Polar Biol (2013) 36:1857–1864
DOI 10.1007/s00300-013-1400-y

SHORT NOTE

# Proximity of krill and salps in an Antarctic coastal ecosystem: evidence from penguin-mounted cameras

**Nobuo Kokubun · Jeong-Hoon Kim · Akinori Takahashi**

Received: 6 November 2012 / Revised: 13 July 2013 / Accepted: 12 August 2013 / Published online: 13 September 2013


**Abstract** Antarctic krill (*Euphausia superba*) and salps (mainly *Salpa thompsoni*) are main components of Southern Ocean ecosystem, but little is known about their coastal distribution at a fine scale (<1 km). We deployed miniaturised cameras on breeding chinstrap ($n = 9$ birds) and gentoo penguins ($n = 9$ birds) in the Antarctic Peninsula region and obtained 2,333 krill images, 93 salp images and 609 sea floor images from 1,843 dives. 51.2 % of penguin dives that had salps present in the images occurred near the dives with krill images (within 5 min). The vertical distribution of salp images showed overlap with the upper depth zone of krill images. While 16.3 % of dives with krill images were associated in time with the sea floor, only 1.2 % of dives with salp images did. These results revealed close proximity between krill and salps within the penguin's foraging range in an Antarctic coastal ecosystem. These results also imply that krill patches were common in both pelagic and benthic habitat, whereas salps were common mainly in pelagic habitat. If the effects of deployments are similar between the years or regions, inter-annual or regional comparison using the penguin-mounted camera will be valid for characterising prey environment in the penguin foraging area.

N. Kokubun (✉) · A. Takahashi
National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo 190-8515, Japan
e-mail: nkokubun@hotmail.co.jp; kokubun@nipr.ac.jp

N. Kokubun
Australian Antarctic Division, 203 Channel highway, Kingston, TAS 7050, Australia

J.-H. Kim
Korea Polar Research Institute, Songdo Techno Park, 7-50 Songdo-dong, Yeonsu-gu, Incheon 406-840, Korea

**Keywords** Animal-borne camera · Chinstrap penguin · Gentoo penguin · Antarctic krill · *Salpa thompsoni* · Antarctic Peninsula

## Introduction

Antarctic krill (*Euphausia superba*) and salps (mainly *Salpa thompsoni*) are the most abundant components of the Southern Ocean ecosystem (Pakhomov 2004; Loeb and Santora 2011). A decline in krill abundance accompanying an increase in salp abundance over recent decades has been highlighted in relation to regional warming events and consequent ecological changes in the pelagic Southern Ocean food web (Atkinson et al. 2004). Documented habitat segregation generally shows salps in the warmer water masses and krill in the colder water masses (Nishikawa et al. 1995; Nicol et al. 2000; Pakhomov 2004). On the other hand, particularly in the Antarctic Peninsula region, basin-scale co-existence of krill and salps has been reported in recent years (Kawaguchi et al. 1998; Loeb and Santora 2011). Increasing water temperature and a recent change in phytoplankton community towards a smaller size are considered to be factors that allow salps to have expanded their habitat off the Antarctic Peninsula (Moline et al. 2004; Meredith and King 2005). Because of high reproductive rates and an ability to filter a wide range of particles, salps might compete for existing food resources with krill if they occur in close proximity (Alldredge and Madin 1982; Siegel and Loeb 1995). Changes in the availability of krill are considered to have significant effects on the feeding and breeding performance of a wide range of apex predators in the Antarctic Peninsula and Scotia Arc regions (Reid and Croxall 2001). However, only a few studies have investigated the interactions (segregation or co-existence) between krill and salps at a local-scale (but see Pakhomov et al. 2006; Catalan et al. 2008; Loeb et al. 2010), at which predators exploit prey. In addition, there is ongoing discussion regarding whether salps are consumed by predators such as seabirds (Dubischar et al. 2012) in relation to increasing records of salps in higher latitudes.

The methodologies to investigate both krill and salp distribution have been restricted to ship-based survey such as net tow or hydro-acoustic measurements (Woodd-Walker et al. 2003; Wiebe et al. 2010; Loeb and Santora 2011). It is difficult to apply these methodologies in the Antarctic coastal area because of the complex sea floor topography, although this area is one of the important foraging habitats for land-based predators (Takahashi et al. 2003; Kokubun et al. 2010). Recently developed miniaturised animal-borne camera/video technology allows us to determine the predator–prey field in relation to their behaviour (Fuiman et al. 2002; Hooker et al. 2002). While this technology has the limitations that sampling space and time is not evenly distributed because of the predator behaviour, this is a unique method to monitor the foraging habitat and environment of the predators. We studied the foraging behaviour of Antarctic penguins in the 2009–2010 breeding season using penguin-mounted cameras and obtained images of krill patches. The images allow us to characterise krill patches and the surrounding environment (including salps) under natural conditions (e.g. Takahashi et al. 2008). In the present study, we aimed (1) to provide information about encounter rates of penguins with both krill and salps using underwater images, (2) to investigate the potential contribution of krill and salps to penguin's diet and (3) to explore the relationship between krill, salps and other environmental features.

