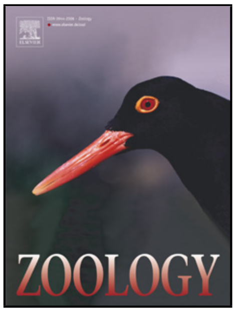

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Whale and dolphin behavioural responses to dead conspecifics

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Highlights

- Effort-weighted study of 'postmortem attentive behaviour' (PAB) in cetaceans.
- Dolphins (Delphinidae) accounted for 92.3% of 78 PAB records, baleen whales 1.3%.
- Encephalisation was an important predictor of PAB across taxa.
- Female PAB towards dead calves (75%) may have been rescue attempts or grieving.
- Male PAB was rare and possibly not caregiving.

Abstract

The scientific study of death across animal taxa—comparative thanatology—investigates how animals respond behaviourally, physiologically and psychologically to dead conspecifics, and the processes behind such responses. Several species of cetaceans have been long known to care for, attend to, be aroused by, or show interest in dead or dying individuals. We investigated patterns and variation in cetacean responses to dead conspecifics across cetacean taxa based on a comprehensive literature review. We analysed 78 records reported between 1970 and 2016, involving 20 of the 88 extant cetacean species. We adopted a weighted comparative approach to take observation effort into account and found that odontocetes (toothed cetaceans) were much more likely than mysticetes (baleen whales) to attend to dead conspecifics. Dolphins (Delphinidae) had the greatest occurrence of attentive behaviour (92.3% of all records, with a weighed attendance index 18 times greater than the average of all other cetacean families). Two dolphin genera, *Sousa* and *Tursiops*, constituted 55.1% of all cetacean records (N = 43) and showed the highest incidence of attentive behaviour. Results of analyses intended to investigate the reasons behind these differences suggested that encephalisation may be an important predictor, consistent with the "social brain" hypothesis. Among attending individuals or groups of known sex (N = 28), the majority (75.0%) were adult females with dead calves or juveniles (possibly their own offspring, with exceptions), consistent with the strong mother-calf bond, or, in a few cases, with the bond between mothers and other females in the group. The remaining records (25.0%) involved males either showing sexual interest in a dead adult or subadult, or carrying a dead calf in the presence of females. Because an inanimate individual is potentially rescuable, responses to dead conspecifics—especially by females—can be explained at least in part by attempts to revive and protect, having a clear adaptive value. In some cases such responses are followed by apparently maladaptive behaviour such as the long-term carrying of, or standing by, a decomposed carcass, similar to observations of other terrestrial mammals. Among the possible explanations for the observed cetacean behavioural responses to dead conspecifics are strong attachment resulting in a difficulty of "letting go"—possibly related to grieving—or perhaps individuals failing to recognise or accept that an offspring or companion has died. Our current understanding is challenged by small sample size, incomplete descriptions, and lack of information on the physiology and neural processes underpinning the observed behaviour. We provide research recommendations that would improve such understanding.

Keywords: Cetaceans; epimeletic behaviour; caregiving behaviour; comparative thanatology; grieving

1. Introduction

The scientific study of death across animal taxa—comparative thanatology—investigates how animals respond behaviourally, physiologically and psychologically to dead conspecifics, and the processes behind such responses. The discipline offers insight into evolutionary and social adaptations, for instance how responses are influenced by the identity, kinship and social role of the dead individual (e.g. offspring, partner, relative, group member or stranger). The field is also concerned with whether nonhuman species share aspects of the human concept of death (for instance, whether some species grieve or exhibit compassionate behaviour; Anderson, 2016). Scientific studies of death have become increasingly interdisciplinary in recent years, encompassing a variety of taxa and topics such as necrophoresis or interment behaviour (including corpse removal, burial, cannibalism, and avoidance or necrophobia, e.g. among insects; Sun and Zhou, 2013), bird "funerals" (Iglesias et al., 2012), and behavioural responses to dead conspecifics among mammals. The latter includes mainly primates (Anderson et al., 2010; Anderson, 2011; De Marco et al., 2018), but also species such as the African elephant *Loxodonta africana* (Douglas-Hamilton et al., 2006), the dingo *Canis dingo* (Appleby et al., 2013), the collared peccari *Pecari tajacu* (de Kort et al., 2018) and the giraffe *Giraffa camelopardalis* (Bercovitch, 2013).

Several species of cetaceans (whales, dolphins and porpoises) have been long known to care for, attend to, be aroused by, or show interest in dead or dying individuals (Hubbs, 1953; Norris and Prescott, 1961; Caldwell and Caldwell, 1966). This behaviour has been often labelled as "epimeletic" or "caregiving"—terms that imply a supposedly altruistic action toward an injured animal. In addition to assisting an individual in distress, epimeletic behaviour involves one or more adults attending to a dead individual, keeping it afloat if sinking, lifting or pushing it down if buoyant, performing "resuscitation" attempts, and carrying it on the dorsum, head or rostrum (Fig. 1), or in the mouth (Reggente et al., 2016; Bearzi and Reggente, 2017). Cetaceans have been documented carrying a dead and decomposing individual for up to about one week (Porter, 2002; Ritter, 2007; Krasnova et al., 2014). While present understanding of cetacean behaviour toward the dead is poor, and risks of over-interpretation are high (Anderson, 2016), some responses to deceased individuals—primarily involving adult females and their dead calves—have been interpreted as expressions of bereavement resulting from the breaking of strong social bonds (Bearzi et al., 2017). The prevalence and specific attributes of this behaviour appear to vary among cetacean species, but such variability has not been formally assessed.

[INSERT FIG. 1]

Reports describing responses of cetaceans to dead conspecifics have been based largely on opportunistic observations in the wild. These reports are scattered across a variety of species, and the number of reports per species depends in part on the ease of observing natural behaviour, which varies with species abundance, distribution and behaviour, in particular: proximity to shore, dive duration, and responsiveness to vessels (Bearzi et al., 2017). In addition, cetaceans are typically long-lived animals with low birth rates and high adult survivorship, which further limits the opportunities to observe behaviour toward dead individuals. The chances of documenting infrequent behaviour also depend on the amount and intensity of observation effort, and there are great differences in the extent of research effort directed toward the various species. Some of the beaked whales, for example, are known only from stranded specimens, and have never been identified alive in the wild (Jefferson et al., 2015). Clearly, one would not expect to find published reports documenting instances of epimeletic behaviour for species that are rarely if ever encountered at sea.

Phylogenetic variation in the number of reported responses to dead conspecifics may also be attributed to biological and ecological differences among cetacean taxa. Currently, extant cetaceans comprise 88 known species (Committee on Taxonomy, 2017) that vary in distribution, habitat, ecology, social organisation, behaviour, body size, and encephalisation. As a group, cetaceans have exceptionally large and sophisticated brains, though measures of relative brain size show great diversity across taxa (Ridgway et al., 2017). Brain size, in particular, was recently shown to predict a variety of social and cultural behaviours in cetaceans (Fox et al., 2017) and might, therefore, also correlate with variation in the responses to dead conspecifics. The investigation of this phylogenetic variation may help unravel the evolutionary, biological and cognitive processes that determine and shape the diversity of responses to dead conspecifics, elucidate the adaptive value of such responses, and perhaps initiate a debate over whether epimeletic responses can be framed in the larger context of emotional and mental sensitivity to another's state (de Waal, 2008; de Waal and Preston, 2017).

Here, we conduct a literature review to identify all verifiable reports of cetaceans exhibiting attentive behaviour toward dead individuals. Because we found only one case of interspecific response between a live and a dead cetacean, and it was in a captive setting (see Materials and methods), we concentrate on attentive behaviour toward dead conspecifics. Then, we use a weighted comparative approach to investigate whether, and how, a given type of behaviour varies across taxa, and in that way obtain insight into taxon-specific responses. In addition, we attempt to identify links between behavioural responses toward dead conspecifics and metrics of relative brain size and encephalisation, to help explain some of the variability of behaviour across taxa. Lastly, we discuss the implications of our findings with regard to the potential for animal comprehension of death and grieving.

2. Materials and methods

2.1 Terminology

For cetaceans, the terms "caregiving" and "epimeletic" have been used almost interchangeably since the early 1960s to describe "the giving of care or attention" toward distressed, dying or dead conspecifics (Caldwell and Caldwell, 1964, 1966). The term epimeletic (Bearzi and Reggente, 2017) and its variants, nurturant and succorant (Caldwell and Caldwell, 1966; Reggente et al., 2016), have implicit altruistic and empathic connotations, which may or may not reflect reality. In this study, we address cetacean responses to dead (and not distressed or dying) conspecifics, and we use the phrases "postmortem attentive behaviour" (PAB) when referring to cetacean behaviour directed at a dead conspecific, and "postmortem attender" (PA) to identify the individual engaged in these behavioural responses. PAB normally involves close proximity with a dead conspecific, repeated physical contact (which may be either gentle or rough, and may include sexual arousal), keeping the carcass from sinking or pushing it down if afloat, mouthing, or carrying the carcass. Carrying includes pushing the carcass with the rostrum, melon, dorsal fin or flipper, transporting it out of the water using the top of the head or back, or carrying in the mouth. Finally, we use "bystanders" to refer to individuals that were present at the scene but did not perform PAB.

