USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

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Once you have Acrobat Reader open on your computer, click on the Comment tab (right-hand panel or under the Tools menu).

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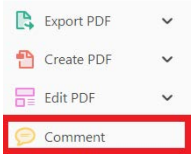

1. Replace (Ins) Tool – for replacing text.

Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it:

- Highlight a word or sentence.
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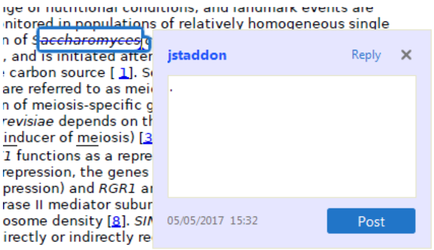
- Type the replacement text into the blue box that appears.



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2. Strikethrough (Del) Tool – for deleting text.

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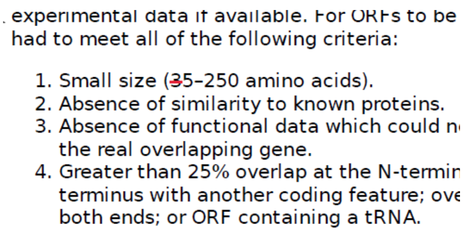
- Highlight a word or sentence.
- Click on .
- The text will be struck out in red.



experimental data if available. For ORFs to be had to meet all of the following criteria:

1. Small size (~~3~~5–250 amino acids).
2. Absence of similarity to known proteins.
3. Absence of functional data which could n
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4. Greater than 25% overlap at the N-termin
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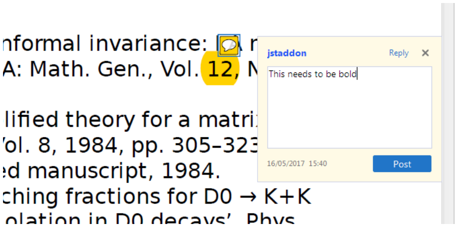
3. Commenting Tool – for highlighting a section to be changed to bold or italic or for general comments.

Use these 2 tools to highlight the text where a comment is then made.

How to use it:

- Click on .
- Click and drag over the text you need to highlight for the comment you will add.
- Click on .
- Click close to the text you just highlighted.
- Type any instructions regarding the text to be altered into the box that appears.



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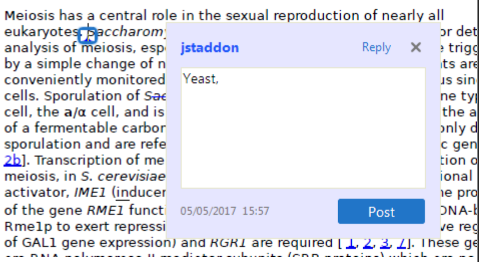
4. Insert Tool – for inserting missing text at specific points in the text.

Marks an insertion point in the text and opens up a text box where comments can be entered.

How to use it:

- Click on .
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the box that appears.



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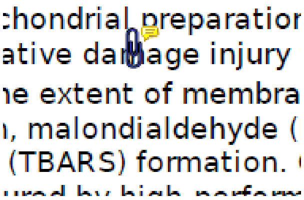
5. Attach File Tool – for inserting large amounts of text or replacement figures.

Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it:

- Click on .
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

  The attachment appears in the right-hand panel.



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6. Add stamp Tool – for approving a proof if no corrections are required.

Inserts a selected stamp onto an appropriate place in the proof.

How to use it:

- Click on .
- Select the stamp you want to use. (The Approved stamp is usually available directly in the menu that appears. Others are shown under *Dynamic*, *Sign Here*, *Standard Business*).
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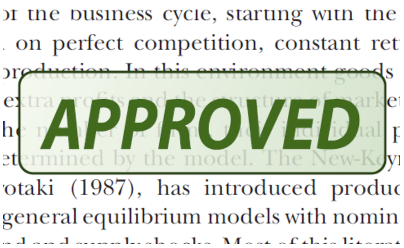

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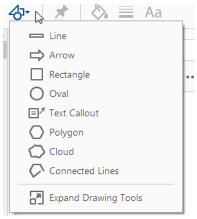
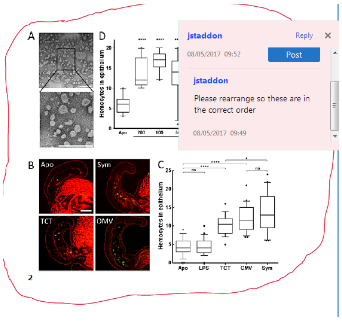


7. Drawing Markups Tools – for drawing shapes, lines, and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines, and freeform annotations to be drawn on proofs and for comments to be made on these marks.

