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Food for Thought

Why do marine endotherms eat gelatinous prey?

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There is growing evidence that gelatinous zooplanktonic organisms (“gelata”) are regular prey for marine endotherms. Yet the consumption of gelata is intriguing in terms of the energy reward, because endotherms have a high energy demand and the consumption of gelata provides little energy return. In this paper, we take advantage of recent advances in diet analysis methods, notably animal-borne video loggers and DNA analysis in seabirds, to examine our current understanding of this interaction. We suggest that several hypotheses commonly raised to explain predation on gelata (including increased biomass, reduced prey availability, and secondary ingestion) have already been tested and many lack strong support. We emphasize that gelata are widely consumed by endotherms (121 cases reported across 82 species of seabirds, marine mammals, and endothermic fishes) from the Arctic to the Antarctic but noticeably less in the tropics. We propose that in line with research from terrestrial ecosystems atypical food items might be beneficial to the consumers in a non-energetic context, encompassing self-medication, and responding to homeostatic challenges. Changing the “last resort” context for a “functional response” framework may improve our understanding of widespread predation on gelata. Further biochemical analyses are needed to formally examine this perspective.

Keywords: ctenophores, diet, DNA analysis, endothermy, gelatinous zooplankton, jellyfish, predation, predator–prey, salps, video data logger

Introduction

Nearly three decades ago, Alverson (1992) proposed the “junk food” hypothesis to explain the dramatic decline of Steller sea lions *Eumetopias jubatus* in the Gulf of Alaska since the 1970s. According to this hypothesis, poor food quality, beside food quantity, can affect the population dynamics of predators. Specifically for Steller sea lions, a shift in the availability of a high-lipid prey to low-lipid prey item in the area (Anderson and Piatt, 1999) led to a dietary switch to prey of low energy content (Sigler *et al.*, 2004; Womble *et al.*, 2005; Trites *et al.*, 2007). This dietary switch had detrimental effects on the population of sea lions, as the low-energy prey were of poor quality for them to build sufficient energy reserves (Rosen and Trites, 2004, 2005). The relevance of the junk-food hypothesis for the sea lion case is still subject to debate (e.g. Fritz and Hinckley, 2005), however, this concept has found a large echo in marine ecology. Indeed, further studies on seabirds and marine mammals have provided substantial support for this hypothesis in food webs where predator populations face different levels of food resource quality, in

response to oceanographic variability or anthropogenic disturbances (reviewed in Grémillet *et al.*, 2008; Österblom *et al.*, 2008; Ludynia *et al.*, 2010).

Jellyfishes and other pelagic gelatinous organisms (“gelata”; Table 1) have sometimes been described as an energetic “dead end” in pelagic food webs (Sommer *et al.*, 2002; Robinson *et al.*, 2014; but see Verity and Smetacek, 1996). They are yet a well-known food source for a variety of ectothermic predators, including the oceanic sunfish and marine turtles (reviewed in Arai, 2005; Houghton *et al.*, 2006b), and are currently getting more attention from scientists to re-assess their potential contribution to marine food webs through such diverse ectothermic consumers (Choy *et al.*, 2017; Diaz Briz *et al.*, 2017; Dunlop *et al.*, 2017; Aubert *et al.*, 2018). However, because of their relatively low energy reward as food (Doyle *et al.*, 2007; Spitz *et al.*, 2010; Schaafsma *et al.*, 2018), gelata would constitute a sub-optimal diet for endothermic predators, which have higher energy demands than ectotherms. Accordingly, the occurrence of gelata in endotherms’ diets may be considered an extreme case of the

Table 1. Animal groups considered as “gelatum” prey items in this paper.

Phylum	Class	Order	Family	Genus	Common name, or example
Cnidaria	Scyphozoa				“True” jellyfishes; moon jelly <i>Aurelia aurita</i> ; giant jellyfish <i>Nemopilema nomurai</i>
	Hydrozoa	Siphonophora			“Portuguese man o’ war” <i>Physalia physalis</i>
Ctenophora	Hydrozoa	Anthoathecata	Porpitidae	Velella	Chondrophores; “by-the-wind sailor” <i>Velella velella</i>
Chordata (subphylum Tunicata)	Appendicularia	Copelata			Ctenophores, comb jellies; <i>Mnemiopsis leidyi</i> , <i>Beroe cucumiris</i> Larvaceans
	Thaliacea	Salpida	Salpidae		Salps; <i>Salpa thompsoni</i>
Mollusca	Gastropoda	Pyrosomida	Pyrosomatidae	Pyrosoma	Pyrosomes; <i>Pyrosoma atlanticum</i>
		Doliolida			Doliolids; <i>Doliolotta gegenbauri</i>
		Clades Thecosomata and Gymnosomata Clade Heterobranchia: Opisthobranchia	Superfamily Pterotracheoidea		Pteropods, pelagic sea snails, sea butterflies, sea angels Heteropods, sea elephants (holo-planktonic snails)

junk-food hypothesis, a “last resort” in prey selection, temporary or not. For example, the presence of salps in the diet of Antarctic seabirds in spring was interpreted as a last resort for the predators, “forced to be opportunistic” in the likely absence of high quality prey at that time (Ainley *et al.*, 1991).

There is growing evidence though that gelata are routinely consumed by a variety of marine predators including endotherms (Pakhomov *et al.*, 2002; Hays *et al.*, 2018). Studies have shown that consumption of gelata by endotherms does not seem restricted to certain individuals (Sutton *et al.*, 2015), gender (Thiebot *et al.*, 2016), demographic categories (McInnes *et al.*, 2016), species (Harrison, 1984; Fraija-Fernández *et al.*, 2018), seasons (Carroll *et al.*, 2019), years (Jarman *et al.*, 2013), poor breeding conditions (Cavallo *et al.*, 2018), or marine regions (McInnes *et al.*, 2017). Yet these prey remain unexpected by observers of endotherm diets, and their occurrence is poorly explained or underreported (Ates, 1991; Henschke *et al.*, 2016). It is thus problematic that these persisting issues are likely to bias our perception of the natural importance of jellies in marine food webs (Pauly *et al.*, 2009; Lamb *et al.*, 2019a).

In this paper, we question the paradigm that gelata should be dismissed as anomalies in the diet of marine endotherms. In fact, the frequency of occurrence of gelata in predator diets is likely to be underestimated because of the lack of hard parts distinguishable by visual examination, compared with other prey remains (Cattray *et al.*, 2004; Arai, 2005). In line with the current re-evaluation of the ecological role of jellyfish (Hays *et al.*, 2018), we gather published information on predation on gelata by endotherms, and review the energetic- and nonenergetic-based hypotheses that have been tested or speculated to explain this behaviour. We notably examine these hypotheses in the light of recent research using DNA dietary analysis and predator-borne video logging, mostly conducted on seabirds (e.g. Deagle *et al.*, 2010; Sutton *et al.*, 2015). In exploring whether a single framework may be applicable to all reported cases, we finally propose new perspectives to elucidate why endotherms consume gelata.