## Materials and methods

The field study was conducted on Barton Peninsula, King George Island, Antarctic Peninsula region (Antarctic Specially Protected Area 171: Narębski point) from 21 December 2009 to 8 February 2010, which covered the chick-guarding period of chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins.

Miniaturised cameras (DSL-380, housed in a cylindrical container: 22 mm diameter, 133 mm length, mass 82 g; Little Leonardo, Tokyo, Japan) were deployed on the backs of 9 chinstrap and 9 gentoo penguins to obtain underwater still images. Amongst them, small accelerometers (ORI-380 D3GT, housed in a cylindrical container: 12 mm diameter, 45 mm length, mass 10 g; Little Leonardo) were deployed on the heads of 3 chinstrap and 5 gentoo penguins at the same time, for determining their underwater head movement (as a proxy of their feeding behaviour: Kokubun et al. 2011). Details of deployment procedures and potential effects of deployments on penguin behaviour are described in Kokubun et al. 2011. Underwater still images were taken every 15 s for 5 chinstrap penguins and 5 s for 4 chinstrap and 9 gentoo penguins, and dive depth was recorded every second. Because camera images do not provide information on foraging locations, we deployed GPS-depth loggers (GPL380-DT, housed in a rectangular container with a cylindrical battery section: 92 g; Little Leonardo) on 17 chinstrap and 17 gentoo penguins to determine potential foraging ranges and locations of penguins during the study. Maximum distance from the colony during the trips was $22.3 \pm 9.9$ and $17.7 \pm 6.7$ km for chinstrap and gentoo penguins, respectively (GLM with likelihood ratio test, $\chi^2 = 1.34$, $p = 0.25$). There was no interaction between data logger types (camera vs. GPS depth) and the penguin species for trip duration (GLM with likelihood test, $\chi^2 = 0.47$, $p = 0.53$). Thus, we believe that the penguin foraging habitats investigated with GPS-depth loggers were representative of those covered by camera loggers.

Depth profiles were analysed with Igor Pro (Wave Metrics) software. Dive depth was calculated for each dive that was more than 5 m deep (Takahashi et al. 2008). Underwater still images were sorted visually. If the images were light enough that existence or absence of any features could be determined, they were classified as "light" and the other images were classified as "dark". The presence of krill, salps, fish or sea floor was checked visually for each light image. All dives were classified as "light" or "dark" because darker images reflected deeper or nighttime dives (Fig. 1), and the higher proportion of dark images during a dive makes it less likely to detect any features appropriately. Dives were classified as "light" when the proportion of light images was more than 50 % of the images taken at depths greater than half of the maximum dive depth, and only data from "light" dives were used in subsequent analyses to avoid uncertainty in detection according to darkness of deep or nighttime dives (Kokubun et al. 2011). In addition, we set a practical limitation that eliminates trips covered less than 50 % or trips with percentage of light dives less than 50 %, to enhance confidence and future comparability between years and regions.

Encounter rates of penguins and any features (krill, salps, fish or sea floor) in a trip were defined as the proportion of dives with that feature out of the total "light" dives from the trip. We explored the relationships between encounter rates of penguins and krill, salps or sea floor, with Generalised Linear Models (GLMs: Crawley 2007). In the models, the response variables (the encounter rates of penguins and krill or salps) were fitted by explanatory variables (combinations of the effect of penguin species, encounter rates with krill, salps or sea floors) with logistic

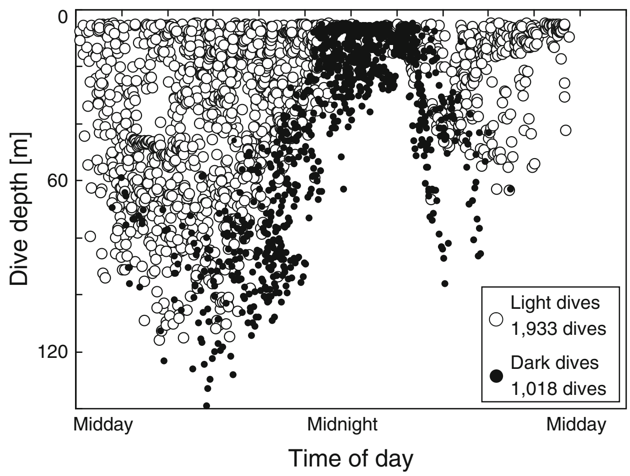


**Fig. 1** Distribution pattern of dive depth of the penguins and "light" and "dark" dives. *Open circles* represent the "light dives", and *black dots* represent the "dark dives"

curves. A binomial error distribution with logit link function was used.