How to use it:

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, right-click on shape and select *Open Pop-up Note*.
- Type any text in the red box that appears.



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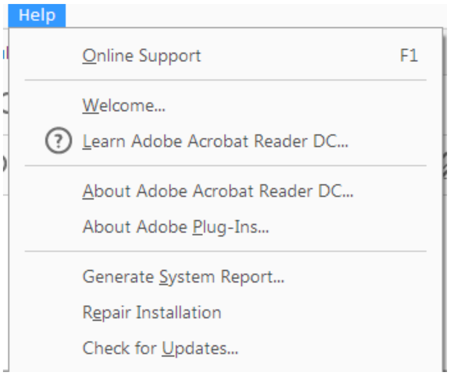

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Jellyfish and other gelata as food for four penguin species – insights from predator-borne videos

Jean-Baptiste Thiebot[1]*, John PY Arnould[2], Agustina Gómez-Laich[3], Kentaro Ito[4], Akiko Kato[5], Thomas Mattern[6], Hiromichi Mitamura[7], Takuji Noda[7], Timothée Poupart[2,5], Flavio Quintana[3], Thierry Raclot[8], Yan Ropert-Coudert[5], Juan E Sala[3], Philip J Seddon[6], Grace J Sutton[2], Ken Yoda[9], and Akinori Takahashi[1,4]

Jellyfish and other pelagic gelatinous organisms ("gelata") are increasingly perceived as an important component of marine food webs but remain poorly understood. Their importance as prey in the oceans is extremely difficult to quantify due in part to methodological challenges in verifying predation on gelatinous structures. Miniaturized animal-borne video data loggers now enable feeding events to be monitored from a predator's perspective. We gathered a substantial video dataset (over 350 hours of exploitable footage) from 106 individuals spanning four species of non-gelatinous-specialist predators (penguins), across regions of the southern oceans (areas south of 30°S). We documented nearly 200 cases of targeted attacks on carnivorous gelata by all four species, at all seven studied localities. Our findings emphasize that gelatinous organisms actually represent a widespread but currently under-represented trophic link across the southern oceans, even for endothermic predators, which have high energetic demands. The use of modern technological tools, such as animal-borne video data loggers, will help to correctly identify the ecological niche of gelata.

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Studying the ocean's food webs, and quantifying the trophic relationships between taxa within them, allows scientists to refine their perception of the ecological niche of marine predators and prey. In turn, improved knowledge about these ecological niches is essential to predict how variation in environmental conditions may affect ecosystem functioning (eg Moline *et al.* 2004). Considerable progress is being made in understanding the ecological niche of jellyfish and other "gelata" (see below). For example, these organisms may be more important in the ocean's carbon cycle than previously thought (Lebrato *et al.* 2012; Doyle *et al.* 2014). However, quantifying the ecological interactions of gelata in marine food webs is still challenging, for several reasons: gelata not only exhibit very diverse ecology (taxa encompassing carnivores and herbivores), with complex life cycles and fluctuating population size (Boero *et al.* 2008; Condon *et al.* 2013), but also are difficult to sample and study in the field due to logistical and methodological constraints (Arai 2005; Hamilton 2016). Quantifying their importance as prey for marine predators is especially challenging because of the difficulties associated with collecting fragile gelatinous tissues in stomach content analyses.

