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SHORT NOTES

On the significance of Antarctic jellyfish as food for Adélie penguins, as revealed by video loggers

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Abstract Concern of pelagic gelatinous organisms taking over perturbed marine ecosystems has led to a recent increase in research into this group. However, the significance of this group as prey remains challenging to assess, and hence, gelatinous consumers are often depicted incorrectly as dead ends of pelagic food webs. In the Southern Ocean, where a shift in trophic webs may favour gelatinous animals, we video-monitored prey intake of a key predator. Twenty-eight chick-rearing Adélie penguins *Pygoscelis adeliae* from Dumont d'Urville station (66°40′S, 140°01′E) were instrumented with miniaturized video loggers in 2014–2015. Among other items (krill, fish), 101 gelatinous organisms ($n = 79$ jellyfish, 6 salps and 16 unidentified) were observed on 13 of 21 exploitable video footages (total: 59 h). Importantly, 65.3 % of gelatinous organisms were attacked, but among them salps were not attacked. Attacks on jellyfish were significantly associated with the visible presence of the jellyfish's gonad. Jellyfish were encountered at an average depth of 26.2 ± 10.4 m, significantly shallower than krill. Attacks occurred mostly during bottom, but also descent or ascent dive phases. Concomitant GPS location for four birds revealed that attacks on jellyfish occurred above the shelf, 35 km north from the colony, where sea ice concentration reached 88 %. These results indicate that Adélie penguins occasionally feed on jellyfish, even though other prey types are also available. Refining our perception of scyphozoans' niche may thus help anticipate the functional response of the food webs to the extensive changes witnessed in the Antarctic environment.

Introduction

There is a major concern that pelagic gelatinous organisms are taking over perturbed marine ecosystems (e.g. Richardson et al. 2009; Greene et al. 2015), as these organisms may develop in simplified ecosystems resulting from climate changes, overfishing or eutrophication (reviewed in Howarth et al. 2014). Increasing interest in this issue raised the need for a better knowledge on the ecological niche of these animals (Fleming et al. 2015), which encompass cnidarians (e.g. Scyphozoa: "true" jellyfish; Siphonophora), ctenophores ("comb jellies") and chordates (Salpida: salps). They are indeed widely recognized as significant consumers (e.g. Purcell et al. 2010), but their importance as prey is still difficult to quantify in the pelagic trophic webs (Pauly et al. 2009) despite evidence that a large variety of taxa may feed on this group (reviewed in Arai 2005). This is mainly

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due to methodological issues, such as the challenge to monitor predation events in the wild or to detect the fragile gelatinous tissues in the predators' diet (Arai 2005). Consequently, gelatinous organisms are sometimes depicted incorrectly as dead ends in pelagic food webs because of their supposedly low nutritional value, and the existence of separate "jellyweb" versus "fishweb" in trophic chains has been suggested (Sommer et al. 2002; Robison 2004).

In the Southern Ocean, the structure and processes of trophic webs are being significantly altered, as a consequence of environmental changes (Constable et al. 2014; Gutt et al. 2015). Current ecosystem shifts may favour gelatinous consumers across Antarctic regions, while being locally detrimental to the Antarctic krill *Euphausia superba*, the main food resource of vertebrate predators (Atkinson et al. 2004). Therefore, it is desirable to clarify the ecological niche of the abundant but complex gelatinous community in the Antarctic (Lindsay et al. 2014), and more specifically to determine whether these taxa could represent an alternate prey item for krill-dependent predators.

The Adélie penguin *Pygoscelis adeliae* is a key krill consumer in the Antarctic (Ainley 2002; Ratcliffe and Trathan 2011). Surprisingly, recent DNA-based diet studies detected significant proportions of gelatinous organisms' sequences in faecal samples from this predator (Jarman et al. 2013; McInnes et al. 2016). However, the latter approach does not allow ruling out secondary ingestion (through other prey), raising the need to clarify this trophic relationship.

Over the past three decades, predator-based biologging techniques have shown their potential to complement knowledge on elusive prey taxa in remote marine environments (e.g. Cherel and Weimerskirch 1995; Rodhouse et al. 1996; Xavier et al. 2006). Animal-borne video loggers further allow detailing individual prey captures (Watanabe and Takahashi 2013): for example, a recent study using this technique newly reported predation on jellyfish by little penguins *Eudyptula minor* in Australia (Sutton et al. 2015). In our study, we mounted miniaturized video loggers on Adélie penguins to directly monitor predator–prey interactions taking place in the Antarctic pelagic food web and examine the occurrence of capture of gelatinous organisms by this predator.