Proximity of each feature (krill, salps, fish or sea floor) was examined by measuring the time intervals between two dives with the feature present in the images. If the time interval was less than 5 min, the features were regarded as "clustered" or "associated in time", otherwise they were regarded as "not clustered" or "not associated in time". If the number of "dark" dives exceeded the number of "light" dives between images with the two features, proximity was regarded as "unknown". In addition, if there were no sea floor images in a trip, proximity of features (krill, salps or fishes) and sea floor was regarded as "unknown".

The depth of the features was defined as the depth that the images were taken. The mean depth was compared between krill and salps present in images with generalised linear mixed model (GLMM) and likelihood ratio test (LRT) (Faraway 2006). Depth distribution of krill and salps in relation to time of day was described by kernel density analysis (Worton 1989) to investigate their vertical overlap. For kernel analysis, both depth and time of day were converted into a scale ranging from 0 to 1 as follows:

$$d = \frac{D}{117} \tag{1}$$

where $D$ was depth (in metres: the denominator 117 was determined from the deepest depth where krill image was taken amongst the light dives) and $d$ was the depth converted to range between 0 and 1, and

$$t = \frac{T}{24} \tag{2}$$

where $T$ was time (in hours) starting on midday and ending the following midday, and $t$ was the time converted to range between 0 and 1.

We collected stomach contents from 6 chinstrap and 7 gentoo penguins to examine prey items using the standard stomach-flushing method (CCAMLR 1997). The samples were obtained from individuals with GPS-depth loggers. Detailed description of these samples is shown in Kokubun et al. (2011). Even though the stomach contents reflect actual food items, gelatinous plankton (i.e. salps) can be digested more rapidly than the other solid foods (Arai 2005). Salps have a potential to be food item of penguins as they have slightly larger energy content (0.20 $kJg^{-1}$) than those required to heat water-rich food from 0 to 37 °C (0.16 $kJg^{-1}$) (Dubischar et al. 2012). Thus, we also examined the temporal concordance of images with krill or salps with underwater active head movements to examine penguin's response when they encounter krill or salps. Head movement measured by accelerometers has been previously demonstrated to be a good proxy of underwater feeding events (Kokubun et al. 2011; Watanabe and Takahashi 2013).

We used the Spatial Analyst extension of ArcGIS 10.0 for kernel analysis, and R 2.7.0 for GLM, GLMM and LRT analyses (R Development Core Team 2008).

## Results

### Device and data recovery

We obtained a total of 38,182 underwater images covering 2,951 dives (>5 m) and 17 foraging trips from 6 chinstrap and 8 gentoo penguins. We excluded 4 birds (one bird that was not recaptured, one bird that did not depart for a foraging trip, one bird that had a failed battery in the camera and one bird that had a failed depth sensor in the camera). Of all images, 24,985 images (65.4 %) were taken during "light dives", whereas 13,197 images (34.6 %) were taken during "dark dives". "Light dives" were distributed at shallower depth or during the daytimes, whereas "dark dives" were distributed at deeper depth or during nighttime (during the study period, sunrise and sunset ranged between 02:56–04:58 and 21:19–22:51) (Fig. 1). Four of the 17 trips were not used for further analysis because of a low proportion of "light dives" (0.0–30.0 %) and/or low coverage rate of trips (1.5 and 1.7 h: equal to 12.9 and 25. 9 % of the trip duration). Images taken during "light dives" included 2,333 krill images (in 582 dives: Fig. 2a, b, d), 93 salp images (in 82 dives: Fig. 2c, d), 19 fish images (in 13 dives: Fig. 2e) and 609 sea floor images (in 219 dives: Fig. 2b, e, f) (Table 1). There is a possibility that two species of krill (*E. superba* and *E. crystallorophias*) can be observed in the study area (Volkman et al. 1980; Stępnik 1982). From our underwater images, all recognisable krill seemed to be *E. superba*. Images taken during "dark dives" included 430 krill images (15.6 % of total krill images; in 183 dives), 26 salp images (21.8 % of total salp images; in 24 dives), no fish or sea floor images. To avoid uncertainty in the detection of features according to darkness, only images taken during "light dives" were used for further analysis.