2.2 Accounts of postmortem attentive behaviour

We searched the cetacean literature and online sources for reports describing behavioural responses to dead individuals, irrespective of interpretation provided by the authors. Observations of cetaceans attending their dead were commonly perceived as important and were typically reported as single events or series of events, often including detailed information. Individual cases can be used to create an inventory of the reported occurrence of specific types of behaviour among taxa (Table 1; the common names and author citations for all cetacean species are listed in Supplementary material A.1). While species-by-species compilations cannot be considered statistical samples, they offer the possibility of identifying general behavioural patterns if the information is authoritatively selected, treated with caution, and used carefully as a basis to formulate hypotheses (Bates and Byrne, 2007).

Reports of cetacean behaviour toward the dead and distressed in early literature tend to be more difficult to interpret than recent reports. Most cases reported prior to the 1970s refer to animals killed or wounded by whalers, animals deliberately killed (or otherwise harmed) "for science", or animals held in captivity. These are not ideal circumstances for unbiased observations of natural behaviour (Bearzi et al., 2017). In addition, pre-1970 output by literature search engines (used as a weight in this study, as explained below) can be misleading, for instance due to the comparatively poor legibility of digitised documents or the use of obsolete and inconsistent scientific names. To mitigate these problems, we considered only information produced between 1970 and 2016, encompassing 47 y of cetacean research (which also approximately coincides with the flourishing of cetacean research in the wild; Samuels and Tyack, 2000).

The decision to include a given account in our dataset (Table 1) was based on the description provided by the account authors as well as on our own judgment as experienced cetacean field researchers. While a variety of situations may be relevant to the understanding of attending to dead conspecifics, for the purposes of quantitative assessment we excluded from our sample: 1) reports of PAB that were inferred rather than observed (e.g. based on tooth rakes on stranded individuals; Pilleri, 1971; Cremer et al., 2006; Haelters and Everaarts, 2011); 2) one poorly documented and undated second-hand report of an adult female *Sousa* sp. carrying a dead *Tursiops truncatus* calf, observed in captivity at Seaworld Australia (Porter, 2002; and see the Discussion); 3) cases involving captive individuals attending dead conspecifics under conditions not found in the wild (three published records: Tayler and Saayman, 1972; Kilborn, 1994; Porter, 2002); 4) all cases involving attempts to protect living conspecifics from predators (e.g. Jefferson et al., 1991; Pitman et al., 2001, 2015, 2017) not followed by documented action toward the dead individual; 5) all cases of infanticide (e.g. Patterson et al., 1998; Dunn et al., 2002; Kaplan et al., 2009; Nery and Simão, 2009; Robinson, 2014; Perrtree et al., 2016; Zheng et al., 2016); 6) all cases of entrapment in ice (e.g. Siegstad and Heide-Jørgensen, 1994; Heide-Jørgensen et al., 2002); and 7) all cases involving mass strandings of cetaceans (Geraci et al., 1999).

[INSERT TABLE 1]

2.3 Analyses of postmortem attentive behaviour

Culturomics (the analysis of large electronic datasets for the study of human culture) is increasingly used to investigate trends, with search-engine output serving as a proxy for the nature and scale of interest in a range of topics (Michel et al., 2011; Stergiou, 2017). Search engines such as Scopus, Web of Science, PubMed and Google Scholar are tools for assessing trends related to scientific interest and to control for observation effort (Shultz, 2007; Nourbakhsh et al., 2012; Harzing and Alakangas, 2016; Fox et al., 2017). Identification of the most appropriate search engine with a culturomics approach is becoming a scientific branch in its own right (Pechenick et al., 2015), but clearly each search engine has its strengths and weaknesses and the choice of tools ultimately depends on what one is attempting to investigate. Google Scholar (GS) stands out as an appropriate specialist search engine to retrieve information from multiple electronic resources, including peer-reviewed journals, books, abstracts, technical reports and conference proceedings. A recent study concluded that in virtually all cases, GS provided the highest citation count, reflecting its broader coverage in terms of sources compared to both ISI and Scopus—particularly in the life sciences sector (Harzing and Alakangas, 2016). While other literature search engines are restricted to certain parts of a publication (e.g. title, abstract, keywords), GS is known to encompass the entire body of a text and has the potential of providing access to at least a portion of the immense grey literature (Shultz, 2007). Because the "best" search strategy ultimately depends on the question being asked (Nourbakhsh et al., 2012), we chose to rely on GS as a way of broadening our survey coverage, consistent with our primary aim of assessing scientific interest in a given cetacean species as a proxy of observation time. Such a choice is also consistent with the inclusion of grey literature reports in our dataset (Table 1).

We used the scientific name of each of the 88 currently recognised and extant cetacean species as a query (e.g. "*Megaptera novaeangliae*" for the humpback whale, using the "exact phrase" and "dated between" functions in GS advanced search), relying on the fact that 1) the full scientific name of a given species is routinely included in the scientific literature, and 2) the scientific names of cetaceans are intended to be unique and, for the most part, do not match pairs of words that appear in the same combination in the scientific literature (e.g. as names of persons or locations; Stergiou, 2017). GS provided the frequency of times the scientific name of a given cetacean species appeared in the scientific literature published between 1970 and 2016, a time interval matching the events dataset in this study. The ratio between number of reported cases of PAB (Table 1) and log-transformed GS metric for a given taxon, arbitrarily called "PAB index", was then used as a rough proxy of the frequency of occurrence of PAB, normalised for observation effort (see Supplementary material A.1).

Issues of inconsistent and changing taxonomic nomenclature resulting from changes having occurred during the study period were addressed by searching for obsolete scientific names and combining the metrics (for instance, both "*Physeter macrocephalus*" and the obsolete "*Physeter catodon*" for the sperm whale were searched and combined; see Supplementary material A.2). In other cases, species were split during the study period, for instance within the genus *Sousa*, resulting in new species under the same genus. In such instances, information must be interpreted with caution and ideally at broader taxonomic levels (as we have done in the analyses), recognizing that some true differences in PAB at the species level can be obscured.

Although our PAB index already incorporates GS metric, we wanted to be transparent toward the potential influence of research effort on our ability to compare variability in PAB among taxa. Therefore, we calculated Pearson correlation coefficients between both the number of PAB records and the PAB index with GS metric for species, genera, and families. We also calculated correlation coefficients for taxa whose GS metric was within the range that PAB events were observed. For these exploratory correlations, $\alpha = 0.05$.

We also investigated if residual brain size and/or encephalisation quotient (EQ) were associated with the likelihood of exhibiting any PAB among genera and families using logistic regressions. We used only genus- and family-specific data due to the aforementioned issues in inconsistent nomenclature. The binary response variable in logistic regressions was whether or not a family or genus exhibited any PAB (among genera with GS metric ≥ 2480, i.e. the lowest metric for any genus with PAB; see Supplementary material A.1). EQ and residual brain size of species were first calculated using brain mass and body mass data from Ridgway et al. (2017). EQ was calculated as equal to brain mass (g) divided by 0.12*body mass (g) to the two-thirds power (Jerison, 1973). Residuals of brain size for species were calculated as the residuals of a quadratic relationship fitted between the logarithms of brain size and body size. For each genus and family, a single value for EQ and residual brain size was calculated by taking the average across all species within that genus or family. To further account for the influence of research effort, GS metric (log-transformed) was also used as an explanatory variable. Due to the small sample size (26 out of 27 genera with GS metric ≥ 2480 and 12 out of 13 families had brain information), only a single variable was entered into each logistic regression (residual brain size, EQ, or GS metric). As closely-related taxa may be expected to have similar brain characteristics, the family of each genus was added as a random effect in genus-specific logistic regression models. The performance of each model was assessed using 1) the Akaike Information Criterion (AIC), 2) change in AIC between the best and other competing models (ΔAIC), 3) AIC weights (w_i), which represent the probability that a model is the best among a candidate set of models, 4) pseudo-R^2. Logistic regressions and model weights were generated using 'lme4' (Bates et al., 2015) and 'MuMIn' (Barton, 2017) packages, and pseudo-R^2 values (Nagelkerke R^2 index) were calculated using the 'rms' package (Harrell, 2018) in R (R Core Team, 2017).

3. Results

Information derived from the literature and online sources is summarised in Table 1, which includes 78 records of PAB. When checking and validating the available data sources we bent on the side of precaution. For instance, we amended our dataset whenever text, photographs, video or other information appeared inconsistent (e.g. the sex of a PA was considered unknown if the reported sex was inferred, debatable, or inconsistent with the available visuals).