Carnivorous gelata – such as scyphozoans ("true" jellyfish, phylum Cnidaria) and ctenophores ("comb jellies", phylum Ctenophora) – naturally exhibit cyclic, global blooming patterns, although very little information is available from the southern hemisphere (Condon *et al.* 2013). In the southern oceans (ie the portions of various oceans and seas that are south of 30°S; important note: southern oceans are not to be confused with the Southern Ocean, the ring-shaped body of water extending northward from the Antarctic continent to 60°S), environmental variability occasionally promotes an increase of nano-phytoplankton that supports gelatinous herbivores such as salps (Tunicata, phylum Chordata), instead of fueling large endothermic predators such as penguins and whales (Chiba *et al.* 1998; Moline *et al.* 2004).

In this context, are southern marine predators able to exploit this variable gelatinous biomass as a food source? At the global scale, the existence of "jellyvore" species (sea turtles, ocean sunfish) demonstrates that despite their relatively low energy density, gelata might nevertheless sustain large animals (Arai 2005; Doyle *et al.* 2007, 2014). Furthermore, many other non-specialist species – including endotherms, which characteristically have high energetic demands – occasionally consume

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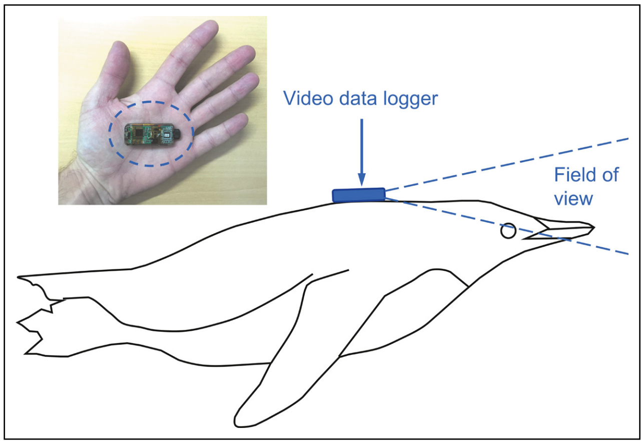

Figure 1. *Illustration of one type of video data logger used in this study (Little Leonardo DVL200; 15 gr; dimensions: 20 mm × 10 mm × 52 mm; 2.5-hr recording capacity), and its position when attached onto the back of a penguin to monitor feeding events.*

gelatinous prey (Harrison 1984; Arai 2005; Cardona *et al.* 2012).

Modern approaches to determining predator diets (including stable isotope analyses or scat DNA sequencing) have overcome limitations regarding the detection of fragile gelatinous tissues but still cannot rule out secondary ingestion of gelata by predators targeting other associated prey (Cardona *et al.* 2012; Jarman *et al.* 2013; McInnes *et al.* 2016). Consequently, to clarify the role that gelatinous organisms play in southern oceans' trophic webs, we used recently developed animal-borne video data loggers to record direct observations of predation events. Using a similar approach, Sato *et al.* (2015) demonstrated how jellyfish can serve to aggregate fishes, which predators such as diving seabirds can feed upon. We set out to quantify ingestion of the gelata themselves as food for such predators. Penguins are endothermic, presumed non-gelatinous-specialist marine predators, and a key component of consumers' biomass from the southern oceans (Brooke 2004). We video-monitored prey intake in four penguin species – Adélie penguins (*Pygoscelis adeliae*), yellow-eyed penguins (*Megadyptes antipodes*), Magellanic penguins (*Spheniscus magellanicus*), and little penguins (*Eudyptula minor*) – at seven breeding localities across regions of the southern oceans ranging from polar to temperate habitats. By doing so we hoped to provide an improved assessment of the importance of gelata in the southern oceans' food webs, and to support the use of a video-logging approach to conduct innovative and robust ecological assessments.

Methods

The study was conducted during the chick-rearing period for each penguin species at each site. Penguins of both sexes were captured at the nest or when leaving the colony to forage at sea. The video logger (facing forward) was attached to the median dorsal line of the penguins, positioned on the scapular joint (Figure 1); for detailed information about the video data loggers, see WebPanel 1.

The potential adverse effects of instrumentation on the foraging performance of individual penguins was expected to be small and transitory given the very short-term attachment of the loggers (one at-sea foraging trip per bird). Returning birds were recaptured ashore, loggers removed, and data downloaded onto a computer.

