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Past, present and future of the ecosystem services provided by cetacean carcasses

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ABSTRACT

Ecosystem services associated with cetacean strandings have been altered by humans through exploitation of wild populations during the whaling era and more recently by regulations on carcass management and disposal to abide by environmental health requirements. Here, we systematically review the scientific literature and gather data on cetacean strandings worldwide to: 1) identify the ecosystem services provided by stranded cetacean carcasses in the past and present; 2) estimate the density of cetacean strandings currently occurring in selected coastal areas around the globe, and analyse its association with human population density and regulations; and 3) identify and discuss the regulations and methods concerned with whale carcass disposal in specific regions of the world. Our literature review revealed that stranded cetacean carcasses have provided a rich and varied array of provisioning, regulating, cultural, and supporting ecosystem services to ancient and modern civilisations worldwide. Also, we found that the current density of stranded carcasses (mean: 0.090 strandings • year^{-1} • km^{-1}; range: 0.001–0.978) and the disposal methods widely varied across the studied regions and countries. In addition, neither human population density nor the existence of regulations were good predictors of stranding densities. Finally, we provide recommendations for the future management of stranded cetacean carcasses, by identifying those disposal methods that minimize costs and maximize ecosystem functions and services. In particular, we encourage natural decomposition *in situ* whenever possible; otherwise, the present coastal management strategies could be improved by including zoning, seasonal use limitation and educational outreach depending upon the local scenario. Overall, further socio-ecological research is strongly needed to guide stranded cetacean carcass management towards enhancing the net benefits that humans and ecosystems gain from carcasses, especially considering that coastal areas become more populated, new disposal regulations are approved, and cetacean populations are recovering – and thus strandings may become more frequent.

1. Introduction

Modern societies are increasingly disconnected from nature (Dijkstra, 2016). One of the many manifestations of such disconnection is the growing implementation of “aseptic” strategies in natural resource management. For instance, carcasses of both domestic (Donázar et al.,

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2009) and wild animals (Margalida and Moleón, 2016) are frequently removed from the field to minimize disease transmission risk in many regions, often mandated by regional, national or international regulations. This management scenario largely ignores the pivotal ecological role of carrion (DeVault et al., 2003; Wilson and Wolkovich, 2011) and the many contributions that dead animals can offer to humans (Moleón et al., 2014).

Cetacean carcasses are a naturally occurring element of the coast and humans have been exploiting them for millennia (Seersholm et al., 2016), providing coastal inhabitants with goods such as food, oil and bones, but also with knowledge of the sea while observing them stranded on the shore (Ellis, 1991). Also, stranded cetaceans are a key source of food to scavengers, and nutrients to the sediments (e.g. Laidre et al., 2018; Tucker et al., 2019a), thus being an integral part of coastal ecosystems (Panels 1 and 2, Figs. 1 and 2). However, about forty percent of the human population currently lives within 100 km of the coast, and as a result, many coastal areas have been transformed (Crossland et al., 2005). The changes include not only the intense urbanization of the coast and subsequent alteration of ecological processes (e.g. Huijbers et al., 2013), but also the application of policies urging the removal of carcasses from the coastal areas to protect human health (Tucker et al., 2018). Combined with the past depletion of cetacean populations (Hacquebord, 2001; Panel 3), the existing regulations on removal of stranded carcasses has led to radical changes in the abundance and availability of large marine biomass inputs, which has greatly altered the ecosystem functions and services associated with marine carrion over time.

Fig. 1. Cetacean carcasses support a wide range of scavengers, both vertebrates and invertebrates, in different habitats. See photo credits in Appendix A.

Fig. 2. Andean condors (*Vultur gryphus*) used to intensively exploit stranded whale carcasses. However, the current scarcity of stranded whales has induced important changes in condors' behaviour (see Panel 2). Adult Andean condor soaring above a living whale in Peru (a); several Andean condors of different age feeding upon a stranded whale carcass in Patagonia, Argentina (b). See photo credits in Appendix A.

In this study, we review the scientific literature and gather data on cetacean strandings to: 1) identify the ecosystem services provided by stranded cetacean carcasses. Here, ecosystem services are defined as the benefits people obtain from ecosystems (Millennium Ecosystem Assessment, 2005). These include provisioning, regulating, and cultural services that directly influence people, as well as supporting services (or ecosystem functions) necessary to maintain the other services. While the recently developed Nature's Contributions to People framework (NCP) includes both the beneficial (i.e. ecosystem services) and detrimental (i.e. disservices, conflicts or damages) contributions of nature to societies' quality of life (see Díaz et al., 2018 for an overview of the evolution of the concept), here we deliberately focus on the beneficial side of stranded cetacean carcasses; 2) estimate the density of cetacean strandings occurring in selected coastal areas around the world and analyse whether human population density and the presence of regulations affect these recordings, in order to gain understanding on the spatial distribution and the factors affecting the potential provision of ecosystem services by stranded cetaceans; and 3) enumerate the regulations and methods concerned with whale carcass disposal in specific regions of the world, and discuss the pros and cons associated with each method in terms of ecosystem service provision. Based on the findings of the paper we provide recommendations for future research and the management of cetacean strandings in an increasingly aseptically managed world.

