

Collecting whales. Processes and biases in Nordic museum collections

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Abstract

Whales are unique museum objects that have entered collections in many ways and for different reasons. Understanding these processes and the resulting biases is important for research, outreach, and conservation. This work studies three Nordic natural history museum collections, in Norway and Denmark, with more than 2500 whale specimens in total, and gathers available biological and collection data on the specimens. It finds that influx of specimens to the collections mainly happened in the latest 1800s and earliest 1900s, ~~fueled~~fuelled by research trends, nation building, local whaling, and colonial mechanisms. Norway was a major whaling nation, but the largest hunt for whales in the Southern Ocean in the mid-1900s is not reflected in the collections.

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Introduction

Whales have always been important to humans, as a natural resource, as a research subject and in many cultures (Burnett 2012; Gatesy et al. 2013). The invention of industrial whaling in the late 19th century changed this relationship, and the hunt for whales from the 1890s to the 1980s, mainly for production of fats used in food, medicines, and machinery, has been called “the largest hunt in history” (Rocha et al. 2014; Tønnesen & Johnsen 1982). From 1900 to 1999, 2.9 million large whales (baleen and sperm whales) were killed, a reduction of up to 99-100 per cent for some populations (Rocha et al. 2014; Roman & Palumbi 2003). After the cessation of large-scale whaling, some populations show signs of recovery, whereas others do not, and some respond negatively to new anthropogenic pressures (Albouy et al. 2020; Edwards et al. 2015; Savoca et al. 2021). A few countries were responsible for most of the whaling both regarding income, technological innovations, and skilled labour. Among these is Norway, a small country that came to dominate global whaling from the late 1800s (Tønnesen & Johnsen 1982).

Commented [JB2]: Industrial whaling was not 'invented', it a process that develop from the long term interests and motivations to explore an ubiquitous resources. This sentence needs to be rewritten to encompass the multiplicity of whaling practices across the centuries until reaching industrial whaling in late 19th and 20th century.

Today, whales are ~~still~~ important to humans, not just as a resource, at least, in the same dramatic scale, but as part of healthy ocean ecosystems, as local food resources, and as symbols of fascinating biodiversity, for cultural practices and religion. On the other hand, news economic practices have developed from this interest on whales, and ~~The~~ whale watching industry ~~is~~ has been growing from many decades now (Suárez-Rojas et al. 2023). Not of least importance, but most people probably encounter whales in natural history museums, as whales are centrepiece objects in exhibitions all over the world.

The exhibited specimens only represent a fraction of the specimens held by museums, as they usually have larger collections aimed for education and research purposes (Fig. 1)(Pyenson 2017). Museums are again experiencing increased research focus towards the use of collection specimens for understanding, among other aspects, e.g., changing biodiversity patterns, and spread of diseases and toxins, using a range of methods (reviewed in e.g. Bakker et al. 2020; Hilton et al. 2021; Meineke et al. 2019). Because whales will not be targeted by humans on a large scale in the foreseeable future, many specimens in museum collections are unique objects that will not be replaced. However, using historically collected specimens in modern research is not straight-forward, and not all types of research are suited, because of inherent collection bias (Bakker et al. 2020; Boakes et al. 2010; Pyke & Ehrlich 2010; Uhen & Pyenson 2007; Wehi et al. 2012). Because museum collections have been built up over hundreds of years, the aim, strategy and what is economically and logistically possible, has shifted repeatedly (Bakker et al. 2020). Understanding collection history is thus vital for understanding what the collections represent and how they are biased, and what they can contribute in terms of scientific results (Pyke & Ehrlich 2010), as they often represent the most comprehensive data available, despite the biases (Boakes et al. 2010). Using a

framework on collection bias, one can imagine nature going through a series of sieves, where only a fraction of the original biodiversity pass through each one, because bias either from natural or anthropologic causes are introduced at all steps in the process (Uhen & Pyenson 2007; Whitaker & Kimmig 2020).

Collection bias should be investigated for different groups in order to be most precisely understood (Benton et al. 2011). This work uses three Nordic museum collections of whale specimens to map and discuss the collection processes. The aims are to gather datasets for the whale specimens in the three collections including both biological data as well as the available knowledge for how the specimens were collected; discuss the collection processes and sampling regime and how this has affected the resulting collections; and detect possible biases. It also asks how the collections were impacted by whaling, and whether the extensive removal of whales from the oceans is reflected in museum **collections**. A review of the previous and future research based on the specimens in these collections is outside the scope of this paper.