In the Supplementary material (A.1) we report GS metrics obtained for each taxon, together with number of PAB records (obtained from Table 1) and computed PAB indices. Results on correlations between research effort and PAB indices for species, genera, and families are given in the Supplementary material (A.3).

3.1 Postmortem attentive behaviour by taxon

PAB was documented in 20 of 88 cetacean species (22.7%), of which only one was a mysticete (*M. novaeangliae*; Table 1). Nine species had a single PAB report. PAB was most prevalent within the family Delphinidae (72 reports; 92.3%), followed by Monodontidae (3 reports; 3.8%) and the families Iniidae, Physeteridae and Balaenopteridae (each with a single report; 1.3%). All other cetacean families had no records of PAB.

PAB indices ranged between 0 and 14.19 for families (Fig. 2), between 0 and 5.46 for genera, and between 0 and 5.05 for species (Table 2). The main contributing families were Delphinidae (comprising 37 species, with a PAB index of 14.19), Monodontidae (2 species; 0.72), and Iniidae (1 species; 0.28). PAB was not recorded for 5 cetacean families: Ziphiidae (22 species), Phocoenidae (7 species), Kogiidae (2 species), Platanistidae (1 species) and Pontoporiidae (1 species). Two genera within the Delphinidae stand out: *Sousa* (PAB index = 5.46) and *Tursiops* (5.20), followed by *Globicephala* (2.33), *Stenella* (1.41), *Orcinus* (0.96), *Steno* (0.88), *Delphinapterus* (0.74), *Grampus* (0.54), *Lagenorhynchus* (0.51), and all other genera (below 0.30).

[INSERT FIG. 2]

3.2 Age and sex of attenders and dead individuals

Some of the reports in our dataset did not provide detailed information on the age, sex and number of individuals involved in PAB (Table 1). To investigate age, sex and number of PAs we removed from our dataset 11 records with insufficient detail (marked with * in Table 1), resulting in 67 acceptable records. Of these, 53 (79.1%) were single adults (34 of unknown sex and 19 females). Two reports of "subadult" *Sousa chinensis* PAs likely referred to younger adults with a spotted pigmentation (Reeves et al., 2002; Hung, 2014) and were considered adults for the purposes of our study. Among 14 (20.9%) cases involving more than one PA, there were 1) seven groups composed of 2–23 individuals that included one or more adult males (four of these groups also included adult females), 2) five groups composed of 2–4 individuals of unknown sex, 3) one group composed of an adult female (possibly the mother of the dead individual) with her live juvenile son, and 4) one group composed of two females (not closely related based on genetic analyses; Quintana-Rizzo and Wells 2016), one of which was the mother of the dead individual. Calf occurrence in PA groups was limited to the single case of one calf within a group composed of two adult females and 20 adult and subadult males (Dudzinski et al., 2003). The age class was reported for all the dead individuals in our dataset (N = 78): 63 (80.8%) calves, 8 (10.2%) juveniles, 5 (6.4%) adults, and 2 (2.6%) subadults. Sex was known for 21 dead individuals: 13 females and 8 males.

Two reports described a dead calf being carried by a male accompanied by females. The first was a report of an adult male short-finned pilot whale *Globicephala macrorhynchus* swimming with a dead calf in his mouth. The male was accompanied by two adult females, possibly mother and daughter, of which the daughter was reported to have had distended mammary glands suggesting that "she may be the mother of the dead calf and had not nursed for several days" (Baird, 2016). The second report was the unpublished observation of a dead killer whale *Orcinus orca* calf carried by an adult male that pushed the carcass at the surface with his head; bystanders included three adults reported to be females and one juvenile, later joined by a few other females (van Ginneken, 1994, 1996). Apart from these two cases, where the dead individual was a calf, all other cases of PAB involving adult males ($N = 5$) targeted a dead adult or subadult individual, and included evidence of sexual behaviour, but no carrying (*T. truncatus*, *Delphinus delphis* and *M. novaeangliae*; Pack et al., 1998; Dudzinski et al., 2003; Park et al., 2013; Kuczaj et al., 2015).

Table 1 also shows the occurrence, number and composition of bystanders. These reportedly included individuals of both sexes and all age classes, varying in numbers from 1 to 28. Details on the numbers and demographics of bystanders, however, were not consistently reported, and in most cases the observers appeared to focus on PAs and paid limited or no attention to the occurrence and behaviour of conspecifics in the larger area. In publications having a wider scope, PAB was reported with limited detail. As a consequence, absence of information on bystanders in Table 1 should be interpreted to indicate that they were sometimes unreported rather than absent. Finally, some reports mention the occurrence of other groups farther away, but only provide information on the most nearby individuals.

3.3 Correlates of postmortem attentive behaviour

Among the covariates assessed via logistic regressions, residual brain size was the strongest predictor of a taxonomic family exhibiting any records of PAB ($w_i = 0.69$; Table 2), with more than four-times the weight of the next best predictor. As residual brain size increased, and in particular as it transitioned from negative to positive, the probability of observed PAB increased (Fig. 3). Of the 12 families investigated, 80% of those with positive brain size residuals (4 of 5) had at least one record of PAB, compared to only ~14% of those with negative brain size residuals (1 of 7). GS metric ($w_i = 0.15$) performed slightly better than the intercept-only model ($w_i = 0.10$). EQ ($w_i = 0.06$) did not perform better than an intercept-only model, and thus does not help predict PAB among families. Among genera with GS metric ≥ 2480, we also identified residual brain size as the strongest predictor of PAB occurrence (see Supplementary material A.4 for details).

[INSERT TABLE 2]
[INSERT FIG. 3]

4. Discussion

Our results suggest that PAB is distributed unevenly across cetacean taxa, with a higher occurrence among odontocetes (particularly Delphinidae; Fig. 2), and largely absent among mysticetes. Most incidents of PAB involved females (most likely mothers) with dead calves (most likely their offspring); but there were notable exceptions. Below, we acknowledge some of the potential biases and we frame our results in the context of animal cognition, sociality and possible comprehension of death. We conclude by making research recommendations intended to help generate datasets and other information relevant to a better understanding of cetacean responses to dead conspecifics.

4.1 Postmortem buoyancy

Success in this study depended on the likelihood of observing and reporting cetaceans responding to dead conspecifics. Because most observations of wild cetaceans are conducted from boats, rather than underwater, one must consider the relative chances of observing a given type of behaviour at the surface. Therefore, attentiveness to a consistently buoyant carcass would have a higher chance of being reported than when the carcass sinks, even considering that PAs often try to keep non-buoyant carcasses at the surface. Buoyancy varies greatly among cetaceans, depending on species, blubber thickness, age/size, water temperature/salinity and a number of other factors (Kipps et al., 2002; Noren and Wells, 2009). Postmortem buoyancy also depends on air temperature, amounts of gas in the lungs and intestines, how long the animal has been dead (gas build-up in the stomach can cause a carcass to refloat), and intactness of the abdominal wall. Balaenopterid mysticetes have thinner blubber layers and their carcasses are more likely to sink than those of balaenid mysticetes, which are often positively buoyant (Nousek-McGregor et al., 2014). Peltier et al. (2012) tested the buoyancy of carcasses of two small odontocetes (*Stenella coeruleoalba* and *Phocoena phocoena*) and reported that they floated for the first ten days or so, and then progressively started to sink. Bearzi (2000) reported on a *D. delphis* that sank in a catatonic vertical position, head up, after being struck by a biopsy dart. In our dataset, the carcass was positively buoyant in 19 (24%) of 78 cases, negatively buoyant in 15 (19%), and unknown or unreported in the remaining cases (Table 1). Finally, the age/size of the dead individual may influence the feasibility and energetic costs of carrying or supporting a carcass that naturally tends to sink. Species that tend to be positively buoyant at birth (e.g. *T. truncatus*; Cockcroft and Ross, 1990; Mann and Smuts, 1999; Noren and Wells, 2009) would presumably offer better chances of observing PAB directed at dead neonates, and possibly also a higher likelihood of such behaviour being performed and sustained.

4.2 Attentiveness to non-conspecifics and inanimate objects

In our sample, the dead individuals that cetaceans responded to were always conspecifics. To our knowledge, only one (undated) second-hand report exists of PAB targeting a dead non-conspecific cetacean: an adult female *Sousa* (reported as *S. chinensis*, but likely belonging to the recently recognised species *S. sahulensis*) supporting a dead *T. truncatus* calf in captivity (Porter, 2002). Interspecific PAB has yet to be reported in the wild.