2. Materials and methods

2.1. Literature review

We conducted a systematic literature review according to the PSALSAR method (Mengist et al., 2020), which is an extension of the SALSA framework that has frequently been used in systematic reviews (Grant and Booth, 2009) and that guarantees conceptualization, accuracy and reproducibility. In the first step, we defined our study scope: ecosystem services provided by stranded cetacean carcasses. Secondly, we defined our search string (see Table B1) and used Web of Science to search for articles (published until 6th August 2020) containing these keywords in the entire article. In summary, our search protocol used the terms “humans” and “ecosystem services” in combination with various synonyms for cetacean carcasses (i.e. “stranded whale”, “whale carcass”, “stranded cetacean”). This yielded 484 articles (Table B1), including repeated articles resulting from different searches. Thirdly, we restricted the search to peer-reviewed articles. Then, we screened titles and abstracts to identify those articles that dealt with the ecosystem services provided by cetacean carcasses, and we fully read the selected articles. This led to a final selection of 27 articles dealing with services provided by cetacean carcasses (Table B1). Fourthly, we extracted the following information from the selected articles: 1) ecosystem services mentioned (separating them into provisioning, regulating, cultural and supporting services), 2) cetacean species or group to which the ecosystem services were related, 3) study area, and 4) study period (prehistoric, historic –i.e. before the start of the 19th century when the onset of commercial whaling occurred– and modern –i.e., after the start of 19th century–). Fifthly, we categorised the selected articles according to these former factors (ecosystem service type, cetacean group, area and period). Species were grouped according to families and parvorders of Cetacea: a) baleen whales, b) toothed whales (excluding small-toothed whales), and c) dolphins and porpoises, which were separated from the other toothed whales because of their smaller body size and generally higher abundance.

2.2. Data collection on strandings and regulations

We retrieved data on cetacean stranding events from 29 countries or regions (Table B3) and regulations from 23 of them (Table B4), from an initial list of 67 coastal countries in all continents that were considered and asked for information. Data on strandings and regulations were directly shared either by the marine mammal network established in these countries or by scientists working on cetacean strandings in different academic organisations, governmental institutions or independent societies. In addition, we extracted complementary information from local grey and primary scientific literature. We selected stranding datasets that were representative of the species occurring in each study area and covered multiple years. Records of cetaceans that stranded as carcasses, died after stranding or were unsuccessfully re-floated (re-stranded and died) were grouped as mentioned above: a) baleen whales, b) toothed whales (excluding small-toothed whales), c) dolphins and porpoises, and d) unidentified cetaceans. For each group, the total number of strandings was divided by the number of years covered by the dataset and the coastline length (km) of the territory or country (see more details in Table B3). Few datasets also provided information related to the fate of the stranded carcasses in terms of disposal, which will be summarised in the Results.

2.3. Analysis of stranding data

To understand if stranding reporting rate in each region could be explained by the population density and existence of stranding management policy or regulations, we used the 23 regions for which we were able to gather information on the existence of management policy or regulations (Table B4), coast length and human population density. The existence of stranding management policy or regulations was coded as: “yes”, if present and known; “no”, if not present and known; and “na” for unknown (five regions). We used the decimal logarithm of human population by coastal km^2 as a proxy of human coastal population density. We performed model selection using the Akaike’s information criterion (AIC; Burnham and Anderson, 2004). We considered models to be equivalent when the difference in AIC with the best model was ΔAIC < 2 (Burnham and Anderson, 2004). All were Generalized Linear Mixed models (GLMMs) built in R (R Core Team, 2013) using a Gaussian link function.

3. Results

3.1. Ecosystem services provided by cetacean carcasses

Our literature review showed that cetacean carcasses have mainly supplied provisioning services, followed by cultural, supporting and regulating services (Fig. 3; Table B2). Most articles referred to modern times, though those mentioning provisioning services mostly related to prehistoric times (Fig. 3). In our search, the keyword “human” was included in more articles than “ecosystem service”. This reveals that, despite the scientific literature acknowledging the association between humans and cetacean strandings, little of this association is explained in terms of ecosystem services. Here, we present an overview of the historical and current role of cetacean strandings as providers of ecosystem services for humans by compiling the examples produced by our literature search and further pertinent articles (see also Panel 1).

Cetacean carcasses provided food and raw material to early civilisations worldwide (Fig. 4). For instance, remains of two barnacle species, originally attached to the body of southern right whales (*Eubalena australis*), were found in a cave at a prehistoric site in southern Spain, suggesting that primitive humans used to consume stranded whale meat (Álvarez-Fernández et al., 2014). Bone fragments belonging to cetacean specimens were also identified in the Mesolithic deposits of other prehistoric caves (e.g., Grotta dell’Uzzo, Italy; Mannino et al., 2015). The discovery, in Angola, of numerous tools made from whale bone, such as choppers and flakes, indicated that many components of carcasses were used in the Lower Palaeolithic (Gutierrez et al., 2001).