## Occurrence pattern of krill and salps

The encounter rate of penguins and krill (dives with krill images amongst all "light" dives) was 232 out of 808 dives (28.7 %, ranging 3.3–70.7 %) for chinstrap and 350 out of 1,035 dives (33.8 %, ranging 3.7–61.3 %) for gentoo penguins and that of penguins and salps (dives with salp images amongst all "light" dives) was 54 out of 808 dives (6.7 %, ranging 2.2–20.2 %) for chinstrap and 28 out of 1,035 dives (2.7 %, ranging 0.0–6.8 %) for gentoo penguins, but please note that these values had individual variability (Table 1). Logistic regression models (GLM) showed that the presence of sea floor had a negative effect on encounter rate of penguins and salps (Table 2b). Also, the presence of both sea floor and salps had a negative effects on encounter rate of penguins and krill (Table 2a).

The dives that had krill images were clustered (87.3 % of dives with krill occurred within 5 min each other). In comparison, the dives that had salp images were less clustered than those of krill (20.7 % of dives with salps occurred within 5 min each other). The dives that had krill images and those with salp were often clustered together (51.2 % of dives with salps occurred within 5 min from the nearest dives with krill, vice versa 21.0 % of dives with krill occurred within 5 min from the nearest dives with

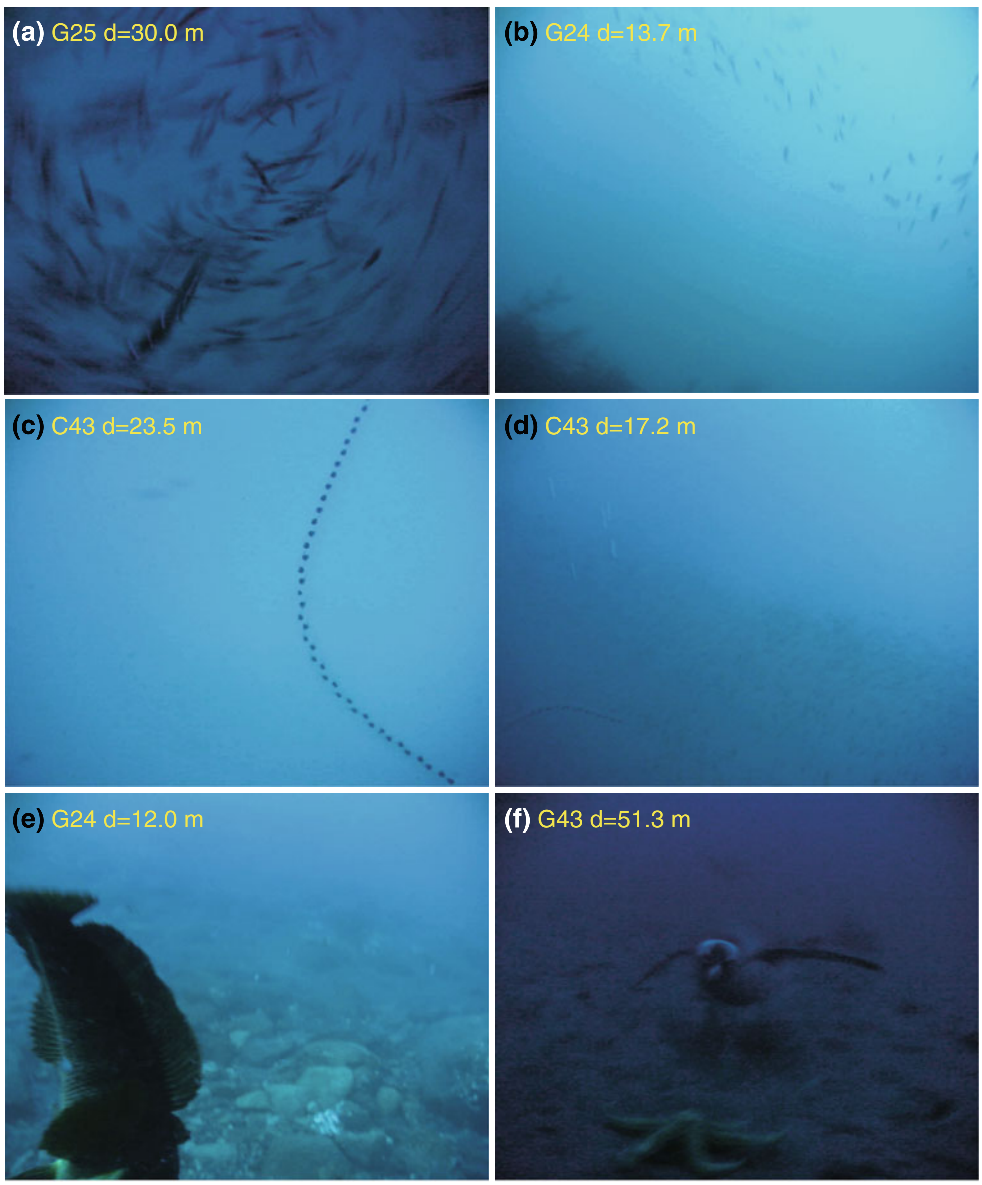


**Fig. 2** Underwater images taken by camera loggers mounted on penguins. **a** Pelagic krill swarm with bio-luminescence, **b** dispersed krill swarm above sea floor, **c** chain-formed salp, **d** chain-formed salp with krill swarm background, **e** a fish (*Notothenia coriiceps*) above sea floor and **f** a starfish, another gentoo penguin and sea floor

**Table 1** Data summary of underwater still images taken by cameras mounted on five chinstap and eight gentoo penguins

| BirdID | Number of images with the features | | | | | Number of dives with the feature images | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Krill | Salps | Fish | Sea floor | No obvious features | Krill | Salps | Fish | Sea floor | No obvious features | All light dives | Penguin species |