Some observations of captive and wild belugas *Delphinapterus leucas* responding to inanimate objects have been interpreted as indicative of the need for a surrogate, perhaps to mitigate separation distress following the death of an offspring. When the dead calf of a captive beluga was removed from the pool postpartum, the mother started carrying her own placenta, and after the placenta was removed she resorted to a buoy, which she continued carrying for several months (Kilborn, 1994). Wild belugas of undetermined sex have at different times been observed carrying a dead neonate, a placenta and amniotic sac, a piece of seine net, planks up to 2–2.5 m long (four cases), and the skeleton of a dead caribou *Rangifer tarandus* (Smith and Sleno, 1986). The authors postulated surrogate epimeletic behaviour following perinatal death of previous calves as a possible explanation (Kilborn, 1994; Smith and Sleno, 1986). Other interactions with non-cetacean marine life, however, are known—or were credibly interpreted by the source authors—to represent play, socio-sexual display, tool-use, feeding-related behaviour or other functions inconsistent with the hypothesis of surrogates (e.g. Würsig et al., 1989; Smolker et al., 1997; Krützen et al., 2005; Fertl and Fulling, 2007; Martin et al., 2008; Allen et al., 2011, 2017; Patterson and Mann, 2011; Araújo and Wang, 2012; Krasnova et al., 2014; Barber, 2016). Finally, several cases of *G. macrorhynchus* carrying dead sea lions *Zalophus californianus* (Shane, 1994) or fish-eating *O. orca* carrying dead salmon (Whitehead et al., 2004) may be fads, confer status or other advantages to the carriers (Shane, 1994; Whitehead et al., 2004; Allen et al., 2017), or possible prey caching.

4.3 Age and sex of postmortem attenders

In our sample, the dead individuals that cetaceans responded to were mostly calves. Calves have high mortality rates (Caughley, 1966; Reznick et al., 2002; Stolen and Barlow, 2003), tend to be more buoyant (Noren and Wells, 2009), and due to their small size are energetically less costly to carry (Fig. 1). Perhaps more importantly, mothers are naturally pre-disposed to take care of their calves. When the sex of the calf attender was known ($N = 20$), females were always present as single PAs (with or without bystanders; $N = 16$), as a PA pair (with another female or with their grown-up offspring; $N = 2$), or with other females and one male ($N = 2$). Most cases of PAB towards a calf by single adult PAs of unknown sex ($N = 27$) might also have been females. A mother attending her dead offspring would seem to have been the most common case. If all single adults with dead calves were assumed to be mothers, then this would account for 55% of all PAB records (43 of 78). PAs, however, were only occasionally known to be the actual mothers (9% of cases). Related and even unrelated females may attend a dead calf, either by assisting a PA or, on occasion, being a PA themselves. For instance, a female *T. truncatus* was reported to attend the dead offspring of a long-term female associate, interest in the dead calf possibly reflecting the social bond between the PA and the calf's mother rather than kinship between the PA and the calf (Quintana-Rizzo and Wells, 2016). Potentially related behaviours include allomothering, babysitting and non-offspring nursing observed in several cetacean species

(Whitehead, 1996; Mann and Smuts, 1998; Best et al., 2015), with at least one documented case involving an unrelated calf (*T. aduncus*; Sakai et al., 2016).

Two records exist of male PAB toward a dead calf: 1) an adult *G. macrorhynchus* carrying a calf in his mouth in the presence of two adult females, of which one was suggested to be the calf's mother (Baird, 2016), and 2) the unpublished observation of a male *O. orca* carrying a calf in his mouth in the presence of adult females and one juvenile (van Ginneken, 1994, 1996). Considering the occurrence of infanticide among odontocetes such as *T. truncatus* (e.g. Patterson et al., 1998; Dunn et al., 2002; Kaplan et al., 2009; Robinson, 2014; Perrtree et al., 2016), *S. chinensis* (Zheng et al., 2016) and *Sotalia guianensis* (Nery and Simão, 2009), and the recent observation of infanticide in *O. orca* (Towers et al., 2018), it cannot be ruled out that in some cases a male may be "attending" a dead calf after having killed it (Bearzi et al., 2017). Whether or not related to infanticide, male PAB may prevent a female from attending a dead calf while ensuring that she does not leave, possibly facilitating immediate or eventual sexual access to that female. The recent observation of a male *T. truncatus* attacking a calf that was already dead, and attended by a female, may be consistent with the hypothesis of calf PAB by males being unrelated to caregiving ('case 2' in Díaz López et al., 2017; not included in our dataset of scientific literature published between 1970 and 2016).

Cases of cetacean PAB involving dead adults or subadults are particularly interesting, as these cases may represent expressions of long-lasting attachment and enduring social bonds. In our study, most cases of PAB targeting dead adults (including males or females) involved male PAs and occurrence of sexual behaviour (Table 1). In one of these observations, the target of sexual behaviour was an adult male *M. novaeangliae*, which had possibly died during a competitive interaction with other males (Pack et al., 1998). As noted by Bearzi et al. (2017), sexual arousal may be triggered by physiological responses related to stress, or be an expression of dominance devoid of a reproductive purpose. However, no occurrences of sexual behaviour have been reported when the dead individual was a calf. Only two observations exist of PAB by single adults targeting dead adults or subadults: a *T. truncatus* of unknown sex attending to an adult non-lactating female (Cape Lookout Studies, 2015) and an *S. coeruleoalba* of unknown sex attending to a subadult female, described below. PAB by groups including calves or juveniles were infrequent (3 of 67 records with information) and there were no records of single calves or juveniles attending to a dead adult (e.g. to their dead mother). Such a low occurrence, at least in social species, may be explained in part by alloparental behaviour (Packer et al., 1992) and adoption by other females occurring soon after the death of a parent (Simard and Gowans, 2004; Sakai et al., 2016).

4.4 Prevalence of postmortem attentive behaviour

A key assumption is that our GS metric is an unbiased relative estimator of the kind of research effort likely to result in observations of PAB. Although there are correlations between research effort and our PAB indices (see Supplementary material A.3), we suggest that there is variability in PAB across cetacean taxa. Much of the correlation among genera was driven by little-researched genera, indicating that—as discussed earlier—it is indeed unlikely to observe PAB in rarely-studied cetaceans. When focusing on those genera having adequate research effort (GS metric ≥ 2480, see Materials and methods), there was no significant correlation, indicating true variability among taxa. Similarly, correlations among families were driven by Delphinidae, which represent the clear majority of PAB records (Fig. 2). Positive correlation between GS metrics and PAB indices at the species level indicate that results at this taxonomic level must be interpreted with caution. Even so, some of the species with notably high GS metrics (*M. novaeangliae*, *P. macrocephalus* and *D. delphis*, all above 10000) had only a single record of PAB, suggesting a relatively lower occurrence of responses to dead conspecifics.

Mysticete species had a particularly low occurrence of PAB and, perhaps more tellingly, none was reported toward calves. The only observation of mysticete PAB was the already mentioned group of humpback whales with an adult male that died possibly during a competitive interaction (Pack et al., 1998). Humpback whales (presumably mothers, often assisted by an escort) have been consistently observed protecting their calf and fighting back when killer whales attack (Pitman et al., 2015, 2017). They are also known to mob killer whales in apparent attempts to protect other species (Pitman et al., 2017), but PAB with a dead calf has not been reported so far. Besides, PAB has not been reported among other baleen whales characterised by Ford and Reeves (2008) as "fight" species with regard to their anti-predator strategies. The protective females of "fight" species might be less inclined to abandon their dead offspring (beside humpback whales, fight species also include *Eubalaena* spp., *Balaena mysticetus*, and *Eschrichtius robustus*; Ford and Reeves, 2008). However, a frequent source of mortality among several mysticete species is predation (particularly by killer whales; Jefferson et al., 1991; Pitman et al., 2015) and in those cases dead calves are mostly towed away by predators and therefore unavailable for PAB. Conversely, a higher occurrence of infanticide by the males of some odontocete species (e.g. *T. truncatus*) might contribute to a higher occurrence of female PAB in those species.

The average PAB index of odontocetes was 69 times higher than that of mysticetes (Table 2). Among odontocete families, indices range between 0 for Kogiidae, Ziphiidae, Platanistidae, Pontoporiidae and Phocoenidae and 14.19 for Delphinidae, with only a few genera and individual species having indices above 1 (Fig. 2). Most ziphiids tend to be evasive or otherwise cryptic at the sea surface and therefore opportunities to observe their behaviour are rarer than indicated by the GS metrics, resulting in possible bias. However, even among those beaked whale species that have been studied relatively intensively (including *Ziphius cavirostris*, *Mesoplodon densirostris* and *Hyperoodon ampullatus*) and for which there are detailed descriptions of behaviour (e.g. Gowans and Rendell, 1999), none have records of PAB. Sperm whales are well-studied and highly social (Whitehead, 2003), and they actively protect their offspring (Jefferson et al., 1991; Pitman et al., 2001), but only one second-hand report exists of an adult sperm whale carrying a dead calf in its mouth (Reggente et al., 2016), therefore the species had a relatively low PAB index (0.24, same as the humpback whale). The sperm whale's low occurrence of observations may be related in part to the species' low reproductive rate (Best et al., 1984) and offshore distribution, resulting in rare sightings of calves in some populations (Whitehead and Weilgart, 2000).