Historical context

~~Because collection of~~Collecting natural history specimens is largely influenced by history (Anderson & Pietsch 1997), ~~a short context is provided~~. In 1814, Norway got its own constitution and entered a loose union with Sweden after being part of Denmark for several hundred years. In the last decades of the 1800s, Norwegian national identity grew, with increased demand for national institutions and full independence, which happened in 1905. As a part of this, and because of the focus on science in many countries, also museums were established; In 1813 the Natural museum in Oslo, and in 1825 Bergen Musæum (Aslaksen 2020; Wiig & Bachmann 2013). In the latter, the exhibition in the "Whale hall" has been an

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attraction since its first opening in 1865, with ~~approx~~around 20 complete whale skeletons, including an iconic blue whale, caught in 1878 in Finnmark in Northern Norway (Bergen 2011).

Denmark started their expansion in Greenland in the mid-1700s. In 1953, Greenland went from being a colony to a part of the Danish nation, and in 1979 home rule was granted, and expanded in 2008 (Gabriel 2009). The natural history museum in Copenhagen can be traced back to the 17th century Museum Wormianum. The Zoological Museum was established in 1862 by three institutions merging: the Royal Kunstkammer, The Royal Natural History Museum and the Zoological University Museum (~~Copenhagen~~; Copenhagen).

Whales have been hunted along the coasts of Europe and in the Arctic for hundreds of years.

The whaling in the Arctic and North Atlantic from the 1600s largely affected bowhead whales and Atlantic right whale, for which the populations became severely reduced (Cerca et al. 2022; Moore et al. 2021; Tønnesen & Johnsen 1982). From the late 1800s onwards, Norway became the world's dominating whaling nation. This started in 1864 when sealer Svend Foyn invented the steam-powered whale catcher and the exploding harpoon gun, as well as improved on-shore whale processing, inventing modern whaling (Tønnesen &

Johnsen 1982). This made it possible to catch fast-swimming baleen whales that did not float after death, the rorquals, and made whaling far more efficient. Consequently, it shifted the focus of the targeted species and changed the impacts on whales populations and their ecosystems. Geographically, modern whaling started in northernmost Norway, along the coast of the Finnmark county and northwards in the Barents Sea, dominated by Svend Foyn's company. In this period, at least 18 000 whales were caught (blue, sei, fin and humpback whales) (Davis et al. 1997; Ringstad 2011; Tønnesen & Johnsen 1982; Øien 2010). The

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largest catches were made in the 1890s (Tønnesen & Johnsen 1982). Whaling increasingly took place further and further from the shore because the populations were reduced, and in 1904, whaling was prohibited in Northern Norway. Norwegian whaling industry then turned to other hunting grounds, first in the Northern Hemisphere (Iceland, Faroe Islands and Newfoundland). After depleting the populations there, the industry moved to the Southern Hemisphere, along the southern African coast and in the Antarctic. The whaling station in Grytviken at South Georgia was the main hub until full pelagic catch and processing made shore-based stations unnecessary (Rocha et al. 2014; Sanger & Dickinson 1997; Tønnesen & Johnsen 1982).

The largest numbers of whales were killed in the last decades before bans on whaling, between 1950 and 1970. Norway had the largest fleet, and provided technology, knowledge transfer and skilled labour to other nations (Schladitz 2014; Tønnesen & Johnsen 1982). This industry provided large incomes to Norwegian actors. In 1957, “whale oil” had a value of 300 mill NOK – approx. half the value of the fisheries. Increasingly stricter international regulations on whaling came in place from 1931 to 1982 (Rocha et al. 2014). Norway objected repeatedly to these but ceased whaling in the Southern Hemisphere in 1961. Minke whales are still hunted along the Norwegian coast, in small numbers. In addition to the industrial hunt for the large whales, there was a continuous hunt for tooth whales along the Norwegian coast (Kalland 2014).