| C026 | 324 | 10 | 0 | 0 | 2,962 | 81 | 9 | 0 | 0 | 74 | 159 | Chinstrap |
| C030 | 64 | 25 | 0 | 0 | 1,757 | 45 | 23 | 0 | 0 | 327 | 393 | Chinstrap |
| C033 | 56 | 8 | 0 | 0 | 747 | 39 | 8 | 0 | 0 | 61 | 104 | Chinstrap |
| C043 | 272 | 2 | 0 | 0 | 1,148 | 65 | 2 | 0 | 0 | 26 | 92 | Chinstrap |
| C048 | 2 | 16 | 0 | 0 | 1,182 | 2 | 12 | 0 | 0 | 46 | 60 | Chinstrap |
| G024 | 98 | 0 | 17 | 318 | 2,787 | 45 | 0 | 11 | 132 | 77 | 232 | Gentoo |
| G025 | 759 | 17 | 1 | 0 | 3,624 | 136 | 15 | 1 | 0 | 83 | 222 | Gentoo |
| G027 | 236 | 3 | 0 | 0 | 1,590 | 30 | 3 | 0 | 0 | 65 | 95 | Gentoo |
| G037 | 105 | 0 | 0 | 107 | 1,409 | 38 | 0 | 0 | 28 | 22 | 87 | Gentoo |
| G038 | 117 | 4 | 0 | 2 | 1,940 | 23 | 4 | 0 | 1 | 63 | 88 | Gentoo |
| G039 | 17 | 4 | 0 | 18 | 1,861 | 4 | 2 | 0 | 9 | 92 | 107 | Gentoo |
| G043 | 230 | 1 | 0 | 135 | 2,481 | 62 | 1 | 0 | 45 | 73 | 148 | Gentoo |
| G044 | 53 | 3 | 1 | 29 | 1,098 | 12 | 3 | 1 | 4 | 38 | 56 | Gentoo |

Number of images with underwater features (krill, salps, fish and sea floor) and number of dives with the features are shown for each individual foraging trip. All pictures shown here were taken during "light dives" (please see "Materials and methods")

**Table 2** Summary for generalised linear models (GLMs) explaining encounter rates of penguins and (a) krill and (b) salps

(a) Encounter rates of penguins and krill

| Explanetory variables | *df* | Estimates | | | | AIC |
|---|---|---|---|---|---|---|
| | | Intercept | Penguin species | Salp | Sea floor | |
| Salp + Sea floor | 3 | −0.156 | | −0.049 | −0.009 | **380.8** |
| Salp + Sea floor + Penguin species | 4 | −0.265 | 0.139 | −0.044 | −0.010 | **381.7** |
| Penguin species + Sea floor | 3 | −0.909 | 0.488 | | −0.007 | 411.2 |
| Salp | 2 | −0.558 | | −0.025 | | 423.6 |
| Penguin species + Salp | 3 | −0.526 | −0.036 | −0.026 | | 425.5 |
| Sea floor | 2 | −0.684 | | | −0.004 | 428.2 |
| Penguin species | 2 | −0.909 | 0.238 | | | 435.6 |
| None | 1 | −0.773 | | | | 439.1 |