In the pre-Columbian era, indigenous people, such as Arawak and Carib groups from Barbados (Caribbean), also consumed stranded dolphins and sperm whales (*Physeter macrocephalus*; Romero and Creswell, 2010). Stranded carcasses have been of crucial importance to the survival and cultural development of other traditional coastal communities, such as the Inuit living in the Arctic region (Katona and Whitehead, 1988), the “canoe people”, and the Fuegians, inhabiting the southernmost Patagonian coast. The latter considered stranded cetaceans a “great

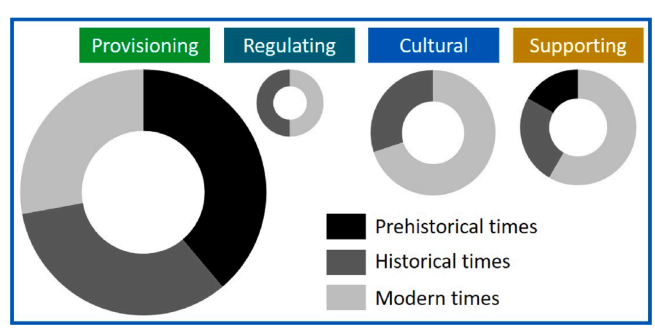

Fig. 3. Results of the systematic literature review on the ecosystem services associated with cetacean carcasses, according to service type and period of time. Ring size is proportional to the number of articles found in the review. For more details, see Table B2.

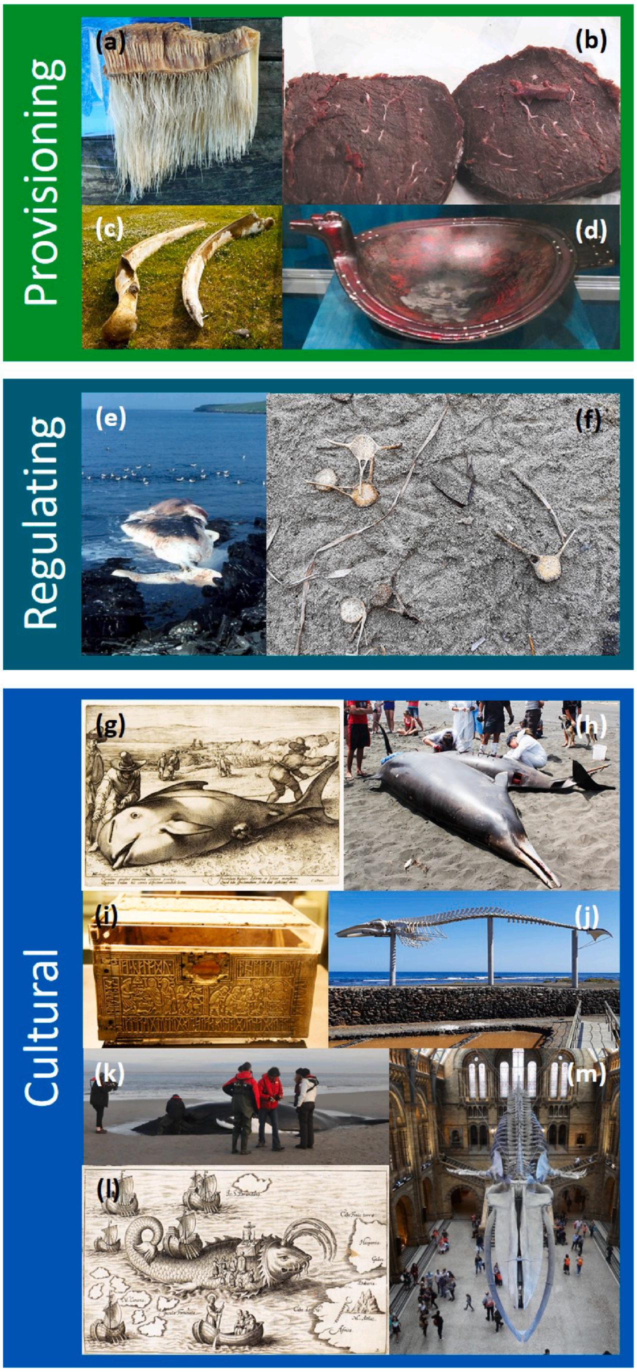

Fig. 4. Examples of ecosystem services associated with cetacean carcasses. Provisioning services: production of tools (baleen plates used as broom; a), meat (b), fertilizers (c) and oil (oil dish for whale oil; d). Regulating services: CO_2 sequestration in the form of floating carcasses before sinking (e) before undergoing nutrient recycling through action of scavengers and decomposers (f). Cultural services: scientific advancement in the past (g) and present (h); production of art (Frank Casket, an Anglo-saxon box made of whalebone; i); educational value in outdoor (j) and indoor museums (m); ecotourism (k); and religious significance (l). See photo credits in Appendix A.

gift of nature" to be shared with the entire community (Quiroz et al., 2016), whereas Australian Aborigines and islanders from the Torres Strait believed that strandings could connect them to ancestral lands, seas, and their ancestors (Harcourt et al., 2014). Similarly, in New Zealand, Māori regarded whale strandings as a symbol of abundance and richness because they were great sources of protein and material: these resources were extracted following strict protocols to respect their spiritual importance (Rodgers, 2017).

In the later medieval period, both Anglo-Saxons and Nordic coastal communities used to exploit stranded marine mammals (Brito et al., 2011; Parsons and Monaghan-Brown, 2017). Since the eleventh century, cetaceans stranded on English shores have been known as "Royal Fish", following a statute enacted by Edward II (Gardiner, 1997). The cetaceans' flesh was consumed by wealthy citizens whereas the remains of the carcass were rendered to produce oil and the bones used as utensils or artistically carved (e.g. the Franks Casket which is a small decorated box made of whale bone from the 8th century, representing Anglo-Saxon art). For the medieval English, whales were "sea-monsters" and according to the popular superstition, their strandings predicted the imminent occurrence of extraordinary events (Gardiner, 1997; Fig. 4).