After removing video footage that was blurry or obstructed by the penguin's feathers, we visually inspected the remaining exploitable footage to identify and quantify interactions with prey within the camera's field of view. Gelatinous organisms observed on the videos were counted when penguins visibly modified their behavior to attack them (visible head and/or bill movements in contact with the prey). All observed gelata were categorized into three main taxonomic groups: scyphozoans, ctenophores, and salps. Further identification was conducted to the lowest possible taxonomic level, with the help of specialists.

Results

A total of 106 individual penguins were studied across four different years, and over 350 hours of exploitable footage were collected (Figure 2; WebTable 1). The observed gelatinous species included the jellyfish *Diplulmaris antarctica* and the salp *Ihlea racovitzai* on the videos collected from Adélie penguins; the jellyfish *Aequorea forskalea* from the yellow-eyed penguin video; the jellyfish *Chrysaora plocamia* and *Aequorea* sp, as well as the ctenophore *Mnemiopsis leidyi*, from the Magellanic penguin videos; and the jellyfish *Cyanea* sp from the little penguin videos. Importantly, the footage revealed predation on gelata by individual penguins, in all surveyed populations. The penguins apparently targeted gelata as a food source, and were seen swallowing entire specimens, tearing off and consuming parts of them, or pecking at their surface (WebVideo 1). Jellyfish (187 in total, none of them harboring fish) were attacked by all four penguin species. The Magellanic and little penguins also ingested 11 ctenophores. In contrast, salps were visible in the Adélie, yellow-eyed, and little penguin videos but were never observed being targeted. Overall, approximately one-third of the instrumented birds (n = 34) interacted with a gelatinous organism, and the penguins captured on average 0.91 gelatum per hour. Capture of previously known prey (fish and crustaceans) was also observed, and gelata amounted to an average of 3.9%, 4.9%, and 42.4% of prey events in individual Adélie, Magellanic, and little penguins, respectively (WebPanel 2; details of prey given in Sutton *et al.* 2015; Thiebot *et al.* 2016). Unexpectedly, Magellanic penguins twice captured a gelatum after swimming through, and not attacking, a swarm of lobster krill (*Munida gregaria*). In