(b) Encounter rates of penguins and salps

| Explanatory variables | *df* | Estimates | | | | AIC |
|---|---|---|---|---|---|---|
| | | Intercept | Penguin species | Krill | Sea floor | |
| Sea floor | 2 | −2.714 | | | −0.077 | **63.7** |
| Species + Sea floor | 3 | −2.636 | −0.233 | | −0.069 | **64.8** |
| Krill + Sea floor | 3 | −2.598 | | −0.002 | −0.081 | **65.3** |
| Krill + Sea floor + penguin species | 4 | −2.572 | −0.201 | −0.001 | −0.072 | 66.7 |
| Penguin species | 2 | −2.636 | −0.946 | | | 91.2 |
| Penguin species + krill | 3 | −2.793 | −0.974 | 0.003 | | 92.5 |
| None | 1 | −3.067 | | | | 106.1 |
| Krill | 2 | −3.129 | | 0.001 | | 107.9 |

A binominal error distribution and logit link function were used for the analysis. Combination of explanatory variables, degree of freedom (*df*), estimates of intercept, coefficients for each explanatory variables and Akaike's information criteria (AIC) are shown. Bold texts mean those within 2 AIC from the minimal value

salps). 16.3 % of dives that had krill images were associated in time with the dives with sea floor images (occurred within 5 min from the nearest dives that had sea floor images). In comparison, only 1.2 % of dives that had salp images were associated in time with the dives with sea floor images. Krill images were typically taken at deeper depths than salp images (krill: 48.7 ± 28.4 m, salps: 30.2 ± 12.8 m, GLMM with LRT, $\chi^2 = 12.21$, $p < 0.01$). The mean depth of krill and salps did not differ between the penguin species (GLMM with LRT, $p > 0.05$). The deviation of depths of both krill and salps became larger towards daytime and were smaller towards nighttime (Fig. 3). This distribution pattern seems to reflect the diving pattern of the penguins (Fig. 1). The depth distribution of salp images in relation to time of the day showed overlap with those of the upper part of krill images (Fig. 3), under the situation that the sample size was different between the species (2,333 points for krill and 93 points for salps). Sea floor and fish images were taken only during several gentoo penguin trips (Table 1). This result is consistent with that gentoo penguins sometime utilised benthic foraging habitat (Takahashi et al. 2008; Kokubun et al. 2010). The average depths were 19.2 ± 14.1 m for sea floor and 11.1 ± 3.6 m for fishes. 17 out of 19 fish pictures were taken during a gentoo penguin trip whose dive depth was shallow (12.5 ± 4.5 m, $n = 293$ dives).

### Potential contribution of krill and salps to penguin's diet

More than 99 % of the stomach contents (in wet weight) was Antarctic krill (*E. superba*) for both chinstrap and gentoo penguins. No evidence of eating salps was found in the stomach contents. Accelerometer data showed the rate of strong head movement within ± 2.5 s from images (a proxy of underwater feeding events; Kokubun et al. 2011) was higher for krill than salps. 944 out of 999 krill images (94.5 %) and only 3 out of 49 salp images (6.1 %) were

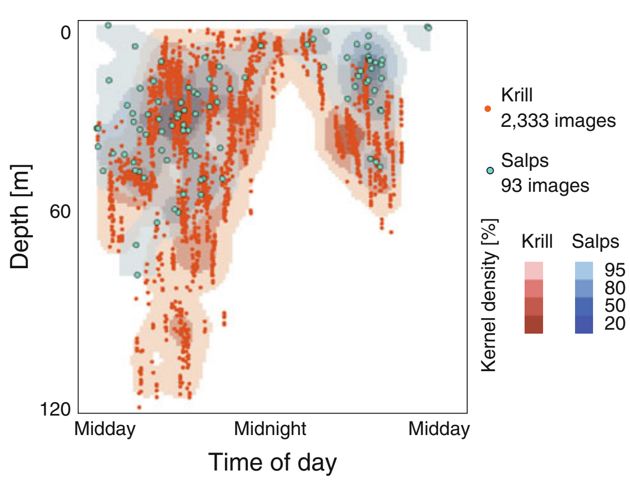


**Fig. 3** Depth distribution pattern of krill and salp images in relation to time of day shown by kernel density analysis. Please note that all pictures from different birds ($n = 13$ birds) were pooled and that the sample size was different between the species. For kernel analysis, both depth and time of day were converted into a scale ranging from 0 and 1 (please see "Materials and methods")

accompanied with head movement (GLMM with LRT, $\chi^2 = 57.1$, $p < 0.01$). This means that penguins rarely attempted to catch salps compared with krill when the penguins encountered them (Kokubun et al. 2011; Watanabe and Takahashi 2013).