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~~Norway and Denmark are today rich welfare states with a highly educated population and relatively small inequality. Norway's main exports are petroleum and fish, whereas Denmark exports industry goods and agricultural produce (Stugu 2018).~~

Material and methods

The Natural History Museum in Oslo (hereafter NHM Oslo), Natural history of the University Museum in Bergen (hereafter NHM Bergen), and the Natural History Museum in Copenhagen (hereafter NHM Copenhagen) where the places and collections selected ~~The natural history museum collections in Oslo and Bergen were selected~~ because they are the largest in Norway, and the one in Copenhagen, Denmark is larger and serves as a comparison to the former two. Datasets of the whale specimens present in ~~the three~~ collections as of 2022 ~~in each of the three collections~~ were assembled, and are openly shared at the Dryad depository and serve as a result on its own in the process of producing open science, and it hoped that they can be used for future research. The datasets were built on existing databases, with information added from other sources such as intake journals, and from personal observation during collection visits by LLD in April 2022 – January 2023. Museum specimen numbers have several different abbreviations: BM, B, ZMUB and ZU at NHM Bergen; NHMO-DMA and M at NHM Oslo; and CN, MCE, M, FM at NHM Copenhagen. All three museums also have several specimens marked with a museum number without letters. To understand the collection history, interviews with curators and collections managers were conducted. With regard to NHM Bergen, the book by A. Kalland (Kalland 2014) has provided important documentation and analysis.

All whale specimens were treated as separate entries, regardless of preservation technique and completeness. Subfossil specimens have been removed. The museums' taxonomic assignments were not evaluated, but nomenclature was updated to follow the Society for Marine Mammalogy (Taxonomy 2022). Data recorded for each specimen are: species, ontogenetic stage, sex, geographic location, collection year, collector, the role of the

collector, and how the specimen was acquired by the museum. Preparation types were recorded as ~~either~~: OT Osteological specimens, including teeth (some specimens have dried soft tissue attached); B Baleen; WF Complete foetus or small juvenile with soft tissue, stored in ethanol or formalin; WO Organs or stomach content stored in ethanol or formalin or DO Organs, preserved as dry specimen.

The collections in NHM Bergen and NHM Oslo ~~both~~ have more than one database, which were manually merged and checked for duplicates. In addition, the original intake journals at NHM Bergen were searched for additional information. At NHM Bergen, 267 out of 509 specimens were personally inspected by LLD. 194 remaining specimens belong to the wet collection, which is recently inventoried and well-organized, and were included in this analysis. The 49 last specimens are present in the database but were not observed during the visits in 2022. Most likely these are present in the collection, and they are included in the analysis, even if some of them might have been discarded, introducing some bias.

~~According to the~~ NHM Oslo ~~database, the~~ collection holds 317 whale specimens, and of these, 196 were personally inspected. In addition, 188 other specimens were also inspected, but could not be matched with the database, often because of missing labels. Many of these probably represent the specimens in the database. At least 60 are not registered. The 84 inspected specimens that were not found in the database, and where genus was unknown, were removed from the analysis. Most of these also lack other data. This leaves 421 specimens for analysis. The analysis is thus biased by collection management: some specimens might be counted twice, whereas others are not included. The general trends are deemed to be representative. For the timeline, specimens registered for 1820 and 1834 are left out, as the oldest specimen that was physically located is from 1839.

For NHM Copenhagen, only the osteological collection is included. The museum does not have a digital specimen database, and the dataset used here is assembled by personal observation by LLD in June 2022. The osteological collection contains 1780 whale specimens. Out of these were 36 lacking information on genus or species, leaving 1744 specimens for analysis.

Even if not stated in writing, the collections have aimed to include all “local” whale species (C. Kinze, H. Meijer, pers. comm.). The species compositions in the collections were compared to species occurrences in Norway (including Svalbard, Jan Mayen and the Barents Sea) (Artsdatabanken 2021; Kovacs & Lydersen 2006), Denmark and Greenland. At NHM Bergen, 79 specimens lack information on geographical origin, and in NHM Oslo the number is 94. Some specimens are labelled very generally (e.g., “Atlantic Ocean” or “Africa”).

We also had to deal with the possibility of missing data in the collections.—As this study collected many types of data from an extended time span, with a biased collection history, *and* many specimens miss some or all accompanying information. It has been made sure that corresponding values are compared, e.g., only specimens with known collection year were compared when discussing temporal trends (Figs. 2-3). Regarding collection year, the year mentioned on the label or in the database sometimes refer to the actual collection, and in other instances to inclusion in the museum collection. In most cases, these lie within 1-3 years of each other, and the oldest value was always used. At NHM Bergen, 135 specimens lack information on collection year, and for NHM Oslo, 89 specimens. For NHM Copenhagen, collection year is known only for 205 specimens, based on labels.

Most specimens are not labelled with ontogenetic stage, and many of these are assumed to be adult (Table 1). At NHM Bergen and NHM Oslo, ~~the majority of most~~ specimens for which ontogenetic stage is recorded, are fetuses in the wet collection. At NHM Copenhagen, ontogenetic stage is provided for 25 non-adult specimens.