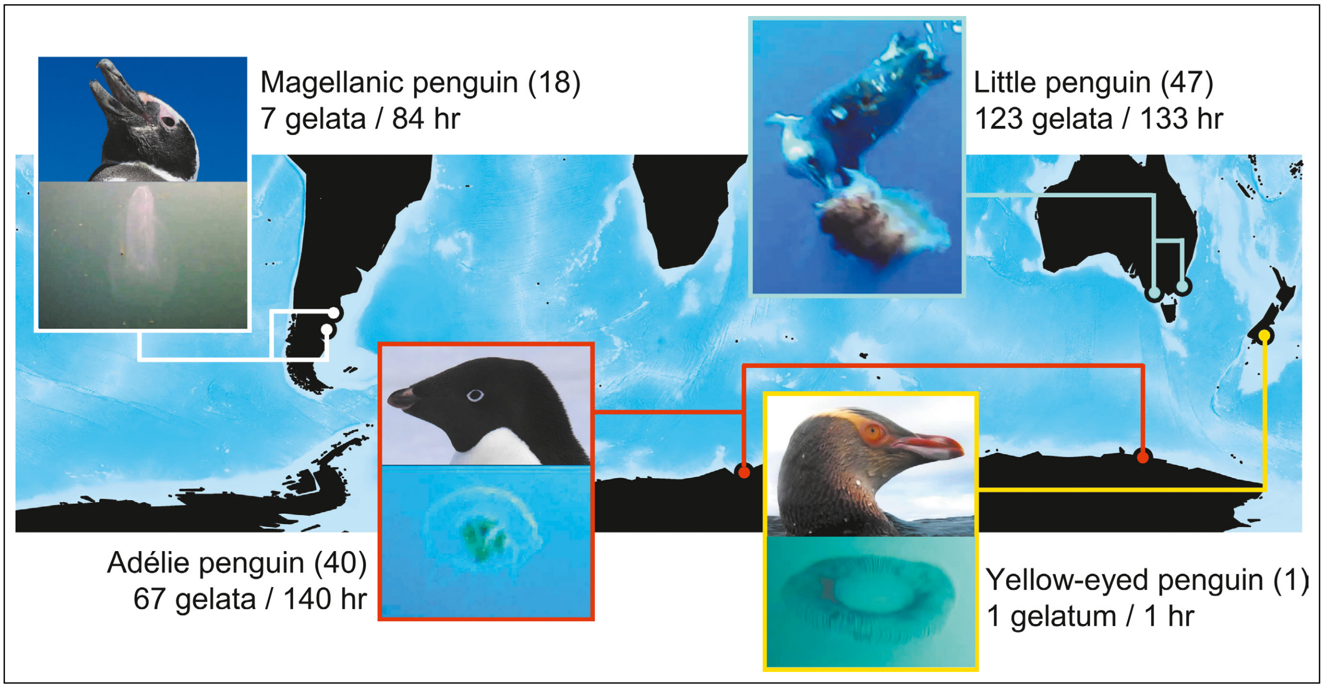

Figure 2. *Map of the seven localities for the four penguin species surveyed across the southern oceans. For each species, the number of individual penguins instrumented with video loggers, the number of observed interactions with gelata (jellyfish or ctenophore), and the amount of recorded footage (hours) are indicated. The gelatum images were taken from the analyzed videos.*

Adélie and little penguins, birds were observed repeatedly attacking individual gelatinous specimens. Furthermore, in Adélie, Magellanic, and little penguins, an individual bird successively attacked several gelata (up to 42 specimens attacked by one Adélie penguin). Repeated surveys with video loggers at Magellanic and little penguin sites confirmed the capture of gelata over 2 years. Predation on gelatinous organisms is estimated to account for >1% (for Adélie, Magellanic, and yellow-eyed penguins) and up to >2% (for little penguins) of the birds' daily energetic needs (WebPanel 2).

Discussion

Our observations establish that carnivorous gelata are more than just an incidental food source for the endothermic, non-gelatinous-specialist penguins, across regions of the southern oceans. Whereas stomach content and stable isotope analyses have previously suggested that seabirds and tunas might occasionally feed on jellyfish in the northern hemisphere (Harrison 1984; Cardona *et al.* 2012), our video logger study rules out secondary ingestion as the only explanation for the occurrence of gelata in southern predator diets. Moreover, repeated individual observations exclude the possibility that penguins only peck at gelatinous organisms as unidentified objects, or swallow them by mistake. Battery life limited the extent of our video recording to <25% of complete foraging trips, such that actual encounter and predation rates of gelata might differ over the course of an entire foraging trip. However, our results suggest that penguins may interact with a potentially large number of gelatinous organisms across the southern oceans each year. Our study, based on central-place foraging animals (that is, animals tied to a location from where they must commute to exploit feeding sites), supports the role of carnivorous gelata as a trophic link to apex levels within the coastal component of the southern oceans. By contrast, our video data suggest that penguins did not prey on herbivorous gelata: we seldom, if ever, observed salps, in contrast to studies in the pelagic component of the southern oceans (Pakhomov *et al.* 2002; Atkinson *et al.* 2004).

Our findings are consistent with the DNA sequencing of Adélie penguin scats that revealed the ingestion of various carnivorous gelata over several years and on occasion in unexpectedly large proportions (Jarman *et al.* 2013; McInnes *et al.* 2016). It is not known whether the routine consumption of gelata by penguins (in addition to other prey) is a recently developed behavior, potentially resulting from a "regime shift" in food webs (Richardson *et al.* 2009), or whether it occurred previously. Our video data show that the penguins consumed gelatinous organisms even when other prey items were available. Thus, the widespread capture of gelata does not reflect a situation of locally altered prey choice that would be caused by severe ecosystem perturbations (Richardson *et al.* 2009; Howarth *et al.* 2014). Gelata may indeed be naturally and cyclically important in the marine food web dynamics, without necessarily reflecting an anomaly (Boero *et al.* 2008; Condon *et al.* 2012, 2013). Nevertheless, whether penguin populations could be sustained on a predominantly gelatum diet under massive bloom conditions is currently unknown.