Literature search and cases found

We conducted a literature search in June 2019 using Web of Science. Search terms were “gelatinous,” “jelly*,” “salp*,” “tunicat*,” “scyphozoa*,” “hydrozoa*,” “cnidaria*,” “pteropod*,” or “heteropod*” combined with: “endotherm,” “whale,” “cetacean,” “seal,” “seabird,” or “tuna,” in any field. Articles were

included if they contained diet information for any endotherm which consumed a gelatinous organism. Reference lists of articles, including reviews identified in the literature search, were checked for additional studies.

A total of 66 papers from the literature review contained data of gelatinous prey in the diet of endotherms, encompassing birds, mammals, and endothermic fishes. These reports covered virtually all oceans in both hemispheres (Figure 1), although fewer observations were found for tropical regions. Nearly half (45.8%) of all sites with reported cases were at high latitudes spanning 45°–71°, whereas only 11.7% of them were from the intertropical zone (<23.4°; Supplementary Figure S1). This spatial pattern is consistent with the latitudinal ratio of endothermic versus ectothermic predator richness (Grady *et al.*, 2019). More specifically, we found 121 cases where an endothermic predator was reported to consume gelatinous prey (Supplementary Table S1). This encompassed 82 predator species, with some species represented in several studies. In mammals, 15 cases of consumption of gelata were reported from 11 species, representing 8.9% of the 123 known species of marine mammals. In birds, 84 cases were reported from 60 species of seabirds and shorebirds, representing 10.8% of the 346 species of seabirds and 212 species of shorebirds combined. In fishes, 22 cases were reported from 11 species (31.4% of the 35 known species of endothermic fishes; Dickson and Graham, 2004). The higher number of cases observed for seabirds and shorebirds may therefore reflect the higher avian species diversity compared with other groups of endotherms. In addition, the foraging ecology of birds is typically more easily observable by scientists and amateur wildlife enthusiasts than for other groups, and observations on the detailed composition of their diet accordingly seem more commonly available. The proportion of endothermic species observed to consume gelata was the highest among fishes, in which gelata can form a major component of the diet (Cardona *et al.*, 2012). On the contrary, it is remarkable that some taxa scarcely appear in Supplementary Table S1, and this is particularly the case of pinnipeds (seals). Similarly to seabirds, pinnipeds breed ashore: thus it could have been expected that detailed, long-term diet studies in this group that are outstanding among marine mammals would aptly reveal jelly consumption, but this was not the case. This is likely explained by detection biases, given pinniped diet is predominantly studied by identifying hard parts in faecal samples (Bowen and Iverson, 2013),

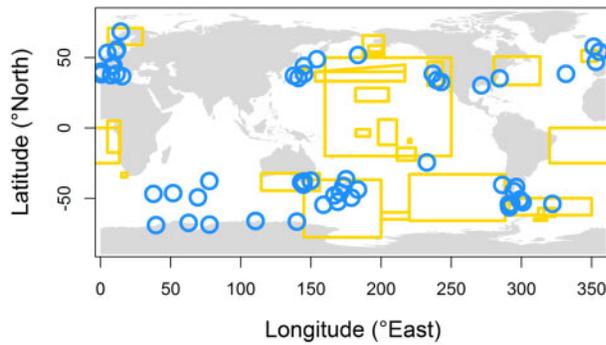


Figure 1. Map showing the location of the study sites where cases of predation on gelata by endotherms have been reported in the literature (references in Supplementary Table S1). Circles mark the sites for which a specific location was indicated in the publications (for example, a study colony where the predator diet was sampled, or a direct observation of predation for which geographic coordinates were recorded). The regions outlined with polygons show the boundaries of study areas from publications covering a large spatial range and/or not providing a specific location (for example: mention of a geographic region, reports on at-sea observations without recorded coordinates, or diet studies with samples collected from vast regions).

whereas for seabirds diet is mostly studied through visual identification of regurgitated stomach contents (Barrett *et al.*, 2007).

Finally, different types of gelata seemed to be consumed unevenly among endothermic predators (Figure 2). Mammals were reported to consume mostly tunicates among gelatinous prey (74.1%), with a lesser proportion of cnidarians (14.8%) and minor proportions of ctenophores, molluscs and other/unidentified gelata. In contrast, in birds the cnidarians were the gelatum taxa most often reported to be consumed (59.6%), followed by tunicates (28.1%), ctenophores (8.8%), and others. Finally, endothermic fishes were reported like marine mammals to consume predominantly tunicates among gelatinous prey (56.5%), with notably more cnidarians (34.8%) and the highest reported proportion of molluscs (8.7%).

The energetic return of gelata

Based on metabolic and thermodynamic estimates, it is possible to estimate whether a marine endotherm may compensate its energetic expenditure when ingesting gelata (Figure 3a). Using calorimetric and composition measurements, the average energetic content of three species of jellyfishes (*Cyanea capillata*, *Rhizostoma octopus*, and *Chrysaora hysoscella*) were estimated to reach $\sim 130 \text{ J g}^{-1}$ of wet mass (Doyle *et al.*, 2007). From this value, we calculated the energy that an endothermic predator may extract per gram of ingested jellyfish, by multiplying it by the predator's assimilation efficiency (e.g. 77% in penguins; Cooper, 1977):

$$0.77 \times 130 \text{ J g}^{-1} \text{ wet mass} = 100 \text{ J g}^{-1} \text{ wet mass.}$$

The energetic cost C undertaken by the predator to bring 1 g of the ingested tissue to its internal temperature (T_i , $\sim 38^\circ\text{C}$), depends mainly on the ambient seawater temperature (T_w , 14°C on average in temperate regions), as well as the specific heat capacity of the sea (K) and the water contents of the prey (W):

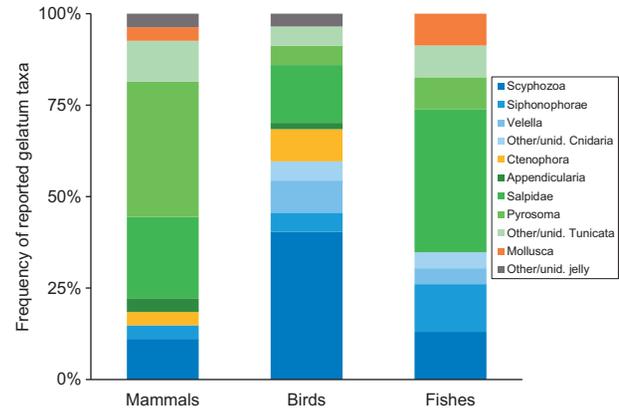


Figure 2. Frequency of the different gelatum taxa reported in the diet of marine endotherms. Number of reported cases of consumed gelatum taxa: 27 in mammals, 57 in birds, 23 in endothermic fishes.

$$C = K \times W \times (T_i - T_w)$$

$$C = 4.17 \times 0.96 \times (38 - 14) \text{ Jg} - 1.$$

This predicts an energetic cost of $\sim 96 \text{ J g}^{-1}$ for a penguin in temperate waters, which is 96% of the maximum expected energetic gain (without accounting for costs related to capture and prey handling). In polar waters ($\sim 0^\circ\text{C}$), this thermodynamic cost rises to $\sim 152 \text{ J g}^{-1}$ of ingested jellyfish, and thus exceeds the maximum expected energetic gain (152% of the gain). Hence, there would be very little energetic benefit for an endotherm to ingest jellyfish in temperate waters, and no energetic benefit (but a net cost) in colder waters, where many of the examples collated in Supplementary Table S1 originate. These calculations would predict greater benefits for endotherms in warmer (tropical) waters, yet comparatively few observations were available at lower latitudes (Supplementary Figure S1). By comparison, the same above approach applied to ingestion of fish flesh (5 kJ g^{-1} and 75% water contents, reviewed in Doyle *et al.*, 2007) predicts that gains are systematically higher than the costs: 51 times higher than the costs in temperate waters, and 32 times higher in polar waters.

