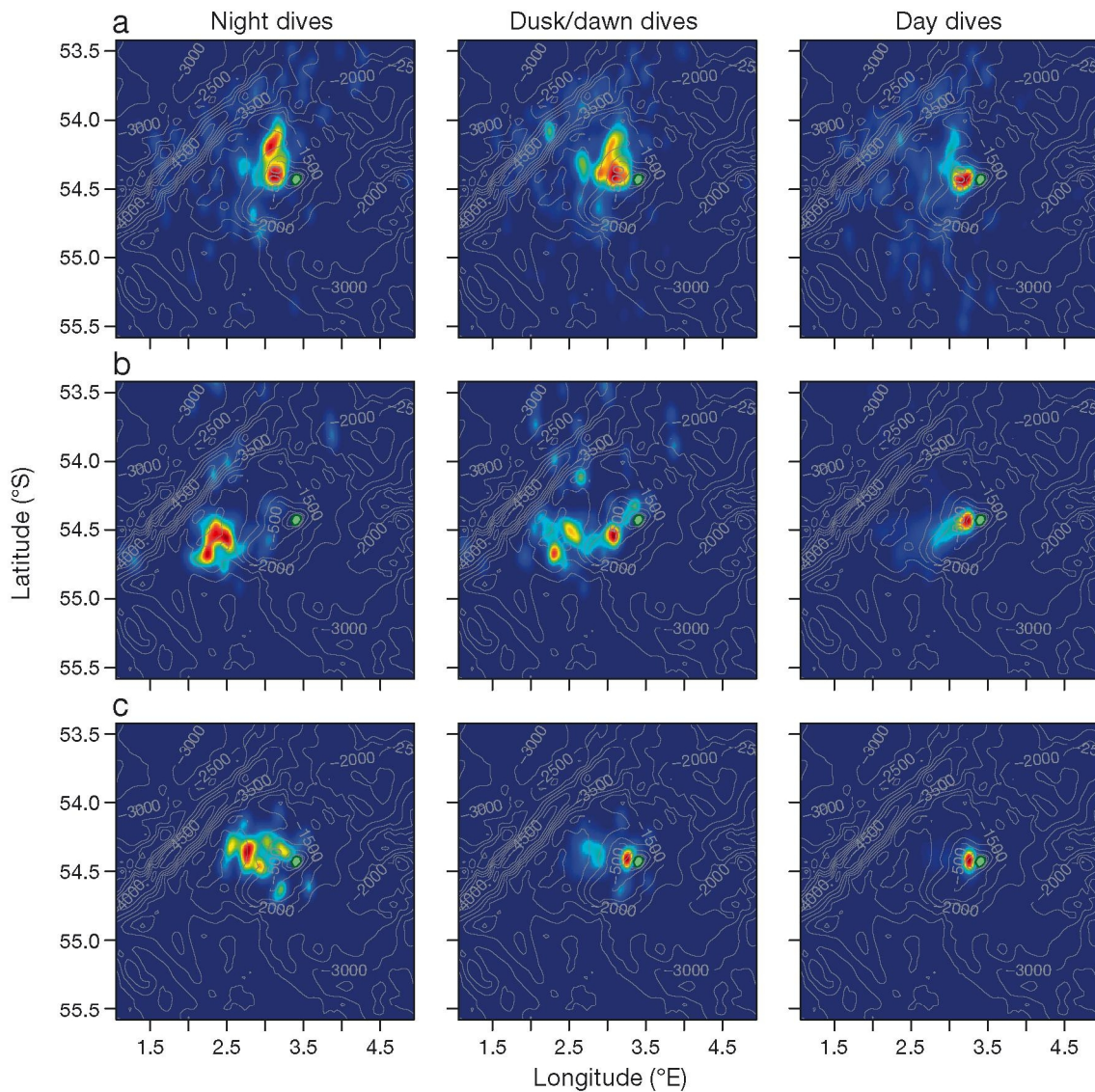|	AFS	MAC	CHIN
Whole 24 h period			
AFS	–	62	90
MAC	40	–	81
CHIN	15	21	–
2 other spp.	43	63	99
Day			
AFS	–	11	11
MAC	15	–	27
CHIN	6	9	–
2 other sp.	30	26	57
Night			
AFS	–	6	23
MAC	3	–	3
CHIN	4	1	–
2 other sp.	7	8	26
Dusk or dawn			
AFS	–	5	27
MAC	2	–	4
CHIN	7	3	–
2 other sp.	10	13	31