For predators (especially energy-demanding endotherms), the energetic benefits of feeding on gelata appear to be very low relative to those from other food sources, such as crustaceans or fish (Doyle *et al.* 2007). Furthermore, animals living in extremely cold water, such as Antarctic penguins, experience a substantial heat cost when ingesting prey. Therefore, how can predation on gelata, which are renowned for their high salt and water content (95–98% wet mass; Doyle *et al.* 2007), be metabolically profitable for penguins? First, the low energy reward of gelatinous prey for penguins might be balanced by their ease of capture as compared with fish, which require greater effort to chase, manipulate, and assimilate (Arai 2005; Sutton *et al.* 2015). This is especially true for penguins during the breeding season, which are usually losing body mass while rearing chicks and may not be meeting their daily energy requirements (eg Green *et al.* 2009). Ingesting any additional source of energy during this period, even a small amount of energy, could be critical to chick-rearing penguins. Second, predators may be selecting specific gelatinous tissues, such as gonad or arm tissues, which have an energy density about five times that of the bell (Doyle *et al.* 2007). Given that jellyfish may reach large sizes and their gonads are rich in lipids and proteins, predators that preferentially target these tissues could gain substantial energetic benefits. Third, gelatinous carnivores may act as a simple vector of nutrients, with penguins benefitting from the food being assimilated by these consumers. For example, DNA sequences of calanoid copepods (Crustacea), animals too small for the penguins to visually detect and capture, were commonly identified in Adélie penguin scats (Jarman *et al.* 2013; McInnes *et al.* 2016). Interestingly, this approach also revealed that approximately 15% of copepod genetic sequences were co-detected with jellyfish or ctenophore sequences, suggesting that such prey were repeatedly captured concomitantly. Consuming jellyfish arm tissues, where nutrients from the jellyfish's prey are being assimilated and may be concentrated, could be energetically profitable for penguins. Yet Thiebot *et al.* (2016) examined and rejected the hypothesis that Adélie penguins target jellyfish to ingest parasitic hyperiid amphipods (Crustacea), hence supporting the value of jellyfish themselves (not the energetic value of their parasites) for penguins. Finally, we suggest that penguins might target gelata as food for purposes beyond energetic ones. For example, the jellyfish mesoglea is a good source of collagen fibers, and scyphozoans can actively incorporate and concentrate free amino acids from organic matter dissolved in seawater (reviewed in Pitt *et al.* 2009), such that penguins might benefit from consuming gelata to enhance physiological or biochemical processes. This hypothesis, however, needs additional investigation.

The results of our multi-site, -species and -year survey challenge traditional perspectives that marine predators consuming gelata are an anomaly or indicative of a perturbation in ecosystem food web dynamics. Here, we emphasize the "supporting" service of gelatinous carnivores in marine systems, raised by previous studies (Doyle *et al.* 2014, Hamilton 2016), among other ecological benefits. Furthermore, regular predation on gelata by a larger community of predators than previously known could reduce the estimated rates of carbon advection to the benthos through so-called "jelly-falls". Sinking gelatum bodies facilitate the transfer of particulate organic matter to the seabed, mitigating some of the expected losses of carbon from the declining phytoplanktonic flux (Lebrato *et al.* 2012).

Predation on carnivorous gelata needs to be appropriately acknowledged to better understand and predict the ecosystem dynamics of the southern oceans. Our study shows that the use of modern tools such as predator-borne video data loggers may be instrumental in helping to quantify this impact. Indeed, such methods allow biologists to conduct studies that are typically only possible under lab conditions (eg functional responses, prey ingestion rates, handling times). Additionally, animal-borne videos are able to capture invaluable information regarding predators' foraging decisions (eg prey encounter rates, characteristics of the prey fields, intraspecific competition for prey), and this technology is readily transferable to many other marine predators. Quantifying the potential benefits (other than energetic gains) and costs (such as detoxification processes) for predators capturing gelata may help to refine current understanding of such interactions, at the start of a predicted global bloom of jellyfish (Condon *et al.* 2013).

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