Large salps, such as *Thetys vagina*, would have higher energetic values (11 kJ g^{-1} dry weight, DW) than that of jellyfish (4 kJ g^{-1} DW); and *Salpa thompsoni* and *Ihleia racovitzai* have high protein (10 and 32% DW, respectively) and carbon (15 and 22% DW) contents (Dubischar *et al.*, 2012; Henschke *et al.*, 2016). However, improved estimates for assimilation efficiency are currently needed for many of the gelatinous prey, hence limiting predictions on assimilation costs. Such costs may greatly reduce energetic benefits for the consumer, and in the case of tunicates, the cellulose-like polysaccharide “tunic” that encloses salps’ bodies might be hardly digestible for predators (Pakhomov, 1993; Dubischar *et al.*, 2012). In conclusion, it seems possible that endotherms might have little to no energetic benefit from ingesting gelata. An energy-based framework might hence not be systematically relevant to understand why endotherms consume gelata, especially in polar regions. Consequently, in this paper we also examine hypotheses associated with non-energetic drivers of such behaviour. The ingestion of food for non-energetic reasons (encompassing the acquisition of certain minerals or essential

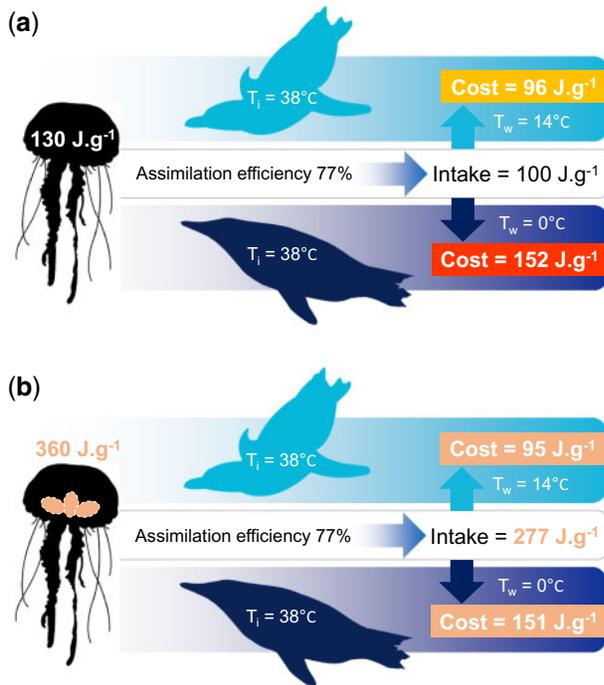


Figure 3. Estimates of energetic cost and reward for the ingestion of jellyfish tissue by an endothermic predator. Here is shown the example of a penguin (internal temperature $38\text{--}39^\circ\text{C}$) in two contrasted environments: temperate versus polar regions (sea surface temperature $T_w=14^\circ\text{C}$ versus 0°C), with energy estimates (a) from average jellyfish tissue (130 J.g^{-1} wet mass; 96.0% water content) and (b) specifically from gonad tissue (360 J.g^{-1} wet mass; 95.1% water content). Note that lower gain estimates are obtained when considering the ingestion of the jellyfish bell (57 J.g^{-1} wet mass; 96.3% water content) versus oral arm (223 J.g^{-1} wet mass; 95.5% water content) tissues, providing an assimilated gain of 44 versus 172 J.g^{-1} wet mass, and costs of 221 versus 56% this gain in temperate waters, and 350 versus 88% in polar waters, respectively. Energy density of tissues from Doyle *et al.* (2007).

amino acids, practicing foraging techniques, enhancing physiological processes or responding to homeostatic challenges) is in fact widespread among wild animals, and although it has been documented mostly in terrestrial ecosystems (e.g. Weeks, 1978; Perrins, 2008; Forbey *et al.*, 2009), there is no reason to suspect that this behaviour would not be exhibited by marine organisms.

Assumptions generally not supported to explain consumption of gelata by endotherms

High gelatinous biomass

Alarming titles about gelatinous biomass flourish in the literature (e.g. “attack of the blobs”: Schroepe, 2012; “rise of the slime”: Grémillet *et al.*, 2017; issue discussed in Doyle *et al.*, 2014; Duarte *et al.*, 2015). One could thus be tempted to relate the recently highlighted cases of predation on gelata to an increased abundance of such prey in the oceans. However, many gelatum populations have naturally cyclic abundance patterns (Boero *et al.*, 2008; Condon *et al.*, 2013). Their blooms may be spectacular at times, and regular (e.g. *Rhizostoma* blooms, Houghton *et al.*, 2006a) or not (e.g. *Pelagia noctiluca* bloom, Doyle *et al.*, 2008), but these phenomena may well not represent large-scale, long-

term trends (Mills, 2001; Condon *et al.*, 2012; Richardson *et al.*, 2012). Indeed, there is limited evidence for a prolonged, global increase in gelatum biomass, with the majority of long-term monitoring datasets not supporting this trend (Brodeur *et al.*, 2008; Condon *et al.*, 2013). However, over-fishing of forage fish may provide a competitive release for gelata in some regions (Lynam *et al.*, 2006; Richardson *et al.*, 2009), especially when combined with eutrophication or coastal anthropogenic activities (Daskalov *et al.*, 2007; Uye, 2014; Greene *et al.*, 2015). It could thus be expected that occasionally high biomass of gelata in time and/or space would increase their probability of consumption by predators, and contribution to the predators’ diets. Nevertheless, gelatum consumption by endotherms has been reported regularly for decades or even more than a century (Supplementary Table S1) and across diverse regions (Figure 1), even in periods of low abundance. For example, in one of the most significant reports of gelatum consumption by seabirds (Harrison, 1984), individuals from 11 out of 17 species of birds shot in the eastern Bering Sea in 1982–1983 included jellyfish as part of their diet, with gelatinous tissue regularly occurring in up to 50% of the birds sampled per species. However, long-term monitoring data on jellyfish in the eastern Bering Sea (1979–2011) reveals that although large variations have occurred across decades, jellyfish abundance was low, and even minimal, at the time of that seabird survey (Condon *et al.*, 2013).

More recently, inter-annual DNA dietary analyses combined with data from fisheries showed that black-browed albatrosses *Thalassarche melanophris* from the Falkland Islands/Islands Malvinas in the southern Atlantic Ocean included jellyfishes in their diet, whether or not jellyfishes were abundant in trawl fisheries’ catches off the islands (McInnes *et al.*, 2017). Importantly, the frequency of jellyfish occurrence in albatross diets was similar in years of high and low jellyfish availability, suggesting that jellyfish consumption is independent from the local biomass available to the predators. The survey on seabirds in the Bering Sea tends to further support this conclusion, with several seabird species preying on jellyfish even at times of year when they are less abundant (Harrison, 1984).