Within the family Delphinidae, the two genera *Sousa* and *Tursiops*, combined, constituted 55% of all records of PAB among cetaceans (43 of 78 records). The genus *Sousa* had the highest PAB index (5.46). The high number of reports ($N = 17$) for *S. chinensis*, resulting in an index of 4.83, come from Hong Kong coastal waters. While it is possible that these dolphins have a higher propensity to attend dead conspecifics, such finding must be considered in the light of the fact that calf (particularly neonatal) mortality in the Hong Kong area is exceptionally high and the population has been the focus of behavioural studies for 25 years (Jefferson, 2000; Porter, 2002; Jefferson et al., 2006). Seven cases of PAB in this area were recorded over a period of only 6 months, and of these five occurred during 6 weeks, in stark contrast with PAB occurrence in the previous 10 years (four confirmed cases; Hung, 2010, 2014). The genus *Tursiops* also had a high PAB index (5.20) and, compared to *Sousa*, records were more evenly distributed in time and space. Apparent differences among species within the genera *Tursiops* and *Sousa* may arise in part from changing scientific names and identification issues (Committee on Taxonomy, 2017).

4.5 Postmortem attentive behaviour and the "social brain" hypothesis

Sociality in mammals is closely associated with encephalisation (Jerison, 1973). The "social brain" hypothesis holds that "excess brain mass", beyond that needed to run the body machinery, has evolved not only in response to environmental challenges but also to the complexity of social life (Dunbar, 1998; Shultz and Dunbar, 2010). Connor (2007) argued that in odontocete cetaceans, as well as in primates and elephants, strong selective pressure towards a large brain resulted from cognitive demands imposed by mutual dependence within a network of associates, and the benefits of developing complex social skills. Consistent with that argument, Fox et al. (2017) suggested that cetacean encephalisation is predicted by social organisation, brain size being indicative of the breadth of social and cultural behaviour across cetacean species. Measures of brain complexity such as specific cortical surface area per unit brain mass (cortical folding; Ridgway et al., 2017) may also be related to cognition and sociality. Encephalisation and brain complexity were found to be low in mysticetes relative to odontocetes, consistent with a lower overall degree of sociality among baleen whales (Fox et al., 2017; Ridgway et al., 2017). Such findings might help explain the great difference in PAB indices between the two taxonomic groups.

Beyond the major phylogenetic differences, a positive correlation between sociality and attentiveness to dead conspecifics may be expected across odontocete taxa, considering that life within structured social groups offers the opportunity for establishing strong and enduring bonds, even beyond those of mother-calf pairs, and these bonds are unlikely to vanish immediately when severed by death. Small sample size, inconsistency in reports, and paucity of information in the existing accounts all conspire to frustrate robust statistical analyses relevant to the evolutionary understanding of behavioural responses to dead conspecifics. However, even with small sample sizes, we identified a relationship between the probability of observed PAB and residual brain size that was consistent within both families and genera—taxa with larger relative brain sizes being apparently more likely to attend to their dead. These findings, taken together with those of Fox et al. (2017), provide indirect evidence that PAB may be tied to encephalisation and sociality. As Pilleri (1971) suggested: "It may be presumed that epimeletic behaviour in cetaceans is an expression of their very highly developed social instinct and as such is dependent on the degree of cerebralization."

Several of the species with high PAB indices (Supplementary material A.1) rank high in terms of encephalisation, brain complexity and social complexity (Fox et al., 2017; Ridgway et al., 2017). Still, the low PAB indices of some intensely social species which live in small groups of related individuals deserves further investigation. Sperm and killer whales are cases of well-studied species (GS metrics > 12000) with low PAB indices (0.24 and 0.96, respectively). Pending more systematic and careful reporting of PAB, comparisons across cetacean taxa of weighted measures of PAB with social and brain complexity indices may provide useful insight. If PAB was correlated with sociality, it would be important to assess how its occurrence varies according to the social structure and duration of bonds within each taxon. For instance, mysticete calves tend to stay with their mothers for relatively short periods of time, while in many odontocetes social bonds can last for decades. Inclusion of additional variables in the analyses, such as measures of swimming speed and dive duration, may be relevant, considering that members of fast-swimming gregarious groups or deep-diving species might have less opportunity to stay behind and attend to dead individuals.

4.6 The debate on animal grieving

The question of whether it is possible to know the mind state of other organisms has been vigorously debated (Nagel, 1974; Griffin, 1981), *inter alia* because each species presumably perceives its own environment in a different way, and an animal's *Umwelt*—meaning the environment as an organism perceives it and interacts with it—must be taken into account (von Uexküll, 1909). Despite the challenges, the field of "cognitive ethology" contends that it is possible to imagine and describe some of the experience of other organisms (Griffin, 1981; Ristau, 2013). In modern terms, understanding animal emotions may stem in part from similarities (or lack thereof) in physiology and neural processes across different species (Panksepp, 1998; Ristau, 2013; Sapolsky, 2017). For instance, Engh et al. (2006) documented increased glucocorticoid levels (associated with bereavement in humans), as well as increased grooming rates suggestive of stronger and broader social relationships, in female chacma baboons *Papio hamadryas ursinus* that had lost a close relative (i.e. mother, maternal sibling, offspring) to observed or suspected predation, compared to matched controls whose relatives had not died.

Mammalian responses to dead conspecifics raise the question of whether some of the observed behaviour can be considered an expression of grieving. According to Archer (1999), grief in humans is a reaction to a social and emotional deficit broadly similar to that generated by impermanent separation, though often more extreme and pronounced. Grieving ultimately results from the breaking of social or familial bonds and its intensity is thought to parallel the strength of attachment. Grief represents "the cost of commitment" (Parkes, 1972) and its emotional expressions have evolved from a basic inclination or wish to maintain connectivity with an offspring, other relative or partner. When the offspring or partner dies, the longing remains largely intact and the experience of loss may produce various negative responses including distress, anxiety, bewilderment, depression and compulsive behaviour, any of which may undermine the survivor's own health and well-being. These apparently maladaptive aspects of grieving in humans must be weighed against the adaptive advantages (immediate and evolutionary) of the attachment and commitment needed to maintain a stable relationship with another individual (Archer, 1999). Among cetaceans, examples of such bonding include primarily those between a mother and her calf (a bond that may extend to grown-up offspring), those between related females, or unrelated females in a similar reproductive state, and even allies in male coalitions (Mann et al., 2000).

Are some of the behavioural responses to dead conspecifics observed in cetaceans an expression of stress resulting from emotional attachment, roughly equivalent to grieving as described in terrestrial mammals including primates or elephants? Some accounts of cetacean responses to dead conspecifics do explicitly mention grieving or mourning, if only as a possibility (Kilborn, 1994; Baird, 2016; Reggente et al., 2016). Unfortunately, studies such as that conducted by Engh et al. (2006) on baboons have never been conducted on cetaceans and at present the existence of physiological and psychological processes related to, or at least similar to, grieving cannot be proven beyond dispute one way or another. Whether or not cetacean PAB can be interpreted as being a manifestation of grieving (or bereavement) also depends on how these words are defined, as well as on the sensitivity attributed to emotional states often regarded as being uniquely human, and on the importance given to awareness of death as a point of non-return (King, 2013, 2016; Anderson, 2016). Awareness of death is regarded as a human attribute, with notable and sometimes striking differences among age classes, individuals, cultures and peoples (Hollan, 1995; Tamm and Granqvist, 1995; Archer, 1999). Behavioural patterns and emotional responses to death, however, are deeply rooted in our evolutionary and cultural history and consistent responses may be found in other highly social mammals. Charles Darwin was among the first to postulate an evolutionary continuity of mental experience in "The Expression of Emotions in Man and Animals", where he described outward emotional states including grief in monkeys (though he nonetheless posited that expressions of grief and anxiety are eminently human; Darwin, 1872). Notwithstanding the writings of Darwin, interpreting animal behaviour as grieving has long been taboo in science (King, 2013). Still, such interpretation and wording has become increasingly accepted since Jane Goodall first provided detailed accounts of grieving in wild chimpanzees *Pan troglodytes* (Goodall, 1986).