The sex of most whale specimens is also unknown. At NHM Bergen, among the 130 specimens where sex is registered, were 70 male and 60 female (54:46 ratio). At NHM Oslo, 83 specimens (18%) are registered. At NHM Copenhagen, 222 specimens are labelled as females and 233 as males. In the two latter NHMs the vast majority of specimens for which sex is known, are harbour porpoise (*Phocoena phocoena*) osteological material.

Results

Characterization of the collections

The University Museum in Bergen

At NHM Bergen, the collection of whales started in 1834 (Aslaksen 2020; Kalland 2014). This study shows that most of the whale specimens were collected between 1880 and 1920 (Fig. 2), similar to other zoological objects in the same collection (Bergen). After 1920, more toothed whales than baleen whales were collected; 21 percent of the toothed whales and 13 percent of the baleen whales.

The collection houses 24 whale species, out of which 159 specimens are baleen and 347 toothed whales (Fig. 4A). The most common species is harbour porpoise (*Phocoena phocoena*, 127 specimens) followed by minke whale (*Balaenoptera acutorostrata*, 113). Eighteen specimens are not identified to species level. Among species occurring in Norway,

Grampus griseus and *Tursiops truncatus* are not represented. Nearly all specimens of species that occur in Norway originate from locations in Norway. Only a few specimens are species not occurring in Norway: *Platanista gangetica*, *Inia geoffrensis*, *Sotalia fluviatilis* and *Stenobredaensis* (one specimen each).

Many specimens lack information about the collector, and how the museum acquired them. However, it is known that many were bought from people hunting toothed whales in the areas around Bergen in the last half of the 19th century (Aslaksen 2020; Kalland 2014), which is confirmed by data assembled for this study (see Database); when acquisition mode is known, specimens bought by the museum are most common, and all of these, except one sperm whale, are toothed whales from the county, collected before 1910. This collection method resulted in many wet collection fetuses, and skeletons (Fig. 1B, C). Among the 509 whale specimens, more than half (58%) are fetuses preserved in ethanol or formalin, and 31% are osteological specimens. The remaining specimens are organs, preserved in the wet (6%) or dry (2%) collection; and baleen (2%).

Twenty-one specimens are registered as gifts, but it can be assumed that this is true for many more. The museum actively asked for donations and cooperated with the industry and the public (Kalland 2014). People with a job in the marine sector are the most common donors, but there is also one writer, one schoolboy, two businessmen and one kindergarten. There has always been extensive interaction with other institutions, such as the Institute for marine research, the whaling museums, and the natural history museums in Oslo and Copenhagen.

Eight specimens result from Southern hemisphere whaling, mostly from South Georgia and one (a 1914 sperm whale) from South Africa. Three specimens are from 1913, and four from

1948. Six are fetuses, one is a set of hypophyses of minke whale (*Balaenoptera acutorostrata*), all in the wet collection.

The Natural history museum in Oslo

The first collected whale specimen was probably an orca killed in the Oslo fjord in 1820 (NHMO-DMA-25160/1-O). It could not be confidently located in 2022 but might be one of the unlabelled specimens. This study shows that most specimens that are still in the collection, came to the museum between 1860 and 1910 (Fig. 3), like other parts of the zoological collections (Johannessen et al. 2023; Johannessen & Lifjeld 2022). There is also an intake spike in 1999-2000, which is specimens of *Phocoena phocoena* for a research project (Ø. Wiig pers. comm.).

Today, three quarters of the specimens are osteological, 15% are fetuses/juveniles and 10% are organs in the wet collection, whereas 1.5% are baleen (Fig. 3B). Twenty different species are represented. Like the collection in NHM Bergen, harbour porpoise (*Phocoena phocoena*, 107 specimens) is the most common, for which the majority are osteological specimens, as well as some fetuses and inner organs. The second most common is blue whale (*Balaenoptera musculus*, 36 specimens). Note that the latter are not complete osteological specimens, but rather disarticulated osteological elements, fetuses, and a few inner organs in the wet collection.

Compared to NHM Bergen, there is a larger geographical spread, with more specimens from other countries. Among species not occurring in Norwegian waters, NHM Oslo holds one *Eubalaena australis* and one *Balaenoptera brydei* specimen. For species occurring in Norway, NHM Oslo misses *Grampus griseus*, *Tursiops truncatus* and *Ziphius cavirostris*.

Among the species occurring in Norwegian waters, most specimens originate from Norway, except the sperm whale (*Physeter macrocephalus*), for which the specimens originate from the UK, Iceland, and Saint Helena.