In conclusion, endothermic predators appear to consume gelata even when gelatinous biomass is not high. However, diet techniques rarely allow the ingested gelatum biomass to be calculated, and therefore comparisons of its contribution to the predators’ diet between varying conditions of availability are limited. It would be desirable to examine this further in detail to relate the consumed amounts of gelata to the available biomass. Besides, the hypothesis of a long-term increasing trend in gelatum biomass, which has emerged from actual supporting cases observed at several sites (e.g. Utne-Palm *et al.*, 2010; Lynam *et al.*, 2011), is questionable at the global scale. Fluctuating populations of jellyfish in some areas, regular and predictable seasonal blooms in many coastal areas, and large increases in jellyfish populations in other areas seem to compose a more complex picture than the above hypothesis may account for (Sanz-Martin *et al.*, 2016).

Reduced prey availability

In this context, endotherms would consume gelata when they cannot find enough higher-energy prey in their environment (see above example, Ainley *et al.*, 1991). As a consequence, the proportion of gelatum prey in the diet should be negatively correlated with local availability of the main prey. However, multi-year

dietary studies on penguins suggest that despite potential variation in prey supply, the intake of gelata by these predators is relatively consistent between years (Jarman *et al.*, 2013; Thiebot *et al.*, 2017). More specifically, in the case of the diet of Adélie penguins *Pygoscelis adeliae* examined at four Antarctic sites, across 4 years and three different breeding stages through faecal DNA sequencing (Jarman *et al.*, 2013), the proportion of various gelatinous taxa DNA detected was not clearly correlated with the proportions for the two main prey (krill and bony fish; Spearman's rank correlation $\rho = 401.2$, $p = 0.097$). However, it may be difficult to translate DNA readings into local biomass levels of prey (Lamb *et al.*, 2019b), and other approaches may be more relevant to examine this point.

Penguin-borne video data enabled this hypothesis to be specifically tested, over the shorter term (Sutton *et al.*, 2015; Thiebot *et al.*, 2016). First, the footage showed that crustacean and/or fish prey were locally available, irrespective of gelatum ingestion; second, the penguins which consumed gelata were primarily eating other prey, and finally gelatum consumption was not related to the time elapsed since the last successful prey capture. Thus, in these examined cases, the ingestion of gelata did not seem to occur as a consequence of poor availability of other prey.

In conclusion, recent empirical evidence suggests that the current assumption, according to which the ingestion of gelata would only occur as a consequence of reduced availability of the first choice prey, should be looked with greater scepticism. The growing number of studies using animal-borne video data may bring further information on this point, by examining the *in situ* prey capture events in relation to the local prey availability.

Accidental or inadvertent captures

Marine predators may sometimes ingest non-food items if they mistakenly catch them for prey: this has been reported for a wide array of consumers, including fish, marine turtles, cetaceans, and seabirds (e.g. Fukuoka *et al.*, 2016; Hyrenbach *et al.*, 2017; Savoca *et al.*, 2017; Fraija-Fernández *et al.*, 2018). This behaviour may be stimulated by the fact that these non-food items look, smell, and/or taste similarly to proper food items.

Accordingly, gelata could be ingested by marine endotherms as they are mistaken for other prey items, or ingested inadvertently while the predator targets other prey items.

For example, diet studies on northern elephant seals *Mirounga angustirostris* by stomach lavage revealed the recurrent occurrence of bioluminescent pyrosomes among other food items, in both sub-adult males and adult females (Antonelis *et al.*, 1987). It is thus possible to assume that these bioluminescent organisms have been ingested in lieu of mesopelagic lantern-fishes, which are also bioluminescent and consumed by this predator (e.g. Naito *et al.*, 2013).

However, underwater footage collected from 106 individuals across four penguin species (Sutton *et al.*, 2015; Thiebot *et al.*, 2016, 2017) showed that predators can repeatedly attack the same jellyfish, as well as successively attack several jellyfishes in a row (up to 42 gelata attacked by 1 Adélie penguin). These elements suggest that in penguins, gelata are not predominantly captured inadvertently together with the main targeted prey, but seem to be themselves the targeted item. Presumably, albatrosses would actively select jellyfishes too, because these prey occurred more consistently in their diet than in the environment across years (McInnes *et al.*, 2017).

In cetaceans, many cases of ingestion of tunicates involve suction-feeding predators (reviewed in Fraija-Fernández *et al.*, 2018): adults and/or juveniles of Risso's dolphin (*Grampus griseus*), sperm whale (*Physeter macrocephalus*), Baird's beaked whale (*Berardius bairdii*), southern bottlenose whale (*Hyperoodon planifrons*), and Stejneger's beaked whale (*Mesoplodon stejnegeri*) were all found to have ingested tunicates, among which *Salpa maxima* (up to 123 individuals in a Risso's dolphin calf), *Salpa fusiformis*, *Iasis zonaria*, *T. vagina*, and most commonly *Pyrosoma atlanticum*. It could thus be assumed at first glance that individuals may inadvertently ingest gelatum along with the main target prey; however, some of these predators were found with tunicates as the only prey in the stomach contents (a Risso's dolphin calf with exclusively *S. maxima* and *P. atlanticum*; and a southern bottlenose whale calf with exclusively *P. atlanticum* and *T. vagina*), suggesting these captures were deliberate in these cases. Direct observations of predation on "jellyfishes" by a killer whale *Orcinus orca* (Similä *et al.*, 1996) and several seabird or shorebird taxa (Supplementary Table S1) further support the widespread, non-inadvertent nature of these captures.

In conclusion, recent research conducted on seabirds, and empirical observations from marine mammals tend to consistently reject the hypothesis that at least in these predators, gelatum captures are inadvertent. However, the consumer's intent cannot be directly inferred from these observations and further experimental research on animal cognition would be needed to ascertain the deliberate nature of these captures, and that the gelata are recognized as food items.

Secondary ingestion

In diet studies based on the examination of stomach contents, but more particularly in DNA dietary analyses, one acknowledged consideration is that a detected prey might have originally been contained in the stomach of a first consumer, which was subsequently ingested by the studied predator. This incidental, indirect interaction between the prey and a second predator is known as "secondary ingestion." The secondary ingestion of gelata is possible given the higher prevalence in the diet of ectotherms (Diaz Briz *et al.*, 2017; Dunlop *et al.*, 2017; Aubert *et al.*, 2018) and may cause an over-estimate of primary predation of gelata in the endothermic, second predators. However, co-occurrence analyses of DNA sequences and examination of the proportion of sequences can be used to ascertain which prey are likely primary prey items. Such analyses show that gelata are consumed as primary prey items in the examined cases (Jarman *et al.*, 2013; McInnes *et al.*, 2017). This inference combined with more than a century of direct observation of predation events and stomach contents examination (Supplementary Table S1), as well as recent remote observations using predator-borne video loggers (Sutton *et al.*, 2015; Thiebot *et al.*, 2016, 2017) have largely discredited this theory, with clear empirical evidence of primary predation on gelata by various predators (see above section). However, the inference on primary ingestion made from the co-occurrence analyses of DNA sequences (Jarman *et al.*, 2013; McInnes *et al.*, 2017) cannot be extended with confidence to all cases of DNA-based gelatum detection in the predators' diet. In conclusion, secondary ingestion is not, or very unlikely in some taxa, the cause of the detected gelata in the diet of endothermic predators.