As humans developed towards modern society, their relationship with marine mammals also changed. Provisioning ecosystem services attributable to strandings were slowly substituted for cultural services (Fig. 4). Starting from the 18th century, stranded carcasses were studied and Latin names were given to cetacean species. Stranded carcasses on beaches, particularly of large cetaceans, also frequently generated high public interest (Sousa and Brito, 2012).

From the 20th century, it became common for scientists to collect stranded specimens to improve their understanding of these aquatic mammals (Fig. 4). The skeletons were collected by museums for public exhibition, education (Weir and Pierce, 2013) or future research (Borella and Borrero, 2017). Cetaceans and their carcasses are now viewed as indicators of ocean health, and strandings provide important information that enhances our scientific understanding of marine ecosystems and the effects of anthropogenic impacts (Bossart, 2011). Receiving much attention from the media and the public, strandings of large cetacean specimens became sources of sustainable environmental education. In addition, the work of volunteer–based organisations responding to marine mammal strandings is of great value in raising public awareness, which can potentially enhance animal welfare and conservation (Roman et al., 2018).

Whale carcasses are also providers of supporting services, such as subsidies to scavengers. They greatly contribute to nutrient cycling and carbon sequestration, representing – in the case of whale falls – a potential sink for anthropogenic carbon that may be important for mitigating global climate change (Pershing et al., 2010; see Panel 1).

3.2. *Strandings around the world*

Mean density of stranding per country/region was 0.09 strandings • $year^{-1}$ • km^{-1} (SD = 0.21). Northern Territory (Australia) had the lowest annual density of stranding events (0.001 strandings • $year^{-1}$ • km^{-1}), whereas Belgium the highest (0.978 strandings • $year^{-1}$ • km^{-1}; Fig. 5). In general, as expected from their relative abundances (Hammond et al., 2013), dolphins and porpoises were the most abundant group across all countries (Fig. 5), with the exception of Argentina and Chile, where baleen whales dominated the recorded stranding events (Figure B.1).

Regarding the GLMMs exploring if the stranding densities recorded could be predicted by the presence of management policy or human population density across the studied areas, the set of best competing models (see Table B5) comprised the model including the effect of human density (M_1) and the model including the effect of legislation presence (M_2). However, these models were not significantly different from the constant model, and their effects were not significant (i.e. none of the betas was significantly different from zero; see Table B5 and Figure B.2). Thus, neither of the abovementioned factors were good predictors of recorded stranding densities.

3.3. *Regulations around the world*

The implementation of regulations for carcass management is a

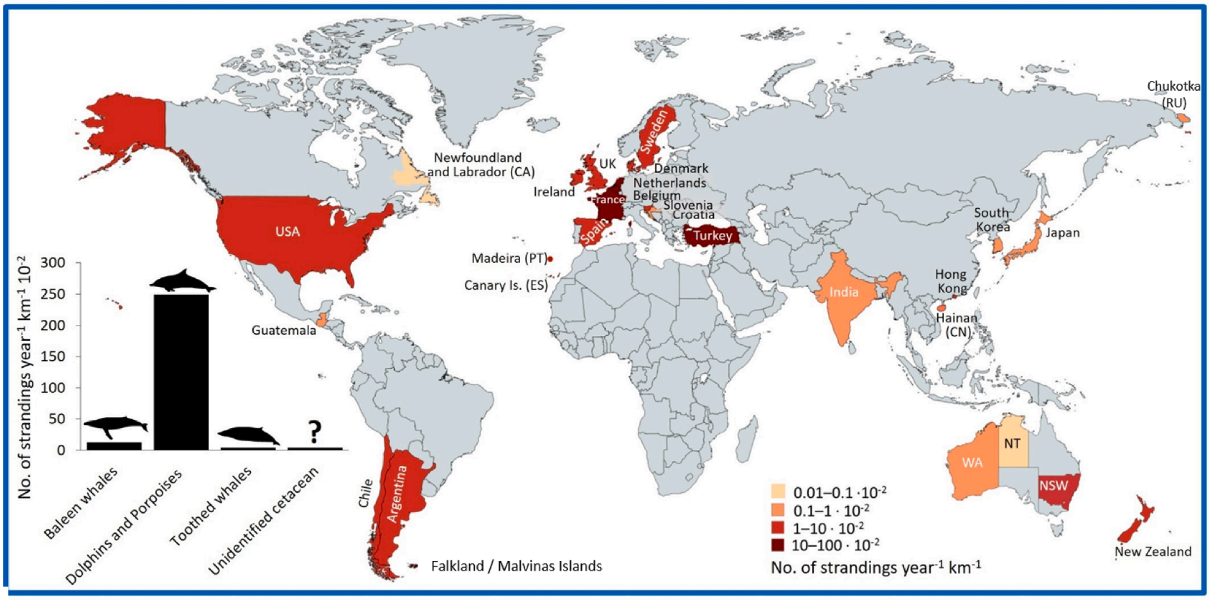

Fig. 5. Cetacean stranding density map (N strandings • year^{-1} • km^{-1}) and absolute abundance of strandings per group of cetaceans (Baleen whales or Mysticeti; Toothed whales or Odontoceti, excluding small toothed whales like dolphins and porpoises; Dolphins and Porpoises; and Unidentified cetaceans) for all study countries/regions.