For approximately half of the specimens (189), the collector is known. Early in its history, the museum bought many specimens and received many as gifts; mainly from people working in the marine sector, but also citizens in Southern Norway who found stranded whales. An important source for specimens were the active measures taken by Professor Robert Collett (Fig. 2), who travelled in northern Norway and cooperated with the whaling companies, including Svend Foyn.

Twenty-one specimens originate from the Southern Hemisphere and likely result from whaling. Most of these are humpback whales *Megaptera novaeangliae* (9 specimens), whereas the rest are large baleen whales, two sperm whales and two *Delphinus delphis*. They reflect the international Norwegian whaling; most are from South Georgia, and some from Angola, Namibia, South Africa, and the Kerguelen Islands.

The Natural history museum in Copenhagen

This is the largest osteological collection, with larger variation in species composition than the two Norwegian ones. More than half of the specimens are harbour porpoise (*Phocoena phocoena*, 988 specimens), followed by narwhal (*Monodon monoceros*, 113), beluga (*Delphinapterus leucas*, 111) and white-beaked dolphin (*Lagenorhynchus albirostris*, 101) (Fig. 4C). There are 136 baleen whale specimens, among them complete or close to complete skeletons of blue, sei, minke, bowhead and humpback whales (Fig. 1A).

This study shows that the specimens in the osteological collections were collected from 1838 to 2017. Because so few specimens have a known collection year, temporal trends are not discussed. The collection includes all species that occur in the waters of both Greenland and Denmark. The *Eubalaena glacialis* specimens originate from Iceland and Spain, and the *Tursiops truncatus* from Azores and Faroe Islands. Marine species not occurring in either Denmark, Faroe Islands or Greenland waters in the collection are *Berardius arnuxii* (2 specimens), *Mesoplodon grayi* (1), *Globicephala macrorhynchus* (3 specimens, Senegal) and *Stenella longirostris* (4 specimens, Australia). There are also coastal *Orcaella brevirostris* (Thailand, 1 specimen) and *Pontoporia blainvillei* (6 specimens, Argentina), as well as freshwater toothed whales *Platanista gangetica* (India, 3 specimens) and *Inia geoffrensis* (4 specimens, Venezuela).

Discussion

The making of the collections

This work is based on studies of three collections as they were in 2022. The combination and interaction of natural and anthropogenic factors in the preservation and collection processes have formed the collections as they are today and will continue to do so in the future (Anderson & Pietsch 1997; Whitaker & Kimmig 2020). The collections are the results of aims to build museums, combined with chance; a museum sometimes cannot decide which specimens they should acquire, but rather must act on what is available.

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Whales enter museum collections in different ways, after being killed or because of stranding. The museum acquires a specimen either because it is donated, because the museum buys it, or exchanges it for another specimen, or it enters as part of a research project (see Supp. mat. 1 Database) (Aslaksen 2020; Bakker et al. 2020). Sometimes the decision to

include a specimen happens first, such as when a museum actively orders a specimen of a particular species; in other instances, the museum is offered a specimen, and can either accept or decline. The museums studied here, seldom received whales in exchange, but especially NHM Bergen has exchanged a large number of whales for other animal specimens (Aslaksen 2020; Kalland 2014), which is to some degree reflected in the intake journals. The also sold whale specimens to other museums (Torino & Nicola 2013). Both the opportunistic, ad hoc collection mode and the dependence on the collector's interest is commonly seen in biological collections (Ponder et al. 2001; Pyke & Ehrlich 2010).

A specimen often passes via at least one person before it enters a museum collection. Who collected and who took decisions, and their interest at a certain point in time, has largely influenced the resulting collections. Many people were involved: scientists, other museum employees, local industry, natural history traders and the public. Museum employees, especially the scientists, largely influence which specimens enter the collections; R. Collett in Oslo, D. F. Eschricht in Copenhagen, and W. Christie, F. Nansen and G. Guldberg in NHM Bergen actively collected, and ordered specimens, including from each other (Fig. 2) (C. Kinze, pers. comm.)(Guldberg 1885; Kalland 2014).

The people were given opportunities or limited by society, and temporal patterns illuminate how the collection processes are closely related to society and history (Fig. 2-3). The major influx of whale specimens to the collections happened between 1860s to 1920s (Fig. 2-3, database), at the same time as the rise of modern science, the establishment of natural history museums in many countries (Farber 1982), and for Norway, with nation building. For the collection in NHM Copenhagen, the colonial relationship to Greenland and the stranding programme, that started already in 1885, are the most important contributors (Ijsseldijk et al.