The first author of this paper, together with his colleagues, observed, photographed and filmed the behaviour of an adult *S. coeruleoalba* of unknown sex toward a freshly dead female subadult conspecific, which was floating at the surface in the Gulf of Corinth, Greece (Fig. 4). The PA maintained consistent physical contact with the dead individual, making repeated and persistent attempts to push its buoyant carcass underwater, nudging it with the head and rostrum, swimming around it, and moving it away when the observers' boats approached too closely. When placing its "chin" on the carcass, the eyes of the PA consistently looked down at the carcass rather than up at the nearby boats. The PA was alone with the dead individual—a highly unusual occurrence considering the large groups of this species normally seen in the study area (Bearzi et al., 2016). In this and other cases, behavioural patterns exhibited by some cetacean species resemble those observed in certain terrestrial mammals—most notably upon the death of an offspring (Nakamichi et al., 1996; Warren and Williamson, 2004; Douglas-Hamilton et al., 2006; Engh et al., 2006; Biro et al., 2010; Fashing et al., 2011; Appleby et al., 2013; Bercovitch, 2013; de Kort et al., 2018).

[INSERT FIG. 4]

4.7 Do cetaceans recognise or comprehend death?

At first, a seemingly dead individual may simply appear to be unconscious and thus require rescue. In such cases, the PA may not be certain that the other individual is dead. An inanimate conspecific can sometimes be revived by forceful manipulation (Krasnova et al., 2014) and the PA may act with the primary aim of achieving reanimation (Bearzi et al., 2017). The carrying of a calf may also be interpreted as a protective response. For instance, a mother *T. truncatus* was observed pushing a neonate to the surface and carrying it on her back during an infanticide attempt by male conspecifics (Perrtree et al., 2016). Some individuals may fail to acknowledge that a conspecific has died, and sometimes continue to care for their charges as if they were still alive. However, a lack of awareness that the individual under duress has died would seem inexplicable when the PAB continues for days and even until the point of putrefaction (Hubbs, 1953; Reggente et al., 2016), when the limp carcass has decomposed beyond recognition or is only a body part (e.g. a severed head; Moore, 1955), let alone when it is replaced by a placenta or another surrogate object (Smith and Sleno, 1986; Kilborn, 1994). Such apparently maladaptive behaviour may result from strong attachment (Parkes, 1972) and a difficulty of "letting go," as observed in bereaved humans (Archer, 1999). Following the loss of a close relative, several terrestrial mammals have been known to show long-term evidence of compassionate behaviour (Douglas-Hamilton et al., 2006), stress (Engh et al., 2006) or attentive behaviour (Biro et al., 2010; Fashing et al., 2011; Bercovitch, 2013; de Kort et al., 2018). When confronted with the variety of published reports (and the plethora of videos available online), we must acknowledge that an awareness of death among cetaceans is still largely unknown territory. Though research into this realm started over fifty years ago (Caldwell and Caldwell, 1964), there has been little directed research on this topic and the matter is still open to investigation and debate.

Action toward a dead individual and time spent in its proximity comes at a cost to the attendant (e.g. due to energy expenditure, stress, increased exposure to predation risk, risk of infection or a temporary loss of foraging opportunities). However, action aimed at reanimation (Mann and Barnett, 1999)—especially of one's own offspring—might have adaptive advantages at times. In fact, it is reasonable and parsimonious to assume, unless and until proven otherwise, that PAB towards dead conspecifics is adaptive in some way(s), regardless of whether such behaviour signifies grieving. For instance, if an individual cetacean is rendered unconscious (or nearly so) during some social interaction or aggression and its companions keep it at the surface until it is able to breathe again, it might survive and recover. The long-term and adaptive benefits of sympathetic concern, cognitive empathy, consolation, empathic perspective-taking, targeted helping, and reciprocal altruism have been described in nonhuman mammals (e.g. de Waal, 2008; de Waal and Preston, 2017; Pérez- Manrique and Gomila, 2018). Such benefits likely apply to cetaceans as well (Connor and Norris, 1982) and may encompass responses to dead individuals perceived as rescuable.

If one accepts the notion that at some point cetaceans do "recognise" death (an aspect that is still controversial among cetacean scientists, including some co-authors of this study), three phases of PAB may be considered, at least in the context of female responses to dead conspecifics: a first phase, during which the attender perceives an apparently inanimate individual as being potentially rescuable, followed by a second phase when the finality of death is cognitively recognised but possibly not emotionally accepted. The ability to determine with certainty whether cetaceans recognise death may require detailed observations (visual and acoustic) to see if, and how, a PA's behaviour changes after the other animal dies, i.e. at the beginning of that second phase. Realisation of separation through ultimate loss, combined with attachment resulting from strong familial or social bonds, may prompt behaviour related to grieving, or at least behaviour that could be interpreted as a precursor to grieving in its truest sense. Group members and other individuals at the scene (particularly females) may be either grieving on their own, or trying to assist and participate via sympathetic concern and empathic perspective-taking (de Waal and Preston, 2017; Pérez- Manrique and Gomila, 2018). In the third phase, the attender may either lose interest or become concerned with its own survival, ultimately abandoning the dead individual.

An additional hypothesis that seems unlikely but cannot be entirely dismissed is that the dead conspecific may represent a potential source of nutrition for the PA. Cases of cannibalism by mothers were recorded in several primate species, though these cases are rare and often refer to habituated, captive, semi-wild or rehabilitated individuals (including some confiscated from the pet trade; Dellatore et al., 2009; Fowler and Hohmann, 2010; Watson et al., 2015; Tian et al., 2016; Tokuyama et al., 2017). For instance, a captive Tonkean macaque *Macaca tonkeana* mother was reported carrying her deceased offspring for a period of 25 days, and at the end of such period she was observed gnawing and consuming its mummified remains (De Marco et al., 2018). The authors suggested that by the stage of cannibalism the mother had lost any clear understanding of what the mummified remains of her infant were. To our knowledge, potential cases of cannibalism among cetaceans are limited to one uncertain report of killer whale remains in the stomachs of two conspecifics caught by whalers (Shevchenko, 1976; originally in Russian): "It is possible that owing to the insecure food supply in the warm zone, cases of cannibalism have also been recorded: killer whale remains about 820 cm long [first digit of length estimate in Russian original is illegible; more likely should be 3 rather than 8, thus 320 cm] were found in two males belonging to the same group".

4.8 Recommendations for future research

Many experienced field researchers have had chances to observe cetacean behaviour toward dead and distressed conspecifics, and such observations may occur on a fairly regular, albeit infrequent, basis. However, only a small portion of these observations ends up being systematically reported or published in peer-reviewed journals. Because our understanding of PAB relies on detailed reports, having a central repository for these cases (e.g. an online database with photos and videos), combined with suitable data collection protocols and an expert validation system, would improve such understanding.

Reporting the number, age class and behaviour of bystanders would contribute valuable insight into cetacean PAB. In this study, only about 20 PAB reports included relevant information on individuals other than the PA(s). Longer-term and more in-depth observations are needed to understand the duration of PAB and the relatedness of the cetaceans involved. For instance, an adult carrying a decomposed calf is often inferred to be a mother that has been carrying her calf continuously since the calf's death. While that may be a reasonable inference, these aspects need to be confirmed, e.g. through repeated observations or long-term follows, photo-identification and sexing of the individuals involved, and genetic analyses to assess kinship. Monitoring should be balanced with ethics, to ensure that an animal's stressful situation is not worsened by invasive research. The well-intentioned and relatively common practice of removing a dead individual from the scene (in our dataset, 73% of carcasses were removed; Table 1) should be discouraged, considering that removal prevents a scientific assessment of the duration and pattern of PAB, unless there are pressing conservation concerns making prompt necropsy necessary. In addition, maintaining proximity with a dead offspring is likely to mitigate the mother's trauma caused by separation (Archer, 1999; Bearzi et al., 2017).

Non-invasive ways of collecting relevant information include the use of small, remotely operated photo and video cameras (including underwater filming and the use of drones), and acoustic recordings. Because cetaceans are primarily acoustic animals, this last approach can be a suitable unobtrusive way to document any changes in behaviour, that might indicate changes in an animal's emotional state (Kuczaj et al., 2013, 2015). Ideally, this should include comparison of vocalisation patterns before, during and after the death, as well as under "normal" circumstances when no dead or dying conspecific is present. Creative and non-intrusive ways may be devised to collect samples (e.g. Rolland et al., 2005, 2006) for genetic, hormonal and other analyses, e.g. before-and-after analyses of stress hormone levels (as done by Engh et al., 2006 with baboons) and to investigate changes in affiliation patterns and social behaviour (Mann and Barnett, 1999). Focusing on the measurable expressions of stress in cetaceans during and after an encounter may contribute to our understanding of "what it would be like to be a cetacean" (paraphrasing Nagel, 1974) confronted with the death of a conspecific.

Interest in, and attentive behaviour towards the dead is not an attribute exclusive to our species (Archer, 1999; King, 2013; Anderson, 2016). Whether or not cetacean PAs realise the finality of death, mammals as evolutionarily distant from *Homo sapiens* as cetaceans seem to share behavioural traits that include a strong, sometimes fairly long-lasting attachment to dead conspecifics. Investigating the factors triggering such behaviour and its underlying mental processes would require a willingness on the part of cetacean researchers to engage (e.g. through scholarly collaborations) with other disciplines such as affective neuroscience (Panksepp, 1998), comparative psychology, neurophysiology and cognitive ethology (Ristau, 2013).