Methods

The study was conducted at Dumont d'Urville, Pétrels Island (66°40′S, 140°01′E; Adélie Land, East Antarctica), where *c.* 34,000 Adélie penguins breed (Ropert-Coudert et al. 2015). Between 26 December 2014 and 11 January 2015, 28 chick-rearing penguins (20 males, 8 females; sex inferred from morphometric measurements: Kerry et al. 1992) were captured when leaving their nest after switching guarding duties with their partner. The video logger (facing forward) was attached to the median dorsal line of the penguins, positioned on the scapular joint. The matchbox-shaped video loggers were developed at the National Institute of Polar Research, Japan (manufactured by Little Leonardo, Tokyo). Two models were used: DVL200 (15 g, 20 mm × 10 mm × 52 mm, 2.5 h recording capacity) and DVL200 M (22 g, 21 mm × 11 mm × 63 mm, 4 h recording capacity), both recording videos at 30 frames s^{-1}. The devices were attached to the back feathers using mastic and waterproof adhesive Tesa® tape (Wilson et al. 1997). Because recording duration was limited and our aim was to capture the periods of feeding at sea, the video loggers were programmed to start recording only in the morning of the following day (i.e. generally 15 h start delay, range 8–24 h, after deployment). This delay was expected to cover the penguins' commuting time over the extended sea ice to the open water. Each video-surveyed bird was also instrumented with either two time–depth recorders ($n = 24$ birds) or a GPS logger ($n = 4$ birds). The 24 birds also instrumented with time–depth recorders (9 g each, ORI400-D3GT, Little Leonardo) had one device attached to the top of the head, the other one taped aside of the video logger (a design following Watanabe and Takahashi 2013 for purposes which are not addressed in the present paper). Time–depth recorders were programmed to record depth every second. The recording was expected to last 50 h. The four other video-surveyed birds (three males, one female) were also instrumented with a GPS logger (CatLog™, 16 Mb memory, 380 mA lithium-ion battery, Catnip Technologies, USA) customized by the engineers of MIBE (IPHC-CNRS, UMR7178, Strasbourg, France), as described in Cottin et al. (2012). The GPS loggers were placed in waterproof heat-shrink tubes (final weight: 30 g, final size: 14 mm × 35 mm × 70 mm). They were attached to the birds' lower back feathers using mastic and waterproof adhesive Tesa® tape and tightened up with two Colson® plastic clamps. GPS loggers were programmed to record latitude and longitude every 3 min; however, location acquisition was possible only when not underwater. The potential adverse effect of instrumentation on individual foraging performance of the penguins was expected to be small given the very short-term attachment of the loggers (one at-sea foraging trip per bird) and the smaller size of the video logger used here compared to previous, successful studies (e.g. Watanabe and Takahashi 2013).

Each nest was checked every 1–4 h until the return of the instrumented bird. The returning birds were then recaptured outside of or on their nest, loggers removed

Fig. 1 Selected images of encountered gelatinous animals, from video loggers attached to Adélie penguins at Pétrels Island, Adélie Land: jellyfish (likely *Diplulmaris antarctica*) (**a**–**e**); and aggregated salps (detail; likely *Ihlea racovitzai*) (**f**). Notice the parasitic amphipods on (**c**, **d**) pointed out with *white arrows*

and data downloaded onto a computer. After removing the blurry videos or that hindered by the penguin's feathers, we visually inspected a total of 59 h of exploitable footage obtained from 21 birds, to determine prey encounter and capture events in the field of the camera. Time–depth data were processed using IGOR Pro (WaveMetrics Inc., USA). For each dive, descent/bottom/ascent phases were identified from depth patterns. GPS location coordinates were processed in R 3.2.0 software (R Development Core Team; www.R-project.org). We used passive microwave estimates of daily sea ice concentration from the Australian Antarctic Division (https://github.com/AustralianAntarcticDivision/raadtools; 0.025° resolution) to characterize the ice conditions encountered by the tracked animals. These data were analysed using "raadtools" (Sumner 2015), "raster" (Hijmans 2015), "sp" (Pebesma and Bivand 2005) and "rgdal" (Bivand et al. 2015) packages on R.