Fig. 8. *Arctocephalus gazella, Eudyptes chrysolophus, Pygoscelis antarctica.* Density plots highlighting the regions of high diving intensity based on the total number of dives performed by (a) Antarctic fur seals, (b) macaroni penguins and c) chinstrap penguins, instrumented on Bouvetøya, according to the different periods of the day. Warm colours: high density; cold colours: low density. The densities are calculated relative to the number of dives occurring during each diel period; therefore, the plots are not directly comparable within a species

lewska & Klusek 1987, Zhou & Dorland 2004). Thus, it was not surprising that the AFSs and penguins in this study displayed diel diving patterns. The 3 species all performed dives that were concentrated in the upper 20 m during the night, while dives were more scattered in the water column and generally deeper during the day. AFSs performed most of their daytime dives above 60 m. MACs seemed to target 2 different layers, as shown by the bimodal distribution of their maximum dive depths, with a shallow peak at ~10 m and an other deep one at ~70 m, both occurring

throughout the day. This suggests that the MACs were perhaps alternating between energy-costly but profitable deep dives and less profitable but less energy-demanding shallower dives. Similar to the AFS, CHINs dove to depths of ~60 m during their daytime diving.

Diving frequency varied according to diel period among the 3 predator species. Female AFSs dive mainly during the night in order to target krill when it is the closest to the surface, maxi mising their energy intake compared to the energy spent diving

(e.g. Costa 1991, Ichii et al. 2007, Staniland & Robinson 2008, Biuw et al. 2009). Like most pinnipeds, AFSs use their tactile senses (especially their whiskers) extensively and are hence not strictly limited by ambient light, which allows them to forage during the night or below the photic zone (Schuster-man et al. 2000, Dehnhardt et al. 2001). In addition, energy-rich, deep-dwelling myctophid fish are associated with krill shoals at the surface during the night (Tomo 1983, Ichii et al. 2007), enhancing the advantages of night-time predation. However, although night dives were definitively more numerous, the AFSs also performed occasional longer, deeper dives during the day to depths of 80 to 100 m (Zhou & Dor-land 2004, Ichii et al. 2007). The diel pattern observed for the AFSs was in marked contrast to that observed for both species of penguins, which per-formed most of their diving during the day with a few dusk/dawn or night-time dives. This is consistent with previous studies of MACs and CHINs conducted elsewhere (Jansen et al. 1998, Hart et al. 2010, Ainley & Ballard 2012). Penguins typically forage during the day and stay on shore at night, although some species, including MACs and CHINs, have bimodal foraging strategies, alternating day and overnight trips (Croxall et al. 1988, Jansen et al. 1998, Ichii et al. 2007), as was observed in this study. It has been suggested that penguins tend to use vision as their primary sense while foraging, partly explaining the preference for daytime diving (Bengston et al. 1993, Jansen et al. 1998, 2002). Previous studies have shown that king penguins *Apten-odytes patagonicus* have a lower prey ingestion rate when foraging during the night than during the day (Kooyman et al. 1992). In Adelie penguins *Pygoscelis adeliae* dive depth has been shown to be directly cor-related to ambient light levels, suggesting that light was a limiting factor for these birds (Wilson et al. 1993, Ainley & Ballard 2012). Light also seems to be a key factor governing the MACs and CHINs diving behaviour at Bouvetøya given that solar elevation had a significant influence on the number of dives per hour. However, the preference for daytime diving might also be linked to non-foraging issues, such as predator avoidance (Ainley & Ballard 2012). Penguins are thought to be less visible to predators during the day because their counter-shaded plumage render them difficult to see from beneath when light is above them (Tickell 2003). In contrast, their white bellies might stand out against the darker surface during the night. Penguin predators in the sub-Antarctic region include leopard seals *Hydrurga lepto nyx*, killer whales *Orcinus orca* and also AFSs

(Hofmeyr & Bester 1993, Casaux et al. 2004, Daneri et al. 2008, Charbonnier et al. 2010). However, no leo -pard seal observations have ever been reported from Bouvetøya, and killer whales are not regular visitors to the island's coastal areas (Guinet 2000, Lauriano et al. 2007, Andrews et al. 2008, Pitman & Durban 2010, Reisinger et al. 2011). Predation on penguins by AFSs, particularly non-breeding males, has been documented on several occasions on the Antarctic Peninsula, and penguin remains have been identified in a large proportion of scats at some sub-Antarctic islands — contributing in some cases up to 75% of the dietary biomass of the AFSs (Casaux et al. 2004, Daneri et al. 2008, Charbonnier et al. 2010). Daneri et al. (2008) suggest fur seals turn to preying on penguins in periods of low krill abundance, when the energetic cost of foraging for krill becomes too high. Bitten penguins are observed on Bouvetøya with some regularity; the bite marks match the gape of large fur seals (Norwegian Polar Institute unpubl. data). Penguins might avoid foraging and transiting around the island at the same time as the AFSs to the degree that is possible. However, both MACs and CHINs do some night diving (although daytime diving was much more prevalent). This is likely facilitated by krill and mycto phids being somewhat bio -luminescent (Tomo 1983, O'Brien 1987) and at least intermittently visible to these predators at night or at depth (i.e. in low light conditions).