recent and ongoing phenomenon. Out of the 23 study countries/regions, five did not have regulations related to strandings (22%; Table B4). The lack of legislation was justified by the institutions involved in stranding management because the areas were remote and had low human population density (e.g. Newfoundland and Labrador in Canada and Northern Territory). The absence of a stranding response network and a competent national authority also determined the lack of regulations (e.g. Ireland, which, however, has an efficient volunteer network; IWC, 2016). In some countries/regions, official permissions are needed to handle stranded cetaceans in distress, or their carcasses, and specific stakeholders are responsible for the intervention and the carcasses' fate. Several stakeholders are involved in these processes. These may include local governments, such as the city council and the municipality, and/or land managers, academic institutions, stranding networks, local NGOs and museums. Their role in the management of carcasses varies from country to country. In some countries, like New Zealand, indigenous people are also involved in the process: for instance, Māori would pray for the dead cetaceans before their disposal (Butterworth, 2017). Protocols may be implemented to guide and facilitate the process of carcass disposal (Table B4). This is the case in New South Wales (Australia), where the National Parks and Wildlife Services developed a checklist to guide land managers when disposing of whale carcasses (NPWS, 2020).

A wide spectrum of carcass disposal methods exists, from completely or relatively natural procedures, such as natural decomposition *in situ* of the whole carcass or in pieces, burial of the carcass, towing out to sea (offshore), to land (inshore) or composting, to methods that involve

	Ecosystem services				Costs			
Method of disposal	Supporting	Regulating	Provisioning	Cultural	Technical	Social	Economic	Environmental
Natural decomposition in situ	yes	yes	yes	yes		yes		
Burial	yes	yes			yes		yes	
Incineration plant					yes		yes	yes
Landfill		yes			yes		yes	
Ocean tow	yes	yes			yes		yes	
Educational & scientific collection			yes	yes	yes		yes	
Rendering		yes		yes	yes		yes	
Composting	yes	yes		yes			yes	

+ Frequency in regulations −

Fig. 6. Different methods of stranded cetacean carcass disposal and associated ecosystem services and costs, ordered according to their frequency in regulations of countries/regions considered in this study.

more intervention, such as disposal at a local landfill, incineration or rendering (Fig. 6). In Western Australia, most carcasses are buried (30%), and only 8% of them are left *in situ*. Excluding the carcasses whose fate is unknown, in New Zealand and USA most of the carcasses are left on site or buried (NZ: 39% and 38%; USA: 28% and 21%, respectively). Also, in New Zealand, mass strandings have forced authorities to use natural tide driven decomposition. Carcass transportation to landfills or incineration plants is common in many European countries. For instance, in Belgium and France, which are characterised by high densities of strandings, the only option is to destroy cetacean carcasses in appropriate facilities. Multiple disposal methods are allowed in other European countries (e.g. Spain). In USA, the third most used method is the landfill (18%). Specimens that will be used for scientific and educational purposes are either collected, buried or consumed by scavengers prior to recovery of the skeleton. In Western Australia and New Zealand, only a small number of carcasses are collected for scientific (WA: 0.7%; NZ: 1.3%) or educational (WA: 1.2%) purposes. When carcasses are removed, they are often necropsied, so they still may provide a scientific and veterinary service. However, in some cases, the necropsy *per se* is the ultimate goal, which usually means moving the carcass to a wildlife rescue centre, where it is eliminated or cleaned to obtain the skeleton. Necropsies of large whales are normally done *in situ*.

The method of carcass disposal is context-dependent in 45% of countries/regions, as it may change depending on the exact location where the animal strands (Table B4). Generally, when the carcass is found in a remote or difficult to access area, the common procedure is to let it decompose naturally, whereas its removal is considered preferable when occurring in a populated or touristic area. This is the case in New South Wales and Western Australia (Australia; NPWS, 2020; DPAW). However, this choice is not contemplated when the removal of the carcass is compulsory (France and Belgium), or there are no regulations in place because they are considered unnecessary (Newfoundland and Labrador, and Falkland Islands). Regulations vary when strandings occur in protected areas, depending on the potential contamination and impact on the existing flora and fauna. Special concerns arise when stranded large whales are euthanized, as toxic chemicals used in some methods may pose a possible risk to scavengers and the surrounding environment (relay toxicity), potentially affecting humans negatively (Harms et al., 2014). In these cases, carcasses are always removed for appropriate disposal (e.g. UK). In the case of Denmark, removal of the carcass is not location-, but species-dependent, as only harbour porpoises are left at site to decompose.

4. Discussion

Ancient and modern civilisations worldwide have benefited from the rich and varied array of provisioning, regulating, cultural, and supporting ecosystem services associated with stranded cetacean carcasses. From Palaeolithic Africans and Europeans to pre-Columbian Americans, and from boreal Inuits and Icelanders to Pacific Māori, pre-industrial humans living in or near the coast viewed strandings as a gift from nature (e.g. *hvalreki* in Icelandic, meaning “windfall”, Fielding, 2018), and cetacean carcasses were widely used for food and as source of raw material for hunting and butchering tools and ornaments (e.g. Gardiner, 1997). Cetaceans also produced a deep spiritual and artistic inspiration (e.g. Harcourt et al., 2014). More recently, cultural services became the dominant benefits associated with stranded cetaceans (as happened with other faunal groups; e.g. Moleón et al., 2014), including scientific discovery, *in situ* and *ex situ* education, public awareness raising, and ecotourism. Overall, for many ancient and modern people, cetacean carcasses signify an apparent manifestation of nature’s magnificence. All this reveals the important cultural heritage that humanity has constructed around stranded cetaceans. In addition, through the key ecological effects of cetacean carcasses, which pervade well beyond the coastal systems and may last for years, strandings have also led to relevant supporting services for past and present ecosystems. However, currently, ecosystem services provided by stranded cetaceans are greatly threatened by both the results of reduction in cetacean populations due to hunting (see Panel 3) and modern policies regarding the disposal of these carcasses. From the International Whaling Commission 1982 moratorium on commercial whaling, the number of countries adhering to the International Convention for the Regulation of Whaling (1946) increased year after year (IWC). In addition to this international agreement, many countries have put forward national legislation to protect marine mammals, including their remains. As a result, the management of any type of operation involving marine mammals (from first intervention to disposal of the carcass) is often regulated at national or infra-national levels. Because of the natural recurrence of stranded animals on the coast, these regulations are indispensable for not only the conservation of cetaceans and their full ecological role, but also human well-being.