## Discussion

In this study, we have described characteristics of the occurrence of krill and salps and their proximity within penguin foraging ranges using miniaturised penguin-mounted cameras. This sampling method has limitations in that sampling location and time may be concentrated near krill patches because penguins spend longer in these, the depth reflects the diving pattern of the penguins, and clear images can only be obtained during relatively shallow dives or daylight hours (Fig. 1). Therefore, the quantitative density or abundance estimation of the underwater features is difficult especially for the purpose of comparing density of two taxa directly. Despite these animal-specific limitations, basic parameters such as encounter rate of penguins with features (krill, salps, fishes and sea floor) or proximity of the features will be comparable between different years and/or locations, assuming that the effect of the deployments will be similar between years or locations. Such comparison will be valid based on statistics that can deal with behavioural individual variability (Tables 1, 2b), and it will help to characterise the prey environment in the penguin foraging habitat, complementing ship-based surveys.

Our results show some aspects of the interaction between krill and salps in an Antarctic coastal ecosystem. First, salps were found around the krill patches that were utilised by penguins. Given that *Pygoscelis* penguins swim at a mean speed of 2.1 $ms^{-1}$ (Culik and Wilson 1994), 51.2 % of dives with salps in the images occurred within 5 min of krill patches (i.e. <630 m). Also, 21.0 % of dives with krill in the images occurred near salps. Krill and salps were often observed in similar depths especially during nighttime, presumably reflecting diving pattern of penguins and/or vertical migration pattern of krill and salps (Figs. 1, 3). Habitat segregation of krill and salps seems common over large scale in several areas in the Southern Ocean according to their different preference of water temperatures (Nicol et al. 2000; Pakhomov 2004) or diel vertical migration patterns (Nishikawa and Tsuda 2001). We have demonstrated here the evidence of proximity between krill and salps, at a micro-habitat scale (<1 km) in the Antarctic Peninsula region. Salps were found in images (Fig. 2c, d; Table 1), but penguins rarely attempted to catch them. These results are consistent with reported penguin's diet (Volkman et al. 1980) and suggest that penguins did not consume salps actively as long as Antarctic krill are available.

Second, encounter rate of penguins and sea floor negatively correlated with that of penguins and salps (Tables 1, 2). Similarly, salps were rarely seen in association in time with the sea floor in contrast to krill which were sometimes observed in association in time with the sea floor (Fig. 2b). These results imply that salps are more common in offshore pelagic habitat rather than in on-shelf benthic habitat. According to recent penguin population studies in this region, chinstrap penguins which mainly use pelagic habitat have decreased, whereas gentoo penguins which use both benthic and pelagic habitats have not decreased (Hinke et al. 2007; Kokubun et al. 2010; Miller et al. 2010). Because krill formed the main component of the penguin diet, the presence of salps in their foraging habitat can potentially be a factor altering availability of prey, especially for pelagic krill feeders.

In conclusion, this study presents new evidence on the proximity between krill patches and salps using penguin-mounted cameras in an Antarctic coastal marine environment. Both krill and salps were found in images, but salps were not found in the penguin's diet and penguins rarely try to capture them. Krill patches tended to be found in both pelagic and benthic habitat, whereas salps tended to be found mainly in pelagic habitat. In the Antarctic Peninsula region, there has been increasing interest in distributional shifts of krill and salps in response to rapid regional warming (Moline et al. 2004). A multiple-year study using the penguin-mounted camera technique will provide a unique opportunity to monitor changes in the Antarctic coastal marine ecosystem.

**Acknowledgments** We would like to thank Dr S.-H. Kang and all members of the King Sejong Station, Korea Polar Research Institute (KOPRI) for logistic supports in the field. Dr. H.-C. Shin provided the basis for our fieldwork. Drs. I.-Y. Ahn and E. J. Choy helped us to conduct the fieldwork. We are grateful to Dr L. Emmerson, for reviewing the manuscript, providing helpful comments and improving the English. We also thank an anonymous reviewer who kindly provided suggestion for improving the English. This work was supported by the Japan Society for the Promotion of Science (JSPS) Research Fellowship for Young Scientists to N.K., JSPS research Grant 20310016 to A.T. and the programme "Bio-logging Science, The University of Tokyo (UT-BLS)" led by Drs N. Miyazaki and K. Sato. A research Grant PE11030: Studies on biodiversity and changing ecosystems in King George Island, Antarctica funded by the KOPRI provided support for this work. This study was conducted under permits issued by the Ministry of the Environment, Japan.