Fisher's exact test for count data was used in R to examine the association between (1) observed feeding success during the current dive or previous one, or prey characteristics, and (2) the ratio of attacked/all prey encounter events. One-way ANOVA was used to test for differences in depth range between prey types. Statistical significance was assumed under a p value threshold <0.05. Normality of variables was assessed with the Shapiro–Wilk test. Unless otherwise stated, values are mean ± SD.

Results

Krill was the prevailing prey item of the monitored penguins ($n = 2017$ captures by the 21 birds). Fish ($n = 25$ captures) and unidentified taxa ($n = 347$ captures) were also recorded. Noteworthy 101 gelatinous organisms were encountered, of which 65.3 % were attacked by the penguins from both sexes (Fig. 1; Table 1). The large majority of the encountered gelatinous organisms were jellyfish ($n = 79$), versus 6 salps and 16 unidentified animals. None of the encountered salps was attacked.

Thirteen of 21 penguins (62 % of the instrumented birds) encountered gelatinous animals, between 27 December 2014 and 12 January 2015. One to 58 (median = 3.0) gelatinous organisms were encountered by each of these birds, amounting to 7.3 ± 12.3 items seen per hour underwater. All identifiable jellyfish ($n = 27$) were *Diplulmaris antarctica*. The aggregated or solitary salps were presumably *Ihlea racovitzai*.

The small-sized gelatinous organisms could be fully engulfed; however, in the case of large jellyfish, the penguins attacked the oral arms or bell edge only ($n = 15$, see online video), and further shook the jellyfish to fragment it ($n = 9$). Occasionally, penguins only briefly pecked at the bell edge ($n = 8$), without ingesting a visible part of it. Attacks were usually conducted either from the side ($n = 41$) or from below ($n = 21$), thus making the penguins exposed to the nematocysts, and rarely from above ($n = 4$).

Table 1 Comparison of attack versus non-attack prevalence of gelatinous organisms by Adélie penguins, accounting for the penguins' previous feeding success or the characteristics of the encountered jellyfish; in bold are highlighted the statistically significant relationships

Situation (n = number of observed cases)		Encountered gelatinous animals			Fisher's exact test for count data
		Number attacked	Number not attacked	Ratio attacked/total (%)	
All ($n = 101$)		66	35	65.3	
During the previous dive, was other prey captured?	Yes ($n = 58$)	31	27	**53.4**	**$P < 0.002$**
	No ($n = 42$)	35	7	**83.3**	
	Undistinguishable ($n = 1$)	0	1		
During this dive, was other prey already captured?	Yes ($n = 59$)	37	22	62.7	$P = 0.45$
	No ($n = 30$)	20	10	66.7	
	Undistinguishable ($n = 12$)	9	3		
Are amphipods present on the jellyfish's bell?	Yes ($n = 9$)	8	1	88.9	$P = 0.066$
	No ($n = 9$)	4	5	44.4	
	Undistinguishable ($n = 61$)	42	19		
Is the jellyfish's gonad visible?	Yes ($n = 28$)	28	0	100	**$P < 0.001$**
	No ($n = 11$)	1	10	9.1	
	Undistinguishable ($n = 40$)	25	15		

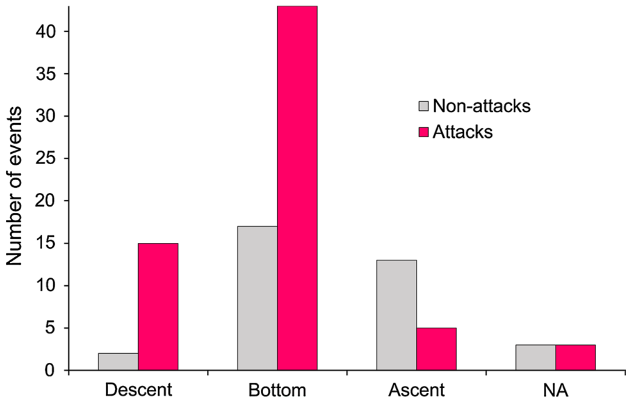

Fig. 2 Prevalence of attack versus non-attack of the encountered gelatinous organisms according to the dive phase of Adélie penguins (descent, bottom or ascent; NA when no depth data available)

Afterwards, remains of jellyfish could be observed on the penguins' head, twice. On two other occasions, a penguin (same individual) approached a jellyfish but suddenly got away as another penguin attacked the jellyfish first. Finally, each non-attacked jellyfish was scrutinized beforehand by the penguin, as inferred from its head movements. No jellyfish was observed having captured prey.