Decomposing cetacean carcasses are a potential safety hazard to human health, and a nuisance for some locals and beach users when occurring in populated areas (Tucker et al., 2018). Thus, the systematic removal of carcasses is often applied to avoid health-related risks and/or people’s malcontent. The latter could be considered the main disservices that stranded cetacean carcasses provide to humans. Avoiding these detriments, however, often requires complex logistics and important economic costs, which could also be viewed as a sort of disservice. For instance, in Australia, the beach burial of a whale can reach up to approximately $18,000 (USD) when including all the costs of the machinery, operations and consultation with stakeholders. The transport and destruction of a small whale at a dedicated facility, instead, is around $15,000 (USD), with costs varying according to carcass size (Tucker et al., 2018). Moreover, as the coastal areas become “cleaned” and the coastal ecosystems “aseptic” to fulfil these human necessities, the structure of natural communities is destabilised and their ecological functionality lost (Huijbers et al., 2013), and the provision of other human demands such as aesthetic enjoyment, education and other cultural services is compromised. Thus, understanding the ecosystem service potential associated with cetacean strandings is the first step to fully recognise and establish the direct and indirect benefits to human society and its needs (Malinauskaite et al., 2021a).

4.1. Policy and management recommendations

Stranded cetacean carcass management will be an increasing global matter as coastal areas become more populated, new regulations are approved, and cetacean populations recover (Clapham et al., 1999; see Panel 3). In addition, climate change and population shifts may potentially lead to strandings in regions which may not have previously encountered them, and strandings may involve different species than previously seen (Williamson et al., 2021). Thus, management strategies may need to adapt in response.

One way to maximise the benefits derived by cetacean carcasses is identifying those disposal methods that can preserve and/or enhance ecosystem functions and services. All the existing disposal methods can support ecosystem services, but some better than others (Fig. 6). Management of cetacean carcasses needs to balance their ecological importance, the ecosystem services they may provide, costs of management actions, biodiversity conservation regulations and legal and public health requirements (Fig. 6). When left *in situ*, a cetacean carcass can provide all the types of ecosystem services, with very low management costs, but social discontent may rise. Burial is a cost-effective option; but if the carcass is buried close to the shoreline, the nutrient enrichment of the surrounding environment may contaminate the ground waters and potentially attract sharks to the shore, which may diminish the recreational use of the beach (Tucker et al., 2018; Tucker et al., 2019a; Heiss, 2020). Returning the carcass to the sea by towing it would allow its natural decomposition and provision of regulating and supporting services. However, a floating carcass could also become a safety hazard in areas of high maritime traffic (Tucker et al., 2018). The full removal of stranded cetaceans from the coastal area leads to the loss of ecosystem services and increase of the costs related to their transport and disposal. In particular, incineration is more expensive than other methods and is a source of greenhouse gas emissions (Morales-Reyes et al., 2015). Among the options requiring the removal and transport of carcasses, composting costs (per unit weight) half of the price of the disposal in a landfill or incineration plant (King et al., 2018). Moreover, this option comes with environmental benefits too, e.g. improved soil quality and break-down of contaminants and pollutants (King et al., 2018).

Given the prominent importance of stranded cetacean carcasses for endangered scavengers in some areas/regions (Chamberlain et al., 2005; Lambertucci et al., 2018, see Panel 2) and ecosystem functions (Smith and Baco, 2003; Bui, 2009; Smith et al., 2015), we encourage natural decomposition *in situ*, provided that legal and safety needs are fulfilled. This measure, which is the cheapest one, can obviously be easily applied in remote coasts and/or protected areas, as some countries already do. In more populated and touristic areas leaving carcasses *in situ* may raise problems of sight, smell, changes in sediment and groundwater chemistry, and shark and feral dog attraction (Tucker et al., 2018). In these cases, management may be season- and/or location-dependent. When strandings take place during the low-tourism season, carcasses may be left *in situ*. When strandings occur in the high-tourism season, a temporal restriction, covering the main decomposition period, could be applied to the vicinity of the carcass. The implementation of zonation maps identifying remote and urban beaches could also be implemented in order to facilitate the decision making. Alternatively, carcasses could be chopped into smaller parts to accelerate their consumption or decomposition.