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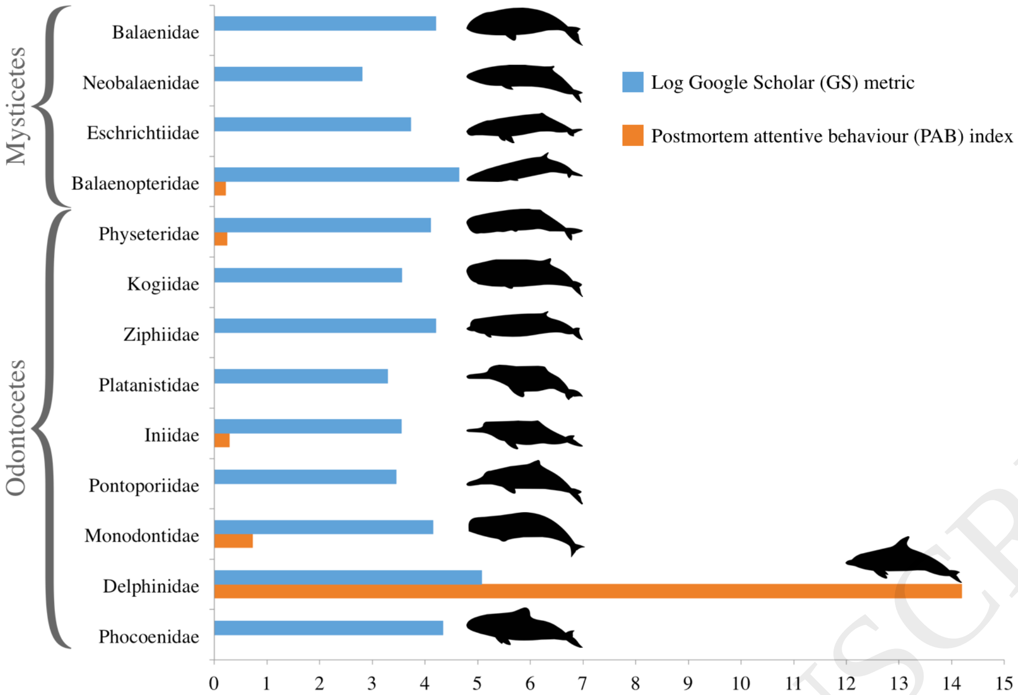
Figure captions

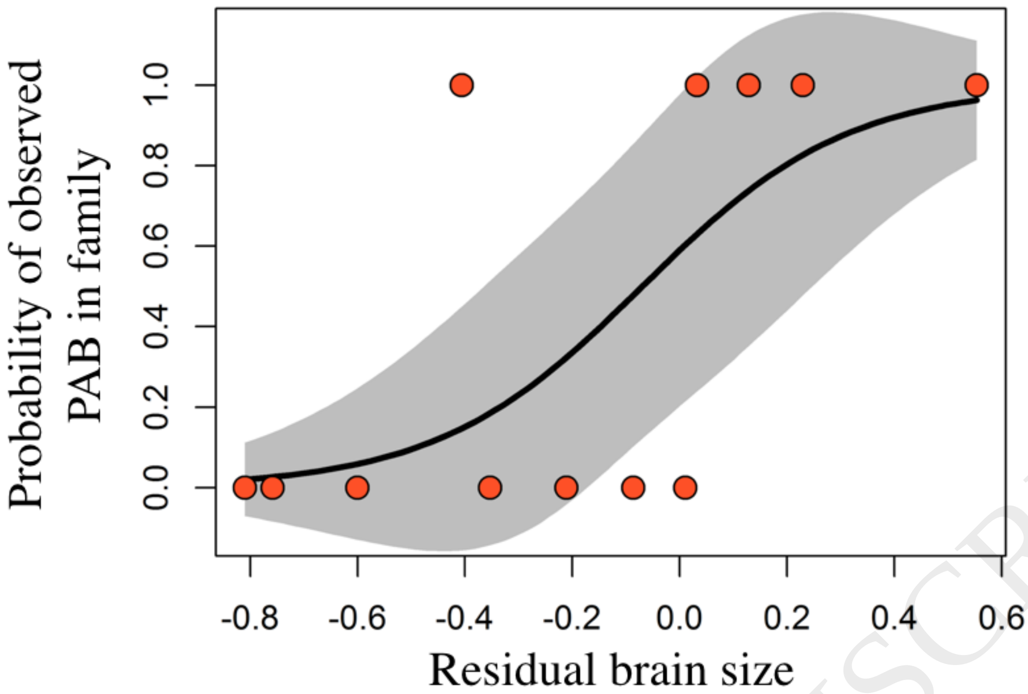
Fig. 1. A common bottlenose dolphin *Tursiops truncatus* carrying a dead neonate on its rostrum. Taylor's Creek, Beaufort, NC, USA; 5 April 2010. Photo by Keith Rittmaster / North Carolina Maritime Museum.

Fig. 2. Log-transformed Google Scholar (GS) metrics (blue) and postmortem attentive behaviour (PAB) indices (orange) for mysticete and odontocete families. Credit: silhouette images, Chris Huh (Creative Commons Attribution-ShareAlike 3.0 Unported).

Fig. 3. Logistic relationships between the probability of a cetacean family having at least one record of postmortem attentive behaviour (PAB) and either residual brain size (top) or GS log-transformed metric (bottom). Lines represent predicted relationship from logistic regression and shaded areas indicate 95% confidence interval of the mean response. Individual circles represent family-specific values. Circles are jittered along the horizontal axis slightly to prevent overlap of two data points. These two variables represent those that performed better than an intercept-only model (see the Results).

Fig. 4. An adult striped dolphin *Stenella coeruleoalba* attempting to push down a dead and buoyant subadult conspecific. Gulf of Corinth, Greece; 9 June 2016. Photo by Silvia Bonizzoni / Dolphin Biology and Conservation.


Mysticetes
Odontocetes
Balaenidae
Neobalaenidae
Eschrichtiidae
Balaenopteridae
Physeteridae
Kogiidae
Ziphiidae
Platanistidae
Iniidae
Pontoporiidae
Monodontidae
Delphinidae
Phocoenidae
Log Google Scholar (GS) metric
Postmortem attentive behaviour (PAB) index
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15


Probability of observed PAB in family
0.0
0.2
0.4
0.6
0.8
1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
Residual brain size

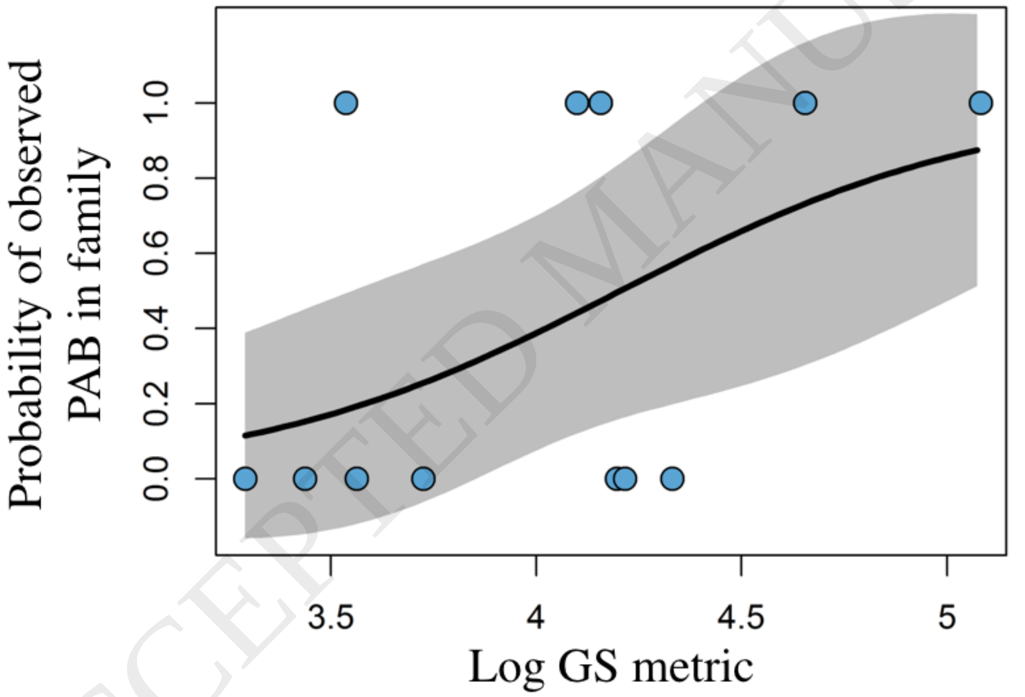

Probability of observed PAB in family
0.0
0.2
0.4
0.6
0.8
1.0
3.5
4
4.5
5
Log GS metric

Table 1. Summary of 78 reported cases of postmortem attentive behaviour (PAB), and cetacean species involved. Age class and sex of postmortem attender(s) (PA(s)) / reported bystanders / dead individual: A = adult, S = subadult, J = juvenile, C = calf, newborn or miscarried fetus, M = male, F = female, Fmo = known mother. Sexual behaviour by PAs: Y = reported occurrence of visible penis or belly-to-belly contact with the carcass. Buoyancy: B = carcass buoyant, NB = carcass non-buoyant, U = carcass buoyancy unknown or unreported. Removal: Y = carcass removed by observers, Failed = removal of carcass attempted but failed, N = carcass not removed by observers, or unreported. A blank cell indicates unreported occurrence. An asterisk (*) indicates information (or lack thereof) not used for PA group size and composition analyses.