Penguins encountered gelatinous organisms mostly during the bottom phase of the dives ($n = 60$ events out of 95 for which video and depth data were available, Fig. 2), compared to the descent and ascent phases ($n = 17$ and 18 events, respectively). Similarly, attacks mostly occurred during the bottom phase of dives (68.3 % of cases, versus 23.8 and 7.9 % during the descent and ascent phases, respectively). There were more "attack" than "non-attack" cases during the descent and bottom phases, but that was the opposite during the ascent phase.

Attacking the encountered gelatinous organisms in a given dive was significantly enhanced if the penguin did not capture prey (other than gelatinous) during the previous dive (Table 1). However, previous prey captures during the given dive did not significantly affect the attacks prevalence. When jellyfish were clearly visible ($n = 18$ cases), the number of parasitic amphipods on the jellyfish could be noted ($n = 1.8 \pm 2.5$, range 0–8 amphipods per jellyfish). There was no significant association between the occurrence of amphipods and attacks; however, there were significantly more amphipods on the 12 attacked jellyfish than on the 6 non-attacked ones, on average (2.5 ± 2.8 vs. 0.3 ± 0.8, respectively; Wilcoxon signed-ranks test, $T = 26.5$, $N = 18$, $P = 0.006$). Finally, in clear enough images, the jellyfish's gonad was noted as either visible or not ($n = 39$ cases), and the presence of visible gonad was significantly associated with the attacks prevalence (Table 1).

The observed taxa (krill, fish, jellyfish or salps) were encountered at significantly different depths, on average (ANOVA, $F_3 = 44.25$, $P < 0.001$). Jellyfish were encountered at 26.2 ± 10.4 m (range 2.7–52.8, from $n = 74$ cases with concomitant video and depth data); that is significantly shallower than for krill (40.6 ± 15.9 m; range

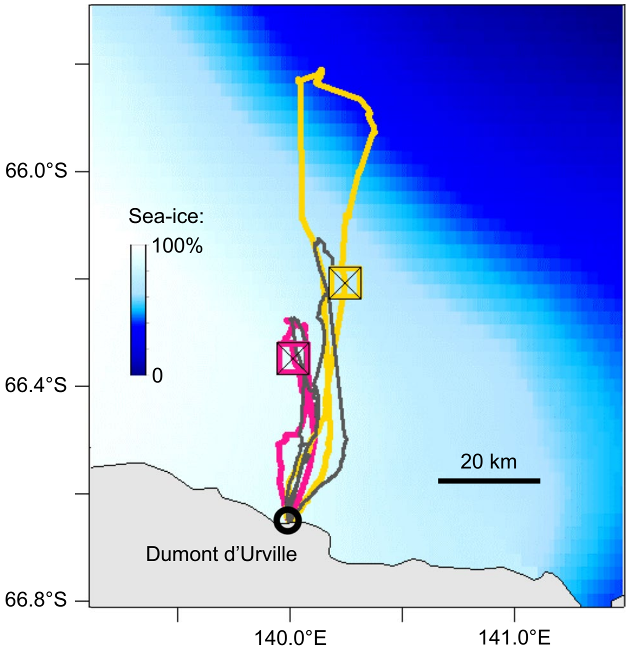

Fig. 3 Spatial location of jellyfish or salp encounters by the four Adélie penguins GPS tracked from Pétrels Island, Adélie Land (background: sea ice concentration on 11 January 2015). One penguin (pink track) attacked two jellyfish on 11 January 2015. Another bird (orange track) encountered salp once on 12 January 2015. The square boxes symbolize the respective location of these events

3.1–110.4, from $n = 1859$ cases; Tukey post hoc comparisons of means, adjusted $P < 0.001$), but deeper than for fish (7.7 m ± 20.1 m; range 1.9–90.5, from $n = 19$ cases; adjusted $P < 0.002$) and similar to salps (30.4 ± 16.9 m; range 3.9–47.0, from $n = 5$ cases; adjusted $P = 0.97$).