Minerals and water

Ingestion of specific food for its essential minerals that are otherwise rare in the environment has been documented or suspected for decades (Weeks, 1978; Perrins, 2008). It could thus be assumed that gelata represent “concentration hotspots” of such elements in the marine environment. However, there is no evidence that gelata have the general capacity to osmo-regulate significantly. Composition analyses in the moon jellyfish *Aurelia aurita* showed that sodium and chloride concentrations are virtually identical with seawater; only divalent sulphate ion concentrations reflect some capacity for active regulation (Robertson, 1957; Mackay, 1969). Some jellyfish species might show higher concentrations in N and P than their environment, but this is not a general rule (Uchida *et al.*, 2005). Similarly, with water contents of typically 94–97% (reviewed in Doyle *et al.*, 2007), gelata may be seen as a source of water for predators, but the lack of significant osmo-regulation for sodium and chloride again suggests that this would not be a valid option for predators. In this context, it would seem more efficient for predators to simply ingest seawater, as this would provide easier access to salt or water for marine predators, rather than relying on encountering gelata across their foraging trip. Hence, this hypothesis does not seem to be generally supported.

Plausible arguments, but lacking consistent empirical support

Opportunistic ingestion

Capturing gelata, which move slowly and may reach large sizes, presumably costs little energy to a predator, as opposed to more mobile and/or smaller prey (Henschke *et al.*, 2016). Hence, predators may simply seize the opportunity of a low-cost capture when encountering gelata, even for a presumably low energy reward; but importantly must balance these opportunities with the need to keep their body streamlined and manoeuvrable (Verity and Smetacek, 1996; Hays *et al.*, 2018). This strategy, and notably its limits, would explain why gelata are generally found in minor proportions of predators’ diets, even in fishes which do not share the time constraints of air-breathing marine predators for underwater foraging.

This hypothesis is consistent with the observation that not all encountered gelata were attacked by the video-monitored penguins (Thiebot *et al.*, 2016), suggesting that predators do not maximize their gelatum intake when they could. Foraging penguins, which usually capture their prey during the bottom and ascent phases of their dives, attacked jellyfishes mostly during the descent and bottom phases (Thiebot *et al.*, 2016). These captures, especially when energy-rich tissues are targeted (see below), may thus ensure minimum energy gains for penguins at the start of a dive when upcoming prey capture success is unknown. This hypothesis therefore seems plausible. Quantifying the energy expenditure of capturing gelata versus other prey would allow this hypothesis to be formally tested, especially for predators that must return to the surface to breathe.

Further work using acceleration and video data loggers could examine the cost for air-breathing predators to ingest gelatum parts at depth, especially when these predators undertake multiple consecutive dives to feed on gelata and higher energy prey are locally available. This behaviour would not always support the argument of low-cost predation on gelata, depending on the local availability of other prey types (Sutton *et al.*, 2015). Furthermore,

examples exist where predators were directly observed to engulf large quantities of jellyfishes, to the point of exhibiting difficulties to flee (Anthony, 1895), and several dietary studies found that jellyfishes could make up to the majority, or even the total, of prey items found (birds: Hatch, 1993; in fishes: Cardona *et al.*, 2012). Finally, this hypothesis does not explain why predators seem to consume relatively consistent proportion of gelata, despite variations of available biomass in the environment (McInnes *et al.*, 2017; although this may not always be the case: Anthony, 1895). Further studies using video-logging techniques in several taxa are thus warranted to further support this explanation, and to better understand the decision of predators knowing local availability in gelata versus other prey.

Playing, practicing prey capture and the ontogeny of predatory behaviours

Handling of living or inanimate objects by predatory animals may be carried out for a non-nutritious purpose, notably playing and practicing prey capture (e.g. Marchetti and Price, 1989; Hall, 1998). These two types of behaviour may have different or similar purposes, and are difficult to separate from each other in observations carried out in the wild. Playing can be observed in both juvenile and adult animals, and its function for predators may be to enhance individual success by reducing shyness or fear of a novel prey, and to reduce predation time through practice with non-prey objects (see Hall, 1998 and references therein). Besides, juveniles often exhibit a different foraging behaviour or diet than adults (e.g. Marchetti and Price, 1989). These differences originate from the existence of structural (skeletal-muscular and/or neurological systems) and time constraints to learn foraging skills, and are under strong natural selection as foraging skills are crucial for survival.

Gelata are slow-moving animals and would thus represent easy targets for predators playing or practicing prey capture, especially in young, inexperienced individuals who have not yet fully developed their foraging techniques. Indeed, calves of cetaceans show a more limited ability to capture mobile prey than adults, and often select slower prey that are easier to catch (reviewed in Fraija-Fernández *et al.*, 2018). For example, stomachs examined from dead calves from three cetacean species contained only tunicates, suggesting that these were the only prey type that could be caught by these young individuals (Fraija-Fernández *et al.*, 2018). But these behaviours are not just restricted to juvenile animals, with adult killer whales “often” observed playing with jellyfishes in northern Norway (Similä *et al.*, 1996). Therefore this hypothesis might be valid for juveniles, inexperienced individuals and/or in predators known to play or actively practice their foraging skills, e.g. cooperative hunting behaviour. Yet, even in cases comparing the diet of adult and younger individuals, this hypothesis is sometimes not supported.

Foraging ontogeny in juvenile predators, or practicing group foraging skills are unlikely to be the primary reason for predation on gelata, as most reported cases involve adult individuals foraging solitarily, or at least not cooperatively. The majority of surveys used indirect dietary methods where the predation behaviour was not observed, but video data show that predators do not seem to play with the gelata before ingesting them (Sutton *et al.*, 2015; Thiebot *et al.*, 2016, 2017). In addition, DNA dietary analyses showed that the scats of non-breeding birds (which included at least some immatures) contained less jellyfish sequences

than that of breeding adults, over the two examined seasons (McInnes *et al.*, 2016). Nevertheless, the practice component of this behaviour still cannot be excluded, even in these cases. Hence, further studies would be needed, especially from direct observations or video logging, so that special attention could be given to assess the importance of this playing/practicing behaviour in the predators ingesting gelata.

Prey aggregation

Certain organisms may harbour large numbers of smaller animals, whereby the latter locally reach greater density than elsewhere in the environment, hence providing a concentrated food source for predators (e.g. Valburg, 1992). In the context of the marginal value theorem for optimal foraging in animals (Charnov, 1976), this situation is highly beneficial to the predators as it enhances foraging success and decreases search effort. Similarly, marine predators may target gelata because these organisms could harbour a higher density of potential prey than in the ambient environment.