## References

Alldredge AL, Madin LP (1982) Pelagic tunicates: unique herbivores in the marine plankton. Bioscience 32:655–663

Arai MN (2005) Predation on pelagic coelenterates: a review. J Mar Biol Assoc UK 85:523–536

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Science 432:100–101

Catalan IA, Morales-Nin B, Company JB, Rotllant G, Palomera I, Emelianov M (2008) Environmental influences on zooplankton and micronekton distribution in the Bransfield Strait and adjacent waters. Polar Biol 31:691–707

CCAMLR (1997) CCAMLR ecosystem monitoring program: standard methods for monitoring studies. Commission for the conservation of Antarctic marine living resources (CCAMLR), Hobert, Australia

Crawley MJ (2007) The R book. Wiley, West Sussex, pp 569–591

Culik BM, Wilson RP (1994) Underwater swimming at low energetic cost by *Pygoscelid penguins*. J Exp Biol 197:65–78

Dubischar CD, Pakhomov EA, von Harbou L, Hunt BPV, Bathmann UV (2012) Salps in the Lazarev Sea, Southern Ocean: II. Biochemical composition and potential prey value. Mar Biol 159:15–24

Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall/CRC, Boca Raton, pp 153–183

Fuiman LA, Davis RW, Williams TM (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. Mar Biol 140:815–822

Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ (2007) Divergent responses of *Pygoscelis penguins* reveal a common environmental driver. Oecologia 153:845–855

Hooker S, Boyd IL, Jessopp M (2002) Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. Mar Mamm Sci 18:680–697

Kawaguchi S, Ichii T, Naganobu M (1998) Do krill and salps compete? Contrary evidence from the krill fisheries. CCAMLR Sci 5:205–216

Kokubun N, Takahashi A, Mori Y, Watanabe S, Shin H-C (2010) Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Mar Biol 157:811–825

Kokubun N, Kim JH, Shin H-C, Naito Y, Takahashi A (2011) Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. J Exp Biol 214:3760–3767

Loeb VJ, Santora JA (2011) Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: growth rates and interannual variations in reproductive activity (1993–2009). Prog Ocenogr 96:93–107

Loeb VJ, Hofmann EE, Klinck JM, Holm-Hansen O (2010) Hydrographic control of the marine ecosystem in the South Shetland-Elephant Island and Bransfield Strait region. Deep Sea Res II 57:519–542

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Miller EK, Kappes MA, Trivelpiece SG, Trivelpiece WZ (2010) Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. Condor 112:683–695

Moline MA, Claustre H, Frazer T, Schofield O, Vernet M (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Glob Chang Biol 10:1973–1980

Nicol S, Pauly T, Bindoff NL, Wright S, Thiele D, Hosie GW, Strutton PG, Woehler E (2000) Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. Nature 406:504–507

Nishikawa J, Tsuda A (2001) Diel vertical migration of the tunicate *Salpa thompsoni* in the Southern Ocean during summer. Polar Biol 24:299–302

Nishikawa J, Naganobu M, Ichii T, Ishii H, Terazaki M, Kawaguchi K (1995) Distribution of salps near the South Shetland Islands during austral summer, 1990–1991 with special reference to krill distribution. Polar Biol 15:31–39

Pakhomov EA (2004) Salp/krill interactions in the eastern Atlantic sector of the Southern Ocean. Deep Sea Res II 51:2645–2660

Pakhomov EA, Dubischar CD, Strass V, Brichta M, Bathmann UV (2006) The tunicate *Salpa thompsoni* ecology in the Southern Ocean. I. Distribution, biomass, demography and feeding ecophysiology. Mar Biol 149:609–623

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proc R Soc Lond B 268:377–384

Siegel V, Loeb V (1995) Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Mar Ecol Prog Ser 123:45–56

Stępnik R (1982) All-year populational studies of *Euphausiacea (Crustacea)* in the Admiralty Bay (King George Island, South Shetland Islands Antarctic). Pol Polar Res 3:49–68

Takahashi A, Dunn MJ, Trathan PN, Sato K, Naito Y, Croxall JP (2003) Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. Mar Ecol Prog Ser 250:279–289

Takahashi A, Kokubun N, Mori Y, Shin H-C (2008) Krill-feeding behaviour of gentoo penguins as shown by animal-borne camera loggers. Polar Biol 31:1291–1294

Volkman NJ, Presler P, Trivelpiece W (1980) Diets of *Pygoscelid penguins* at King George islands, Antarctica. Condor 82:373–378

Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. Proc Natl Acad Sci USA 100:1971–1972

Wiebe PH, Chu D, Kaartvedt S, Hundt A, Melle W, Ona E, Batta-Lona P (2010) The acoustic properties of *Salpa thompsoni*. ICES J Mar Sci 67:583–593

Woodd-Walker RS, Watkins JL, Brierley AS (2003) Identification of Southern Ocean acoustic targets using aggregation backscatter and shape characteristics. ICES J Mar Sci 60:641–649

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168