Among the four birds that had concurrent GPS location, two encountered gelatinous organisms (Fig. 3). One penguin attacked jellyfish twice in a 4-min interval, 35.1 km north from the colony (over the shelf area, bathymetry: −198 m; sea ice concentration: 88 %). The other bird encountered salp once, farther from the colony (51.8 km away; bathymetry: −482 m; sea ice concentration: 74 %). In both penguins, these events occurred during the outbound phase of the trip.

Discussion

Our data demonstrate that Adélie penguin, a major Antarctic marine predator, occasionally feeds on jellyfish, despite other prey types being available. Jellyfish therefore appear as an alternate prey choice for this krill-dependent predator. Scyphozoan DNA was previously detected in Adélie penguins' faecal samples from East Antarctica (Jarman et al. 2013; McInnes et al. 2016), but the latter approach could not rule out secondary ingestion through other prey. Here, the video loggers revealed a direct trophic link and confirm the non-negligible fraction that scyphozoans may represent in Adélie penguins' diet. These results demonstrate that jellyfish are not a dead end of the Antarctic trophic web, but a non-krill pathway to transfer matter/energy to higher trophic levels. High abundances of cnidarians were reported from the neritic zone of the Dumont d'Urville Sea in summer 2008 (Toda et al. 2014). In particular, *Diplulmaris antarctica* was collected at stations situated south of 66°S only, where it was found at various depth ranges (from 0–50 to 200–500 m). Greatest numbers for that species were recorded at the closest sampling stations north of our survey colony (down to 38 km; Toda et al. 2014). This is within the foraging radius of our tracked birds (Fig. 3; Widmann et al. 2015) and such rich cnidarian community would indeed represent a considerable biomass available for these predators provisioning in a limited area from the colony. *Diplulmaris antarctica* also was one of the most abundant jellyfish species reported three decades ago in the coastal Ross Sea (depth 0–20 m; Larson and Harbison 1990), whereabouts large numbers of Adélie penguins breed (Ainley 2002).

It is often considered that gelatinous animals might constitute poor diets because of the low ratio of organic material to salt and water (Sommer et al. 2002). Typically, calorimetric values reported for gelatinous animals per unit of wet weight confer on them low energy density when compared with other taxa: only less than 20 % of those of arthropods (Arai 1988) and up to 58 times less energy per gram of wet mass than herring flesh (reviewed in Doyle et al. 2007). We may therefore wonder whether jellyfish would actually be a beneficial—yet underestimated—prey item for penguins. Video monitoring recently revealed that jellyfish can be profitable to seabirds, not because they have intrinsic energetic content but because they serve as a "reservoir" of other prey items (Sato et al. 2015). The main identified jellyfish species in our study, *Diplulmaris antarctica*, is regularly infested with the parasitic hyperiid amphipod *Hyperiella dilatata* (up to 54 individuals on one bell; Larson and Harbison 1990). From the footage, it is difficult to determine whether penguins were targeting the amphipods; however, our observations (Table 1) comprised four cases of attacks though no amphipod was visible on the jellyfish. This shows that the presence of amphipods was not a prerequisite of attack for the penguin, though it might enhance the profitability of such attacks. Similarly, no jellyfish was observed with its captured prey; thus, the monitored penguins were not depredating them. Consequently the motivation for the penguins to attack the jellyfish was not, at least in some cases, to consume the associated parasites or prey, but the jellyfish itself.

Closer examination of the intrinsic value of jellyfish as food reveals differences in energy density both between species and between body components, which may better explain the attacks by Adélie penguin. For example, Doyle et al. (2007) showed that energy density of specimens varied twofold between species and that either gonad or oral arm tissue contained ~5 times more energy than bell tissue. The energetic content of *D. antarctica* is unknown, and thus, we cannot infer whether this species would be more profitable than others to penguins; but coherently with the latter study, our instrumented birds attacking a large jellyfish mainly targeted the gonad and/or oral arms only, which suggests that consuming these tissues may be particularly beneficial to the penguins. Our analyses further revealed a significant association between the penguin attacks and the visible presence of the jellyfish gonads. The carbon and protein content of the gonads is indeed greater than that of any other tissues in gelatinous animals (Arai 1997), and it is plausible that such structure may benefit to penguins from its energy content (quantitatively), and perhaps also by providing specific elements (qualitatively) that the penguins may seldom find in other food items. Therefore, Adélie penguins from East Antarctica may indeed prey on scyphozoans for the intrinsic value of their tissues. In that aim, approaching the jellyfish from below may help the penguins in silhouetting the gonads against the light background of the surface and evaluating its energy content. King penguins *Aptenodytes patagonicus* targeting myctophid fish exhibit a similar silhouetting strategy (Ropert-Coudert et al. 2000).