Indeed, jellyfishes' tentacles sometimes harbour juvenile fish, and predators may attack jellyfishes to access these fish (Duffy, 1988; Brodeur, 1998; Sato *et al.*, 2015). Similarly, numerous taxa of amphipods (Crustacea) live in close association with gelata and may constitute non-negligible food sources for predators. For example, amphipods in the sub-order Hyperiidia are famous symbionts of gelata (Harbison *et al.*, 1977; Madin and Harbison, 1977). The association between amphipod and gelatinous host, although probably parasitic (Ohtsuka *et al.*, 2009), is often highly specific and can involve salps, siphonophores, scyphozoans, ctenophores, or other gelatinous organisms (Harbison *et al.*, 1977; Madin and Harbison, 1977). Hence, gelata may represent prey aggregating systems for predators targeting fish and/or crustaceans, and this trait could explain the presence of gelatum parts entering in the predators' diet. There is empirical evidence supporting this hypothesis. For example, hyperiid amphipods were frequently found in Arctic seabird stomach contents, and the most well-preserved specimens were individual amphipods enveloped in gelatinous tissue found in Northern fulmar *Fulmarus glacialis* samples (Harrison, 1984).

However, animal-borne video data (Sutton *et al.*, 2015; Thiebot *et al.*, 2016, 2017) revealed that the jellyfishes attacked by penguins (i) did not harbour fish and (ii) sometimes had not a single associated amphipod (4 cases over a total of 12 examined jellyfishes, Thiebot *et al.*, 2016), although on average they hosted more amphipods than the non-attacked ones. Furthermore, other video footage revealed that in the Bering Sea, thick-billed murre *Uria lomvia* would be able to discriminate the targeted prey, and to capture only the juvenile fishes harboured within the jellyfishes' tentacles, without ingesting parts of the jellyfish (Sato *et al.*, 2015). Consequently, although some observations support the hypothesis that predators may benefit from the prey associated with the ingested gelata, there is a lack of consistent support from the available *in situ* observations to conclude on the significance of this perspective.

Klepto-predation

In a slightly different context from the previous section, diet studies showed that marine predators can also capture unusual prey to benefit from the food previously ingested by this prey ("klepto-predation"; see Willis *et al.*, 2017). In this perspective,

gelata may be ingested by marine endotherms if they contain sufficient prey items recently captured in their feeding apparatus, to constitute a valuable energy intake for the predators. DNA dietary analyses on penguins highlighted a relatively high co-occurrence of jellyfishes and calanoid copepod (Crustacea) sequences (Jarman *et al.*, 2013). Copepods are presumably too small to be visually detected and captured by penguins in the open water: it might hence be profitable for penguins to consume jellyfishes, which routinely capture these prey. However, in albatrosses, no other prey DNA was detected in 25% of samples containing jellyfish (McInnes *et al.*, 2017), suggesting these jellyfish did not provide additional gains. Therefore, this hypothesis also seems plausible, but needs further empirical evidence, most likely to be brought from DNA dietary analyses.

Energy-rich tissues

It is a widespread behaviour in both terrestrial and marine environments that predators do not fully eat their captured prey: this behaviour has been extensively documented for example in the killer whale (reviewed in Jefferson *et al.*, 1991). Killer whales may consume only minute portions of their prey (for obvious reasons when the prey is very large), such as targeting the tongue and lips of captured baleen whales. This selective feeding may be to avoid the danger of fluke movements of the prey, or possibly because the killer whales favour these parts and target them in particular (reviewed in Jefferson *et al.*, 1991). Similarly, it could be assumed that because gelata as food confer little energetic benefit to their consumers and may reach large sizes, the endothermic consumers would benefit from consuming only gelatum tissues with the highest energy density. In scyphozoans for instance, body components such as the gonads or oral arms may contain up to five times more energy than that of the bell (Doyle *et al.*, 2007).

This hypothesis has been specifically tested with video data of Adélie penguins. The presence of a well-developed gonad in a jellyfish was associated with a higher probability of predation (Thiebot *et al.*, 2016), which suggests that the penguins may be targeting jellyfishes to specifically consume this energy-rich tissue. By doing so, penguins ingest $\sim 360 \text{ J g}^{-1}$ of gonad wet tissue (Figure 3b; estimates from Doyle *et al.*, 2007), and may assimilate 277 J g^{-1} wet mass. Accordingly, this gain from ingesting gonad tissue compares more favourably to the thermodynamic costs estimated above, which decrease to only 34 and 54% of the gain estimated in temperate and polar regions, respectively. On the other hand, the fact that the penguins usually avoid attacking the jellyfish from below could also suggest that they targeted the upper parts simply to avoid the tentacles. However, penguins were also seen ingesting full (smaller) jellyfishes and ctenophores (Sutton *et al.*, 2015; Thiebot *et al.*, 2016, 2017), supporting the hypothesis that they actively select the energy-rich tissues in the larger jellyfishes, not primarily to avoid stings.

This hypothesis of selecting energy-rich tissues seems to provide a solid framework to explain the capture of jellyfishes by endothermic predators. In fact, this may also be significant in ectotherms: video data showed that ocean sunfish (Nakamura *et al.*, 2015) and marine turtles (Fukuoka *et al.*, 2016) similarly targeted the most energetic parts of jellyfishes. Notably, sunfish consumed large scyphozoa, ctenophores and various siphonophore chains, but in the case of scyphozoan jellyfishes they only fed on gonads and oral arms, leaving the bell intact.

In conclusion, it seems highly beneficial for marine consumers to select only those gelatum tissues that maximize energy gains.

Nevertheless, this hypothesis provides limited understanding for the consumption of other types of gelata than scyphozoan jellyfishes. For example, even though tunicates may reach relatively high energy density among gelata ($5\text{--}11\text{ kJ g}^{-1}\text{ DW}$, reviewed in Doyle *et al.*, 2007; Henschke *et al.*, 2016), the biochemically stable structure of their envelope may limit the efficiency of the consumer in assimilating this energy. Furthermore, in addition to having low energy densities, gelata such as siphonophores (and possibly tunicates; see Doyle *et al.*, 2007 for a review), do not build up large, prominent energy-rich organs like the gonads found in scyphozoan jellyfishes. In conclusion, this hypothesis provides a valid framework, but is, to this day, mostly relevant to predation of scyphozoan jellyfishes.

Exploring new perspectives: consuming gelata as a functional response

The context of response to homeostatic challenges

Consumption of unusual food items with a weak nutritional benefit has been observed across the animal kingdom (reviewed in Forbey *et al.*, 2009; Huffman, 2010). This type of behaviour was first investigated in non-human primates specifically to understand leaf-swallowing, which was devoid of solid energetic gain for the consumer (reviewed in Huffman, 2015). The potential benefit of leaf-swallowing for parasite expulsion from the consumer generated new hypotheses in a functional interpretation framework. Using food item components to respond to homeostatic challenges is not a new concept (Janzen, 1978). However, this idea has developed immensely through a growing number of observations, both anecdotal and empirical, that show a diverse array of animal species engage in such forms of self-medication (e.g. Huffman, 1997; Villalba and Landau, 2012; Su *et al.*, 2013; Suárez-Rodríguez *et al.*, 2013). Many cases have been documented in which animals specifically target non-energetic, or even toxic, items, to exploit biological properties that reduce costly homeostatic challenges. This has mostly been documented so far in terrestrial ecosystems where animals exploit secondary metabolites from plants (reviewed in Forbey *et al.*, 2009), but the same theoretical framework could be applied to understand similar interactions between organisms in a variety of ecosystems. In this context, this behaviour may serve to mitigate the costs of homeostatic challenges, including, but not restricted to, infection by parasites, moderating thermoregulation, and increasing alertness (detailed below).