The timing of movements to or from the island was linked to light levels and the day or night foraging strategies of each species. AFSs departed from the breeding beach in the late afternoon to reach for -aging areas at night, when krill availability at the surface is at its maximum. The more dispersed distribution of arrival times reflects the variability in their trip durations and distances travelled from the island. The penguins foraged mostly during daytime, and their departures were mainly clustered in the early morning and arrivals in the evening. This was in accordance with trips lasting either ~18 h (day trips) or ~35 h (overnight trips) for the MACs. In CHINs, the switching between short and long trips was reflected in the bimodal distribution of departures, allowing mates to each perform a short day trip or one partner to do an overnight trip while the other did only a day trip (see Ichii et al. 2007). Whether the penguins were at sea or on land, low light levels seemed to result in avoidance of transiting from or to the island. This avoidance might be related to higher predation risks (see above) or the lack of prominent navigation cues used by penguins at night. Birds generally use a combination of magnetic and visual

cues for navigation (Jansen et al. 1998). Adelie penguins require a minimum light intensity to navigate around the ice edge (Emlen & Penney 1966). Similarly CHINs and MACs might need a minimum amount of light to travel across the terrain of the intertidal zone, particularly given the rough weather conditions that dominate around Bouvetøya. The large body size of AFSs might make them less sensitive to the rough seas around the island, allowing them to transit through the narrow shelf region around the island in the dark.

Defining foraging areas using only position data can be quite challenging, because behavioural states have to be inferred from animals' 2-dimen-sional movements (Hart et al. 2010). However, position data in combination with TDR data allow us to look at positions and behavioural state simultaneously. Dive intensity can then be used as a proxy for foraging intensity, assuming that when an animal dives below a certain threshold, it is foraging (regardless of the actual foraging success). Locations of areas where diving intensity was high showed that AFSs and MACs dove mostly over slopes and in the top layers of oceanic waters (up to 1000 m deep) at somewhat greater distances from the island than the CHINs. The latter species mainly foraged close to the island in shallower waters (<500 m). However, the specific locations of foraging areas were influenced by the diel period in which the diving occurred, particularly for the penguins. Differences between diel periods were not striking for AFSs, but MAC and CHIN night dives were mainly located over deeper oceanic waters as opposed to day dives, which were concentrated in shallower waters closer to the island. This reflects a trade-off faced by the penguins and illustrates the differences in life history between mammalian and avian predators. In contrast to mammals, which produce milk, most penguins cannot concentrate the material fed to their young so they need to provision their offspring at short intervals with regurgitated food (Costa 1991). This time-minimising strategy has been shown to be the case for CHINs as opposed to the energy-maximising strategy used by AFSs (Ichii et al. 2007). These 2 strategies are also illustrated by the low proportion of time spent diving by the AFSs looking for the most profitable areas and the higher proportion of time spent diving by the penguins that must target areas closer to home. In this study both penguin species alternated multiple short, day foraging trips near the colony with less frequent but longer overnight trips to areas at greater distances. CHIN

overnight foraging in other areas has been shown to target energy-rich myctophids associated with krill swarms that would cover the additional energy expenses of a longer trip (Jansen et al. 1998). These longer overnight foraging trips might serve as self-provisioning of the adult birds, as has been shown in procellariiform seabirds and little auks *Alle alle*, while the short day trips likely provision only the chicks (Waugh et al. 2000, Steen et al. 2007).

Instrument attachments can alter the behaviour of animals (see Wilson & McMahon 2006 for a review) by creating discomfort or causing additional energy expenditure. However, results of studies designed to explore the potential effects of instruments are conflicting (Boyd et al. 1991, Croll et al. 1991, Walker & Boveng 1995, Francis & Boness 1998), and there is no clear evidence as to which behavioural parameter is the most affected. Nevertheless, we respected the rule proposed by Hawkins (2004), suggesting that animals should not carry devices that exceed 5% of their mass to avoid unsustainable additional energetic costs (range: 0.4 to 3.1% in our study) and careful attention was paid to the frontal area and hydrodynamic shape of the instruments used, which is likely more important than the actual mass carried (see Ballard et al. 2012 for a review). Body mass records for the study animals over the deployment periods suggest that the energetic cost of carrying the instruments was either negligible or compensated for behaviourally.