Breeding success in the survey plot was poor in 2014–2015 (10 %) compared to the long-term monitoring of this colony (Ropert-Coudert et al. 2015; Barbraud et al. 2015). Poor breeding success often reflects inadequate foraging conditions for Adélie penguins (e.g. Emmerson et al. 2015). Hence, it could be argued that our observations, carried out during this single field season, may reflect an odd behaviour of the penguins possibly linked to unusual foraging conditions. However, the previous DNA-based studies of Adélie penguins' diet covered, in all, five breeding seasons in East Antarctica (Jarman et al. 2013; McInnes et al. 2016). In four out of these five different seasons with presumably variable foraging conditions, scyphozoan DNA was detected in the penguins' faecal samples (in variable proportions). Hence, Adélie penguins may regularly prey on jellyfish across years, at least in East Antarctica. This prey item may dominate at times, while being undetected at others (Jarman et al. 2013; Watanabe and Takahashi 2013; McInnes et al. 2016). However, it is unlikely that in a "bad" year, Adélie penguins may prey exclusively on jellyfish. Indeed, the East Antarctic epipelagic (0–200 m) cnidarian community decreases in abundance and biomass when primary production is low, due to bottom-up control, while only the upper mesopelagic community (200–500 m) remains stable (Toda et al. 2010). This upper mesopelagic community being vertically out of reach of Adélie penguins (Ropert-Coudert et al. 2001), they may not rely on it as an alternate to krill under reduced productivity.

Besides, our analyses (Table 1) suggest that penguins attacked jellyfish, especially when they did not feed during the previous dive, but whatever was their feeding success during the current dive. This apparent paradox shows that it is not the lack of recent feeding that led penguins to target jellyfish. Indeed, because jellyfish are little mobile, with poor escape capacity, and of possibly large size (Larson and Harbison 1990), they constitute an easy target for predators such as penguins. Hence, capturing gonad-prolific jellyfish when it is encountered seems valuable for these predators even if the energy reward is low, because the expenditure for its capture would be very small. Prey captures are usually more numerous during the ascent versus descent dive phases in penguins (including the Adélie; Ropert-Coudert et al. 2000, 2001, 2006), yet our penguins most often neglected jellyfish during the ascent dive. These results suggest that jellyfish may represent an opportunistic prey for Adélie penguins, presumably allowing them to fine-tune their food intake, at both the dive and dive bout scales.

The increasingly used animal-borne video approach greatly contributes to better understanding ecosystem processes, especially in the marine realm, by pinpointing predator–prey interactions that are challenging to measure otherwise. In the case of Adélie penguins, it appears desirable to repeat such video monitoring in order to assess the proportion of consumed jellyfish according to other prey abundance, and particularly in contrasted foraging conditions. Kokubun et al. (2013) previously noted the occurrence of salps in the feeding environment of Antarctic penguins, but neither their study nor ours did reveal salps were consumed by the birds. This may be due to the salp tunica consisting mainly of tunicin, a cellulose-like polysaccharide that is hardly split into monosaccharides, and may thus be equally hard to digest for predators (Dubischar et al. 2012). Yet, Antarctic salp species in general, and *I. racovitzai* in particular, have relatively high carbon and protein contents per dry weight (Dubischar et al. 2012), which may in turn support their occurrence in minute proportions in the diets of seabirds in the Southern Ocean (Cherel and Klages 1998), including Adélie penguins (Jarman et al. 2013). Longer video recording may hence be needed to study the rarest trophic interactions and to demonstrate direct ingestion of salps by penguins. At the ecosystem level, our video-monitoring data show the need to better depict the niche of jellyfish in the Antarctic food webs, apart from that of salps (Melbourne-Thomas et al. 2013; Gutt et al. 2015). The significance of jellyfish as prey may indeed buffer the predicted impacts of the rapid and extensive environmental changes on Antarctic biota (Constable et al. 2014), although further monitoring will be required in order to better understand these ecological interactions.

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