Potential roles for gelata in homeostatic challenges

Ingesting gelata may provide individual endotherms with physiological benefits and solutions to homeostatic challenges, in conjunction with one or several of the hypotheses presented earlier. This hypothesis of “unusual and bioactive foods” (Masi *et al.*, 2012) would account for the large variation in behaviour observed between individuals in a given situation (e.g. McInnes *et al.*, 2016). In fact, despite the low energy reward of gelata (which can be seen as “the green tea of the sea”; Hamilton, 2016), they may be targeted because they would provide consumers with particular components that can be directly beneficial against homeostatic challenges temporarily affecting individuals.

Gelata as a diet item could meet two of the five defined levels of response to homeostatic challenges (Huffman, 2010): either

(i) as items routinely selected in the diet in small quantities or with limited occurrence, with a preventative or health maintenance effect; or (ii) their ingestion would represent a direct self-meditative behaviour by the predator, for a curative treatment using toxic or biologically active components of the ingested item, devoid of nutritional value. Evidence for food utilization at these two levels has been found across the animal kingdom (Huffman, 1997), with similar behaviours appearing in phylogenetically distant taxa. For example, plants are ingested by apes, bears, and geese at key phases of their life cycle (during the rainy season months, and prior to hibernation and migration, respectively), even when regular food items are locally available, and while the plant does not contribute directly to the energy balance (reviewed in Huffman, 2010). However, the benefit of ingesting these non-energetic items could outweigh the cost of energy loss from high parasite loads prior to hibernation or migration. This is especially the case in those two examples, where the consumers have restricted energy stores available to complete these challenges. It is thus possible that gelata could have a similar role against gut parasites in endothermic consumers, although the gelata may themselves be hosts to various parasites. This hypothesis would definitely deserve further investigation, with individual parasitic load measured concurrently with gelatum consumption.

Endothermic animals have also been shown to use secondary metabolites to maintain homeostatic body temperatures. Hypothermia notably represents a costly homeostatic challenge in the marine medium where heat conductivity is 30-fold that of air (Dejours, 1987), and research shows that such challenge can be alleviated through the use of peculiar molecules. For example, alkaloids in tall fescue grass and terpenes in pine trees can cause vasoconstriction that limits heat loss (Oliver *et al.*, 1993; Gardner *et al.*, 1998). In the wild, woodrats consume more juniper in cold conditions (Dearing *et al.*, 2008), presumably taking advantage of secondary metabolites to minimize heat dissipation (McLister *et al.*, 2004). This suggests that endotherms can boost their body temperature through this strategy without increased energetic costs, with these components decreasing the lower critical temperature triggering a thermoregulatory response (Forbey *et al.*, 2009). Physiological mechanisms such as vasoconstriction can indeed elicit reduced heat loss, whereas heat production may be obtained through the biochemical process of detoxification. This aspect definitely deserves further research in the case of gelatum consumers. It would seem particularly beneficial to marine endotherms indeed, because of the great heat dissipation in water; moreover, it is supported by the higher number of reports on gelatum ingestion by endotherms in colder environments (but not limited to this explanation; see Grady *et al.*, 2019). It is also remarkable that in cetacean calves, necropsy revealed that gelata were sometimes the only food items found in the stomach (Fraija-Fernández *et al.*, 2018): although we cannot exclude the possibility that the slow-moving gelata may have been the only prey that these predators were capable of capturing before death, these observations may also reflect an active response of these consumers facing a severe homeostatic challenge associated with hypothermia. This hypothesis on thermoregulation may therefore be relevant to gelata ingestion, but currently remains to be tested.

As a last example, animals are expected to benefit from maintaining a high level of alertness (i.e. vigilance) through maximized ability to detect predators, and may achieve this by consuming stimulating substances. In the wild, scientific documentation of animals affected by the stimulatory activities of food compounds

is rare. However, gorillas, wild boars and porcupines have been observed digging up and eating the roots of the plant *Tabernanthe iboga* to increase stamina (reviewed in [Forbey et al., 2009](#)), with the principle component ibogaine having stimulating effects similar to caffeine ([Dubois, 1955](#); [Szumlinski et al., 2001](#)). Such properties might also exist in gelata and be desirable for consumers, especially meso-predators living in cold waters where endothermic top predators dominate ([Grady et al., 2019](#)). Increased alertness may benefit a range of species also through improved individual memory of quality habitats and foods ([Forbey et al., 2009](#)) and increasing reaction times ([Michael et al., 2008](#)) which would be advantageous for marine predators to capture and handle prey.

In conclusion, many cases have been documented where animals may exploit specific, bio-active food compounds in ways that reduce various homeostatic challenges. This framework for food use, although often correlative, suggests that ingesting gelata could also serve such a function in marine endotherms.

Potential bio-active components of gelata

Four basic requirements have been listed for demonstrating self-medication in animals ([Huffman, 2010](#)): (i) identify the homeostatic challenge or symptom(s) being treated; (ii) distinguish the use of a therapeutic agent from that of routine food items; (iii) demonstrate a positive change in homeostatic condition following self-meditative behaviour; and (iv) provide evidence for the bio-activity of compounds extracted from these therapeutic agents. If we consider that examples for the first part have been listed above, and that in the second part, we assume that gelata may fill this role, the third and fourth parts still need detailed examination. As stated above, experiments could be undertaken in which monitoring the ingestion of gelata would be concomitant with individual examination for, e.g. parasitic load, and therefore formally test this hypothesis. But regarding the bio-active properties of gelatum compounds, we need to look at research from the human medical and food sciences, where scyphozoan jellyfishes, among all gelata, have received considerable attention.

As a food item, jellyfish is low in fats and cholesterol but rich in proteins ([Hsieh et al., 2001](#)), and notably more than 40% of its dry weight consists of collagen ([Kimura et al., 1983](#); [Nagai et al., 1999](#)). Collagen is a group of fibrous proteins of very high tensile strength that form the main component of connective tissues in animals: it is indeed an essential component of muscle tissue, cartilage and bone and has been recognized as very suitable material for cartilage tissue engineering ([Leone et al., 2015](#)). Experimental studies on mice revealed its anti-fatigue and anti-oxidation properties ([Ding et al., 2011](#)), as well as immunological effects leading to autoimmune and inflammatory responses ([Firestein and Corr, 2005](#)). Moreover, collagen is an important platelet agonist that is thought to be involved in the early stages of platelet activation during both hemostasis and thrombosis ([Sugiyama et al., 1987](#); [Pignatelli et al., 1998](#)). In humans, jellyfish collagen has been shown to stimulate the acquired immune system, by enhancing the production of immunoglobulins (up to 34-fold) and cytokines ([Sugahara et al., 2006](#); [Nishimoto et al., 2008](#)). These results suggest that jellyfish collagen facilitates the immune response, in addition to antibody production. Further, more recent studies showed that jellyfish collagen enhanced not only the acquired, but also the innate immune response through cytokine production and the activation of phagocytotic activity of macrophages

and dendritic cells ([Putra et al., 2012, 2014](#)). Beyond immunostimulation, it was shown that jellyfish collagen peptides also had an effect on regulating blood pressure ([Zhuang et al., 2012](#)). In the wild, consuming jellyfish for its collagen content might hence contribute to protecting the consumer from infectious agents, diseases, or other homeostatic challenges. The many bio-active properties of collagen supports the hypothesis that ingestion of gelata may constitute a self-medication behaviour by marine endotherms ([Thiebot et al., 2017](#); [Hays et al., 2018](#)).