2020; Kinze 2023). This also shows that regulations by law are important, for instance on ownership to stranded whales, which was and is important for NHM Copenhagen, as for other museums around the world (Kinze 2023; Kinze 2017; Lotzof 2023; Yamada et al. 2006). This contrasts the situation in Norway, which has not had the same framework for stranded whales in modern times.

Greenland has unique access to Arctic cetaceans, and because it was a Danish colony, this is evident in the collection in NHM Copenhagen, as it has been for cultural heritage (Gabriel 2009). This is a common situation in European museums (Bakker et al. 2020). Several specimens in the collection are a result of D. F. Eschricht's cooperating with captain Holbøll, who organized for narwhal and beluga specimens to be sent to the museum (C. Kinze, pers. comm.). Indigenous hunters and traders in Greenland were and are very important for the acquisition of specimens, but none of their names are present on the specimen labels, which means they receive less recognition than the Danish people involved.

Some specimens result from expeditions, which is typical for the 1800s and 1900s and still is today (Heyning 2002). At NHM Oslo this includes a foetal narwal skull Jan Mayen, donated by Roald Amundsen, from the first Gjøa expedition in 1901, a *Delphinus delphis* specimen from Australia from Carl Lumholtz in 1880, and two *Balaenoptera* specimens from South Africa 1912-1914 from Ørjan Olsen (see Supp. mat. 1 Database). At NHM Copenhagen, one specimen (*Platanista gangetica*) result from the first, and four (*Delphinus*, *Stenella* and *Globicephala*) from the second Galathea expedition (Bruun 1957).

Today, fewer whale specimens enter the collections in the three NHMs. They accept some donations and sometimes collect stranded specimens, especially if they complement the

existing collection (History) and there are examples of recent collecting for research purposes (Lislevand, Wiig pers. comm.). At NHM Copenhagen, the stranding programme has made available a number of specimens in much more recent times than at the other two NHMs (Kinze 2017).

The effect of whaling

Whaling has largely influenced the collections. In quantity of specimens, the collection at NHM Bergen most clearly reflects the local hunt on toothed whales, which took place in a more opportunistic manner than the hunt for baleen whales (Collett 1911-1912; Kalland 2014). For instance, in 1885, a group of approx. 1000 *Lagenorhynchus acutus* assembled in a fjord close to Bergen, out of which 200-300 were killed (Collett 1911-1912; Rasch 1845). Then curator at NHM Bergen, Fridtjof Nansen, arranged for the museum to buy foetuses and skeletons (Collett 1911-1912), out of which approx. 20 are still part of the collection (Fig. 2, Supp. mat. 1 Database). Whaling was also the method for acquiring large baleen whale specimens from northern Norway, both for NHM Bergen and NHM Oslo.

However, an interesting trend is that the magnitude of the largest scale industrial whaling, in the Southern Ocean, is not reflected in the Norwegian collections. The few specimens present do not represent a systematic collection. Some were bought and some were donated, but for most of them, acquisition mode is unknown. There are more Southern Ocean specimens at NHM Oslo (21) than at NHM Bergen (8 specimens), reflecting the more diverse geographical scope of the museum in the capital.

Why did so few specimens enter the collections from the largest scale whale hunt? It might result from inherent factors in the industry, or the time when this happened. In the 1900s,

biological sciences changed away from specimen-based natural history to studies on ecosystems and molecular studies (Burnett 2012; Farber 1982; Gippoliti et al. 2014). Many museums also experienced limited space for growing collections (von Achen 2019). The set-up of the whaling itself was targeted for industrial purposes, and had a long distance to Norway, and gradually changed to pelagic factory ships. The large-scale whaling was a sheer industrial endeavour, which to a very limited degree affected the museums. There is however one exception: The collections at the Anatomical institute in Oslo, that through cooperation with whaling ship medical doctors, received approximately 300 whale brains and foetuses, which were used for neurobiological comparative studies (Dietrichs 2018; Jansen & Osen 1984). The collection has recently moved to NHM Oslo but is not part of this study.

Species composition

Whenever the collections deviate from nature, there might be two types of biases at work that are intertwined: natural- and human-induced. One example is the differing blubber amount among whale species, which means that some whales float after death whereas others sink (e.g., thick blubber in bowhead whales). This influences stranding potential and is thus a natural-induced bias, acting together with ecology of the species. The blubber content however also influences whether humans hunt certain species, showcased by the invention of modern whaling where rorquals became more easily available for hunt and thus for museum collections (Collett 1911-1912).