Our analysis of strandings around the world revealed that not all countries or regions will face the same challenges, as both the density and size of the stranded cetaceans were highly spatially heterogeneous. In general, those countries with the highest densities of stranded cetaceans and more restrictive regulations for carcass removal (e.g. France, Belgium and the Netherlands) mostly received small-sized cetaceans. A sensible policy might take into account both the size and number of carcasses. The disposal and transport of smaller carcasses generally cost less, both in terms of manpower, logistics and overall financial cost. In a country where strandings are dominated by small cetaceans such as dolphins and porpoises, a proportion of carcasses may, therefore, be chosen to be left *in situ*, or transported to a more remote area with limited costs. If both small and large whales occur at a similar extent, then logistics may be eased and costs reduced by removing the small size carcasses, whereas large carcasses could be chopped *in situ* after necropsy avoiding transport costs, but potentially increasing staff efforts.

Finally, we recommend that the past and present value of strandings, and cetacean carcasses in general, are included in educational initiatives. In remote areas, like in the Arctic regions, information on whale carcasses can be incorporated as an educational resource for the locals and used to promote the increasing tourist industry alongside with the one existing on living whales (Geraci and Lounsbury, 1993; Malinauskaite et al., 2021a). This, and other ecotourism experiences, could be enhanced and exported to other places worldwide, as scavengers provide important recreational, aesthetic, learning and inspiration experiences to people (Aguilera-Alcalá et al., 2020). An increased public awareness of the ecological and cultural role of cetacean strandings could help reduce negative attitudes towards these phenomena and thus balancing ecosystem services and disservices.

5. Conclusions and future research

We have provided a comprehensive overview that could be used to raise public awareness of the benefits that cetacean carcasses have provided to our ancestors, and the services from which modern humans could benefit. Thus, future steps should identify the main social actors involved and evaluate the public perception of strandings and associated services, which could eventually improve current regulations on carcass disposal (Malinauskaite et al., 2021b). Further, we encourage the implementation of innovative science outreach via citizen science and education to foster enhanced local ecological knowledge and appreciation of ecosystem services provided by cetacean carcasses, which may lead towards more sustainable practices. Finally, both use and non-use values of cetacean carcasses should be estimated in different local social contexts by integrating market and non-monetary valuations to each ecosystem service provided (Cook et al., 2020).

We recommend enhancing the present coastal management strategies by widening their ecosystem perspective by including zoning, seasonal use limitation and science outreach. Undoubtedly, these management actions need to be supported by a better scientific knowledge of cetacean strandings – and populations. Long-term monitoring of stranding events, especially if coordinated at the supranational level, should be a basic component for the conservation of marine megafauna and the ecosystem services they provide. These programs may supply detailed data on cetacean stranding numbers and their spatiotemporal distribution, which is relevant to refine our understanding of the factors affecting stranding dynamics and to improve the efficiency of carcass detection and decision making. These data and knowledge are also essential for clarifying the relationship between stranding events and multiple explanatory factors in addition to human density and presence of regulations here explored. Importantly, this information should be made easily accessible to researchers. In addition, further evaluation of the ecological impact of the different management techniques of strandings and comparing their costs and benefits is essential (Tucker et al., 2018). Only through a deeper scientific knowledge of the socio-ecological context that characterizes the carcasses of stranded cetaceans, we will be able to delineate the most efficient management strategies in coastal areas in an increasingly populated (by both humans and cetaceans) world.

Panel 1. Ecological effects of cetacean carcasses.

Whale carcasses are a significant source of carrion in the marine system (Baco and Smith, 2003), representing a huge food supply to scavengers and decomposers, both marine and terrestrial (Fig. 1). “Whale falls” attract and sustain a diverse and abundant deep-sea community of vertebrate and invertebrate scavengers. By providing intermediate habitats to be colonised, whale carcasses link chemosynthetic communities together, enhance the structural complexity of the seabed for years (Smith and Baco, 2003) and promote adaptive radiation of certain organisms such as the bone-eating worm (*Osedax* spp.; Smith et al., 2015). Most dead whales sink to the bottom, but about 10% may become buoyant because of gas produced during decomposition (Pyenson, 2010). While floating, carcasses become an easy and energy-rich source of food for orcas and sharks (Whitehead and Reeves, 2005; Leclerc et al., 2011; Tucker et al., 2019a). Of these, some carcasses eventually become stranded on the shore (Roman et al., 2014). The ecological impact of these stranded carcasses on the coastal scavenging community is substantial, attracting a wide range of marine and terrestrial scavengers and eliciting numerical and/or functional response in consumers (Polis et al., 1996; Fig. 1). Giant petrels (Warham 1990), skuas (Lönnberg 1906) and polar bears all scavenge on stranded cetaceans, providing the fat and protein necessary to cope with extensive periods of fasting (Laidre et al., 2018). Whale carcasses may have supported polar bears in past warmer interglacial periods, when seal availability was limited (Laidre et al., 2018), and thus, may play a crucial role in their adaptation to ongoing climate change. At more temperate latitudes, terrestrial scavengers such as brown bears, wolves (Lewis and Lafferty, 2014), foxes (Katona and Whitehead 1988), hyenas and jackals (Skinner et al., 1995) also move to the coast to feed on dead marine mammals. The extinct California grizzly bear is reported to have fed upon salmonids and stranded marine mammals (Laidre et al., 2018). In addition, condors, which are obligate scavengers, largely specialised on stranded whales (Chamberlain et al., 2005; Lambertucci et al., 2018; for more details, see Panel 2, Fig. 2). Finally, similarly to whale falls, stranding events are likely to enrich substrata with nutrients (as happens with buried cetaceans; Bui, 2009) and be discharged into coastal waters potentially attracting sharks (Tucker et al., 2019b; Heiss, 2020). These nutrients may also provide supplements to algae and plants in the surrounding environment, as well as to increase landscape heterogeneity.