Species	PA(s)	Age class and sex of reported bystanders	Sexual beha. by PA(s)	Dead individual / carcass				References
	Age class and sex			Age class and sex	Status	Buoyancy	Removal	
Megaptera novaeangliae	3AM		Y	AM	Possibly killed by conspecific	B	N	Pack et al., 1998
Physeter macrocephalus	1A	8 individuals		C	Dead	U	N	Espaço Talassa, 1997; Reggente et al., 2016
Inia geoffrensis	1A	1A, 1J		C	Dead	NB	N	Henningsen, 1998
Delphinapterus leucas	1A			C	Dead	U	N	Smith and Sleno, 1986
	1AF	1AF, 2A, 2C		C	Dead	U	N	Krasnova et al., 2014
	1A			C	Dead	U	N	Cabana, 2015
Cephalorhynchus hectori	1AF			CM	Dead	U	Y	Stone and Yoshinaga, 2000
Delphinus delphis	5–12A (including 1AM)	5–10A	Y	AF	Alive then dead	NB	Failed	Park et al., 2013
Globicephala macrorhynchus	1AF			C	Dead	U	N	Heimlich-Boran, 1993
	1AF			C	Dead	U	N	Heimlich-Boran, 1993
	1AM, 1AFmo?, 1AF			C	Dead	U	N	Baird, 2016
	1A	8 individuals		C	Dead	U	N	Reggente et al., 2016
	1A	28 individuals		C	Dead	U	N	Reggente et al., 2016
	1A	8 individuals		C	Dead	U	N	Reggente et al., 2016
	1A	6 individuals		C	Dead	U	N	Reggente et al., 2016
	1A	9 individuals		C	Dead	U	N	Reggente et al., 2016
	1A	13–18 individuals		J	Dead	U	N	Reggente et al., 2016
Grampus griseus	1A			C	Dead	U	N	Palacios and Day, 1995
	1A			C	Dead	U	N	Reggente et al., 2016
Lagenorhynchus obliquidens	1A			JM	Dead	B	Y	Kasuya and Miyazaki, 1976
	10 individuals*			C	Dead	NB	N	Black 1994
Orcinus orca	1AM, up to 7AF, 1J			C	Dead	U	N	van Ginneken, 1994, 1996
	1AF			C	Dead	U	N	Olesiuk et al., 2005

	1AF	1S		C	Dead	NB	N	Baird, 2010; Calloway Whiting, 2010; Reggente et al., 2016
	1AF, 1JM (son of AF)			C	Dead	NB	N	Durban et al., 2016
Sousa chinensis	1A			C	Dead	U	N	Parsons, 1998
	"Group"*			C	Dead	U	N	Parsons, 1998
	1A	3A		C	Dead	U	N	Porter, 2002
	1A			C	Dead	U	N	Porter, 2002
	1A			C	Dead	U	N	Porter, 2002
	4A			C	Dead	U	N	Porter, 2002
	*			C	Dead	U	N	Hung, 2010, 2014
	*			C	Dead	U	N	Hung, 2010, 2014
	*			C	Dead	U	N	Hung, 2014
	*			C	Dead	U	N	Hung, 2014
	1A	11 individuals		C	Dead	NB	N	Hung, 2014
	1AF	7 individuals		C	Dead	U	N	Hung, 2014
	1A	3 individuals (1C)		C	Dead	NB	N	Hung, 2014
	1AF	7 individuals (2C)		C	Dead	U	N	Hung, 2014
	5 individuals?*			CF	Dead	U	N	Hung, 2014
	7 individuals (?J, 1C)*			C	Dead	B	N	Hung, 2014
	7 individuals?*			C	Dead	NB	N	Hung, 2014
Sousa sahulensis	1AF	1J		C	Dead	B	N	Reggente et al., 2016
	1AFmo	4A, 2J		C	Dead	B	N	Reggente et al., 2016
	1A	2A, 1J		C	Dead	U	N	Reggente et al., 2016
Sotalia fluviatilis	1A	4–8 individuals		CF	Dead	B	Y	Santos et al., 2000
Stenella attenuata	5 individuals*			C	Dead	U	N	Rinaldi et al., 2006
Stenella coeruleoalba	1A			SF	Dead	B	N	Bearzi et al., 2016; and see the Discussion
Stenella frontalis	4A	16 individuals		C	Dead	U	Y	Alves et al., 2015
	1A			C	Dead	U	Y	Alves et al., 2015
Stenella longirostris	1AF	15 individuals (including J and C)		CM	Dead	B	N	Rickards et al., 2001
	1A	"Group"		CF	Dead	B	Y	Reggente et al., 2016
Steno bredanensis	1AF	6A		JF	Dead	U	Y	Lodi, 1992
	3A	15–17 individuals		C	Dead	NB	Y	Ritter, 2007
	2 individuals*			JM	Dead	B	N	de Moura et al., 2008
Tursiops aduncus	1A			J	Dead	U	Y	Reggente et al., 2016
Tursiops truncatus	2A	4A		C	Dead	NB	Failed	Cockcroft and Sauer, 1990
	1AFmo	1A, 3AM		CM	Dead	B	Y	Connor and Smolker, 1990

	1AFmo	1AF		C	Dead	U	N	Wells, 1991
	1A	10–13A, 2C		C	Dead	NB	N	Harzen and dos Santos, 1992
	1A	13–14 individuals, 1C		CM	Dead	B	Y	Harzen and dos Santos, 1992
	1A	10 individuals with "a few" C		C	Dead	U	N	Harzen and dos Santos, 1992
	1A	3AF, ?A, 3C		JF	Dead	B	Failed	Félix, 1994
	1A	"Several" individuals		C	Dead	B	Y	Fertl and Schiro, 1994
	1A			C	Dead	U	N	Fertl and Schiro, 1994
	1AF	1A		C	Dead	U	N	Rollo and Monteiro-Filho, 1994
	1AFmo	2AF, 2C		CF	Killed by shark	B	Y	Mann and Barnett, 1999
	1A, 1S	26A, 2C		C	Dead	B	N	Delgado-Estrella, 2002
	1AF	"Other" individuals		C	Dead	B	N	Bearzi, 2007; Hooper, 2011; Calloway Whiting, 2010
	2AM		Y	AF	Dead	NB	N	Dudzinski et al., 2003
	4AM, 2AF, 16SM, 1C		Y	SM	Dead	NB	Y	Dudzinski et al., 2003
	1AF	2A, 1J		JF	Alive then dead	U	Y	Warren-Smith and Dunn, 2006
	1AF			JF	Dead	B	Y	Rittmaster, 2011
	1A	"Other" individuals		C	Dead	U	N	Anderson, 2013; Thomas, 2013
	1A			AF	Dead	B	Y	Cape Lookout Studies, 2015
	3-5A (M, F)	4-11A	Y	AF	Alive then dead	NB	N	Kuczaj et al., 2015
	1AF, 1AFmo			C	Dead	NB	Y	Quintana-Rizzo and Wells, 2016
	1A	1A		C	Killed by conspecifics	U	N	Verborgh et al., 2013; Reggente et al., 2016

Table 2. Results from logistic regressions describing probability of at least one postmortem attentive behaviour (PAB) record within a family. Models, in order of relative Akaike Information Criterion (AIC) weight, include a single explanatory variable: residual brain size, GS metric (log-transformed), encephalisation quotient (EQ), or none (intercept only). ΔAIC represents the difference in AIC between the model and the best performing model. The AIC weight (w_i) represents the probability that the model is the best among the candidate set of models. Pseudo-R^2 represents the Nagelkerke R^2 index.

Variable	df	Coeff	SE	Pseudo-R^2	AIC	ΔAIC	w_i
Residual brain size	2	5.2	3.0	0.52	14.4	0	0.69
Log GS metric	2	1.0	0.7	0.28	17.5	3.1	0.15
Intercept	1	-0.3	0.6	-	18.3	3.9	0.10
EQ	2	0.6	0.6	0.19	19.2	4.8	0.06