Apart from collagen, a new polysaccharide composed of mannose, galactose, and glucuronic acid was extracted from jellyfish tissue, and shown to also have bio-active property in the immune response through the activation of macrophages ([Li et al., 2017](#)). Furthermore, other components extracted from jellyfishes were suggested to have “nutraceutical value” (reviewed in [Leone et al., 2015](#)). For example, high anti-oxidant activity measured from peptides extracted in all tested jellyfish samples ([Leone et al., 2015](#)) suggests that gelata as food may serve self-treatment purposes. Their contents in essential amino acids is also to be noted (e.g. [Kimura et al., 1983](#); [Pitt et al. 2009](#); [Leone et al., 2015](#)). Essential amino acids are needed by organisms for vital processes like the building of proteins and synthesis of hormones and neurotransmitters, and unlike nonessential ones, must be obtained through diet.

The lipid content of jellyfish tissue is also noteworthy. Among fatty acids examined in the analysed jellyfish species, a relatively high proportion (~25–30%) were polyunsaturated fatty acids, among which the ω -3 types were abundant and predominant compared with the ω -6 types ([Uchida et al., 2005](#); [Leone et al., 2015](#)). The ω -3 polyunsaturated fatty acids are well known for being involved in a number of biological processes including growth, development, tissue, and cell homeostasis, as well as for having health benefits including hypo-triglyceridemic, anti-inflammatory antihypertensive, anticancer, antioxidant, antidepressive, antiaging, and anti-arthritis effects (reviewed in [Leone et al., 2015](#)).

Finally, examining the natural compounds of venoms and associated biotoxins from jellyfishes revealed promising sources of bioactive compounds (reviewed in [Mariottini and Pane, 2010](#)). Some bioactive substances were actually discovered in cnidarians, such as the Palytoxin local anaesthetic and vasoconstrictive agent. Cytolytic and antitumoral substances have also been found that inhibit the growth of leukemic cells. Further, venom of scyphozoan jellyfishes has been shown to adversely affect or inhibit growth of tumours.

The study of the physiological benefits of jellyfish components is a dynamic research field, however, these results are yet to percolate through to wildlife ecology. Research on scyphozoan jellyfishes' collagen and venom has already revealed immense potential for bio-active substances beneficial to humans and possibly the natural jellyfish consumers; however, much less is known about the compounds of Thaliaceans and other gelata. Exploring properties of the acidic mucopolysaccharides constituting the gelatinous body of the tunicates, and that of the tunicin, the polysaccharide enclosing the body of adult tunicates (reviewed in [Henschke et al., 2016](#)), may reveal further support for the natural and extra-energetic benefits for marine consumers to ingest gelata, possibly including self-medication. We propose that such benefits may widely apply to wild animals consuming gelatum tissues, although further analyses are needed to formally examine this hypothesis. The use of modern tools for molecular

Box 1. Why are gelata not found more commonly in endotherm diets?**1. Methodological biases**

It is likely that gelata are naturally consumed more frequently than currently reported, but this interaction remains difficult to quantify with traditional dietary methods. Direct at-sea observations of predators feeding on gelata are understandably not frequent, but are occasionally reported in air-breathing species (Supplementary Table S1 and Figure S2). Consequently, information relies largely on indirect dietary methods; however, gelata are difficult to identify visually from diet samples (Arai, 2005; but see Harrison, 1984). The fragile gelatinous tissues devoid of hard parts break down much faster than other prey such as fish, crustaceans, and cephalopods: therefore these tissues are likely to be partially or totally degraded in the examined stomach contents or scats. These detection biases from traditional diet approaches also provided the basis for fewer reports of gelatum occurrence in the diet of certain taxa such as pinnipeds. Indeed, even when using modern approaches such as DNA-based analysis, biases can exist if markers used cannot detect DNA from gelatum groups (Deagle *et al.*, 2009; Hardy *et al.*, 2017; Jeanniard-Du-Dot *et al.*, 2017), hence limiting our ability to quantify the importance of these groups in the actual diet. Further work using video cameras on a range of predator species as well as DNA methods with group-specific markers to detect gelata will help clarify this point.

2. Observer biases

Authors previously suggested that there may be a “reluctance of observers to accept [gelata] as being a useful source of food” (Ates, 1991), which again may prevent gelata from being adequately reported among the prey items of studied predator species. This point was one of the motivations to write the current paper, and we hope that in further studies, authors may report even traces of gelatum tissues whenever it is the case found in the diet samples.

3. Potential cost to the predator

There may be specific costs incurred to the predator when consuming gelata. Gelata are not all equivalent and differ considerably between taxa, and thus may not confer the same benefits and have the same costs to the consumers. Specific costs may include the difficulty of digesting certain tissues (e.g. tunicates; Dubischar *et al.*, 2012), avoiding or detoxifying the venomous components of gelata (Mariottini and Pane, 2010) or their defence mechanisms (e.g. distasteful organic compounds from tunicates, Pisut and Pawlik, 2002). For these reasons, consumers may also avoid consuming gelata more often than it could be expected from the hypotheses listed above.

investigation including metabolomics may further help highlighting bio-active compounds of gelatum tissues, which could directly or indirectly stimulate a number of physiological functions in the consumers. If consuming gelata does indeed provide predators with homeostatic benefits, it would be valuable to know whether there are associated costs, e.g. related to the lysis of the tunicin or venom components, which could explain why gelata are not detected more often in the diets (Box 1).

Conclusions

This paper highlights that gelata regularly appear among the prey consumed by marine endotherms. Although pelagic gelatinous organisms are not a major prey for endotherms worldwide, from recent research conducted using modern approaches we can clarify that gelata (i) do not necessarily reflect an anomaly in the food webs when they are ingested by endotherms; and (ii) can be a primary target for a range of predators, in a routine fashion. In line with recent works, we believe that the role of gelata as a prey for endotherms should be better acknowledged in trophodynamic models of marine food webs (Henschke *et al.*, 2016). Finally, we suggest that a change of paradigm may be needed to clarify how endotherms may benefit from ingesting gelata: the “junk-food hypothesis” generally associated with energy-poor diets might actually limit our understanding of these interactions, whereas non-energetic approaches, including the practice for prey capture, opportunism, or self-medication, may bring a more relevant, functional vision on the role of these ingestions. This latter point, however, deserves further experimental research, and does not preclude that several hypotheses among all those examined may be valid and would operate in conjunction. This paper provides frameworks to stimulate research and debate on the question of gelatinous organisms as prey in marine ecosystems. By reviewing

the documented cases of ingestion and confronting them with new perspectives brought by modern diet approaches, we intend to refine the general perception of the natural importance of gelata in marine food webs, and to propose further experimental studies to formally test the hypotheses underlying this role.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Authors' contributions

J.B.T. conceived the manuscript; J.B.T. and J.M. wrote the manuscript.

Statement of competing interest

None declared.

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