Panel 2. Ecological and conservation consequences of marine carcass depletion: the case of condors.

Cetacean strandings provide long-lasting pulses of food, which may determine local changes in distribution and abundance of scavenging organisms and populations, as well as changes in the energy flux of food webs. Whales in particular were an important carrion source for scavengers in historic and prehistoric times. Pleistocene megafaunal extinction strongly impacted terrestrial mammals and, to a lesser extent, marine mammal populations. After the late Pleistocene terrestrial megafaunal extinction in North America, the California condor (*Gymnogyps californianus*) became extinct in the areas where they fed mostly on terrestrial animals. The condor's distribution range was restricted to the Pacific coastal area, where they exploited the abundant carrion resources provided by strandings (Chamberlain et al., 2005). The severe depletion of marine mammals during the whaling era forced condors to shift back to terrestrial food resources in the late 1700s, which has caused a serious conservation problem due to lead poisoning from bullets found in the terrestrial carcasses (Chamberlain et al., 2005).

In Patagonia, South America, the Andean condor (*Vultur gryphus*) has traditionally nested on the Pacific slope of the Andes, allowing efficient exploitation of the cetacean carrion that was once abundant on the coast (Lambertucci et al., 2018; Fig. 2). Those breeding areas close to the Pacific Ocean are maintained even today, when few whale carcasses are available on the western Patagonian coast. Thus, condors are forced to routinely cross the Andes to the east to scavenge on ungulate carcasses from the Patagonian steppe, increasing the energy expenditure and potential risks that threaten this species (Lambertucci et al., 2018).

Populations of both condor species decreased until almost the extinction in high risk areas associated with human impacts. These threats include safe native wild food reductions, and the increasing use of anthropogenic food sources (Plaza and Lambertucci, 2020). In the past, before the severe declines in whale populations, strandings could have been so common that coastal ecosystem structure and function may have been different from those known today, and their effects could have even permeated inland. Under this scenario, the historic lack of whale strandings has played an important role in the loss of safe abundant food sources for condors, and potentially many other scavengers.

Panel 3. The global decline of cetacean populations.

Hunting of whales, especially baleen whales (suborder Mysticeti) and the sperm whale (*Physeter macrocephalus*; suborder Odonotoceti), has been practiced for centuries by some civilisations such as the Japanese and Inuit (Shoemaker, 2005). More recently, whaling started to be practiced also across different populations such as the Basques in the 11th century, Norsemen in the early medieval period, and Dutch, Caribbeans and European colonists of America in the 15th century (Romero and Creswell, 2010; Parsons and Monaghan-Brown, 2017). Whaling began in Svalbard in 1611 and lasted about three hundred years. By around 1850, the Greenland right whale was completely removed from marine ecosystems around Svalbard (Hacquebord, 2001).

The advent of modern, commercial whaling with more sophisticated vessels and the use of explosives (late 1800; Ellis, 1991) permitted whalers to catch larger and faster cetacean species (Parsons and Monaghan-Brown, 2017). With the expansion into Antarctic waters and the establishment of whaling stations, whaling reached its historical peak in the early 20th century. The lack of sustainability of this industry, which drastically reduced whale stocks at a global scale, led first to the signing of the Convention for the Regulation of Whaling (Sept. 24, 1931, 155 L.N.T.S 349) in Geneva for Antarctic whale fishery in 1931, and eventually the International Whaling Commission (IWC) to take action and regulate whale catches as early as 1946 (IWC). In 1982, a ten-year moratorium was decided and then applied in 1986 to permit whale populations to recover, but at the end of it, the pause in commercial whaling was extended for indefinite time (IWC). Currently there are 88 participant member governments, as Japan withdrew its membership in 2013 and resumed whaling in 2019. In addition, Norway is still hunting minke whales (*Balaenoptera acutorostrata*) for internal consumption and export to Japan (Leclerc et al., 2011). Iceland and Faroe Islands also continue to practice whaling. Aboriginal subsistence whaling is also currently allowed in Greenland, Chukotka, Bequia and Alaska, although its effect on whale populations is considered negligible (Clapham et al., 1999).

With millions of cetaceans killed (Clapham et al., 1999), large-scale commercial whaling is one of the greatest episodes of unsustainable wildlife exploitation in human history (Clapham et al., 2008). As a result, several species were depleted almost to extinction, although some sign of recovery have been observed in some populations in recent decades (Clapham et al., 1999). Because of the slow population growth rate characterising these K-strategy animals, some whale species (*B. musculus*, *B. physalus* and *Eubalena australis*) will take more than a century to recover to half of their original pre-exploitation numbers, although others may recover sooner (e.g. *Megaptera novaeangliae*; Tulloch et al., 2018). The cascading effects of the huge decrease in whale populations have profoundly altered the functioning of whole ecosystems (e.g. Hacquebord, 2001).

Although it has not been investigated, it can be assumed that the number of stranded cetaceans has reduced in proportion to the decrease in living whales. The diminished availability of cetacean carcasses has almost certainly also affected the provision of ecosystem services and functions. The carbon sequestration through sinking carcasses, for instance, would be an order of magnitude greater if whale populations were restored to pre-whaling numbers (Pershing et al., 2010).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2022.101406.

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