Our study indicates overlapping resource use by krill predators at Bouvetøya. They appear to exploit the same krill population and their areas of high diving intensity overlap significantly. However, there was also evidence of partial resource partitioning via temporal segregation between the species. The ob served vertical segregation in dive depth per diel period is also consistent with some resource partitioning (Friedlaender et al. 2009, 2011), particularly between MACs and CHINs which foraged at the same time. The distribution of dive depths for MACs was clearly bimodal with peaks at ~10 and ~70 m, showing that they targeted 2 distinct layers in the water column during the day. The upper one (<60 m) was exploited by all 3 predator species, while the deeper one (>60 m) was only intensely targeted by MACs. Therefore, competitive pressure is likely re duced by both temporal and vertical segregation.

It is also possible that the competitive pressure is further reduced by subtle dietary differences be -tween species. Diet analyses from Bouvetøya have

shown that AFSs and MACs have a more diverse diet than CHINs, although they all rely heavily on krill. Krill was present in >80% of the samples in MACs and in 99% of the AFS and CHIN samples. Fish was an important dietary component by mass only in the MACs diet, which also consume a greater variety of fish species (Krafft et al. 2002, Hofmeyr et al. 2010, Norwegian Polar Institute unpubl. data). This suggests that some dietary segregation occurs among the 3 species and that at least MACs would be able to niche shift in periods of low krill abundance, as has been demonstrated at South Georgia (Barlow et al. 2002, Waluda et al. 2010).

Despite the potential for competition among the 3 krill predators at Bouvetøya, the available evidence suggests that the recently observed declines in penguin numbers at Bouvetøya are due to a shortage of breeding space created by landslides and the presence of the large AFS colony, rather than food limitation. This is in contrast to the conclusions of Trathan et al. (2012), who suggested that MAC declines at South Georgia are linked to food competition created by the expanding AFS colonies in the region. But, these authors noted that the implied resource competition and the observed population changes may be exacerbated by recent reductions in Antarctic krill abundance, which have in turn been linked to reductions in seasonal sea ice following rapid regional warming. AFS numbers are currently quite stable at Bouvetøya (Hofmeyr et al. 2005, Norwegian Polar Institute unpubl. data for 2007–2008), and maternal attendance patterns do not show the signs of vari ability that accompanies food shortages in this species (see Boyd 1993, Krafft et al. 2002, Biuw et al. 2009). But, perhaps even more importantly, two-thirds of the CHINs tagged at Bouvetøya during the 2007/2008 season raised 2 chicks; the lack of brood reduction strongly suggests that they had abundant food. It has also been shown that this portion of the Southern Ocean is quite productive, and currently the region of Bouvetøya experiences relatively little human fishing pressure compared to other regions (Atkinson et al. 2008, Krafft et al. 2010, Nicol et al. 2012). Additionally, the extreme regional warming in the western parts of the South Atlantic has not been documented for the Bouvetøya area, or areas to the east (Turner et al. 2009, Huang et al. 2011).

If krill stock reduction takes place around Bouve -tøya in the future, it would likely be most disadvantageous to the penguins, particularly the CHINs. AFSs might be able to adjust the duration and direction of their foraging trips more readily (see Barlow et al.

2002). In such circumstances, penguins might have to exploit alternative, lower quality prey resources, which might result in decreased reproductive success. They would also likely be subjected to greater predation risks from AFSs. Between the 2 penguin species, MACs appear to have the greatest ability to niche shift, due to their more diverse diet (Barlow et al. 2002, Krafft et al. 2002, Waluda et al. 2010), their capability to exploit a larger portion of the water column and their abilities to travel greater distances than CHINs. It is important to note that only breeding female AFSs and MACs were tagged during this study, while CHINs of both sexes were instrumented. The pressure of intensive foraging during the breeding period is shared by both sexes of CHINs, while only the female AFSs and primarily the female MACs support this cost. In the context of competition it would also be interesting to have information about the foraging behaviour of males and non-breeding individuals, which might influence the distribution of the breeding individuals.