Many whale species migrate over large distances, but geographical origin of specimens is interesting for the aim of this study. The species composition in the collections show the same trend; local and common species are abundant, in addition to the strong colonial bias towards Arctic species from Greenland in NHM Copenhagen (Fig. 4). One of the most

common species in coastal waters and in the collections is the harbour porpoise (Fig. 4). The species that occur in Norwegian waters but are not present in the collections, are those only rarely observed, and not reproducing. Geographical information that can be gained from collections often limited due to bias (Bakker et al. 2020; Pyke & Ehrlich 2010), which is also likely the case here.

In all the three collections, as in nature, there are more toothed whales than baleen whales. At NHM Bergen, 71% of the baleen whale specimens belong to one species, the minke whale (*Balaenoptera acutorostrata*). The reason is probably a combination of natural abundance and human factors; minke whales are the most common baleen whales and have been hunted for a long time. NHM Oslo in comparison has few minke whale specimens, possibly because of its position further from the hunting grounds or because of a different research focus.

For whales, timing is crucial when discussing abundance and distribution, as this group has already experienced a severe extinction event due to large scale whaling which means that available species have changed significantly throughout the period when the collections have been assembled. In modern whaling, the largest species were usually hunted first, and this is reflected in the collections. After the halt in whaling in Norway (1904), baleen whales in the collections (except minke whale) are very few or originate from the Southern Ocean (see Supp. mat 1 Database). One example is the North Atlantic right whale *Eubalaena glacialis*, where no specimens entered NHM Oslo or NHM Bergen after 1904. Today, the species is regionally extinct in Norway and a critically endangered species worldwide (Artsdatabanken 2021).

The “local” species composition has not only changed in the past but is still changing. One species composition bias in NHM Oslo and NHM Bergen caused by timing, is the lack of *Tursiops truncatus* specimens. This species was uncommon when the collections were mostly assembled but is increasingly more common today because of increased sea temperatures (Artsdatabanken 2021). The same is true for *Mesoplodon bidens* and *Ziphius cavirostris* in Denmark, the latter had its first stranding in 2020 and was added to the museum collection in, which previously had a specimen from New Zealand (Alstrup et al. 2021; Stavenow et al. 2022). Non-native and invasive species are often overlooked in collecting (McLean et al. 2016). The number of strandings might increase in the future, because some populations are growing, but it has also been argued that anthropogenic pressures might induce strandings (Aniceto et al. 2021; Ijsseldijk et al. 2020; Stavenow et al. 2022).

Among the few non-local specimens, freshwater toothed whales are more common than coastal or open ocean species. A possible reason is that these were “exotic” and thus interesting either for comparison to local species or for exhibition purposes (Bakker et al. 2020). The one *Platanista gangetica* specimen (not located) in NHM Bergen was received from the Ganges, India, from G. A. Frank in 1898. Frank was a natural history dealer in Amsterdam with a large global network, and one of museum’s most important trade partners (Kalland 2014; Largen 1985). He also traded *P. gangetica* specimens to the natural history museums in Leiden and Pisa, and to the former, whale specimens from Norway e. g. two *Lagenorhynchus* specimens (Braschi et al. 2007; Broekema 1983). Such trade networks were common and important for the museums (Coote et al. 2017), and this indicates that NHM Bergen actively wanted a *Platanista* specimen. The *P. gangetica* specimens in NHM Copenhagen were collected 1840-1845 by a Dr. Mundt, and by the first Galathea expedition. At least the latter points to intentional collection.

NHM Bergen has one complete *Inia geoffrensis* skeleton, collected in 1924, from Manacapuru, Brazil. W. Ehrhardt is the collector, probably the German taxidermist and collector who supplied museums with vertebrates from Brazil (Gutsche et al. 2007). At NHM Copenhagen are four *Inia* specimens. Two of the skulls were collected in 1892 in Rio Apure, Venezuela, by van Dockum, probably the captain in the Danish fleet, on trips to the colony “Danish West Indies” (Islands St. Thomas, St. Jan and St. Croix)(Garde 1952). There is also an almost complete skeleton of *Sotalia fluviatilis* in NHM Bergen (BM 414) from Rio de Janeiro, Brazil, given by professor van Beneden. Van Beneden is the author of *Sotalia guianensis* (van Beneden 1864), but this specimen might have been collected by his son Edourd van Beneden in his 1872 Brazil travel.