In summary, we present the first simultaneous observations of at-sea behaviour and attendance patterns of the 3 krill-predator species breeding at Bou-vetøya. Our major findings are consistent with patterns recorded at other locations in the Scotia Sea and off the Antarctic Peninsula. At Bouvetøya, AFSs, MACs and CHINs rely mainly on krill of similar size (and associated fish communities), thus sharing a common resource. Currently, it ap pears that modest (or little) competitive pressure drives a limited degree of niche partitioning, which is achieved via geographic, temporal and vertical segregation of foraging effort. The overall abundance of prey in the area appears to be adequate to meet the current predator populations' needs. However, if re gional warming reduces krill recruitment, or human fishing pressure increases markedly, penguin populations, particularly CHINs, might experience direct competitive pressure from (and perhaps also increased pre-dation by) AFSs.

LITERATURE CITED

Ainley D, Ballard G (2012) Non-consumptive factors affecting foraging patterns in Antarctic penguins: a review and synthesis. Polar Biol 35: 1-13

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr 19: 716-723

Alanärä A, Burns MD, Metcalfe NB (2001) Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. J Anim Ecol 70: 980-986

Alley TR (1982) Competition theory, evolution, and the concept of ecological niche. Acta Biotheor 31: 165-179

Andrews RD, Pitman RL, Ballance LT (2008) Satellite tracking reveals distinct movement patterns for Type B and C killer whales in the southern Ross Sea, Antarctica. Polar Biol 31: 1461-1468

Atkinson A, Shreeve RS, Hirst AG, Rothery P and others (2006) Natural growth rates of Antarctic krill (Euphausia superba). II. Predictive models based on food, tem -perature, body length, sex, and maturity stage. Limnol Oceanogr 51: 973-987

Atkinson A, Siegel V, Pakhomov EA, Rothery P and others (2008) Ocean circumpolar habitats of Antarctic krill. Mar Ecol Prog Ser 362: 1-23

Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012) Co -existence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biol Conserv 156: 72–82

Barlow KE, Boyd IL, Croxall JP, Reid K, Staniland IJ, Brierley AS (2002) Are penguins and seals in competition for Antarctic krill at South Georgia? Mar Biol 140: 205-213

Barton K (2012) MuMIn package: model selection and model averaging based on information criteria. R package Version 1.7.11, R Foundation for Statistical Computing, Vienna

Beauplet G, Dubroca L, Guinet C, Cherel Y, Dabin W, Gagne C, Hindell M (2004) Foraging ecology of sub-antarctic fur seals Arctocephalus tropicalis breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. Mar Ecol Prog Ser 273: 211-225

Bengston JL, Croll DA, Goebel M (1993) Diving behaviour of chinstrap penguins at Seal Island. Antarct Sci 5: 9-15

Biuw M, Krafft BA, Hofmeyr GJG, Lydersen C, Kovacs KM (2009) Time budgets and at-sea behaviour of lactating female Antarctic fur seals Arctocephalus gazella at Bou-vetøya. Mar Ecol Prog Ser 385: 271-284

Biuw M, Lydersen C, De Bruyn PJN, Arriola A, Hofmeyr GJG, Krintzinger P, Kovacs KM (2010a) Long-range migration of a chinstrap penguin from Bouvetøya to Montagu Island, South Sandwich Island. Antarct Sci 22: 157-162

Biuw M, Nøst ØA, Stien A, Zhou Q, Lydersen C, Kovacs KM (2010b) Effects of hydrographic variability on the spatial, seasonal and diel diving patterns of southern elephant seals in the eastern Weddell Sea. PLoS One 5: e13816

Boyd IL (1993) Pup production and breeding of Antarctic fur seals (Arctocephalus gazella) at South Georgia. Antarct Sci 5: 17-24

Boyd IL (1998) Time and energy constraints in pinniped lactation. Am Nat 152: 717-728

Boyd IL (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets.

Behav Ecol 10: 198-208

Boyd IL, Lunn NJ, Barton T (1991) Time budgets and foraging characteristics of lactating Antarctic fur seals. J Anim Ecol 60: 577-592

Boyd IL, Staniland IJ, Martin AR (2002) Distribution of foraging by female Antarctic fur seals. Mar Ecol Prog Ser 242: 285-294

Bretz F, Hothorn T, Westfall P (2010) Multiple comparisons using R. CRC Press, Boca Raton, FL

Burnham KP, Anderson DR (2002) Model selection and multi model inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

Casaux R, Bellizia L, Baroni A (2004) The diet of the Antarctic fur seal Arctocephalus gazella at Harmony Point, South Shetland Islands: evidence of opportunistic foraging on penguins? Polar Biol 27: 59-65