Bias in the collections

Intake bias can be nature-induced due to abiotic factors, taphonomy and decay, or anthropogenic due to societal factors, technological possibilities and limitations, economy and trends in culture and science (Whitaker & Kimmig 2020). Collecting whales can be a logistical challenge because of their size and smell (Heyning 2002; Pyenson 2017). Whales have not only come into the collections, they have also left; through discarding due to decay or space limitations, through exchange or due to random incidents (Pyke & Ehrlich 2010). Discarding seems to have been a more common practice for whale specimens previously than now, and to more frequently happen to older specimens, organs in the wet collections and taxa that are seen as common. Correct cataloguing and labelling of museum specimens is crucial for later use and analyses of historical specimens, but missing data was the case for many specimens in this study, hindering insights and (Lane 1996; Pyke & Ehrlich 2010).

Whale specimens are preserved in different ways (Fig. 1, 2B, 3B). This is a human decision, made at an intersection of wanting to preserve as much information as possible, research trends, but also what is logistically possible. In the early natural history museums, only skulls or skeletons with sketches were collected (Heyning 2002). In the early 1900s, following lead by those cooperating with whaling stations, museum scientists started documenting more of each specimen (Burnett 2012). In the three collections studied here, organs preserved dry were only found in the older part of the collections (see Supp. mat. 1 Database).

In the two Norwegian collections the large number of fetuses preserved in ethanol or formalin is noteworthy. In collections elsewhere, fetuses are often few or lacking completely, but can be important for research, and might enable e.g., studies of soft tissue (Heyning 2002; Lotzof 2023; Yamato & Pyenson 2015). One reason for collecting fetuses in this way can be traced back to D. F. Eschricht quoting Georges Cuvier about whales being too large to be preserved completely. Eschricht argues that fetuses are important study subjects that are not interesting for other people, adding that collecting fetuses make possible to study the entire anatomy of the whale, only on a miniaturized scale (Eschricht 1844).

Sex bias is common in museum collections. Many specimens are needed to understand sexual dimorphism, and not knowing sex can lead to errors (Cooper et al. 2019; Heyning 2002). In the three collections, sex is known for too few specimens to infer any collection-wide trend. A possible bias that is sex-related is that narwhal specimens with a tooth are usually interpreted as male, even if some females also develop a tusk, and some males are toothless (Petersen et al. 2012).

Commented [JB7]: Overall, the discussion is long and a bit confusing, and I could not follow some of the ideas

Conclusion

The natural history museum whale collections in Oslo, Bergen, and Copenhagen ~~together~~ document life in the oceans. ~~They, and~~ have been and will continue to be important for research, especially in a time of environmental change ~~and because for which~~ museum collections can provide long time series ~~and historical and cultural background~~. By focusing on collection history and possible biases, this work ~~can contribute~~ to ~~more the continuous building of~~ knowledge ~~being~~ derived from the ~~specimens~~.

Commented [JB8]: I would refer the idea of the afterlives of cetaceans

Natural museum collections played a role in nation building projects that took place in the era of industrial whaling and are ways to present ourselves to each other and to the world.

~~Knowing Norway's extensive whaling,~~ the number of specimens from the South Ocean is surprisingly small. It seems that the actions taken by the museum itself are more important for the resulting collections than large scale industrial trends. A very important factor is thus the museum employees involved in decision-making and their collaboration with the industry, public and traders. ~~The colonial history is also clearly visible, especially in the large number of Arctic specimens in Copenhagen.~~

Commented [JB9]: See my comment in the beginning of the manuscript. Is the whaling history of Norway represented in the museums, because if it is not (as I think it is not), this cannot be stated at all. In my view, the whales' collections do not add information to this practice in the past as in current day. I believe this is a silenced practice in the museums, but I might be wrong (just consider this hypothesis).

The increased focus on museum specimens hopefully can result both in important science and in the long-time management of these unique objects, which is sometimes lacking resources (Bakker et al. 2020; Boakes et al. 2010; Gippoliti et al. 2014; Vane-Wright & Cranston 1992).

Commented [JB10]: Without context in the exhibitions and collections, the bones tell us nothing about the historical moments on which they were obtained. I think you have room here to explain the value of well contextualized specimens.

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Commented [JB11]: Please check and eventually cite the work by Sophia Nicolov on the afterlives of whales: <https://www.researchgate.net/profile/Sophia-Nicolov>
See also the work by Nina Vieira, for instance: <https://www.mdpi.com/2076-0787/9/3/90>