Charbonnier Y, Delord K, Thiebot JB (2010) King-size fast food for Antarctic fur seals. Polar Biol 33: 721-724

Costa DP (1991) Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. Am Zool 31: 111-131

Croll DA, Osmek SD, Bengston J (1991) An effect of instrument attachment on foraging trip duration in chinstrap penguins. Condor 93: 777-779

Croll DA, Demer DA, Hewitt RP, Jansen JK, Goebel ME, Tershy BR (2006) Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). J Zool 269: 506-513

Croxall JP, Davis LS (1999) Penguins: paradoxes and patterns. Mar Ornithol 27: 1-12

Croxall JP, Everson I, Kooyman GL, Rickett C, Davis RW (1985) Fur seal diving behaviour in relation to vertical distribution of krill. J Anim Ecol 54: 1-8

Croxall JP, Davis RW, O'Conell MJ (1988) Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. Condor 90: 157-167

Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD (1993) Diving patterns and performances in the macaroni penguin Eudyptes chrysolophus. J Zool 230: 31-47

Daneri GA, Carlini AR, Harrington A, Balboni L, Hernandez CM (2008) Interannual variation in the diet of non-breeding male Antarctic fur seals, Arctocephalus gazella, at Isla 25 de Mayo/King George Island. Polar Biol 31: 1365-1372

David JHM, Meyer MA, Best PB (1990) The capture, hand ling and marking of free-ranging adult South African (Cape) fur seals. S Afr J Wildl Res 20: 5-8

de Bruyn PJN, Tosh CA, Oosthuizen WC, Bester MN, Arnould JPY (2009) Bathymetry and frontal system interactions influence seasonal foraging movements of lactating subantarctic fur seals from Marion Island. Mar Ecol Prog Ser 394: 263-276

Dehnhardt G, Mauck B, Hanke W, Bleckmann H (2001) Hydrodynamic trail-following in harbor seals (Phoca vitulina). Science 293: 102-104

Emlen JT, Penney RL (1966) The navigation of penguins. Sci Am 215: 104-113

Francis J, Boness D (1998) A protracted foraging and attendance cycle in female Juan Fernandez fur seals. Mar Mamm Sci 14: 552-574

Friedlaender AS, Lawson G, Halpin P (2009) Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. Mar Mamm Sci 25: 402-415

Friedlaender AS, Johnston DW, Fraser WR, Burns J, Halpin PN, Costa DP (2011) Ecological niche modelling of sym-patric krill predators around Marguerite Bay, West Antarctic Peninsula. Deep-Sea Res II 58: 13-16

Godlewska M, Klusek Z (1987) Vertical distribution and diurnal migrations of krill *Euphausia superba* Dana from hydroacoustical observations, SIBEX, December 1983/ January 1984. Polar Biol 8: 17-22

Goldsworthy SD, Page B, Welling A, Chambellant M, Brad-shaw CJA (2010) Selection of diving strategy by Antarctic fur seals depends on where and when foraging takes place. Mar Ecol Prog Ser 409: 255-266

Green JA, Butler PJ, Woakes AJ, Boyd I (2002) Energy requirements of female Macaroni penguins breeding at South Georgia. Funct Ecol 16: 671-681

Guinet C (2000) Coordinated attack behaviour and prey sharing by killer whales at Crozet Archipelago: strategies for feeding on negatively-buoyant prey. Mar Mamm Sci 16: 829-834

Hardin G (1960) The competitive exclusion principle. Science 131: 1292-1297

Hart T, Coulson T, Trathan P (2010) Time series analysis of biologging data: autocorrelation reveals periodicity in diving behaviour in macaroni penguins. Anim Behav 79: 845-855

Hawkins P (2004) Bio-logging and animal welfare: practical refinements. Mem Natl Inst Polar Res (Jpn) 58: 58-68

Hofmeyr GJG, Bester MN (1993) Predation on king penguins by Antarctic fur seals. S Afr J Antarct Res 23: 71-74

Hofmeyr GJG, Krafft BA, Kirkman SP, Bester MN, Lydersen C, Kovacs KM (2005) Population changes of Antarctic fur seals at Nyrøysa, Bouvetøya. Polar Biol 28: 725-731

Hofmeyr GJG, Bester MN, Kirkman SP, Lydersen C, Kovacs KM (2010) Intraspecific differences in the diet of Ant arctic fur seals at Nyrøysa, Bouvetøya. Polar Biol 33: 1171-1178

Huang T, Sun L, Stark J, Wang Y, Cheng Z, Yang Q, Sun S (2011) Relative changes in krill abundance inferred from Antarctic fur seals. PLoS ONE 6: 1-4

Hutchinson GE (1957) Population studies: animal ecology and demography: concluding remarks. Cold Spring Harb Symp Quant Biol 22: 415-427

Huyser O (2001) Bouvetøya. In: Important bird areas in Africa and associated islands. Birdlife Conserv Series No. 11. Pices Publications and Birdlife International, New-bury, p 113-115

Ichii T, Bengston JL, Boveng PL, Takao Y and others (2007) Provisioning strategies of Antarctic fur seals and chin-strap penguins produce different responses to distribution of common prey and habitat. Mar Ecol Prog Ser 344: 277-297

Jammalamadaka S, SenGupta A (2001) Topics in circular statistics, Section 1.3. World Scientific Press, Singapore

Jansen JK, Boveng PL, Bengtson JL (1998) Foraging modes of chinstrap penguins: contrasts between days and night. Mar Ecol Prog Ser 165: 161-172

Jansen JK, Rusell RW, Meyer WR (2002) Seasonal shifts in the provisioning behaviour of chinstrap penguins *Pygo -scelis antaictica*. Oecologia 131: 306-318

Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, Ridoux V, Kooyman CA (1992) Diving behaviour and energetics during foraging cycles in king penguins. Ecol Monogr 62: 143-163

Kovacs KM, Lavigne DM (1992) Maternal investment in otariid seals and walruses. Can J Zool 70: 1953-1964

Krafft B, Hofmeyr GJG, Keith D, Harck BIB, Kovacs KM

(2002) Studies of seals and seabirds on Bouvetøya 2000-2001—field work and preliminary results. Norwegian Polar Institute Rep Ser 120: 62-71

Krafft B, Melle W, Knutsen T, Bagøien E, Broms C, Ellertsen B, Siegel V (2010) Distribution and demography of Antarctic krill in the Southeast Atlantic sector of the Southern Ocean during the austral summer 2008. Polar Biol 33: 957-968

Lauriano G, Fortuna CM, Vacchi M (2007) Observation of killer whale (*Orcinus orca*) possibly eating penguins in Terra Nova Bay, Antarctica. Antart Sci 19: 95-96

Lea MA, Dubroca L (2003) Fine-scale linkage between the diving behaviour of Antarctic fur seals and oceano-graphic features in the southern Indian Ocean. ICES J Mar Sci 60: 990-1002

Lea MA, Hindell M, Guinet C, Goldworthy S (2002) Variability in the diving activity of Antarctic fur seals *Artco-cephalus gazella,* at Iles Kerguelen. Polar Biol 25: 269-279

Lunn NJ, Boyd IL (1993) Effect of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. J Zool 229: 55-67

McCafferty DJ, Boyd I, Walker T, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. Mar Ecol Prog Ser 166: 285-299

Meeus J (1991) Astronomical algorithms. Willmann-Bell, Richmond, VA

Meyer RW, Bengston JL, Jansen J, Russell R (1997) Relationships between brood size and parental provisioning performance in chinstrap penguins during the chick guard phase. Polar Biol 17: 228-234

Miller A, Trivelpiece W (2008) Chinstrap penguins alter foraging and diving behaviour in response to the size of their principle prey, Antarctic krill. Mar Biol 154: 201-208

Miller A, Kappes M, Trivelpiece S, Trivelpiece W (2010) For-aging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. Condor 112: 683-695

Nicol S, Foster J, Kawaguchi S (2012) The fishery for Antarctic krill—recent developments. Fish Fish 13: 30-40

O'Brien DP (1987) Description of escape responses of krill (Crustacea: Euphausiacea), with particular reference to swarming behaviour and the size and proximity of predator. J Crustac Biol 7: 449-457

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs DR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, p 154-177

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Mat thio -poulos J (2008) State-space models of individual animal movement. Trends Ecol Evol 23: 87-94

Patterson TA, McConnell B, Fedak M, Bravington MV, Hindell MA (2010) Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. Ecology 91: 273-285

Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team (2012) nlme: linear and nonlinear mixed effects models. R package Version 3.1-104, R Foundation for Statistical Computing, Vienna

Pitman RL, Durban JW (2010) Killer whale predation on penguins in Antarctica. Polar Biol 33: 1589-1594

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: www.R-project.org

Reid K, Watkins JL, Croxall JP, Murphy EJ (1999) Krill pop-

ulation dynamics at South Georgia 1991-1997, based on data from predators and nets. Mar Ecol Prog Ser 177: 103-114

Reid K, Davis D, Staniland IJ (2006) Spatial and temporal variability in the fish diet of Antarctic fur seals *(Arcto-cephalus gazella)* in the Atlantic sector of the Southern Ocean. Can J Zool 84: 1025-1037

Reisinger RR, de Bruyn PJN, Tosh CA, Oosthuizen WC, Mufanadzo NT, Bester MN (2011) Prey and seasonal abundance of killer whales at sub-Antarctic Marion Island. Afr J Mar Sci 33: 99-105

Schoener TW (1974) Resource partitioning in ecological communities. Science 185: 27-39

Schusterman RJ, Kastak D, Levenson D, Reichmuth C, Southall B (2000) Why pinnipeds don't echolocate? J Acoust Soc Am 107: 2256-2264

Staniland IJ, Robinson S (2008) Segregation between sexes: Antarctic fur seals, *Arctocephalus gazella* at South Georgia. Anim Behav 75: 1581-1590

Staniland IJ, Reid K, Boyd IJ (2004) Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella.* Mar Ecol Prog Ser 275: 263-274

Staniland I, Morton A, Robinson SL, Malone D, Forcada J (2011) Foraging behaviour in two Antarctic fur seal colonies with differing population recoveries. Mar Ecol Prog Ser 434: 183-196

Steen H, Vogedes D, Broms F (2007) Little auks *(Alle alle)* breeding in a High Arctic fjord system: Bimodal foraging strategies as a response to poor food quality? Polar Res 26: 118-125

Thorpe SE, Murphy EJ, Watkins JL (2007) Circumpolar connections between Antarctic krill *(Euphausia superba)* populations: investigating the role of ocean and sea ice transport. Deep-Sea Res II 54: 792-810

Tickell WLN (2003) White plumage. Waterbirds 26: 1-12

Tomo AP (1983) Study on the diurnal migration of *Euphausia superba* and the formation of shoals. Ber Polarforsch 4: 191-195

Tou JC, Jaczinsky J, Chen YC (2007) Krill for human consumption: nutritional value and potential health benefits. Nutr Rev 65: 63-77

Trathan PN, Ratcliffe N, Masden EA (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35: 1-11

Trivelpiece WZ, Trivelpiece S, Volkman NJ (1987) Ecological segregation of Adelie, gentoo and chinstrap pen-

guins at King George Island, Antarctica. Ecology 68: 351-361

Trivelpiece WZ, Buckelew S, Reiss C, Trivelpiece SG (2007) The winter distribution of chinstrap penguins from two breeding sites in the South Shetland Islands of Antarctica. Polar Biol 30: 1231-1237

Turner J, Bindschadler RA, Convey P, Di Priso G and others (2009) Antarctic climate change and the environment. SCAR, Cambridge

US Naval Oceanography Portal (2011) Rise, set and twilight definitions from the US Astronomical Applications Dept (USNO). Available at: www.usno.navy.mil/USNO/ astronomical-applications/astronomical- information- center/ rise-set-twi-defs (accessed 10 May 2012)

Van de Putte AP, Jackson GD, Pakhomov E, Flores H, Vol ckaert FAM (2010) Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during the BROKE-West campaign. Deep Sea Res I 9/10: 956-967

Walker BG, Boveng PL (1995) Effect of time-depth recorders on maternal foraging and attendance behaviour of Antarctic fur seals *(Arctocephalus gazella).* Can J Zool 73: 1538-1544

Waluda CM, Collins MA, Black A, Staniland IJ, Trathan PN (2010) Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. Mar Biol 157: 99-112

Wand M, Ripley BD (2005) KernSmooth: functions for kernel smoothing for Wand and Jones. Available at: http: // cran. r-project.org/ web/ packages/ Kern Smooth/ Kern Smooth. pdf (accessed 30 June 2012)

Waugh SM, Weimerskirch H, Cherel Y, Prince P (2000) Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. Condor 102: 804-813

Wilson RP, McMahon CR (2006) Measuring devices on wild animals: What constitutes acceptable practice? Front Ecol Environ 4: 147-154

Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: Whose dinner by candlelight? Mar Ecol Prog Ser 94: 101-104

Woods S (2006) Generalized additive models: an introduction with R. CRC/Chapman & Hall, London

Zhou M, Dorland RD (2004) Aggregation and vertical migration behaviour of *Euphausia superba*. Deep-Sea Res II 51: 2119-2137